

# Canopy gap dynamics, disturbances, and natural regeneration patterns in a beech-dominated Hyrcanian old-growth forest

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## Abstract

Canopy gaps play a crucial role in forest dynamic processes and help preserve biodiversity, influence nutrient cycles, and maintain the complex structure of the forests. This study aimed to quantify the gap dynamics, regeneration establishment, and gap closure in a natural old-growth Hyrcanian forest in the north of Iran. We used a repeated inventory of gap size-frequency and fraction in beech (*Fagus orientalis*) dominant forest over a 9-year interval (2010–2019). The total gap area documented in 2010, 2016, and 2019 was 2,487, 6,890, and 8,864 m<sup>2</sup>, respectively. The gap area ranged from the smallest sizes of 139, 83, and 153 m<sup>2</sup> to the largest sizes 906, 1,668, and 871 m<sup>2</sup> in 2010, 2016, and 2019, respectively. Gap fraction significantly increased from 0.52%, 1.93%, and 3.7% in 2010, 2016, and 2019, respectively. The size distribution of gaps was strongly skewed to the medium class (200–500 m<sup>2</sup>), with approximately 60% of the gaps. Results revealed that total regenerations are not in correlation with gap size. Small gaps were closed within a few years through rapid horizontal canopy expansion of neighboring beech trees. The gap closure rate decreased by increasing the gap size (70% in 71 m<sup>2</sup> to 10% in 1,600 m<sup>2</sup>). The highest density and greatest regeneration growth occurred mostly along the eastern part of gaps. The spatial distributions of regeneration density demonstrated differences in different gap size classes, which probably resulted from heterogeneity in the microenvironment within the gap and the differences in the regeneration responses to these variations. This investigation provided useful data for managing natural regenerations based on forest sustainability. The changes in gap patterns observed between 2010 and 2019 highlight the high value of repeated gap inventories for better comprehending the disturbance regeneration and dynamics of natural gaps.

**Keywords:** Gap size, Gap development, Special distribution, Regeneration density, Gap closure

## Introduction

Due to the increased population and environmental pollution, protection of the environment and natural resources is receiving increasing attention. In the meantime, the importance of forest ecosystems is very high. The forest ecosystem and its dynamics depend on numerous factors, including natural disturbances that affect gap in the forest structure and influence the dynamics of the plant population (Naaf and Wulf 2007). The term gap usually refers to some open space inside the forest canopy caused by the death or injury of trees (Zhu et al. 2014). Canopy gaps play key roles in forest ecosystem development and result from either natural processes or targeted forest management activities (Holik et al. 2018). Gap disturbances are one of the fundamental determinants of the forest structure, composition, and dynamics (Turner 2010, Yang et al. 2017), and their ecological effects vary with size and

frequency (White and Jentsch 2001). Gap distribution is related to the geographical conditions of the region, as well as the climatic conditions and the management history of the forest. (Amiri et al. 2015). It is known that wind disturbances selectively damage larger trees in each stand, and species with heartwood decay are generally vulnerable to wind damage (Peterson 2007). Earlier studies indicated that the functional properties of tree species might be as important as the wind in determining the characteristics of gap formation (Arihafa and Mack 2013, Grainger and Aarde 2013). Gaps are mainly formed by the death of trees and other external destructive factors such as wind, snow, etc. Technically, they act as secondary factors in the weakening of weak trees and the spread of pre-formed gap (Bottero et al. 2011). Gaps from a fallen tree lead to regeneration growth in forests (Almquist et al. 2002). Increasing the sunlight, changing the soil moisture levels, and pro-

viding available nutrients for regeneration lead to heterogeneity in the forest ecosystem (Hart and Grissino-Mayer 2009) which plays a substantial role in species composition, growth rate, density, forest age, and gap dynamics (Weiskittel and Hix 2003, Woods 2004).

The spatial heterogeneity of the canopy structure means that there are different sizes and shapes of gap throughout the forest stand structure, and the creation of sequential mosaics in the forest ecosystem that begins with regenerative cavities plays a significant role in the spatial structure of the stands. Surface soils have different effects on the establishment of regeneration and tree regeneration in managed stands (Almuquist et al. 2002, Zolfaghari et al. 2007). Open forest areas as islands are regarded as having more biomass, more grass layers, and younger cover (Shabani et al. 2009) which increases the abundance, diversity, and composition of plants and the number of forest regenerations (Naaf and Wolf 2007, Dupuy and Chazdon 2008).

According to recent studies, in addition to gap, gap makers are also critical in the structure and dynamic process of forest ecosystems and are even involved in the biogeochemical processes of forest ecosystems (Stella et al. 2015). Forests contain large amounts of terrestrial biomass, so they are a pivotal part of the terrestrial carbon cycle as well (Grace et al. 2014). Gap makers are one of the main structural features of natural and untouched forests and have an important function in maintaining the production, environmental heterogeneity, and biodiversity assessment of forest ecosystems. Also, the diversity of the organisms is strongly influenced by forest gap makers in the forest. Gap makers form a stage of this cycle that is rich in nutrients such as nitrogen, calcium, phosphorus, magnesium, and potassium (Sefidi et al. 2007) and by retaining water and nutrients, they create a suitable microclimate under forest disturbances that help establish natural regeneration (Sefidi and Haghighi 2008).

The quantity of the gap pattern is important for understanding the dynamics of the stands, although the gap opening is a random and time-bound process (Nuske et al. 2009). However, comparing the results of research on bright dynamics in different geographical locations will facilitate the prediction and understanding of the effects of different types of disturbances on various forest ecosystems. The basic characteristics of gap include size, age, shape, and rate, which affect forest components (Weiskittel and Hix 2003). Numerous studies have attempted to determine the best statistical distribution of gap sizes (Sapkota and Oden 2009, Yamamoto et al. 2011, Muscoco et al. 2014, Zhu et al. 2014). The large gaps have a positive effect on tree regeneration (Cuevas 2003, Kathke and Bruelheide 2010), and the shape of gap affects microclimate and species composition (Dam 2001). Several studies have been conducted in old-growth forests to determine the gap characteristics, disturbance regimes, and its dynamics (Kucbel et al. 2010, Muscolo et al. 2014, Orman et al. 2018). Therefore, one should investigate the most important gap factors (struc-

ture and regenerations establishment). Understanding gap dynamics, regeneration establishment, and gap closure is of importance to sustainable forest management practices. Therefore, this study examined the gap creation, dynamics, and regeneration density in 9 years (2010–2019).

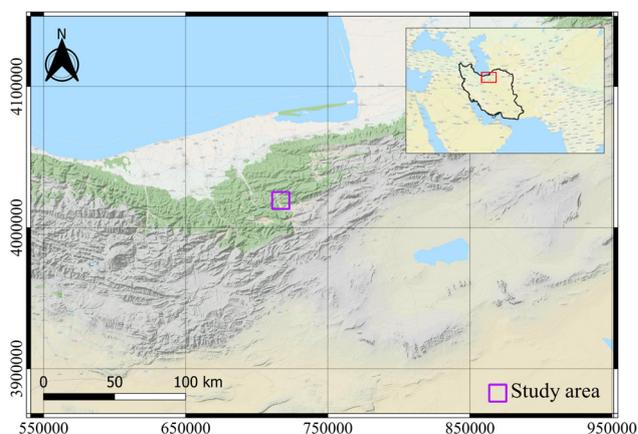
## Materials and methods

### Description of Hyrcanian forests

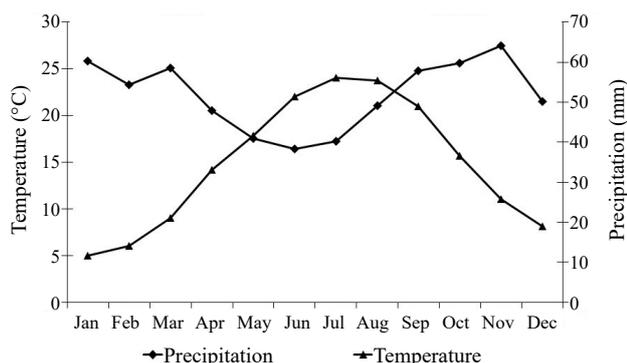
Hyrcanian forests form a unique forested massif that stretches 850 km along the southern coast of the Caspian Sea (across three provinces viz. Gilan, Mazandaran, and Golestan, Iran). The history of these broad-leaved forests dates to 25–50 million years, when they covered most of this Northern temperate region. These ancient forest areas retreated during the Quaternary glaciations and then expanded again as the climate became milder. Their floristic biodiversity is remarkable: 44% of the vascular plants known in Iran are found in the Hyrcanian region, which only covers 7% of the country. The forest is dominated by Oriental beech (*Fagus orientalis* Lipsky), Hornbeam (*Carpinus betulus* L.), Chestnut-leaved oak (*Quercus castaneifolia* C. A. Mey), Caucasian alder (*Alnus subcordata* C. A. Mey.), and Persian maple (*Acer velutinum* Boiss).

### Study site description

The study was conducted in a 50-ha area of Haftkhal series 1 and 4 (between 36°27' and 36°32' N and 53°42' and 53°48' E, DATUM WGS84) of the Hyrcanian old-growth forest located in the Mazandaran Province within the Alborz mountain region in the northern part of Iran (Figure 1). The series is located at an altitude of 1,100 to 1,900 m a.s.l. The origin of the soil in the studied series consists of limestone, marl limestone, and dolomite limestone. The relative humidity fluctuates between 78% and 84%, with the highest in September and the lowest in March and April. There is rainfall in all months of the year, the amount of which varies in different months. The highest amount of rainfall in November is 64 mm and the



**Figure 1.** The studied area of Haftkhal forest (a part of Hyrcanian old-growth forests), northern Iran



**Figure 2.** Embrothermic curve of the study site

lowest in June is 38.2 mm. According to the embrothermic curve, the studied area is climatically temperate (Figure 2).

### Field investigation

A complete gap field survey was conducted from June to September 2019 in a 50-ha forest stand. We found a total of 47 canopy gaps. We recorded physical site characteristics, including slope, aspect, elevation, geographical coordinates, and canopy height when gaps were not identified as closed.

Gap length was set as the longest distance from one gap edge to another gap edge, and the width was set as the longest perpendicular to length. In irregular-shaped gaps, we measured actual radii as in Lertzman and Krebs (1991). Gap areas were calculated by fitting width and length dimensions to the formula for an ellipse (Lima 2005). Gap-makers were the fallen trees that created gaps, and one, two, or more of these fallen trees could form gaps. From the approximate centre of each expanded gap, we measured distance and direction to all regenerations to determine the detailed position of everyone. We also measured the ground diameter (GD) and height (H) regenerations in the expanded gaps.

To better map the locations of regeneration, only those regeneration with a minimum height of 20 cm (Barbeito et al. 2008) were measured and mapped according to X/Y coordinates. This procedure was followed because the study was focused on established regeneration that had survived for at least one full year since germination. The age of regeneration was estimated by counting the branch whorls or scars on the stem (Wang and Zhang 2009, Dong et al. 2013).

### Statistical analysis

We investigated the canopy gap creation and development within the period 2010–2019. Gap formation and increases in gap area in 2010, 2016, and 2019 were investigated. The distribution of gap size and the cover percentages of canopy gap size classes were compared in 2010–2019. We reported the relative rate of gap closure in relation to the gap size in 2019. The dominant process of gap closure (horizontal and vertical regeneration growth) was assessed in the field basis on measuring the percent

area which filled by regenerations. All the statistical analyses were performed with the SPSS software package, version 19.0 (IBM SPSS Statistics 2010). Significant differences were detected at  $p < 0.05$ .

### The spatial pattern of canopy gaps

The spatial distribution of canopy gaps varied in the different parts of the study area. The univariate Ripley's L-function  $L(r)$ :

$$L(r) = \sqrt{\frac{K(r)}{\pi}} - r,$$

$$\text{where } K(r) = \frac{a}{n \cdot (n-1)} \cdot \text{sum}[i, j] \cdot I(d[i, j] \leq r) \cdot e[i, j],$$

where  $a$  is the area of the window,  $n$  is the number of data points,  $i$  and  $j$  are all ordered point pairs,  $d[i, j]$  is the distance between the two points  $i$  and  $j$ ,  $I(d[i, j] \leq r)$  is an indicator that equals 1 if the distance is less than or equal to  $r$ , and  $e[i, j]$  is the edge correction weight (Wang et al. 2017).  $L(r)$  has an expectation of 0 under the null hypothesis of CSR (complete spatial randomness) and becomes positive or negative when the pattern tends to aggregate or disperse. (Wang et al. 2017).

### Kernel density estimation for gap regeneration density

Kernel density estimation (KDE) is a non-parametric statistical method (Parzen 1962) that is based on the quadratic kernel function and fits a smooth surface to each point to calculate a magnitude per unit area. KDE was calculated for regeneration density in the four gap size classes. The initial X/Y coordinates of the regeneration were converted into a new coordinate system with the centre of each gap as the origin. The gap points were grouped by gap size class (minor, small, medium, and large) and were aligned by the coordinates of each gap centre. Kernel density estimates were first run for each of the 47 gaps. Mean cell statistics were then calculated for all the kernel densities and heights within a particular gap size class, producing a final map of the mean KDE, the mean height, and their corresponding standard deviations. Similarly, the mean edge line of each gap section was plotted for each gap size class. The constant polygon shapefiles of sufficient size to encircle any gap were created to calculate the mean KDE and the mean height. To calculate and graphically display the mean KDE of the gaps and regenerations, QGIS application, v. 3.6.2 (QGIS 2019), was used.

The Kernel density estimator is, where  $K(\cdot)$  is a non-negative function that integrates to 1 and has a mean of 0,  $n$  is the number of data points ( $x$ ), and  $h$  is the search radius. In this study, the default search radius was used for statistical analysis, calculated using the formula:

$$\text{SearchRadius} = 0.9 \cdot \min \left( SD, \sqrt{\frac{1}{\ln(2)} \cdot D_m} \right) \cdot n^{-0.2},$$

where  $SD$  is the standard distance and  $D_m$  is the median distance (Wang et al. 2017).

### Results

The total gap area documented in 2010, 2016, and 2019 was 2,487, 6,890, and 8,864 m<sup>2</sup>, respectively (Figure 3). The gap area in 2010 ranged from 139 to 906 m<sup>2</sup>, with an average of 414 m<sup>2</sup>. In 2016, the gap area was ranged from 83 to 1,668 m<sup>2</sup>, with an average of 383 m<sup>2</sup>. Finally, in 2019, the gap area ranged from 153 to 871 m<sup>2</sup>, with an average of 385 m<sup>2</sup>. Fig. 4 depicts the coordinates of gaps by years 2010, 2016, and 2019, and Table 1 lists the gap geometry characteristics (gap area mean, gap perimeter, gap elongation, and gap-maker volume).

Forty-seven gaps were documented in the *F. orientalis* mixed stand (total area: 50.21 ha) in 2010, 2016, and 2019 (3.7% of the total area of stands). The total area of gaps in 2010 was 0.26 ha (0.5% of the total area of stands). One gap was classified as small (< 200 m<sup>2</sup>), four as medium (200–500 m<sup>2</sup>), and one as large (< 1000 m<sup>2</sup>). From the 18 gaps (1.4% of the total area of stands) registered in 2016, six gaps were classified as small (< 200 m<sup>2</sup>), nine as medium (200–500 m<sup>2</sup>), two as large (< 1000 m<sup>2</sup>), and one as very large (> 1000 m<sup>2</sup>). Finally, in 2019, 23 new gaps were observed, accounting for 1.860% of the forest area. The gap share of 2019 was as follows: four gaps were classified as small (< 200 m<sup>2</sup>), 15 as medium (200–500 m<sup>2</sup>), and four as large (< 1,000 m<sup>2</sup>) (Figures 5 and 6). The size distribution of gaps was strongly skewed to the medium class (200–500 m<sup>2</sup>), with ~60% of the gaps. Six gaps were formed before 2010, and 41 gaps from 2010 to 2019. We recorded 63 gap-makers as fallen trees (51%), uprooting (10%), broken trunks (21%), and standing dead tree (19%) in the 47 gaps.

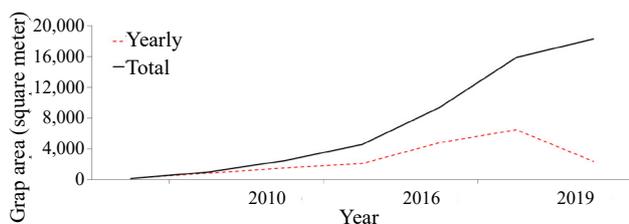


Figure 3. Gap area increase in different years

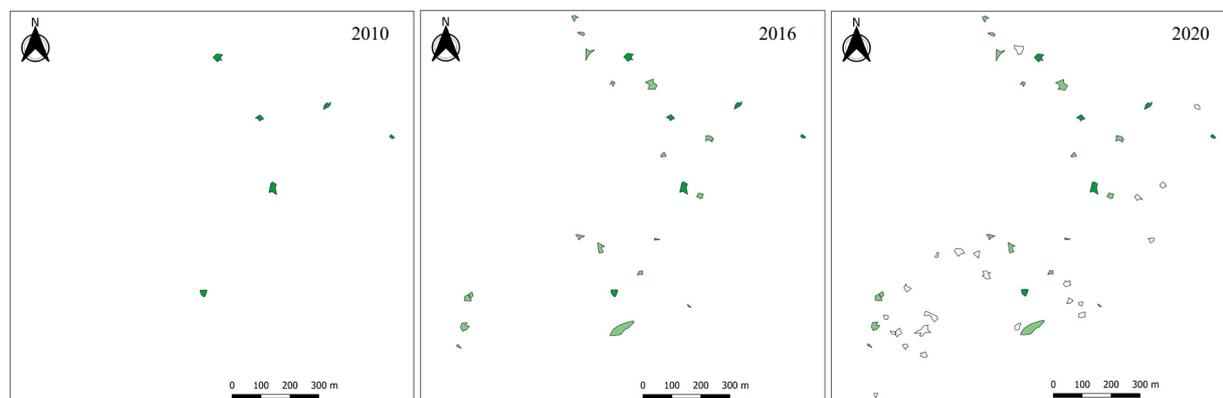


Figure 4. Gap evolution in different years

Eight species were registered as the regeneration composition in all the documented gaps (Table 1). Beech (*F. orientalis*) had the most frequency in the regeneration layer with 86.4%. Total regeneration in 2010, 2016, and 2019 was 39, 117, and 190, respectively. Mean regenerations' cover in 2010, 2016, and 2019 was 10.8%, 11.4%, and 13.5%, respectively.

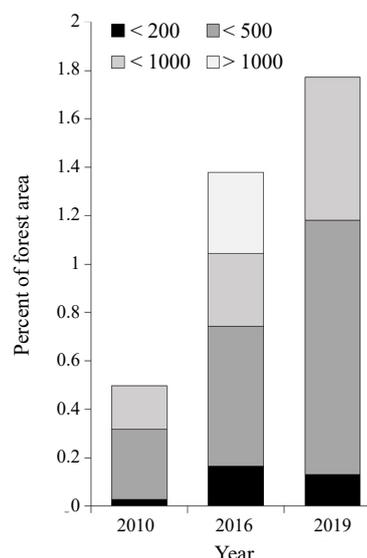


Figure 5. Gap share (%) of the forest area in 2010, 2016, and 2019

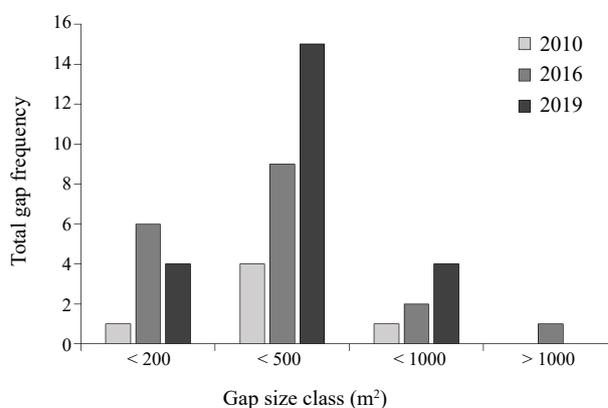


Figure 6. Total gap frequency in different gap size classes

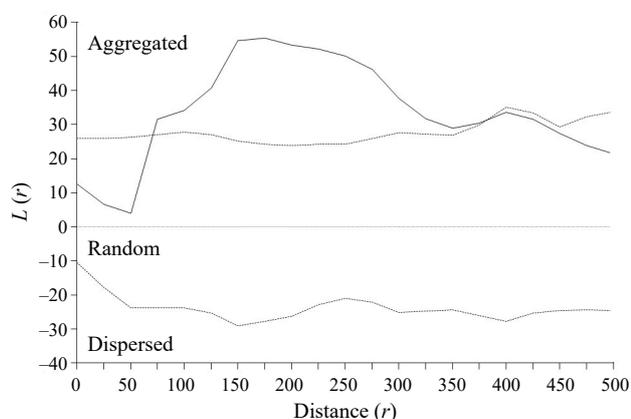
**Table 1.** Gap geometry characteristics (Mean ± Standard deviation) and regeneration species composition divided by years of 2010, 2016 and 2019

|                                    | Year           |                |                |                |
|------------------------------------|----------------|----------------|----------------|----------------|
|                                    | 2010           | 2016           | 2019           | Total          |
| Number of gaps                     | 6              | 18             | 23             | 47             |
| Gap area mean (m <sup>2</sup> )    | 414.5 (261.96) | 382.8 (379.78) | 385.4 (193.42) | 388.1 (280.64) |
| Gap perimeter (m)                  | 82.8 (22.05)   | 77.8 (42.68)   | 81.9 (20.77)   | 80.5 (30.61)   |
| Gap elongation (m)                 | 21.5 (6.02)    | 18.2 (7.22)    | 20.1 (8.18)    | 19.6 (7.52)    |
| Dead tree volume (m <sup>3</sup> ) | 10.4 (4.53)    | 13.5 (7.82)    | 12.1 (8.07)    | 12.4 (7.55)    |
| Regeneration ground diameter (cm)  | 9.1 (4.50)     | 6.2 (2.10)     | 5.5 (2.06)     | 6.2 (2.69)     |
| Regeneration ground height (m)     | 10.5 (4.96)    | 6.4 (2.39)     | 5.4 (1.99)     | 6.4 (3.06)     |
| Regeneration composition           |                |                |                |                |
| <i>Fagus orientalis</i>            | 33             | 93             | 173            | 299            |
| <i>Acer pseudoplatanus</i>         | 2              | 7              | 9              | 18             |
| <i>Acer cappadocicum</i>           | -              | 6              | 2              | 8              |
| <i>Tilia begoniifoliolinden</i>    | 1              | 2              | 5              | 8              |
| <i>Ulmus glabra</i>                | 2              | 5              | -              | 7              |
| <i>Diospyros lotus</i>             | 1              | 1              | 1              | 3              |
| <i>Alder buckthorn</i>             | -              | 2              | -              | 2              |
| <i>Parrotia persica</i>            | -              | 1              | -              | 1              |

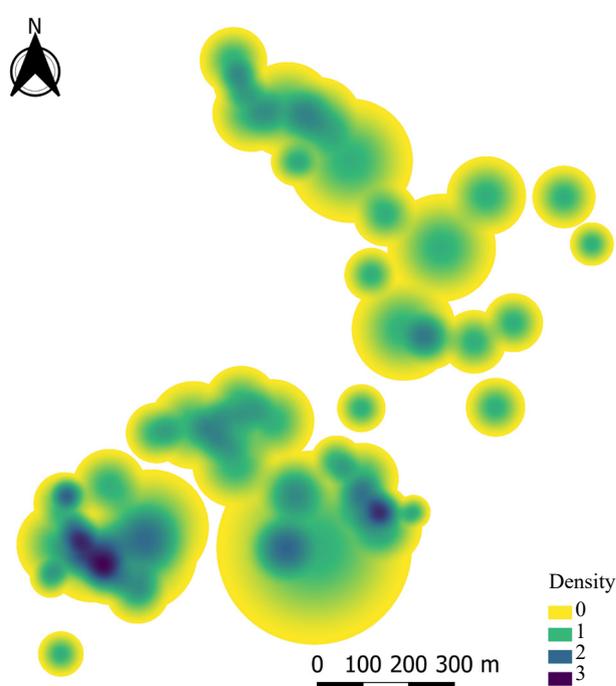
The spatial distribution of canopy gaps changes by increasing the distance. Univariate Ripley’s L-function showed random distribution in the range of 0 to 70 m (Figure 7). The aggregated spatial pattern started at 70 m and continued to 380 m. The spatial pattern of the gaps was random for distances > 380 m. Mean KDE for gap distribution indicated that it is denser (three gaps per ha) in the southern part of the studied area than in the other parts (Figure 8).

The cover of the regeneration layer was investigated horizontally and vertically in 47 gaps (Figure 9). The most successful regeneration of species from small to tall seedlings was beech, which comprised an 80% share of the tall seedlings and an increasing density over the 9 years. The small class of gap area (< 200 m<sup>2</sup>) has a larger closure rate (~70%). Gaps > 500 m<sup>2</sup> had a 20% gap closure rate with >90% probability. Finally, as Fig. 9 shows, the gap closure rate decreased by increasing the gap size (70% in 71 m<sup>2</sup> to 10% in 1,600 m<sup>2</sup>).

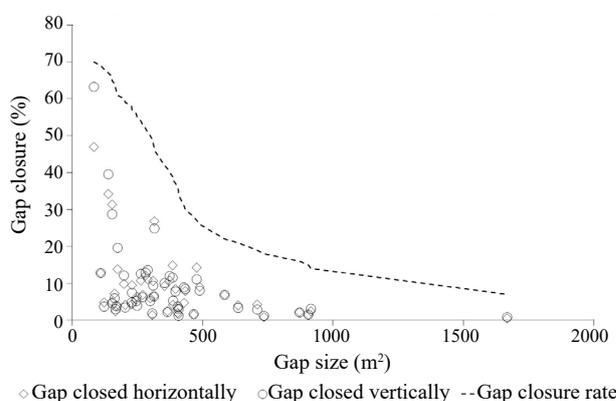
The distance from the gap centre was used to better exhibit the spatial distribution of regeneration density and growth within a gap. The highest regeneration



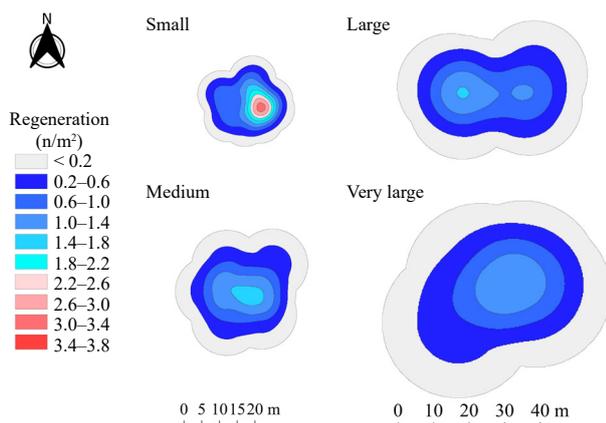
**Figure 7.** Univariate spatial analyses of gaps in 2019; the modified Ripley’s K-function  $L(r)$  for the univariate analyses



**Figure 8.** Mean kernel density (n/ha) estimates for gap distribution in the studied area



**Figure 9.** Gap size development and closure processes



**Figure 10.** Mean kernel density ( $n/m^2$ ) estimates for regeneration dispersion in gaps of the three size classes

density occurred in the centre of all gaps but, in small and medium gaps, regeneration density was skewed mostly in the eastern part (Figure 10). The different pattern observed for all the regenerations was probably because this species (especially beech as the dominant species) is shade-tolerant only in the first stages of its life.

## Discussion

Forest gaps are essential for the maintenance of diversity in old-growth forests, and healthy forest gap dynamics are likewise necessary for guaranteeing their long-term functioning and ecosystem services (Williams et al. 2019). Like the gap formation rate (3.7% points of the stand area in 9 years), the total gap area increased from 2010 to 2019. The frequency of gap creation has important outcomes for the species composition and forest structure. The rate of gap openings in natural mature temperate forests ranges from 0.5 to 2.0% per year (Runkle 1985). In 2019, 85% of the total gap area recorded in 2010 was still present, and gaps older than 9 years still had a share of ~13% in number and 17% in the total area of gaps mapped in 2013. This result is consistent with the findings of a study in a *Fagus sylvatica* virgin forest by Feldmann et al. (2018) who found a significant decrease in average gap fraction within only 10 years. The constant trend was described by Splechtna and Gratzner (2005) for a spruce-fir-beech virgin forest in Austria, where the gap fraction increased from 3.3 to 13.8% within 34 years (1962–1996). Kenderes et al. (2009) found gap fraction (9–11%) and gap frequency distribution to be very stable over 33 years (1971–2004) in a mixed beech virgin forest reserve in the Czech Republic. Bottero et al. (2011) reported the highest gap fraction observed so far (19%) for beech-dominated forests from a mixed beech-spruce-fir forest. However, in this forest, only a small proportion of large gaps existed (~10%). These different findings suggest that regional climate and disturbance regimes, as well as topography and physiog-

raphy, exert a large influence on the temporal dynamics of gap formation. Gaps are often irregularly spaced in relation to stand age, structure, and dynamics (Muscolo et al. 2014). Marthews et al. (2008) showed that spatial gap distributions determine direct light regimes in time and space, increasing germination and the emergence of seedlings. Sharma et al. (2019) focused on the disturbances of different gap sizes and investigated gap spatial distribution, advanced regeneration, and stand structure of five *Shorea robusta*-dominated forests. Gap size is the most important characteristic of the gap, and the microclimatic environment of gap and humidity differs with gap size (Zhang et al. 2019). Gap size differs concerning tree size and crown dimensions, and the differences depend also on single or multiple-tree falls, as well as gap age. Gap size is often used as an indicator of environmental heterogeneity and resource sequestration in gaps. Gélhidy et al. (2006) indicated that gap size had a profound effect on the environmental variables measured, while relative light intensity values in small gaps did not reach those in large gaps. Gap size reflects the magnitude of the disturbance, i.e., the type, number, and size of falls (Lima et al. 2008), which has a direct influence on gap microclimate and understory damage levels (Zhu et al. 2007). The size of a gap can strongly influence vegetation growth and nutrient cycling (Gray et al. 2002) and can have a considerable effect on several biological processes. Çoban et al. (2018) reported that soil moisture levels reached similar maximum values in gap centres regardless of gap size. Gaps create a range of light conditions within and around the gap opening which depend on sun angle (aspect and topography), tree height, and sky condition. The results of the present study showed that most of the gaps were of medium size (200–500  $m^2$ , ~60%), which can provide a suitable condition of relative light intensity for better regeneration. Gap shape is another important descriptor with a substantial influence on gap microclimate (Salvador-Van Eysenrode et al. 1998) and site resource availability (Lertzman and Krebs 1991). Numerous gap shapes have been recognized, including chablis, ellipse, and triangle (Muscolo et al. 2014). Gagnon et al. (2004) reported that gaps are often irregularly shaped. In general, irregular narrow gaps will receive far less PAR (Photosynthetically Active Radiation) at ground level than circular gaps of the same size and have increased competition for light, water, and nutrients (Gagnon et al. 2004).

Gaps of different sizes are among the most important mechanisms for the maintenance of tree species diversity in forests (Zhang et al. 2019), although our findings indicated that regeneration density decreases by increasing the gap size. However, our results are not in line with the conclusions of Kucbel et al. (2010) suggesting that regeneration development increases with gap size. Garbarino et al. (2012) reported that early successional and shade-intolerant species such as *Acer pseudoplatanus* and *Sorbus aucuparia* were present only in larger gaps in a Bosnian old-

growth forest. Zhu et al. (2014) and Mallik et al. (2014) report that all groups of plants, including shade-tolerant ones, have significantly higher densities of seedlings and saplings in gaps compared to under canopy. Environmental heterogeneity, as well as light availability, is higher in the gaps in comparison with under canopy, and one expects to observe higher regeneration success (germination and growth) of tree species in gaps (Ruger et al. 2009, Devagiri et al. 2016). A small gap probably provides the ideal light environment for these shade-tolerant immatures to regenerate and grow (Swaine and Whitmore 1988). Yu et al. (2014) found that the diameter of medium gap regenerations was higher than that of large gaps. They suggested that the middle gap would promote regeneration and high-quality timber cultivation. The *F. orientalis* dominant species regeneration can alter its crown architecture to plagiotropic growth forms, but as an individual it grows and reaches a better light position in the stand, its crown architecture improves, and the number of plagiotropic, forked, and broom-shaped individuals is noticeably decreased (Rozenbergar and Diaci 2014, Orman et al. 2018). Beech is known for its capacity to rapidly expand its crown when light is available (Roloff 1986, Peters 1997). The results provide strong evidence that regenerations established in the forest gap since formation play a major role in the gap closure and canopy rebuilding process in the Hyrcanian forest. We discovered that regenerations are mostly present in the centre to the east part of gaps, which is in line with the findings of Wagner et al. (2010) and Cater and Diaci (2017) who suggested that gap centres are not optimal for the regeneration of this species. Vilhar et al. (2015) state that they expect gap centres to be the most favourable part for the regeneration of tolerant tree species with considering different factors such as high irradiance, increased soil depth, the highest topsoil water content, higher anticipated N availability, and reduced nutrient uptake by the tree roots. Also, Garbarino et al. (2012) confirmed that gap geometry was related to regeneration composition, showing that early successional and shade-intolerant species, such as sycamore maple and rowan, were positively associated with large and elongated gaps. In temperate forests, gap opening is the major process determining regeneration development (Sapkota et al. 2009) and a vast body of literature exists on the effects of canopy gaps on tree recruitment patterns (Yamamoto 2000, Harcombe et al. 2002, Bottero et al. 2011).

Considering the KDE maps, the highest densities of regeneration occurred in small gaps ( $< 200 \text{ m}^2$ ) along the eastern part of gaps with a maximum of  $3.0\text{--}3.4 \text{ n/m}^2$  regenerations. *F. orientalis* was the dominant regeneration of species (86.4%). Therefore, we speculate that the optimal micro-environment for the two age classes of regeneration in the present study might have occurred at different positions within gaps. Regardless of species shade tolerance, results showed that regeneration density was skewed mostly in the eastern part (small and medium gap size) and

centre part (large and very large gap size), probably because of the sun angle. In this vein, Coates (2002) demonstrated that regeneration success depends on mature tree canopy cover, gap size, and position in a gap. This result is consistent with that of Vilhar et al. (2015) who conducted that regenerations increase by increasing the gap size. A similar study of regeneration in gaps in a Hyrcanian forest revealed that total regeneration has no significant correlation with gap size (Mohammadi et al. 2019). However, Cui et al. (2015) found that the regeneration was the most and least distributed in the eastern and northern edge of the gap, respectively. Furthermore, Wang et al. (2017) indicated that no significant difference in regeneration density was observed among different gap sections. Raymond et al. (2006) studied spatial patterns of soil microclimate, light, regeneration, and growth within silvicultural gaps of mixed tolerant hardwood-white pine (*Pinus strobus* L.) stands. They found that their spatial patterns might change and diverge from each other in the future due to differential survival of different species. In this research, the reasons for the regeneration of *F. orientalis* distribution remain unclear, necessitating a study that focuses on the relationships between regeneration and important environmental factors (i.e. light distribution within gaps, soil moisture, temperature, and microclimate), microsite characteristics, and seed dispersal factors (i.e. seed size, seed predation, and the direction of prevailing winds).

The rate of gap closure is partly a consequence of the rapid growth of gap regenerations, which can fill a gap within a few years. Indeed, we found a maximum gap closure rate in small and medium gaps (70%), whereas the large and very large gaps had a minimum gap closure rate ( $\sim 10\%$ ). In temperate forests, a negative relationship is found between seedling height and gap size (Muscolo et al. 2014). Nevertheless, Bullock (2000) reported that larger gaps will be filled in less time due to reduced seedling competition for light, nutrients, and water compared to small gaps. Diaci et al. (2012) found that small gaps will fill in 5–40 years, while medium-size gaps require  $\sim 30\text{--}60$  years for closure. How rapid *F. silvatica* can close the gaps is demonstrated by the observations of Madsen and Hahn (2008) who found medium-sized gaps ( $180\text{--}470 \text{ m}^2$ ) cut into a 110-year old beech stand to be nearly closed after 3 to 4 years. We found a strong decrease in gap closure by increasing the gap size. In contrast with our result, Whitmore (1982) represented  $1,000 \text{ m}^2$  as the minimum gap size needed for the successful regeneration of shade-intolerant species. Zhu et al. (2014) showed that regeneration density exhibited a significantly positive correlation with gap size, providing quantitative evidence for the large effect of gaps on increasing regeneration by woody species. According to Obiri and Lawes (2004) and Nagel et al. (2010), shade-intolerant species or early-successional species are often recruited only in the larger gaps and are usually established after gap formation, or in young gaps, where more light is available. Finally, Fox et al. (2000) and Herwitz et al.

(2000) demonstrated changes in gap dynamics over time, concluding that the total gap area had a clear decreasing trend: Smaller gaps vanished in the course of time, and larger ones tended to shrink.

### Conclusion

The results of this study can support the point of view that the gap dynamics and regeneration patterns of the uneven-aged stands are the most important rules of forest dynamic. The changes in gap patterns observed between 2010 and 2019 highlights the high value of repeated gap inventories for better comprehending the disturbance regeneration and dynamics of natural gaps. Although many studies have been conducted on the gap dynamics of natural forests, few of them have focused on the dynamics of gap closure. However, many studies indicate that accumulated knowledge of gap dynamics and regeneration patterns is useful for sustainable forest ecosystem management. Our results showed a different regeneration pattern in gap size classes from 2010 to 2019. Due to rare gap closure, a high probability of gap recovery will be expected. Finally, our results took a major step towards a general understanding of gap dynamics and regeneration disturbance in Hyrcanian old-growth forests with the dominant species of *F. orientalis*. A longer period of gap data and regeneration information collection is required for characterizing the disturbance gap regime and dynamics in the Hyrcanian forest. More research on other virgin forests would help assess regional and site-specific differences in forest gap dynamics.

### Conflict of interests

The authors declare that they have no conflict of interests.

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