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Trends in genetic diversity of silver birch: Insights from varied planting scenarios

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Abstract

This study explores the impact of planting strategies on genetic diversity in silver birch (*Betula pendula* Roth) stands using simulation models. We examine the influence of different proportions of planted stands and the number of open-pollinated families on genetic diversity, focusing on the Shannon-Weiner Diversity Index and expected heterozygosity. Results indicate optimal genetic diversity increases with 50–55% planted stands. Additionally, using more families in planting enhances diversity, peaking when 30 families are used compared to five. Simulations suggest that combining natural regeneration with planting seed lots from at least 20 families enhances genetic diversity at the landscape level, supporting sustainable forest management. However, using only the top-performing five families does not harm genetic diversity if planted stands remain below 55%. Acknowledging the limitation, this study considers only a single generation, which may affect long-term applicability of the results over multiple generations.

Keywords: expected heterozygosity; Shannon-Weiner Diversity Index

Introduction

Silver birch (*Betula pendula* Roth) is a widespread deciduous tree species in Europe, known for its ecological and economic importance. It thrives in a variety of climates and soil types, which contributes to its widespread distribution and ecological adaptability (Hynynen et al. 2010). Genetic diversity within this species is crucial for its adaptability to changing environmental conditions and for the maintenance of healthy populations (Reusch et al. 2005). This diversity is influenced by various factors including reproductive biology, historical range shifts, and contemporary forest management practices (St. Clair and Howe 2011, Habel and Schmitt 2012, Ivetić et al. 2016).

Silver birch is predominantly an outcrossing species with wind-pollinated flowers, which facilitates extensive gene flow, hence maintaining high genetic diversity within populations (Palmé et al. 2003, Ingvarsson and Dahlberg 2019). This variation is crucial for adapting to local conditions and environmental stressors (Savolainen et al. 2007). Post-glacial colonization patterns have also influenced genetic diversity. Populations that expanded rapidly from glacial refugia tend to show a mix of pioneering and locally adapted genotypes, contributing to a diverse genetic pool (Tenkanen et al. 2020). The ability of silver birch to colonize disturbed sites rapidly, such as those cleared by fire or human activity, allows for continual mixing of genetic material across landscapes (Brzeziecki and Kienast 1994).

Planted stands of silver birch often originate from selected seed sources, which may reduce their genetic diversity compared to naturally regenerated forests (Habel and Schmitt 2012). The use of genotypes aimed at enhancing certain traits (like growth rate or timber quality), yet insufficiently adapted to the location, can limit the genetic pool, potentially making these stands more vulnerable to pests, diseases, and changing climate conditions (Reusch et al. 2005, Ingvarsson and Dahlberg 2019). Planting practices can lead to genetic bottlenecks if a small number of genotypes are applied extensively (Ingvarsson and Dahlberg 2019, Wu 2019). Management practices in planted forests, such as selective thinning can further deplete genetic diversity (Schaberg et al. 2003). Overall, practices that favour certain tree characteristics can lead to selective pressures that may reduce overall genetic variability within the stand (Ivetić et al. 2016).

Therefore, planted stands, while potentially more uniform and productive, may require careful management to maintain genetic diversity and ensure long-term sustainability and resilience. Enhancing genetic diversity in planted stands, possibly through the use of diverse seed sources, could be beneficial for those purposes. In this study, we conduct a comparative analysis of genetic diversity between naturally regenerated and planted silver birch stands, with a focus on two commonly used diversity indices: expected heterozygosity and the Shannon-Weiner Diversity Index (Shannon 1948, Nei 1978). Using simulations, we projected genetic diversity under different management scenarios, considering the proportion of planted stands and the genetic diversity of planted families. Our findings aim

to inform sustainable forest management practices and conservation efforts for silver birch populations in dynamic landscapes.

Materials and methods

Plant material

Samples from 175 birch trees representing natural stands from 16 provenances across Latvia were used for genotyping. For comparison, the progeny of 53 open-pollinated families (total 327 trees) was sampled in a first-generation birch seed orchard (JSC 'Latvia's State Forests'), representing genetically improved forest reproductive material.

DNA was extracted using a modified CTAB method (Porebski et al. 1997). Genotyping was done with 12 SSR markers (L7.8, L7.4, L1.10, L5.1, L3.1, L2.7, L4.4, L2.3, L2.2, L5.4, L022 and L13.1 (Kulju et al. 2004). PCRs were performed in a volume of 10 µl containing approximately 50 ng DNA, 2 µl HOT FIREPol® Blend Master Mix (Solis BioDyne) (containing 10 mM $MgCl_2$), 0.3 µM forward and reverse primers. The PCRs were carried out in a thermocycler (Eppendorf Mastercycler epgradient) using the following protocol: 95°C for 5 min, 35 cycles of 95°C for 30 sec, 50°C – 30 sec, 72°C – 30 sec; 72°C – 7 min. PCR products were diluted 1 : 10 with deionized water and visualised on an Applied Biosystems ABI Prism 3130xl Genetic Analyser. Genotyping was performed using GeneMapper 4.0 software package (Applied Biosystems 2006).

Simulation analysis

The simulation analysis was performed to determine influence of the proportion of the planted stands on the birch genetic diversity. The simulation was organised so that the proportion of the planted stands was set from 0 to 100% of theoretical stands with a 5% increment. Then, the next division level was the number of the open-pollinated families used for the planted stands (5, 10, 15, 20, 25 or 30). For example, 25% of planted stands with 10 open-pollinated families mean that 75% of stands are naturally regenerating and 25% are planted using trees from 10 different open-pollinated families. For each combination of stand proportion and the number of families, 50 replicates were used (the total number of replicates was 6,300). To assess genetic diversity for each replicate, random sample of 2,000 trees data (with replacement) was generated from the database of naturally regenerating trees and open-pollinated families, where for each tree there is information on allele frequencies for 12 loci (Table 1). The proportion of the trees in the replicate depended on the proportion of the planted stands simulated (for example, if 25% of planted stands, then, 500 trees came from the open-pollinated families and 1,500 from the naturally regenerating stands). For the open-pollinated families, the random sample of families from the database according to the chosen simulation scenario was used for the trees employed in selection. For each replicate expected heterozygosity and the Shannon-Weiner Diversity Index was calculated using R 4.3.3 (R Core Team 2024) software library poppr (Kamvar et al. 2015). Afterwards, the mean and 95% confidence interval were calculated for those two parameters for each combination of stand proportion and number of families.

Table 1. Summary statistics over 12 loci for the studied naturally regenerated trees and the progeny of open-pollinated families

Population	Natural regeneration		Families	
	Mean	Standard error	Mean	Standard error
Sample size	93.500	3.039	326.083	5.802
Number of Alleles	13.583	1.520	15.750	1.577
Number of Effective Alleles	5.733	0.799	5.417	0.717
Information Index	1.935	0.135	1.918	0.140
Observed Heterozygosity	0.698	0.050	0.690	0.058
Expected Heterozygosity	0.780	0.034	0.766	0.037
Unbiased Expected Heterozygosity	0.784	0.034	0.767	0.037
Fixation Index	0.101	0.055	0.105	0.053

Results

In the applied simulations, expected heterozygosity was 0.78 for the naturally regenerated stands, while increased with the proportion of planted stands in the landscape of naturally regenerated silver birch up to 45–50% and reached value of ca. 0.86 depending on the number of open-pollinated families in the seed source of the planting stock. Beyond this point, the heterozygosity value decreased with increasing proportion of planted stands, dropping below 0.78 when 90–95% of the stands were planted, corresponding to 5 to 30 families used, respectively (Figure 1). Differences among seed lots with varying numbers of families began to appear when the proportion of planted stands reached 25%. However, a distinctly lower expected hetero-

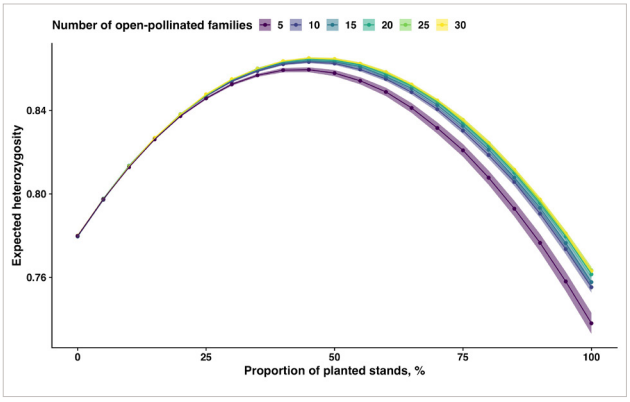

Figure 1. Simulated expected heterozygosity with an increasing proportion of planted silver birch stands and various numbers of families used

The shaded area surrounding each curve represents the 95% confidence interval.

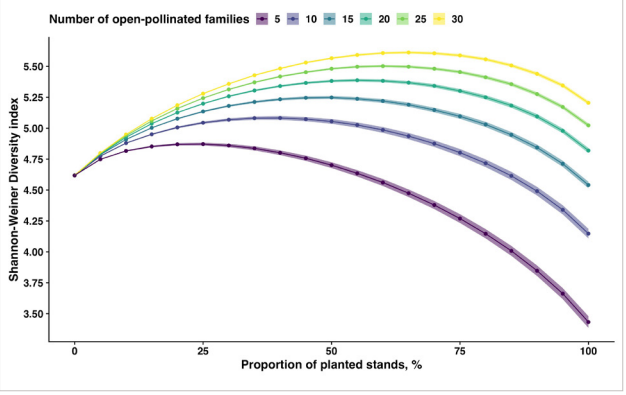

Figure 2. A simulated Shannon-Weiner Diversity Index with an increasing proportion of planted silver birch stands and various numbers of families used

The shaded area surrounding each curve represents the 95% confidence interval.

zygosity was observed only for the lot with five families, with a value of 0.72 for 100% planted stands, compared to the slight variation around 0.76 for other lots with a higher number of families.

Similarly, across all proportions of planted stands, the Shannon-Weiner Diversity Index increased initially, reached a peak, and then declined as the proportion of planted stands continued to rise, but differences among the number of families used were more distinct compared to expected heterozygosity (Figure 2). As the number of open-pollinated families increased (from 5 to 30), the overall diversity increased, and the peak value of the diversity index shifted to the higher proportions of planted stands. For 5 families, the Shannon-Weiner Diversity Index peaked around a proportion of 20% planted stands, with a maximum value slightly below 5.0. The index then declined steadily as the proportion of planted stands increased beyond this point. For 10 families, the peak was higher and occurred at around 25% planted stands. For 15 and 20 families, the peak values were progressively higher and shifted to around 35–40% planted stands. For 25 and 30 families, the highest diversity was achieved at around 50–55% planted stands, with peak values exceeding 5.25. The largest gap in the diversity index value was observed between using 5 and 10 families, while subsequent increments (10 to 15, 15 to 20, etc.) had progressively less effect. The index dropped below the initial value of 4.65 (the naturally regenerated stands) at approximately 55% proportion of planted stands for 5 families, while it was higher up to 100% proportion of planted stands for 30 families.

Discussion

In the observed trends from the study, the initial increase in genetic diversity with the inclusion of a mixture of planted and naturally regenerated silver birch stands suggests a beneficial interaction between these regeneration methods. Specifically, when the planted stands constitute a moderate portion of the landscape (up to approximately 50%), there is a notable increase in genetic diversity, as measured by both the Shannon-Wiener Diversity Index and expected heterozygosity (Figures 1 and 2). This enhancement likely results from the introduction of selected genetic material through planting, which augments the natural genetic pool presented in naturally regenerated areas (Bettinger et al. 2009). This phenomenon might be attributed to the introduction of a wide range of alleles from different families into the forest gene pool (Zeng and Fischer 2021), which may not only complement the existing genetic material but also introduce new genetic variations. Such diversity is vital for the adaptability and resilience of forest ecosystems, allowing them to better withstand environmental changes and pressures (Savolainen et al. 2007, Proschowsky et al. 2020).

Detailed analysis reveals nuanced dynamics between the proportion of planted stands and the number of plant families used. For instance, when utilizing five families, the Shannon-Weiner Diversity Index indicates an increase only up to 20% of planted stands in the landscape. However, when employing 30 families, this index continues to rise up to around 55% of planted stands, with the values still higher for 100% planted stands compared to natural regeneration (Figure 2). Similarly, for expected heterozygosity, an increase is observed up to 40% in the landscape with five families and extends up to 50% when 30 families are used (Figure 1). The degree of heterozygosity correlates directly with the suitability of an individual to a particular environment, thus, the capacity of population for adaptation should also be linked to it (Reed and Frankham 2003). These findings underscore the effect of the diversity within planted families on the genetic structure of forest stands (Ivetić et al. 2016).

As the proportion of planted stands continues to increase beyond these peaks, a decrease in diversity is observed. The rate of decline is more pronounced for scenarios with fewer families (e.g. 5 families), suggesting higher genetic diversity from more families mitigates the reduction in diversity at high planting proportions. This decline may be attributed to the dominance of fewer genetic sources if the diversity among the planted genotypes is not sufficiently broad (Zeng and Fischer 2021). Hence, the number of families used in planting plays a crucial role in mitigating this risk. The findings indicate that using seed lots with 20–30 families consistently promotes higher genetic diversity in the planted stands, as shown by the Shannon-Weiner Diversity Index. This relationship holds true even as the proportion of planted stands increases up to 100% (Figure 2), demonstrating that the diversity of genetic sources is crucial in maintaining broad genetic variability across the landscape. Modelling has indicated that using between 6 and 30 clones optimally reduces risks from known and unknown pests in boreal forest tree species with long growth cycles, with minimal differences between these clone numbers (Yanchuk et al. 2006). In most cases, it is

recommended to collect seeds from at least 20 sources to sustain genetic diversity (Pacalaj et al. 2011). However, our results show that using just 5 families can sustain genetic diversity similar to natural regeneration up to 55% of the planted birch stands. Therefore, while the strategic use of a higher number of diverse families may be necessary to maintain genetic diversity at higher levels of planting, using fewer best-performing genotypes can be effectively employed in intensive forestry when the proportion of planted stands is lower.

Nevertheless, over the past decade in Latvia, the proportion of planted stands in silver birch forest regeneration and afforestation has averaged 20% (Official Statistics of Latvia 2024), indicating a strong prevalence for natural regeneration to maintain genetic diversity in the landscape (Schmidtling 2001). In Sweden, it has been estimated that even under the most intensive management scenarios, 50% of the Norway spruce population will regenerate naturally (Rosvall 2019). It allows for the use of selected genotypes in the production of planting material while still maintaining genetic diversity and a basis for evolution (Ingvarsson and Dahlberg 2019).

We acknowledge that our study has certain limitations. Namely, the simulations conducted in this study consider only a single generation, thereby providing a snapshot of the potential impact of different proportions of the planted stands and the number of families used in planting on genetic diversity. However, it is essential to recognize that forest ecosystems evolve over multiple generations, and the long-term effects of planting strategies may differ from those observed in our simulations. Further research efforts are needed utilizing more sophisticated simulation models that could provide a more comprehensive understanding of how genetic diversity changes at the landscape level over time, considering factors such as gene flow, mating patterns, and natural selection (Sønstebø et al. 2018). Over multiple generations, genetic diversity can be expected to increase due to the mating between planted and naturally regenerating birch, as gene flow and recombination introduce new genetic variations into the population (Savolainen et al. 2007). Despite these limitations, our study contributes valuable insights into the potential implications of different planting strategies for genetic diversity in forest landscapes.

In conclusion, the simulation shows that balancing naturally regenerated and planted silver birch stands enhances genetic diversity across the landscape. Using 30 families may sustain genetic diversity comparable to natural regeneration even when 95–100% of the stands are planted. However, our study supports the strategic use of a limited number of top-performing families in intensive forestry practices, provided the proportion of planted stands among naturally regenerated ones does not exceed 55%. This approach ensures a balance between productivity and genetic diversity conservation in managed forest ecosystems.

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