

# The State of Forest Genetic Diversity: Anthropogenic Impacts and Conservation Initiatives

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Fragmented forest landscape in Upper Austria, Amstetten area (Photo: BFW/Florian Winter)

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## Abstract

Genetic diversity is a key pillar of biodiversity, underlying the adaptive potential of any species. At the same time, it is difficult to quantify this component of biodiversity, and we know very little about the genetic diversity status of most species. A wealth of studies points toward a substantial decline, which is also apparent in numerous forest species. Connectivity is fundamental to maintaining high levels of genetic diversity and adaptability via gene flow between populations. In this chapter, we attempt to elucidate the importance of genetic diversity for the entire forest ecosystem with a focus on its main components: tree species. We elaborate on the anthropogenic factors impacting forest diversity, like exploitation and artificial regeneration, climate change, and introduced pests. An overview of molecular methods for studying genetic diversity and connectivity is presented. Regular genetic monitoring is imperative for optimizing conservation strategies such as the creation of stepping stones to counteract population fragmentation. We highlight the importance of taking genetic diversity into account when sourcing plant material for forest and landscape restoration projects. Finally, international efforts to conserve genetic diversity are presented along with recommendations on suitable indicators to monitor it. Scientists working on genetic diversity are encouraged to actively participate in national and international processes to incorporate genetic principles into policy development as well as conservation and restoration efforts.

## Keywords

Climate change · Forest genetic resources · Forest reproductive material · Genetic rescue · Human impact

# The Importance of Genetic Diversity for Forest Ecosystems

## Processes Affecting Genetic Diversity in a Changing Climate

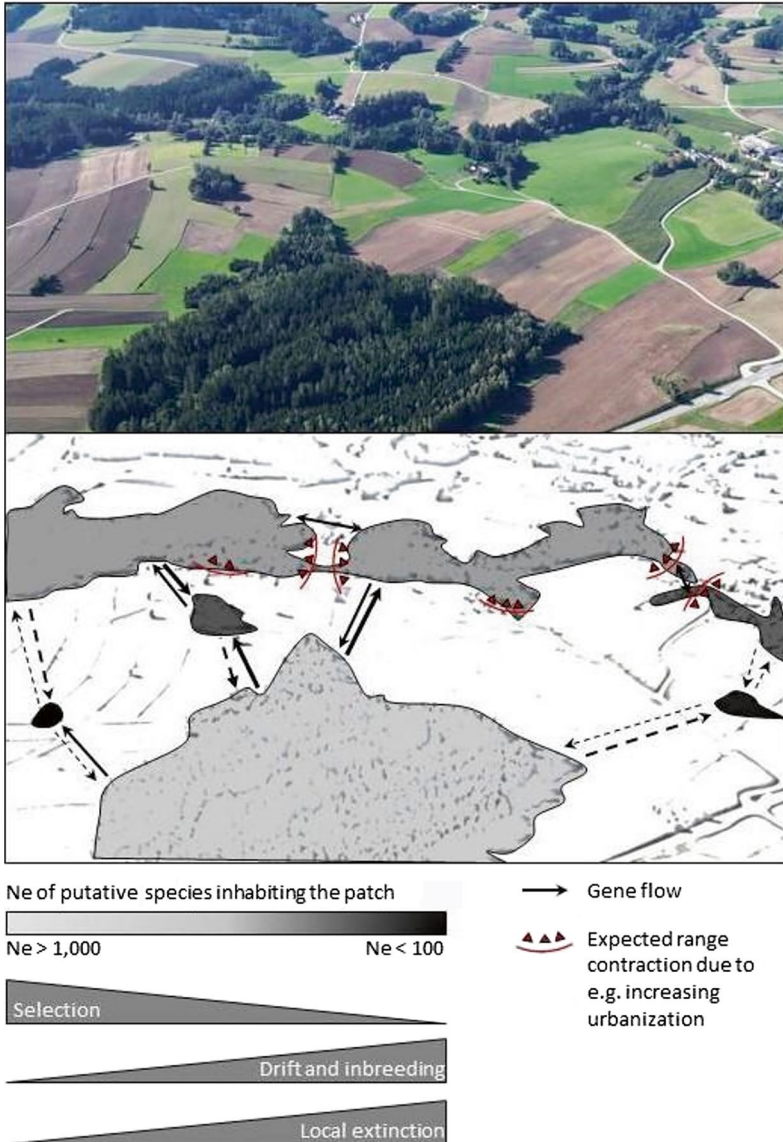
Genetic diversity is an intrinsic and essential element of biodiversity, encompassing the variation of genetic traits within a population, a species, or an entire ecosystem. All forms of biological diversity are based on the genetic variation found within populations. The variability of genetic traits can be seen as the “raw material” of evolution since the change, further development, and *adaptation* (see Box 4.1) of a species in response to changing environmental conditions depend on it. Without a sufficient amount of genetic diversity, the long-term survival of any species is at risk. It is decisive for species’ ability to cope with and adapt to new stresses such as changing site and climate conditions or novel pests (Fisher 1930; Pitelka 1988; Pease et al. 1989; Burger and Lynch 1995; Burdon and Thrall 2001; Etterson 2004; Reusch et al. 2005; Schaberg et al. 2008). Importantly, genetic diversity is a direct function of population and ecosystem connectivity, which determines the extent of

genetic variants exchanged between patches in a fragmented habitat (Lowe and Allendorf 2010).

When it comes to the analysis and conservation of genetic diversity, the *population* emerges as the most significant unit. Population genetic diversity is affected by a range of factors, among which *genetic drift* and *inbreeding* can be considered the most important for biodiversity conservation (Allendorf et al. 2022) since they play a major role in small populations (Fig. 4.1). Drift affects all members of a population equally and has the greatest influence when the *effective population size* ( $N_e$ ) is small (see also Chap. 5). In the majority of species, some populations have undergone a *bottleneck* during their more or less recent evolutionary history, for example, due to range contraction as a consequence of periods of glaciation. These fluctuations in population size lead to recurrent reductions in the genetic variation of populations. The random recruitment of genetic variants by drift causes changes in the genetic composition of populations that may have a negative effect on their fitness and adaptive potential. Therefore, a large  $N_e$  is most important for population and species survival. As discussed in more detail in the following,  $N_e$  is considered a suitable indicator for evaluating whether a population needs conservative intervention (prioritization of conservation efforts), but it is also very difficult to determine in practice (Waples 2002; Santos-del-Blanco et al. 2022).

Through the exchange of genetic variants, *gene flow* shapes the genetic composition of species, maintaining shared diversity across different populations. On the other hand, gene flow also homogenizes genetic variation across populations, thus counteracting *local adaptation*; however, it is generally regarded as beneficial in terms of preserving genetic diversity, enhancing the fitness of fragmented populations, and minimizing the effects of drift and inbreeding (Ralls et al. 2018). Most importantly, gene flow is an immediate and fundamental measure of population connectivity. By reducing the ability of a species to migrate and exchange genes among populations, reduced connectivity exacerbates the effects of climate change. In the geological past, forest species have modified their distribution ranges through migration to more favorable environments multiple times (Bernabo and Webb 1977; Webb III 1981; Davis 1983; Huntley and Birks 1983; and review by Geber and Dawson 1993; Huntley and Webb III 1988). However, the current climate change and habitat fragmentation processes are likely too fast to be compensated by natural migration rates (Huntley 1991; Davis and Shaw 2001; Jump Peñuelas 2005).

*Natural selection* acts against individuals with low fitness, purging deleterious genetic variants while favoring beneficial ones. It can thus change the allelic composition of a population rapidly, for example, in the case of the appearance of a novel pathogen causing a *selective sweep*. Such adaptive shifts leave recognizable signatures at the genomic level (e.g., Pritchard et al. 2010) and can describe certain adaptive patterns in natural populations. Nevertheless, phenotypic traits are often *polygenic* with a complex *genetic architecture* and do not respond to selection via pronounced frequency changes of few genetic variants (Höllinger et al. 2019). Due to *redundancy* in polygenic traits, most genetic loci likely contribute only transiently to a change in the phenotype (Yeaman 2015), meaning that the adaptive trait architecture (Barghi et al. 2019; Pritchard et al. 2010) varies strongly over time and



**Fig. 4.1** A forest landscape in Upper Austria (Schönau im Mühlkreis), typically fragmented by agricultural and urban land (top), along with an idealized and simplistic representation of the degree of gene flow between the forest patches (bottom). Note that the depicted processes are species-specific and cannot be realistically represented for multiple species in a single illustration. Thicker, thinner, and dashed arrows indicate more frequent, less frequent, and rare gene flow, respectively. Note that gene flow between two specific patches is often asymmetrical. Red curves and arrows symbolize the direction of plausible future range contraction in already urbanized areas, leading to further reduction and fragmentation of existing patches. The gray color gradient indicates larger (lighter) to smaller (darker)  $N_e$ , which is accompanied by a parallel decrease in the strength of selection along with increases in the effects of drift and inbreeding as well as the probability of local extinction. (Drone photography by Florian Winter)

multiple molecular mechanisms are available to organisms during adaptation (Leinonen et al. 2013; Luo et al. 2014; Szukala et al. 2022; Yeaman 2022). Several studies have found theoretical and experimental evidence that a sufficient amount of genetic variation must be present in populations for adaptation to take place via small adaptive shifts, as expected under the framework of polygenic adaptation and redundancy (Bakker et al. 2010; Fagny and Austerlitz 2021; Sinclair-Waters et al. 2020; Thornton 2019). Moreover, Bakker et al. (2010) demonstrated that prolonged habitat fragmentation with limited gene flow severely limits the adaptive potential of species, given that adaptive genetic variation is scattered across patches, reducing the adaptive potential of individual subpopulations. Thus, given the complexity of the genetic basis of adaptation, the amount of genetic variation available must be “large enough” (see section “Connectivity Conservation Strategies and Actions” below for further insights on this concept) and/or subpopulations sufficiently connected for adaptation to occur.

Species can also react to differing environmental conditions by way of *phenotypic plasticity*, changing a phenotypic parameter like tree height or behavior in reaction to a change in the environment (Nussey et al. 2005). These phenotypic adjustments are reversible and occur if the underlying genetic architecture permits it and the energetic cost is not too high (DeWitt et al. 1998). Under certain circumstances, plasticity can be adaptive, bringing the phenotype closer to an optimum (e.g., Nicotra et al. 2015), but neutral and even maladaptive effects of plasticity have been documented as well (e.g., Arnold et al. 2019). How and when phenotypic plasticity supplies the variation targeted by selection and contributes to adaptation is a matter of debate (Wund 2012; Levis and Pfennig 2016; Fox et al. 2019; Szukala et al. 2023). In the context of biodiversity conservation, it is important to note that plasticity has intrinsic physiological limits (DeWitt et al. 1998) that are likely exceeded by the demands of climate change for most species, as suggested by several studies (e.g., Forcada et al. 2008; Reed et al. 2011).

Three key means by which species can react to climate change can be determined: (1) Dispersion of seed or vegetative propagules into a more favorable environment (i.e., similar to the native environment prior to climatic change); (2) changes in allelic composition in response to natural selection, resulting in better adaptation to the new environment (Burdon and Thrall 2001; Reusch et al. 2005); or, when the genetic architecture permits it, (3) phenotypic plasticity changes to cope with the new conditions. As mentioned above, both the capacity to migrate—at least, without human intervention—and the ability to respond plastically to changing conditions are limited: Migration rates and plastic reaction norms are mostly exceeded by climate change and human-induced habitat modification. Maintaining sufficient genetic variation through population connectivity is therefore essential for enabling adaptation—or, in a human-driven context, for delivering the material for artificial selection, marker-assisted breeding, assisted migration, and even gene editing. It is important to note that evidence of the positive effects of selection on fitness in the wild has been reported (Bonnet et al. 2022), suggesting that many species do indeed have the potential to adapt to ongoing climate change. Nevertheless, we must also remember that every species has its own reproductive and genetic

systems that interact with the described evolutionary processes in specific ways to shape that species' genetic diversity. Therefore, a profound understanding of species-specific population genetic dynamics and demographic and evolutionary histories is required to carefully evaluate the state of individual species and optimize conservation efforts.

#### Box 4.1 Glossary of classical population genetic terms used in the current chapter

Adaptation	An evolutionary process that increases an individual's probability of survival and reproduction in a given environment.
Bottleneck	A sharp reduction in population size due to stochastic events.
Demographic connectivity	The effects of dispersal on population growth and mortality (Lowe and Allendorf 2010).
Effective population size, $N_e$	The size of a theoretical population in which the genetic composition is affected by the same degree of random change (drift) and inbreeding as the observed population.
Gene flow	Effective transfer of genetic material by pollen containing the haploid male gametophyte resulting in fertilization and development of a diploid embryo.
Genetic architecture	The sum of all genetic loci contributing to a trait of interest, including their effect size on the phenotype, their position in the genome, and their interaction (i.e., linkage disequilibrium, epistatic interaction, and pleiotropy).
Genetic connectivity	The effects of gene flow on population evolution (Lowe and Allendorf 2010).
Genetic drift	Changes in allele frequency due to random effects (e.g., natural catastrophes, such as wildfires and storms).
Inbreeding	The mating of individuals that are genetically closely related, including self-fertilization.
Local adaptation	The process by which a population evolves to be more suited and better adapted to its local environment than other populations within the same species.
Natural selection	The process by which individuals with higher fitness are more likely to survive and produce progeny.
Phenotypic plasticity	The same genotype can modify the expression of the phenotype in different environments (Schlichting and Pigliucci 1998).
Population	A group of interbreeding individuals of the same species that live in the same place at the same time.
Polygenic	Governed by large amounts of genetic variants.
Redundancy	Different combinations of genetic variants can produce the optimal phenotype (Goldstein and Holsinger 1992).
Selective sweep	The process by which positive selection increases the frequency of a beneficial mutation in the population, leading to a frequency increase of other mutations linked to the beneficial one (so-called <i>hitchhikers</i> ) and, in consequence, to a decrease of genetic diversity in the genomic region surrounding the beneficial mutation.

## Genetic Diversity of Forest Foundation Species

Foundation species, such as trees in forest ecosystems, have been defined as species that structure a species community by creating locally stable conditions for other species as well as by modulating and stabilizing fundamental ecosystem processes (e.g., Dayton 1972; Whitham et al. 2003). The field of community genetics has shown that the genetic diversity of the main tree species in a forest can affect the community of dependent species (e.g., microbes, plants, arthropods, birds, and mammals) (Whitham et al. 2003). To cite an example, Tovar-Sánchez et al. (2013) found evidence of higher arthropod diversity in the crown of oaks positively associated with the within-population genetic variation of the host plant. In addition, accumulated evidence shows direct impacts of foundation species' intraspecific genetic diversity on several ecosystem processes such as primary productivity, population recovery from disturbance, interspecific competition, community structure, and energy and nutrient flows (Crutsinger et al. 2007; Hughes et al. 2008). Studying the interactions between the genetic diversity of foundation species and several ecosystem components should allow us to develop better strategies for preserving biodiversity and ecosystem function in the face of forest fragmentation, climate change, and introduced pests (Whitham et al. 2006). Therefore, the conservation of genetic diversity and population connectivity of trees merits special attention. Indeed, the genetic diversity of foundation tree species has been the focus of multiple studies pursuing a better understanding of forest genetic resources (FGR) and how to improve their conservation (e.g., Geburek and Konrad 2008).

Trees are among the organisms with the highest genetic diversity (Hamrick and Godt 1990). This diversity within and among natural populations provides the foundation for forest ecosystem stability in variable and changing environments (Gregorius 1996; Petit and Hampe 2006), as well as for relatively rapid adaptive responses to environmental challenges (Alberto et al. 2013; DeHayes et al. 2000; Davis and Shaw 2001). For example, forest trees reacted to dramatic changes in climate and other stresses several times during the quaternary period, both through adaptation and migration (Davis and Shaw 2001; Petit et al. 2004). Nevertheless, within-species tree genetic diversity must be complemented by diversity at the species level of another organismal group to ensure tree population stability; for example, trees rely on other organisms for their survival, needing pollinators (e.g., insects, bats, and birds) and seed dispersers (e.g., birds and mammals). The survival and genetic diversity of these dispersers are therefore likewise important for the long-term resilience of forest ecosystems. The number of studies on the genetic diversity of organisms associated with forests is large, yet these species are still understudied and the results are scattered among the body of conservation genetics literature. Nevertheless, a large body of literature points toward a strong decline in genetic diversity of pollinator and seed disperser species (Exposito-Alonso et al. 2022; Hoban et al. 2023a, b).

Populations experiencing a rate of environmental change beyond the rate at which they can adapt or disperse are threatened by decline (Lynch and Lande 1993; Burger and Lynch 1995; Visser 2008). At present, anthropogenic climate change is

quickly altering the natural environment: The current biodiversity crisis is manmade and requires active interference to be halted and reversed. We have reached a state in which fragmentation is reducing effective population sizes and impeding gene flow among populations (Fig. 4.1). As a result, the genetic diversity of forest species is under considerable threat due to multiple anthropogenic factors, with climate change, the introduction of novel pests and diseases, and forest fragmentation representing the main threats (which will be discussed in more detail in the following section). Connectivity between forest populations is pivotal to the conservation of genetic diversity and species survival, but it is also one of the aspects most heavily affected by human impact. Every effort needs to be made to maintain forest ecosystems. In particular, since most current threats to biodiversity and the genetic diversity underlying it are manmade, it is our obligation to mitigate anthropogenic impacts and take action to increase or at least preserve the remaining levels of genetic diversity to prevent further loss and, eventually, the collapse of forest ecosystems.

In this chapter, we attempt to review the current state of forest genetic diversity and connectivity, with a special focus on (i) the major anthropogenic threats impacting them, (ii) the available tools used for their assessment, including the respective advantages and limitations, and (iii) the guidelines currently in use for genetic monitoring and global conservation initiatives. We emphasize that genetic diversity and connectivity are difficult to assess, especially on a large scale and for many species, but nevertheless necessary to inform conservation practices. Evaluation is demanding in terms of time, funding, and other resources, especially when molecular methods are used (which is necessary for most species). At the same time, genetic monitoring and easy-to-apply indicators are urgently needed to inform policy makers and define conservation priorities.

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## **Anthropogenic Impacts on Genetic Diversity in Forest Ecosystems**

### **Climate Change**

Human alteration and management of forest ecosystems have heavily impacted the genetic diversity of forests; in some regions, this impact has been ongoing for millennia. Only a brief overview of this topic, which has been more broadly assessed, e.g., by Ledig (1992), Savolainen and Kärkkäinen (1992), and Lefèvre (2004), can be presented here. At present, the primary threat is climate change. It is expected that population dieback and/or increased selection pressure—e.g., due to prolonged periods of drought—may erase genetic variation in populations that have already suffered a loss of genetic diversity due to human activity in the past (Alsos et al. 2012; Armbruster and Reed 2005; Pauls et al. 2012). Due to its crucial importance, the multiple effects of climate change on forest ecosystems are discussed in detail in Chaps. 5 and 6. Here, we will focus on a specific aspect that also impacts reproductive biology, genetic diversity, and the survival of forest species, namely the influence of climate change on the masting behavior of forest trees.

Mast seeding—the large-scale, synchronized interannual variation in seed production among populations of forest trees—is a phenomenon exhibited by many of the foundation tree species in temperate forests, including oak, beech, spruce, and pine. The enhancement of pollination efficiency and the decrease of seed predation in mast years have been suggested as the main benefits of masting for tree reproduction (Kelly et al. 2001). There is now increasing evidence that climate change disrupts masting dynamics, likely leading to a decrease in the long-term regeneration of masting plants (Foest et al. 2024). In turn, decreased regeneration potential is expected to impede the rapid geographic range shifts required to maintain species within suitable habitats under the scenario of climate change (Walther et al. 2002; Chen et al. 2011). Alarming evidence was provided by Bogdziewicz et al. (2020), who showed that climate warming decreased the interannual variability of seed production and the reproductive synchrony among individuals in European beech. These effects led to lower pollination success as well as greater loss of seeds to predators, offsetting the benefits of masting dynamics even though climate warming has increased the overall seed production of European beech over the last few years. Moreover, the authors showed that seed viability is decreasing, especially in old trees. In connection with the effects of forest fragmentation like increased inbreeding and lower fitness among offspring (see below), these findings offer a pessimistic outlook for the future of many forest species if no countermeasures are taken.

## Deforestation

The most profound and direct impact on all levels of forest biodiversity is caused by deforestation, meaning the permanent removal of forest growth, which is equivalent to habitat loss for all forest species. Deforestation has accompanied cultural development since prehistoric times and has resulted in a steady decrease in forest cover on a global scale. Deforestation for agricultural and human development has been less frequent at higher latitudes and high elevations while being most severe in tropical countries (Balboni et al. 2023)—for example in Ethiopia, where 60% of the forest area recorded at the end of the nineteenth century was lost during the twentieth century (Oljirra 2019). Unfortunately, this process is still ongoing. Globally, we are currently still losing more forest than is being restored (ca. ten million ha per year; FAO 2022). The majority of forest area is destroyed for agricultural purposes (including pastures) in the southern hemisphere. By contrast, deforestation has been halted in most countries of the northern hemisphere, where the total forest area is presently increasing again (FAO 2022). Forest restoration is one of the key approaches to mitigating the effects of climate change, with the additional benefit of restoring forest biodiversity, at least in the long term (e.g., European Green Deal; EC 2019). The effects of deforestation on genetic diversity and species survival are most severe when whole populations are lost, or even entire species go extinct. The latter case has primarily been observed for endemic species with restricted distribution, especially on islands (e.g., Madagascar; Allnutt et al. 2008), and should not be underestimated since such events are impossible to reverse.

## Fragmentation

A common result of deforestation is forest fragmentation, which is currently viewed as the greatest issue concerning long-term species survival, particularly in the face of climate change. Forest fragmentation subdivides populations into smaller sections and creates barriers to migration. Eventually, this process leads to inbreeding in the forest fragments, which has long-term negative effects on population fitness and adaptability to environmental change. Moreover, demographic stochasticity or drift effects (the decline of populations due to random effects like browsing or fire) can have an earlier and more immediate effect in small forest fragments, thereby quickly leading to local extinction (Lande 1988). The size of forest fragments is therefore very important: Larger fragments can hold more individuals of more species as well as attract more migrants, which in turn reduces the effects of population isolation. Most tree species have developed mechanisms for long-distance dispersal of their propagules. Nevertheless, a review of the effects of fragmentation on the genetic diversity of plant species shows that tree species are affected by disruptions of their gene flow in the same ways as herbaceous species (Vranckx et al. 2012; Aguilar et al. 2019). The only likely exception to this general rule are species pollinated by vertebrates (birds and bats; mostly in tropical regions), which can fly long distances and are thus able to counteract fragmentation by maintaining pollen flow among population fragments (Hadley and Betts 2009).

The effects of fragmentation extend further than the mere loss of alleles and increased rates of inbreeding in adult individuals: It also causes changes in reproductive output. Due to pollen limitation, both the reproductive output and genetic diversity of the offspring are reduced (Aguilar et al. 2006; Leimu et al. 2006; Honnay and Jacquemyn 2007; Vranckx et al. 2012), and inbreeding strongly affects the performance of the progeny—in other words, fewer offspring with a lower chance of survival are produced (Aguilar et al. 2008; Vranckx et al. 2012). These factors work together to increase seedling mortality, which impedes natural regeneration and leads to local extinction (Charlesworth and Willis 2009; González-Varo et al. 2010; Ashworth and Martí 2011; Aguilar et al. 2012). The quality of planting material is also decisive for the success of forest and landscape restoration (FLR) (Maginnis and Jackson 2007), but this is often neglected in practice (Jalonen et al. 2018). Implications for forest restoration efforts and possible ways to improve the situation are further elaborated and discussed in Box 4.2. A variety of management strategies have been developed to counteract fragmentation, including the creation of habitat corridors and stepping stones, under- and overpasses for animals, and supplementation of populations by adding individuals from other populations to increase genetic diversity and population size, a strategy termed “genetic rescue” (Allendorf et al. 2022).

## Overexploitation

A further anthropogenic impact is overexploitation. With regard to forest trees in particular, excessive harvesting can severely impact a species' genetic diversity, primarily due to a significant reduction in population sizes. Overexploitation will not result in species extinction but can profoundly impact the size of the gene pool, equivalent to a population bottleneck (Allendorf et al. 2022). For instance, selective logging of a large part of a tree population while leaving a small number of undesirably shaped individuals as seed trees can have a lasting negative effect on the growth of future tree generations (Ledig 1992). Research has also shown that while thinning of stands as a silvicultural management practice may not affect the genetic diversity of the main target species, it can, however, have a detrimental effect on the associated secondary tree species when their population size is strongly reduced (El-Kassaby and Benowicz 2000).

Another effect of overexploitation can be an increase in hybridization rates among species that would not have occurred in undisturbed habitats. For example, extensive hybridization between *Picea rubens* and *P. mariana* has been observed as a consequence of extensive logging and wildfires in the maritime provinces of Canada (Ledig 1992). In a situation where *P. rubens* was heavily harvested and simultaneously affected by fires, *P. mariana* was not overharvested and less affected by forest fires due to its more humid habitat; as a consequence, *P. mariana* outnumbered and was able to fertilize *P. rubens*, resulting in large-scale establishment of hybrid offspring in the clearcut areas. This hybridization does not occur to the same extent in undisturbed habitats, and hybrids do not establish as easily, since they tend to grow slower and be more susceptible to pests. A similar example has been reported with regard to *Pinus palustris* and *P. taeda* (Namkoong 1966). Climate change may have a similar effect in certain situations (e.g., Lind-Riehl and Gailing 2017). Hybridization can threaten the genetic integrity of a species, but on the other hand can also provide the genetic variation necessary to adapt to new climate conditions (Brauer et al. 2023; see also Chap. 5).

## Translocation

The anthropogenic translocation of forest plants, animals, and microorganisms has heavily affected the appearance and composition of current forests. Unfortunately, the unintentional introduction of novel pests and diseases can significantly impact the genetic diversity and even survival of many species, and of forest tree species in particular. Among the most severe such cases is the introduction of the chestnut blight pathogen (*Cryphonectria parasitica*) to eastern North America, which has basically eradicated *Castanea dentata* as one of the main tree species from the forests in this geographic region (Anagnostakis 1988). Other examples are the spread of Dutch elm disease (*Ophiostoma novo-ulmi*) to Europe and North America (Brasier 2000), the appearance of the gypsy moth in eastern North America (Liebhold et al. 1992), and more recently the introduction of the ash dieback fungus

(*Hymenoscyphus fraxineus*) to Europe (McMullan et al. 2018) and the emerald ash borer (*Agrilus planipennis*) to North America (Herms and McCullough 2014). These introductions have decimated the population sizes of the affected tree species, causing massive reductions in extant genetic diversity. In combination with fragmentation and climate change, these factors pose further threats to long-term species survival. Efforts should be undertaken to prevent such intercontinental spreading of pests and pathogens by applying strict phytosanitary measures.

The introduction of non-native tree species as an alternative to autochthonous trees for wood production in the face of climate change is a hotly debated topic. Introduced species might become invasive and outcompete native ones with large-scale and long-lasting negative effects on forest ecosystems. Therefore, careful evaluation of species performance is necessary before such introductions are recommended (Brundu et al. 2020). For example, *Robinia pseudoacacia* was introduced to Europe from North America in the seventeenth century and has since invaded many Central European ecosystems, becoming a typical element of the landscape. Though its effects on native forests have mostly been described as negative, this species currently represents an important component of forests of Southeastern Europe, where its eradication has become impossible (and no longer even desirable) for forest managers. The European populations spread out from a small number of founding trees possessing a restricted share of the genetic diversity present in *R. pseudoacacia*'s native range. Interestingly, the seeds of these most successful trees were shown to have significantly higher germination rates than the average native American populations, as well as low pre-adaptation germination requirements (Bouteiller et al. 2021); this provides evidence that anthropogenic selection has favored these provenances without their invasive potential being taken into account.

The translocation of native forest plants as part of reforestation and forest management efforts likewise impacts genetic diversity. Planting can change local patterns of variation, modify the mating system, and impact natural populations in the vicinity through pollen flow and seed migration by reducing local adaptation (outbreeding depression; Frankham et al. 2011). Since often no records are kept on which planting material has been used in which locations, it is difficult to assess associated negative and positive impacts on local performance and diversity patterns. In general, however, the available examples show that effects on local populations seem to be limited or even beneficial (Lefèvre 2004). Complementary planting in small populations of endangered species can actually be seen as a measure of assisted gene flow or genetic rescue, since it provides demographic support (census size) and the introduced migrants reduce the effects of inbreeding depression in the respective population fragment (Allendorf et al. 2022). However, it is essential for this practice to be carried out with proper forest reproductive material (FRM) containing sufficient genetic diversity to avoid negative effects on extant populations: Excessive planting of a rare species to increase its distribution under the neglect of the native gene pool and the genetic diversity of the reproductive material used can result in further erosion of genetic diversity and eventual loss of the entire population. An example is provided by Lefèvre (2004) for *Sorbus domestica* when plants

with low genetic diversity are planted on a large scale, outnumbering the native gene pool (genetic swamping; García-Ramos and Kirkpatrick 1997; Lenormand 2002). Awareness for this issue is increasing and it is becoming common practice to check the genetic diversity of rare species as well as potential source populations before large-scale planting is conducted (e.g., for *Sorbus torminalis*, Kavaliauskas et al. 2021; or *Acer platanoides*, Lazic et al. 2022). In situations where an endangered population needs to be conserved, special attention should be paid to the influx of unwanted immigrant pollen or seeds (Unger et al. 2016).

Widespread plantation failures, poor performance, bole shape of ill-adapted forest tree provenances, and loss of productivity resulting from the use of low-quality planting material led to higher standards being applied by forest managers in the sourcing and employment of FRM. In the European Union, a directive on baselines for the collection of and trade in FRM is in place that is aligned with the respective OECD standards (OECD 2023). Extant guidelines on FRM translocation are mostly based on the assumption that “local is best.” All FRM needs to be labeled properly from seed to plant, and a database of all registered FRM sources has been created (FOREMATIS). The “local is best” paradigm is presently being challenged by the advent of climate change. One generally accepted way to help forests adapt to climate change is the development of assisted migration (or assisted gene flow; Aitken and Whitlock 2013) by planting putatively better-adapted FRM (i.e., provenances from portions of the species’ range that are closer to future climatic predictions for the target site) in addition to natural regeneration. In this way, forests should have the possibility to adapt through natural selection in the long term. Modeling approaches regarding optimal provenance selection are already available and steadily being improved to include various site conditions (Poupon et al. 2021). A more in-depth review of the concept of assisted migration is provided in Chap. 14.

## Artificial Regeneration

Artificial regeneration is considered beneficial to local genetic diversity if the employed FRM is of proper origin and derived from a sufficiently high number of mother trees. In contrast to natural regeneration, planted trees are often unrelated. Plantations can thus feature high genetic diversity, especially when seeds from a large number of unrelated clones are used (Lefèvre 2004). On the other hand, natural regeneration can potentially capture new genetic variation from a larger cohort of pollen donors (Raja et al. 1998). Despite artificial regeneration being challenging for several reasons (see the review on oak artificial regeneration by Dey et al. 2008), it becomes necessary when natural regeneration is too slow or does not meet the required objectives; for instance, after forest decline in large areas. Therefore, both management systems should be practiced and complement each other with the aim of enhancing genetic diversity and fitness (see also preceding section). Importantly, Lefèvre (2004) showed that the majority of economically important tree species harbor moderate to high levels of genetic diversity so that human selection and

breeding do not significantly reduce their genetic diversity, with corresponding effects mostly detectable only in a few genomic regions.

In addition to the selection of FRM sources, cultivation in nurseries can have different effects on the genetic diversity of the resulting plant lots. For instance, common practices such as seed sorting for efficient container plant production and thinning out surplus (i.e., smaller) seedlings after seeding numerous seeds per container have effects equivalent to directional selection for large-sized seedlings, a trait that does not correlate with improved performance in later life stages (Edwards and El-Kassaby 1996). Moreover, seed lots have differing requirements for stratification and substrate conditions, which are mostly not taken into account in nurseries. This becomes particularly problematic when seedling selection is based on performance in the nursery environment rather than at the planting site. Finally, additional challenges are posed by the methods of fertilization, mycorrhization, growth sorting, cold storage, and undercutting of nursery stock and their effects on later performance of trees and their progenies (see the review by Himanen et al. 2021). Direct sowing should be considered an option for artificial regeneration, since it appears to maintain within-seed-source diversity better than planting and because the higher selection intensity during seed germination and seedling establishment results in the establishment of the seedlings best adapted to the respective site (Lefèvre 2004).

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## How Can Genetic Diversity and Population Connectivity Be Measured Using Molecular Tools?

The field of conservation genetics was established to detect and monitor anthropogenic influences on natural populations and develop conservation schemes encompassing genetic principles (Holderegger et al. 2019). As discussed in the previous paragraphs, connectivity is an essential feature affecting the genetic makeup and dynamics of populations in fragmented habitats. The metapopulation concept introduced by Levins (1970) has become a valuable model for conservation genetics (e.g., Wade 2016). A metapopulation is a group of populations of different sizes occupying similar habitat patches within a specific region that are connected via the exchange of migrants. The different patches vary in population size and migrant exchange and are thus affected to differing degrees by drift and inbreeding, with the possibility of local extinction and recurrent natural recolonization of patches (Allendorf et al. 2022; Fig. 4.1). Bigger fragments harboring larger populations, as well as subpopulations located closer to each other, will exchange more migrants. Migration between habitat patches is particularly important because it counteracts population decline and helps to recolonize patches in which individual species have gone extinct. In conservation genetics, the estimation of gene dispersal distances and the rate of exchange among patches is therefore of particular interest, as these factors are decisive for overall (meta-)population survival.

Plant research places a key focus on current rates of pollen and seed exchange to obtain a reliable measure of population connectivity. To achieve this goal, data on

gene dispersal processes at a local, regional, and species-range scale is required (Kremer et al. 2012). Every species has different dispersal capabilities, and a broad range of analytical methods to assess gene flow has been developed (Manel et al. 2005; Smouse and Sork 2004; Burczyk et al. 2006; Robledo-Arnuncio 2012). In general, the available methods can be classified as direct or indirect. Indirect methods offer information on historic, intrinsic dispersal capabilities of a species, both at the intra- and interpopulation level. Indirect approaches to assessing historical gene flow within continuous populations employ the principle that the spatial genetic structure (SGS) displayed by neutral genetic markers is essentially caused by local drift, the effect of which is balanced out by gene dispersal. Under this isolation by distance model, the decay of genetic relatedness with distance has been shown to be inversely proportional to the effective population density (i.e., a measure of population density based on  $N_e$  as defined in Vekemans and Hardy 2004). When a reliable estimate of the latter is available, methods to estimate gene dispersal distance from patterns of SGS exist (Vekemans and Hardy 2004; Rousset 2000).

Despite the importance of non-time-specific estimation methods, most present-day research aims to assess the contemporary gene flow among populations. Estimates of current levels of pollen and seed exchange between populations deliver valuable information for ecological monitoring and conservation management in a wide range of scenarios (Lenormand 2002). These include *genetic and demographic connectivity* after landscape fragmentation, containment of allochthonous (or even genetically modified) populations, or potentially adaptive long-distance gene flow across heterogeneous habitats under climate change (Robledo-Arnuncio 2012). A plant-specific maximum-likelihood approach to jointly estimating contemporary pollen and seed exchange rates was established by Robledo-Arnuncio (2012) and developed further by Unger et al. (2016). This method employs genetic markers that are biparentally inherited (nuclear microsatellite markers) and sampled from the putative target and source populations sequentially, i.e., before and after a reference dispersal event. A major limitation is that the methodology cannot be applied to species with a continuous distribution, including those with long-range dispersal—which includes a majority of economically and ecologically important tree species.

Alternatively, patterns of current gene flow can be estimated “directly” using genetic fingerprint and parentage analyses to assign seedlings to their parent trees and thus infer species-specific pollen and seed dispersal curves (Oddou-Muratorio and Klein 2008; Oddou-Muratorio et al. 2010). Although such results are locally derived, very detailed information about the reproductive system and reproductive biology of a species can be obtained. In plant populations, parentage analysis consists of genotyping a sample of dispersed seeds or established seedlings as well as all reproductive individuals within a circumscribed area using a set of shared polymorphic markers (see Chap. 5 for a more detailed description) to determine the parents of each seedling (Meagher 1986). To distinguish between male and female parentage of seeds and seedlings, maternally inherited tissues collected on dispersed seeds can be genotyped (Jones et al. 2005; Jordano et al. 2007). When already established seedlings are studied, the average effective pollen/seed dispersal distance can be directly estimated from parent–offspring genotype data by model fitting, such as

the neighborhood model (Burczyk et al. 2006). These approaches also enable the detection of ecological factors that are likely to influence patterns of gene flow and relatedness, e.g., parental phenotypic traits (González-Martínez et al. 2006), seed disperser behavior (Jordano et al. 2007), or spatial environmental heterogeneity (Jones et al. 2005). The most advanced approaches additionally allow estimation of selection gradients and detection of fitness-related traits that enhance the reproductive and dispersal success of parental individuals (Chybicki 2018, 2023).

Clustering and assignment methods have also been used to estimate dispersal between population fragments (Berry et al. 2004; Gagnaire et al. 2015); these have mostly been applied to animal populations but are likewise useful in plant studies (e.g., Bizoux et al. 2009; Kassa et al. 2017). In these approaches, a set of reference populations is defined *a priori* and individuals are assigned to their respective population of origin based on multilocus genotypes. In this way, immigrants can be identified when the sampling location and genetic group of origin do not match. These methods also allow the offspring of immigrants and later-generation descendants to be identified (Wilson and Rannala 2003). Rates and direction of dispersal among the studied populations can thus be estimated. Moreover, it is possible to detect natural or anthropogenic barriers as well as other factors with an impact on gene flow (e.g., wind direction and migration corridors). The results of these investigations can inform conservation strategies to restore connectivity (Balkenhol et al. 2015). The research field focused on these aspects by combining population genetics and landscape ecology has been termed “landscape genetics” see also Chap. 5.

There is a wide variety of measures of genetic diversity (see also Chaps. 5 and 8) the most useful for genetic monitoring are allelic diversity (or allelic richness when comparing different sample sizes) and expected heterozygosity. The latter is most sensitive to reductions in  $N_e$  and thus the most suitable for detecting population decline (Allendorf et al. 2022). The estimation of  $N_e$  is particularly important to glean information on the genetic status of a population; for example, a population’s census size ( $N_c$ , the total number of individuals in a population) can be high even though  $N_e$  is low (e.g., when few parents have sired a large part of the population). The effective population size  $N_e$  was introduced by Sewall Wright (1931, 1933) and can be defined as “*the size of an ideal population that would experience the same magnitude of genetic drift and inbreeding as the studied population*”; in other words, it informs us about the “true” size of a population in terms of genetic diversity (Allendorf et al. 2022). An in-depth review of existing methods to infer  $N_e$  based on demographic parameters and genetic data was performed by Wang et al. (2016). For practical applications, thresholds have been suggested (see below) for how large  $N_e$  and  $N_c$  should be to enable a population to survive in the long term. Nevertheless,  $N_e$  estimation is particularly difficult and generally approximate for large populations of forest trees with a continuous distribution (Santos-del-Blanco et al. 2022). Additional limitations of this measure include the impossibility to know whether an estimated  $N_e$  refers to a single population from which samples are taken or to the metapopulation it is a part of, as well as the time point reflected by the measurement (Wang et al. 2016).

Most existing studies on genetic diversity and gene flow have been performed using neutral nuclear microsatellite markers since they are straightforward to score and the obtained results are repeatable and usually show a high number of alleles per studied locus. Technological progress in the development of molecular methods has been rapid thanks to next-generation sequencing, which allows the study of thousands to millions of single nucleotide polymorphisms (SNPs) for any given species (Ellegren 2014). At present, the use of microsatellite markers for parentage analyses is rapidly declining in favor of next-generation sequencing markers—mostly SNPs (Flanagan and Jones 2018). Major challenges arising in the context of next-generation markers include (i) whether the existing software products can handle much greater numbers of markers, (ii) whether the methods can deal with the higher degree of uncertainty of genotype estimation at single loci (e.g., genotype likelihoods), and (iii) whether additional sources of error should be considered (Flanagan and Jones 2018). Moreover, with the steadily increasing number of available reference genomes, whole-genome resequencing of large numbers of individuals is becoming feasible (and affordable) for an increasing number of laboratories. Most of the methods listed above have already been extended to allow the use of SNP data to study connectivity and gene flow as well as considering genotyping errors and rare allele frequencies (e.g., Korneliussen et al. 2014; Chybicki 2018, 2023; Heena et al. 2023).

Although genotyping and sequencing technologies are advancing quickly, monitoring the genetic diversity of one or multiple species remains very resource-intensive. New technologies that allow biological information to be collected for a large number of individuals simultaneously are emerging as a possible solution to this limitation. Remote sensing via imaging spectrometry—i.e., detection of the physical features of an area from its reflected and emitted radiation—provides extensive biochemical information on natural ecosystems including forests, and is increasingly publicly available (see e.g. [www.geo.uzh.ch/en/units/rs.html](http://www.geo.uzh.ch/en/units/rs.html); [www.genesinspace.org](http://www.genesinspace.org)). This data can support an indirect assessment of within-species genetic diversity for many tree species (Cavender-Bares et al. 2022; Jung et al. 2021; Wang and Gamon 2019). Indicators of genetic diversity based on estimated census sizes of reproductively mature individuals in a population (see below) do not require genetic data for estimation. It is therefore potentially feasible to quantify species abundance and characterize populations using remote sensing data from satellite or aircraft images, and to integrate this information with existing field-based knowledge on habitat type and extent. The superposition of spectral information and environmental data can thus provide proxies of genetic variation and identify areas of high or low genetic diversity, as shown by an increasing number of studies (Kivinen et al. 2020; Madritch et al. 2014; D’Odorico et al. 2023; Yamasaki et al. 2017). Despite several technical limitations that still need to be overcome (e.g., Jung et al. 2021; Khanal et al. 2020; Tran et al. 2022), remote sensing data represents a promising new approach for the future of genetic monitoring.

## How Much Genetic Diversity Is Needed?

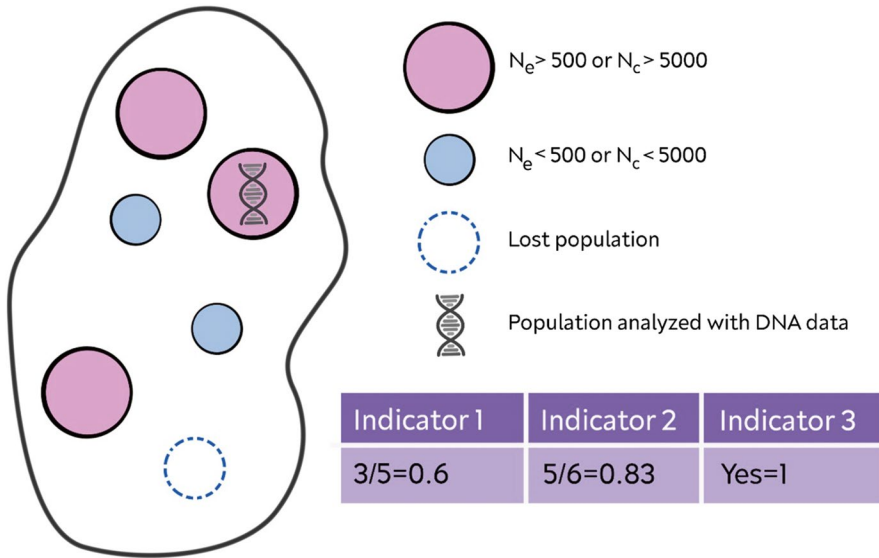
Genetic monitoring can detect long-term changes in genetic diversity. Both *in situ* and *ex situ* approaches to conserving genetic diversity have been suggested and implemented, at least for some of the main forest tree species (e.g., Hoban and Schlarbaum 2014; Lindenmayer and Laurance 2017; Mounce et al. 2017). These concepts are presented and discussed in Chap. 11, and will not be elaborated on any further here. However, the number of populations conserved in either fashion is a good indicator of the conservation status of a species of interest (Hoban et al. 2020).

Most data accumulated so far indicates only rare losses of genetic diversity among the primary tree species in temperate forest ecosystems, mostly due to their large population sizes, frequent wind-pollination, and predominately outcrossing mating systems. Generally, tropical tree species exhibit more evident population structure and enhanced genetic differentiation between populations of the same species than temperate tree species (Dick et al. 2008). This difference is likely caused by low but significant rates of self-fertilization and biparental inbreeding in tropical species, probably due to lower population densities and predominant pollination by insects (Dick et al. 2008). Comparatively little is known in this regard about secondary (i.e., economically less important) tree species, and even less about the vast number of other forest-dwelling organisms. While relatively high levels of genetic diversity are still found even in rare tree species within fragmented habitats, these results are probably strongly biased: Most studies to date have analyzed adult trees, which do not realistically reflect the effects of fragmentation and anthropogenic impact over the last 100 years but rather preceding and historic patterns of genetic diversity. This phenomenon has been termed the “extinction debt” (Aguilar et al. 2008; Vranckx et al. 2012) and describes the time lag between population decline and subsequent measurable changes in genetic diversity; there is increasing evidence showing that offspring generations generally have lower genetic diversity (Aguilar et al. 2018; see also above under fragmentation impacts).

But the question remains how much genetic diversity is needed for a population to survive, or for conservation efforts to be necessary or meaningful. Are small populations doomed because all individuals will be the result of inbreeding after a few generations? These questions cannot be easily answered. There exist examples of populations with very low diversity but no apparent effects of inbreeding depression (Allendorf et al. 2022). The importance of inbreeding depression for the fate of populations has been debated (e.g., Nonaka et al. 2019), but the accumulated evidence clearly indicates that inbreeding depression needs to be considered in the context of the persistence of populations (Frankham et al. 2011; Spurgin and Gage 2019; Allendorf et al. 2022). It is therefore safe to say that small populations will generally have a lower ability to adapt to changing environments or novel pests and be more strongly affected by stochastic effects (drift). Genetic data can provide precise information about the state of a given population: Is its diversity lower than that of other populations of the same species? Is the population connected to other populations or is it relatively isolated?

As a general guideline for management decisions, the so-called 50/500 rule (Franklin 1980) postulates that  $N_e$  should not fall below 50 individuals in the short term and 500 individuals in the long term to prevent erosion of genetic diversity. Later studies have suggested changing these thresholds to 100 and 1000 individuals, respectively (Frankham et al. 2014). In theory, the long-term adaptability of a population remains stable if less than 0.1 of its heterozygosity is lost per generation (Frankham et al. 2010). This preservation of diversity per generation is estimated to be achieved with approximately 1000 randomly mating individuals with a balanced sex ratio (i.e.,  $N_e$  of 1000). In nature,  $N_e$  is around 10% of the  $N_c$  of a population on average; this means that approximately 10,000 individuals would be needed in the long term for a population to remain stable under the influence of factors that erode genetic diversity (Frankham et al. 2014). Such general rules have been widely criticized as being too approximative and far from reality (e.g., Fady and Bozzano 2021; Franklin et al. 2014), and because they do not take species-specific assumptions and constraints into consideration (Flather et al. 2011). Most likely, a more meaningful approach involves avoiding such thresholds as targets but instead considering them as indicators of potential risk of decline (Allendorf et al. 2022). In this way,  $N_e$  approximated on the basis of  $N_c$  can be applied as a suitable pragmatic indicator of “genetic health state” for any species, including forest trees. Such indicators are necessary for decision-making and the prioritization of conservation efforts, since the alternative is to make entirely unscientifically based decisions at the political and bureaucratic levels (Brook et al. 2011).

Practical indicators for monitoring the status and trend of genetic diversity within species have been developed under the Post-2020 Global Biodiversity Framework (GBF; e.g., Hoban et al. 2023a, b) of the Convention on Biological Diversity’s (CBD, i.e., the main legally binding agreement with respect to biodiversity conservation; see also next section). These indicators are partly based on the abovementioned relationships between  $N_e$  and  $N_c$  and were ultimately recommended by the CBD at the Kunming-Montreal Summit in 2022. The purpose of Indicator 1 (fraction of populations with  $N_e > 500$  or  $N_e > 5000$ ) is to provide a baseline for conserving sufficient within-population diversity in case of rapidly changing environmental conditions. By contrast, Indicator 2 (fraction of populations still existing) measures the temporal trends in among-population diversity with a view to providing diverse options for the future adaptability of the species. Indicator 3 is a binary value describing whether the species has been monitored by means of molecular markers or any DNA data that could guide future conservation actions. These three indicators are illustrated for a hypothetical species in Fig. 4.2. While Indicators 1 and 3 are based on a present state (i.e., only current data is required), Indicator 2 is more challenging because it requires historic population data and monitoring efforts. Although such data is presumably available for some of the commercially important tree species (e.g., from national forest inventories), the indicator will likely be difficult to assess for rare species with scattered distributions.



**Fig. 4.2** Illustrative and simplified example of the application of three indicators suggested for monitoring genetic diversity within a hypothetical species. The indicators relate to goals and targets defined by the CBD under the Post-2020 Global Biodiversity Framework: the fraction of populations with  $N_e > 500$  or  $N_c > 5000$  (Indicator 1), the fraction of populations still existing (Indicator 2), and the presence of populations for which genetic data exists (Indicator 3). The black outline represents the species distribution, and the circles inside represent individual populations

## The State of Genetic Diversity at a Global Scale, and Initiatives to Conserve It

The available data on anthropogenic damage to forests and other ecosystems offers a desolating perspective. Hoban et al. (2023a, b) provided an overview of the loss of genetic diversity in the recent past by reporting DNA-based studies documenting high genetic diversity losses over the past 50–100 years, particularly in island species (28% loss), and harvested fish species (14% loss) (Pinsky and Palumbi 2014; Leigh et al. 2019). Over the past few decades, the genetic diversity of International Union for Conservation of Nature (IUCN) Threatened species has declined by 9–33% on average (estimates are based on a mathematical relationship between population loss and genetic diversity loss in several plant and animal species; Exposito-Alonso et al. 2022). Hoban et al. (2021) predicted that, based on population genetic theory and the Living Planet Index ([www.livingplanetindex.org](http://www.livingplanetindex.org)), populations may ultimately lose an average of 19 to 66% of their genetic (allelic) diversity within the next few decades without interventions to stop and reverse species' population declines. More specific numbers for forest ecosystems are hitherto not available. The most striking example of forest habitat loss is South America. Most forest

ecosystems in this region are rapidly declining, and the predictions mentioned above are therefore presumably valid for forest species as well. Projections by Frankham (2022) have shown that a loss of “only” 10% of genetic diversity within a given species in the long term (more than 100 years) will already give rise to increased levels of inbreeding that can severely debilitate that species’ evolutionary potential to adapt to a changing environment. Policymakers are urged to take measures accordingly.

The CBD marked a historic milestone as the world’s first international treaty uniting nearly all nations in a common mission to preserve biodiversity and promote sustainable utilization and equitable distribution of the benefits it generates. Since entering into force in 1993, the CBD has developed multiple frameworks; preparations are currently underway for the Post-2020 GBF (CBD 2022). The Post-2020 GBF is expected to include four high-level goals for 2050 related to the state of nature resulting from conservation, nature’s contribution to people and its sustainable use, shared benefits arising from biodiversity, and means of implementation and resource mobilization, along with 22 action targets for changes in human society and activities required by 2030 to achieve those goals (Hoban et al. 2023a, b). The GBF is currently still being negotiated and must be agreed upon by all parties; it therefore reflects scientific input, political negotiation, perceived feasibility, and compromise. The CBD encourages countries to develop strategies and action plans to conserve and sustainably manage their forest biodiversity.

The signatory states have committed to monitoring and reporting on biodiversity development in their countries. In the original CBD, genetic resources were mentioned, but not explicitly with regard to the conservation of genetic diversity of wild animals and plants. In the new Post-2020 GBF development, this topic is to be extended to include wild animals, plants, and fungi (Laikre et al., 2020). Defining implementable indicators is a prerequisite for countries to report on their respective status, but discussions on this matter are still in progress (Hoban et al. 2023a, b). Frankham (2022) describes the process and recommends that goals, milestones, and targets in the GBF should mention as core elements: (i) the maintenance of sufficiently large populations (rather than permitting an “acceptable loss of genetic diversity”), (ii) sufficient and appropriate genetic exchange among populations (connectivity) and (iii) active monitoring and management of genetic diversity, as well as (iv) no loss of populations. Respective indicators have been described in the previous section. Furthermore, such indicators have been recommended and are also required for reporting under other biodiversity conservation schemes. A more extensive treatment of the topic of biodiversity indicators is presented in Chap. 8.

In connection to the CBD, the European Commission has launched the EU Forest and Biodiversity Strategy 2030 (European Commission 2020), a comprehensive, ambitious, and long-term plan to protect nature and reverse the degradation of ecosystems. The strategy aims to place Europe’s biodiversity on a path to recovery by 2030 and encompasses specific actions and commitments. It is the proposal for the EU’s contribution to the upcoming international negotiations on the Post-2020 GBF and a core element of the [European Green Deal](#) (EC 2019). In particular, it calls for

the establishment of ecological corridors to prevent genetic isolation, allow for species migration, and maintain and enhance healthy ecosystems.

Another important initiative primarily concerned with the genetic diversity of forest trees and other woody species that are of realized or potential economic, environmental, scientific, or societal value is the FAO scheme on forest genetic resources. Work on forest genetic resources at FAO was initiated in the 1950s, and since then FAO has supported countries in their efforts to improve the management of forest genetic resources and promoted regional and international cooperation. Within FAO, the Commission on Genetic Resources for Food and Agriculture requested countries to provide input to and guide the preparation of a report on “The State of the World’s Forest Genetic Resources” (FAO 2014; a second updated report is currently in preparation). Furthermore, FAO agreed on strategic priorities which the FAO Conference adopted in June 2013 as the Global Plan of Action for the Conservation, Sustainable Use, and Development of Forest Genetic Resources. The results of the 2014 report show that studies have thus far described genetic parameters for less than 1 percent of tree species and that no data is available for many countries. Although the Global Plan of Action recognizes that both the number of (molecular genetic) studies and the number of species studied have increased significantly over the past 20 years, it regrets that little of the accumulating knowledge has direct application in management, improvement, or conservation. The report shows that most research on forest genetic resources has been concentrated on temperate conifers, eucalypts, several acacia species, teak, and a few other broadly adapted, widely planted, and rapidly growing species—mostly with the aim of describing genetic resources for breeding rather than for conservation. Genomic or marker-assisted selection is close to being realized, but major gaps still exist in phenotyping and data management. The report also states that many of the species identified as priorities, especially for local use, have received little or no research attention, indicating a need to associate funding with priority-setting practices. An Intergovernmental Technical Working Group on Forest Genetic Resources (ITWG-FGR) was also established within FAO to address issues relevant to the conservation and sustainable use of forest genetic resources as well as advising and making recommendations concerning the report preparation process (see also Chap. 15).

In Europe, a specific network on FGR conservation and use is in place. EUFORGEN—the European Forest Genetic Resources Programme—is an international cooperation program that promotes the conservation and sustainable use of forest genetic resources as an integral part of sustainable forest management. It was established in 1994 as a result of a resolution adopted in 1990 by the first Ministerial Conference of the Forest Europe process. Experts from member countries come together within EUFORGEN to exchange information and experience, analyze policies and practice, and develop science-based strategies, tools, and methods to improve the management of FGR.

The International Union for Conservation of Nature (IUCN) is the main global organization providing expertise, assessments, and guidelines for conservation efforts. It publishes the IUCN Red List of Threatened Species, which includes information on the conservation status of various groups of organisms (mainly plant and

animal species, including many forest species). The Red List is a key data source that also informs CBD reporting, and the respective data could be used as a baseline for genetic monitoring. The Red List also shows that we still lack data on biodiversity: Only 6% and 15% of all known plant and animal species, respectively, have been assessed for their conservation status. The available data show, for example, that an alarming 34% of all conifer species are threatened by extinction and listed in the IUCN Red List (IUCN 2019).

The Living Planet Index and Living Planet Report are published by the World Wildlife Fund (WWF) biannually (Almond et al. 2022), reporting trends in biodiversity for animal species on a global scale. The 2022 edition shows a 69% global decline in the relative abundance of monitored wildlife populations between 1970 and 2018. Latin America exhibits the greatest regional decline in average population abundance (94%), while freshwater species populations have seen the greatest overall global decline (83%). Data for the report are partially provided by IUCN and the Intergovernmental Panel on Climate Change (IPCC).

The United Nations Collaborative Program on Reducing Emissions from Deforestation and Forest Degradation (UN-REDD) supports countries in their efforts to reduce emissions from deforestation and forest degradation while promoting sustainable forest management. It is the UN reference knowledge and advisory platform on forest-related solutions to the climate crisis. UN-REDD promotes approaches that ensure the environmental integrity of carbon emissions reductions while supporting non-carbon benefits—from safeguarding biodiversity to supporting local livelihoods and promoting the rights of indigenous peoples. Genetic diversity preservation is a part of the broader conservation objectives of this program (UN-REDD Program, [www.un-redd.org](http://www.un-redd.org)).

The initiatives mentioned above, along with many others, contribute to the global effort to protect and conserve the genetic diversity of forest ecosystems, acknowledging the importance of biodiversity for ecosystem resilience, sustainability, and human well-being.

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## **Active Participation of Conservation Geneticists in Policy Development Is Needed**

In this chapter, we presented an overview of the knowledge on and status of forest genetic diversity, highlighting the anthropogenic influences on it and the associated policy initiatives to conserve it. Policy developments, implementations, and conservation decisions need to be based on scientific research. To conserve and improve biological and genetic diversity, scientists should actively work to suggest and improve related policy development in close cooperation with policymakers. This can be a difficult process for both sides (Hoban et al. 2023a, b). Typically, foresters and scientists are not involved in political processes, while policymakers are usually not familiar with concepts specific to the field of research. The integration of these two spheres of action is very time-consuming and demanding, yet still frequently does not deliver the output needed by scientists (e.g., peer-reviewed publications).

Nevertheless, steady interaction with decision-makers is the only path toward sustainable and long-term stabilization and conservation of genetic diversity and ecosystem functioning. Research questions often do not directly address the needs of forest or conservation managers (Taylor and Dizon 1999; Geburek and Konrad 2008; Holderegger and Segelbacher 2016). This is currently changing as genetic diversity and connectivity are becoming increasingly recognized as important parts of successful conservation and restoration strategies (Jalonen et al. 2018; Aguilar et al. 2019). Nevertheless, interactions and dialogue need to be intensified to work toward the common goal of sustainable conservation of forest biodiversity. In addition, the general public constantly needs to be informed on initiatives and principles to generate the required attention and (financial) support.

#### **Box 4.2 Providing reproductive material for sustainable forest and landscape restoration (FLR)**

The purpose of forest and landscape restoration (FLR) is to restore ecological processes at the landscape scale to maintain biodiversity and ecosystem functions and enhance resilience to environmental change. FLR has become the aim of a range of multi-million-hectare commitments in many parts of the world to mitigate climate change effects and halt the loss of biodiversity (e.g., European Green Deal; EC 2019). To achieve these ambitious goals, billions of seedlings are needed, yet the provision of seeds has often received little attention in the planning of restoration projects, and Jalonen et al. (2018) reported widespread use of unsuitable reproductive material for FLR. As explained in this chapter, reproductive material to be used in FLR (i.e. seed, seedlings, or vegetatively produced propagules) needs to be locally adapted and provide sufficient genetic diversity to build stable, adaptable, disease-resistant, and self-reliant forests. However, due to a lack of awareness in restoration practices, FLR projects often use seeds that are ill-adapted to the local conditions or offer insufficient genetic variation, for example, when they are collected from a small pool of mother trees (Broadhurst 2013; Liu et al. 2008; Navascués and Emerson 2007; Thomas et al. 2014). On the other hand, habitat loss, fragmentation of source populations, and climate change have a joint negative influence on the genetic diversity of seed lots and their actual availability (Aguilar et al. 2019). To counteract this development, Jalonen et al. (2018) recommend the following policy interventions:

1. *Assembling a national assessment of seed supply and demand for meeting FLR targets.* Identification of gaps in seed supply and development of strategies for sustainable sourcing should occur beyond specific project demand. Seed supply assessments should consider quantity, genetic

(continued)

quality (diversity), and geographic origin. This strategy will be most efficient if applied across national borders.

2. *Adjusting FLR targets and funding cycles.* Building up long-term seed supplies goes beyond the average FLR project duration. FLR projects should include investments in seed availability and access to quality seeds to avoid unfit selection and deployment of low-quality plants. In this context, funding schemes and projects should allow long enough durations to avoid unsuccessful FLR efforts.
3. *Exchanging of knowledge and experiences regarding seed selection and supply options.* The unprecedented amounts of seed and plant material currently needed to meet FLR targets require knowledge sharing among actors to identify functioning approaches for different species and socio-economic contexts, as well as which actors are most efficient at which stage of the process. Multi-stakeholder platforms can efficiently bring together these different actors (e.g., seed suppliers, restoration practitioners, and policymakers). Such platforms already exist in some countries and could be expanded and developed further (Melo et al. 2013).
4. *Facilitating seed exchange across landscapes.* In many cases, seeds for FLR are collected from origins as close as possible to the deployment site, often at the cost of genetic diversity and quality of the seeds. This approach needs to be shifted toward genetically more viable seed sources. Documentation of employed seed sources should also become common practice to allow the performance of different seed origins to be compared. Use of multiple different seed sources and stimulation of natural gene flow by restoring landscape connectivity is also recommended (e.g., Sgrò et al. 2011).
5. *Establishing regulations on seed quality and strengthening capacities for compliance.* Other than in regular forestry, where regulations on the collection and marketing of forest reproductive material exist (e.g., the OECD schemes on forest reproductive material or the EU Directive 105/1999/EU on Forest Reproductive Material in the European Union), this is not the case in many countries where FLR is implemented. Accreditation of seed sources and nurseries is an important step toward ensuring the availability of high-quality plant material from known sources. It should become common practice to only use seeds from accredited sources for subsidized FLR projects.

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