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Towards resilient forest establishment in Europe: functional traits, genetic diversity and multifunctional design

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Abstract
Forest restoration and afforestation across Europe are accelerating, yet the decision-making processes governing forest establishment remain unevenly examined, especially from a biodiversity perspective. Considering this and the global environmental changes of climate shifts, land-use transitions, and biological invasions, the present review provides guidance for planning and establishment of multifunctional forests that enhance biodiversity outcomes without compromising long-term forest productivity or resilience. Aiming to assist both practitioners and researchers, we have particularly focused on tree species selection, plant production and management of forest reproductive material, and on-field establishment practices. Literature revision and expert observations indicate that tree species selection must integrate functional traits, provenance performance, and ecological impact assessments alongside species distribution models, since climatic suitability alone does not predict performance under future conditions. Genetic diversity remains severely underutilized in operational forestry but can be advanced through assisted migration, provenance mixing, and traceable seed sources as practices that need to be better supported and monitored. Concurrently, the plant production chain contains multiple points where genetic diversity is eroded, along with advancement opportunities explored through pan-European projects focusing on diversity standards, regional seed-exchange networks, and low-cost molecular monitoring. On-field, the choice between direct seeding and planting needs to link better genetic diversity targets and site conditions rather than biased preference. And finally, urban forests, increasingly recognized as components of the restoration continuum, require context-specific species selection and a transition from isolated specimen planting to more complex and inclusive design (similar to stand level in natural forests) to deliver meaningful biodiversity and multifunctionality outcomes.

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Introduction

Biodiversity plays a key role in enhancing ecosystem resilience, ensuring the continued provision of ecosystem services, and providing the basis for harmonious coexistence between nature and society (O'Connor et al. 2020). Since 1992, this interconnectedness has been recognized in the Convention on Biological Diversity (CBD), which emphasizes the importance of conserving biological diversity, the sustainable use of its components, and the equitable sharing of benefits arising from genetic resources. In pursuit of the ambitious biodiversity recovery plan outlined with the Kunming-Montreal Global Biodiversity Framework, the Biodiversity Strategy for 2030, and the Green Deal, the European Union (EU) has experienced both notable successes and persistent shortcomings regarding biodiversity conservation efforts (Hermoso et al. 2022; Kangas and Ollikainen 2025). The unfolding of the twenty-first century has especially underlined the challenges with biodiversity conservation. At the core is the increased pressure on natural resources to meet the vital needs of the growing society (Chebby et al. 2023), the supply–demand mismatch of ecosystem services (Van Winckel et al. 2026), land-use changes due to land abandonment (Mantero et al. 2020), the impact of invasive alien plant species (Ceriani et al. 2023, 2024), climate change and natural disturbances, and the uncertain results from assisted migration. The outcome is reflected mainly in biodiversity decline and habitat fragmentation, both in natural and urban areas. Certain events have further highlighted additional specific challenges regarding biodiversity conservation. For instance, the reduced human pressure during the COVID-19 pandemic contributed to short-term benefits for forest biodiversity and associated ecosystems (Lawler et al. 2021). Concurrently, financial support for conservation was reduced, along with research capacity, on-field conservation and restoration activities, and progress on policy agendas (Corlett et al. 2020; Bates et al. 2020; Sandbrook et al. 2022). Another relevant example is the long-lasting and unpredictable impact of armed conflicts on biodiversity, which often extends beyond areas directly affected by military operations (Strange et al. 2022), including critical habitats and biodiversity hotspots (Hanson et al. 2009). Moreover, the deteriorating geopolitical situation has shifted budget priorities in European countries toward security spending at the expense of biodiversity conservation. In this context, sustainable transition, including biodiversity conservation activities, is inevitably shaped by broader economic trends and pressures (Bartkowski et al. 2015; Antonarakis et al. 2022). Therefore, forestry, as both a nature-dependent and an economy-linked sector, offers opportunities to explore and support alternative biodiversity conservation approaches. However, intensive forestry practices have shown limited capacity to sustain ecosystem resilience and multifunctionality (Pohjanmies et al. 2021). Thus, the global economic and ecological challenges are pushing the forestry sector towards sustainability through innovation (Pätäri et al. 2016; Weiss et al. 2021). Indeed, the New EU Forest Strategy for 2030 promotes multifunctional forestry through the implementation of closer-to-nature forest management (European Commission 2021; European Commission, Directorate General for Environment. 2023).

The complexity of managing forest ecosystems for multifunctionality highlights numerous knowledge gaps. Some of them have been addresses in recent reviews on legislation and EU strategies (Hermoso et al. 2022; Adam et al. 2022), biodiversity indicators and monitoring methodologies (Gao et al. 2015; Marín et al. 2021; Moussy et al. 2022; Moersberger et al. 2022, 2024; Safdar et al. 2025), and the outcomes from management of existing forests, i.e, the impact of wood harvesting on species richness (Chaudhary et al. 2016), monitoring biodiversity indicators in relation to silvicultural measures (Oettel and Lapin 2021), management cycles in central European forests (Jandl et al. 2024; Uhl et al. 2025), and effects of forest thinning on biodiversity (Verschuyl et al. 2011). However, far less attention has been given to the relevant decision-making processes and factors during the different phases of forest establishment and restoration. Activities such as species selection, nursery cultivation, genetic diversity of planting stock, site preparation, planting techniques, and post-planting management all affect the long-term biodiversity status and stability of forest ecosystems. Considering the tree-planting targets across Europe under the EU Nature Restoration Regulation, which call for the restoration of degraded ecosystems and the establishment of millions of new trees, it is timely to highlight forestry practices that can better integrate and support biodiversity within these initiatives. While collaborative research has helped identify core concepts bridging biodiversity conservation and forestry, a persistent gap remains between scientific knowledge and its application in operational forest management — driven by differences in institutional mandates, timescales, communication, and incentive structures between researchers and practitioners (Lindenmayer et al. 2012; Craven et al. 2019; Felton et al. 2020). Due to variability in management practices, ecoclimatic conditions, and historical and socio-economic factors, a practical examination of the interconnectedness between forest establishment and restoration activities and biodiversity conservation could benefit both research and practice in the European context. Indeed, most European forests are managed as multifunctional systems in which biodiversity must coexist with timber production, carbon sequestration, water regulation, recreation, and other ecosystem services (Duncker et al. 2012; Bauhus et al. 2017; Gustafsson et al. 2020). These objectives are not always aligned, and trade-offs between biodiversity and production, for example, have been widely documented (Gamfeldt et al. 2013; Felipe-Lucia et al. 2018; Oettel and Lapin 2021). Several optimization strategies aimed at balancing multiple forest functions, ranging from landscape zoning to adaptive silviculture, have been studied across European forest types (Knoke et al. 2008; Triviño et al. 2017; Eyvindson et al. 2021), although further development and implementation are still needed.

In this context, we provide targeted guidance for the planning and establishment of multifunctional forests aimed at enhancing biodiversity outcomes without compromising long-term forest productivity or resilience. Through our daily work, we have observed that key aspects of these early-stage phases are often overlooked or remain unfamiliar to many practitioners involved in forest establishment, thereby threatening the long-term sustainability of new forests. Accordingly, we review and discuss the status in Europe of practices such as the use of diverse species mixtures, access to genetically diverse planting stock, and complementary management techniques in nurseries and on the field. We consider these practices to be compatible with, and beneficial for, multifunctional management objectives both in natural and urban forests under the ongoing climate change.

Tree species selection under climate change: evidence streams, uncertainties, and knowledge gaps

Species selection provides the basis for building a new forest ecosystem

In the context of climate change, the selection of tree species draws on several largely independent lines of evidence, including species distribution models, dendroecological analyses, and functional trait-based methodologies (Hanewinkel et al. 2013; Thurm et al. 2018; Dyderski et al. 2025). As these approaches address different ecological processes and operate at different temporal and spatial scales, they cannot be easily translated into clear decisions regarding tree species selection for forest plantations. Despite the extensive knowledge of the biology and ecology of individual tree species, important species-specific knowledge gaps persist. For example, predicting how species perform based on interactions among climate, site conditions, and biotic context remains difficult. Consequently, current discussions on tree species selection focus on managing uncertainty in species choice under changing climate conditions, as well as on evaluating the potential contribution of non-native tree species to European forests (Thurm et al. 2018; Puchałka et al. 2023b). Changes in species ranges, driven by climate change and competition with non-native tree species, can present challenges and opportunities to different ecosystems. Such species turnover and altered environmental conditions may lead to changes in the structure, functioning, and in the outcome of interspecific interactions within ecosystems (Thuiller et al. 2005; Dyderski et al. 2025). Model-based analyses of approximately 1,350 European vascular plant species suggest that more than half of the studied species may lose part of their potential climatic range under future climate scenarios, with the magnitude of range contraction varying substantially among species (Thuiller et al. 2005; Wen et al. 2022; Puchałka et al. 2023a). These shifts may have further consequences for ecosystem functioning and food-web dynamics (Heleno et al. 2020) but this remains unexplored.

Functional trait-based approaches offer a powerful and increasingly operational framework for translating ecological knowledge into species selection decisions for afforestation and reforestation plantations (Laughlin et al. 2017; Charles 2018; Navarro-Cano et al. 2019). Rather than relying solely on species identity or climatic niche models, trait-based selection identifies candidates by matching plant functional strategies (i.e., traits such as specific leaf area (SLA), wood density, leaf dry matter content (LDMC), root architecture, and seed mass) to the abiotic and biotic conditions of the target site (Reich 2014; Dyderski et al. 2025). This approach is grounded in the plant economics spectrum (Reich 2014), which positions species along a continuum from fast resource acquisition (high SLA, low wood density, high growth rate) to conservative resource use (low SLA, high wood density, high stress tolerance), and has been applied successfully in degraded land restoration, montane forest management, and tropical reforestation contexts (Laughlin et al. 2017; Charles 2018; Xu et al. 2024). In restoration ecology, for instance, matching the functional distance between candidate species and the target community has been shown to improve establishment success and accelerate the recovery of ecosystem functions, since species with trait profiles similar to those of established residents are more likely to integrate into existing biotic networks (Navarro-Cano et al. 2019). For afforestation under climate change, selecting species whose functional traits align with projected future site conditions could increases the likelihood of long-term stand persistence and reduces the risk of maladapta-

tion. In practice, this means prioritising drought-tolerant traits for drier future conditions (high LDMC, deep rooting), selecting for high phenotypic plasticity where environmental uncertainty is larger, and diversifying the functional composition of mixed stands to capture complementarity effects on resource use and resilience. The trait-based framework also provides a principled basis for evaluating non-native species: rather than accepting or rejecting them on the basis of origin alone, their functional compatibility with target community conditions and their potential for habitat transformation can be assessed and compared with the native alternatives (Navarro-Cano et al. 2019; Xu et al. 2024). A practical protocol for such assessments has been demonstrated to be both rapid and effective even in data-limited contexts (Xu et al. 2024), suggesting its applicability to the European forestry where species trait data are increasingly available through databases such as TRY (Kattge et al. 2020).

As widespread economically important tree species are threatened by climate change in Europe, especially conifers such as *Pinus sylvestri*s L. and *Picea abies* (L.) H. Karst. (Thurm et al. 2018; Buksha et al. 2019; Wessely et al. 2024; Dyderski et al. 2025), phylogenetically distant broadleaved species, including *Prunus serotina* Ehrh., *Quercus rubra* L., and *Robinia pseudoacacia* L., are likely to saturate their current niches, particularly given their functional traits such as lower height, larger specific leave areas, and higher wood density (Puchałka et al. 2023b, 2024; Wessely et al. 2024). Research indicates that several non-native species are more likely to be the 'winners' of climate change in Europe with projected range expansion under warming scenarios (Thurm et al. 2018; Puchałka et al. 2023a; Dyderski et al. 2025), while both native and non-native species with thermophilic traits are expected to expand at the expense of the currently dominant conifers (Wessely et al. 2024; Dyderski et al. 2025). Hence, both native and non-native dominant coniferous species are expected to lose their optimal areas (Thurm et al. 2018; Puchałka et al. 2023b; Wessely et al. 2024; Lozano et al. 2024). This climatic matching may facilitate establishment in recipient areas and, under certain conditions, confer a temporary advantage of non-native species over native species that need to adjust to rapidly changing climatic conditions (Dainese et al. 2017; Iseli et al. 2023). Such shifts in tree species composition towards a higher proportion of broadleaved trees can affect forest structure and functioning. In particular, the increasing dominance of broadleaved species can alter light regimes and the whole forest microclimate (Mölder et al. 2014; Piwczyński et al. 2016; Díaz-Calafat et al. 2023; Czortek et al. 2025), the litter type and soil conditions in forests (Aerts et al. 2017; Horodecki and Jagodziński 2017), and reduce the abundance of species evolutionarily adapted to nutrient-poor and moderately shaded coniferous or mixed forests (Dyderski et al. 2025; Bury and Dyderski 2025; Czortek et al. 2026). Climate change poses a threat to species adapted to cold environments, such as conifers and forest specialist species associated with coniferous forests (Dyderski et al. 2018; Puchałka et al. 2023c, a; Puchałka et al. 2023b). However, it will also affect understory species (Kermavnar et al. 2023; Puchałka et al. 2023a, 2023c). In this context, non-native tree species that show functional similarity or phylogenetic closeness to species native to European forests may, under certain conditions, gain an adaptive advantage, here understood as the capacity to exploit similar resources and interact with established communities following the 'join the locals' strategy (Tecco et al. 2010). Examples of such species are *Q. rubra, Abies grandis* (Douglas ex D. Don) Lindl*, Pinus rigida* Mill*.,* and *Pinus radiata* D. Don. Importantly, such an advantage does not imply superior adaptation to climate change per se, but rather context-dependent compatibility with local environmental conditions (Klisz et al. 2023; Medina-Villar et al. 2024). In such cases, their

effects may also be similar to those of the close relatives. For instance, dense canopy shading by non-native *Q. rubra* can result in shade and soil effects comparable to those observed under native *Fagus sylvatica L.*, i.e., limiting the development of understory vegetation due to leaf litter accumulation (Dyderski and Jagodziński 2021) and soil modification (Czortek et al. 2026; Stanek et al. 2020). From a management perspective, species selection should be based not only on the climate of origin but also on functional strategies that reflect trade-offs between productivity and stress resilience. Such a comprehensive approach can be helpful for informed species selection that supports the functional characteristics of ecosystems. It can also serve as a decision-making framework, rather than a prescriptive scheme for replacing native species (Dyderski et al. 2025). Recent research indicates that when used to plan future afforestation under a changing climate, species distribution models primarily provide information on the stability, contraction, or expansion of species ranges. In contrast, provenance trials and analyses of annual tree growth provide direct data on growth efficiency and timber production potential (Klisz et al. 2019). This means that climatic niches identified using species distribution models may not correspond to the growth or regeneration optimum, highlighting the need to distinguish between habitat suitability and species physiological productivity (Popa et al. 2025). Therefore, species distribution models should not be the sole basis for silvicultural decisions, as they describe the stability of species occurrence rather than their growth productivity. The selection of tree species should take greater account of functional traits associated with the Plant Economic Spectrum (Dyderski et al. 2025), which are useful for assessing adaptation to climatic and ecological conditions, as well as for predicting the potential impact of individual tree species on the species and functional diversity of ecosystems (Czortek et al. 2025, 2026; Puchałka et al. 2025).

Concurrently, many species have evolved under different conditions, having different functional traits, which leads to an increased ability to transform habitat conditions (light regime, soil chemistry and moisture, or elemental cycling) and create different inter-species interactions (e.g., *R. pseudoacacia, Ailanthus altissima* (Mill.) Swingle*, Acacia dealbata* Link, *Eucalyptus globulus* Labill. *and Sorbaria sorbifolia* (L.) A. Braun (Castro-Díez et al. 2009; Wohlgemuth et al. 2022; Czortek et al. 2026). These species often exhibit rapid establishment and spread, partly due to their high potential for vegetative reproduction (Kowarik and Säumel 2007; Bouteiller et al. 2023). For instance, both *R. pseudoacacia* and *A. dealbata* are nitrogen-fixing species that significantly alter soil properties (Rice et al. 2004; Rodríguez-Echeverría et al. 2013; Lazzaro et al. 2018; Wohlgemuth et al. 2022), while *A. altissima* successfully inhibits the growth of other plants via allelopathy (Kowarik and Säumel 2007; Constán-Nava et al. 2015). Therefore, these species represent the 'try harder' strategy (Tecco et al. 2010), which confers functional advantages over native species. Such benefits can be attributed to the performance of invasive species (Dyderski and Jagodziński 2019; Milanović et al. 2020) or their ability to facilitate habitat transformation (Aerts et al. 2017); e.g., non-native tree species can either increase (Horodecki and Jagodziński 2017) or decrease (Jo et al. 2016) leaf litter decomposition rates. These strong and often transformative functional effects are variable across environments and frequently alter habitat conditions in ways that disadvantage habitat-specialist species and alter community structure. Ecological risks are inherent to species introductions and the increasing use of non-native taxa, including invasive species such as *A. altissima* and *R. pseudoacacia*, whose short-term functional benefits may conflict with long-term ecological integrity, native biodiversity, and forest management objectives, and these risks need to be carefully

considered. In line with this, a systematic review indicates that non-native tree species more frequently have a negative impact on biodiversity (66%) than a positive one (24%) (Wohlgemuth et al. 2022). In this sense, climate-adaptive and multifunctional forest management can only support biodiversity conservation when the selection of tree species is framed as a flexible decision-making process that integrates ecological evidence, manages uncertainty, assesses ecological impacts, and aligns societal expectations with the long-term functioning of European forest ecosystems (Fig. 1).

Tree genetic diversity as part of forest establishment and management

A further consideration in species selection and functional diversity, both for forestry and conservation, is the role of genetic diversity within tree species—an aspect that remains notably understudied due to the long lifespan of trees, yet it is highly relevant to the selection process. High genetic diversity ensures the current population's fitness and preserves its adaptive potential to respond to environmental change (Fady et al. 2020). However, neither the natural migration of trees by seeds and other propagules nor gene flow by pollen can keep pace with the current rapid temperature increase and the shift in precipitation patterns (Corlett & Westcott 2013; Mátyás, 1996; Williams & Dumroese 2013). Tree populations may persist in a given environment if the rate of adaptation matches or exceeds the rate of environmental change (Jablonski 2008; Siepielski et al. 2009; Charlesworth et al. 2017). Genetic adaptation is not, however, the only mechanism available to trees facing environmental change. Phenotypic plasticity, defined as the capacity of a given genotype to express different phenotypes under varying conditions, represents an additional and often critical buffer. Importantly, evidence from common garden and provenance experiments indicates that intraspecific differences in growth response are most apparent under moderate or suboptimal conditions, whereas under truly adverse conditions, provenance-specific patterns tend to diminish and populations converge toward a common stress response (Klisz et al. 2019). This has important implications: provenances that appear highly differentiated and most promising under current experimental conditions may lose their apparent advantage under the severe conditions projected by climate change when most needed. Moreover,

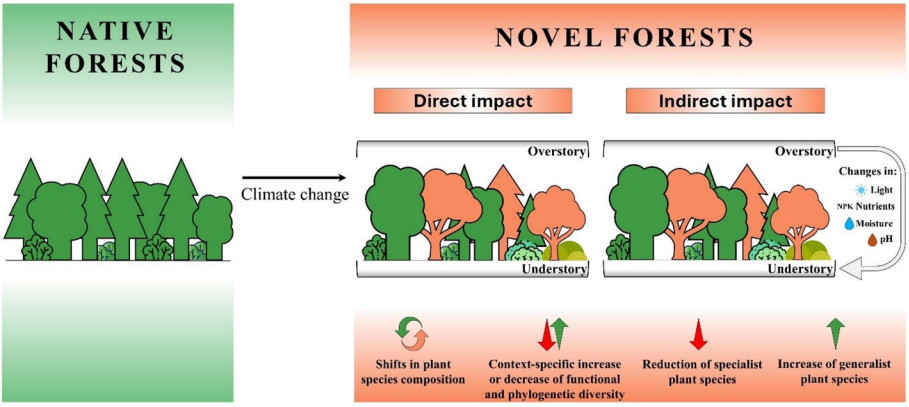

Fig. 1 Direct and indirect impacts of climate change that contribute to the formation of *'Novel Forests'* and how they would reflect on plant species biodiversity

although climate change projections vary among scenarios, all suggested rates of environmental change exceed the capacity rate of plants to adapt or migrate naturally (Gray and Hamann 2013).

In this context, the ongoing loss of tree genetic diversity has become particularly alarming, as it is crucial for securing forest reproductive material (FRM) suitable for current and future afforestation and reforestation activities (Popovic et al. 2022). Accordingly, information on genetic diversity, genetic structure, and inbreeding is key for the effective management of forest tree populations (Šijačić-Nikolić et al. 2023; Pinosio et al. 2026). As core elements of forest ecosystems, the fate of tree populations has cascading consequences for a wide range of forest-dependent organisms. The persistence of tree populations under rapidly changing climate depends on sufficient genetic variation to enable local adaptation, or alternatively, on sufficient phenotypic plasticity (Schlichting and Smith 2002; Anderson 2016; Leites and Benito Garzón 2023). Under adverse environmental conditions, species vulnerability is shaped by both inter- and intraspecific variation, as well as by the ecological tolerance. Vulnerability is particularly high in rare tree species, predominantly inbreeding species, species with long generation time, locally adapted genetic specialists, and species with limited dispersal capacity. Likewise, species or populations characterized by low genetic diversity, resulting from past bottlenecks, small population size and strong isolation, and populations with limited possibilities for range shifts due to habitat loss are particularly threated (St.Clair and Howe 2011; Boonman et al. 2024). Maintaining genetic variation to preserve the evolutionary potential of populations through natural selection, i.e., by increasing the frequencies of advantageous alleles, is a long-term strategy that it is particularly challenging for long-lived trees (Sætre and Ravinet 2019; Alimpić et al. 2022). On the one hand, rapid adaptation may occur even across short spatial scales; on the other hand, adaptive responses are constrained by the generally slow evolutionary rates of trees (Petit and Hampe 2006; Budde et al. 2024; Modica et al. 2024). Furthermore, evolutionary responses to complex selection pressure such as climate change may be limited by trade-offs between fitness-related traits, which are polygenic, as well as by epistatic interactions among the genes that control them (Sthultz et al. 2009; Darychuk et al. 2012). Gene flow represents another mechanism influencing the buffering capacity of natural populations against climate change. By increasing local genetic variation and reducing the effects of genetic drift in small populations, gene flow may enhance adaptation to changing environments (Alleaume-enharira et al. 2006; Krutovsky et al. 2012; Willi et al. 2022; Avanzi et al. 2024; Sexton et al. 2024). However, patterns of gene dispersal are highly skewed, with rare long-distance dispersal events playing a disproportionate role. Empirical studies have shown that in anemophilous species such as pines, viable pollen can travel hundreds of kilometres (Ashley 2010; Kremer et al. 2012; Lindgren et al. 1995; Williams 2017), although the reproductive success of such pollen remains uncertain. Consequently, the net effects of gene flow on the fitness of local populations are difficult to predict. In strongly locally adapted populations, incoming alleles may be maladaptive and disrupt co-adapted gene complexes in subsequent generations (Charlesworth and Willis 2009; Lindtke et al. 2012). However, under unstable or rapidly changing environments, gene flow may introduce adaptive genetic variants that are absent from local population but present within the species' gene pool (Soularue and Kremer 2012; Kremer et al. 2012; Olson-Manning et al. 2012).

Phenotypic plasticity is advantageous for organisms inhabiting heterogeneous environments (Nicotra et al. 2010), particularly for forest trees. This capacity is especially impor-

tant because tree species typically occupy environments that vary widely in microclimate, soil conditions, and biotic communities, while also experiencing substantial fluctuations over their long lifespans. Notably, the complexity of genetic diversity in both theoretical and applied research is further reflected in the fact that forest tree species are rarely selected for genetic diversity as a primary criterion (Climent et al. 2024). However, the consequences of such as selection are unavoidable (Fig. 2), highlighting the need for additional trials specifically designed to address genetic diversity as a primary objective rather than as a by-product of performance-based selection. Likewise, detailed studies of existing natural and managed stands are essential for advancing both forestry and conservation. Common-garden experiments indicate that phenotypic plasticity is a widespread feature of trees, although its magnitude vary among provenances and depends on the species, trait considered, and environmental context. Nevertheless, empirical evidence regarding the response of different provenances to ongoing climate change and associated shifts in temperature regimes remains limited (Wegener et al. 2026). Moreover, because provenance trials have historically focused on economically valuable timber species, the relevance of provenance variation from a conservation perspective within multifunctional forest management remains poorly understood, highlighting an important and pressing knowledge gap. Ultimately, decisions regarding the use of particular species or provenance are typically made by forest managers. Therefore, awareness of the potential practical risks, both short-term and long-term, together with open communication among experts from different disciplines and access to clear, evidence-based information, are essential for informed decision-making. The most effective way to evaluate the responses of native and non-native species, as well as their provenance, to climate change is through investment in well–documented trials conducted under both controlled and natural conditions, combined with long-term monitoring. Such approaches are already being implemented across Europe (e.g., Leverkus et al. 2025; Bison et al. 2026; Martínez-Sancho et al. 2025), although additional efforts will

Fig. 2 Picture of the two European beech trees (*Fagus sylvatica* L.) of different origins taken in spring 2021 at the provenance trial site Vrchdobroc (SK) of the International beech experiment coordinated by the von Thuenen Institute (https://www.thuenen.de/en/cross-institutional-projects/beech-provenances; Photo credit: Dušan Gömöry)

continue to be necessary, particularly in the context of species diversification. Furthermore, involving stakeholders beyond the research community represents another important step towards increasing public awareness of species selection and the conservation of forest genetic resources.

Biodiversity conservation during different stages of plant production

Conserving genetic diversity through targeted sourcing of FRM

Diversifying the genetic material is a well-known strategy for ensuring forest adaptation and ecosystem resilience to new climate conditions (Aitken and Whitlock 2013). Therefore, restoration guidelines recommend considering both among-habitat genetic differentiation and the use of local seed sources (Broadhurst et al. 2008; St. Clair et al. 2022), which requires identifying natural populations as propagule sources. From a conservation perspective, under the current climate pressures, traditional conservation methods of FRM may not be enough, and thus require active conservation and species and/or populations transfer to new areas during forest establishment (Schwartz et al. 2012; Hällfors et al. 2017; Zhao et al. 2023; Szamosvári et al. 2025; Luo et al. 2025). The translocation of reproductive materials from sites currently experiencing climatic conditions to target sites where they are expected to occur in the future has been consistently advocated by many forest geneticists (Mátyás 1994; Winder et al. 2011; Konnert et al. 2015; Aitken and Bemmels 2016; Szamosvári et al. 2025). Several terms are used to name this practice, primarily under the label of 'assisted migration' (AM) (Fig. 3), frequently distinguishing between assisted gene flow, i.e., movement of genetic material within the natural range of a species, and assisted colonization, i.e., translocation of FRM outside the range (Aitken and Whitlock 2013; Chakraborty et al.

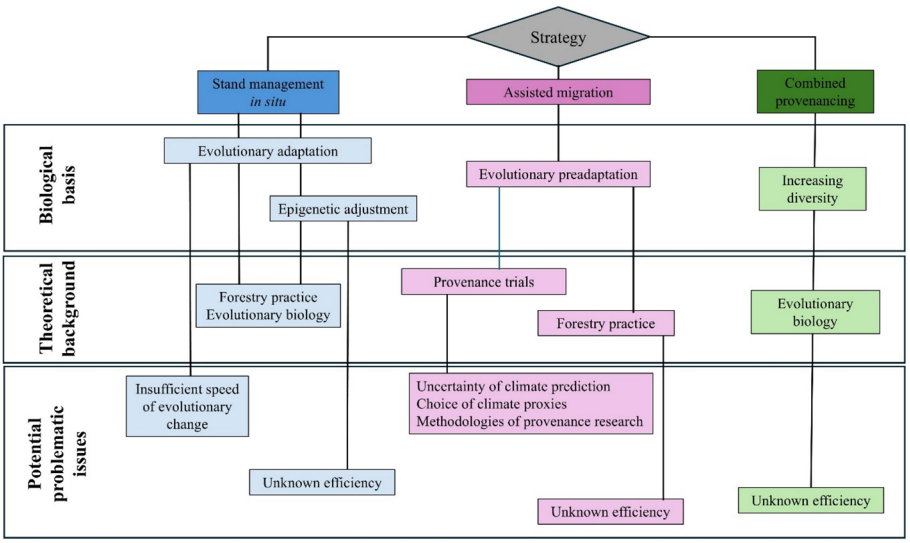

Fig. 3 Alternatives management approaches and their biological basis, theoretical background, and potential issues for forest adaptation and restoration under climate change

2015). These genetic considerations are relevant not only for conservation-focused restoration but also for multifunctional forests established for wood production, carbon sequestration, and other ecosystem services, as genetic diversity underpins long-term productivity and resilience under climate change (Fady et al. 2020). Considering this, the motivation for AM may also differ. Indeed, Pedlar et al. (2012) distinguish between *forest AM*, focusing on the stability or increase of forest productivity, and *species rescue AM*, aimed at saving endangered species and conserving the biodiversity of both tree species and accompanying ecosystem components. At least two information sources guide AM. The first is common garden experiments, especially provenance trials, where the performance (mortality/survival rates, growth, physiology, and phenology) of populations of different origins is tested at sites under different climates. Replication of an identical provenance set across several environments enables modelling population responses using transfer or response functions (Rehfeldt et al. 1999; Wang et al. 2010; Chakraborty et al. 2015; Benito Garzón et al. 2019). Indeed, one of the main benefits of such multi-environmental trials (METs) is the ability to assess genotype-environment interactions (GxE). Another critical but often-neglected information source is experience gained in forestry practice. Seeds and plants have been widely traded and transferred across Europe since the eighteenth century (Tulstrup 1959), and the trade in FRM remains intense (Jansen et al. 2019). In many cases, FRM was moved across climatic zones, predominantly from the South to the North. In contrast to provenance trials, which are often assessed at a juvenile age, adult stands originating from the translocation of FRM have the potential to yield more reliable information about the population's performance.

The absence of the records of seed origin, usually kept only temporarily or not at all, may be the primary reason why FRM transfer history has not been systematically evaluated for successes and failures (Schueler et al. 2014; Pötzelsberger et al. 2020). Despite three decades of policy commitments (see MCPFE Strasbourg Resolution S2 (1990)), documentation of FRM provenance remains inconsistent across Europe (Mataruga et al. 2023), although the recently proposed EU Regulation on forest reproductive material (European Commission 2023) represents a significant step toward mandatory traceability requirements (Aitken and Bemmels 2016; Fady et al. 2016). Information on the origin of planting material is particularly crucial for non-native tree species introduced into Europe, which, within their natural range, are distributed across a wide spectrum of ecological conditions (Alizoti et al. 2022). These experiences can provide substantial input into the decision-making process of choosing whether to adopt AM, since the concept of AM is associated with several risks stemming from information uncertainty across various aspects. In particular, the invasiveness, hybridization potential, and unpredictable impact on local ecosystems are significant shortcomings of AM (Vitt et al. 2010; Bucharova 2017; Szamosvári et al. 2025), as noted above. At the local scale, reliable climatic data for the sites of origin and plantation sites are needed to assess tree–climate relationships, but such data are not readily available everywhere, nor are they regularly updated. At the global scale, the future climate and its dynamics also largely depend on unpredictable political decisions that affect greenhouse gas emissions (Meinshausen et al. 2022; Calvin et al. 2023), making AM decisions even more challenging, considering the long production cycle of forests and biodiversity conservation goals for target species and ecosystems. Different tools can inform decision-making for both researchers and forest managers regarding AM outcomes (O'Neill et al. 2017; St. Clair et al., 2022; Lachmuth et al. 2023; Shalev et al. 2025), which would be especially valuable

in the initial stages of planning for new forest establishment. However, to date, these tools have been more focused on the North American context (e.g., Palik et al. (2022); Clark et al. (2023); Bower et al. (2024)). In Europe, most recently, valuable insights into the potential to improve forest resilience through seed provenance selection for seven of the main forest species have been provided (Chakraborty et al. 2024). Further studies are urgently needed, both on more- and less-frequently used species in planting activities, considering the arguments for species selection presented earlier.

Mixing reproductive materials of different origins to increase genetic diversity in the newly established forest stands has been suggested as another alternative strategy (Prober et al. 2015; Ivetić and Devetaković 2016; Bucharova et al. 2019) (Fig. 3). Several approaches relying on this principle have been developed, united by the expectation that broadening genetic variation allows for the selection of genotypes suitable for unknown future climates, while interbreeding between divergent genotypes and genetic recombination may contribute to increased resilience in future generations (Broadhurst et al. 2008; Breed et al. 2013; Prober et al. 2015). However, practical experience with this strategy is very limited and not fully noted, along with potential risks which include outbreeding depression due to the disruption of coadapted gene complexes and breakdowns in local adaptation to non-climatic environmental factors (Ivetić and Devetaković 2016). Tree breeding programs, as a more specific tool, have traditionally focused on selecting genotypes with high growth rates to optimize timber production (Sheppard et al. 2020; Fugeray-Scarbel et al. 2023; Climent et al. 2024). However, forests are experiencing new disturbance regimes due to ongoing climate change, characterized by increased frequency and magnitude of abiotic extremes and pests (Senf and Seidl 2020; Gomes Marques et al. 2022). Therefore, future breeding programs need to be geared towards selecting tolerant genotypes of various tree species that can withstand abiotic and biotic stresses. Furthermore, early short-term tests and experiments under controlled conditions, which can provide data on the resistance of specific populations to drought and other threats, can guide AM and enable more informed choices (Stojnić et al. 2018). Progress in forest genomics and the accumulation of knowledge about fitness-relevant DNA polymorphisms have also accelerated significantly over the past two decades (Plomion et al. 2016; Borthakur et al. 2022; Grattapaglia 2022; Nelson 2023; Wang and Zhang 2024) and can be used more practically during the early stages of planning new forests. However, until the physiological mechanisms underlying traits related to evolutionary fitness are understood and the genes controlling variation in these traits are identified, the application of genomic tools to guide the transfer of FRM will remain limited (Lind et al. 2018; He et al. 2023; Vajana et al. 2023).

Underscoring and addressing the knowledge gaps regarding nursery cultivation

The potential for biodiversity conservation through various practices during forest establishment should not be compromised by species or genetic diversity losses that may occur during nursery cultivation. A species selection bias arises from the seed availability and reliability of a few core species due to the nurseries' know-how (Clark et al. 2023; Mataruga et al. 2023) and some species attributes (e.g., high germination and seed viability, no need or easily applicable pre-germination treatments, seed that can be easily conserved). The genetic diversity of planted (i.e., artificially regenerated) stands depends on the strategy for seed collection (Hosius et al. 2006; Zinnen et al. 2021) and all subsequent nursery activi-

ties leading to the final selection of the FRM (Villar-Salvador et al. 2026). Selection inevitably results in change, potentially leading to a subsequent reduction in diversity in each newly established forest stand. Therefore, orienting all activities toward optimal sampling of genetic diversity is essential for maintaining biodiversity in newly established forests (Ivetić et al. 2016; Gömöry et al. 2021; Zinnen et al. 2021), thereby balancing conservation goals with the efficiency of FRM production.

The selection of provenances for seed collection is the first step toward supporting multifunctional forests (Hosius et al. 2006; Vajana et al. 2024). Both adaptive and neutral genetic diversity of natural forests are not uniformly distributed in space due to historical processes and selective pressures. On the one hand, genetic diversity is often concentrated in former glacial refugia and post-glacial melting pots (Petit et al. 2003); but it might be eroded by ecological and geographic marginality processes in both genetically enriched and depauperate areas (Hampe and Petit 2005). On the other hand, as already emphasized, trees can adapt at short spatial scales (Petit and Hampe 2006), as it has been demonstrated in tropical and temperate species (Brousseau et al. 2021; Budde et al. 2024). The spatial distribution of selected provenances is crucial for achieving optimal seed collection for the *ex-situ* conservation of genetic diversity (Hoban and Schlarbaum 2014). Analytical tools that help process and connect genetic data and rank natural populations to optimize seed collection are available (Andrello et al. 2022) and have recently been applied to forest trees (Beridze et al. 2023; Vajana et al. 2024). Extensive genetic data at high spatial resolution are needed to sample enough genetic diversity for these approaches to be effective, particularly in regions where genetic structure is complex (Gómez and Lunt 2007; Rodríguez-Quilón et al. 2016; Piotti et al. 2017). When seed collection is carried out adequately—whether deliberately for genetic conservation or not—the levels of neutral genetic diversity of plantations and seed orchards cannot be significantly lowered (Ivetić et al. 2016; Santini et al. 2018). Several national and international guidelines provide precise rules and recommendations to prevent the loss of genetic diversity during seed collection [see Gömöry et al. (2021) for Europe or Zinnen et al. (2021) for a review on the benefits and risks of seed production areas]. Some authors, after considering the biology of plants, collection maintenance, and conservation targets (e.g., avoiding the loss of rare alleles), have shown that seed collection should focus on the total number of seed trees across the entire distribution rather than a specific number of seed trees per population (e.g., Hoban 2019). They emphasized the importance of paying particular attention to rare, genetically depauperate, clonal, and dioecious species, as well as marginal populations and those representing unique genetic lineages. More precisely, the species-specific minimum threshold for seed trees across hierarchical levels can be estimated using simulations based on genetic data (Blanc-Jolivet and Degen 2014). Any strategy for the choice of seed trees should also consider that tree fecundity and the effective number of pollinators per tree (parameters tightly associated with the diversity of the seed crop) are often related to the individual- and population-specific characteristics and can vary over the years (Hoebee et al. 2007; Oddou-Muratorio et al. 2018; Avanzi et al. 2020; Aleksić et al. 2022). Other temporal factors should also be considered, e.g., changes in flowering and fruiting phenology (Gray and Ewers 2021), and economically convenient harvesting during peak seed production may exclude relevant climate-adaptive phenotypes. Finally, when seed collection is carried out in seed orchards, and the main goal is obtaining climate-resilient FRM, one should consider that most seed orchards contain clones of plus trees selected between 1950 and 1990 (Gömöry et al. 2021)—thus highlighting the need for

suitable replacement of the source material or facing a severe lack of planting material in the upcoming years.

Following seed collections, other factors may also contribute to changes in genetic diversity in subsequent nursery production phases. For instance, processing only medium-sized seeds or discarding small seeds during grading may result in genetic loss (Campbell and Sorensen 1984; Ivetić et al. 2016). However, as genetic factors may affect germination more than seed size, advocating a mix of seed sizes to target FRM quality and genetic diversity is a potential solution (Edwards and El-Kassaby 1996; Ivetić et al. 2016). Both seed storage and dormancy-breaking treatments may favour some phenotypes (Schmidt 2000), but their overall effect on genetic diversity appears negligible (Konnert and Hosius 2010). Nursery practices may include a pre-germination phase; for practical reasons, pre-germinated seeds are usually collected when their occurrence is high, potentially excluding valuable adaptive phenotypes that may occur at lower frequencies. Selective processes can also be exacerbated during cultivation. Nursery seedling quality, which goes beyond appearance (Dumroese et al. 2016; Mataruga et al. 2023), is practically associated with easily measurable traits (size or height), and seedlings' morphological uniformity is preferred. At the same time, this mitigates risks associated with underdeveloped seedlings prone to outplanting stress (Andivia et al. 2021), and it may also reduce overall batch diversity. However, as only a few reports have examined the impact of nursery operations on the genetic diversity of forest reproductive material (Ivetić et al. 2016; Konnert & Ruetz 2003), strong recommendations cannot be made at this time.

The various steps of the plant production process (ensuring availability of FRM via AM or breeding programs, informed selection of mother trees, adapted seed collection, seed processing, and nursery cultivation of seedlings) are often overlooked in discussions of biodiversity conservation and ecosystem restoration. This is even more so the case when the production is not focused on directly profitable crops, leading to forest nurseries being underfunded, understaffed, and technologically poor (Haase and Davis 2017). While there is no consensus on the role and acceptability of AM for biodiversity conservation (Hällfors et al. 2017; Charles and Stehlik 2021), climate pressures leave no time for passive adaptation. Considering this, several approaches can be explored. A pan-European traceability system for FRM, modelled on the voluntary certification already used for ornamental plants, would enable practitioners to track seed origin, nursery treatments, and outplanting performance, creating a feedback loop that is currently absent despite the long history of cross-border FRM trade (Jansen et al. 2019). The ornamental plant trade has already demonstrated that cross-border movement of documented plant material is logistically feasible; therefore, the forestry sector could adopt similar standards for restoration. Such a uniform legislation could be indeed helpful, but larger stakeholder involvement would be crucial in the development stage considering that although most European countries follow a unified legislation, dealing with the day-to-day issues (i.e., what to collect, from where to collect, when to collect, and how much to collect) varies on national and even more so on regional and local level (see Mataruga et al. (2023) for an overview of seedling quality control across Europe). Additionally, minimal genetic diversity standards for commercial nursery production could be developed around the target plant concept (Dumroese et al. 2016), specifying thresholds such as a minimum number of mother trees per seed lot (e.g.,$\geq$30 individuals following Hoban (2019)), limits on seed grading that risk excluding rare alleles, and guidelines for retaining a proportion of morphologically non-uniform seedlings in outplanting batches.

The feasibility of nursery-level genetic monitoring has increased with low-cost molecular tools (e.g., DNA barcoding, microsatellite fingerprinting) that can assess genetic diversity at scale (Grattapaglia 2022), and integrating these tools into existing certification schemes or offering subsidies could shift nurseries from passive suppliers to active conservation partners. However, the local context needs to be considered, and the mistakes of uneven integration across Europe should be avoided to preserve biodiversity more systematically and evenly. Finally, regional seed exchange networks that connect collectors, nurseries, and restoration practitioners could aggregate demand for underrepresented species and provenances, making it economically viable for nurseries to diversify beyond the few 'silver bullet' species currently favoured (Clark et al. 2023). Targeted activities through such a network could also help address the workforce shortage in the forestry sector, especially in the field, and provide alternative livelihoods in rural areas. Some models already exist in Scandinavia (Nordic Genetic Resource Center), and Central Europe (EUFORGEN partners), and scaling these regionally could address the fragmentation that currently constrains FRM diversity. At the same time, active involvement of in situ and ex situ genetic conservation programs (e.g., EUFORGEN, Millennium Seed Bank Project of the Royal Botanic Kew Gardens, European Native Seed Conservation Network) in specific regard to forest species could also be beneficial. Encouragingly, several EU initiatives that combine research and practice are also expanding our knowledge of FRM and exploring ways to advance nursery production. Some examples of such initiatives are the OptFORESTS Horizon project, which is surveying European nurseries and expanding common garden networks to 29 locations (Rogelja et al. 2025), and the LIFE ADAPT-ALEPPO project, which has established nursery-grown, labelled provenances of *Pinus halepensis* Mill. in AM trials in Spain. Furthermore, a Horizon Europe call topic explicitly requires AM analysis for dynamic gene conservation (HORIZON-CL6-2024-BIODIV-01-8), supporting the claims of necessary advancement of the field. The ERC-funded FutureNature project (2024-2028) takes a functional approach to AM, shifting focus from minimizing risks to maximizing contributions to novel ecosystem functioning, while the MyGardenofTrees project (2021-2027) aims to develop a Europe-wide predictive tool for selecting climate-resilient tree seed sources by combining large-scale field experiments, genomics, and local environmental data for species like *F. sylvatica* and *Abies alba* Mill. Most recently, the EU Regulation on Forest Reproductive Material (adopted in April 2026) strengthens traceability requirements, ensuring that material can be tracked from registered parent material through collection, certification, and marketing stages (Council of the European Union 2026). Collectively, these activities indicate that the infrastructure for improved FRM governance is either in place or under active development, and that it is intended to be applied at a higher level. Long-term provenance trials and common gardens remain essential as the empirical foundation for validating these approaches; as such, they need to be considered when establishing new forests and during restoration. However, the work needs to be extended beyond establishment to systematically include monitoring and regular data collection to analyse outcomes and respond quickly if issues arise. For this, a coordinated implementation across the nursery sector, supported by targeted funding and next-generation citizen science approaches (Bison et al. 2026; Csilléry et al. 2026), could engage practitioners in monitoring seedling performance and plasticity.

Establishment practices and management of biodiverse and resilient forests

Direct seeding vs. planting

The choice between direct seeding and planting as revegetation techniques is among the most consequential decisions in forest establishment (Lázaro-González et al. 2023), with implications for genetic diversity, establishment probability, structural complexity, and long-term biodiversity in newly created stands. While nursery-grown transplants have dominated European afforestation and reforestation practice for over a century mainly due to their predictable establishment success, survival rates, and the degree of control they allow regarding species composition, provenance, and traits; direct seeding has received renewed interest as an approach that can, under the right conditions, simultaneously reduce costs and better preserve the genetic diversity of the founding population (Dodet and Collet 2012; Palma and Laurance 2015; Grossnickle and Ivetić 2017, 2022). Direct seeding involves broadcasting or spot-sowing seed directly onto prepared sites, allowing germination and early development to occur under the field-specific conditions. Its principal advantage from a genetic perspective is that the number of maternal individuals contributing to the seed lot can be larger, and the previously noted selective pressures from nursery production (grading, density management, and morphological uniformity requirements) will be reduced or removed, allowing space for natural selection (Dodet and Collet 2012; Ivetić et al. 2016; De Souza 2022). Furthermore, because sown seedlings develop their root architecture without the constraints imposed by containers or root pruning, they may form more extensive and functionally diverse mycorrhizal associations from the outset, potentially enhancing long-term stress tolerance (Grossnickle 2012; Juan-Ovejero et al. 2025). However, direct seeding is not universally applicable, and its limitations are particularly acute in the context of climate change and degraded site conditions. Germination and early seedling survival are highly sensitive to soil moisture, temperature fluctuations, competition from herbaceous vegetation, and predation from rodents, birds, and invertebrates, making establishment success variable and difficult to predict (Dodet and Collet 2012; Löf et al. 2012). From a practical aspect, seed storage and application of pre-germination treatments, especially for species with complex long dormancy, can also act as a limiting factor (Lamont and Pausas 2023). Planting of nursery-grown stock offers greater control at the cost of some biological flexibility. Containerized and bare-root seedlings have already passed the most vulnerable early life stages and can be selected for specific traits such as root architecture, shoot-to-root ratio, target seedling quality, etc., thus, reducing establishment risk, particularly on harsh or degraded sites (Andivia et al. 2021; Mataruga et al. 2023). Moreover, a wide range of planting tools and water-saving techniques helps improve the establishment of planted seedlings, especially in dry and harsh environments (Carabassa et al. 2022). From a climate adaptation perspective, planting allows precise deployment of pre-selected provenances or provenance mixtures, enabling the implementation of AM strategies that are difficult to achieve through (often) uncontrolled direct seeding. This predictability is especially valuable when establishing forests under novel climatic conditions and where local seed sourcing is already scientifically supported (Aitken and Bemmels 2016; Chakraborty et al. 2024). The higher costs associated with production, logistics, and field preparation for planting are the main argument against planting, and, as such, have varying degrees of impact depending on the

local context (Raupp et al. 2020). Furthermore, planted stands carry a greater long-term risk of structural instability, as nursery-induced root deformations can compromise anchorage and increase susceptibility to windthrow and drought-related collapse, compared with the naturally-developing root systems of direct-seeded trees (Lindström and Rune 1999). This concern is likely to grow under climate change, as the frequency of extreme drought and wind events increases (Ekeoma et al. 2024); however, long-term studies comparing the structural stability of planted versus direct-seeded stands remain scarce, representing an important direction for future research. An underutilized intermediate approach is to combine both methods at the stand level. Direct seeding of abundant, large-seeded native species alongside planting of less abundant or physiologically demanding species can maximize both genetic diversity and compositional control within a single restoration effort (Löf et al. 2012). Such mixed approaches also support the structural and species heterogeneity objectives by enabling greater inclusivity of species, especially those that cannot be directly seeded due to complex dormancy. Furthermore, the main limitations of direct seeding can be somewhat mitigated by incorporating seed shelters, hydro- and aerial seeding, and drone seeding into the process (Grossnickle and Ivetić 2017; Oliet et al. 2015). From a biodiversity perspective, the choice of establishment method interacts strongly with subsequent understory development. Direct seeding may facilitate the co-establishment of herbaceous and shrub species from the local soil seed bank, potentially accelerating understory diversification (Prach and Hobbs 2008). Conversely, intensive site preparation followed by planting at high densities can suppress this process, particularly if canopy closure is rapid. Retaining patches of natural regeneration or deliberately lowering planting densities in parts of new stands can thus serve as a low-cost strategy to enhance overall stand biodiversity, regardless of the primary establishment method chosen.

In summary, neither direct seeding nor planting is universally superior for biodiversity-conscious forest establishment. The optimal choice will always depend on site conditions, target species, available seed material, climate projections, and management objectives. For instance, larger-seeded species that commonly form a tap-root might benefit more from direct seeding, but their germination rates, seed biology, and storage needs must be considered (Ceccon et al. 2016; Löf et al. 2019; Juan-Ovejero et al. 2025). As is the case with species diversity, monitoring of forests established by direct seeding is rare, and as De Souza (2022) noted, it is mainly concentrated in Brazil and the United States, primarily in tropical forests. Recent pan-European studies have shown that, for oaks, sites that are colder and drier in winter seem to better facilitate seedling emergence and early growth, but also highlight that, even among the 12 oak species studied, species-specific information is needed (Leverkus et al. 2025). In this context, anyone who opts to establish new forests should treat the establishment method not as a simple binary decision but as one component of an integrated planning process that links seed sourcing, genetic diversity targets, site preparation intensity, and long-term monitoring. A particularly valuable and currently underexploited opportunity lies in combining operational planting activities with structured provenance testing: when multiple provenances of a target species are available, deploying them in spatially distinct but systematically documented plots within new stands would generate comparative performance data at minimal additional cost while simultaneously diversifying the stand's genetic composition. This approach can bridge formal research trials and unmonitored operational planting and would help address the current scarcity of empirical data on provenance performance under European field conditions (Bison et al. 2026). How-

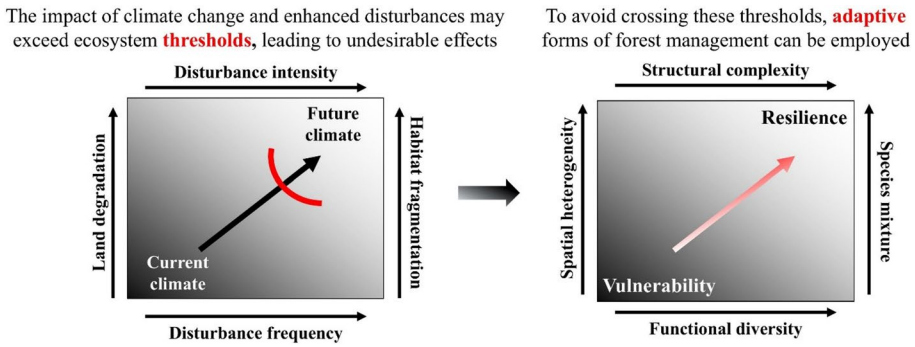

Fig. 4 The impact of disturbances can exceed a threshold, leading to adverse effects such as species loss, population decline, or reduced ecosystem functions. To prevent this, climate-adaptive forest management practices can be used. For instance, promoting functionally diverse mixed-species forests with high structural complexity can enhance forest resilience to climate change and disturbances, as well as productivity

ever, its potential is dependent on consistent record-keeping and long-term monitoring, the same infrastructure whose absence currently limits the use of historical planting records for evaluating past FRM transfers (see the previous section).

Post-establishment management for promoting structural and species heterogeneity

Once a new forest stand has been established, whether by planting, direct seeding, or a combination of both, the management decisions made during and after canopy closure will largely determine its long-term trajectory in terms of both biodiversity and resilience. A general principle of climate-adapted and multifunctional silviculture at this stage is to enhance tree species diversity and shift the developing stand away from monospecific uniformity towards structurally complex mixed composition, either by favouring the establishment and development of accompanying species or through species-enriched supplementary planting (Fig. 4). Substantial evidence supports that mixed forests achieve better multifunctionality and higher biodiversity than monocultures, leading to overall habitat heterogeneity at both stand and landscape scales (Van Der Plas et al. 2016; Duflot et al. 2022), although no universal solution exists across all forest types (Uhl et al. 2025), which is especially relevant in the European context with many diverse forests.

The ecological basis for this principle lies in niche complementarity. Tree species exhibit architectural and physiological differences that influence their size, branching patterns, crown forms, and shade tolerance, which predict greater coexistence likelihood and reduced competition among species with more divergent resource-use strategies (Silvertown 2004). When different species coexist, vertical stratification favours canopy packing (Pretzsch 2014), leading to more efficient use of available growing space and an overyielding effect relative to the respective monocultures (Liang et al. 2016; Pretzsch et al. 2017). Certain species combinations are complementary in their resource-use patterns and can increase productivity (Hooper et al. 2005; Liang et al. 2016; Wiesmeier et al. 2019). Mixed forests generally have higher structural complexity and sometimes higher productivity, which increases available niche space and provides opportunities for less competitive individuals

(Cavard et al. 2011; Stein et al. 2014; Ampoorter et al. 2020). Indeed, a recent meta-analysis confirms that mixed forest plantations also store more carbon than monospecific ones (Warner et al. 2023). Forests harbouring trees with different resource-use strategies have greater resource diversity for consumers and greater heterogeneity in soil resources and microclimate (Keller et al. 2013). At the population level, species mixing increases stability through asynchronous responses to environmental fluctuations and by including species with greater tolerance to perturbations (Morin et al. 2014; Isbell et al. 2015). Thus, admixture can be considered a strategy for promoting long-term resilience, productivity, and adaptation to climate change, while acknowledging that evidence for admixture benefits during extreme climatic events, such as drought, remains limited and context-dependent (Jourdan et al. 2019; Grossiord 2020; Muñoz-Gálvez et al. 2021; Mas et al. 2024). The relationship between stand structural diversity and biodiversity outcomes is strongly influenced by spatial scale, a consideration that is particularly relevant for reforestation and afforestation planning. While uneven-aged management maximizes within-stand heterogeneity, applying this system at the landscape scale can result in lower overall biodiversity in central European beech forests than management under shelterwood systems, because the latter ensures a wider variety of environmental conditions and resources across stands, thereby enhancing beta and gamma diversity (Schall et al. 2020). For newly established forests, this highlights the importance of integrating post-establishment management into afforestation and reforestation planning from the outset, considering not only stand-level structure but also landscape-scale heterogeneity. Such an approach aligns with the view that structurally and functionally diverse forest landscapes require equally diverse management strategies (Uhl et al. 2025).

Soil amendments and mycorrhizae

Soil conditions at the time of establishment profoundly affect both the immediate survival of planted or seeded material and the long-term biodiversity trajectory of the stand. While abiotic factors, such as moisture, temperature, and soil type, primarily govern soil processes (Barré et al. 2017; Wiesmeier et al. 2019; Mayer et al. 2020), the biological dimension of soil health is equally consequential and substantially more tractable as a management target. Trees are closely linked to diverse communities of soil fauna and microorganisms that play a crucial role in the cycling of carbon and nutrients within forest ecosystems (Lange et al. 2015). The microbiome inhabits the soil, rhizosphere, roots, and other plant tissues, establishing complex, dynamic interactions with the host plant that environmental factors can modulate to enhance plant resilience to stress (Naylor and Coleman-Derr 2018; Montagnoli et al. 2019; Singh et al. 2020; Fantozzi et al. 2024). As soil microorganisms are strongly influenced by forest structure and species composition (Beugnon et al. 2023; Baldrian et al. 2023), they are also highly sensitive to alterations induced by site preparation and subsequent management. Mechanical site preparation (e.g., scarification, mounding, and subsoiling or ripping) is widely employed to improve soil conditions for tree regeneration and planting, but it also has negative consequences, including soil compaction, erosion, carbon losses, nutrient leaching, and reduced soil biodiversity; the severity of these effects depends on the intensity and frequency of operations (Löf et al. 2012). Herbicide application has been linked to reduced soil microbial biomass and diversity, potentially lowering mineralization rates (Omidvar et al. 2023). Prescribed fires exhibit contrasting effects depending on soil properties, vegetation type, and fire characteristics: while they can negatively impact fungal

and microbial biomass, they may also improve chemical characteristics such as soil organic matter content and nutrient availability (Alcañiz et al. 2018). Mulching, in contrast, can increase soil organic matter, preserve soil moisture, mitigate temperature fluctuations, and enhance soil microbial biomass and diversity (Huang et al. 2008; Hosseini Bai et al. 2014), making it one of the more biodiversity-compatible site preparation approaches available.

Counterbalancing the disruptive effects of site preparation through targeted interventions at different stages is an increasingly important aspect of multifunctional forest establishment. For instance, mycorrhization of seedlings can be an effective tool for enhancing seedling quality and establishment success. Mycorrhizal fungi have co-evolved with forest trees, contributing to their adaptive potential and playing a central role in forest health (Zanne et al. 2020), particularly on low-quality sites (Geml 2019; Lazarević and Menkis 2020; Usman et al. 2021). Fungi more broadly play critical roles in essential ecological processes, including litter decomposition, nutrient recycling, biodiversity maintenance, nitrogen fixation, and nutrient uptake (Baldrian 2016). Despite its demonstrated potential to improve restoration success and seedling survival under harsh environmental conditions (Asmelash et al. 2016; Medeiros et al. 2021), mycorrhization remains underutilized in commercial forest nurseries across Europe during the plant production phase (Menkis et al. 2005; Cram and Dumroese 2012; Ciadamidaro et al. 2022). Organic amendments during soil preparation have also emerged as a significant strategy, especially on severely degraded or nutrient-poor sites, although in many countries, it is not a common and regular practice. Those suitable for forest planting sites include composts from various sources, sewage sludge, agri-food wastes, biochar, and compost-like outputs from municipal waste (Henry 2005; Carabassa et al. 2020a; Mariotti et al. 2023). In the short term, these amendments provide essential nutrients, stimulate biological activity, enhance soil water retention capacity and aggregate stability, and promote accelerated vegetation growth (Ojeda et al. 2010, 2011; Carabassa et al. 2018; Solé et al. 2023). Mid-term effects include enhanced soil carbon sequestration and favourable vegetation development (Carabassa et al. 2020b). Biochar has received increasing attention as a soil amendment in forest restoration: in addition to its carbon sequestration properties, biochar can improve cation exchange capacity, reduce nutrient leaching, and enhance mycorrhizal colonization, with effects that may persist over decades (Thomas and Gale 2015; Lehmann et al. 2021). While organic amendments offer numerous benefits, their use requires careful monitoring due to potential risks from contamination with heavy metals and persistent organic pollutants (POPs), and the unintentional introduction of propagules from invasive alien species (Düring and Gäth 2002). Managing potential nitrogen leaching and avoiding the ruderalization of vegetation requires optimal application rates (Carabassa et al. 2018), and stable, non-polluted amendments at moderate doses are recommended, alongside ongoing regulatory oversight (Carabassa et al. 2020a). As soil water availability is essential for growth following transplanting, and adequate moisture supports the development of new roots necessary for nutrient and water absorption, superabsorbent polymers (hydrogels) have been widely used to improve tree vigour and reduce mortality under drought conditions. These water-retaining polymers are capable of absorbing approximately 100–150 times their own weight in water, while a considerable proportion of the retained water remains accessible to plants, thereby serving as an additional water reserve. The beneficial effects of hydrogels in mitigating osmotic stress in tree seedlings have been reported for several tree species (Beniwal et al. 2011; Crous 2017; Tomášková et al. 2023). A shift from monospecific plantations to mixed-species stands can further enhance the diversity

and activity of soil biota and increase mineralization rates and litter production, primarily by increasing diversity in leaf and root functional traits (Santonja et al. 2017; Beugnon et al. 2023). This creates positive feedback between the aboveground diversity objectives and the belowground biodiversity outcomes. However, our understanding of how specific establishment and management practices affect soil microbial communities remains limited, due both to research priorities and the logistical constraints of working with soil (Caruso and Bardgett 2021; Kipi et al. 2025). This represents one of the clearest knowledge gaps in forest establishment ecology, and systematic monitoring of soil biological communities in new plantations and reforestation trials alongside standard measures of seedling performance would substantially advance the evidence base.

Urban forests as key elements in the restoration continuum

Alongside forest restoration in natural and semi-natural landscapes, urban environments represent a particular context for new forest establishment in Europe, where the landscape is highly anthropogenic, with numerous species and high movement frequency within a relatively small area. As urbanization occurs disproportionately in biodiversity hotspots (Nilon et al. 2017), centuries of land use have left only remnants of primary forest in Europe (Sabatini et al. 2018). Thus, urban forests represent not only a key element green infrastructure in urban areas but also an opportunity to explore alternative forest establishment outcomes, biodiversity conservation, and ecological connectivity. Furthermore, they can also be the source point of introduction and spread of non-native tree species as well as pests and pathogens, thus directly impacting the surrounding natural forests. Urban forests (vegetation in streets, parks, woodlots, groves, abandoned sites, and residential areas) have also gained increased attention because they comprise a significant percentage of a nation's tree canopy and their well-documented socio-ecological benefits for human well-being (Wolf et al. 2020; Richardson et al. 2021; Pataki et al. 2021; De Carvalho et al. 2022; O'Brien et al. 2022; Rozario et al. 2023; Gillerot et al. 2024). Due to their greater accessibility relative to rural forests, urban green areas have the potential to increase public awareness of nature and address the growing disconnect from natural systems (Beery et al. 2023).

The establishment of urban forests, however, fundamentally differs from natural afforestation and reforestation in species selection, planting techniques, and post-planting management, yet it must be multifunctional at its core. Trees chosen for urban environments must tolerate conditions that often eliminate many native forest species as viable candidates, i.e., compacted and chemically altered soils, elevated ambient temperatures, limited rooting volume, pollution, and periodic drought (Paquette et al. 2021; Esperon-Rodriguez et al. 2022). These constraints, combined with land-use legacies, homeowner preferences, nursery availability, and the socioeconomic characteristics of individual neighbourhoods, drive a tendency towards a narrow set of stress-tolerant taxa (Paquette et al. 2021; Sousa-Silva et al. 2023; Muvengwi et al. 2024). The result, documented across European cities, is a homogenized urban tree flora dominated by a small number of widely planted species and cultivars, that reduces functional and genetic diversity and creates systemic vulnerability to shared pests, pathogens, and climatic extremes (Doroski et al. 2020; Hilbert et al. 2023). Therefore, diversifying species in urban forests is a conservation priority with direct parallels to the provenance and species-diversity arguments made throughout this manuscript.

Species selection and planting design for urban forest establishment

Similar to natural areas, effective species selection for urban forest establishment also requires integrating the functional ecology of candidate species with the specific physical and microclimatic conditions of the planting site. Yet, the spatial integration of grey, blue, and green zones within cities creates highly heterogeneous microclimatic conditions as temperature, moisture, wind exposure, and soil chemistry can vary substantially across short distances (Massaro et al. 2023), necessitating that species selection must be adjusted to the local context rather than applied uniformly across a city. A growing body of research in landscape architecture and urban planning draws on familiar ecological principles (e.g., habitat patch size, landscape configuration, species phenology, structural diversity) to guide these decisions (Speak et al. 2015; Norton et al. 2016; Von Thaden et al. 2021; Piana et al. 2021; Wu et al. 2025b). Several functional traits have emerged as particularly relevant for predicting urban suitability: high stomatal regulation under water deficit and water-use strategy, canopy density, foliage longevity, tolerance of soil compaction and low soil volume, heat tolerance, and resistance to pollution-associated oxidative stress (Grote et al. 2016; Esperon-Rodriguez et al. 2022). Beyond the commonly used genera *Tilia*, *Platanus*, *Acer,* and *Fraxinus*, several native species with documented tolerance to urban stressors appear to be candidates for increasing both functional diversity and conservation value in European urban forests. In temperate Central Europe, these include *Carpinus betulus* L., *Amelanchier* Medik genus, disease-resistant *Ulmus* L. clones, and *Quercus pubescens* Wild.; in Mediterranean contexts, *Celtis australis* L., and *Sorbus* L. genus, which have shown strong performance under urban heat and drought conditions. In all contexts, avoiding species with high invasive potential and those documented to alter soil properties, outcompete native vegetation, or facilitate exotic fauna (Potgieter et al. 2017; Borden and Flory 2021; De Carvalho et al. 2022) is an essential constraint on species selection, since uncontrolled introduction of invasive alien species remains one of the primary risks to biodiversity in urban areas. Non-native tree species with low invasive potential and high functional complementarity may, where ecologically justified and subject to monitoring, be considered as part of a diversified palette; this mirrors the conditional, evidence-based approach to non-native species use developed in the tree species selection section of this manuscript. Urban areas also present an underexploited opportunity in current practice: the deliberate planting of species of high conservation value or threatened provenance, for which urban habitats can serve as supplementary refugia. Where site conditions permit, incorporating species of conservation concern into urban tree planting programmes would allow for closer monitoring of their performance and practical observation of targeted and in this case multifunctional AM, and thus multifunctional forestry (Piana et al. 2021; Schwaab et al. 2021; De Carvalho et al. 2022; Wu et al. 2025a).

In addition to species selection, the design and planting techniques used in urban forest establishment significantly influence both immediate survival and long-term biodiversity outcomes. Standard urban tree planting (single-specimen street trees in constrained pits) provides limited habitat value and exposes individual trees to the full intensity of urban stressors without the buffering effects of canopy cover, humidity, and root-zone competition that characterize forest conditions. Transitioning from isolated specimen planting towards grove- or stand-level establishment, even on small parcels, substantially changes the microclimate experienced by individual trees and the habitat structure available to asso-

ciated fauna (see Gustavsson et al. (2005)). The Miyawaki method, characterized by dense, multi-species planting of native species on small urban parcels to rapidly establish structurally complex, multi-layered vegetation, is another scientifically-supported alternative for increasing urban tree diversity and structural heterogeneity simultaneously (Miyawaki 1998; Schirone et al. 2025). The method's theoretical basis closely aligns with the principles of ecological restoration and has yielded encouraging results in several European urban contexts, particularly in terms of establishment speed and species richness of associated fauna. However, its applicability depends strongly on local conditions and assets: substantial soil preparation, a sufficiently diverse palette of native nursery stock, and high maintenance demands during the establishment phase are considerable.

Conclusions

The establishment of new forests and the restoration of degraded ecosystems across Europe directly determine the success of biodiversity conservation targets under the EU Nature Restoration Regulation. Focusing on multifunctional forests and their potential to support higher levels of biodiversity conservation and nature contributions to people, we highlight several aspects that necessitate greater consideration and recognition, both in research and practice. Tree species selection must move beyond species distribution models alone and integrate functional traits, provenance performance, and ecological impact assessments, since climate suitability alone does not guarantee performance under future climatic conditions. Genetic diversity is foundational for forest resilience but remains severely underutilized in operational forestry. As such, it can be advanced through AM, provenance mixing, and traceable seed sources, but all require close, continuous monitoring. For instance, the 2026 EU Regulation on Forest Reproductive Material strengthens traceability, but its effectiveness requires sustained investment in provenance trials, monitoring, and decision-support tools. The nursery production chains contain multiple points where genetic diversity is inadvertently eroded, and while activities such as minimum genetic diversity standards, regional seed exchange networks, and low-cost molecular monitoring can improve the outcomes, it is still a sector that is severely underfunded and dismissed, especially when it comes to less economically important species. In this sense, an alternative approach could be to support activities that focus on less-studied species but are relevant to the local and regional biodiversity conservation context. Once on the field, the choice between direct seeding and planting requires integrated planning that explicitly considers genetic diversity targets, site conditions, and monitoring capacity rather than binary preference. In this sense, post-establishment management that promotes structural and species heterogeneity through species admixture, extended rotations, soil amendments, and mycorrhizal inoculation could significantly enhance both biodiversity and climate resilience of newly established forests, from their early years onwards. And finally, like in natural forests, questions on how to support multi-functionality in urban forests also arise. Urban forests suffer from taxonomic homogenization; thus, context-specific species selection that prioritizes functional diversity and native conservation value is needed, alongside transitioning from isolated specimen planting to stand-level establishment where feasible.

Across Europe, long-term systematic monitoring of established stands, accessible, evidence-based decision frameworks tailored to European ecoregions, and financial mecha-

nisms that support nurseries and practitioners in diversifying beyond currently favoured species and provenances remain needed. This has been partially addressed through research projects of various sizes, but better targeting of species, inclusion of more diverse regions and contexts, and closing the persistent gap between scientific knowledge and operational practice are the necessary conditions for more significant progress.

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Author contributions AD, MK, and AM developed the concept of the manuscript. All authors participated in the investigation, the preparation of figures for their relevant sections and the writing of the original draft and the revised version of the manuscript. AD and AM conducted the writing (review & editing) of the manuscript. EA, CC, DG, BK, ML, BM, JM, AP, RP, and RT provided valuable feedback during the editing. AD and AM and dealt with the submission process.

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