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A Pollen-Based Assisted Migration for Rapid Forest Adaptation

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ABSTRACT

Climate change poses an unprecedented threat to forest ecosystems, necessitating innovative adaptation strategies. Traditional assisted migration approaches, while promising, face challenges related to environmental constraints, forestry practices, phytosanitary risks, economic barriers, and legal constraints. This has sparked debate within the scientific community, with some advocating for the broader implementation of assisted migration despite these limitations, while others emphasize the importance of local adaptation, which may not keep pace with the rapid rate of climate change. This opinion paper proposes a novel pollen-based assisted migration strategy as a potential middle ground in this debate. By leveraging existing seed orchard infrastructure for controlled pollen transfer, this approach aims to enhance forest resilience through the introduction of genetic material from climatically suitable sources while acknowledging local adaptation. We assess the genetic implications of the proposed strategy through computer simulation. Additionally, we examine the ecological implications of assisted gene flow, discussing the potential benefits of heterosis and the risks of outbreeding depression in intra-specific hybrid populations. We further explore the advantages of pollen-based migration in mitigating phytosanitary risks, reducing economic barriers, and simplifying legal considerations compared to traditional seed or seedling transfer methods. Regional perspectives on adapting pollen-based assisted migration are provided, with specific examples from Northern and Central Europe. We highlight how this approach could be integrated into existing forestry practices and regulatory frameworks within the European Union. We conclude by advocating for the inclusion of pollen-based assisted migration in future international projects and operational forestry, emphasizing the need for adaptable policies that can support innovative forest management strategies in the face of climate change.

1 | Introduction

Forest ecosystems play a crucial role in mitigating climate change through climate regulation (Smith, Baker, and Spracklen 2023) and carbon sequestration, capable of removing billions of tons of carbon from the Earth's atmosphere (Canadell and Raupach 2008). By fully utilizing available resources, knowledge, and technology, their potential for carbon sequestration could be significantly enhanced (IPCC 2022). However, tree species are particularly vulnerable to the adverse effects of climate change, such as rising temperatures and prolonged droughts, which increase their susceptibility to wildfires, diseases, and pests (Lindner et al. 2010).

These factors contribute to landscape changes and a significant decline in forest cover, impeding forests' natural capacity to absorb carbon. Furthermore, the widespread decline of trees in younger age stages is excessively increasing the amount of released carbon that has been previously stored (Gorte and Sheikh 2010), further elevating atmospheric carbon levels.

Trees can withstand shifts in environmental conditions through phenotypic plasticity (Kramer 1995; West-Eberhard 1989), which enables them to adjust to the inherent diversity of landscapes (Schreiber, Hacke, and Hamann 2015), undergoing continual changes. However, it may fall short of addressing the unforeseeable impacts of climate change (Visser 2008). Therefore, long-term responses such as adaptation through selection and natural migration are essential because an inadequate response to unfavorable conditions could result in species decline (Aitken et al. 2008; Ledig, Rehfeldt, and Jaquish 2012).

Natural or artificial selection is an important process that progressively improves the tolerance to the harmful effects of climate change by increasing the frequencies of beneficial alleles in a population over many generations (White, Adams, and Neale 2007). Tree species have a very long reproductive cycle, which makes this inherently slow adaptation process out of step with the speed of contemporary climate change (Rehfeldt et al. 2002). Thus, migration can be a more relevant climate change mitigating mechanism because it can quickly introduce climatically preadapted genotypes or haplotypes to existing populations (Aitken and Whitlock 2013).

Tree species generally disperse seeds within a limited radius, often just a few tens of meters from the parental tree, thereby gradually increasing their spatial distribution (Burns 1990). However, data shows that forests expanded at an accelerated pace after the last glacial period, which could not have been achieved by typical seed dispersal patterns. This phenomenon, known as Reid's paradox (Reid 1899), challenges our understanding of species expansion. Rare long-distance dispersal events, potentially driven by unusual atmospheric conditions (Clark et al. 1998), may explain the rapid spread.

Pollen-mediated gene flow provides valuable insights into migration dynamics, particularly in wind-pollinated forest tree species. Long-distance pollen dispersal has been repeatedly reported, with well-documented cases of grains traveling hundreds to thousands of kilometers from their source (Campbell et al. 1999; Savolainen, Pyhäjärvi, and Knürr 2007). This emphasizes the critical role of both seed and pollen dispersal in how forest tree species cope with changing environmental conditions, including contemporary climate change. However, models indicate that most tree species' migration rates cannot keep up with the speed of climate change, with some species needing to migrate up to a hundred times faster than historical rates suggest (Sáenz-Romero et al. 2016). On top of that, long-distance dispersion's rate and direction are unpredictable (Nathan et al. 2002, 2011). Contrary to what models predict, the actual migration rates are usually slower, likely due to competition at new sites and low seed germination rates (Sittaro et al. 2017; Zhu, Woodall, and Clark 2012).

Given the limitations of natural migration, there has been a notable focus on human-aided migration, coined by a variety of terms such as assisted migration, assisted colonization (Hoegh-Guldberg et al. 2008), assisted gene flow (Aitken and Whitlock 2013), and managed relocation (Richardson et al. 2009). These conceptual frameworks have been suggested for animals (Bouma et al. 2020) as well as plants (McKone and Hernández 2021), including forest tree species (P. W. Clark et al. 2022). They all share a common goal: to relocate populations to areas with favorable projected climate conditions (Mueller and Hellmann 2008; Ste-Marie et al. 2011).

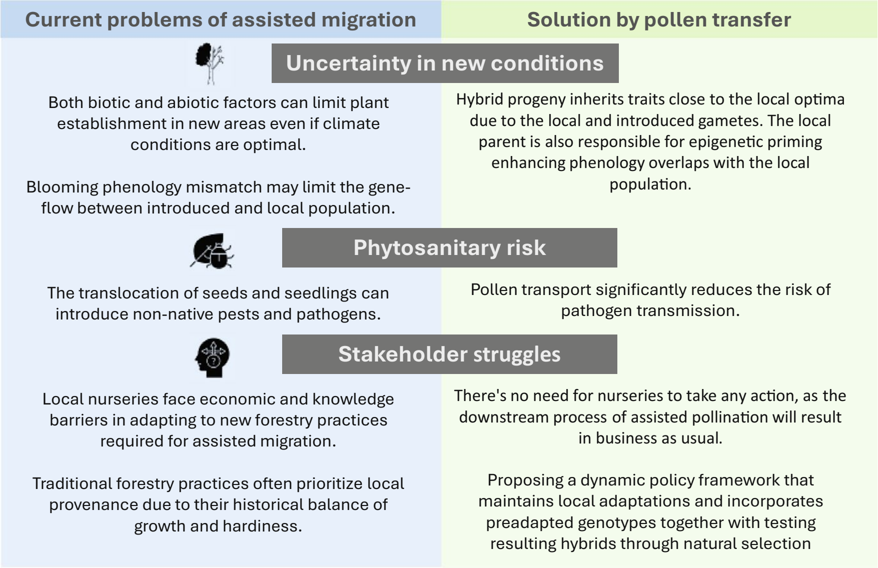
In this opinion paper, we outline several critical challenges associated with current methods of assisted migration. Importantly, we introduce a novel pollen-based approach to assisted migration, which may offer solutions to these challenges, as outlined in Figure 1. We believe that this innovative method, which could be easily integrated into established frameworks, will significantly contribute to the broader acceptance and effectiveness of assisted migration worldwide.

2 | Current State: General Challenges of Assisted Migration

Assisted migration, the deliberate relocation of tree populations, faces several key challenges (Figure 1) limiting its broader application: (1) environmental factors and current forestry practices, (2) insufficient transfer guidelines, (3) phytosanitary risks from seed and seedling translocation, (4) economic and knowledge barriers faced by local nurseries, and (5) legal obstacles in seed and plant material transport.

Plants' phenotypes evolve to cope with specific local conditions, leading to variations in traits within the same species across their distribution range. A notable meta-analysis revealed that 71% of studies across various organisms reported local adaptations, resulting in an average 45% increase in the fitness of native populations compared to non-native ones (Hereford 2009). Additionally, genomic research supports the idea that local populations are adapted to factors beyond climatic variables, namely soil and photoperiodism (Van Daele, Honnay, and De Kort 2022). Local adaptation is especially prevalent in tree species (Aitken and Bemmels 2016), where differentiated populations are referred to as provenances.

The relative differences in growth and hardiness among provenances have been extensively studied over the past centuries (Langlet 1971). These experiments have primarily aimed to identify the best seed sources for forest establishment by testing the effects of the common environment on different populations. By the late nineteenth century, it was concluded that local provenances usually offer the best balance of growth and hardiness, leading to the preference for local seed sources (Aitken and Bemmels 2016; Langlet 1971). This principle, commonly referred to as "local is best," remains widely accepted. Both traditional forestry focusing on maximizing wood production and close-to-nature practices emphasizing complex natural processes and additional forest functions (O'Hara 2016) continue to prefer the "local is best" principle.



	Current problems of assisted migration	Solution by pollen transfer
Uncertainty in new conditions	Both biotic and abiotic factors can limit plant establishment in new areas even if climate conditions are optimal. Blooming phenology mismatch may limit the gene-flow between introduced and local population.	Hybrid progeny inherits traits close to the local optima due to the local and introduced gametes. The local parent is also responsible for epigenetic priming enhancing phenology overlaps with the local population.
Phytosanitary risk	The translocation of seeds and seedlings can introduce non-native pests and pathogens.	Pollen transport significantly reduces the risk of pathogen transmission.
Stakeholder struggles	Local nurseries face economic and knowledge barriers in adapting to new forestry practices required for assisted migration. Traditional forestry practices often prioritize local provenance due to their historical balance of growth and hardiness.	There's no need for nurseries to take any action, as the downstream process of assisted pollination will result in business as usual. Proposing a dynamic policy framework that maintains local adaptations and incorporates preadapted genotypes together with testing resulting hybrids through natural selection

FIGURE 1 | Assisted migration faces numerous challenges, including the unpredictability of local environmental conditions due to climate change, phytosanitary risks associated with the transfer of seeds and live plants, and difficulties faced by stakeholders. Many of these issues can be addressed through a pollen-based approach to assisted migration.

In contrast, earlier recommendations for assisted migration often focused exclusively on climate variables, such as mean annual temperature, while overlooking crucial non-climatic factors like phenological cues and soil properties. These non-climatic factors are highly location-specific and play a vital role in the local adaptation of populations. By ignoring them, one risks overestimating the adaptive potential of assisted migration (Xu et al. 2024; Xu and Prescott 2024). For example, even under optimal climatic conditions, edaphic variables such as soil nutrients, water availability, interactions with soil organisms, and seed predation can significantly limit plant establishment in new areas (Benning and Moeller 2021; Brown and Vellend 2014; Ni and Vellend 2024). Phenological cues are equally important to the success of assisted migration, especially when relocating tree populations over long distances. Many species rely on site-specific day length, rather than temperature, to regulate phenological events (Basler and Körner 2012; Laube et al. 2014; Way and Montgomery 2015). Consequently, translocating these species to areas with different day lengths can cause mismatches in the timing of phenological events, leading to reduced growth and increased vulnerability to spring and autumn frosts (Montwé et al. 2018; Silvestro et al. 2019). This reduces the distances over which populations can be relocated, making it more challenging to align assisted migration efforts with the pace of climate change (Cooper et al. 2019; Stinziano and Way 2014).

However, recent advancements in the collection and availability of high-quality, large-scale landscape data (Dauphin et al. 2023) are addressing these limitations by incorporating a broader range of environmental variables into assisted migration frameworks (Feng et al. 2020). This holistic approach not only aligns with traditional forestry practices that emphasize local adaptation but also offers a more robust basis for assisted migration. Continued research in this field is essential to develop robust recommendations that account for both climatic and non-climatic variables, thereby reducing the risk of maladaptation and promoting population fitness in new environments.

Another significant risk of assisted migration is the potential introduction of non-native pests and pathogens. This risk increases with the growing volume of international trade in plants, including trees (Eschen, Roques, and Santini 2015; Liebhold et al. 2012). As a result, only a small fraction of imported plants undergo inspection (Brasier 2008). Furthermore, the effectiveness of these inspections is limited because infested plants may not show symptoms upon arrival, making it difficult to ensure complete phytosanitary safety through traditional methods (Jung et al. 2016; Liebhold et al. 2012). Phytosanitary risks are not confined to living plants alone. Recent studies suggest that seeds also pose a significant phytosanitary risk, despite previously being considered relatively safe for international transfer. This risk is particularly pronounced in Europe, where regulations for preventing the introduction of seed-borne pathogens are less stringent compared to other regions (Franić et al. 2019; Vettraino, Potting, and Raposo 2018).

Forest nurseries are crucial for forest regeneration, requiring increased seedling production and diversity to address contemporary climate change challenges in forestry. A North American study (P. W. Clark et al. 2023) highlights the need for more ecological diversity in nurseries, as the focus on commercially valuable species often limits conservation and climate adaptation efforts. While there are business opportunities to produce seedlings adapted to future climatic conditions, including those phenotypes resistant to climate extremes and new pests, this bears additional costs, logistical complexities, and financial risks. Nurseries often prioritize uniformity in seed lot germination and growth for easier cultivation and more effective production (Ivetić et al. 2016), which often contrasts with the desired level of genetic diversity.

These challenges, especially when sourcing seeds from distant locations, have hampered investments, particularly in regions where the number of nurseries has declined in recent decades in Europe and North America. Moreover, small nurseries fear competition from larger foreign entities threatening their profitability in an open-market scenario. Nursery managers across Central Europe have also expressed concerns about the impacts of climate change on their operations. Perceptions vary by country, with Austria and Germany expecting higher demand for non-native species, while Poland and Hungary anticipate a need for more resilient local varieties (Hazarika et al. 2021).

Finally, implementing assisted migration requires considering various legal regulations, including the "Nagoya Protocol" (Secretariat of the Convention on Biological Diversity 2011). It may constrain assisted migration in countries that have adopted this international agreement with stringency. Nevertheless, assisted migration is predominantly hindered by laws on a national and regional level, restricting seed usage to specific "seed zones" or "provenance regions", thereby favoring locally adapted populations (Konnert et al. 2015). Thus, a dynamic policy framework adapting to diverse climate change scenarios is essential for ensuring long-term forest health and resilience.

3 | Assisted Gene Flow: Implications of Inter-Provenance Hybridization

Assisted migration methodologies can be categorized into two general approaches: migration outside the species' geographic range and migration within it. It is anticipated that assisted migration of tree species will predominantly occur within the species' geographic range (Sáenz-Romero et al. 2021). This approach poses less ecological risk as it avoids relocating trees to unfamiliar environments where unforeseen interactions could occur (Aitken and Whitlock 2013). Additionally, it is generally more accepted by the public compared to the alternative (Findlater et al. 2020).

Within-range assisted migration has been proposed by Aitken and Whitlock (2013) and Kelly and Phillips (2016). These studies suggest leveraging existing genetic differences among tree populations of a given species by transferring seeds or seedlings to introduce preadapted genotypes and increase adaptive genetic variation of endangered populations, through "assisted gene flow." However, as these authors caution, this strategy carries the risk of unintended interspecific hybridization, particularly with closely related species, leading to genetic incompatibilities (Critchfield 1967). Furthermore, the effectiveness of genetic infusion of preadapted genotypes can be limited by potential mismatches in flowering phenology and will only manifest once the introduced seedlings reach reproductive age.

The timing of flowering events in plants is generally highly variable (Shelton et al. 2024; Weis 2015). While this variability is more pronounced in herbaceous species, it is also observed in tree species, albeit to a lesser extent (Horbach, Rauschkolb, and Römermann 2023). This variation is a result of adaptation to local conditions, which can occur in a relatively few generations. Differences in flowering phenology may result in flowering asynchrony both within and among populations. This asynchrony potentially increases the current variation in the reproductive success of forest tree species, thus affecting genetic diversity. Flowering phenology asynchrony tends to increase with geographic distance, possibly resulting in phenological isolation of populations. As a result, migrants rarely mate with members of the resident population, promoting assortative mating patterns, with a higher rate of mating occurring between migrants and between residents (Wadgymar and Weis 2017). Even when mating between migrants and residents is successful, cones or fruits may not be produced by late-flowering individuals (Wadgymar, Cumming, and Weis 2015). This leads to a reduced rate of hybridization that becomes even more apparent in the second generation of hybrids (F_2) (Wadgymar and Weis 2017).

Apart from flowering asynchrony, assisted gene flow may lead to emergent short-term genetic effects resulting from the hybridization of genetically divergent populations, which might hinder achieving the desired adaptation. These effects can include potential positive impacts such as heterosis in the first generation of hybrids or negative consequences like outbreeding depression and hybrid decay in subsequent generations.

Heterosis, also frequently called hybrid vigor, is the beneficial effect that occurs when a hybrid surpasses the quality of both parents (Shull 1914). This phenomenon was already recognized by Charles Darwin (1876) and is traditionally exploited in agriculture to enhance the yield of inbred crop lines and improve resistance to diseases (e.g., Hei, Hussein, and Laing 2016). The degree of heterosis generally rises with increasing genetic distance up to a certain point, after which it declines (e.g., Moll et al. 1965; Würschum et al. 2023). Heterosis is also apparent in inter-species crosses and is utilized in forestry species, such as in the larch genus, with European larch (*Larix decidua* Mill.) and Japanese larch (*Larix kaempferi* (Lamb.) Carr.). First-generation (F_1) larch hybrid (*Larix* × *eurolepis* Henry) has shown significant genetic response in growth rate, wood quality, and seed yield (Marchal et al. 2017). Thus, they pose overall better performance compared to the parent species and also compared to the second-generation hybrids (F_2). Similar results have been found in poplar (Zanewich, Pearce, and Rood 2018), eucalyptus (Madhibha et al. 2013), silver fir (Stejskal, Horák, and Typta 2016), and pines (Dungey 2001).

There are two prevalent hypotheses that explain the basis of heterosis. The first is the dominance hypothesis, which suggests that in hybrids, harmful recessive alleles are hidden by beneficial alleles from either parent (Bruce 1910; Davenport 1908; Jones 1917). The second is the overdominance hypothesis, which proposes that heterozygosity itself can result in hybrids being more vigorous than either parent (East 1908; Shull 1908). Those approaches were further expanded by the epistatic theory of heterosis, involving interactions among genes (Powers 1944). However, the exact genetic and molecular basis behind heterosis is still not fully understood (Birchler et al. 2010; Yu et al. 2021).

The question arises whether heterosis occurs only in isolated groups, such as between inbred lines and within inter-specific hybrids, or also across populations connected by gene flow, similarly to forest trees. Simulations of these scenarios suggest that heterosis can indeed occur in such cases (Whitlock et al. 2000). Moreover, various forest tree species have been tested for potential heterosis effects in their provenance hybrids (Liesebach, Liepe, and Bäucker 2021). Harfouche and Kremer (2000), Harfouche et al. (2000) reported an 8.4% increase in growth due to heterosis in maritime pine (*Pinus pinaster* Aiton) provenance hybrids. Additionally, Doerksen, Bousquet, and Beaulieu (2014) revealed a heterosis effect in inter-provenance crosses of white spruce (*Picea glauca* (Moench) Voss), with approximately 6% greater height growth at age 15 compared to intra-provenance progenies. In contrast, Eriksson and Ilstedt (1986) observed heterosis in Norway spruce (*Picea abies* (L.) H. Karst) provenance hybrids at only one of three test sites, while Kaya and Lindgren (1992) found no evidence of heterosis. Similarly, Levkoev et al. (2017) did not observe an increase in growth and wood density in hybrids compared to the local population. Although heterosis was observed in several intra-specific scenarios, its impact does not seem to be as pronounced as in the inter-species hybrids of forest trees.

Conversely, outbreeding depression occurs in hybrids of distant populations when local adaptive traits average out, resulting in lower fitness in later generations compared to the parental lineage. Although common in plants (Liesebach, Liepe, and Bäucker 2021), it is rare in forest trees, with Sakhalin fir (*Abies sachalinensis* F. Schmidt) being a single case study (Goto et al. 2011). Outbreeding depression typically appears from the second generation onwards, as hybrid vigor masks these effects in the first generation. From the F_2 generation, recombination disrupts epistatic interactions between coadapted genes (Whitlock et al. 2013). However, these interactions are expected to be restored over several generations, and the fitness of later generations can surpass that of the parental generation as climatically preadapted alleles will become apparent (Aitken and Whitlock 2013; Grummer et al. 2022).

Understanding the genetic architecture of adaptive traits is crucial for evaluating the benefits and risks of assisted gene flow such as the aforementioned heterosis and outbreeding depression. This involves examining the number, position, and effect sizes of individual genes. Genome-wide association studies provide detailed molecular-level insights into gene-trait associations. While detecting gene effects is relatively efficient in inbred lines, it becomes significantly more complex in outbred populations (Lynch and Walsh 1998). Outbred forest tree species present unique difficulties due to their large genomes and growth in highly heterogeneous environments.

Empirical evidence from tree species indicates that adaptive traits, such as resistance to drought, frost damage, and pathogens, often exhibit polygenic or complex architectures (De La Torre et al. 2019, 2021; Depardieu et al. 2021; Milesi et al. 2019; Riehl et al. 2023; Singh et al. 2024). These architectures may consist of a few genes with relatively large effects but are largely controlled by many genes with smaller effects. This predominantly polygenic inheritance of quantitative traits in forest trees is further supported by traditional genetic variance decomposition, based on controlled crosses and progeny trial evaluations (White, Adams, and Neale 2007).

4 | Pollen-Based Assisted Migration as an Innovative Approach

We propose a comprehensive strategy framed around intentional pollen transfer from suitable sources (typically referred to as a population of migrants) to reduce the risk of maladaptation in adverse climates while preserving the integrity of locally adapted populations. This strategy involves collecting pollen from a source seed orchard and transferring it to a target (typically referred to as a resident population) seed orchard for intraspecific hybridization (Figure 2), thereby introducing haplotypes suited for anticipated future climate conditions.

A key advantage of this method is that it capitalizes on existing forestry infrastructure, specifically, seed orchards, which already play a critical role in global forestry for large-scale seed production (White, Adams, and Neale 2007). In Europe specifically, the establishment of seed orchards for seed mass production began in the 1950s (see Faulkner (1975), for early review) and has continued to grow, with the current number exceeding 1500 seed orchards of 40 forest tree species (EU Forest Reproductive Material Information System, https://ec.europa.eu/forematis). Traditionally, seed orchards have been closely linked to tree improvement programs, serving as the primary source for producing bulk seed for afforestation and reforestation efforts. Many seed orchards are also established for tree species of lower economic but significant ecological importance (e.g., So, Theilade, and Dell 2010). Globally, seed orchard networks extend beyond Europe to North America (Li, McKeand, and Weir 1999; Miller and DeBell 2013; Reid 2008), South America (Jayawickrama and Balocchi 1993; Rockwood, Huber, and White 2001), Africa (Gapare 2000; Missanjo, Kamanga-Thole, and Manda 2013; Swain, Verryn, and Laing 2013), Asia (Batkhuu et al. 2010; Chaix et al. 2011; Leksono, Kurinobu, and Ide 2008; Moriguchi et al. 2005; Na et al. 2015; Nicodemus et al. 2009; Shi et al. 2016), Australia (Burczyk et al. 2002; Johnson, Robinson, and O'Hara 1992; Wu et al. 2007), and New Zealand (Burdon, Carson, and Shelbourne 2008; Dickson, Sweet, and Mitchell 2000; Turner 1997).

Collecting pollen in the source orchard is feasible because the trees in orchards are pruned to facilitate seed harvest and control pollination. When choosing a deployment strategy, several suitable source seed orchards can be identified to obtain the desired pollen mixture. Thus, the pollen mixture could be adjusted frequently based on previous experience and the progression of climate change.

Since open pollination (natural random mating) occurs in seed orchards, implementing supplemental mass pollination (SMP) or controlled mass pollination (CMP) in the target orchard is straightforward. SMP or CMP involves disseminating the collected pollen during the peak receptivity of female strobili (Funda and el-Kassaby 2012), promoting gametic exchange between migrant and resident population genotypes. Additionally, SMP or CMP could be combined with the method of delayed blooming, which adjusts flowering times to promote synchronization. This reduces pollen contamination from inferior genotypes in non-selected populations near the seed orchard (Korecký and El-Kassaby 2016; Song et al. 2018) and increases the annual seed set (Pearse et al. 2015), resulting in higher seed orchard production.

In the proposed strategy, seeds produced in the target seed orchard will be sown in local nurseries (Figure 2), allowing progenies to undergo their entire embryogenesis and early growth under local conditions. This contrasts with traditional transfer

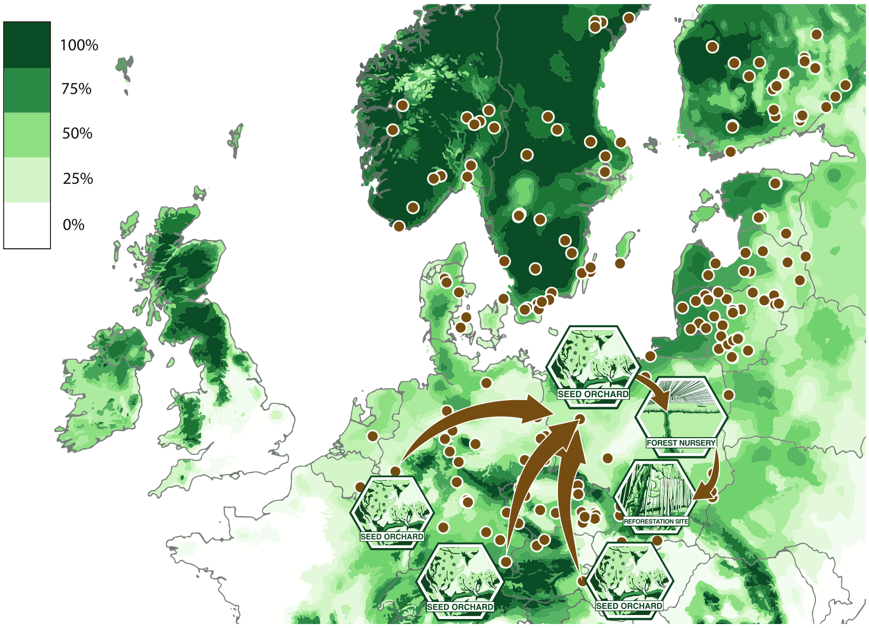


FIGURE 2 | The map is derived from the species distribution model developed by Chakraborty et al. (2021). The green gradient represents the probability of Norway spruce distribution in Europe within the 2041–2060 time range under intermediate climate scenario RCP 4.5. Brown dots show the locations of individual seed orchards across Europe based on the European Union's FOREMATIS database and the internal Norwegian database of seed orchards. The flowchart represents the transfer of desired haplotypes from source to target seed orchards through pollen and subsequent seedling production utilized in target reforestation sites. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

methods where seeds or mature plants carry their original epigenetic profiles when moved to new locations.

Epigenetics, transgenerational changes that modulate phenotype without altering the genetic composition, is increasingly recognized as an important factor in shaping adaptive traits in plant breeding and ecosystem conservation (Bräutigam et al. 2013). Although the effects of epigenetics on tree species remain understudied, its significant role has been suggested in both Norway spruce (Johnsen et al. 2005, 2009) and Scots pine (Bose et al. 2020). Our method may present a significant advantage, as local conditions can modulate gene expression through various epigenetic mechanisms (Franks and Hoffmann 2012), thus enhancing the adaptive potential of these tree species in their native environments and reducing the risk of transferring potentially harmful epigenetic settings.

The pollen-based approach facilitates the production of hybrid offspring with flowering periods that average the flowering times of their parents. Empirical evidence supports this pattern, particularly in fruit trees like apples (Urrestarazu et al. 2017) and Prunus species, such as sweet cherries and almonds (Branchereau et al. 2022, 2023; Castède et al. 2014; Dirlewanger et al. 2012; Sánchez-Pérez et al. 2014). Similar trends have also been observed in outcrossing plants like maize (Buckler et al. 2009). These studies reveal that flowering periods are highly heritable and governed by complex genetic architecture. Moreover, Urrestarazu et al. (2017) highlight that the genes controlling flowering phenology predominantly exhibit additive effects.

The flowering time of hybrids that more closely align with the resident population will gradually increase the proportion of backcrosses and later-generation hybrids within the population. This, in turn, will boost the frequencies of pre-adapted alleles in subsequent generations. This process can be particularly advantageous for enhancing adaptive genetic diversity, as it establishes a solid foundation for natural selection by favoring the best-adapted individuals among a broad range of genotypes, especially under the competitive pressures of a changing climate. To achieve this objective, we recommend supplemental planting of orchard-derived hybrid seedlings in a grid or group planting (Saha et al. 2012) among the naturally grown seedlings in situ.

This approach aligns with close-to-nature forestry principles, where forest stands are primarily restocked by trees growing from seeds that fall and germinate on-site, maximizing the natural processes within the stand (O'Hara 2016). However, in cases where significant heterosis is present, hybrids can surpass all local individuals in fitness, reducing the proportion of naturally regenerated individuals in favor of F_1 hybrids. This poses a risk, as the initial heterosis diminishes in the F_2 generation, leading to a significant decline in overall fitness and resulting in detrimental effects on the stand (Kaya and Lindgren 1992). In such scenarios, a more effective strategy might be to fully utilize the benefits of heterosis in F_1 hybrids by establishing pure hybrid stands and regenerating them through clear cuts. The establishment of pure hybrid stands can lead to increased biomass production and overall forest productivity due to the superior growth characteristics and enhanced resistance to environmental stresses of F_1 hybrids. This method ensures that the hybrids' genetic advantages are fully exploited during their peak growth periods, maximizing yield and economic return. Additionally, this strategy still facilitates the introgression of climatically pre-adapted alleles, as their pollen contribution to the neighboring stands would promote backcrossing, gradually introducing pre-adapted alleles and thereby maintaining the overall fitness. Since this process is more gradual, it helps to mitigate the negative effects of hybrid decay in F_2.

The pollen-based method can also facilitate the adaptation of exotic species. Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco), native to the Pacific Northwest of North America, is a prime example of an introduced species in Europe. Breeding programs for Douglas fir are already established in several European countries, with seed orchards located in Austria, France, Germany, and other regions. In some countries, such as the Czech Republic and Slovenia, these programs are just being established. Another example of a successful introduction is a Turkish fir (*Abies bornmülleriana* Mattf.) and Nordmann fir (*Abies nordmanniana* (Steven) Spach), with seed orchards in Denmark (Nielsen, Xu, and Hansen 2020; Xu, Nielsen, and Hansen 2018).

These exotic species typically underwent intense selection for both adaptation and productivity traits. While the genetic diversity of mature stands after introduction seems to be comparable with the native populations, it can be reduced due to population bottlenecks caused by the variation in reproductive success, which is a specific problem in exotic species as their populations in non-native environments are typically fragmented (Neophytou, van Loo, and Hasenauer 2020). The pollen-based strategy enhances local populations by increasing genetic diversity and introducing climate-adaptive alleles from suitable regions within the native range.

Beyond the aforementioned benefits for native and exotic species, the pollen-based assisted migration strategy offers solutions to remaining challenges, including phytosanitary risks, economic obstacles, and legislative constraints. Managing phytosanitary risks becomes simpler as pollen is typically unsusceptible to pathogens and is expected to be germinated on site. The approach is economically feasible as seed orchard managers could handle a local pollen collection and storage framework. Nevertheless, some investment in pollen storage may be necessary. As both seed and seedlings are locally sourced, forest nurseries can continue business operations without disruption. Considering these advantages, we anticipate a wider acceptance of the pollen-based assisted migration, leading to legislative adaptations enabling pollen transport.

5 | Simulation Insights Into Genetics of an Adaptation Through Pollen-Based Assisted Migration

From a genetic perspective, the effectiveness of the proposed pollen-based assisted migration depends on several factors. These include the degree of population divergence, as reflected by differences in genetic structure (allelic and genotypic frequencies) and fitness distribution between the source and target populations under current environmental conditions; the extent of gametic phase disequilibrium; the genetic architecture of fitness traits (including the number of loci contributing to trait variance and their respective additive, dominance, and epistatic effects); biological mechanisms of heterosis and outbreeding depression; narrow-sense heritability; and the intensity of pollen migration from the source orchard to the target orchard.

To examine the genetic implications of pollen-based assisted migration, we utilized a computer simulation model presented in Supplement S1, which includes parametrization and computer code. A schematic overview of the simulation scenarios is provided in Figure 3. Comparative results for pollen-based assisted migration, conventional assisted migration, and a reference scenario relying solely on local populations are shown in Figure 4. The model incorporates a mixed genetic architecture, with 30% of the genetic variance attributed to 10 quantitative trait loci (QTLs), while the remaining genetic variance is polygenic. Narrow-sense heritability was set at 0.2, reflecting a significant environmental component in adaptive traits. The model is specifically designed to simulate diploid populations and, in its current implementation, does not support the evaluation of interspecific hybridization.

We first evaluated a single reproductive outcome in the target seed orchard subjected to pollen-assisted migration, with fitness assessed in the offspring population (forest stands originating from the orchard). Our model revealed significant initial heterosis, resulting in a mean fitness that exceeded the average of parental populations, and even surpassed the mean fitness of conventional assisted migration (generation 1 in Figure 4). However, we should note that the initial population divergence (difference between the allelic frequency of the two founder populations) was assumed to be very large which promoted the initial heterosis and outbreeding depression. Typically, differences between allelic frequencies would be lower, thus the mean fitness would more closely resemble the average of parental populations in the same figure. However, the real adaptive response of the pollen-based assisted migration might be underestimated in our simulations given additional components, such as retaining the local adaptation when using the seed orchard in the target location and additional beneficial factors that were discussed in Section 4.

The dynamic nature of climate change necessitates frequent recalibration of assisted migration models and optimization of pollen mixtures. This also highlights the importance of periodical updates of the genetic composition of seed orchards in both source and target populations adopting a dynamic system that leverages both local (e.g., Lstibůrek, García-Gil, and Steffenrem 2023) and distant adaptation, ensuring proper synchronization with practical forest management as discussed in the previous chapter.

In line with these options, Figure 4 also illustrates the potential for maintaining forest plantations established in generation 1 and allowing natural regeneration in subsequent generations. In generation 2, the model predicts an initial outbreeding depression from reduced initial heterosis and unfavorable epistatic effects. In subsequent generations, however, outbreeding depression is purged and the higher overall genetic diversity in the population leads to higher subsequent adaptive response, eventually resulting in mean fitness comparable to that of conventional assisted migration (assuming the population remains in situ and continues to reproduce locally).

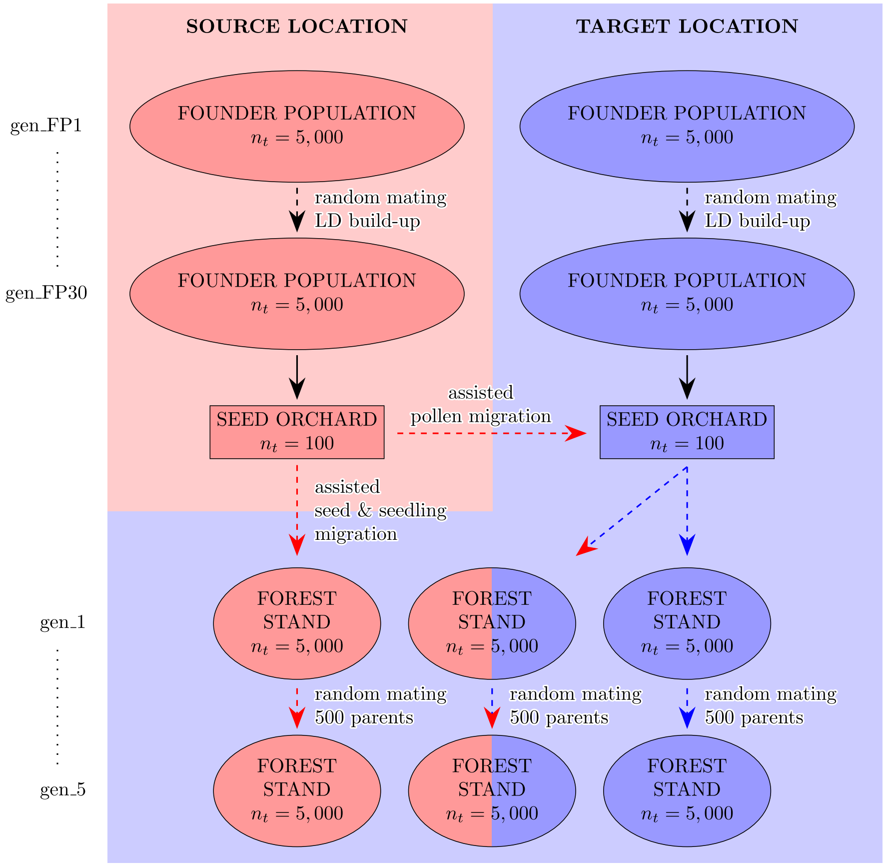


FIGURE 3 | Schematic representation of the computer simulation process. The simulation begins with the creation of two founder populations, distinguished by allelic frequencies: One in the source location (light red background) and the other in the target location (light blue background). Thirty generations of random mating with a constant population size of 5000 individuals facilitated the build up of linkage disequilibrium (LD). The source founder population was modeled with a higher mean fitness compared to the target population, indicating adaptive superiority when introduced to the target environmental conditions. Subsequently, a seed orchard containing 100 individuals was established in each location, derived from their respective founder populations. Assisted migration was then simulated, wherein random mating occurred in the source seed orchard, and a forest stand of 5000 trees was established in the target location (generation 1). From this stand, 500 trees with superior phenotypes (top fitness) were selected and subsequently randomly mated to generate 5000 offspring. Further generations of natural regeneration (2–5) maintained a population size of 5000 individuals through successive cycles of natural selection. This process is represented by the leftmost forest stands in the target location (darker red ellipses). Alternatively, an additional forest stand was established via assisted pollen migration. In this scenario, male haplotypes from the source seed orchard were combined with female haplotypes from the target seed orchard. The resulting forest stand underwent similar mating and natural selection processes up to generation 5, depicted by the middle forest stands in the target location (darker red/blue split-color ellipses to signify mixed haplotypes). For reference, a control scenario without assisted migration was simulated, where random mating occurred within the target seed orchard. This scenario is represented by the rightmost forest stands in the target location (darker blue ellipses).

While we aimed to align simulation parameters with empirical evidence, caution is warranted in generalizing our findings across species. We propose systematic computer modelling research to explore complex dynamics of the proposed system. Fine-tuning simulation parameters for specific species is necessary to evaluate feasibility and account for additional consideration, including benefits of pollen-based assisted migration discussed in our manuscript but not incorporated into the current simulation.

6 | Regional Perspective: Adapting Pollen-Based Assisted Migration in Northern and Central Europe

The Scandinavian region has a long history of successfully introducing and transferring seed sources of Norway spruce and Scots pine (*Pinus sylvestris* L.) (Myking et al. 2016). Consequently, both selectively bred populations and commercially produced seed lots contain a significant proportion of non-local genotypes transferred from various regions within and between Northern European countries and beyond. Given this established practice, current official transfer guidelines are based on past provenance testing and practical regeneration experience, often tolerating substantial transfers from local origin.

New transfer effect models have been developed for both species to predict performance in future climates and facilitate assisted migration (Berlin et al. 2016; Liziniewicz et al. 2023). These models utilize tree phenotype data from all Scandinavian countries to provide uniform deployment recommendations across the region and to develop joint decision support tools. Implementing such a framework requires addressing national transfer rules, legal barriers, and differences in seed orchard definitions.

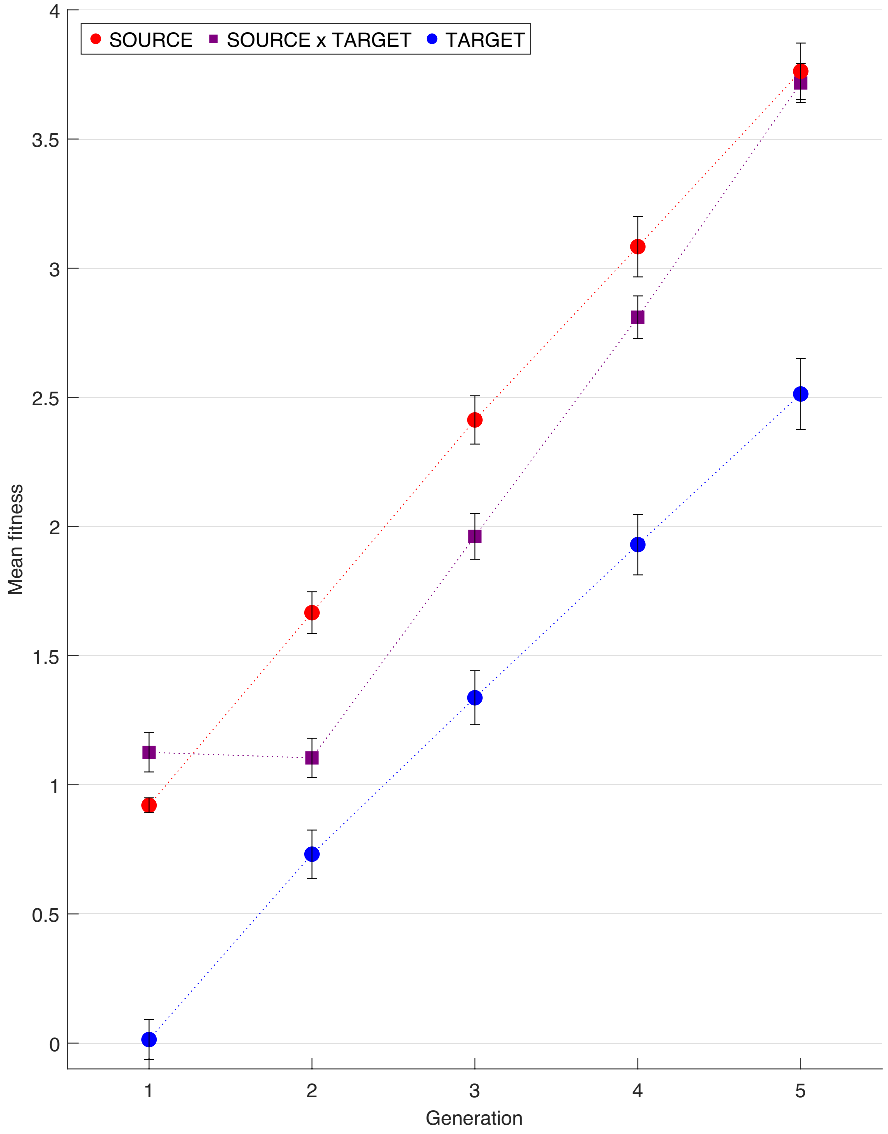


FIGURE 4 | Predicted mean fitness values in the target location based on computer simulation. The three scenarios include: (1) seedling-based assisted migration (red circles), where seedlings derived from the source seed orchard are planted in the target location; (2) pollen-based assisted migration (violet squares), where pollen is transferred from the source orchard to the target orchard, and the resulting offspring are planted in the target location; and (3) local offspring (blue circles), where offspring derived from the orchard in the target location are planted in the same area. Generation 1 represents forest stands established using seeds collected from the target seed orchard for each respective scenario. Generations 2–5 represent hypothesized forest stands resulting from natural mating among the top 500 individuals in each stand.

For Scots pine, common deployment recommendations have been successfully developed and officially approved in Sweden and Finland (Berlin et al. 2019). Additionally, a joint Swedish-Finnish decision support tool called "Plantval" (Skogforsk 2024) aids in selecting optimal seed sources. The tool considers the origin of both the seed orchard parents and the pollen, which is assumed to come from the orchard itself or surrounding populations (e.g., Heuchel et al. 2022). Introducing external pollen with known origin and genetic gain through a pollen-based approach can easily be integrated into the tool, directly influencing the model's predictions and deployment recommendations.

In the Nordic region, seed orchards have undergone genetic thinning and selective harvesting to enhance adaptive properties, increase tolerance to pests/diseases (e.g., Scots pine blister rust and root rot), and boost genetic gain. However, these methods are limited to existing orchard genotypes. A pollen-based approach would enable a rapid and substantial improvement in one or more desired traits, particularly if those traits are not achievable with the current genetic variation within the orchard.

In contrast to Northern Europe, Central Europe encompasses a broader range of ecoregions and forest types, from xerophytic mixed oak forests to subalpine mountain forests, providing habitat for a diverse array of woody plant species. Forest genetic resource management in Central European countries has traditionally focused on selecting and transferring genetic material with superior growth characteristics, as well as the conservation of major and rare tree species. Notably, conifers such as European Larch and Norway spruce have been historically transferred over larger distances, often outside their native range

(Jansen, Konrad, and Geburek 2017; Jansen and Geburek 2016). However, rare and scattered tree species were often neglected in historical forest management practices, potentially impacting their genetic variation (Hemery et al. 2010; Lefèvre 2004).

Genetic studies on many Central European species have revealed that populations south of the Alps, in refugial areas, exhibit the highest genetic differentiation, while populations north of the Alps display the highest genetic diversity, likely due to the admixture of lineages during recolonization (Petit et al. 2003). Awareness of genetic resources, particularly for scattered tree species, increased towards the end of the 20th century, leading to the establishment of several national gene conservation programs (Müller 1997; Tabel 1997) and the EUFORGEN Network for scattered broadleaves. Additionally, the EC directive for forest reproductive material (1999/105/EC) was enacted, regulating the management of 47 tree species across Europe. These efforts have resulted in the establishment of numerous seed orchards for gene conservation.

Given anticipated shifts in tree species composition due to climate change, there is an increasing need to diversify tree species mixtures and incorporate drought-tolerant species from continental or Mediterranean climates. Central Europe has over a century of experience in assisted migration. One example could be a successful transfer of exceptional “Slavonian oaks”, valued for their high genetic quality and adaptability, from the Save and Drava river plains in Southeastern Europe to Northwestern Germany (Gailing et al. 2012). Similarly, “Calabrian” silver firs from South Italy have been successfully used for reforestation in Denmark (Larsen 1981). Extensive provenance experiments for various tree species were conducted in Europe during the 20th century, and recent comprehensive analyses of these experiments have led to transnational transfer guidelines (Chakraborty et al. 2024). Central European countries can leverage their existing network of 717 seed orchards (encompassing 23 native species and hybrids) to implement pollen-based assisted migration. These orchards are expected to serve as both pollen sources and recipients across a wide range of climatic conditions.

7 | Conclusions

We propose a pollen-based assisted migration strategy as an effective and scalable solution for adapting forests to climate change. Through reasoned examples, we discuss the potential benefits and practicalities of implementing this approach in Scandinavia and Central Europe and its compatibility with broader EU frameworks. We strongly advocate for its consideration in future international projects and operational forestry. A dynamic policy framework adaptable to diverse climate scenarios is essential to fully capitalize on this innovative strategy. Such a framework could serve as a catalyst for revising current EU regulations, thereby enabling more agile and effective forest adaptation strategies, crucial for long-term societal resilience against climate change. Since pollen-based assisted migration relies methodically on seed orchards, we advocate for conventional assisted migration in species and regions where seed orchards are unavailable.

Author Contributions

David Chludil: conceptualization, data curation, investigation, visualization, writing – original draft. **Jaroslav Čepl:** formal analysis, software, visualization, writing – review and editing. **Arne Steffenrem:** investigation, resources, writing – review and editing. **Jan Stejskal:** data curation, writing – review and editing. **Christi Sagariya:** data curation, formal analysis, software. **Torsten Pook:** formal analysis, resources, software. **Silvio Schueler:** writing – review and editing. **Jiří Korecký:** writing – review and editing. **Curt Almqvist:** writing – review and editing. **Debojyoti Chakraborty:** writing – review and editing. **Mats Berlin:** writing – review and editing. **Milan Lstibůrek:** conceptualization, formal analysis, investigation, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.28033913. Due to privacy concerns, the locations of the Norwegian seed orchards are not publicly available, but can be obtained by contacting Dr. Arne Steffenrem at arne.steffenrem@nibio.no. The species distribution model can be accessed from Zenodo at http://doi.org/10.5281/zenodo.3686918.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.