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Research article

From breeding to landscape: how genetic improvement and forest management shape multifunctionality in Norway

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A B S T R A C T

Balancing wood production, biodiversity, and climate regulation is increasingly challenging for forest management, particularly as societal demands intensify. Despite growing interest in genetic improvement to enhance forest productivity, its implications for multiple ecosystem services (FES) remain poorly quantified. To address this gap, we assessed how genetically improved regeneration material, combined with alternative management regimes, influences FES provision in Norway. Using National Forest Inventory data, a climate-sensitive single-tree simulator, and multi-objective optimization, we projected 100-year outcomes under three strategies: no genetic gain, growth-focused improvement, and combined improvement in growth and wood quality.

The strongest responses occurred when genetic improvement targeted both growth and wood quality. Under this scenario, harvest net value increased, ecological hotspot areas expanded, and larger set-aside areas were maintained while meeting national harvest demands. Carbon storage in harvested wood products also increased, whereas carbon sequestration in living biomass showed no consistent trend. Genetic gain reinforced positive interactions between bioenergy and climate regulation but left most other FES relationships broadly unchanged. Varying genetic gain levels produced only minor differences across most indicators, suggesting that long-term outcomes depend more on how improved material is integrated within a flexible management portfolio than on the exact magnitude of genetic gain. Positive responses in the structural biodiversity indicators should be interpreted cautiously, as these proxies capture only a limited subset of ecological dimensions and likely underestimate broader biodiversity trade-offs. Overall, genetically improved material represents a complementary tool for enhancing forest multifunctionality when integrated with adaptive, landscape-scale management.

1. Introduction

Increasingly, sustainability-oriented forest management requires balancing wood production with multiple forest ecosystem services (FES), including provisioning, regulating, and cultural services (Tischenko et al., 2024). As bioeconomy strategies become more central in forest policy, forest management faces growing pressure to reconcile these diverse objectives while meeting increasing wood demand. This may intensify trade-offs among FES, particularly those involving biodiversity, climate regulation, freshwater provision, and recreation (Blattert et al., 2023). Climate change is expected to further amplify these challenges by altering growing conditions and increasing tree vulnerability (Weiskopf et al., 2020). These challenges highlight the need for diversified forest management approaches, such as the integration of genetic improvement with adaptive management strategies.

Tree breeding has increased forest productivity and wood quality globally while also improving resilience to climate change (Fugeray-Scarbel et al., 2024). Forest management, in turn, influences ecosystem services and their trade-offs by altering forest structure and age composition (Triviño et al., 2022). For instance, the increasing adoption of Continuous Cover Forestry (CCF) and related silvicultural approaches can provide multiple ecosystem services and enhance forest resilience (Eyvindson et al., 2021).

Since the late 1940s, tree breeding programs in Scandinavia have focused on Norway spruce (*Picea abies* L.) and Scots pine (*Pinus sylvestris* L.) by selecting phenotypically superior "plus trees" (Jansson et al., 2017). Although these programs have primarily targeted volume production, improvements in stem and wood quality have also been considered (Stener, 2015). In Norway, breeding efforts mainly target Norway spruce for sawn timber production, reflecting its importance to

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the forest industry, as the species accounts for approximately 73% of harvested roundwood volume.

Integrating improved genetic material into silvicultural practices can increase harvest potential while reducing pressure on natural forests (Jansson et al., 2017). Combined with diversified management, improved regeneration material may enhance carbon sequestration and timber yield (Heinonen et al., 2018). For example, Pikkarainen et al. (2024) found that combining improved regeneration material with fertilization can offset timber deficits associated with expanded conservation while increasing long-term yields. Similarly, Ahtikoski et al. (2013) showed that improved regeneration material increased growth and economic returns, while Ruotsalainen (2014) reported improved wood quality and long-term profitability.

Field trials across the Nordic region indicate that genetically improved material can increase volume growth by approximately 10–25%, depending on breeding generation, site productivity, and climate (Jansson et al., 2017). First-generation Norway spruce seed orchards increase volume by around 20%, while tested 1.5-generation orchards may achieve gains close to 37%. These gains have increasingly been incorporated into forest growth simulations through adjusted site-index values or genetic-gain multipliers. For example, Rosvall and Lundström (2011) projected a 10% increase in Swedish forest growth using improved seedlings, while simulations in Finland reported 7–24% higher volume production for improved Scots pine material (Juutinen et al., 2018). Such simulations are commonly embedded within scenario analyses evaluating long-term forest development under alternative management and climate pathways (Sevillano et al., 2025).

However, these studies have mainly focused on individual FES, particularly timber production or carbon sequestration, without explicitly addressing trade-offs among multiple services. Although multi-objective optimization approaches have recently been applied at national scales in Fennoscandia (Vergarechea et al., 2023; Blattert et al., 2023; Toraño Caicoya et al., 2023b), they have not incorporated genetic improvement into the optimization framework. Consequently, the combined effects of genetic improvement and forest management on FES provision remain poorly understood. This question is particularly relevant for Norway, where genetically improved material is actively promoted through national forestry guidelines and improved seeds currently account for the majority of planted Norway spruce across productive forest land (Myre et al., 2021). To address this gap, we used scenario analysis to assess how integrating genetic improvement into forest management influences multiple FES and their trade-offs in Norway. We compare three strategies: conventional management, genetic improvement aimed solely at increasing growth, and combined growth and wood-quality improvement. Specifically, we address the following research questions.

1. How can genetic improvements in Norway be combined with forest management to maximize the provision of several FES?
2. How do different breeding strategies (e.g., growth-focused vs. quality-focused) affect trade-offs among FES?
3. How do varying levels of genetic gain affect future FES indicators?

We simulated different ecosystem services under the three scenarios and applied a multi-objective optimization framework to identify management and breeding combinations that maximize timber production, biodiversity, and climate change mitigation (Fig. 1). The optimized scenarios were then evaluated in terms of harvest demand, long-term FES trajectories, spatial patterns, and sensitivity to different levels of genetic gain.

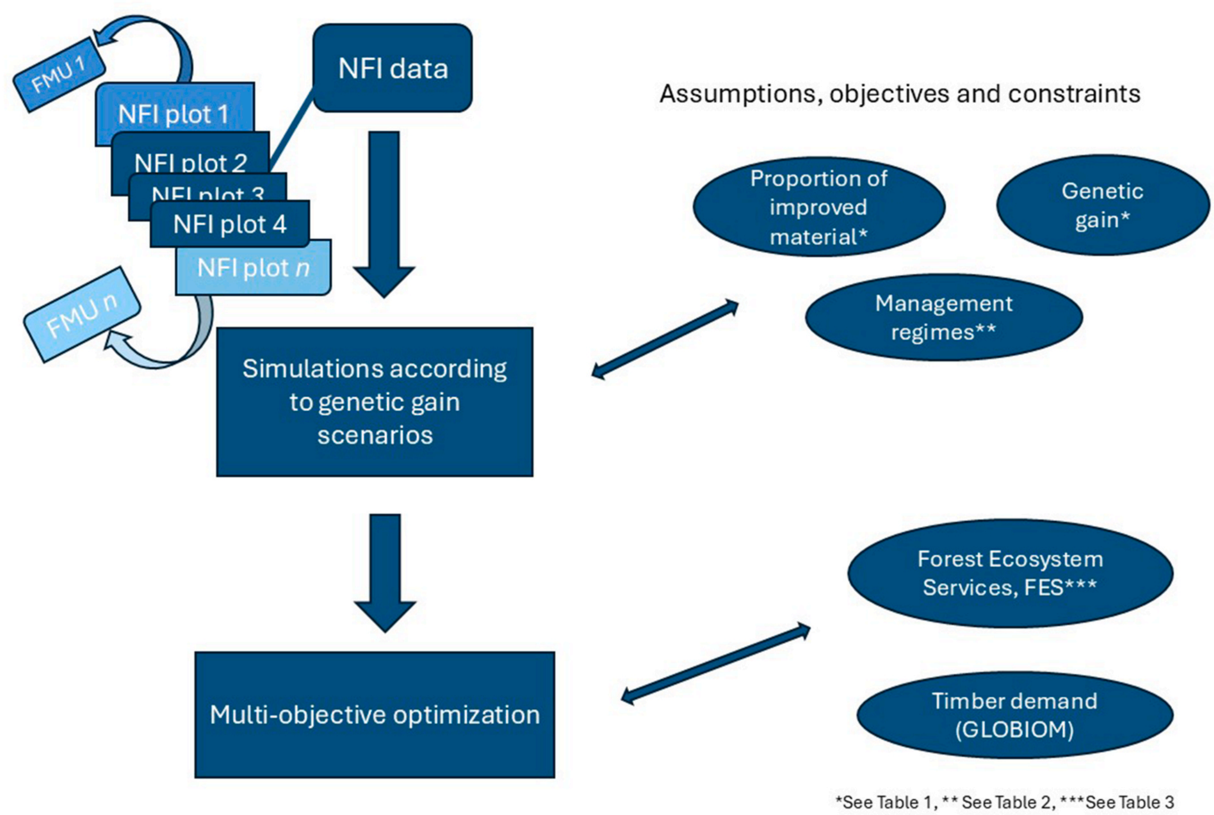

Fig. 1. Study workflow. Norwegian national forest inventory (NFI) data were used to simulate genetic-gain scenarios and management regimes, forming the solution base for the multi-objective optimization of FES indicators under timber-demand constraints.

2. Material and methods

2.1. Forest data and Sitree simulation

In Norway, forests cover approximately 37.6% of the mainland, of which 71% is classified as productive forest land, defined by an annual growth rate exceeding $1\,m^3\,ha^{-1}\,yr^{-1}$ including bark (FAO, 2020). Forests are dominated by Norway spruce, Scots pine, and birch (*Betula spp.*), with spruce and pine covering roughly 64% of productive forest. Our 100-year simulations were based on Norwegian National Forest Inventory (NFI) data from 2018 to 2022 (Breidenbach et al., 2020).

Forest dynamics and management were projected using a single-tree growth simulator implemented in SiTree (Antón-Fernández and Astrup, 2022). SiTree uses single-tree models calibrated with NFI data and simulates growth, mortality, and ingrowth using nearest-neighbor imputation based on the three most recent NFI cycles. Climate effects were incorporated using a climate-sensitive site index model driven by 30-year averages of growing-season temperature sum and June moisture surplus for 1971–2100 (Antón-Fernández et al., 2016).

2.2. Genetic gain

The proportion of harvested areas regenerated by planting was derived from annual forest regeneration surveys for 2018–2022 (Resultatkartleggingen, unpublished data), which indicated that 77% of harvested Norway spruce areas and 10% of harvested Scots pine areas were replanted. Of these, the proportion established with genetically improved material — broken down by species, breeding zone, and altitude — was estimated from Myre et al. (2021). These proportions (Table 1) were achieved through random allocation of eligible stands. Genetic gain was not applied to stands with $SI \leq 8$ unless the target proportion could not be reached from $SI > 8$ stands alone (Baardsen, S., Eid, T. & Hoen, H.F.). Random allocation was not replicated, as the aim of the simulations was to identify optimal management strategies rather than to quantify uncertainty associated with the spatial allocation of improved material.

In SiTree, genetic gain was incorporated by adjusting the site index (SI), which is the primary driver of stand productivity. Specifically, SI was multiplied by the expected height-growth increase (Table 1) at the time of planting and held constant during the rotation length. Modifying SI causes stand development to follow production tables reflecting enhanced productivity, thereby affecting waiting time, tree density, and early growth characteristics (Table S2).

Table 1
Proportions of the area planted with genetically improved material, expressed relative to the planted area, and their respective height gains (in brackets) for Norway spruce and Scots pine in each breeding zone.

Breeding zones	First 10 years[a]		After 10 years	
	Spruce	Pine	Spruce	Pine
Eastern Norway; < 350 m	95% [8%]	90% [6%]	95% [10%]	90% [8%]
Eastern Norway; 350 - 650 m	95% [8%]	90% [6%]	95% [10%]	90% [8%]
Eastern Norway; 650 m	95% [8%]	65% [6%]	95% [10%]	65% [8%]
Western Norway; 350 m	100% [8%]	25% [6%]	100% [10%]	25% [8%]
Trøndelag/Helgeland; 250m	90% [8%]	50% [6%]	90% [10%]	50% [8%]
Trøndelag/Helgeland; 250 - 450 m	25% [8%]	50% [6%]	25% [10%]	50% [8%]
Nordland north and Troms/ Finnmark; 250m	25% [8%]	25% [6%]	25% [10%]	25% [8%]

[a] 'First 10 years' refers to the initial 10-year period of the simulation (2023–2033). For all plots harvested after 2033, the 10-year post-harvest gain is applied.

2.3. Management regimes

In Norway, clearcutting is the dominant silvicultural practice, used on approximately 71% of productive forest area, followed by seed-tree cutting (20%) and other methods such as selective cutting (9%) (Granhus, 2021). To represent this diversity, we defined seven management regimes differing in harvest intensity, rotation length, green-tree retention, thinning, and regeneration method. **Set-aside (SA)** excludes all interventions, allowing natural forest development. **Business as usual (BAU)** represents conventional even-aged management with final clearcutting and artificial regeneration. Extensive **BAU (EBAU)** extends the BAU rotation period by 40%, while **Intensive (INT)** increases planting density, fertilization, and thinning intensity. **Short intensive (SINT)** follows INT but with a 20% shorter rotation period. **Continuous cover forestry (CCF)** avoids final clearcutting by harvesting incremental growth every 15 years while maintaining permanent canopy cover. **Multispecies (MULT)** promotes mixed-species stands through the regeneration of spruce, pine, and birch mixtures. BAU, EBAU, INT, SINT, and MULT were also simulated with genetically improved regeneration material; although MULT only for Norway spruce (e.g., BAU_gen). Full regime specifications are provided in Table S1.

2.4. Genetic gain scenarios

Three scenarios were defined based on genetic gain implementation and timber quality assumptions.

(a) ***No genetic gain* scenario**: Management regimes described above were applied without incorporating any genetic improvements.
(b) **Growth-Focused scenario (*Genetic Growth*):** Genetic gain was incorporated into SiTree by adjusting the site index (SI) as described in Section 2.2, increasing tree growth and forest yield.
(c) **Quality-Focused scenario (*Genetic Growth & Quality*):** The same SI adjustment was applied in SiTree as in the Growth-Focused scenario. Additionally, the proportion of stem volume allocated to sawlog was increased from 55% to 65%, reflecting the expected reduction in stem defects from genetic improvement (Ruotsalainen, 2014; Malinen et al., 2018), although direct experimental validation of this assumption for genetically improved material is currently lacking.

2.5. Indicators for ecosystem services provision and definition of optimized scenarios

To assess the effects of genetic gain and management regimes, we defined four categories of FES based on international classification and European policy analyses (Primmer et al., 2021): (i) timber production, (ii) bioenergy, (iii) biodiversity conservation and (iv) climate regulation. These services were selected using indicators measurable from the available NFI data and consistent with previous studies on Norwegian forest multifunctionality (Toraño Caicoya et al., 2023b; Vergarechea et al., 2023).

Timber production was evaluated as net harvest income (NOK), calculated as revenues minus silvicultural and transportation costs. Harvest costs were estimated using standard Norwegian procedures reflecting terrain and road accessibility (Granhus et al., 2011), while timber prices and costs were held constant throughout the simulations (Vennesland et al., 2014). Bioenergy was measured as the harvested volume of logging residues (GROT; *greiner og topper*). Biodiversity conservation was assessed using ecological hotspot area and deadwood volume. Here, NFI plots were classified as binary hotspots (1/0) based on the presence of large trees and broadleaves. Deadwood volume (lying and standing deadwood >30 cm in diameter) was estimated using species and diameter-specific decomposition functions calibrated with NFI mortality data (Müller and Bütler, 2010). Climate regulation was evaluated using carbon sequestration in living trees and carbon storage in harvested wood products (HWP). Carbon sequestration was estimated by converting tree biomass to carbon by applying a conversion factor of 0.5, while HWP carbon storage was estimated for sawn wood and panels, with half-lives of 35 and 25 years (IPCC, 2019).

2.6. Timber demands as climate mitigation targets

Wood and biomass demand projections for Norway were derived from the GLOBIOM-forest model (IIASA's Global Biosphere Management Model), which represents forestry, the forest industry, and forest bioenergy in detail (Lauri et al., 2021; see Supplementary Material S5 for further details). The model provides demand projections for sawlogs, pulpwood, other industrial roundwood, fuelwood and logging residues. Our analysis focused on sawlogs and pulpwood, which were combined as "total wood demand." These projected wood and biomass demands were then incorporated as constraints within the multi-objective optimization framework to evaluate whether Norway could meet future climate-mitigation targets under the different management and genetic gain scenarios.

2.7. Optimization method

We incorporated FES indicators and harvest demands aligned with EU climate change mitigation targets into the multi-objective optimization framework MultiOptForest (Eyvindson et al., 2024), which has been widely applied in forest management planning across Fennoscandia (Blattert et al., 2022; Vergarechea et al., 2023) and Germany (Toraño- Caicoya et al., 2023a).

Our optimization approach was based on Vergarechea et al. (2023), who evaluated policy impacts on biomass supply and forest ecosystem services under the Norwegian National Forest Strategy ("Verdier i vekst"; NMAF, 2016). Building on this framework, the optimization incorporated objectives representing the four ecosystem-service categories evaluated in this study, together with constraints reflecting biodiversity targets and future wood demand. For timber production, harvest net value was maximized as an even flow, defined as the minimum periodic income over the planning horizon. Harvested residues for bioenergy (GROT) were maximized only in plots where roadside extraction costs were below 150 NOK t^{-1}. For biodiversity, ecological hotspot area and deadwood volume were constrained to non-declining trajectories relative to current levels. For climate regulation, carbon storage in HWP and carbon sequestration in living biomass were maximized, with HWP also constrained to remain above its initial level. In addition, harvested timber volume was included as a hard constraint to ensure that projected national wood demand was met.

For each scenario, MultiOptForest optimized 5-year indicator trajectories under alternative management regimes at the forest management unit (FMU) level, identifying Pareto-optimal solutions that balanced trade-offs among competing objectives. The optimization problem was formulated as:

$$\begin{aligned} &\textit{minimize}\ x\ \{f_1(x), \ldots, f_n(x)\} \\ &\qquad \textit{subject}\ x \in S \end{aligned} \qquad \text{[Eq. 1]}$$

where $f_1(x)$ represents the objective functions, x the vector of management regimes, and S the feasible set of regimes defined by constraints. Maximization objectives were reformulated as minimization problems.

Trade-offs among ecosystem services were handled using the achievement scalarizing function (ASF), which guides the search toward solutions that improve all objectives as evenly as possible relative to user-defined reference points (Eyvindson et al., 2024). Constraints were implemented using the ε-constraint method and consisted of two categories. Hard constraints ensured that timber harvest volumes met projected national wood demand. In contrast, threshold-based constraints required biodiversity indicators and carbon storage in HWP to remain above predefined levels but could be progressively relaxed when no feasible solution could be found. The remaining ecosystem-service objectives were then optimized simultaneously within the resulting feasible solution space.

Indicators were modeled individually, each with its own objective function, while aggregation into FES categories was performed afterward for reporting purposes (see Section 2.8). Convergence was reached when the ASF value no longer improved and constraint feasibility remained stable. Full mathematical details are provided in Supplementary Material S6 and in Eyvindson et al. (2023).

2.8. Ecosystem services aggregation, normalization and assessment analyses

We evaluated each FES indicator across the full planning horizon by scaling plot-level outputs to the represented forest area and aggregating them nationally. Differences from the reference scenario (*No genetic gain*) were used to assess the effects of genetic improvement, and time-series were produced for key indicators. Harvest volume and ecological hotspots were also mapped to evaluate spatial patterns and landscape-level trade-offs.

To facilitate comparisons among FES, indicators were normalized to a 0–1 scale using scenario-specific minimum and maximum values (Equation (2)) and aggregated with equal weights within each FES category. This approach assumes equal importance among indicators within a category and enables direct comparison across services and scenarios. However, alternative weighting schemes could influence multifunctionality outcomes and the interpretation of trade-offs. Spatio-temporal relationships among FES were analyzed using bootstrapped Pearson correlations (1000 replicates) to identify synergies and trade-offs over time. Correlations strength were classified as weak (0–0.2), moderate (0.2–0.6), or strong (0.6–1) (Toraño Caicoya et al., 2023b).

$$f\left(x_{i,j,k,}\right) = \frac{x_{i,j,k} - Ind_{min}}{Ind_{max} - Ind_{min}} \qquad \text{[Eq. 2]}$$

Where $f\left(x_{i,j,k}\right)$ is the normalized landscape-average indicator (i), at simulation period (j), under genetic gain scenario (k).

To evaluate the sensitivity of FES provision to genetic gain, we performed additional simulations for the *Genetic Growth* and *Genetic Growth & Quality* scenarios by proportionally adjusting the baseline gain values (Table 1). Low-gain conditions reduced projected height growth to 5% for the first 10 years and 8% thereafter, while high-gain conditions increased gains to 10% and 15%, respectively. We then repeated simulations for both scenarios under these adjusted assumptions. A total of seven simulations and optimizations were conducted. Sensitivity results are presented in Section 3.4, while the main text focuses on the three primary scenarios.

3. Results

3.1. Effect of genetic gain on ecosystem service provision

Fig. 2 shows the projected differences in FES indicators under the two genetic gain scenarios, *Genetic Growth* and *Genetic Growth & Quality*, relative to the baseline (*No Genetic Gain*) .

Both genetic gain scenarios increased economic returns, with the strongest gains under *Genetic Growth & Quality*. GROT remained close to baseline levels, although variability was slightly greater under *Genetic Growth*. Ecological hotspot area increased in both scenarios, particularly under *Genetic Growth & Quality*. Deadwood volumes remained near baseline levels under *Genetic Growth*, with only minor deviations over time, whereas *Genetic Growth & Quality* produced a gradual long-term increase after 2070. Carbon stored in HWP consistently exceeded baseline levels in both scenarios, again with stronger responses under *Genetic Growth & Quality*. In contrast, carbon sequestration in living

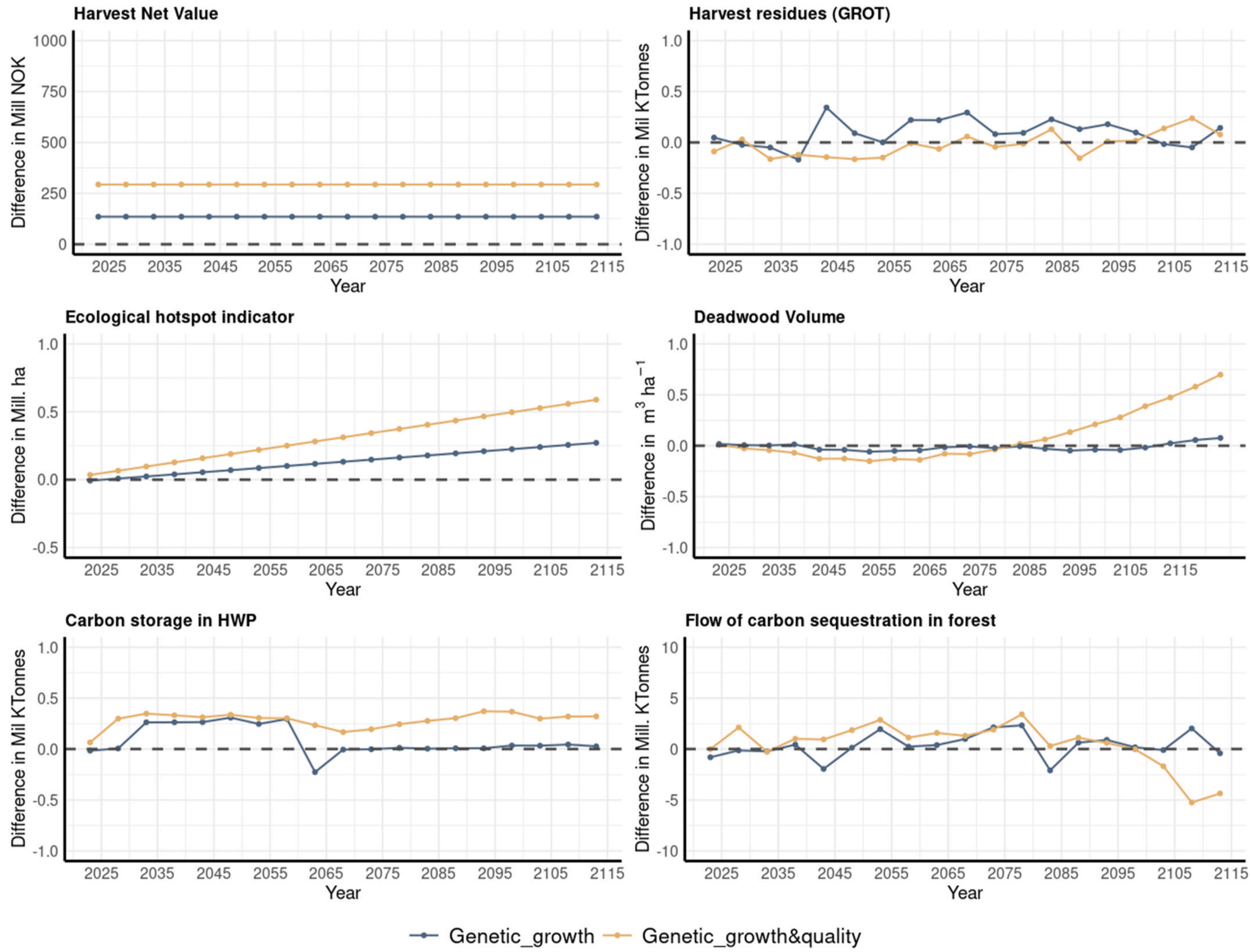

Fig. 2. Differences in FES indicators under the *Genetic Growth* and *Genetic Growth & Quality* scenarios relative to the *No genetic gain* scenario over time (2023–2113). Long-term projections of indicators are presented in Supplementary Material S1.

biomass fluctuated over time without a consistent trend relative to the baseline.

3.2. Trade-offs and synergies among ecosystem services

Correlations were analyzed among the aggregated FES categories (Wood, Bioenergy, Biodiversity, Climate), each defined as the equal-weight mean of its normalized indicators (Section 2.8).

Wood–Bioenergy correlations remained strongly positive across all scenarios. In contrast, Wood–Biodiversity and Biodiversity–Bioenergy correlations stayed near zero, suggesting limited interaction. Wood–Climate and Bioenergy–Climate correlations increased from near zero to moderately positive values after mid-century. The genetic gain scenarios maintained higher correlations for much of the period, before converging with the baseline toward the end of the simulation period (see Fig. 3).

Overall, although the general correlation patterns remain broadly consistent across scenarios, the inclusion of genetic gain slightly modified the magnitude of key relationships. For instance, the genetic gain scenarios maintained higher Bioenergy–Climate correlations through much of the simulation period, particularly under *Genetic Growth & Quality*.

3.3. Harvest distribution and management prescriptions

Fig. 4 shows the spatial distribution of harvest volumes across Norway under the *Genetic Growth* scenario. Spatial patterns were broadly similar across scenarios, reflecting the dominant role of site productivity in shaping harvest allocation regardless of genetic strategy. Higher harvest volumes were consistently concentrated in southern and central regions, a pattern also observed for other indicators, such as the ecological hotspot area (Fig. S3 in the Supplementary Material).

All scenarios met the projected harvest demand, although production patterns differed slightly among them (Fig. 5). Sawlog production increased over time in all scenarios, with the highest volumes under *Genetic Growth & Quality*. Pulp production gradually declined over the simulation period, while harvested residues remained relatively stable with only a slight upward trend toward the end of the century.

The proportion of set-aside (SA) increased from 34.2% (*No Genetic Gain*) to 39% (*Genetic Growth & Quality*). BAU and its extended version (EBAU) together covered 44.9% of the area in the baseline scenario and remained similar under *Genetic Growth*, although BAU variants alone declined slightly from 21.2% to 19% under *Genetic Growth & Quality*. Meanwhile, intensive regimes (INT and SINT, with or without genetic gain) remained stable across scenarios, ranging from 16.8% to 17.5%. Genetically enhanced variants (e.g., EBAU_gen, MULT_gen) became more prominent under both genetic gain scenarios, leading to a more

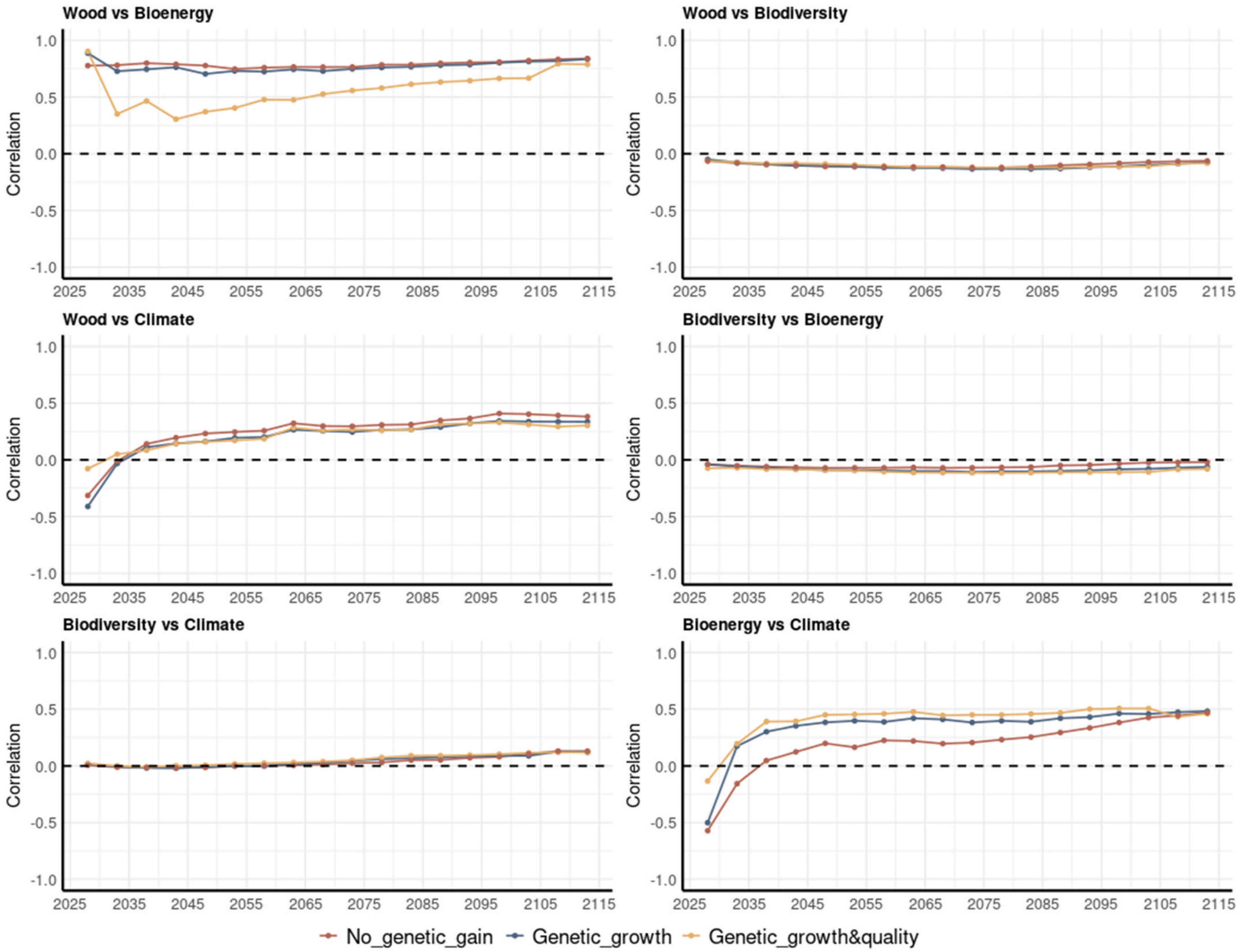

Fig. 3. Bootstrapped Pearson correlations of paired normalized FES over time (2023–2113) under the three scenarios: *No genetic gain, Genetic Growth, Genetic Growth & Quality*. Each panel displays temporal trends across all NFI plots. Correlation strength: 0–0.2 weak, 0.2–0.6 moderate, 0.6–1 strong. The dashed line indicates zero correlation.

balanced mix of management strategies. Continuous Cover Forestry (CCF) remained limited but increased from 0.2% to 0.8% under *Genetic Growth & Quality*.

3.4. Impact of varying genetic gain rates on simulations

When testing different genetic gain rates, noticeable effects appeared only for harvest net value and the ecological hotspot area (Fig. 7). Consequently, the sensitivity analysis focuses on these two indicators.

For harvest net value, the *high*−gain scenario (yellow) produced slightly higher returns than the *baseline* (green), while the *low*−gain scenario (red) remained close to it. This pattern held for both *Genetic Growth* and *Genetic Growth & Quality*, indicating that the optimization framework stabilized economic outcomes through management reallocation despite differences in genetic gain magnitude.

Ecological hotspot area increased steadily over time in all scenarios. Under *Genetic Growth*, differences among gain levels were more visible: high gain (yellow) led to the largest expansion of hotspot areas, while baseline (green) and low gain (red) increased more slowly. Under *Genetic Growth & Quality*, trajectories largely converged by the end of the century, indicating that hotspot-area gains were broadly consistent across gain levels once wood quality was also targeted.

4. Discussion

4.1. Impact of genetic improvement on the forest ecosystem services

While previous research has mainly focused on the effect of genetic gain on timber production and tree growth (Ahtikoski et al., 2020; Sevillano et al., 2025), its broader implications for other FES remain largely unexplored. Recent studies suggest that tree breeding can enhance multiple services, particularly carbon sequestration, through improved regeneration material (Fugeray-Scarbel et al., 2023).

Combining genetic improvement with diversified management can enhance several FES (Section 3.1), with the greatest effects when genetic gain targeted both growth and wood quality. This suggests that genetic improvement may support not only forest productivity but also landscape-scale multifunctionality. Among the affected services, harvest net value showed the most pronounced and consistent response. Its benefits appeared early in the simulations because the optimization framework maximizes an even flow over the full planning horizon, anticipating the future value of improved stands and adjusting harvest allocation accordingly. Thus, long-term gains are internalized early, creating a strong economic incentive to adopt genetically improved seed material. Under the fixed timber prices and management costs assumed here, the *Genetic Growth & Quality* scenario increased harvest net value

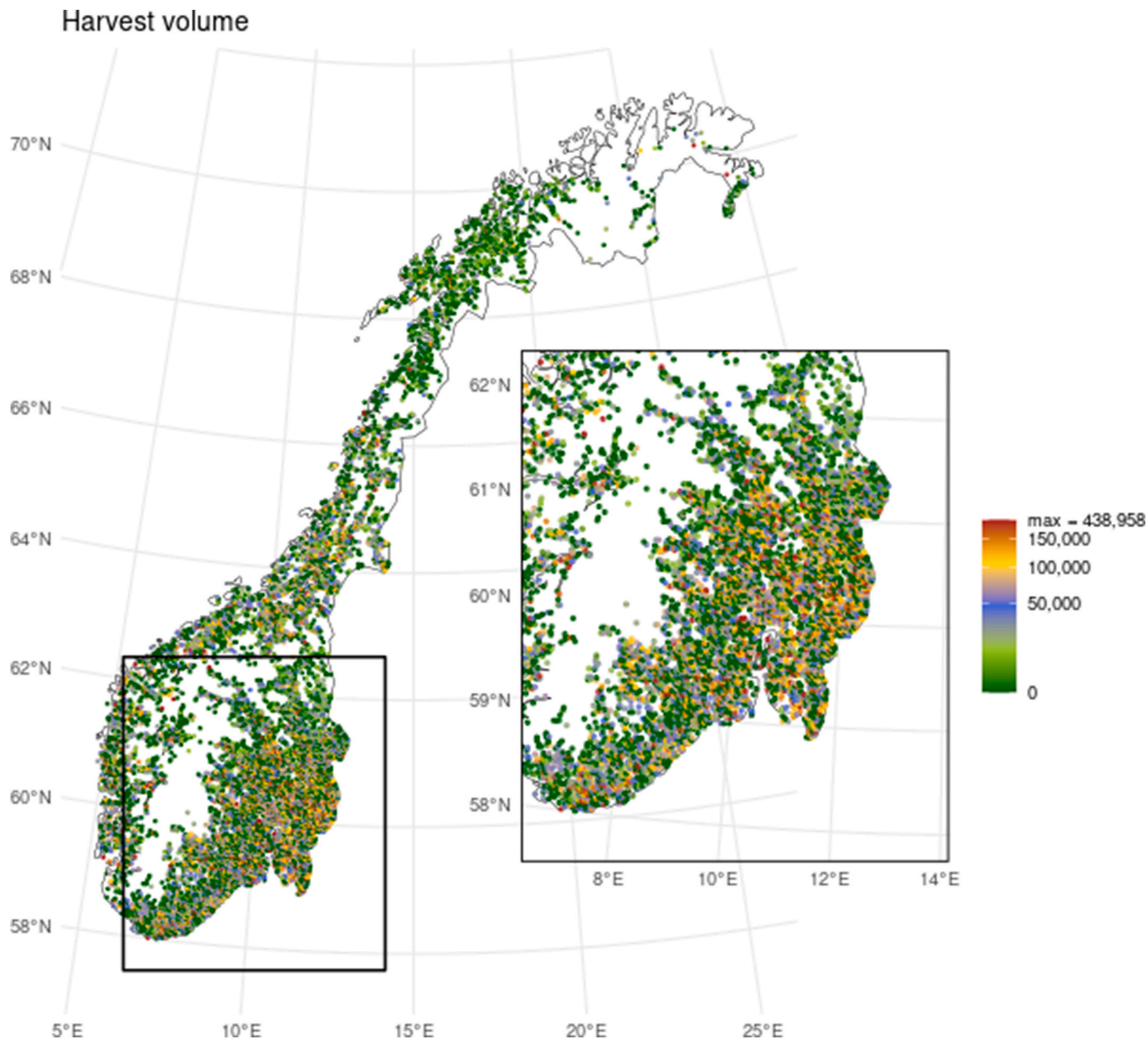

Fig. 4. Map of harvest volume distribution (m^3 cumulative 100 years) per represented NFI plot for 2023–2113 under the *Genetic Growth* scenario. Plot-level values were expanded to the corresponding forest area represented by each plot.

by approximately 51 million NOK per year (about 5 million EUR at 2025 exchange rates) relative to the baseline. This result highlights the economic potential of genetically improved regeneration material and supports previous findings that long-term productivity gains can justify investments in tree breeding (Ahtikoski et al., 2013). Nevertheless, the magnitude of this economic benefit is conditional on the market assumptions adopted and should therefore be interpreted as a scenario-specific comparison rather than a robust forecast.

Beyond economic performance, our results suggest that genetic gain can also expand ecological hotspot area, a structural proxy for stands with large and old trees, generally associated with higher biodiversity potential. Large trees and old-growth structures are generally associated with higher biodiversity potential (Kebrle et al., 2021), making these responses particularly relevant in intensively managed Fennoscandian forests (Lunde et al., 2025). The longer-term increase in deadwood under *Genetic Growth & Quality* likely emerged indirectly through optimization-driven management allocation rather than through direct modifications of mortality or decay dynamics, which were treated similarly across scenarios. Higher sawlog value improved the efficiency of wood production, allowing harvest targets to be met with a larger share of set-aside and lower-intensity regimes, favoring deadwood accumulation at the landscape-scale. Thus, the positive responses observed in ecological hotspot areas and deadwood likely reflect landscape-level management reallocation rather than through direct effects of genetic improvement on ecological processes. However, the indicators used here likely capture only part of the ecological response and should therefore be interpreted cautiously.

Higher carbon storage in HWP under *Genetic Growth & Quality* is consistent with increased sawlog production and highlights the potential contribution of genetic improvement to climate mitigation (IPCC, 2019). In contrast, effects on carbon sequestration in living trees were less consistent. Similar results were reported by Sevillano et al. (2025),

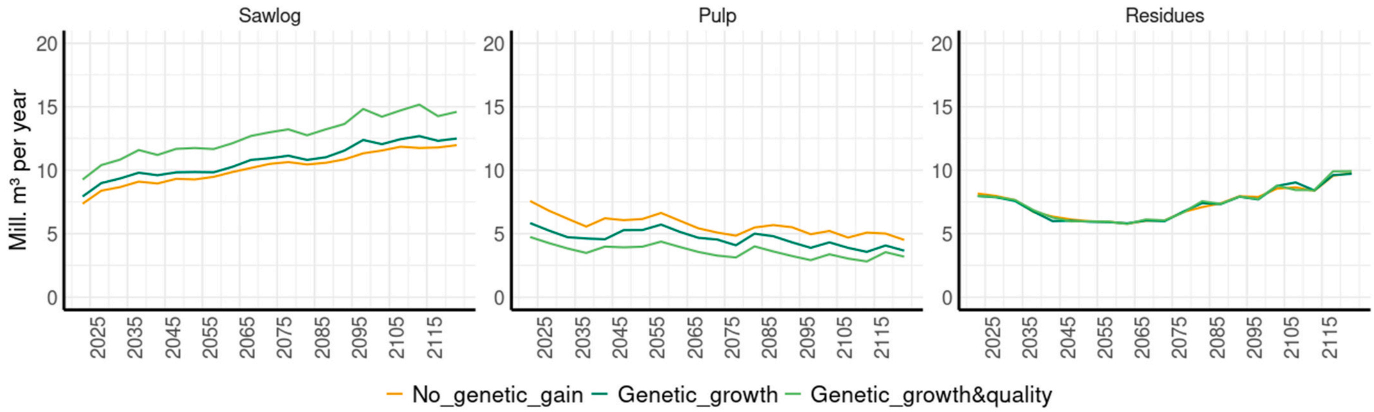

Fig. 5. Provision of different timber assortments (sawlogs, pulp, and residues; million m^3 per year) under the three optimal management scenarios (*No genetic gain, Genetic Growth, Genetic Growth & Quality*) over the simulation period (2023–2113).

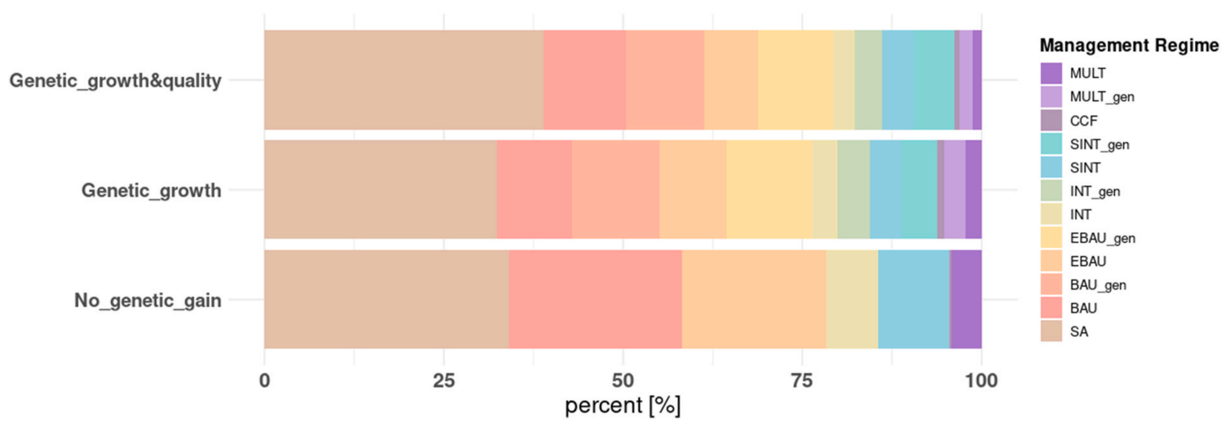

Fig. 6. Share of management regimes across the three scenarios (*No genetic gain, Genetic Growth, Genetic Growth & Quality*). SA: set-aside; BAU: business as usual; EBAU: extensive BAU; INT: intensive; SINT: short-rotation intensive; CCF: continuous cover forestry; MULT: mixed-species stands. Variants with the suffix "_gen" indicate regimes including genetic gain.

who found that genetic improvement alone had limited effects on forest carbon stocks in Norway, whereas measures such as post-harvest reforestation and pre-commercial thinning were more effective. These findings suggest that the climate benefits of genetic improvement depend on its integration with management practices that maintain stand productivity and resource availability (Pretzsch, 2009).

The overall pattern of FES relationships remained broadly consistent across genetic gain scenarios, suggesting that genetic improvement does not fundamentally restructure FES interactions at the national scale. Differences emerged mainly in their temporal dynamics. The Wood–Climate correlation started at approximately −0.5 in all scenarios, reflecting early carbon losses from harvesting, but shifted to positive values roughly five years earlier under *Genetic Growth & Quality* (∼2035) than under *No genetic gain* (∼2040). This suggests that the higher sawlog value under the quality-focused scenario enabled harvest targets to be achieved more efficiently, shortening the initial production–climate trade-off. The Bioenergy–Climate relationship followed a similar pattern.

The weak relationships between biodiversity-related indicators and production should be interpreted cautiously. Previous studies have reported highly context-dependent biodiversity–production relationships, ranging from strong trade-offs under intensive management (Triviño et al., 2022) to weaker or mixed responses depending on forest structure, management intensity, and the indicators considered (Schulze, 2018). The biodiversity proxies used here capture only a limited subset of ecological dimensions and do not represent broader aspects such as species diversity, habitat connectivity, or understory composition. Consequently, the positive responses observed for hotspot area and deadwood should be interpreted as improvements in selected structural biodiversity indicators rather than evidence that biodiversity trade-offs are broadly avoided. Additional biodiversity metrics would likely reveal stronger ecological trade-offs.

4.2. Impact of genetic gain on harvest distribution

Although spatial harvest patterns remained largely unchanged, site productivity remained the dominant driver of harvest allocation. Genetic gain amplified existing productivity differences between plots but did not alter their relative ranking, so management intensity was redistributed within the existing landscape structure rather than shifting harvest geographically.

However, site productivity alone did not explain the allocation of set-aside area. Set-aside increased from 34.2% under the *No Genetic Gain* baseline to 39.0% under *Genetic Growth & Quality* (Fig. 6; Table S6), whereas it decreased slightly to 32.4% under *Genetic Growth*. This indicates that increased productivity alone was insufficient to expand conservation areas. Instead, the larger set-aside area under *Genetic Growth & Quality* may reflect optimization reallocating management because the higher value of sawlogs allowed harvest targets to be met with a smaller area under intensive management. This reallocation could support conservation-area targets such as the EU goal of protecting 30% of land (European Commission, 2020). Previous studies

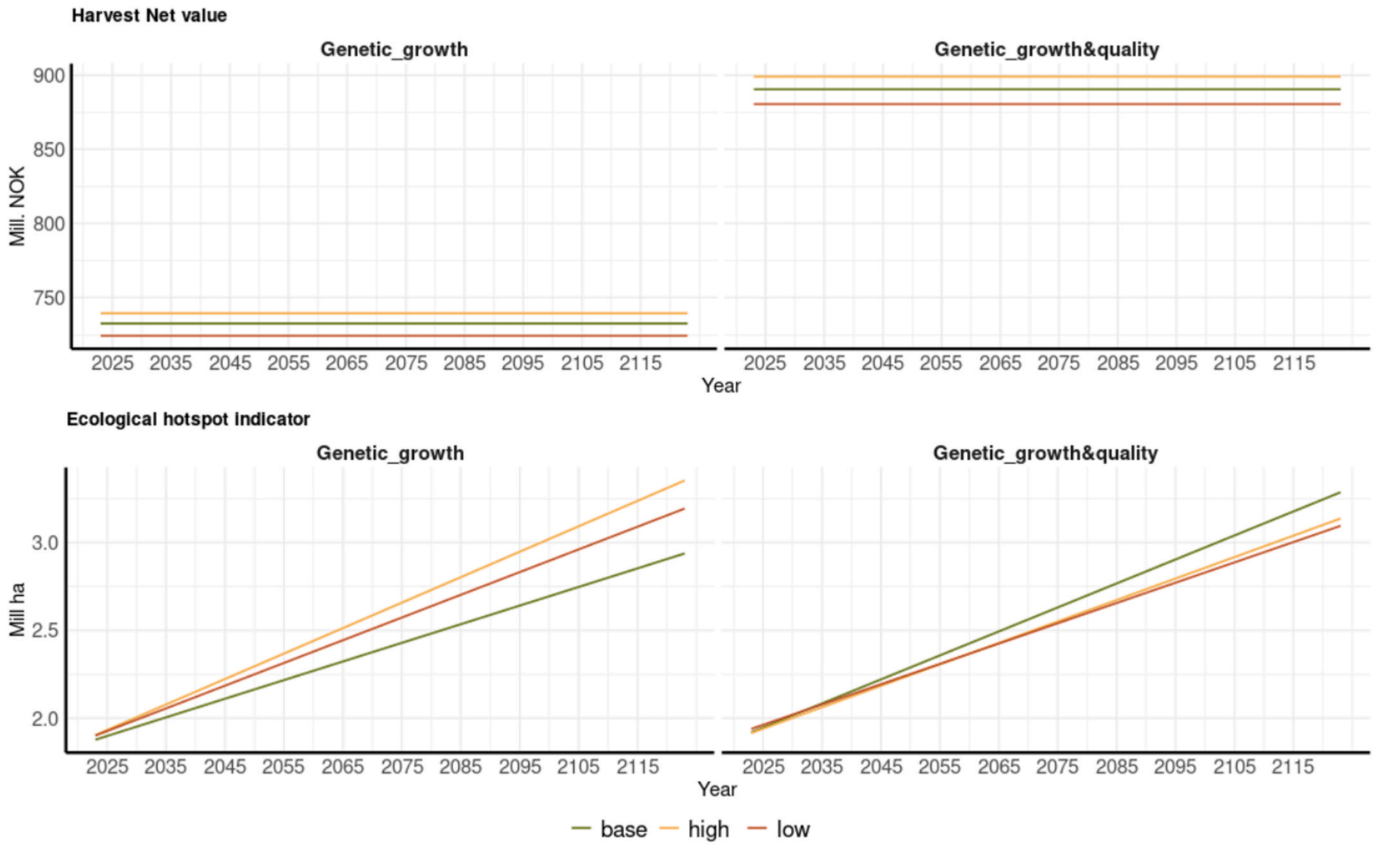

Fig. 7. Harvest net value (Mill. NOK per 5-year period) and ecological hotspot area (Mill. ha) under the *Genetic Growth* and *Genetic Growth & Quality* scenarios at different genetic gain levels. Green: baseline gain; orange: high gain (10% for the first 10 years, 15% thereafter); red: low gain (5% for the first 10 years, 8% thereafter).

indicate that achieving such targets without reducing harvest would require intensification or expansion of harvesting elsewhere (Duncker et al., 2012). Pikkarainen et al. (2024) similarly suggested that genetically improved regeneration material can help offset conservation-related harvest losses through increased productivity. While our results support the broader conclusion that genetic improvement may facilitate conservation without reducing harvest, they indicate that, under the present optimization framework, this outcome was achieved through a different mechanism.

The increased use of set-asides and the more diverse mix of management regimes observed under the genetic-gain scenarios may also contribute to landscape resilience and multifunctionality. More heterogeneous management mosaics can reduce disturbance risks and support habitat diversity (Messier et al., 2021). However, the contribution of some management approaches remained limited in all scenarios. CCF increased from only 0.2% to 0.8% under *Genetic Growth & Quality*, likely reflecting the lower short-term sawlog yields and less predictable harvest flows than even-aged systems, making it less competitive within an even-flow optimization framework under strict demand constraints. These benefits, however, should be interpreted from a long-term perspective, as genetic gains require decades to fully manifest (Heinonen et al., 2018).

4.3. Impact of varying genetic gain rates on FES projections

The limited response of most ecosystem-service indicators to variation in genetic gain suggests a threshold effect, in which further increases beyond a minimum level provide diminishing marginal returns. This is consistent with the larger differences observed between the no-gain baseline and the genetic gain scenarios than among the different gain levels themselves. In addition, because genetic gain affects only a fraction of the landscape, sensitivity to gain-level variation at the national scale is further reduced. Strategic deployment of genetically improved material may therefore be more important for stable FES provision than the precise magnitude of genetic gain, reinforcing the finding that integration strategy—rather than gain level—is the primary driver of multifunctional outcomes.

This limited sensitivity is particularly evident for harvest net value. Earlier studies in Finland found that genetically improved Scots pine remains financially viable even at low gain levels (3%) (Ahtikoski et al., 2013). Our results similarly indicate that reducing gain from 8–15% to 5–6% does not substantially reduce harvest net value, nor does increasing gain to 10–15% provide markedly higher benefits. These results should, however, be interpreted within the assumptions of the optimization framework. Timber prices and silvicultural costs were held constant throughout the simulation period, so the relatively stable harvest net values across gain levels reflect optimization-driven management under fixed market assumptions rather than dynamic economic conditions. Changes in the relative value of sawlog and pulpwood could alter the attractiveness of quality-focused versus growth-focused management, although this remains speculative because dynamic market conditions were not modeled.

4.4. Limitations and methodological aspects

Although the simulation and optimization framework applied here has been validated in previous studies (Vergarechea et al., 2023; Ahtikoski et al., 2025), the results remain dependent on the models and assumptions used. SiTree determines how forest growth, mortality, and management responses are represented over time, thereby shaping ecosystem-service trajectories available to the optimization. Optimization constraints, together with the GLOBIOM demand projections, restrict feasible management allocations and influence the resulting Pareto-optimal solutions. Consequently, alternative growth models, optimization settings, or future demand pathways could lead to different FES outcomes and trade-offs. In particular, the conclusion that national harvest targets can be maintained under genetic gain scenarios is conditional on the GLOBIOM demand pathway used, and alternative socioeconomic scenarios could alter this result. The same applies to the expansion of set-aside area (Section 4.2), which reflects the interaction between harvest-value targets under the adopted demand pathway and the optimization constraints. Alternative demand pathways or optimization settings could therefore alter this outcome.

Additional uncertainty arises from the stochastic components of the simulations, which likely contributed to patterns such as the slight decline in ecological hotspot area under the *Genetic Growth* scenario. In addition, the use of 5-year planning periods may have masked short-term fluctuations, particularly in carbon sequestration, where high interannual variability limits the interpretation of scenario differences.

Another important assumption concerns the proportion of planted area receiving genetically improved material (37.1% on average; Table 1), which was fixed based on current regeneration practices and allocated preferentially to more productive stands. Varying this assumption would not necessarily produce proportional changes in outcomes, as the effects would depend on where improved material is deployed across the landscape and how management is subsequently reallocated within the optimization framework. In addition, the site-index multipliers used to represent genetic gain were assumed to remain constant throughout the rotation. Although this assumption is consistent with most previous simulation studies (Jansson et al., 2017; Serrano-León et al., 2021), empirical evidence suggests that realized genetic gains may vary with stand age (Joo et al., 2020). Consequently, the projected long-term effects of genetic improvement should be interpreted as conditional on constant genetic gain over time.

Economic outcomes are also influenced by assumptions regarding wood quality. The increase in sawlog shares from 55% to 65% under the *Genetic Growth & Quality* scenario represented an additional source of uncertainty. This assumption is supported by evidence of genetic variation in stem quality traits (Stener, 2015) and variation in sawlog recovery across quality classes (Malinen et al., 2018), but has not been validated experimentally through direct comparisons of genetically improved and unimproved material during sawmill processing. Varying the magnitude of this sawlog share increase would not necessarily translate into a proportional change in harvest net value, as the optimizer selects management regimes based on relative economic returns; a different assumption could also shift the balance between quality-focused and growth-focused rotations, with consequences for rotation length and associated ecological indicators. Combining genetic field trials with sawmill conversion data would help reduce this uncertainty.

Finally, disturbances could offset the positive effects of genetic gain. Enhanced growth may lead to larger, older trees, more vulnerable to disturbances like spruce bark beetle (López-Andújar Fustel et al., 2024), potentially reducing long-term gains in timber production and carbon storage. Genetic strategies focused primarily on growth could unintentionally increase susceptibility if resilience traits are not simultaneously improved. This highlights the importance of breeding not only for growth and wood quality, but also for drought tolerance and pest resistance (Sniezko and Koch, 2017). Future research should therefore integrate resilience traits into strategies aimed at sustaining ecosystem services under increasing environmental uncertainty.

5. Conclusions

Integrating genetic improvement with forest management offers a viable approach to reconciling timber production with other FES. The strongest effects occurred when genetic improvement targeted both growth and wood quality, increasing harvest value while improving selected structural biodiversity indicators, particularly ecological hotspot areas, and allowing larger set-aside areas without compromising harvest demands.

A key finding is that genetic improvement influenced management allocation and ecosystem-service provision without fundamentally restructuring spatial harvest patterns or ecosystem-service relationships. Long-term multifunctional outcomes depend more on how genetically improved material is integrated into management systems than on the precise magnitude of genetic gain itself. Varying gain levels produced little variation in most FES indicators, suggesting that even moderate genetic improvements can support stable multifunctional outcomes under flexible landscape-scale management.

In terms of trade-offs, genetic gain slightly shifted some trade-offs among services, particularly between production and climate regulation, though the magnitude of this effect varied over time. Regarding biodiversity, responses in the structural biodiversity indicators should be interpreted cautiously, as these proxies capture only a limited subset of ecological dimensions and likely underestimate broader biodiversity trade-offs. Broader biodiversity metrics and more spatially explicit approaches are needed to fully capture ecosystem-service interactions under genetic improvement.

Overall, our findings position genetically improved material as a complementary tool within multifunctional forestry—one that enhances economic performance alongside improvements in selected structural indicators without fundamentally altering existing ecosystem-service relationships. Future assessments should incorporate broader biodiversity metrics, more spatially explicit approaches, and breeding strategies that explicitly integrate resilience traits alongside productivity goals.

CRediT authorship contribution statement

M. Vergarechea: Writing – review & editing, Writing – original draft, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **I. Sevillano:** Writing – review & editing, Methodology, Formal analysis. **A. Steffenrem:** Writing – review & editing, Methodology, Conceptualization. **A. Ahtikoski:** Writing – review & editing, Methodology, Conceptualization. **H. Holmström:** Writing – review & editing, Methodology, Conceptualization. **C. Antón-Fernández:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work, the authors used Claude (Anthropic) to assist with language editing, proofreading, and improving the clarity and coherence of the manuscript. The authors reviewed and edited all AI-assisted content and take full responsibility for the content of the published article.

Declaration of competing interests

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. Supplementary data

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Data availability

The authors do not have permission to share data.

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