Disrupting tree continuity through clearcut forestry can alter the climate sensitivity of future tree growth in northern Sweden

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ABSTRACT

Disrupting tree continuity through clearcut forestry is a widespread management practice across the boreal biome. However, concerns remain that forests regenerated after clearcutting may be more sensitive to climatic fluctuations. We examined how clearcutting affects tree growth responses to weather variability, focusing particularly on the extreme 2018 drought. We collected tree-ring width data from forests in northern Sweden that either were clearcut ~60 years prior to the study or never had been clearcut but exposed to past selective logging. We tested whether growth responses to interannual weather variations variables differed between these forest types and assessed how the differences were mediated by soil organic matter, soil temperature stability, and variations in tree age, size, and early growth rates. Forests regenerated after clearcutting showed greater responsive to interannual variation in weather, being more negatively affected by increasing temperature but more positively affected by precipitation. During the 2018 drought, clearcut forests exhibited a mean growth reduction of 19 %, compared to 11 % in non-clearcut forests. The higher drought resistance in non-clearcut forests was primarily associated with greater mean tree age and slower early growth rate. However, as these variables are strongly correlated with clearcutting history, their independent mediation effects are difficult to interpret. Our results suggest that clearcut forestry may increase the sensitivity of regenerating forests to climatic variability. Further research is needed to disentangle the underlying mechanisms and to determine how forest management practices can promote greater climatic resilience in boreal ecosystems.

1. Introduction

The boreal forest constitutes more than a quarter of the world's forested area (FAO, 2020). Despite its relatively low productivity, it provides wood products of global importance (Burton et al., 2010) and plays a key role in climate change mitigation, as a substantial portion of the world's terrestrial carbon is stored in boreal ecosystems (Gauthier et al., 2015). Consequently, changes in tree growth may have significant economic and climate-regulating implications, underscoring the importance of a deeper understanding of the factors that control tree growth.

Over the past century, the global temperature has increased by ~1.1 °C, and current climate change projections estimate a future increase ranging from 1.5 °C to as much as 4 °C (IPCC, 2023). In the boreal forest, the warming has been thought to result in accelerated tree growth (Zhu et al., 2016). However, recent observations of forest productivity declines in the Fennoscandian boreal forest contradict these predictions (Henttonen et al., 2024; Laudon et al., 2024; Breidenbach et al., 2024) and suggest that global warming may instead have a negative effect on tree growth. Even small shifts in temperature and precipitation can influence tree growth (Huang et al., 2010), while extreme environmental events, such as droughts, have the potential to significantly reduce growth and cause tree mortality (Spiecker and Kahle, 2023). However, considerable uncertainty remains regarding which factors interact with climate change to affect tree growth. For instance, tree response to rising temperatures vary among species (Huang et al., 2010) and across geographical regions (Jiang et al., 2016). Temporal tree continuity may be an equally important, yet understudied, factor influencing tree

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growth responses to climate change (Mausolf et al., 2018; Oheimb et al., 2014; Wolf et al., 2023).

The boreal forest contains some of the largest pristine forested areas (Potapov et al., 2008), but parts of the biome, such as northern Fennoscandia, are experiencing a rapid increase in disrupted tree continuity through clearcutting (Ahlström et al., 2022; SLU, 2023). Under natural disturbance regimes, northern Fennoscandian pine forests (*Pinus sylvestris*) generally regenerate under cohort or gap dynamics, while stand-replacing disturbances, similar to the type that follows after clearcutting, are less common (Kuuluvainen and Aakala, 2011). Clearcutting results in nutrient mobilisation (LeDuc and Rothstein, 2007) and relax competition from large trees (Kärenlampi and Riekkinen, 2004) and thereby promote the growth rate of the emerging tree regeneration. However, forests of long tree continuity may be more resilient to environmental changes than those that have undergone a disruption event (Oheimb et al., 2014). Indeed, impacts of the Europe-wide summer drought in 2018 suggest that primary forests may be less sensitive to droughts than secondary forests (Wolf et al., 2023). However, the underlying mechanisms driving this difference remain unknown.

One possible explanation as to why forests that have undergone clearcutting are more susceptible to weather variability and may be more sensitive to climate change is that they have a less stable soil climate. Longer continuity allows greater build-up of soil organic layers and provides greater water storage capacity (Oheimb et al., 2014), which in turn potentially alleviate trees from drought stressors during periods of high temperature and low precipitation. In addition to these soil-related changes, clearcutting may also affect tree-root dynamics. Disrupted tree continuity may reduce tree root production (Mausolf et al., 2018) and thereby decrease the root:shoot ratio (Lim et al., 2015), as increased nutrient availability (LeDuc and Rothstein, 2007) lowers the need for resource allocation to root growth (Poorter et al., 2012). A reduced root:shoot ratio limit water uptake in relation to transpiration (Chen et al., 2022) and will increase tree susceptibility to elevated temperatures and drought stress. These effects are further compounded by rising soil temperatures, which not only influence root function (Pregitzer et al., 2000) but may also aggravate tree water loss through increased transpiration (Wieser et al., 2015). Therefore, the belowground micro-climate may be of great importance for trees' ability to withstand climatic changes.

Aside from soil associations, factors intrinsic to the trees themselves may also influence the responsiveness to interannual weather variability following clearcut forestry. Clearcutting inherently lowers the average tree ages within a forest. Tree age can affect growth responses to weather variability. For instance, younger trees may be more resilient to drought due to lower hydraulic constraints compared to older, taller, trees (Ryan and Yoder, 1997). Conversely, younger trees may have shallower root systems, making them more drought sensitive (Zhang et al., 2022). Hence, it remains unclear if changed tree age, as a consequence of clearcutting, will increase or decrease the stand's overall drought resistance. Furthermore, the regeneration of a forest through clearcutting will likely cause a homogenization of the trees' ages and sizes. Such a reduction in functional diversity may decrease ecological redundancy, and possibly lower drought resistance at the stand scale (Anderegg et al., 2018). For instance, a stand with higher tree heterogeneity (age, size, species etc.) would have a higher probability of containing individuals that are highly resilient to a specific stressor (Mori et al., 2013). Therefore, tree traits and functional diversity may play a critical role in supporting a forest's resilience to climatic change.

Given that clearcut forestry is the dominant management practice across large areas of the boreal biome, and considering the biome's significant economic and climate-regulating importance, it is crucial to develop a deeper understanding of how this management approach influences tree growth and climate sensitivity. In this study, we investigate detailed growth patterns following a continuity disruption event in northern Sweden caused by clearcutting by examining tree ring widths. We hypothesize that (I) the stand-level growth in trees regenerated after

clearcutting exhibits greater interannual variation due to the homogenization of tree characteristics, resulting in reduced functional diversity. Furthermore, we hypothesize that (II) clearcutting reduces drought resistance in tree growth by decreasing functional diversity and altering key tree and ecosystem attributes, such as tree age and soil organic layer thickness.

2. Methods

2.1. Study area

In order to explore the consequences of disrupted tree continuity, we compared 9 forests that had been clearcut ~60 years prior to the study (hereafter referred to as Clearcut forests) with 9 forests that have never been clearcut, but exposed to selective logging in the past (hereafter referred to as Non-clearcut forests) (Fig. 1). The studied forests are located in northern Sweden and spans a distance of approximately 250 km. The area has a mean annual temperature of ~0 °C, with monthly average temperatures ranging from −15 °C in January to 13 °C in July, and a mean annual precipitation of ~500–600 mm (SMHI, 2009). The studied forests are dominated (>50 % of trees) by pine (*P. sylvestris*), but also contain some spruce (*Picea abies*) and birch (*Betula pubescens*). The understory vegetation is dominated by ericaceous dwarf-shrubs, predominantly *Vaccinium* and *Empetrum* species, and the forest floor is dominated by feather mosses and ground-living lichens. The geology consists mainly of granite moraine, but is also scattered with glaciofluvial deposits (SGU, 2023). The 18 forests were selected from a dataset on stand characteristics compiled by the Swedish forestry company Sveaskog. To ensure that tree growth was not influenced by other underlying differences in site conditions than the management type, we made an effort to select stands with similar conditions in terms of annual temperature sums, altitude, latitude, and estimated site productivity prior to clearcutting. Information on the latter was derived from the forest company's stand database and based on the original forest owners' estimation of site productivity. To select Non-clearcut forests, we used information from the forest company Sveaskog's database on sites with long tree continuity. To ensure that sites with long tree continuity are not harvested (as part of the company's biodiversity conservation strategy), Sveaskog determines each stand's mean tree age by systematically coring trees in forests that might have long tree continuity. This involves coring trees at the base of the stem in a systematic grid until an average mean tree age is established. Sites where at least 30 % of the trees have an age greater than 140 years are classified as having long tree continuity and are subjected to special consideration if logging is planned. Our Non-clearcut forests were selected from this subset. Since a proportion of the trees in these forests predate the introduction of clearcutting in the area (Östlund et al., 1997), we can state with high confidence that the forests we identified as Non-clearcut have never been clearcut. To further verify our classification, we used aerial imagery from the 1960s that confirmed that the selected Non-clearcut forests had a continuous canopy, while the Clearcut forests were open, non-forested sites during the same period. Variation in tree age structure among the Non-clearcut forests, and the lack of such variation in the Clearcut forests, further indicates that these forests are regenerated following non-stand-replacing disturbances and stand-replacing disturbances, respectively (Figure S1). It is important to note that the Non-clearcut forests should not be regarded as pristine, as they all show evidence of past selective logging, such as the presence of old tree stumps. Although logging in some areas may have been relatively intensive, it was not stand-replacing in the way clearcutting is. Since the transition from selective logging to clearcut forestry, these forests have only experienced low-intensity management. In each forest, we randomly selected three circular plots (20 m ø) with at least 30 m distance between two adjacent plots. This resulted in a total of 54 plots across the 18 forests. To avoid the influence of edge-effects, we ensured that no plot was situated closer than 30 m to the edge of the stand.
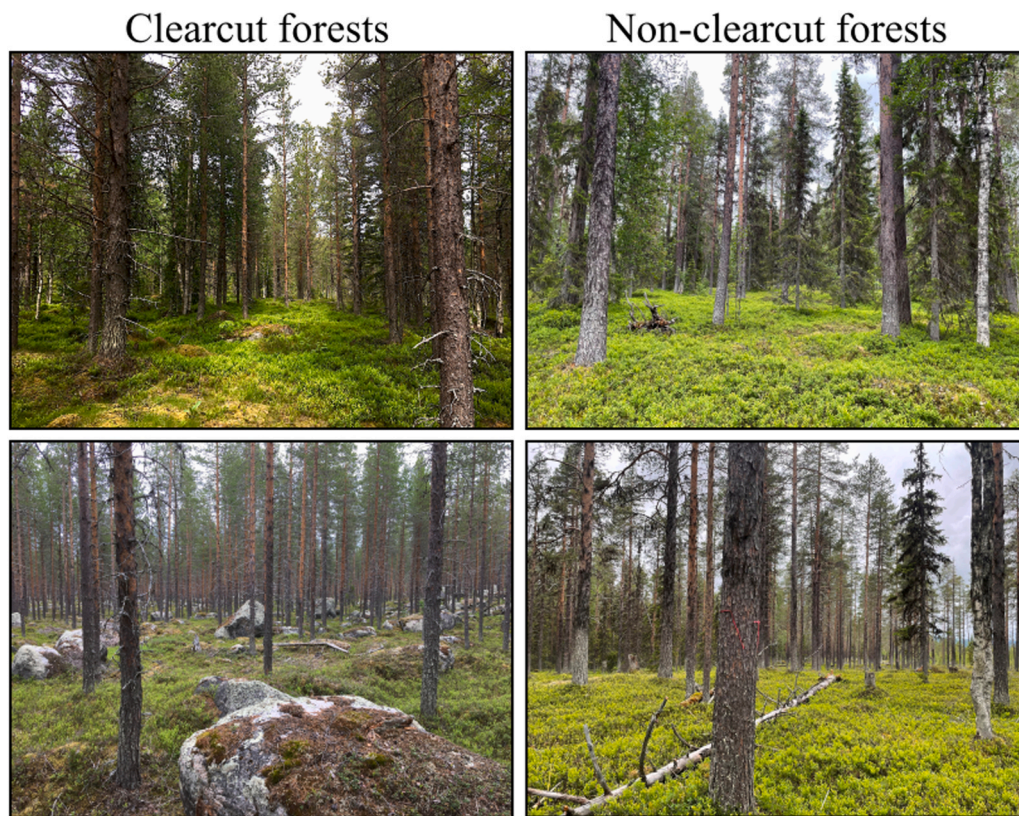
Fig. 1. Example images of the studied forests. Pictures to the left show forests that have been clearcut ~60 years ago. Pictures to the right show forests that have never been clearcut.

2.2. Tree variables

To study the growth patterns of the trees, we collected tree cores. In every plot, we cored all trees > 5 cm DBH (at 1.3 m) with a 5 mm tree borer in July-August 2022 (a total of 1249 trees). We dried the cores at 50 °C and then mounted and sanded them to enhance the ring visibility. Where tree rings were unclear, we treated the cores with zinc paste. We measured the tree ring widths (TRW) using the R package MtreeRing (Shi and Xiang, 2021). Due to difficulties in accurately assessing TRWs, all deciduous trees (2 aspen, 7 sallows, and 131 birches) as well as two pine trees, whose rings were too unclear to allow visual inspection of tree rings even after zink paste treatment, were excluded from analysis. Of the excluded trees, 83 belonged to the Clearcut category and 59 belonged to the Non-clearcut category. We detrended the TRW series to produce ring width indices (RWI) using a spline function from the dplR package in R (Bunn et al., 2025), in accordance with standard dendrochronological procedures (Frank et al., 2022). To ensure accurate assignment of growth years in the RWI series, we computed estimates of inter-series correlations (Rbar) and the Expressed Population Signal (EPS) for each of the 54 plots. We excluded a total of 71 RWI series (32 from Clearcut and 39 from Non-clearcut forests) with an inter-series correlation below the critical level of 0.3281 which is the recommended default value used in the dendrochronological software COFE-CHA (Holmes, 1983). Low correlations between individual RWI series and mean RWI series may be produced either by dating errors of individual year TRW, or due to individual trees producing growth patterns that differ from the mean. Because of this, we also conducted analyses on the dataset including the 71 RWI series and found the results to be similar. However, to present results that are as reliable as possible in terms of data quality, we present only the results based on analyses where we excluded the 71 RWI series of low inter-series correlations. The resulting rbar was on average 0.57 ($\pm$0.02) and 0.56 ($\pm$0.02) for Clearcut forests and Non-clearcut forests, respectively. Due to the high

number of trees sampled (~20 per plot), the retained EPS-values were on average 0.96 ($\pm$0.05) and 0.95 ($\pm$0.06) for Clearcut forests and Non-clearcut forests, respectively. To illustrate growth patterns of the different forests, we transformed TRWs to biomass estimates using allometric functions for pine and spruce (Marklund, 1988). Since a tree's size traits are potential mediators of differences in drought resistance, we also measured all sampled trees for circumference at breast height using a tape measure, and height using a Vertex IV and Transponder T3.

2.3. Soil variables

To test if soil climatic stability is a potential mechanism that mediates differences in growth responses during extreme droughts, we collected data on variations in soil temperature. We placed temperature data loggers ~10 cm below the soil surface in all sample plots during June 2023 and retrieved them in June 2024. We used the coefficient of variance from each temperature logger's time series to examine the soil temperature variability. As the timing of placement and recovery of the temperature loggers differed somewhat among sites, we only used the period when all loggers were buried in the soil for further analysis (July 1st to May 15th). Data from one temperature logger in a Clearcut forest was excluded as it was deemed unreliable after showing a heat anomaly in March (reaching >20 °C and then remaining above 5 °C for a full month).

Further, to explore differences in the soil organic layer, we collected fifteen soil samples, 2.5 cm diameter each, of the organic soil layer from each plot. We estimated organic matter in the soil samples through loss on ignition (LOI) by drying and weighing samples and then burning them at 550 °C for 6 h to remove all organic matter. We calculated the organic matter as the fraction of weight lost after burning. As we are interested in the total amount of organic matter as a potential mediator of drought resilience, we extrapolated the fraction of organic matter to the total collected soil mass for each plot. Thus, we present the data here

as organic matter in terms of kg per m^{-2}.

2.4. Weather data

To explore the effects of climatic variables on tree growth, we retrieved data on daily precipitation, maximum (T_{max}), minimum (T_{min}) and mean temperature (T_{mean}) from the Swedish Meteorological and Hydrological Institute's (SMHI) weather station in Arjeplog. The Arjeplog station is located in the centre part of the study area (N: 66.0513, E: 17.8396) and contains the most cohesive dataset of the nearby stations. Using this data, we also calculated Standardized Precipitation Evapotranspiration Index (SPEI) based on precipitation and temperature measurements of 6 months prior to the indexed month (e.g. Jevšenak, 2019), with potential evapotranspiration calculated through the Hargreaves method (Vicente-Serrano et al., 2010). To test the tree growth responses to an extreme drought year, here 2018, we analysed the growth changes during 2018 which has been noted as an extreme drought year in the region (Martín-Gómez et al., 2017; Toreti et al., 2019; Wolf et al., 2023; SMHI, 2019).

2.5. Data analysis

All statistical tests and descriptive statistics were done in R (version 4.4.1; R Core Team 2022).

To test our first hypothesis on whether there are differences in growth stability caused by clearcutting, we analysed the mean sensitivity of inter-annual variability in RWI (Fritts, 2012). In short, a high value of mean sensitivity indicates high growth variability and a low value indicates low growth variability. We used limited time series of 54 years since all forests had trees that were at least 54 years old (i.e. contained 54 annual rings at breast height). As the Clearcut forests are even-aged, increasing the length of the studied time series quickly decreases the number of Clearcut forest sites (e.g. from 9 forests to 3 forests between age 54 and age 61). Prior to analysis of mean sensitivity, we detrended the TRW series to RWI to avoid long-term intrinsic patterns of growth decline due to aging trees. The TRW series were detrended using a spline function with a 50 % cutoff after 36 years (2/3 of the studied 54 years). We used two separate analyses to study the growth variability of the different forest types on an individual tree level and on a forest stand level. To compare the growth variability of individual trees, we calculated mean sensitivity for individual trees prior to pooling the data in each plot for statistical analysis, so that the variability of the first 54 years was compared between individual trees of the different forest types. In the second analysis, we compared stand-wide growth sensitivity by calculating mean sensitivity during the 54 year study period based on the within-plot mean RWI. We then analysed tree-level and stand-level sensitivity statistically with linear mixed models from the lme4 package (ver. 1.1–35) in R (Bates et al., 2015) with sensitivity as the response variable and forest type as the explanatory variable and plot as a random variable. Given the extensive geographical spread of the sites, we added latitude and altitude as covariates to ensure that potential differences were not artefacts of geographical variation. Furthermore, to control for between stand variation in pine dominance, we included the proportion of cored trees that are not pine (i.e. spruce) as a covariate. We tested the fixed effects of the models with Type II SS ANOVAs using Kenward-Roger corrected degrees of freedom in the lmerTest package (ver. 3.1–3) in R (Kuznetsova et al., 2017).

To explore the forests' growth dependency on weather variability, we tested the effect of monthly values for precipitation, minimum temperature, mean temperature, maximum temperature, and SPEI on RWI. For each climatic variable and month, we used linear mixed models fitted with the nlme package (ver. 3.1–167) in R (Pinheiro and Bates, 2025) with RWI as the response variable and each respective climatic variable and forest type (Clearcut and Non-clearcut) as explanatory variables. Since the RWI and climatic variables are measured over multiple years, creating temporal autocorrelation in the

data, we included an AR1 covariance structure in our model. To address the spatial autocorrelation primarily caused by multiple trees per plot, we added plot as a random variable.

To test our second hypothesis that clearcutting causes reduced drought resistance in tree growth, we focused on the year 2018 and analysed indices of resistance, recovery, and resilience (Lloret et al., 2011). Here, resistance is calculated as the ratio between the RWI of 2018 and the average RWI of three years prior; recovery is calculated as the ratio between the average RWI three years after the drought and the RWI of 2018; and resilience is calculated as the ratio between the RWI after drought and the RWI prior to the drought. Finally, we fitted linear mixed models using the lme4 package in R with the drought indices as response variables, forest type as the explanatory variable, plot as a random variable, and the aforementioned covariates. We tested the fixed effects of the models with Type II SS ANOVA using Kenward-Roger corrected degrees of freedom in the lmerTest package.

To explore potential mechanisms that explain the variation between the two forest types regarding the aforementioned drought indices, we conducted mediation analyses (Imai et al., 2010). A mediation analysis is a form of path analysis that examines the direct and indirect effects of a variable, in this case clearcutting, on the response variable through a mediator (Fig. 2). As mediator variables, we used mean tree age and age heterogeneity (calculated as the tree age coefficient of variance within each plot), mean tree height and height heterogeneity, mean tree circumference and circumference heterogeneity, early growth rates (calculated as the mean biomass (kg) gained during the first 20 years), soil temperature variability, and the mass of the soil organic layer. We here assume that the relative differences between forest types were the same during the drought year 2018 as when the data were collected in 2022–2023. We calculated the mediation of the effect from forest type as $\beta_{my} * \beta_{xm} / \beta_{xy}$, where β_{my} = regression coefficient of the mediator variable on the response variable when controlling for forest type; β_{xm} = regression coefficient of forest type on the mediator variable; and β_{xy} = regression coefficient of forest type on the response variable. While standardization of data is common within path analysis, it has no effect on the outcome of the mediation analyses. Therefore, we have chosen to report each coefficient in the mediation equation as based on raw data, so that the coefficients represent the change in the response variables per unit in the explanatory or mediator variable. With the mediation analysis approach, a high positive value indicates that much of the effect of clearcutting on the response variable is *because of* the mediator variable. A high negative value indicates that clearcutting affects the response variable *despite* directionally opposite differences in the mediator variable (i.e. the mediator variable has a weakening effect on
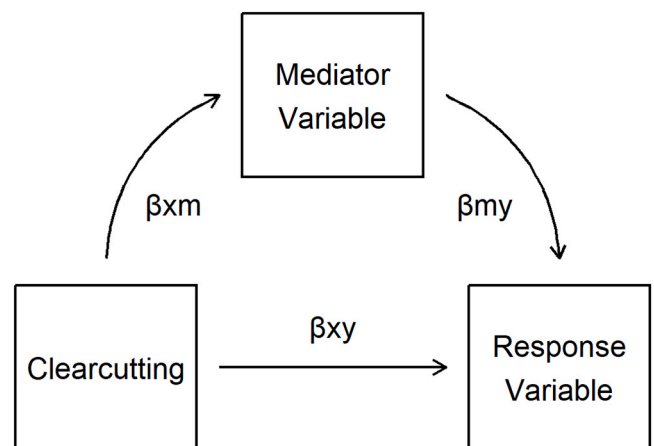

Fig. 2. Illustration of the parameters in a mediation analysis depicting the direct effect of clearcutting on a response variable where the mechanisms remain unidentified (β_{xy}), and the effect mediated through a mediator variable (β_{xm} x β_{my}), attributing the effect of clearcutting to a specific mechanism.

the differences between the forest types). A value close to 0 indicates that little of the clearcutting effect is mediated through the mediator variable, i.e. that the difference between the two forest types cannot be explained by variation in the particular variable.

Data are available at: https://doi.org/10.5281/zenodo.16037934

Code is available at: https://github.com/LundgrenAndreas

3. Results

3.1. Tree and soil characteristics

The mean tree age was higher in Non-clearcut forests than in Clearcut forests (Figure S1; Table 1). Likewise, the age heterogeneity (measured as tree age coefficient of variance) was greater in Non-clearcut forests than in Clearcut forests. The mean tree height and circumference were similar between the two forest types, but the size heterogeneity (measured as height and circumference coefficient of variance) was greater in Non-clearcut forests (Table 1). Trees growing in Clearcut forests had a higher rate of early biomass accumulation than those growing in Non-clearcut forests (Figure S2; Table 1). After 20 years, the growth rate in Clearcut forests plateaued at $\sim$3 kg tree^{-1} year^{-1} while the trees in Non-clearcut forests continued to increase their growth rate until they reached a maximum of $\sim$4.8 kg tree^{-1} year^{-1}. However, this maximum was reached after $\sim$140 years, which extends well beyond the age of the oldest trees that we currently have data on from Clearcut forests.

Temperature variability (measured as temperature coefficient of variance) of the soil was somewhat lower in Clearcut forests than in Non-

clearcut forests, but the difference was not statistically robust due to confounding effects of the geographical covariates (Table 1). The mean soil temperature throughout the measuring period (July 1st to May 15th) was 4.4 ± 0.1 and 4.1 ± 0.2 °C in Clearcut and Non-clearcut forests, respectively. The minimum soil temperature was -1.3 ± 0.3 and -3.1 ± 1.0 °C and the maximum soil temperature was 24.7 ± 1.0 and 25.4 ± 1.3 °C in Clearcut and Non-clearcut forests, respectively. There was no difference between the forest types in the amount of soil organic matter (Table 1).

There were some correlations among the tree and soil characteristics (Figure S4). The mean tree age and tree age heterogeneity were both negatively correlated to early growth rates. Tree height was positively correlated to tree circumference, and the heterogeneity of tree height was positively correlated to the heterogeneity of tree circumference. Additionally, the soil temperature variability was positively correlated to the mean tree age and circumference.

3.2. Growth sensitivity

Patterns of mean sensitivity differed depending on whether it was expressed per individual tree or as stand-wide mean sensitivity (Fig. 3; Table 1). The mean sensitivity, when calculated for each individual tree, did not differ much between the two forest types. However, when mean sensitivity was calculated based on the stand's mean annual growth, Non-clearcut forests showed lower mean sensitivity than Clearcut forests.

3.3. Impact of weather variability

During the period 1970–2020, the mean annual temperature in the study region rose by an average of 0.033 °C year^{-1} (Figure S3; Table S1). Despite a large inter-annual variation in precipitation (ranging from 345 to 774 mm year^{-1}), there was no directional trend in annual precipitation over time while SPEI decreased by $\sim$0.02 year^{-1} over the study period.

Tree growth of Clearcut forests showed greater responsiveness to weather variability than the tree growth of Non-clearcut forests (Fig. 4). The RWI of Clearcut forests was more affected by all temperature variables than those of Non-clearcut forests. Specifically, high temperatures in previous year autumn months (October, November) and current year August had a stronger negative effect, while high mean and minimum temperatures in current year September had a more positive effect on RWI in Clearcut forests compared to Non-clearcut forests. The effect of higher precipitation and SPEI on RWI was generally greater in Clearcut than Non-clearcut forests. Mainly, the precipitation and SPEI of current year summer months (June – September) had a greater positive effect on RWI in Clearcut forests than in Non-clearcut forests. In general, the effects of precipitation and SPEI on RWI were stronger than the effects of temperature.

3.4. Impact of the 2018 drought

The growth was greatly reduced in both forest types during the drought year of 2018 (TRW decline from the average growth of the three preceding years was 19 ± 1.3 % and 11 ± 1.3 % for Clearcut and Non-clearcut forests, respectively). Tree growth was more influenced by the 2018 drought in Clearcut than Non-clearcut forests, indicated by the reduced resistance values in the disturbance indices (Fig. 5; Table 1). Mediation analyses showed that the difference in resistance to the 2018 drought was mostly mediated by differences in mean tree age and early growth rate and, to a lesser extent, by age heterogeneity (Table 2). However, there was a strong correlation between the greatest mediating factors and forest type, leaving little variation explained by the mediating variables when forest type was accounted for (i.e. coefficient β_{my} was small for all mediating variables). Hence, the mediation analysis could not reveal if mean tree age, early growth rate, and age

Table 1

Descriptive statistics (mean $\pm$ standard error) of response and mediator variables, as well as mixed effects model statistics (F- and p-values) testing the effect of forest type. Latitude, altitude, percentage non-pine trees, and Al/Ca ratio are added as covariates (see Tables S2-S3 for details on full models). For the purpose of readability, mean sensitivity values have been multiplied by 100. Note that mean sensitivity is calculated from data over a time period of 54 years, while drought indices (Resistance, Recovery, Resilience) are calculated from the years around 2018 (2015–2021). CoV indicates the coefficient of variance for the given parameter. CC = Clearcut; NC = Non-clearcut. Sample sizes: n = 54 nested in 18 forests.

Response variable	CC	NC	df	F	p
Tree mean sensitivity (val x 100)	8.00 ± 0.2	8.87 ± 0.3	1, 12.5	0.91	0.36
Stand mean sensitivity (val x100)	4.43 ± 0.2	3.38 ± 0.2	1, 12.6	4.66	0.05
Resistance	0.88 ± 0.0	0.95 ± 0.0	1, 11.9	11.1	< 0.01
Recovery	1.17 ± 0.0	1.03 ± 0.0	1, 12.3	4.47	0.06
Resilience	1.03 ± 0.0	0.98 ± 0.0	1, 12.4	0.04	0.85
Mediator variables used for 2018 drought indices	**CC**	**NC**	**df**	**F**	**p**
Mean tree age (years)	49.0 ± 1.6	99.0 ± 4.3	1, 12.5	43.0	< 0.01
Age heterogeneity (CoV)	15.8 ± 1.6	40.2 ± 4.5	1, 12.8	8.96	0.01
Early growth rate (kg year^{-1})	1.77 ± 0.1	0.55 ± 0.0	1, 12.5	10.2	< 0.01
Mean tree height (m)	12.2 ± 0.4	12.8 ± 0.4	1, 12.7	0.41	0.53
Height heterogeneity (CoV)	22.1 ± 1.4	31.0 ± 2.2	1, 12.4	7.82	0.02
Mean tree circumference (cm)	51.7 ± 1.7	57.1 ± 2.4	1, 12.5	1.18	0.30
Circumference heterogeneity (CoV)	32.4 ± 1.9	48.2 ± 2.5	1, 12.5	13.1	< 0.01
Soil temperature variability (CoV)	138 ± 3.2	160 ± 6.2	1, 12.8	3.10	0.10
Soil organic matter (kg m^{-2})	12.9 ± 1.6	12.7 ± 1.1	1, 12.3	0.19	0.67
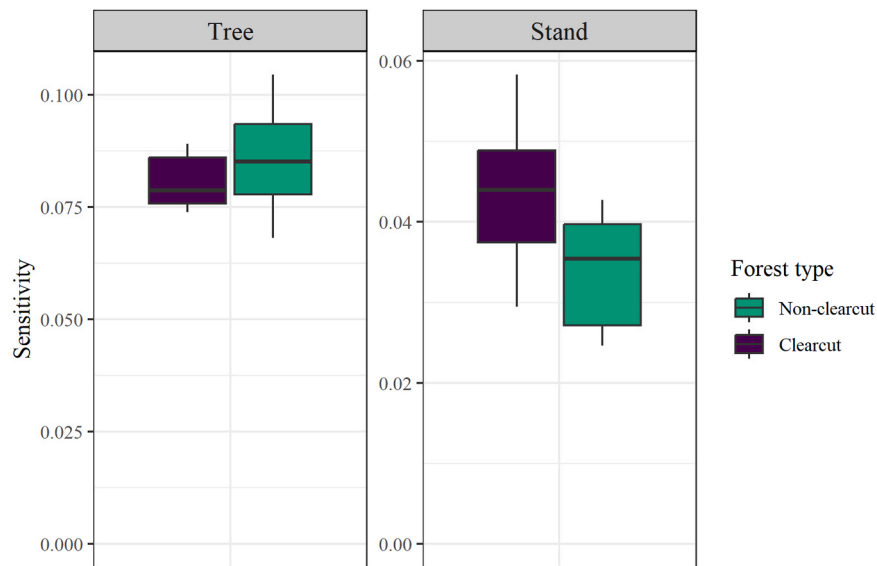
Fig. 3. Difference in mean sensitivity (inter-annual growth variability) between Clearcut forests and Non-clearcut forests. On the left, the data is presented for individual trees, and the mean sensitivity is calculated for each individual tree and then averaged per forest. On the right, the data is presented as a standwide mean average, and the mean sensitivity is calculated based on the forests' mean annual growth. Note the difference in scale between the two facets. In both cases, N = 18.
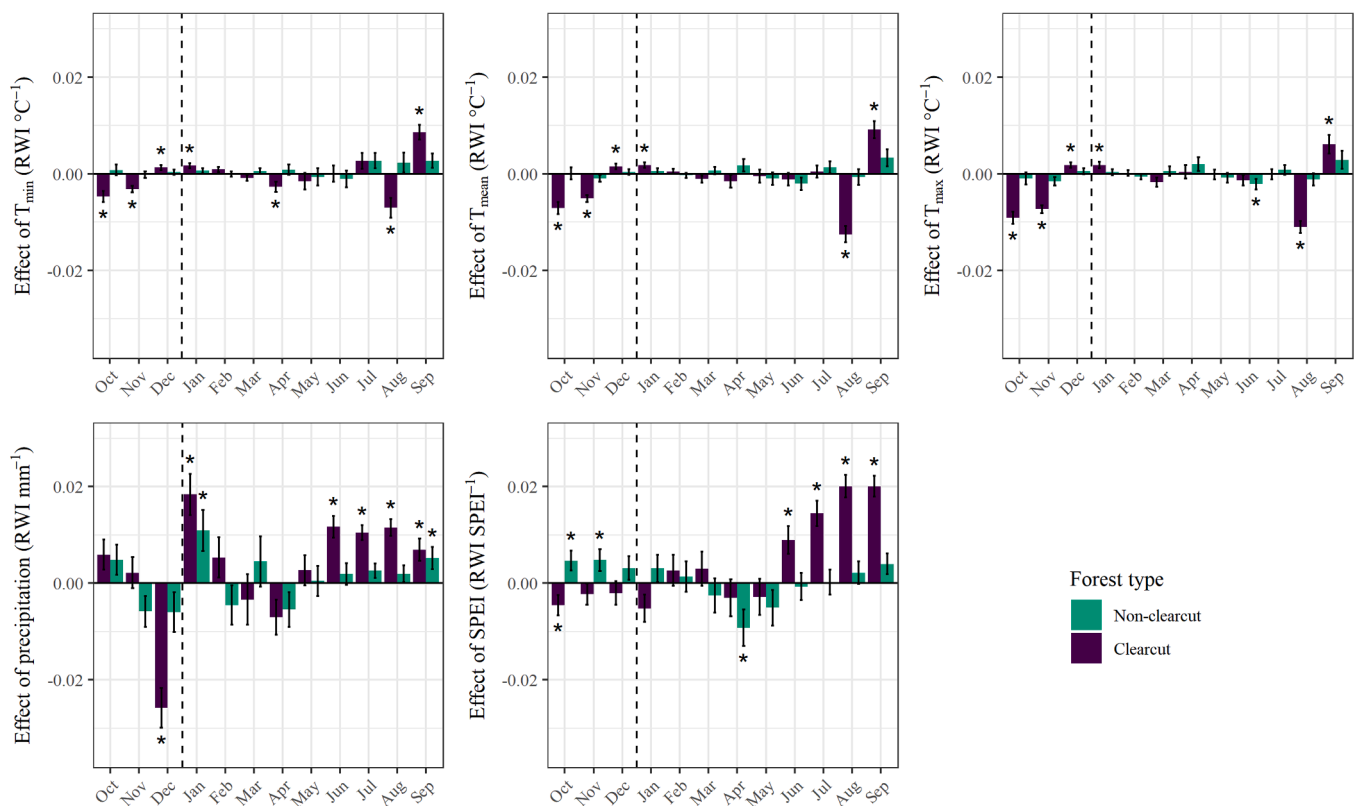
Fig. 4. Model output of the effects of climatic variables (maximum, mean, and minimum temperature, precipitation, and SPEI) on RWI in Non-clearcut forests (green) and Clearcut forests (purple). Asterisks indicate months where the main effect of the respective climatic variable on RWI in the indicated forest type shows a p-value < 0.05. In each month and climatic variable, N = 18.

heterogeneity, are true mediators of the effect of clearcutting or if their apparent effects resulted from multicollinearity with forest type.

Since the growth rates of both forest types returned to normal values in the years that followed the drought year of 2018, the recovery rate was greater in Clearcut forests due to their more substantial growth decline during the drought (Fig. 5). None of the studied variables

mediated much of the differences in drought recovery (Table 2). Instead, the differences in mean age as well as heterogeneity in age, height, and circumference all weakened the differences in drought recovery.

The opposing directions of differences with greater resistance in Non-clearcut forests and greater recovery in Clearcut forests resulted in a similar resilience index for the two forest types (Fig. 5).
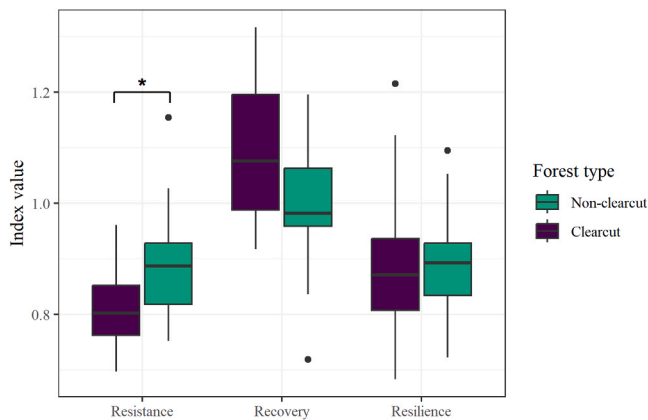
Fig. 5. Index values of resistance, recovery, and resilience, to the 2018 drought, based on RWI data for Clearcut forests (purple) and Non-clearcut forests (green). Asterisk indicates differences between forest types with a p-value < 0.05 (see Table 1 for detailed statistical output). In each index, N = 18.

4. Discussion

In this study, we examined the differences in tree growth sensitivity and response to weather variability between forests that had been clearcut ~60 years prior to the study and forests that have never been clearcut in northern Sweden. We found that disrupting tree continuity by clearcutting generally decreases the forests' ability to withstand extreme drought events. This is in accordance with similar findings from temperate forests (Alfaro-Sánchez et al., 2019; Mausolf et al., 2018; Oheimb et al., 2014), as well as recent findings from the Swedish boreal forest (Wolf et al., 2023). Our results further suggest that the increased drought sensitivity in forests regenerated after clearcutting is mediated through changes in tree characteristics such as decreased mean tree ages and increased early growth rates.

4.1. Growth sensitivity

We found modest support for our first hypothesis that tree growth stability would decrease following clearcutting. When examining the effect of clearcutting on tree growth stability, as measured by mean sensitivity scores, we found minor differences in mean sensitivity between Clearcut and Non-clearcut forests. Overall, the general mean sensitivity score in our study was slightly lower than those previously reported from forests in the region. For example, Linderholm and Linderholm (2004) showed mean sensitivity scores of 0.15 – 0.21 in pine trees, which is higher than the numbers we recorded (0.06 – 0.12). Interestingly, we found that the difference in mean sensitivity between Clearcut and Non-clearcut forests differed depending on whether it was expressed at the tree or stand level. When expressed as mean sensitivity at the individual tree level, the mean sensitivity score was slightly higher in Non-clearcut forests. Older trees may exhibit greater mean sensitivity (Carrer and Urbinati, 2004), which may explain our result, but the difference between forest types in our study was very small. In contrast, when we expressed mean sensitivity as the plot mean sensitivity across the stand, the mean sensitivity score was lower in Non-clearcut forests. Hence, the trees of the Non-clearcut forests showed more complementary growth patterns than the Clearcut forests, so that low growth for some trees was compensated by higher growth of other trees in the same plot.

4.2. Impact of weather variability

We found that tree growth in Clearcut forests showed greater responsiveness to temperature and precipitation than tree growth in Non-clearcut forests. Generally, growth in Clearcut forests was more

Table 2
Mediation analyses of the effect of forest type mediated through mediator variables (mean tree age, age heterogeneity, mean tree height, height heterogeneity, mean circumference, circumference heterogeneity, early growth rate, soil temperature variability, and soil organic matter) on response variables (resistance to, and recovery from, the 2018 drought), based on detrended tree-ring series. Mediation values correspond to the proportion of the effect of clearcutting on the response variable that is explained by the mediator variable (calculated by: $\beta_{my} * \beta_{xm} / \beta_{xy}$). Note that negative mediation values indicate weakening effects. Path coefficient values are reported as mean (with standard deviation in parentheses), while the Mediation values are reported based on the means of the path coefficients.

Mediator variable	β_{my}	β_{xm}	β_{xy}	Mediation
Response variable: Resistance to 2018 drought				
Mean tree age	4.9×10^{-4}	49.4	0.08	0.30
	(6.8×10^{-4})	(7.53)	(0.02)	
Age heterogeneity	4.9×10^{-4}	25.4	0.08	0.15
	(7.2×10^{-4})	(8.50)	(0.02)	
Early growth rate	-1.8×10^{-2}	-1.12	0.08	0.25
	(1.5×10^{-2})	(0.35)	(0.02)	
Mean tree height	-4.9×10^{-3}	0.63	0.08	-0.04
	(6.0×10^{-3})	(0.99)	(0.02)	
Height heterogeneity	-6.5×10^{-4}	9.66	0.08	-0.08
	(1.4×10^{-3})	(3.46)	(0.02)	
Mean tree circumference	-1.2×10^{-3}	5.12	0.08	-0.08
	(1.1×10^{-3})	(4.71)	(0.02)	
Circumference heterogeneity	3.7×10^{-4}	15.9	0.08	0.07
	(1.2×10^{-3})	(4.38)	(0.02)	
Soil temperature variability	-3.2×10^{-4}	18.8	0.08	-0.08
	(5.0×10^{-4})	(10.5)	(0.02)	
Soil organic matter	-1.7×10^{-4}	-8.76	0.08	0.02
	(2.3×10^{-4})	(20.3)	(0.02)	
Response variable: Recovery from 2018 drought				
Mediator variable	β_{my}	β_{xm}	β_{xy}	Mediation
Mean tree age	3.6×10^{-4}	49.4	-0.09	-0.21
	(9.4×10^{-4})	(7.53)	(0.04)	
Age heterogeneity	9.1×10^{-4}	25.4	-0.09	-0.27
	(1.0×10^{-3})	(8.50)	(0.04)	
Early growth rate	2.1×10^{-3}	-1.12	-0.09	0.03
	(2.0×10^{-2})	(0.35)	(0.04)	
Mean tree height	-7.0×10^{-3}	0.63	-0.09	0.05
	(8.4×10^{-3})	(0.99)	(0.04)	
Height heterogeneity	1.5×10^{-3}	9.66	-0.09	-0.17
	(2.0×10^{-3})	(3.46)	(0.04)	
Mean tree circumference	8.8×10^{-4}	5.12	-0.09	-0.05
	(1.5×10^{-3})	(4.71)	(0.04)	
Circumference heterogeneity	7.2×10^{-4}	15.9	-0.09	-0.13
	(1.7×10^{-3})	(4.38)	(0.04)	
Soil temperature variability	2.2×10^{-5}	18.8	-0.09	0.00
	(9.1×10^{-4})	(10.5)	(0.04)	
Soil organic matter	-3.5×10^{-4}	-8.76	-0.09	-0.04
	(3.0×10^{-4})	(20.3)	(0.04)	

negatively affected by temperature (with the exception of September temperature which showed an opposite pattern) and more positively affected by precipitation and SPEI than growth in Non-clearcut forests. As both temperature and precipitation are expected to increase in the studied area as a result of global warming (IPCC, 2023 – and temperature data from the Arjeplog weather station in this study), it is difficult to predict if and how the forest types will diverge in their growth-weather response. Furthermore, we found temporal discrepancies revealing that summer precipitation (and SPEI) generally had a positive effect on growth while winter and spring precipitation had a more modest effect. This is possibly due to winter precipitation delaying the start of the growing season (Yun et al., 2018), and thereby limiting the otherwise positive effect of precipitation. Projected precipitation show an increase mainly during the winter months rather than the summer months (Alcamo et al., 2007). Such temporal dependency complicates the prediction of future tree growth responses as the differing effects of precipitation on tree growth was mostly apparent in summer months. Furthermore, while increased precipitation had a generally greater effect on growth than temperature in our study, future precipitation

increases are predicted to be more unevenly distributed, featuring more distinct periods of heavy rainfall interrupted by droughts, rather than a uniform increase (IPCC, 2021). Periods of heavy rainfall generally weaken a tree's positive relationship with precipitation (Land et al., 2017), and droughts are generally negative for tree growth. Hence, the potential positive effects of increased precipitation in Clearcut forests may be double-edged. If droughts become more frequent between periods of heavy rainfall, the positive growth effects stimulated by higher precipitation may be offset, or even reversed, due to increased drought sensitivity during low precipitation periods.

4.3. Impact of the 2018 drought

We found support for our second hypothesis that forests regenerated after clearcutting would be less resistant to droughts. This reasonably follows from the Clearcut forests' greater responsiveness to temperature and precipitation, and is in line with previous studies, finding similar differences in the response to 2018 between old and more recently established forests in Sweden (Wolf et al., 2023), and in general drought responses in temperate regions (Alfaro-Sánchez et al., 2019; Mausolf et al., 2018; Oheimb et al., 2014). While the climatic data from the Arjeplog station did not reveal extreme values for 2018 in terms of annual mean temperature or precipitation (Figure S3), the year of 2018 has been noted as an extreme drought year in several previous studies (e. g. Martínez-García et al., 2024; Toreti et al., 2019). Importantly, the forest productivity of this study region was especially negatively affected by the 2018 drought (Wolf et al., 2023). Hence, the difference observed in our study may be exacerbated compared to a larger, biome-encompassing scale. However, if extreme droughts become more common in the boreal biome (Toreti et al., 2019; IPCC, 2021), the results of our study may be indicative of future drought effects on a larger scale.

There are many potential explanations to our observed differences in drought response between Clearcut and Non-clearcut forests. Here we have examined the mediation of the drought tolerance through differences in both tree and soil characteristics. Importantly, the mediators that appeared most influential (i.e. those that accounted for a large proportion of the effect of clearcutting on drought resistance) were strongly correlated with forest type. This indicates that the observed mediation partly reflects shared variance with forest type rather than independent effects. Keeping this in mind, one of the most important mediating factors in our study was early growth rate. This is consistent with previous studies that have found strong negative correlations between early growth and stress tolerance (Bigler, 2016; Bigler and Veblen, 2009; Di Filippo et al., 2015; Tao et al., 2024; Zang et al., 2014). Here, we found clear differences in growth patterns between forests that have been clearcut and those that have not. Most apparently, the early growth of Clearcut forests was substantially greater than that of Non-clearcut forests. This is not surprising, considering that clearcutting increases access to both nutrients and light (LeDuc and Rothstein, 2007), two of the most important growth-influencing factors in boreal forests (Kärenlampi and Riekkinen, 2004). Potentially, increased resource allocation to stem radial growth may come at the cost of reduced resource allocation to stress tolerance (Loehle, 1988) which could explain the detrimental effect of high early growth rates. Furthermore, the higher nutrient availability following clearcutting may have shifted the allocation patterns of trees in Clearcut forests, resulting in reduced resource allocation to belowground growth (Lim et al., 2015; Mausolf et al., 2018). This could lead to smaller root systems and, consequently, a reduced ability to access water during drought years.

Differences in soil properties have been shown to influence trees' drought tolerance, where drought sensitivity is generally higher in forests with greater soil bulk density (Cartwright et al., 2020), or poorly developed organic layers (Oheimb et al., 2014). Accordingly, drought tolerance in forests of disrupted continuity can be mediated by characteristics of the soil organic layer (Oheimb et al., 2014). However, the forests in our study exhibited minimal variation in soil organic mass,

thereby disabling it as an important mediating factor in the observed reduced drought tolerance. Although we cannot rule out that the soil organic layer does play a role in drought tolerance even within our study system, we can show that similarities in soil organic layers do not equate to similar drought tolerance. Interestingly, in our study, the Non-clearcut forests had slightly more variable soil temperatures than Clearcut forests, while at the same time retaining greater drought resistance. Warmer soils have the potential to increase water loss in trees (Wieser et al., 2015), especially in isohydric species such as pine (Hu et al., 2024; Martín-Gómez et al., 2017). This may potentially explain why we found that the soil temperature variability had a weakening effect (although very minor) on the resistance values. In turn, this suggests that the Non-clearcut forests could potentially show even greater drought resistance if soil temperature variability would have been equal.

5. Conclusion

We found that trees growing in forests regenerated after clearcutting were more affected by temperature and precipitation patterns compared to stands that had been logged but never clearcut in northern Sweden. Further, we found that tree growth in forests regenerated after clearcutting was more severely affected by the extreme drought of 2018. The decrease in drought resistance was mainly mediated by a decrease in mean tree age as well as increased early growth rates in forests that have regenerated after clearcutting. It remains to be clarified whether the differences we have observed between clearcut forests and forests with long uninterrupted tree continuity represent an inherent effect of clearcutting, or whether they are primarily explained by the fact that clearcutting results in stands with lower average age and higher growth rates during the early stages of development, which generally make such forests more sensitive to weather variability. Nevertheless, our results demonstrate that clearcut forestry increases the responsiveness of tree growth to weather, which may be an important consideration for future forest management.

CRediT authorship contribution statement

Joachim Strengbom: Writing – review & editing, Writing – original draft, Conceptualization. **Gustaf Granath:** Writing – review & editing, Writing – original draft, Conceptualization. **Andreas Lundgren:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

Acknowledgements

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123295.

Data availability

Data are available at: https://doi.org/10.5281/zenodo.16037934 and Code at: https://github.com/LundgrenAndreas

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