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Effect of canopy openness and canopy type on the natural regeneration of *Abies numidica* in a mixed forest of the Babor Massif, Algeria

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Abstract: Natural regeneration is a key process for the persistence and long-term conservation of the endangered Numidian fir (*Abies numidica* de Lannoy), a relict endemic conifer restricted to the Babor-Tababort massif in northern Algeria. Light availability is a fundamental factor influencing juvenile establishment and survival across forest stand types, while canopy structure strongly regulates the amount and spatial distribution of light reaching the understory. Yet, their influence on the regeneration of *A. numidica* remains poorly documented. This study aimed to evaluate the effects of canopy characteristics and light availability on the natural regeneration of *A. numidica* using hemispherical photography acquired with a smartphone-based imaging approach.

The study was conducted in the mixed Numidian fir forests of Babor-Tababort National Park, Algeria. Hemispherical photographs were collected at 30 sampling sites distributed within the mixed forest according to the dominant canopy type (*A. numidica*, *C. atlantica*, and *Q. canariensis-P. tremula* mixed canopy). At each site, one hemispherical photograph was taken at the sampling point, and the density of *A. numidica* juveniles was recorded within a 100 m² sampling area around the corresponding point. The 30 sites were selected to represent the range of canopy conditions encountered in the study area, then we processed in R using the *hemispheR* package to derive canopy structural attributes, including Gap Fraction and Diffuse Non-Interceptance (DIFN). The density of *A. numidica* juveniles was recorded around each sampling point. Gaussian regression models were then applied to investigate the relationship between regeneration density, light availability, and canopy type.

The results revealed a non-linear response of regeneration to light availability. Juvenile density was highest under intermediate canopy openings, indicating the existence of optimal light conditions for establishment and early growth. Very dense canopies limited regeneration by reducing light penetration, whereas large canopy openings were associated with lower juvenile abundance. Regeneration also differed among canopy types, being generally most abundant under mixed (*Quercus canariensis* and *Populus tremula*) canopies, intermediate beneath *A. numidica* canopies, and lowest under *Cedrus atlantica* canopies.

These findings demonstrate that moderate canopy openings and heterogeneous stand conditions promote the regeneration of *A. numidica*. They also highlight the usefulness of smartphone-based hemispherical photography as a cost-effective tool for assessing canopy structure in montane forests. The study provides valuable insights for the conservation and sustainable management of this endangered endemic conifer in the Babor massif.

Keywords: canopy heterogeneity, hemispherical photography, DIFN, juvenile establishment, Numidian fir, Mediterranean conifers

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Introduction

Natural regeneration plays a key role in the dynamics of montane and Mediterranean forests, ensuring the renewal and persistence of forest stands (Erdozain et al., 2023). In mixed forests, where several species coexist and interact, regeneration strongly depends on inter- and intraspecific interactions that influence the survival, growth, and spatial distribution of juveniles (Pretzsch, 2014), as well as on abiotic factors such as light availability which can strongly influence seedling emergence, survival, and early development (De Lombaerde et al., 2020). The spatial distribution of seed-producing trees, seed dispersal patterns, soil conditions suitable for juvenile establishment, and light intensity may also play important roles in the determining the probability of juvenile establishment (Nathan & Muller-Landau, 2000).

The probability of an individual reaching the adult stage is closely associated with the environmental conditions experienced during its development, particularly resource availability, shade tolerance at different ontogenetic stages, and the capacity to withstand natural or anthropogenic disturbances (Kobe et al., 1995; Clark et al., 1999). Indeed, canopy structure and attributes are critical to the functioning of forest ecosystems (Nakamura et al., 2017; He et al., 2023), controlling the interception and redistribution of solar radiation, and influencing understory microclimatic conditions, and, consequently, affecting regeneration processes (Canham et al., 1990; Kobe et al., 1995). The architectural characteristics of forest cover are essential for mechanistically describing energy exchanges between vegetation and its environment, as well as for understanding interactions between forest structure and ecological dynamics (Zhou et al., 2023). Opening the forest canopy, either through gap creation or reduced tree density, can increase light availability and soil temperatures, thereby influencing natural tree regeneration (Kremer & Bauhus, 2020; Xu et al., 2023).

Located within the Babor-Tababort National Park in northeastern Algeria, the forest of Mount Babor constitutes one of the most remarkable montane ecosystems in the Mediterranean basin (Quézel & Médail, 2003). It is distinguished by a high level of species diversity, including, depending on site-specific conditions, the Numidian fir *Abies numidica*, the Atlas cedar *Cedrus atlantica* (Endl.) Manetti ex Carrière, zeen oak *Quercus canariensis* Willd., afares oak *Quercus afares* Willd., as well as the yew *Taxus baccata* L. and aspen *Populus tremula* L. (Gharzouli & Djellouli, 2005). This mosaic of forest tree species, structured by pronounced altitudinal and edaphic gradients, provides the massif with a high level of ecological heterogeneity, favoring the coexistence of species with varied biogeographic affinities, especially Euro-Siberian and Mediterranean (Médail & Quézel, 1997; Yahi et al., 2011). The Babor massif is thus acknowledged as a regional biodiversity hotspot and glacial refuge for several relict taxa (Quézel, 1998). In the core of this ecosystem lies *A. numidica*, a conifer strictly endemic to the twin Babor-Tababort massifs, whose extremely limited distribution and vulnerability to climate change and anthropogenic disturbances make it a species of major conservation interest (Farjon, 2010; Linares et al., 2011). This rare species is classified as Critically Endangered according to the IUCN (Yahi et al., 2011). Therefore, understanding the dynamics of the mixed stands in the Babor massif is crucial for clarifying the mechanisms governing the regeneration and perennity of this emblematic species.

From a structural perspective, Mount Babor forest stands show an irregular, multilayered configuration, characterized by high variability in tree diameters, as well as a mosaic of gaps that create marked canopy heterogeneity (Laidi et al., 2025). This heterogeneous canopy structure is expected to generate substantial spatial variation in the amount of radiation reaching the forest floor, thereby creating contrasting light environments for natural regeneration.

Quantifying this variation requires methods that characterize canopy openness and radiation transmission through the forest canopy. Hemispherical photography (HP) provides a practical approach for characterizing canopy structure and estimating the light environment beneath forest canopies (Depauw et al., 2020; Chianucci, 2020). Today, hemispherical photography is widely recognized as a reference

method for the precise characterization of forest cover structure and its effect on the understory light microclimate (Cameron et al., 2021; Hederová et al., 2023). By providing an indirect estimation of solar radiation transmission, this approach allows the quantification of the proportion of diffuse radiation penetrating the canopy (Rich, 1990; Hu et al., 2009).

Among the indicators derived from HP analysis, Diffuse Non-Interceptance (DIFN) constitutes a synthetic and ecologically relevant metric representing the fraction of diffuse radiation not intercepted by the canopy (Rich, 1993; Frazer et al., 1999). Because light availability influences the growth, survival, and establishment of natural regeneration, DIFN can provide a useful proxy for the understory light environment experienced by regenerating trees (Canham et al., 1990; Valladares & Niinemets, 2008). More recently, smartphone-based hemispherical photography has emerged as an accessible alternative to conventional fisheye cameras for assessing forest canopy structure. Indeed, many studies used smartphones for canopy analysis (Bianchi et al., 2017; Chianucci, 2020; Arietta, 2021; Cameron et al., 2021; Beeles et al., 2022; Lusk, 2022; Díaz, 2023, 2024; Brown et al., 2024; Baul et al., 2025). The increasing use of smartphones for this purpose reflects their potential for obtaining reliable estimates of canopy structural attributes while providing a more accessible and cost-effective approach than conventional fisheye cameras.

In this context, assessing the relationship between *A. numidica* regeneration and understory light availability can provide valuable insights into the environmental conditions governing the recruitment and persistence of this rare and threatened species. In the present study, smartphone-based hemispherical photography was used to characterize forest canopy openness in the mixed stands of the Babor massif, while the DIFN was used as an indicator of light availability in the forest understory. This approach allowed us to investigate how variation in canopy openness and associated light conditions relates to the density of *A. numidica* juveniles.

Three main canopy types were identified in the study area based on the dominant species forming the upper canopy layer: (1) *A. numidica*-dominated canopies, where the canopy was predominantly formed by *A. numidica* crowns; (2) *C. atlantica*-dominated canopies, where *C. atlantica* was the predominant canopy-forming species; and (3) mixed canopies, mainly composed of *Q. canariensis* and *P. tremula*. These canopy types were considered to assess the influence of canopy composition on local light conditions and the natural regeneration of *A. numidica*.

Based on field observations indicating greater regeneration abundance under moderately open canopies, together with previous evidence that light availability and canopy structure influence the regeneration of shade-tolerant tree species (De Lombaerde et al., 2020; He et al., 2023), we hypothesize that light is a key factor in the recruitment of *A. numidica*, and that its establishment is maximal under intermediate levels of canopy openness. We further hypothesize that differences in canopy composition are associated with contrasting light environments and, consequently, with differences in the density of *A. numidica* juveniles. Therefore, this study aims to assess the relationship between canopy openness, canopy type, and the natural regeneration of *A. numidica* in the mixed forest stands of Mount Babor. Specifically, it seeks to identify the light conditions most suitable for *A. numidica* regeneration and to improve our understanding of the ecological mechanisms governing its persistence in a heterogeneous forest environment.

Material and methods

Study area

This study was conducted in the mixed Numidian fir forest of Mount Babor (Fig. 1), located within the Babor-Tababort National Park (northeastern Algeria). Mount Babor culminates at 2004 m a.s.l. (36°30'06"N, 5°28'27"E), making it the highest point of the Babor range in the eastern Tell Atlas. This massif is characterized by a montane Mediterranean climate, with cold and humid winters often associated with snowfall, annual precipitation generally exceeding 1000 mm on the summit ridges, and relatively dry summers tempered by altitude (Quézel, 1985).

The vegetation consists of mixed forest stands where *A. numidica* is associated with several forest tree species, such as *C. atlantica*, *Q. canariensis*, *P. tremula,* and *T. baccata*. Nonetheless, this study was carried out specifically in areas where *A. numidica* dominates the tree layer. It is worth highlighting that *A. numidica* always occurs within mixed forest formations, though with varying degrees of dominance, and holds the status of a strictly endemic relict species of the adjacent Babor and Tababort massifs. Its extremely restricted distribution range, covering approximately 300 ha, confers major biogeographical and heritage value on these stands (Yahi et al., 2011). The species is described in the literature as shade-tolerant during its early developmental stages, often occurring under forest cover (Aussenac, 2002; Linares et al., 2011).

Given the restricted distribution of *A. numidica* and its predominantly mixed occurrence with other tree species, the plots were selected across representative sites in the Babor and Tababort massifs to capture variation in species composition, canopy

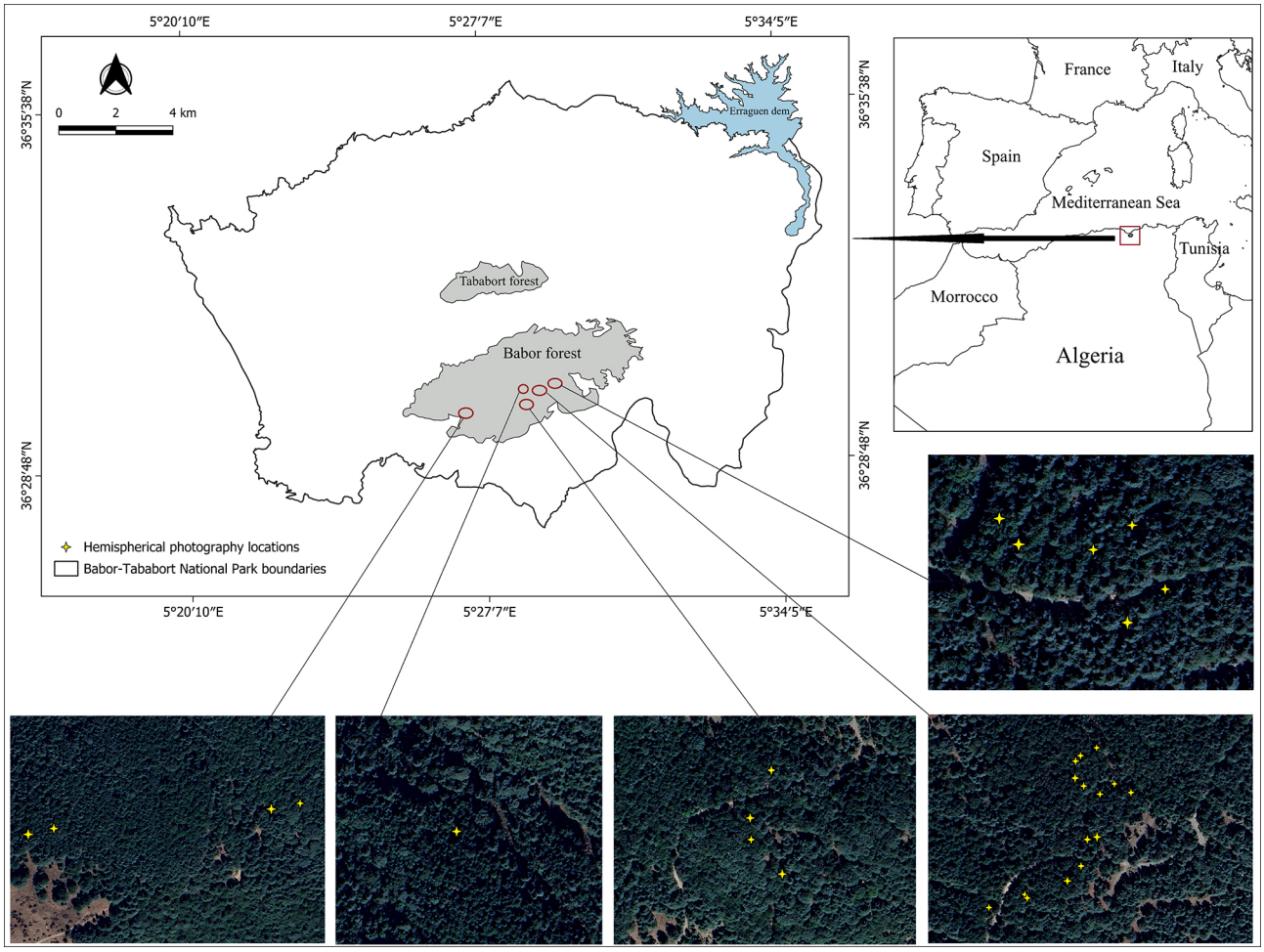


Fig. 1. Location of the study sites where hemispherical photographs were taken. Map created using QGIS version 3.10, projected in the UTM Zone 31, WGS 84 coordinate system

structure, and *A. numidica* dominance. This approach allowed the investigation of *A. numidica* regeneration under a broad range of canopy conditions and light environments representative of its natural habitat (Fig. 1).

Acquisition of hemispherical photographs

To capture a broad range of canopy openness and associated light conditions, HPs were taken in adjacent areas with comparable ecological conditions (similar altitude, soil type, and floristic composition). Images were acquired under three dominant overstory conditions: *A. numidica*, *C. atlantica*, and *Q. canariensis- P. tremula* mixed canopy. Canopy types were defined according to the dominant tree crowns surrounding each sampling point. A total of 30 HPs were retained for analysis.

Fieldwork was conducted in spring, either before 8:00 a.m. or at 7:00 p.m. (Arietta, 2021; Von Meijenfeldt et al., 2025), under diffuse light conditions to ensure homogeneity and high-quality images and minimize illumination artefacts (Fournier & Hall, 2017; Chianucci, 2020; Diaz, 2024).

Image acquisition was performed using a Vivo V30 smartphone based on the spherical photography described by Arietta (2021). The application "360 Photo Sphere Camera" was used to capture 29 individual images, which were automatically merged to generate a spherical projection. Thus, each image taken with the main camera of the Vivo V30 has a field of view (FOV) of 119°. However, the final result covers up to 360° horizontally and 180° vertically, corresponding to a hemispherical FOV (180°) or even a full spherical FOV, depending on the reconstruction method. The images were acquired by rotating the camera around a central point, guided by the camera's spatial mapping system and assisted by the smartphone's internal gyroscope and compass. The smartphone's camera software automatically merges individual images into a spherical projection by detecting interest points and using scale-invariant feature transforms to compensate for variations in distance and viewing angle between images (Szeliski

& Shum, 1997; Brown & Lowe, 2007). The resulting panoramas have a resolution of 3584 × 1792 pixels, allowing reliable estimation of canopy structural attributes.

Image processing

The obtained HPs were processed in R (R Core Team, 2025) using the "*hemispheR*" package, which is designed for HP analysis and the computation of canopy structural and radiative parameters, particularly DIFN, leaf area index (LAI), and gap fraction (Bréda, 2003; Soudani et al., 2006; Ben Yahia et al., 2020; Ben Yahia et al., 2023; Chianucci & Macek, 2023). This package enables automated execution of processing steps, sky/vegetation classification, and extraction of light-related metrics, thereby providing reliable and reproducible estimates. Complementary packages, such as "*imager*" (used in image manipulation and enhancement) and "*tidyverse*" (adapted for data organization and analysis), allowed the standardization of the processing workflow and the integration of canopy data into statistical analyses.

Following image acquisition, the spherical panoramas were converted into 2D equirectangular images, in which the vertical axis represents the zenith angle (0–180°) and the horizontal axis the azimuth (0–360°). The upper hemisphere (sky and canopy) was then extracted and remapped into a polar projection to generate a circular hemispherical (fish-eye) image, with the zenith at the center and the horizon at the periphery, following Arietta (2021). Although the theoretical foundations of hemispherical photography are well established (e.g., Welles, 1990; Rich, 1990), the present study employed a recent workflow based on smartphone-generated spherical panoramas and their processing with the R package *hemispheR* (Chianucci & Cutini, 2022), following the image conversion procedure proposed by Arietta (2021).

The analysis of the circular image includes a key binarization step to distinguish sky and vegetation pixels. This classification relies on thresholding methods based on luminance or spectral values, particularly in the blue channel, where the sky/vegetation contrast is maximal (Nobis & Hunziker, 2005). The first approaches were based on empirical thresholds that are sensitive to lighting conditions (Rich, 1990). Later, automated techniques, such as the method outlined by Otsu (1979), enabled statistical optimization of class separation by minimizing within-class variance, thereby improving productivity (Macfarlane et al., 2014).

Despite these methodological improvements, segmentation remains sensitive to exposure conditions, to light artefacts, and to atmospheric variations (Díaz

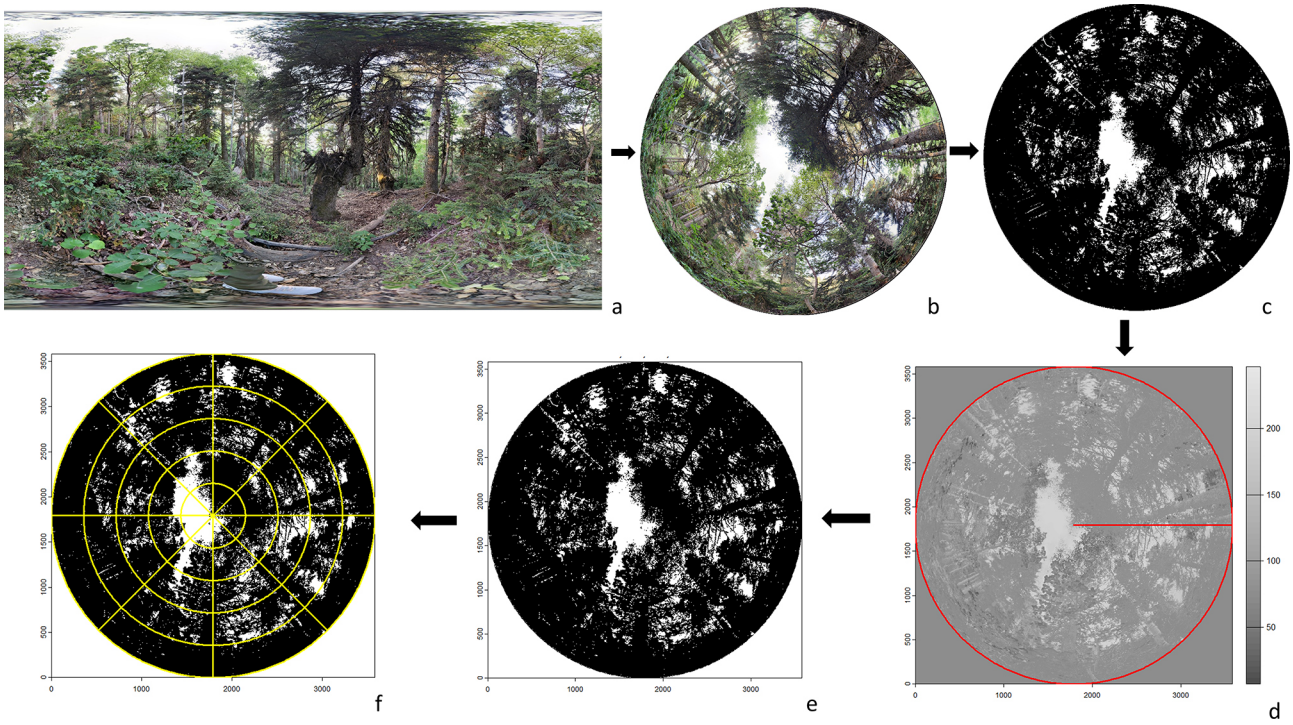


Fig. 2. Steps of hemispherical photograph processing and analysis. (a) Original HP acquired in the field using a smartphone in 360° mode, positioned at the center of the plot. (b) Circular projection of the HP after geometric correction and cropping. (c) Binary image obtained after thresholding, distinguishing canopy (black pixels) from openings (white pixels). (d) Grayscale image indicating the hemispherical circle delimitation and the azimuthal orientation. (e) Final binary image used for quantitative extraction of hemispheric parameters. (f) Overlaid angular grid (concentric rings and azimuthal sectors) used to calculate canopy structural indices (gap fraction, light transmission, and DIFN)

& Lencinas, 2015). Any classification errors directly affect the estimation of LAI and derived light-related parameters (Bréda, 2003; Jonckheere et al., 2004). Therefore, the choice and the rigor of the thresholding method are crucial to ensure reliable comparative analyses and ecological investigations based on HPs. The steps of the image-processing workflow adopted in this study are illustrated in Fig. 2.

Measurement of the DIFN

The diffuse non-intercepted fraction (DIFN) represents the proportion of sky visible from a given point, taking into account the angular weighting associated with the distribution of diffuse radiation. In contrast to transmittance metrics, which quantify the amount of light transmitted through the canopy, DIFN measures the fraction of sky unobstructed by vegetation based on a model of diffuse radiation (Jonckheere et al., 2004). Consequently, an open canopy results in a high DIFN, whereas a closed canopy yields a low DIFN. Moreover, DIFN is closely related to the gap fraction but integrates a weighting based on diffuse radiation, making it more directly applicable for deriving LAI and particularly important for forest regeneration studies (Macfarlane et al., 2014). The calculation is based on the principles described by Norman and Campbell (1989) and subsequently implemented in canopy analysis methods developed for hemispherical photography and LAI estimation (Welles & Norman, 1991; Macfarlane et al., 2014) representing by the equation 1.

$$DIFN = \sum_{\theta} \sum_{\emptyset} T(\theta, \emptyset) \times W(\theta, \emptyset) \quad (1)$$

Where:
- $T(\Theta, \emptyset)$ is the transmittance (proportion of canopy openness) at a given zenith angle (Θ) and azimuth angle ($\emptyset$);
- $W(\Theta, \emptyset)$ is the weighting factor of diffuse radiation at the angle.

Inventory of regeneration

The quantification of *A. numidica* regeneration was carried out within the same 10 × 10 m plots where the hemispherical photographs (HPs) were taken. All juvenile *A. numidica* individuals present within each plot were counted, and regeneration density was expressed as the number of juveniles per 100 m². No dendrometric measurements were taken on individual juveniles. This procedure allowed regeneration density to be directly related to the local light conditions quantified from the corresponding hemispherical photograph, providing a spatial correspondence between canopy openness and the abundance of *A. numidica* regeneration. This method enables the spatial linking of the variations in the light regime under the forest cover to the distribution and establishment patterns of juveniles, in accordance with the methodological protocols recommended in studies integrating light ecophysiology and forest regeneration dynamics (Beaudet & Messier, 2002).

Modeling *Abies numidica* regeneration density as a function of DIFN

The relationship between *A. numidica* juvenile density and DIFN was modeled under three canopy types: i) *A. numidica* adults, ii) *C. atlantica* adults, and iii) mixed species canopies, using a nonlinear Gaussian model (Eq. 2), following Ter Braak (1987) ecological response curve theory. This approach allows testing the hypothesis that light availability promotes the establishment of young individuals.

$$Y(x) = a.\exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right) \quad (2)$$

Where:
- $Y(x)$ is the predicted juvenile density (juveniles per 100 m²);
- x is the canopy openness (DIFN, %);
- a is the predicted maximum juvenile density;
- μ is the optimal DIFN value (ecological optimum);
- σ is the standard deviation of the curve (light niche breadth).

The Gaussian model relies on the assumption of a symmetric response around the optimum and is commonly applied in ecological studies. However, ecological datasets may exhibit skewed distributions or heterogeneous variances, which can affect model performance (Lichti et al., 2021). Therefore, it is important to evaluate the goodness of fit of the model. The predictive quality of the model was assessed using the coefficient of determination R^2, although this statistic should be interpreted with caution in the context of nonlinear models (Bates & Watts, 1988).

The significance of the nonlinear model parameters is assessed through the estimated standard errors and 95% confidence intervals, computed using asymptotic approximation. A parameter is considered significant if its confidence interval does not include zero.

The comparison of light optima among canopy types is performed using a nonparametric bootstrap (1000 iterations), based on resampling with replacement of the observations. The model is refitted and the optimum reestimated at each iteration. The bootstrap confidence intervals are obtained from the 2.5% and 97.5% percentiles of the empirical distribution. The difference between optima is considered

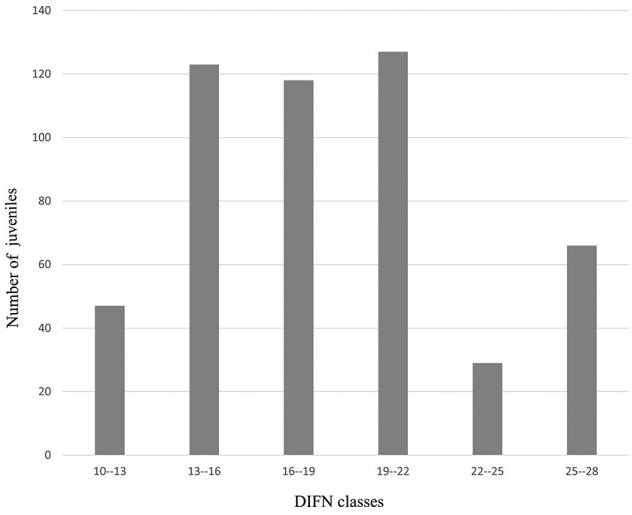


Fig. 3. Distribution histogram of *Abies numidica* juvenile number according to canopy openness (DIFN) classes

significant if the confidence interval of this difference excludes zero. All analyses were performed in R (R Core Team, 2025).

Modeling *A. numidica* regeneration density as a function of canopy type

Post-hoc pairwise comparisons were performed using Tukey's Honestly Significant Difference (HSD) test to control for Type I error across multiple comparisons (Tukey, 1949; Quinn & Keough, 2002). Tukey's HSD test was used to identify significant differences between the means of the different canopy types following the ANOVA. All statistical analyses were performed in R (R Core Team, 2025).

Results

Relationship between DIFN and regeneration

The descriptive statistics of DIFN values, used as an indicator of understory light availability, are summarized in Table 1. The stand exhibited a mean DIFN value of 19.06 ± 4.54%, with values ranging from 11.04% to 28.39% among sampling plots. This range reflects the heterogeneity of light conditions within the forest stand.

Table 1. Descriptive statistics of DIFN values.

Variable	Mean	Min	Max	σ
DIFN (%)	19.06	11.04	28.40	4.54
Juvenile density (juvenile/100 m^2)	17	0	55	15.53

Estimated parameters and goodness of fit

The results of modeling *A. numidica* regeneration as a function of DIFN using a Gaussian function revealed a well-structured, nonlinear response (Table 2). The model is statistically significant and explains 59.7% of the observed variability ($R^2 = 0.597$) with an optimum at $\mu = 17.67 \pm 1.21$ ($p < 0.001$). Both the amplitude ($a = 129.06 \pm 26.15$; $p = 0.015$) and the standard deviation ($\sigma = 5.04 \pm 1.40$; $p = 0.036$) were statistically significant.

Analysis of the 95% confidence intervals exhibits robust evidence of *A. numidica* regeneration response to the light gradient (Table 2). The ecological optimum (μ), ranging from 15.30 to 20.05% of DIFN, is relatively narrow. In contrast, the amplitude (*a*), ranging from 77.82 to 180.31, exhibits greater uncertainty. Likewise, the standard deviation (σ), ranging from 2.29 to 7.78, demonstrates a moderate but variable ecological tolerance to light.

Bootstrap analysis of the light optimum for *A. numidica* regeneration

The bootstrap analysis showed that the estimated difference in the optimum μ is not statistically significant ($p = 0.216$; mean difference = 0.216), and 95% confidence interval (−1952.52 to 3770.49) includes zero.

Figure 4 illustrates the nonlinear relationship between juvenile density and DIFN. Juvenile density increases with DIFN up to an optimum of approximately 17–18% DIFN, after which it declined.

Juvenile density also varied among canopy types (Table 3), with the highest estimated mean under mixed canopy (26.20 ± 4.87 juveniles), followed by *A. numidica* canopy (15.20 ± 4.22) and *C. atlantica* canopy (10.10 ± 4.87). However, the effect of canopy type was only marginally significant (deviance = 1229.3, $p = 0.056$; Table 4).

Table 2. Parameters of the Gaussian model fitted to regeneration density as a function of canopy openness (DIFN) for *Abies numidica* and results of analysis of the 95% confidence intervals

Parameter	a (± SE)	μ (± SE)	σ (± SE)	R^2	RSE
Juvenile density of *A. numidica*	129.06 ± 26.15	17.67 ± 1.21	5.04 ± 1.40	0.597	35.24
p-value	0.015	<0.001	0.036	–	–
95% confidence interval	77.82–180.31	15.30–20.05	2.29–7.78	–	–

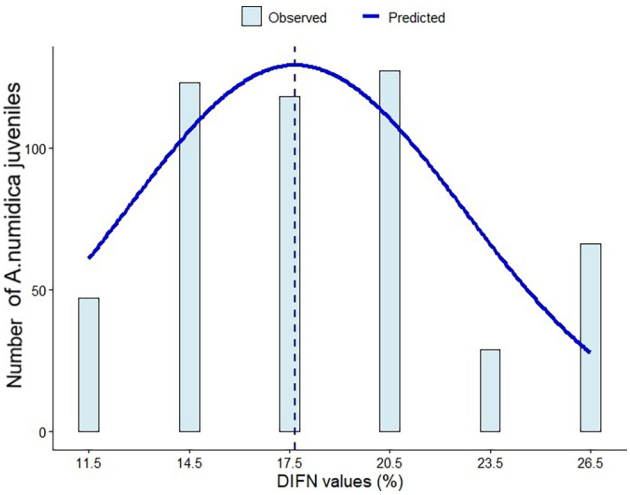


Fig. 4. Gaussian model fit showing the relationship between *Abies numidica* juvenile density and canopy openness (DIFN)

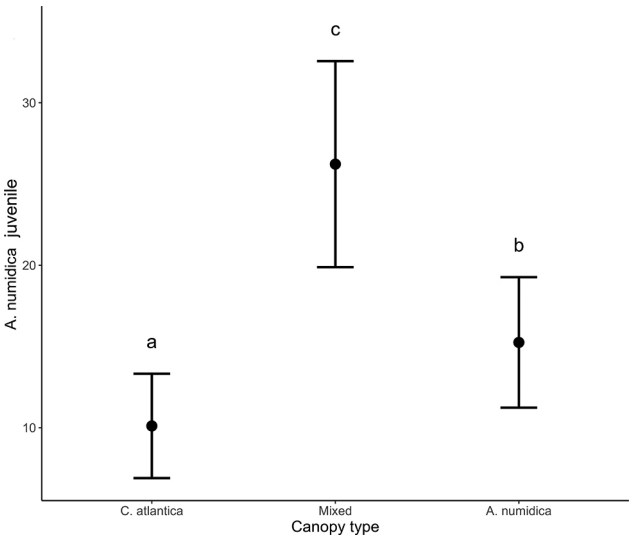


Fig. 5. Effect of canopy type on *Abies numidica* juvenile density (Tukey's HSD post-hoc test)

Effect of canopy type on regeneration

Table 3 shows that *A. numidica* juvenile density varied among canopy types, although the differences were not statistically significant at the 5% level (Table 4). The highest estimated mean density was observed under mixed canopy (26.20 ± 4.87 juveniles; 95% CI: 16.23–36.20), followed by *A. numidica* canopy (15.20 ± 4.22; 95% CI: 6.60–23.90), while the lowest density was recorded under *C. atlantica* canopy (10.10 ± 4.87; 95% CI: 0.12–20.10). The effect of canopy type was marginal but not statistically significant ($p = 0.056$).

The Tukey's HSD post-hoc test revealed differences in *A. numidica* juvenile density among canopy types (Fig. 5). The highest estimated juvenile density was observed under mixed canopy, followed by *A. numidica* and *C. atlantica* canopies.

The deviance analysis also shows that canopy type explained part of the variation in *A. numidica* juvenile density, with a deviance reduction of 1229.3. However, this effect was not statistically significant at the 5% level ($p = 0.056$) (Table 4).

Table 3. Estimated means of *Abies numidica* juvenile numbers according to canopy type

Canopy type	Estimated juvenile mean	SE	95% CI
A. numidica canopy	15.20	4.22	6.60–23.90
C. atlantica canopy	10.10	4.87	0.12–20.10
Q. canariensis-P. tremula mixed canopy	26.20	4.87	16.23–36.20

Table 4. Deviance analysis of the Gaussian model testing the effect of canopy type on *Abies numidica* juvenile numbers

Source of variance	Degrees of freedom	Deviance	Residual deviance	p-value
Null model	–	–	6994.0	–
Canopy type	2	1229.3	5764.7	0.056

Discussion

Regeneration of *A. numidica* showed a non-linear response along the canopy openness gradient, with an optimum juvenile density occurring under moderate openness levels (approximately 17–19%); for higher values, the density rapidly declines. This pattern is characteristic of species tolerating shade at juvenile stages, but whose optimal growth requires an alleviation of light limitation (Chianucci & Cutini, 2013). Also, the optimal DIFN value (17.67%) falls within the range of light conditions considered favourable to regeneration in other *Abies* species. Similar responses have been reported for *Abies alba* Mill., a shade-tolerant species whose regeneration can occur under relatively low to moderate light availability rather than under completely open conditions (Szymura, 2005; Linares et al., 2009; Kupferschmid et al., 2013; Dobrowolska et al., 2017). Among other closely related Mediterranean firs, *Abies pinsapo* Boiss. also exhibits a physiological plasticity allowing efficient light capture in the understory, while sustaining increased growth once irradiance exceeds a minimum threshold of 5–10% (Sancho-Knapik et al., 2014).

In Mediterranean ecosystems, such an intermediate light optimum reflects a trade-off between sufficient photon availability for photosynthesis and the maintenance of favourable microclimatic conditions, particularly soil moisture, which is critical for juvenile survival (Carvajal et al., 2014). A very closed canopy limits the energy available for photosynthesis whereas excessive forest cover openness, on the other

hand, increases soil temperature and evapotranspiration, thereby raising the risk of desiccation, whereas (Rodríguez-García et al., 2011). Similar relationships were described for *Abies alba*, for which as little as 10–11% canopy opening is sufficient to improve juveniles' growth, but excessive light access can lead to increased mortality (Kupferschmid et al., 2013). The forest cover thus acts as a thermal and hydric buffer, representing a key facilitation mechanism for a relic and endemic species such as *A. numidica*, which is particularly vulnerable to climatic stress.

The good fit of the Gaussian model indicates that light availability may be one of the main factors controlling *A. numidica* regeneration. Explaining approximately 60% of the variability with a single environmental factor may be considered relatively high, as the regeneration process also depends on other environmental and biotic variables (Vilhar et al., 2015). The relatively narrow confidence interval for the μ parameter suggests that the light optimum was estimated with high precision. It is worth emphasising that the bootstrap did not show a significant difference from the estimated optimum, which further confirms the stability of the obtained results.

The influence of canopy type showed that, although the light optimum remains relatively stable across different contexts, recruitment intensity varies significantly and may partly depend on the characteristics of the canopy formed by the associated tree species. The different canopy types differ in tree species composition and crown architecture, which can influence both the degree and spatial heterogeneity of light transmission to the understory. *A. numidica* generally develops a dense, conical crown with relatively continuous foliage, whereas *C. atlantica* forms broader crowns with a more discontinuous foliage structure. In the mixed canopy, *Q. canariensis* generally develops broad and relatively dense crowns, while *P. tremula* has a lighter and more open crown structure. These differences in crown architecture can generate contrasting patterns of canopy openness and light availability beneath the canopy.

Under *A. numidica* canopies, homogeneous shading and a thick litter amplify juveniles' dependence to fine-scale changes in canopy openness. Under *C. atlantica* canopies, the more discontinuous crown structure generates a more heterogeneous light environment, attenuating the effect of mean DIFN and pointing to the potential impact of additional factors such as root competition or soil properties (Navarro-Cerrillo et al., 2013). Microhabitat conditions can also be taken into account, as cedar generally shows greater tolerance to lack of water and short periods of drought than fir (Ben Said et al., 2022). Under mixed canopies (*Q. canariensis* and *P. tremula*), regeneration appeared higher, likely due to a combination of favourable conditions, including increased canopy openness, non-uniform light distribution, faster litter decomposition, and enhanced nutrient availability. This type of canopy thus creates intermediate optimal conditions that are both sufficiently illuminated and relatively protective, promoting juvenile establishment and survival.

However, the overlap of confidence intervals from the bootstrap analysis confirms the stability of *A. numidica*'s light niche, regardless of the specific canopy composition. This result is consistent with the observations reported by Linares et al. (2011) in mixed forests of southern Europe.

Finally, previous work showed that *A. numidica* regeneration exhibits an aggregated spatial distribution across different canopy types (Laidi et al., 2025), suggesting that local spatial processes may contribute to its regeneration patterns. In the present study, however, spatial distribution was not quantified, and the analysis focused specifically on the relationship between regeneration density and light availability. Emphasizes the importance of favourable microsites in the regeneration process. Indeed, recruitment tends to occur within "regeneration nuclei" where moisture and fertility conditions are optimal (Kobe et al., 1995; Gómez-Aparicio et al., 2008). In North African massifs like the Babor, where stands often display aging and heterogeneous structures, these dynamics are particularly pronounced. In this context, excessive forest cover closure in certain relatively undisturbed stands may limit the establishment of new cohorts by reducing light availability below the critical threshold required for juvenile development (Muscolo et al., 2017).

From a species conservation perspective, our results suggest that maintaining heterogeneous canopy conditions and avoiding extensive canopy opening may favour the regeneration of *A. numidica*. The relatively high regeneration density observed under mixed canopies further suggests that maintaining species and structural diversity could provide suitable light conditions for regeneration within the Babor forests. However, the mechanisms underlying these patterns remain uncertain, as water availability, interspecific competition, and stand structural dynamics were not directly assessed in this study. The observed response is consistent with findings reported for other relict Mediterranean firs, such as *Abies pinsapo* and *Abies marocana* Trab., for which regeneration has also been associated with heterogeneous canopy conditions and moderate light availability (Linares & Carreira, 2009; Ben Said et al., 2022).

Conclusion

This study examined the relationship between the regeneration of *A. numidica* and light availability

estimated from hemispherical photographs in Babor-Tababort National Park (northeastern Algeria). It demonstrates that the regeneration of the investigated species is not determined solely by light availability, but rather results from complex interactions among light conditions, and stand structure.

The identification of an intermediate light optimum, supported by bootstrap resampling, highlights the nonlinear and context-dependent response of *A. numidica* juveniles to canopy openness.

These findings suggest that, although *A. numidica* is shade-tolerant during the juvenile stage, moderate light conditions may favour its establishment. This response may reflect the species' ability to benefit from increased light availability while remaining under relatively shaded conditions. However, the present study did not investigate stand structure, soil moisture, or microclimatic conditions; therefore, it cannot directly assess the potential contribution of these factors to the observed regeneration patterns. These findings indicate that, although *A. numidica* is shade-tolerant during the juvenile stage, its regeneration density was highest under moderate light conditions, with an estimated optimum DIFN of 17.67%. This suggests that intermediate canopy openness may provide suitable conditions for regeneration, although the physiological mechanisms underlying this response require further investigation.

From a practical perspective, this study provides key information for the management and conservation of this species, which has a very restricted distribution. It suggests that silvicultural practices promoting a mosaic of stand structures, combining shaded areas with moderate canopy openings, represent an appropriate strategy to support natural regeneration.

Within the framework of climate change, characterized by rising temperatures and recurrent drought events, these findings hold particular relevance. They offer a scientific basis for steering conservation actions aimed at enhancing the resilience of relict populations of *A. numidica*. In this regard, identifying micro-environmental conditions that favor regeneration constitutes a key lever for adaptive management, particularly in the most vulnerable areas.

Finally, several research perspectives emerge from this investigation. Temporal monitoring of *A. numidica* regeneration could provide a better understanding of juvenile growth and mortality dynamics in response to seasonal variations in light availability and climatic conditions. Integrating complementary factors, such as soil moisture, root competition, and edaphic properties, could further help refine explanatory models. Furthermore, ecophysiological approaches centered on the responses of *A. numidica* to water and heat stress appear crucial to anticipating the species' trajectory under ongoing global change. In the long term, combining these approaches with distribution models and climate scenarios would allow for more precise identification of priority areas for the conservation and restoration of this emblematic species.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare that they have no competing interests.

Authors' contributions

Keyssa Laidi: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Khellaf Rabehi:** Supervision, Methodology, Conceptualization, Data curation, Formal analysis, Validation, Visualization, Writing, Review & editing. **Said Slimani:** Writing – Review & editing, Validation. **Łukasz Walas:** Writing – Review & editing, Validation.

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