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Stand density and structural complexity modulate the effects of restorative selective cutting on aboveground carbon stocks

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ABSTRACT

Forest management is increasingly recognized as a strategic adaptative measure to climate change, aiming to integrate biodiversity conservation and move beyond traditional even-aged systems globally. Selective cutting is thereby attracting attention as it is expected to maintain complex forest structure and provide multiple ecosystem services including aboveground carbon stocks. However, whether selective cutting modifies the relationships between stand structure and aboveground carbon stocks in uneven-aged, mixed species forests remains poorly understood. Using restorative selective cutting experiments conducted in southern Norway and Sweden, we investigated how selective cutting influences stand structural attributes and structural complexity, as well as the relationships between stand structure and aboveground carbon stocks in mixed stands. We found that stand density and tree size variation are the key factors determining stand structural complexity. In addition, both stand density and structural complexity drive aboveground carbon stocks. In contrast, species diversity did not significantly affect stand structural complexity, while it did negatively impact aboveground carbon stocks in selectively cut stands. We showed that selective cutting does not alter stand structural complexity nor the relationships between stand structure and aboveground carbon stocks. Therefore, selective cutting may present a promising strategy for maintaining complex stand structures beneficial for biodiversity conservation and enhancing aboveground carbon stocks. Consequently, selective cutting practices can prioritize the retention of greater tree size variation to foster both complex forest stand structure and increased aboveground carbon stocks.

1. Introduction

Over recent decades clear-cutting-based even-aged management has increasingly dominated production forests in Scandinavia, largely driven by the development of modern industrial-scale forestry (Kuuluvainen et al., 2012; Puettmann et al., 2015). However, the viability of intensively-managed and simplified production forest systems is being challenged by climate change (Patacca et al., 2023), biodiversity loss (IPBES, 2019), and broadening societal demands for the forest environments provided (Felton et al., 2024; Winkel et al., 2022). As a result, there is a growing need for forest management strategies to prioritize resilience and a breadth of forest ecosystem services, including carbon sequestration and biodiversity conservation, that go beyond the production of traditional forest commodities such as timber (Ekholm et al., 2023; Felton et al., 2024; Uhl et al., 2024). Thus, the application of uneven-aged forest management systems, also referred to as continuous cover forestry (CCF), has gained increasing interest (Peura et al., 2018; Hertog et al., 2022; Mason et al., 2022). CCF is a silvicultural technique characterized by the removal of individual trees of all sizes or small group of trees, often involving the use of natural regeneration (Pommerening and Murphy, 2004). Selective cutting is one approach to implementing CCF, involving the cutting of individual trees throughout the entire stand area. In contrast to clear-cutting, selective cutting can enhance ecosystem services and biodiversity by preserving a multi-layered stand structure (Schütz, 2002).

Selective cutting can be guided by different management objectives, resulting in varied forest outcomes. When primarily intended for timber production (production-oriented selective cutting), selective cutting is

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focused on promoting economically desired tree species (Owari et al., 2016; Owari, 2026). In contrast, when used to restore forest ecosystems (restorative selective cutting), selective cutting may be used to promote compositional, structural and functional diversity (Götmark, 2009; Stanturf et al., 2014). Restorative selective cutting is increasingly being implemented in Sweden to promote biodiversity (Götmark, 2005; Nordén et al., 2019; Nordén et al., 2025; Torres-García et al., 2026). This use of restorative selective cutting is also providing opportunities to assess how selective cutting affects forest stand structure, as well as associated changes in aboveground carbon stocks. For our purpose, the term "selective cutting" will hereafter be used to indicate restorative selective cutting to simplify the terminology. In this context, the selective cutting prescriptions involved removing only certain tree species without focusing on sustained yields (Ford-Robertson, 1971).

Forest stand structure is an important indicator of a forest's potential to contribute to habitat availability, and thus managing stand structure is a critical aspect of managing production forests for biodiversity (Staudhammer and LeMay, 2001). It is largely for this reason that, for example, the European Union (EU) Biodiversity Strategy recommends CCF as a biodiversity friendly forest management practice (Mason et al., 2022). Stand structure is typically characterized by two components; stand structural attributes and stand structural complexity (McElhinny et al., 2005). Stand structural attributes include stand density, tree species diversity, tree size variation, and tree spatial distribution. In contrast, stand structural complexity refers to the variety and abundance of different structural attributes within a stand (Zenner and Hibbs, 2000; McElhinny et al., 2005), which is determined by the underlying stand structural attributes (Zenner, 2000; Neumann and Starlinger, 2001; Ehbrecht et al., 2017; Seidel et al., 2019b). Both stand structural attributes and structural complexity can be directly modified through silvicultural interventions (Schütz, 2002; Schall et al., 2018). The vertical structure and diameter distribution of forest stands managed under selective cutting are hereby generally considered to more closely emulate the disturbance regime characteristics of primary or unmanaged forests compared to even-aged systems (Kuuluvainen et al., 2012; O'Hara, 2016). Selective cutting may also have lower impact on the species diversity of a range of forest-dependent taxa relative to unmanaged stands (Götmark et al., 2005; Dieler et al., 2017; Schall et al., 2018; Ekholm et al., 2023). Despite these findings, considerable uncertainty remains over whether structural modifications caused by selective cutting affect the relationships between stand structural attributes and stand structural complexity, as well as the relationships between forest stand structure and specific ecosystem services; such as aboveground carbon stocks.

The relationships between stand structure and ecosystem functions and services, as well as aboveground carbon stocks, have been examined across different forest ecosystems (Paquette and Messier, 2011; Zhang et al., 2012; Liang et al., 2016; van der Plas, 2019; Yuan et al., 2020). However, much debate has centred on the role of forest stand structure in promoting aboveground carbon stocks. The three fundamental mechanisms - niche complementarity, selection, and mass-ratio hypothesis, have often been used to explain these relationships (Grime, 1998; Loreau and Hector, 2001; Fotis et al., 2018; Ullah et al., 2021). In the niche complementary effect, higher stand density, species diversity, and tree size variation improve canopy packing and stratification (Jucker et al., 2015; Ali et al., 2016) and promote aboveground carbon stock to the efficient utilization of resources by the component tree species of different sizes in a forest stand (Paquette and Messier, 2011; Ali et al., 2016; Liang et al., 2016; Yuan et al., 2020). The selection effect suggests that a higher aboveground carbon stocks occurs due to the higher probability occurrence of few productive tree species in dense and highly diverse stands (Loreau and Hector, 2001). As an alternative yet mutually exclusive mechanism to niche complementarity, the mass-ratio hypothesis (Grime, 1998), suggests that the most dominant species largely drive ecosystem functions and aboveground carbon stocks. Based on these ecological mechanisms, the selective removal of trees from a stand to alter their density, size variation and species diversity, can be expected to affect stand structural complexity, and the relationships between forest stand structure and aboveground carbon stocks (Pretzsch and Hilmers, 2025). Nevertheless, few studies have evaluated how selective cutting may alter these relationships and the mechanisms that underly these relationships.

Here we aimed to (1) assess whether selective cutting modifies the relationships between stand structural attributes and stand structural complexity; and (2) evaluate how selective cutting regulates the relationships between stand structure and aboveground carbon stocks. We expected that, although selective cutting modified stand structural attributes and aboveground carbon stocks by reducing stand density, stand structural complexity was not influenced by selective cutting. In addition, we also anticipated that selective cutting does not change relationships between stand structure and aboveground carbon stocks.

2. Materials and methods

2.1. Study area and design

The study sites were located in southern Sweden (33 sites) and southern Norway (8 sites) (Fig. 1) in the transition zone between boreal and temperate forests (Sjörs, 1999). The plots have dry to mesic soil types often with stones at the ground surface (Götmark et al., 2005; Nordén et al., 2019). The altitude of the plots ranged from 14 to 277 m above sea level. The forests are cold temperate forests with a mixture of broadleaved species and conifers. All stands had been regenerated naturally.

The experiments were established in 2002 (21 sites) and 14 years later in 2016 (20 sites). At each site, two 1-ha plots (100 ×100 m each) were established, of which one plot was selected randomly to be a selective cutting plot (S), and the remaining assigned as the control plot (C). Selective cutting in the S plots was carried out during the winters of 2002/03 and 2016/17. The selective cutting was mainly implemented for restoration and nature conservation purposes and not for increasing wood production. Thus, trees of low timber value but high expected importance for biodiversity, such as cavity-bearing or injured trees, were retained. Norway spruce (*Picea abies* L.), birch (*Betula* spp) and other sub-canopy woody species such as Common hazel (*Corylus avellana* L.) were the tree species most commonly selected for cutting. Selective cuttings more closely resembled single-tree selection than group selection, target diameter cutting, or gap cutting. In addition, selective cutting operations are more similar to thinning from below than thinning from above. The spatial distribution of harvested trees was relatively even throughout the plots, with all felled trees removed. On average, 25–30% of the basal area was removed. Characteristics of the 41 study sites are listed in Table S1.

2.2. Forest inventory

Within each of the S and C plots, three circular subplots ($r = 10$ m) were established (Fig. 1). The total number of inventory plots was 245 across 41 sites. One subplot was not measured due to high water levels during the field survey period.

In each circular subplot, all individual trees with a diameter at breast height (DBH) ≥ 5 cm were measured in the spring 2024. Individual tree information, such as species, DBH, tree height, and survival status (live or dead) was recorded. The DBH (in millimetre) was measured using a tape measure at a height of 1.3 m above ground, and tree height (in meter) was measured using a Vertex Laser Geo 2 (Haglöf Sweden AB). The coordinates at the centre of each circular subplot were recorded with a Garmin handheld GPS, and the centre points were marked with aluminium poles for subsequent measurements. The distance and compass bearing from each tree with a DBH ≥ 5 cm to the plot centre were also measured. We used the build-in compass of the Vertex Geo 2 to measure the compass bearing. The compass has a resolution of 0.1° and

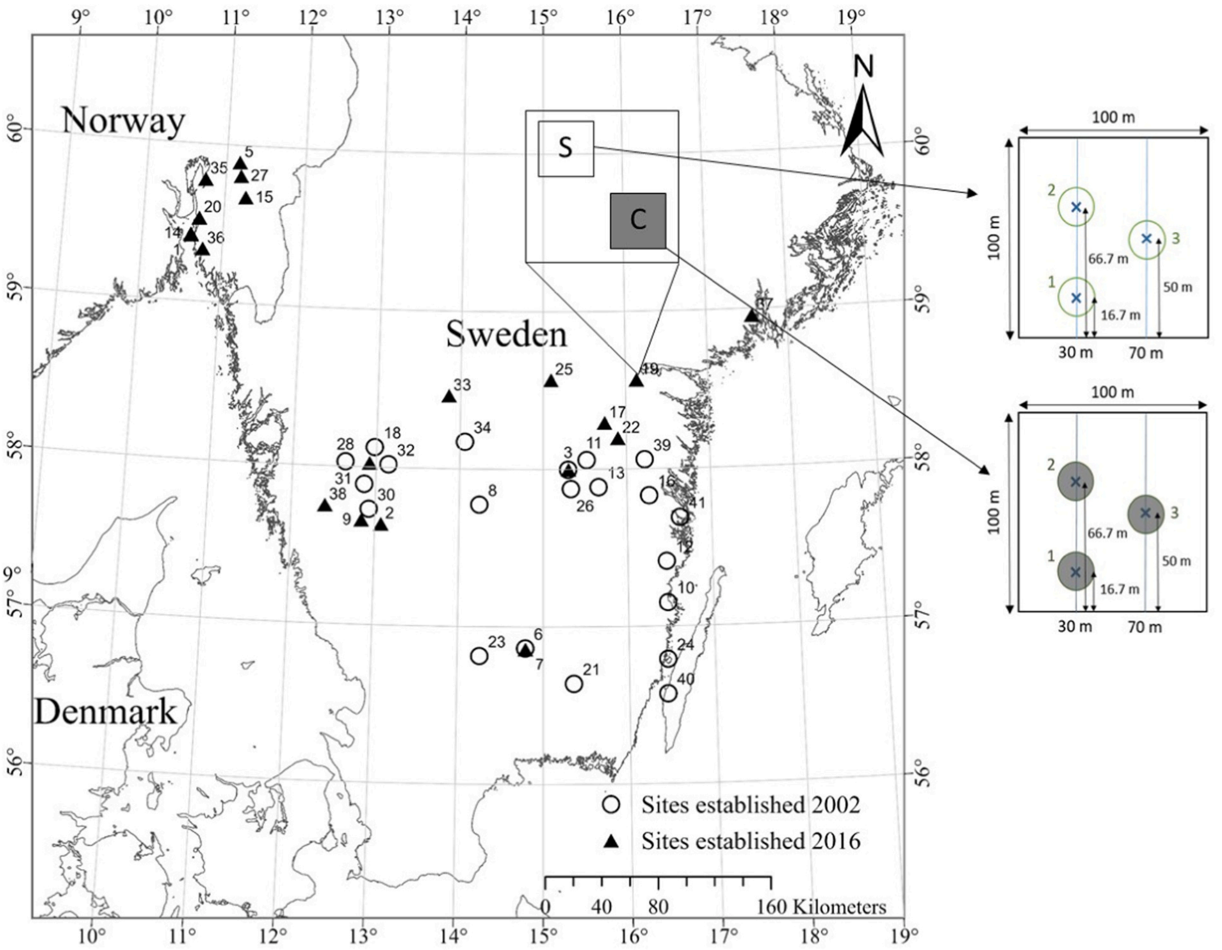

Fig. 1. Location of study sites in southern Sweden and Norway (Selective cutting = S, and a control without cutting = C) where sites with triangles were established in 2016/17 and sites with open circles were established in 2002/03. Numbers 1–41 in the map correspond to the site numbers in the Table S1. In each of the two treatments, three circular subplots (radius =10 m) were established for tree and deadwood inventories.

accuracy of 1.5° RMSE. Distances were also measured with the Vertex Laser Geo 2, with a resolution of 10 cm. In total, twenty-three species were recorded. The most common tree species were oak (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.) (42% of total basal area), followed by Norway spruce (12%), birch (10%), aspen (*Populus tremula* L.) (9%), Scots pine (*Pinus sylvestris* L.) (6%) and linden (*Tilia cordata* Mill.) (5%). The remaining tree species each constituted 3% or less of the total basal area. The proportion of each species by basal area in both C and S plots is described in Table S2.

Deadwood within each subplot was measured according to Jönsson et al. (2023). All standing and fallen dead trees, cut-stumps, and branches were measured and identified to species-level where possible, using the following inclusion criteria. The DBH of all standing dead trees with DBH $\geq$ 10 cm was measured. For fallen deadwood the minimum diameter was 10 cm, and the minimum length of fallen deadwood was 1.30 m. For standing dead trees shorter than 6 m, mid diameter was measured. The height of all standing dead trees taller than 1.3 m was measured. For each fallen deadwood longer than 1.3 m, the length of the log up to a small-end diameter of 10 cm, and the diameter at the mid-point were measured. All deadwood that originated inside the subplot was included in the measurement. If the origin was unclear, the deadwood was included if a minimum of 50% of the part with a diameter of $\geq$ 10 cm was within the plot. In addition, the four decay classes (1 – 4) of deadwood were recorded. Decay class 1 was the least decayed, in which more than 90% of the stem volume consists of hard wood and is only slightly affected by decomposing organisms. Decay class 2 consisted of stems that are only slightly decomposed, and the stem contains 10–25% soft wood. In decay class 3, the stem was decomposed to the extent of containing 26–75% soft wood; and if the stem was 76 – 100% soft and very decomposed, it was regarded as decay class 4.

2.3. Quantification of stand structural attributes and stand structural complexity

We calculated traditional stand structural attributes, such as tree density (tree ha^{-1}) and basal area (m^2 ha^{-1}), species diversity, and tree size variation for each subplot. For the quantification of tree species diversity (Hs), we used Shannon's diversity index (Eq. 1), as it incorporates both species richness and evenness. In Eq. 1, species abundances were represented by species-specific basal area, and Hs was calculated using these basal area values, resulting in a basal area-weighted measure of species diversity.

$$Hs = -\sum_{i=1}^{s} p_i \ln p_i \tag{1}$$

where *Hs* is the species diversity, p_i is the proportion of basal area of *i*th species and *S* is the number of species within a subplot. Hs was calculated using the *vegan* package (Oksanen et al., 2024). To account for tree size variation, we derived coefficient of variation of DBH (CV-DBH) and Gini coefficients of DBH (Gini-DBH). Gini-DBH was calculated using *ineq* package (Zeileis, 2014). We also derived additive stand density index (ASDI) using following equation (Long and Daniel, 1990).

$$ASDI = \sum_{i=1}^{n} \left(\frac{DBH_i}{25}\right)^{1.6} \tag{2}$$

where ASDI is the additive stand density index (Long and Daniel, 1990; Chivhenge et al., 2024) and DBH_i is the DBH (in cm) of *i*th tree in the subplot, and ASDI was standardized to a per-hectare value.

To quantify the stand structure complexity, the structural complexity index (SCI) was calculated. SCI is a three-dimensional (3D) metric that describes stand structural heterogeneity based on the spatial distribution and height of individual trees within a plot (Zenner, 2000; Zenner and Hibbs, 2000). Each triangular unit is defined by three neighbouring trees represented as 3D points using their spatial position (x, y) and height (z), forming an irregular spatial pattern. The spatial (x, y) positions of trees define the base of the triangle, and heights (z) contributes to the 3D surface of the triangle. When applied across an entire stand, this method generates a triangulated irregular network (TIN), a network of non-overlapping triangles that captures spatial variation in tree sizes. The SCI was then calculated (Eqs. 3 and 4) as the sum of the 3D surface areas of the TIN divided by the horizontal ground area covered by all triangles (Zenner, 2000). The following equations were used to calculation SCI (Zenner and Hibbs, 2000).

$$\mathrm{SCI} = \mathrm{SCI}^{*} \ / \ \mathrm{A_T} \tag{3}$$

$$\mathrm{SCI}* \quad = \sum_{j=1}^{N} \frac{1}{2} |\mathrm{a} \times \mathrm{b}| \tag{4}$$

where, N is the number of triangles in the subplot, A_T is the total area of non-overlapping two-dimensional triangles, $|a \times b|$ is the absolute value of the vector product of vectors AB and AC with coordinates $a = (x_b - x_a, y_b - y_a, z_b - z_a)$, and $b = (x_c - x_a, y_c - y_a, z_c - z_a)$. The x and y coordinates of individual trees were calculated using the distance and compass bearing from each tree to the plot centre, and tree height was used as the z coordinate. All standing trees with DBH $\geq$ 5 cm, including standing dead trees due to their importance in the forest stand structure, were used for the SCI calculation. The effect corrections (Fig. S1) were conducted by omitting triangles whose neighbours may have been outside of the subplot boundary subplot as described in Zenner (2000). For each triangle, a midpoint was first determined between the two trees closest to the plot centre. A triangle was excluded if the distance from this midpoint to the third tree was greater than the distance from the midpoint to the edge of the subplot. However, this criterion was applied only to triangles containing trees located more than 7.5 m from the subplot centre, to avoid zero or high SCI values in subplots with few, widely spaced trees.

2.4. Quantification of aboveground carbon stocks

We used biomass equations to derive individual living tree aboveground biomass (see Table S3 for the biomass functions used). We used biomass functions of Marklund (1988) for Norway spruce, Scots pine and Birch, and Husmann et al. (2018) for oak, beech, and ash. The biomass functions of birch were applied to other broadleaved species except oak, beech and ash (Table S3). We converted the living tree biomass into living tree carbon stocks using the carbon fraction of 0.5 for all species (Neumann et al., 2016; Martin et al., 2018).

To estimate the carbon stocks in deadwood, we first calculated the deadwood volume. We used the formula for volume of a cylinder to calculate the volume of the fallen logs and branches, and standing dead trees up to 6 m. To estimate the volume of the standing dead trees over 6 m, we followed the method used in the study by Puletti et al. (2019) using the formula;

$$V_{deadtree} = f.\ \mathrm{H.}\ \pi/4.\ \mathrm{DBH}^2 \tag{5}$$

where $V_{deadtree}$ is the volume of standing dead trees/snags and high stumps, *f* is the shape coefficient, which was set equal to 0.5, and H is the tree total height.

We then applied biomass expansion factors (BEF) for each decay class (Sandström et al., 2007) to convert deadwood volume into biomass. BEF are only available for Norway spruce, Scots pine and birch. The species-specific BEF for these species were applied, and BEF of birch was applied for other broadleaved species. To convert the deadwood biomass into deadwood carbon stocks, we multiplied deadwood biomass with 0.5, which is the rounded carbon conversion factor (Neumann et al., 2016; Martin et al., 2018). Total carbon aboveground stocks (CST) is the sum of living tree and deadwood carbon.

2.5. Statistical analysis

All statistical analyses were performed in R (R Core Team 2024). Fourteen of the 245 inventory plots were excluded from the analysis because they overlapped with different cutting treatments.

A generalized linear mixed-effects model (GLMM) was used to test whether selective cutting influences stand structural attributes and stand structural complexity (SCI). We tested the treatment effect on seven stand structural attributes: tree density, ASDI, basal area, species diversity, CV-DBH, Gini-DBH, and aboveground carbon stocks. We considered the treatments (C and S) and years since cutting as fixed effects and subplots nested within sites were considered as random effects. The overview of the models is described in Table S4. GLMMs were performed using the “glmmTMB” package (Brooks et al., 2017). Post-hoc tests were conducted with the “emmeans” package (Lenth, 2025), and model evaluation, including residual diagnostics and assumption checks, was conducted with “DHARMa” package (Hartig, 2025).

To test whether selective cutting modifies the relationships between stand structural attributes and stand structural complexity, we used piecewise structural equation modelling (pSEM). We examined the relationships among stand structural attributes and stand structural complexity using pSEM because it enables the assessment of multiple interdependent relationships among variables while accounting for mixed-effects models (Lefcheck, 2016). A conceptual model was constructed based on the fixed hypothesized paths, in which stand density affects species diversity and variation in tree size dimensions, and stand density, species diversity and variation in tree size dimensions affect SCI (Fig. S2a). We then fitted the linear mixed-effects models using lmer function in “lme4” package (Bates et al., 2015) for each hypothesized path. Treatments nested within sites were considered as random factors. Model residuals and fitted values plots, along with residual QQ plots, were used to test the homogeneity of variance and normality of residuals. pSEM was then fitted using “*piecewise*SEM” package (Lefcheck, 2016). To determine whether selective cutting alters the relationships between stand structural attributes and structural complexity, we also used pSEM to test the same hypothesized paths separately for C and S plots, with sites considered as a random effect.

To investigate whether selective cutting regulates the relationships between stand structure and aboveground carbon stocks, the constructed hypothesized paths were modified by adding more paths, as stand density, species diversity, variation in tree size and SCI affect aboveground carbon stocks (Fig. S2b). We then examined the relationships among stand structure and aboveground carbon stocks and tested if the selective cutting altered these relationships using the same methods described above.

For pSEM, the variables were log-transformed and standardized using z-score normalization to ensure the same range of values and comparison of effect sizes. Stand density index (ASDI), rather than tree density, was included in the model because stand density index accounts for both the number of trees per hectare and tree size. We used CV-DBH and Gini-DBH to represent variation in tree size dimensions. However, Gini-DBH was included in the model because it exhibited higher correlations with both SCI and aboveground carbon stocks (Fig. S3). The pSEM models were evaluated using Fisher’s C statistic and its associated p-value (Lefcheck, 2016). The conditional R^2 (R^2 c) and marginal R^2 (R^2 m) were calculated to examine the variance explained by fixed effects (R^2 m) and by the combination of fixed and random effect (R^2 c).

3. Results

Total tree density, stand density index (ASDI) and total basal area were higher in the control ($p < 0.05$) compared to selective cutting plots (Fig. 2; Table S5). Similarly, higher aboveground carbon stocks ($p < 0.05$) were observed in the control plots. However, there were no significant differences in tree species diversity, SCI, CV-DBH, or Gini-DBH between control and selective cutting plots. Year since selective cutting did not significantly influence tree density, ASDI, basal area, carbon stocks, SCI, or species diversity. However, longer post-cutting periods were associated with higher tree size inequality (CV-DBH and Gini-DBH) (Table S5).

Stand density and tree size variation contributed to increased structural complexity (Fig. 3**a**; Table S6). However, tree species diversity had no significant influence on stand structural complexity. Stand density had no significant influence on tree size variation or species diversity. The pSEM predicting stand structural complexity from stand structure attributes indicated that the fixed effects accounted for 19% of variation, while both fixed and random effects together accounted for 40%. Stand density showed no significant influence on tree size variation in either control or selective cutting stands (Figs. 3**b and** 3**c**). Stand density had a significant positive effect on species diversity in stands subjected to selective cutting (Fig. 3**c**), while exhibiting no significant influence in control stands. In contrast, increased stand density promoted structural complexity in control stands, whereas no significant effect of stand density on structural complexity was observed in selective cutting stands. Variation in tree size drove stand structural complexity in both stands, and the selective cutting did not alter these relationships.

Stand density drove the aboveground carbon stocks in all stands (Fig. 4; Table S7). Similarly, aboveground carbon stocks were consistently increased by stand structural complexity across all study stands. Tree size variation did directly promote aboveground carbon stocks. Species diversity exhibited a negative relationship with aboveground carbon stocks (Fig. 4**a**). Significant positive relationships between stand density, structural complexity, and aboveground carbon stocks were observed in both the control and selective cutting stands (Figs. 4**b and** 4**c**). Variation in tree size and species diversity did not directly affect the aboveground carbon stocks in control stands. However, the significant negative effect of species diversity on aboveground carbon stocks was observed in the selective cutting stands, whereas tree size variation promoted carbon stocks (Fig. 4**c**). Stand density and stand structural complexity drove the aboveground carbon stocks across all study stands. Selective cutting did not alter these relationships.

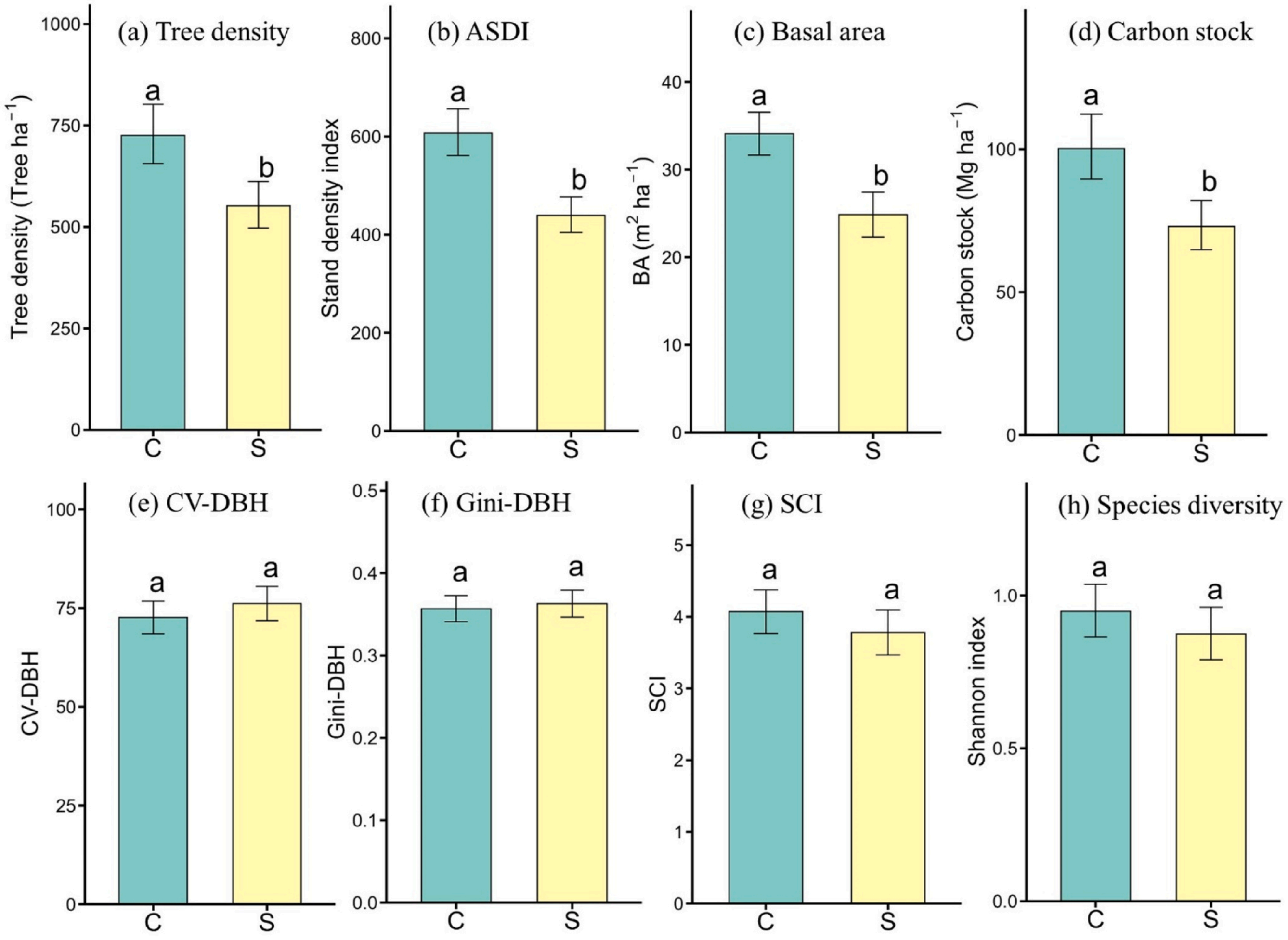

Fig. 2. Comparison of stand structural attributes and stand structural complexity between control (C) and selective cutting (S) stands in temperate mixed broadleaved forests in southern Norway and Sweden. Error bars indicate the ± standard error. Letters in common indicate no significant differences. Significant level used in all comparisons was 0.05.

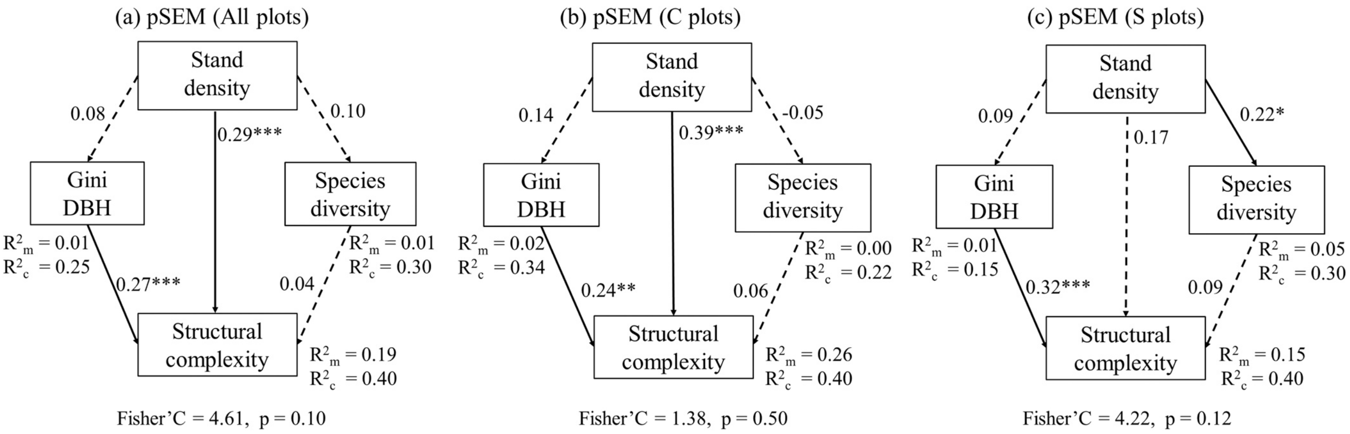

Fig. 3. The effects of stand structural attributes on stand structural complexity in (a) all plots, (b) control plot (C) and (c) selective cutting (S) plots. Dashed arrows indicate non-significant paths, while solid arrows represent significant paths below the 0.05 significance level. The numbers beside the arrows represent the standardized regression coefficients for the path (see Table S6 for the summary of the models).

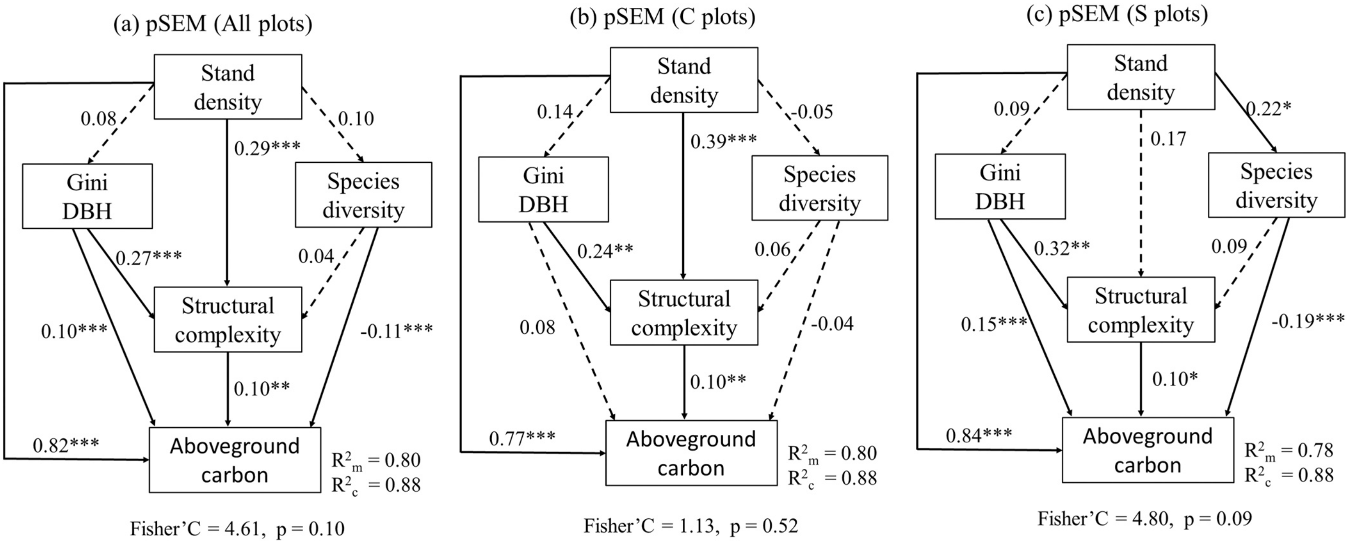

Fig. 4. The effects of stand structure on aboveground carbon stock in (a) all plots, (b) control plot (C) and (c) selective cutting (S) plots. Dashed arrows indicate non-significant paths, while solid arrows represent significant paths below the 0.05 significance level. The numbers beside the arrows represent the standardized regression coefficients for the path (see Table S7 for the summary of the models).

4. Discussion

4.1. Effects of selective cutting on stand structural attributes and stand structural complexity

We found that while selective cutting reduced stand structural attributes such as tree density, stand density index (ASDI), basal area, and aboveground carbon stocks compared to control, it did not affect species diversity and tree size variation. Stand structural attributes, such as tree density, basal area, and aboveground carbon stocks are largely shaped by forest management (Zhou et al., 2013; Schall et al., 2018). Consistent with previous studies (Dieler et al., 2017; Ekholm et al., 2023), our results also indicate that selective cutting did not significantly affect tree species diversity and tree size variation. We could also not confirm that selective cutting reduced stand structural complexity (SCI). This is in line with previous studies indicating that the selective cutting system does not alter stand structure complexity (Ehbrecht et al., 2017; Stiers et al., 2018). SCI calculation in our study was based on the spatial distribution of individual trees and their heights (Zenner, 2000; Zenner and Hibbs, 2000). SCI is therefore sensitive to changes in spatial and vertical height distributions. Although the selective cutting in our study sites was mainly implemented for restoration and conservation purposes, the cut trees were distributed fairly evenly across the experiment plots (Götmark et al., 2005; Götmark, 2007; Nordén et al., 2019). Therefore, selective cutting did not significantly alter the structural complexity of the remaining stands.

Tree density, ASDI, carbon stocks, SCI, and species diversity in both control and selective cutting stands remained relatively stable over time. However, tree size variation (CV-DBH and Gini-DBH) increased over time regardless of treatment. Tree size variation in uneven-aged multi-species forests may be largely controlled by asymmetric competition, where the growth of larger trees dominates (Binkley et al., 2006). Although reduced stand density in selective cutting stands could likely promote the growth of remaining trees (Götmark, 2009), tree size variation is largely dependent on stand structure and site quality (Pretzsch et al., 2022; Pretzsch and Hilmers, 2025). In addition, reduced stand density in selective cutting stands was mainly due to the removal of relatively small trees. In both control and selective cutting stands at our study sites, where large and old oak trees were common, the growth of larger trees could outperform that of other species resulting in higher tree size variation.

4.2. Tree size variation as the main driver of stand structural complexity

We observed that tree size variation determined stand structural complexity in both control and selective cutting stands. Higher tree size variation increased stand structural complexity. These results are in line with previous studies that highlight the importance of variability of tree traits, for the creation of complex stand structure (Ehbrecht et al., 2017). We also found, in line with previous studies (Neumann and Starlinger, 2001), that species diversity did not influence stand structural complexity. However, positive effects of tree species diversity were reported by other studies (Juchheim et. al., 2019, Põldveer et al., 2021). The pattern observed in our study, i.e., there was no significant influence of species diversity on structural complexity, may be attributed to the dominance of oak in both the control and selective cutting stands at our study sites. The selective cutting experiment deliberately retained large and old trees; as these trees are among the key elements for forest biodiversity (Lindenmayer and Laurance, 2017; Torres-García et al., 2024). Stands possessing multiple trees with large crowns highly contributed to structural complexity (Seidel et al., 2019a, 2019b). Selective cutting that favours the retention of large oak trees may alter relationships between stand density and structural complexity (Figs. 3**b and** 3**c**). In this study, the reduction in stand density within selective cutting stands primarily occurred due to the removal of smaller trees rather than dominant canopy trees. Since stand structural complexity calculations were based on the spatial distribution of individual trees and their tree height, the lower stand density in the selective cutting stands had no significant influence on stand structural complexity. At the stand level, tree size variation and structural complexity characterize habitat heterogeneity, a key factor for maintaining biodiversity (McElhinny et al., 2005; Neumann and Starlinger, 2001). Previous studies suggested that selective cutting had no negative impacts on herbaceous plant species, bryophytes and wood-inhabiting fungi (Götmark et al., 2005; Ekholm et al., 2022) and may benefit insect diversity (Nordén et al., 2025). Thus, maintaining diversity in tree sizes can be used to support the complex stand structures in forests that in turn promote biodiversity.

4.3. Selective cutting did not alter the relationships between stand structure and aboveground carbon stocks

We observed that higher aboveground carbon stocks were associated with increased stand density and structural complexity in both the control and selective cutting stands. The observed negative effects of species diversity on aboveground carbon stocks in our study may be explained by the mass-ratio hypothesis (Grime, 1998), which suggests that higher aboveground carbon stocks are largely determined by dominant species associated with increased carbon stocks. Although tree species diversity was not significantly different between the control and selective cutting plots, aboveground carbon stocks were nevertheless largely determined by the dominant tree species (Table S2). Because the dominant tree species accounts for the largest share of total aboveground carbon, the addition of species that contribute less to this total share may not substantially increase carbon storage. In other words, the dominant tree species drive aboveground carbon stocks (e.g., Lohbeck et al., 2016). Consequently, increasing tree species diversity exerted a negative effect on overall aboveground carbon stocks. The high dominance of oak, among other factors, contributed to the negative effects of tree species diversity on carbon stocks. Our results are consistent with previous studies (Szwagrzyk and Gazda, 2007; Fotis et al., 2018; He et al., 2025) that reported negative or negligible effects of tree species diversity on aboveground carbon stocks. In contrast to our findings, other studies have observed an increase in aboveground carbon stocks with higher tree species diversity (Zhang et al., 2012; Liang et al., 2016). These contradictory results could be due the spatial scale of the analysis, as species diversity is more likely to have positive effects on aboveground carbon stocks at smaller scale (0.04–0.1 ha), but neutral or negative effects at larger spatial scales (0.25–1 ha) (Chisholm et al., 2013). The negative effects of tree species diversity on aboveground carbon stocks that were observed in this study, are consistent with these previous study findings, if we consider the spatial scale at which our study was conducted.

Tree size variation in selective cutting stands promoted aboveground carbon stocks, whereas no significant effect was observed in control stands. Although tree growth was not specifically examined in this study, it was likely enhanced by reduced stand density and increased canopy openness, as previously observed by Götmark (2009) at the same study sites. The significant positive effects of tree size variation on aboveground biomass and productivity were also reported by previous studies (Ali et al., 2016; Dănescu et al., 2016; Fotis et al., 2018). In contrast, tree growth in control stands may be limited by higher stand density and resource competition. Consequently, structural heterogeneity (Gini-DBH) alone is insufficient to significantly enhance aboveground carbon stocks in the control stands (e.g., Forrester, 2019).

Aboveground carbon stocks are largely determined by stand density and structural complexity rather than species diversity. In consistent with our results, the positive effect of stand density and stand structural complexity on aboveground carbon stocks has been found in previous studies (Zhang and Chen, 2015; Forrester and Bauhus, 2016; Fotis et al., 2018; Ullah et al., 2021). Higher stand density and greater variation in tree size can promote canopy packing (Jucker et al., 2015; Morin et al., 2025), leading to higher structural complexity, and greater efficiency light interception, which together increase aboveground carbon stocks. Selective cutting did not alter these underlying relationships in our study. Balancing stand structure and carbon storage is key to sustainable forest management, as it can foster both resilient forest ecosystems and contribute to climate mitigation. We therefore suggest that selective cutting can represent an alternative management approach to even-aged management preserving fundamental ecological processes in these forests.

4.4. Limitations of the study

The results of the study highlight that stand density management, as well as maintaining structural complexity and different size classes, play a crucial role in maintaining aboveground carbon stocks in selective cutting stands. Selective cutting in this study was mainly implemented as conservation thinning, in which large and old oak trees were deliberately retained, and tree removal was biased toward promoting their long-term persistence. In addition, the selective cutting was implemented only once. Therefore, caution is warranted if attempting to generalize the results of this study. We also suggest that further research is needed in forest stands with repeated selective cutting involving the removal of trees of different sizes. This can substantially alter size structure and spatial distribution of trees, and thereby potentially influence stand structural complexity and aboveground carbon stocks. Differences in selective cutting intensity may influence the relationships between stand structure and carbon stocks (e.g., Pretzsch and Hilmers, 2025).

When a particular tree species was deliberately retained during selective cutting, changes in stand structure - in terms of tree size distribution and spatial pattern - were highly associated with the remaining tree species composition. Consequently, the observed relationships between stand structure and aboveground carbon stocks are highly context-dependent. In this study, basal area-weighted Shannon diversity index was used as a measure of species diversity. Previous studies (Laliberté and Legendre, 2010; Fotis et al., 2018; Hisano et al., 2024) found that functional diversity drives forest productivity and aboveground biomass and that increasing functional trait diversity may increase productivity of forest ecosystems. The observed relationships in our study may also be driven by functional diversity, and aboveground carbon stocks may depend more on which functional tree types are present or removed during selective cutting than on the tree species diversity. However, the initial stand conditions and the identity of tree species removed during selective cutting could not be incorporated in this study, mainly due to differences in sampling procedures, i.e., circular subplots in the current inventory compared to transect sampling in the previous inventory.

It should also be noted that the relationships among stand structural attributes, structural complexity and aboveground carbon stocks may be nonlinear (e.g., Fraser et al., 2015; Pretzsch et al., 2024). However, as we used pSEM to examine linear causal relationships among stand structural attributes, structural complexity and aboveground carbon stocks, the potential nonlinear responses could not be accounted for in our analysis.

5. Conclusion

In this study, we investigated the influence of restorative selective cutting on stand structural complexity and the relationships between stand structure and aboveground carbon stocks. We showed that selective cutting does not alter stand structural complexity, nor the relationships between stand structure and aboveground carbon stocks. Tree size variation promoted stand structural complexity, which in turn influenced aboveground carbon stocks. Thus, maintaining diverse tree size is essential for sustaining greater stand structural complexity and enhancing aboveground carbon stocks. In addition, the application of selective cutting should foster tree size variation, thereby promoting structural complexity and contributing to increased aboveground carbon stocks. These processes are crucial for biodiversity conservation and climate change mitigation because maintaining structurally complex forest stands provide diverse habitats that sustain ecosystem resilience, while increasing carbon sequestration. As biodiversity conservation and climate adaptation are central priorities for future forestry, our results suggest that the regulation of stand structure through selective cutting represents a viable strategy to achieve these goals by sustaining complex stand structure and aboveground carbon stocks.

CRediT authorship contribution statement

Adam Felton: Writing – review & editing, Funding acquisition. **Björn Nordén:** Writing – review & editing, Funding acquisition. **Magnus Löf:** Writing – review & editing, Supervision, Funding acquisition. **Kyaw Thu Moe:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Julia Schmucker:** Writing – review & editing. **Jorge Aldea:** Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123670.

Data availability

Data will be made available on request.

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