Translating conservation genetics into management

Jarkko Koskela, Francois Lefèvre, Silvio Schueler, Hojka Kraigher, Ditte C. Olrik, Jason Hubert, Roman Longauer, Michele Bozzano, Leena Yrjänä, Paraskevi Alizoti, et al.

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Translating conservation genetics into management: pan-European minimum requirements for dynamic conservation units of forest tree genetic diversity

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Abstract

This paper provides a review of theoretical and practical aspects related to genetic management of forest trees. The implementation of international commitments on forest genetic diversity has been slow and partly neglected. Conservation of forest genetic diversity is still riddled with problems, and complexities of national legal and administrative structures. Europe is an example of a complex region where the distribution ranges of tree species extend across large geographical areas with profound environmental differences, and include many countries. Conservation of forest genetic diversity in Europe has been hampered by lack of common understanding on the management requirements for genetic conservation units of forest trees. The challenge resides in integrating scientific knowledge on conservation genetics into management of tree populations so that recommendations are feasible to implement across different countries. Here, we present pan-European minimum requirements for dynamic conservation units of forest genetic diversity. The units are natural or man-made tree populations which are managed for maintaining evolutionary processes and adaptive potential across generations. Each unit should have a designated status and a management plan, and one or more tree species recognized for as target species for genetic conservation. The minimum sizes of the units are set at 500, 50 or 15 reproducing individuals depending on tree species and conservation objectives. Furthermore, silvicultural interventions should be allowed to enhance genetic processes, as needed, and field inventories carried out to monitor regeneration and the population size. These minimum requirements are now used by 36 countries to improve management of forest genetic diversity.

Keywords

Forest genetic resources; genetic diversity; genetic conservation unit; genetic management; in situ

1. Introduction

Forests harbour most of Earth's terrestrial biodiversity (Millennium Ecosystem Assessment, 2005) and trees are the keystone species of forest ecosystems maintaining their structure and function. Between 50 000 (National Research Council, 1991) and 100 000 (Oldfield et al., 1998) tree species are estimated to exist globally and many of them are also an important component in other ecosystems, such as savannas and agricultural landscapes. The genetic diversity of trees is crucial for adaptation of forests to climate change (Hampe and Petit, 2005; Neale and Kremer, 2011) and for sustaining other species and entire forest ecosystems (Whitham et al., 2006).

International efforts to improve the management of tree genetic diversity were initiated more than 40 years ago (Palmberg-Lerche, 2007) focusing on forest genetic resources, i.e. genetic variation in trees valuable for present or future human use (FAO, 1989). Lack of research on the minimum size of a genetic conservation unit for forest trees was recognized early as a problem (FAO, 1975). Later on, the concepts of minimum viable population (MVP, a population size that ensures the persistence of a population for a given period of time) (Shaffer, 1981) and evolutionary significant units (ESU, populations having independent evolutionary histories) (Ryder, 1986) paved the way to incorporating genetics into conservation work and developing a dynamic approach to the conservation of genetic diversity (e.g. Lande and Barrowclough, 1987).

Soon after the MVP and ESU debate started, the dynamic conservation approach was also applied and further developed for forest trees (Ledig, 1986; Eriksson et al., 1993; Namkoong, 1997). It is based on managing tree populations at their natural sites within the environment to which they are adapted (in situ), or artificial, but dynamically evolving populations elsewhere (ex situ). Ex situ conservation stands of forest trees contribute to dynamic conservation only if natural selection predominates. Climate change makes it even more important to apply the concept of dynamic conservation to ensure the long-term sustainability of tree populations.

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Many countries have developed specific national programmes or strategies for managing their forest genetic diversity based on the dynamic conservation approach (e.g. Graudal et al., 1995; Behm et al., 1997; Teissier du Cros, 2001). Unfortunately, the progress in implementing these programmes and strategies has been slower than expected and the practical conservation of forest genetic diversity is still riddled with methodological and political problems, and complexities of national legal and administrative structures (Geburek and Konrad, 2008). These problems are not uniquely related to forest genetic diversity but to genetic conservation in general. As a result, many national and international actions on biodiversity conservation have largely neglected genetic diversity (Laikre et al., 2010).

The lack of genetic management in biodiversity conservation is no longer due to a lack of research or guidelines, but due to failure to incorporate genetic aspects into practical management (Frankham, 2010). In case of trees, forest conservation genetics has improved the theoretical basis of genetic management of tree populations (e.g. Young et al., 2000; Geburek and Turok, 2005; Hamann et al., 2005) and various guidelines are available for this purpose (e.g. FAO, DFSC, IPGRI, 2001; FAO, FLD, IPGRI, 2004). However, a persisting problem is that the national programmes apply the theory and the guidelines in different ways. As a result, the effectiveness of the conservation efforts varies to a large degree between countries. This has also led to difficulties in assessing the status of genetic conservation of forest trees as they often have large distribution areas covering several countries, sub-regions or even continents. Furthermore, without a common and operational definition for the genetic conservation unit, it is impossible to develop range-wide conservation strategies for forest trees.

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Europe is an example of a complex region where the distribution ranges of forest trees extend across large geographical areas with profound environmental differences, and include many countries with different forest management practices and forest owners. Conservation status assessment of forest genetic diversity in Europe has been hampered by a lack of common understanding on the management requirements for the genetic conservation units. This has also made it difficult to identify gaps in the conservation efforts and to develop genetic conservation strategies at the pan-European level.

In this paper, we discuss theoretical and practical aspects of genetic management of forest trees. We use Europe as a case study and present pan-European minimum requirements for genetic conservation units of forest trees that are scientifically sound and practically feasible to implement in different countries. We also suggest further actions for improving the genetic management of tree populations. The term "dynamic conservation of genetic diversity" used throughout the text is defined as in situ or ex situ conservation aimed at conserving evolutionary processes and adaptive potential of natural or man-made tree populations across generations.

2. Methods

This review was carried out in the context of the European Forest Genetic Resources Programme (EUFORGEN) and the EUFGIS project (Establishment of a European Information System on Forest Genetic Resources, 2007-2011). The process of developing the pan-European minimum requirements for dynamic conservation units of forest tree genetic diversity is presented in Figure 1. The inputs to the process included relevant literature and various results of EUFORGEN, such as species-specific requirements for the units (unpublished), conservation guidelines (e.g. Koski et al., 1997; Lefèvre et al., 2001) and descriptors for inventories of forest genetic resources (e.g. Jensen, 1998; Kleinschmit et al., 1998; Alba, 2000). Furthermore, a large group of experts contributed to a survey and a workshop organized as part of the EUFGIS project. A smaller group of experts then reviewed all input information and drafted the minimum requirements. The drafting process included pilot testing of the minimum requirements in six countries (Austria, Denmark, France, Slovakia, Slovenia and the United Kingdom) before they were finalized. The literature selected for the review focuses on key issues, i.e. genetic diversity and related processes in tree populations, dynamic conservation of genetic diversity, sampling for genetic conservation, forest management and monitoring (Figure 1). We considered these as the most important issues for integrating genetics into the management of the conservation units and we only referred to main publications (in our opinion).

3. Conservation of forest tree genetic diversity

3.1. Genetic diversity in forest trees

Forest trees differ from other plant species in their capacity to maintain high levels of genetic diversity within populations rather than among populations (Hamrick, 2004), with some exceptions to the rule (e.g. Vendramin et al., 2008). This is partly due to extensive gene flow as dispersal distances of effective pollen flow (i.e. pollination leading to successful mating) and seeds can reach up to 100 km and tens of kilometres, respectively (Kremer et al., 2012). Trees also have a long generation time, characterized by a long juvenile stage and overlapping generations (Austerlitz et al, 2000). However, despite the extensive gene flow, tree populations also demonstrate adaptation to local environmental conditions (Aitken et al., 2008). Such local adaptation can develop rapidly, i.e. within one or a few generations (Namkoong, 1998). Despite of

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local adaptation, genetic variation in adaptive traits is generally maintained at a high level within tree populations (Savolainen et al., 2007).

It seems that the counter-acting processes of extensive gene flow and local adaptation (through strong selection pressures on seedlings and young trees in each generation) have shaped the genetic constitution of European forest trees during their range expansion after the last glaciations to a high degree. Extensive gene flow is constantly mixing genes and alleles, offering a multitude of new combinations for selection. In contrast, forest trees have low evolutionary rates at the DNA sequence level (Petit and Hampe, 2006). The rapid local adaptation is most likely caused by the intergenic allelic associations created in this constant 'mixing' process facilitated by high gene flow rates (e.g. De Carvalho et al., 2010). These associations explain the coexistence of phenotypic differentiation among tree populations in the presence of extensive gene flow (Kremer et al., 2010). An epigenetic mechanism may also play a significant role in the rapid local adaptation of forest trees, as shown in Norway spruce (*Picea abies*). Variation in environmental signals, such as temperature, during embryo development influences the expression of adaptive traits in the offsprings (Kvaalen and Johnsen, 2008). This epigenetic mechanism in Norway spruce seems to be controlled by a set of largely unknown genes, which have been identified by microRNAs (Yakovlev et al., 2010).

During the past 2.6 million years (Quaternary Period), the distribution ranges of tree species have not been stable but dynamically contracting, expanding or shifting as a response to climate changes. These changes had a profound impact on boreal and temperate tree species but they also influenced the distribution of tropical forests (Hewitt, 2000) as well as the migration of tropical tree species (e.g. Kadu et al., 2011; Logossa et al., 2011). Genetic and paleoecological studies have provided insights into the past dynamics of the distribution ranges by locating refugia areas and postglacial migration routes (Petit et al., 2002; Magri et al., 2006; Cheddadi et al., 2006; Liepelt et al., 2009). Refugia populations, which are often found at the current low-latitude regions of temperate tree species' distribution ranges, have been assigned a high priority for the long-term conservation of genetic diversity (Hampe and Petit, 2005). In Europe, the refugia populations are mostly found in the Mediterranean Basin which harbours high within-population genetic diversity in vascular plants (Fady and Conord, 2010) and where species introgression took place during the last glaciation (Hatziskakis et al., 2008; Scaltsoyiannes et al., 1999). However, recent studies have provided evidence that small tree populations also survived at intermediate or even high latitudes throughout the Quarternary glacial episodes (Hu et al., 2009; Parducci et al., 2012).

Range expansions generally reduce genetic diversity along the migration path owing to recurrent bottleneck effects and they can also create patterns of genetic diversity that can be difficult to separate from adaptive events (Excoffier et al., 2009). However, when multiple founder events are unrelated, due to long distance dispersal, a high level of genetic diversity is conserved in the colonisation domain (Fayard et al., 2009). Successful migrating tree populations obviously maintained sufficient genetic variation to allow them to adapt to newly colonized areas (Hamrick, 2004). Furthermore, so called mid- or high-latitude contact zones, where different refugial lineages mixed, had an important role in creating new gene combinations and adaptations to environmental conditions along the migration routes (Liepelt et al., 2009; De Carvalho et al., 2010). Tree populations in the contact zones still harbour high levels of genetic diversity (Petit et al., 2003; Liepelt et al., 2009; De Carvalho et al., 2010) and thus they are considered of a high conservation priority in addition to the refugia areas.

3.2. Conservation goal and approaches

Genetic diversity includes both the diversity of alleles and the diversity of genotypes, i.e. allelic combinations. The diversity of genotypes is particularly important for organisms having long generation time, such as forest trees, because they have few opportunities of recombination to create new allelic associations. The frequencies of alleles and genotypes are continuously changing over time as a result of evolutionary processes (natural selection, genetic drift, gene flow and mutation) and tree populations have rarely, if ever, reached an optimum degree of adaptation to given environmental conditions (Eriksson, 2005). Thus, the goal of genetic conservation of forest trees should be the maintenance of a diverse group of mating individuals and populations across different environmental gradients to ensure continued evolutionary processes, not only the preservation of the existing frequencies of alleles and genotypes.

In situ conservation is commonly the preferred approach for maintaining the genetic diversity of forest trees and other wild plant species, while domesticated plants are conserved in genebanks (ex situ) or on farms (circa situm). Genetic material of forest trees is also conserved ex situ in seed banks, seed orchards, clone collections, provenance trials, planted conservation stands and botanical gardens to complement in situ conservation efforts (particularly when population size is critically low in the wild). In situ conservation of forest trees has several advantages as compared to ex situ conservation (Rotach, 2005). Firstly, in situ conservation is dynamic allowing temporal and spatial changes in genetic diversity while ex situ conservation is mostly static maintaining the once-sampled genetic diversity. The second advantage is that trees within in situ conservation units remain exposed to evolutionary processes, as they continue interacting with their environment and competing with individuals of the same or other species. Thirdly, it is easier and

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cheaper to conserve tree populations in their natural habitat than under ex situ conditions. Finally, larger population sizes can be managed in situ than ex situ.

3.3. Management aspects

Dynamic conservation of genetic diversity can be integrated into the management of both protected areas and forests used for different purposes (FAO, FDL, IPGRI, 2004). However, from the genetic management point of view, both protected areas and managed forests often have some limitations. Most protected areas are established for conserving endangered animal and plant species or specific habitats, and their suitability for long-term genetic conservation of forest trees has rarely been assessed prior to their establishment. It is assumed that habitat conservation and natural regeneration also maintain the genetic diversity of tree populations in an optimum and stable state. However, this assumption has been challenged by many theoretical and empirical studies (e.g. Rauch and Bar-Yam, 2005; Faith et al., 2008). Furthermore, genetic conservation of forest trees often has a low priority in the management of protected areas and typically no silvicultural treatments are allowed in these areas to enhance genetic processes within tree populations.

When protected areas or genetic conservation units in managed forests are being established, it is commonly assumed that seemingly natural forests consist of autochthonous, genetically diverse tree populations. However, historical records show that forest reproductive material (typically seeds or seedlings) has been traded and distributed across Europe for hundreds of years (König, 2005). There is usually no documentation available where the transferred material was planted in

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the past. Genetic studies have shown that such human interventions have shaped the pattern of genetic diversity in forest trees in Europe (e.g. Fineschi et al., 2000; Vendramin et al., 2008).

As part of today's forest management, stands are often regenerated by planting or seeding with genetic material originating from other locations but the use of forest reproductive material is still poorly documented in most countries. Of the whole silvicultural chain, the regeneration phase is the most significant one as it largely determines the amount of genetic diversity in subsequent mature stands while other phases, such as thinning, have a lesser impact on genetic diversity (Savolainen and Kärkkäinen, 1992; Lefèvre, 2004). The impact of forest management on genetic diversity depends on the silvicultural system applied and many systems actually maintain genetic diversity rather well (Geburek and Müller, 2005). However, forest management usually focuses on one or relatively few tree species and may even aim at removing non-commercial species from production stands.

A particular concern is the use of non-certified reproductive material for amenity tree planting along roads and for other similar purposes. These activities rarely follow well-regulated forestry practices and they often use reproductive material which does not comply with the international labelling schemes of the material, such as those developed by the European Union or the Organization for Economic Co-operation and Development (OECD) (Ackzell and Turok, 2005). Assisted migration can enhance adaptation to climate change (Hewitt et al., 2011) but in case of amenity tree planting, the risks of introducing alleles resulting in maladaptive traits into nearby genetic conservation units is higher than in the forestry operations which are obliged to use well-documented reproductive material that is usually also tested in different site conditions prior to its deployment.

In Europe, most national conservation strategies for forest genetic resources are based on the dynamic approach and several countries have also revised their strategies based on the expected impacts of climate change (e.g. Hubert and Cottrell, 2007; Lefèvre, 2007). The national strategies aim at conserving dynamically a representative sample of the genetic diversity found within a country and for this purpose, many countries have created a network of genetic conservation units (Graudal et al., 1995; Behm et al., 1997; Teissier du Cros, 2001). The networks are typically based on ecogeographical zonation and the distribution of tree species in a given country. In other regions, such as Asia and Africa, similar conservation networks have also been established for some commercially important species (FAO,DFSC, IPGRI, 2001). However, these networks are still largely based on tree populations occurring in protected areas and production forests (see Eyog-Matig et al., 2002; Luoma-aho et al., 2004) rather than populations which are specifically managed for genetic conservation. Ideally, if all countries had national conservation strategies in place, the conservation networks would cover the whole distribution range of a tree species. In practice, however, countries have different priorities for implementing genetic conservation and selecting tree species, as well as different levels of resources available for this work. As a result, there are often gaps in genetic conservation networks in Europe and elsewhere.

4. Pan-European minimum requirements for the dynamic conservation units

4.1. Basic requirements

Genetic management of forest trees requires long-term commitment, planning and action. Therefore, we identified several basic requirements for genetic conservation units of forest trees (Table 1). Firstly, each unit should have a *designated status* as a genetic conservation area, recognized by the appropriate authorities or agencies in a country to ensure its long-term management for this purpose. The designated status does not necessarily mean that the units should have a legal status. As countries have organized their conservation work in various ways, the designated status can also be based on an administrative decree or other similar arrangement.

Secondly, the units should have a *basic management plan* that includes generation turnover and genetic conservation of forest trees should be recognized as a major management goal. All management efforts carried out within a unit should also be documented in detail and the records should be maintained either by the landowner, the organization responsible for the management of the unit or a relevant national authority. The management plan should be updated based on systematic field inventories conducted every five or ten years, depending on the planning cycle.

The third basic requirement is related to tree species and the genetic background of their populations. For each unit, one or more tree species should be recognized as *target tree species* for genetic conservation in the management plan. This means that management efforts to maintain genetic processes are applied to favour these species. If a genetic conservation unit has several target species, each target species must meet the appropriate minimum population size as described in detail below.

The target tree species can be either native or introduced ones. In the case of native tree species, the units should ideally consist of autochthonous tree populations but well-adapted populations originating from other locations can also be designated as conservation units. Several introduced tree species have been used for forestry and environmental restoration in Europe for decades or even hundreds of years. Many of these species have developed into landraces that are adapted to

European conditions and have, in some cases, developed distinct characteristics from their original source populations (König, 2005). Such landraces constitute a valuable genetic resource that needs to be managed according to the principles of dynamic conservation. Furthermore, genetic material of both native and introduced tree species conserved in Europe may be useful in the future for restoring lost tree populations in their original locations (König, 2005; Chalupka et al., 2008). The target tree species may grow in pure or mixed stands and a unit may consist of one or more stands of different age classes. No unknown or maladapted genetic material of the target tree species should be growing within a unit.

The reasons for establishing genetic conservation units often depend on where a country is located in respect to the distribution range of a target tree species. Many stand-forming tree species have large, continuous populations at the centre of their distribution range while they grow in disjunct populations at the margins. There are scattered tree species which rarely, if ever, form stands and subsequently their population density is low throughout their distribution range. Furthermore, a tree can be rare or endangered in one country but more common in another country. There are also endemic tree species which may occur only in specific areas within a country. Thus conservation objectives for tree species often vary among countries. The objectives for the genetic conservation units can be classified into the following categories; 1) to maintain genetic diversity in large tree populations, 2) to conserve specific adaptive or other traits in marginal or scattered tree populations which are often relatively small, and 3) to conserve rare or endangered tree species with populations consisting of a small number of remaining individuals. The fourth basic requirement is that one of these objectives has been clearly stated for each target tree species within a unit.

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4.2. Size of a dynamic conservation unit

The size of conservation populations is commonly determined with two goals in mind; 1) to increase the probability of capturing the existing diversity of alleles (sampling perspective), and 2) to reduce the risk of loosing genetic diversity during the course of evolution (dynamic perspective). To our knowledge, no theoretical or let alone practical recommendations have yet been elaborated based on the concept of allelic associations which play an important role in adaptation of forest trees (Kremer et al., 2010).

4.2.1. Sampling perspective

Marshall and Brown (1975) presented a conceptual framework for prioritizing genetic conservation efforts and grouped alleles into four classes, 1) common and widespread, 2) common and local, 3) rare and widespread, and 4) rare and local. They argued that common and local alleles should be given a priority in genetic sampling as this class presumably includes those alleles behind adaptation to the local conditions. Brown and Hardner (2000) recommended that a sampling strategy targeting this same allele class is also well suited for forest trees as their populations demonstrate geographical patterns in adaptive traits. However, recent work based on DNA sequencing suggests that these highly differentiated adaptive alleles are also rare (Grivet et al., 2011). Any sampling strategy will capture the first allele class while the sampling of the third allele class depends on the number of units within the species' distribution range and not on the number of trees within a unit (Brown and Hardner, 2000).

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The alleles in the fourth class are the most difficult ones to sample but they are of low priority for two reasons (Brown and Hardner, 2000). Firstly, conserving all rare and local alleles is practically impossible considering the resources available for conservation work and secondly, even with unlimited resources available to sample all these alleles, it would be difficult to maintain them in the long-term as they include recent and deleterious alleles which are likely to be eliminated by natural selection. Yanchuk (2001) calculated that almost 280 000 trees would need to be sampled to include 20 individuals with recessive alleles of low frequency (less than 1%). This would require an area of nearly 700 ha (assuming an average density of 400 reproducing trees per hectare) and would make the establishment of genetic conservation units nearly impossible not only for most tropical tree species but also for many scattered or rare tree species in the temperate and boreal zones.

In forest trees, some 10-20% of allozyme alleles are common and local (Brown and Hardner, 2000). Considering this, the same authors defined an adequate sampling strategy as one that captures with 95% certainty at least one copy of alleles with a frequency of 0.05 and stated that this requires 59 unrelated gametes. Taking into consideration differences in the breeding systems of trees, Brown and Hardner (2000) recommended that a sample should include a minimum of 50 random and unrelated trees. As a worst-case scenario, Brown and Hardner (2000) concluded that open-pollinated seed collected from a minimum of 15 maternal trees would sample a large part of genetic diversity within a population.

4.2.2. Dynamic perspective

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Applications of MVP and ESU to improve the genetic management of conservation populations have been debated extensively during the past 30 years (see Traill et al. (2010) and Flather et al. (2011) for MVP; Fraser and Bernatchez (2001) for ESU). Various MVP and ESU approaches have been defined using different criteria but they all have a common goal, i.e. long-term conservation of evolutionary processes and adaptive diversity. However, no single ESU approach is the best one for all situations (Fraser and Bernatchez, 2001) and there is no universal threshold for MVP either (Flather et al., 2011). MVP also depends on context-specific factors (Traill et al., 2007).

The minimum size of a genetically viable population is commonly defined using effective population size (N_e), which is a parameter measuring the intensity of random genetic drift in the Wright-Fisher model population (e.g. Hartl and Clark, 1997). Based on theoretical studies, recommendations for the minimum population size range from N_e=500 (Franklin, 1980; Soulé, 1980; Lande and Barrowclough, 1987) to N_e=5000 (Lande, 1995) when the goal is to maintain evolutionary potential. A meta-analysis by Traill et al. (2007) found a median, standardized MVP estimate of 4169 individuals based on published studies on 212 species (mainly animals). If the goal is to maintain reproductive fitness in the short term (over a few generations), the minimum population size of N_e=50 has been suggested by many studies (see Frankham et al., 2002).

The question of how many individuals should be included in a conservation unit has also been studied extensively in forest trees. However, as N_e is extremely difficult to determine accurately in tree populations, it is frequently approximated by the number of reproducing trees (N_r), i.e. the effective size of an observed biological population instead of a model one (e.g. Hattemer, 2005a). The recommendations for N_r range from 50 (e.g. Brown and Hardner, 2000) to 500 (e.g. Hattemer, 2005b) and 1000 (Lynch, 1996).

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Franklin (1980) and many other theoretical studies on MVP are based on the assumption that additive genetic variance (V_a) rather than allelic diversity determines evolutionary potential, and that its level depends on the balance between random genetic drift and mutation. The change in additive genetic variance (ΔV_a) is calculated as the difference between the increase in genetic variation per generation due to mutation (V_m) and the loss of additive genetic variation per generation due genetic drift ($V_a/2N_e$) (e.g. Frankham et al., 2002). At mutation-drift equilibrium ($\Delta V_a=0$), N_e equals $V_a/2V_m$. Various theoretical studies have estimated V_m differently and this explains the large variation in the recommended minimum population sizes. These recommendations can thus be debated until it is better known which mutations are always deleterious, and which ones are deleterious in some conditions and beneficial in others (Frankham et al., 2002).

Expected heterozygosity (H_e) and V_a are expected to decline in a population by a factor of $1-1/2N_e$ per generation (e.g. Hartl and Clark, 1997). The assumptions of this model include equal sex ration, random mating and non-overlapping generations, and that no selection, mutation or migration take place. However, these assumptions do not often hold in case of tree populations. Furthermore, this model probably over-estimates the decrease of V_a because they do not take into account the role of linkage disequilibrium and interactions among loci (Carter et al., 2005; Kremer and Le Corre, 2012).

4.2.3. Recommendations for the sizes of the dynamic conservation units of forest trees

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Genetic conservation is obviously more secure with a population size of a few thousand trees instead of a few hundred or tens. However, setting thousands of trees as the minimum population size is not practically feasible. The size requirement should be reasonable and flexible for different kinds of tree species. It should also take into account different conservation objectives across species' distribution ranges. Considering resource allocation at the range-wide level, the size requirement for a unit needs to be set at a level which allows establishment of a network of units to cover all ecogeographical zones within a species' distribution range.

Considering the real-life fact that resources are limited for conservation, Frankham et al. (2002) proposed that maintaining 90% of genetic diversity for 100 years is a reasonable goal for genetic management of conservation populations. Using this goal, we first considered how long period is 100 years in terms of tree generations (t), and then calculated, based on the random genetic drift model, the decline in genetic diversity during this period as $(1\text{-}1/2N_e)^t$ using different values of N_e.

Generation time in forest trees, i.e. the time from seed to seed (Petit and Hampe, 2006), is somewhat difficult to establish accurately for a number of reasons. Temperate and boreal tree species, for example, reach reproductive maturity typically at the age of 20-30 years but in open and dense stands, this takes place several years earlier or later, respectively. The reproductive cycle usually takes two or three years, year-to-year variation in seed production is large and mast years occur infrequently. It may then take several years, decades or even centuries before a new tree generation has been established successfully, depending on whether a species is a pioneer or climax one, and how a forest is managed. The life span of individual trees can extend up to several hundreds of years and as a result, tree populations often consist of overlapping generations.

However, assuming that the average generation time of a European tree species is 50 years, a model population with N_e=500 would maintain 99.8% of its original genetic diversity after 100 years. Smaller populations with N_e=50, 15 or 5 would maintain 98.0%, 93.4% and 81.9% of their genetic diversity, respectively. These calculations do not take into account any outside gene flow which is likely to offset some part of the loss of in genetic diversity, nor bi-parental inbreeding that, on the contrary, can reduce the diversity. Furthermore, spatial genetic structure is not considered. Using a simulation approach and the most realistic seed dispersal functions for a model population, Sagnard et al. (2011) showed that a spatial genetic structure (non-random distribution of related genotypes in space) could result from a single mating event when $N_e < 16$.

Migration can play a significant role in maintaining genetic diversity in tree populations. Long-distance gene flow via seed and pollen dispersal increases genetic variation in tree populations in two ways (Kremer et al., 2012). Firstly, long-distance effective pollen dispersal increases the genetic diversity in seeds produced by the current tree generation. Secondly, migrant seeds can accumulate in a population over many years, increasing the number genotypes in the next tree generation. This suggests that long-distance gene flow can compensate partly or fully the loss of genetic diversity due to genetic drift in small tree populations or even increase their genetic diversity, depending on the situation.

Based on the theoretical considerations and practical aspects, we propose that the minimum size of a genetic conservation unit should be either 500, 50 or 15 reproducing individuals depending on tree species and conservation objectives (Table 1). As some tree species are capable of vegetative reproduction (through root sprouts or partially buried shoots), efforts should be made to check if there are identical genotypes (clones) of such tree species present within a unit and take this into consideration when estimating the number of reproducing genotypes.

In Cases 1 (N_r=500) and 2 (N_r=50) (Table 1), the minimum number of reproducing trees can be temporarily lower than what is indicated if it is necessary to create gaps to promote natural regeneration, for example. The prerequisite is that the minimum number of reproducing trees has contributed to mating (and seeding depending on the species) before the regeneration process has been initiated with silvicultural measures. Furthermore, N_r should recover to the minimum level or above in the near future after a management intervention. We consider Case 3 (N_r=15) as an exceptional case. All units with such a low number of reproducing trees should be subjected to appropriate measures to increase their population size. Furthermore, seed or other reproductive material from these units should be collected urgently for ex situ conservation.

4.3. Management of dynamic conservation units

Management of the units should aim to maintain and enhance the long-term evolutionary potential of the target tree populations. Subsequently, two management objectives are necessary for reaching this goal (Table 1). Firstly, management should ensure the continued existence of target tree populations and secondly, it should create favourable conditions for growth and vitality of the target tree species and their natural regeneration (Rotach, 2005). This means that management should be active, i.e. various measures and silvicultural techniques are applied, whenever needed, to enhance genetic processes that maintain the long-term viability of the target tree populations. The management interventions should also favour all tree species that have been recognized as target species and result in adequate natural regeneration, both in terms of

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quantity and genetic quality. In some particular cases, such as riparian pioneer tree species, ecological engineering may be needed to ensure natural regeneration (Lefèvre et al., 2001).

Under the first objective, management efforts should aim to protect the units against natural or man-made catastrophes. Obviously, the units can never be fully protected against these stochastic events but management can increase the resilience of the tree populations so that they can persist during a catastrophe and recover from it. In the absence of any catastrophe, successional development may also threaten the existence of tree populations and management efforts are needed to halt or reverse this natural process, depending on the target species.

Under the second objective, silvicultural techniques, such as thinning, are often needed to maintain the vitality of the target tree populations and to avoid stands becoming too dense with reduced health, vigour and seed production. Thinning typically removes out-competed individuals or it can be applied in a systematic way but as long as stand density remains above a certain threshold, thinning usually has limited genetic consequences (El-Kassaby and Benowicz, 2000; Lefèvre, 2004). After thinning, target tree populations should still have a sufficient number of effectively mating and reproducing trees to prevent reduction of genetic diversity through demographic bottlenecks and consanguineous mating, and to maintain genetic diversity. Furthermore, the spatial distribution of trees should be such that it is reasonable to assume that sexual reproduction takes place randomly, and that the level of relatedness among the next generation of trees, or spatial genetic structure, is as low as possible (Sagnard et al, 2011).

Silvicultural techniques should be applied in such a way that they support reproductive processes and result in adequate regeneration of the target tree species. Natural regeneration should be

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favoured as a regeneration method, but tree populations can also be regenerated by planting or seeding. If stands are regenerated artificially, the reproductive material should originate from the same genetic conservation unit, or, if not available, from another autochthonous stand nearby. In this case, the number of trees which contributed to the artificial regeneration process should also meet the minimum requirements. If a unit is large, different selective cutting and regeneration techniques could be used within and among the units to promote variability in mating patterns (e.g. clustered, random and regular spacing of seed trees).

Genetic conservation of forest trees can be integrated fairly easily with other management goals of forests and it does not prevent forests from being used for different purposes. As dynamic conservation of genetic diversity may require active management, it can be easier to implement it in forests that are managed for multiple-uses as compared to nature reserves and other protected areas which are often managed passively without silvicultural interventions. However, it is important to note that genetic conservation of forest trees cannot be practised in all managed forests. For example, stands established using reproductive material from unknown sources do not meet the minimum requirements. Furthermore, seed orchards and many seed stands, i.e. areas identified as being suitable for seed collection for forestry, do not meet the requirements for dynamic genetic conservation either.

Detailed guidelines for field-level management of the units are already available (e.g. Koski et al., 1997; FAO, DFSC, IPGRI, 2001; Lefèvre et al., 2001; Rotach, 2005) so we do not discuss them here. However, we want to highlight the importance of relevant practices and policies in supporting management of the units. As countries are ultimately responsible for conserving genetic resources within their territory, management of the units needs overall coordination at the national level.

The management of networks of units across a country is best undertaken by a designated authority working in collaboration with relevant agencies, forest owners and other interested parties. This often facilitates the process of obtaining the designated status for a unit and incorporating genetic conservation as a management goal into the management plan. Furthermore, conservation of forest genetic resources should be incorporated into relevant national policies, such as national forest programmes, national biodiversity action plans and national adaptation strategies to climate change (see Koskela et al., 2007).

4.4. Monitoring of dynamic conservation units

Monitoring is crucial for the successful management of the units. Once basic information on the target tree populations has been collected for the establishment of the units and for the development of a management plan, field inventories should ideally be carried out every five or ten years to assess the success of the conservation work and to update the management plan.

As a minimum level of monitoring, the field inventories should collect data on natural regeneration of target tree species and their population sizes. In case natural regeneration is inadequate or if the number of reproducing trees has decreased, urgent management interventions may be necessary to improve the situation. Between the inventories, the units should also be visited regularly to check for any damages caused by storms, forest fires or insect outbreaks, for example. Regular visits can also detect problems in the viability or reproduction of target tree populations before they become a serious threat.

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Ideally, monitoring efforts should also track temporal changes in the genetic variation and structure of the target tree populations, as this is the only way to verify directly how well genetic diversity is maintained over time. Namkoong et al. (1996; 2002) proposed a genetic monitoring system for forest trees based on four indicators (levels of variation, directional changes in allele or genotype frequencies, migration among populations and reproductive system) and a combination of demographic and genetic verifiers. However, this system is rather expensive and time-consuming to be used as part of practical conservation work, and it requires a high level of scientific skills. Furthermore, several difficult questions remain unsolved. These include selection of species, how to characterize genetic variation, what threshold values of different verifiers should be used and how to combine information from multiple indicators to reach clear conclusions on the success of genetic management (Boyle, 2000).

Development of a more operational genetic monitoring system for forest trees is a necessary and urgent task as problems in the genetic processes of tree populations are usually not immediately observable by measuring natural regeneration or vitality of seeds (Konnert et al., 2011). Aravanopoulos (2011) proposed a simplified genetic monitoring approach which includes only three indicators (natural selection, genetic drift and a gene flow-mating system), to be evaluated based on three demographic (age and size class distribution, reproductive fitness and regeneration abundance) and four genetic (effective population size, allelic richness, latent genetic potential and outcrossing/actual inbreeding rate) verifiers. This new scheme is a useful step towards making genetic monitoring more feasible and cost-effective in terms of field and laboratory work, but it does not solve all the problems (e.g. multiple indicators may still give conflicting results) and it still needs to be tested.

As development of more powerful and affordable molecular markers and novel statistical and modelling tools is making genetic monitoring more feasible and cost-effective, it is reasonable to expect that an operational genetic monitoring system can be established for the dynamic conservation units in the near future. Genetic monitoring systems have also been proposed for other plant species and animals (Schwartz et al. 2007; Laikre et al., 2008).

4.5. Deployment of the pan-European minimum requirements

The pan-European minimum requirements for genetic conservation units of forest trees are now being used by 36 countries to improve management of forest genetic diversity. To support the related documentation efforts, the countries have also agreed common data standards for the units. The data on those units which meet the minimum requirements was collected by a network of national focal points for the EUFGIS Portal (http://portal.eufgis.org). This new database provides geo-referenced data on the genetic conservation units based on 26 data standards at the unit level (geographical area) and 18 data standards at the population level (target tree species within a unit). In January 2012, the portal contained data on 2369 units, which are managed for genetic conservation of nearly 100 tree species in Europe. The units harbour a total of 3154 tree populations. In addition to conservation work at the national level, the countries have used the EUFGIS Portal for international reporting efforts, such as the State of Europe's Forests 2011 report (FOREST EUROPE et al., 2011) and the forthcoming State of the World's Forest Genetic Resources report.

5. Conclusions

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The pan-European minimum requirements for genetic conservation units of forest trees presented in this paper constitute a major step in improving genetic management of forest trees in a large geographical scale. They provide managers, forest owners and policy makers with practical, science-based recommendations for implementing dynamic conservation of forest trees in a coordinated manner across different countries and situations. The presented requirements were developed for the European tree species and conditions so they cannot be applied to other regions without modifications. However, we believe that they provide other regions with a useful example on how such requirements can be developed through regional collaboration. Furthermore, as range-wide genetic studies and mapping of valuable populations are increasingly carried out also for tropical and sub-tropical tree species (e.g. Kadu et al., 2011; van Zonneveld et al., 2012), countries in other regions would also benefit from having common requirements for genetic conservation units of forest trees modified for their conditions.

In addition to secured regeneration and adequate number of reproducing trees within a conservation unit, it is crucial that a network of the units has a sufficient coverage of the spatial genetic variation present in a given species (Koski et al., 1997; Crandall et al., 2000). As it is very difficult to define a universal minimum number of units for a conservation network that could be justified for all tree species (Brown and Hardner, 2000), we did not include this aspect to the minimum requirements. Instead, we argue that the minimum number of units for conservation networks of forest trees should be defined species by species using available data on the existing conservation units, species distribution, range-wide genetic diversity studies and results of common garden tests or other information on adaptive traits. This would also allow assessment of duplication in conservation efforts between countries and, considering the level of threats for a

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given species, decisions on what level of duplication is needed to minimize the risks of loosing genetic resources within a species.

The minimum requirements have prompted various actions by European countries to improve the management of their forest genetic resources and to better document their conservation units. They have been particularly useful for countries with limited budgets and human resources available for genetic conservation by focusing their efforts to key issues. In other countries, they have increased collaboration between forest owners and managers, forest geneticists and the broader biodiversity conservation community to explore whether existing protected areas or production forests meet the minimum requirements and whether such areas can also obtain designated status as genetic conservation units. There are a few countries which have no units that meet the minimum requirements. The reason for this is usually missing designated status or a management plan which includes genetic considerations. Therefore, the minimum requirements have also been useful for pointing out these shortcomings to managers and policy makers.

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Legends

Figure 1. Illustration of the development process of the pan-European minimum requirements for genetic conservation units of forest trees.

Table 1. Pan-European minimum requirements for genetic conservation units of forest trees.

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Figure 1

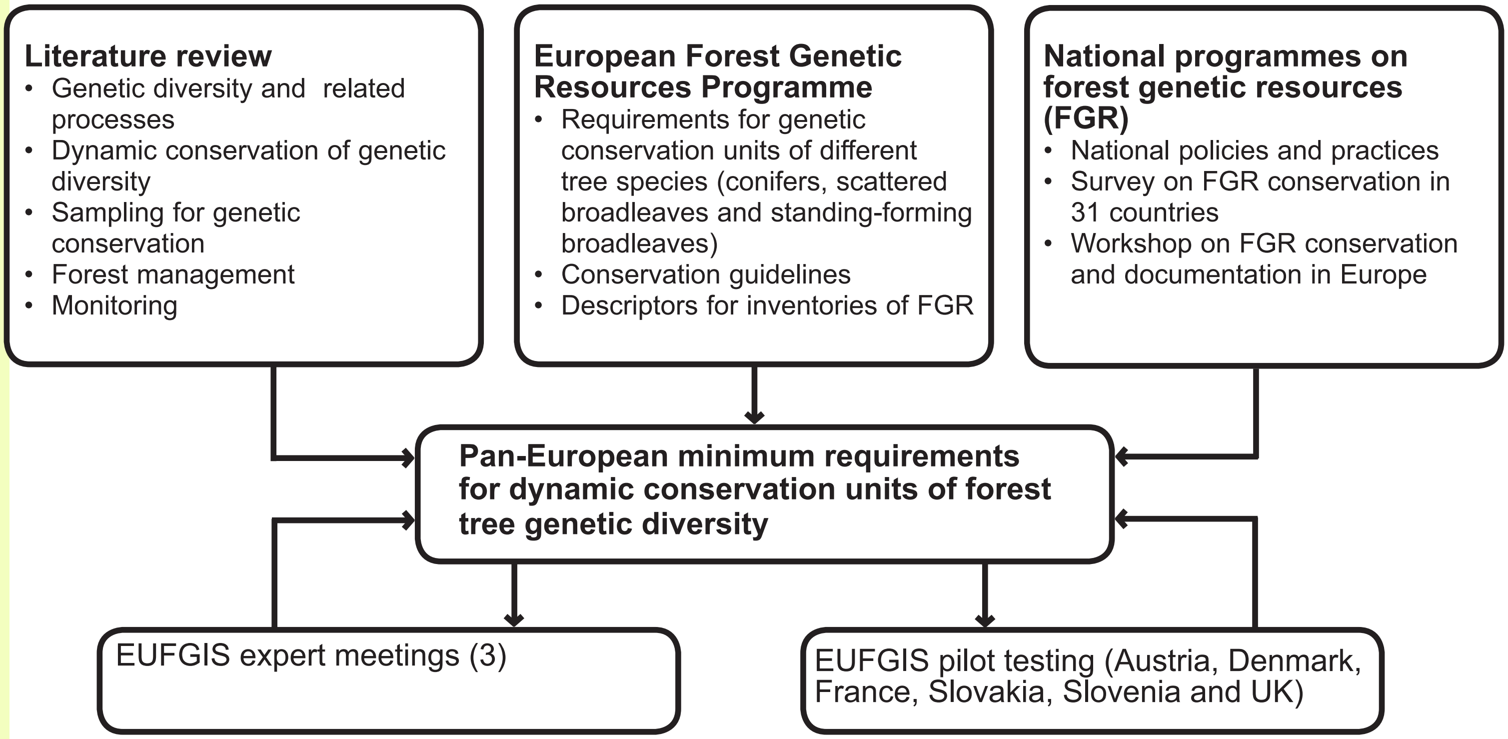

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Table 1. Pan-European minimum requirements for genetic conservation units of forest trees.

Requirement group	**Detailed requirements**
Basic requirements	The unit has 1) a designated status as a genetic conservation area of forest trees, recognized by the appropriate authorities or agencies in a country. 2) a management plan in which genetic conservation of forest trees is recognized as a major management goal. One or more tree species have been recognized as target tree species for genetic conservation in the management plan. One of the following conservation objectives has been clearly stated for each target tree species within a unit: 1) to maintain genetic diversity in large tree populations; 2) to conserve specific adaptive or other traits in marginal or scattered tree populations; or 3) to conserve rare or endangered tree species with populations consisting of a small number of remaining individuals.
Population size	The minimum population size depends on the conservation objective as follows: Case 1: If the purpose of the unit is to maintain genetic diversity of widely occurring and stand-forming conifers or broadleaved species, the unit must consists of 500 or more reproducing trees. Case 2: If the unit was established to conserve specific adaptive or other traits in marginal or scattered tree populations, the unit must harbour a minimum of 50 reproducing trees or, in the case of dioecious tree species with sexual dimorphism, 50 seed bearing trees. Case 3: If the unit is aiming to conserve remaining populations of rare or endangered tree species, it must harbour a minimum of 15 unrelated reproducing trees.
Management	Silvicultural interventions are allowed within the unit and they are actively applied, as needed, to: 1) ensure the continued existence of target tree populations; and 2) create favourable conditions for growth and vitality of the target tree species and their natural regeneration.
Monitoring	Field inventories are carried out every five or ten years to assess regeneration success and the population size, and to update the management plan. Between the inventories, the units are visited regularly to observe that they still serve their purpose and that they have not been damaged or destroyed.

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