CHAPTER 9

Biodiversity conservation for climate adaptive forest restoration and reforestation

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The role of biodiversity in forest ecosystem stability

Ecosystem services provided by forests

Forests provide multiple ecosystem services (ES) to human societies, thus contributing to human well-being (Haines-Young and Potschin, 2018; MEA, 2005). Forests are a source of a wide variety of raw materials (e.g., food, fodder, water, wood, firewood, fibers, and medicines) that have a monetary value in the market. They are called “provisioning ecosystem services” (PES). Primary PES include wood or wood-derived products. Indeed, a major reason for forestation is the enhancement of wood production (FAO, 2001; FRA, 2020). Forests also provide nonwood products with different types of industrial use, such as cork, tannins, and resins, which often do not require felling the trees (FAO, 2016; Krumm and Vítkov� 2016). Certain tree species produce appreciated edible fruits or nuts (e.g., chestnuts produced by *Castanea sativa* and pinyons produced by *Pinus pinea* in South Europe, or *Araucaria araucana* in South America). Other species are used for honey production (e.g., *Robinia pseudoacacia*, *Eucalyptus* sp., *Melaleuca* sp.; Dickie et al., 2014; Loock, 1948; Nicolescu et al., 2020). Indirectly, forests are also responsible for the provision of other products by providing habitat for other nontree species, such as berry-producing plants, mushrooms, or game, which represent an additional income source in some rural areas (Gamfeldt et al., 2013; Mann et al., 2022).

Beyond provisioning services, forests also regulate many ecosystem processes that contribute to people’s safety and well-being (e.g., climate, water supply and quality,

Guidelines for Climate Adaptive Forest Restoration and Reforestation Projects
ISBN 978-0-443-34086-4
https://doi.org/10.1016/B978-0-443-34086-4.00006-2

flood mitigation, pest and disease control, soil fertility, and protection from soil erosion). These services are called “regulating and maintenance ecosystem services” (RMES) (Haines-Young and Potschin, 2018). Generally, RMES have no commercial value, which makes them less acknowledged by the public. However, their loss or degradation may cause important socio-economic losses (Haines-Young and Potschin, 2018). For instance, forests contribute to climate regulation globally, annually sequestering an estimated 30% of the CO_2 liberated from fossil fuels (Ballantyne et al., 2012; Bellassen and Luyssaert, 2014). Although forests tend to consume more water than other vegetation types and may reduce water yield (Ge et al., 2023; Maitre et al., 1996), they also regulate the water cycle, promoting water infiltration and reducing runoff and flooding (Dutta, 2016). Moreover, montane cloud forests intercept fog and cloud droplets, adding substantial amounts of water to the hydrologic system (Bruijnzeel et al., 2011).

Forests play a major role in the protection of soils against erosion, reducing the amount of sediment transported by rivers and the rate of silting of water reservoirs (Dutta, 2016; Ju�sko et al., 2022). Some forests protect riverbanks and coastal zones from the erosion associated with river flooding, storm surges, king tides, or tsunamis (Forbes and Broadhead, 2008). Stabilization of noncohesive sandy soils and protection from wind erosion is another RMES provided by forests and other vegetation. Many sand dunes have been planted with pines, acacias, or other species able to colonize such soils, to prevent sand drifting (Gadgil and Ede, 1998; Li et al., 2013), although some planted species became invasive, replacing the native vegetation and altering the nutrient cycles and fire regimes of the afforested area (Marchante et al., 2008).

Cultural ecosystem services (CES) from forests are intangible assets that contribute to spiritual and mental health and well-being of people (Haines-Young and Potschin, 2018; MEA, 2005). For example, forests provide shade and buffer temperatures, which may be a relevant amenity sought by people in hot regions. Forests also provide aesthetic assets, such as the bright and varied colors of deciduous forests in autumn, or opportunities for recreation, which may become a tourist attraction and contribute to the local economy (Dickie et al., 2014) (Fig. 9.1).

Other forests attract tourism due to certain remarkable characteristics, such as California’s redwood forests that are home to some of the largest trees in the world. Wealthy societies usually value forests as providers of aesthetic values, and opportunities for recreation and tourism (Vaz et al., 2018), whereas indigenous societies highlight other cultural services, such as tribal identity, sense-of-place and heritage, religious values, or knowledge systems (Brockerhoff et al., 2017). The difficulty of quantifying CES and the variety of perceptions across different cultures and through time make them the least studied ES (Brockerhoff et al., 2017).

Figure 9.1 Beech (*Fagus sylvatica*) forest (on the right, with orange color) and oak (*Quercus pyrenaica*) forest (on the left with yellow colors) in autumn (Valporquero, Leo�n, Spain). The colors of the deciduous forests in autumn are a tourist attraction for the region. *(Credit: Alberto Ferna�dez Medarde)*

Biodiversity and forest ecosystem services

Biodiversity is known to be relevant for ecosystem functioning and the ability of forests to provide ecosystem services (Diaz and Cabido, 2001; Hooper et al., 2005). Some evidence points to a direct link between biodiversity and productivity in forests (Gamfeldt et al., 2013; Ruiz-Benito et al., 2014). Forest productivity underpins the provision of wood and other forest-derived products (Diaz et al., 2005), as well as the forest capacity to sequester atmospheric CO_2 (Poorter et al., 2015; Ruiz-Benito et al., 2014). Other provisioning services of forests, such as production of edible berries and fungi and game habitat, were also found to increase with tree species richness (Felipe-Lucia et al., 2018; Gamfeldt et al., 2013).

The link between forest diversity and productivity may be explained by three mechanisms, with some involvement of other ES. First, diverse forests could host functionally dissimilar species with complementary resource use strategies, which promotes resource partitioning and enhances resource use efficiency at the community level (Loreau and Hector, 2001; Ruiz-Benito et al., 2014). Second, plant diversity promotes belowground microbial/mycorrhizal abundance and activity, which in turn contributes to soil formation and fertility (Balvanera et al., 2006; Thompson, 2009). Plant diversity also enhances belowground plant and microbial biomass, thus positively contributing to soil erosion control (Balvanera et al., 2006). Third, diverse forests are less affected by herbivores and pests, as they enhance populations of natural enemies that contribute to disease and pest control (Balvanera et al., 2006; Jactel and Brockerhoff, 2007; Tylianakis et al., 2008).

Even-aged monospecific forests usually show reduced diversity and abundance of pollinators compared with more diverse forests (Taki et al., 2011), although other forest structural features, such as tree gaps, reduced density, or uneven distribution of tree ages might enhance pollinators (Taki et al., 2010). Less information on the relations between cultural services and biodiversity is available (Brockerhoff et al., 2017), as the value that people assign to different ecosystems is influenced by a wide range of factors. Even so, some evidence supports that people prefer mixed forests over monocultures for recreation and aesthetic value (Almeida et al., 2018; Gundersen and Frivold, 2008; Tew et al., 2019).

Biodiversity contributes to forest multifunctionality

The multiple ES provided by forests represents a challenge for forest managers, who should maximize as many services as possible, that is, multifunctionality. It is well known that ES are not independent of each other; some of them are positively related, but others show notable trade-offs (Castro-Díez et al., 2019; Felipe-Lucia et al., 2018; Gamfeldt et al., 2013; Rodríguez et al., 2006). Thus, maximizing a single ES may decrease others, which represents a challenge for managers (Thompson et al., 2011). For example, maximizing the production of tree biomass that increases shade and water shortage under the canopy, could increase the risk of wildfire due to the accumulation of fuels (Castro-Díez et al., 2019), reduce berry production, or the potential for game production (Gamfeldt et al., 2013), and it often reduces forest aesthetic value (Edwards et al., 2012; Gundersen and Frivold, 2008). On local scales, given that different tree species provide different functions and services, forest multifunctionality generally increases with tree diversity (Gamfeldt et al., 2013; Van Der Plas et al., 2016). On larger spatial scales, different species composition among forests within a region (i.e., high beta-diversity) promotes multifunctionality at landscape scale, because different localities complement each other in the services they provide (Brockerhoff et al., 2017; Felipe-Lucia et al., 2018). Promoting forest diversity is not only relevant for forest multifunctionality but also contributes to meeting the increasingly exigent conservation targets of developed countries.

Biodiversity and forest resilience

Forest resilience, i.e., the ability to endure environmental changes while retaining their functionality, is essential for sustaining ES over time in the current context of climate change. Evidence suggests that more diverse forests are more resistant to loss of functionality and recover earlier from disturbances than less diverse forests (Mori et al., 2017; Thompson, 2009). For instance, wind damage to forests can be reduced by using multiple species and variable forest structures. Multistory forest structure, which is often associated with species-diverse forests, reduces wind loading on the tallest trees. Different species vary in their resistance to wind damage, so that more stable species can help prevent damage propagation during a storm (Brockerhoff et al., 2017).

Global change is altering wildfire regimes and increasing the frequency of catastrophic fires, negatively impacting human well-being and reducing ES supply (Brockerhoff et al., 2017). Active management to maintain a certain fuel load and fuel continuity is essential to regulate the risk of catastrophic fires (Sturtevant et al., 2009; Wunder et al., 2021). The effect of forest diversity on fire regulation at the stand level has been rarely addressed (Brockerhoff et al., 2017). Given that resistance of trees to fire is species-specific, mixing species with different traits does not necessarily enhance resistance to fire, but may allow a faster postfire recovery of the vegetation cover, that is, resilience (Martín-Alc�n et al., 2015).

Strong evidence supports the positive effect of forest diversity on pest regulation; tree species growing in pure stands are more affected by insect herbivory than the same species growing in mixed stands (Jactel et al., 2017). The mechanism underpinning the greater resistance and resilience of a diverse forest relies on the dissimilarity of responses to herbivory among different species, mainly within groups of species with a similar function. Thus, species with different susceptibility to herbivory but similar functions reduce fluctuations in functioning over space and time (Elmqvist et al., 2003; Mori et al., 2013). This "insurance" diversity involves not only different species, but also applies at multiple scales, through heterogeneity of genetics within species, functional groups, and landscape configuration (Aitken et al., 2008; Anderson, 2016; Diaz et al., 2005; Thompson, 2009).

The theoretical background of biodiversity

Biodiversity refers to the variety of all living things and their interactions. Biodiversity changes over time from extinctions and evolution of new species. There are three levels of diversity: genetic, species, and ecosystem diversity. A brief discussion of each level of diversity is in order.

Genetic diversity

Genetic diversity (Fig. 9.2) is defined as the variation that occurs within species (Barua et al., 2024). Genetic diversity among individuals is based on the presence of variable alleles in the gene pool and, consequently, different genotypes within populations of plant species. Genetic diversity is a crucial element of tree species adaptation to climate change, and it is essential to preserve the vitality of forests and to deal with pests and diseases. Genetic diversity is higher in large, connected populations with intensive gene flow. Small, isolated populations usually have low genetic diversity and thus are more in danger of extinction. The populations of forest trees reveal a notable variety in their biochemical markers. This variation stems from prolonged events such as the shifting of continents, the rise of mountain ranges, and changes in climate that led to the isolation of forest populations. These historical challenges significantly impacted the survival of the species that exist today (Conkle, 1992).

Genetic diversity is responsible for forest trees' survival, adaptation, and evolution under changing environmental conditions (Koskela et al., 2007). With more variation, it is more probable that some individuals within a population will contain variations of alleles that are suitable for survival in a given environment (Mukhopadhyay and Bhattacharjee, 2016). Conservation of genetic diversity is important in many contexts. Ex situ conservation using gene banks of seeds in storage is one possibility, but the best way to protect forest genetic resources is to conserve trees in situ, directly in the field together with the whole ecosystem they are part of, including shrub and understorey species (Koskela et al., 2007).

The linkage between genetic and species diversity is significant. For example, changes in tree species composition lead to changes in microenvironmental conditions (Mikulov�a et al., 2020; Slabejov�a et al., 2019) and consequently to adaptation of the remaining species of forest understory. The loss of species that are not able to adapt, for example, shade-tolerant or moisture-demanding forest species, leads to a loss of biodiversity.

Species diversity

Species diversity (Fig. 9.2) is a function of the number of species within a plant community. which can be expressed in multiple ways. Species diversity is distributed unevenly across space, with increasing diversity from the poles toward the equator (MacArthur, 1965). On a regional level, significant differences in species richness among vegetation units were identified, for example, between forest and grassland (MacArthur, 1965). The highest numbers of plant species found in small areas have been reported in three types of ecosystems: tropical rainforests (Duivenvoorden, 1994), Mediterranean vegetation (Naveh and Whittaker, 1980), and temperate grasslands (Chytrý et al., 2015; Zobel et al., 1996).

Species diversity can be represented by species richness, the total number of species present in a plot, stand, or locality. It can also be measured by the relative abundance of individuals of a species in a community. Species richness is influenced by environmental factors such as geology, soil characteristics, nutrient supply, moisture, light availability, and the intensity of disturbances. These abiotic characteristics shape community composition through the process called "habitat filtering." The most species-rich forest plots in Central Europe generally occur on limestone or other base-rich rocks (Chytrý et al., 2015) and they include variable forest types, for example, floodplain forests, mesic oak-hornbeam forests, calcicolous beech forests, mixed deciduous scree-slope forests, thermophilus oak forests, pine forests on limestone outcrops, and Carpathian high-mountain forests (Chytrý et al., 2015).

The other process responsible for community composition is competition among species. Within a local community, competition leads to ecological differentiation of coexisting species, while habitat filtering reduces the number of species and variability of their traits, according to shared ecological claims (Cornwell et al., 2006). Since plant community composition is dependent on environmental conditions and reacts to its changes, plant species richness and abundance are often used to assess ecosystem health, restoration success, human impact (positive or negative), and other important aspects of ecosystem functions (Miedema Brown and Anand, 2022).

Species richness is also called *taxonomic diversity* that considers higher taxonomic ranks, in addition to species, or *functional diversity,* the variation in plant functional groups. A functional group refers to plant species that utilize similar resources. Another definition describes these group characteristics as functional traits—morphological, biochemical, physiological, structural, or phenological characteristics of organisms influencing how they respond to the environment (Violle et al., 2007). Well-known groups are linked with plant strategies (competitors, stress tolerators, and ruderals) (Grime, 1979), or life forms (phanerophyte, chamaephyte, hemicryptophyte, geophyte, helophyte, hydrophyte, therophyte, and epiphyte) (Raunkiaer, 1934), or functions in the ecosystem (producers, consumers, decomposers) (Odum, 1971). Functional diversity could significantly vary between different levels of succession or within an invasion process. It is high at the onset of an invader community colonization, while it is more stable at intermediate and high levels of invasion (Renault et al., 2022).

Phylogenetic diversity is a quantitative measure of the evolutionary history of a group of species, and the breadth of ecological functions they represent. It can be used to predict functional similarity (Webb et al., 2002; Srivastava et al., 2012). Phylogenetic diversity is a biodiversity measure defined as a phylogenetic difference between species (Faith, 1992). This measure is calculated as the branch lengths in a phylogenetic tree, and it provides a comparable, evolutionary measure of biodiversity not possible with species counts (Miller et al., 2018). Competitive relationships and stability of habitat conditions over a long time usually lead to phylogenetic overdispersion, where functional diversity is higher than expected. On the contrary, historically unstable environments, occurrence of disturbances, or extreme conditions are considered to result in a phylogenetically closer pattern due to environmental filtering (Kooyman et al., 2011; Webb et al., 2002).

Ecosystem diversity

Ecosystem diversity (Fig. 9.2) is described as the variety of ecosystems that occurs within a larger landscape unit, ranging from biome (the largest ecological unit) to microhabitat site

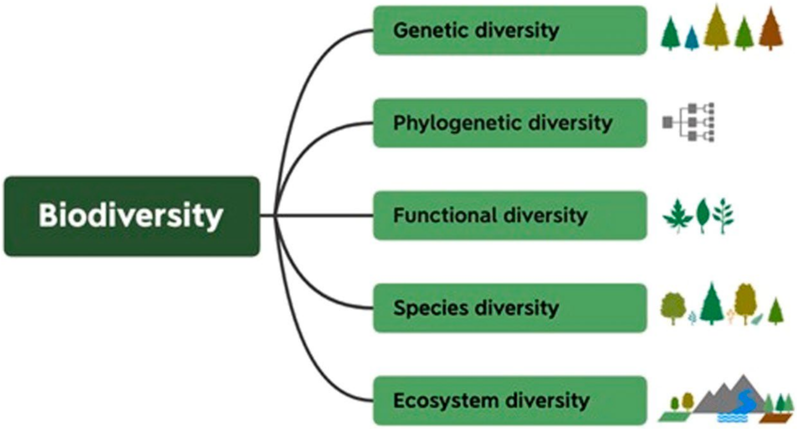

Figure 9.2 Different levels of biodiversity. *(Credits: Mária Šibíková)*

(EEA, 2024). Ecosystem diversity greatly influences both genetic and species diversity. Ecosystem heterogeneity positively influences the alpha and gamma diversity of plant species (Dufour et al., 2006; Geri et al., 2010; Liu et al., 2019; Lundholm, 2009). Higher landscape structure variability is likely to increase the number of patches of different vegetation types, providing more opportunities for different species to occur and thus increasing species diversity (Dufour et al., 2006; Gabriel et al., 2005; Pausas et al., 2003; Tscharntke et al., 2012). In some specific cases, for example forest fragmentation, increasing landscape heterogeneity could have the opposite effect on diversity (Steiner and Köhler, 2003; Tamme et al., 2010) because the increase in the number of patches results in a reduction in the core area of each forest patch which reduces the diversity of some specialized, shade-tolerant forest species dependent on internal forest habitat conditions (Dufour et al., 2006; Fahrig, 2003; Petrášová-Šibíková et al., 2017).

Measuring and assessing biodiversity in practice

Depending on the aims of biodiversity assessment, there are three basic types of diversity: alpha, beta, and gamma diversity (Fig. 9.3) (Whittaker, 1972). Alpha diversity is the species diversity (number of species) present within each forest patch (or vegetation plot) in the landscape. Beta diversity is represented by the difference of species diversity between any two forest patches. Gamma diversity is the species diversity along the whole range of the forest patches in the landscape.

Alpha diversity

For plant species, alpha diversity is usually equated to the number of species identified within a defined area (Revermann et al., 2016). Together with the total number of

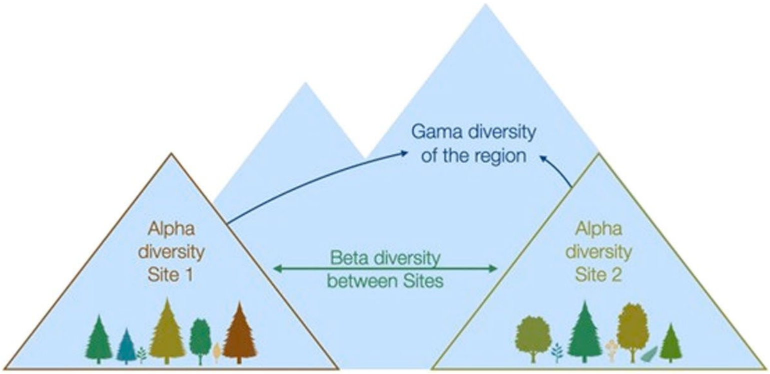

Figure 9.3 Scheme of alpha, beta, and gamma diversity *(Credits: Ma�ia �ibíkova�*

species, the distribution of species abundances is also an important measure of diversity. If a species is represented by only a few individuals, it contributes less to the diversity of the plant community than a species represented by a large number of individuals (Daly et al., 2018). Diversity measures that combine species presence and abundance are, for example, Simpson or Shannon–Wiener indexes. Another measure of diversity is the equitability of a species' abundance, which is referred to as its evenness. Evenness is how similar the abundances of different species are in the community. A community is deemed even if every species is present equally and uneven if a single species is dominant.

Alpha diversity is based on sampling lists of tree species only or all vascular plants including shrubs and the herb layer. One of the important methodologies is the Braun-Blanquet approach, which places a strong emphasis on plant species composition (Braun-Blanquet, 1964; Westhoff and Van Der Maarel, 1978). With this approach, cover-abundance values are assigned to every plant species commonly in 400 m^2 plots. This approach deals with plant species compositional patterns and gradients at the scale of the plant community (Dengler, 2008; Ewald, 2003; Westhoff and Van Der Maarel, 1978).

Beta diversity

Beta diversity describes the amount of differentiation between plant communities, forest patches, or other defined plots. Beta diversity can be computed between all kinds of alpha diversity measured on sites (taxonomic, functional, or phylogenetic diversity). Beta diversity is also called dissimilarity or the distance between two samples. It is traditionally measured by dissimilarity indices such as Jaccard's index and others that are designed for cover-abundance data (e.g., Similarity ratio, Euclidean distance, Sørensen dissimilarity index).

The processes opposite to species presence processes shaping plant community composition are species replacement and species loss (Baselga and Araújo, 2009). There are two components of beta diversity, species turnover and nestedness of assemblages. Species turnover is defined as a change in the species composition between areas due to the extinction of some species and their replacement by incoming species (Gaston, 2000). Nestedness occurs when the diversity of sites with smaller numbers of species are subsets of the diversity at richer sites (Ulrich and Gotelli, 2007), reflecting a process of species loss (Baselga and Araújo, 2009). Depending on the study or monitoring aims, basic beta diversity or its components can be analyzed.

Gamma diversity

Gamma diversity describes the total species diversity among plant communities within a larger geographic area or across biogeographic or political units, such as landscapes, ecoregions, or countries (Brummitt et al., 2021; Kier et al., 2005). The basic idea of gamma diversity is that the total species diversity in a landscape is formed by the diversity of sites/patches at a local scale and the differentiation among these sites (Whittaker 1972). Geographic units with high ecosystem diversity also have high gamma-diversity. Conversely, processes such as land use changes and the unifying of landscape units (e.g., establishment of large croplands or monodominant forest plantations) that lead to biotic homogenization reduce gamma diversity.

The choice and sources of plant material

Genetic diversity of forest reproductive material

Increasing genetic diversity in the Forest Reproductive Material (FRM) used for forestation is a strategy for adapting to climate change. Although the relationship between diversity and stability of a biological system is not straightforward, genetic diversity is seen as a sort of insurance against environmental change (Koskela et al., 2007; Naeem and Li, 1997; Yachi and Loreau, 1999). The underlying idea is that a large genetic variability allows for selection of genotypes matching (almost) whatever future climate. The choice of FRM used for reforestation has always been an important issue but has become increasingly critical.

Traditionally, many foresters throughout Europe relied on the "local-is-the-best" principle, preferring local FRM (although the understanding of what "local" means varies substantially). This principle is frequently reflected in recommendations for species choice (Konnert et al., 2015). Several countries, especially in Central Europe, have legal restrictions on the use of nonlocal provenances and sometimes have banned introduced tree species countrywide or in specific territories, for example protected areas (see Chapter 1). Many European countries promote tree planting through legal and policy instruments but often have specific provenance requirements as part of their grant schemes supporting tree planting efforts (Gömöry et al., 2021; Konnert et al., 2015). There is growing agreement among forest geneticists and breeders that such a policy is no longer tenable, and more flexibility is needed in the transfer of FRM to ensure that planted forests will be adapted to future climates.

Several approaches have been developed, focusing primarily on increasing genetic diversity in planted forests (for an overview, see Bucharova et al., 2019; Ivetić and Devetaković, 2016). One method is the composite provenancing strategy that combines local seed sources of native species with FRM coming from more distant and climatically variable sites (Broadhurst et al., 2008). The goal is to introduce new genetic variants while preserving local adaptation. Under the admixture provenancing approach (Breed et al., 2013) seeds are collected in a wide array of provenances, usually over large spatial scales and without a preference for local sources, aiming at maximizing adaptive potential. Climate-adjusted provenancing (Prober et al., 2015) combines admixtures with climatic transfer by introducing several nonlocal provenances collected along a climatic gradient to introduce genotypes adapted to future climate.

Risks of composite provenancing are common with other forms of assisted migration (see Table 9.1) and are related mainly to future generations: outbreeding depression due to the disruption of coadapted gene complexes, and breakdown of local adaptation to nonclimatic environmental factors (Ivetić and Devetaković, 2016). The benefit of broadening the array of available genotypes is immediate, while the build-up of evolutionary resilience through interbreeding and genetic recombination is also expected in the offspring generation. Again, the problem may be restrictive legislative and regulatory frameworks. The EU Directive 105/1999/EC on the marketing of forest reproductive material requires that reproductive material shall, during all stages of production, be kept separated by reference to individual units of approval, while mixing is allowed for the categories Source-identified and Selected within the same region of provenance. This actually prohibits mixing FRM from different sources, at least this is the way the Directive is often interpreted by the responsible official bodies.

Moreover, both seed sources and the process of FRM production need to be managed in a way that guarantees preserving genetic diversity. An expert group of the EUFORGEN program formulated several recommendations concerning this issue (Gömöry et al., 2021). In Europe, the selection criteria and management rules for basic materials vary considerably among countries, but some common features exist. In seed stands (category Selected), selection criteria related to genetic diversity include population size (defined by minimum area or the minimum number of reproducing trees), spatial arrangement, and (sometimes) isolation from inappropriate pollination sources (poor stands, related species, etc.). For seed collection, the minimum number of maternal trees is usually defined by legislation, and seed harvest is recommended to be performed during mast years to ensure maximum genetic contribution of the whole population to the seed crop (see Chapter 4).

Seed orchards (category Qualified) are small populations by definition; the number of genotypes used to establish a seed orchard rarely exceeds a few tens. Replacement of infertile clones, supplemental pollination, and flowering stimulation (e.g., by pruning, phytohormones, or fertilizers) may improve parental balance and genetic diversity of the seed crop. As parental contributions may vary strongly between years, controlled mixing of seedlots from different harvest years was recommended both for seed stands and seed orchards to promote genetic diversity. This is a consequence of the genetic structure of the seed crop deviating considerably from the genetic structure of the parental population. Although this practice is allowed under the Directive 105/1999/EC, it is prohibited by legislation in several countries. During the plant production stage, all steps introducing unnecessary selection pressure are to be avoided. For instance, seed fractioning by size or weight removes small, but viable seeds, which may discard families with smaller seed size (Ivetić et al., 2016). Culling of seedlings based on size can have a similar effect on genetic variation, depending on the genetic control of culling criteria (typically physical damage, height, and diameter; cf. Campbell and Sorensen (1984).

Transfers of forest reproductive material

At least since the 18th century, FRM has been transferred across Europe. At first, the search was for the cheapest seed sources; later, the goal was to improve stand performance, wood yield, or timber quality (Tulstrup, 1959). Currently, the adaptation of forest ecosystems to rapidly changing climate has become the main objective. Transfer of reproductive materials from sites currently experiencing climatic conditions similar to what is expected at a target site in the future is called assisted migration (AM). This term is not exclusively applied to forest trees, as AM is often taken into consideration in conservation biology and restoration ecology, mostly in relation to keystone species (Frascaria-Lacoste and Fernández-Manjarrés, 2012; Hällfors et al., 2016; Kreyling et al., 2011; Richardson et al., 2009). Assisted migration is currently advocated by many (if not a majority of) forest geneticists (Aitken and Bemmels, 2016; Aitken and Whitlock, 2013; Konnert et al., 2015; Matyas, 1994).

The terms associated with AM are confusing, but it is useful to distinguish between AM objectives and the distance FRM is moved (Fig. 9.4, cf. Hällfors et al., 2014). Pedlar et al. (2012) described forestry AM, focusing primarily on maintaining productivity and health of stands of widespread and commercially important forest species, and species rescue AM, aiming at the prevention of extinction of threatened species. In general, genetic material can be moved within the natural range of a species, called assisted gene flow (Aitken and Whitlock, 2013) or assisted population migration (Williams and Dumroese, 2013). Material transferred outside the range is called assisted colonization (Aitken and Whitlock, 2013), managed relocation (Richardson et al., 2009), or predictive provenancing (Breed et al., 2013). Williams and Dumroese (2013) distinguished in

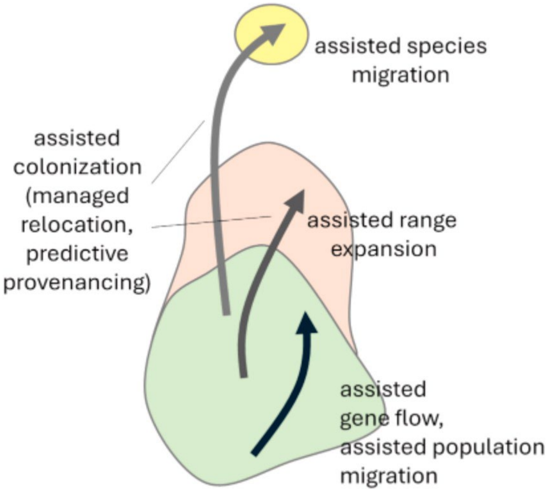

Figure 9.4 Schematic explanation of terms used in the context of assisted migration. green—natural range of species, pink—adjacent areas, yellow—disconnected areas. *(Credits: Du�an Go€mo€ry)*

this case between *assisted range expansion*, when FRM is placed close to the original range, and *assisted species migration*, which means translocation to distant sites (including the use of exotic species, cf. Chakraborty et al., 2015).

Assisted gene flow includes "transfer of gametes" (Aitken and Whitlock, 2013), which actually means transfer of pollen as male gametophytes. In practice, such transfer is limited to supplemental pollination in seed orchards, employing pollen collected in sources located at drier or warmer sites (G€m€ry et al., 2021). In the conservation literature, the concept of assisted migration covers practices that are not necessarily linked to climate change adaptation, such as species reintroduction (movement of organisms into a part of its range, from which it has disappeared in historic times) or species reinforcement (movement of organisms to build up an existing population) (IUCN/SSC, 2013).

As with every practical solution with uncertain outcomes, AM is debated among both conservationists and foresters. Kreyling et al. (2011) summarized the arguments supporting and contradicting the use of AM (Table 9.1), focusing primarily on biological aspects. Assisted gene flow has risks that could appear in the offspring generation. It may result in fitness loss due to outbreeding depression, which may persist for several generations (Grummer et al., 2022; Keller et al., 2000), or dilute local adaptations not related to climatic factors that could compromise the short- or long-term viability of the population (Torres et al., 2023). There are additional biological aspects of AM that need to be considered. As stressed by Frascaria-Lacoste and Fern�andez-Manjarr� (2012), tree species represent mostly keystone species of forest ecosystems, and transfer of specific genotypes or population may largely and irreversibly affect the associated biotic communities. They recommended favoring population mixes of the foundation species and collecting from adjacent populations along ecological clines of the foundation species

Table 9.1 Arguments in favor or against assisted migration (Kreyling et al., 2011).

Pros	Cons
• Reduced risk of extinction of focal units which lack adaptation and dispersal abilities to cope with climate change (intensified by fragmentation) • Conservation of genetic diversity • Conservation and restoration of diverse forests in the face of climate change • Maintenance of the productive potential and stability (of forests) • Active conservation as opposed to documentation of losses for conservationists • Pragmatic and cost-effective approach • Risks generally low, as the majority of studied historical species introductions were not detrimental • Risk of adverse effects on biodiversity from inaction higher	• Risk of adverse effects on native species composition and ecosystem functioning (as shown by examples of invasive species) • Risks for recipient ecosystems even for short-distance translocations • Problematic identification of recipient localities with imperfect knowledge on ecology and climate change • Some current climate conditions are without future definition, and assisted colonization for species from these climates is not feasible • Technical feasibility generally questionable • Technical feasibility for rare and endangered species not provided • Lack of predictive methods for risk assessment • Unknown costs and acceptability • Single species approach untimely in conservation • Impediment of efforts to preserve or restore habitats • Creation of a biased flora or fauna • Biological homogenization

to mimic natural processes of migration, in effect, assisted population migration. Bucharova (2017) expressed similar concerns about the effects of AM on biotic interactions in the target ecosystems.

The main source of information to guide AM is provenance research. For several commercially or ecologically important species, large-scale international provenance experiments have been established, where the performance of populations of different origins in terms of mortality and growth as well as traits of interest such as tree architecture, phenology, or physiology is assessed at sites situated under different climates. Such experiments comprising tens of provenances planted across climatically diverse test sites covering substantial parts of species' ranges are available for Norway spruce (Krutzsch, 1974), Scots pine (Oleksyn, 1988), European beech (von Wühlisch, 2007), and white oaks (Kleinschmit, 1993). Provenance responses to climatic transfer (usually measured as the difference in climate characteristics between the site of origin and the site of plantation; Mátyás, 1994) can be assessed by various types of transfer or response functions (Benito Garzón et al., 2019; Chakraborty et al., 2015; Rehfeldt et al., 1999; Wang et al., 2010). Although this approach was originally developed to guide geographic transfer, it can equally be used to choose appropriate FRM for future climates (Chakraborty et al., 2019).

Forestry practice is another important information source, although generally neglected in AM considerations. As FRM has been traded across Europe for centuries (Tulstrup, 1959; Myking et al., 2016; Brus et al., 2019), adult stands originating from FRM translocation are available, sometimes even in the second generation (e.g., Budde et al., 2023). This allows reliable assessment of the yield potential and evolutionary fitness of transferred populations under a new climate, wherever reliable records of seed origin have been preserved.

The future development of such a complex system as climate is associated with a considerable uncertainty related both to climate tipping points and political decisions affecting greenhouse gas emissions (Meinshausen et al., 2022). Modeling future climate at a sufficient resolution to allow prediction of temperatures and precipitations for a particular location is thus not an easy task. To a certain degree, the problems of uncertainty and insufficient spatial resolution also apply to modeling of past climate, which is based on spatial interpolation and thus loaded by error. The methodology of provenance research is another problematic aspect. Representativeness of the FRM used to establish provenance trials is not guaranteed, the collected material need not necessarily properly reflect the genetic setup of the maternal stand due to unbalanced family sizes, few families are collected, and poor fecundity in the year of seed collection are some of the potential shortcoming (Gömöry et al., 2020). For outplanting, wide spacing, weed control, and fencing against deer are used; this may distort mortality rate as an important indicator of the suitability of a particular seed source. Provenance trials are often assessed only at a young age; later, when measuring becomes difficult, trials are often abandoned. Thus, it is questionable whether such results can be extrapolated to the age of stand rotation.

The theoretical framework for AM has been elaborated and validated worldwide for several commercially important tree species (Beaulieu and Rainville, 2005; Chakraborty et al., 2024; O'Neill, 2017; Rehfeldt et al., 1999; Ukrainetz et al., 2011). However, the application in practice has moved slowly. Although the need for action is urgent, it seems to be insufficiently reflected in forestry practice and by political decision-makers. One of the reasons is legislation. In most countries, forest seed transfer rules have remained unchanged or have changed insufficiently. For instance, in the Canadian provinces of Alberta and British Columbia, seed transfer guidelines have been revised to allow seed of most species in most regions to be moved up to 200 m higher in elevation (Pedlar et al., 2011). To show another example from Europe, the last update of the FRM bill in Slovakia (138/2010 Z.z.) also allows FRM transfer by 200 m upwards, which corresponds to an average temperature shift of 1.3°C. It is questionable whether such moderate modifications of rules are sufficient. Even though revision of provenance recommendations is ongoing in many European countries, the current versions generally prefer local FRM or basic materials (seed sources) within the same region of provenance (Konnert et al., 2015). In spite of these difficulties, a variety of decision-support tools have appeared in the meantime, offering the choice of appropriate seed sources under consideration of particular climate change scenarios, such as Optisource (Beaulieu, 2009), SusSelect[1], or Seedlot Selection Tool (St.Clair et al., 2022).

Genetic diversity in the forest nursery supply chain

The genetic diversity of artificially regenerated forest stands relies on the choice of seed lots and seedling collections used for reproductive purposes (Hosius et al., 2006), starting with the selection of stands, provenances, and trees from which seeds are collected, through seed storage and germination, to the final selection of FRM. The criteria used to select seed stands and trees, to conduct seed collection, storage, and grading, as well as the selection of seedlings, inevitably changes the genetic diversity originally found in the source population. In the worst case scenario, a reduction in diversity occurs at each phase. This issue highlights the need to balance the conservation of biodiversity with the efficiency of FRM production throughout the nursery cultivation process, ensuring the production of FRM maintains the genetic diversity essential for maintaining forest biodiversity (Gömöry et al., 2021; Ivetić et al., 2016).

Seed stand selection

Selecting provenances for seed collection represents the initial, critical phase of *ex situ* conservation of forest genetic resources as well as production of FRM (Hosius et al., 2006; Vajana et al., 2024). Genetic diversity is often large in former glacial refugia and at the crossroads of different postglacial recolonization routes (Petit et al., 2003) and could be affected by factors linked to ecological and geographic marginality (Hampe and Petit, 2005). Conversely, a high genetic diversity of trees in combination with large juvenile population sizes allows local adaptation in spite of typically high levels of gene flow (Petit and Hampe, 2006) as recently shown in both tropical and temperate species (Brousseau et al., 2021; Budde et al., 2024).

Regardless of its spatial scale, when a population genetic structure exists, the spatial distribution of selected populations is critical to achieve optimal sampling of seeds. Thus, seed collection plans should incorporate considerations based on the spatial distribution of genetic diversity, in particular for species characterized by limited dispersal capabilities (Hoban and Schlarbaum, 2014). Extensive genetic data, especially in areas where several differentiated genetic groups are present (e.g., Gómez and Lunt, 2007; Rodríguez-Quilón et al., 2016; Piotti et al., 2017), are needed to sample enough genetic diversity for these optimizations to be effective, paying particular attention when species are rare

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[1] https://play.google.com/store/apps/details?id=com.topolynx.susselect&hl=en.

or widespread but characterized by low genetic diversity (e.g., Mataruga et al., 2020; Vendramin et al., 2008). There is evidence that, if seed collection is done correctly, at least the levels of neutral genetic diversity of plantations/seed orchards will be comparable to those of the original populations (Ivetić et al., 2016; Santini et al., 2018).

Selection of seed trees within seed stand

Approved seed stands are usually a small fraction of mature forest stands, and a limited number of seed stands are used for collecting seeds for producing FRM (Gömöry et al., 2021). A critical factor in preserving as much genetic diversity and representativeness as possible in nursery-produced FRM is defining a minimum number of seed trees and rules for their spatial distribution. Several national and international guidelines indicate that 15 to 50 seed trees per stand, spaced at least 50 m apart, should be enough to reach this goal (Gömöry et al. (2021). Some sources, instead of indicating a number of seed trees per population, state that seed collection should be preferentially focused on the total number of seed trees at the whole distribution level (Hoban, 2019), after due consideration of a species biology, collection maintenance, and conservation targets (e.g., avoiding the loss of rare alleles), although this approach may not be allowed under current European regulations (e.g., Directive 105/1999/EC).

Special attention should be paid to species with sporadic seed production (i.e., masting), clonal species, and dioecious species. Also, pay heed to extremely isolated populations or populations representing unique genetic lineages, which are typical conditions toward range margins. A more precise, species-specific determination of the minimum threshold of seed trees at various hierarchical levels can be achieved through simulations based on real genetic data. This approach was used for *Prunus avium*, a sporadic species prone to the development of clonal groups through root suckers. Recommendations similar to the ones generally found in available seed collection protocols were reached (i.e., collecting seeds from ≥25 genetically distinct, geographically distant seed trees to attain 90% of the extant genetic diversity; Blanc-Jolivet and Degen, 2014).

Any strategy for the choice of seed trees should consider that tree fecundity and the effective number of pollinators per tree are parameters tightly associated with the genetic diversity of the seed crop. They are often related to population and individual characteristics (e.g., stand density and isolation, individual phenology and growth rate) as well as climatic features (e.g., wind direction, humidity; Aleksić et al., 2022; Avanzi et al., 2020; Hoebee et al., 2007; Oddou-Muratorio et al., 2018). In rare cases when individual pollen flow dynamics were studied in different reproductive seasons, it was shown that mating patterns might substantially vary among years (Hoebee et al., 2007). All these issues must be carefully considered to collect seeds, guaranteeing the highest possible adaptive potential and survival in the climate of the future.

Seeds from seed orchards

For production of climate-adaptive FRM, it is important to emphasize that most seed orchards established from plus trees selected between 1950 and 1990 still exist and produce seed. Thus, seed orchards often use old plus trees (Gömöry et al., 2021) and consist of genotypes possibly adapted to climates significantly different from those projected for the future. Hence, the establishment of new seed orchards is timely, as well as understanding potential limitations of existing orchards.

The assessment of seed quality from seed orchards is closely related to the criteria that drove planning the orchard (Funda and El-Kassaby, 2012; Hosius et al., 2006; Lefèvre, 2004). A key-point is whether the establishment of the orchard was guided by prioritizing the maintenance of genetic diversity or other selection criteria (e.g., growth, quality timber production, pest or damage resistance). The criteria used for the selection of the material affect the genetic diversity introduced in the orchard (Funda and El-Kassaby, 2012). Another critical consideration is the scale of represented stands; seed orchards can include trees selected at the national, regional, or local scale. In addition, selection of single trees is also significant; the trees selected to provide vegetative material for the orchards are the so-called plus trees that exhibited the best growth and health conditions in the stand sampled. Such a criterion makes sense, because genetically inferior trees cannot be visually distinguished from trees affected by competition and unfavorable microsite conditions. Nevertheless, the use of phenotypic selection is generally thought to be effective in maintaining genetic diversity within natural populations and provides a cost-effective method of selecting reproductive material (Ivetić et al., 2016). New techniques of marker-assisted selection and association mapping in natural populations, however, are becoming affordable options to select material with features resistant to biotic and abiotic stressors (Ray et al., 2022; Santure and Garant, 2018).

The distribution of trees within the seed orchard plays a pivotal role in genetic diversity preservation because it affects the spatial patterns of gene flow by pollen. When controlled cross-breeding is not applied, the interplay among the size and isolation of the seed orchard, as well as spacing and the degree of phenological overlap with surrounding conspecific trees, can influence the levels of undesired pollination from outside (Burczyk et al., 2004). Seed orchards can boost genetic diversity of sporadic species or endangered species suffering dispersal limitations, enabling pollen exchange in situations where geographic distances would otherwise hinder exchange among trees or populations (Aleksić et al., 2022; Hoebee et al., 2007).

Seed collection

Despite careful selection of a sufficient number of seed trees, the family ratio in the collected seed lot may be uneven (Ivetić et al., 2016). Variations in the quantity of collected seeds, fruits, or cones, and differences in seed viability due to factors such as maturity, insects, or infections can contribute to these disparities (Schmidt, 2000). Mast years in heavy-seeded species affect seed availability that, in turn, could change the quality and diversity of the seed lot. Seeds collected during non-mast years can have diminished genetic diversity. Seeds collected from a limited number of trees or from trees that produce few seeds underrepresent the overall diversity of the population (Ivetić et al., 2016). Mixing seed lots of different years is recommended when mast years occur at longer intervals.

The timing of collection plays a role in seed selection. Seed maturity may be linked to individual genetic characteristics, and not solely influenced by microenvironmental or climatic conditions. Within a stand, seeds from different trees may not ripen at the same time due to individual variation in fruiting phenology (Schupp et al., 2019). Typically, seed collection is done when a sufficient number of trees have mature seeds, primarily due to cost effectiveness. Therefore, collecting only during the time when the bulk of seed maturation occurs can exclude early or late maturing individuals. This could miss traits associated with the ability to cope with unfavorable early or late conditions. In addition, when seed collection is limited to the more easily accessible parts of the canopy, there could be a decrease in genetic diversity due to the position in the crown of the collected seeds. All these considerations underscore the need to carefully balance economic gains and genetic diversity losses when collecting seeds.

Seed processing, grading, storage, and treatment

Seeds may vary in size, weight, morphology, and physiology, and these traits are strongly related to the genotype of seed trees (Ivetić et al., 2016). Generally, small seed size is related to smaller seedlings (Bonito et al., 2011; Campbell and Sorensen, 1984) that might have lower chances of survival (Andivia et al., 2021). Mechanical seed processing and grading are customized for medium-sized seeds. Since it is not cost-effective to process the progenies separately, systematically excluding families producing smaller seeds from the final seed lot might reduce genetic diversity (Ivetić et al., 2016). Germination is more influenced by genetic factors than seed size, however, and quick development of a quality plantlet and seedling is believed to be impacted by germination (Ivetić et al., 2016). Consequently, selecting only larger seeds might lead to a decline in quality and diversity. Therefore, it is recommended to utilize a mixture of seeds of varying sizes (Edwards and El-Kassaby, 1996; Ivetić et al., 2016).

Genetic changes are possible during seed storage since storability of seeds is significantly influenced by genetic characteristics (Roos, 1980; Schmidt, 2000). However, the potential loss of viability in seeds with relatively low vigor mainly occurs during over-extended storage periods with no major impact on randomly selected seeds with different sizes, weight, and other physical or physiological traits. Studies suggest that seed treatment and stratification have minimal effects on the genetic structure of reproductive material (Konnert and Hosius, 2010). The breaking of dormancy—a trait with a strong genetic basis—through specific treatments may lead to the loss of seeds that do not respond quickly, however, leading to a selection bias favoring seeds that promptly respond to treatment.

Germination and emergence selection of plantlets

Germination is strongly genetically controlled, but low germination capacity results in low seedling availability of smaller plants, which generally will be discarded, that is, culled (Ivetić et al., 2016). Nursery practices may include a pregermination phase to sow only viable seeds (i.e., seeds that already have initiated germination), an emergence phase where seeds are placed in a seedbed to select the plantlets to be transplanted into containers, or both. Pre-germinated seeds are generally collected when there are enough for practical and economic reasons, excluding early or late germinating individuals that may carry adaptive capacity to unfavorable germination conditions that may occur at the beginning or end of the growing season.

Seedling production and selection

Quality in nursery seedlings goes beyond appearance (Dumroese et al., 2016; Grossnickle and MacDonald, 2018) yet the traditional criteria for plant culling and grading often focus on easily measured morphological characteristics such as size or height. While nursery practices tend to uniformly favor all seedlings, selecting the material according to phenotypic criteria might inadvertently lead to a reduction in the overall diversity of the batch. Nonetheless, the exclusion of very small seedlings is a common practice to mitigate the risk of incorporating underdeveloped plants or those more susceptible to outplanting stress (Andivia et al., 2021). It is crucial to recognize that treatments aimed at standardizing growth may mask inherent variability and potentialities among plants. The choice between average-sized seedlings or larger ones involves a trade-off, as it influences the diversity and individual characteristics within the selected material. Striking the right balance in selection criteria becomes important to ensure a robust and diverse pool of trees for various planting scenarios. For instance, a trend toward a slight reduction in genetic diversity among larger individuals was shown by assessing the genetic diversity among seedlings sorted by dimension during nursery practices (Konnert and Ruetz, 2003).

Nursery production may cause a significant change in genetic diversity according to the production method and mechanization level. For example, a loss of genetic diversity due to size selection was observed in *Picea engelmannii* and *Picea abies*, even though such reduction can be relatively small as was observed in *Fagus sylvatica* (Hosius et al., 2006). Bareroot production can expose the seedlings to more severe environmental conditions than experienced by seedlings grown in containers, possibly causing a higher selection pressure (Iveti� et al., 2016). However, there is no evidence suggesting that nursery operations have a significantly negative impact on the genetic diversity of FRM (Iveti� et al., 2016).

The impact of site preparation and forest management on biodiversity

Goals of restoration and reforestation may differ, for example, promoting species diversity versus shortening rotation cycles. Although survival and development of tree seedlings are common targets, costs and benefits may differ between practices, environmental and economic targets are not necessarily mutually exclusive (Stanturf et al., 2001). At the landscape scale, multipurpose forest management may balance public and private interests in biodiversity conservation, timber production, and provision of ecosystem services. A landscape management regime that balances these three components has the potential to minimize trade-offs between the global need for meeting climate targets and the local demand for providing ecosystem services (Muys et al., 2021). Diverse forest structures, with trees of varying sizes and ages located across different horizontal and vertical spaces within forest stands (i.e., functional diversity) and among stands across the landscape (i.e., ecosystem diversity), play a crucial role in increasing ecosystem function, niche occupancy, and resource use (Millar et al., 2007; Forrester et al., 2018).

Regeneration

Traditional forest management practices have simplified stand structures, reduced species richness and landscape diversity, and altered forest microclimate. These effects will continue to influence ecosystem functions, processes, and services for a long time. The reduction in habitat diversity and spatial complexity adds to the decrease in habitat amount and in ecosystem connectivity that shapes landscape structure (Lecoq et al., 2021). Forest regeneration and seedling establishment offer the first opportunity to adapt species composition and stand structure to projected environmental conditions (L6f et al., 2015). Reversing the simplification of landscape structure by fostering landscape heterogeneity, in terms of high diversity of land cover types and small patch size, can help select multifunctional forest communities comprising species with generalized and specialized traits, despite high levels of management intensity (G�amez-Viru� et al., 2015).

Forest harvesting is a disturbance that alters ecosystem structure, but forest ecosystems may regenerate and reconstitute their equilibrium after the cessation of the disturbance. Small-scale mechanical disturbances may resemble localized natural soil disturbances caused by tree falls or animal activity, however, mechanical disturbances from modern land management equipment are often more intense, frequent, and widespread. This can exceed the recovery capacity of native plant and animal species, affecting their composition and richness. Their extensive use can alter community composition for decades or even centuries. As an example, frequent soil disturbance can lower the activity of carabids, thereby lowering their impact on weeds (Blubaugh and Kaplan, 2015).

Forestation (reforestation, afforestation, or restoration) treatments include planting seedlings or cuttings, direct seeding, coppicing, or natural regeneration with or without site preparation (Oliet and Jacobs, 2012; Stanturf et al., 2014a). These treatments typically start at the initial phases of forest regeneration following natural disturbance events, planned silvicultural interventions, or land use change. Assessing the ability of forests to recover either naturally or through planting is essential to meet land management objectives and regimes. When stand-replacing disturbances make natural regeneration unreliable, planting may help trigger or accelerate the development of forested ecosystems. Forestation priorities also need to be identified in partnership with stakeholders for developing adaptive forest plans and ensuring resilient future forests. Establishing resilient forests requires naturally regenerating or planting the right species or provenance, considering the landscape context, and proper site preparation (Oliet et al., 2019; Castro et al., 2021). Nurturing forests as they develop promotes structural, compositional, and functional diversity, in support of ecosystem benefits and services.

Young forests can require treatments to ensure stand development and sustain forest health over time. Site preparation and forest management practices for restoration objectives borrow from traditional silviculture, although we must bear in mind the goals and costs may differ (L6f et al., 2019; Stanturf et al., 2014b). In addition, efficient site preparation and forest management practices must consider local contexts and multiple species with different traits (Castro et al., 2021). Competing plant species can provide suitable environmental conditions for the proliferation of other organisms (e.g., fungi, nematodes, deer, and small mammals, such as voles and rabbits) also harmful for seedling recruitment (Bergman et al., 2005; Bucyanayandi and Bergeron, 1990). Ungulates are key drivers of forest regeneration (Fig. 9.5) leading to reduced seedling growth and survival and changes in plant assemblages by benefiting species that are less palatable or more tolerant to browsing (Boulanger et al., 2015; Laurent et al., 2017). Although postharvest site preparation is more common, preharvest site treatments, such as chemical spraying and prescribed burning, may reduce postharvest site-preparation costs.

Eradicating vegetation other than the planted trees can be counterproductive because other plants may help retain nutrients on the site, provide wildlife habitat, help maintain biodiversity, and promote erosion control. Herbaceous vegetation may protect tree seedlings from adverse environmental conditions or herbivory (St-Denis et al., 2018). Although the survival and growth of pioneer species (e.g., *Pinus* sp.) can be enhanced through site preparation treatments that reduce competition for resources, seedlings exposed to high levels of solar radiation may also show increased mortality and deformed growth (Lambers et al., 2008). Nevertheless, herbaceous communities often are strong

Figure 9.5 Clearcutting has been applied to progressively remove maritime pine infected by maritime pine bast scale, concurrent with planting of holm oak seedlings. Establishment of holm oak regeneration has, however, been severely constrained by fallow deer browsing pressure. Herbivory pressure on planted holm oak seedlings is significantly related to mechanical protection exerted by natural regeneration of abundant maritime pine saplings (and secondarily shrub species) that interfere with the detection of, access to, and consumption of the target species. See Maltoni et al. (2019) for details. *(Credits: Roberto Tognetti)*

direct and indirect competitors, and their control may become necessary to secure tree planting on abandoned agricultural fields (Cogliastro et al., 2006). Dense herbaceous cover colonizing open spaces and abandoned lands may impair the establishment, growth, and survival of planted or regenerating seedlings for several years (Benjamin et al., 2005).

Site preparation effects on biodiversity

Lands previously used for agriculture or pasture are difficult to regenerate due to compacted soils with few nutrients, low water retention capacity, and impoverished microbial communities (Foley et al., 2005). Harvested forest sites can have accumulated logging residue, stumps, and roots that impede planting. In either case, managers often use heavy equipment in mechanical site preparation to aid regeneration by plowing the soil, killing and incorporating existing vegetation and other plant debris, cultivating the soil layers, and removing logging slash to facilitate planting or direct seeding (Löf et al., 2012). Although mechanical site preparation may benefit seedling establishment, survival, and growth (Löf et al., 2006, 2012), soil conditions can be altered and competing vegetation also may take advantage of practices such as scarification and mounding (Löf et al., 2015).

Mechanical treatments include scarification, subsoiling, ripping, mounding, or bedding of soils (Chapter 6). The choice of methods depends on soil type, terrain topography, and disturbance degree beyond which regeneration and restoration, or conservation can be impaired. In hilly or mountainous areas with steep slopes, terracing can reduce steepness by dividing the slope into smaller, gently sloping sections that prevent rainfall runoff and accumulate soil organic carbon (Deng et al., 2021). Terracing can enhance regional landscape diversity, providing habitats, fostering symbiotic relationships among organisms, and crucially contributing to habitat reconstruction and improvement, thus maintaining biodiversity (Merino et al., 2010). Negative effects of terracing may also arise, such as interference with the hydrologic cycle caused by poorly designed or mismanaged terraces that increase soil erosion and water runoff, which can indirectly harm biodiversity.

Competition for resources (e.g., light, nutrients, and water) may also endanger seedling survival and growth during the regeneration stage (Balandier et al., 2006). Using chemicals to remove or control competitive plants, without damaging the planted seedlings, may be important to maximize seedling establishment and reforestation or restoration success. Unfortunately, herbicides are partially responsible for biodiversity loss worldwide, as they significantly reduce food sources for birds, insects, and mammals. They can also damage or kill nontarget vegetation or other organisms. Indeed, many chemicals are potentially toxic to biota (including humans) in terrestrial and aquatic environments.

Reducing effects on biodiversity and ecosystem services

Site preparation following forest harvest represents the initial step for increasing regeneration survival and growth. Nevertheless, forest management activities preharvest affect the site conditions for regeneration. Since site preparation may alter vegetation composition, wildlife occurrence, water quality, and aesthetic features; forest management should be planned and implemented carefully to drive restoration and reforestation projects. Human pressure through land management has impacted the landscape with varying intensity, leaving long-term legacies in today's forests and their dynamics (Giesecke et al., 2017; Jɵgiste et al., 2018). Fire and pasture regimes are examples that have been greatly altered by human activity, with impacts on the current response of forest ecosystems to these disturbances. Altered fire regime and intensity because of climate and land use changes profoundly affect the structure and composition of forest ecosystems (Brown and Smith, 2000). Legacies of past management approaches need to be considered when planning for restoration or reforestation. Restoring ecological processes such as fire or inundation regimes, nutrient cycling, and landscape connectivity may be necessary (Stanturf et al., 2014a).

Figure 9.6 In the mixed fir-beech-spruce old-growth forest of Lom in Bosnia-Herzegovina, regeneration processes are initiated by natural disturbances that happen at different times and are unevenly distributed across the area. Canopy gaps caused by the death of individual trees or groups of trees, along with the presence of deadwood, play a crucial role in the widespread establishment of natural regeneration. *(Credits: Roberto Tognetti)*

In addition to harvesting, other disturbances are stand-replacing extreme events, such as wildfires, windstorms, droughts, and pest outbreaks (Fig. 9.6). Salvage logging that removes timber before it deteriorates is common after extreme events but also reduces the amount of deadwood. Postdisturbance salvage logging may have long-lasting impacts on microhabitats and soils, affecting biodiversity and hydrology (Thorn et al., 2017). Snags anchor soils reducing chronic runoff of sediment to streams, while deadwood provides habitat sustaining the richness of many taxonomic groups and the abundance of saproxylic species and other wood-dependent organisms (Bani et al., 2018; Parisi et al., 2018). Thus, retaining as much standing and downed woody debris as possible during site preparation reduces impacts on biodiversity.

Partial removals of overstory trees can provide opportunities for planting that can alter stand composition over time. Retention forestry is an alternative to even-aged methods such as clearcutting. Retention practices release individual trees and tree patches with a primary aim to promote biodiversity (Löf, 2017). Variable density or nonuniform thinning may also create heterogeneous conditions (Puettmann et al., 2016). Thinning approaches that seek to enhance and restore forest heterogeneity may increase tree microhabitat for wildlife species that prefer dense canopy layers and, at the same time, regulate stand density to mitigate the risk of stand replacing fire or drought-related tree mortality (Knapp et al., 2017; North et al., 2009). Underplanting in areas skipped in thinning, or by creating gaps, can enrich diversity (Stanturf et al., 2014a).

Because the degree of soil disturbance during site preparation and effects on biodiversity differ according to methods used and site conditions, the trade-offs with costs and benefits are difficult to generalize. Piling and raking clear loose debris, roots, and stumps remaining after harvesting and shearing facilitates bedding and planting operations and minimizes sprouting from remaining roots. Logging debris should be left on site as much as possible as a future substrate for the next generation of tree seedlings and for the species richness of saproxylic organisms (Bani et al., 2018; Parisi et al., 2018). Scattering the logging debris without burning postharvest debris can be a solution, although logging debris increases the difficulty of other operations and increases fuel loads. Burning in winter reduces hazardous fuels and provides easy movement during planting.

Mechanical site preparation and tree planting may increase greenhouse gas emissions from soils (Jandl et al., 2007) and trigger soil erosion processes (Alcázar et al., 2002), especially on slopes. Restricting site preparation to tree planting spots (e.g., mounding with an excavator) or reduced density (planting fewer spots) in combination with large seedlings and may provide an operational solution (Löf et al., 2015). Large but more expensive seedlings, in fact, have greater survival-to-cost ratio and competitive strength than smaller seedlings.

Where the intensification of management aims at increasing the average rate of wood production per unit of land, for example in short rotation forestry for bioenergy, fertilization can be required (Smethurst, 2010). Fertilizers used in forestry are aimed at increasing biomass production for wood volume and intensification reduces the length of harvesting cycles. On phosphorus (P) deficient soils, tree survival and growth may benefit from preplant phosphorus applications. Monospecific plantations are often limited by nitrogen (N) and fertilizer rates and timing can be calibrated for cost-effective growth response. Including N-fixing tree species in mixed-species plantings might improve conditions for co-existing trees (Battipaglia et al., 2017), although N-fixing trees can outcompete the growth of the target species and may need to be removed at some point. Increased N-availability benefits in agroforestry systems have been well-documented (Binkley and Giardina, 1997; Forrester et al., 2006).

Introducing non-native species and management of existing ones

Although there is a long history of introductions of non-native tree (NNT) species in European forests and despite the fact that hundreds have been trialed, so far only about 150 non-native species are of major ecological and economic importance (Brus et al., 2019; Hermann, 1987). The extent of introductions of NNT species varies greatly among countries, depending on climatic conditions, but also on historical, socio-economic, and legislative factors (Pötzelsberger et al., 2020). Some were deliberately introduced to increase timber production, cultivated for phytomelioration, or to stabilize soils and to reclaim degraded land areas. Introduced species include *Eucalyptus* spp., *Picea sitchensis*, *Pinus strobus, Pseudotsuga menziesii*, *Quercus rubra* (Brundu and Richardson, 2016)*, Prunus serotina* (Starfinger et al., 2003), *Acacia* spp., and *Robinia pseudoacacia* (Brundu and Richardson, 2016). Some other species were not introduced for forestry but spread from nearby green spaces or orchards, for example, *Acer negundo, Ailanthus altissima*, *Fraxinus pennsylvanica,* and *Prunus cerasifera* (Czortek et al., 2024; Puchałka et al., 2023b).

Even though non-native woody species have significantly enriched the taxonomically and functionally impoverished European dendroflora and provide many important ecosystem services, negative impacts on biodiversity and soil properties have been documented for many of them. On the one hand, particularly adverse impacts have been observed for NNT species that are phylogenetically and functionally distant from native species (Wohlgemuth et al., 2022). On the contrary, species closely related to native trees are sometimes hosts of common pathogens and pests (Pötzelsberger et al., 2020) and can be vectors for new pests that threaten native species (Green et al., 2023; Santini et al., 2013; Seidl et al., 2018). The introduction of NNT species also can contribute to the invasion of symbiotic species, which can lead to unpredictable changes in the mycorrhizae of trees, especially phylogenetically close ones, such as the North American *Aureoboletus projectellus*, which can compete with native fungi from the Boletaceae family for symbiosis with *Pinus sylvestris*, thus affecting Scots pine adaptation to the environment (Wrzosek et al., 2017).

The diversity of the economic and ecological importance of NNTs, as well as their life history traits and dispersal abilities, means that each of these species requires a different approach to their management in forests. Despite many studies, knowledge of the ecology and impacts of non-native tree species on European forest ecosystems is still insufficient (Dimitrova et al., 2022). Moreover, studies on the effects of better understood non-native species on biodiversity and soil properties often yield contradictory results (Wohlgemuth et al., 2022). Recent work suggests that the spread of NNT species can significantly reduce the quality of ecosystem services such as habitat maintenance, crop provisioning, and soil and nitrogen storage, and NNTs represent one of the greatest threats to forest ecosystems (Gallardo et al., 2024). Hence, the introduction of NNT species should consider both the economic benefits and the ecological risks it entails (Brundu et al., 2020). This is especially relevant for species that can spread aggressively from forest plantings.

Non-native tree species cultivated and spreading in European forests are highly variable in terms of phylogenetic position, functional traits, and autecology. Their invasiveness and economic importance can be highly variable, depending on the habitat conditions and plant communities into which they are introduced (Wohlgemuth et al., 2022). For example, some *Pinaceae* species are highly invasive in the southern hemisphere, where closely related species do not occur (Moran et al., 2000), whereas in Europe, they are generally considered as low invasive and some species have naturalized (Carrillo-Gavilán and Vilà, 2010). Non-native conifers rarely colonize forests in Europe because their seeds often end up in habitats that are not conducive to seedling establishment (Adamowski, 2004). The conifer seedlings also are less competitive than angiosperm seedlings due to the lower efficiency of the wood transport system by tracheids, less efficient photosynthetic apparatus, and lower ecological plasticity (Becker et al., 1999).

The most naturalized species in Europe, including *Picea sitchensis, Pinus contorta, P. strobus* and *Pseudotsuga menziesii*, are relatively easy to control in their abundance and distribution (Wohlgemuth et al., 2022). Their impact on the habitat diversity of European pine forests is also poorly documented (Carrillo-Gavilán and Vilà, 2010). This is likely to be due to their functional similarity to native congeners. Although non-native conifers can negatively affect the forest understory, birds, insect biodiversity, and soil properties of fertile deciduous forests (Bärmann et al., 2023; Wohlgemuth et al., 2022), native pine species introduced into spruce and beech habitats have similarly negatively impacted biodiversity (Budde et al., 2011; Petersson et al., 2019). Thus, it is inconclusive that native species always have less negative impact on ecosystems than functionally similar non-native congeners.

The management of non-native deciduous species poses a more complicated challenge because many of them are highly invasive. Projected climate change will favor their further expansion as many of them are from warmer and drier conditions similar to the projected future European climate (Dyderski et al., 2018; Puchałka et al., 2023b). Even though many European countries restrict them due to their invasiveness, some are considered important alternative species as conditions for native trees deteriorate (Dyderski et al., 2018; Thurm et al., 2018; Wohlgemuth et al., 2022). For example, *Acacia* spp., *Ailanthus altissima*, *Q. rubra,* and *R. pseudoacacia* are more suitable for land reclamation than native species and can play an important role in the first stages of restoration of forest ecosystems (Enescu, 2014; Horodecki and Jagodziński, 2017; Papaioannou et al., 2016). These fast-growing species with low water and soil requirements may competitively displace native trees, of which only a few will benefit from climate change (Dyderski et al., 2018; Konatowska et al., 2023; Puchałka et al., 2021, 2023b).

Climate change is threatening European conifer forests, which are giving way to native and non-native deciduous species (Carnicer et al., 2014; Galiano et al., 2013). The shift of deciduous species ranges toward higher latitudes and elevations, however, does not mean that they will have favorable growing conditions, particularly on poor sandy soils (Dyderski et al., 2018; Puchałka et al., 2023b). Recent studies of *F. sylvatica* and *Q. petraea* near the northeastern, cooler margin of their current natural ranges, suggest that climate warming may cause premature cessation of the cambial activity due to summer droughts and heat waves (Puchałka et al., 2024). An earlier phenology can also increase the risk of frost injury due to the increasing frequency of late spring frosts (Puchałka et al., 2016).

Deciduous species in poor pine forest habitats not only could be unproductive but also cause deterioration of habitat for many species that evolved in low-trophic and moderately shaded forests by altering light regimes, litter characteristics, and soil chemistry (Aerts et al., 2017; Horodecki and Jagodziński, 2017; Woziwoda et al., 2014). Hence, some closely related conifers from drier and warmer European climates may provide an alternative to receding *A. alba*, *P. sylvestris,* and *Picea abies* (Buksha et al., 2019; Dyderski et al., 2018). For example, the closely related and functionally similar *P. nigra* could replace *P. sylvestris*. On the contrary, comparative studies in Poland of native *P. sylvestris* and introduced *P. nigra* and North American *P. rigida* found growth increment in all three species were very similar (Klisz et al., 2023), failing to confirm that species from drier and hotter climates tolerate meteorological extremes better.

Recent studies suggest that the most economically important introduced conifers in Europe, such as *A. grandis, P. sitchensis, P. contorta,* and *P. menziesii*, will lose their climatic optima in southern and central Europe and continued planting of these species is risky in many areas of central and southern Europe in the coming decades. Areas suitable for their cultivation will remain mainly in northern and western Europe, in areas influenced by a humid oceanic climate, and in mountainous areas (Dyderski et al., 2018; Puchałka et al., 2023b). Many otherwise promising drought and heat-wave tolerant conifers suffer from late frosts at a young age, as evidenced by frequent frost-rings (Klisz et al., 2022). In the changing European climate, the frequency of this factor is unfortunately increasing (Zohner et al., 2020). This highlights that multiple factors can affect potential adaptation and species and their ecotypes for cultivation should include both early and late frost tolerance and summer drought resistance, which may be mutually incompatible (Silvestro et al., 2019).

Non-native conifers may be considered as alternatives to native conifers, as they alter ecosystem functioning less than deciduous species, especially non-native species such as *Quercus rubra, Prunus serotina,* and *Robinia pseudoacacia*. These NNT species are currently expanding, tolerate poor sandy soils well, and climate change will expand their potential ranges in Europe (Dyderski et al., 2018; Puchałka et al., 2023b). These deciduous NNTs are functionally and ecologically distinct from conifers, thereby significantly altering light regimes, litter properties, and soil conditions, consequently altering understory species composition and abundance, changing entire trophic networks, and ecosystem functioning (Chabrerie et al., 2010; Halarewicz and Pruchniewicz, 2015; Woziwoda et al., 2021). It seems sensible to seek alternatives to native conifers among phylogenetically and functionally similar species that would play a similar role in ecosystems. Some of the introduced conifers, for example, *Pinus contorta*, perform better in dune fixation than native pines threatened by climate change and could reduce the risk of soil degradation by aeolian processes (Schwendiman, 1977).

Climate change will alter the composition of forests by favoring the spread of species that are less economically attractive. This may come from species dispersing from parks, orchards, and gardens such as *Acer negundo*, *Fraxinus pennsylvanica*, *Prunus cerasifera,* and *Prunus serotina* (Czortek et al., 2024; Fernandez et al., 2023; Zajdler et al., 2018). Other native species that currently have little economic importance in timber production will benefit from climate change and increase in dominance, for example *Acer pseudoplatanus, Prunus avium,* and *Sorbus torminalis* (Dyderski et al., 2025; Konatowska et al., 2023). In addition to the negative impact on the forest environment of some of these species, they also can hamper current forest management and attempts to remove them are costly and not always effective (De Wit et al., 2001; Fernandez et al., 2023). Also, it should be borne in mind that forest trees are part of an ecosystem linked by trophic networks to other species of plants, animals, and fungi, whose climatic niches are also subject to shifts. Climate-driven range shifts also apply to the most common and widespread forest understory species (Kermavnar et al., 2023; Puchałka et al., 2023b, 2023c).

Climate-driven shifts in species ranges are expected, where most native species will mainly lose rather than gain new climatically optimal areas (Bellard et al., 2012; Thuiller et al., 2005a, 2005b). This also applies to most of Europe's major forest-forming trees (Dyderski et al., 2018). Despite the general pattern of shifts in ranges toward higher latitudes and elevations, both the magnitude, direction, and importance of particular climatic factors differ considerably among species (Kermavnar and Kutnar, 2024; Puchałka et al., 2023a, 2023b, 2023c). Nevertheless, the persistence of NNT species in forests may become a reality in the near future and strategies for shaping them is a challenge, and at the same time, an urgent need for mitigating the negative effects of climate change (Alaniz et al., 2024; Bellard et al., 2012; Hanewinkel et al., 2013).

Instead of communities developed as a result of natural ecological and evolutionary processes, shortly we may have to manage forests formed by species that have not yet occurred with each other, functioning in interspecies interactions hitherto unknown in our experience. Such novel ecosystems formed by accidental or intentional species introductions and range shifts are becoming a fact of life (Evers et al., 2018; Hobbs et al., 2006). Hence, when introducing or removing NNT species, it is important to keep in mind their ecological and economic importance (Bonanno, 2016; Nyssen et al., 2024), not only in the present, but also the role they will play under future climate conditions. Rational management of NNT species can mitigate the adverse effects of climate change and help keep forest ecosystems functioning while maintaining their economic productivity. Inappropriate decisions, on the contrary, can exacerbate their effects.

Guidelines for biodiversity conservation

- Promote multifunctional forests and multispecies stands
- Maintain or increase all forms of biodiversity (genetic, species, ecosystem)

- Increase functional diversity
- Increase flexibility in regulations governing transfers of forest reproductive materials
- Avoid unnecessary selection pressure at all stages of the FRM production processes
- Ensure that FRM maintains as much genetic diversity as possible
- Fully consider trade-offs and balance economic benefits with loss of genetic diversity when collecting seeds
- Minimize soil disturbance during site preparation
- Retain snags and deadwood on regeneration sites including during salvage logging
- Consider trade-offs between economic benefits and ecological risks when introducing non-native tree species
- Prepare to manage novel ecosystems

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