

Forest developmental stages override canopy gap attributes in shaping natural regeneration in Hyrcanian beech forests

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Abstract

Natural regeneration is a fundamental ecological process determining the long-term structure, composition, and resilience of forest ecosystems. Although canopy gaps are widely recognized as key drivers of regeneration dynamics, the relative importance of gap characteristics and broader forest developmental conditions remains poorly understood, particularly in the Hyrcanian temperate forests of northern Iran. This study investigated the effects of forest developmental stages, canopy gap area, and gap-maker abundance on regeneration abundance in natural Oriental beech (*Fagus orientalis* Lipsky) forests. A total of 26 naturally formed canopy gaps distributed across six developmental stages (pre-forest stage, young forest, canopy closure, mature forest, old-growth, and disturbance and legacy creation) were surveyed. Regeneration abundance was quantified using 9,460 regeneration subplots established within gap environments. Generalized linear mixed models (GLMMs) with negative binomial error structure were employed to evaluate the relative contributions of developmental stage, gap area, and gap-maker abundance while accounting for the hierarchical sampling design. Forest developmental stage emerged as the strongest predictor of regeneration abundance. Regeneration differed significantly among developmental stages, with mature forests exhibiting the lowest regeneration abundance, whereas canopy closure, old-growth, and disturbance and legacy creation stages supported substantially higher regeneration densities. In contrast, neither canopy gap area nor the number of gap-making dead trees significantly affected regeneration abundance. Marginal and conditional R^2 values indicated that developmental-stage-related variation explained a substantial proportion of observed regeneration patterns. Furthermore, although canopy gap area varied among developmental stages, pairwise comparisons revealed limited differentiation among individual stages, suggesting that gap size alone provides an incomplete explanation of regeneration dynamics. These findings challenge traditional gap-centered interpretations of forest regeneration and highlight the importance of considering forest developmental context when evaluating regeneration processes. The results suggest that regeneration patterns in Hyrcanian beech forests are governed primarily by stand-level structural and ecological conditions associated with developmental stages rather than by individual gap attributes. From a management perspective, maintaining developmental heterogeneity across forest landscapes may be more effective for sustaining regeneration resilience than focusing exclusively on canopy gap characteristics. This study provides new evidence supporting the integration of developmental-stage concepts into close-to-nature forest management and conservation strategies in temperate old-growth forests.

Introduction

Natural regeneration is a fundamental ecological process governing forest persistence, resilience, and long-term ecosystem functioning. Regeneration determines future stand composition, structural complexity, and the capacity of forests to respond to environmental change and natural disturbances (Drössler et al., 2016). Consequently, understanding the mechanisms that regulate regeneration is essential for both ecological theory and sustainable forest management (Yamamoto & Nishimura, 1999).

Forest ecosystems are inherently dynamic systems characterized by continuous changes in structure, composition, and ecosystem functioning (Etemad et al., 2019). These changes are commonly described through the concept of forest developmental stages, which represent distinct structural and ecological phases arising from interactions among disturbance regimes, competition, mortality processes, and resource availability (Korpel, 1995; Franklin et al., 2018). Developmental stages are not merely temporal phases of succession; rather, they reflect integrated expressions of ecosystem processes that influence forest structure and habitat conditions at the stand scale (Kuuluvainen & Gauthier, 2018).

Different developmental stages are associated with substantial variation in canopy architecture, tree density, vertical stratification, deadwood accumulation, microsite heterogeneity, and disturbance legacies (Oliver & Larson, 1996, Palik et al., 2020). These structural attributes directly affect the availability of critical resources such as light, moisture, nutrients, and establishment sites, thereby influencing regeneration processes (Sefidi et al., 2011). As a result, regeneration patterns are expected to differ among developmental stages because each stage provides a unique ecological environment for seedling establishment, survival, and growth (Feldmann et al., 2018).

Within this broader developmental framework, canopy disturbances and gap formation represent important mechanisms generating structural heterogeneity (Weber et al., 2014). According to gap-phase theory, canopy openings modify understory environmental conditions by increasing light availability, altering microclimatic conditions, and creating regeneration niches (Runkle, 1982; Yamamoto, 2000). Numerous studies have demonstrated that canopy gaps contribute to species coexistence and structural diversity by promoting spatial variation in regeneration opportunities (Diaci et al., 2012; Muscolo et al., 2014). However, canopy gaps are not independent ecological entities. Their formation, size, persistence, and ecological effects are strongly influenced by the developmental context in which they occur (Dahir & Lorimer, 1996).

Increasing evidence suggests that regeneration responses cannot be adequately explained by gap characteristics alone (Drössler et al., 2016, Mazdi et al., 2021). Similar-sized gaps may exhibit markedly different regeneration patterns depending on stand developmental stage, surrounding canopy structure, deadwood availability, competitive environments, and disturbance history (Nagel et al., 2014). Consequently, developmental stages may function as higher-order ecological filters that mediate the effects of local gap attributes on regeneration dynamics (Frelich, 2002). Under this perspective, canopy gap area and the number of gap-forming trees are expected to influence regeneration primarily through their interactions with broader stand structural conditions.

The importance of developmental-stage context may be particularly pronounced in old-growth and near-natural forests, where structural complexity and ecological heterogeneity are exceptionally high. Such forests contain diverse microsites, multi-layered canopies, abundant deadwood resources, and complex disturbance legacies that collectively regulate regeneration processes across spatial and temporal scales. Understanding how regeneration varies among developmental stages in these systems therefore

provides valuable insights into the mechanisms maintaining forest resilience and long-term ecosystem stability.

The Hyrcanian forests of northern Iran represent one of the largest and most ecologically intact temperate broadleaf forest ecosystems in the world. Dominated by Oriental beech (*Fagus orientalis* Lipsky), these forests have persisted for millions of years and retain substantial areas of near-natural structure and ecological continuity (Javanmiri Pour et al., 2019 & 2024). Compared with many European temperate forests, where unmanaged stands are increasingly rare, the Hyrcanian forests provide a unique opportunity to investigate natural forest developmental processes under relatively undisturbed conditions.

Although canopy gap dynamics and regeneration ecology have been widely investigated in temperate forests, relatively little is known about how regeneration patterns vary among clearly defined developmental stages in Hyrcanian forests. In particular, the relative importance of stand developmental context versus local gap attributes remains poorly understood. This knowledge gap limits our understanding of the mechanisms controlling forest renewal and structural dynamics in one of the world's most important temperate forest ecosystems.

To address these questions, this study examined regeneration abundance across six developmental stages in canopy gaps within the Gorazbon compartment of the Kheyroud Forest. Specifically, we aimed to: (1) quantify variation in regeneration abundance among developmental stages; (2) evaluate the influence of canopy gap attributes, including gap area and the number of gap-makers, on regeneration abundance; and (3) determine the relative importance of developmental-stage context and local gap characteristics in explaining regeneration dynamics.

We hypothesized that regeneration abundance would differ significantly among developmental stages because each stage represents distinct structural and ecological conditions affecting resource availability, microsite heterogeneity, and competitive interactions. In contrast, we expected canopy gap attributes to exert comparatively weaker effects on regeneration abundance once developmental-stage context was considered. The conceptual framework guiding this study is presented in Fig. 1, where forest developmental stages are considered the primary drivers of structural and ecological conditions regulating regeneration, whereas gap attributes act as secondary modifiers of regeneration responses.

Materials and Methods

Site description

The study area is located in the Kheyroud Research and Educational Forest, which is situated 7 kilometers east of Nowshahr in Mazandaran Province, Iran. Its geographic coordinates range from 27°36" to 40°36" North and 32°51" to 43°51" Longitude. The Gorazbon section is the third part of the forest managed by the Faculty of Natural Resources at the University of Tehran, with elevations ranging

from 540 to 1,350 meters above sea level (M.A.S.L.). This section encompasses 27 parcels, covering an area of 24.934 hectares.

The Gorazbon section is bordered to the north by the southern ridge of the Chelandar forests, to the east by the forests of the Chelir district, to the south by the Kheyroud River, and to the west by the forests of the Namkhaneh district. In this study, parcel 326 was specifically examined; it serves as one of the control parcels in Kheyroud Forest (Fig. 2). Parcels 326 and 327 are designated as control plots, where no exploitation will occur, making them suitable for long-term research activities. Typological studies indicate that the pure beech type predominates in these two parcels. The study was conducted in a designated control parcel, where no silvicultural interventions have been carried out in recent decades. This status allowed the observation of naturally occurring canopy gaps and regeneration patterns, providing an ecologically undisturbed baseline for analyzing forest developmental stage.

The Kheyroud Forest in Noshahr, particularly the Gorazbon district, is notable for its significant species diversity. This forest serves as a rich ecosystem that includes various tree species at different stages of growth and ecological succession. The most important forest species in the Gorazbon area consist of beech (*Fagus orientalis*), hornbeam (*Carpinus betulus*), velvet maple (*Acer Velotinum*), and chestnut-leaved oak (*Quercus castaneifolia*).

These species contribute to the overall biodiversity and ecological health of the region, playing crucial roles in habitat formation, soil stabilization, and carbon sequestration. The presence of diverse tree species also supports a wide range of wildlife, enhancing the forest's ecological functions and resilience.

Beech is one of the most important tree species in the forests of northern Iran, with significant economic and environmental value. These trees are part of the Hyrcanian forests, which date back to the Jurassic period, playing a key role in maintaining biodiversity and ecosystem health. Beech is used for construction, wood products, and cellulose due to its high-quality timber. Additionally, these forests are major tourist attractions with pristine natural landscapes that require protection alongside environmental conservation.

Permanent plot establishment

A 25-ha permanent research plot was established within compartment 326, a predominantly pure Oriental beech stand representative of mature Hyrcanian forest conditions. The plot was systematically divided into twenty-five contiguous one-hectare subplots (100 × 100 m) to facilitate detailed spatial monitoring and standardized measurements across the entire study area.

All living and dead trees within the permanent plot were mapped and recorded. Subplot boundaries were permanently marked in the field, and individual trees were numbered to support long-term monitoring of forest structure, disturbance processes, and regeneration dynamics.

2.3 Identification of forest developmental stages

Forest developmental stages were identified based on stand structural characteristics, canopy conditions, regeneration patterns, and disturbance history following the framework of natural forest development described by Korpel (1995) and subsequent studies of temperate old-growth forests.

Six developmental stages were distinguished within the study area include Pre-forest stage, Young forest, Canopy closure, Mature forest, Old-growth forest and Disturbance and legacy creation.

Classification was based on field observations of canopy structure, stand density, regeneration abundance, deadwood occurrence, and gap characteristics. These developmental stages represent distinct structural and ecological conditions influencing resource availability and regeneration opportunities.

2.4 Canopy gap inventory and measurements

Naturally formed canopy gaps were identified and mapped throughout the study area using the FieldMap® forest inventory system. Gap boundaries were delineated according to the canopy opening definition proposed by Runkle (1981), whereby a canopy gap represents an opening extending through all vegetation layers to a height of approximately two-thirds of the surrounding canopy.

All gap boundaries were georeferenced and digitized in the field. Gap dimensions, shape, area, and the number of gap-makers (dead trees responsible for gap formation) were recorded for each canopy opening. The FieldMap system was calibrated daily following manufacturer guidelines, and independent validation measurements confirmed a positional accuracy within 3%.

Gap area was calculated according to gap geometry. For elliptical gaps, which represented the most common gap form, area was estimated as:

$$A = \frac{\pi LW}{4} \text{ (Eq. 1)}$$

Where, (L) is the major diameter and (W) is the minor diameter of the gap (Runkle, 1982).

For circular gaps, area was calculated as:

$$A = \pi r^2 \text{ (Eq. 2)}$$

Where, (r) is the radius of the gap.

Irregularly shaped gaps were digitized as polygons and subdivided into non-overlapping triangles. Total gap area was obtained by summing the areas of individual triangles:

$$A = \sum_{i=1}^n \frac{1}{2} (b \times h) \text{ (Eq. 3)}$$

Where, (b) and (h) represent the base and height of triangle (i), respectively.

Gap-maker abundance was recorded as the number of standing dead trees or recently fallen trees directly responsible for canopy opening formation. In total, 26 canopy gaps were identified and analyzed across the developmental stages.

For descriptive purposes, canopy gaps were classified into three size categories following commonly used thresholds in temperate forest gap studies: small ($< 200 \text{ m}^2$), medium ($200\text{--}500 \text{ m}^2$), and large ($> 500 \text{ m}^2$) (Brokaw, 1985; Yamamoto, 2000; Fahey & Lorimer, 2014). These categories were used only for ecological interpretation and were not included as explanatory variables in the final statistical models.

2.5 Regeneration sampling

Natural regeneration was sampled within each canopy gap using a systematic microplot design adapted from Clinton and Boring (1988). Nine square regeneration microplots ($2 \times 2 \text{ m}$; 4 m^2 each) were established within every canopy gap, resulting in a sampled area of 36 m^2 per gap.

One microplot was positioned at the geometric center of the gap, four were located along the major and minor gap axes at intermediate positions, and four were established near the gap margins. This arrangement was designed to capture spatial variation in regeneration conditions from the gap center to the edge.

Within each microplot, all regeneration individuals were identified to species and classified according to height ($< 30 \text{ cm}$, $30\text{--}130 \text{ cm}$, and $> 130 \text{ cm}$) and root-collar diameter ($< 2.5 \text{ cm}$, $2.5\text{--}7.5 \text{ cm}$, and $> 7.5 \text{ cm}$). Regeneration abundance was calculated as the total number of individuals recorded within each microplot.

Conceptual framework and explanatory variables

The present study was designed to evaluate whether natural regeneration patterns are primarily controlled by local gap characteristics or by the broader developmental context of the forest. Based on current theories of forest development and gap dynamics, canopy gap area and gap-maker abundance were selected as structural attributes representing local disturbance characteristics, whereas developmental stage represented the broader stand-level structural condition.

Gap area was measured because it directly influences light availability, microclimatic conditions, and resource distribution within canopy openings. Similarly, gap-maker abundance (i.e., the number of dead trees responsible for creating a canopy gap) was quantified as an indicator of disturbance intensity and structural legacies associated with gap formation.

These variables were incorporated into the statistical analyses not only as predictors of regeneration abundance but also as components of a conceptual framework linking disturbance processes to stand development. Specifically, the study tested whether regeneration responses could be explained by individual gap attributes alone or whether forest developmental stages—which integrate multiple

structural characteristics such as canopy architecture, disturbance history, deadwood accumulation, and microsite heterogeneity—provide a stronger explanation for observed regeneration patterns.

Accordingly, developmental stage, gap area, and gap-maker abundance were included simultaneously in the generalized linear mixed-effects models to evaluate their relative contributions to regeneration abundance. This approach allowed direct comparison between local gap-scale controls and broader stand-scale developmental influences on regeneration dynamics.

2.6 Statistical analyses

Differences in canopy gap area among developmental stages were initially evaluated using the non-parametric Kruskal–Wallis test because gap-area data did not satisfy assumptions of normality and homogeneity of variance. When significant differences were detected, pairwise comparisons were conducted using Dunn's post hoc test with Bonferroni adjustment.

To investigate factors influencing regeneration abundance, generalized linear mixed-effects models (GLMMs) were fitted using a negative binomial distribution with a log-link function. Regeneration abundance was included as the response variable, while developmental stage, gap area, and gap-maker abundance were treated as fixed effects.

To account for the hierarchical sampling design, plot identity and gap identity nested within plots were included as random effects:

Estimated marginal means were calculated using the emmeans package, and pairwise comparisons among developmental stages were adjusted using Tukey's method. Model performance was evaluated using marginal and conditional R^2 values.

All analyses were performed in R version 4.5.1 using the packages glmmTMB, emmeans, performance, FSA, and ggplot2.

Results

Patterns of regeneration abundance across developmental stages

A total of 9,461 regeneration observations were recorded across six developmental stages of natural Hyrcanian beech forests. Regeneration abundance exhibited considerable variation among developmental stages (Table 1). The highest mean regeneration abundance was observed during the canopy closure stage (58.0 ± 9.76), followed by disturbance and legacy creation stages (47.3 ± 18.2) and old-growth forests (44.1 ± 6.89). In contrast, mature forests supported the lowest regeneration abundance (26.0 ± 4.57). Pre-forest stages exhibited relatively low regeneration abundance (28.8 ± 0.39),

whereas young forests showed intermediate values (41.4 ± 4.90), although this stage was represented by a comparatively small sample size ($N = 50$).

The wide variation observed within disturbance and legacy creation stages suggests substantial heterogeneity in regeneration responses following canopy disturbances, whereas the low variability recorded in pre-forest stages indicates more homogeneous regeneration conditions. Overall, the descriptive statistics suggest that regeneration dynamics vary markedly among developmental stages, with canopy closure and old-growth conditions generally supporting higher regeneration abundance than mature forest conditions.

Table 1
Descriptive statistics of regeneration abundance across developmental stages of natural Hyrcanian beech forests.

Developmental stage	N	Mean	SD	Median	Minimum	Maximum
Canopy closure	1,243	58.0	9.76	51.0	50.7	73.0
Disturbance and legacy creation	2,233	47.3	18.2	55.0	26.2	74.0
Mature forest	1,239	26.0	4.57	24.0	13.3	31.0
Old-growth	3,889	44.1	6.89	45.0	31.5	68.0
Pre-forest stage	807	28.8	0.39	29.0	28.0	29.0
Young forest	50	41.4	4.90	41.5	40.0	75.0
Note: N represents the number of regeneration observations recorded within each developmental stage.						

Canopy gap area differed significantly among developmental stages of the Hyrcanian beech forests (Kruskal–Wallis test: $\chi^2 = 11.31$, $df = 5$, $P = 0.046$; Fig. 3). However, pairwise comparisons using Dunn's test with Bonferroni correction did not reveal significant differences between individual developmental stages (all adjusted $P > 0.05$). These findings suggest that although gap size distributions varied across the developmental mosaic, the limited number of canopy gaps within each stage reduced the statistical power to detect specific pairwise differences.

A total of 9,460 regeneration records were analysed across 25 plots and 26 canopy gaps representing six developmental stages of natural Hyrcanian beech forests. The generalized linear mixed-effects model (GLMM) with a negative binomial distribution revealed that developmental stage significantly influenced regeneration abundance, whereas canopy gap area and the number of gap-making dead trees did not exert significant effects (Table 2).

Compared with the canopy closure stage, regeneration abundance was significantly lower in mature forests ($\beta = -0.906 \pm 0.236$ SE, $z = -3.844$, $P < 0.001$) and pre-forest stages ($\beta = -0.715 \pm 0.294$ SE, $z = -2.437$, $P = 0.015$). In contrast, disturbance and legacy creation stages ($P = 0.317$), old-growth forests ($P = 0.436$), and young forests ($P = 0.230$) did not differ significantly from canopy closure conditions.

Neither mean canopy gap area ($\beta = 2.61 \times 10^{-5} \pm 1.36 \times 10^{-4}$ SE, $z = 0.192$, $P = 0.848$) nor the number of gap-making dead trees ($\beta = -1.49 \times 10^{-4} \pm 2.53 \times 10^{-4}$ SE, $z = -0.589$, $P = 0.556$) significantly affected regeneration abundance. These findings indicate that the broader structural and ecological context represented by developmental stages was more important in determining regeneration patterns than the physical attributes of canopy gaps.

Random-effect estimates showed that variation among gaps nested within plots (variance = 0.084; SD = 0.290) exceeded variation among plots (variance < 0.001; SD = 0.019), suggesting that local-scale heterogeneity contributed substantially to unexplained variability in regeneration abundance.

Table 2
Results of the generalized linear mixed-effects model (GLMM)

Fixed effect	Estimate	SE	z	P-value
Intercept (Canopy closure)	4.030	0.178	22.621	< 0.001
Disturbance and legacy creation	-0.251	0.251	-1.001	0.317
Mature forest	-0.906	0.236	-3.844	< 0.001
Old-growth	-0.176	0.226	-0.780	0.436
Pre-forest stage	-0.715	0.294	-2.437	0.015
Young forest	-0.321	0.267	-1.201	0.230
Gap area	0.000026	0.000136	0.192	0.848
Number of gap-makers	-0.000149	0.000253	-0.589	0.556
Response variable: Regeneration abundance				
Distribution: Negative binomial (nbinom2)				

Random structure

Gap nested within plot (Gap $\subset$ Plot)

Random effects

Random effect	Variance	SD
Gap (nested within plot)	0.084	0.290
Plot	0.0004	0.019
Observations = 9460		
Plots = 25		
Gaps = 26		

Predicted regeneration abundance

Estimated marginal means derived from the GLMM further illustrated the influence of developmental stage on regeneration abundance (Fig. 4). The highest predicted regeneration abundance occurred during the canopy closure stage (57.0 individuals; 95% CI: 39.6–82.1), followed by old-growth forests (46.1 individuals; 95% CI: 37.4–56.8) and disturbance and legacy creation stages (48.4 individuals; 95% CI: 37.9–61.7). In contrast, mature forests exhibited the lowest predicted regeneration abundance (23.3 individuals; 95% CI: 17.6–30.9). Pre-forest stages (28.6 individuals; 95% CI: 19.2–42.5) and young forests (41.6 individuals; 95% CI: 27.6–62.8) showed intermediate values.

Overall, these findings demonstrate that regeneration dynamics in Hyrcanian beech forests are strongly associated with forest developmental stages, while canopy gap size and the number of gap-forming dead trees play relatively minor roles. The observed patterns suggest that regeneration processes are governed primarily by stage-dependent ecological conditions rather than by gap characteristics alone.

Pairwise comparisons among developmental stages

Tukey-adjusted post hoc comparisons revealed several significant differences among developmental stages (Table 3). Regeneration abundance was significantly higher in canopy closure stands than in mature forests (estimate = 0.891, $P = 0.001$). Similarly, disturbance and legacy creation stages supported significantly greater regeneration abundance than mature forests (estimate = 0.726, $P = 0.001$). Old-growth forests also exhibited significantly higher regeneration abundance compared with mature forests (estimate = 0.678, $P = 0.002$).

No significant differences were detected between canopy closure and disturbance and legacy creation stages, canopy closure and old-growth forests, or among the remaining pairwise comparisons after Tukey adjustment ($P > 0.05$). These results indicate that mature forests consistently supported lower regeneration abundance relative to several other developmental stages, whereas canopy closure, disturbance and legacy creation, and old-growth stages tended to maintain comparatively high levels of regeneration.

Table 3

Pairwise comparisons of regeneration abundance among developmental stages based on Tukey-adjusted estimated marginal means

Comparison	Estimate	SE	z-ratio	P-value
Canopy closure – Disturbance and legacy creation	0.165	0.198	0.835	0.961
Canopy closure – Mature forest	0.891	0.219	4.065	0.001
Canopy closure – Old-growth	0.213	0.198	1.075	0.892
Canopy closure – Pre-forest stage	0.692	0.262	2.643	0.087
Canopy closure – Young forest	0.317	0.262	1.209	0.833
Disturbance and legacy creation – Mature forest	0.726	0.180	4.033	0.001
Disturbance and legacy creation – Old-growth	0.048	0.153	0.310	1.000
Disturbance and legacy creation – Pre-forest stage	0.527	0.230	2.291	0.198
Disturbance and legacy creation – Young forest	0.152	0.231	0.659	0.986
Mature forest – Old-growth	-0.678	0.180	-3.767	0.002
Mature forest – Pre-forest stage	-0.199	0.248	-0.801	0.967
Mature forest – Young forest	-0.574	0.249	-2.300	0.194
Old-growth – Pre-forest stage	0.479	0.230	2.083	0.296
Old-growth – Young forest	0.105	0.231	0.453	0.998
Pre-forest stage – Young forest	-0.375	0.287	-1.303	0.784

Discussion

Forest developmental stage overrides gap attributes in shaping regeneration patterns

The results largely supported the conceptual framework proposed in Fig. 1, indicating that developmental-stage-specific structural conditions explained regeneration patterns more effectively than local gap attributes. Developmental stages represent integrated outcomes of past disturbances, competitive interactions, and successional trajectories, each providing unique ecological conditions for regeneration establishment and persistence. Similar concepts have been described for primeval European beech forests, where recurring developmental stages have been identified as fundamental components of long-term forest dynamics (Korpel, 1995; Glatthorn et al., 2018). In Hyrcanian forests, studies have increasingly emphasized that developmental stages constitute meaningful ecological units that reflect variations in stand structure, deadwood accumulation, and regeneration niches (Sefidi et al.,

2018). Therefore, regeneration patterns observed in the present study are likely driven by the cumulative effects of developmental context rather than by isolated structural attributes.

More broadly, our findings suggest that canopy gaps should not be viewed as independent drivers of regeneration dynamics, but rather as structural components embedded within broader developmental trajectories of forest ecosystems. While classical gap-phase theory emphasizes the role of canopy openings in controlling regeneration processes, the present study indicates that the ecological context in which gaps occur may be more important than the gap characteristics themselves. Developmental stages integrate multiple structural attributes, including canopy organization, deadwood accumulation, competitive interactions, and microsite diversity, thereby providing a more comprehensive framework for understanding regeneration dynamics in natural temperate forests.

Low regeneration abundance in mature forests

Among the developmental stages investigated, mature forests exhibited the lowest regeneration abundance. This pattern likely reflects the ecological constraints associated with prolonged canopy closure and competitive exclusion. Mature stands are generally characterized by relatively homogeneous canopy structures, reduced spatial heterogeneity, and limited light penetration into the understory. Under such conditions, seedling establishment and survival may be restricted, particularly for species with intermediate light requirements.

Similar regeneration bottlenecks during mature developmental stages have been reported in several European beech forests. In primeval and old-growth beech ecosystems of Central Europe, mature developmental phases are commonly characterized by relatively closed canopies, reduced structural heterogeneity, and intense competition for light and belowground resources, resulting in limited regeneration establishment and recruitment (Korpel, 1995; Emborg et al., 2000). Studies conducted in unmanaged beech forests across Europe have further demonstrated that regeneration abundance often declines during periods of canopy stability and increases only after the emergence of structural complexity associated with disturbance events and subsequent developmental transitions (Commarmot et al., 2005; Diaci et al., 2012). The low regeneration abundance observed in the mature stage of the present study therefore appears consistent with general patterns reported from temperate beech forests, where prolonged canopy closure constrains regeneration opportunities until new structural heterogeneity is created through gap formation and stand development processes. In Hyrcanian forests, previous studies have likewise demonstrated that regeneration dynamics are strongly associated with variations in stand structure, canopy stratification, and developmental conditions rather than with gap characteristics alone. Research conducted in natural oriental beech stands has shown that developmental stages differ markedly in terms of canopy architecture, deadwood accumulation, and microsite availability, all of which influence regeneration establishment and survival (Sefidi et al., 2011; Sefidi et al., 2018). Similarly, studies from unmanaged and close-to-natural Hyrcanian forests have reported that regeneration abundance and composition are closely linked to structural heterogeneity and successional status, emphasizing the importance of stand-scale developmental processes in shaping forest renewal dynamics (Mataji et al., 2010; Javanmiri Pour et al., 2019; Akbari Mazdi et al., 2021).

These findings support the view that regeneration should be interpreted within the broader context of forest development rather than solely through the characteristics of individual canopy gaps.

Structural complexity and regeneration resilience in old-growth forests

The comparatively high regeneration abundance observed in old-growth forests highlights the ecological importance of structural complexity as a driver of forest renewal processes. Unlike mature forests, which are often characterized by relatively uniform canopy conditions and limited spatial heterogeneity, old-growth stands contain a diverse array of structural features that create a broad spectrum of regeneration opportunities. Multi-layered canopies, standing and downed deadwood, pit-and-mound microtopography, and spatially heterogeneous light environments collectively increase the availability and diversity of regeneration microsites. This process, often referred to as regeneration niche diversification, enhances the establishment, persistence, and coexistence of seedlings under a wide range of environmental conditions.

The ecological significance of regeneration niche diversification has been widely documented in primeval and old-growth European beech forests. Korpel (1995) described old-growth developmental stages as structurally heterogeneous phases characterized by continuous small-scale disturbances and abundant biological legacies that facilitate forest renewal. Similarly, studies in unmanaged European beech forests have shown that structural complexity promotes regeneration by generating diverse microsites that differ in light availability, substrate conditions, moisture regimes, and competitive environments (Commarmot et al., 2005; Král et al., 2014; Čada et al., 2016). In Hyrcanian beech forests, developmental heterogeneity and deadwood accumulation likewise increase across late developmental stages and contribute substantially to ecosystem stability and regeneration opportunities (Etemad et al., 2019). Rather than being concentrated within a limited number of favorable locations, regeneration in old-growth forests is distributed across numerous ecological niches created by the interaction of canopy dynamics, deadwood accumulation, and fine-scale topographic variation.

A similar mechanism is likely operating in the Hyrcanian old-growth beech forests examined in this study. The higher regeneration abundance observed in the old-growth stage may therefore reflect not only the presence of canopy openings but also the cumulative effects of long-term structural diversification. From this perspective, regeneration success in old-growth forests is best interpreted as an emergent property of ecosystem complexity rather than as a direct response to individual gap characteristics.

Gap size alone is an insufficient predictor of regeneration abundance

Contrary to classical expectations derived from gap-phase theory, canopy gap area did not significantly influence regeneration abundance once developmental stage was incorporated into the model. This observation is consistent with previous studies conducted in Hyrcanian beech forests, which reported

weak or non-significant relationships between total regeneration density and gap size (Akbari Mazdi et al., 2021). Similarly, investigations in intact Hyrcanian stands have shown that medium-sized gaps dominate natural disturbance regimes, while regeneration responses remain strongly mediated by microsite heterogeneity and stand structural conditions (Kian et al., 2017). These findings suggest that gap size alone may be insufficient to explain regeneration dynamics in shade-tolerant forest systems such as Hyrcanian beech forests.

In European beech forests, regeneration success has likewise been linked to local environmental heterogeneity rather than canopy opening dimensions per se. Factors including litter characteristics, substrate availability, browsing pressure, and neighbourhood competition may modify or even override the influence of gap size.

The absence of a significant relationship between canopy gap area and regeneration abundance suggests that regeneration dynamics in Hyrcanian beech forests cannot be explained solely by the size of canopy openings. Classical gap-phase theory predicts that larger gaps generally increase light availability and may therefore enhance regeneration establishment and growth (Runkle, 1982). However, in shade-tolerant forest ecosystems dominated by European and Oriental beech, regeneration responses are often less dependent on gap size than in forests containing light-demanding tree species. Numerous studies have shown that beech regeneration can successfully establish and persist beneath relatively low light conditions and within small canopy openings, where favorable microclimatic conditions reduce environmental stress and improve seedling survival (Yamamoto, 2000; Diaci et al., 2012). Consequently, increases in gap area do not necessarily translate into proportional increases in regeneration abundance.

Furthermore, canopy openings represent only one component of the regeneration environment. The ecological effects of a gap are mediated by multiple interacting factors, including understory competition, litter accumulation, deadwood availability, soil moisture, browsing pressure, and microsite heterogeneity. In structurally complex forests, these factors may either reinforce or offset the influence of light availability, thereby weakening direct relationships between gap size and regeneration density. The present findings therefore support the view that regeneration responses in natural Hyrcanian beech forests are governed primarily by the broader structural and ecological context of forest development rather than by canopy opening dimensions alone. This interpretation is consistent with the conceptual framework of the study, which proposes that developmental-stage-specific structural conditions constitute the principal drivers of regeneration dynamics.

Limited influence of gap-maker abundance

The absence of a significant relationship between regeneration abundance and the number of dead trees responsible for gap formation further suggests that the origin of canopy openings may be less important than the ecological conditions prevailing after disturbance. Although multiple-tree mortality events can potentially generate larger and more heterogeneous canopy openings, our results indicate that such differences did not translate into detectable changes in regeneration density.

This outcome may reflect the buffering capacity of structurally diverse forests, where regeneration processes are maintained through multiple pathways irrespective of disturbance origin. It also emphasizes the need to distinguish between disturbance agents and disturbance effects when assessing forest regeneration dynamics.

This finding further supports the hypothesis that post-disturbance structural conditions, rather than the specific mechanism of disturbance initiation, are the primary determinants of regeneration outcomes. In other words, the ecological legacy created by disturbance appears to be more important than the number of trees involved in gap formation.

Implications for close-to-nature forest management

From a silvicultural perspective, the present findings question management approaches that rely predominantly on canopy gap size as a surrogate for natural regeneration processes. Although gap-based silviculture seeks to emulate natural disturbances, our results indicate that maintaining developmental heterogeneity across the landscape may be more important than reproducing specific gap dimensions. Silvicultural systems designed to emulate natural forest dynamics should therefore focus not only on creating canopy openings but also on conserving the full spectrum of developmental stages. Management strategies that generate gaps without preserving developmental-stage diversity may fail to reproduce the ecological processes responsible for long-term forest renewal. Consequently, developmental-stage diversity may represent a more ecologically meaningful management target than gap-size distributions alone. Such an approach is fully consistent with the principles of close-to-nature forestry, which emphasize the integration of natural disturbance regimes, structural complexity, and developmental processes into forest management planning.

Limitations and future research directions

Several limitations should be acknowledged. The relatively small number of canopy gaps reduced the statistical power of pairwise comparisons and may have limited the detection of subtle differences among developmental stages. Furthermore, the present study focused primarily on regeneration abundance and did not explicitly examine species-specific regeneration responses, seedling performance, or environmental variables such as soil properties and browsing pressure.

Future research should investigate how developmental stages interact with regeneration composition, functional traits, and microsite characteristics to shape forest renewal processes. Long-term monitoring across developmental gradients would also provide valuable insights into the temporal stability of regeneration patterns and the mechanisms underlying forest resilience in Hyrcanian ecosystems.

More broadly, the present study contributes to a growing body of evidence suggesting that regeneration dynamics in natural temperate forests should be interpreted within a developmental-stage framework rather than through a purely gap-centered perspective. While canopy openings remain important structural components of forest dynamics, their ecological significance depends strongly on the developmental context in which they occur. Developmental stages integrate the cumulative effects of

disturbance history, structural complexity, biological legacies, and resource heterogeneity, thereby providing a more comprehensive explanation of regeneration patterns than individual gap attributes alone.

Conclusions

This study provides evidence that forest developmental stage constitutes a stronger determinant of regeneration abundance than canopy gap characteristics in natural Hyrcanian beech forests. Regeneration patterns were primarily associated with the broader structural and ecological context represented by developmental stages, whereas gap area and gap-maker abundance exerted comparatively limited effects. These findings challenge simplified gap-based interpretations of regeneration dynamics and underscore the importance of developmental heterogeneity in sustaining the long-term functioning and resilience of temperate old-growth forest ecosystems.

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Figures

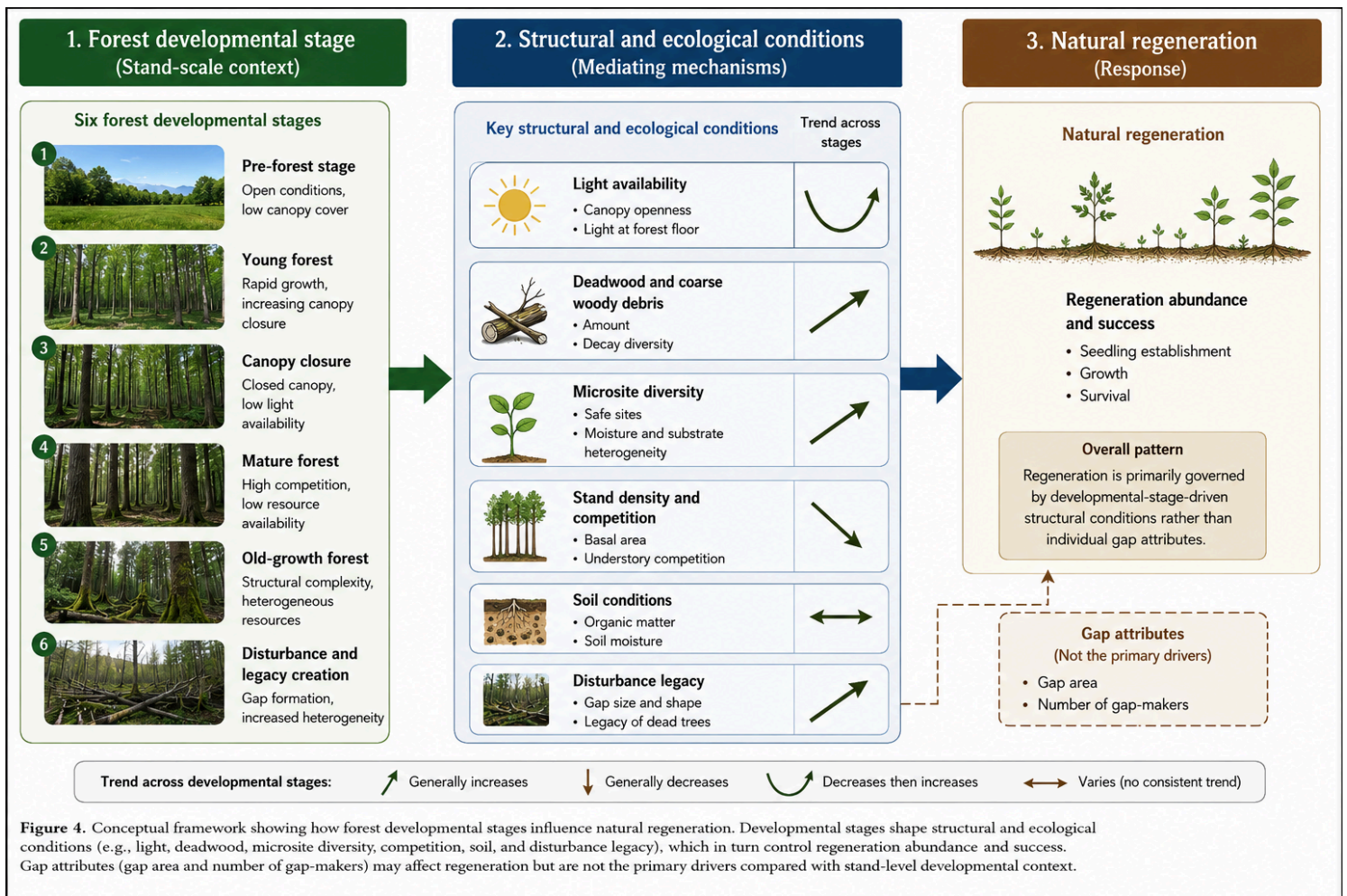


Figure 1

Conceptual framework illustrating the hypothesized relationships among forest developmental stages, structural and ecological conditions, and natural regeneration within canopy gaps. Developmental stages represent the primary ecological context shaping light availability, deadwood accumulation, microsite diversity, competition intensity, soil conditions, and disturbance legacies. These structural and ecological conditions collectively regulate regeneration abundance and establishment success. Gap attributes, including gap area and the number of gap-makers, may influence regeneration locally but are expected to exert weaker effects than the broader developmental-stage context. The framework guided the formulation of hypotheses and interpretation of results in the present study.

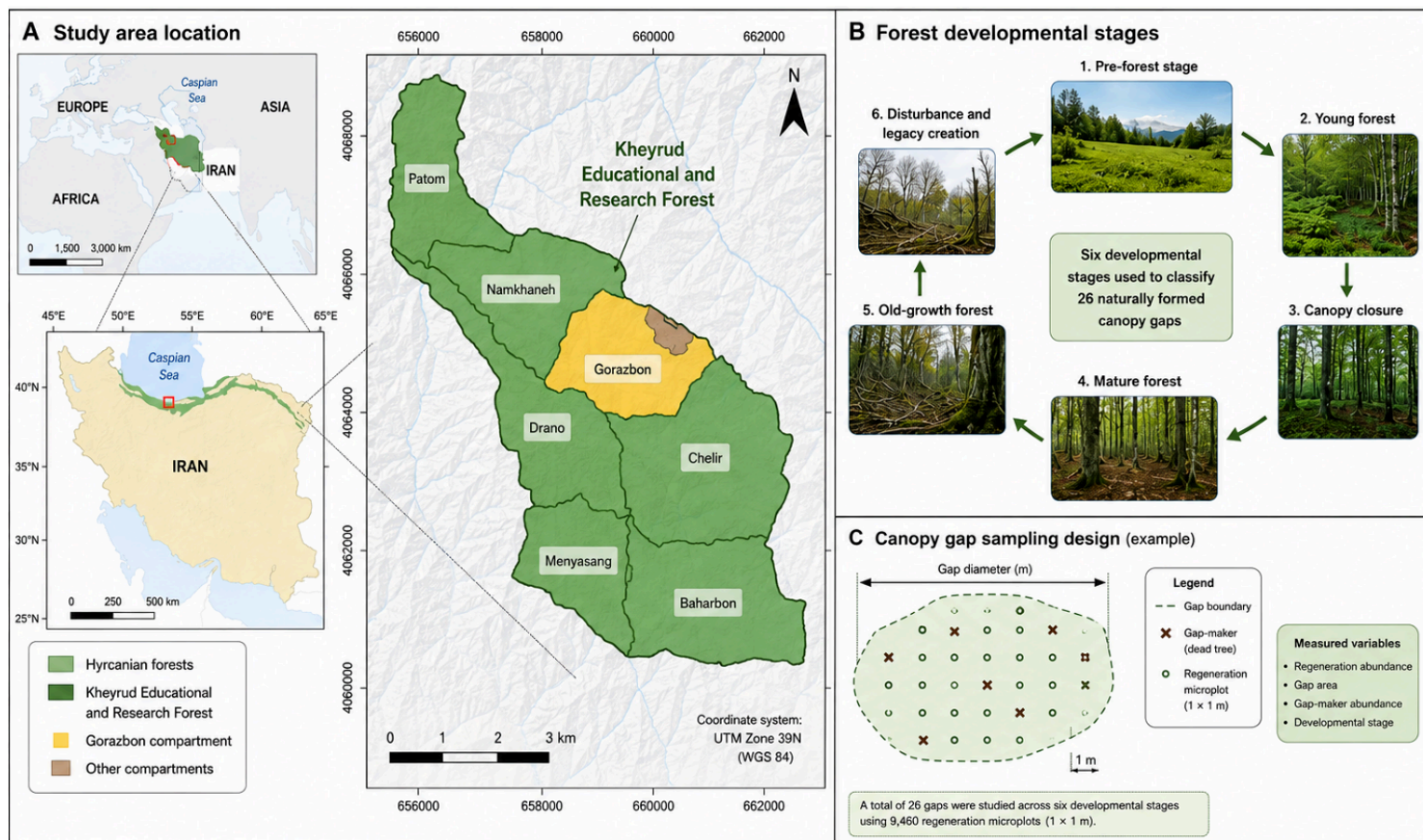


Figure 1. Study area and sampling design. (A) Location of the Gorazbon compartment (yellow) within the Kheyroud Educational and Research Forest (dark green) in northern Iran, part of the Hyrcanian forests along the southern coast of the Caspian Sea. (B) The six forest developmental stages used to classify the 26 naturally formed canopy gaps. (C) Schematic illustration of canopy gap sampling design showing gap boundary, gap-makers (dead trees), and the systematic grid of regeneration microplots used to quantify regeneration abundance and gap attributes.

Figure 2

Study area and sampling design. (A) Geographic location of the Gorazbon compartment within the Kheyroud Educational and Research Forest, located in the Hyrcanian temperate forest region of northern Iran. (B) Distribution of the 26 naturally formed canopy gaps across six forest developmental stages. (C) Schematic representation of canopy-gap sampling showing regeneration micro_plots established within each gap, gap-making dead trees, and canopy-gap boundaries used to quantify regeneration abundance, gap-maker abundance, and gap area.

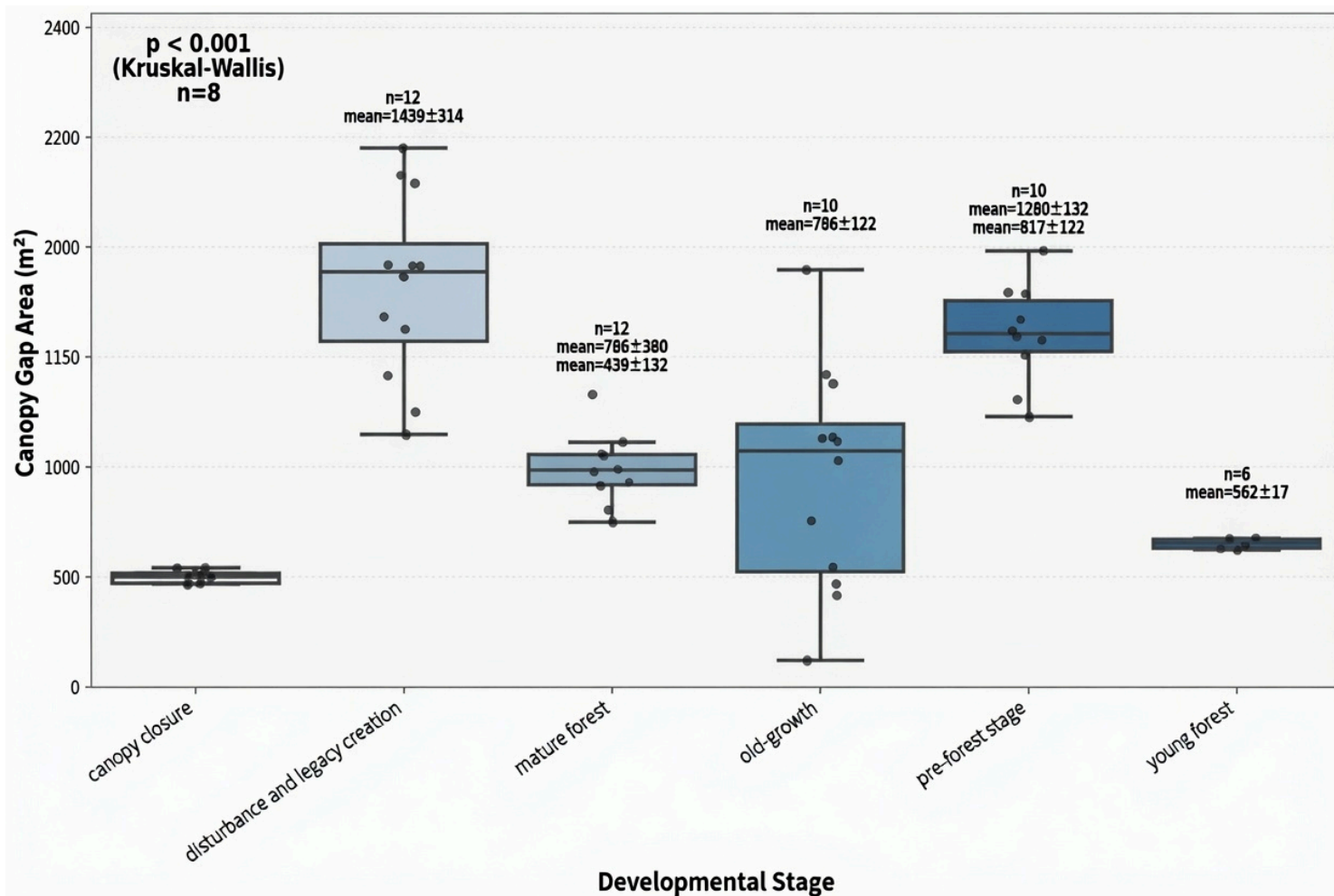


Figure 3

Variation in canopy gap area across forest developmental stages in the Gorazbon old-growth beech forest. Points represent individual canopy gaps ($n = 26$), boxplots indicate medians and interquartile ranges, and diamonds denote stage means. Canopy gap area differed significantly among developmental stages (Kruskal–Wallis $\chi^2 = 11.31$, $p = 0.046$). The largest gaps occurred during the disturbance and legacy creation stage, whereas canopy closure and young forest stages were characterized by smaller canopy openings.

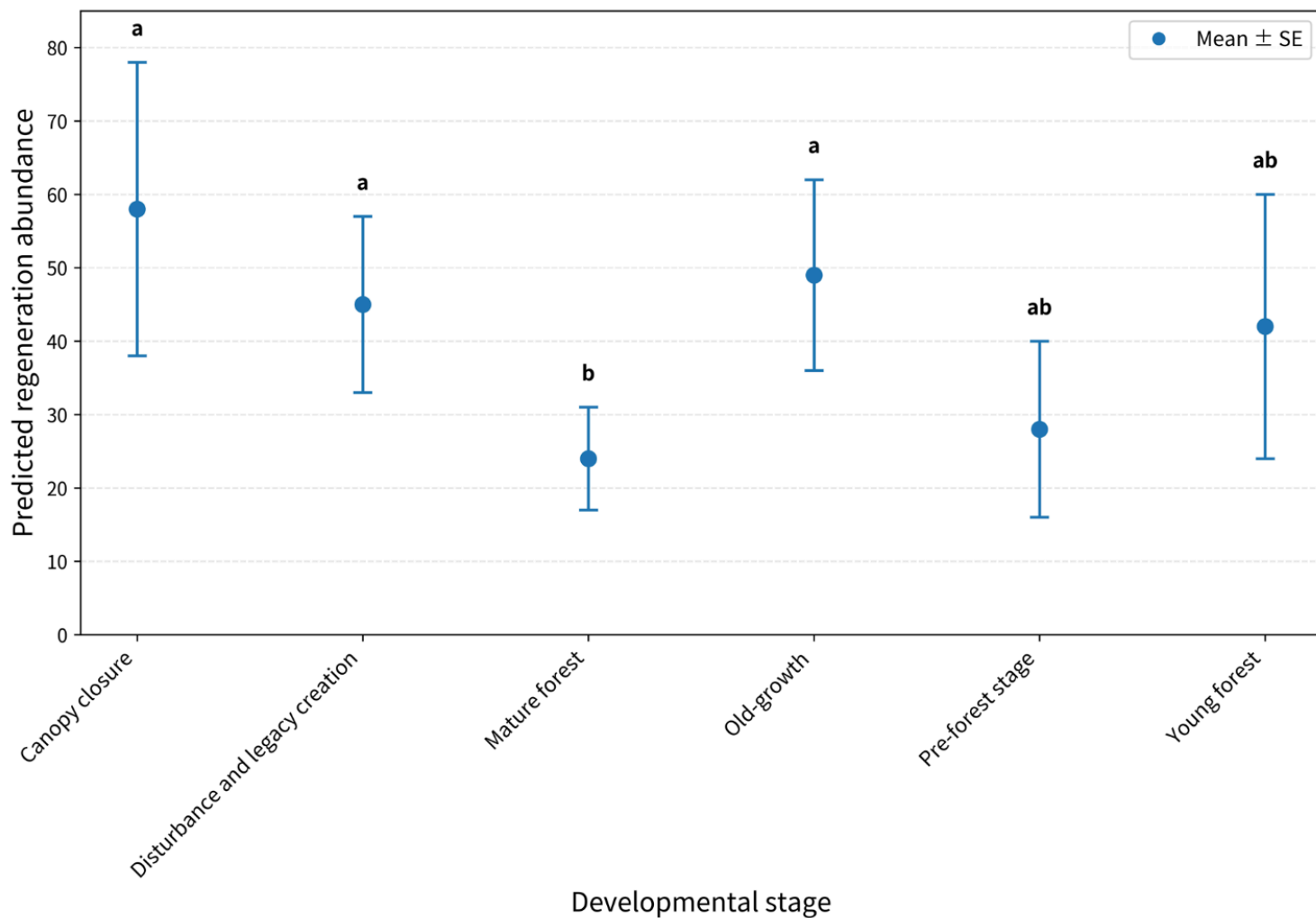


Figure 4

Predicted regeneration abundance (means $\pm$ 95% confidence intervals) across developmental stages of natural Hyrcanian beech forests derived from the generalized linear mixed model (GLMM). Different letters indicate significant differences among developmental stages based on Tukey-adjusted pairwise comparisons ($P < 0.05$).