Beyond single species seed orchards: A multi-species framework for tropical tree breeding and forest management

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Abstract

Conventional forest tree breeding has largely focused on species that perform well in monoculture systems, where genetic evaluation, seed production, and management can be optimized under uniform conditions. While this approach has delivered substantial genetic gains, it does not adequately address the growing demand for forests that function as diverse, climate resilient ecosystems. Most tropical tree species occur native in species diverse ecosystems, where species have co-evolved under various degrees symbiotic interactions from mutualism to commensalism. It is reflected in plantings, where many of the species therefore grow best/only in mixed species stands, where ecological interactions shape their performance, adaptability, and long-term survival. Yet breeding strategies specifically designed for such mixed systems remain largely unexplored. While the concept of mixed-species evolutionary breeding has been explored in crop systems, comparable approaches remain largely unexplored in tree breeding. This is paradoxical, given that the genetic basis of interspecific interactions is likely to be particularly important for tree species that exhibit reduced fitness in monocultures. Rather than exploiting the genetics underlying species interactions, conventional tree breeding has largely focused on selecting individual genotypes that perform best under single-species conditions. In response to this discrepancy, we propose a shift toward designing and selecting seed sources based on their performance, ecological function, and economic value within relevant species mixtures rather than in single-species systems. We advocate breeding programs that maintain high levels of genetic diversity in planting material to enhance the resilience and adaptive capacity of restored forests, while simultaneously providing a cost-effective framework capable of accommodating multiple tree species. Such an approach reflects the growing recognition that future forestry and restoration efforts will increasingly rely on diverse, mixed-species plantings to deliver resilient and multifunctional forest ecosystems. Based on these considerations, we propose the novel concept of Multi-species Breeding Seed Orchards (MBSOs) as a transformative approach to tropical tree improvement. Unlike traditional single-species orchards, MBSOs are designed to mimic natural forest dynamics while enabling systematic genetic improvement, and to serve as a reliable source of genetically improved seeds for diverse applications including plantation forestry, landscape restoration, agroforestry, and broader tree planting and climate-smart forestry initiatives. By integrating ecological principles with quantitative and genomic breeding methods, this concept seeks to reconcile productivity, biodiversity, and resilience within a single breeding framework. We discuss the scientific and operational challenges including species compatibility, reproductive synchrony, spatial design and competition management, maintenance of genetic integrity within and across species, and the complexity of estimating genetic parameters such as heritability and breeding values in mixed species contexts. We critically examine these biological, genetic, and design constraints and discuss emerging methodological and analytical solutions to overcome them. Finally, we present the conceptual design and layout of a planned MBSO to be established at Karura forest in Nairobi, Kenya, envisioned as the first breeding seed orchard of its kind. This novel initiative will serve as both a research platform and a demonstration site, advancing the science of breeding trees for mixed species systems and redefining the future of tropical tree improvement under the pressures of climate change and the urgent need for tree plantings as

part of a sustainable green transition toward biobased and resilient economies.

1. Ecological foundations: Forest dynamics and successional guilds

The majority of native natural tropical forests are multi-species systems structured along successional gradients, where tree species occupy distinct ecological niches defined by their light requirements, growth strategies, and life-history traits. A widely recognized classification distinguishes pioneer species, non-pioneer light-demanding (NPLD) species, and shade-tolerant late-successional species, each playing a specific role in forest development and regeneration (Hawthorne, 1995). These guilds are not static categories but represent dynamic strategies that interact across space and time to shape forest structure and function. Insights from long-term tropical forest plot networks have substantially advanced our understanding of the mechanisms underlying species coexistence and community assembly. Empirical studies have demonstrated that processes such as stabilizing density dependence, abiotic niche partitioning, and interspecific interactions collectively regulate seedling survival, species diversity, and forest composition (Adler et al., 2018; Hülsmann et al., 2024; Johnson et al., 2017; Pretzsch and Schütze, 2021). These mechanisms operate across environmental gradients and disturbance regimes, reinforcing the importance of both intra- and interspecific interactions in maintaining diverse and resilient forest ecosystems (Adler et al., 2018; Lan et al., 2012; Pretzsch et al., 2026). A central concept emerging from this body of work is that of the regeneration niche, which defines the specific environmental conditions required for successful seedling establishment. Pioneer and NPLD species typically recruit in canopy gaps where light availability is high, whereas shade-tolerant, late-successional species establish under closed canopies or beneath nurse vegetation (Fagundes et al., 2018). Facilitative interactions, particularly during early establishment, are therefore critical, as many late successional species depend on moderated microclimatic conditions provided by existing vegetation. These ecological dynamics have important implications for managed systems. Classical short rotation plantation systems may fit well with the regeneration niche of pioneer species, but less so for NPLD species. Similarly, conventional single-species breeding approaches may effectively capture and use genetic variation in vigor and fitness for pioneer species, but largely overlook successional processes and interspecific interactions when testing shade-tolerant species in conditions that are suboptimal for growth and survival (Valladares et al., 2016). In contrast, incorporating ecological principles such as stratified canopy structure and facilitative interactions can enhance the ability to select trees with high establishment success and long-term stability. Recent advances in understanding early life-stage dynamics further emphasize the importance of these processes. Studies on tropical tree demography have shown that seedling survival and persistence are strongly influenced by species-specific responses to competition, light availability, and microsite conditions, ultimately shaping forest composition over time (Condit et al., 2025). Together, these findings provide a robust ecological foundation for designing systems that integrate species with complementary functional traits and successional roles (Ashton et al., 2001). Overall, tropical forest dynamics are governed by the interplay of disturbance, succession, and species interactions. Recognizing and incorporating these processes is essential for developing multi-species breeding approaches that more closely reflect natural forest systems, thereby supporting both ecological functionality and long-term productivity.

2. Evolution of forest tree breeding and the rationale for evolutionary multi-species breeding

Tree breeding has long been a cornerstone of sustainable forestry, delivering genetic gains in productivity, wood quality, and resistance traits while enhancing adaptability to environmental change (Fady et al., 2016; Graudal et al., 1995). Conventional breeding is based on continuous cycles of testing and selection with deployment. The best genotypes are deployed in each generation and breed to create the next generation (Eriksson et al., 2020). The gain depends on the efficiency of the selection, and the genetic material is therefore carefully evaluated under controlled conditions, typically in field trials established and managed under relatively uniform conditions, and almost always in single species trials(Chakrabarty and Külheim, 2025; White et al., 2007). This approach has proven effective for many traditional forest plantation species, but it does not reflect the ecological context in which most forest trees naturally grow and regenerate (Namkoong et al., 1988). As a result, restoration programs that deploy planting material developed for classical short rotation plantation programs may rely on genetic material selected for environmental conditions that are fundamentally different from those in which it is expected to establish, compete, and persist.

An alternative to conventional breeding for short rotation plantations is a multi-species testing approach that evaluates fitness in terms of survival, growth, and reproductive success under ecologically realistic conditions, where traits such as shade tolerance and competitive ability play pivotal roles and cannot be reliably predicted from monoculture trials. Both species-level traits (Davrinche and Haider, 2024) and genotype- or seed-family-level responses (Hoeber et al., 2017; Tang et al., 2025) can shift, and even reverse in ranking, once individuals are grown alongside heterospecific neighbors. A genotype selected for fast height growth under open, uniform spacing may be a poor competitor for light once placed beside other species, while a genotype that performs modestly alone may hold a decisive advantage once shade tolerance becomes the limiting trait (Szwagrzyk et al., 2012). This is not simply environmental noise; it may reflect a genetic effect that single-species trials cannot capture. A tree's phenotype depends not only on its own genotype (a direct genetic effect) but on the genotype of its neighbors (an indirect, or associative, genetic effect). Because every neighbor in a conventional progeny trial belongs to the same species, only conspecific indirect effects are ever estimated, the interspecific indirect genetic effects that will govern performance in a mixed planting are structurally invisible to the trial design (Bourke et al., 2021).

From an ecological perspective, single-species stands are also more vulnerable to pests, diseases, and climatic extremes, because host concentration reduces the structural and functional diversity that buffers natural forests against disturbance (Bauhus et al., 2017; Ingvarsson and Dahlberg, 2019; Liu et al., 2022; Messier et al., 2022). As climate change accelerates and environmental uncertainty intensifies, forests are increasingly expected to deliver resilience alongside productivity (Gould et al., 2024). In Europe, tree breeders are already responding through breeding strategies that have been reoriented toward supporting mixed-species, close-to-nature forest restoration rather than continued reliance on even-aged monoculture deployment (Larsen et al., 2022; Ray et al., 2022). However, in much of the tropics, genetically improved seed sources remain scarce despite rising demand from plantation forestry, landscape restoration, agroforestry systems, and broader tree planting initiatives (Graudal et al., 2022), and restoration efforts often rely on material collected from natural forests or remnant trees without knowledge of genetic quality or provenance suitability (Dawson et al., 2011; Jalonen et al., 2018; Lillesø et al., 2011; Roshetko et al., 2022).

Mixed-species approaches have been explored more extensively in crop breeding than in forestry, and the findings are directly relevant. Across wheat-legume and cereal-pea systems, genotypes selected for high monocrop yield have repeatedly failed to predict performance in mixture, prompting calls to re-design breeding programs around interspecific rather than purely intraspecific performance (Bančič et al., 2021). To operationalize this, crop breeders have extended the combining-ability framework long familiar from progeny testing (general and specific combining ability), into general and specific mixing ability, which describe a genotype's average performance across mixture partners and its performance with a particular partner, respectively (Haug et al., 2021). No equivalent framework currently exists for forest trees, despite the underlying concept being the same that tree breeders already use. This gap reflects a broader disconnect between the ecological complexity of natural forests and the predominantly single-species frameworks used in tree improvement programs.

The concept of Breeding Seed Orchards (BSOs) was developed for breeding of tropical trees species in the 1980'ties in order to integrate breeding, seed source development and gene conservation (Barnes, 1995). The Multi-Species Breeding Seed Orchard (MBSO) expands the concept by integrating species mixtures into the breeding populations, so that mixing ability becomes a selectable trait alongside growth, form, and resistance. While traditional breeding seed orchards are confined to single-species systems (Funda and El-Kassaby, 2012; Wright, 2012), MBSOs are designed to test genetic material under species mixtures that more closely mimic natural forest environments, allowing assessment of growth dynamics, interspecific interactions, and complementary ecological functions such as differing successional roles. This approach has the potential to facilitate the selection of superior genotypes of shade-tolerant and late-successional species that are adapted to natural ecological conditions and biotic interactions, thereby providing high-quality genetic material for the establishment of structurally diverse, functionally resilient, and ecologically sustainable plantings.

The adoption of MBSOs extends the principles of conventional breeding seed orchards by integrating evolutionary ecology and community assembly into tree breeding. MBSOs share many of the genetic management considerations of single-species breeding systems, including the maintenance of genetic diversity, control of relatedness among selected trees, and balanced seed and pollen production (Galeano et al., 2021; Hall et al., 2023; Neophytou et al., 2020; Wang et al., 2023), but provide a framework for breeding tree populations that are tested and selected to function within diverse forest communities. A key strength of MBSOs lies in their ability to mimic the structure and ecological functioning of natural mixed forests. By combining species with complementary ecological strategies, growth rates, light requirements, and successional roles, MBSOs can foster stable species coexistence, promote functional complementarity, and support ecosystem processes that underpin productivity, resilience, and long-term forest stability. The deliberate integration of species occupying different ecological niches also provides opportunities to maintain breeding populations that are directly relevant to operational restoration and mixed-species forestry, where trees are expected to establish, grow, and reproduce under complex biotic interactions rather than in monocultures. Further, a seed source design based on species mixture simply allows easier and more abundant seed procurement from many shade tolerant species that thrive poorly in monocultures. The ecological foundation of MBSOs provides opportunities to capture interactions that are largely absent from conventional breeding systems. Tropical tree species have coevolved with diverse pollinators and seed dispersers, and these interactions strongly influence reproductive success, gene flow, and species persistence (Fleming and Kress, 2013).

Realizing these benefits requires careful orchard design and management. Species should be selected based on functional compatibility, including complementary light requirements, growth rates, and successional status, while ensuring that the resulting species mixtures reflect vegetation types targeted for restoration and operational forestry. Phased establishment can reduce early competition and facilitate canopy stratification, particularly for breeding shade-tolerant and late-successional species. Balanced representation of species and genotypes at planting, together with adaptive management through thinning and density regulation, helps maintain both ecological functioning and genetic diversity throughout orchard development. Taken together, these principles allow MBSOs to serve simultaneously as breeding populations, seed production systems, and experimental platforms for developing genetically improved planting material suited to diverse forest ecosystems. The practical implementation of these systems, however, introduces a number of ecological, genetic, and management considerations that differ from those encountered in conventional single-species breeding programs. Accordingly, the following section examines these challenges in detail and discusses potential strategies for addressing them.

3. Challenges in establishing MBSO and potential solutions

3.1 Orchard design complexity

Traditional tree seed orchards are typically established as single-species systems, either as clonal seed orchards (CSOs) or seedling seed orchards/breeding seed orchards (BSOs), designed to maximize genetic gain, seed production efficiency, and ease of management (Funda and El-Kassaby, 2012). These orchards consist of selected plus trees arranged in spatially balanced layouts to minimize inbreeding and facilitate effective pollination (White et al., 2007). Their efficiency is supported by the relative uniformity in species biology such as synchronized flowering, comparable growth rates, and similar silvicultural requirements, which enables coordinated management and optimized seed production (Wang et al., 2023; Xie et al., 2022). In contrast, MBSOs are inherently more complex because tree performance reflects not only genetic potential but also interspecific interactions for resources such as light, water, nutrients, and space. This adds a layer of heterogeneity associated with species identity and community composition that complicates the estimation of genetic parameters and breeding values (El-Kassaby and Askew, 1991; Rodionov et al., 2019; Tsumura, 2011). At the same time, this complexity creates unique opportunities. By combining species with complementary ecological traits, MBSOs can harness niche complementarity, whereby resource partitioning and facilitative interactions among species enhance stand productivity beyond that achieved by individual species grown in isolation (Loreau and Hector, 2001). In some cases, the presence of one species can directly improve the survival and growth of another (Lan et al., 2012). Consequently, MBSOs provide an opportunity to evaluate and select genotypes under ecologically realistic mixed-species conditions, where positive interspecific interactions contribute to resource-use efficiency, stand resilience, and ecosystem functioning. This approach enables the production of genetically improved reproductive material better suited for establishing diverse, multifunctional, and climate-resilient forests.

A central challenge in the design of MBSOs is the selection of species combinations that realistically reflect the mixed species stands used, or expected to be used, in forestry and restoration practice. Achieving this objective is not straightforward, as species compatibility depends on a range of ecological characteristics, including growth rates, light requirements, reproductive phenology, and establishment dynamics. Furthermore, the classification of species into successional guilds and ecological niches is often uncertain and context-dependent, varying among regions, forest types, and studies. Consequently, species selection should be guided by site-specific ecological knowledge and, where possible, local silvicultural experience. The challenge is further complicated by the fact that natural forest mixtures are shaped by dynamic ecological processes operating over long time scales. Successional development results from a combination of facilitative and competitive interactions, disturbance regimes, environmental filtering, and trade-offs among species. In contrast, the objective of an MBSO is not to replicate these processes themselves, but rather to create a stable representation of species mixtures that occur in practice. To achieve this, orchard design should seek to minimize the role of competition as a driver of species composition. Wide initial spacing and carefully planned thinning interventions can help prevent competitive exclusion and ensure the long-term representation of all target species. At the same time, unlike single-species systems where selective thinning may lead to dysgenic outcomes (Silva et al., 2008), the management of MBSOs is expected to act in the opposite direction and help maintain genetic diversity and adaptive potential.

Spatial arrangement follows from this. Unlike conventional breeding seed orchards, which favor regular plantation-style row arrangements, MBSOs may benefit from spatial designs that more closely resemble natural forest ecosystems. Species can be arranged in heterogeneous and seemingly random spatial patterns that mimic natural stand structure and species associations, thereby creating a more ecologically realistic environment for evaluating genetic performance in mixed-species systems and better capturing the spatial and temporal dynamics through which species interactions develop (Forrester, 2014). Interspersion also carries a functional advantage: tree diversity reduces herbivory by specialist forest insects, but this associational resistance depends on non-host neighbors being close enough to disrupt host-finding, not merely present elsewhere in the orchard (Jactel and Brockerhoff, 2007). An alternative approach is grouped or segregated planting, where species are established in discrete blocks within a shared orchard. While this configuration facilitates species-specific management and simplifies seed collection, it may reduce ecological interactions and limit the structural complexity characteristic of natural forests. Besides, intra-specific competition is more critical than inter-specific competition affecting survival, growth performance and seed production. Segregated planting therefore does not fully align with the primary objectives of MBSOs and is therefore generally not recommended as the preferred design approach.

Spatial design alone cannot ensure reproductive compatibility among component species. Although grouping species with compatible flowering phenology remains important, additional management interventions, such as controlled pollination and the phased establishment of species with contrasting growth rates, may help synchronize reproductive dynamics and reduce early competitive effects (Webber, 1995). MBSOs also provide opportunities to enhance pollination through the deliberate design of species mixtures that support diverse and abundant pollinator communities. For many tropical tree species, particularly those dependent on insect pollination, pollinator availability can be a major constraint on seed production. Incorporating species with complementary flowering periods or shared pollinator guilds may increase pollinator abundance and visitation, thereby improving pollination efficiency, seed set, and the reliability of seed production. Where closely related species are included, orchard design should also consider the potential for interspecific hybridization and unwanted gene flow (Kremer et al., 2012) through appropriate species selection and spatial arrangement.

3.2 Challenges in genetic parameter estimation

Maintaining adequate genetic diversity within each species remains a fundamental requirement, as in conventional BSOs (Funda and El-Kassaby, 2012; Namkoong et al., 1988; White et al., 2007). Each species should be represented by a sufficient number of unrelated individuals to ensure effective population size and avoid inbreeding depression. These genetic management principles remain unchanged in MBSOs, although their implementation becomes more complex due to the presence of multiple species.

In traditional forest tree breeding programs, quantitative genetic analyses have played a central role in estimating genetic parameters such as heritability, genetic correlations, and breeding values, primarily within single-species seed orchards(Funda and El-Kassaby, 2012; White et al., 2007; Wright, 2012). These analyses often rely on linear mixed models and variance component estimation using pedigree based methods such as restricted maximum likelihood (Falconer and Mackay, 1983). The relatively uniform genetic background and controlled environmental conditions in field tests of genetic material make it feasible to partition phenotypic variance into its genetic and environmental components with reasonable accuracy (White et al., 2007). This framework has enabled tree breeders to select individuals based on estimated general or specific combining ability, as well as to predict genetic gains under different selection intensities and mating designs (Zobel and Talbert, 1984).

However, applying these traditional approaches in MBSOs remove that uniformity: heritability estimation must now disentangle species specific genetic effects from shared and heterogeneous environmental influences. Standard single-species Best Linear Unbiased Prediction (BLUP) models (Isik et al., 2017) are not built to capture the additional level of interspecific variance and covariance structures (Lo et al., 1997). Moreover, predicting breeding values in a multi-species context requires moving beyond classical models that assume uniform genetic structures and selection pressures (Lo et al., 1997). Conventional single-species BLUP or GBLUP (genomic BLUP) models will therefore need reformulation to account for interspecific trait correlations, non-additive genetic effects, and genotype by species or genotype by environment interactions that are common in mixed species systems. A quantitative genetics framework recently developed for intercropping systems offers a direct template: it extends mixed-model theory to jointly estimate direct and indirect genetic effects across both single-species and multi-species groupings, so that genetic gain can be predicted simultaneously within and across species combinations (Salomon et al., 2026). Adapting this framework to trees would require extending BLUP and genomic BLUP models to account for interspecific trait correlations, non-additive genetic effects, and genotype-by-species interactions, thereby providing the methodological foundation required for reliable estimation of breeding values in MBSOs.

Crop breeding offers a second, more immediately transferable tool: the general and specific mixing ability (GMA/SMA) framework, which extends the combining-ability concepts already used in tree progeny testing to describe a genotype's average performance across mixture partners (GMA) and its performance with a specific partner (SMA) (Wright, 2012). This has since been argued as a necessary, rather than optional, addition to breeding programs wherever mixtures are the deployment target (Annicchiarico et al., 2019). Unlike the mixed-model framework above, GMA/SMA requires no reformulation of the underlying genetic model: it maps directly onto the combining-ability selection tree breeders already practice in progeny testing, which is what makes it the more immediately applicable of the two tools. The practical obstacle is trial size, full factorial trials across all species combinations quickly become infeasible as the number of candidate species grows, incomplete factorial designs have been developed to estimate GMA and SMA variance with a fraction of the plots a full factorial would need (Haug et al., 2021). No equivalent trial-design framework yet exists for forest trees, despite MBSOs facing precisely the estimation problem GMA/SMA was built to solve. This gap reflects a recent call for breeding programs to shift toward multicrop systems in agriculture (Moore et al., 2023), a shift that has not yet occurred in forestry.

Genomic selection (GS) is already established in single-species tree breeding, improving prediction accuracy over pedigree-based BLUP in several breeding programs (El-Kassaby et al., 2024; Grattapaglia and Resende, 2011; Lobo et al., 2026). Extending it to MBSOs means predicting breeding value from a genomic relationship matrix that spans species boundaries, combining shared genomic information where pedigree or marker data allow it, with species-specific heritability and variance structure where they don't. Crop breeders working on intercrop systems have already begun building this: genomic selection models incorporating mixture performance have been shown to improve selection efficiency in intercrop breeding programmes(Bančič et al., 2021), and a multi-species genomic selection framework has been proposed explicitly for agroecosystems spanning several crop species and planting configurations (Wolfe et al., 2021). No forest-tree equivalent exists yet. If developed, such a framework would also alleviate the trial-size constraints identified above. Genomic prediction could reduce the number of species combinations requiring direct phenotyping to estimate GMA and SMA, making incomplete factorial designs even more resource-efficient than the framework proposed by Haug (Haug et al., 2021).

3.3 Management challenges

Establishing a MBSO presents substantial logistical and silvicultural challenges, primarily due to differences in seed availability, propagation requirements, growth dynamics, and early stand development among species. Differences among species in traits such as phenology, growth rates, and propagation requirements can present both challenges and opportunities for efficient orchard management. For example, variation in flowering and fruiting times among species could be advantageous by distributing labour requirements for pollination, seed collection, and nursery operations more evenly throughout the year, rather than concentrating them in a single season. To effectively manage these complexities and capitalize on potential benefits, it is essential to build a strong knowledge base on the biological and ecological characteristics of each species. The development and use of accessible, comprehensive databases on species traits, phenology, and management requirements will be critical for informed planning and successful implementation of MBSOs. Unlike conventional single-species orchards, where seed sourcing and nursery protocols are standardized, MBSOs require the coordinated procurement of reproductive material from multiple species, often across different populations and numerous mother trees. Ensuring adequate representation of genetically diverse and well documented seed sources can be difficult, particularly when species vary in fruiting periodicity, seed longevity, and storage behavior (e.g., orthodox vs. recalcitrant seeds). However, in practice, the number of species included in an MBSO is typically limited, (3-4 species) making the logistical challenge comparable to planning several BSOs simultaneously. For most candidate species, flowering and fruiting tend to occur within the same season, and differences in seedling age or growth rates can be accommodated through phased or staggered planting, which is a standard part of orchard design. While species may differ in germination requirements, shade tolerance, root architecture, and susceptibility to pests and pathogens (Blakesley et al., 2002; Elliott et al., 2003; Khurana and Singh, 2001) these differences are not fundamentally different from those encountered in the establishment and management of single-species BSOs.

The regeneration dynamics of tropical forests are governed by interactions among species traits, disturbance regimes, and successional processes. Typically, forest recovery follows a sequence in which fast-growing pioneer or non-pioneer light-demanding species colonize canopy gaps or disturbed sites, creating conditions that facilitate the establishment of shade-tolerant, late-successional species beneath a developing canopy (Ashton et al., 2001). This sequence is the ecological basis for MBSO planting design. Species vary in shade tolerance and early survival strategy - some establish under partial or closed canopy, others need high light, and planting schedules should be built around these differences. Empirical evidence on tropical tree survival from seed through the earliest sapling stage highlights the importance of aligning species' ecological requirements with their spatial and temporal placement within the orchard (Condit et al., 2026), and recent restoration trial evidence supports staggered spacing and planting order between early- and late-successional species as a determinant of late-successional seedling survival (Bürli et al., 2026).

The sequence of establishment is especially critical. Light-demanding species are often introduced first to rapidly occupy the site and can function as nurse trees, moderating microclimatic conditions and facilitating the establishment of shade-tolerant species (Lu et al., 2017; Padilla and Pugnaire, 2006). However, delayed introduction of slower-growing species must be carefully managed to prevent competitive suppression once early established species dominate canopy space. Alternatively, simultaneous planting may require early interventions such as thinning or spacing adjustments to maintain balanced growth. Either way, early-stage monitoring is therefore essential as survival, growth rates, and crown development can quickly alter stand structure and species representation. These dynamics should inform initial species combinations and guide adaptive management interventions, including selective thinning, gap creation, replacement planting, and density regulation. Continuous monitoring during the initial years is particularly important to detect mortality patterns, competitive exclusion, or site-species mismatches that may compromise long term orchard performance.

3.4 Practical and socioeconomic constraints

Policy and regulatory barriers also pose a significant challenge. In many regions, regulations on seed certification and the movement of seed materials are structured around single-species systems (Nanson, 2001), which complicates the transfer and sale of seeds from MBSOs. Existing certification and approval frameworks, such as the OECD Forest Seed and Plant Scheme (Nanson, 2001), were developed for conventional single-species breeding populations. Consequently, MBSOs may face challenges in gaining regulatory recognition, particularly where seed orchards are required to qualify as "tested" reproductive material under current national or international certification systems (Gömöry et al., 2021; Konnert et al., 2015; Koskela et al., 2014). However, since MBSOs are established as planted seed sources with a clearly documented design and origin, they should be compatible with OECD certification requirements. The OECD scheme is designed to accommodate planted seed sources with known provenance and management, so MBSOs that meet these criteria are unlikely to face significant barriers to certification. While the development of appropriate certification and regulatory frameworks for MBSOs may take many years, these challenges are not fundamentally greater than those faced when managing several single-species BSOs simultaneously. The main difference lies in the need to coordinate across multiple species within a single orchard, but the underlying regulatory and certification issues are similar in scope and complexity. In practice, the primary objective of both conventional BSOs and MBSOs is to supply seed for the national market, with international seed sales being of limited relevance. Therefore, regulatory and certification frameworks should prioritize facilitating the movement and certification of seed within national boundaries, as this is the main context in which MBSOs are likely to operate.

To support the successful implementation and management of MBSOs, targeted policy and capacity building measures are essential just as they are for ordinary BSOs. First, developing best practice guidelines for MBSO management is crucial. These guidelines should provide clear protocols for species selection, orchard design, genetic management, and pest control, ensuring that breeding professionals can effectively navigate the complexities of managing mixed species systems. Standardized best practices can also improve the consistency and efficiency of MBSOs across regions. Additionally, capacity building initiatives for breeding professionals, especially in genetic analysis in a multi-species setup are necessary to equip individuals with the skills and knowledge required to manage these more complex systems. Training programs, workshops, and collaborative research projects can enhance the expertise of local professionals in areas such as genetic modeling, orchard design, and long-term monitoring, strengthening the overall effectiveness of multi-species breeding programs.

4. Designing an MBSO: the Karura forest in Kenya

Building on the conceptual opportunities and practical challenges outlined above, we initiated the design of what is, to our knowledge, the first MBSO in an urban tropical forest context at Karura Forest, Nairobi, Kenya. The model is intended to function as an ecologically integrated component of the forest ecosystem. Its design is guided by the long-standing restoration philosophy jointly advanced by Friends of Karura Forest and the Kenya Forest Service, which prioritizes the restoration and maintenance of diverse, indigenous and naturally functioning forest ecosystems rather than monoculture plantations.

Karura Forest is classified under the Afromontane Dry Transitional Forest (Fh) vegetation type according to regional vegetation mapping, representing a mosaic of light demanding and shade tolerant native tree species typical of East African highland systems. The site provides a strategic setting to operationalize the MBSO concept by integrating ecological realism with structured tree breeding objectives. Based on the regional potential natural vegetation map (Lillesø et al., 2014) and documented species composition of the Afromontane Dry Transitional Forest zone, we identified a shortlist of eight native tree species representing three functional canopy categories: (i) canopy light demanding species, (ii) canopy shade tolerant species, and (iii) sub canopy shade tolerant species (Table 1). This functional stratification was intended to reflect natural forest structure while enabling controlled genetic management within species. The selection process considered ecological compatibility, successional status, availability of genetically diverse seed sources, and feasibility of coordinated establishment within a shared orchard framework.

Table 1: Tree species selection representing functional canopy categories for the design of a multi-species breeding seed orchard (MBSO) in the Afromontane Dry Transitional Forest zone at Karura.

Species	Canopy Characteristics	Characteristics
Albizia gummifera	Top canopy Light demanding	Tall, deciduos tree, non pioneer light demanding (NPLD)
Croton megalocarpus	Top canopy Light demanding	Tall, deciduos tree, non pioneer light demanding (NPLD)
Dombeya kirkii	Top canopy Light demanding	Tall, deciduos tree, non pioneer light demanding (NPLD)
Diospyros abyssinica	Top canopy Shade tolerant	Tall, evergreen tree, late successional
Olea europaea ssp. cuspidata	Top canopy shade tolerant	Tall, late successional, evergreen tree
Suregada procera	subcanopy shade tolerant	late successional, evergreen tree
Strychnos mitis	subcanopy shade tolerant	late successional, evergreen tree
Ehretia cymosa	subcanopy shade tolerant	late successional, deciduous tree

To operationalize the MBSO concept, we propose selecting one to two species from each functional canopy category resulting in an initial assemblage of up to four carefully selected native species. As illustrated in the conceptual design (Figure 1), the orchard is structured to mimic the vertical stratification described by Ashton (Ashton et al., 2001), with light demanding canopy species forming the main canopy layer, shade tolerant canopy species occupying intermediate positions, and subcanopy shade tolerant species developing beneath them. In natural tropical forests, emergent species, those that eventually rise above the main canopy - are also recognized as a distinct functional group (Ashton et al., 2001), though these are not included in the current MBSO design. Rather than including short lived pioneer species, which are typically unsuitable for long term breeding objectives due to their limited lifespan, we propose incorporating long-lived, non-pioneer light demanding (NPLD) species that has the same regeneration niche as pioneer species. These species combine relatively rapid early growth with extended longevity, allowing them to provide canopy structure and nurse effects while remaining compatible with long term genetic management goals.

The classification of Karura Forest as an Afromontane Dry Transitional Forest and the selection of characteristic species for this vegetation type are supported by foundational studies such as Trapnell's work on Kenyan forests (Kindt et al., 2011; Trapnell CG & Brunt MA, 1987) and the Kenya potential natural vegetation (Lillesø et al., 2024, 2014), which provide detailed descriptions and species lists for regional forest types. Incorporating these sources will ensure that species selection for the MBSO is ecologically grounded and aligned with established vegetation classifications. Given that Karura Forest is often described in vegetation studies as a *Diospyros–Olea* forest type, species within these genera are considered priority candidates for inclusion, as they represent key structural and ecological components of the Afromontane Dry Transitional Forest. Final species selection will be validated in consultation with botanical and ecological experts to ensure accurate successional classification and alignment with the site's natural forest dynamics and potential vegetation. Because Karura is an urban forest embedded within Nairobi, species selection was informed not only by successional guild classification and potential vegetation suitability, but also by local community perceptions, cultural value, aesthetic preferences, and stakeholder acceptance. Incorporating socially valued native species strengthens public support, enhances educational potential, and improves long term stewardship of the orchard.

To facilitate structural development and minimize early competitive imbalances, a phased establishment strategy is proposed. In the first phase, NPLD species will be planted to form the initial structural framework and create moderate microclimatic conditions. And in phase 2 shade tolerant top canopy and sub canopy species will be introduced beneath the developing canopy layer. This staggered approach allows early canopy formation to function as a nurse layer, buffering microclimatic extremes and improving establishment conditions for shade tolerant species, while maintaining the intended vertical stratification shown in Figure 1.

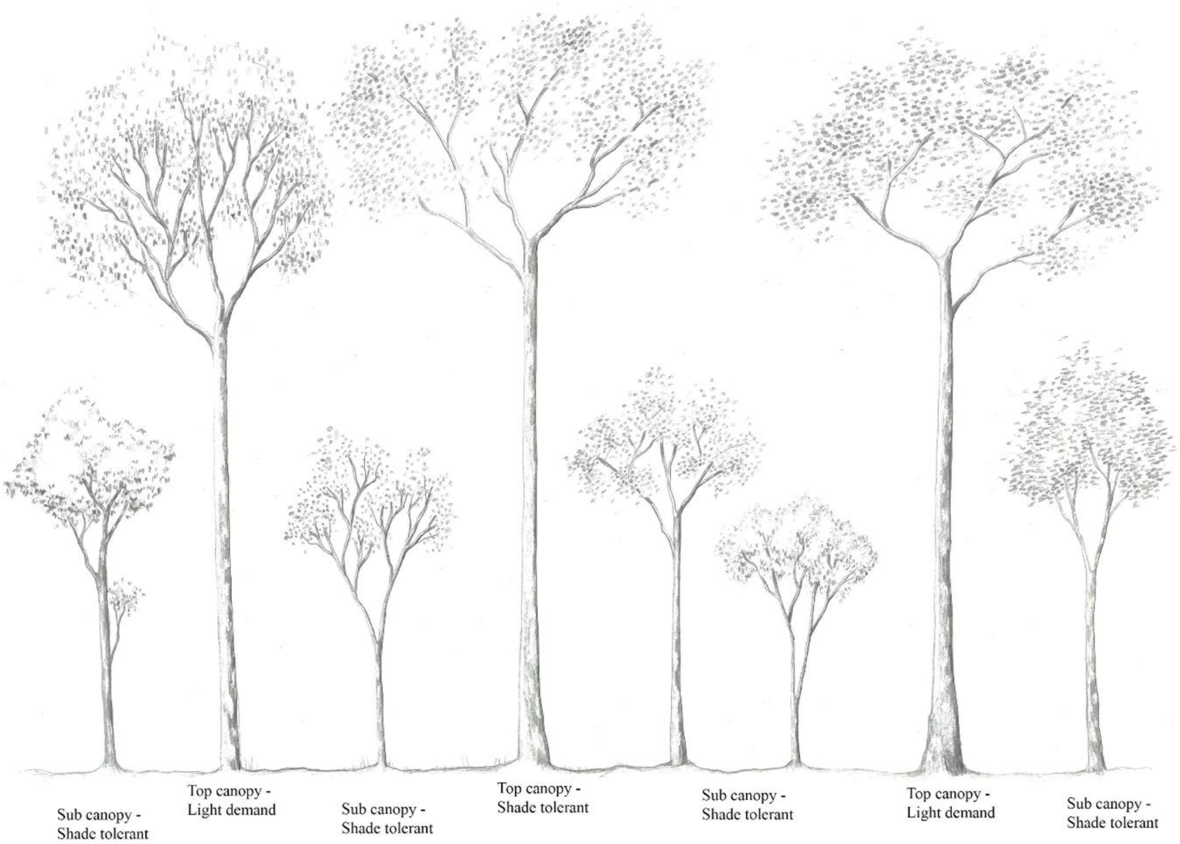

Figure 1: Conceptual layout of a multi-species breeding seed orchard (MBSO) showing the spatial distribution of native tree species from different successional guilds and functional canopy categories.

5. Future perspectives and research needs

Looking ahead, several key areas of research and innovation are critical to advancing the management and success of MBSOs. First, there is a pressing need for improved statistical models for genetic evaluation. Developing more refined models that can better account for the complexities of multi-species interactions, environmental variation, and interspecies genetic dynamics will enable more accurate heritability estimates and breeding value predictions. Modelling approaches, as recently discussed in the context of mixed-species crop breeding (Bančič et al., 2021), may also be valuable for optimizing the design and management of multi-species breeding seed orchards. Early data collected from MBSOs - such as growth rates, reproductive phenology, and interspecific interactions - could support the development of such models, ultimately informing more efficient stand design and management. These advanced models will be essential for optimizing the genetic potential of MBSOs and ensuring efficient breeding outcomes. Additionally, long term monitoring strategies are needed to track genetic diversity and species adaptation over time. Establishing robust monitoring frameworks will allow for the continuous assessment of genetic variation within orchards, providing valuable insights into how species respond to environmental changes and ensuring that genetic diversity is maintained. This will be crucial for adapting breeding strategies to future climate conditions and promoting the resilience of forest ecosystems. Finally, emerging technologies, such as AI driven genetic analysis, hold significant potential for revolutionizing MBSO management. Continued investment in these research areas will be crucial for the future success of MBSOs, ensuring that they can contribute to sustainable forest management, biodiversity conservation, and climate resilience in the years to come.

6. Conclusion

The MBSO concept represents a novel integration of ecological principles and structured tree breeding. While its implementation presents clear challenges including complex establishment logistics, interspecific differences in growth dynamics, seed sourcing constraints, and long-term structural management, these challenges are not insurmountable. Rather, they highlight the need for careful species selection, adaptive silvicultural planning, and coordinated genetic management from the outset. The Karura Forest initiative constitutes, to our knowledge, the first operational attempt to design and implement a structured MBSO within a natural forest framework. By aligning successional guild structure, vertical canopy stratification, and genetic representation within species, the MBSO moves beyond conventional single-species seed orchard systems and more closely reflects the ecological complexity of natural forests. Although this pilot is established within a tropical Afromontane system, the conceptual framework is transferable to other forest types, including temperate and boreal ecosystems. Mixed species stands, successional gradients, and functional canopy stratification are universal features of forest systems. With appropriate species selection and adaptation to local ecological conditions, the MBSO approach may have potential for application as a climate responsive breeding and restoration strategy. In an era of accelerating climate change and increasing demand for resilient forest landscapes, integrating genetic improvement with ecological realism offers a forward-looking pathway. The MBSO concept may provide a foundation for breeding programs that aim to maintain genetic diversity, enhance adaptive potential, and better emulate natural forest dynamics, thereby supporting long term forest sustainability. As highlighted throughout this paper, selecting species that are ecologically compatible and ensuring high genetic diversity within each species are critical for the successful establishment and functioning of MBSOs.

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