RESEARCH ARTICLE

Gap expansion is the dominant driver of canopy openings in a temperate mountain forest landscape

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Abstract

1. Natural disturbances are important drivers of forest dynamics, and canopy gaps are their fingerprints in forest ecosystems. Gaps form and persist because of the interplay of tree mortality and regeneration. They can have long-lasting impacts on ecosystems, yet the temporal dynamics of gap formation and closure remains poorly quantified.

2. We analysed 11,331 canopy gaps and their changes through time across 3999 ha of unmanaged temperate mountain forests at Berchtesgaden National Park (Germany). We assessed gap formation and closure using three repeat lidar acquisitions between 2009 and 2021, analysing canopy height changes at 1 m horizontal resolution. Our objective was to determine the dominant mode of gap formation, distinguishing the creation of new gaps from the expansion of existing ones. Additionally, we studied the rate of gap closure, considering closure from tree regeneration and lateral crown expansion.

3. Gap formation was primarily driven by gap expansion rather than the initiation of new gaps. Gap expansion accounted for 81.3% of gap formation, although new gaps were on average twice as large as gap expansions. Only 1.4% of gaps did not expand over the 12-year study period, and Norway spruce forests had the highest rate of gap expansion.

4. Overall, gap closure rate (0.74 ha 100 ha^{-1} year^{-1}) was higher than gap formation (0.58 ha 100 ha^{-1} year^{-1}) in our study system. Ingrowth of the regenerating tree cohort was the primary mode of gap closure, with lateral crown expansion accounting for 20% of all gap area closed. Mixed-species stands had the highest rate of gap closure, and gaps <0.1 ha closed faster than larger gaps.

5. *Synthesis.* While canopy openings are generally small in the European Alps, we show that they keep growing over multiple years, underlining that gap expansion is an important driver of temperate forest dynamics. Canopy gaps closed faster than they were created, highlighting the resilience of European mountain forests to natural disturbances. However, as disturbances are projected to increase under climate change, this resilience might be challenged in the future, requiring

a continuous monitoring of gap dynamics as an important early warning indicator of forest change.

KEYWORDS

forest disturbance, gap dynamics, gap formation and closure, gap-phase regeneration, landscape ecology, lidar, temperate mountain forest

1 | INTRODUCTION

Gaps are the fingerprint of disturbances in forest canopies (Jucker, 2022). Disturbances are 'any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment' (Pickett & White, 1985). They range from the death of individual trees to large but rare mortality events, such as windthrows, insect outbreaks or wildfires, and play a crucial role in the dynamics of forest ecosystems. Disturbances, for instance, alter forest structure and species composition for decades to centuries, depending on disturbance magnitude, frequency and severity, and modulate key ecosystem fluxes such as carbon uptake and nutrient cycling (Maltamo et al., 2014; Muscolo et al., 2014). As forest disturbance regimes are changing in response to climate change (Seidl et al., 2017), a better quantitative understanding of disturbances and the gaps they create in forest canopies is needed.

Canopy gaps span a wide range of scales across at least four orders of magnitude (from approximately 10^2 to $10^6 \, \text{m}^2$). Also, gap characteristics vary with biome and forest type, as different biomes are affected by different disturbance agents (Jentsch & von Heßberg, 2022) and different forest types are more or less prone to various types of disturbance (Griffiths et al., 2014; Seidl et al., 2020; Sommerfeld et al., 2018). In the forests of Central Europe, for example, large-scale stand-replacing disturbances are usually found within conifer-dominated forests (Potterf et al., 2023; Sommerfeld et al., 2018), while small canopy gaps typically occur in broadleaved forests (Hobi et al., 2015), with mixed forests experiencing the full spectrum of gap sizes (Frankovič et al., 2021; Nagel et al., 2021). The gaps observed in a forest canopy at any given point in time are thus the cumulative effect of all disturbance agents acting within a landscape. They are furthermore modulated by forest type-related traits, for example tree species diversity (Jactel et al., 2017) and land-use legacies (Munteanu et al., 2015; Thom et al., 2018). The variability in canopy gaps (resulting from the diverse forces that create them and the manifold responses to them) is a crucial factor creating beta diversity in forest ecosystems (Mori et al., 2018; Senf et al., 2020). However, many studies of forest mortality focus on either one end of the spectrum of gaps (e.g. either on small-scale mortality or landscape-scale disturbances) and rarely investigate canopy gap dynamics across the continuum of interactive processes that create them (Fisher et al., 2008; Hobi et al., 2015; Hurtt et al., 2016).

Forest canopy gaps are not static but change dynamically over time. A number of previous studies have analysed gap structure at a single point in time, creating important insights into structural patterns created by various gap-forming processes (Asner et al., 2013; Goodbody et al., 2020; Goulamoussène et al., 2017; Reis et al., 2022; Vehmas et al., 2011; Vepakomma et al., 2011). These studies showed that gap characteristics vary considerably among boreal and tropical forests (Goodbody et al., 2020; Goulamoussène et al., 2017). The variation in canopy openings is typically lower within forest biomes (Asner et al., 2013) than across them. Differences in gap characteristics within forest biomes are often driven by variation in soil fertility and human-induced disturbances (Reis et al., 2022). However, what remains understudied is how canopy gaps change over time. For instance, do newly formed gaps go through a phase of expansion before they eventually close? And if so, what is the relative importance of new gap formation versus gap expansion in shaping canopy dynamics? In this regard it is important to note that gap dynamics reflect the interactions inherent in forest disturbance regimes (Buma, 2015; Canelles et al., 2021). For example, windthrow creates edges that are more susceptible to subsequent wind disturbance (Ruck et al., 2012; Zeng et al., 2009). Moreover, forest edges receive more direct radiation, leading to warmer microclimate which, can further promote disturbances (e.g. by bark beetles, Kautz et al., 2013). Understanding and quantifying the dynamic nature of gaps is important because the transient edges that they create are important habitat features (Reiner et al., 2023) and modulate manifold ecosystem processes (Pöpperl & Seidl, 2021).

Besides gap formation, gap closure is an equally important process for understanding the long-term impact of disturbances on forest ecosystems (Turner et al., 1993). The main mode of gap closure is by tree regeneration within gaps. Gaps in the forest canopy increase the resource availability on the forest floor (i.e. light, water, nutrients), which facilitates the establishment of a new cohort of trees and enhances the growth of regeneration already present on the forest floor before canopy opening (Muscolo et al., 2014; Thom et al., 2023; Zhu et al., 2014). However, lateral crown expansion of trees growing at the edge can also contribute to gap closure, either partially (in larger gaps) or completely (in small gaps) (Leitold et al., 2022; Vepakomma et al., 2011). To date, the overwhelming majority of studies on gap dynamics have focused on the process of gap formation (e.g. Asner et al., 2013; Dalagnol et al., 2019; Goodbody et al., 2020; Goulamoussène et al., 2017; Hobi et al., 2015; Koukoulas & Blackburn, 2004; Reis et al., 2022; Vehmas et al., 2011; Vepakomma et al., 2010), while studies on gap closure and different closure mechanisms remain more scarce (e.g. Blackburn et al., 2014; Coates, 2000; Fujita et al., 2003; Gorgens

et al., 2023; Hunter et al., 2015; Leitold et al., 2022; Rodes-Blanco et al., 2023; Vepakomma et al., 2011). Consequently, the contribution of different mechanisms of gap closure (i.e. lateral crown expansion versus regenerating trees) and the modulating role of gap size remain poorly understood. On the one hand, we might expect small gaps to close faster than large gaps due to higher seed input (Masaki et al., 2019) and favourable microclimate (Thom et al., 2023). On the other hand, larger gaps favour the establishment of early-seral species, which are at a disadvantage in small gaps because of limited light availability, but have faster height growth (Muscolo et al., 2014). Early-seral species are thus generally able to close gaps faster than shade-tolerant, late-seral species, but require more light and thus larger gaps. Further, the influence of tree species diversity on gap closure rates remains uncertain. For mature trees, there is evidence for a positive relationship between species diversity and productivity in general (Madrigal-González et al., 2016; Williams et al., 2017) and for a positive effect of niche complementarity on tree growth in particular has been reported (Jucker et al., 2015). How these effects translate to the regeneration stage of forest development, however, remains widely unclear (Grossman et al., 2017; Lang et al., 2012).

The net outcome of gap formation and closure is an important indicator of forest change, yet remains poorly quantified. At the landscape scale, the relationship between these two rates determines whether a forest remains ecologically resilient (Senf & Seidl, 2022)—defined here as having higher rates of gap closure than gap formation. Conversely, higher rates of gap formation than closure are an indicator of ongoing structural changes in forest canopies, and can precede a possible reorganization trajectory towards alternative states (Seidl & Turner, 2022). As both disturbance and recovery are influenced by ongoing global change, studying their net outcomes can serve as an important means to monitor ongoing changes in forest canopies.

Recent developments in the field of remote sensing have transformed the spatial scale and temporal resolution at which we can study gap dynamics in forest ecosystems (Senf, 2022). Moderate-resolution optical sensors like Landsat provide insights into large-scale forest disturbance patterns (Griffiths et al., 2014; Masaki et al., 2019; Senf & Seidl, 2021), and high resolution data from aerial images and high resolution satellites allow the characterization of gap patterns on a finer scale (Fujita et al., 2003; Henbo et al., 2006). However, fine-grained analyses distinguishing individual processes of gap dynamics, such as lateral crown expansion, remain beyond the reach of current satellite sensors, as they cannot capture vertical forest dynamics well. Airborne lidar (light detection and ranging) has expanded the capacity to identify gaps beyond satellite data (Dalagnol et al., 2019; Goodbody et al., 2020), and study tree recovery at fine spatial grain. The main advantage of lidar is the use of an active sensor which provides information on the 3D structure of forest vegetation (Leitold et al., 2022; Senf & Seidl, 2022; Stritih et al., 2023; Vepakomma et al., 2011). Moreover, repeated lidar acquisitions enable researchers to track gap development over time, allowing for a fine-grained analysis of gap formation and closure (Jucker, 2022; Maltamo et al., 2014). The increasing availability of repeated lidar

acquisitions and a rapidly developing processing infrastructure (Roussel et al., 2020; Silva et al., 2019) make multi-temporal lidar a powerful tool for understanding forest canopy dynamics (Blackburn et al., 2014; Dalagnol et al., 2019; Gorgens et al., 2023; Leitold et al., 2022; Rodes-Blanco et al., 2023; Vepakomma et al., 2012).

Our aim was to quantify canopy gap formation and closure in an unmanaged temperate mountain forest landscape—allowing us to focus on natural forest dynamics in the absence of human interventions—in the Northern Front Range of the European Alps. Our specific objectives were (i) to understand the rates and modes of canopy gap formation by contrasting the formation of new gaps with the expansion of existing ones, (ii) to study the rates and modes of gap closure, considering closure from tree regeneration as well as from lateral crown expansion, and (iii) assess drivers of gap closure, including elevation, forest type and aspect. We hypothesized that (H1) gap expansion is more important than the formation of new gaps due to prominent disturbance interactions in the disturbance regime of our study system, such as bark beetle spread after wind disturbance (Seidl & Rammer, 2017; Senf, Pflugmacher, et al., 2017). We furthermore expected that (H2) small gaps close faster than large ones, and that gaps in mixed forests of coniferous and broadleaved species close faster than in forests of either conifers or broadleaved species due to niche complementarity (Jucker et al., 2015). We also hypothesized that (H3) vertical ingrowth of the regenerating cohort is the predominant process of gap closure (Winter et al., 2015), while lateral crown expansion plays a substantial role only in broadleaved forests, as these have higher crown plasticity (Schröter et al., 2012). Lastly, we contrasted gap formation and closure rates at the landscape scale, hypothesizing that (H4) gaps are created faster than they close, based on the observation of strong increases in tree mortality in Europe in recent years (Patacca et al., 2022; Senf & Seidl, 2021), and the broader expectation of the emergence of more open forests under climate change (McDowell et al., 2020).

2 | METHODS AND MATERIALS

2.1 | Study area

We studied canopy gap dynamics in Berchtesgaden National Park (BGNP), Germany's only national park in the Alps. Located at the border to Austria in south-eastern Germany, BGNP was established in 1978 and is an IUCN category II protected area, with 75% of the total area of 20,808 ha being unmanaged (referred to here as core zone). Forests in BGNP extend over an elevation gradient of approximately 1150 m, ranging from 603 m a.s.l. (Lake Königssee) to 1750 m a.s.l. (treeline). The natural vegetation of the submontane zone (<800 m a.s.l.) is characterized by European beech (*Fagus sylvatica* L.), while the montane zone (800–1400 m a.s.l.) features mixed forests of Norway spruce (*Picea abies* (L.) Karst.), European beech and silver fir (*Abies alba* Mill.). The subalpine zone (from 1400 m a.s.l. to the treeline) is dominated by Norway spruce, European larch (*Larix decidua* Mill.), Swiss stone pine (*Pinus cembra* L.) and mountain pine

(*Pinus mugo* Turra) (Thom et al., 2022; Thom & Seidl, 2022). The area was used intensively by humans before 1978, mainly for timber production. As a legacy of past land use, the share of Norway spruce on the landscape is elevated in the submontane and montane zones relative to natural vegetation conditions, and canopy structures in these secondary forests are largely homogeneous (Knott, 1991). The major natural disturbance agents in the area are bark beetles (mostly *Ips typographus* L.) and wind-throw, besides smaller areas affected by avalanches.

We here focus on the forests of the core zone of BGNP (Figure 1), to exclude effects of restoration management ongoing in the management zone of the park. Furthermore, we only analyse closed-canopy forests, defined by the FAO as areas with canopy cover of at least 40% (FAO, 2020). The resultant research area was 3999 ha of forest. For our analyses, we distinguished four forest types based on current vegetation (data derived from forest inventory, see Thom and Seidl (2022)): Spruce forests (42.56%), larch-pine forests (35.09%, combining forests dominated by either European larch, Swiss stone pine or mountain pine, and mixtures of these species), spruce-fir-beech forests (18.76%) and beech forests (3.59%).

2.2 | Data acquisition and canopy gap identification

We utilized three airborne lidar acquisitions available for BGNP, covering all 3999 ha of closed forests in the core zone and spanning a period of 12 years (2009, 2017 and 2021). The 2009 and 2017 acquisitions have a minimum point density of 4 pt m^{-2}, while the 2021 acquisition has a minimum point density of 30 pt m^{-2}. We have no scanner information on the 2009 and 2017 acquisitions, which were conducted in winter by the Bavarian Agency for Digitalization, High-Speed Internet and Surveying (see details in BayernAtlas (2023)), while the 2021 acquisition was performed with a VQ-780i Riegel Laserscanner in September 2021. To account for different point densities we generated a 1 m resolution canopy height model (CHM) for each acquisition from top returns (a total of 422,524,296 pixels in three time steps), representing vegetation height above the ground surface per cell, using the LidR package in R (Roussel et al., 2020). CHMs were derived from the difference between the digital surface model (DSM), representing the elevation of the canopy surface, and the digital terrain model (DTM), representing the ground surface (for more details see Supporting information). We cut all points above the height of 50 m to exclude outliers before CHM generation and manually masked rock formations that were clearly visible on aerial photographs. Different point densities can lead to differences in the accuracy of gap delineations, but according to Vepakomma et al. (2011) a return density of 3 pt m^{-2} or more is sufficient for detecting forest canopy gaps. We hence kept the original point densities and did not subsample the 2021 dataset.

We used CHMs to identify canopy gaps, defined as areas with vegetation less than 5 m in height, a minimum area of 400 m^2 and a minimum extension of 20 m in each cardinal direction. The later filter serves to remove narrow, elongated spaces between the
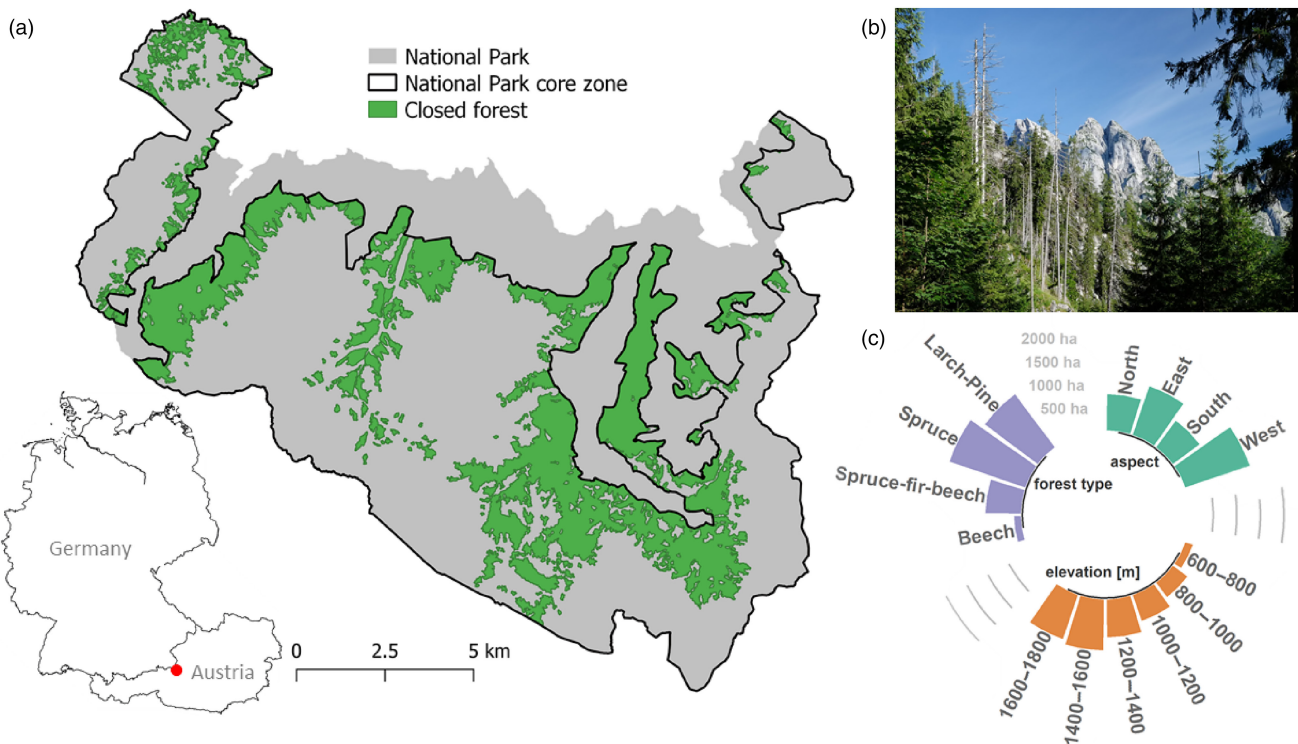
FIGURE 1 (a) Distribution of closed-canopy forests in the core zone of Berchtesgaden National Park, located in the south-eastern corner of Germany. (b) Example of a forest gap in Berchtesgaden National Park. (c) Distribution of the study area across aspects, elevation and forest types.

crowns of individual trees, which we do not consider as gaps. The minimum gap size corresponds to the canopy area taken up by between one to four trees in late forest development stages (Heurich et al., 2004) and lies within the range of gap sizes used in quantitative ecology (varying between 100 and 1000 m², Bugmann, 2001). The vegetation height threshold was chosen to mark the transition from the regeneration stage to stem exclusion stage, and is the minimum tree height for woody vegetation to be considered a forest by FAO (2020). A sensitivity analysis revealed that our results were qualitatively similar for a range of different gap size and vegetation height thresholds (see Figures S4–S10). A minimum connection requirement of 2 m in width was set for two neighbouring openings to be considered a single gap, and queen contiguity was used for establishing neighbourhood.

2.3 | Analyses

All gap change processes were analysed on a pixel-by-pixel basis at 1 m horizontal resolution and continuous vertical resolution. We stacked the gap layers from 2009, 2017 and 2021, and analysed them for (i) gap formation–distinguishing newly created gaps from expanding gaps, and (ii) gap closure–separating ingrowth of a regenerating cohort from lateral closure via crown expansion of edge trees. Gaps were considered newly created when they did not exist in the previous time step and when they were not connected to a previously existing gap. Gap expansion areas are those where newly created gap areas were connected to a previously existing gap. To identify if new gaps emerge in close proximity to existing gaps, we calculated the distance of new to existing gaps. As a reference for random gap placement, we sampled random locations in closed forests throughout the landscape and compared their distance to previous gaps to that from the actually observed newly created gaps.

We identified closure rates and modes of gap closure (lateral crown expansion versus regeneration) following the approach of Leitold et al. (2022). To distinguish between lateral canopy expansion and regeneration (vertical gap closure), we considered the neighbourhood of each gap pixel to trees >5 m height and its height change from one time step to the next. Lateral closure was only considered for pixels directly adjacent to canopy trees >5 m. We distinguished between lateral closure and regeneration ingrowth via a threshold for maximum tree height growth. This assumes that if pixel-level height changes are above realistic maximum tree height growth rates, they stem from expanding crowns of neighbouring trees. Maximum tree height growth rates were derived via two approaches: First, we assessed the average height growth of canopy trees in our study area from lidar data. Using the lidR package (Roussel et al., 2020), we identified single trees in the 2009, 2017 and 2021 CHMs for a subset of our study area, which comprise 214 ha across different forest types and elevation zones. The tree objects served as input for the dalponte2016 algorithm (Dalponte & Coomes, 2016), delineating tree crowns above the height of 10 m. The crown objects were used as a mask to extract height growth

within individual crowns. For both observation periods, the 80th percentile of annual height growth was around 0.5 m (0.48 and 0.52 m year⁻¹) across all 173,550 trees analysed. Second, we consulted maximum annual height growth estimations of regenerating trees reported in the literature. Reported height growth rates vary between 0.1–0.3 m year⁻¹ (Coates, 2000) and 0.4–0.55 m year⁻¹ (Schelhaas, 2014) for conifer seedings in different gap sizes and species, which corresponded well with the values estimated from lidar data. We consequently set 0.5 m as a realistic maximum annual tree height growth rate in our analysis. If the annual height change in a pixel was >0.5 m and the respective pixel was located next to a tree >5 m in height, we considered the change to be from crown expansion (i.e. lateral closure). If one of the two criteria (neighbourhood and height change above threshold) was not met, we considered the change to be from ingrowth of regenerating trees (i.e. vertical gap closure).

We stratified all results by aspect, elevation and forest type. We calculated rates of gap formation and closure on an annual basis per 100 ha of forest area. In addition, we expressed gap closure rates as the percentage of gap area closing per year. We performed gap delineation in Python (Python Software Foundation, 2022) with the support of the osgeo and scikit-image libraries (GDAL/OGR contributors, 2024; van der Walt et al., 2014). All other analysis were performed with the terra library in R (Hijmans et al., 2023; R Core Team, 2022).

3 | RESULTS

3.1 | Gap formation

Overall, we identified 11,331 gaps (comprising an area between 784.43 ha in 2017 and 1031.84 ha in 2009), whereof 819 gaps (52.00 ha) were newly created and 6737 gaps expanded during the observation period (226.72 ha expansion area) (Table 1). Gap formation (a total of 278.72 ha in 12 years) was primarily driven by gap expansion (81.3% of the newly formed gap area) rather than the initiation of new gaps, with gap expansion causing 4.4 times more gap area than gap formation (Figure 2). In contrast, newly created gaps were on average two times larger than the instances were gaps expanded, highlighting that gap expansion is a relatively slow, continuous process occurring over multiple years. New gaps typically ranged from 0.04 to 0.25 ha in size, with a median size of 0.05 ha, and often emerged in close proximity to existing gaps, with a median distance of 203 m between new gaps and previously existing ones (see Figure 3a; Figure S12). In contrast, randomly selected locations in closed forests had a median distance of 485 m to existing gaps, highlighting the spatial contagiousness of gaps (see Figure S13). In highly dynamic areas of canopy change, expanding gaps tended to merge with neighbouring gaps to form networks of open areas with interspersed close canopy forests (Figure 3b).

Norway spruce forests exhibited the highest rate of gap formation (median rate of 1.00 ha 100 ha⁻¹ year⁻¹; 2.5th–97.5th percentile range

TABLE 1 Gaps analysed and their modes of change.

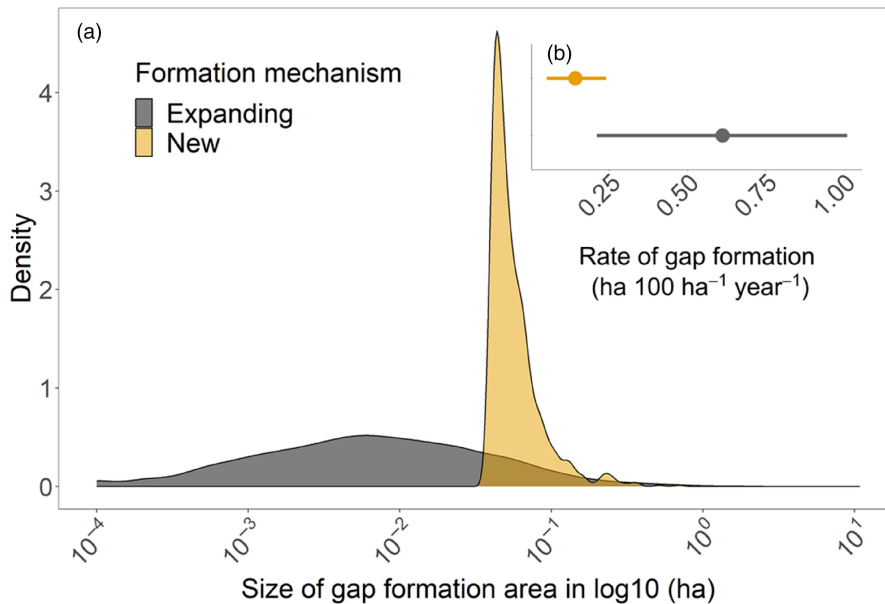| Year	No. gaps	Gap area (ha)	No. new gaps	New gap area (ha)	No. exp gaps	Exp gap area (ha)	No. stable or closing gaps
2009	3669	1031.84					
2017	3798	784.43	195	13.50	3497	61.72	105
2021	3864	914.26	624	28.50	3240	165.00	0
Σ	11,331		819	52.00	6737	226.72	105

Abbreviation: Exp, expanding gaps.

FIGURE 2 (a) Gap size distributions per mode of gap formation. Expanding gaps are canopy openings created adjacent to previous gaps, new gaps are those created in a previously closed forest canopy. Data here show the distribution across the full observation period from 2009 to 2021, for an analysis at the level of individual time steps between lidar acquisitions see Figure S11. (b) Annual gap formation rate (in hectares per 100 ha per year) by mode of gap formation. Point shows the median, whiskers indicate the 2.5th–97.5th percentile range of all observations.

0.43–1.57 ha $100\,ha^{-1}year^{-1}$), while beech forests had the lowest rate of canopy opening (median rate 0.30 ha $100\,ha^{-1}year^{-1}$; 2.5th–97.5th percentile range 0.05–0.54 ha $100\,ha^{-1}year^{-1}$) (Figure 4). The rate of new gap formation was comparable across all forest types (median rate between 0.08 and 0.19 ha $100\,ha^{-1}year^{-1}$; 2.5th–97.5th percentile range 0.01–0.31 ha $100\,ha^{-1}year^{-1}$). In contrast, gap expansion differed significantly with forest type, with gaps expanding at a two-fold rate in spruce forests compared to mixed forests of spruce, fir and beech, and with beech forests having the lowest gap expansion rate among all forest types (amounting to only 30% of the rate observed for spruce forests). Gap formation per aspect and elevation did not reveal a distinct pattern (see Figures S14 and S15).
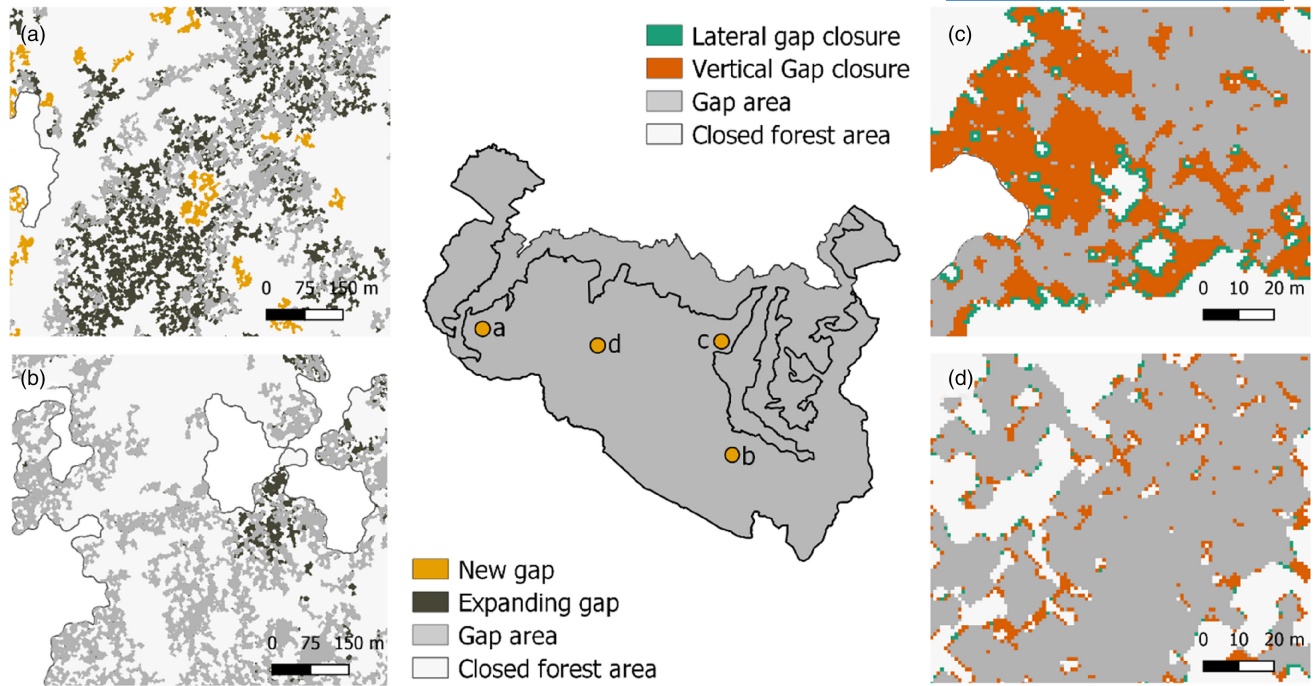
3.2 | Gap closure

Of the gaps identified in 2017 and 2021 (Table 1) only 111 experienced no gap closure. Overall, 3.80% of the gap area closed per year on average (29.78 ha year^{-1}), with very small gaps (<0.1 ha) closing faster than medium-sized and large gaps (Figure 5). Gap closure rates decreased with increasing elevation (Figure 5). Beech forest types had the highest closure rates, while coniferous forest types closed gaps considerably more slowly. Gap closure occurred primarily as

a result of ingrowth of the regenerating cohort (vertical gap closure), which contributed approximately four times more to overall gap closure than crown expansion (horizontal closure). The relative importance of these two processes was very similar across forest types, with lateral crown expansion accounting for 20% of all gap area closed for larch-pine forests, 21% for spruce-fir beech forest and for 22% in spruce and beech forest.

3.3 | Net gap area change

Contrasting gap formation and closure rates revealed a clear dominance of gap closure over the study period, with 278.72 ha of gap area formed versus 357.38 ha of gap area closed (formation rates of 0.58 ha $100\,ha^{-1}year^{-1}$ versus closure rates of 0.74 ha $100\,ha^{-1}year^{-1}$). Gap closure was particularly prevalent at the lowest and highest elevations of BGNP, where gap closure rates were between 1.6 and 2.5 times higher than gap formation rates (0.71 ha $100\,ha^{-1}year^{-1}$ versus 0.45 ha $100\,ha^{-1}year^{-1}$ in the submontane zone and 1.03 ha $100\,ha^{-1}year^{-1}$ vs. 0.41 ha $100\,ha^{-1}year^{-1}$ in the subalpine zone). In contrast, average rates of gap formation and closure were nearly balanced in the montane zone (0.64 ha $100\,ha^{-1}year^{-1}$ versus 0.68 ha $100\,ha^{-1}year^{-1}$).

FIGURE 3 Examples of spatial patterns of new and expanding gaps as well as lateral and vertical gap closure for the period 2009 to 2021. The middle map insert shows the study area (see Figure 1) and the location of the respective panels. Panels show (a) a mixture of new and expanding gaps (montane spruce-fir-beech forest type) and (b) an area where the dynamics are driven exclusively by gap expansion (subalpine spruce forest type). Panel (c) shows large portions of a big gap closing through both lateral and vertical gap closure (submontane beech forest type), while (d) shows slow gap closure with almost no lateral crown expansion (montane larch-pine forest type).
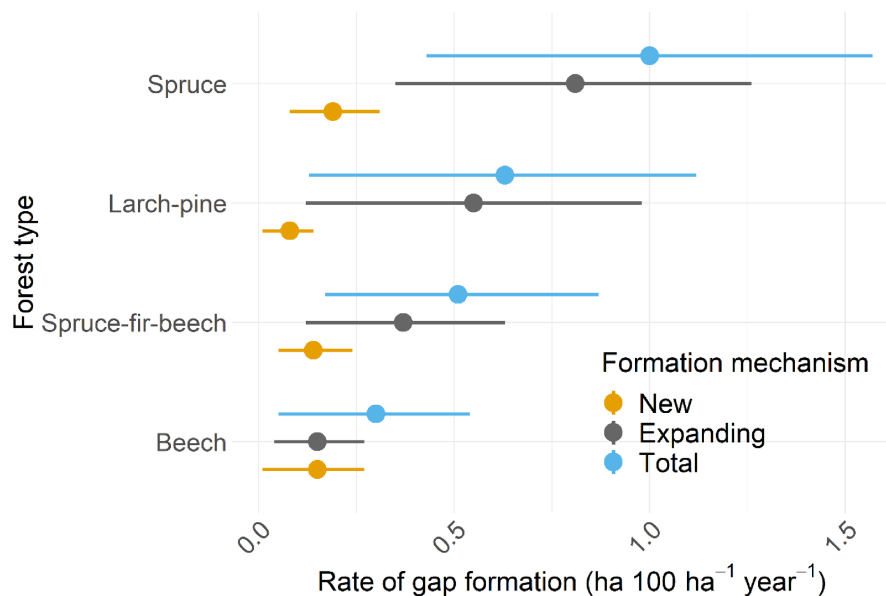

FIGURE 4 Annual rate of gap formation per forest type and mode of formation. Points indicate the median, whiskers the 2.5th–97.5th percentile range of the data distribution.

4 | DISCUSSION

4.1 | Gap dynamics

Analysing multi-temporal Lidar data, we show that gap expansion is the dominant process of canopy opening in a temperate mountain forest landscape in Europe's Northern Alps. In line with our initial hypothesis (H1), new gaps started relatively small but kept growing over the years of our observation period. This finding highlights at least two important aspects: First, annual rates of canopy gap formation, such as determined from remote sensing (e.g. Senf & Seidl, 2021), should not be confused with realized gap sizes in temperate
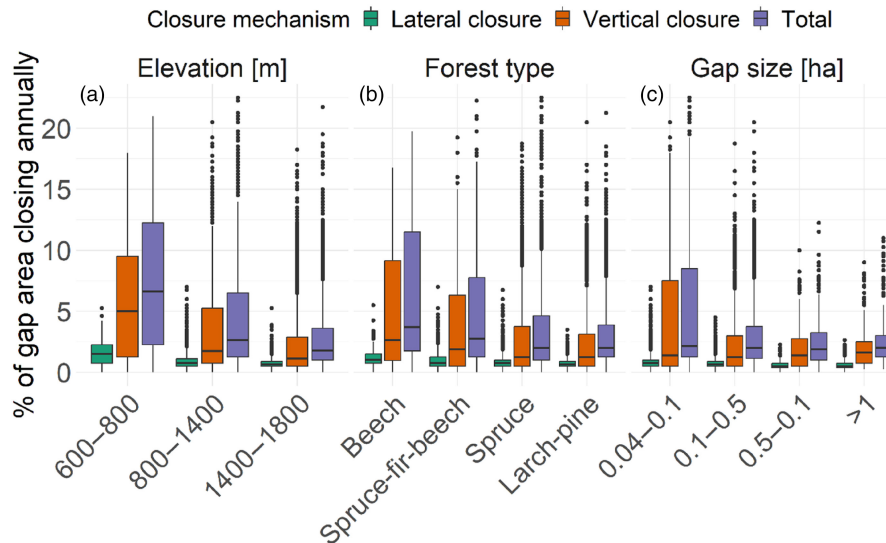
FIGURE 5 Canopy gap closure rates by closure mechanism across (a) elevation, (b) forest type and (c) gap size (ha). Boxes mark the median and inter-quartile range, whiskers indicate 1.5×IQR and dots are values beyond that range.

forest landscapes; the latter are considerably larger than the former due to the multi-year process of gap expansion. Second, canopy gaps have a long-lasting impact on forest dynamics due to their tendency to continue expanding, and due to the likelihood of new gaps emerging in their vicinity. Spruce forests exhibited the highest rate of canopy opening. On the one hand this is partly the result of human land use legacies, which promoted spruce in pure and structurally homogeneous stands that are prone to disturbance (Knott, 1991; Stritih et al., 2021). On the other hand this partly reflects the particular vulnerability of spruce to the ongoing changes in the climate system, with an increasing impact of important species-specific disturbance agents such as *Ips typographus* (Jakoby et al., 2019). The observation of highest canopy opening rates in spruce forests is thus in line with an ongoing reorganization towards less spruce dominance in Central Europe, observed for BGNP (Hartl-Meier et al., 2014; Winter et al., 2015) and elsewhere in the Alps (Stritih et al., 2021; Temperli et al., 2013). Interestingly, spruce forests did not differ from other forest types in the formation of new gaps, but had a higher gap expansion rate than the other forest types. This might be the result of the increased susceptibility of edge trees to bark beetles (Kautz et al., 2013) and wind-throw (Davies-Colley & Payne, 2000; Zeng et al., 2004) in spruce forests. In areas where spruce occurs in mixtures with other species, the rates of canopy openings were considerably reduced, potentially due to an increased resistance of spruce in mixed-species stands (Jactel et al., 2017; Sebald et al., 2021).

In contrast to gap formation rates, gap closure rates were less influenced by forest type. Broadleaved and mixed forest types had the highest capacity to close gaps, which partly reflects their high ability to regenerate in small canopy gaps (Collet et al., 2008; Huth & Wagner, 2006; Ishikawa & Ito, 1988). However, these forest types also occur predominately at lower elevations, where more favourable growing conditions facilitate seedling establishment and sapling growth (Hartl-Meier et al., 2014; Rapp et al., 2012). Mixed species

stands including spruce demonstrated a higher capacity to close gaps compared to spruce-dominated forest types, possibly due to the effect of niche complementarity, better utilizing free growing space and available resources (Jucker et al., 2015; Madrigal-González et al., 2016; Williams et al., 2017). We found that small gaps (<0.1 ha in size) closed faster than larger ones, which supports our initial hypothesis (H2) and is generally in line with Kern et al. (2013), who report increasing competition from shrubs with increasing gap size. In contrast, Coates (2000) found the opposite relationship between seedling height growth and gap size, indicating that larger gaps take less time to fill due to higher light availability. The effect of gap size was, however, only apparent for very small gaps in our study, and gaps greater than 0.2 ha in size closed at a rate that was independent of their size. This is an important finding because it suggests that even the largest gaps in our landscape are not limited by seed delivery (Hansen et al., 2018), and that more extreme microclimatic conditions in large gaps do currently not impede canopy recovery (Abd Latif & Blackburn, 2010; D'Odorico et al., 2013; Thom et al., 2023). Vertical closure of gaps (i.e. ingrowth of a regenerating tree cohort) was more important than lateral gap closure (crown expansion of edge trees), supporting our hypothesis on the paramount importance of tree regeneration for gap closure (H3). Nonetheless, crown expansion contributed to approximately 20% of all gap closures in our analysis and is thus a relevant—and to date often overlooked—response of temperate forests to canopy gaps. Interestingly, the rate of lateral crown expansion was largely independent of gap size and forest type, suggesting that not only forests dominated by European beech, which is known to have a highly responsive crown architecture (Schröter et al., 2012), but also coniferous forests respond to gaps with increasing their crown dimensions. This finding is also supported by an analysis from conifer-dominated boreal forests, in which lateral crown expansion accounted for 22% of all gap closures (Vepakomma et al., 2011).

4.2 | Limitations

Some methodological aspects need consideration when interpreting the results presented here. First, all analyses and findings are contingent on the underlying definition of a canopy gap, gap formation and gap closure. We conducted a sensitivity analysis on gap size to determine the influence of these definitions on our results, finding that our findings remain robust also under different gap definitions (see Figures S4–S9). Our results are least robust in areas where stocking density is naturally low, such as larch-pine forest types occurring at high elevations. Here, the death of only some individuals (or a change in the threshold applied for detecting gaps) can result in a large change in gap area. Further uncertainty relates to our classification of lateral and vertical gap closure. We used spatial proximity to edge trees and survivors within a gap in combination with a potential height growth threshold to discriminate between these two modes of gap closure. Better data on height growth in the regeneration, such as more nuanced and site-specific height growth rates, could help to make this discrimination more robust. We tested the effect of the maximum annual tree growth rate choice and found that the closure patterns over gap sizes remain consistent across different thresholds (see Figure S10). Furthermore, analyses based on terrestrial laser scanning could give insights into canopy expansion rates at the level of individual trees (Calders et al., 2020; Seidel et al., 2011).

While using repeat Lidar data has many advantages and allows for a detailed picture of forest canopy change, it also has shortcomings that need to be considered. First, the surveys in 2009 and 2017 were conducted in winter and hence under leaf-off conditions, which impacts the generated CHMs, also due to the possible presence of snow. The higher resolution and leaf-on conditions in the 2021 survey could thus introduce a positive bias in rates of closure between 2017 and 2021. Second, while Lidar data allows detailed inferences on (changes in) forest structure, it does not contain information on species composition. We thus do not know whether canopy gaps are closed by early successional or late-successional species, nor if there is a compositional species change compared to the canopy before gap formation. To address these ecologically relevant questions terrestrial inventories should be used to complement remote sensing-based analyses (Tomppo et al., 2008). Repeated multi- and hyperspectral campaigns can further aid the analysis of compositional responses to gap formation (Hycza et al., 2018; Modzelewska et al., 2020). Furthermore, given the time scales of mountain forest dynamics, our observation period is short (12 years). This is particularly relevant as some of our findings might reflect the particular management and disturbance history of our study area (e.g. with a big wind-throw and subsequent wave of bark beetle outbreak affecting the area right before the onset of our study period in 2007 (Winter et al., 2015)). It is thus important to note that our results only present a snapshot of the longer-term dynamics of forests in the Northern Front Range of the Alps. We are nevertheless confident that our findings provide important and broadly applicable insights into temperate mountain forest dynamics, not least because

they are congruent and complementary to approaches extending over much longer time frames (Thom et al., 2022).

4.3 | Implications

Our findings have important implications for the understanding of forest dynamics in Central Europe where canopy disturbance rates are increasing sharply (Patacca et al., 2022; Senf et al., 2018; Senf & Seidl, 2021). In particular, our results highlight the importance of gap expansion for forest canopy dynamics, with new gap formation being independent of forest type. This suggests that focusing future investigations on gap expansion could be an important avenue to better understanding forest dynamics. Possible questions arising from our findings are: Does gap expansion follow geographical or environmental features? Which factors drive or impede gap expansion? Our findings also highlight the importance of spatial contagion in forest change. Once a gap is created, the course for the surrounding forests is set for the coming years, as new gaps are more likely to emerge next to existing gaps, and as gaps keep growing over multiple years. This pattern of spatial dependence was found also in other studies in temperate (Blackburn et al., 2014; Senf, Campbell, et al., 2017), tropical (Gorgens et al., 2023) and boreal forests (Hytteborn & Verwijst, 2014; Vepakomma et al., 2012). Potential processes contributing to the contagious nature of canopy gaps are edge effects (Hunter et al., 2015; Pöpperl & Seidl, 2021), as edge trees are more susceptible to drought and wind (Buras et al., 2018; Seidl et al., 2014); but also dispersal mechanisms, such as the flight of bark beetles, which can contribute to spatially clustered canopy openings (Kautz et al., 2011; Seidl et al., 2016; Senf, Campbell, et al., 2017).

Our results also have considerable relevance in the context of forest management. The typical regeneration method in mountain forests of the Alps—creating small gaps and then slowly enlarging them (Hilmers et al., 2020; Streit et al., 2009)—aligns well with the natural dynamics observed in our study. Regenerating the forest via small canopy openings is thus not only favourable in the context of maintaining ecosystem services of high relevance in mountain forests, such as the protection against natural hazards (Teich et al., 2022), but also mimics natural processes and is in line with the intention to manage forests 'closer to nature' (Larsen et al., 2022). However, our results also highlight that management should be cautious with creating gaps, as they might continue to grow once the canopy has opened. This process of gap expansion might be hard to contain once it has started, particularly in conifer-dominated forests. Given the high rate of natural disturbances in the recent past, gaps created naturally can be utilized to reach silvicultural goals such as forest restoration (Dollinger et al., 2023), while retaining some closed-canopy tracts on the landscape.

We found that gap closure outweighs gap formation in our study landscape. This generally underlines the high resilience of Central European forests to disturbance (Senf & Seidl, 2022), and their ability to regenerate well after canopy openings (Winter et al., 2015).

Specifically, we did not detect a signal towards more open forests, such as expected for many ecosystems under global change (McDowell et al., 2020), but rather found indications of a densification of forests in our study system. This is well in line with terrestrial observations from earlier studies both in BGNP (Thom & Seidl, 2022), in the Alps more broadly (Kulakowski et al., 2017), and was also reported for other systems (Gorgens et al., 2023; Rodes-Blanco et al., 2023). Nonetheless, emerging novel disturbance regimes and ecological responses will likely continue to alter ecosystem dynamics (Seidl, & Turner, 2022). Our analyses, for instance, indicated that gap formation and closure rates are currently close to balancing each other out in the montane elevation belt of our study system. The two- to four-fold increase in disturbance rate that is expected for the 21st century in our study area (Albrich et al., 2023; Thom et al., 2022) could thus tip the system towards more open forests, highlighting the need for a continued monitoring of forest change.

We conclude that while canopy openings might be small in the European Alps (Maroschek et al., 2024), they keep growing over multiple years by way of gap expansion. Once created, gaps thus have a long-lasting impact on forest dynamics. However, we also show that trees regenerate well in canopy gaps, underlining the resilience of forests in Central Europe. We highlight that studying forest gap dynamics with high resolution, multi-temporal Lidar data allows important insights into the ongoing changes in forest ecosystems. Improved process understanding on the formation and closure of gaps can, for instance, provide important benchmarks for developing and evaluating process-based models used to simulate forest resilience under global change (Albrich et al., 2020). We conclude that a continued monitoring of forest gaps is important as global change progresses, as they are the fingerprints of disturbance and regeneration processes in forest canopies and are thus important early warning signals of forest change.

AUTHOR CONTRIBUTIONS

Kirsten Krüger: Conceptualization, methodology, formal analysis, writing—original draft and visualization. **Cornelius Senf:** Conceptualization, methodology, and writing—review and editing. **Tommaso Jucker:** Writing—review and editing. **Dirk Pflugmacher:** Conceptualization, methodology, writing—review and editing. **Rupert Seidl:** Conceptualization, methodology, writing—review and editing, and supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest. Tommaso Jucker is an Associate Editor for *Journal of Ecology* but took no part in the peer review or decision making process for this manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The code for reproduction of all analyses as well as data used is available at Zenodo: https://zenodo.org/records/10966262 (Krüger, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Changes in canopy height (height gain) between the years 2009 and 2017 within tree crowns of trees >10 m height (crown center) and the surrounding forest vegetation (non-crown).

Figure S2: Changes in canopy height (height gain) between the years 2017 and 2021 within tree crowns of trees >10 m height (crown center) and the surrounding forest vegetation (non-crown).

Figure S3: Subset of the study area for which we performed the sensitivity analyses.

Figure S4: Abundance of gap sizes per formation mechanism and minimum mapping unit in m^2 on log scale.

Figure S5: Gap formation rate as area of annual gap formation per process and minimum mapping unit in m^2.

Figure S6: Distribution of closure rates for total closure (lateral + vertical) in different gap size bins.

Figure S7: Abundance of gap sizes per formation mechanism and height thresholds on log scale.

Figure S8: Gap formation rate as area of annual gap formation per process and height threshold. Points show the median, point range the 5th–95th percentile.

Figure S9: Closure rates for total gap closure across gap sizes for different height thresholds in m.

Figure S10: Annual gap closure rates per gap size bin and varying height growth threshold (the top of each panel).

Figure S11: Gap size distributions per mode of gap formation.

Figure S12: Distance between new and previously existing gaps.

Figure S13: Distance between random new and previously existing gaps.

Figure S14: Annual rate of gap formation per aspect and mode of formation.

Figure S15: Annual rate of gap formation per aspect and mode of formation.

Figure S16: Gap closure rates per closure mechanism across aspects.

Figure S17: Detailed breakdown of gap closure rates by smaller categories per elevation and gap size.

Table S1: Average closure shares for different maximum annual tree growth thresholds across the whole sub-region used for sensitivity analysis.

Table S2: Distribution of gap formation area for new gaps and the expanding gap area.

Table S3: Gap formation rates in ha $100\,\text{ha}^{-1}\text{year}^{-1}$ per forest type and mechanism.

Table S4: Gap closure rates in annual % of gap area closed per forest type and closure mechanism.