

RESEARCH ARTICLE

Drivers of snag fall rates in Fennoscandian boreal forests

Tuomas Aakala¹  | Ken Olaf Storaunet² | Bengt Gunnar Jonsson³ | Kari T. Korhonen⁴¹School of Forest Sciences, University of Eastern Finland, Joensuu, Finland²Norwegian Institute of Bioeconomy Research, Ås, Norway³Mid-Sweden University, Sundsvall, Sweden⁴Natural Resources Institute Finland, Joensuu, Finland**Correspondence**

Tuomas Aakala

Email: tuomas.aakala@uef.fi**Funding information**

Kone Foundation

Handling Editor: Pieter De Frenne**Abstract**

1. Persistence of standing dead trees (snags) is an important determinant for their role for biodiversity and dead wood associated carbon fluxes. How fast snags fall varies widely among species and regions and is further influenced by a variety of stand- and tree-level factors. However, our understanding of this variation is fragmentary at best, partly due to lack of empirical data.
2. Here, we took advantage of the accruing time series of snag observations in the Finnish, Norwegian and Swedish National Forest Inventories that have been followed in these programs since the mid-1990s. We first harmonized observations from slightly different inventory protocols and then, using this harmonized dataset of ca. 43,000 observations that had a consistent 5-year census interval, we modelled the probability of snags of the main boreal tree species *Pinus sylvestris*, *Picea abies* and *Betula* spp. falling, as a function of tree- and stand-level variables, using Bayesian logistic regression modelling.
3. The models were moderately good at predicting snags remaining standing or falling, with a correct classification rate ranging from 68% to 75% among species.
4. In general, snag persistence increased with tree size and climatic wetness, and decreased with temperature sum, advancing stage of decay, site productivity and disturbance intensity (mainly harvesting).
5. *Synthesis and applications:* The effect of harvesting demonstrates that an efficient avenue to increase the amount of snags in managed forests is protecting them during silvicultural operations. In the warmer future, negative relationship between snag persistence and temperature suggests decreasing the time snags remain standing and hence decreasing habitat availability for associated species. As decomposition rates generally increase after fall, decreasing snag persistence also implies substantially faster release of carbon from dead wood.

KEYWORDS

boreal forest, coarse woody debris, Fennoscandia, forest management, standing dead tree

1 | INTRODUCTION

The presence of intact and broken standing dead trees (snags) is a characteristic feature of most forests. Their importance

for a well-functioning forest ecosystem is well established (Thomas, 2002) and, above all, they provide the basis for broad networks of deadwood-dependent species, some of which are highly specialized on snags (Larsson Ekström et al., 2023; Stokland

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Author(s). *Journal of Applied Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

et al., 2012). In forest ecosystems where snags are common, their persistence, that is the time they remain standing, can have major implications for the whole ecosystem carbon cycling (Hilger et al., 2012) and may also play an important role for forest nutrient dynamics (Krankina et al., 1999). For both issues—biodiversity and carbon and nutrient cycling—snag persistence is a key factor: habitat availability and stability, and how long carbon and nutrients keep locked away in dead wood are greatly dependent on how quickly snags fall.

To manage snags, we need to understand factors influencing their rates of fall. Here, the mechanisms that determine the resistance of live trees to wind and snow (e.g. Peltola et al., 1999), are also applicable to understanding snag dynamics. In general, the probability of a tree falling depends on (i) the structural strength of the stem and on (ii) the external forces exerted on the stem (Oberle et al., 2018).

Out of these two, the structural strength and consequently the resistance to fall of an individual tree develops during its lifetime. While alive, a tree benefits from structural strength that can withstand the external forces on the stem, usually from winds and snow. This resistance carries over to the standing dead trees. Studies of live tree resistance to winds have shown that important variables at the tree level include tree species and size, which influence allometry and mechanical resistance and physical and chemical properties of the wood material (Peltola, 2006). At the level of a forest stand, this is influenced by variables such as soil conditions, topographic position and stand composition and density (Elie & Ruel, 2005; Suvanto et al., 2016). Jointly with the species properties, these influence tree allometry, rooting depth and anchorage, canopy surface roughness and wind exposure. Higher stand density also dissipates energy from the wind to a larger number of individuals (Oberle et al., 2018), but stand density may also increase the chance of a tree being knocked down by a neighbouring tree (Pelz & Smith, 2013). Trees also acclimate to winds during their lifetime (e.g. Larson, 1965), and hence changes in the exposure to high winds for instance due to clearcutting adjacent the trees leads to an increased chance of falling over.

These factors at the level of the tree and the forest stand, together with the changes occurring at tree death and the possible activity of saprotrophic fungi while the tree was alive then determine the mechanical strength at the time of tree death. Following the death of the tree, the joint effect of decomposers and the structural strength at death then determine how long the snag remains standing. As the wood is invaded by decomposers that begin to cleave apart cellulose, hemicellulose and lignin, the mechanical strength progressively erodes, and hence the external force needed to topple the tree is reduced. On the other hand, as foliage and branches of gradually increasing order begin to drop, the sail area of the tree crown decreases, reducing the turning moment towards the stem or the root system, and consequently the mechanical force the tree has to withstand. Snag fall occurs latest at the point where the stem can no longer support its own mass.

In Fennoscandia, both the long-term human influence on forests and the current intensive forest management have reduced snag

densities to a fraction of their natural levels (Kalliola, 1966; Linder & Östlund, 1998; Storaunet & Rolstad, 2002). Although the amount of dead wood in general has lately increased, snags remain few, averaging less than 4 m³/ha throughout Fennoscandia (Korhonen et al., 2020; Nilsson et al., 2020; Storaunet & Rolstad, 2015). Consequently, the lack of dead wood of different species, sizes and degrees of decomposition is one of the main causes for the decline in forest habitat quality, and reasons underlying the decline of populations of many forest-dwelling species (Stokland et al., 2012). In managed forests, low snag densities implies that they play a minor role for carbon storage and fluxes. However, in protected areas the amount of dead wood is higher than in the managed forests, and their amount has been increasing faster (Korhonen et al., 2020; Kyaschenko et al., 2022).

Forest management guidelines and certification standards emphasize leaving dead trees during silvicultural operations, but current models predicting snag fall lack generality that could be used in management planning. Understanding snag dynamics, especially understanding factors that increase their persistence could feed into management planning aiming at producing long-lived habitats and long-term carbon storage. This also influences the assessment of the role and potential of snags in forest carbon fluxes, where snags are often treated in a simplistic manner (Hilger et al., 2012; Oberle et al., 2018; Woodall, Domke, et al., 2012).

An obstacle to analysing factors influencing snag fall and for developing predictive models has been the lack of empirical data, which is partly explained by the low density of snags in forests and the slow nature of snag dynamics. Permanent plots, where snags can be tracked through time are superior data source for these types of analyses. However, as permanent plots are usually not specifically designed for monitoring snag populations, the numbers of observations have remained low relative to the number of factors influencing the fall rates.

During recent decades, large-scale forest inventory programs have accrued data suitable for such studies in North America (Hilger et al., 2012; Oberle et al., 2018) and central Europe (Oettel et al., 2023). Similarly, these earlier data limitations are gradually disappearing also from northern Europe despite the low snag densities, as Finland, Norway and Sweden (henceforth: Fennoscandia) all incorporated dead wood in the permanent plot measurements of their National Forest Inventories (NFIs) in the 1990s. The exact protocols differ among these countries, but similar basic data is collected in all three inventory programs, and many of the variables can be readily harmonized (Stokland, 2003).

Using harmonized snag measurements from the Fennoscandian NFIs, we developed statistical models for predicting snag fall, and analysed the tree- and site-level factors that influence fall rates in Fennoscandian boreal forests. The variables were chosen so that the models can be used for predicting snag fall from attributes readily available and easily measurable on any snag found in Fennoscandian forests. Our analyses focused on the main tree species in the region: Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and two birch species grouped together (silver

birch *Betula pendula* and pubescent birch *Betula pubescens*). For other deciduous trees species, although important components in Fennoscandian forests, the current data from the NFIs is too limited to allow for a similarly detailed analysis as the main tree species.

2 | MATERIALS AND METHODS

2.1 | Fennoscandia

The study area consists of the forested areas of Finland, Norway and Sweden, stretching from 55°N in southern Sweden, to 69°N in northern Norway. Longitudinally, the area is demarcated by the Atlantic Ocean at the Norwegian coast at approx. 5°E and the eastern border of Finland at approx. 32°E. The area exhibits a varied topography, with highest areas in the Scandes with elevations between 1000 and 2500m above sea level, to lowland areas in Finland and the southern and coastal areas of Sweden and coastal Norway.

The main factor influencing the climate in Fennoscandia is its position between the Atlantic Ocean and Eurasia. The Scandes Mountains in the west give rise to major differences in precipitation particularly between the western and eastern parts of the region. The Norwegian coast is highly maritime, while the eastern parts of Fennoscandia are intermediate between maritime and continental. However, in all parts of the area at least moderate precipitation is recorded throughout the year. Mean temperature of the warmest month (July) ranges from 17°C in the southern Sweden to 13°C in some areas of the North. The mean temperature of the coldest month (February) varies from -3.5°C in southern Sweden to -14.7°C in northern Finland (Grieser et al., 2006). Annual precipitation sum also varies from over 2000mm on the Norwegian coast to 450–500mm in the interior of northern Lapland (Tikkanen, 2005). In southwestern Norway 11% and in northern Sweden 38% of the precipitation falls as snow (Grieser et al., 2006).

Forests cover approximately 72%, 35% and 69% of the land area in Finland, Norway and Sweden. Most of this area is managed: of productive forest land (annual growth >1.0m³/ha), 6.1%, 3.8% and 5.9% is formally protected from harvesting in Finland (Suojelualueet, 2022), Norway (Hysten et al., 2022) and Sweden (Statistics Sweden, 2021), respectively. Most of the forests are managed as rotations of even-aged stands, with intermediate thinnings from below. The main forest-forming tree species in the region are Scots pine, Norway spruce and birches. Deciduous co-dominants include aspen (*Populus tremula*), and other boreal deciduous species such as alders (*Alnus incana* and *Alnus glutinosa*), rowan (*Sorbus aucuparia*) and goat willow (*Salix caprea*). The hemiboreal and temperate forests in southern Sweden and Norway can also be dominated by nemoral deciduous species, such as oaks (*Quercus robur*, *Quercus petraea*), or beech (*Fagus sylvatica*).

2.2 | National forest inventories

National forest inventories (henceforth NFIs) are detailed elsewhere (Breidenbach et al., 2020; Fridman et al., 2014; Korhonen et al., 2021), but in short, data is collected on stand, plot and tree levels. The Finnish NFI (maintained by Natural Resources Institute Finland, <https://www.luke.fi/fi/seurannat/valtakunnan-metsien-inventointi-vmi>) is based on a systematic cluster sampling. Within-cluster configuration varies throughout the country, with the shortest distance between sample plots varying from 250 to 300m. Every fourth cluster is permanent and hence applicable here. Earlier, the plot remeasurement interval varied, but from the 10th NFI 10 (2004–2008) onwards, remeasurement interval for each permanent plot was 5 years. The Norwegian NFI (maintained by Norwegian Institute of Bioeconomy Research, <https://www.nibio.no/en/subjects/forest/national-forest-inventory>) is a systematic permanent inventory since the 1990s, where plots allocated on a 3km×3km grid are measured every 5 years. The Swedish NFI (maintained by Swedish University of Agricultural Sciences, <https://www.slu.se/en/Collaborative-Centres-and-Projects/the-swedish-national-forest-inventory>), plots are clustered into quadratic tracts (clusters) with eight circular sample plots, located evenly along the tract sides. The length of the tract sides varies, from 300m in the south to 1200m in the north for the permanent tracts. The remeasurement interval varied before 2003, and after that every 5 years.

2.3 | Snags in the NFIs

In the Finnish NFI, snag measurements are made on circular sample plots with a radius of 7m, and all snags with diameter at breast height (i.e. 1.3m, DBH) ≥10cm are included. Here, we used data from three NFI cycles with a fixed 5-year measurement interval. As dead wood pieces were not explicitly followed through time but needed to be matched between inventories, tracking the fate of snags required developing a 'piece-matching algorithm' (Woodall, Walters, & Westfall, 2012) to pair observations of snags on the same permanent plot between two inventory cycles. In short (see Data S1), at each permanent plot we used tree species, size and decay class to match the observations. A snag recorded in an inventory cycle was compared with snags measured on the same plot in the next cycle, and snag of the same species, approximately the same DBH, and the same or more advanced stage of decay was considered a match. Snags without a matching tree in the following inventory were considered fallen.

In the Norwegian NFI, snags are tracked through time, from living trees until they fall to the ground. Pairing of observations between measurements was, therefore, straightforward. Tree measurements (including snags) are made on circular sample plots of 250m², where all trees with DBH ≥5cm are included. Tree species, DBH and decay class are recorded.

In the Swedish inventory, dead wood is measured on a plot with a radius of 10m. Variables for each dead wood unit (≥ 10 cm in basal diameter and ≥ 1.3 m in length) are tree species, size (maximum basal diameter), decay stage (see below) and position (standing or downed). A standing dead tree is defined as being any stump or snag higher than 1.3m and is recorded separately from downed logs originating from the same tree. Snags are tracked through time.

While permanent plot data is ideal for studying snag dynamics, our approach overestimates snag fall for two reasons: snags that fall or that were deliberately harvested cannot be separated in the data (this information is available only in the Norwegian records). Second, snags with erroneous field records (e.g. wrong species, more recent decay class in later inventory cycle, etc.) would be considered fallen in the Finnish data matched here (Data S1). On the other hand, the 5-year remeasurement interval may also overestimate the standing times, as trees that died standing and fell during the remeasurement interval are not captured. Hence only a part of this 'fastest' fraction of snags leaves any record, whereas slower fraction of snags that remains standing for >5 years is fully recorded.

We visualized the geographical pattern of proportion of snag fall, by calculating the proportion of snags that were observed to fall in cells of a $10\text{km} \times 10\text{km}$ grid. We then calculated a smooth surface (a grid of $5\text{km} \times 5\text{km}$ cells) over the entire area, using inverse-distance-weighted interpolation (with a maximum of 100 closest points and parameter 0.5).

2.4 | Factors influencing snag fall and how they are derived from the NFIs

Separate models were built for Scots pine, Norway spruce, and the two birch species combined. The two birch species were combined, as they are not separated in the Swedish data. For the other species, their numbers were too low to allow analyses with similar level of detail, with 1210 observations of aspen, 6112 observations of boreal deciduous species (including alders, rowan, goat willow) and 1558 of nemoral deciduous species (such as oaks and beech).

Predictor variables were chosen as variables that were found important in earlier studies and that are readily available or measured. Tree-level predictor variables included DBH and decay class. Of these tree-level predictors, DBH was similarly recorded in all three NFI protocols. However, decay classifications were all slightly different. We thus used the harmonization developed by Aakala and Heikkinen (2024) that uses wood density in decay classes to group similar decay classes into a new, harmonized classification that has three decay classes for snags: early, intermediate and advanced. Of these, early decay class includes snags that are recently dead and/or only modestly influenced by decomposers. Intermediate snags are characterized by somewhat decayed trees in which a knife can be pressed through the outer parts of the stem. In the advanced stages, snags are becoming increasingly decomposed, until the point where they can barely maintain their own stem upright. Of tree-level variables, height (and stem taper) influences probabilities of trees

falling (Peltola, 2006), but because it has not been systematically recorded on all snags in the dataset, we fitted the models without height information.

Site-level predictors included site type, stand live tree basal area, and disturbances during the remeasurement interval. We also used climatic variables that are important determinants for decomposer activity and wood properties as plot-level predictors. For temperature, we used growing degree days accumulated over the growing season, with a 0°C threshold (i.e. temperature sum). For moisture conditions, we used the climatic moisture index (Willmott & Feddema, 1992) that describes the relative wetness or dryness of a location based on precipitation and evapotranspiration, varying between -1 (dry) and 1 (wet). Both climate variables were obtained from the openly available gridded Envirem data set (Title & Bemmels, 2018), based on climatic averages over 1970–2000, and with a $16\text{m} \times 16\text{m}$ resolution. Climate variables were assigned to each snag based on plot coordinates (permanent plot coordinates are classified, and thus have a 1-km accuracy). We note that although topography and slope may also influence probability of a tree falling (Elie & Ruel, 2005), these were not recorded in the different NFIs in a manner that would make them readily harmonizable and were thus not included here.

Of the plot-level candidate predictors, basal area was available from the original data sets. However, the site type variable required harmonization to be useable here. In short (listed in Data S2), site type was harmonized so that Norwegian site types (30 site types) and Swedish site types (16 site types) were each assigned to a corresponding Finnish site type (6 in total), based on expert opinion on the closest-matching site type. Out of these six types, the most productive and the least productive had a low number of observations, and they were thus assigned into the closest site type class. Thus, four site types were used in the analyses.

For disturbances, we used change in stand basal area during the remeasurement interval as an index of disturbance intensity. We divided these into three categories: low intensity (reduction of less than $1/3$ of basal area), intermediate intensity, (reduction of basal area between $1/3$ and $2/3$) and high intensity (reduction of over $2/3$ of basal area). As harvesting causes a vast majority of the basal area removal in Fennoscandian forests, this variable represents mainly the effect of harvesting.

2.5 | Logistic regression models

Factors influencing snag fall (i.e. snag either standing [1] or fallen [0]) were modelled with generalized linear mixed models with a logit-link, binomial error distribution and with tree and plot identities as nested random effects (trees nested within plots). The reasoning behind the choice of the analysis method was to build a parametric model where the fixed part is easy to use for prediction, while dealing with the violations of independence due to multiple observations of the same tree, and trees in the same plot. We further assumed that plots are independent of one another.

In the analyses, we used only the observations with 5-year remeasurement interval. Hence, the variable of interest was the probability of snag remaining standing over a 5-year period. In fitting the models, we included all trees in the dataset so that data from Norway had a smaller minimum DBH (5 cm) than the Finnish and the Swedish data (both with a minimum DBH of 10 cm).

We used Bayesian MCMC methods for fitting the models, as implemented in the *brms* package in R (Richardson et al., 2017). Two chains were run for 10,000 iterations, preceded by a burn-in phase of 10,000 iterations. Model validation consisted of visual inspection of trace plots (to assess mixing of chains), and an assessment of overdispersion. Model performance was approximated with posterior predictive checks, where we calculated the correct classification rates, and the area-under-the-curve (AUC) statistics with fixed effects models only (to approximate the skill of the model to predict unseen data).

Residual spatial autocorrelation is often problematic when analysing ecological data. As individual snags are not mapped in the NFIs, we tested for spatial autocorrelation of residuals, using the grouped residuals at the plot-level, and conducted the Moran's *I* test for spatially correlated residuals, as implemented in the *DHARMA* package in R (Hartig, 2022). We further explored the large-scale patterns in model residuals, using interpolated maps (Data S3).

We visualized the influence of climate on snag persistence, predicting probability of snag remaining standing over the region where snags were measured in the NFI data sets. The visualization was based on the values of the climate data set and was predicted on a contiguous grid of 16 m × 16 m cells and setting all other predictors to fixed values.

Data analyses relied on R (version 3.5), and packages *brms* (Richardson et al., 2017), *sf* (Pebesma, 2018) and *raster* for spatial data (Hijmans, 2020), *pROC* (Robin et al., 2011) for area-under-the-curve calculations, and *ggplot2* (Wickham, 2016) and *tmap* (Tennekes, 2018) for visualizations. Inverse distance weighted (IDW) interpolations were done with the package *gstat* (Pebesma, 2004).

3 | RESULTS

The compiled dataset consisted of 42,729 observations of a total of 25,610 individual snags. Scots pine, Norway spruce, and the two birch species combined all had a relatively similar number of observations (12,945, 14,278 and 15,569, respectively). In all, the records contained observations of 12,857 snag falls, and 29,935 snags remaining standing over the 5-year periods (details on the dataset, Data S3). On the map, the proportion of snags that survived showed a clear pattern from South to North (Figure 1).

The models predicted snag persistence over the 5-year period moderately well, based on posterior predictive checks (using fixed effects only). Correct classification rate for snags remaining standing was higher for the two conifers Scots pine (0.73) and Norway spruce (0.75), and somewhat lower for birch (0.68). Evaluated using the AUC, the values were 0.71 for pine, 0.72 for spruce and 0.68 for birch.

Factors that influenced snag persistence were consistent among tree species (Figure 2). Out of the tree-level variables, DBH had a consistently positive influence on probability of snags remaining standing, and advancing decay stage (from early to intermediate to advanced) a consistently negative influence. The change from intermediate to advanced decay stage had a particularly large influence on the 5-year probability of a snag remaining standing (Figure 2, parameter estimate values in Data S3).

Decreasing site productivity increased the probability of snag remaining standing consistently among different species. Site productivity differences were the greatest for spruce and birch, but discernible also for Scots pine (Figures 2 and 3). Basal area had a consistently negative, but modest influence on probability of snag remaining standing.

In addition to the influence of decay stage, the occurrence of harvesting or natural disturbances on the plot had a profound influence on snag persistence. In particular, the persistence of Norway spruce snags in any decay stage, and Scots pine and birch in the advanced decay stage was very low in plots subjected to clear-cut or

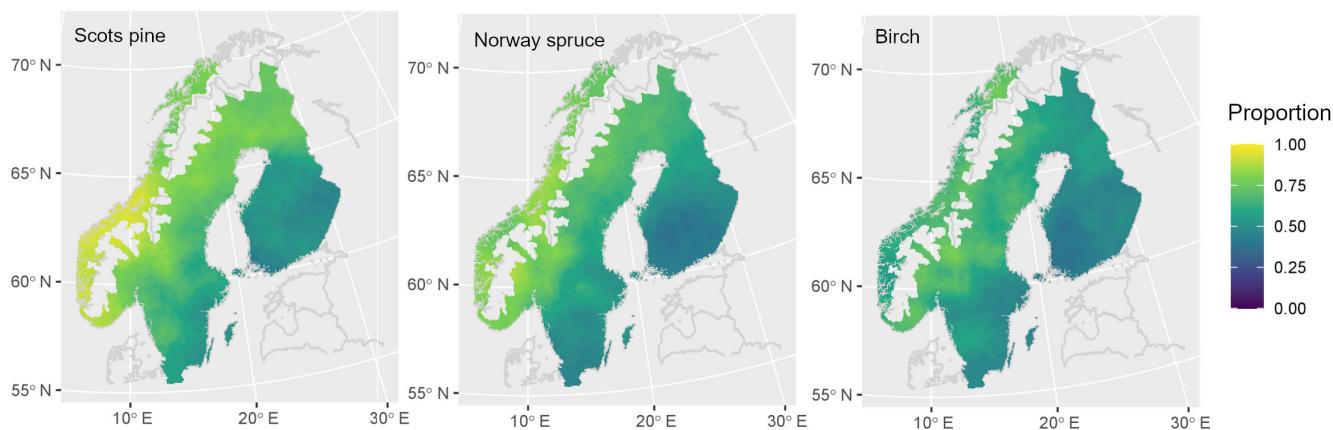


FIGURE 1 Smoothed maps of observed proportion of snags that survived during any of the 5-year intervals, for Scots pine, Norway spruce and the two birch species combined.

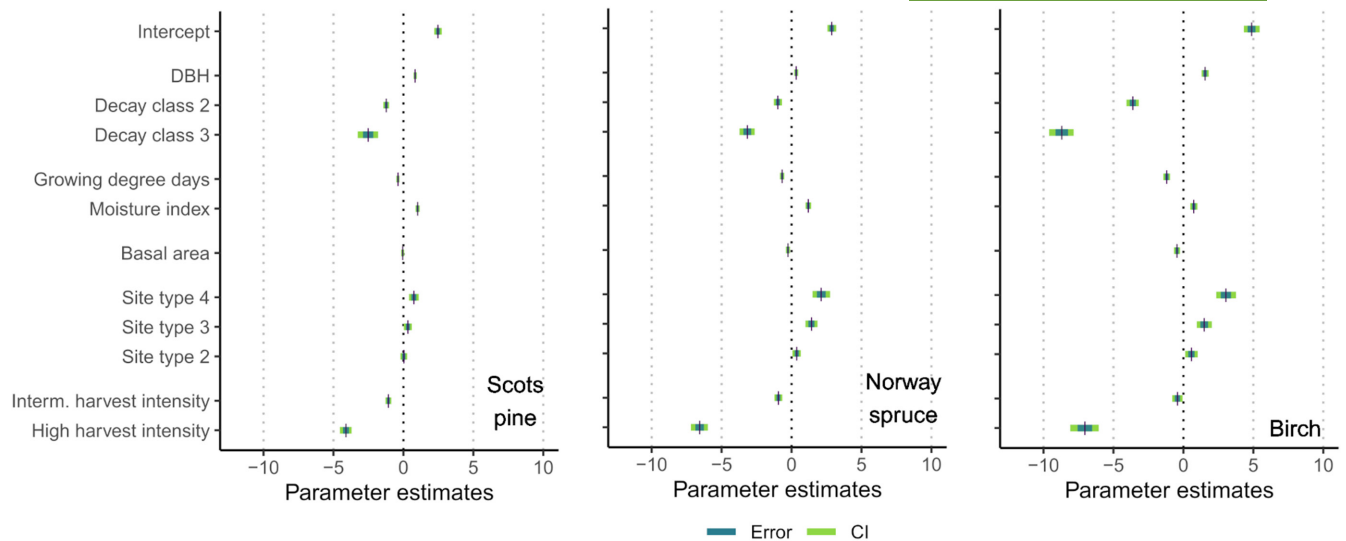


FIGURE 2 The influence of different variables on probability that a snag remains standing over a 5-year period, shown as posterior distributions of parameter estimates (\pm error, 95% credible intervals, CI) for each species. Parameter estimates, errors and credible interval values are in Data S3. DBH, diameter at breast height.

severe natural disturbance (i.e. at least 2/3 of basal area removed; Figures 2 and 3).

Climate imposed a varying, but discernible influence on the probability of snags remaining standing. Overall, the climate-driven North–South gradient visible in the predictions (Figure 4) followed a largely similar variation as the larger geographic trends in the observed snag persistence and fall (Figure 1). The effects of temperature here included as growing degree days were consistently negative, whereas the moisture index had a consistently positive influence on snag persistence. Jointly, these two variables imposed broad geographic gradients, in which the dominant feature is the high snag persistence in the mountains, and low snag persistence in southernmost Sweden (Figure 4).

Residual spatial autocorrelation was either absent or very weak. Moran's I may take values between -1 and 1 , but varied in our analyses over a very narrow, and probably biologically insignificant range of values, from <0.001 for birch, to 0.002 for Scots pine and 0.005 for Norway spruce. Although for Norway spruce, the residual spatial autocorrelation was statistically significant at the 0.05 level ($p=0.012$), this was probably mainly the result of the large sample size.

4 | DISCUSSION

The ability of predicting how long snags remain standing from easily measurable parameters and understanding which factors influence standing times is paramount to incorporating snags into forest management. Here, we developed one of the largest datasets of snag observations to date and models for snag persistence and fall for the main tree species over Fennoscandia.

The models were moderately good at predicting snag persistence over the 5-year periods, with correct classification rate

varying between 0.68 for birch and 0.75 for Norway spruce that was also the most common species in the dataset. The classification accuracy was within the same range, or somewhat better compared to Oberle et al. (2018), who had more data (close to 100,000 records), but also a much greater number of tree species within a broader climatic range.

4.1 | Factors influencing snag fall at the level of the tree individual

Variables applied here have the advantage of being easily measured and hence making the models useful for predictions, based on routinely collected forest inventory data. The disadvantage is that many of them incorporate a number of potential mechanisms, which makes it difficult to link snag fall rates to specific causes. Nevertheless, consistency among tree species (as we fit the models separately), understanding of how trees stay upright, and findings from earlier studies helps in refining our understanding of the potential drivers and their effects and relative importance.

At the tree level, diameter had a consistently positive effect on snag persistence for each of the species. The strength of the effect varied among species so that a unit change in diameter had a stronger influence on the probability of a snag remaining standing for birch compared to the coniferous Scots pine and Norway spruce. Diameter-persistence relationship has been shown mechanistically for live trees (Peltola et al., 1999) and is also identified in a number of observational studies on snag dynamics (Garber et al., 2005; Keen, 1955; Oberle et al., 2018; Russell & Weiskittel, 2012), but not always (Holeksa et al., 2008; Vanderwel et al., 2006). Our results are well in line with Oberle et al. (2018), who showed a clear increase in the 5-year probability of snag persistence with increasing diameter. In our models, the diameter effect was particularly clear in trees in

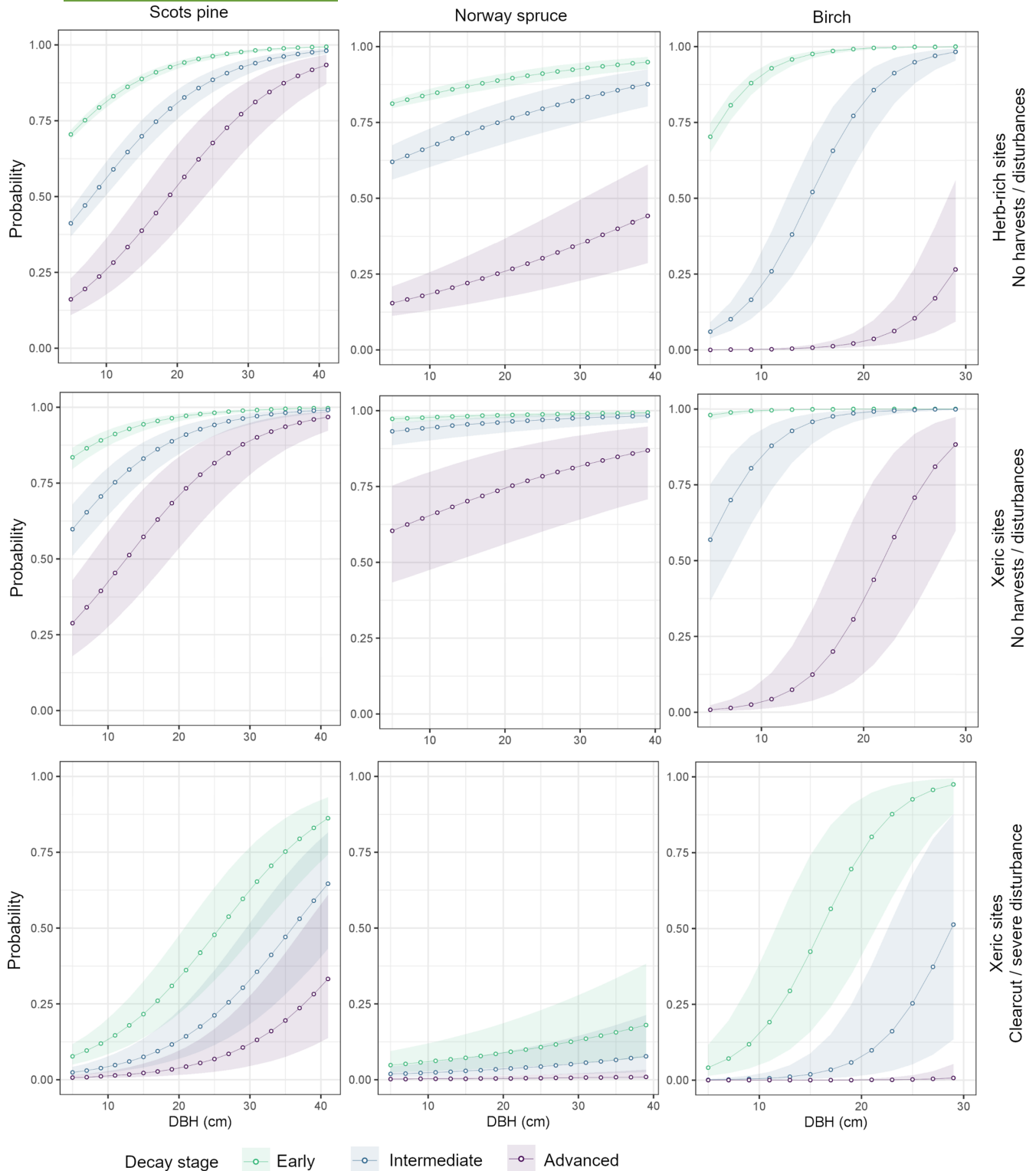


FIGURE 3 Examples of how decay stage, site type and harvesting/natural disturbance influences snag persistence (i.e. probability for a snag to still be standing after a 5-year period) of different-sized snags of each species. Top row shows probability of a snag remaining standing on herb-rich (most productive) sites in the absence of harvesting or natural disturbances, middle row the probability of a snag remaining standing on xeric (poorest) sites in the absence of harvesting or natural disturbances, and the bottom row the probability of a snag remaining standing on xeric sites in clear-cut harvests or severe natural disturbance (over 2/3 basal area decrease in the sample plot). Other parameters are fixed for climatic conditions of southern Finland and basal area of 20 m²/ha. DBH, diameter at breast height.

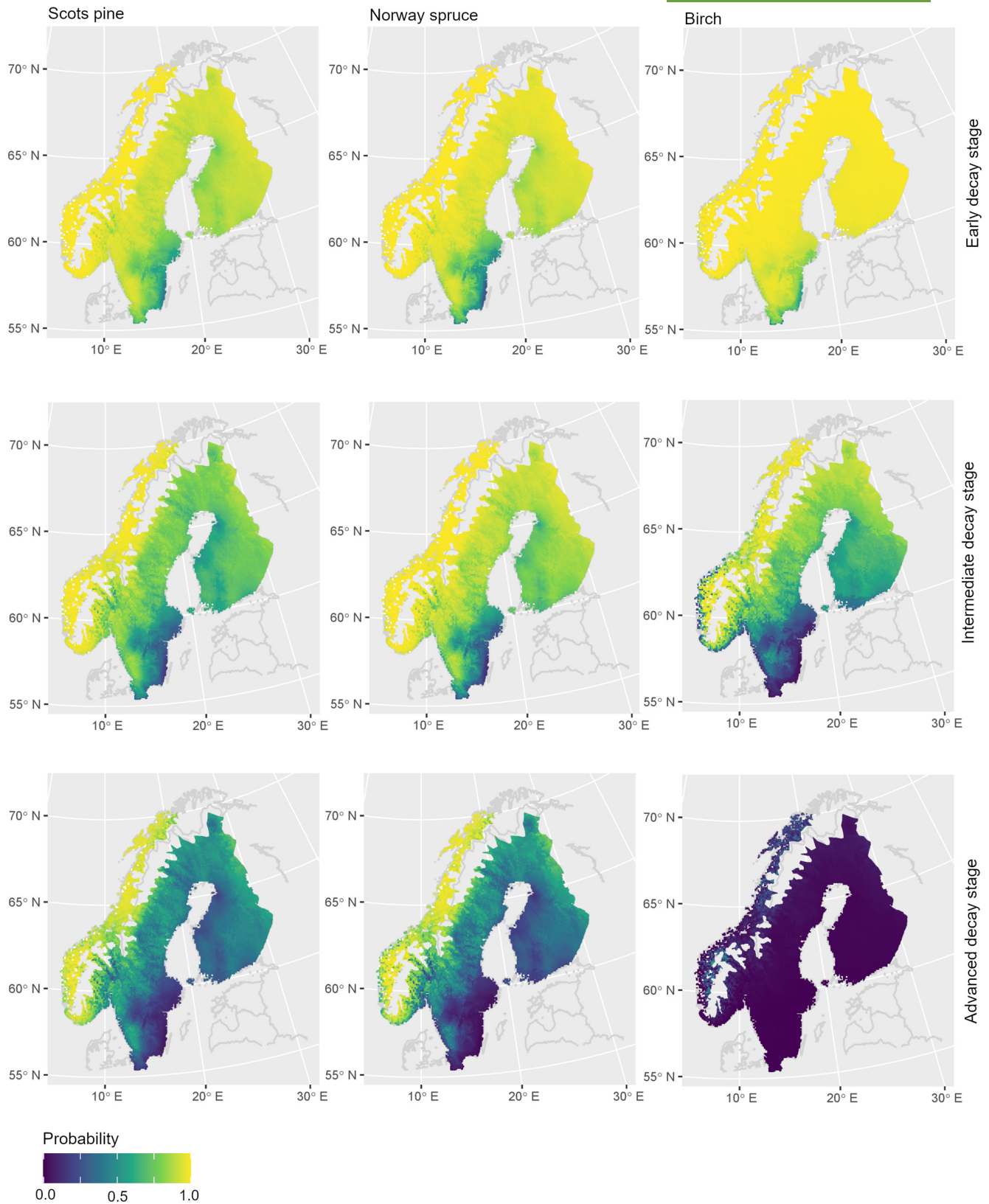


FIGURE 4 The influence of climatic conditions on the probability for a snag to remain standing after a 5-year period based on predictions from models for each species. Snag persistence is shown here for trees with the average DBH for that species in the dataset (Scots pine 15.4 cm, Norway spruce 14.9 cm, birch 11.8 cm; see Data S3 for details on the DBH distributions), on mesic sites with a 20 m²/ha basal area, in early (top row), intermediate (middle row) and advanced (bottom row) decay stage and without harvesting/disturbances. The geographical differences originate from differences in temperature sum and the moisture index in 16 m × 16 m grid cells. DBH, diameter at breast height.

advanced stages of decay (Figure 3). Onodera and Tokuda (2015) also showed that whether the effect is detectable may depend on the species. For instance, the increasing heart-rot or hollowing-out of larger trees may confound this relationship (Onodera & Tokuda, 2015). In general, the influence of tree size originates from the larger diameter stems being stronger (Peltola, 2006), but also from the higher proportion of decay-resistant heartwood in conifers (Taylor et al., 2002).

In our approach (as opposed to many detailed studies on snag dynamics), we did not consider the time the snag has remained standing. Instead, we used decay class as a measure of the snag history and otherwise considered each observation independent of its past. Snag persistence was relatively stable at early- and mid-stages of decay, but greatly reduced when moving to advanced stage of decay. This change was especially prominent for birch (Figure 3), which could be due to the differences in the decomposition pathways between birch and the two conifers. Birch tends to decay from inside-out and retain its bark (Krankina et al., 1999). By the time it is classified into advanced decay stage (assigned by how well a sharp object penetrates the wood), it is only held upright by the bark and falls easily. Overall, the pattern of increasing probability of falling with increasing decay class is mostly consistent with studies from boreal North America and Europe (Aakala, 2010; Vanderwel et al., 2006), and especially with the rapid increase in fall rates in the most advanced decay class reported for black spruce and balsam fir in northeastern Canada (Aakala et al., 2008).

Although our findings are not directly comparable with studies using snag time since death as a predictor (as in most studies on snag dynamics), the general trends seen in many of those studies are in line with what we observed (see also Vanderwel et al., 2006). The development of fall rates as a function of decay class reflected the patterns in studies of dynamics on snag age, where a reverse sigmoid curve has been shown to depict snag fall rate change with age. In our approach the fall rate obviously depends on how quickly the snags move from early to intermediate and to advanced stages of decay, but considering a given species, size and environment, our results are in line with this shape with an initial lag period that has been described in a number of studies (Garber et al., 2005; Keen, 1955; Lee, 1998; Mäkinen et al., 2006; Taylor & MacLean, 2007).

4.2 | Non-climatic site-level predictors

Of the stand-level variables, both live tree basal area and site type (an indicator of productivity) had a consistent effect on snag persistence so that both decreasing live tree basal area and productivity increased snag persistence. Site type influences through differences in soil water holding capacity and capillary rise of water, which on higher productivity sites contribute to keeping the stem base moist enough for decomposer activity (Harmon, 1982; Keen, 1955). Site productivity also increases growth rates and hence influences the wood density (slower-growing conifers are denser; Eriksson et al., 2006), and higher nutrient availability may also increase

decomposition rates of nutrient-poor substrates such as stemwood (Allison et al., 2009). Another potential effect of site productivity could be through its influence on tree allometry: shorter stature (Mäkelä et al., 2016), and deeper root systems (Pretzsch et al., 2012) in poorer productive sites, would both increase snag persistence.

Live tree basal area had a negative effect on snag persistence. Similar to what Oberle et al. (2018) reported on the effects of stand structure on snag persistence, the effect detected here was weak, but nevertheless consistent among the three species analysed. Live tree basal area captures multiple potential effects. Low basal area means more open stands, with lower humidity and higher winds that reduce snag wood moisture content, potentially low enough to influence the decomposer activity (Fahey, 1983; Johnson & Greene, 1991). Sparser stands with low basal areas also reduce the probability of knock-down when neighbouring trees fall, and high stem tapering in sparse stands might be more favourable to withstand bending forces on the stem (Peltola, 2006; Peltola et al., 1999). On the other hand, snags in stands with high basal areas may be more protected from wind, as wind energy dissipates faster in a higher-density stand (Oberle et al., 2018).

Disturbance severity (quantified as change in live tree basal area), had a clear effect on snag persistence so that snags were very likely to fall in the high intensity category. In Fennoscandia, most disturbances are due to harvesting, which may influence snag fall in a number of ways. Snags can be deliberately felled (e.g. for safety concerns), snags can be harvested for bioenergy, or they can be accidentally knocked down when harvesting nearby living trees. In earlier studies, harvest frequency is shown to have a negative impact on snag persistence in forests managed under the selection logging system (Garber et al., 2005; Vanderwel et al., 2006). As continuous-cover forestry with more frequent harvest entries is increasing in Fennoscandian forests, these findings imply that maintaining snags under this system requires explicit attention.

4.3 | Climatic variables

One major advantage of this large dataset was that the same species covered a wide climatic gradient, from the hemiboreal forests to the Arctic. Temperature had a clearly negative effect on snag persistence and this effect can be explained by at least two different mechanisms. First, temperature has a generally positive influence on decomposer activity and wood decomposition rates, so that the integrity of the stem is reduced more quickly in warmer environments. The second effect comes through the influence of temperature on growth rates in the boreal forests, and the related influence on wood strength, as faster-growing trees tend to have a lower wood density (Eriksson et al., 2006). The influence temperature observed here is similar in magnitude to that reported by Oberle et al. (2018), who showed an increase in mean annual temperature of 0 to 20°C reduced probability of remaining standing from ca. 0.8 to ca. 0.1 (figure 3 in Oberle et al., 2018). The reduction is similar, or even slightly stronger compared to the 5-year probability difference

in snag persistence between the southernmost and northernmost regions in our analyses (Figure 4).

The observed positive influence of the moisture index on snag persistence is less straightforward to explain. We would have expected drier climatic conditions to increase the probability of snag remaining standing, as moisture availability influences decomposers. Growing degree days and the moisture index were not correlated within the dataset ($r < 0.01$), but it may be that the moisture index is reflecting other temperature effects and that in general precipitation is not limiting snag decomposition, unlike what is observed from moisture-limited systems (e.g. Palmero-Iniesta et al., 2017). For reducing the strength of the base of the stem, soil hydrology might have an overriding role as a determinant of moisture conditions at the base of the stem. This effect would most likely partially be included in the site type variable as the poorer productive sites are typically dry sites on coarse soils.

4.4 | Implications for forest management, biodiversity and carbon

In the Fennoscandian region, snags are of major biodiversity concern as dearth of dead wood is listed among the main causes of biodiversity decline (Junninen & Komonen, 2011; Löfroth et al., 2023). A wide consensus exists in all three countries on the importance of increasing the amount and variability of dead wood in the managed forest landscapes. Because the functioning of dead wood as a habitat greatly changes when it falls (Runnel et al., 2013), managing snags requires understanding snag fall and factors influencing it.

To reach such aims of increasing the amount of dead wood, leaving snags as retention trees is nowadays recommended in forest management guidelines and forest certification requirements. Despite this, the development of snag volumes has been modest. In Finland, the amount of standing dead wood according to the 12th NFI (2014–2018) in productive forest land was 1.6 m³/ha. At the national level, this value is similar to the mid-1990s, when dead-wood measurements started (Korhonen et al., 2021). The amount of standing dead wood in Sweden is not directly comparable to the Finnish figures as published data are available only for managed forests. In those, the amount of standing dead wood has increased from 1.6 m³/ha in 1996, to 2.9 m³/ha in 2017 (SLU, 2020). The increase can at least partly be attributed to increased conservation efforts (Kyaschenko et al., 2022). In Norway, standing deadwood in productive forest land also increased, from 2.5 m³/ha in 1994–1998 to 4.1 m³/ha in 2017 (Storaunet, 2021).

Most of the standing deadwood in the data used here, and reported in the Finnish NFI is in early stages of decay (Korhonen et al., 2021). The small proportion in more advanced decay stages obviously reflects the high probability of fall in the intermediate and especially advanced decay stages as shown also in our models (Figures 3 and 4). However, it also reflects the deliberate removal of dead wood (e.g. for bioenergy) during harvesting operations or by

selective harvesting by the forest owner, and, importantly, the high probability of snags falling during or after the harvesting operations (Figure 3). This finding points to the need to retain and protect snags during management interventions as a potentially effective measure to increase their persistence in the managed forest landscapes. This applies to long-standing snags that are critical for slow-colonizing dead wood dependent species, such as many red-listed lichen species (Larsson Ekström et al., 2023; Nirhamo et al., 2023), but similarly also to species relying on more ephemeral dead wood substrates, such as deciduous snags in advanced stages of decay [e.g. the endangered *Poecile montanus* (Vatka et al., 2014)]. Moreover, the negative influence of warmer temperatures on snag persistence means that in a warmer climate, habitat availability for species dependent on snags will decrease further, unless compensated for by increased standing-tree mortality.

In addition to protecting existing snags during harvesting operations, the findings here point to two additional considerations if managing for increasing snag persistence. First, complementary to their importance as a habitat (Siitonen, 2001), larger diameter snags are also more persistent. This further adds to their value when deciding which structures to retain in managed forests. Second, decreasing stand basal area increased snag persistence. Although this effect was relatively weak, it points to the potential of increasing snag persistence in the forests with lower stocking densities.

Properly accounting for dead wood and dead wood dynamics can increase the accuracy of forest carbon models (Domke et al., 2011). Snags are not considered to be of major importance in the carbon cycling in the Fennoscandian forests due to their low numbers. Relative to the live tree volumes, the volume of snags is low, in Finland 1.3% (Korhonen et al., 2021), in (managed forests of) Sweden 2.6% (SLU, 2020) and in Norway, 3.3% (Storaunet, 2021). With climate change, increases in disturbances that lead to trees dying standing, such as drought, bark beetles, or fires, may change their importance in the future. After such a disturbance, considerable amount of the forest aboveground C may be in snags with low decomposition rates.

However, warming climate will potentially change the role of snags in the cycling of carbon, regardless of changes in mortality. Due to the consistent increase in snag fall rates with warmer climate identified here, the effect on carbon cycling will be stronger than what could be expected from the temperature effect on decomposer activity alone. This is due to the strong moisture-limitation of decomposer activity (Cornwell et al., 2009): as snag fall brings previously dry wood material in contact with the ground, snag fall increases decomposer activity and further accelerates the release of carbon (and nutrients) stored in the wood material (Hilger et al., 2012; Johnson & Greene, 1991).

5 | CONCLUSIONS

The models presented here increase the possibilities for more informative approaches to reaching targets associated with standing

dead wood. Fitted separately for each of the species analysed, the models consistently indicated that leaving larger snags in low productive edaphic and climatic conditions and in open forests maximizes their persistence. Using this as management recommendation would also slow forest carbon turnover, although for biodiversity reasons large snags in different environments are habitats for different species and not substitutes for one another. The detrimental effect of harvesting on snag persistence identified here suggests that an efficient avenue to increasing and maintaining snags in managed forests is protecting them during silvicultural operations and management planning.

AUTHOR CONTRIBUTIONS

Tuomas Aakala conceived the ideas and designed the methodology; Tuomas Aakala, Kari T. Korhonen, Ken Olaf Storaunet and Bengt Gunnar Jonsson compiled and harmonized the data; Tuomas Aakala analysed the data and led the writing of the manuscripts. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank Bertil Westerlund (SLU Sweden) for providing the Swedish NFI data. The paper benefited from discussions with Shawn Fraver, Christopher W. Woodall and Pekka Punttila. We further thank the Associate Editor and two anonymous reviewers for their constructive comments that greatly improved the paper. The work was supported by the Kone Foundation (grant to TA).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data used in the modelling are available from the Dryad Digital Repository, available at <https://doi.org/10.5061/dryad.37pvmcvt> (Aakala et al., 2024). The climate data is originally from the Envirem data set (Title & Bemmels, 2018), available at: envirem.github.io.

ORCID

Tuomas Aakala  <https://orcid.org/0000-0003-0160-6410>

REFERENCES

- Aakala, T. (2010). Coarse woody debris in late-successional *Picea abies* forests in northern Europe: Variability in quantities and models of decay class dynamics. *Forest Ecology and Management*, 260, 770–779.
- Aakala, T., & Heikkinen, J. (2024). Harmonized decay classification for dead wood in Nordic National Forest Inventories. *Scandinavian Journal of Forest Research*, 39, 1–7.
- Aakala, T., Kuuluvainen, T., Gauthier, S., & De Grandpré, L. (2008). Standing dead trees and their decay-class dynamics in the north-eastern boreal old-growth forests of Quebec. *Forest Ecology and Management*, 255, 410–420.
- Aakala, T., Storaunet, K. O., Jonsson, B. G., & Korhonen, K. T. (2024). Data from: *Drivers of snag fall rates in Fennoscandian boreal forests*. Dryad Digital Repository. <https://doi.org/10.5061/dryad.37pvmcvt>
- Allison, S. D., LeBauer, D. S., Ofrecio, M. R., Reyes, R., Ta, A.-M., & Tran, T. M. (2009). Low levels of nitrogen addition stimulate decomposition by boreal forest fungi. *Soil Biology and Biochemistry*, 41, 293–302.
- Breidenbach, J., Granhus, A., Hysten, G., Eriksen, R., & Astrup, R. (2020). A century of National Forest Inventory in Norway – Informing past, present, and future decisions. *Forest Ecosystems*, 7, 46.
- Cornwell, W. K., Cornelissen, J. H. C., Allison, S. D., Bauhus, J., Eggleton, P., Preston, C. M., Scarff, F., Weedon, J. T., Wirth, C., & Zanne, A. E. (2009). Plant traits and wood fates across the globe: Rotted, burned, or consumed. *Global Change Biology*, 15, 2431–2449.
- Domke, G. M., Woodall, C. W., & Smith, J. E. (2011). Accounting for density reduction and structural loss in standing dead trees: Implications for forest biomass and carbon stock estimates in the United States. *Carbon Balance and Management*, 6, 14.
- Elie, J. G., & Ruel, J.-C. (2005). Windthrow hazard modelling in boreal forests of black spruce and jack pine. *Canadian Journal of Forest Research*, 35, 2655–2663.
- Eriksson, D., Lindberg, H., & Bergsten, U. (2006). Influence of silvicultural regime on wood structure characteristics and mechanical properties of clear wood in *Pinus sylvestris*. *Silva Fennica*, 40, 743–762.
- Fahey, T. J. (1983). Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. *Ecological Monographs*, 53, 51–72.
- Fridman, J., Holm, S., Nilsson, M., Nilsson, P., Ringvall, A. H., & Ståhl, G. (2014). Adapting National Forest Inventories to changing requirements – The case of the Swedish National Forest Inventory at the turn of the 20th century. *Silva Fennica*, 48, 1095.
- Garber, S. M., Brown, J. P., Wilson, D. S., Maguire, D. A., & Heath, L. S. (2005). Snag longevity under alternative silvicultural regimes in mixed-species forests of central Maine. *Canadian Journal of Forest Research*, 35, 787–796.
- Grieser, J., Gommers, R., & Bernardi, M. (2006). New LocClim – The local climate estimator of FAO. *Geophysical Research Abstracts*, 8, 08305.
- Harmon, M. E. (1982). Decomposition of standing dead trees in the southern Appalachian Mountains. *Oecologia*, 52, 214–215.
- Hartig, F. (2022). DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R Package version 0.4.6.
- Hijmans, R. J. (2020). *raster: Geographic data analysis and modeling*. R package version 3.3-7.
- Hilger, A. B., Shaw, C. H., Metsaranta, J. M., & Kurz, W. A. (2012). Estimation of snag carbon transfer rates by ecozone and lead species for forests in Canada. *Ecological Applications*, 22, 2078–2090.
- Holeksa, J., Zielonka, T., & Żywiec, M. (2008). Modeling the decay of coarse woody debris in a subalpine Norway spruce forest of the West Carpathians, Poland. *Canadian Journal of Forest Research*, 38, 415–428.
- Hysten, G., Fernández, C. A., & Granhus, A. (2022). *Skogressurser i Norge: Status og framtidsscenarier*. NIBIO.
- Johnson, E. A., & Greene, D. F. (1991). A method for studying dead bole dynamics in *Pinus contorta* var. *latifolia*–*Picea engelmannii* forests. *Journal of Vegetation Science*, 2, 523–530.
- Junninen, K., & Komonen, A. (2011). Conservation ecology of boreal polypores: A review. *Biological Conservation*, 144, 11–20.
- Kalliola, R. (1966). The reduction of the area of forests in natural condition in Finland in the light of some maps based upon National Forest Inventories. *Annales Botanici Fennici*, 3, 442–448.
- Keen, F. P. (1955). The rate of natural falling of beetle-killed ponderosa pine snags. *Journal of Forestry*, 53, 720–723.
- Korhonen, K. T., Ihalainen, A., Kuusela, S., Punttila, P., Salminen, O., & Syrjänen, K. (2020). Metsien monimuotoisuudelle merkittävien rakennepiirteiden muutokset Suomessa vuosina 1980–2015. *Metsätieteen aikakauskirja*, 2020, 10198.
- Korhonen, K. T., Ahola, A., Heikkinen, J., Henttonen, H. M., Hotanen, J.-P., Ihalainen, A., Melin, M., Pitkänen, J., Rätty, M., Sirviö, M., &

- Strandström, M. (2021). Forests of Finland 2014–2018 and their development 1921–2018. *Silva Fennica*, 55, 10662.
- Krankina, O. N., Harmon, M. E., & Griazkin, A. V. (1999). Nutrient stores and dynamics of woody detritus in a boreal forest: Modeling potential implications at the stand level. *Canadian Journal of Forest Research*, 29, 20–32.
- Kyaschenko, J., Strengbom, J., Felton, A., Aakala, T., Staland, H., & Ranius, T. (2022). Increase in dead wood, large living trees and tree diversity, yet decrease in understory vegetation cover: The effect of three decades of biodiversity-oriented forest policy in Swedish forests. *Journal of Environmental Management*, 313, 114993.
- Larson, P. R. (1965). Stem form of young *Larix* as influenced by wind and pruning. *Forest Science*, 11, 412–424.
- Larsson Ekström, A., Sjögren, J., Djupström, L. B., Thor, G., & Löfroth, T. (2023). Reinventory of permanent plots show that kelo lichens face an extinction debt. *Biological Conservation*, 288, 110363.
- Lee, P. (1998). Dynamics of snags in aspen-dominated midboreal forests. *Forest Ecology and Management*, 105, 263–272.
- Linder, P., & Östlund, L. (1998). Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. *Biological Conservation*, 85, 9–19.
- Löfroth, T., Birkemoe, T., Shorohova, E., Dynesius, M., Fenton, N. J., Drapeau, P., & Tremblay, J. A. (2023). Deadwood biodiversity. In M. M. Girona, H. Morin, S. Gauthier, & Y. Bergeron (Eds.), *Boreal forests in the face of climate change: Sustainable management* (pp. 167–189). Springer International Publishing.
- Mäkelä, A., Pulkkinen, M., & Mäkinen, H. (2016). Bridging empirical and carbon-balance based forest site productivity – Significance of below-ground allocation. *Forest Ecology and Management*, 372, 64–77.
- Mäkinen, H., Hynynen, J., Siitonen, J., & Sievänen, R. (2006). Predicting the decomposition of Scots pine, Norway spruce, and birch stems in Finland. *Ecological Applications*, 16, 1865–1879.
- Nilsson, P., Roberge, C., & Fridman, J. (2020). *Forest statistics 2020*. Swedish University of Agricultural Sciences.
- Nirhamo, A., Pykälä, J., Jääskeläinen, K., & Kouki, J. (2023). Habitat associations of red-listed epiphytic lichens in Finland. *Silva Fennica*, 57, 22019.
- Oberle, B., Ogle, K., Zanne, A. E., & Woodall, C. W. (2018). When a tree falls: Controls on wood decay predict standing dead tree fall and new risks in changing forests. *PLoS One*, 13, e0196712.
- Oettel, J., Zolles, A., Gschwantner, T., Lapin, K., Kindermann, G., Schweinzer, K.-M., Gossner, M. M., & Essl, F. (2023). Dynamics of standing deadwood in Austrian forests under varying forest management and climatic conditions. *Journal of Applied Ecology*, 60, 696–713.
- Onodera, K., & Tokuda, S. (2015). Do larger snags stand longer? Snag longevity in mixed conifer-hardwood forests in Hokkaido, Japan. *Annals of Forest Science*, 72, 621–629.
- Palmero-Iniesta, M., Domènech, R., Molina-Terrén, D., & Espelta, J. M. (2017). Fire behavior in *Pinus halepensis* thickets: Effects of thinning and woody debris decomposition in two rainfall scenarios. *Forest Ecology and Management*, 404, 230–240.
- Pebesma, E. (2018). Simple features for R: Standardized support for spatial vector data. *The R Journal*, 10, 439.
- Pebesma, E. J. (2004). Multivariable geostatistics in S: The gstat package. *Computers & Geosciences*, 30, 683–691.
- Peltola, H., Kellomäki, S., Väisänen, H., & Ikonen, V.-P. (1999). A mechanistic model for assessing the risk of wind and snow damage to single trees and stands of Scots pine, Norway spruce, and birch. *Canadian Journal of Forest Research*, 29, 647–661.
- Peltola, H. M. (2006). Mechanical stability of trees under static loads. *American Journal of Botany*, 93, 1501–1511.
- Pelz, K. A., & Smith, F. W. (2013). How will aspen respond to mountain pine beetle? A review of literature and discussion of knowledge gaps. *Forest Ecology and Management*, 299, 60–69.
- Pretzsch, H., Uhl, E., Biber, P., Schütze, G., & Coates, K. D. (2012). Change of allometry between coarse root and shoot of lodgepole pine (*Pinus contorta* DOUGL. ex. LOUD) along a stress gradient in the sub-boreal forest zone of British Columbia. *Scandinavian Journal of Forest Research*, 27, 532–544.
- Richardson, T. S., Robins, J. M., & Wang, L. (2017). On modeling and estimation for the relative risk and risk difference. *Journal of the American Statistical Association*, 112, 1121–1130.
- Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.-C., & Müller, M. (2011). pROC: An open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics*, 12, 77.
- Runnel, K., Rosenvald, R., & Löhmus, A. (2013). The dying legacy of green tree retention: Different habitat values for polypores and wood-inhabiting lichens. *Biological Conservation*, 159, 187–196.
- Russell, M. B., & Weiskittel, A. R. (2012). Assessing and modeling snag survival and decay dynamics for the primary species in the Acadian forest of Maine, USA. *Forest Ecology and Management*, 284, 230–240.
- Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins*, 49, 11–41.
- SLU. (2020). *Forest statistics Sweden 2020*. Swedish University of Agricultural Sciences.
- Statistics Sweden. (2021). *Protected nature 2021*. Sweden.
- Stokland, J. N. (2003). *Forest biodiversity indicators in the Nordic countries: Status based on National Forest Inventories*. Nordic Council of Ministers.
- Stokland, J. N., Siitonen, J., & Jonsson, B. G. (2012). *Biodiversity in dead wood*. Cambridge University Press.
- Storaunet, K. O. (2021). *Død ved. Page Bærekraftig skogbruk i Norge*. Norsk Institutt for Bioøkonomi.
- Storaunet, K. O., & Rolstad, J. (2002). Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest. *Canadian Journal of Forest Research*, 32, 1801–1812.
- Storaunet, K. O., & Rolstad, J. (2015). *Mengde og utvikling av død ved i produktiv skog i Norge. Med basis i data fra Landsskogtakseringens 7. (1994–1998) og 10. takst (2010–2013)*. Oppdragsrapport fra Skog og landskap.
- Suojelualueet. (2022). *Suojelualueet, talousmetsien monimuotoisuuden suojeluhoiteet ja luontoarvojen suojelua tukevat alueet, koko maa*. Luonnonvarakeskus.
- Suvanto, S., Henttonen, H. M., Nöjd, P., & Mäkinen, H. (2016). Forest susceptibility to storm damage is affected by similar factors regardless of storm type: Comparison of thunder storms and autumn extratropical cyclones in Finland. *Forest Ecology and Management*, 381, 17–28.
- Taylor, A. M., Gartner, B. L., & Morrell, J. J. (2002). Heartwood formation and natural durability – A review. *Wood and Fiber Science*, 34, 587–611.
- Taylor, S. L., & MacLean, D. A. (2007). Dead wood dynamics in declining balsam fir and spruce stands in New Brunswick, Canada. *Canadian Journal of Forest Research*, 37, 750–762.
- Tennekes, M. (2018). tmap: Thematic maps in R. *Journal of Statistical Software*, 84, 1–39.
- Thomas, J. W. (2002). Dead wood: From forester's bane to environmental boon. *Proceedings of the symposium on the ecology and management of dead wood in western forests*. USDA Forest Service General Technical Report PSW-GTR 181, pp. 3–9.
- Tikkanen, M. (2005). Climate. In M. Seppälä (Ed.), *The physical geography of Fennoscandia* (pp. 97–112). Oxford University Press.
- Title, P. O., & Bemmels, J. B. (2018). ENVIREM: An expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. *Ecography*, 41, 291–307.

- Vanderwel, M. C., Malcolm, J. R., & Smith, S. M. (2006). An integrated model for snag and downed woody debris decay class transitions. *Forest Ecology and Management*, 234, 48–59.
- Vatka, E., Kangas, K., Orell, M., Lampila, S., Nikula, A., & Nivala, V. (2014). Nest site selection of a primary hole-nesting passerine reveals means to developing sustainable forestry. *Journal of Avian Biology*, 45, 187–196.
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.
- Willmott, C. J., & Feddema, J. J. (1992). A more rational climatic moisture index. *The Professional Geographer*, 44, 84–88.
- Woodall, C. W., Domke, G. M., Macfarlane, D. W., & Oswald, C. M. (2012). Comparing field- and model-based standing dead tree carbon stock estimates across forests of the US. *Forestry: An International Journal of Forest Research*, 85, 125–133.
- Woodall, C. W., Walters, B. F., & Westfall, J. A. (2012). Tracking downed dead wood in forests over time: Development of a piece matching algorithm for line intercept sampling. *Forest Ecology and Management*, 277, 196–204.

SUPPORTING INFORMATION

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

Data S1. Piece-matching dead wood in the Finnish NFI.

Data S2. Harmonized site types.

Data S3. Predictor variable distributions, parameter estimates and residual spatial autocorrelation.

How to cite this article: Aakala, T., Storaunet, K. O., Jonsson, B. G., & Korhonen, K. T. (2024). Drivers of snag fall rates in Fennoscandian boreal forests. *Journal of Applied Ecology*, 61, 2392–2404. <https://doi.org/10.1111/1365-2664.14729>