

Comparison of long-term gap dynamics of two beech-dominated Central European forest reserves with different management history

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Abstract

Understanding forest development following the cessation of management remains a key challenge in forest ecology. Gap dynamics, a driver of structural and compositional change, might serve as an important indicator of progression toward old-growth conditions. This study investigates and compares the long-term gap dynamics of two Central European forest reserves (Kékes—old-growth and Óserdő—long untouched) dominated by European beech (*Fagus sylvatica* L.) over a 42–45-year period, using aerial imagery. Our aim was to assess how historical management legacies influence gap size, formation, persistence, and closure, and to evaluate these processes relative to the forests' naturalness levels. Gap fractions ranged between 4.9%–9.9% in Kékes and 2.3%–10.7% in Óserdő. These values are mostly consistent with previous reports for primary European beech forests. In Kékes, smaller gaps (<200 m²) predominated, while in Óserdő, following a sequence of recent disturbances, gaps of 200–499 m² became dominant. Statistical analyses revealed a significantly steeper increase in total gap area in Óserdő, reflecting greater sensitivity to exogenous disturbances, likely due to its more homogeneous stand structure and residual management effects. Site conditions, browsing pressure, and topography might have further contributed to the observed divergence. Our results indicate that the fine-scale endogenous dynamics, typical of old-growth forests (characterized by small, recurring gaps of endogenous processes), develop only several decades after the last human intervention. The study highlights that gap dynamics might serve as an indicator of forest naturalness and can guide restoration planning. Promoting structural heterogeneity and mimicking natural gap processes may accelerate recovery toward old-growth characteristics in formerly managed forests.

Keywords Kékes Forest Reserve, Óserdő Forest Reserve, naturalness, long-term gap dynamics, airborne imagery

Introduction

The concept of forest naturalness has been interpreted in multiple ways (Peterken 1996). One approach examines the degree to which a forest resembles its natural, undisturbed state. However, defining an appropriate reference condition remains inherently challenging, as different classification systems tolerate varying levels of past human influence. Due to the diverse interpretations of naturalness, Buchwald (2005) proposed a unified nomenclature, which we adopt throughout this paper. Recently, a classification of all European primary forests based on Buchwald's naturalness-level system has been completed (Sabatini *et al.* 2018). This standardization reduces inconsistencies among definitions of naturalness by applying uniform criteria. According to this framework, primary forests are relatively intact ecosystems that have remained largely unmodified by human activity, either throughout their entire history or, at minimum, for the past 60–80 years. Within this category, several subtypes can be distinguished,

ranging from long untouched (n5) to primeval forests (n10). In long untouched forests, several decades may have elapsed since the last human intervention. While certain categories of naturalness cannot be reached over time, others can gradually develop through natural succession and increase in structural complexity. Forests exhibiting a more advanced successional and structural state are classified as old-growth forests (n6), a primarily descriptive category (Meyer *et al.* 2021) rather than one based on historical land use. Distinguishing between long untouched and old-growth forests is essential: old-growth forests possess unique structural and functional attributes (e.g. multiaged tree stands, abundant deadwood, dynamic equilibrium at the landscape scale) that are often absent from long untouched stands (Vandekerkhove *et al.* 2009, Paillet *et al.* 2015, Kunca *et al.* 2022). The spontaneous recovery of these characteristics in formerly managed forests may take decades, even centuries (Bauhus *et al.* 2009, Wirth *et al.* 2009, Albrich *et al.* 2021); furthermore, their gradual

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development contributes to increasing levels of naturalness (Di Filippo *et al.* 2017). Consequently, the transition between these two categories represents a significant, but less studied phase of forest development.

Managed forests with homogeneous structure tend to respond more sensitively to exogenous disturbances (exhibiting larger and more frequent canopy gaps or even domino-like cascading effects) (Nagel and Diaci 2006, Kenderes *et al.* 2007, Seidl *et al.* 2011). Similar processes can also be observed in forests that have been recently abandoned, because it takes decades to buffer the legacy of former management (e.g. to develop a heterogeneous structure, canopy trees typically experience several gap formation and closure cycles and may remain suppressed for decades before eventually reaching dominance (Trotsiuk *et al.* 2012; Di Filippo *et al.* 2017)). With the increasing frequency and intensity of natural disturbances driven by climate change (Schelhaas *et al.* 2003), the differences between the (recently) managed and old-growth forests may be amplified.

Research tracking such long-term succession remains rare. One approach to study forest development in self-organized stands is the observation of gap dynamics processes. However, significant variation exists among gap-dynamics studies, largely due to differences in definitions (e.g. gap) and methodologies (e.g. gap age estimation and sampling methods) (Runkle 1992). Many studies on canopy gap dynamics rely on short-term observations, which may be misleading since they capture only the most recent disturbance events. Although empirical research on local disturbance regimes is growing, limited geographic coverage and methodological inconsistencies still hinder broader generalizations (Nagel *et al.* 2014). This highlights the need for long-term, systematically designed investigations with the application of harmonized definitions. We did not find any research investigating long-term gap dynamics changes during the development of former commercial forests towards the old-growth phase. Among primary European temperate forests, beech-dominated (*Fagus sylvatica* L.) stands have been most thoroughly studied (Standovár and Kenderes 2003, Nagel *et al.* 2017), providing the richest empirical basis for comparative analyses.

The objective of the present study is to quantify and compare the processes of gap dynamics (formation, persistence, and closure) and their changes over time in a long-untouched and an old-growth beech-dominated forest reserve in Central Europe. The analyses conducted in this study span a 42–45-year period. We use canopy gap data obtained from a multi-temporal series of aerial imagery. We hypothesize that the old-growth forest is characterized by smaller gaps that close more rapidly, reflecting greater resistance and resilience to natural disturbances. Contrarily, we assume that the long-untouched forest with visible traces of past management shows distinct gap patterns (smaller gaps that close more slowly). We suggest that the gap dynamics of the first decades of abandonment as obtainable with historic aerial imagery can be used as an indicator of naturalness.

Methods

Study areas

The Kékes Forest Reserve (total: 142.8 ha, core area: 54.8 ha) is located in the Mátra Mountains (47°52′51.0″N 19°59′58.0″E) at elevations of 700–950 m, on predominantly north-facing slopes with an average inclination of 30–50 degrees. The mountains are of volcanic origin, with bedrock composed predominantly of andesite (Führer 2017). In the reserve, the mean annual precipitation ranges from 760 to

840 mm, while mean annual temperatures range between 5.6 and 5.7°C (Horváth *et al.* 2021). The history of the forest areas is well documented (Czajlik and Pászty 2009). The forest has been protected since 1949, but in the first decades, salvage logging was permitted. This led to significant logging in certain parts of the stand after a windthrow in 1960. This part of the reserve is not included in this study (Fig. 1). This salvage logging event represents the last and only forest management intervention in the reserve. More recently, major windthrows occurred in 2012, accompanied by rockfalls (Horváth *et al.* 2016), and in 2014, the reserve was affected moderately by a glaze storm. The species composition of the stand (expressed as mixture ratio) is dominated by European beech (83%) growing in characteristic forest communities including Aconito-Fagetum Soó 1960, Mercuriali-Tilietum Zólyomi et Jakucs 1958, and Phyllitidi-Aceretum subcarpathicum Soó 1960 (Ódor 2000). *Tilia platyphyllos* Scop. (5%), *Acer platanoides* L. (5%), *Acer pseudoplatanus* L. (5%), furthermore occasionally *Fraxinus excelsior* L., *Ulmus glabra* Huds., *Carpinus betulus* L., *Larix decidua* Mill., *Sorbus aucuparia* L., and *Quercus petraea* (Matt.) Liebl. also occur in the reserve. The stand structure is characterized by a mosaic of patches representing different developmental stages (Horváth and Borhidi 2002, Czajlik *et al.* 2003). The average height of the stand is 32 m, and some specimens exceeding 40 m (Horváth *et al.* 2024). According to Sabatini *et al.* (2018), the site qualifies as an old-growth forest (n6).

The Őserdő Forest Reserve (total: 375.3 ha, core area: 59.3 ha) lies on the limestone karstic plateau of the Bükk Mountains (48°03′28.0″N 20°27′22.0″E) (Führer 2017) (Fig. 1). Elevations range from 830 to 900 m, with a diverse (micro)topography. In the Central Bükk, mean annual precipitation is 702 mm, and mean annual temperature is 7.9°C (Führer 2017). The dominant tree species (expressed as mixture ratio) is also European beech (84%), with Aconito-Fagetum Soó 1960 as the characteristic forest association (Horváth and Borhidi 2002). On steeper north-facing slopes of our study site, mixtures of associated species (*A. pseudoplatanus*—12%, *F. excelsior*—4%, and occasionally *Picea abies* (L.) H. Karst. and *U. glabra*) occur, while on south-facing slopes, large beech specimens dominate. For the initial decades, the management of the site was conducted in accordance with an age-class silvicultural system, characterized by the implementation of uniform tending cuts. Subsequently, the decision was taken to set the area aside ca. 100 years ago and it was declared protected in 1942. The current canopy is the result of a century of spontaneous development formed by 170–220 years old trees with 41–47 m maximum height (Kenderes *et al.* 2008). Since 2001, our study site has been enclosed by a game exclusion fence. It is no longer fully intact; however, it still significantly reduces herbivore pressure within the reserve (Ódor 2005). Major natural disturbances included an ice storm in 2004 and a windthrow in 2010. The gap dynamics of this site were first investigated in our earlier studies for the period 1975–2005 (Kenderes *et al.* 2008). According to Sabatini *et al.* (2018), the forest qualifies as a long untouched forest (n5).

Data and methods

In both study areas, we examined parts of the core areas, which are considered to be in the best condition. We set a buffer of two canopy heights to avoid edge effects; therefore, the study areas narrowed two canopy lengths inward from the edge of each designated area. Accordingly, the total study areas were 37.275 ha in Kékes and 21.344 ha in Őserdő. To track stand dynamics, we collected aerial photographs from as many points of time as possible. For Őserdő, eight images were

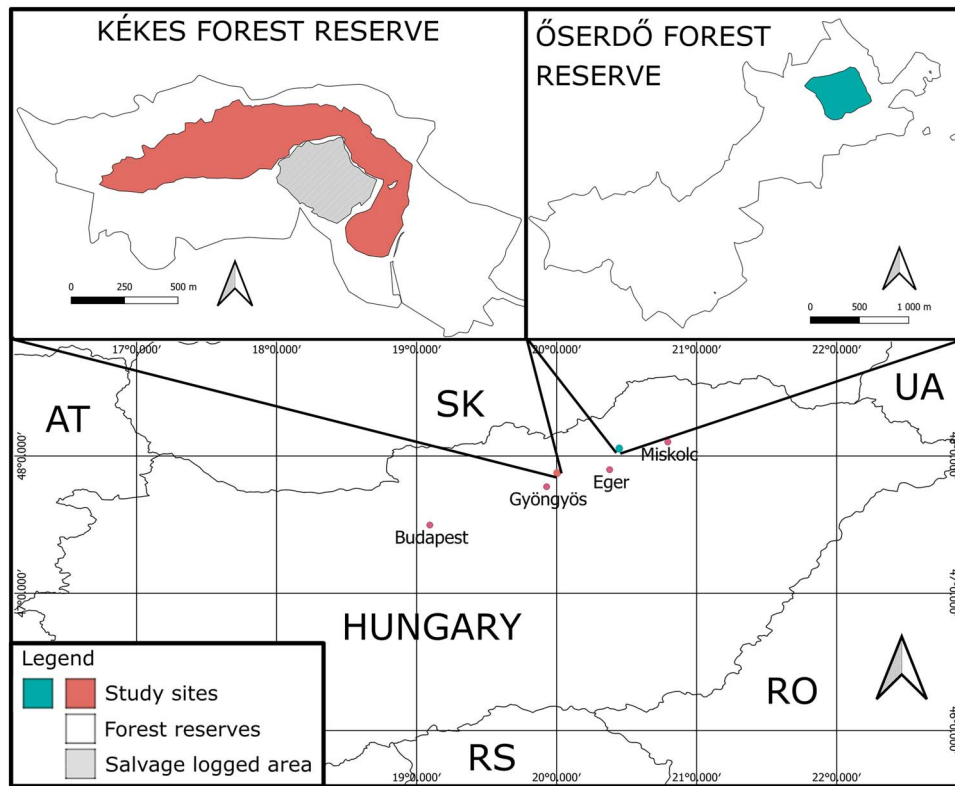


Figure 1 Location of the study areas within Hungary.

available with the following resolutions: 1975 (0.2 m), 1980 (0.5 m), 2000 (0.75 m), 2005 (0.8 m), 2007 (0.5 m), 2011 (0.4 m), 2015 (0.4 m), and 2020 (0.4 m). For Kékes, nine suitable images were available with the following resolutions: 1977 (1 m), 1990 (0.2 m), 1997 (0.4 m), 2000 (0.8 m), 2002 (0.5 m), 2005 (1 m), 2010 (0.5 m), 2015 (0.5 m), and 2019 (0.4 m). Only images with sufficient quality and resolution were selected for analysis. Gap outlines were manually digitized on screen from the geocoded aerial photographs, and for each year for which photographs were available (referred to as “snapshot” in the following), a vector layer was created. This study builds upon our previous research (including earlier datasets), during which we performed a field validation of the gap maps (Kenderes *et al.* 2008). Drawing on the experience gained from that work, we continued the mapping of canopy gaps based on aerial imagery. A gap was defined as the land surface area directly beneath a canopy opening (Runkle 1982). Any canopy opening larger than 4 m² was classified as a gap. If trees were present within an opening, the horizontal projection of their crowns was excluded from the gap area. If the regeneration in the gap reached a height of 8 m, it was considered closed, which can be reliably recognized based on previous field validation. Gap mapping was processed using an ArcView GIS 3.1 extension (Patch Structure). This older software was used to ensure methodological consistency with our earlier work and because the Patch Structure tool was specifically developed for this purpose. The program calculates the area of individual gaps for each snapshot, and tracks overlaps between gaps over time, thereby enabling the reconstruction of gap development sequences. Based on unique identifiers, gaps that closed or merged could be easily identified. This allowed us not only to quantify structural attributes at a given time, but also to quantify stand dynamical events between two snapshots. The area of opening,

closing, or persisting gap values between two periods was divided by the number of years between the two snapshots, thus showing average annual changes.

Statistical analysis

For each observation year, we determined gap characteristics including number, size distribution (mean, standard deviation, minimum, and maximum), and the proportion of gap area relative to the total study area (gap fraction). Using the gap succession sequences, we calculated the number and area proportions of newly formed, persisting, and closed gaps for each period. Due to the unavailability of suitable aerial imagery, the temporal distribution of data is uneven in Óserdő (the 1980–2000 interval is longer than the others). Consequently, dynamic attributes were analyzed only for 4–6-year periods (1975–1980, 2000–2005, 2005–2011, 2011–2015, and 2015–2020).

Comparisons between the two reserves were made primarily by analyzing descriptive statistics. Temporal changes in total gap area were further assessed using a negative binomial generalized linear model (nbGLM) to account for strong overdispersion and non-normal residuals. The dependent variable was gap area (m²), and independent variables included year (numeric), site (categorical), and their interaction. The model was fitted with a log link function. The fitted model had the following structure: gap area ~ year × site. Analyses were performed in R 4.4.1 (R Core Team 2025). Some gap sections remained continuously open throughout the entire observation period. This was identified by intersecting gap polygon maps across all years and classifying sections exceeding 4 m² as persistent gaps. Descriptive statistics of these non-closing gaps were also compared between the two reserves.

Table 1 Summary of gap dynamics in the forest reserves. Data represent eight snapshots for Óserdő (1975–2020) and nine snapshots for Kékes (1977–2019). Ranges show minimum and maximum values, while averages are given in parentheses.

	Kékes Forest Reserve [min–max (avg.)]	Óserdő Forest Reserve [min–max (avg.)]
Number of gaps/ha	6–10 (8.3)	6–9 (7.8)
Mean gap size (m ²)	67–111 (81.3)	40–121 (83.3)
Maximum gap size (m ²)	751–1946 (1063)	378–1276 (861)
Gap fraction (%)	4.90–9.97 (6.97)	2.30–10.70 (6.73)
Change in total gap area (%/year)	–0.70–0.81 (0.03)	–0.55–0.65 (0.17)
Number of new gaps/ha	1.0–2.8 (1.6)	0.8–3.5 (2.0)
Percent of total area covered by new gaps (%/year)	0.07–0.42 (0.15)	0.10–0.34 (0.21)
Number of gaps that closed/ha	0.5–2.3 (1.2)	0.7–1.9 (1.4)
Percent of total area covered by gaps that closed (%/year)	0.01–0.13 (0.07)	0.05–0.14 (0.08)
Percent of change in the area of persistent gaps (%/year)	–0.72–0.49 (–0.05)	–0.51–0.43 (0.05)
Proportion of area where canopy dynamics occurred (%/year)	0.09–0.99 (0.46)	0.26–0.80 (0.54)

Results

The gap maps produced for each year are presented in [Supplementary Figs S1 and S2](#), while [Figs S3 and S4](#) show all the maps superimposed on each other in high resolution (with persistent gaps). The detailed gap dynamics for each observation year are provided in [Supplementary Tables S1–S5](#). The ranges and mean values of the dynamic processes observed during the study periods in the forest reserves are summarized in [Table 1](#). These results reveal that dynamic processes were more pronounced in Óserdő. Although the mean change in total gap area was several times higher in Óserdő compared to Kékes, the average number of newly created gaps was lower. This indicates that in Óserdő, fewer but larger gaps were formed. Despite this, the mean gap area created per observation period was relatively low in Óserdő, pointing to high interannual variability and occasional outlier values. Overall, gap formation and persistence were more characteristic in Óserdő, whereas gap closure played a more significant role in Kékes.

In Óserdő, the distribution of gap fraction and frequency among size categories showed continuous change ([Fig. 2b and d](#)). Initially, the total gap fraction was low, and the 20–49 m² category accounted for the largest proportion until 2005. From 2000 onwards, the 200–499 m² category represented the largest share (28%–34%). Beginning with the 2005 imagery, a relatively stable distribution pattern emerged: the frequency of gap categories gradually increased up to the 200–499 m² class, which consistently dominated in the distribution of the gap fraction data too. Larger gaps were also present, and even the >999 m² category gained significance in 2007, 2015, and 2020. Since large gaps had closed and decreased in size by 2011 ([Fig. 2b and f](#)), new large gaps appeared in subsequent years.

In Kékes, the distribution of gap fraction and frequency among categories exhibited small changes ([Fig. 2a and c](#)). During the first 3 observation years, the 100–199 m² category accounted for the largest area, followed closely by the 200–499 m² category. In the final 3 observations, dominant gap sizes alternated between categories. Across all observations, the 20–499 m² size classes were consistently the most frequent and provided the dominant category in most cases. Following exogenous disturbances, the 500–999 m² category occasionally increased in prominence, but such gaps shrunk and closed relatively quickly ([Fig. 2a and e](#)). Larger gaps than 999 m² were also created multiple times.

The nbGLM revealed a significant interaction between year and site ($\beta = 0.11$, $P < .001$), confirming disparate temporal trajectories

Table 2 Characteristics of gaps that remained continuously open throughout the entire study period (Kékes: 42 years, Óserdő: 45 years).

	Kékes Forest Reserve	Óserdő Forest Reserve
Number of gaps	40	2
Total gap area (m ²)	838.13	119.08
Mean gap size (m ²)	20.95	59.54
Maximum gap size (m ²)	117.89	100.80
Persistent gap fraction (%)	0.22	0.06
Initial mean gap size (m ²)	187.65	564.68

between the two reserves. The baseline intercept was lower for Óserdő ($\beta = -0.16$, $P = .036$), but the slope was steeper compared to Kékes, suggesting a faster increase in gap area over time. Although the model's explanatory power was low (McFadden's pseudo-R² = 0.017), this is typical for ecological datasets with high variability. The analysis of deviance confirmed the significance of the interaction effect ($\chi^2 = 15.88$, $P < .001$), supporting the conclusion that the two sites show statistically robust and diverging trends in gap area dynamics.

Some gaps partially closed and later reopened in other directions, while certain sections remained continuously open throughout the observation period ([Fig. 3](#)). Analysis of these persistent gaps revealed that in Kékes they were generally more numerous and smaller, whereas in Óserdő they were fewer but larger ([Table 2](#), [Supplementary Fig. S5](#)).

Discussion

Gap dynamics

The gap fraction was in the range 4.90%–9.97% in Kékes and 2.30%–10.70% in Óserdő. Comparative syntheses have reported gap fractions of 1.7%–16% ([Hobi et al. 2015](#)), 3.3%–6.6% ([Meyer et al. 2003](#)), and 3%–19% ([Feldmann et al. 2018](#)) in beech-dominated primary forests, with higher values occurring where exogenous disturbances are significant ([Table 3](#)). Within this context, Óserdő was initially below most of these ranges, but later both of the reserves fell within the expected range.

[Meyer et al. \(2003\)](#) found that gaps in beech-dominated old-growth forests were generally smaller than the crown size of canopy trees,

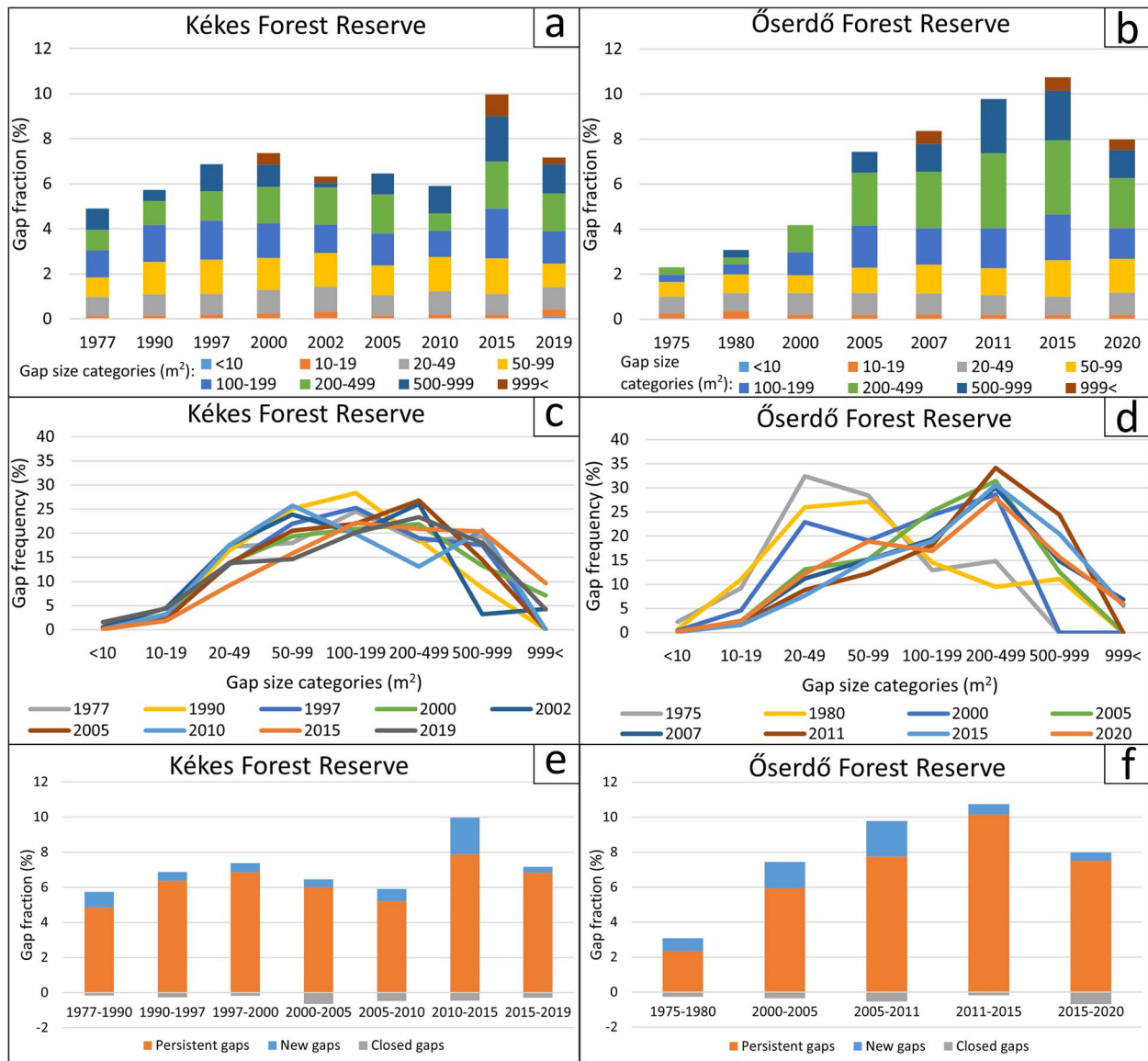


Figure 2 Gap area distribution indexes in the reserves: gap fraction (a, b) and gap frequency (c, d) among size categories in each observation year; the dynamic processes between the observation periods (e, f), where the closed gap areas were referred to as negative numbers.

Table 3 Gap dynamics in beech-dominated, primary, Central European forest reserves.

Reserve	Naturalness level ^a	Time period (yrs.)	Sample sets	Most frequent gap size	Average gap area	Gap fraction	Reference
Uholka	n7	2012 (1)	1	<200 m ²	28 m ²	<1%	(Hobi <i>et al.</i> 2015)
Krokar	n6	2000 (1)	1	<200 m ²	137 m ²	5.6%	(Zeibig <i>et al.</i> 2005)
Gorjanci	n6	1986–2006 (20)	2	100–300 m ²	294–317 m ²	9.1%–10.6%	(Rugani <i>et al.</i> 2013)
Havešová	n6	2003 (1)	1	<62.5 m ²		16%	(Drößler and von Lüpke 2005)
Kyjov	n6	2003 (1)	1	<62.5 m ²		14.6%	(Drößler and von Lüpke 2005)
Kyjov	n6	2003–2013 (10)	2	<100 m ²	96–261 m ²	13.6%–8.2%	(Feldmann <i>et al.</i> 2018)
Kopa	n5	1998–2006 (8)	2	<200 m ²	118–141 m ²	3.2%–4.5%	(Rugani <i>et al.</i> 2013)

^aNaturalness categories follow Sabatini *et al.* (2018): n7—near-virgin forest; n6—old-growth forest; n5—long untouched forest.

indicating that endogenous dynamics predominated. A synthesis suggests that in most of these forests, gap sizes typically fall within the 34–50 m² range (Wagner *et al.* 2010). In our study, the largest

share of gap areas in Kékes were in the 20–499 m² classes (mean 67–111 m²; Table 1, Fig. 2). Studies of beech-dominated forests with natural dynamics in Central Europe generally report a predominance

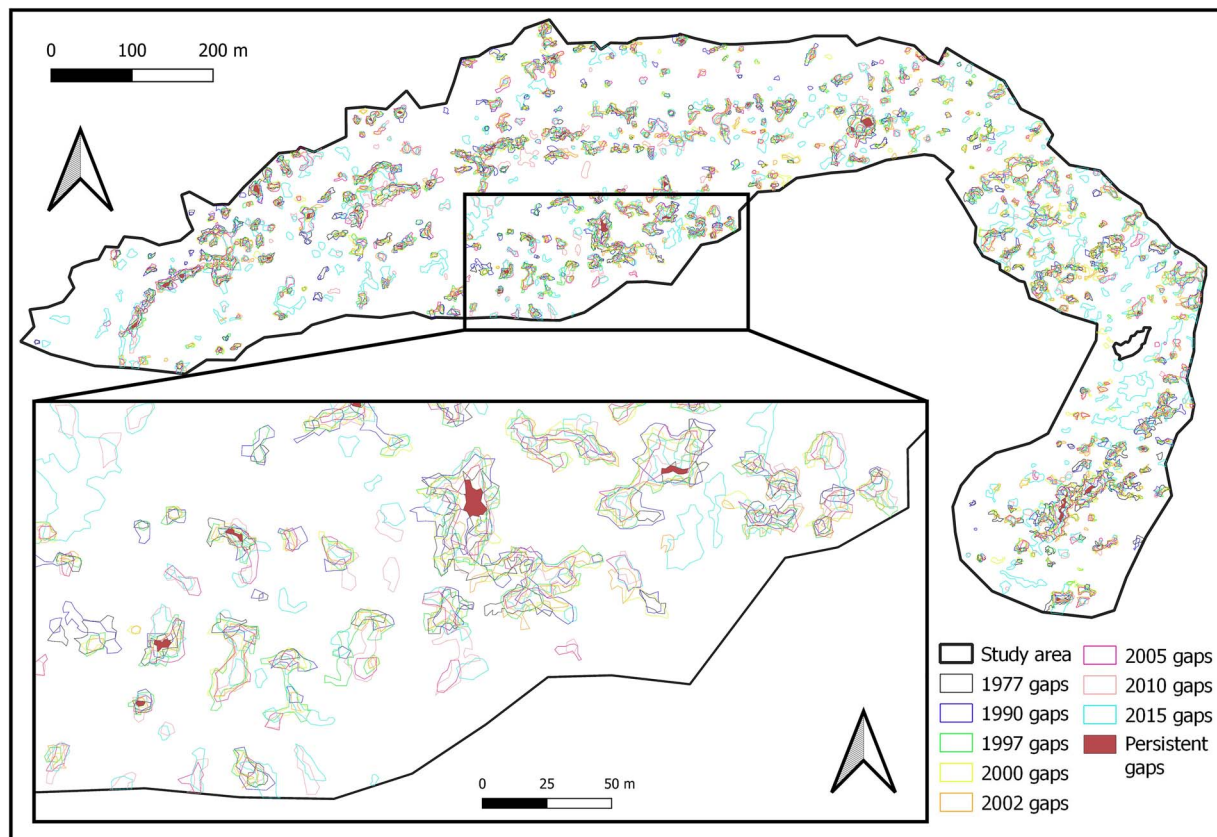


Figure 3 The change in the area of gaps, illustrated with the example of Kékes Forest Reserve.

of small gaps (Table 3, n6 and n7 categories). Among these, Uholka exhibits the highest level of naturalness (near-virgin). Near-virgin forests primarily differ from old-growth ones in their spatial extent (Buchwald 2005); however, significant differences were found in Uholka compared to them. The survey of Uholka combined remote sensing with field validation (Hobi *et al.* 2015). The terrestrial data indicated a lower proportion of small, spectrally detected gaps and a higher share of larger gaps. Remote sensing identified only gaps without regeneration and visible soil surface, whereas field surveys defined gaps as canopy openings where regeneration did not exceed one-third of canopy height. Consequently, these methodological limitations could have caused a distortion of the gap fraction value (Table 3) and can explain the striking differences found in Uholka. Taking these into account, no major difference or trend pattern can be found between Kékes and the other reserves.

In Óserdő, the mean gap size was 40–121 m² over the examined 45-year period (Table 1). Initially smaller gaps dominated, but following a series of disturbances, the 200–499 m² category became prevalent (Fig. 2). The Kopa Forest Reserve, unmanaged for more than 50 years (Rugani *et al.* 2013), can thus be classified as a long untouched forest, similar to Óserdő (Table 3, n5 category). However, when comparing the two sites, there are clear differences: in Óserdő, small canopy gaps (below 50 m²) are frequent and consistent (Fig. 2b), and in Kopa, where gap delineation was based on aerial photographs, larger openings are generally more common, and the gap fraction can also be described in a narrower interval (Rugani *et al.* 2013). Although both reserves have similar site conditions, they differ in topography and consequently, in species composition. The Óserdő includes steeper

slopes and supports a locally higher proportion of admixing species. Outside this area, the stand is more homogenous, which could explain the formation of larger gaps. Smaller gap formation potential can be explained by the earlier abandonment of management: similarly smaller gaps form in old-growth and near-virgin forests (Wagner *et al.* 2010). According to this, management history is still significantly reflected in the low rate of formation of smaller gaps in the first decades after the abandonment of forests, while in forests without intervention for ca. 100 years, fine-scale natural dynamic processes may also be initiated. This result partially confirms our hypothesis that smaller gaps are created in forests with higher naturalness level.

Drößler and von Lüpke (2005) recorded significantly higher gap fraction than in a re-survey a decade later (Feldman *et al.*, 2018). While their study covered 10 years, our work spans nearly 5 decades, allowing for a broader evaluation of dynamic processes. Their results nonetheless fit within the framework suggested by our study, namely that recurring exogenous disturbances create larger gaps, which subsequently regenerate and close, before new disturbance events initiate similar cycles. This highlights a limitation of many comparative studies that assess only short-term periods or snapshots, thereby providing information biased toward recent disturbances. Dendroecological research in primary beech forests has confirmed that mixed-severity disturbance regimes predominate (Frankovič *et al.* 2021), though occasionally extensive (but not catastrophic) events also occur (Janda *et al.* 2025). This suggests that even the nearly 5 decades covered by our study are insufficient to fully characterize the dynamic processes of an area and draw attention to the need for long-term monitoring and dendrochronological studies.

Differences between the examined reserves

The most pronounced difference between the two forest reserves lies in the frequency of small-gap categories (Fig. 2). In Óserdő, gaps smaller than 200 m² were considerably less frequent than in Kékes until 2005. The Kékes pattern corresponds to the widely recognized 200 m² threshold, with smaller gaps being the most frequent in beech-dominated old-growth forests (Wagner *et al.* 2010, Hobi *et al.* 2015, Feldmann *et al.* 2018). By contrast, in Óserdő the 200–499 m² category has the largest share in 6 snapshots (Fig. 2). This difference is also reflected in the gap fraction values, and it occurs simultaneously with the appearance of more frequent and intense disturbances experienced after 2000. Overall, fewer but larger gaps were created in Óserdő (Table 1). The nbGLM model further confirmed that the increase in gap area was significantly steeper in Óserdő than in Kékes.

One explanation for the differences found is probably the extent of human influence. Managed forests with homogeneous stands tend to respond more sensitively to exogenous disturbances (Nagel and Diaci 2006, Kenderes *et al.* 2007). Previous regional analyses have also confirmed these differences between managed and abandoned forests (Zoltán and Standovár 2018); however, it was not explicitly considering gap dynamics. In Óserdő, in addition to small gaps, due to the intense appearance of natural disturbances, larger gaps than in Kékes were also formed. This is probably due to the characteristics of the management-related even-aged stands: the stand is aging, the crowns of the trees are large, so the uprooting/snapping of these trees can result in large gaps, while broken branches can manifest in the formation of smaller gaps. In our opinion, this does not fully correspond to what is experienced in forests with natural structure. Gap size may also depend on the vertical stand structure. In forests with a well-developed understory, saplings and sub-canopy trees can rapidly occupy canopy openings and contribute to gap closure or modify apparent gap size (Feldmann *et al.* 2018). Furthermore, due to the uneven-aged stands, the uprooting/snapping of younger trees can also cause the formation of smaller gaps (Nagel and Svoboda 2008). These phenomena are confirmed by the total gap fraction distribution: Óserdő showed a much lower initial value, which gradually increased (death of old individuals, without a well-developed understory), while in the case of the Kékes, a small fluctuation but no trend-like increase is visible (Fig. 2a and b). As a result of the detailed comparison, it can be stated that our hypothesis has been proven true: it seems that the gap dynamics of long untouched and old-growth forests differ.

However, several other additional factors may influence these differences. First, site conditions influence the observed dynamics. Much of Kékes consists of rocky terrain, with locally varying species composition and additional processes such as rockfall, which do not occur in Óserdő. Due to data limitations, we were unable to stratify our study area accordingly. Second, browsing pressure differs between the reserves. The Óserdő study site has benefited from a game-exclusion fence (Ódor 2005), whereas Kékes experiences high browsing pressure (Zoltán *et al.* 2024), which makes regeneration difficult. Third, studies of understory dynamics in Kékes have shown that gaps between 2000 and 2004 almost exclusively closed via lateral canopy expansion due to their small size (Kovács 2009), while the less frequent larger gaps closed slower through the advanced regeneration. Based on our current, qualitative field experience, this distinction persists.

Gap age also provides important insights. In a mixed beech-spruce-fir forest, Bottero *et al.* (2011) determined that the majority of gaps

ranged in age from 50 to 100 years, with the maximum estimated age reaching 140 years. Drößler and von Lüpke (2005) reported a lower maximum gap age of ~60 years in a beech-dominated forest, while Feldmann *et al.* (2018) documented a gap closure speed that was substantially faster than the rates reported in the aforementioned studies. These divergences in documented gap ages highlight the sensitivity of gap dynamics to site-specific conditions, species composition, and critically, the methodology applied for estimation. In these studies, the gap age was determined using indirect methods, but in our work, we were able to measure it explicitly; therefore, comparable long-term studies remain scarce. In our results, 40 gap(-section)s in Kékes persisted throughout the 42-year observation period without complete closure, whereas only 2 such gaps were recorded in Óserdő across 45 years. In Kékes, these long-lived gaps were generally small (Table 2), found mostly on steep rocky slopes, while in Óserdő, we found only 1 small and 1 medium-sized gap that failed to regenerate over nearly 5 decades—highlighting a notable difference between the 2 reserves. There is also a possibility that these gaps closed and then reopened during the years between measurements, which adds some degree of uncertainty to our results.

Limitations and further research directions

The presented approach can be readily applied to other forest reserves where aerial image series are available. This provides opportunities for broader spatial comparisons of disturbance patterns. However, some limitations should be acknowledged: (i) gap delineation from aerial photographs involves a certain degree of subjectivity, even though efforts were made to standardize the procedure; (ii) the varying quality of the images introduce additional uncertainty; and (iii) as the method is not based on canopy height models, gap boundaries cannot always be clearly defined and no information on understory structure can be obtained.

Despite all this, our results align broadly with findings from forests of similar types. Variations in definitions (gap) and methodologies (sampling method, gap age estimation) influence comparability. Moreover, local topographic, habitat, and biotic factors likely shape gap dynamics and should be considered when interpreting our results. Consequently, (i) harmonization of definitions (like naturalness) and surveys using uniform methods should be pursued; (ii) due to the small number of forests without human intervention and the variability experienced among them, data on the gap dynamics of forests that have not yet been analyzed would also be necessary; and (iii) long-term monitoring in these forests is essential, particularly during the initial decades following the last human intervention (even with retrospective methods).

Conclusion

Our findings suggest that in temperate mesic deciduous forests free from direct human intervention for 100 years, small canopy gaps continuously form and close over nearly 5 decades as a result of endogenous processes. The initiation of such fine-scale dynamics appears to occur after several decades following the last human intervention, suggesting that it may serve as a valuable indicator of forest naturalness. Periodic exogenous disturbances of varying intensity seem to contribute to the formation of additional small to medium-sized gaps, particularly in older, more even-aged stands. This transitional phase distinguishes such forests from old-growth stands characterized by a

more complex stand structure. In contrast to the gradual, fine-scale gap turnover driven by endogenous processes, these disturbances produce more episodic and structurally pronounced canopy openings.

These results offer valuable insights for forest restoration and management. Restoration targets can be designed to accelerate the development of natural stand structures and gap dynamics. Starting from homogeneous, commercially managed forests, structural and compositional diversity can be promoted through the deliberate creation of canopy openings (even just by removing large branches) at controlled intervals. Previous studies have highlighted that silvicultural interventions can accelerate the development of old-growth structural attributes and increase structural complexity in forest stands (Keeton 2006). Such interventions can expedite the formation of a heterogeneous stand structure that would otherwise take much longer time to develop naturally. In the absence of such management, the whole stand may reach the degradation phase in a more synchronized manner; hence, the sufficiently diverse stand structure will not be able to develop in the next generation. Active restoration approaches, including density regulation and the promotion of regeneration and canopy structural diversity, may therefore offer more predictable pathways for restoring complex stand structures than passive development alone (Bauhus *et al.* 2009).

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Author contributions

László Zoltán (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing—original draft), Kata Kenderes (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing—review & editing), and Tibor Standovár (Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing—review & editing)

Supplementary material

Supplementary material is available at *Forestry: An International Journal of Forest Research* online.

Conflicts of interest

None declared.

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Data availability

The data presented in this study are available on request from the corresponding author.

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