

CHAPTER 4

Species selection under predicted climate change: Opportunities and limitations

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Introduction

Globally, most forests are naturally regenerated, and only 7% of the total global forest area is planted forests (294 million ha). Less than half (45%) of the planted forest area is managed for timber production, fiber, energy, and non-wood forest products, and 55% of the planted forests are for ecosystem restoration and protection of soil and water (FAO, 2020a, b). Plantation forestry, an intensively managed subset of planted forests, supplies 33% of the roundwood harvested globally, of which 44% is nonnative species. Planted forests provide a range of other ecosystem services, including carbon sequestration and water retention. Moreover, even forestry plantations play a role in achieving biodiversity conservation objectives (Brockerhoff et al., 2008; Balieiro et al., 2020) by offsetting the need to extract resources from native forests and reducing land-use pressure on forests (Verheyen et al., 2016; Depauw et al., 2024).

Both regionally and globally, rapid environmental changes may alter species ranges and lead to the extinction of tree species and associated organisms (Dyderski et al., 2018). At larger spatial scales, climate is one of the most important drivers of tree distribution (Pearson and Dawson, 2003; Thuiller et al., 2011), while at smaller scales, other factors such as topography, soil nutrients and biotic interactions are more important and alter the climatic drivers of species distribution (Thurm et al., 2018; Dyderski and Pawlik, 2020). Given the pace of global climate change and the limited adaptive capacity of long-lived organisms such as trees, human intervention to assist the migration of species and populations seems necessary to ensure the stability of forest ecosystems.

The concept of assisted migration, originally intended to increase the productivity of forest stands, is gaining new importance as it aims to increase the resilience of species to novel climate and abiotic and biotic threats and to maintain rare and endangered species (Williams and Dumroese, 2013; Stanturf et al., 2020). The emergence of nonnative tree

(NNT) species that are artificially introduced or spontaneously spread outside their native range is linked to biogeographical and reproductive barriers (Blackburn et al., 2011; Soto et al., 2024). The rate at which they can spread, in turn, defines their invasive potential, which should be considered when assessing their impact on local habitats and biodiversity (Richardson et al., 2000). Therefore, knowledge of the invasiveness and reproductive potential of NNTs is crucial when selecting NNT species for reforestation and restoration (Brundu et al., 2020).

Selection of species and provenances is one of the most crucial decisions in forestry, determining not only productivity but also the stability of forests under changing environmental conditions. Selecting species for planting has always been a complex issue that must consider site conditions, future market conditions for production forests, and changes in regulation and society's expectations. The complexity and importance of the decision have increased considerably due to the uncertainty of future growing conditions due to climate change. Decisions on the selection of target species and provenances can require a trade-off between growth performance and the ability to persist under changing environmental conditions. Therefore a proper assessment of the ecological requirements of target species and provenances, as well as their plasticity and adaptability, determines the factors to consider in the decisions. The objectives of this chapter are to describe the factors to consider in selecting species for planting, including choice of native versus nonnative species, monospecific versus mixed stands, and to describe species distribution models (SDM) as a tool for selecting species adapted to the future climate. We should always remember the conclusion of Toumey and Korstian (1942): "No combination of silvicultural methods will mitigate mistakes in planting an inappropriate species or setting them out in an improper arrangement across a site."

Species selection: State-of-the-art

The choice of species to plant is a complex process with far-reaching implications (Poskin, 1926; Boudru, 1992). Matching tree species to site conditions is one of the most important decisions in forestry because a bad one can lead to many long-term problems or even the loss of a plantation (Kerr and Evans, 1993; Savill et al., 1997). In the period between planting and harvesting a managed forest, tree requirements must be continuously matched to the chosen site. The species selected for planting should therefore be those whose requirements throughout their lives are likely to be satisfied by the prevailing climate. The species must also fulfill the objectives of the planting program. Ecological considerations should be the first ones used when making the choice to match species with a site. Other considerations (e.g., social and economic) should not be ignored but used in conjunction with the ecological ones.

The economic and social suitability of a species for a forestation project/program is important, but must recognize basic biological considerations (Evans, 1992; Evans and

Turnbull, 2004; Fremout et al., 2022). Nevertheless, the purpose or objectives of growing trees are critical. Without a clear idea of why trees are planted, consideration of the technical aspects of species choice becomes arbitrary. As soon as the objectives are clear and agreed upon, it is possible to consider the tree species that satisfy the main objective and eliminate species that are inappropriate for the site, unavailable, or otherwise undesirable.

Forests are multifunctional, in that a particular stand will have several productive and protective functions. An established stand must fulfill the main role, or the function assigned to it, as much as possible. Where once economic criteria were paramount in species selection for planted forests, today the choice of species is based on multiple principles and considerations (Damian, 1969; Abrudan, 2006). Especially for restoration, native species have been emphasized, and one or more species from the regional species pool have been promoted in particular (Lu et al., 2017). Mixed stands with native species, without totally ignoring nonnative species, are advocated for climate adaptation (Kelty, 2006; Felton et al., 2022). The species chosen for mixed plantings should be compatible to reduce the negative effect of interspecific competition. Current tree planting programs aiming to reforest or restore land generally follow a conservative “local-is-best” approach for selecting appropriate species. But, given current and predicted climate change, locally sourced trees may lead to higher risks of planting failure, declining tree vigor, and suboptimal long-term forest conditions (MacKenzie and Mahony, 2021).

Whatever the purpose of a tree planting program is, along with matching the site, the selected species must also fit the needs of a landowner (Nyland, 2016). If the role of the forest is primarily production, the chosen species should ensure the highest profit. Plantation forestry has been heralded as a “win-win” that should provide both opportunities for forest owners to generate income and preserve the ecosystem services of a forest cover. These potential benefits, however, are not always realized; the factors that limit the positive socio-economic aspects of forests for low-resource producers include insecure land rights, long return times on initial financial investments, insufficient technical support, and lack of access to markets (Marshall et al., 2022). In addition, landowners and farmers may be hesitant to plant trees or may have negative attitudes toward the expansion of forest cover. Financial incentives from government bodies may encourage farmers to implement afforestation under certain conditions. Appropriate and well-functioning grant schemes are widely agreed to be an essential factor for increasing forestation rates.

Matching species with sites is fundamental to good silviculture. In particular, local climate factors that influence species choices are the incidence of drought, winter cold, and infrequent frosts in autumn or spring. Other factors that should be considered include aspect, especially for broadleaves that grow best on moister north and east facing slopes. Important soil factors are the presence (too much, as the effect of waterlogging) or

absence of water (too little, due to summer drought), fertility, and acidity or base saturation (see [Chapter 3](#) for details).

Species chosen should ensure a stand with a high structural diversity, which is more stable and can offer more future use options. Species selection must also consider the risks that reduce production or compromise the persistence of a species by the intensity, recurrence, and severity of disturbances. Examples include biotic agents such as insects (e.g., defoliating, sap-sucking, shoot/stem-boring and cutting, and root-feeding), fungi (e.g., *Ophiostoma ulmi* (Buisman) Melin & Nannf. in *Ulmus* spp.), and animals (e.g., depredation by cattle, sheep, goats, deer, moose, wild boar, squirrels, rodents). Risks of abiotic disturbances include wildfires, wind storms, mass movements such as landslides and avalanches, and increasingly extreme meteorological events, including drought and heat waves ([Seidl et al., 2017](#); [Stanturf et al., 2020](#)).

In addition to the selection of suitable tree species, whether native or nonnative, high-quality planting material is no less important for successful forestation. On the one hand, forest reproductive material (FRM) used for reforestation in Europe is largely categorized as “selected” under the EU Directive on Forest Reproductive Material 1999/105/EC ([Jansson et al., 2017](#)). On the other hand, sufficient quantities of suitable plants of the desired species may be unavailable because (i) the chosen species is locally unusual, (ii) the chosen provenance or seed origin is difficult to obtain, (iii) seed supply is poor owing to lean seed years, and (iv) there are trade losses, as production from nurseries is disrupted owing to weather, pests, and disease problems.

Species selection in the future

Climate change may represent the greatest challenge ever faced by forest managers, conservation biologists, and ecologists, with already realized and projected impacts that include changes in forest productivity ([Bottero et al., 2017](#)), tree habitat suitability ([Peters et al., 2020](#); [Cvijetković et al., 2021](#)), catastrophic tree mortality, and altered pest behavior ([Bentz et al., 2010](#)). Currently and in the future, forests are and will be frequently exposed to extreme events (e.g., droughts, wildfires, windstorms, and pest outbreaks) that interact and potentially cascade ([Burton et al., 2020](#); [Niggli et al., 2022](#)). Moreover, these disturbances are likely to increase their frequency and intensity with global change affecting the delivery of ecosystem services such as wood supply, resulting in severe economic, ecological, and social consequences ([Verheyen et al., 2016](#); [Jactel et al., 2017](#)).

Climate change already threatens European forests; therefore the selected species should be adapted not only to current conditions but also to changing conditions over the life of the future forest. The mean annual temperature has increased 1.7–1.9°C from the pre-industrial reference to the last decade—far stronger than the global average of 0.94–1.03°C, and climate models predict temperature to rise another

0.9–3.5°C by 2100 (Mette et al., 2021). The exceptionally dry summers in the early decades of the 21st Century have led to widespread forest dieback in Middle Europe, affecting not only boreal tree species such as Norway spruce (*Picea abies* (L.) Karst) and Scots pine (*Pinus sylvestris* L.) but also temperate tree species such as European beech (*Fagus sylvatica* L.) and others (Mette et al., 2021; Karrer et al., 2022; Montagnoli et al., 2023).

Changing the forest management paradigm to face climate change

Forest managers currently confront the task of integrating a forward-looking outlook into forestry decision-making protocols (Brang et al., 2014) by incorporating strategies and guidelines into forest management plans (Vacek et al., 2023). The decision-making process in forestation programs carries inherent risks due to the long lifespan of trees and their role as key species in forest biomes (Brang et al., 2014). Uncertainties in the future economics of forestry create problems for species selection as well (Klinka and Feller, 1984); the future economic costs and returns associated with forest products and markets cannot be accurately predicted at the time species are selected. Foresters and restorationists therefore need up-to-date knowledge and tools to help them make decisions on species selection for afforestation, reforestation, and restoration practices.

The evidence suggests that climate change will increase drought risk and severity, with specific regions including western North America, Central America, Europe, the Mediterranean, the Amazon, southern Africa, China, Southeast Asia, and Australia experiencing strong drying trends (Cook et al., 2020). In Europe, the greatest impact of these changes is currently being observed in forest ecosystems in the Mediterranean region (Rubio-Cuadrado et al., 2021). In addition, more frequent and more intense heatwaves and droughts are predicted for Central and Southern Europe. A Mediterranean-like climate can also be expected in Central Europe this century (Vacek et al., 2023). This increasing environmental pressure on trees is manifested locally and regionally through increased mortality (Sáenz-Romero et al., 2016; Seidl et al., 2017; Senf et al., 2020), disrupted balance of forest ecosystems due to changes in the dynamics of insects and pathogens, as well as an increase in the frequency of wildfires (Sierota et al., 2019; Wales et al., 2020; Rocas-Díaz et al., 2021).

In a regional and global context, these changes may involve species extinction, changes in species range, and associated organisms (Dyderski et al., 2018). Therefore the selection of species for future forests is the most important ecological, social, and economic decision determining the stability of forest ecosystems for the next decades, and as such, it should be based on continuously updated knowledge, risk analysis, and operational flexibility.

Traditionally, forest management strategies and growth and yield models supporting decision-making have assumed stable climatic conditions. As a result, forestation

practices have been based on a conservative “local-is-best” approach in selecting suitable species (MacKenzie and Mahony, 2021). However, this approach may become outdated in the face of rapidly occurring climatic changes (Thackeray et al., 2022; Zhou et al., 2023) that are manifested by fast shifts in air temperature, water availability, increasing risk of drought periods, and a shift in the regimes of both wildfires and storms (Dumroese et al., 2019; Cook et al., 2020; Somorowska, 2022; Montagnoli et al., 2023). Given current and predicted climate change, locally sourced trees may lead to higher risks of planting failure, declining tree vigor, and suboptimal forest conditions due to different climates in the future compared to those in which they evolved (Aitken and Whitlock, 2013).

Suitable tools for studying the characteristics of source material include provenance tests, progeny tests, common gardens, and others. Starting material from multiple seed sources is collected and tested, and based on long-term test results, the optimal transfer of starting material from these seed sources to suitable habitats is determined, ensuring that the new forest meets the objectives of its establishment (Fig. 4.1). Many such tests have been conducted for commercial species, but older installations likely have not experienced the expected climate extremes. Needed are new trials that build on the accumulated knowledge but test new species or provenances beyond their native range, that is, in assisted migration (Sáenz-Romero et al., 2021; Lindback et al., 2023; Park and

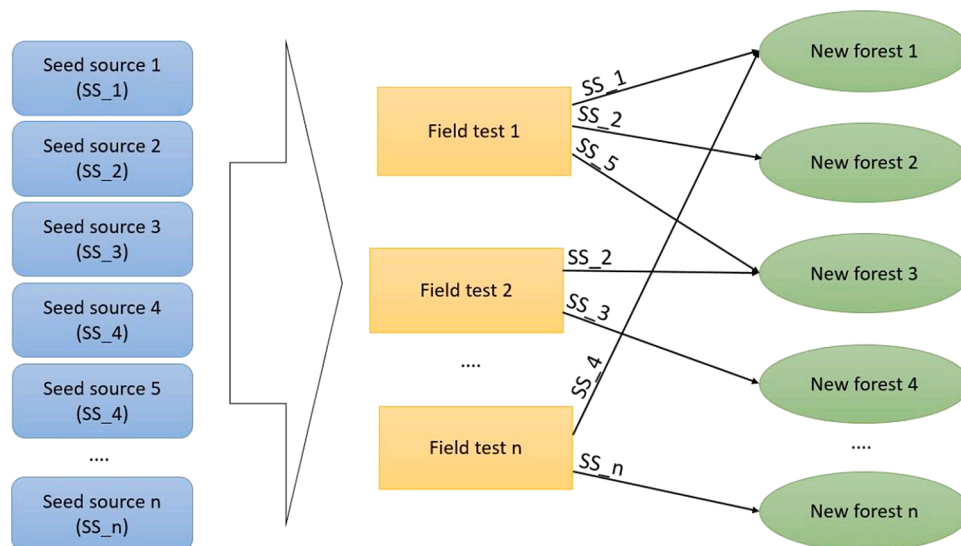


Figure 4.1 Testing seed sources in field tests for adaptability to new habitats with many different seed sources spread through all native range (left), tested in different environmental conditions (middle), and recognized as suitable for transfer to new habitats (right) due to ongoing and/or predicted climate changes or other unfavorable environmental conditions. (Credit: Authors).

Rodgers, 2023; Royo et al., 2023; Twardek et al., 2023; Bower et al., 2024; Chakraborty et al., 2024).

Mechanisms of tree response to climate that impact species selection

A growing body of research demonstrates that both inter- and intraspecific variability significantly impact the responses of trees to climate change (Aitken et al., 2008; Leites and Benito Garzón, 2023). Tree populations can respond to new conditions by adapting, which is achieved through the process of evolution, or by migrating to a more favorable niche; extinction is an undesirable response to changes and signifies a lack of adaptation (Valladares et al., 2014; Benito Garzón et al., 2019; Gárate-Escamilla et al., 2019) (Fig. 4.2). Both mechanisms of tree responses to climatic factors, adaptation, and migration can be utilized in knowledge-based forest resource management in the face of climate change (Aitken and Whitlock, 2013; Valladares et al., 2014; Leites and Benito Garzón, 2023).

Genetic adaptation refers to long-term changes in the gene pool of a population, on the one hand, allowing for better adaptation to local climatic conditions. It is a slow process, but it is crucial for the survival of species in the long term (Leites and Benito Garzón, 2023). On the other hand, phenotypic plasticity (Fig. 4.2) allows tree species to quickly respond to changing environmental conditions through changes in phenotypic functional traits without the need for genetic changes. This allows trees to survive

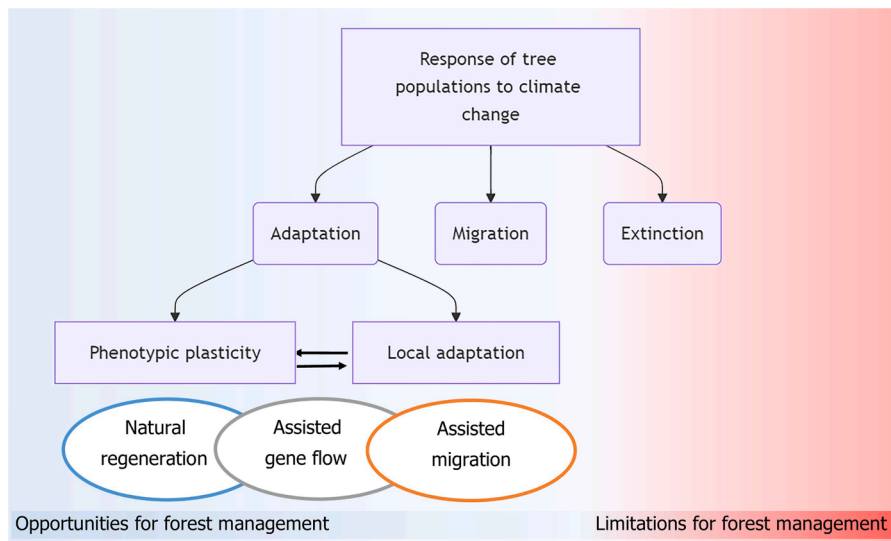


Figure 4.2 Ecological or biological responses of tree populations to climate change; opportunities and limitations for forest management associated with responses of trees in adaptation possibilities to environmental changes. (Credit: Authors).

and thrive in diverse climatic conditions, which is particularly important in the context of rapid climate change.

Understanding phenotypic plasticity and local adaptation enables better predictions regarding the response of individual tree species to climate change and facilitates the formulation of strategies that promote forest stability. This knowledge can inform the selection and transfer of FRM that is better adapted to the anticipated climatic conditions in a specific area (Leites and Benito Garzón, 2023). The dominance of a specific evolutionary strategy differs among forest tree species, but it may also vary across different regions within a species' distribution range. Some species show strong local adaptation, for example, Scots pine and Norway spruce (Sáenz-Romero et al., 2019), while others, such as European beech (Müller et al., 2020), pedunculate oak, and sessile oak (Mátyás, 2021), show a greater reliance on phenotypic plasticity. This suggests that assisted gene flow may need to be considered more frequently in populations of species with established local adaptation than in those with high phenotypic plasticity. Assisted gene flow is an intentional translocation of individuals within a species range to facilitate adaptation to expected local conditions, also called assisted population migration (Aitken and Whitlock, 2013; Williams and Dumroese, 2013).

When choosing native species for planting in new areas within their native range, it is essential to consider the potential impact—both positive and negative—on existing forests. Gene flow can be particularly significant for most commercial species (Burczyk et al., 2004), as it can enrich the existing gene pool and improve the resistance to different impacts (Koskela et al., 2014). For some species with disjunct distributions, poor gene flow can decrease the ability of a species to adapt to climate change (Aleksić et al., 2022). A concern is that using non-local seed sources means the seedlings—and later, the planted trees—will have a different genetic composition from the native stands. Crossing between introduced and existing populations may dilute and eventually lead to the loss of the unique diversity found in local populations, resulting in a breakdown of coadapted gene complexes, potentially leading to outbreeding depression (Ledig, 1992). This effect, known as “genetic pollution,” highlights the importance of testing provenances in selecting species (Koskela et al., 2014).

Different approaches in selecting species and provenances

Selecting species and provenances is a trade-off between growth rate and ability to persist under unfavorable conditions and requires a good assessment of the ecological requirements of target species and provenances. No matter the moment—past, present, future—of species selection, the need to consider so many factors complicates the decision process. When selecting a species for planting, it is crucial to start with genetically high-quality material. Species selection cannot be separated from some level of species breeding. Seed sources can be at a different level of breeding. Selected provenances,

population groups, and individual trees are classified as sources of FRM. These sources form the basis for further breeding processes, such as hybridization or subsequent selection within offspring, where the best individuals are identified and selected again. From these breeding efforts, recommendations can be developed for the use of different FRM sources in varying environmental conditions (West, 2014). The selection of suitable FRM is the oldest and the best-investigated breeding method in forestry. Selection and assisted migration are interrelated and complement each other, primarily based on information about expected climate change in a particular region. Matching climates in which seed sources evolved with near-future climates projected for planting sites should help reduce maladaptation and increase forest health and productivity.

The primary task for reforestation and afforestation has been to maintain and increase productivity by selecting appropriate initial populations and the transfer of FRM to new habitats. The first controlled transfer of FRM and the establishment of seed zones for the purpose of maintaining and increasing productivity were recorded in the early 20th century, when the transfer of Douglas fir (*Pseudotsuga menziesii*) was conducted in North America. Subsequently, similar processes were undertaken for other significant forest species. By monitoring the behavior of transferred populations in new environmental conditions, it was possible to establish the first guidelines for sustainable transfer of FRM (St. Clair et al., 2020). Today, the selection process is linked to the ecological conditions of the habitat and is implemented operationally through provenance recommendations.

Field tests, as a tool for adaptation assessment, provide indications of the climate sensitivity of a particular forest species (Konnert et al., 2015; Royo et al., 2023). To support the selection process, botanical collections and common garden experiments are used to assess growth performance and adaptability to a changing climate (Berend et al., 2019; Fanal et al., 2021). Common garden experiments with NNT species compare the potentially best-suited species for introduction. Provenance trials provide detailed measurements of species and provenance fitness to particular climatic conditions. The difference in tested provenances' survival and growth across field trials may indicate specific provenances with the potential for successful transfer to the new sites (Fig. 4.3). At the same time, it is necessary to preserve or increase productivity. This approach requires many resources and a long time after planting to obtain results. Under current schemes of science financing that provide support only for 3–5 years, there are few such experiments.

Provenance trials are designed studies aiming to select species and provenances for forest management adapted to particular climatic and soil conditions (Booth et al., 2014). When a number of provenances are evaluated under varied conditions in multi-environmental trials, an assessment of genotype–environment interactions is possible. Provenance trials provide some empirical evidence for predicting the effects of climate change on the growth and survival of particular provenances, provided the trials

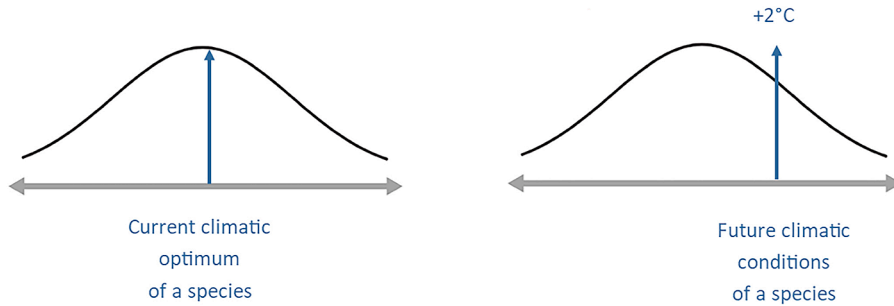


Figure 4.3 Climatic optimum for the growth of a hypothetical tree population (left) and future climate change with a shift in mean temperature ($+2^{\circ}\text{C}$) over one generation of the tree population's lifespan, leading to suboptimal climatic conditions for growth of the population (right). The Gaussian function illustrates how this shift leads to suboptimal climatic conditions for population growth. (Credit: Authors).

experience the range of climate conditions. For example, [Reich and Oleksyn \(2008\)](#) found that a warming climate will affect the growth and survival of Scots pine and Norway spruce, leading to a decrease in the southern and intermediate populations and an increase in northern populations. [Pretzsch et al. \(2023\)](#) used a set of provenance trials across Europe to determine regions with increases and decreases, in particular, in tree growth. [Chakraborty et al. \(2016\)](#) used provenance trials to select optimal regions of origin for Douglas fir in Central Europe under a changing climate. Although provenance trials provide reliable measurements under experimental rigor, they require a lot of resources; therefore they provide only a limited amount of data, covering a few species.

Effects of selection

Selection, as a breeding method, can significantly increase the genetic goal compared to the average value of the observed parameter in existing forests. For example, the volume of wood produced in artificially established forests established from selected seeds in some Scandinavian countries increased by 10%–25% ([Jansson et al., 2017](#)). On the one hand, many other genetic goals have been achieved using selection as a breeding tool (e.g., resistance to adverse environmental conditions, disease resistance, shape of trunks, branching, and homogeneity of new forests). On the other hand, during any kind of selection, genetic diversity is reduced ([St Clair and Howe, 2011](#)). Selection from a small number of individuals presents a significant problem in terms of reducing genetic diversity ([Thomas et al., 2014](#)), which can lead to failures in establishing new forests. Selection can lead to genetic drift, the random reduction of genetic variation in a population of finite size. Genetic drift affects mostly neutral genetic diversity. It increases when population size decreases through the process of selection. Reduction of genetic diversity, occurring through the reduction of rare alleles, can lead to erosion of the genetic potential of species. Therefore to preserve an appropriate level of genetic

diversity when establishing new forests, it is necessary to consider a larger number of parent trees, at least 50 for the widespread species (Gaisberger et al., 2023).

Some populations and individual trees, not selected in the selection process, may contain genes whose expression could avoid or reduce some negative effects of the external environment. For example, beech from marginal populations with characteristics of mixed forests has been found to have high drought tolerance, even though individuals show an average level of quality in terms of desired phenotypic traits (Bolte et al., 2016; Stojnić et al., 2018).

From a genetic point of view, three methods can be distinguished by artificially establishing forests and thus mass production of FRM for their needs. These are seedling, family, and clonal forestry. The number of genotypes in the new seedling forests is equal to the number of planted seedlings. The number of genotypes in family forestry is equal to the number of seedlings from controlled crossing, thus small since vegetative multiplication takes place after crossing. In clonal forestry, the number of genotypes is equal to the number of clones. Genetic diversity has to be reduced to attain the planned genetic gain, and therefore it is crucial to find a balance between these two objectives: genetic diversity and genetic gain.

The genetic diversity of seed lots is influenced by the size of the parent population, the balance in parental reproductive success, the relatedness of its members, and the level of inbreeding (Funda et al., 2012). A large variability in fertility is observed between and within populations (Kang et al., 2003). The main question that arises is how much genetic diversity is necessary to maintain during the mass production of FRM. Ivetić et al. (2016) provided a clear overview of how genetic diversity decreases over time in the breeding process. At the same time, the risk of unwanted effects on newly established forests increases due to reduced genetic diversity. Over a longer time, most of the non-adapted FRM sources are identified and excluded further in the selection process; as the risk begins to decrease, quality starts to increase in new forests (Fig. 4.4).

Tree species migration

Tree species migration, alongside adaptation, is one of the key survival strategies (Aitken et al., 2008; Wang et al., 2010; Vacek et al., 2023). Tree populations initiate migration when existing habitat conditions do not favor their survival, gradually leading to changes in the species distribution area. Although our knowledge of the pace of tree migration in the context of current climate change is still limited, the migration of tree species in the past has been fairly well documented and closely linked to global climatic cycles (Aitken et al., 2008). The maximum migration rate spreading from the south range for pioneer, early successional species, such as birch, willow, or pine is estimated at 225–540 m year⁻¹, while for mid- and late-successional trees such as silver fir, spruce, and European beech the rate can range from 115 to 385 m year⁻¹, depending on the method of seed dispersal by wind or animals (Feurdean et al., 2013). However, the observed historical migration rates differ significantly from the pace required to keep up with current climate

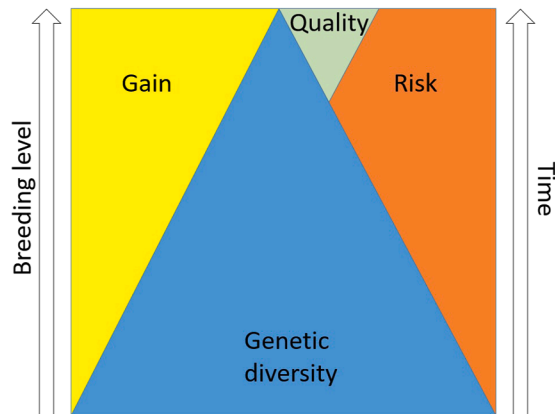


Figure 4.4 Breeding level over time, genetic diversity, and genetic gain risk and quality are highly dependent on each other. As the breeding process advances, the genetic diversity of the starting material decreases, increasing the risk of unwanted factors. At the same time, the desired results of breeding—such as improved quality—become more pronounced. After some time, this risk in the starting material is reduced through the selection process by a decrease in the proportion of sensitive individuals participating in breeding. (Credit: Ivetić, V., Devetaković, J., Nonić, M., Stanković, D., Šijacić-Nikolić, M., 2016. Genetic diversity and forest reproductive material—from seed source selection to planting. *iForest-Biogeosciences and Forestry* 9, 801).

change, which may necessitate movement up to 1000 m year^{-1} (Aitken et al., 2008; Woodall et al., 2009). Therefore in the face of climate change, forestry should favor the potential migration of native tree species by adjusting management and planning practices to support natural migration and adaptation processes (Bruchwald et al., 2016; Vacek et al., 2023). This may involve increasing connectivity between forests, creating ecological corridors that facilitate the movement of species, as well as the implementation of assisted migration (Aitken and Whitlock, 2013; Williams and Dumroese, 2013).

Assisted migration

In addition to assisted population migration (i.e., assisted gene flow), assisted range expansion refers to the intentional translocation of individuals to suitable areas just outside the native range of a species. This involves the deliberate introduction of species into new areas where they can survive better under changing climatic conditions (Vacek et al., 2023). Assisted species migration, the movement of species to locations far outside current ranges, can be used in areas where native species show signs of weakening or decline of entire stands, such as spruce (Hentschel et al., 2014; Kamińska et al., 2021; Krejza et al., 2021), and there is no alternative to replacement by other native species. The farther a species is moved outside its native distribution, the more controversial assisted migration is (Aubin et al., 2011; Pedlar et al., 2012; Bucharova, 2017). Nevertheless, assisted migration is a conservation option to improve species' adaptive capacity and facilitate persistence (Chen et al., 2022). By nudging tree populations in the

direction of climate change, assisted migration is expected to help maintain forest health and productivity by restoring populations to climates where they are best adapted (Wang et al., 2006; Nigh, 2014). Assisted species migration in particular is an instrument that can help forests adapt to climate change (Gömöry et al., 2020). However, all forms of assisted migration require careful planning and monitoring to avoid unintended consequences, such as disruption to local ecosystems.

Assisted species migration has long been used in forestry to increase wood production, habitat quality, or forest species richness. Formerly, forest management focused mainly on maximizing yield and wood product dimensions. For that reason, botanical expeditions aimed to find new species of trees to introduce to their homelands. Primarily, these species were planted as ornamentals and later introduced into the forest (Starfinger et al., 2003; Cierjacks et al., 2013), sometimes in large areas (Nyssen et al., 2016b). The commonly moved tree species are in the families of *Pinaceae* and *Fagaceae*. Movement was most common among the genera *Pinus* and *Quercus*, followed by *Picea*, *Pseudotsuga*, and *Populus* (Twardek et al., 2023). The process of selecting initial populations and evaluating them in new habitats, often through provenance trials and progeny tests, indicates the direction in which selected material should be transferred to new habitats. Testing must be conducted regardless of costs because it represents a valid means of confirming the suitability of certain populations for establishing new forests and preserving the goal of forest establishment at other locations (Chen et al., 2022; Palik et al., 2022; Royo et al., 2023; Sáenz-Romero et al., 2020).

There is an urgent need to adapt the forests to climate change; however, many forest owners hesitate to adapt their forests to a new climate. Climate change remains an abstract risk as long as people are not affected directly, although this may be changing. Nevertheless, the introduction of new tree species requires daring to do something unknown, and local knowledge is scarce (Mette et al., 2021). Therefore the need to adapt forests to climate change has led to a higher level of debate on two major questions: (1) What species should we use in the future, native or nonnative? (2) What kind of plantations should we establish, pure or mixed?

Native vs. nonnative species

Native species have co-evolved over thousands of years and contribute to ecosystem functioning in a balanced way (Karrer et al., 2022). Consequently, under natural conditions (i.e., quasi-stable), an equilibrium has been reached between site conditions and the native vegetation. This has led to the preference in forestation decisions for planting native tree species for the transformation of forests according to climate change (Fig. 4.5). The use of native species is ecologically sound and avoids the risk associated with planting some NNTs that might become invasive and alter ecosystem services (Dimitrova et al., 2022; Karrer et al., 2022). Especially for restoration of drylands,

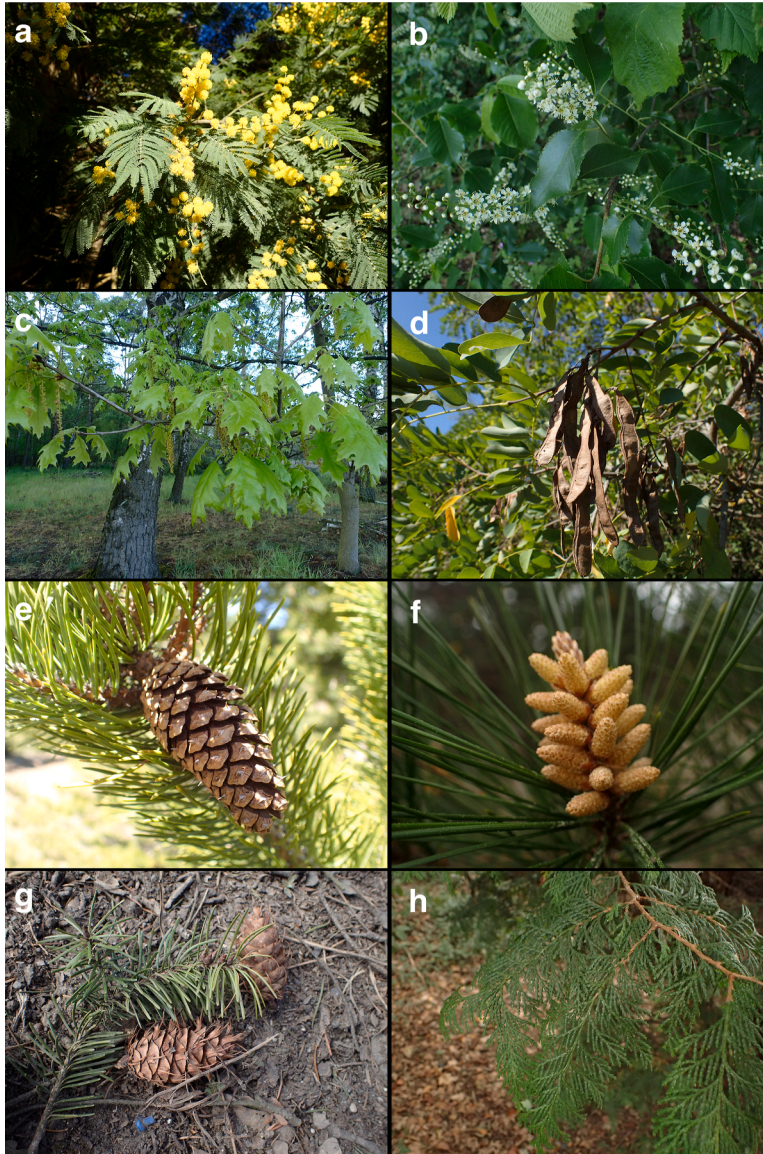


Figure 4.5 Examples of nonnative tree species used in forestry: (a) *Acacia dealbata* Link, (b) *Prunus serotina* Ehrh., (c) *Quercus rubra* L., (d) *Robinia pseudoacacia* L., (e) *Pinus contorta* Douglas, (f) *Pinus radiata* D. Don, (g) *Pseudotsuga menziesii* (Mirbel) Franco, (h) *Thuja plicata* Donn. ex D. Don. (Credit: Marcin K. Dyderski).

however, insisting on the exclusive use of local plant material may be consigning restoration projects to a genetic dead end that does not allow for rapid adaptation to changing environments in the era of climate change (Reisman-Berman et al., 2019).

Planting native species in mixtures can restore ecosystem functions, conserve biological diversity, and diversify forest products in degraded landscapes (Lu et al., 2017). For native species, the use of local provenances has been advocated (Damian, 1969). Yet, provenances from across the range of potentially suitable native species, as part of assisted migration of populations and species into areas of future climate feasibility, may be needed and require consideration (Evans and Turnbull, 2004; MacKenzie and Mahony, 2021). Investigating tree species from regions where the climate already resembles projections for future climates in Central Europe can give important insights into the suitability of new tree species adapted to future climates (Heinrichs et al., 2021). Accounting for climate variability potentially avoids the mistake of using very productive provenances on sites of variable water supply that suffer extensive dieback in dry summers (Karrer et al., 2022).

Nonnative tree species: definition and introduction pathways

NNT are those species that were artificially introduced (i.e., assisted species migration) or spontaneously dispersed outside their native range after breaking a biogeographical barrier due to human intervention (Richardson et al., 2000; Blackburn et al., 2011; Dimitrova et al., 2022; Soto et al., 2024). Introduction can be related to different pathways, deliberate or accidental, but is always connected with breaking biogeographical barriers, e.g., mountain ranges or oceans. When new species were introduced and survived, we can say that they crossed the first barrier, related to geographic distance and environmental filters, mainly climatic (Blackburn et al., 2011).

When the NNT species can reproduce out of the cultivation site, i.e., crossing the reproduction barrier, it is an established species (Nyssen et al., 2024; Soto et al., 2024) that can spread into natural and semi-natural ecosystems. Some NNT species can become invasive species, that is, they not only establish successive populations beyond the introduction points but also replace the native taxa (Soto et al., 2024). The purely biogeographical definition of invasive accounts for their spread rate; plants are labeled as invasive species by reproducing generatively (spreading over 100 m in less than 50 years) or vegetatively (6 m in 3 years) (Richardson et al., 2000). By this definition, however, not all invasive species need to have negatively impacted biodiversity, native species, or the human economy and health. In turn, the nature conservation-based definition, included in the Convention on Biological Diversity, defines species as invasive when they can reproduce and have negative impacts on native species (CBD, 2002).

Not all introduced tree species became established, and among those that were established, only a small part became invasive (Williamson and Fitter, 1996). However, assessing the potential of NNT species to become invasive may take time. For many invasive trees, the time lag between introduction and the start of massive spread can take 100–200 years (Kowarik, 1995), indicating the uncertainty related to future invasiveness and the need to account for propagule pressure, i.e., number of propagule sources introduced to the focal region, and the time since introduction (Blackburn et al., 2011). The area of NNT species cultivation or the number of seed sources is strictly related to species spread capacity (Křivánek et al., 2006; Jagodziński et al., 2019), showing that even species not regarded to be invasive can effectively spread (Czortek et al., 2024; Jagodziński et al., 2024).

Before introducing additional NNT species into forestation practice, it is important to thoroughly analyze potential benefits (e.g., productivity) and negative impacts, such as unintended ecological consequences like changes in host pathogens for native species and/or potential to invade nontarget habitats (Dyderski and Jagodziński, 2020; Dimitrova et al., 2022). The invasive potential of a species is a function of its competitiveness, seed dispersal efficiency (mechanism and distance), seed bank survival, and vegetative reproduction capacity (Fanal et al., 2021). A full accounting of the potential for invasion must also consider the vulnerability of the ecosystem, i.e., its invasibility (Lonsdale, 1999; Alpert et al., 2000). When it comes to introducing NNT species into stands of native species, it is essential to monitor their competitive interactions because none of the species (native or introduced) has evolved together in the same climatic conditions (Bolte et al., 2009).

NNTs under climate change

Under a changing climate, established NNT species can either contract their climatic optima or expand, depending on their life history traits and ecological requirements in their native range. Recent studies evaluated predicted niche dynamics of NNT species in Europe and revealed that most nonnative coniferous trees will lose their climatic optimum, while most broadleaves will expand their climatic niches under climate change (Table 4.1) (Thurm et al., 2018; Puchałka et al., 2023b). Exceptions are *Quercus rubra* L., which is expected to lose more climatic suitability than other broadleaved NNTs, and *Pinus strobus* L., expected to lose less climatic suitability than other conifers. In general, species with high growth rates, reflected by low wood density and high specific leaf area, are predicted to contract their potential climatic niches more than expand (Fig. 4.6).

Positive impacts of NNTs

NNTs are usually referred to as transformers (*sensu* (Richardson et al., 2000)), species able to modify inhabited environments, especially resource availability and biotic interactions

Table 4.1 The most frequent nonnative tree species in Europe and predictions of their climatic optima under climate change.

Species	Predicted shifts	Source
<i>Abies grandis</i> (Douglas ex D. Don) Lindl.	High contraction	(Thurm et al., 2018; Puchałka et al., 2023b)
<i>Acer negundo</i> L.	High expansion	Puchałka et al. (2023b)
<i>Ailanthus altissima</i> (Mill.) Swingle	High expansion	Puchałka et al. (2023b)
<i>Fraxinus pennsylvanica</i> Marshall	High expansion	Puchałka et al. (2023b)
<i>Juglans nigra</i> L.	High expansion	Puchałka et al. (2023b)
<i>Larix kaempferi</i> (Lamb.) Carrière	High contraction	Thurm et al. (2018)
<i>Picea sitchensis</i> (Bong.) Carr.	High contraction	Puchałka et al. (2023b)
<i>Pinus contorta</i> Douglas	High contraction	Puchałka et al. (2023b)
<i>Pinus strobus</i> L.	Moderate contraction, moderate expansion	Puchałka et al. (2023b)
<i>Prunus serotina</i> Ehrh.	High expansion, moderate contraction	Puchałka et al. (2023b)
<i>Pseudotsuga menziesii</i> (Mirbel) Franco	Low expansion, high contraction	(Dyderski et al., 2018; Puchałka et al., 2023b)
<i>Quercus rubra</i> L.	Moderate expansion, moderate contraction	(Dyderski et al., 2018; Puchałka et al., 2023b)
<i>Robinia pseudoacacia</i> L.	High expansion, moderate contraction	(Dyderski et al., 2018; Thurm et al., 2018; Puchałka et al., 2023b)
<i>Thuja plicata</i> Donn. ex D. Don	High contraction	Puchałka et al. (2023b)

(Crooks, 2002; Corenblit et al., 2012). For that reason, NNT species positively or negatively affect ecosystem services (Castro-Díez et al., 2019). NNT species can modify light availability and microclimate (García et al., 2023), nutrient content, and decomposition rates (Horodecki et al., 2019), as well as communities of other organisms (Gentili et al., 2019).

Some impacts of NNT species on ecosystem services are positive, such as increased carbon sequestration rates in biomass of NNTs (Grotkopp et al., 2010) that can be perceived as positively impacting climate regulation (Castro-Díez et al., 2019). Higher timber production is highly biome- and country-specific, with high effect sizes in countries with high-intensity plantations of highly productive species, e.g., *Eucalyptus globulus* Labill., *Pinus radiata* D. Don, *Pinus contorta* Douglas, and *Acacia saligna* (Labill.) H.L. Wendl. in South Africa, Southern South America, and New Zealand, or *P. contorta* and *Picea sitchensis* (Bong.) Carr. in the UK and Ireland. Potential benefits related to timber production might also be related to the demand for particular wood types, e.g., coniferous roundwood in the British Isles. Also, they can provide cultural services,

Figure 4.6 Production of seedlings of sessile oak (*Quercus petraea* (Matt.) Liebl.), a major native tree species in Europe (south of Romania). (Credit: V.N. Nicolescu).



especially for old trees (Sádlo et al., 2017; Castro-Díez et al., 2019). Another benefit from NNTs might be related to non-wood products, such as fruits.

NNTs can reach remarkable growth rates in their new environment; however, this is also related to vulnerability to climate change. Among species assessed for the relationship between site index and climate change vulnerability, Thurm et al. (2018) found only two NNT species on top of alternative tree species: *Robinia pseudoacacia* L. and northern red oak. Decisions about planting these species require consulting future climatic suitability maps and checking local adaptation. For example, black locust will lose the majority of its current climatic suitability in Hungary and Romania, where it is widely planted (Puchałka et al., 2021).

NNTs also can be better adapted for reclaiming degraded, post-industrial sites (Spyroglou et al., 2021) or for erosion control (Castro-Díez et al., 2019). Their habitat-shaping abilities can be especially important for increasing soil fertility and supporting soil formation, especially nitrogen-fixing species (Von Holle et al., 2013; Castro-Díez et al., 2019). Species such as *Acacia dealbata* or black locust increase soil nitrogen and cation content (Wohlgemuth et al., 2022). Also, broad-leaved NNT species that do not fix nitrogen, like *Prunus serotina* Ehrh., can accelerate nutrient cycling and increase P content in the ecosystem (Aerts et al., 2017; Horodecki et al., 2019; Wohlgemuth et al., 2022). Conversely, nonnative conifers usually decrease soil pH and calcium content, leading to nutrient leaching (Augusto et al., 2003). Changes in resource availability caused by NNTs can significantly alter successional dynamics, for example, positively on post-mining sites (Nicolini and Topp, 2005; Rawlik et al., 2018) or negatively in valuable non-forest ecosystems (Vitousek, 1990; Yelenik et al., 2004).

Negative impacts of NNTs

The biggest threat of NNTs is related to potential invasiveness and negative effects on other components of ecosystems, especially biodiversity. However, their impacts are species- and case-specific (Castro-Díez et al., 2019; Sapsford et al., 2020; Wohlgemuth et al., 2022). For example, an invasive species may reach large dimensions and colonize the sub-canopy layer, negatively affecting regeneration of native trees and the shrub layer (Peterken, 2001; Dyderski and Jagodziński, 2020). Impacts on understory diversity may vary; however, more negative than positive (Wohlgemuth et al., 2022). Most of the positive effects are related to an increase in species richness, mainly generalist, ruderals, and nonnative herbs (Gentili et al., 2019; Slabejová et al., 2019; Dyderski and Jagodziński, 2021).

Invasive NNTs may transform habitats so much that the habitat becomes more vulnerable to invasion by other nonnative species, the phenomenon of facilitating secondary invasions known as “invasional meltdown” (Simberloff and Von Holle, 1999; Kurokawa et al., 2010). Non-forest habitats are the most threatened; the occurrence of invasive trees can significantly alter ecosystem functioning (Yelenik et al., 2004; García et al., 2023), increase fire susceptibility, and decrease groundwater table level (Crooks, 2002; Taylor et al., 2017). Loss of biodiversity can also be related to hybridization between nonnative and native taxa, leading to the loss of genetic distinctiveness of native ones (Vilà et al., 2000). For example, native and threatened *Populus nigra* L. hybridize with nonnative *P. ×canadensis* Moench, leading to the retreat of pure black poplar (Smulders et al., 2008). In total, NNT can generate economic costs that are usually not fully recognized (Fernandez et al., 2023).

Management of NNTs is context-dependent

The spread success and impact of NNT species depend on characteristics of the recipient ecosystem, that is, its invasibility (Sapsford et al., 2020; Catford et al., 2022). For example, black cherry in Europe leads to a greater decrease in forest specialists in nutrient-poor than in nutrient-rich habitats (Chabrerie et al., 2010; Halarewicz and Pruchniewicz, 2015; Dyderski and Jagodziński, 2021). The negative effects of northern red oak on understory dwarf shrubs are also greater in post-agricultural lands than in forest sites (Woziwoda et al., 2019). Moreover, the effects of NNTs are scalable over their abundance gradients (Pearse et al., 2019; Catford et al., 2022). Impacts can be linearly negative (García et al., 2023) or positive up to a certain threshold, and then negative (Dickie et al., 2010). However, these effects depend on the width of the abundance gradient (Sapsford et al., 2020). Including this dimension in assessments of NNT impacts can help determine management thresholds for multifunctional forest management. Therefore assessing the invasiveness of NNTs should account for context dependence and abundance gradients of NNTs. This can lead to case-specific guidelines for

managing NNTs that depend on the aims and functions expected for a particular site (Nyssen et al., 2016a; Sádlo et al., 2017). Such guidelines require more empirical data, especially assessments of the effects of NNT across habitat types and along abundance gradients.

Pure or mixed stands

When the question “What kind of forests should we establish, pure or mixed?” arises, we should remember that only a tiny proportion (less than 0.1%) of today’s plantation forests worldwide are tree species mixtures (Jactel et al., 2017). Mixed forests favoring native trees are considered the key climate adaptive forestry practice that fulfill the multiple functions of productive ecosystems (Mette et al., 2021; Karrer et al., 2022). Diverse forests are said to be more resilient to climate change (Brang et al., 2014; Grossiord, 2020). The planned species mixture should include not only the main tree species but also admixture tree species that occupy ecologically different niches, thereby enhancing the biodiversity of forest ecosystems. Admixture species potentially contribute to increasing biological resilience or reducing wildfire risk (Bernier et al., 2016). For example, site-adapted admixed tree species can reduce the susceptibility of mature European beech to drought (Metz et al., 2016). Furthermore, selected admixture species trigger resistance associated with certain pests, thus emphasizing the potential of admixture species to improve the overall health and resilience of forest ecosystems (Castagneyrol et al., 2014).

Mixed-species forests may provide many benefits such as provision of a wider range of ecosystem goods and services, higher productivity, increased carbon storage, early financial returns from species with different rotations, fuller site utilization, increased resilience to disturbance, greater resistance to small mammalian herbivores, less susceptibility to soil-borne fungal diseases and specialized insect herbivores, and more resistance to wildfire and windstorms (Schueler et al., 2014; Jactel et al., 2017; Depauw et al., 2024). On the contrary, biodiversity in mixed stands is not always better than in monocultures, and differences in understory biodiversity may only be reflected in species composition rather than species number (Luo et al., 2024). Mixed stands are also difficult to manage (e.g., it is difficult to ensure that the final crop is not swamped by the admixture species), and landscape aesthetics suffer when planting is done in bands or strips on a regular pattern (Evans, 1984).

In general, monospecific, even-age stands are considered to be simpler to manage, less expensive, and more profitable than mixed-species stands (Klinka and Feller, 1984). Forest owners and managers have identified multiple constraints that are still hindering wider adoption of mixed stands, including logistical (e.g., requirements for highly trained workers and specialized machinery), economic (e.g., costs of more complex management operations), cultural and historical (e.g., professional and public

perceptions, prejudices) challenges (Klinka and Feller, 1984; Verheyen et al., 2016; Jactel et al., 2017). The most important constraint, which is likely at the root of landowners' and stakeholders' reluctance to adopt mixed plantings, is the lack of information on how they can be successfully established and maintained, and evidence for the benefits of mixtures (Depauw et al., 2024). The reality for restoration, especially, is that species selection and seed-sourcing decisions are commonly driven by the availability of material. This often results in the selection of a few well-known, sometimes NNT species, rather than those species that best match the restoration site conditions and objectives. This lack of suitable FRM constrains the wider use of more diverse tree species (Fremout et al., 2022).

As a complement to the dominant use of native species, commonly used NNT species such as black locust, Douglas fir, Sitka spruce, northern red oak, some of which originated from warmer climates, could be planted in Europe, as pure or mixed stands, or for enriching the native or artificial stands dominated by native species. Indeed, NNTs can offer greater productivity and resilience to climate change than native species, without jeopardizing the provision of ecosystem services (Nicolescu et al., 2020a,b, 2023; Nyssen et al., 2024).

The selection of a suitably adapted provenance can be critical when planting NNT species with a widespread native distribution, and the knowledge of the pattern of natural variation is of considerable practical importance (Savill and Evans, 1986; Savill et al., 1997). However, foresters must use caution in selecting NNT species and avoid large plantings of those not previously tested in the region (Nyland, 2016). It is insufficient to decide simply which species to plant without considering the original geographic source of the seed as well. Some of the worst mistakes in forestation have been the result of well-intentioned foresters importing seed from stands that looked good but were unsuited to the new environment.

Species distribution models and other selection tools

SDM are a method for projecting future forest composition (Booth, 2018; Lozano et al., 2024). The first models of tree distributions were generalized linear models or climate envelope models that correlated physical conditions necessary for tree growth with species occurrence. Variables included climate data such as temperature and precipitation, or growing degree days. These climate envelope models described a species' climate "envelope," the climate where it currently occurs, and then mapped the geographic shift of that envelope under climate change. Mechanistic SDMs are based on processes and species traits, and use independently derived information about a species' physiology to develop a model of the environmental conditions where the species can exist. The development of BIOCLIM in 1984 (Booth, 2018) and MaxEnt models were milestones, providing tools allowing for easy development of SDM (Fig.4.7). The

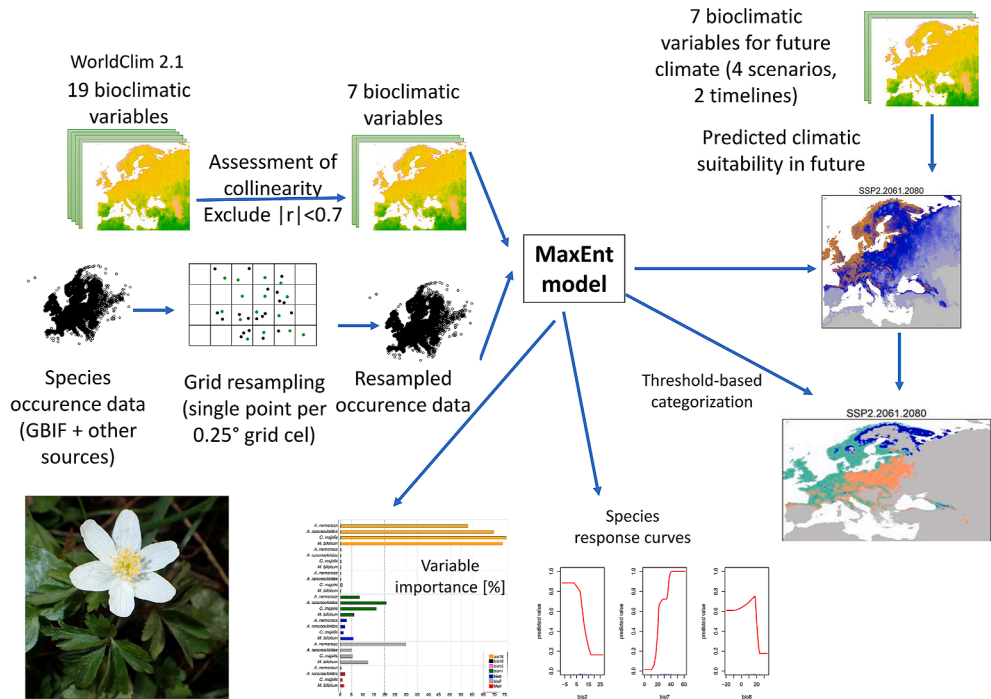


Figure 4.7 Scheme of species distribution model development on the example of *Anemone nemorosa*. Using data about species distribution and current climate, the MaxEnt algorithm can predict climatic suitability in each pixel of the map. Binary classification of climatic suitability allows us to translate it into presence-absence categories. Using future climate change scenarios allows us to predict future range dynamics. (Credit: Scheme modified from Puchałka, R., Paż-Dyderska, S., Dylewski, Ł., Czortek, P., Vítková, M., Sádlo, J., Klisz, M., Koniakin, S., Čarni, A., Rašomavičius, V., De Sanctis, M., Dyderski, M.K., (2023). Forest herb species with similar European geographic ranges may respond differently to climate change. *Science of The Total Environment* 905, 167303).

main advantage of BIOCLIM was preparing a standardized set of 19 bioclimatic variables, describing the variability of monthly temperatures and precipitation (Booth, 2018). These variables are easy to obtain both from climatic stations and open databases and are useful not only for the analysis of current conditions but also for projections under different climate change scenarios. MaxEnt (i.e., maximum entropy) modeling predicts species occurrences considering the limits of the environmental variables of known locations (Elith et al., 2011; Soley-Guardia et al., 2024). Other statistical methods were also used to develop SDMs, such as logistic regression, generalized additive models, or point-process models, providing similar output—climatic suitability, quantitatively expressing how much climate is suitable for species occurrence in a particular place.

Developing species distribution models—what affects their reliability?

Regardless of the algorithm used for developing an SDM, the reliability of its outcome is mostly defined by the quality of input data, describing both climate and species distributions (Elith et al., 2011; Larson et al., 2014). Climatic conditions might be available at different spatial scales, and most of the bioclimatic variables are collinear (Puchałka et al., 2023b), meaning that two (or more) variables explain the same process and are highly correlated. Using correlated variables together in a model could decrease their importance, thus underestimating the effect of a particular resource availability (García et al., 2015). For that reason, the selection of variables requires assessing collinearity and understanding their importance.

Gridded climatic data are available for the whole world in databases such as WorldClim (Fick and Hijmans, 2017) or Chelsea (Karger et al., 2017), facilitating model development. The accuracy and availability of species distribution data are more problematic. Due to uneven sampling intensity in some regions (Cornwell et al., 2019), large databases of species distribution, such as the Global Biodiversity Information Facility or Botanical Information and Ecology Network, do not always provide observations with similar densities of points in particular regions. Only part of the data comes from regular surveys, while many are from incidental observations, with varying precision of spatial accuracy. For that reason, a crucial part of developing SDMs is an assessment of occurrence data accuracy and supporting it with unpublished sources (Puchałka et al., 2021). In recent years digitalization of natural history collections and citizen science has significantly increased the availability of occurrence data for many species (Wood et al., 2015; Steen et al., 2019; Jarić et al., 2020).

The results of SDMs require a statistical assessment of their accuracy. In most cases, SDMs have been developed using part of the data, and the remaining 20%–30% of observations serve for independent validation (Elith et al., 2011; Roberts et al., 2017). As these data are not included in the model, checking how an SDM predicts a species distribution allows an evaluation of whether the model is overfit, meaning that it performs well only within a dataset and has limited applicability outside of it. The goodness of SDMs fit can be evaluated using a confusion matrix, and a table comparing the number of correctly and incorrectly classified presences and pseudoabsences. These values provide measures of sensitivity (probability of true positive outcome) and specificity (true negative outcomes). Models with high specificity and low sensitivity would identify most of the absences but underestimate some sites where particular species occur, while models with low specificity and high sensitivity would overestimate them (Allouche et al., 2006; Hanspach et al., 2010).

The balance between specificity and sensitivity is important for determining the reliability of an SDM. Most studies report on the value of the area under the receiver operating curve (AUC), showing a trade-off in model performance. The ideal model

has an AUC of 1.0, indicating a perfect match of model and source data, while the random assignment of cases would result in an AUC of 0.5. Most SDMs report values from 0.75 (fair) to 0.98 (excellent fitness). Assessing the quality of an SDM based on the AUC, however, it needs to account for prevalence, where high prevalence is when most of the area of interest is covered by species presence. In such cases, it is harder to detect the zone of transition between species presence and absence, and for these cases, usually, values of AUC are lower (Allouche et al., 2006).

Applications of species distribution models

Early developed SDMs provided important insights into the biology and ecology of trees and their potential responses to a changing climate. Booth (2018) used an SDM for the assessment of potential niches of Australian *Eucalyptus citriodora* in Africa. Sykes et al. (1996) assessed the distributional patterns of 19 tree species in Europe, predicting a serious threat to Norway spruce and the northward shifts of European beech and English oak. Iverson and Prasad (1998) analyzed 80 tree species in the USA, indicating about 30 species that will expand their ranges and the same number of species that will retreat. Further studies also covered other regions and species, providing forecasts from a very local scale (Sarikaya et al., 2022) to global (Kozhoridze et al., 2015). They provided insights into extinction risk (Zhang et al., 2017), threats to genetic diversity (Schueler et al., 2014), invasion risk (Puchalka et al., 2023b), or suitability for assisted migration (Beridze et al., 2023). Results of SDMs can be easily communicated to a wider audience using web applications such as FutureForests (<https://connect.appsilon.com/future-forests/>) that presents maps for 12 European tree species (Dyderski et al., 2018) or Seed4forest (<https://www.seed4forest.org/>) that presents not only predictions of climatic optimum shifts but also suitable provenances of seeds (Chakraborty et al., 2021, 2024).

Limitations of species distribution models

Despite the large applicability of SDMs, this method has several limitations that need to be considered in using them for decision-making. First of all, climatic suitability (or habitat suitability, in the case of models including other variables) is commonly mistaken with the probability of species occurrence in a given place. As SDMs are based on presence and pseudoabsence, and do not include many factors determining species occurrence, but rather a range of conditions where species could occur, this cannot be treated as a probability. SDMs usually do not include biotic interactions, which can be crucial for particular tree species. For example, Dyderski et al. (2018) predicted a low level of climate-related threat for *Fraxinus excelsior* that suffers a lot from ash dieback, but adding this disease to the model changed predictions (Goberville et al., 2016). Another important issue is the assumed lack of dispersal limitation, which is usually related to predicted range expansion. In areas remote from current seed sources, we

cannot expect that particular species will spontaneously appear, despite high climatic suitability. The differences in range expansion between limited and unlimited dispersal scenarios are high (Meier et al., 2012). Also, the results of particular models are not transferable across spatial scales (Sallmannshofer et al., 2021).

The outcome of an SDM strongly depends on climate change scenarios; thus many studies use more than one intensity of climate change to show the range of uncertainty. This way of presenting results shows the range of possibilities depending on future policies. Moreover, scenarios of climate change are calculated by various global circulation models (GCMs); therefore it is good to include an ensemble of more than one GCM, as it can also significantly affect the results (Goberville et al., 2015; Paż-Dyderska et al., 2021). Additionally, although GCMs are improving, their output is generally too coarse to provide the spatial detail needed for management decisions. Thus regional climate downscaling using statistical or dynamic downscaling would improve decisions (e.g., Jacob et al., 2020; Kotamarthi et al., 2021). Moreover, the spatial scale of prediction also decreases differentiation related to local microhabitat, potentially missing local refugia. Microclimatic diversity can significantly alter predicted climatic suitability (Lembrechts et al., 2018), as well as geomorphometric diversity (Dyderski and Pawlik, 2020). For that reason, a future step in refining SDMs will take advantage of microclimate maps and predictions of how future microclimate will change (De Frenne et al., 2021). Another limitation of SDMs is not accounting for intraspecific variability, especially different responses to the climate of particular provenances. However, recent studies provide some approaches that will allow including that variability in predictions. An interesting step forward, Δ TraitSDMs, include local adaptation and phenotypic plasticity (Benito Garzón et al., 2019) and the approach proposed by Vajana et al. (2023).

Other tools

Selecting the most suitable tree species composition for a managed stand on a given site can benefit from using decision support tools. Examples of some available tools are the Climate-Change Informed Species Selection (CCISS) tool and Tree Species Selection Tool in Canada (MacKenzie and Mahony, 2021)¹ and the Diversity for Restoration tool in Columbia². These tools should always be used along with the advice of experts on local flora (Gastón et al., 2014). The selection of tree species for future forests should be based on continuously updated knowledge and analysis of changes in potential climate niches in relation to climate change scenarios.

¹ Government of British Columbia, Tree Species Selection Tool (TSST), <https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/silviculture/tree-species-selection/tool-introduction> [Accessed 14 October 2024].

² Diversity for Restoration, D4R, www.diversityforrestoration.org [Accessed 14 October 2024].

The existing knowledge related to the species distribution modeling capabilities incorporating intraspecific variability, and the integration of ecological and physiological traits of individual tree species, alongside high-resolution soil and terrain data, form a robust basis for making informed decisions in response to climate change (MacKenzie and Mahony, 2021). In addition, the availability of various climate databases provides a strong foundation for developing decision support systems. In British Columbia, Canada, the practitioner-focused CCISS model uses the biogeoclimatic ecosystem classification system and machine learning and serves as a successful illustration of such a decision-making framework. This model predicts the redistribution of bioclimate units induced by climate change, offering practical guidance for practitioners (MacKenzie and Mahony, 2021). It can also serve as a model for developing similar applications for European conditions to assess the adaptive potential of key tree species under various climate scenarios.

A range of conceptual frameworks (Yousefpour et al., 2017) and applications have been developed for European conditions to assess the adaptive potential of key tree species, such as SUSselect, which displays the current and future vulnerability of 7 European tree species and suggests locations for selecting species (Chakraborty et al., 2021). Nevertheless, to date, no complex decision support system has been developed for European conditions. A significant limitation stems from the fragmented approaches and diverse forest owner structures across EU countries, making it challenging to harmonize practices related to the trade of FRM and seed zones. To address this, it is important to consider greater flexibility in seed regionalization (Gömöry et al., 2020) to ensure broad and adaptable actions in response to climate change that transcend borders. In addition, it is essential to develop species selection recommendations early in the process of preparing forest management plans to ensure inclusion of adaptive forestry practices.

Guidelines

- Recommend tree species for selection in forestation in close consultation with local stakeholders, considering local cultural preferences, subject to availability of desired planting material.
- Account for species-specific responses to climate change, basing species selections on knowledge of local adaptation, phenotypic plasticity, and functional traits of forest trees.
- Use a species selection support system with high spatial resolution, down to the level of individual forest stands, based on comprehensive knowledge, possible options (scenarios, simulations), and decision support with risk assessment.
- Ensure planting material derives from environmental conditions that reflect current as well as projected future climatic conditions at the restoration site.

- Ensure that planting material derives from many widely spaced trees—more than 50 reproductive trees per species—from at least one and, preferably several, large and viable populations.
- Take an adaptive management approach that continuously incorporates scientific research, expert judgment, and operational experience.
- In planting mixed species, choose species that are compatible with each other, such as those with similar growth rates, shade tolerance, and rooting depths, and adapted to likely future climatic conditions.
- Incorporate NNTs adapted to the future climate, accounting for multiple functions, expectations of the wide range of stakeholders, and low risk of negative effects.
- Use climate change models for various periods, and analytical tools such as SDM, to effectively advise practitioners and incorporate risk into the decision-making process.
- Highlight the significant uncertainties in modeling future climates to emphasize the need for risk management.
- Implement range-wide strategies to protect large native tree populations and vulnerable tree populations as seed sources for reforestation and restoration.
- Encourage the implementation of long-term provenance trials that will provide valuable information on the adaptive capacity of tree species to climate change and abiotic stresses.
- Devote time and resources to sourcing quality seeds in projects.
- Work with suppliers who follow best seed collection practices that are transparent and include proper management of metadata associated with those collections.

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