Evolutionary and operational trade-offs in assisted gene flow for climate-adaptive forestry

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Abstract

Assisted gene flow (AGF) is an adaptive forest management strategy to increase forests' resilience to climate change, yet little is known about how management decisions interact with the strength of natural selection and introgression dynamics that co-determine relative stand productivity. We used individual-based, spatially explicit simulations to investigate how spatial configuration (ranging from clustered to dispersed) and introduction intensity influence introgression and relative stand productivity in the case of AGF of Oriental beech (*Fagus orientalis*) to European beech (*Fagus sylvatica*), two closely related species that hybridize, across a range of realistic selection scenarios. AGF scenarios were obtained based on questionnaires completed by forest researchers and practitioners at an international workshop. We found that clustered introductions consistently promoted hybrid formation and maintained higher levels of introgression, reaching 50% hybrid proportions 50–120 years earlier than dispersed configurations across selection scenarios. In contrast, when selection favoured either the introduced or the resident species, dispersed introductions achieved up to 15% higher relative stand productivity after 100 years, while rapidly diluting hybrids. Transect introductions generally produced intermediate outcomes for both introgression and relative stand productivity. To further evaluate trade-offs among introgression, relative stand productivity, and implementation cost, we conducted a Pareto frontier analysis. As expected, no single AGF strategy simultaneously maximized relative stand productivity and minimized implementation costs, and strategies that performed best after 100 years were not necessarily performing best after 500 years. Since AGF outcomes emerge from interactions between uncertain future selection regimes and controllable management decisions, our results highlight the importance of integrating evolutionary, demographic, and operational trade-offs when designing climate-adaptive forest management strategies.

Keywords: assisted gene flow, climate change, hybridization, European beech, Oriental beech, stand productivity

1 Introduction

The persistence and functioning of temperate forests is today challenged by climate change and habitat loss. Long-lived tree species will likely not adapt fast enough to keep pace with rapidly changing environmental conditions [Aitken et al., 2008, Fréjaville et al., 2020, Leites and Benito Garzón, 2023]. In Europe, this lag is already manifesting as a widespread decline in growth and increased mortality in many forest tree species following recurrent drought events and rising temperatures (e.g., [Knutzen et al., 2025]). These trends raise concerns about the persistence of forests and the ecosystem services they provide. In this context, assisted migration (AM), the intentional translocation of individuals to facilitate adaptation to anticipated local conditions, can accelerate adaptation to climate change [Aitken and Bemmels, 2016, Chakraborty et al., 2024, Erlichman et al., 2024, Chludil et al., 2025]. Assisted Gene Flow (AGF) is a special case of AM in which individuals or genes are translocated within the species' range [Aitken and Whitlock, 2013]. Empirical and theoretical studies suggest that transferring pre-adapted genotypes can increase resilience to climatic stressors, particularly when resident populations are maladapted to emerging conditions [Aitken and Bemmels, 2016, Bontrager and Angert, 2018, Browne et al., 2019, Grummer et al., 2022, Woolridge et al., 2023].

Past introductions of foreign species and provenances provide evidence of the adaptive advantages of introducing pre-adapted genes or mixing gene pools, but also their biological complexities. Several studies reported enhanced growth and productivity following the transfer of pre-adapted seed sources, including southern provenances of Norway spruce in Sweden and directional transfers of southern pine sources in North American forestry programs [Williams and Dumroese, 2013, Milesi et al., 2019a]. However, these benefits may be context-dependent or time-limited. For example, gains in productivity observed in translocated black spruce populations in Canada declined after approximately 15 years after planting [Girardin et al., 2021], while restoration trials in California found that the increased performance of non-local provenances of incense cedar and Jeffrey pine under extreme climatic conditions varied across sites [Young et al., 2020]. A simulation study also suggests that short-term gains in growth or survival do not necessarily predict long-term genetic and demographic consequences, especially for traits with complex polygenic architectures, common in trees [Grummer et al., 2022]. Such introductions frequently result in hybridization and introgression between resident and introduced populations. For example, substantial bidirectional gene flow has been documented following translocations of European larch from the Alps into native Carpathian populations [Jansen and Geburek, 2016, Raffl et al., 2018]. However, whether these processes ultimately enhance adaptive potential or instead generate maladaptive consequences remains largely unclear, as the effects of introductions can differ across environments, change over time, and lead to uncertain genetic consequences [Park and Talbot, 2018]. Given these uncertainties, it is challenging to balance potential benefits against risks such as maladaptation or disruption of locally adapted gene complexes [Williams and Dumroese, 2013, Hällfors et al., 2014, Dimitrova et al., 2022].

Designing operational guidelines for implementing AGF under changing environmental conditions is a major challenge [Aitken and Bemmels, 2016], because AGF outcomes emerge from an interplay between management decisions and multiple ecological and evolutionary processes. For example, the introduction intensity or relative abundance of introduced and native individuals can influence mating dynamics and the direction of introgression. Empirical and modeling studies in hybridizing oak systems have shown that hybridization tends to increase when introduced individuals are rare because of the increased exposure of heterospecific pollen, consistent with the minority or Hubbs' principle, whereas more balanced abundances can promote bidirectional introgression [Nason et al., 1992, Lepais et al., 2009, Lagache et al., 2013, Klein et al., 2017]. The spatial configuration may further modulate gene flow, with the same studies suggesting that clustered distributions tend to maintain locally conspecific pollen pools and limit hybridization, whereas intermixed configurations increase interspecific contact and gene flow [Lagache et al., 2013, Klein et al., 2017]. In the hybrid beech system, Stefanini et al. [2025] found that introducing Caucasian beech into European beech stands at different proportions resulted in substantial differences in hybridization rates, with a higher proportion of F1 seedlings in the stand where Caucasian beech was rare, in agreement with Hubbs' principle.

The persistence of introduced, native, and hybrid genotypes also depends on their relative fitness under future climatic changes. Different selective scenarios are possible depending on how genotypes respond to environmental cues. Under the most commonly assumed climate change scenario, resident populations are maladapted, resulting in directional selection favouring introduced individuals pre-adapted to warmer or drier conditions. Conversely, introduced genotypes may themselves be maladapted to local conditions, including unforeseen climatic factors or competitive environment [Young et al., 2020] and pathogens [Grady et al., 2015]. Hybrids may also exhibit superior performance relative to parental species, a phenomenon called hybrid vigor or heterosis [Shull, 1948], which can enhance growth, survival, or stress tolerance [Dungey, 2001, MacLachlan et al., 2018, Clifton-Brown et al., 2019, Labroo et al., 2021, Li et al., 2024, Hord et al., 2025]. For example, in the Caucasian-European beech system, hybrid vigor was observed only at the seedling stage and was replaced by mild outbreeding depression in adult trees, resulting in limited spatial spread of introgressed individuals despite 100 years of coexistence Stefanini et al. [2025]. Evidence of outbreeding depression following introgression has also been reported in reciprocal crosses between local and non-local populations of *Abies sachalinensis*, where hybrids exhibited reduced growth and potentially lower reproductive success [Goto et al., 2011].

Forestry AGF is mostly explored through provenance trials and common-garden experiments, which provide valuable insights into early performance but typically capture short-term establishment and rarely resolve multi-generational genetic and demographic dynamics [Milesi et al., 2019b, Girardin et al., 2021], or through retrospective analyses of past introductions [Kurz et al., 2023, Budde et al., 2023, Stefanini et al., 2025]. Moreover, implementing AGF strategies is costly and difficult to reverse, making it challenging to experimentally compare alternative planting designs and introduction intensities before deployment. Spatially explicit simulation models, therefore, provide a powerful complementary approach by functioning as virtual management experiments. To effectively inform AGF decisions, such models must integrate spatial structure, tree life history, genetic inheritance, and selection acting across generations, while allowing the evaluation of alternative management-relevant scenarios. However, most existing simulation frameworks capture only a subset of these processes, either focusing on long-term evolutionary dynamics but lacking realistic spatial structure, or focusing on detailed demographic processes and spatial dynamics without integrating genetic processes [Eggers et al., 2020, Lees et al., 2021, Fouqueray et al., 2022, Hallberg-Sramek et al., 2023, Zimmerman and Oyler-McCance, 2025]. As a result, few tools explicitly integrate demographic, genetic, and spatial processes within a unified, decision-oriented framework. Bridging this gap is crucial to evaluate how management strategies interact with hybridization dynamics and selection over the long time scales relevant for forest trees.

Our work is inspired by the repeated introductions of Caucasian beech (*Fagus hohenackeriana* Palibin; [Denk et al., 2024]) into European beech (*Fagus sylvatica* L.) forests over 100 years ago [Kurz et al., 2023]. The two species have recently been reclassified as separate species and no longer referred to as subspecies of *Fagus sylvatica* species complex [Denk et al., 2024]. While they exhibit distinct morphological features, they can also hybridize and produce viable offspring [Kurz et al., 2023, Budde et al., 2023, Stefanini et al., 2025]. Therefore, even if this system is strictly speaking no longer a case of AGF, we shall refer to it as such for the sake of simplicity and also because the introduction of other species of this newly defined species complex, such as Oriental beech (*Fagus orientalis* Lipsky) [Denk et al., 2024], is increasingly considered as a candidate for AM/AGF decisions in Europe. This is because the native resident species, European beech (*Fagus sylvatica* L.), has shown increasing sensitivity to drought and heat stress across large parts of its range [Leuschner, 2020, Martinez del Castillo et al., 2022, Rukh et al., 2023]. Thus, in this context, beech species/genotypes originating from warmer or drier regions may have a selective advantage under future climates.

In this study, we perform spatially explicit demographic-genetic simulations to evaluate their medium- and long-term outcomes in terms of hybridization and relative stand productivity, used here as a measure of stand-level demographic performance, under alternative climate-change scenarios. Our starting assumption is that forest management aims to maintain forest productivity and ecosystem services while accounting for uncertainty in the future performance of resident European beech, potentially introduced Oriental beech, and their hybrids. We distinguish between management decisions that can be controlled, including whether Oriental beech is introduced, introduction intensity, and spatial planting configuration, and factors that cannot be controlled, namely the direction and strength of selection acting on parental and hybrid genotypes. Further, we investigate the implementation costs to assess the operational feasibility of alternative strategies. Our simulation parameters are motivated by a stakeholder questionnaire to ensure that we explore realistic scenarios. Specifically, we evaluate how introduction intensity and spatial configuration affect hybridization and relative stand productivity over medium and long time scales, how these outcomes vary under alternative selection scenarios, and which introduction strategies best balance hybridization, relative stand productivity, and implementation cost. By explicitly linking management decisions to long-term genetic and demographic consequences, this study provides a quantitative framework for evaluating and refining AGF strategies under climatic and biological uncertainty.

2 Materials and Methods

2.1 Stakeholder questionnaire

A Forester–Researcher Workshop on Oriental beech was held on 10–11 June 2025 in Wasselonne, France. The workshop is described here to define the respondent pool and the context in which the questionnaire was completed. The workshop provided a forum for presenting and discussing research results from a network of 11 Oriental beech stands located across France, Germany, and Switzerland [Kurz et al., 2023]. The workshop included 39 unique registered participants from seven countries: Germany ($n = 14$), France ($n = 11$), Switzerland ($n = 9$), Belgium ($n = 2$), Sweden ($n = 1$), Slovakia ($n = 1$), and Turkey ($n = 1$). The first day consisted of presentations by researchers comparing European and Oriental beech in terms of phenology, growth, wood anatomy, physiology, genetics, and hybridization. These presentations were followed by a participatory workshop focused on the potential risks and benefits of using Oriental beech or other Eurasian beech species for AM in Western Europe. Stakeholder questionnaires were distributed at the beginning of the day. During the workshop session, foresters and researchers completed a structured questionnaire, available in English, German, and French, developed by members of the organizing committee (see Acknowledgments; questionnaire provided in the Supplementary Material). Participants completed the questionnaire in one of four moderated roundtable discussion groups: one French-speaking group, two German-speaking groups, and one English-speaking group composed mainly of researchers. Respondents first identified themselves by name and indicated whether they were participating as a forester or a researcher.

The questionnaire consisted of two parts. In the first part, participants assessed existing introductions by comparing Oriental beech from the Greater Caucasus with European beech in the Rhine valley, as well as potential future introductions, including other Oriental or Eurasian beech origins specified by the respondent. Questions regarding existing introductions focused on perceived ecological risks and benefits associated with Oriental beech already established in Europe, including resilience to climatic stress, regeneration capacity, invasive potential, susceptibility to pests and diseases, legal acceptability, and potential forestry applications. The questionnaire used a semi-quantitative coding system in which participants scored whether a given characteristic applied, did not apply, partially applied, was assumed to apply, or was unknown.

In the second part, participants were asked to draw assisted gene flow (AGF) management scenarios on a 100 m × 100 m grid, with the stated objective of maximizing hybridization between European and Oriental beech. Participants were also asked to specify the spatial placement of European or Oriental beech, the planting method (direct seeding or planting seedlings of different ages), and potential management interventions to maximize species hybridization. Participants provided schematic representations of planting layouts under three initial stand conditions: (i) European beech-dominated stands,

(ii) mixed stands, and (iii) open, treeless conditions. The latter was excluded from further analysis because respondents consistently found it unrealistic due to insufficient shading for beech establishment.

Of the 39 unique registered participants, 19 completed the questionnaire. Of these respondents, 7 identified themselves as foresters and 12 as researchers. The first part of the questionnaire was digitized and analyzed to compare foresters' and researchers' perceptions of the risks and benefits of Oriental beech introductions. The second part of the questionnaire was used to parameterize the simulations. All responses were digitized, and we quantified the spatial distribution and proportional representation of Oriental beech from the resulting layouts.

Based on both spatial patterns and accompanying participant descriptions, planting designs were classified into four representative configuration types: (i) dispersed, corresponding to mixed individuals, (ii) single cluster, (iii) multiple clusters, and (iv) transects, approximating linear disturbances such as skid trails (Figure 1a). These configuration types were implemented in the simulation model at three introduction intensities: 10%, 25%, and 40% of the stand area planted with Oriental beech. This classification captured the main gradients in stakeholder-proposed strategies while reducing the diversity of proposed designs into a feasible set of scenarios. For simplicity, simulations were restricted to a European beech-dominated stand to maintain a standardized baseline.

2.2 Individual-based spatially explicit population genetic simulations

We conducted individual-based, forward-time simulations using Nemo-age v0.32.6 [Cotto et al., 2020]. The model simulates overlapping generations through annual cycles of mating, reproduction, seedling competition (density-dependent regulation), and survival (viability selection). Selection was implemented as genotype-dependent survival in specific life stages. For simplicity, all adult trees were considered potentially reproductive. All parameters used are summarized in Table 1. Summary statistics were recorded every 20 years, including the number of individuals, genotype proportions, and individual fitness for each age class.

Spatially explicit simulations were implemented through a custom R wrapper (available at `https://github.com/path` - *to be completed after manuscript is accepted for publication*). The 1-ha landscape was represented as a 25 × 25 grid of 4 × 4 m patches, with individuals located at patch centers. Seed and pollen dispersal were modeled using two-dimensional exponential kernels, discretized into custom $n_p \times n_p$ matrices (where $n_p =$ number of patches). Dispersal parameters were parameterized using empirical values from the literature (Table 1). The spatial configurations and introduction intensities used in the simulations were derived from the stakeholder questionnaire described above.

We defined four life stages: seedlings (year 1), saplings (years 2-4), juveniles (5-39), and adults, i.e., mature reproductive individuals ($\geq$ 40 years). Stage-specific survival rates were derived from the COMPADRE Plant Matrix Database (2023, Version 6.23.5.0; `https://compadre-db.org/`). Density dependence acted on seedlings and juveniles through a Beverton–Holt competition function [Beverton and Holt, 2012], in which survival decreases with increasing local population size. This choice is motivated by the fact that seedlings mostly compete against individuals previously established in favourable local conditions. After conducting a sensitivity analysis on the competition coefficient (b) and patch carrying capacity (K), values were fixed $b = 0.03$ and $K = 30$ individuals per 16 m^2 patch, consistent with reported regeneration densities of European beech under favourable conditions (Supplementary Material, Figure S2) [Dobrovolnỳ and Tesař, 2010, Dobrowolska, 2015, Axer et al., 2021]. Excess seedlings and saplings were randomly culled each year. Species identity was modeled as a quantitative trait determined by 10 additive diallelic loci following the framework developed in [Stefanini et al., 2025], where the resulting trait value served as a measure to track the introgression through time, enabling the classification of the individuals as parental, F1 hybrids and advanced-generation introgressed individuals across a continuous phenotypic gradient.

Simulations were initialized with a spatially heterogeneous but demographically stable *F. sylvatica* stand. To generate this baseline state, we first ran a 500-year burn-in simulation including only European beech. Patch-specific stage abundances from the burn-in were then extracted and used to initialize all scenario simulations. Introduction intensity was defined as the proportion of patches in which the baseline initialization was replaced by Oriental beech saplings (20 seedlings per patch). For each spatial configuration (dispersed, single-cluster, multiple clusters, and transects) and introduction intensity (10%, 25%, or 40% of the total area), a nested replication design was implemented. First, we generated five spatial replicates to capture model sensitivity to specific spatial layouts. Across these replicates, the total number and relative abundance of the two species remained constant, while the locations of clusters or planted trees were randomly assigned while preserving configuration type and introduction intensity. Second, to account for stochastic process noise within a fixed layout, we ran 10 stochastic replicates per spatial replicate, resulting in 50 replicates per parameter combination.

To establish a neutral baseline, we ran simulations without selection, assuming equal survival probabilities across all phenotypes. In selection scenarios, viability selection selectively removes individuals from a patch based on their survival probability given by their individual fitness (W), which follows a quadratic function:

$$W(z_{i,k}) = 1 - \frac{(z_{i,k} - \theta_k)^2}{\omega_k^2}$$

where $z_{i,k}$ is the phenotype (defining the species identity) of individual i in patch k, θ_k is the phenotypic optimum, and ω_k^2 determines the strength of selection in patch k. We defined three alternative selection regimes by varying the phenotypic optimum θ_k. First, to represent conditions favouring Oriental beech under drier climates, we set $\theta_k = +1$. Second, to represent maladaptation of Oriental beech in the non-native environment, we set $\theta_k = -1$. Third, to simulate selection favouring intermediate hybrid phenotypes, as expected under heterosis, we set $\theta_k = 0$. For each scenario, we tested three values of selection strength by varying ω^2, with lower values corresponding to stronger selection against maladapted phenotypes while maintaining relatively higher fitness for intermediate phenotypes. Selection strength was allowed to vary across life stages, reflecting stronger mortality during establishment and weaker selection in later stages [Harper, 1977, Will et al., 2013, Masaki et al., 2021, Lalor et al., 2023]. Accordingly, we imposed a stronger selection (lower ω_k^2) during the seedling and sapling stages, with progressively weaker selection in older stages (Figure 2b). Finally, to isolate the effects of climate-driven maladaptation in the absence of AGF, we simulated additional scenarios in which selection acted against European beech (across all three selection strengths) without introducing Oriental beech. This "no-intervention" scenario provides a baseline for assessing the extent to which management interventions mitigate climate-induced fitness declines.

2.3 Characterizing hybrid proportions and relative stand productivity

We classified genotypes into three categories: pure European beech (phenotypic value < -0.9), pure Oriental beech (phenotypic value > 0.9), and hybrids (phenotypic values between -0.9 and $+0.9$). These thresholds distinguish individuals carrying only species-specific alleles from those carrying mixed ancestry in our 10-locus coding of phenotypic values. For simplicity, all hybrid classes were pooled into a single category, without distinguishing among hybrid generations. To compare the different spatial configurations and introduction intensity, we quantified relative stand productivity (RSP) as the fitness-weighted adult abundance of adult trees, calculated as the number of adults multiplied by the mean individual fitness ($N \times W$) at time t. Higher RSP values indicate that the stand is composed of a greater number of adults with higher average fitness. Then, for each simulation, we extracted the proportion of hybrids and the RSP at $t = 100$ and $t = 500$. Further, to compare the scenarios, we extracted two reference values: the time to reach 50% hybrids and the time to achieve 80% of RSP relative to equilibrium. Since the establishment phase (the first 75 years) was characterized by strong transient demographic fluctuations, we considered data from the subsequent phase. For each parameter combination, Kruskal-Wallis tests were used to test for differences in the distributions of the two metrics between the spatial configurations.

2.4 Assessment of cost-efficiency

Because management interventions are also constrained by operational costs, we estimated a relative cost index for each introduction strategy by combining planting intensity with the expected operational efficiency of the spatial configuration, with more aggregated designs assumed to be less labor intensive (see Supplementary Material).

We then evaluated how introduction scenarios balance multiple objectives using the Pareto optimality framework [Pareto et al., 1971, Farnsworth and Niklas, 1995, Shoval et al., 2012]. strategies that represent the best trade-offs among competing objectives, such that no alternative strategy performs at least as well for all objectives and better for at least one. In our case, we treated hybrid proportion and RSP as objectives to maximize, and estimated implementation cost as an objective to minimize. For each combination of selection scenario, selection strength, introduction configuration, introduction intensity, and year, we summarized stochastic simulation outputs across replicates using the median hybrid proportion and median RSP. We then assigned each strategy its estimated implementation cost. Pareto-optimal strategies were identified separately for each selection scenario, selection strength, and year. A strategy was considered dominated if another strategy had equal or higher RSP, equal or higher hybrid proportion, and equal or lower cost, with at least one of these criteria being strictly better. Strategies that were not dominated constituted the Pareto front. We used these non-dominated strategies to compare how the set of cost-efficient introduction strategies changed through time and across selection regimes.

3 Results

3.1 Stakeholder-derived AGF strategies

19 responses (7 foresters and 12 researchers) were obtained for the first part of the questionnaire, which assessed existing and future introductions, and 16 responses (4 foresters

and 12 researchers) for the second part on spatial configurations. Responses indicated that Oriental beech was perceived as a potentially useful but uncertain option for AM, whereas European beech was viewed as familiar, legally acceptable, and useful, but less adapted to climate extremes (Figure S1). For Oriental beech from the Greater Caucasus, respondents more frequently selected positive or assumed responses for drought resilience, heat tolerance, and resistance to pests and pathogens. In contrast, assessments of European beech in the Rhine valley were more often negative or partial for drought and heat tolerance. Respondents also recognized potential genetic benefits of Oriental beech, including high genetic diversity and hybridization with native European beech, but expressed greater uncertainty regarding whether hybrids would outperform parental species. The strongest contrast between the two taxa concerned legal status: European beech was consistently perceived as native and legally unproblematic, whereas responses for Oriental beech reflected greater uncertainty and potential regulatory constraints. Researchers tended to provide more positive or assumed assessments for adaptive and genetic benefits, whereas foresters more often selected partial, negative, or uncertain responses, particularly for legal and ecological-risk categories.

In European beech-dominated stands (N = 16), most respondents proposed multiple-cluster configurations (11 cases), with fewer dispersed (3) and single-cluster (2) designs. Responses for mixed stands (N = 13) showed similar patterns, including multiple clusters (5), dispersed (4), single clusters (2), and transects (2). Across all responses, the proportion of Oriental beech introduced ranged between approximately 10% and 40%. This variability motivated the choice of three introduction intensities (10%, 25%, and 40%) and four spatial configurations (dispersed, single cluster, multiple clusters, and transects) implemented in the simulations (Figure 2a).

3.2 Selection scenario determines long-term stand composition

Across simulations, the direction and intensity of selection emerged as the primary determinants of long-term genetic composition (Figure 3). During the first century following introduction, demographic dynamics and genotype frequencies fluctuated strongly due to the rapid expansion of introduced Oriental beech and the formation of hybrids, however, trajectories subsequently stabilized, reaching equilibrium within 300 to 500 years (Figure 3, Figure S3, Figure S4). Replicate variability (central 80% interval) in genotype proportions remained moderate overall, although it increased through time under scenarios favouring one parental species, particularly under strong selection, where variability reached values of 0.6 (Figure S4).

Despite these early fluctuations, long-term outcomes consistently reflected the selective regime. Even weak selection substantially altered genetic trajectories relative to neutral expectations (Figure 3, Figure S3, Figure S4). Under weak to intermediate selection favouring Oriental beech, introgression increased progressively through time, whereas selection favouring European beech limited hybrid persistence and drove stands back toward the local European beech genotype. When selection mildly favoured Oriental beech, European beech persisted for approximately 150–200 years before progressively declining, whereas strong selection accelerated its disappearance to within a few decades (Figure 3). Stronger selection favouring parental genotypes also reduced the generation of introgressed individuals, resulting in stands dominated by the favoured species with relatively limited hybrid representation. In contrast, when selection favoured hybrids, hybrid genotypes accumulated rapidly, and progressively replaced both parental types, resulting in highly introgressed stands (Figure 3, Figure S3, Figure S4).

3.3 Introduction intensity and spatial configuration modulate short and medium term AGF outcomes

While selection direction and strength determined whether the introduced alleles spread, declined, or accumulated as hybrids, introduction intensity and spatial configuration modulated the rate and magnitude of these outcomes.

When selection favoured Oriental beech, introduction intensity shaped the balance between hybrid formation and RSP (Figure 4). Higher introduction intensity accelerated demographic recovery, with introductions of 40% Oriental beech approaching the neutral RSP range within approximately 100–150 years, whereas introductions of 10% or 25% Oriental beech recovered more slowly and remained below the neutral expectation at $t = 100$ (Figure 4c and d). However, higher introduction intensity did not maximize hybrid proportions. Instead, adult hybrid proportions at $t = 100$ were generally highest under low introduction intensity and declined as the proportion of Oriental beech increased (Figure 4b). Under low to intermediate selection, hybrid frequencies at $t = 100$ reached median values of 35–40% when only 10% Oriental beech was introduced, approximately 15–20% higher than under high introduction intensity. Under strong selection, hybrid frequencies remained below 20% across all introduction intensities because Oriental beech rapidly replaced European beech before extensive introgression could occur. Together, these results indicate that intensive introductions promoted faster replacement of European beech by Oriental beech, whereas lower introduction intensity favoured hybrid formation.

Spatial configuration further modified these outcomes. Clustered introductions generally produced higher hybrid proportions than dispersed and transect configurations (Figure 4a and b). This effect was most evident under intermediate and strong selection favouring Oriental beech, where clustered introductions maintained higher hybrid proportions despite the overall decline in hybrid formation at high introduction intensity. Single-cluster configurations, in particular, accelerated hybrid formation, reaching 50% hybrids 50-120 years earlier than dispersed configurations (Figure 4a, Figure S5a). In contrast, spatial configuration had little effect under weak selection favouring Oriental beech at $t = 100$ (Figure 4b). While clustered configurations promoted hybrid persistence, RSP recovery was faster in dispersed and transect configurations (Figure 4c and d). Increasing selection strength amplified these differences, with dispersed and transect introductions reaching neutral RSP expectations 50–100 years earlier than clustered configurations (Figure S5b). After 100 years, clustered introductions showed reductions in RSP of approximately 10–15% compared with dispersed and transect configurations (Figure 4d).

When selection favoured European beech, the introduction strategy had weaker effects on both hybrid proportions and RSP because Oriental beech declined over time and RSP rapidly approached the neutral baseline (Figure S6a). Introgression generally remained limited, with most scenarios producing hybrid frequencies between 0–26% and median values below 20% (Figure S4, Figure S6a and b). Nevertheless, moderate to high introduction intensity combined with clustered configurations, particularly single clusters, retained the highest levels of Oriental beech ancestry after 100 years, whereas dispersed and transect configurations showed little remaining spatial genetic structure (Figure S7). In contrast to the scenarios favouring Oriental beech, spatial configuration had weaker effects on RSP and differences among configurations were mostly independent of selection strength (Figure S6c and d). Single-cluster configurations produced only slightly lower RSP, delaying recovery to 80% RSP by approximately 20 years relative to other configurations (Figure S5b). Overall, spatial configuration had the strongest effects on RSP, either when the native species was strongly maladapted or when the introduced species was both abundant and maladapted.

Under selection favouring hybrids and under neutral conditions, increasing introduction intensity accelerated hybrid formation and increased hybrid proportions, as expected (Figure S4, Figure S6a and b). High introduction intensity reduced the time required to reach 50% hybrids by approximately 100–200 years relative to lower introduction intensity, depending on selection strength and spatial configuration (Figure S5a). Under selection favouring hybrids, hybridization was pervasive across all introduction strategies, with both parental genotypes replaced by introgressed individuals within approximately 200 years (4–5 generations), around 100–150 years earlier than under neutral conditions (Figure S4). Nevertheless, low introduction intensity (10%) allowed pure European beech genotypes to persist over longer time scales, whereas higher introduction intensities resulted in populations composed almost entirely of introgressed individuals (Figure S3). Under these conditions, the effect of spatial configuration was strongest at intermediate hybrid proportions, when either introduction intensity was high and selection was weak, or when selection was intermediate, or when selection was strong but introduction intensity was low (Figure S6b). In these cases, after two to three generations, multiple-cluster and transect configurations produced the highest hybrid proportions, whereas single-cluster and dispersed configurations generally led to slightly lower proportions (Figure S6b). Effects on RSP were much weaker, with significant differences among configurations detected only under strong selection favouring hybrids combined with high introduction intensity; in these cases, multiple-cluster and transect configurations achieved the RSP, although values remained approximately 10% below neutral expectations (Figure S6c and d).

3.4 Operational trade-offs among hybridization, relative stand productivity, and estimated cost

Pareto frontiers revealed scenario-dependent trade-offs among hybrid proportion, RSP, and the estimated cost of introduction. Across selection regimes, long-term Pareto-optimal strategies tended to converge toward clustered configurations, especially single-cluster introductions, whereas dispersed configurations were rarely retained among optimal strategies at $t = 500$ (Figure 5, Figure S8). These trade-offs were strongest when selection favoured Oriental beech over European beech (Figure 5): 100 years after introduction, low-cost strategies, including low introduction intensity (10%) and clustered configurations, were associated with higher hybrid proportions but lower RSP. In contrast, higher-cost strategies increased RSP but reduced hybrid proportions, resulting in a negative relationship between RSP and hybrid proportion.

Although most strategies appeared Pareto-optimal at $t = 100$, clear differences emerged over longer time scales (Figure 5). Within the Pareto-optimal set, faster recovery of RSP was generally achieved through higher introduction intensities, often in clustered configurations (Figure 5a). In contrast, dispersed configurations showed more variable outcomes across introduction intensities and were retained among optimal strategies mainly under low to intermediate selection strength. Under strong selection favouring Oriental beech, low introduction intensity combined with dispersed configuration provided relatively rapid short-term RSP recovery at low relative operational cost (Figure 5b). However, these strategies were not maintained among Pareto-optimal solutions over longer time scales (t = 500).

When selection favoured European beech, trade-offs among RSP, hybrid proportion, and estimated cost were relatively weak, as most introduction strategies converged toward similarly high RSP values and/or returned low hybrid proportions (Figure S8). Thus, Pareto-optimal sets were smaller and mainly restricted to scenarios with low or moderate selection strength. Across both short- and long-term time scales, clustered configurations consistently outperformed dispersed introductions and dominated the Pareto frontiers. Similar levels of introgression could be achieved with 25% and 40% Oriental beech introductions in clustered configurations, indicating low returns of higher introduction intensity despite greater relative operational costs. Dispersed configurations were rarely retained among Pareto-optimal strategies at $t = 100$ and were absent at $t = 500$ (Figure S8b).

When selection favoured hybrids, increasing introduction intensity simultaneously increased hybrid proportion and RSP, leading to positive relationships between estimated cost and both outcomes (Figure S8). Clustered and transect configurations consistently ranked among the most efficient strategies and showed similar long-term recovery trajectories (Figure S8b). Dispersed configurations were only retained among optimal strategies at high introduction intensity and were generally absent from long-term Pareto frontiers.

4 Discussion

Climate change is already altering forest disturbance regimes, increasing tree mortality, reducing regeneration success, and shifting the climatic suitability of forest tree species, creating major risks for forest persistence, productivity, and ecosystem services [Seidl et al., 2017, Senf and Seidl, 2021, Forzieri et al., 2021]. These risks are particularly challenging for long-lived forest trees because rapid environmental change contrasts with long generation times, slow migration, and the long planning horizons of forest management. AM and AGF are therefore increasingly discussed as tools for adaptive forest management in Europe and worldwide [Aitken and Bemmels, 2016, Chakraborty et al., 2024], but their operational implementation remains difficult. While forest managers can decide whether to introduce non-local material, at what intensity, and in which spatial configuration, they cannot know in advance the future selective environment or the relative performance of resident, introduced, and hybrid genotypes. Here, we explicitly frame this uncertainty as variation in the direction and strength of selection acting on local, introduced, and introgressed genotypes. Our simulations show that identical management interventions can lead to contrasting long-term outcomes depending on the realized selective regime: AGF may promote adaptive introgression, fail to establish, or lead to genetic replacement. At the same time, introduction intensity and spatial configuration shaped the trajectory and pace of introgression in the short- and medium-term. These findings indicate that AGF outcomes emerge from the interaction between climate-driven selection under uncertainty and controllable management decisions, and that spatially explicit simulations can help identify the conditions under which alternative strategies are likely to support demographic recovery, introgression, or both (Figure 4).

Spatial configuration had a significant impact on the introgression dynamics in our individual-based simulations. Clustered introductions consistently promoted hybrid formation and maintained higher hybrid proportions than dispersed configurations, particularly at low to intermediate introduction intensities. Although spatial configuration to our knowledge was not yet explicitly examined in the context of AGF, similar patterns have been reported in systems where dense human-mediated introductions created local aggregations of conspecifics, often promoting elevated hybridization and introgression rates in *Juglans* [Hoban et al., 2012], *Platanus* [Johnson et al., 2016], and *Populus* [Meirmans et al., 2010]. Our simulations demonstrate that this clustering effect may arise from the interaction between local mating environments and the demographic persistence of introgressed genotypes across generations. By concentrating introduced individuals in space, clustered configurations create localized regions where heterospecific mating opportunities repeatedly occur over generations. These areas may function as "hybridization hotspots", continuously producing hybrids and backcrossed individuals that subsequently disperse into the surrounding population. In contrast, dispersed introductions spread heterospecific pollen at lower local densities, and hybrids are diluted into the resident gene pool more rapidly. Thus, clustering may enhance introgression not only through mating opportunities, but also through positive demographic feedback that facilitates the local persistence and cumulative spread of introgressed lineages over successive generations [Buerkle, 2009, Field et al., 2011, Lepais and Gerber, 2011, Beatty et al., 2016, Janes et al., 2017]. This result appears to contrast with Klein et al. [2017], who predicted that spatial aggregation should reduce hybridization by increasing the local proportion of conspecific pollen received by rare individuals. However, this discrepancy likely reflects differences in temporal scale and response variables. Klein et al. [2017] focused on immediate pollen composition and first-generation hybridization, whereas our simulations measured hybrid proportions as the cumulative outcome of mating, establishment, survival, backcrossing, and spatial spread over multiple generations. Thus, spatial clustering may reduce heterospecific pollen exposure in some contexts, while still promoting the long-term persistence and spread of introgressed lineages once hybrids emerge. This result highlights an overlooked dimension of AGF design, since the spatial configuration of introduced individuals can influence mating opportunities and thus the persistence of introgressed individuals.

In line with previous studies, our results also indicate that relative species abundance substantially shapes introgression dynamics and forest trajectories [Vanden Broeck et al., 2012, Lagache et al., 2013, Klein et al., 2017, Janes and Hamilton, 2017, Ortego et al., 2017, Irwin and Schluter, 2022]. When selection favoured the introduced genotype, high introduction intensity accelerated stand recovery by increasing the proportion of pre-adapted individuals (Figure 3). However, the same conditions also promoted faster genetic replacement rather than gradual adaptive introgression. In contrast, when the introduced genotype had a lower fitness than the residents, high introduction intensity combined with clustered configurations was the only intervention that allowed the formation and maintenance of introgressed lineages over longer periods (Figure S6). Introduction intensity therefore emerges as a useful management lever modulating both RSP recovery and the extent of introgression.

AGF decisions are also constrained by economic cost and competing management objectives. Although our cost estimates remain approximate, simulations suggest that it is generally not possible to simultaneously maximize RSP, maintain introgressed variation, and minimize intervention costs. Instead, management outcomes were characterized by clear trade-offs among demographic recovery, genetic diversity, and economic investment. When selection favoured Oriental beech over European beech, strategies maximizing short-term RSP typically involved high introduction intensities and, in some cases, more spatially dispersed planting, thereby increasing both demographic impact and implementation costs. In contrast, strategies promoting hybridization and introgressed diversity generally relied on lower introduction intensities and clustered spatial configurations, which slowed demographic recovery but favoured the persistence and spread of hybrid lineages over time (Figure 4). Consequently, the most appropriate introduction strategy depends strongly on management objectives. If the primary goal is to maximize stand productivity or wood production, introducing a large number of performant Oriental beech individuals into declining European beech stands may be advantageous regardless of the long-term genetic outcome. In contrast, if the objective is to increase adaptive potential and maintain genetic diversity to better deal with uncertain future climates, lower introduction intensities that favour gradual but sustained introgression may represent a more appropriate strategy. Together, our results suggest that AGF should be viewed as a multi-objective optimization problem, in which productivity, evolutionary potential, and economic costs may not always be maximized simultaneously.

Pareto optimality framework highlight that favorable introduction scenarios over short time scales were not always optimal over longer periods. Interventions identified as best-performing after only two or three generations, particularly low-intensity dispersed introductions that rapidly increased RSP, were not optimal over longer time scales (Figure 5). Although these strategies initially improved demographic performance, they ultimately led to lower adaptive introgression while still requiring substantial operational investment. These results highlight that short-term demographic gains may not reliably predict long-term evolutionary outcomes, but also why spatially explicit simulations can be relevant for operational forestry. The spatial scenarios explored here are not only theoretical planting patterns, but could increasingly be implemented through precision forestry and precision forest restoration approaches that combine ecological knowledge with remote sensing, artificial intelligence, field monitoring, and targeted planting or seeding technologies to place individuals in specific landscape positions or microsites where establishment and long-term persistence are more likely [Castro et al., 2021]. In this context, simulations such as ours can help define not only which genetic material to introduce and at what intensity, but also where to place introductions to balance establishment, introgression, and cost. At the same time, the value of these technologies depends on ecological guidance: technological capacity alone does not guarantee restoration success unless seeds or seedlings are placed in suitable microsites and followed through the demographic bottlenecks of establishment and early survival [Castro et al., 2023]. Thus, spatially explicit AGF simulations may provide an important link between evolutionary theory and the emerging operational capacity to implement targeted, adaptive, and monitored forest interventions.

Finally, while throughout this work we focused on hybridization as an adaptive forest management tool for AGF, it can also be viewed as a conservation risk. Indeed, hybridization often represents a source of adaptive variation under rapid environmental change [Janes and Hamilton, 2017], but it may also lead to genetic swamping, loss of autochthonous gene pools, or disruption of locally adapted genetic combinations [Todesco et al., 2016]. Our results illustrate why the same outcome, increased introgression, may be interpreted differently depending on management objectives and conservation context. If the aim is to preserve local genetic identity, persistent introgression may be undesirable even when demographic performance is improved. If the aim is to maintain adaptive potential under uncertain climates, controlled introgression may instead be beneficial. This distinction is important because neutral genetic diversity and adaptive variation do not necessarily respond in the same way to management: planted stands may maintain overall genetic diversity while showing weaker signals of local adaptation and greater future maladaptation risk [Eklöf et al., 2026]. Historical translocations of Norway spruce further demonstrate that the movement of forest reproductive material can leave persistent signatures in forest genetic composition and complicate the identification of autochthonous populations for gene conservation [Jansen et al., 2017]. Thus, AGF should be evaluated not only in terms of productivity and hybrid proportion, but also in terms of how introgression affects adaptive variation, local genetic identity, and conservation value.

Beyond biological complexity and operational feasibility, AGF implementation also depends on stakeholder acceptance and governance. This is particularly important because AM and AGF require decisions that cross boundaries among forest management, conservation, and policy, and therefore depend on collaboration among researchers, practitioners, conservation agencies, and decision-makers [Palik et al., 2022]. Our questionnaire suggests that Oriental beech is perceived as a promising but uncertain option for climate-adaptive forestry: respondents associated it with drought and heat tolerance, resistance to pests and pathogens, and potential genetic benefits, but also expressed uncertainty about hybrid performance, ecological risks, and legal status (Figure 1). In contrast, European beech was perceived as familiar and legally unproblematic, but less promising under future climate extremes. These contrasting perceptions illustrate why AGF decisions are not purely biological. They also depend on how stakeholders evaluate the adaptive potential relative to ecological and regulatory risks, and on whether introducing non-native or non-local material is perceived as a legitimate intervention rather than a departure from established conservation or forestry paradigms [Hagerman et al., 2010]. In Europe, this challenge is further amplified by heterogeneous forestry traditions, ownership structures, and regulatory frameworks, which can make the operational implementation of AM/AGF highly context dependent [Pötzelsberger et al., 2020]. The few differences between researchers and foresters in our questionnaire further suggest that AGF objectives are not universally shared, reinforcing the need to integrate stakeholder perspectives early in the design of operational AGF strategies.

Several simplifying assumptions should be considered when interpreting these results. First, unlike many natural hybrid zones where parental species and hybrids coexist, our model assumes unrestricted gene flow and no ecological niche differentiation, which together favoured genetic homogenization. It was observed, however, that disturbances and altered landscapes can facilitate species hybridization in the context of introductions [Hoban et al., 2012, Ortego et al., 2017]. Second, hybrid vigor was constant across time in our simulations, although empirical studies indicate that heterosis may decline across generations due to genetic recombination and breakdown of favourable gene combinations [Fenster and Galloway, 2000, Burke and Arnold, 2001, Stefanini et al., 2025]. If hybrid fitness advantages decrease over time, introgression rates would likely be lower, leading to reduced hybrid proportions and potentially faster return toward neutral RSP expectations. Our results also highlight the importance of considering genotype gradients rather than discrete hybrid classes (Figure S4), because binary classifications may overestimate the extent of genetic variation within the stand. In this context, hybrid proportion should also not be interpreted as a direct proxy for adaptive potential, because the conservation value of introgression depends on which genomic regions are introgressed, whether they contribute to climate-relevant traits, and whether they maintain or erode locally adapted variation. Another potential limitation is that we explored only three levels of selection strength, representing a limited set of plausible scenarios rather than precise predictions of future outcomes. Consequently, our simulations should be interpreted as exploratory assessments of potential dynamics under contrasting selective pressures, rather than forecasts of specific ecological trajectories. Finally, we did not include additional ecological processes such as interspecific competition, potential phenological differences, or explicit management interventions (e.g., thinning or protection of the introduced individuals), all of which may influence hybridization dynamics in real forests.

5 Conclusion

AM and AGF outcomes emerge from the interaction between controllable management decisions and uncertain future selective conditions. In our simulations, selection determined long-term genetic trajectories, whereas introduction intensity and spatial configuration shaped the rate, spatial dynamics, and demographic consequences of introgression. High-intensity introductions promoted faster recovery of relative stand performance when the introduced genotype was favoured, but also accelerated the replacement of resident genotypes when they had a lower fitness due to climate change. Lower-intensity and spatially clustered introductions favoured the persistence of hybrid and introgressed lineages, highlighting a trade-off between short-term productivity and long-term adaptive potential. These results show that AM/AGF should be evaluated as a set of alternative strategies rather than as a single intervention. Whether introgression is desirable depends on management objectives: it may increase adaptive potential under uncertain climates, but it may also raise concerns about genetic swamping or erosion of locally adapted gene pools. By combining spatially explicit simulations with stakeholder-informed introduction scenarios, our approach provides a framework for comparing demographic, evolutionary, operational, and conservation consequences before implementation. As targeted restoration and precision forestry become more feasible, such simulations can help guide what to introduce, how much to introduce, and where to plan introductions.

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Figure 1: Summary of questionnaire responses collected during the workshop regarding existing introductions of Oriental beech in European forests. Questions are grouped into thematic categories with (A) factors that may facilitate AGF and (B) factors that may constrain or limit its implementation. Bars indicate the proportion of participants selecting each answer category for a given question.

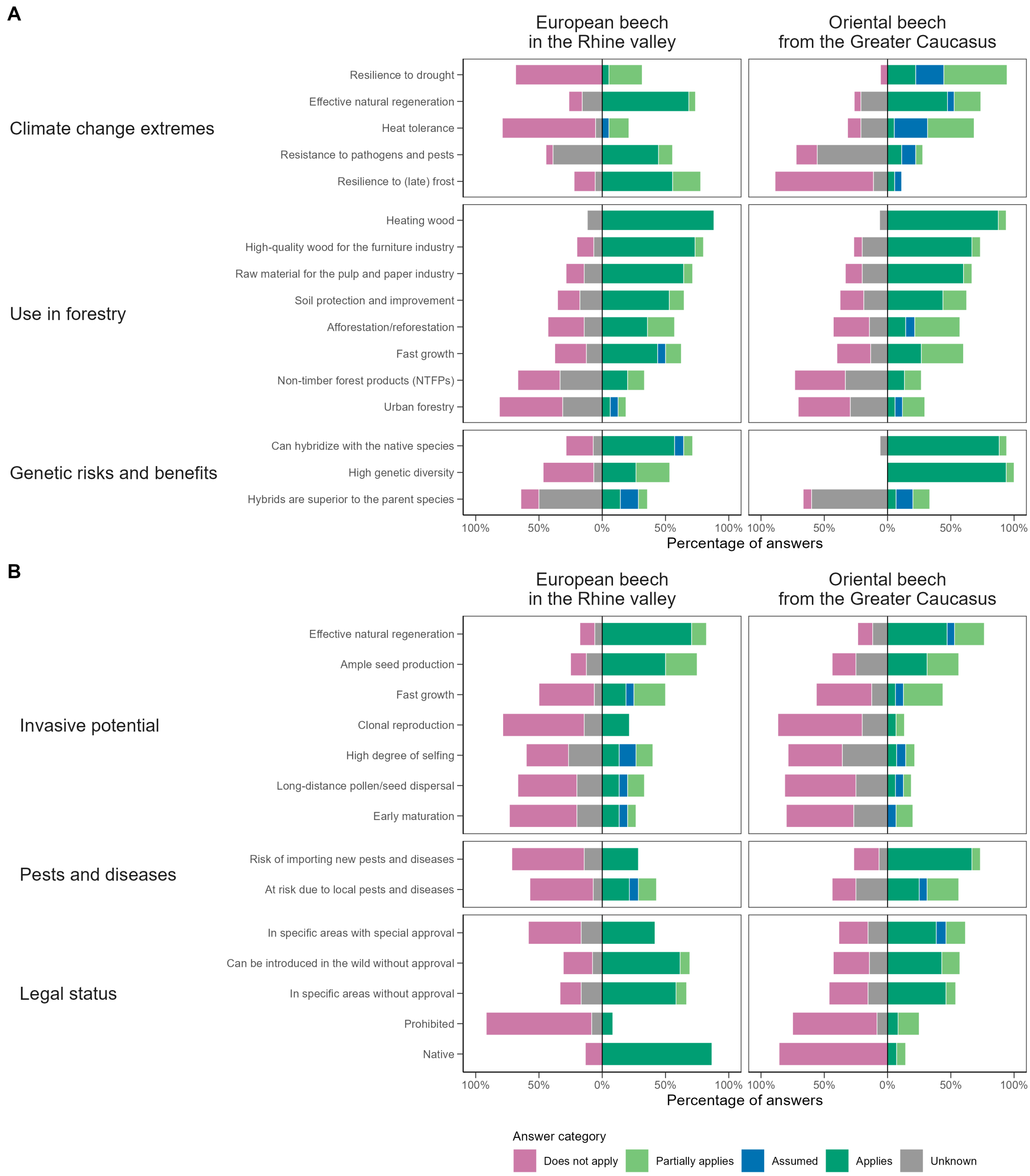


Figure 2: Simulation scenarios. (A) Starting planting configurations derived from workshop questionnaires and used as initial conditions in Nemo-age simulations. Each panel represents a 1-ha virtual stand (100 × 100 m), divided into 4 × 4 m grid cells. Configurations illustrate four spatial arrangements of Oriental beech introduction (dispersed, single cluster, multiple clusters, and transects) at varying introduction intensities. (B) Relative fitness (W) of European beech, F1 hybrids, and Oriental beech across life stages under weak, intermediate, and strong selection regimes used in the spatially-explicit simulations. Columns represent alternative phenotypic optima favouring Oriental beech, F1 hybrids, or European beech, whereas rows indicate the strength of selection applied across ontogenetic stages.

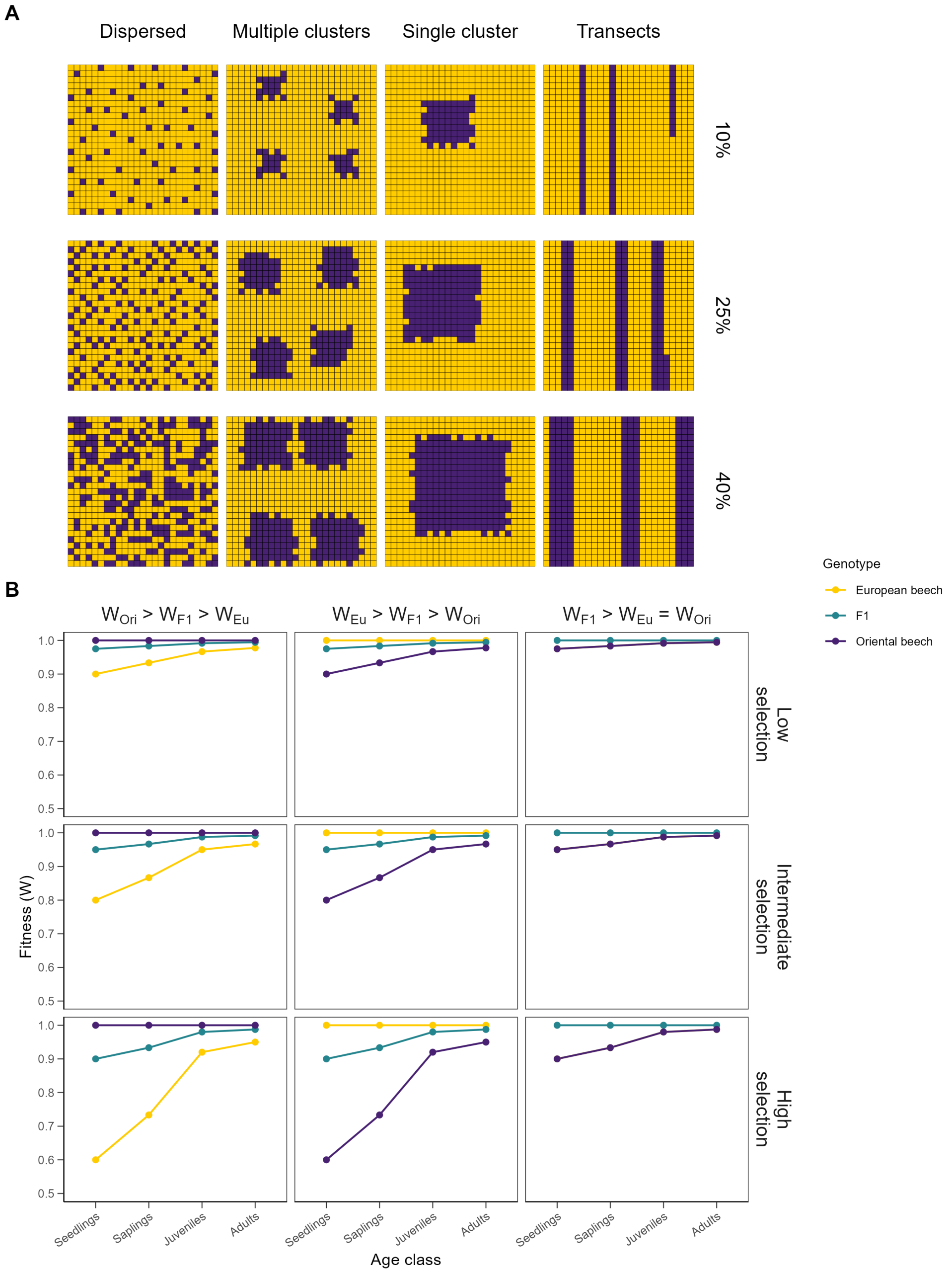


Figure 3: Example simulations illustrating the genetic outcomes of the introduction of Oriental beech in four different selection scenarios with different selection strength. In each case, ten additive loci determine a genotype ranging from -1 (European beech) to $+1$ (Oriental beech). For each simulation, the proportion of adult individuals (median of $n = 50$ stochastic replicates) for each genotype and for each generation are shown.

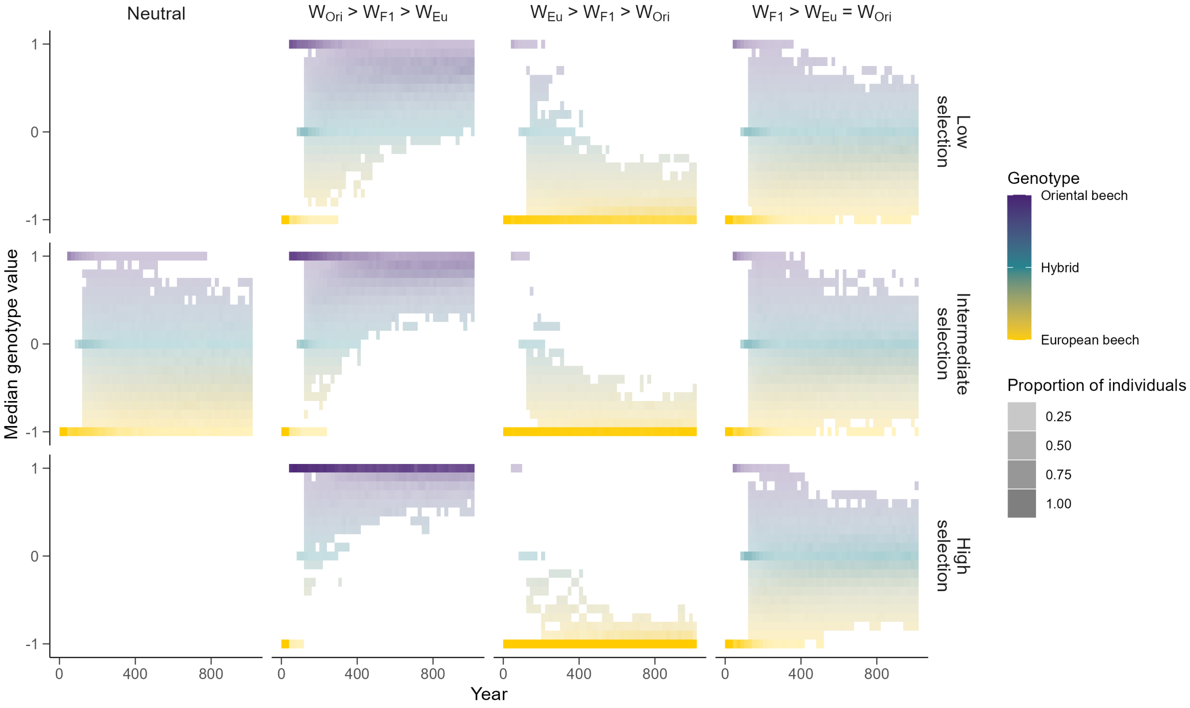


Figure 4: Results of simulations with selection favouring Oriental beech over European beech. Median hybrid proportions (A-B) and relative stand productivity (RSP) (C-D) are shown for each configuration and introduction intensity across $n = 50$ stochastic replicates. Panels (A) and (C) present temporal dynamics, while panels (B) and (D) show values at $t = 100$. In (A) and (B), hybrid proportion is shown; in (C) and (D), RSP is shown. Grey areas denote the 10th–90th percentile range under the neutral scenario. In panel (C), the black line indicates the median RSP under selection against European beech without introduction of Oriental beech. Panels (B) and (D) summarize, respectively, the proportion of hybrids in the adult class and RSP at $t = 100$ across parameter combinations. Grey areas again represent the 10th–90th percentile range of the neutral scenario. Significance of the Kruskal-Wallis test: ****: $p < 0.0001$, ***: $p < 0.001$, ** : $p < 0.01$, *: $p < 0.05$.

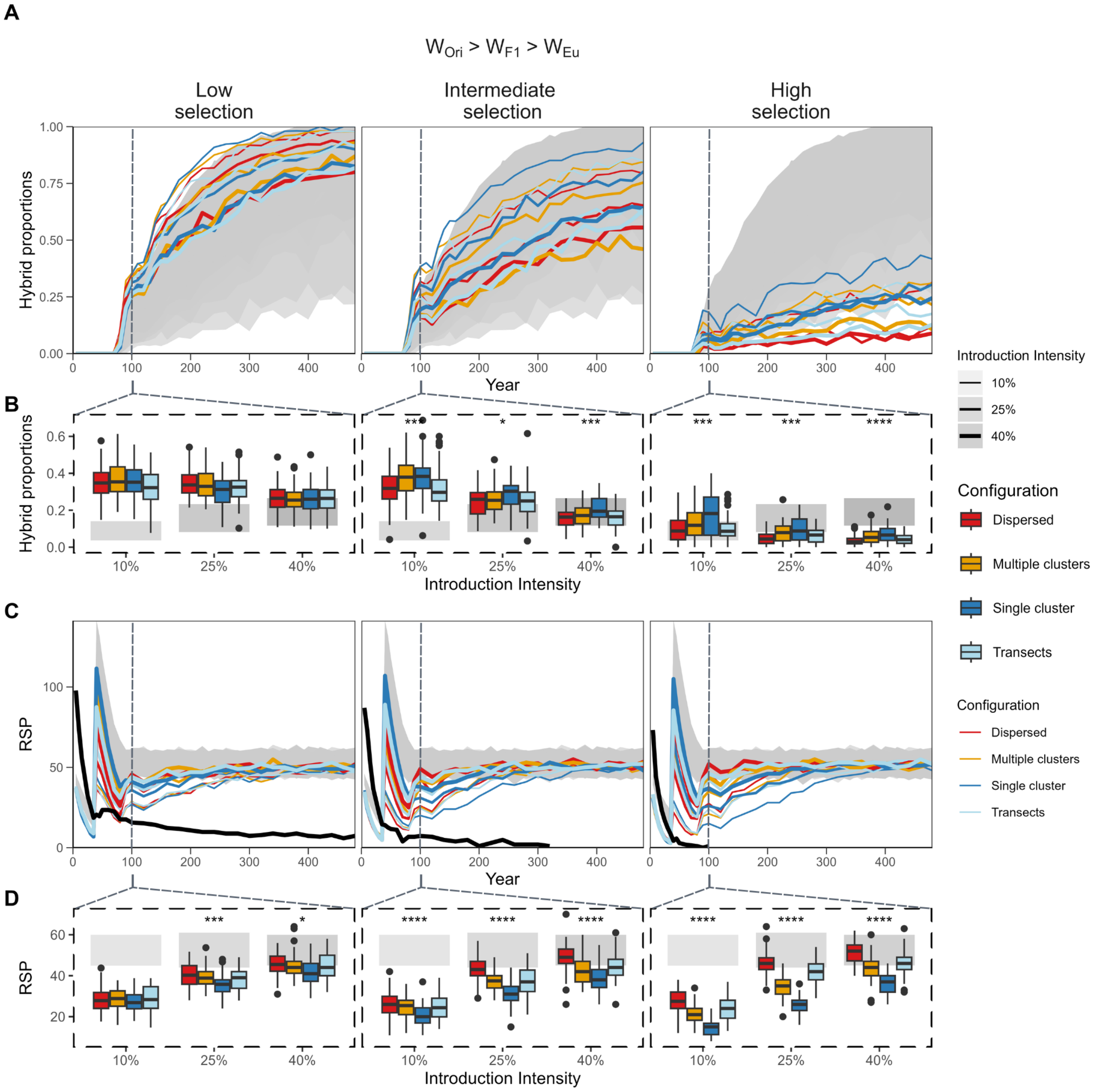
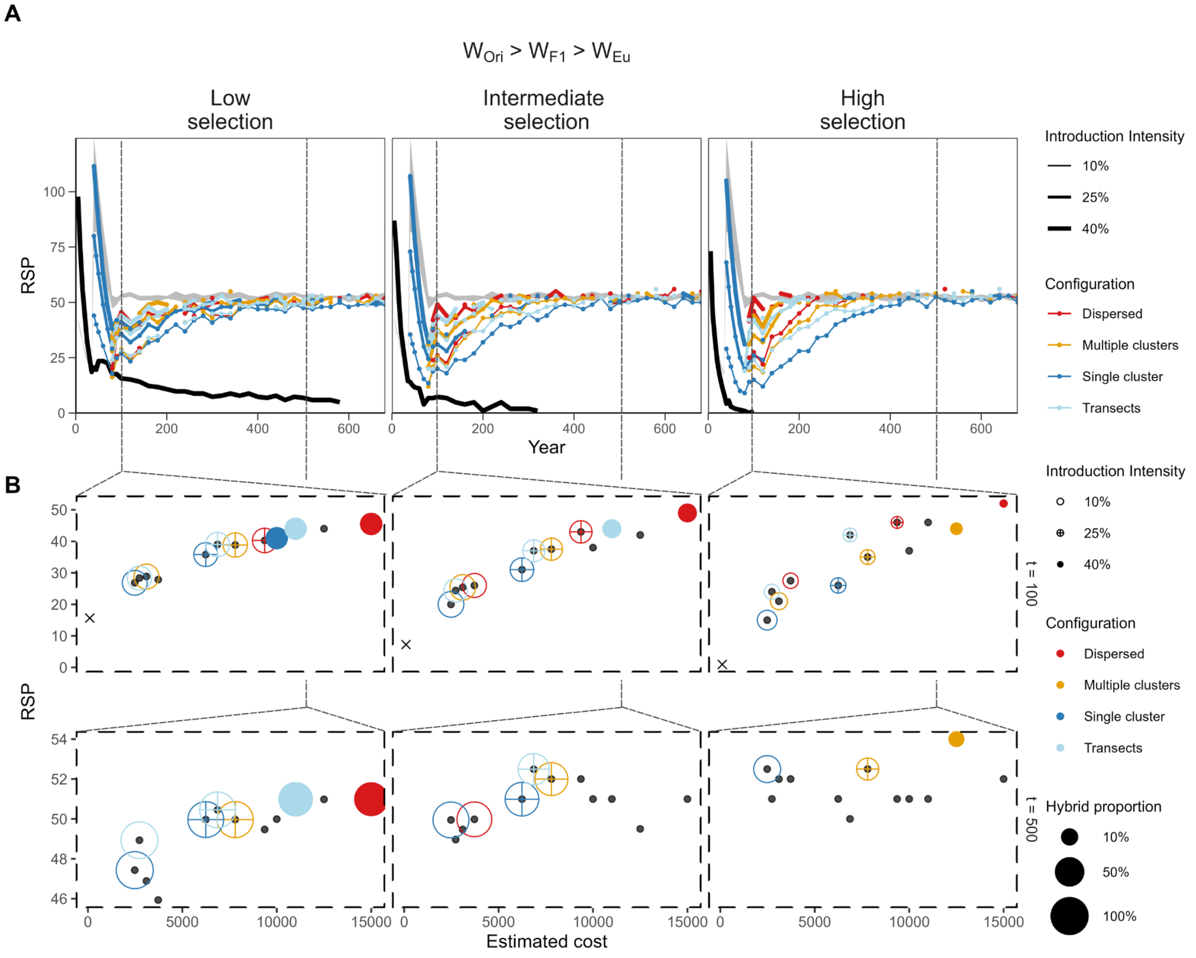


Figure 5: Cost–efficiency Pareto frontiers showing the trade-offs between hybrid proportion, relative stand productivity (RSP), and estimated introduction cost under different introduction intensities and spatial configurations, for the scenario where selection is in favour of Oriental beech (low, medium, and high selection strength). (A) Temporal dynamics of RSP for the best-performing strategies. Grey area denotes the productivity range under the neutral scenario (10th–90th percentile), while the black line shows median productivity under selection against European beech without introduction of Oriental beech. Vertical dashed lines at $t = 100$ and 500 indicate the time points shown in panel (B). (B) Trade-offs between productivity, introduction cost, and achieved hybrid proportions for selected strategies after 100 (top row) and 500 (bottom row) years following the introduction of Oriental beech. Crosses indicate RSP in case of no introduction of Oriental beech.



Tables

Table 1: Parameters used in the Nemo-age simulations and relative references.

Parameter	**Name**	**Value**	**References**
Demographic and dispersal parameters			
–	Population structure (years)	Seedlings (1), Saplings (2–4), Juveniles (5–39), Adults (> 40)	Genet et al., 2010; Wagner et al., 2010
N_p	Number of patches	625	–
K	Patch carrying capacity	30	Dobrovolny et al., 2010; Dobrowolska et al., 2015; Axer et al., 2021
b	Competition coefficient	0.03	Demographic calibration (Supplementary Material)
s_p	Selfing rate	0.005	Westergren et al., 2023; Stefanini et al., 2025; Oddou-Muratorio et al., 2010
S_0	Offspring survival	0.3	COMPADRE Plant Matrix Database
S_1	Seedling survival	0.7	COMPADRE Plant Matrix Database
S_2	Juvenile survival	1	COMPADRE Plant Matrix Database
S_3	Adult survival	0.97	COMPADRE Plant Matrix Database
f	Adult fecundity	1000	COMPADRE Plant Matrix Database
d_s (m)	Seed dispersal distance	5	Oddou-Muratorio et al., 2010; Westergren et al., 2023; Stefanini et al., 2025
d_p (m)	Pollen dispersal distance	30	Oddou-Muratorio et al., 2010; Westergren et al., 2023; Stefanini et al., 2025
II (%)	Introduction intensity	10, 25, 40	–
Selection parameters			
θ	Selection optima	-1 (European beech), 0 (F1), $+1$ (Oriental beech)	–
w^2 (high)	High selection strength	(S_0: 10, S_1: 15, S_2: 50, S_3: 80)	–
w^2 (intermediate)	Intermediate selection strength	(S_0: 20, S_1: 30, S_2: 80, S_3: 120)	–
w^2 (low)	Low selection strength	(S_0: 40, S_1: 60, S_2: 120, S_3: 180)	–

Supplementary Material for:

Evolutionary and operational trade-offs in assisted gene flow for climate-adaptive forestry

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Contents

1 Stakeholder perceptions of Oriental beech introductions

1.1 Existing introductions of Oriental beech

Responses regarding existing introductions of Oriental beech were obtained from 19 participants (12 researchers and 7 foresters). These responses reflect the views of researchers and foresters who were informed about recent scientific findings, as questionnaires were completed after presentations on Oriental beech ecology, genetics, and hybridization. Across all question groups, the highest levels of uncertainty concerned invasive potential, resistance to pathogens and pests, and whether hybrids are superior to parental species. Overall, researchers and foresters showed qualitatively similar response patterns across question groups (Figure 1). Fisher's exact tests comparing positive versus negative responses between respondent groups did not detect statistically significant differences after correction for multiple testing. Before correction, only one question showed a significant difference between researchers and foresters, concerning the perceived degree of selfing within the invasive potential category (Fisher's exact test, $p = 0.008$). Nevertheless, we observed different patterns between groups in some thematic categories.

For climate-related traits, Oriental beech was generally perceived positively regarding drought resilience, heat tolerance, and effective natural regeneration, whereas responses were more negative or uncertain for resistance to pathogens and pests and resilience to late frosts. In contrast, European beech was viewed positively for effective natural regeneration, resistance to pathogens and pests, and tolerance to late frosts, but negatively for drought resilience and heat tolerance. Foresters tended to provide more negative assessments than researchers regarding the resilience of European beech to drought and heat stress.

Regarding forestry use, both species were generally perceived positively for heating wood, furniture production, soil protection and improvement, paper industry use, fast growth, and reforestation potential. In contrast, responses were more negative or uncertain for non-timber forest products and urban forestry applications. Foresters and researchers largely agreed on these patterns, with particularly strong support for the use of both species as heating wood and for furniture production. One forester additionally highlighted the importance of "logistic/selection diagrams on a mixed plantation area".

For traits associated with invasive potential, both species were generally considered capable of effective natural regeneration and ample seed production. Responses regarding fast growth were more evenly divided, whereas respondents mostly disagreed or expressed uncertainty about high levels of selfing, early maturation, long-distance dispersal, and clonal reproduction. The main difference between foresters and researchers concerned selfing rates: foresters tended to provide more positive responses, whereas researchers were more negative or uncertain for both species.

Assessments related to pests and diseases showed broad agreement between foresters and researchers. Oriental beech was more frequently perceived as carrying risks associated with importing new pests and diseases and as potentially being more susceptible to local pests and pathogens. In contrast, respondents generally disagreed that European beech posed similar risks.

For genetic risks and benefits, respondents generally agreed that both species harbour high genetic diversity, particularly Oriental beech, and that Oriental beech can hybridize with native European beech. These perceptions were likely influenced by the preceding presentations, which included examples of hybridization and data on the high genetic diversity of Oriental beech populations. In contrast, respondents were largely uncertain regarding whether hybrids outperform parental species. This was also the question showing the clearest qualitative disagreement between respondent groups: foresters tended to respond positively, whereas researchers were mostly negative. Additional comments highlighted that legal regulations regarding hybridization and reproductive material differ among countries, with one respondent noting that introductions may be "legally forbidden in Switzerland" and that "legal status differs by country/administration". The generally cautious perception regarding whether hybrids outperform parental species likely reflected information presented during the talks.

Concerning the legal status, respondents generally agreed that European beech could be introduced without approval and widely considered it native, whereas Oriental beech was associated with greater uncertainty and potential regulatory constraints. Both species were generally not considered prohibited, although Oriental beech more often required special approval. Foresters tended to provide slightly more positive responses toward European beech across legal categories, although overall agreement between groups remained high.

1.2 Future introductions of Oriental beech

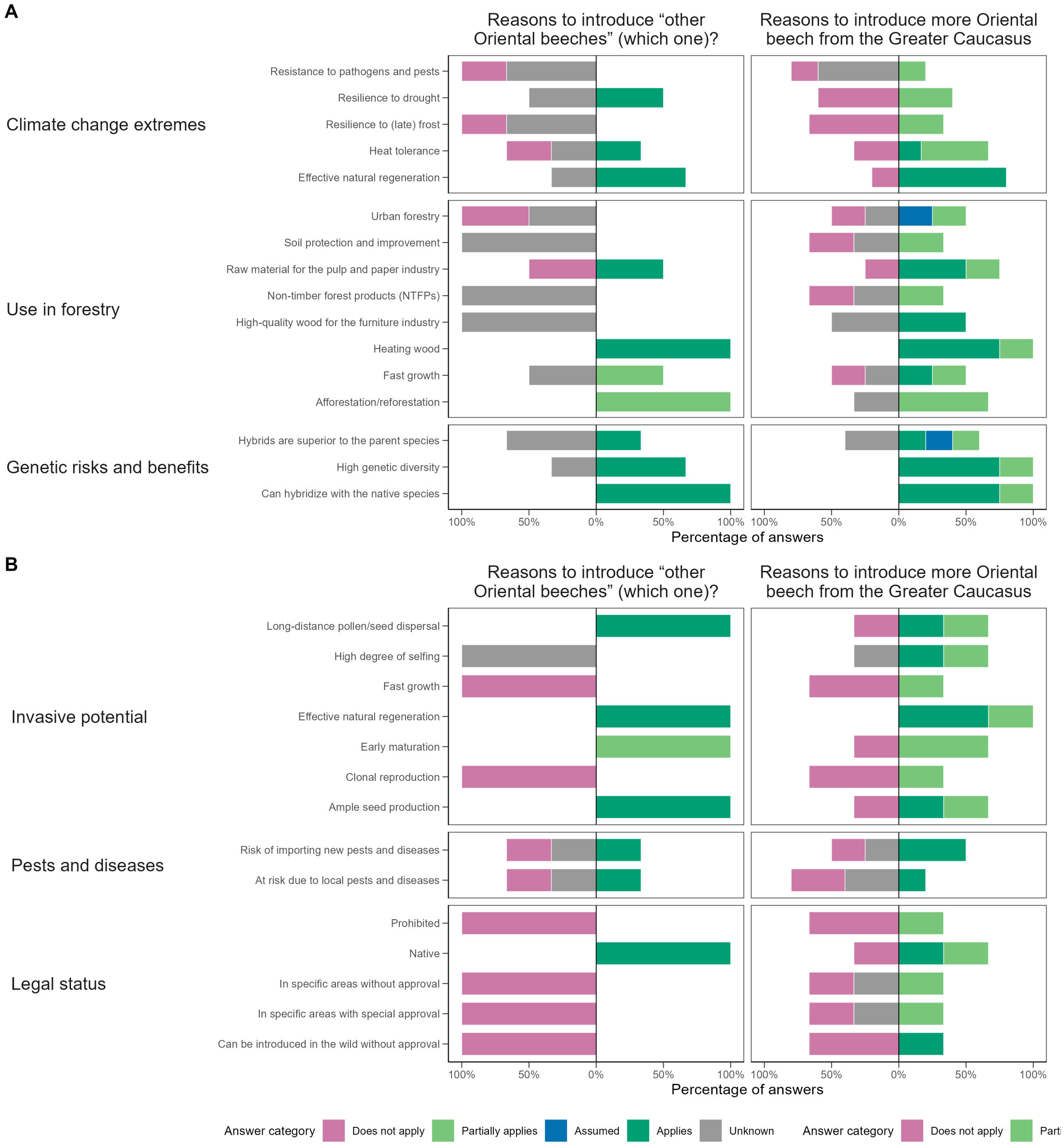
Future introductions of Oriental beech were addressed by relatively few participants and responses were often incomplete, limiting the representativeness of the results. Of the 19 participants, only seven provided at least partial answers regarding the potential introduction of additional Oriental beech from the Greater Caucasus, and only three respondents completed most or all questions (Figure S1). This low response rate itself reflected substantial uncertainty and hesitation regarding future introduction scenarios.

Among respondents who provided substantial answers, additional introductions of Oriental beech from the Greater Caucasus were generally perceived positively with respect to effective natural regeneration, high genetic diversity, and the capacity to hybridize with native European beech. Some respondents also identified potential benefits for heating wood, furniture production, afforestation/reforestation, and, to a lesser extent, fast growth and paper production. Similar to the responses regarding existing introductions, respondents largely agreed that Oriental beech may contribute adaptive and genetic benefits under future climatic conditions.

At the same time, responses showed substantial disagreement and uncertainty for several ecological traits. Perceptions of drought resilience, heat tolerance, frost resilience, and growth performance varied strongly among respondents, indicating limited consensus regarding the adaptive performance of additional Oriental beech provenances under future environmental conditions. Uncertainty was also high regarding invasive potential, particularly for selfing rates, clonal reproduction, long-distance dispersal, and early maturation.

Concerns regarding pests and diseases remained important in future introduction scenarios. Several respondents considered additional introductions to carry risks associated with importing new pests and pathogens or increasing susceptibility to local pests and diseases. Legal status also remained uncertain, with respondents differing in whether additional introductions would require approval or could be considered acceptable within existing regulations. Overall, the responses suggested that future introductions were perceived as potentially beneficial but associated with substantial ecological, legal, and management uncertainty.

Figure S1: Summary of questionnaire responses collected during the workshop regarding potential future introductions of Oriental beech in European forests. Questions are grouped into thematic categories with (A) factors that may facilitate AGF and (B) factors that may constrain or limit its implementation. Bars indicate the proportion of participants selecting each answer category for a given question.



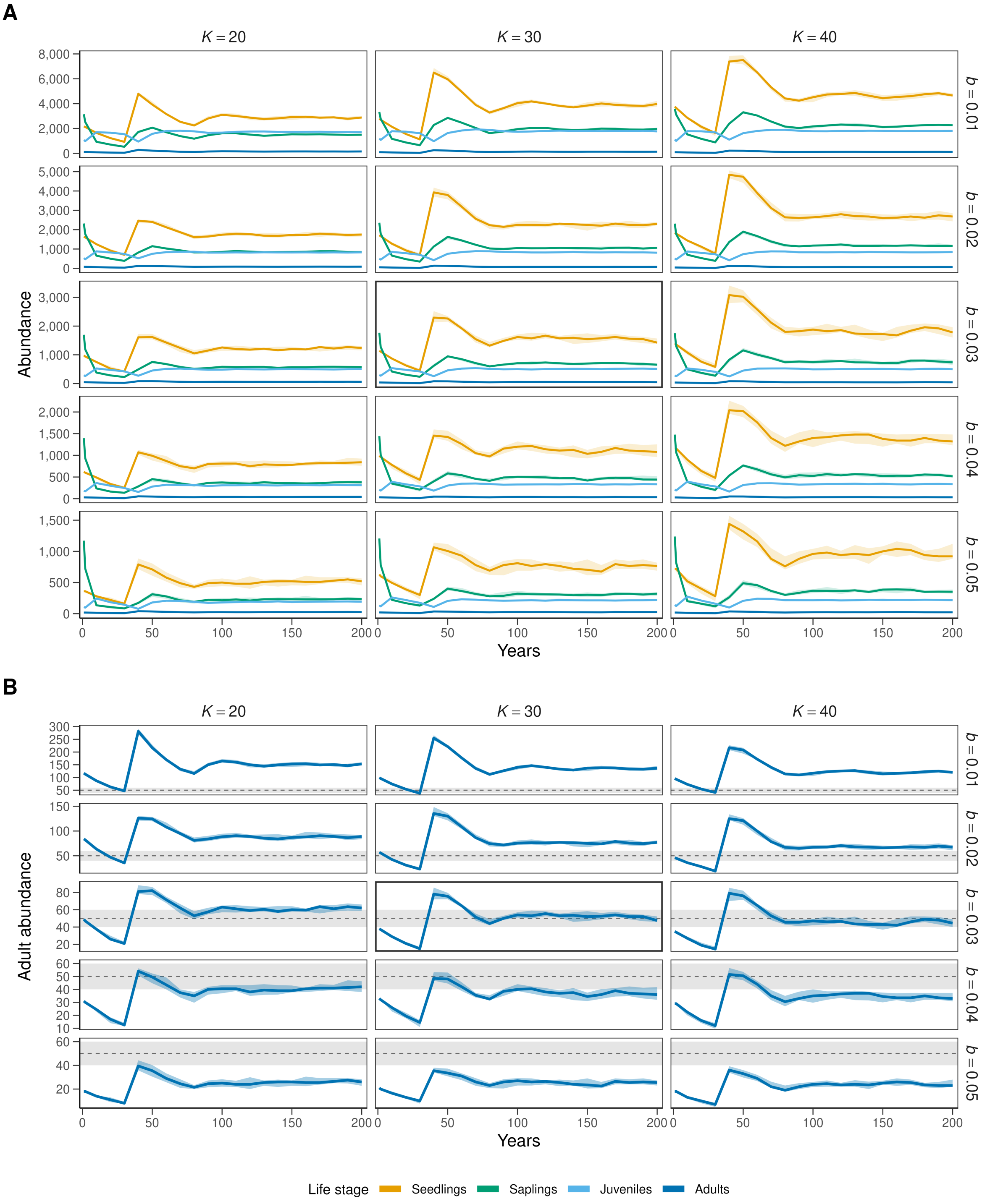
2 Demographic calibration and selection of density-regulation parameters

We calibrated density-regulation parameters to obtain a stable, biologically realistic demographic structure for a 1 ha beech stand simulated in Nemo-age. All life-history parameters, including stage transitions, survival probability, fecundity, mating system, and dispersal kernels, were fixed based on biological knowledge and literature sources (Table 1). In our framework, fecundity is defined as the number of viable seeds, corresponding to realized germination (i.e. the number of seedlings entering the population as seedlings).

We performed a sensitivity analysis on two parameters expected to most strongly influence equilibrium population density and demographic structure: patch carrying capacity (K; maximum density per 4 m × 4 m patch) and the Beverton-Holt competition coefficient (b), which determines the strength of density-dependent competition. Simulations were run using a single representative planting configuration (dispersed introduction; 25% introduction) with $n = 20$ stochastic simulation replicates per parameter combination to quantify replicate variance. We explored combinations of $K = \{20, 30, 40\}$ and $b = \{0.01, 0.02, 0.03, 0.04, 0.05\}$. Each simulation was run for 500 years, and demographic outputs were recorded every 50 years, including year two to capture both early transient dynamics and long-term equilibrium.

We evaluated parameter combinations using three criteria: (i) stable adult abundance at the stand scale, targeting approximately 50 mature individuals per hectare as expected in closed-canopy beech forests; (ii) a biologically realistic stage structure characterized by progressively declining abundances from seedlings (stage 0) to adults (stage 3); and (iii) realistic spatial distributions of adults, assessed through nearest-neighbor distances among occupied adult patches at equilibrium. Among tested combinations, $K = 30$ and $b = 0.03$ consistently produced stable population dynamics, adult densities close to the target range, and a plausible demographic structure (Figure S2). These parameter values were therefore retained for all subsequent simulations.

Figure S2: Demographic calibration of the density-regulation parameters for the Nemo-age simulations, across combinations of patch carrying capacity (K) and the Beverton–Holt competition coefficient (b). Simulations used a single configuration (dispersed, 25 % introduction) with $n = 20$ stochastic replicates per parameter combination. In each panel the line is the median across replicates and the shaded ribbon the interquartile range (25th–75th percentile). (A) Abundance of all four life stages (seedlings, saplings, juveniles, adults). (B) Adults only; the grey band marks the target range of 40–60 mature individuals and the dashed line the target of approximately 50 individuals ha^{-1} expected in closed-canopy beech stands. The retained combination ($K = 30$, $b = 0.03$) is outlined.



3 Estimating operational cost

To compare the economic implications of alternative planting designs, we estimated the relative operational cost associated with each simulation scenario. In our framework, cost differences arise from two factors: (i) the number of introduced seedlings and (ii) the operational efficiency of the planting configuration. Because seedling price is identical across designs, variation in total cost is primarily driven by labor efficiency during planting.

Operational forestry costs depend strongly on country, labor prices, terrain, and machinery availability, and are therefore difficult to generalize. Instead of estimating absolute operational costs, we used a relative cost approach. First, we identified the main cost components associated with enrichment planting. Total cost per hectare typically includes seedling purchase, transport, site preparation, planting labor, protection, maintenance, and supervision. Among these components, planting labor is most directly affected by the spatial arrangement of planted trees. We therefore focused on planting efficiency while assuming that other cost components remain constant across scenarios.

Spatial configurations differ in the movement required for workers, the ease of layout and supervision, and the possibility of concentrating operations within limited areas. Designs with stronger spatial aggregation generally increase operational efficiency because they reduce walking time and allow planting to be performed in more continuous blocks. Based on these considerations, we ranked the expected operational cost of the four spatial configurations from lowest to highest as follows: (1) one cluster, (2) transects, (3) multiple clusters, and (4) dispersed planting.

To integrate this ranking with the simulated introduction intensities, we assigned each configuration a relative cost multiplier representing differences in operational efficiency. Baseline planting cost was estimated as the number of introduced seedlings multiplied by an average forestry seedling price of 2€ per plant. This value reflects approximate bulk nursery prices for broadleaf forest species and avoids the inflated prices typical of retail garden nurseries. The baseline cost was then multiplied by the configuration-specific cost index to obtain the estimated operational cost of each scenario.

For each introduction intensity, the number of planted Oriental beech seedlings was determined by the number of selected patches and the fixed planting density of 20 seedlings per patch, resulting in 1240 seedlings (10% patches), 3120 seedlings (25%), and 5000 seedlings (40%). The final estimated cost of each scenario was calculated by combining these baseline costs with the spatial configuration cost multipliers.

Figure S3: Proportion of adult individuals for each genotype (values close to -1 and $+1$ correspond to European and Oriental beech genotypes, respectively, while intermediate values represent varying degrees of admixture) across time and across parameter combinations. The value of proportion reported correspond to the median of $n = 50$ stochastic replicates.

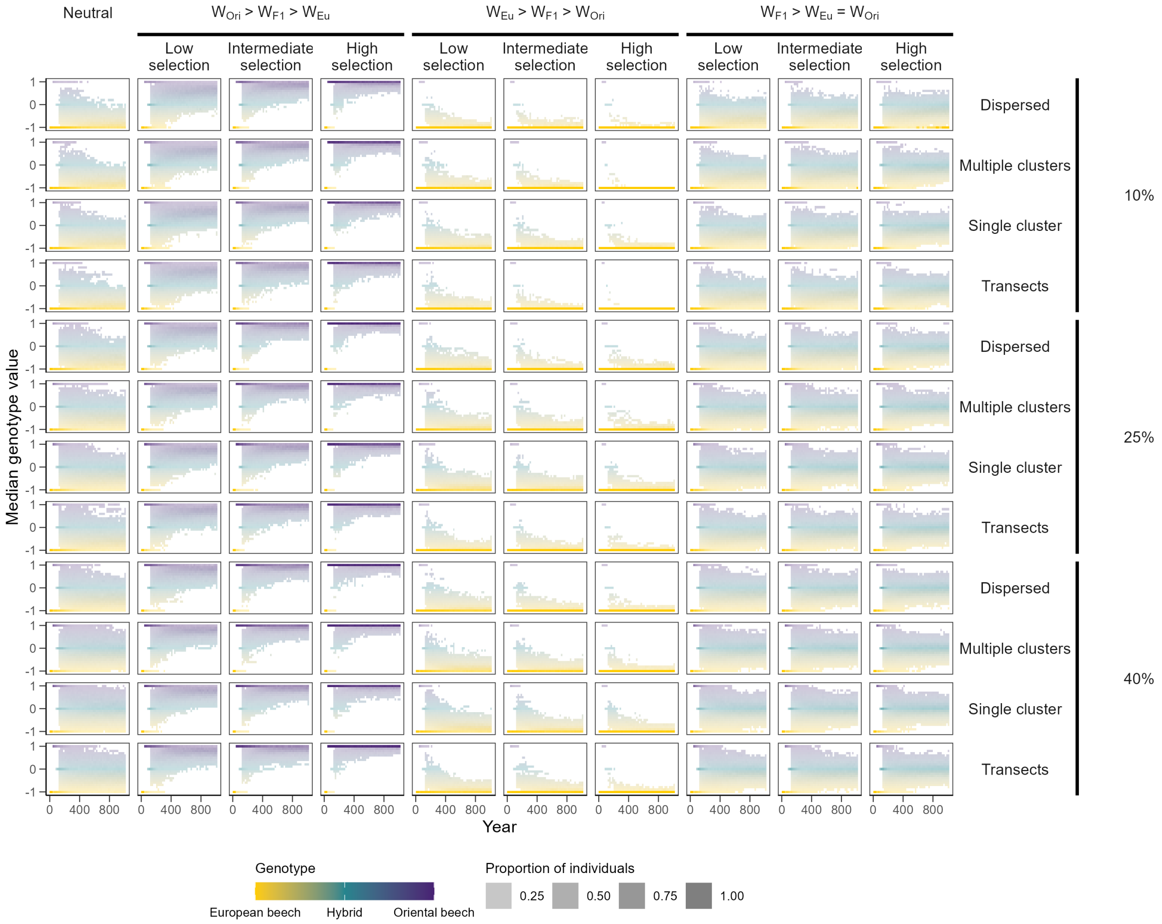


Figure S4: Temporal dynamics of adult genotype proportions across parameter combinations. Lines show the median proportion across n = 50 stochastic replicates, while shaded areas represent the 10% and 90% quantiles.

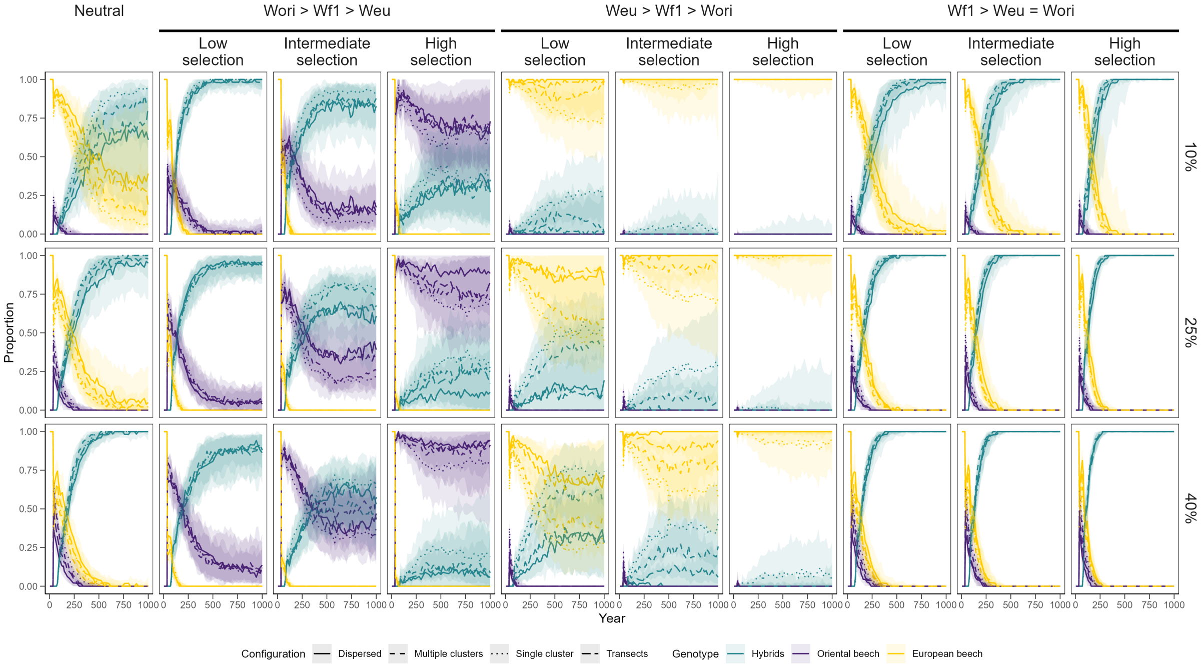


Figure S5: Time required to reach 50% hybrids (A) and 80% of equilibrium relative stand productivity (RSP) (B) in individual-based simulations. Boxplots summarize stochastic simulation replicates across introduction intensities and planting configurations. Facets represent combinations of selection scenarios and selection strength. Asterisks denote significant differences among configurations within introduction intensities (Kruskal–Wallis tests). Significance of the Kruskal-Wallis test: ****: $p < 0.0001$, ***: $p < 0.001$, ** : $p < 0.01$, *: $p < 0.05$.

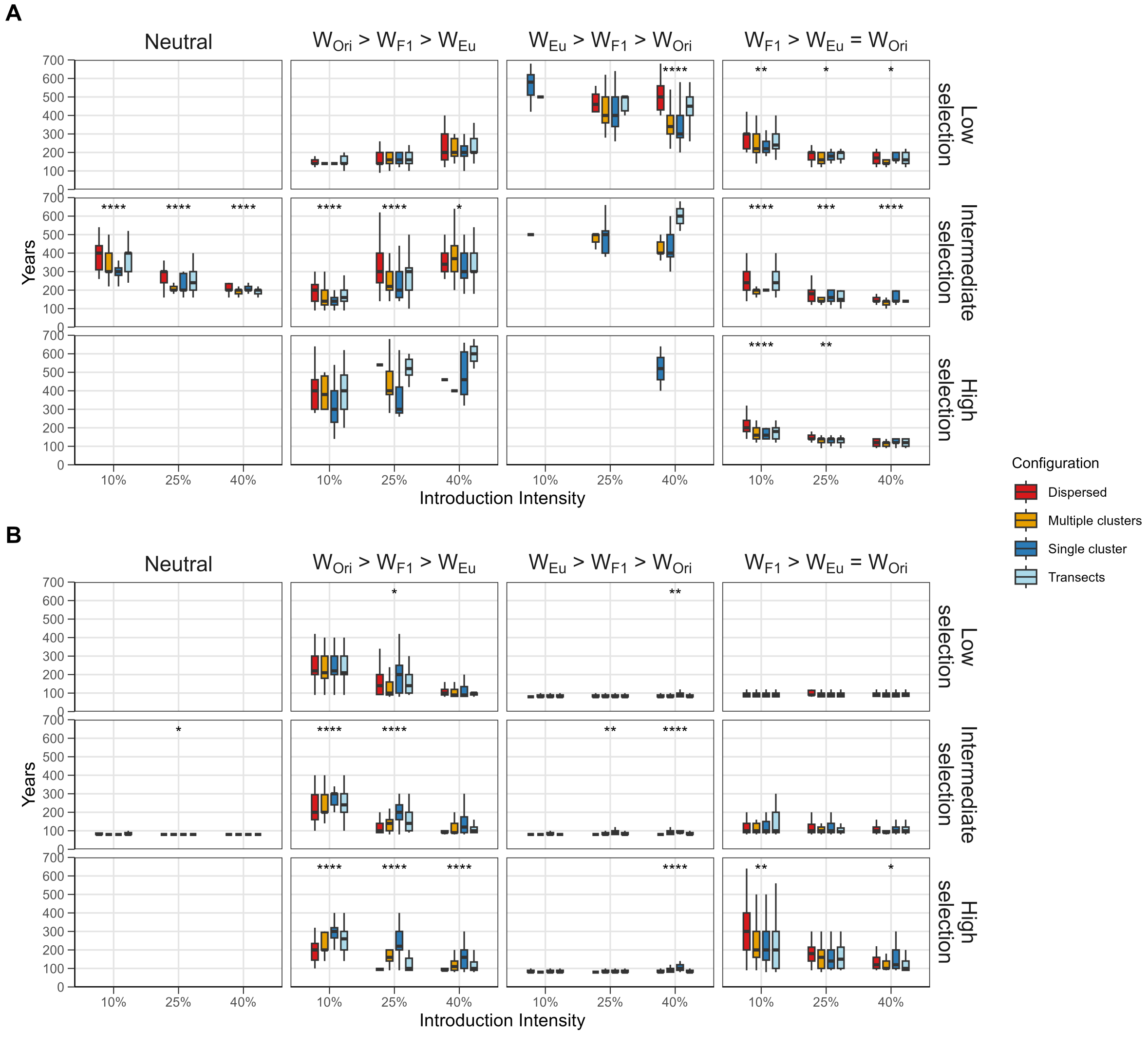


Figure S6: Results of simulations with selection favouring European beech and hybrids. Median hybrid proportions (A-B) and relative stand productivity (RSP) (C-D) are shown for each configuration and introduction intensity across n = 50 stochastic replicates. Panels (A) and (C) present temporal dynamics, while panels (B) and (D) show values at $t = 100$. In (A) and (B), hybrid proportion is shown; in (C) and (D), RSP is shown. Grey areas denote the 10th–90th percentile range under the neutral scenario. Panels (B) and (D) summarize, respectively, the proportion of hybrids in the adult class and RSP at $t = 100$ across parameter combinations. Grey areas again represent the 10th–90th percentile range of the neutral scenario. Significance of the Kruskal-Wallis test: ****: $p < 0.0001$, ***: $p < 0.001$, ** : $p < 0.01$, *: $p < 0.05$.

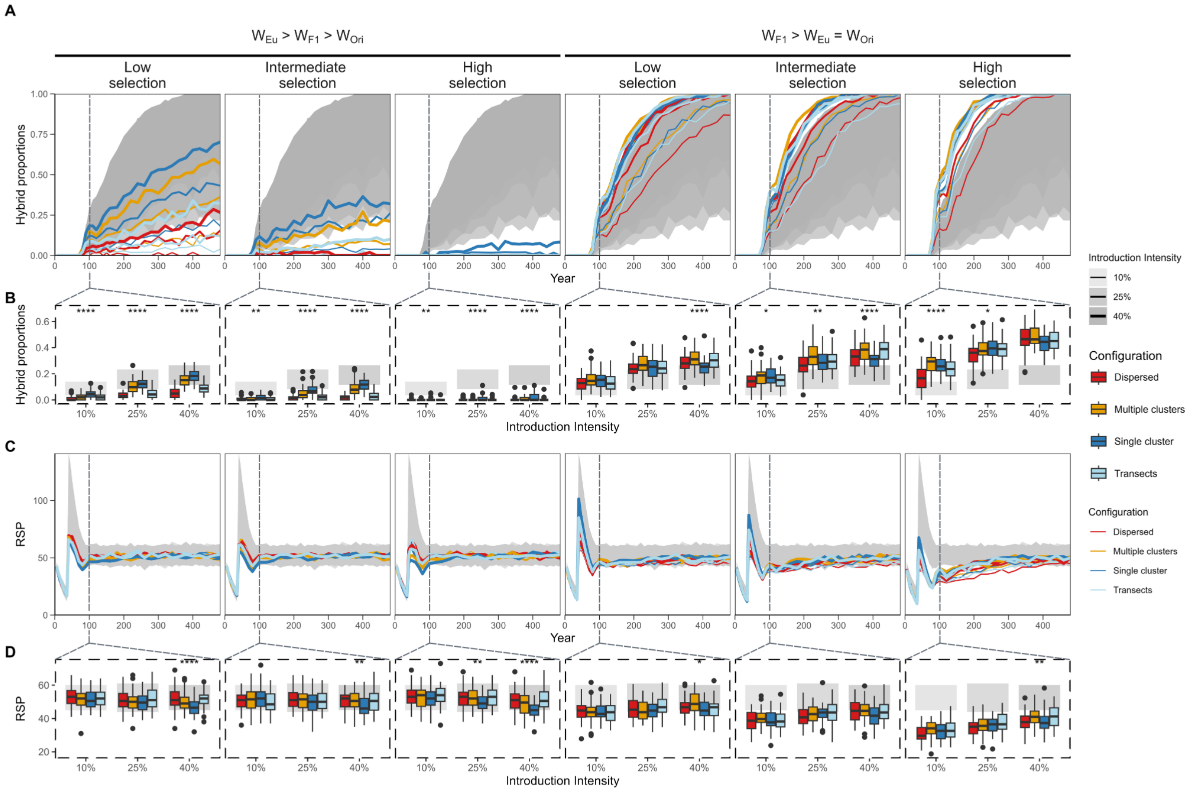


Figure S7: Spatial distribution of proportion of Oriental beech ancestry at $t = 100$, for each parameter combination and selection scenario (median across replicates in each patch).

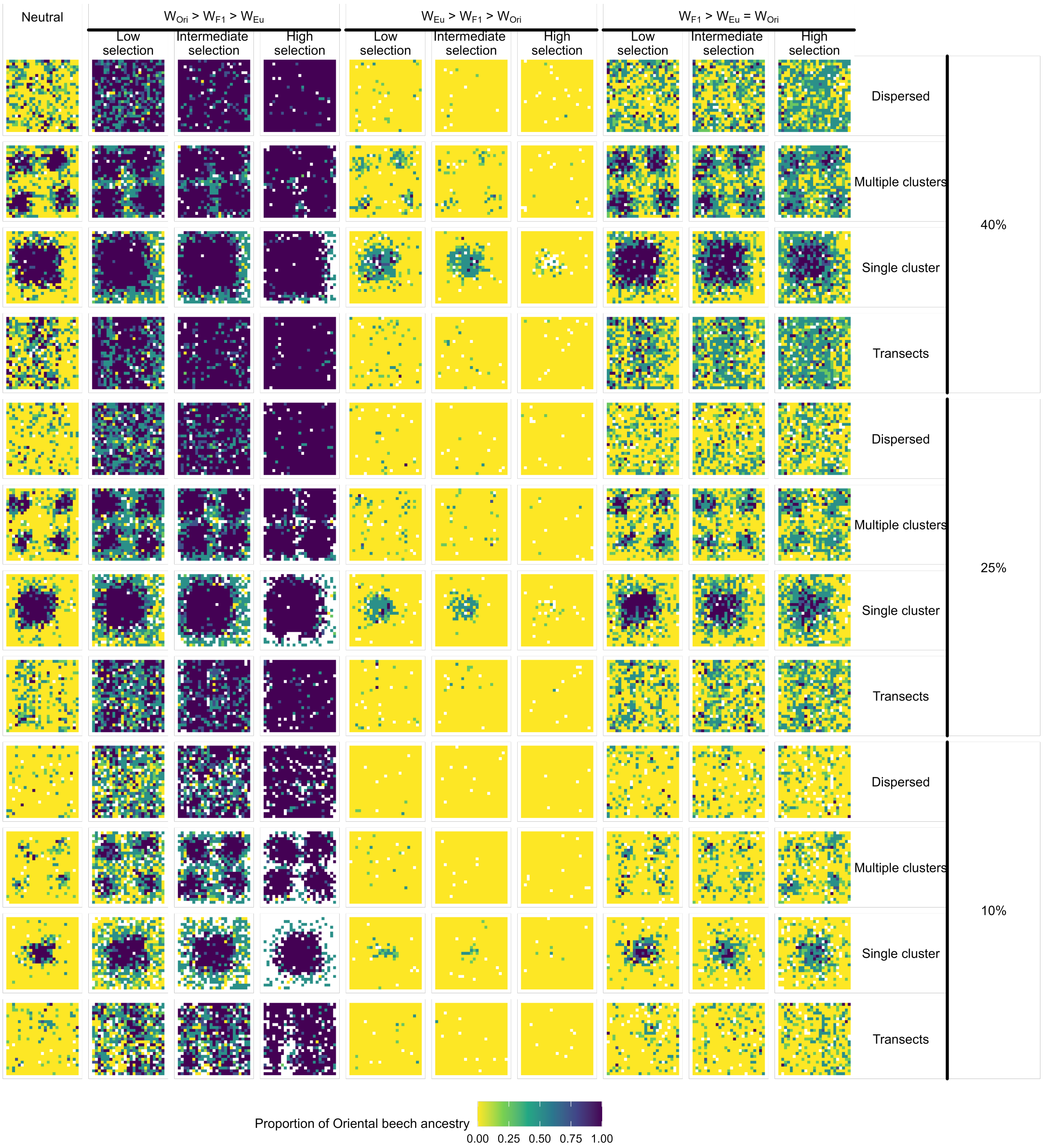


Figure S8: Cost–efficiency Pareto frontiers showing the trade-offs between hybrid proportion, RSP, and estimated introduction cost under different introduction intensities and spatial configurations, for selection in favour of European beech and in favour of hybrids. (A) Temporal dynamics of RSP for the best-performing strategies. Grey area denotes the RSP range under the neutral scenario (10th–90th percentile). Vertical dashed lines at $t = 100$ and 500 indicate the time points shown in panel (B). (B) Trade-offs between RSP, introduction cost, and achieved hybridization for selected strategies after 100 (top row) and 500 (bottom row) years following the introduction of Oriental beech.