ARTICLE

Vegetation Ecology



Check for updates

Tree damage risk across gradients in tree species richness and stand age: Implications for adaptive forest management

Micael Jonsson¹ | Jan Bengtsson² | Jon Moen¹ |

Revised: 14 August 2024

Tord Snäll³

¹Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden

²Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

³SLU Swedish Species Information Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden

Correspondence Micael Jonsson Email: micael.jonsson@umu.se

Handling Editor: Emanuele Ziaco

Abstract

Forest disturbances are expected to increase in severity with climate change and intensified land use, threatening future delivery of several ecosystem services, including the climate-mitigating potential of forests. Alleviating these consequences through adaptive forest management demands a greater understanding of what drives the impacts of disturbances on forests, which, in turn, requires collection of high-quality data through large-scale and long-term monitoring programs. The Swedish National Forest Inventory has been recording "damages" on living trees across a forest area of 230,000 km², in addition to a wide range of stand characteristics and environmental conditions. Using 15 years of these data, we investigated the frequency of different types of tree damages and the causes of these damages and modeled damage risk among tree species and across gradients in stand attributes and environmental conditions. We found that 94% of all surveyed trees had some type of damage, but for 65% of these, the underlying cause was not identified. Nevertheless, for all damage types and causes, we found that damage risk varied considerably among tree species and across gradients in tree species richness, tree height, and stand age. For a few damages, stand age or tree species richness interacted with climate to influence risks. Among identified causes of damage, "wind and snow" was most common (11.9% of surveyed trees), followed by "forestry" (6.9%). Further, for most causes of damage where stand age was significant, the risk was highest in young or the youngest stands. As such, our results indicate that there is great potential for reducing the risk of tree damages via adaptive management, such as altered tree species composition and increased rotation length. However, for a greater understanding of what is driving the frequency and magnitude of forest damages, and to be able to provide specific, useful information to stakeholders, collection of higher-quality data must be prioritized by monitoring programs.

KEYWORDS

boreal forest, disturbance, forestry, herbivory, snow damage, survey, temperate forest, wind damage

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Author(s). Ecosphere published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

.....

INTRODUCTION

Trees in forests are subject to a wide variety of disturbances that cause "damages" by various biotic and abiotic factors, including humans (e.g., forestry-related damages). In most cases, these damages are natural features in the life cycles of trees, representing interactions among trees, other organisms, and the environment, driving forest ecosystem dynamics and nutrient recycling, resulting in the formation of critical resources (e.g., dead wood) and habitat heterogeneity that support ecological processes and biodiversity (Lindenmayer & Noss, 2006; Patacca et al., 2023; Turner, 2010). Sometimes, damages occur outside their "natural" range in space, frequency, or magnitude. These instances are often attributed to climate change or intensified land use and are expected to become more common in the future (Patacca et al., 2023; Seidl et al., 2011). Subsequent increased tree mortality may threaten the delivery of forest ecosystem services, not least the production and quality of wood products, as well as the climate-change mitigation potential of forests (Liu et al., 2023; Patacca et al., 2023; Seidl et al., 2011; Thom & Seidl, 2016). To improve our ability to predict how damages respond to changed environmental conditions, forest attributes, and dynamics of mammal or insect populations, it is important to monitor forest damages on a large temporal and spatial scale (Gauthier et al., 2015; Patacca et al., 2023; Seidl et al., 2011; Thom & Seidl, 2016).

In boreal and temperate forests, damages from wind, snow, fire, mammals, insects, and fungi are common. These damages are largely determined by environmental conditions and forest attributes and their interactions (Gauthier et al., 2015; Seidl et al., 2011, 2017) and can fundamentally affect human use of forest resources and associated economies. For example, during the last 70 years, more than 130 storms have caused substantial damage to boreal and temperate forests across Europe, resulting in substantial financial losses (Gardiner et al., 2010). Due to climate change and an increasing growing tree stock, devastating storms are projected to increase in frequency and severity, causing even more extensive forest damages and greater financial losses (Gauthier et al., 2015). More recently, extensive bark beetle outbreaks have damaged and killed coniferous trees in central Europe and southern Scandinavia (Hlásny et al., 2021), and, across Europe, extensive wildfires have ravaged forests after summer heat waves and subsequent droughts (Tedim et al., 2015). In northern Scandinavia, storm damages and wildfires have been less prevalent, partly due to successful fire elimination programs. However, browsing from large mammals (mainly moose [Alces alces]; Ezebilo et al., 2012) and fungal outbreaks (e.g., Gremmeniella abietina; Sonesson et al., 2007)

on commercial tree species (primarily Scots pine [*Pinus sylvestris*] and the introduced lodgepole pine [*Pinus contorta*]) are considered major threats to forest economics.

To counteract increased forest damages, various management actions have been proposed, and some of them involve managing the forest to contain certain tree species and stand attributes (Gauthier et al., 2015; Hahn et al., 2021; Swedish Forest Agency, 2022; Triviño et al., 2023). For example, increasing the proportion of broadleaf tree species in otherwise coniferous-dominated forest landscapes has been proposed to lower the frequency of stand-replacing wildfires (Astrup et al., 2018) and may reduce forest damage from strong winds (Valinger & Fridman, 2011). Similarly, thinning has been proposed to improve the resistance and resilience of trees to biotic and abiotic stressors, although the evidence for this is still equivocal (Moreau et al., 2022). Further, high tree diversity has been shown to reduce insect herbivory on trees (Jactel & Brockerhoff, 2007; Stemmelen et al., 2022) and may reduce bark beetle infestation on conifer species (Berthelot et al., 2021), calling for inclusion of a wider variety of tree species in managed forests. A higher tree diversity may also decrease the risk of drastically reduced economic returns after disturbances (e.g., Knoke, 2017). Nevertheless, to find practical solutions that successfully mitigate impacts of forest damages, we must better understand what drives damage frequency and magnitude, and especially how these drivers might be affected by climate and forest management methods (Gauthier et al., 2015; Patacca et al., 2023).

In Fennoscandia, forests are mainly managed through large-scale clear-cutting and planting of Norway spruce (Picea abies) or Scots pine seedlings. Further, precommercial thinning is performed 1-3 times before final felling to remove unwanted trees and improve growth and quality of remaining ones. These management actions result in even-aged stands that rarely become over 100 years old, are dominated by one tree species, and generally lack characteristics of more natural, old-growth forests (Esseen et al., 1997). They also result in forests that likely are more susceptible to disturbances (Seidl et al., 2011; Stritih et al., 2021; Vacek et al., 2021; Wolf et al., 2023). Final felling in clear-cut forestry and subsequent soil scarification have been claimed to mimic natural regeneration after wildfire (Mielikäinen & Hynynen, 2003), which is the most important natural disturbance in boreal forests, and to benefit disturbance-dependent species (Paillet et al., 2010), but support for this argument is lacking (Kuuluvainen, 2009).

In Sweden, damages from large, browsing mammals (i.e., cervids) alone are estimated to cost Swedish forestry in excess of US \$740 million (\notin 700 million) annually, and added costs due to damages from wind, snow, fungi, and insects would significantly increase this number

(Swedish Forest Agency, 2021, 2022). Hence, an improved understanding of what drives forest damages would be invaluable to enable management strategies that mitigate adverse effects of global change, for securing future provisioning of several forest ecosystem services, including wood production (Gauthier et al., 2015; Triviño et al., 2023). The overall aims of this study were therefore to investigate how different stand characteristics affect the frequency of different damage types and what the potential is of a high-quality national forest monitoring program to shed light on such questions. In Fennoscandia, clear-cut forestry reduces tree species richness, by locally favoring mainly one commercial tree species and typically restricting stand age to less than 100 years (Esseen et al., 1997). As tree species richness and composition and stand age are important determinants of several forest ecosystem services (Baeten et al., 2019; Gamfeldt et al., 2013; Jonsson et al., 2020; Jönsson & Snäll, 2020), these stand attributes might be important also for disturbance resistance (here, risk of tree damage). Hence, we primarily ask three questions:

- 1. Which types of tree damages are most common in boreal and temperate forests dominated by intensive forestry?
- 2. Does tree vulnerability to different types of damages in boreal and temperate forests vary across stand attributes and environmental conditions?
- 3. Are present monitoring programs sufficient to understand the causes underlying forest damages, or are additional damage inventories or methodological improvements needed to obtain useful information to stakeholders?

We use data from the Swedish National Forest Inventory (NFI; Axelsson et al., 2010) that since 2003 performs a detailed large-scale inventory of tree damages and therefore potentially collects a wealth of information that may increase our understanding of how, why, and where forest damages occur. Our main hypotheses are that tree damage risk will decrease with increasing tree species richness, stand age, and tree age.

METHODS

We used data from the Swedish NFI, which uses a regular sampling grid, with a randomly selected starting point, across the entire 400,000 km² of Swedish land (Axelsson et al., 2010) of which 230,000 km² is covered by productive boreal or temperate forests. It includes approximately 4500 permanent tracts (Appendix S1: Figure S1) with each tract

being surveyed once every 5 years. The quadratic tracts have different sizes in different parts of the country and consist of eight (in the north) to four (in the south) circular sample plots (radius 10 m). From the NFI database, we extracted data from three complete survey cycles, conducted 2003-2007, 2008-2012, and 2013-2017. We used only plots on "productive forest" (mean production of standvolume, stem volume over ing bark >1 m³ ha⁻¹ year⁻¹), excluding plots (n = 853) that had been harvested, cleared, or thinned in the 5-year period before each survey, as this reduces the frequency of live trees and, thus, potentially the number of trees that are surveyed for damages (see below). Further, to be included in our analyses, the plots had to be located on only forest land, for example, not partly including river, road, grassland, or other land types. We also excluded plots where trees were older than 300 years, as these plots were too rare (n = 9) for reliable estimation of relationships to the covariate forest age (see below).

In the NFI, "damages" are recorded only for living so-called "sample trees" (1-6 trees, mean = 3) on each plot. This includes determining the type and the cause of a damage; all damages are classified to type, with the possibility to record several types for each tree. The types of damages are "mechanical," "crack," "resin," "necrosis," "stem break," "dry treetop," "bent stem," "root damage," "root stem damage" (i.e., root damage leading to leaning stem), "leaf and needle loss," and "foliage discoloration." Causes of damages are "natural," such as from large mammal herbivores, insects, snow, wind, fire, and fungi, as well as "human," the last essentially always from forest management activities. Finally, "unidentified" cause is specified. Moreover, damage from "wind and snow" is lumped together, due to difficulties in teasing these apart. In this study, we analyzed only types and causes of damage that were common enough to produce viable statistical models, that is, damages that occurred on $\geq 1.5\%$ of the surveyed trees.

As explanatory covariates available in the NFI database, we used stand characteristics that are calculated based on all tree individuals with a diameter \geq 40 mm at breast height (i.e., 1.3 m): mean stand height (in meters), stand volume (in cubic meters per hectare), stand age (in years), tree species richness, and stand growth (in cubic meters per hectare for every 5 years). We also used temperature sum (in degrees Celsius) and humidity (in millimeters). We also used data on the sample trees: that is, tree species and tree height (in meters). All these selection criteria resulted in two datasets, each with a total of 59,933 (damage types) and 57,840 (damage causes) observations, each representing a tree. For more detailed description of methods, see Appendix S1.

Statistical analyses

We modeled the probability of damage on the living sample trees, that is, the response was Bernoulli (0/1), being of a specific type or due to a specific cause, using a complementary log-log ("cloglog") link function, as occurrences of certain damages often were very low, and we wanted to allow for asymmetrical damage response to the covariates. Probability of being damaged is henceforth termed "risk." We used a generalized linear mixed-effect model ("glmr"), with plot, tract, and year as random variables (i.e., a nested design), to account for the fact that there can be several sample trees within plots, there are several plots within tracts, and plots were surveyed three times over 15 years. As covariates, we used the continuous variables described above (all log-transformed) and tree species as a factor, specifically testing whether the risk was different for the 10 different species compared to the risk for Norway spruce, which was coded to be the intercept term.

For model selection, we used forward stepwise selection, with a predetermined order of adding the predictor variables. This order was based on knowledge from previous ecological studies in this region (e.g., Esseen et al., 1997; Gamfeldt et al., 2013; Valinger & Fridman, 2011; Wallgren et al., 2013) and differed slightly among damage types and causes, but we always added tree species first, as this arguably is the most important predictor of damage risk (Felton et al., 2020). We also used natural tree mortality (total volume of all species that had died during the preceding survey period, in cubic meters, obtained from a separate dataset in the Swedish NFI) as a covariate. This variable can be considered a response to tree damage. However, because of the way in which the damage survey is performed-that is, on living trees only—mortality during the survey period may influence damage frequency, as it potentially reduces the number of living sample trees. We wanted to remove this potentially confounding factor, which we did by excluding plots that had been harvested within 5 years before each survey (as explained above). In the forward stepwise selection, we started by testing predictors one by one and kept those with a p value <0.1. Next, we added predictors one by one and kept those with p values <0.2. In the selection process, we always also included the predictor squared, with the linear term always kept if the squared term showed a *p* value of below 0.1. The two-way interaction terms with the two climate variables, tree species richness, and stand age were also added and was kept if the *p* value was <0.1. Within the factor tree species, all levels were kept as long as at least one level showed a p value <0.05. This model selection was made for each of the damage types "mechanical," "stem break," "necrosis," "stem root," "root," "resin," "dry treetop," "leaf and needle loss," and "crack," and each of the damage causes "wind and snow," "forestry,"

"large mammal herbivores," "moose," "fungi," "rust fungi," and "unidentified." Further, as a contrast to "unidentified" causes (likely a combination of several agents), we selected a model where all identified causes were combined, with the aim to disentangle what "unidentified" in fact could be.

All analyses were performed with R (R Core Team, 2023), using the package "lme4" (Bates et al., 2015) and nAGQ set to zero. nAGQ (Adaptive Gauss-Hermite Quadrature) is the number of points (n) per axis for evaluating the adaptive Gauss-Hermite approximation of the log-likelihood. Setting nAGQ to zero is considered less accurate than setting nAGQ > 0 but is sometimes necessary to avoid extremely long runtimes for complex models (https://stats.stackexchange.com/questions/544937/ when-is-it-appropriate-to-set-nagq-0-in-glmer). Before fitting our models, subsets of data were used to compare the outcome of using nAGQ = 0 and nAGQ = 1. The differences were negligible, so nAGQ = 0 was judged to be sufficient for fitting models on the full dataset. For each significant covariate (x) in each final model, we plotted the partial relationship $y \sim x + x^2$, with other significant covariates kept at their mean values. The 95% confidence bands of the relationships were calculated using the package "effects" (Fox et al., 2022). Finally, we plotted spatial distribution of yearly climate (i.e., temperature sum), stand age, and plot-scale tree species richness across Sweden to visualize gradients in these important predictor variables. Similarly, for the three most common causes of damage, we plotted the spatial distribution of predicted damage risks (from model output) across Sweden.

RESULTS

Damages were recorded for 94% of the sample trees (i.e., 5.9% were undamaged). Natural mortality occurred for 5.4% of the surveyed trees. There was a gradient in climate, from the warmest southeast to the coldest northwest of Sweden (Appendix S1: Figure S2). Further, older stands (>120 years) were most common in the northwest, whereas younger stands (<91 years) dominated in the southern half of Sweden (Appendix S1: Figure S2). Plot-scale tree species richness varied mostly on a smaller spatial scale and therefore showed no strong spatial gradients across Sweden (Appendix S1: Figure S2).

Frequency of damage types and causes

The most common damage type was "mechanical" (found on 17.8% of all surveyed trees), followed by "stem

break" (17.2%), and among identified causes of damage, "wind and snow" was most common (11.9%), followed by "forestry" (6.9%), but the by far most frequently occurring cause was "unidentified" (64.5%). For the frequency of all damage types and causes, including the ones that were too rare (<1.5%) to be statistically analyzed, see Appendix S1: Table S1. There were also a few categories and subcategories of damage causes that were too rare to be included in the statistical analyses. These were "rotting fungi," "other fungi," "Gremmeniella," "other vertebrate," "other large mammal," "insect," "fire," and "bark beetles," followed by a tail of even rarer (<0.1%) categories. However, in this study, all large mammal subcategories (except beaver; see supporting methods in Appendix S1) were included in analyses of "large mammal herbivores," and all fungal subcategories were included in analyses of "fungi," independent on level of rarity.

Damage risk with increasing tree species richness

With increasing tree species richness, the risk of stem break increased from 8% to 11% (Figure 1a), whereas the risk for root damage decreased, but at overall very low levels (<1%; Figure 1b). There was an increased risk of root stem damage from 1 to about 4 tree species, but only in the warmest climates (Figure 1c). The risk of damage from wind and snow increased from 4% to 6% from 1 to about 4 tree species (Figure 2a), whereas the risk of forestry damage decreased with increasing tree species richness (Figure 2b). In the warmest climate, the risk of damage from identified causes decreased from ~25% to ~12% with increasing tree richness, whereas the risk remained unchanged at 10%–15% with increasing richness in colder climates (Figure 2c).

Damage risk with increasing stand age

The damage *types* "mechanical," "necrosis" (in spruce), "root stem damage," "resin" (in spruce), "dry treetop," and "crack" showed an increasing risk with increasing stand age (Figure 3), whereas other types did not vary with stand age. However, the risk of mechanical damage (Figure 3a) and cracks (Figure 3f) was similarly high for the youngest and the oldest stands.

For most *causes* of damage where stand age was significant, the risk was highest in the youngest or young stands (Figure 4), except for wind and snow damage, where the risk increased linearly from very low levels to 20% in the oldest stands (Figure 4a). The damage risk from unidentified causes approached 80% in young



FIGURE1 Probability of damage types (a) stem break, (b) root damage, and (c) root stem damage against tree species richness and for different temperature sums (*T* sum). Error bands show 95% CIs.





FIGURE 2 Probability of damage causes (a) wind and snow and (b) forestry, and (c) combined identified, against tree species richness and for different temperature sums (*T* sum). Error bands show 95% CIs.

stands (Figure 4b) and decreased to ~35% in the oldest stands. Counterintuitively, damage risk of unidentified causes approached 80% also with increasing tree height (Appendix S1: Figure S5f), but, statistically, this is for stands of mean age. The highest risk (~35%) for damage from identified causes was found in both the youngest and oldest stands and the lowest risk (~15%) in young stands (Figure 4e).

The risk of forestry damage was highest (2%-5%) in the youngest stands, except in the coldest climate where there was a very low, age-independent risk (Figure 4c). The risk of herbivore damage was highest (~1% risk) in young stands and decreased slightly with increasing stand age (Figure 4d). This was true also for moose damage, but only in the warmest climate, whereas there was no increased risk with increasing stand age in colder climates (Figure 4f). Sample tree height, which largely reflect tree age, was an important predictor of damage risk, with increasing risk of damage with increasing tree height for most damage types, except for dry treetop, which decreased with tree height (Appendix S1: Figure S5). For damage causes, the risk increased with tree height for fungi, forestry, and unidentified cause, whereas it decreased with tree height for wind and snow, herbivore (in particular moose), and combined identified causes (Appendix S1: Figure S6).

Importance of other forest stand and environmental factors for damage risk

As expected, tree species was important, as damage risks always differed among some of the 11 tree species (Appendix S1: Tables S2-S18, Figures S3 and S4), with birch and lodgepole pine being the most sensitive to wind and snow damage, some of the broadleaf tree species having the highest risk of being damaged by large mammal herbivores (particularly moose), and European aspen, Salix sp., and Scots pine suffering the most from fungi (Appendix S1: Tables S2-S18, Figures S3 and S4). Considering commercial species, the (by Swedish forestry) less preferred birch species exhibited much lower risks of being damaged by unidentified causes than the preferred Scots pine and Norway spruce, and the potentially commercial European aspen showed the lowest risk. Moreover, the introduced lodgepole pine showed among the highest risks (~80%) of being damaged by unidentified causes (Appendix S1: Figure S4).

Climate (i.e., temperature sum) was often an important predictor of damage risk (Appendix S1: Tables S2–S18). Besides climate interacting with tree species richness (Figures 1c and 2c) or stand age (Figure 4c,f) to influence damage risk, climate was also positively (linear or



FIGURE 3 Probability of damage types (a) mechanical damage, (b) necrosis (in Norway spruce only), (c) root stem damage, (d) resin (in Norway spruce only), (e) dry top, and (f) crack across against stand age (years). Error bands show 95% CIs.

nonlinear) related to damage risk for mechanical damage (Appendix S1: Table S2), necrosis in spruce (Appendix S1: Table S3), root damage (Appendix S1: Table S9), wind and snow damage (Appendix S1: Table S9), wind and snow damage (Appendix S1: Table S11), herbivore damage (Appendix S1: Table S13), and unidentified causes of damage (Appendix S1: Table S13), and unidentified causes of rust fungal damage, there was an interaction between climate and stand age (Appendix S1: Table S16). Mean stand height, stand volume, and stand growth were sometimes significant predictors for the risk of different damage types (Appendix S1: Tables S2–S10) and causes

(Appendix S1: Tables S11–S18), and for rust fungal damage, humidity was included in the best-fitting model (Appendix S1: Table S16). Model outputs for all 17 response variables are presented in Appendix S1: Tables S2–S18.

Spatial patterns in damage risk from wind and snow, forestry, and unidentified cause

There was a higher proportion of plots with high (>30%) risk of damage from wind and snow in the north



FIGURE 4 Probability of damage causes (a) wind and snow, (b) unidentified, (c) forestry, (d) herbivore, (e) combined identified, and (f) moose against stand age (in years), and, for (e) and (f), for different temperature sums (*T* sum). Error bands show 95% CIs.

compared to in the southern half of Sweden (Appendix S1: Figure S7). In contrast, the risk of damage from forestry was generally higher in the south, with a higher proportion of plots with high (>25%) or very high (>50%) risk of damage compared to in the north, where the risk was mostly below 10% (Appendix S1: Figure S7). The risk of damage from unidentified causes, on the other hand, show smaller-scale variation in risk and no clear spatial gradient in risk across Sweden (Appendix S1: Figure S7).

DISCUSSION

8 of 12

The risks of damage often changed substantially with tree species richness, but the shape, direction, and magnitude of this change varied among types and causes of damages. We thus fail to provide unequivocal support for our hypothesis that damage risk is lower in stands with many tree species. As changes in the risk of damage across gradients in stand and tree height (assumed to reflect tree age) similarly varied among damage types and causes, our results suggest that changes in the number of tree species or rotation length (i.e., period between clear-cut events) through adaptive forest management will influence damage risk, but differently so depending on which type and cause of damage are regionally the most prevalent.

Despite this substantial and highly unique dataset, there are limitations as to what knowledge can be extracted from it, due to only living trees being surveyed, difficulties in identifying cause of damage, and too broadly defined damage types. For example, the damage type "stem break" is caused by several agents, such as various mammal herbivores, wind, snow, and human activities, impeding a mechanistic understanding of damage risk. Nevertheless, damage risk for identified causes often differed as expected among tree species (Appendix S1: Figure S4) and changed as expected across stand attributes, indicating reliability of those data despite high frequency of "unidentified" cause. Thus, the discussion will henceforth be limited to the different causes of damage.

The increased damage risk from wind and snow from 1 to about 3 tree species suggest that monocultures are more resistant to damage from wind and snow, contradicting earlier studies on stand composition and wind damage (e.g., Valinger & Fridman, 2011), whereas the increased risk of damage from wind and snow with increasing stand age makes sense, as older trees have larger crowns and therefore are more exposed to wind and snow. However, we also found that the highest risk of wind and snow damage was for younger trees. Our best explanation for these results is that most recorded damages of this type are due to snow rather than wind. This is supported by the observed high damage risks for lodgepole pine and warty birch (Appendix S1: Figure S4). For lodgepole pine, smaller trees in dense stands are most sensitive to snow damage (Teste & Lieffers, 2011), and snow is known to damage young birches (Martiník & Mauer, 2012), while wind generally has smaller effects on birch compared to coniferous tree species (Valinger & Fridman, 2011). This strongly suggests that combining damages from wind and snow results in confounding different or even opposing factors behind damage risks. It is therefore doubtful whether the present damage variable classification provides meaningful information to forest owners aiming to decrease damage risks through adaptive management. Instead, these causes should be recorded independently, to inform forest owners if they should, for example, manage for a greater proportion of birch to mitigate wind damage (Valinger & Fridman, 2011) or avoid forest characteristics that increase the risk of snow damage (e.g., lodgepole pine; Teste & Lieffers, 2011).

The decreasing risk of forestry damages with increasing tree species richness can be explained by the dominating Fennoscandian clear-cut management aiming to decrease tree species numbers (Esseen et al., 1997) and the low risk of forestry damage in older (>200 years) forests due to low management activity in most of these forests. However, the higher risk of forestry damage in warmer than in colder climates (Appendix S1: Figure S7), and the highest risk in younger forests in warmer climates, suggest that a warm climate exacerbates the risk of forestry damages, possibly through lack of frozen soil conditions in winter and more frequent precommercial thinnings as trees grow faster in these climates. Nevertheless, forestry was identified as a cause of damage for only 6.9% of the trees. However, mechanical damages, stem break, and root damages, which together were found on 42.8% of the sample trees, are likely caused by management but not identified as such. These damages are also known to cause secondary damages, such as infestation from rotting fungi. Hence, there is an urgent need to quantify the role of forest management for damage risk, tree mortality, and delivery of ecosystem services

(Gauthier et al., 2015; Swedish Forest Agency, 2022; Triviño et al., 2023). Much attention in Sweden today is given to forest damages caused by herbivores (i.e., moose) and insects (i.e., bark beetles), and it is surprising that damages caused by forestry go largely unnoticed, especially as current management methods have been suggested to cause a general loss of disturbance resistance and resilience in forests, thus far unquantified (Seidl et al., 2011; Stritih et al., 2021; Vacek et al., 2021; Wolf et al., 2023).

The interactive influence of climate and tree species richness on damage risk warrants further investigation. It suggests that tree species mixtures act as an "insurance" against tree damage in a warmer climate (Astrup et al., 2018; Berthelot et al., 2021; Hahn et al., 2021; Jactel & Brockerhoff, 2007; Stemmelen et al., 2022; Valinger & Fridman, 2011). Mechanistically, this could be explained by species-rich stands always containing some tree species that tolerate a warmer climate or that mixed stands exhibit reduced drought stress for all species (Aldea et al., 2022), whereas managed monocultures are more likely to experience drought stress (Wolf et al., 2023) and therefore are more vulnerable to secondary damages. Obtaining a greater understanding of which stand characteristics should be promoted to mitigate adverse effects of drought in a warming climate must be a priority in forestry research.

The greater damage risk from large herbivores, especially moose, for most tree species compared to Norway spruce supports the replacement of Scots pine and broadleaf tree species with Norway spruce to reduce browsing damages in managed forests, although such action likely increases the risk for insect damages (Hlásny et al., 2021) and reduces other forest values, such as biodiversity and recreation (Felton et al., 2020). The higher risk of herbivore and moose damage in young stands and on low (young) trees is expected, and the high uncertainty in damage risk from large mammal herbivores in a cold climate is likely due to clustered, high-frequency damages, as expected from mammal browsing in managed boreal forests (Wallgren et al., 2013). This great risk for young trees questions the economic sustainability of clear-cut forestry, as it creates a situation where mammal herbivores can find large patches of preferred food resources (i.e., young trees) and thereby cause extensive, localized damages (Wallgren et al., 2013). Further, the shorter the rotation length, the more abundant these patches will be at the landscape scale. Hence, an extended rotation length would reduce the occurrence of patches of preferred resources, and thus likely reduce the risk of browsing damage and subsequent production losses for forest owners and industry, at the same time as several other forest values would be promoted (Jonsson et al., 2020; Jönsson & Snäll, 2020).

Wind damage causing tree mortality is not recorded in the damage survey, resulting in fewer than expected cases of "stem break" for larger/older trees. Similarly, the relatively low frequency of damage due to wind and snow (12%, compared to 46% in Patacca et al., 2023) and the very low frequency of insect and fire damage are probably partly due to the definition of the variable, which ignores damages that have resulted in tree mortality, but also due to problem with identifying causes of damage. Hence, the true impact from some damage agents is certainly underestimated, especially for fire, but probably also for wind and snow, forestry, insects, and fungi. Nevertheless, the low natural mortality (5.4%) suggests that mortality is too low to have any marked impact on detection rate of damages. Accordingly, in a study from Czech Republic, Martiník and Mauer (2012) found that only 4% of birches were killed by snow, despite snow damage occurring on 67%-95% of the trees. Hence, not being able to identify damage causes seems to be a greater problem with the survey than the exclusion of dead trees.

The high frequency of unidentified damage, and the likelihood that this classification contains damages caused by a wide variety of agents that vary in their responses to different stand attributes and environmental conditions, is problematic for interpretation and generalization of our results. Unidentified damage often showed other relationships to the investigated explanatory covariates than identified causes, suggesting that it is caused by agents that respond differently to stand attributes and environmental conditions than the causes of identified damages do. Nevertheless, similarities between patterns of unidentified damage across stand ages and patterns of herbivore and moose damage in a colder climate across the same stand ages suggest that moose is an underlying cause of many of the unidentified damages, especially in northern Sweden. This would also explain the large discrepancy between the low frequency (3%) of herbivore damage in our study and the known high browsing impact of herbivores on Swedish forests (Swedish Forest Agency, 2021, 2022). In addition, the decreased damage risk from unidentified causes with a warmer climate suggests that the highest risk for damage from unidentified cause occurs in northern Sweden and therefore are related to weather conditions such as snow. In any case, that a large proportion of detected damages is unidentified is problematic and calls for modification of the NFI methodology.

Reduced damage risks of identified causes with increasing stand age and the high risk of wind and snow damage for low trees suggest that extended rotation lengths would lower the risk of tree damage from browsing mammals (Milligan & Koricheva, 2013; Nichols

et al., 2015), snow (Martiník & Mauer, 2012), and forestry. Further, our results indicate that a greater inclusion of broadleaf species (in particular, birch and aspen) in Swedish managed forests would lower the risk of tree damages (Appendix S1: Figure S4) and thus, potentially, production losses (Astrup et al., 2018; Valinger & Fridman, 2011). Conversely, the introduction of lodgepole pine in Swedish managed forests may have increased overall damage frequency and thus production losses (Teste & Lieffers, 2011). As such, our results indicate that there is potential for reducing overall damage risk via adaptive management of tree species composition but highlight the need to further investigate how forest management can be modified to alleviate damage risk, especially in the face of a changing climate (Patacca et al., 2023; Thom & Seidl, 2016; Triviño et al., 2023). Our results also show that despite the highly detailed Swedish NFI, there is high uncertainty in estimated risks in all except the most common damage causes. Hence, factors contributing to damages-knowledge that is needed to make recommendations to forest owners about how to adapt management to alleviate risks-are guite uncertain, and methodological improvements are needed to increase this certainty.

CONCLUSIONS

Patacca et al. (2023) states that "adaptation to changing disturbance regimes must be placed at the core of the European forest management and policy debate" and that "a coherent and homogeneous monitoring system of natural disturbances is urgently needed in Europe, to better observe and respond to the ongoing changes in forest disturbance regimes." In this study, we found both expected results on drivers of tree damages in boreal and temperate forests and some new, interesting patterns on how damage risks vary across environmental conditions and strand attributes. Our results indicate that forest management that favors coniferous monocultures over mixed or broadleaf forests and short over longer rotation length increases the overall risk for a wide range of tree damages, including those caused by forestry itself. However, this said, we are concerned about the large uncertainty in identification of causes of damage in the comprehensive and detailed Swedish NFI. In line with Patacca et al. (2023), we therefore recommend that efforts are made to improve methods for identifying causes of damages, for example, by using DNA to identify mammal herbivores (e.g., Nichols et al., 2015). Only then will data be practically useful to those that want to utilize adaptive management to mitigate effects of climate change on a range of forest values.

AUTHOR CONTRIBUTIONS

All authors helped to formulate the initial idea, study questions, and analyses. Micael Jonsson managed the data, performed the statistical analyses, and wrote the first version of the manuscript. All authors commented on subsequent versions of the manuscript.

ACKNOWLEDGMENTS

We acknowledge help with data extraction and delivery from the Swedish NFI, Swedish University of Agricultural Science, Umeå.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Jonsson, 2024) are available from the Svensk nationell datatjänst: https://doi.org/10.5878/3fcc-7594.

REFERENCES

- Aldea, J., R. Ruiz-Peinado, M. del Río, H. Pretzsch, M. Heym, G. Brazaitis, A. Jansons, et al. 2022. "Timing and Duration of Drought Modulate Tree Growth Response in Pure and Mixed Stands of Scots Pine and Norway Spruce." *Journal of Ecology* 110: 2673–83.
- Astrup, R., P. Y. Bernier, H. Genet, D. A. Lutz, and R. M. Bright. 2018. "A Sensible Climate Solution for the Boreal Forest." *Nature Climate Change* 8: 11–12.
- Axelsson, A.-L., G. Ståhl, U. Söderberg, H. Petersson, J. Fridman, and A. Lundström. 2010. "National Forest Inventory Report Sweden." In National Forest Inventories – Pathways for Common Reporting, edited by E. Tomppo, T. Gschwantner, M. Lawrence, and R. E. McRoberts. Dordrecht, The Netherlands: Springer.
- Baeten, L., H. Bruelheide, F. van der Plas, S. Kambach, S. Ratcliffe, T. Jucker, E. Allan, et al. 2019. "Identifying the Tree Species Compositions that Maximize Ecosystem Functioning in European Forests." *Journal of Applied Ecology* 56: 733–744.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effect Models Using lme4." *Journal of Statistical Software* 67: 1–48.
- Berthelot, S., T. Frühbrodt, P. Hajek, C. A. Nock, C. F. Dormann, J. Bauhus, and J. Fründ. 2021. "Tree Diversity Reduces the Risk of Bark Beetle Infestation for Preferred Conifer Species, but Increases the Risk for Less Preferred Hosts." *Journal of Ecology* 109: 2649–61.
- Esseen, P. A., B. Ehnström, L. Ericson, and K. Sjöberg. 1997. "Boreal Forests." *Ecological Bulletins* 46: 16–47.
- Ezebilo, E. E., C. Sandström, and G. Ericsson. 2012. "Browsing Damage by Moose in Swedish Forests: Assessments by Hunters and Foresters." Scandinavian Journal of Forest Research 27: 659–668.
- Felton, A., L. Petersson, O. Nilsson, J. Witzell, M. Cleary, A. M. Felton, C. Björkman, et al. 2020. "The Tree Species Matters: Biodiversity and Ecosystem Service Implications or Replacing Scots Pine Production Stands with Norway Spruce." *Ambio* 49: 1035–49.

- Fox, J., S. Weisberg, B. Price, M. Friendly, J. Hong, R. Andersen, D. Firth, S. Taylor, and R Core Team. 2022. "Effect Displays for Linear, Generalized, and Other Models. Version 4.2-1." https://www.r-project.org, https://socialsciences.mcmaster.ca/ jfox/.
- Gamfeldt, L., T. Snäll, R. Bagchi, M. Jonsson, L. Gustafsson, P. Kjellander, M. C. Ruiz-Jaen, et al. 2013. "Higher Levels of Multiple Ecosystem Services Are Found in Forests with More Tree Species." *Nature Communications* 4: 1340.
- Gardiner, B., K. Blennow, J.-M. Carnus, P. Fleischer, F. Ingemarson, G. Landmann, M. Lindner, et al. 2010. Destructive Storms in European Forests: Past and Forthcoming Impacts. DG Environment, European Forest Institute. https://edepot. wur.nl/162053.
- Gauthier, S., P. Bernier, T. Kuuluvainen, A. Z. Shvidenko, and D. G. Schepaschenko. 2015. "Boreal Forest Health and Global Change." Science 349: 819–822.
- Hahn, T., J. Eggers, N. Subramanian, A. Toraño Caicoya, E. Uhl, and T. Snäll. 2021. "Specified Resilience Value of Alternative Forest Management Adaptations to Storms." *Scandinavian Journal of Forest Research* 36: 585–597.
- Hlásny, T., L. König, P. Krokene, M. Lindner, C. Montagné-Huck, J. Müller, H. Qin, et al. 2021. "Bark Beetle Outbreaks in Europe: State of Knowledge and Ways Forward for Management." *Current Forestry Reports* 7: 138–165.
- Jactel, H., and E. G. Brockerhoff. 2007. "Tree Diversity Reduces Herbivory by Forest Insects." *Ecology Letters* 10: 835–848.
- Jonsson, M. 2024. "Data for Tree Damage Risk across Gradients in Tree Species Richness and Stand Age: Implications for Adaptive Forest Management." Dataset. https://doi.org/10. 5878/3fcc-7594.
- Jonsson, M., J. Bengtsson, J. Moen, L. Gamfeldt, and T. Snäll. 2020. "Stand Age and Climate Influence Forest Ecosystem Service Delivery and Multifunctionality." *Environmental Research Letters* 15: 0940a8.
- Jönsson, M., and T. Snäll. 2020. "Ecosystem Service Multifunctionality of Low-Productivity Forests and Implications for Conservation and Management." *Journal of Applied Ecology* 57: 695–706.
- Knoke, T. 2017. "Economics of Mixed Forests." In *Mixed-Species Forests. Ecology and Management*, edited by H. Pretzsch, D. I. Forrester, and J. Bauhus, 545–577. Berlin: Springer.
- Kuuluvainen, T. 2009. "Forest Management and Biodiversity Conservation Based on Natural Ecosystem Dynamics in Northern Europe: The Complexity Challenge." *Ambio* 38: 309–315.
- Lindenmayer, D. B., and R. F. Noss. 2006. "Salvage Logging, Ecosystem Processes, and Biodiversity Conservation." *Conservation Biology* 20: 949–958.
- Liu, Q., C. Peng, R. Schneider, D. Cyr, N. G. McDowell, and D. Kneeshaw. 2023. "Drought-Induced Increase in Tree Mortality and Corresponding Decrease in the Carbon Sink Capacity of Canada's Boreal Forests from 1970 to 2020." *Global Change Biology* 29: 2274–85.
- Martiník, A., and O. Mauer. 2012. "Snow Damage to Birch Stands in Northern Moravia." *Journal of Forest Science* 58: 181–192.
- Mielikäinen, K., and J. Hynynen. 2003. "Silvicultural Management in Maintaining Biodiversity and Resistance of Forests in Europe-Boreal Zone: Case Finland." *Journal of Environmental Management* 67: 47–54.

- Milligan, H. T., and J. Koricheva. 2013. "Effects of Tree Species Richness and Composition on Moose Winter Browsing Damage and Foraging Selectivity: An Experimental Study." *Journal of Animal Ecology* 82: 739–748.
- Moreau, G., C. Chagnon, A. Achim, J. Caspersen, L. D'Orangeville, M. Sánchez-Pinillos, and N. Thiffault. 2022. "Opportunities and Limitations of Thinning to Increase Resistance and Resilience of Trees and Forests to Global Change." *Forestry* 95: 595–615.
- Nichols, R. V., J. P. G. M. Cromsigt, and G. Spong. 2015. "DNA Left on Browsed Twigs Uncovers Bite-Scale Resource Use Patterns in European Ungulates." *Oecologia* 178: 275–284.
- Paillet, Y., L. Bergès, J. Hjältén, P. Ódor, C. Avon, M. Bernhardt-Römermann, R.-J. Bijlsma, et al. 2010. "Biodiversity Differences between Managed and Unmanaged Forests: Meta-Analysis of Species Richness in Europe." Conservation Biology 24: 101–112.
- Patacca, M., M. Lindner, M. E. Lucas-Borja, T. Cordonnier, G. Fidej, B. Gardiner, Y. Hauf, et al. 2023. "Significant Increase in Natural Disturbance Impacts on European Forests since 1950." *Global Change Biology* 29: 1359–76.
- R Core Team. 2023. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.
- Seidl, R., M.-J. Schelhaas, and M. J. Lexer. 2011. "Unraveling the Drivers of Intensifying Forest Disturbance Regimes in Europe." *Global Change Biology* 17: 2842–52.
- Seidl, R., D. Thom, M. Kautz, D. Martin-Benito, M. Peltoniemi, G. Vacchiano, J. Wild, et al. 2017. "Forest Disturbances under Climate Change." *Nature Climate Change* 7: 395–402.
- Sonesson, J., G. Swedjemark, C. Almqvist, G. Jansson, B. Hannrup, O. Rosvall, and J. Kroon. 2007. "Genetic Variation in Responses of *Pinus sylvestris* to Natural Infection by *Gremmeniella abietina.*" Scandinavian Journal of Forest Research 22: 290–98.
- Stemmelen, A., A. Paquette, M.-L. Benot, Y. Kadiri, H. Jactel, and B. Castagneyrol. 2022. "Insect Herbivory on Urban Trees: Complementary Effects of Tree Neighbours and Predation." *Peer Community Journal* 2: e22.
- Stritih, A., C. Senf, R. Seidl, A. Grêt-Regamey, and P. Bebi. 2021. "The Impact of Land-Use Legacies and Recent Management on Natural Disturbance Susceptibility in Mountain Forests." *Forest Ecology and Management* 484: 118950.
- Swedish Forest Agency. 2021. "Skogsskador i Sverige 2020." Rapport 2021/702. Skogsstyrelsen, mars 2021. https://skogsstyrelsen.se/ globalassets/nyheter/skogsstyrelsens-nationella-skogsskaderapport-2020.pdf.
- Swedish Forest Agency. 2022. "Skogsskador i Sverige 2021." Rapport 2022/6. Skogsstyrelsen, April 2022. https://www. skogsstyrelsen.se/globalassets/om-oss/rapporter/rapporter-20222021202020192018/rapport-2022-06-skogsskador-i-sverige-2021.pdf.

- Tedim, F., G. Xanthopoulos, and V. Leone. 2015. "Forest Fires in Europe: Facts and Challenges." In Wildfire. Hazards, Risks, and Disasters, edited by J. F. Shroder and D. Paton, 77–99. Oxford, UK: Elsevier.
- Teste, F. P., and V. J. Lieffers. 2011. "Snow Damage in Lodgepole Pine Stands Brought into Thinning and Fertilization Regimes." *Forest Ecology and Management* 261: 2096–2104.
- Thom, D., and R. Seidl. 2016. "Natural Disturbance Impacts on Ecosystem Services and Biodiversity in Temperate and Boreal Forests." *Biological Reviews* 91: 760–781.
- Triviño, M., A. Morán-Ordoñez, K. Eyvindson, C. Blattert, D. Burgas, A. Repo, T. Pohjanmies, L. Brotons, T. Snäll, and M. Mönkkönen. 2023. "Future Supply of Boreal Forest Ecosystem Services Is Driven by Management Rather than by Climate Change." Global Change Biology 29: 1484–1500.
- Turner, M. G. 2010. "Disturbance and Landscape Dynamics in a Changing World." *Ecology* 91: 2833–49.
- Vacek, Z., A. Prokůpková, S. Vacek, D. Bulušek, V. Šimůnek, V. Hájek, and I. Králíček. 2021. "Mixed vs. Monospecific Mountain Forests in Response to Climate Change: Structural and Growth Perspectives of Norway Spruce and European Beech." *Forest Ecology and Management* 488: 119019.
- Valinger, E., and J. Fridman. 2011. "Factors Affecting the Probability of Windthrow at Stand Level as a Result of Gudrun Winter Storm in Southern Sweden." Forest Ecology and Management 262: 398–403.
- Wallgren, M., R. Bergström, G. Bergqvist, and M. Olsson. 2013. "Spatial Distribution of Browsing and Tree Damage by Moose in Young Pine Forests, with Implications for the Forest Industry." *Forest Ecology and Management* 305: 229–238.
- Wolf, J., J. Asch, F. Tian, K. Georgiou, and A. Ahlström. 2023. "Canopy Responses of Swedish Primary and Secondary Forests to the 2018 Drought." *Environmental Research Letters* 18: 064044.

SUPPORTING INFORMATION

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

How to cite this article: Jonsson, Micael, Jan Bengtsson, Jon Moen, and Tord Snäll. 2024. "Tree Damage Risk across Gradients in Tree Species Richness and Stand Age: Implications for Adaptive Forest Management." *Ecosphere* 15(11): e70071. <u>https://doi.org/10.1002/ecs2.70071</u>