

Climate warming strengthens the effect of silviculture on ecosystem services in uneven-aged mountain forests

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2 ecosystem services in uneven-aged mountain forests

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5 Abstract

6 In high-altitude forests, climate warming is expected to reduce cold limitations on tree growth,
7 potentially intensifying competition for light and altering stand dynamics. Such changes may
8 affect the effectiveness of silvicultural strategies that rely on releasing trees from light competition,
9 including continuous cover forestry, with consequences for the ecosystem services provided by the
10 forest.

11 We used the individual-based forest simulator Samsara2 to analyse the combined effects of
12 climate warming and silviculture on light interception, mean tree growth and mortality rates,
13 stand structure and ecosystem services in uneven-aged spruce–fir–beech mountain forests. We
14 simulated stand dynamics in colder and warmer climates without water limitation, under two
15 thinning intensities and three tree-selection strategies: random, aggregated and crop-tree selection.

16 A warmer climate increased stand productivity by accelerating tree growth, particularly that
17 of dominant trees. This intensified size-asymmetric competition, accentuating tree size differenti-
18 ation and accelerating self-thinning. While these changes had a strong positive effect on timber
19 production, deadwood volume and carbon storage, they had a more limited effect on tree-related
20 biodiversity.

21 Selective silvicultural strategies became more economically efficient in a warmer climate, espe-
22 cially under higher thinning intensity, by maximising the growth advantage of the most valuable
23 trees through release from light competition. Redirecting productivity gains towards specific size
24 classes and species induced climate-driven structural changes, leading to stands of lower density
25 dominated by larger conifers. However, it also simplified size distribution and limited the propor-
26 tion of beech, thereby reducing tree-related biodiversity and carbon storage.

1 Introduction

High mountain forests are particularly vulnerable to climate change (Palomo, 2017). The rate of warming increases with altitude, leading to more rapid temperature changes than in lowland areas (Pepin et al., 2015). In addition, high mountain forests are severely limited by cold temperatures, resulting in forests with unique structures dominated by large, cold-resistant conifers (Albrich et al., 2020a). Rising temperatures could therefore increase mountain forest productivity by increasing individual tree growth, provided that water and nutrient availability are not limiting (Elkin et al., 2013; Zlatanov et al., 2017). The effects of climate warming on tree growth and survival may also vary with the level of light competition (Beauchamp et al., 2025). This could have drastic consequences for demographic processes (*i.e.* growth, mortality and regeneration) (Lindner et al., 2010), thus affecting stand structure and composition with predicted changes towards stands dominated by broadleaved species in mountainous areas (Albrich et al., 2020a). In Europe, most mountain forests are managed, and harvesting has complex effects on the process of light competition. Thus, how climate change impacts on individual tree growth and survival translate into changes in forest structure, functions and services may be highly dependent on silviculture.

European mountain forests are traditionally managed under continuous cover forestry (also called uneven-aged management) (Brang et al., 2014). Operationally, this management is achieved through frequent, extensive silvicultural operations with selective thinning to maintain continuous forest cover, species diversity and an irregular structure of trees of different sizes and ages (Pommerening, 2023). This strategy is based on natural forest processes, in particular the natural regeneration of native species. The aim is to promote timber production while maintaining biodiversity (Lafond et al., 2015), mitigating climate change through carbon storage (Hetemäki et al., 2022), providing enhanced recreational experiences (Peña et al., 2015) and ensuring protec-

tion against natural hazards and erosion (Dorren et al., 2004). Maintaining the sustainability of these functions and services is key to forest multifunctionality (Plas et al., 2018). In European mountains, continuous cover forestry has been adopted due to (1) the importance of protection against natural hazards (*e.g.* rockfalls or avalanches), which encourages foresters to avoid large-scale felling, (2) the heterogeneity of the environment and the frequency of disturbances, which naturally lead to forest mosaics, and (3) the steep terrain, which prevents intensive mechanisation (Cerbu et al., 2013). More recently, with climate change threatening the sustainable provision of key forest functions and services (Elkin et al., 2013), continuous cover forestry has been proposed as a promising solution (Mina et al., 2017) in line with the recent emergence of climate-smart forestry (Bowditch et al., 2020). Both the resulting complexity of the forest and the flexibility provided by selective thinning allow for greater resilience and adaptability faced with the uncertainties of global change (O’Hara, 2014).

Continuous cover forestry relies on the precise control of light distribution within the stand and therefore strongly shapes tree competition for light (Pommerening, 2023). Light competition directly influences individual tree performance and seedling development, with sensitivity varying according to species shade tolerance (Valladares et al., 2008). The asymmetric nature of light competition (Weiner, 1990) leads to tree size differentiation (Oliver et al., 1996), whereby larger trees disproportionately capture more light and progressively increase their growth advantage, while smaller trees experience decreasing light availability over time, leading to suppression and eventual mortality (*i.e.* self-thinning). In addition, tree growth tends to be more sensitive to light availability in highly productive climates (Beauchamp et al., 2025), and may amplify the role of size differentiation under such conditions. Consequently, changes in mean climatic conditions may alter the effectiveness of silvicultural operations based on light competition, with implications for timber production and other ecosystem services.

74 In continuous cover forestry, light competition can be controlled through two complementary
75 levers. Firstly, at the stand level, foresters can reduce overall light competition by increasing
76 thinning intensity. This generally promotes faster growth and regeneration by increasing light
77 availability, at the cost of a lower biomass (Lafond et al., 2014). Secondly, at the tree level, through
78 targeted selection and thinning, silviculture can concentrate light resources locally on vigorous trees
79 that best meet the forester’s objectives (Pretzsch, 2009). This typically involves identifying and
80 releasing crop trees from their immediate competitors to maximise their growth potential. However,
81 such fine-scale selection and harvesting is labour-intensive and may be more challenging in steep
82 mountainous terrain (Cerbu et al., 2013). An alternative strategy is to create aggregated gaps
83 centred around mature harvested trees, by removing all or almost all trees within a defined small
84 area. Unlike crop-tree selection, this approach aggregates harvesting operations spatially rather
85 than selectively releasing individual crop trees, facilitating harvesting operations and favouring the
86 regeneration of light-demanding species in canopy gaps (Ligot et al., 2014). Overall, thinning and
87 tree selection play an important role in shaping how individual trees experience light competition
88 and, consequently, how silvicultural strategies mediate stand responses to climate change.

89 Investigating the joint effects of climate, light and silviculture requires long-term, tree-based
90 studies. Field experiments can be difficult to conduct due to the long temporal scale of forest
91 dynamics, difficulties in controlling environmental factors, or laborious surveying protocols (Ganio
92 et al., 2008). Forest simulation models allow us to make predictions about the trajectories of
93 complex systems while controlling for other factors over a long period of time with multiple repli-
94 cations (Peng, 2000). Among the various forest simulators, individual-based models are key tools
95 for understanding how tree-tree processes scale up into stand structure and demographic processes
96 (Seidl et al., 2012). Here we adapted the tree growth and mortality models from Beauchamp
97 et al. (2025), which consider the interactive effect between climate and light competition, and

98 implemented them in the spatially-explicit, individual-based Samsara2 forest simulator (Courbaud
99 et al., 2015). The key features of this simulator are its ability to account for light competition
100 through the SamsaraLight ray-tracing model (Courbaud et al., 2003) and its coupling with a sil-
101 vicultural algorithm allowing automatic, adaptive and selective harvesting (Courbaud et al. in
102 prep). These features help represent how foresters apply selective harvesting rules in continuous
103 cover forestry (Lafond et al., 2014).

104 This study investigates the combined effects of silviculture and climate warming on typical
105 managed European mountain forests: uneven-aged mixed stands managed for timber production
106 with high-value Norway spruce (*Picea abies*) and silver fir (*Abies alba*) and lower-quality European
107 beech (*Fagus sylvatica*), generally used for fuel wood. We examined (i) how silviculture and cli-
108 mate jointly affect stand structure and dynamics, (ii) whether this joint effect can be explained by
109 climate-induced changes in light competition effects on stand dynamics, and (iii) the resulting con-
110 sequences for three ecosystem services: timber production, biodiversity conservation, and carbon
111 storage. To address these questions, we used the updated Samsara2 forest simulator (Courbaud
112 et al., 2015; Beauchamp et al., 2025) to simulate the changes in mature stands over 300 years
113 under two contrasting climates. We applied six uneven-aged silvicultural scenarios, varying thin-
114 ning intensity (with a target post-thinning basal area of either 20 or 30m².ha⁻¹) and tree-selection
115 strategy (random, aggregated and crop-tree selection). We hypothesized that climate warming
116 would strengthen size-asymmetric light competition, thereby amplifying the effects of selective
117 silviculture on stand structure, species composition and, consequently, ecosystem services.

2 Material and methods

2.1 The Samsara2 forest simulator

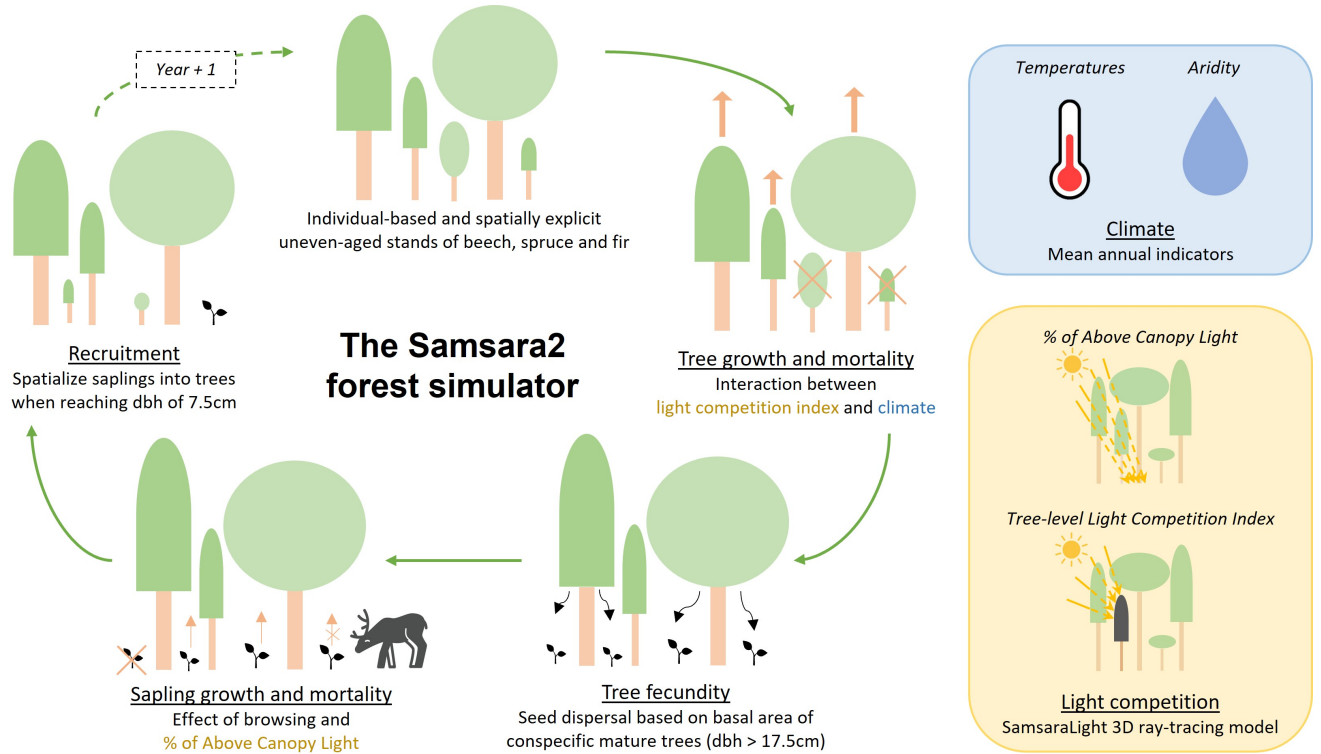


Figure 1: Demographic processes and submodels driving sapling and tree dynamics in Samsara2.

2.1.1 Predicting stand dynamics

The Samsara2 forest simulator is an individual-based and spatially-explicit model (Courbaud et al., 2015) where individuals are classified as either saplings (diameter at breast height, $DBH < 7.5cm$) or trees ($DBH \geq 7.5cm$) (Figure 1). Tree dynamics and regeneration processes (tree fecundity, sapling dynamics and recruitment) are calculated for each year and for each individual. A key feature of the Samsara2 simulator is the integration of the SamsaraLight ray tracing model (Courbaud et al., 2003), which estimates the light intercepted by each tree and the light on the forest floor (Appendix S1-1), used to predict tree and sapling' growth and mortality.

Specifically, we adapted, then implemented, the recently calibrated individual-based tree growth and mortality models from Beauchamp et al. (2025) (Appendix S1-3), which explicitly account for interactions between light competition and mean climatic conditions. In these models, the negative effect of light competition on tree growth and mortality increases under warmer, or wetter, more productive climates and weakens under colder, or drier, more stressful conditions. We also updated the regeneration models with data from Unkule et al. (2022) (Appendix S1-4), which were jointly calibrated for tree effective fecundity and sapling growth and mortality in alpine forests (Unkule, 2022, chapter 4). The sapling sub-models explicitly accounted for the effect of browsing by ungulates, but did not account for climate effects. Finally, to provide a more robust estimation of light interception, we revised the tree crown structures in the simulator based on the recent species-specific allometric relationships from Touzot et al. (2025) (Appendix S1-2).

2.1.2 Simulating uneven-aged silvicultural operations

An adaptative silvicultural algorithm (Courbaud et al. in prep) is implemented in the Samsara2 simulator to represent uneven-aged operations with an automatic selection of trees (Appendix S1-5). Trees are classified into five categories: those to be conserved for biodiversity, those to harvest for timber production, crop-trees to be promoted, trees to be thinned for stand improvement, and other trees to be left growing for the time being. The user defines the number of trees to be conserved and promoted, the target basal area after the operation and the percentage of trees to be harvested for timber/improvement. For each category, the user weights various criteria such as species, diameter, biodiversity potential, market value, relative market value increase and distance to trees of the same or different categories. The trees within each category are then selected through multi-criterion optimisation.

150 2.1.3 Deriving indicators of ecosystem services

151 **Timber production** We calculated the standing timber capital, defined as the sum of the market
152 value of each tree in the stand at a given moment. For the market value of a tree, we estimated its
153 merchantable volume and defined a price per unit volume (*euros.m⁻³*) for each species, diameter
154 class and tree quality (Appendix S1-5). For each silvicultural operation, we also derived the volume
155 (*m³.ha⁻¹*) and income (*euros.ha⁻¹*) from the harvested timber. It was not possible to consider the
156 costs associated with the operation due to a lack of data.

157 **Tree-related biodiversity** We considered tree-related microhabitats (TreMs) to be indirect
158 biodiversity indicators for specialised forest species (Larrieu et al., 2018). TreMs are an important
159 tool in forest management to help foresters select the trees to conserve for biodiversity (Asbeck
160 et al., 2021). Samsara2 includes a model that estimates, for 11 TreM types, the annual probability
161 of formation on individual trees based on tree size and species (Courbaud et al., 2017; Courbaud
162 et al., 2022). We were therefore able to derive a tree-related biodiversity score at the stand scale
163 to take into account the abundance, diversity and rarity of the TreMs on the trees that make up
164 the stand (Appendix S1-6).

165 **Deadwood** We considered stand deadwood volume, an important indicator of biodiversity and
166 sustainable forest management. Deadwood provides key habitats and resources for saproxylic and
167 other forest organisms (Stokland et al., 2012; Augustynczyk et al., 2024). Samsara2 simulates
168 transitions among deadwood decomposition stages and the associated volume loss during decom-
169 position (Lafond (2014), Chapter 3.4) (Appendix S1-6). We assumed that randomly 50% of dead
170 trees remained as standing deadwood (snags).

171 **Carbon storage** We used the CAT carbon accounting tool (Pichancourt et al., 2018) to estimate
172 the total carbon stored in the above- and below-ground living biomass (Appendix S1-6).

173 **2.2 Simulation design**

174 We simulated mixed spruce–fir–beech stands (paragraph 2.2.1) under contrasting climatic condi-
175 tions (paragraph 2.2.2) and silvicultural scenarios (paragraph 2.2.3). Simulations were run over
176 300 years, with uneven-aged silvicultural operations applied every ten years. The first 200 years
177 were treated as a burn-in period and excluded from the analyses to ensure that the stand dynamics
178 were independent of the initial conditions and had reached equilibrium between silviculture and
179 climatic conditions.

180 **2.2.1 Initial stands**

181 We selected ten plots from the French National Forest Inventory (FNFI) database to represent
182 realistic initial conditions that are representative of mountainous, uneven-aged, mature stands of
183 spruce and fir, accompanied by understorey beech. To account for the sampling design of FNFI
184 plots, the sampled trees were replicated according to their weights, then randomly positioned
185 within a 100×100 m plot (1 ha). To account for stochasticity in stand reconstruction, we
186 created three replicates per plot, resulting in 30 initial virtual stands. Initial sapling distributions,
187 not available in the FNFI data, were generated through a 100-year regeneration-only simulation
188 phase to approximate equilibrium with the adult trees. The FNFI protocol, plot selection, stand
189 virtualisation and characteristics of the initial stands are detailed in Appendix S2-1.

190 2.2.2 Climatic conditions

191 We defined two climatic conditions, kept constant throughout the simulation: a cold-limited climate
 192 (*i.e.* Sum of Growing Degree-Days, $SGDD = 1000^{\circ}C$) and a warmer climate ($SGDD = 2000^{\circ}C$),
 193 representing an altitudinal gradient from the subalpine to the collinean zone. The $SGDD$ values
 194 were chosen to represent the observed climatic space shared by fir, spruce and beech in the model
 195 calibration dataset. Water limitation was not considered (aridity index fixed to 1), in order to
 196 isolate the effect of temperature on the altitudinal productivity gradient.

197 2.2.3 Silvicultural scenarios

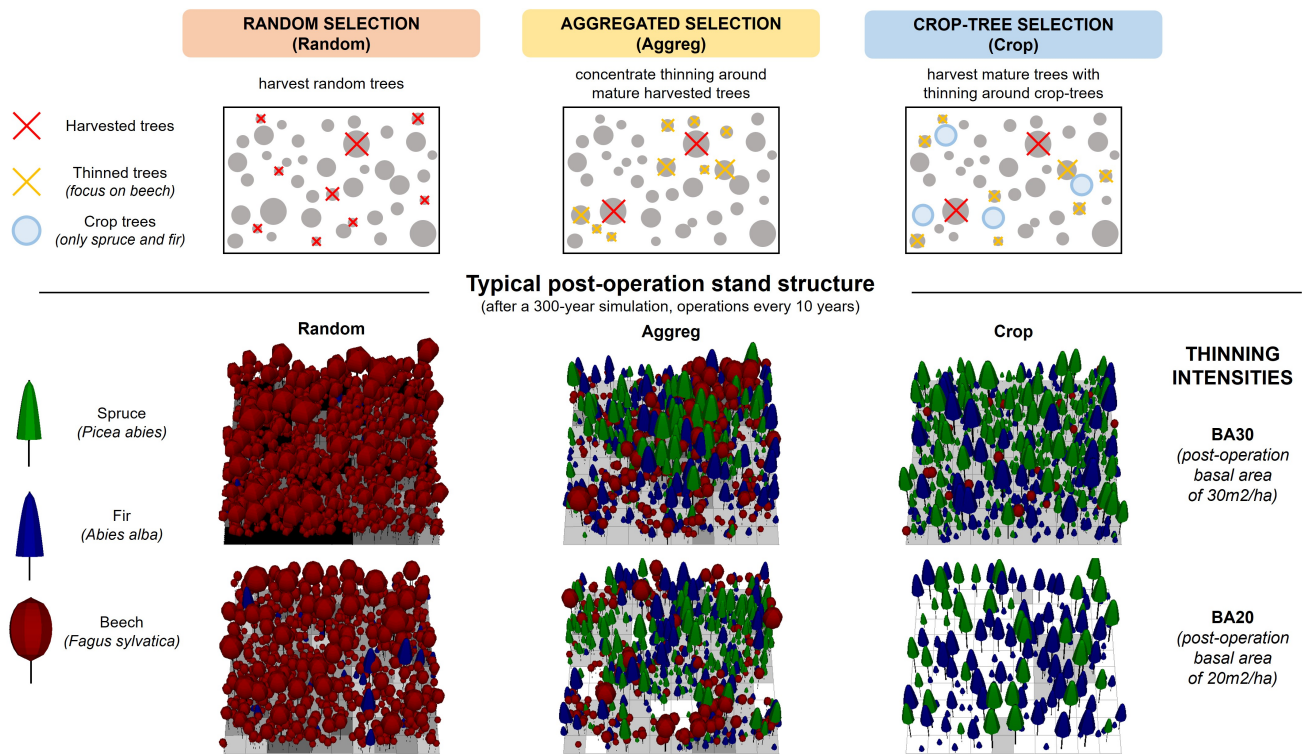


Figure 2: Conceptual representation and simulated post-operation stand structures for the three tree-selection strategies (*Random*, *Aggreg* and *Crop*) and the two thinning intensities (*BA20* and *BA30*).

198 Following discussions with local forest managers (T.C., C.D., J.B. and C.R.) from the French
 199 National Forest Service, we identified two tree-selection strategies representative of uneven-aged

200 mountain forests managed for conifer timber production: crop-tree selection (*Crop*) and aggre-
 201 gated selection (*Aggreg*). Both strategies involve harvesting large, high-value mature conifers
 202 with limited future timber value increment relative to their size, while preferentially thinning
 203 European beech (*Fagus sylvatica*) to favour conifer growth and regeneration. However, the two
 204 strategies differ in how the trees are selected for thinning. The crop-tree selection strategy (*Crop*)
 205 concentrates thinning around retained selected crop-trees to release them from light competition.
 206 In our simulations, we defined crop trees as large, vigorous spruce and fir individuals with a high
 207 conversion efficiency of intercepted light into economic value. We distributed them throughout
 208 the stand. In contrast, the aggregated selection strategy (*Aggreg*) concentrates thinning around a
 209 lesser number of harvested mature trees, thereby creating localised canopy openings and heteroge-
 210 neous light conditions. To isolate the effects of the selection criteria, we also simulated a random
 211 selection strategy in which trees were randomly selected until a target basal area was reached.
 212 Each of the three tree-selection strategies was applied under two thinning intensities correspond-
 213 ing to target post-operation basal areas of $20m^2.ha^{-1}$ (*BA20*) and $30m^2.ha^{-1}$ (*BA30*), with *BA20*
 214 representing the more intensive management. This resulted in a total of six silvicultural modalities
 215 (Figure 2). The parametrisation of the silvicultural algorithm for the *Random*, *Aggreg* and *Crop*
 216 tree-selection strategies is detailed in Appendix S2-2.

217 **2.3 Output analysis**

218 We analysed the joint effect of climate and silviculture on various indicators of stand structure,
 219 stand demographic processes, timber production and environmental functions (see Appendix S2-3
 220 for indicator definitions). The indicators were computed with the average value over the last 100
 221 years of a stand's history (or between each operations for timber production indicators). We tested
 222 each indicator for differences between climates and silvicultural treatments using Student's t-tests.

223 To further characterise stand structure, we analysed the tree size distribution, computed as
224 the mean density over years of all the simulations for each size class (5 cm width, from 7.5 cm to
225 122.5 cm, plus a class for larger trees). We applied a $\log(x + 1)$ transformation on tree density for
226 a better visualisation of climate effect between abundant small trees and fewer very large trees.

227 To investigate the mechanisms underlying the joint effects of climate and silviculture, we anal-
228 ysed how light competition modulated demographic processes under each climate. We used the
229 Proportion of Above-Canopy Light reaching the forest floor (PACL) as a proxy for stand-level
230 light competition. Mean stand PACL $PACL_{mean}$ was computed as the average PACL at the scale
231 of 10 x 10 m grid cells within each 1-ha stand over the last 100 years of the simulation. We used
232 the SamsaraLight ray tracing model (Courbaud et al., 2003) to compute the PACL for each cell as
233 the ratio between the energy reaching the cell and the incoming radiation above the canopy. We
234 then used linear models to predict stand volume increment, mean tree growth, mortality rate and
235 recruitment rate as functions of interaction between $PACL_{mean}$ and climate.

236 Finally, we analysed the consequences of both climate and silviculture on ecosystem services.
237 All the indicators were independently standardised between 0 and 1 by min-max scaling across all
238 the simulations. They were grouped into two categories: economy (standing timber capital and
239 timber income) and environment (tree-related biodiversity score, deadwood volume and carbon
240 storage). We computed the economic score and the environmental score for each simulation as the
241 mean of the standardised indicators within each category.

242 3 Results

243 3.1 The joint effect of climate and silviculture impacted stand struc- 244 ture and composition

245 All tree-selection strategies produced the typical J-shaped size distribution of uneven-aged stands
246 (Appendix S2-7), particularly under random selection (*Random*), where tree density decreased
247 smoothly across size classes towards individuals with a $DBH > 120cm$ (Figure 3). Size-specific
248 harvesting modified this distribution under the selective strategies (*Aggreg* and *Crop*). Com-
249 pared with *Random*, aggregated selection (*Aggreg*) limited maximum tree size and increased the
250 proportion of medium-sized trees, whereas crop-tree selection (*Crop*) promoted the retention and
251 growth of very large trees at the expense of medium- and large-sized individuals (Appendix S2-6).

252 Climate warming altered stand structure only under the selective strategies, especially when
253 lower thinning intensity (*BA30*) was applied (Figure 3; Appendix S2-6). In both *Aggreg* and *Crop*,
254 warming increased the proportion of very large trees while reducing the proportion of smaller size
255 classes, particularly medium-sized trees under *Crop*. This resulted in lower stand densities and
256 larger mean tree diameters. In contrast, *Random* showed no significant climatic effect on stand
257 density or mean diameter, with only a slight increase in the basal area of very large trees.

258 Climate effects on species composition also depended strongly on tree-selection strategy (Figure
259 3). Under *Aggreg*, beech remained stable at approximately 25% of stand basal area regardless
260 of climate or thinning intensity. Under *Crop*, beech was nearly excluded under *BA20* in both
261 climates and under *BA30* in the warmer climate, whereas it remained close to 25% under *BA30*
262 in the cold climate. In contrast, under *Random*, beech became highly dominant, especially in the
263 warmer climate where it exceeded 75% of stand basal area.

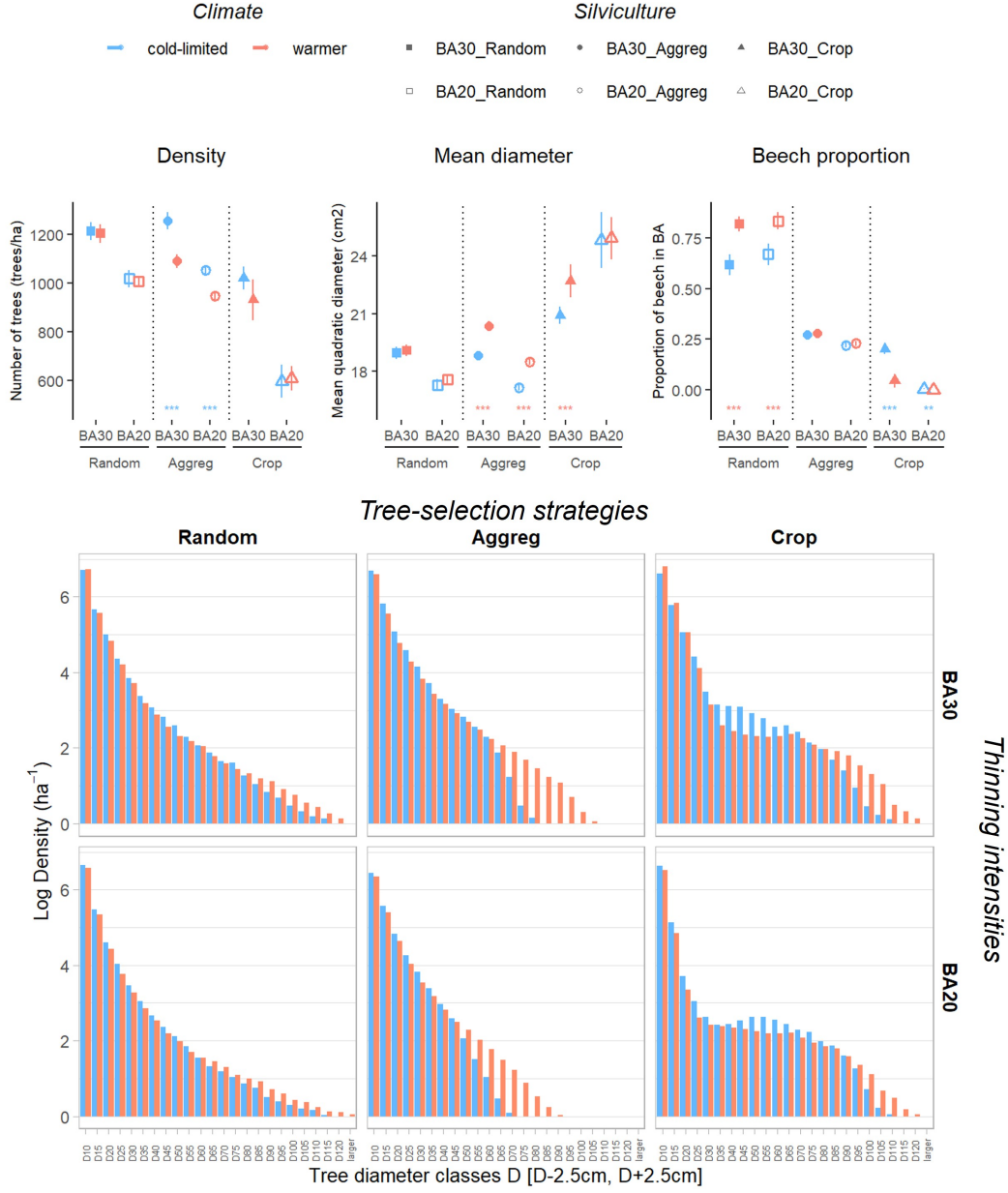


Figure 3: Joint effect of climate and silviculture on stand structure indicators (top panel) and on size distribution in tree basal area (bottom panel). Blue represents simulations in a cold-limited climate and red in a warmer climate. *Random*, *Aggreg* and *Crop* correspond to the tree-selection strategies. *BA20* and *BA30* correspond to the thinning intensities. In the top panel, points show the mean value for each indicator over all the simulations in the specified climate and silviculture, with error bars computed as the 95% confidence intervals around the mean. The significance of the climate effect in a given silvicultural treatment is signified by *** if $pvalue < 0.001$, ** if $pvalue < 0.01$ and * if $pvalue < 0.05$. In the bottom panel, size distribution is computed as the mean density over all years for each size class and all simulations in the specified climate and silvicultural treatment, with a $\log(x + 1)$ transformation. Appendix S2-6 shows the basal area per climate and silvicultural treatment for small, medium, large and very-large trees. Appendix S2-7 shows the size distribution without the log-transformed tree density.

3.2 The effect of climate on stand demographic processes varied with silvicultural treatment due to changes in light competition

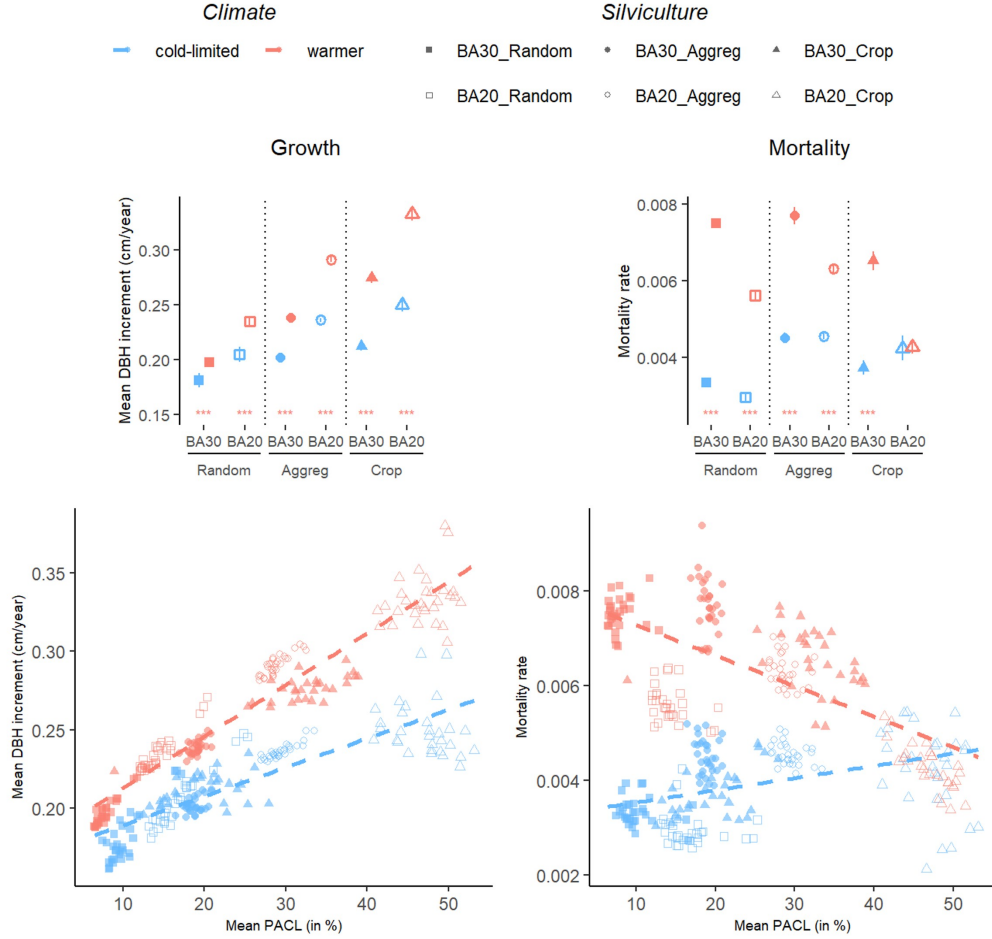


Figure 4: Joint effect of climate and silviculture on stand demographic processes (top panel) and relationships with the interaction between mean percentage of above canopy light $PACL_{mean}$ and climate (bottom panel). Blue indicates simulations in a cold-limited climate and red in a warmer climate. *Random*, *Aggreg* and *Crop* correspond to the tree-selection strategies. *BA20* and *BA30* correspond to the thinning intensities. In the top panel, point show the mean value for each indicator over all the simulations in the specified climate and silvicultural treatment, with error bars computed as the 95% confidence intervals around the mean. The significance of the climate effect in a given silviculture is signified by *** if $pvalue < 0.001$, ** if $pvalue < 0.01$ and * if $pvalue < 0.05$. In the bottom panel, points show the output indicators from a single simulation and the dashed lines are the predictions from the linear regression. The output coefficients and significance of the regressions are presented in the Appendix S2-8. The same analysis was performed for recruitment rate and stand volume increment and is presented in Appendix S2-9.

Average tree growth rate increased in a warmer climate (Figure 4), particularly when thinning was more selective ($Crop > Aggreg > Random$) and more intensive ($BA20 > BA30$). Mor-

268 tality rates also increased with warming (Figure 4) and silvicultural treatment modulated this
 269 response but in the opposite direction from that observed for growth: the climate effect on mor-
 270 tality was stronger under less selective (*Random* > *Aggreg* > *Crop*) and less intensive thinning
 271 (*BA30* > *BA20*). Stand volume increment was higher under the warmer climate, reflecting higher
 272 productivity, and this increase was consistent across all the silvicultural treatments (Appendix S2-
 273 8). Recruitment rate was not impacted by climate but was highly influence by silviculture, which
 274 was much greater in crop-tree selection (*Crop*), especially with more intensive thinning (*BA20*)
 275 (Appendix S2-8).

276 The demographic responses to climate were mediated by changes in stand-level light competi-
 277 tion (see Figure 4 for mean tree growth and mortality rate, and Appendix S2-9 for stand volume
 278 increment and recruitment rate). The mean Percentage of Above Canopy Light $PACL_{mean}$ had
 279 a positive effect on mean tree growth, and this relationship was significantly stronger under the
 280 warmer climate. Consequently, warming had a much higher effect on growth at high light lev-
 281 els (a difference of +31.0% [28.2, 33.8] in yearly DBH increment from the cold-limited to the
 282 warmer climate when $PACL_{mean} = 50\%$) than it did at low light levels (+12.5% [10.2, 14.9] when
 283 $PACL_{mean} = 10\%$). Mortality responded differently to light availability depending on the climate:
 284 an increase in light levels led to a decrease in mortality under the warmer climate, but to an
 285 increase in mortality under the cold-limited climate. As a result, the effect of climate on mortality
 286 was non-significant at high light levels (a difference of +2.85% [-5.76, 11.5] in mortality rate from
 287 the cold-limited to the warmer climate when $PACL_{mean} = 50\%$), but extremely strong at low light
 288 levels (+106.29% [94.53, 118.10] when $PACL_{mean} = 10\%$).

289 $PACL_{mean}$ was primarily driven by stand structure and composition, with lower ground-level
 290 light availability in stands characterised by higher beech proportion, greater total basal area and
 291 lower mean quadratic diameter (*i.e.* mature, homogeneous, dense beech stands) (Appendix S2-5).

As a major driver of stand structure, silviculture strongly affected $PACL_{mean}$ which increased under more selective ($Crop > Aggreg > Random$) and intensive thinning ($BA20 > BA30$) (Appendix S2-4). These differences explained the observed interaction between climate and silviculture: a silvicultural treatment promoting higher light availability ($Crop$ and $BA20$) maximised the positive effect of warming on tree growth while limiting climate-induced mortality associated with self-thinning.

3.3 Consequences of the joint effect of climate and silviculture on ecosystem services

The economic and environmental scores showed contrasting responses to silvicultural treatment but similar responses to thinning intensity, which were greater at a lower thinning intensity ($BA30$). The selective strategies ($Aggreg$ and $Crop$) produced a much higher economic score, whereas the random strategy ($Random$) produced a much higher environmental score. Climate warming significantly increased the economic scores of the two selective strategies, and the environmental score of the random strategy. Consequently, climate warming amplified the effects of tree selection on the provision of ecosystem services.

Economic indicators The economic differences among tree-selection strategies reflected contrasting contributions of timber capital and timber income. Timber capital was highest under the crop-tree strategy ($Crop$), intermediate under $Aggreg$, and lowest under $Random$ (Figure 5). Reducing target basal area ($BA20$) resulted in a homogeneously lower timber capital due to reduced stand biomass. In contrast, timber income was highest under $Aggreg$, slightly lower under $Crop$, and much lower under $Random$. For $Crop$ and $Aggreg$, incomes were lower at $BA20$ than at $BA30$ under cold conditions, but these differences disappeared with a warmer climate.

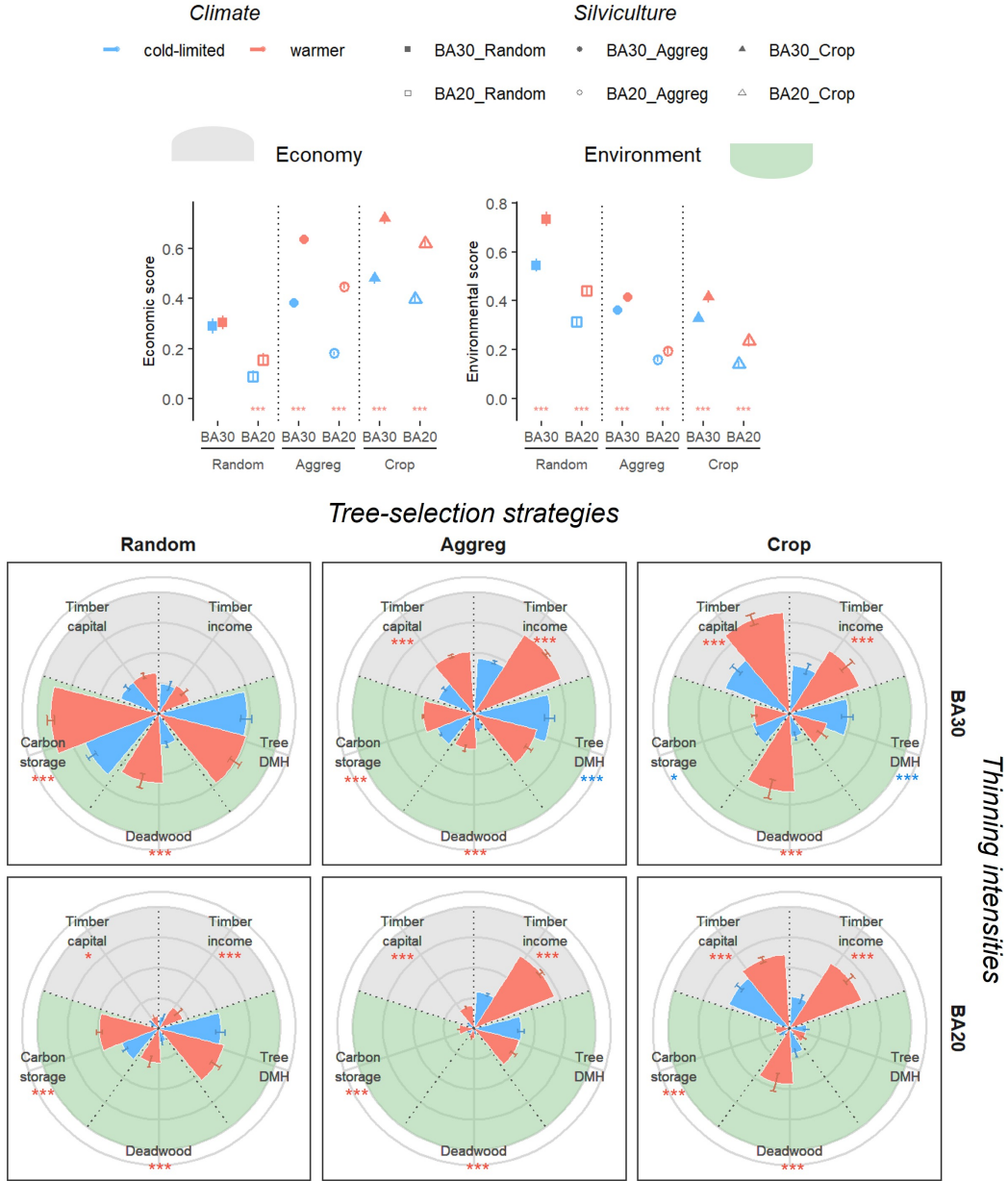


Figure 5: Joint effect of climate and silviculture on economic and environmental scores (top panel), and on each ecosystem service (bottom panel). Blue represents simulations in a cold-limited climate and red in a warmer climate. *Random*, *Aggreg* and *Crop* are the tree-selection strategies. *BA20* and *BA30* are the thinning intensities. In the top panel, points show the mean value for each indicator over all the simulations in the specified climate and silvicultural treatment, with error bars computed as the 95% confidence intervals around the mean. The significance of the climate effect in a given silviculture is signified by *** if $pvalue < 0.001$, ** if $pvalue < 0.01$ and * if $pvalue < 0.05$. All indicators were independently min-max standardised between 0 and 1 across all the simulations, then averaged into an economic score (gray background) and an environmental score (green background). Appendix S2-10 shows the mean size distribution of the harvested trees. Appendix S2-11 shows the same graphical representation as the top panel for each ecosystem service. Appendix S2-12 shows the relationships between the economic and environmental scores.

314 Climate warming significantly increased the total harvested wood volume and the size of the
315 harvested trees (Appendices S2-10 and S2-11). More specifically, harvested volumes were similarly
316 high under *Random* and *Aggreg*, whereas *Crop* produced lower harvested volumes, particularly
317 under *BA20* (Appendix S2-10). Under *Random*, the harvested trees were distributed relatively
318 evenly across size classes, while the two selective strategies preferentially removed larger trees
319 (Figure 3). In addition, *Crop* combined the removal of small and medium-sized trees with the
320 retention of large trees, resulting in a bimodal distribution of the harvested volume and larger
321 harvested tree size than *Aggreg*.

322 **Environmental indicators** Differences in environmental scores among tree-selection strategies
323 were primarily driven by contrasting contributions of the various ecosystem services, with con-
324 sistently higher values under less intensive thinning (*BA30*). Carbon storage and biodiversity
325 were higher under *Random* than under *Crop* or *Aggreg*, with especially low carbon storage under
326 *Aggreg* and low tree-related biodiversity under *Crop*. Deadwood volumes were the highest under
327 *Crop*, intermediate under *Random* and lowest under *Aggreg*.

328 Climate warming generally increased carbon storage and deadwood volume, but its effect on
329 deadwood strongly depended on silviculture, with the largest increases under *Crop* and *Random*
330 and consistently lower values under *Aggreg*. In contrast, tree-related biodiversity showed weak
331 climatic responses overall, and even declined with climate warming under *Crop* and *Aggreg* under
332 less intensive thinning (*BA30*).

333 4 Discussion

334 4.1 Climate warming increased stand productivity and intensified light 335 competition

336 Our simulation study focusing on high-altitude mountain forests showed that the transition from
337 a cold-limited climate to a warmer climate increased stand productivity through enhanced mean
338 tree growth, with positive effects on timber production, deadwood volume and carbon storage.
339 Previous simulation studies consistently projected substantial increases in forest biomass under
340 warming in high-elevation forests (Elkin et al., 2013; Zlatanov et al., 2017), but these projections
341 become negative at lower elevations where water supply becomes limiting. A 60-year observational
342 study (Hilmers et al., 2019) found no net change in productivity of European fir–spruce–beech
343 mountain forests, as the gains for fir were offset by declines in spruce. Although warming may
344 eventually constrain growth through increased vapour pressure deficit (McDowell et al., 2020), the
345 Samsara2 growth model (Beauchamp et al., 2025) can not capture the associated drought-induced
346 decline in spruce growth under drier conditions.

347 As productivity increased, we observed that light competition exerted stronger control over
348 both growth and mortality, reinforcing size-asymmetric dynamics within the stands. These pat-
349 terns reflect the scaling-up to population level of the individual-based interactions between light
350 competition and climate represented in the Samsara2 model (Beauchamp et al., 2025), consistent
351 with ecological theories predicting stronger competition effects in more productive environments
352 (Craine, 2005; Maestre et al., 2009). Likewise, a field study in Central European forests showed
353 that competition for light becomes stronger along fertility gradients in Central European forests
354 (Pretzsch et al., 2010). Under a warmer climate, stronger competition increased the growth ad-

355 vantage of the dominant trees while reducing the survival of the suppressed individuals, thereby
356 intensifying tree size differentiation and accelerating self-thinning dynamics. Similarly, Pretzsch
357 et al. (2011) showed that limiting site conditions reduced the competitive superiority of dominant
358 trees in European spruce and beech forests. Pretzsch et al. (2022) also reported that the increased
359 tree growth resulting from nitrogen fertilisation during the 20th century intensified self-thinning
360 in Scots pine stands in southern Germany.

361 In our simulations, the intensified self-thinning with climate warming resulted in increased
362 deadwood volume, particularly with lower thinning intensity. This is consistent with Augustynczyk
363 et al. (2024), who also predicted increasing deadwood volumes in cold-limited European forests
364 under warmer conditions, driven by higher productivity and stronger competition, especially in
365 denser stands. Deadwood inputs were also strongly influenced by silviculture through differences
366 in the size of dead trees: crop-tree selection promoted particularly high deadwood volume through
367 the occasional mortality of very large trees. However, there is a trade-off with economic objectives,
368 as any climate-driven increase in deadwood is strongly contingent on whether or not the dead trees
369 are retained in the stand (here retention was fixed at 50%), making deadwood provision highly
370 sensitive to the forester's priorities (Stokland et al., 2012).

371 **4.2 Silviculture redistributed the climate-driven increase in produc-** 372 **tivity**

373 Silvicultural treatments combining thinning intensity and tree-selection strategy strongly ampli-
374 fied the response of stand dynamics to climate warming by modulating light competition across
375 organizational levels. At the stand level, reducing the basal area decreased overall competition,
376 thus enhancing dominant tree growth under warmer conditions while limiting density-dependent

377 mortality through the earlier harvesting of suppressed individuals. Similarly, a field study by Ford
378 et al. (2017) showed that climate warming in cold-limited montane forests in the USA resulted
379 in a positive effect on mean tree growth, which was stronger in less crowded stands where com-
380 petition did not constrain growth responses. The aggregated selection strategy created highly
381 heterogeneous light environments and redistributed increased productivity towards the smaller
382 trees in canopy gaps, thereby maximising their growth while increasing self-thinning in the denser
383 patches. The crop-tree selection strategy concentrated the increased resource availability on a
384 limited number of large, vigorous individuals. This mechanism is well established in silvicultural
385 theory, where selective release enhances crop-tree growth, especially in productive environments
386 (Pretzsch, 2009).

387 Consequently, climate warming increased timber income more strongly under the more selective
388 crop-tree strategy, highlighting the ability of silviculture to redirect enhanced productivity towards
389 economically valuable trees. This effect was particularly pronounced under higher thinning inten-
390 sity, where reduced competition maximised the growth of the selected individuals. Such economic
391 gains depend on the sustained growth and survival of high-value large conifers that support both
392 regeneration processes and timber production; these gains may become less reliable under more se-
393 vere climatic conditions where warming is accompanied by drought stress, as observed by Heinonen
394 et al. (2018) in boreal forests. With global change, these high-value individuals may become in-
395 creasingly vulnerable to drought-, heat-, and pest-related mortality in European mountain forests
396 (Mina et al., 2017; Albrich et al., 2020a). This is particularly true for species such as Norway
397 spruce (Piedallu et al., 2023; Hallas et al., 2026), and may have potentially strong impacts on the
398 economic value of the European forest landscape (Hanewinkel et al., 2013). We therefore highlight
399 the high potential for greater economic gain with climate warming in high-elevation mountains,
400 but also remind managers that there is a high risk of disproportionate economic loss associated

401 with concentrating investments on a limited number of highly valuable, but more vulnerable trees
402 (Detten et al., 2017).

403 Accurately representing silvicultural decision-making in continuous cover forestry remains a
404 major challenge for forest modelling (Söderbergh et al., 2003). Our individual-based silvicultural
405 algorithm successfully captured some key aspects of the targeted operations, as illustrated by the
406 very low economic performance of the random selection strategy. However, the higher timber
407 income observed with aggregated selection compared to crop-tree selection was somewhat un-
408 expected. Aggregate thinnings promoted growth in canopy gaps, which primarily favoured the
409 growth of abundant medium-sized trees, for which timber values increase non-linearly with diame-
410 ter before plateauing at larger sizes. This pattern may reflect a modelling limitation related to the
411 absence of explicit intra-specific variations in wood quality, since we assumed all the spruce and
412 fir trees would produce uniformly high-quality timber. Although such variations may be lower in
413 conifers than in broadleaved species, wood quality remains a central criterion in crop-tree silvicul-
414 ture, which aims to select defect-free individuals while maintaining sufficient lateral competition
415 to promote natural pruning and stem straightness (Pretzsch et al., 2016; Pommerening, 2023).
416 Improving the representation of wood quality in forest simulators therefore remains an important
417 step towards more realistic assessments of continuous cover strategies (Drew et al., 2022).

418 **4.3 Silviculture induced climate-driven changes in stand structure and** 419 **composition**

420 Climate warming induced structural changes only under the two selective strategies *Crop* and
421 *Aggreg*, despite enhanced growth and mortality under random selection. Because harvesting was
422 not size-specific in the random selection strategy, the natural size distribution generated by self-

423 thinning was preserved, so warming mainly accelerated stand development without substantially
424 altering stand structure. Pretzsch et al. (2022) also reported that increased growth from nitrogen
425 fertilisation accelerated self-thinning in dense, unthinned Scots pine stands while maintaining stable
426 density–size relationships. In contrast, selective silviculture redirected productivity gains toward
427 targeted size classes through size-specific harvesting and tree release. Under these conditions,
428 climate warming shifted stands towards lower densities with larger trees, while the fixed target basal
429 area constrained biomass accumulation. More generally, our results illustrate how tree selection
430 during thinning modifies tree size–growth relationships, identified by Forrester (2019) as a key
431 determinant of stand structure and functioning.

432 By selectively focusing thinning on beech, the two selective strategies effectively controlled
433 stand composition and maintained spruce and fir dominance. In contrast, the random selection
434 strategy revealed the strong competitive potential of European beech, whose proportion was much
435 greater in warmer climate and reached 75% of the stand basal area. This late-successional species
436 is highly competitive in mountain forests (Heiland et al., 2023), and its expansion under climate
437 change has been widely reported in empirical and modelling studies (Aertsens et al., 2014; Tegel
438 et al., 2014). The aggregated selection strategy also limited beech expansion by creating canopy
439 gaps that reduced local competitive pressure and promoted Norway spruce regeneration, maintain-
440 ing beech proportions below 25%, a threshold commonly recommended by forest managers in this
441 context. The crop-tree selection strategy nearly excluded beech through the repeated thinning of
442 small- and medium-sized trees, particularly under the lower target basal area, while maintaining
443 mature reproductive conifers and more homogeneous light conditions favourable to Norway spruce
444 regeneration. These results are consistent with uneven-aged silvicultural theory (Schutz, 1999)
445 and simulation studies (Ligot et al., 2014), and emphasize the importance of retaining reproduc-
446 tive conifers while selectively removing smaller competing individuals to ensure long-term species

447 control.

448 Silviculture was therefore the main driver of the structure-dependent ecosystem services we
449 studied. It shaped stand biomass, size distribution and species composition, while climate warm-
450 ing primarily amplified these structural effects. Similarly, Mina et al. (2017) found that silvicultural
451 operations exert a stronger influence on ecosystem services than does climate change. Thinning
452 intensity was the primary determinant for carbon storage and tree-related biodiversity, with in-
453 tensive management reducing both carbon stocks and habitat availability. Selective strategies
454 increase the dominance of economically valuable trees but reduce both stand structural complex-
455 ity and the abundance of European beech, which are critical for carbon storage (Pichancourt et al.,
456 2018; Cuny et al., 2026) and habitat provision (Courbaud et al., 2022). This is consistent with
457 studies showing that structurally complex stands, particularly unmanaged and mixed-species ones,
458 support greater microhabitat diversity and abundance (Augustynczyk et al., 2019; Asbeck et al.,
459 2022; Asbeck et al., 2019). Such production-biodiversity trade-offs are widely reported in managed
460 forest systems (Lafond et al., 2017), although habitat-tree retention and increased structural and
461 species diversity may mitigate these effects and still respect production objectives (Lafond et al.,
462 2015).

463 **4.4 Perspectives on resilience under global change**

464 Adapting silviculture to future conditions will require considering the increasing frequency and
465 intensity of disturbances under climate change (Patacca et al., 2023). Climate-driven structural
466 and compositional shifts towards fewer but larger dominant trees, lower abundance of smaller in-
467 dividuals, and beech exclusion may simultaneously increase sensitivity to disturbance and reduce
468 recovery potential. On the other hand, enhanced productivity could accelerate post-disturbance
469 growth and stand reorganisation. Future studies should therefore consider how changes in stand

470 structure, composition, and dynamics driven by the interactive effect of climate and silviculture
471 may influence forest vulnerability and recovery processes in increasingly disturbance-prone envi-
472 ronments (Seidl et al., 2017; Albrich et al., 2020b).

473 **5 Conclusion**

474 Although our study focused on mountain forests, the mechanisms we identified may apply more
475 broadly across productivity gradients. Increased resource availability, whether driven by tem-
476 perature, water availability, or nutrient supply, can strengthen size-asymmetric light competition
477 and promote structural differentiation within forest stands. More productive environments may
478 therefore increase the importance of selective silviculture as a tool to redirect productivity gains
479 towards vigorous trees and maximise their growth response. However, concentrating productivity
480 gains on a limited number of large, high-value trees may lead to more economic specialisation of
481 stand management and increase the risk of losing a substantial fraction of future returns following
482 disturbances. Ensuring structural and compositional diversity therefore appears essential in highly
483 productive forests, not only to mitigate trade-offs between ecosystem services, but also to enhance
484 resilience under increasingly frequent and more intense disturbance regimes.

References

- Aertsen, W., E. Janssen, V. Kint, J.-D. Bontemps, J. Van Orshoven, and B. Muys (2014). “Long-term growth changes of common beech (*Fagus sylvatica* L.) are less pronounced on highly productive sites”. *Forest Ecology and Management* 312, pp. 252–259. DOI: 10.1016/j.foreco.2013.09.034.
- Albrich, K., W. Rammer, and R. Seidl (2020a). “Climate change causes critical transitions and irreversible alterations of mountain forests”. *Global Change Biology* 26.7, pp. 4013–4027. DOI: 10.1111/gcb.15118.
- Albrich, K., W. Rammer, M. G. Turner, Z. Ratajczak, K. H. Braziunas, W. D. Hansen, and R. Seidl (2020b). “Simulating forest resilience: A review”. *Global Ecology and Biogeography* 29.12, pp. 2082–2096. DOI: 10.1111/geb.13197.
- Asbeck, T., J. Großmann, Y. Paillet, N. Winiger, and J. Bauhus (2021). “The Use of Tree-Related Microhabitats as Forest Biodiversity Indicators and to Guide Integrated Forest Management”. *Current Forestry Reports* 7.1, pp. 59–68. DOI: 10.1007/s40725-020-00132-5.
- Asbeck, T., D. Kozák, A. P. Spînu, M. Mikoláš, V. Zemlerová, and M. Svoboda (2022). “Tree-Related Microhabitats Follow Similar Patterns but are More Diverse in Primary Compared to Managed Temperate Mountain Forests”. *Ecosystems* 25.3, pp. 712–726. DOI: 10.1007/s10021-021-00681-1.
- Asbeck, T., P. Pyttel, J. Frey, and J. Bauhus (2019). “Predicting abundance and diversity of tree-related microhabitats in Central European montane forests from common forest attributes”. *Forest Ecology and Management* 432, pp. 400–408. DOI: 10.1016/j.foreco.2018.09.043.
- Augustynczyk, A. L. D., M. Gusti, F. di Fulvio, P. Lauri, N. Forsell, and P. Havlík (2024). “Modelling the effects of climate and management on the distribution of deadwood in European

forests”. *Journal of Environmental Management* 354, p. 120382. DOI: 10.1016/j.jenvman.2024.120382.

Augustynczyk, A. L. D., T. Asbeck, M. Basile, J. Bauhus, I. Storch, G. Mikusiński, R. Yousefpour, and M. Hanewinkel (2019). “Diversification of forest management regimes secures tree microhabitats and bird abundance under climate change”. *Science of The Total Environment* 650, pp. 2717–2730. DOI: 10.1016/j.scitotenv.2018.09.366.

Beauchamp, N., G. Kunstler, L. Touzot, P. Ruiz-Benito, E. Cienciala, J. Dahlgren, P. Hawryło, M. Klopčič, A. Lehtonen, V. Šebeň, J. Socha, M. A. Zavala, and B. Courbaud (2025). “Light competition affects how tree growth and survival respond to climate”. *Journal of Ecology* 113.3, pp. 672–688. DOI: 10.1111/1365-2745.14489.

Bowditch, E., G. Santopuoli, F. Binder, M. del Río, N. La Porta, T. Kluvankova, J. Lesinski, R. Motta, M. Pach, P. Panzacchi, H. Pretzsch, C. Temperli, G. Tonon, M. Smith, V. Velikova, A. Weatherall, and R. Tognetti (2020). “What is Climate-Smart Forestry? A definition from a multinational collaborative process focused on mountain regions of Europe”. *Ecosystem Services* 43, p. 101113. DOI: 10.1016/j.ecoser.2020.101113.

Brang, P., P. Spathelf, J. B. Larsen, J. Bauhus, A. Boncčina, C. Chauvin, L. Drössler, C. García-Güemes, C. Heiri, G. Kerr, M. J. Lexer, B. Mason, F. Mohren, U. Mühlethaler, S. Nocentini, and M. Svoboda (2014). “Suitability of close-to-nature silviculture for adapting temperate European forests to climate change”. *Forestry: An International Journal of Forest Research* 87.4, pp. 492–503. DOI: 10.1093/forestry/cpu018.

Cerbu, G., M. Hanewinkel, G. Gerosa, and R. Jandl (2013). *Management Strategies to Adapt Alpine Space Forests to Climate Change Risks*. en. BoD – Books on Demand.

530 Courbaud, B., V. Lafond, G. Lagarrigues, G. Vieilledent, T. Cordonnier, F. Jabot, and F. R. d. Col-
531 igny (2015). “Applying ecological model evaluation: Lessons learned with the forest dynamics
532 model Samsara2”. *Ecological Modelling* 314, p. 1. DOI: 10.1016/j.ecolmodel.2015.06.039.

533 Courbaud, B., L. Larrieu, D. Kozak, D. Kraus, T. Lachat, S. Ladet, J. Müller, Y. Paillet, K.
534 Sagheb-Talebi, A. Schuck, J. Stillhard, M. Svoboda, and S. Zudin (2022). “Factors influencing
535 the rate of formation of tree-related microhabitats and implications for biodiversity conservation
536 and forest management”. *Journal of Applied Ecology* 59.2, pp. 492–503. DOI: 10.1111/1365-
537 2664.14068.

538 Courbaud, B., C. Pupin, A. Letort, A. Cabanettes, and L. Larrieu (2017). “Modelling the proba-
539 bility of microhabitat formation on trees using cross-sectional data”. *Methods in Ecology and*
540 *Evolution* 8.10, pp. 1347–1359. DOI: 10.1111/2041-210X.12773.

541 Courbaud, B., F. de Coligny, and T. Cordonnier (2003). “Simulating radiation distribution in a
542 heterogeneous Norway spruce forest on a slope”. *Agricultural and Forest Meteorology* 116.1,
543 pp. 1–18. DOI: 10.1016/S0168-1923(02)00254-X.

544 Craine, J. M. (2005). “Reconciling plant strategy theories of Grime and Tilman”. *Journal of Ecology*
545 93.6, pp. 1041–1052. DOI: 10.1111/j.1365-2745.2005.01043.x.

546 Cuny, H., J.-D. Bontemps, N. Besic, A. Colin, L. Hertzog, A. Le Squin, W. Marchand, C. Vega,
547 and J.-M. Leban (2026). “Wood density variation in European forest species: drivers and im-
548 plications for multiscale biomass and carbon assessment in France”. English. *Biogeosciences*
549 23.7, pp. 2365–2388. DOI: 10.5194/bg-23-2365-2026.

550 Detten, R. von and M. Hanewinkel (2017). “Strategies of Handling Risk and Uncertainty in Forest
551 Management in Central Europe”. *Current Forestry Reports* 3.1, pp. 60–73. DOI: 10.1007/
552 s40725-017-0050-7.

553 Dorren, L. K. A., F. Berger, A. C. Imeson, B. Maier, and F. Rey (2004). “Integrity, stability
554 and management of protection forests in the European Alps”. *Forest Ecology and Management*
555 195.1, pp. 165–176. DOI: 10.1016/j.foreco.2004.02.057.

556 Drew, D. M., G. M. Downes, T. Seifert, A. Eckes-Shepard, and A. Achim (2022). “A Review
557 of Progress and Applications in Wood Quality Modelling”. en. *Current Forestry Reports* 8.4,
558 pp. 317–332. DOI: 10.1007/s40725-022-00171-0.

559 Elkin, C., A. G. Gutiérrez, S. Leuzinger, C. Manusch, C. Temperli, L. Rasche, and H. Bugmann
560 (2013). “A 2 °C warmer world is not safe for ecosystem services in the European Alps”. *Global*
561 *Change Biology* 19.6, pp. 1827–1840. DOI: 10.1111/gcb.12156.

562 Ford, K. R., I. K. Breckheimer, J. F. Franklin, J. A. Freund, S. J. Kroiss, A. J. Larson, E. J.
563 Theobald, and J. HilleRisLambers (2017). “Competition alters tree growth responses to climate
564 at individual and stand scales”. *Canadian Journal of Forest Research* 47.1, pp. 53–62. DOI:
565 10.1139/cjfr-2016-0188.

566 Forrester, D. I. (2019). “Linking forest growth with stand structure: Tree size inequality, tree growth
567 or resource partitioning and the asymmetry of competition”. *Forest Ecology and Management*
568 447, pp. 139–157. DOI: 10.1016/j.foreco.2019.05.053.

569 Ganio, L. M. and K. J. Puettmann (2008). “Designing Long-Term, Large-Scale Forestry Exper-
570 iments with Research Objectives at Multiple Scales”. *Journal of Sustainable Forestry* 26.1,
571 pp. 1–18. DOI: 10.1300/J091v26n01_01.

572 Hallas, T., G. Hoch, T. Kirisits, and S. Netherer (2026). “Assessing disturbance risks of the Eu-
573 ropean spruce bark beetle under climate change: a review of model approaches and future
574 perspectives”. en. *European Journal of Forest Research* 145.2, p. 23. DOI: 10.1007/s10342-
575 025-01841-x.

576 Hanewinkel, M., D. A. Cullmann, M.-J. Schelhaas, G.-J. Nabuurs, and N. E. Zimmermann (2013).
 577 “Climate change may cause severe loss in the economic value of European forest land”. *Nature*
 578 *Climate Change* 3.3, pp. 203–207. DOI: 10.1038/nclimate1687.

579 Heiland, L., G. Kunstler, V. Šebeň, and L. Hülsmann (2023). “Which demographic processes con-
 580 trol competitive equilibria? Bayesian calibration of a size-structured forest population model”.
 581 *Ecology and Evolution* 13.7, e10232. DOI: 10.1002/ece3.10232.

582 Heinonen, T., T. Pukkala, S. Kellomäki, H. Strandman, A. Asikainen, A. Venäläinen, and H. Peltola
 583 (2018). “Effects of forest management and harvesting intensity on the timber supply from
 584 Finnish forests in a changing climate”. *Canadian Journal of Forest Research* 48.10, pp. 1124–
 585 1134. DOI: 10.1139/cjfr-2018-0118.

586 Hetemäki, L., J. Kangas, and H. Peltola, eds. (2022). *Forest Bioeconomy and Climate Change*.
 587 Vol. 42. Managing Forest Ecosystems. Cham: Springer International Publishing. DOI: 10.1007/
 588 978-3-030-99206-4.

589 Hilmers, T. et al. (2019). “The productivity of mixed mountain forests comprised of *Fagus sylvat-*
 590 *ica*, *Picea abies*, and *Abies alba* across Europe”. *Forestry: An International Journal of Forest*
 591 *Research* 92.5, pp. 512–522. DOI: 10.1093/forestry/cpz035.

592 Lafond, V. (2014). “Sylviculture des forêts hétérogènes de montagne et compromis production-
 593 biodiversité : une approche simulation”. These de doctorat. Grenoble.

594 Lafond, V., T. Cordonnier, and B. Courbaud (2015). “Reconciling Biodiversity Conservation and
 595 Timber Production in Mixed Uneven-Aged Mountain Forests: Identification of Ecological Inten-
 596 sification Pathways”. *Environmental Management* 56.5, pp. 1118–1133. DOI: 10.1007/s00267-
 597 015-0557-2.

598 Lafond, V., T. Cordonnier, Z. Mao, and B. Courbaud (2017). “Trade-offs and synergies between
599 ecosystem services in uneven-aged mountain forests: evidences using Pareto fronts”. en. *Euro-
600 pean Journal of Forest Research* 136.5, pp. 997–1012. DOI: 10.1007/s10342-016-1022-3.

601 Lafond, V., G. Lagarrigues, T. Cordonnier, and B. Courbaud (2014). “Uneven-aged management
602 options to promote forest resilience for climate change adaptation: effects of group selection
603 and harvesting intensity”. *Annals of Forest Science* 71.2, pp. 173–186. DOI: 10.1007/s13595-
604 013-0291-y.

605 Larrieu, L., Y. Paillet, S. Winter, R. Bütler, D. Kraus, F. Krumm, T. Lachat, A. K. Michel, B.
606 Regnery, and K. Vandekerkhove (2018). “Tree related microhabitats in temperate and Mediter-
607 ranean European forests: A hierarchical typology for inventory standardization”. *Ecological
608 Indicators* 84, pp. 194–207. DOI: 10.1016/j.ecolind.2017.08.051.

609 Ligot, G., P. Balandier, B. Courbaud, M. Jonard, D. Kneeshaw, and H. Claessens (2014). “Man-
610 aging understory light to maintain a mixture of species with different shade tolerance”. *Forest
611 Ecology and Management* 327, pp. 189–200. DOI: 10.1016/j.foreco.2014.05.010.

612 Lindner, M., M. Maroschek, S. Netherer, A. Kremer, A. Barbati, J. Garcia-Gonzalo, R. Seidl,
613 S. Delzon, P. Corona, M. Kolström, M. J. Lexer, and M. Marchetti (2010). “Climate change
614 impacts, adaptive capacity, and vulnerability of European forest ecosystems”. *Forest Ecology
615 and Management. Adaptation of Forests and Forest Management to Changing Climate* 259.4,
616 pp. 698–709. DOI: 10.1016/j.foreco.2009.09.023.

617 Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie (2009). “Refining the stress-
618 gradient hypothesis for competition and facilitation in plant communities”. *Journal of Ecology*
619 97.2, pp. 199–205. DOI: 10.1111/j.1365-2745.2008.01476.x.

620 McDowell, N. G. et al. (2020). “Pervasive shifts in forest dynamics in a changing world”. *Science*
621 368.6494, eaaz9463. DOI: 10.1126/science.aaz9463.

622 Mina, M., H. Bugmann, T. Cordonnier, F. Irauschek, M. Klopčič, M. Pardos, and M. Cailleret
623 (2017). “Future ecosystem services from European mountain forests under climate change”.
624 *Journal of Applied Ecology* 54.2, pp. 389–401. DOI: 10.1111/1365-2664.12772.

625 O’Hara, K. (2014). *Multiaged Silviculture: Managing for Complex Forest Stand Structures*. DOI:
626 10.1093/acprof:oso/9780198703068.001.0001.

627 Oliver, C. and B. Larson (1996). “Forest Stand Dynamics, Update Edition”. *Yale School of the*
628 *Environment Other Publications*.

629 Palomo, I. (2017). “Climate Change Impacts on Ecosystem Services in High Mountain Areas: A
630 Literature Review”. *Mountain Research and Development* 37.2, pp. 179–187. DOI: 10.1659/
631 MRD-JOURNAL-D-16-00110.1.

632 Patacca, M. et al. (2023). “Significant increase in natural disturbance impacts on European forests
633 since 1950”. en. *Global Change Biology* 29.5, pp. 1359–1376. DOI: 10.1111/gcb.16531.

634 Peña, L., I. Casado-Arzuaga, and M. Onaindia (2015). “Mapping recreation supply and demand
635 using an ecological and a social evaluation approach”. *Ecosystem Services*. Best Practices for
636 Mapping Ecosystem Services 13, pp. 108–118. DOI: 10.1016/j.ecoser.2014.12.008.

637 Peng, C. (2000). “Understanding the role of forest simulation models in sustainable forest man-
638 agement”. *Environmental Impact Assessment Review* 20.4, pp. 481–501. DOI: 10.1016/S0195-
639 9255(99)00044-X.

640 Pepin, N. et al. (2015). “Elevation-dependent warming in mountain regions of the world”. *Nature*
641 *Climate Change* 5.5, pp. 424–430. DOI: 10.1038/nclimate2563.

642 Pichancourt, J.-B., R. Manso, F. Ningre, and M. Fortin (2018). “A carbon accounting tool for com-
643 plex and uncertain greenhouse gas emission life cycles”. *Environmental Modelling & Software*
644 107, pp. 158–174. DOI: 10.1016/j.envsoft.2018.06.005.

645 Piedallu, C., D. Dallery, C. Bresson, M. Legay, J.-C. Gégout, and R. Pierrat (2023). “Spatial
646 vulnerability assessment of silver fir and Norway spruce dieback driven by climate warming”.
647 en. *Landscape Ecology* 38.2, pp. 341–361. DOI: 10.1007/s10980-022-01570-1.

648 Plas, F. van der et al. (2018). “Continental mapping of forest ecosystem functions reveals a high
649 but unrealised potential for forest multifunctionality”. *Ecology Letters* 21.1, pp. 31–42. DOI:
650 10.1111/ele.12868.

651 Pommerening, A. (2023). *Continuous Cover Forestry: Theories, Concepts, and Implementation*.
652 John Wiley & Sons. 421 pp.

653 Pretzsch, H. (2009). *Forest dynamics, growth and yield*. Vol. 684. Springer.

654 Pretzsch, H. and P. Biber (2010). “Size-symmetric versus size-asymmetric competition and growth
655 partitioning among trees in forest stands along an ecological gradient in central Europe”. *Can-
656 dian Journal of Forest Research* 40.2, pp. 370–384. DOI: 10.1139/X09-195.

657 — (2022). “Fertilization modifies forest stand growth but not stand density: consequences for
658 modelling stand dynamics in a changing climate”. *Forestry: An International Journal of Forest
659 Research* 95.2, pp. 187–200. DOI: 10.1093/forestry/cpab036.

660 Pretzsch, H. and J. Dieler (2011). “The dependency of the size-growth relationship of Norway
661 spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in forest stands on
662 long-term site conditions, drought events, and ozone stress”. en. *Trees* 25.3, pp. 355–369. DOI:
663 10.1007/s00468-010-0510-1.

664 Pretzsch, H. and A. Rais (2016). “Wood quality in complex forests versus even-aged monocultures:
665 review and perspectives”. en. *Wood Science and Technology* 50.4, pp. 845–880. DOI: 10.1007/
666 s00226-016-0827-z.

667 Schutz, J. (1999). “Close-to-nature silviculture: is this concept compatible with species diversity?”
668 en. *Forestry* 72.4, pp. 359–366. DOI: 10.1093/forestry/72.4.359.

Seidl, R., W. Rammer, R. M. Scheller, and T. A. Spies (2012). “An individual-based process model to simulate landscape-scale forest ecosystem dynamics”. *Ecological Modelling* 231, pp. 87–100. DOI: 10.1016/j.ecolmodel.2012.02.015.

Seidl, R., D. Thom, M. Kautz, D. Martin-Benito, M. Peltoniemi, G. Vacchiano, J. Wild, D. Ascoli, M. Petr, J. Honkaniemi, M. J. Lexer, V. Trotsiuk, P. Mairota, M. Svoboda, M. Fabrika, T. A. Nagel, and C. P. O. Reyer (2017). “Forest disturbances under climate change”. en. *Nature Climate Change* 7.6, pp. 395–402. DOI: 10.1038/nclimate3303.

Söderbergh, I. and T. Ledermann (2003). “Algorithms for simulating thinning and harvesting in five European individual-tree growth simulators: a review”. *Computers and Electronics in Agriculture* 39.2, pp. 115–140. DOI: 10.1016/S0168-1699(03)00022-X.

Stokland, J., J. Sitonen, and B. Jonsson (2012). “Biodiversity in Deadwood”. *The Forestry Chronicle* 88, pp. 660–660. DOI: 10.5558/tfc2012-123.

Tegel, W., A. Seim, D. Hakelberg, S. Hoffmann, M. Panev, T. Westphal, and U. Büntgen (2014). “A recent growth increase of European beech (*Fagus sylvatica* L.) at its Mediterranean distribution limit contradicts drought stress”. *European Journal of Forest Research* 133.1, pp. 61–71. DOI: 10.1007/s10342-013-0737-7.

Touzot, L., N. Beauchamp, A. Baranger, B. Courbaud, T. Cordonnier, B. Olivier, S. Delzon, S. Etzold, C. Fischer, A. Gessler, T. Jucker, P. Ruiz-Benito, M. A. Zavala, and G. Kunstler (2025). “Shade tolerance controls the spectrum of crown sizes and its response to local competition across European and North American tree species. Implications for light interception strategies”. en. *Oikos* 2025.8, e10603. DOI: 10.1002/oik.10603.

Unkule, M. (2022). “Regeneration of spruce - fir - beech mixed forests under climate and ungulate pressure”. Theses. Université Grenoble Alpes [2020-....] DOI: 10.70675/129604caze95ez452ezb03dz2f3cb

692 Unkule, M., C. Piedallu, P. Balandier, and B. Courbaud (2022). “Climate and ungulate browsing
693 impair regeneration dynamics in spruce-fir-beech forests in the French Alps”. *Annals of Forest
694 Science* 79.1, p. 11. DOI: 10.1186/s13595-022-01126-y.

695 Valladares, F. and Ü. Niinemets (2008). “Shade Tolerance, a Key Plant Feature of Complex Nature
696 and Consequences”. *Annual Review of Ecology, Evolution, and Systematics* 39, pp. 237–257.

697 Weiner, J. (1990). “Asymmetric competition in plant populations”. *Trends in Ecology & Evolution*
698 5.11, pp. 360–364. DOI: 10.1016/0169-5347(90)90095-U.

699 Zlatanov, T., C. Elkin, F. Irauschek, and M. J. Lexer (2017). “Impact of climate change on vul-
700 nerability of forests and ecosystem service supply in Western Rhodopes Mountains”. *Regional
701 Environmental Change* 17.1, pp. 79–91. DOI: 10.1007/s10113-015-0869-z.

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