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How large-scale bark beetle infestations influence the protective effects of forest stands against avalanches: A case study in the Swiss Alps

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A R T I C L E I N F O

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A B S T R A C T

Large-scale bark beetle outbreaks in spruce dominated mountain forests have increased in recent decades, and this trend is expected to continue in the future. These outbreaks have immediate and major effects on forest structure and ecosystem services. However, it remains unclear how forests recover from bark beetle infestations over the long term, and how different recovery stages fulfil the capacity of forests to protect infrastructures and human lives from natural hazards.

The aim of this study was to investigate how a bark beetle infestation (1992–1997) in a spruce dominated forest in the Swiss Alps changed the forest structure and its protective function against snow avalanches. In 2020, i.e. 27 years after the peak of the outbreak, we re-surveyed the composition and height of new trees, as well as the deadwood height and degree of decay in an area that had been surveyed 20 years earlier. With the help of remote sensing data and avalanche simulations, we assessed the protective effect against avalanches before the disturbances (in 1985) and in 1997, 2007, 2014 and 2019 for a frequent (30-year return period) and an extreme (300-year return period) avalanche scenario.

Post-disturbance regeneration led to a young forest that was again dominated by spruce 27 years after the outbreak, with median tree heights of 3–4 m and a crown cover of 10–30%. Deadwood covered 20–25% of the forest floor and was mainly in decay stages two and three out of five. Snags had median heights of 1.4 m, leaning logs 0.5 m and lying logs 0.3 m. The protective effect of the forest was high before the bark beetle outbreak and decreased during the first years of infestation (until 1997), mainly in the case of extreme avalanche events. The protective capacity reached an overall minimum in 2007 as a result of many forest openings. It partially recovered by 2014 and further increased by 2019, thanks to forest regeneration. Simulation results and a lack of avalanche releases since the infestation indicate that the protective capacity of post-disturbance forest stands affected by bark beetle may often be underestimated.

1. Introduction

Natural disturbances are important drivers of forest dynamics and ecosystem services in forested landscapes (Kulakowski et al. 2017). The frequency and severity of disturbances in the form of windthrows and bark beetle infestations have increased considerably in European mountain forests during the last decades (Hlásny et al. 2021). This is particularly relevant for Norway spruce dominated mountain forests, which are often in a stage of high susceptibility to windthrow and bark beetle outbreaks, owing to intensive management up to the 19th century and the subsequent decrease in land-use intensity (Bebi et al. 2017). Climatic changes, particularly increased drought stress, reduce resistance and further increase the vulnerability of trees to bark beetle outbreaks (Netherer et al. 2015). A warmer climate also favours the development of new large bark beetle populations (Jakoby et al. 2019) that are more likely to succeed in overcoming tree defences

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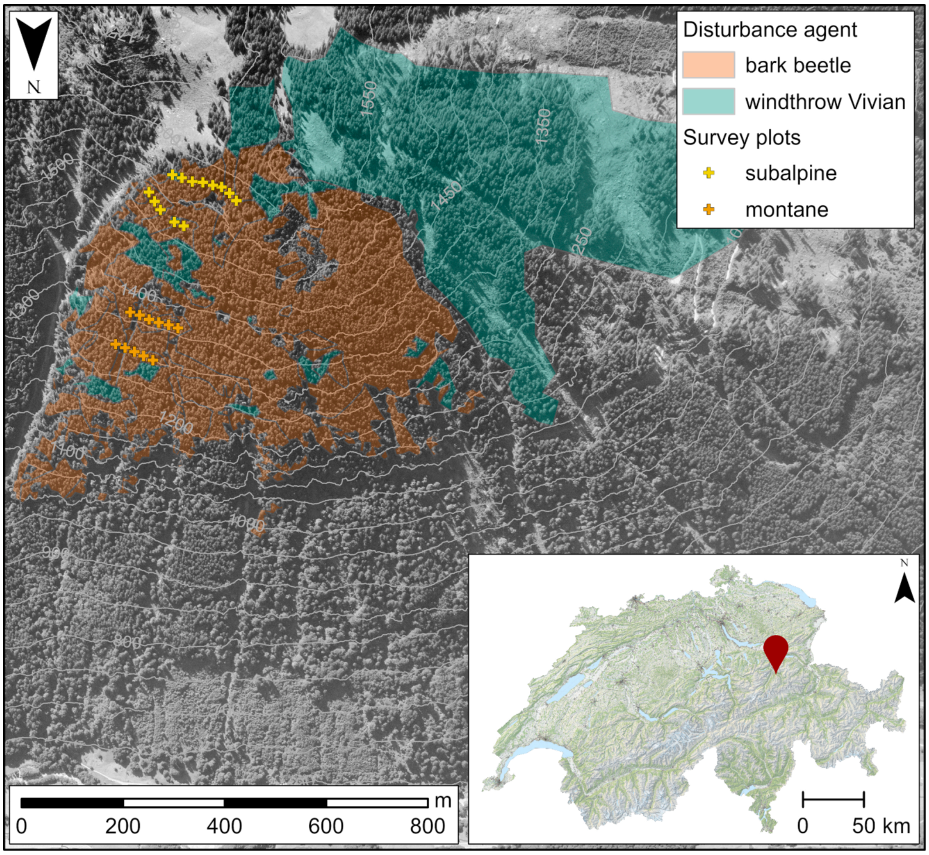

Fig. 1. The study area Gandberg, with orange shading indicating the bark-beetle-induced die-back in 1990 s, and the adjacent and overlapping windthrow area resulting from the storm Vivian in 1990 (turquoise shading). Data from Kupferschmid Albisetti (2003). The orthophoto from 1989 shows the dense forest before the disturbances (© swisstopo). In a total of 24 plots, we surveyed the structure of the forest, which was affected by bark beetles, in the montane zone (orange crosses) and subalpine zone (yellow crosses). Map of Switzerland showing Gandberg © swisstopo. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Wermelinger 2004). Higher temperatures in mountain regions allow bark beetles to increase in the number of generations per year (Jönsson and Bärring 2011) and to spread to higher elevations (Mezei et al. 2017). This often corresponds to a spread from the montane to the subalpine zone, where forests naturally tend to have a large share of coniferous trees.

Long-term legacies of natural disturbances in forests with a long-lasting management history are often characterized by a return to a more natural condition (Kulakowski et al. 2017). Further, reforestation pathways of disturbed forests frequently lead to higher diversity compared with the original forest stands (Scheidl et al. 2020). However, in the case of bark beetle, these pathways strongly depend on: (i) management and disturbance history; (ii) initial stand complexity and diversity; (iii) environmental conditions; and (iv) browsing pressure (Andrus et al. 2020, Fischer et al. 2015, Senf et al. 2019). These changes in structure and structural diversity are expected to have implications for the susceptibility of a stand to subsequent disturbances (Sommerfeld et al. 2021).

The short- and long-term impacts of natural disturbances affect various ecosystem services, such as carbon storage, habitat and recreation (Stritih et al. 2021). Another ecosystem service of major importance in many mountain forests is the capacity to protect human lives and infrastructures against natural hazards, such as snow avalanches (McClung and Schaerer 2006). The importance of such protection forests has increased in many mountain regions as human infrastructures have expanded due to the extension of important transit routes, population growth and a growing tourist industry (Sebald et al. 2019). While intact forests are able to reduce the likelihood of avalanche formations, as well as their runout distances (Feistl et al. 2014, Teich et al. 2012), there is clearly less confidence in the protective effect of forests that have been affected by natural disturbances (Bebi et al. 2015). Specifically, bark beetle infestations may influence the ability of a forest to protect against natural hazards (Teich et al. 2019), but our understanding is still limited regarding the effect of infestations on parameters related to protective function and on the development of protective function over time.

Some disturbances create a large amount of lying or standing deadwood on the ground, which increases ground roughness (e.g. Ulanova 2000, Storaunet and Rolstad 2002). Terrain roughness in turn has the ability to hinder the formation of snow avalanches (McClung 2001, Rammig et al. 2007, Schweizer et al. 2003, Wohlgemuth et al. 2017) and rockfall (Fuhr et al. 2015, Wang and Lee 2010). As wood decay proceeds, the height and strength of deadwood elements decreases (Ammann 2006). If young trees do not grow fast enough during regeneration to compensate for the decreasing height of deadwood elements, a so-called 'gap' in the protective function of a forest may occur (Frey and Thee 2002, Wohlgemuth et al. 2017). In past studies, it has been estimated that deadwood might be an effective avalanche barrier in the first 10–30 years after a windthrow event (Frey and Thee 2002, Schönenberger et al. 2005). Unlike after windthrow, trees die while still standing after a bark beetle infestation and may remain upright for several years. Such standing deadwood elements, so called snags, dry out faster than lying deadwood because of greater exposure to sun radiation and less contact with the moist forest floor (Storaunet and Rolstad 2002). In stands affected by bark beetle, less decayed deadwood is therefore supplied continuously from breaking snags (Schwitter 2011). Due to the slower decomposition of snags, it is possible that the period of reduced protective capacity in stands affected by bark beetle occurs later than in windthrow stands (Bebi et al. 2015) or not at all. However, trees killed by bark beetles normally decay faster than living trees felled suddenly (e.g. by windthrow) once they fall to the ground, as they have already lost their needles and branches (Raphael and Morrison 1987), and therefore settle closer to the ground after breaking (Kupferschmid Albisetti et al. 2003).

Several studies have addressed how the composition and structure of living trees and deadwood elements have changed up to 10 years (Červenka et al. 2020, Kupferschmid and Bugmann 2005a, Kupferschmid et al. 2002, Kupferschmid Albisetti et al. 2003) or up to 20 years (Fischer et al. 2015, Nováková and Edwards-Jonášová 2015, Winter et al. 2015, Zeppenfeld et al. 2015) after bark-beetle-induced dieback. To our knowledge, no European studies have considered a period longer than 20 years (but see long-term studies from the US: Schmid and Hinds 1974, Veblen et al. 1991) and only one study addressed the impacts of bark beetle outbreaks on the protective function of forests (Teich et al. 2016). We therefore conducted a case study in uncleared bark beetle stands in the Swiss Alps, 27 years after the peak of the dieback. The study area was already surveyed ca. 7 years after the outbreak (Kupferschmid and Bugmann 2005a, Kupferschmid Albisetti et al. 2003) and therefore offers an ideal study site to assess the long-term development of stands in which the Norway spruce (*Picea abies*) trees had been killed by the European spruce bark beetle (*Ips typographus*), hereafter called 'bark beetle stands'. Using a field survey, remote sensing data and avalanche simulations, we aimed to answer the following questions:.

1. What were the long-term impacts of the bark beetle outbreak on forest structure, including parameters related to avalanche hazard: (i) the cover, height and decay stage of deadwood elements; (ii) the occurrence of new trees on deadwood; and (iii) the composition and height of new trees?
2. Did the remaining snags, stumps and logs and/or the new trees offer sufficient protection against avalanche formation, and how did the protective function change over time?
3. How did the number and size of potential snow avalanches in the bark beetle stands change over time, from before the disturbance up to 27 years after the peak of the outbreak?

2. Materials and methods

2.1. Study site

The study site Gandberg (46°59′25″N 9°06′28″E) is located south-east of the village of Schwanden in the canton of Glarus in Switzerland (Fig. 1). It is located on the north face of Gandstock mountain. Many parts of Gandberg are relatively steep, with slopes > 35°, which creates favourable conditions for natural hazard processes like snow avalanches and rockfall. Maximum snow heights on Gandberg were calculated to be 2.5 m in the montane zone (1200–1450 m a.s.l.) and 3.2 m in the subalpine zone (1450–1600 m a.s.l.) for avalanches with a return period of 30 years (Kupferschmid Albisetti 2003). According to the forest management authorities of the canton of Glarus, the forest in the montane zone originated from a clearcut carried out between the years 1842 and 1846. Even though some high thinning was done in both elevation zones (Forstverwaltung Kanton, 1949), these interventions were too small to prevent the formation of dense and homogeneous stands with little advanced regeneration (Kupferschmid et al. 2002). Before the disturbances, the growing stock was very high in the montane zone (820 $m^3\ ha^{-1}$) and also high, compared with regional averages for similar forest types, in the subalpine zone (590 $m^3\ ha^{-1}$). The pre-disturbance forest was dominated by Norway spruce (*Picea abies* (L.) H. Karst.), with 1% silver fir (*Abies alba* Mill.) and 3% Sycamore maple (*Acer pseudoplatanus* L.) (Kupferschmid Albisetti et al. 2003). In the year 1990, the storm Vivian caused scattered windthrows and felled a forest area of about 3.4 ha. A bark beetle outbreak followed on Gandberg between 1992 and 1997, peaking in 1993, killing a further 30 ha of trees (Kupferschmid 2002, Kupferschmid Albisetti et al. 2003). Almost all spruce trees died, whereas many silver fir and maple trees survived. As the forest on Gandberg has no direct protective function, it was not cleared and was declared a natural forest reserve. The forest below 1200 m a.s.l. was not affected by bark beetles and today consists of broadleaved and mixed stands which are still managed.

2.2. Field survey

The field campaign took place in October 2020, i.e. 27 years after the peak of the bark beetle outbreak. In previous studies on Gandberg around 20 years ago, four strip transects were surveyed, with a width of 5 m and a length ranging from 100 to 160 m (Kupferschmid Albisetti et al. 2003). For our study, we used the same sampling location, but we sampled circles with a radius of 5 m, spaced 20 m from one plot centre to the next. This method resulted in a total of 24 survey plots, 13 of which were in the subalpine zone and 11 in the montane zone (Fig. 1). Within every plot we collected data on deadwood, seedlings/saplings and ground vegetation.

Seven deadwood elements were surveyed per plot: (i) the tallest element within the plot and (ii) the three snags and three logs closest to the plot centre (even if they were outside of the 5 m radius). This method resulted in a total of 168 deadwood elements. The following variables were measured for every deadwood element: type (snag, log), height, diameter, decay stage, and movability. Snags were defined as standing deadwood elements. Logs were classified as lying (more than half of the stem touching the ground), leaning (less than half of the stem touching the ground) or root plates.

The height of the deadwood elements was measured either with a Vertex clinometer (Haglöf, Sweden) or with a folding meter stick. The diameter was measured using a sliding calliper (accuracy of 1 cm). For snags, the diameter at breast height (DBH) or, if broken below DBH, at the highest circumference was measured. The diameter and height of logs were measured at the closest point to the plot centre. To evaluate the decay stage, the method proposed by Lachat et al. (2019) was used; depending on how far a knife penetrates the wood, five stages of decay are distinguished: stage 1 (fresh wood), stage 2 (sapless wood), stage 3 (less solid wood), stage 4 (soft wood) and stage 5 (very loose wood). The movability of the elements was tested by trying to push them over by hand. Finally, the tree seedlings and saplings growing on each deadwood element were counted, the species was identified, and the height of the tallest seedling/sapling was measured.

All trees within a plot were surveyed by classifying them as seedlings (0.2–1.3 m height) or saplings (>1.3–10 m height). The term tree regeneration is used for the whole process of new tree establishment. We recorded the number of trees, tree species, tree height, DBH of saplings, and percentage of terminal shoot browsing of seedlings (browsing intensity). As only one willow sapling was found, it was excluded from the analysis. In addition, the crown cover of saplings within the 5 m radius was estimated visually with 5% increments. The length and width of all gaps (tree-free areas) which intersected a plot were measured. Gaps were defined as being longer than 10 m and wider than 5 m, and having neither elements taller than 50 cm nor trees with a DBH > 8 cm. Finally, we visually estimated the percentage of cover of the three main types of ground vegetation per plot (with 5% increments). Some of the vegetation types were present at multiple heights, meaning that the total cover could exceed 100%. We chose the three most abundant types from: fern, grass, bramble, dwarf shrubs, herbs, moss and bare soil.

The data collected on Gandberg were analysed using R (R core team 2021) paired with RStudio (version 4.0.2; RStudio Team 2020). To test for significant differences between groups, nonparametric two-sided tests were used. The Wilcoxon rank-sum test ('wilcox.test' function in the *stats* R package) was used for the comparison of two variables. For the height of deadwood elements, the regression analysis was conducted using the 'lm' function, also in the *stats* R package. For the number of seedlings and saplings growing on deadwood elements we calculated a zero-inflated negative binomial model ('zeroinfl' function from the *pscl* package), as the count data were zero-inflated. Reduced models omitting the non-significant variables were calculated and the best model was chosen based on the lowest Akaike information criterion (AIC approach, as in Stauffer 2008). *P*-values > 0.05 were regarded as indicating no statistical significance, ≤ 0.05 as showing a trend (*), < 0.01 as signifying statistical significance (**), and < 0.001 as indicating high

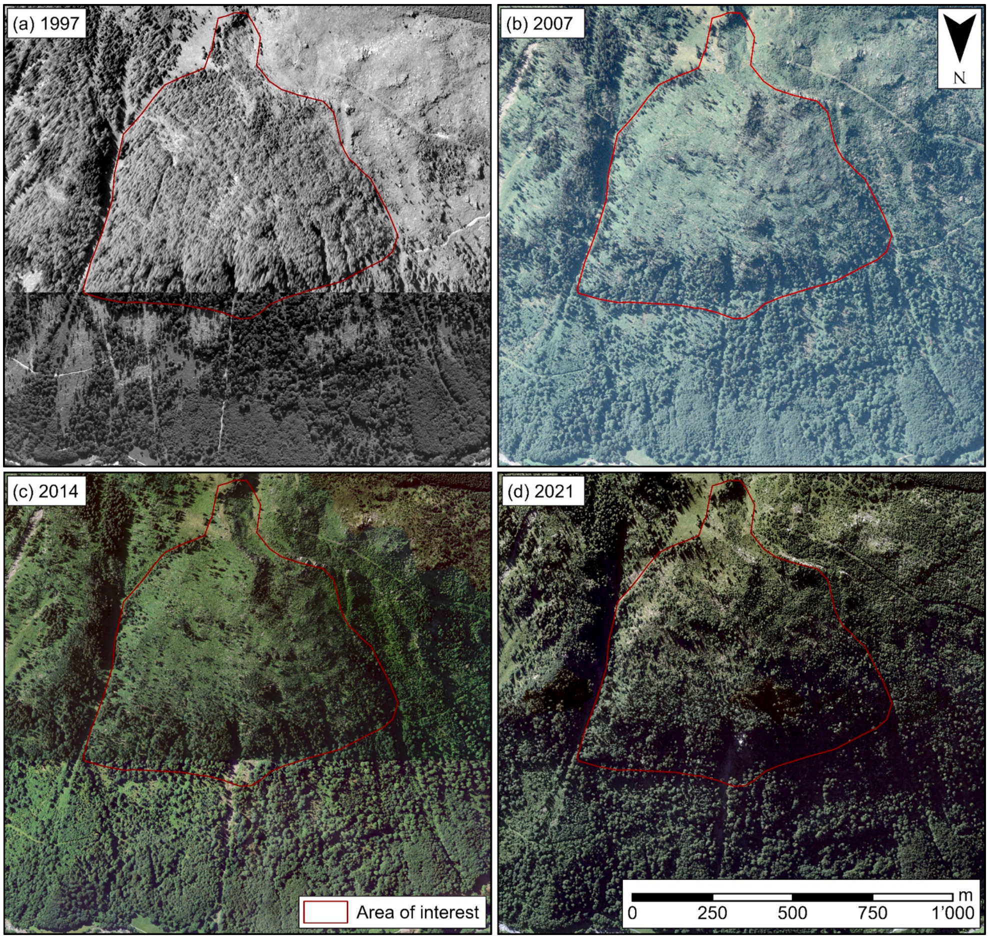

Fig. 2. Four orthophotos showing the change in the Gandberg forest affected by a bark beetle infestation (© swisstopo). Four years after the peak of the outbreak most trees were dead but still standing (a), 14 years after the peak most dead trees were lying on the ground (b), 21 years after the peak new tree regeneration had started (c), and 28 years after the peak the tree cover increased further (d). Note: the image in (d) shows the situation in 2021, but for the avalanche simulations we used the most recent data available, from 2019.

statistical significance (***).

2.3. Avalanche simulations

To evaluate the change in the potential avalanche hazard on Gandberg over time, we used the scientific version of RAMMS (Rapid Mass Movement Simulation) EXTENDED BETA (Feistl et al. 2014). To reflect changes in the forest structure, five points in time were chosen: (i) before storm Vivian (1985, orthophoto in Fig. 1), (ii) four years after the peak of the bark-beetle-induced die-back (1997, Fig. 2a), (iii) 14 years after peak die-back (2007, Fig. 2b), (iv) 21 years after peak die-back (2014, Fig. 2c), and (v) 26 years after peak die-back (2019, no image).

For the five selected years we simulated avalanche scenarios with return periods of 30 years (frequent scenario) and 300 years (extreme scenario) in RAMMS. We used the Swiss elevation model SwissAlti3D (2019) resampled from 0.5 to 1 m resolution for the simulations. To calculate the release height, we used the cumulative snow height, which covers a period of three days (Burkard and Salm 1992). To create an extreme value statistic, we fitted a Gumble distribution to the data from the Braunwald weather station (10 km horizontal distance) using an online tool called EVA+ (ZAMG, Vienna, Austria). We applied the method proposed by Burkart and Salm (1992) and extrapolated the values to Gandberg. The release heights on Gandberg were calculated to be 0.65 m (montane) and 0.75 m (subalpine) for the frequent scenario and 0.9 m (montane) and 1.0 m (subalpine) for the extreme scenario.

We estimated the location and size of the potential release areas (PRAs) in the geospatial processing program ArcGIS Desktop 10.8.1 (Esri, Redlands, CA, USA), using slope and aspect maps. We defined threshold values based on: the vegetation height model (VHM), a protection forest layer according to Bebi et al. (2021) and used an orthophoto from each year (1984, 1997, 2007, 2014, 2019). The combination of these datasets allowed us to account for the effect of different forest structural characteristics and tree heights, as well as any roughness features present on the ground (e.g. deadwood). In particular, the protection forest layer combined different forest parameters, such as tree height and crown cover, which directly influence the potential establishment of release areas (Bebi et al. 2021). We then used VHMs and orthophotos to determine, for each PRA, if high surface roughness is present.

Friction parameters, which determine the flow behaviour of avalanches, depend on: (i) topographic data (slope angle, elevation and curvature), (ii) forest information and (iii) global parameters (return period and avalanche volume), and they can be calculated automatically within RAMMS (Bartelt et al. 2017). Our automatically calculated friction values resulted in Mu = 0.55 and Xi = 1800 for the frequent scenario (30-year return period) and Mu = 0.42 and Xi = 1900 for the extreme scenario (300-year return period). The extended version of RAMMS accounts for snow detrainment within forests, which decelerates avalanches by removing mass (Feistl et al. 2014), and also calculates the damage to trees based on the species and DBH. The detrainment coefficient (K-value) is based on forest type, crown cover and surface roughness. We used orthophotos, VHMs, forest inventory maps and data from the Swiss National Forest Inventory plots (WSL 2021) to assign the K-values, tree species and DBH. The two latter parameters define the tree breakage threshold within the simulation (Feistl et al. 2014). We represented the areas with visible deadwood elements, i.e. the former bark beetle stands, as open deciduous forest (because trees shed their needles after the bark beetle outbreak) with high roughness and assigned K-values accordingly. The avalanche type "Mixed Powder" was selected and the pre-programmed standard

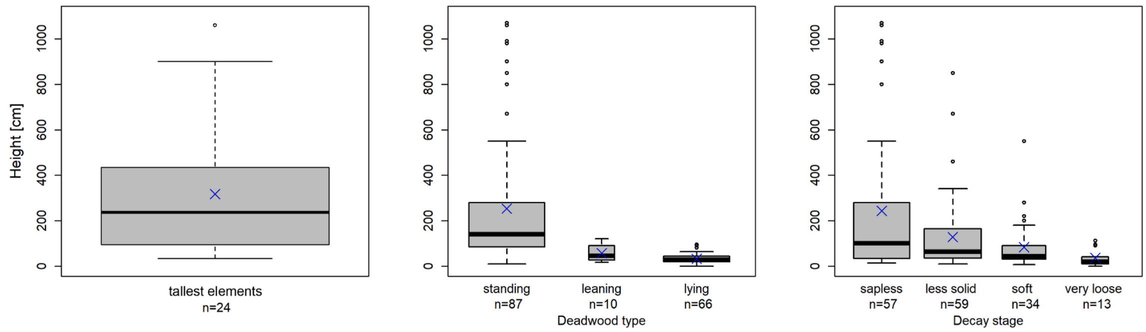

Fig. 3. Boxplots showing the height of the tallest deadwood element per plot (left), as well as the height of all measured elements separated by deadwood type (middle) and decay stage (right). The total sample size was n = 163, due to the exclusion of four root plates and one NA value. The middle and right graphs exclude one sapless snag which had a height of 18.6 m. The boxes represent values ranging from the 25th to 75th percentile, whiskers represent the lower and upper 25% of the data, and points indicate outliers. Median values are indicated with a bold line and mean values with a blue ×. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Zero-inflated Poisson regression of the number of spruce seedlings and saplings growing on deadwood. We used the following reference types for our variables: elevation zone = montane, movability = not movable, deadwood type = standing, and decay stage = sapless (stage 2, since we did not find stage 1 [fresh deadwood] on Gandberg). Because there were no seedlings or saplings on leaning elements (n = 10) we excluded them from the analysis. The count model part of the regression shows how many seedlings and saplings were found growing on deadwood, and the zero-inflated model part predicts the probability of observing a zero.

	Estimate	Standard deviation	Significance	Estimate	Standard deviation	Significance
	Count model			Zero-inflated model		
Subalpine zone	1.319	0.356	***			
Movable	2.407	0.724	***	3.277	1.135	**
Decay: less solid	0.893	0.417	*	−0.440	0.800	.
Decay: soft	0.937	0.311	**	−1.820	0.893	*
Decay: very loose	1.733	0.513	***	−0.087	1.128	
Type: lying	1.284	0.325	***			
Type: root plate	2.788	0.380	***			
Constant	−2.267	0.511	***	0.781	0.686	
Observations	158					
Log(theta)	13.259					

P-values > 0.05 were regarded as indicating no statistical significance, ≤ 0.05 as showing a trend (*), < 0.01 as signifying statistical significance (**), and < 0.001 as indicating high statistical significance (***).

Table 2
Density of saplings and seedlings in the two elevation zones.

	Montane		Subalpine	
	All species [trees ha^{-1}]	Norway spruce [trees ha^{-1}]	All species [trees ha^{-1}]	Norway spruce [trees ha^{-1}]
Seedlings	1042	463	921	735
Saplings	1215	845	950	901
Total	2257	1308	1871	1636

RAMMS parameters for this avalanche type were used.

3. Results

3.1. Field survey: Structure of deadwood

Deadwood was still an important structural element on Gandberg 27 years after the peak of the bark beetle outbreak. Most of the deadwood was lying on the ground (82%), whereas only 12% was still standing and 6% was leaning. The deadwood cover was similar in the two elevation zones, with a median of 25% of the ground covered with deadwood in the montane zone and 20% in the subalpine zone (Wilcoxon test, $P > 0.05$, see also Fig. B.1 in the appendix).

The tallest elements within the 5 m plot radius were often standing snags (67%), which had a median height of 2.4 m (Fig. 3, left). The median height of the three closest snags was 1.4 m, whereas leaning logs were 0.45 m tall and lying logs 0.28 m tall (Fig. 3, middle). The median DBH of the deadwood elements was 34 cm (q1 = 24.5 cm, q3 = 44.0 cm). Most of the deadwood on Gandberg was in an early or middle decay stage. More decomposed deadwood had smaller heights than fresher deadwood. Sapless wood had a median height of 1 m, less solid wood 0.64 m, soft wood 0.44 m and very loose wood 0.20 m (Fig. 3, right; see also regression analysis Table A.1 in the appendix). Out of the 163 deadwood elements (excluding the 4 root plates and 1NA value), 25 elements could be moved by hand (18%).

3.2. Field survey: Seedlings and saplings on deadwood elements

In 2020, a larger percentage of deadwood elements tended to nurse seedlings and saplings in the subalpine zone (25%) than in the montane zone (13%) (Wilcoxon test, $P < 0.05$). We also found a larger number of seedlings and saplings growing on deadwood in the subalpine zone (101 in total) than in the montane zone (20 in total). The most common species growing on deadwood was Norway spruce (97%). The only other species growing on deadwood was rowan (3%) (*Sorbus aucuparia*, L.).

A zero-inflated negative binomial model of the number of spruce seedlings and saplings growing on deadwood for the variables elevation zone, movability, deadwood type and decay stage showed that more spruce trees were found in the subalpine zone than in the montane zone (Table 1, count model). Further, we found more spruce trees on deadwood elements that could be moved by hand than on those that could not be moved. Compared with decay stage 2 (sapless wood), there were increasingly more spruce trees on deadwood in decay stage 3 (less solid), 4 (soft wood) and 5 (very loose). Compared with snags, the lying elements and the root plates nursed significantly more spruce trees (leaning elements nursed no trees at all and were thus omitted from the model).

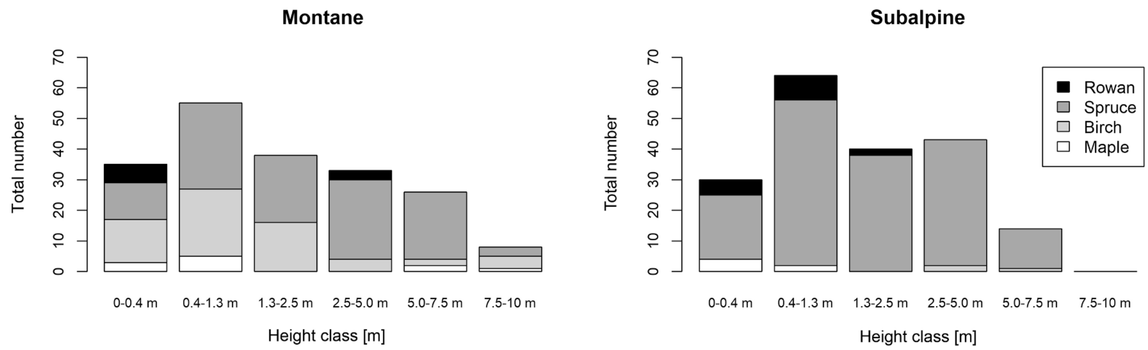

Fig. 4. Height distribution of the seedlings and saplings in the montane and subalpine zone, separated by tree species.

Table 3
Comparison of the values of forest structure parameters measured in this study to values reported in past studies which took place around 20 years earlier.

	Value in 2020	Value in 2000/2001
Deadwood cover		
Montane	25%	19% (1)
Subalpine	20%	12% (1)
Deadwood taller than 10 *m*	<5%	50% (2)
Height of logs		
Montane	32 cm	92 cm (2)
Subalpine	26 cm	78 cm (2)
Logs with ground contact		
Montane	85%	25% (2)
Subalpine	88%	32% (2)
Deadwood (created by the outbreak) that nursed new trees		
Montane	13%	0% (2)
Subalpine	25%	0% (2)
Dominant ground vegetation		
Montane	fern > grass > bramble	bramble > fern > moss (3)
Subalpine	grass > fern > dwarf shrub	moss > fern > grass (3)
Density of spruce seedlings		
Montane	463 ha^{-1}	1961 ha^{-1} (5)
Subalpine	735 ha^{-1}	3906 ha^{-1} (6)
Median height of spruce		
Seedlings	0.56–0.60 *m*	0.14 m (3, 4)
Saplings	2.9–3.9 *m*	NA (3, 4, 5)
Percentage of spruce trees		
Montane	58%	42% (6)
Subalpine	87%	80% (6)

(1) Kupferschmid and Bugmann 2005b, (2) Kupferschmid Albisetti et al. 2003, (3) Kupferschmid and Bugmann 2005a, (4) Kupferschmid et al. 2002, (5) Kupferschmid et al. 2006, (6) unpublished original data on all tree species in the 128 transects analysed in Kupferschmid and Bugmann 2005a and used for model validation in Kupferschmid et al. 2006. (Note that in Kupferschmid et al. 2006 only the upper subalpine level was used for characterizing the subalpine, while here the data for the lower and upper subalpine were taken together).

The zero-inflated model part of the analysis shows that the occurrence of spruce trees itself was influenced negatively by deadwood movability and positively by decay stage 4 (soft).

3.3. Field survey: Tree regeneration

In 2020, the total tree density was 1871 trees ha^{-1} in the subalpine zone and 2257 trees ha^{-1} in the montane zone (Table 2). The crown cover of saplings did not differ significantly between the montane zone (30%) and the subalpine zone (10%) (Wilcoxon test, $P > 0.05$, see also Fig. B.1 in the appendix). More than half of the studied plots were intersected by a gap (54%, i.e. 13 plots: 4 in the montane and 9 in the subalpine zone). Beneath the tree crowns the vegetation covered large amounts of the survey plots, with a similar median cover of 100% in the montane and 120% in the subalpine zone (Wilcoxon test, $P > 0.05$, see also Fig. B.1 in the appendix). The three most common vegetation types in the montane zone were fern, grass and bramble. In most plots in the subalpine zone grass was the most common type with the highest coverage, followed by ferns and dwarf shrubs.

Spruce was the dominant species in both elevation zones (Fig. 4), accounting for 87% in the subalpine zone but only 58% in the montane zone, where birch (32%) co-dominated. Seedlings in the montane and subalpine zones had similar heights, i.e. median of 0.6 m (q1 = 0.31 m, q3 = 1.02 m) and 0.56 m (q1 = 0.40 m, q3 = 0.92 m), respectively (Wilcoxon test, $P > 0.05$). Saplings, however, were significantly taller in the montane zone (median 3.9 m, q1 = 2.10 m, q3 = 5.90 m) than in the subalpine zone (median 2.9 m, q1 = 1.97 m, q3 = 4.12 m; Wilcoxon test, $P < 0.01$). The largest spruce saplings were almost 10 m tall (Fig. 4). The DBH of saplings was larger in the montane zone (median 6 cm, q1 = 3 cm, q3 = 9 cm) than in the subalpine zone (median 4 cm, q1 = 3 cm, q3 = 6 cm) (Wilcoxon test, $P < 0.05$). Browsing intensity was higher for broadleaved species than for spruce. Sycamore maple had the highest browsing intensity (86%), followed by rowan (63%), birch (31%) and spruce (17%). For an overview of the differences between the two elevation zones, see also Table A.2 in the appendix.

3.4. Comparison with past surveys

By comparing our field survey with the surveys undertaken in 2000/2001 on Gandberg, it is apparent that deadwood continued to decompose and trees continued to grow. Some noticeable changes happened within these last 20 years: the deadwood cover, the percentage of logs with ground contact, the percentage of deadwood nursing new seedlings, and the median height of spruce trees increased, while the height of snags and logs, as well as the density of spruce seedlings, decreased. The percentage of spruce in comparison to the other tree species increased in the montane zone and remained stable in the subalpine zone. The most common vegetation type shifted from bramble to fern in the montane zone and from moss to grass in the subalpine zone (Table 3).

3.5. Avalanche simulations

Before the disturbances, the Gandberg forest offered sufficient protection against avalanche formation. We could not identify any potential release areas (PRAs) and therefore simulated no avalanches. Four years after the peak of the bark beetle outbreak (1997), only a few PRAs could be identified (Fig. 5a and b). They were mostly created by the scattered windthrows of 1990. The bark-beetle-infested trees were almost all still standing and therefore prevented avalanche formation. The largest number of PRAs was identified in 2007, 14 years after the peak of the outbreak, when most of the trees killed by bark beetles had been broken and many openings within the infested stands had been created. By

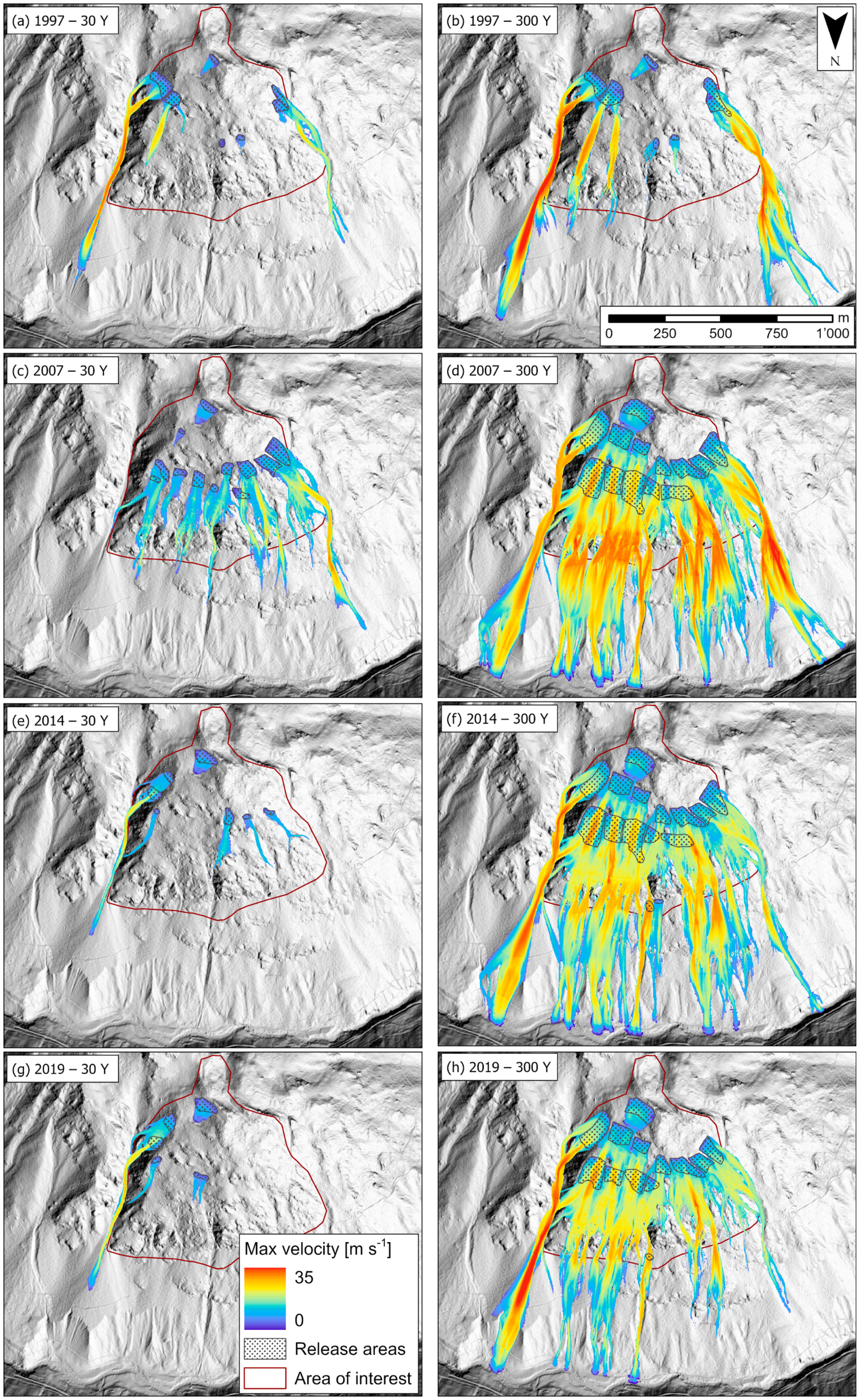

Fig. 5. Avalanche simulations with RAMMS EXTENDED, representing four time-steps after the bark beetle outbreak under a frequent (30-year return period) and an extreme scenario (300-year return period) (hillshade © swisstopo).

2014, the number of PRAs had decreased compared with 2007 under the frequent (30-year return period) avalanche scenario, thanks to the advancing tree regeneration during forest recovery, and even fewer PRAs were identified in 2019 (Fig. 5c, e and g). The growing seedlings and saplings had less of a protective effect in the extreme avalanche scenario (300-year return period): the number of PRAs stayed the same but their sizes decreased slightly from 2007 to 2014, and again from 2014 to 2019 (Fig. 5d, f and h).

Fig. 6. The Gandberg bark beetle stands in 1999/2000 a few years after the disturbance (a, c) and in 2020 (b, d). Photos (a) and (b) were taken from a large outcropping overlooking the montane zone. Images (c) and (d) show part of the upper subalpine transect.

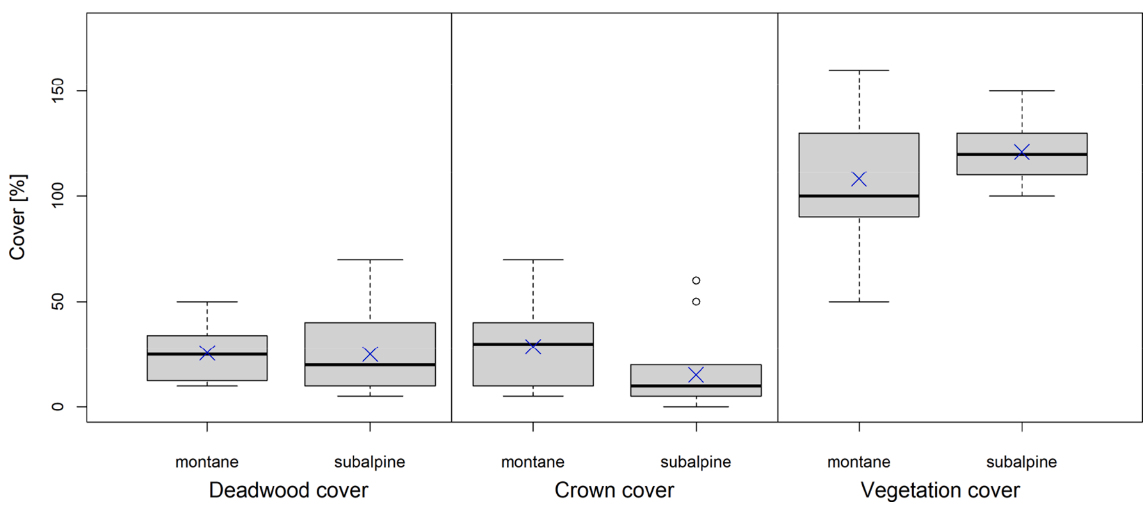

Fig. B1. Percentage of ground covered by deadwood (left), tree crowns (middle) and vegetation (right), per elevation zone. The boxes represent values ranging from the 25th to 75th percentile, whiskers represent the lower and upper 25% of the data, and points indicate outliers. Median values are indicated with a bold line and mean values with a blue ×. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The changing forest affected not only the size of the PRAs, but also the runout distance of the simulated avalanches. In 1997, when most of the trees were still standing, the forest stopped most avalanches: none of the simulated avalanches under the frequent scenario and only two under the extreme scenario reached the valley bottom (Fig. 5a and b). Ten years later (in 2007), there were many simulated avalanches in the frequent scenario, but none of them reached the valley bottom (Fig. 5c). However, in the extreme scenario, many of the simulated avalanches had long runout distances and reached the valley with high velocities (Fig. 5d). Twenty-one years after the bark beetle outbreak (in 2014), avalanches under the frequent scenario were stopped within the regenerating forest, resulting in shorter runout distances in some parts of the slope (Fig. 5f). Similarly, in the extreme scenario, some of the avalanches reached lower velocities and were stopped higher on the slope than in 2007. Further decreases in avalanche runout distance were observed in 2019 under both scenarios (Fig. 5g and h). Some of the simulated avalanches under the extreme scenario stopped within the dense forest below Gandberg (right side) and did not reach the valley bottom (Fig. 5h).

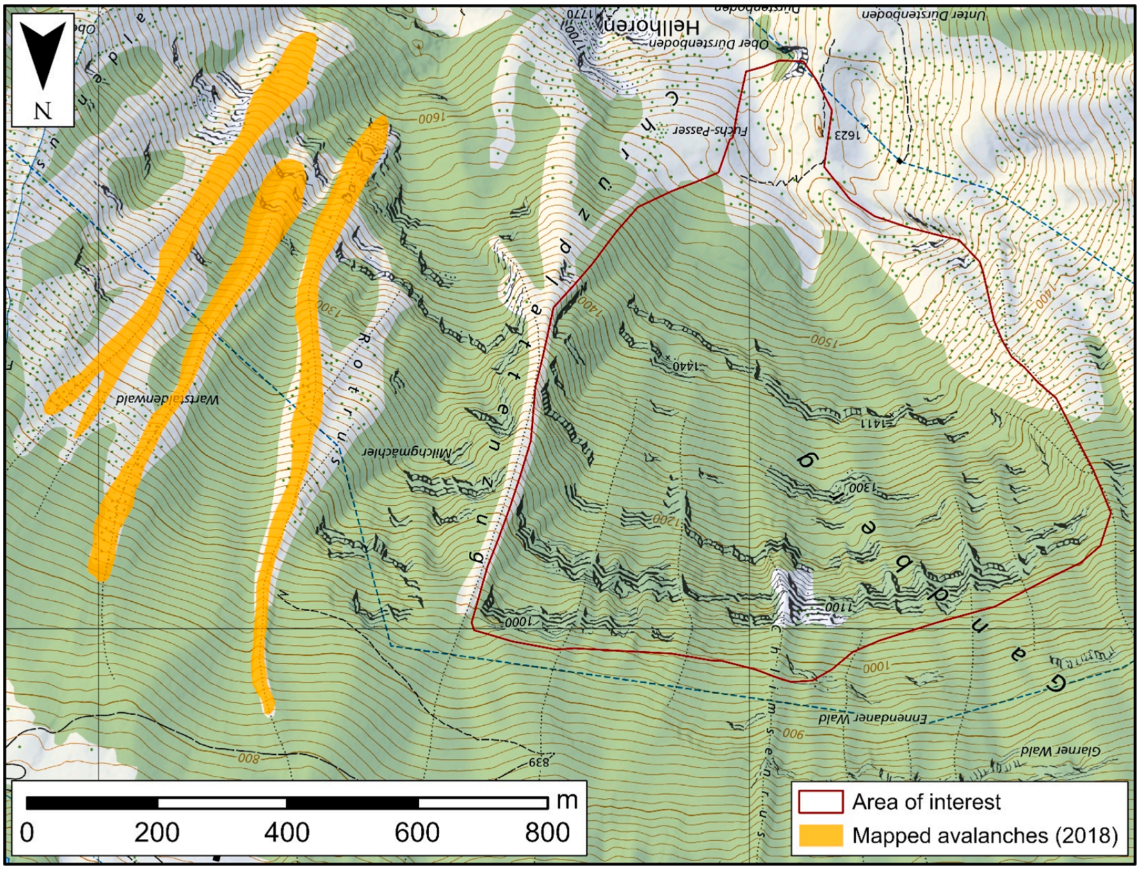

Fig. B2. Three avalanches were recorded between 1990 and 2018 on Gandberg (detected with the method of Bühler et al. 2019). These avalanches released in an area that had been affected by scattered windthrows and bark beetle infestations (©swisstopo).

Table A1
Regression analysis of the height of deadwood elements. The reference was 'standing' for deadwood type and 'sapless' for decay stage. The number of observations was 162, excluding 4 root plates and 2NA values (1 for height and 1 for DBH). There was no detectable difference in the deadwood height between the elevation zones, and elevation zone thus was not included in the final model. The height was $\log_{10}$ transformed after adding 0.001.

Variable	Estimate	Standard deviation	Significance
Type: leaning	−0.453	0.125	***
Type: lying	−0.639	0.069	***
Decay: less solid	−0.059	0.071	
Decay: soft	−0.143	0.084	.
Decay: very loose	−0.325	0.124	**
DBH	0.006	0.002	*
Constant	2.019	0.092	***
Observations		162	
R^2		0.527	
Adjusted R^2		0.509	
Residual std. error		0.364 (DF = 155)	
F statistic		28.814*** (DF = 6, 155)	

P-values > 0.05 were regarded as indicating no statistical significance, ≤ 0.05 as showing a trend (*), < 0.01 as signifying statistical significance (**), and < 0.001 as indicating high statistical significance (***).

Table A2
Comparison of the forest structure in the montane and the subalpine elevation zone.

	Montane zone	Subalpine zone	*P*-value (Wilcoxon test)
Deadwood cover	25%	20%	> 0.05
Deadwood nursing spruce seedlings and saplings	13%	25%	< 0.05
Tree density	2257 ha^{-1}	1871 ha^{-1}	–
Crown cover	30%	10%	> 0.05
Number of gaps/number of plots	4/11	9/13	–
Vegetation cover	100%	120%	> 0.05
Spruce percentage	58%	87%	–
Median height of spruce seedlings	0.60 *m*	0.56 *m*	> 0.05
Median height of spruce saplings	3.9 *m*	2.9 *m*	< 0.01
DBH of spruce saplings	6 cm	4 cm	< 0.05

4. Discussion

4.1. Long-term development of the bark beetle stands

About 27 years after the bark beetle outbreak, deadwood was still a prominent structural feature of the bark beetle stands on Gandberg. Compared with a survey of the same strip transects shortly after the die-back in 2000 (Kupferschmid and Bugmann 2005b), deadwood cover had increased from 12% to 20% in the subalpine zone and from 19% to 25% in the montane zone (Table 3). The increase in deadwood cover can be explained by the fact that many snags broke over the years, especially as a result of weakening through wood decay and tree breakage by storms (Kupferschmid Albisetti et al. 2003). In 2000, 50% of the snags were broken above a height of 10 m (Kupferschmid Albisetti et al. 2003), whereas in 2020 this value was<5%. The height of the logs also decreased over the past 20 years.

As logs settled closer to the ground, more of their length came in contact with the forest floor. In a past survey 25–32% of the logs had ground contact (Kupferschmid Albisetti et al. 2003), whereas in 2020 this value was 85–88%. More ground contact is expected to speed up decay, as more moisture is absorbed from the ground (Harmon et al. 1986). In the last 20 years the decay of the deadwood elements has progressed, and most elements have become sapless or less solid (decay stages 2 and 3). Brožová et al. (2022) found that most deadwood was already soft (decay stage 4) 30 years after the windthrow caused by storm Vivian (montane and subalpine zones; monitoring sites Schwanden, Disentis and Zweisimmen from Schönenberger 2002), indicating that decay is faster in windthrow sites than in bark beetle sites. Slower decay of bark beetle wood occurs because it remains standing for several years, allowing it to dry out (Storaunet and Rolstad 2002), and because it loses its bark before falling. Trees that retain their bark decay faster, as bark retains moisture well (Harmon et al. 1986).

Deadwood becomes a suitable seedbed for trees with increasing decay stage (Bače et al. 2012). While in 2000 there were no seedlings or saplings on the deadwood elements that originated from the bark beetle infestations (Kupferschmid Albisetti et al. 2003), 13% of the deadwood elements in the montane zone and 25% in the subalpine zone acted as nurse logs in 2020. This is less than in comparable windthrow sites, where 47% of all logs and root plates harboured seedlings (Brožová et al., 2022). The lower regeneration densities on bark beetle wood compared with windthrow wood may be related to: (i) the less advanced decay stages after bark beetle infestation; (ii) the larger number of root plates in windthrow areas, which are particularly favourable for regeneration of spruce (Ulanova 2000) and birch (Kuuluvainen and Juntunen 1998); or (iii) the presence of different, less favourable wood-decaying fungi in wood killed by bark beetles (Bače et al. 2012).

As deadwood decay proceeded the new trees gained in height, dominating Gandberg by 2020 (Fig. 6). However, the regeneration process differed between elevation zones. Due to the harsher growing conditions, the height and density of new trees are expected to be lower and forest gaps to be more frequent in the subalpine zone compared with the montane zone. Such cluster-like forest structures with lower tree cover and more gaps are typical for subalpine forests close to the upper treeline (Schönenberger 2001). After a disturbance, the density of trees first increases, because seedlings benefit from resources and space, and subsequently decreases again, due to inter- and intraspecific competition (Bače et al. 2012). In 2001, the densities of the new spruce seedlings were 1961 ha^{-1} in the montane zone (Kupferschmid et al. 2006) and 3906 ha^{-1} in the subalpine zone (Table 3), and there were no saplings, i.e. no advanced regeneration (Kupferschmid et al. 2002). In 2020, the density of spruce seedlings and saplings decreased to 1308 ha^{-1} in the montane and 1636 ha^{-1} in the subalpine zone (Table 2). The most common limiting factors for the establishment of new trees after a bark beetle outbreak are competition with herbs or a thick layer of undecomposed litter (Prach et al. 1996). The amount of ground vegetation on Gandberg increased after the spruce die-back (Kupferschmid 2002) and was still considerable in 2020, therefore likely competing with the tree seedlings and saplings. The vegetation cover did not differ between the two zones, but we found more seedlings and saplings on deadwood in the subalpine zone. It is likely that deadwood is a more important substrate in the subalpine zone, where favourable growing substrates are generally sparse (Brang et al. 2003). The saplings on Gandberg reached heights (3 m in the subalpine and 4 m in the montane zone) similar to values observed in comparable windthrow sites. Wohlgemuth et al. (2017) found average heights of 2.2 m in uncleared windthrow areas 20 years after the storm Vivian.

Before the bark-beetle-induced die-back, the Gandberg forest was very homogeneous and consisted almost exclusively of spruce. In 2020, spruce was still the most common tree species in both elevation zones. However, the percentage of broadleaved species increased considerably, especially in the montane zone, where 32% of all trees were birch. Changes from pure spruce forest to mixed mountain forests are enhanced by the changing climate (Cailleret et al. 2014, Scheller and Mladenoff 2005). We thus might observe a continuing shift of tree species composition in the montane zone in the future. The observed spruce re-establishment can be explained by the fact that: (i) Gandberg is a natural spruce site, in particular in the subalpine zone (Kägi 1992); (ii) there were not many seed trees of other species, such as silver fir and sycamore maple; and (iii) after a bark beetle attack hardly any mineral soil is exposed, which would promote the establishment of pioneer tree species (Fischer et al. 2015). The re-establishment of climax species after bark beetle outbreaks has been described by several other authors (Červenka et al. 2020, Fischer et al. 2015, Nováková and Edwards-Jonášová 2015, Zeppenfeld et al. 2015). In our study, the spruce recovery was also favoured by high browsing pressure on broadleaved species, as well as on silver fir. In the year 2001, maple was among the most frequent tree species (Kupferschmid et al 2002). Almost no maple trees, however, managed to grow taller (Fig. 4), probably due to the heavy browsing (Kupferschmid et al 2002, Kupferschmid & Bugmann 2005a). Such a strong effect of browsing on forest recovery and species composition after bark beetle outbreaks is also known from other studies (Andrus et al. 2020). In our study area, this effect may lead to decreased species diversity and slower climate adaptation. Nonetheless, due to the likely increase in seedlings and saplings growing on deadwood, we expect stands affected by bark beetle to have more heterogeneous structures with more age classes, making them less susceptible to future disturbances and thus dampening the amplifying effect of climate change (Sommerfeld et al. 2021). Apart from enhancing tree species diversity, positive effects on biodiversity more generally are to be expected when deadwood is not removed (Thorn et al. 2017, Thorn et al. 2018).

4.2. *Current protective function*

Traditionally, guidelines for protection forests have focused on the protective effect of living mature trees, neglecting the influence of deadwood and small trees. Nonetheless, several authors have argued that both deadwood and living trees are beneficial, as they enhance the surface roughness of the forest floor (Feistl et al. 2014, Rammig et al. 2007, Schönenberger et al. 2005). The percentage of deadwood cover 27 years after the bark beetle disturbance on Gandberg was high (20–25%), compared with the average in managed forests (Brändli et al. 2020, Paletto et al. 2014, Vítková et al. 2018) or in windthrow sites with similar tree ages and environmental conditions (15%, Brožová et al., 2022). We assume that a large area covered by deadwood decreases the avalanche hazard at least partially, because it enhances surface roughness. Next to cover, deadwood height is also an important factor determining roughness. The maximum snow depth for an avalanche scenario with a return period of 30 years was 2.5 m in the montane and 3.2 m in the subalpine zone on Gandberg (Kupferschmid Albisetti 2003). There were still some very tall snags on Gandberg in 2020, but most of the deadwood elements were significantly shorter than 2 m. Most deadwood elements would therefore be completely covered by snow in the frequent avalanche scenario, which would allow homogeneous snow layers to form on top of them (Veitinger and Sovilla 2016). However, deadwood shorter than the snow height might still prevent the formation of homogeneous snow layers, as vertical cracks can form around the stems (Frey and Thee 2002).

According to the Swiss guidelines for protection forests, the trees in avalanche protection forests should have at least twice the height of the maximum snow depth (Frehner et al. 2005). In 2020, these criteria were fulfilled (with a tree height of up to 10 m and a considerable impact on the snow structure) only with the tallest trees, but not considering the median height of saplings on Gandberg. After a bark beetle outbreak, our findings indicate that forests in the montane zone can recover faster than in the subalpine zone. Based on the current tree heights and growth rates observed in our study, we estimate that the montane stands will fulfil the requirements for protection forests set by Frehner et al. (2005) within the next 10–15 years, whereas recovery could take several additional decades in the subalpine zone.

The effect of smaller trees on snow structure, avalanche releases and avalanche propagation is less clear. However, Teich et al. (2012) found that the occurrence of small trees, 1–15 cm in diameter, in the starting zone and in the first 200 m of the avalanche path had a significant effect on the runout distances of medium and small avalanches. They attributed this effect mainly to a decrease in avalanche mass with increasing density of small diameter stems (Teich et al. 2012). We observed that the forest floor was covered with deadwood and young trees, and that, despite the unfulfilled requirements for protection forests, the forest showed signs of a residual protective function.

It is well known that intact forests reduce the likelihood of avalanche formation in potential starting zones (Bebi et al. 2009), decelerate small to medium sized avalanches (Teich et al. 2012), and reduce their runout distances (Brožová et al. 2020, Feistl et al. 2014, Fischer et al. 2015). This was reflected in our RAMMS simulations for the year 1985; before the bark beetle infestation, the forest offered protection against both frequent and extreme avalanches. However, the avalanche hazard increased after the disturbances.

The protective effect of the forests affected by windthrow and bark beetles was assessed differently by the spatial models. The areas that were affected by the scattered windthrow of 1990 (Fig. 1) resulted in potential avalanche release areas (PRAs) during the first years of post-windthrow development. This was reflected in our simulation results, which showed that these areas did not provide sufficient protection against frequent or extreme avalanches in 1997. The estimation of no PRAs in stands affected by bark beetle using the combination of a protection forest layer, orthophotos and a vegetation height model, is further supported by our field surveys and earlier field surveys in the same study areas from the year 2000, where a large number of snags (with height > 10 m) were found (Kupferschmid Albisetti et al. 2003). Trees killed by bark beetles may remain standing and retain their branches for a few years after death, intercept snow, and thus maintain a protective function to some extent (Teich et al. 2019). Field investigations on Gandberg and observations elsewhere thus largely confirm the results of the spatial modelling.

As decay proceeds, the protective function of the dead trees decreases, and if new trees do not grow fast enough a gap in the protective function of a forest can occur (Wohlgemuth et al. 2017). This was the case in our simulations of the years 2007, 2014 and 2019. In 2007, 14 years after the peak of the bark beetle outbreak, the minimum protective function was reached on Gandberg. PRAs were located both in the small areas affected by windthrow and in the more extensive bark beetle stands. This value is similar to findings from studies on the impact of storm Vivian on the protective function of forests, where the minimum was estimated to occur after 10–15 years (Baggio et al. in review; Bebi et al. 2015).

The gaps caused by the scattered windthrows, as well as some of the bark beetle areas, recovered their protective capacity at least partially by 2014 and 2019. Compared with 2007, there were fewer PRAs in these years under the frequent avalanche scenario. The extent of the PRAs under the extreme avalanche scenario, however, remained similar. By 2019, i.e. 26 years after the peak of the bark beetle outbreak, forest regeneration proceeded. In our field survey we found trees reaching 3–4 m in height, which may offer protection against most frequent avalanches but not yet against extreme events.

It is important to keep in mind that the RAMMS simulations are only models of avalanches that could potentially have occurred. Since the year 1990, no avalanche has been recorded in our study area (Canton Glarus, personal communication). During the avalanche winter of 1999, the maximal snow height reached 304 cm at the weather station Braunwald (10 km horizontal distance), corresponding to an event with a return period of 40 years. The lack of avalanches during this winter may be explained by the fact that standing deadwood decays slowly and was therefore still tall in 1999 (Kupferschmid Albisetti et al. 2003), hindering the formation of avalanches. Similarly, at the windthrow sites the considerable amount of lying deadwood may have had a positive influence on the snowpack stability, as no avalanches were observed in Vivian windthrow areas (Bebi et al. 2015).

In 2018 three avalanches were detected with the method of Bühler et al. (2019) in three channels outside of the studied bark beetle stands (Fig. B.2 in the appendix), but no avalanches occurred in the Gandberg study area itself. Regardless of the fact that our simulations for 2019 showed several PRAs and that the forest parameters measured in 2020 did not meet the requirements for protection forests, no avalanches occurred in the snow-rich winter of 2021 either (Canton Glarus, personal communication). These differences between simulated and observed avalanches in our study area can be seen as a further indication that the effect of young trees and deadwood elements on the avalanche hazard may often be underestimated. Therefore, we believe that a better representation of disturbed forests within RAMMS would be highly valuable.

5. Conclusion

Twenty-seven years after the peak of a bark beetle outbreak, the formerly dense spruce forest on Gandberg is on its way to structural recovery and to becoming a more diverse forest than before the disturbance. Spruce will likely remain the most important tree species, in particular at higher elevations, in areas where seed trees and ingrowth from adjacent broadleaved stands are lacking, and where ungulate browsing is intensive.

The natural post-bark-beetle forest development is comparable in many aspects to the development of post-windthrow stands under similar environmental conditions. However, the remaining standing snags are more dominant in the bark beetle stands, the deadwood decay is slower, and tree regeneration on deadwood is less advanced.

Our field data and simulation results confirm the important residual protective effect of bark beetle stands against snow avalanches in the first years following the disturbance. Furthermore, they indicate that forest structures with potentially insufficient provision of avalanche protection occur ca. 10–15 years after the outbreak and that the protective function increases again afterwards. During the minimum, the snags may already be largely decayed but the new trees might not yet be able to take on a protective function.

Our simulations, along with the fact that no avalanche events have been observed within the study area since the bark beetle outbreak, indicate that the protective effect of bark beetle stands may be sufficient, at least for frequent events. Nonetheless, careful planning of silvicultural, technical and organizational measures, along with more research, are necessary to keep the risks from natural hazards following bark beetle outbreaks at an acceptable level while natural processes which foster the development towards more resilient forest structures are given time to occur.

CRediT authorship contribution statement

Marion E. Caduff: Formal analysis, Writing – original draft, Visualization. **Natalie Brožová:** Conceptualization, Methodology, Formal analysis, Writing – review & editing, Visualization. **Andrea D. Kupferschmid:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Frank Krumm:** Writing – review & editing. **Peter Bebi:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

See the Figs. B1 and B2 and Tables A1 and A2.

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