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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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.

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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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95 Many countries have developed specific national programmes or strategies for managing their
96 forest genetic diversity based on the dynamic conservation approach (e.g. Graudal et al., 1995;
97 Behm et al., 1997; Teissier du Cros, 2001). Unfortunately, the progress in implementing these
98 programmes and strategies has been slower than expected and the practical conservation of
99 forest genetic diversity is still riddled with methodological and political problems, and complexities
100 of national legal and administrative structures (Geburek and Konrad, 2008). These problems are
101 not uniquely related to forest genetic diversity but to genetic conservation in general. As a result,
102 many national and international actions on biodiversity conservation have largely neglected
103 genetic diversity (Laikre et al., 2010).
104
105 The lack of genetic management in biodiversity conservation is no longer due to a lack of research
106 or guidelines, but due to failure to incorporate genetic aspects into practical management
107 (Frankham, 2010). In case of trees, forest conservation genetics has improved the theoretical basis
108 of genetic management of tree populations (e.g. Young et al., 2000; Geburek and Turok, 2005;
109 Hamann et al., 2005) and various guidelines are available for this purpose (e.g. FAO, DFSC, IPGRI,
110 2001; FAO, FLD, IPGRI, 2004). However, a persisting problem is that the national programmes
111 apply the theory and the guidelines in different ways. As a result, the effectiveness of the
112 conservation efforts varies to a large degree between countries. This has also led to difficulties in
113 assessing the status of genetic conservation of forest trees as they often have large distribution
114 areas covering several countries, sub-regions or even continents. Furthermore, without a common
115 and operational definition for the genetic conservation unit, it is impossible to develop range-wide
116 conservation strategies for forest trees.
117

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.

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

166 local adaptation, genetic variation in adaptive traits is generally maintained at a high level within
167 tree populations (Savolainen et al., 2007).
168
169 It seems that the counter-acting processes of extensive gene flow and local adaptation (through
170 strong selection pressures on seedlings and young trees in each generation) have shaped the
171 genetic constitution of European forest trees during their range expansion after the last glaciations
172 to a high degree. Extensive gene flow is constantly mixing genes and alleles, offering a multitude
173 of new combinations for selection. In contrast, forest trees have low evolutionary rates at the DNA
174 sequence level (Petit and Hampe, 2006). The rapid local adaptation is most likely caused by the
175 intergenic allelic associations created in this constant 'mixing' process facilitated by high gene flow
176 rates (e.g. De Carvalho et al., 2010). These associations explain the coexistence of phenotypic
177 differentiation among tree populations in the presence of extensive gene flow (Kremer et al.,
178 2010). An epigenetic mechanism may also play a significant role in the rapid local adaptation of
179 forest trees, as shown in Norway spruce (*Picea abies*). Variation in environmental signals, such as
180 temperature, during embryo development influences the expression of adaptive traits in the
181 offsprings (Kvaalen and Johnsen, 2008). This epigenetic mechanism in Norway spruce seems to be
182 controlled by a set of largely unknown genes, which have been identified by microRNAs (Yakovlev
183 et al., 2010).
184
185 During the past 2.6 million years (Quaternary Period), the distribution ranges of tree species have
186 not been stable but dynamically contracting, expanding or shifting as a response to climate
187 changes. These changes had a profound impact on boreal and temperate tree species but they
188 also influenced the distribution of tropical forests (Hewitt, 2000) as well as the migration of
189 tropical tree species (e.g. Kadu et al., 2011; Logossa et al., 2011). Genetic and paleoecological

190 studies have provided insights into the past dynamics of the distribution ranges by locating refugia
191 areas and postglacial migration routes (Petit et al., 2002; Magri et al., 2006; Cheddadi et al., 2006;
192 Liepelt et al., 2009). Refugia populations, which are often found at the current low-latitude regions
193 of temperate tree species' distribution ranges, have been assigned a high priority for the long-
194 term conservation of genetic diversity (Hampe and Petit, 2005). In Europe, the refugia populations
195 are mostly found in the Mediterranean Basin which harbours high within-population genetic
196 diversity in vascular plants (Fady and Conord, 2010) and where species introgression took place
197 during the last glaciation (Hatziskakis et al., 2008; Scaltsoyiannes et al., 1999). However, recent
198 studies have provided evidence that small tree populations also survived at intermediate or even
199 high latitudes throughout the Quarternary glacial episodes (Hu et al., 2009; Parducci et al., 2012).

200

201 Range expansions generally reduce genetic diversity along the migration path owing to recurrent
202 bottleneck effects and they can also create patterns of genetic diversity that can be difficult to
203 separate from adaptive events (Excoffier et al., 2009). However, when multiple founder events are
204 unrelated, due to long distance dispersal, a high level of genetic diversity is conserved in the
205 colonisation domain (Fayard et al., 2009). Successful migrating tree populations obviously
206 maintained sufficient genetic variation to allow them to adapt to newly colonized areas (Hamrick,
207 2004). Furthermore, so called mid- or high-latitude contact zones, where different refugial
208 lineages mixed, had an important role in creating new gene combinations and adaptations to
209 environmental conditions along the migration routes (Liepelt et al., 2009; De Carvalho et al.,
210 2010). Tree populations in the contact zones still harbour high levels of genetic diversity (Petit et
211 al., 2003; Liepelt et al., 2009; De Carvalho et al., 2010) and thus they are considered of a high
212 conservation priority in addition to the refugia areas.

214 3.2. Conservation goal and approaches

215

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

226

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

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

240

241 *3.3. Management aspects*

242

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

255

256 When protected areas or genetic conservation units in managed forests are being established, it is
257 commonly assumed that seemingly natural forests consist of autochthonous, genetically diverse
258 tree populations. However, historical records show that forest reproductive material (typically
259 seeds or seedlings) has been traded and distributed across Europe for hundreds of years (König,
260 2005). There is usually no documentation available where the transferred material was planted in

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.

285

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

302

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

304 *4.1. Basic requirements*

305

306 Genetic management of forest trees requires long-term commitment, planning and action.
307 Therefore, we identified several basic requirements for genetic conservation units of forest trees
308 (Table 1). Firstly, each unit should have a *designated status* as a genetic conservation area,

309 recognized by the appropriate authorities or agencies in a country to ensure its long-term
310 management for this purpose. The designated status does not necessarily mean that the units
311 should have a legal status. As countries have organized their conservation work in various ways,
312 the designated status can also be based on an administrative decree or other similar arrangement.
313
314 Secondly, the units should have a *basic management plan* that includes generation turnover and
315 genetic conservation of forest trees should be recognized as a major management goal. All
316 management efforts carried out within a unit should also be documented in detail and the records
317 should be maintained either by the landowner, the organization responsible for the management
318 of the unit or a relevant national authority. The management plan should be updated based on
319 systematic field inventories conducted every five or ten years, depending on the planning cycle.
320
321 The third basic requirement is related to tree species and the genetic background of their
322 populations. For each unit, one or more tree species should be recognized as *target tree species*
323 for genetic conservation in the management plan. This means that management efforts to
324 maintain genetic processes are applied to favour these species. If a genetic conservation unit has
325 several target species, each target species must meet the appropriate minimum population size as
326 described in detail below.
327
328 The target tree species can be either native or introduced ones. In the case of native tree species,
329 the units should ideally consist of autochthonous tree populations but well-adapted populations
330 originating from other locations can also be designated as conservation units. Several introduced
331 tree species have been used for forestry and environmental restoration in Europe for decades or
332 even hundreds of years. Many of these species have developed into landraces that are adapted to

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333 European conditions and have, in some cases, developed distinct characteristics from their original
334 source populations (König, 2005). Such landraces constitute a valuable genetic resource that needs
335 to be managed according to the principles of dynamic conservation. Furthermore, genetic material
336 of both native and introduced tree species conserved in Europe may be useful in the future for
337 restoring lost tree populations in their original locations (König, 2005; Chalupka et al., 2008). The
338 target tree species may grow in pure or mixed stands and a unit may consist of one or more stands
339 of different age classes. No unknown or maladapted genetic material of the target tree species
340 should be growing within a unit.
341
342 The reasons for establishing genetic conservation units often depend on where a country is
343 located in respect to the distribution range of a target tree species. Many stand-forming tree
344 species have large, continuous populations at the centre of their distribution range while they
345 grow in disjunct populations at the margins. There are scattered tree species which rarely, if ever,
346 form stands and subsequently their population density is low throughout their distribution range.
347 Furthermore, a tree can be rare or endangered in one country but more common in another
348 country. There are also endemic tree species which may occur only in specific areas within a
349 country. Thus conservation objectives for tree species often vary among countries. The objectives
350 for the genetic conservation units can be classified into the following categories; 1) to maintain
351 genetic diversity in large tree populations, 2) to conserve specific adaptive or other traits in
352 marginal or scattered tree populations which are often relatively small, and 3) to conserve rare or
353 endangered tree species with populations consisting of a small number of remaining individuals.
354 The fourth basic requirement is that one of these objectives has been clearly stated for each target
355 tree species within a unit.
356

4.2. Size of a dynamic conservation unit

358

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

365

4.2.1. Sampling perspective

367

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

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

391
392 In forest trees, some 10-20% of allozyme alleles are common and local (Brown and Hardner, 2000).
393 Considering this, the same authors defined an adequate sampling strategy as one that captures
394 with 95% certainty at least one copy of alleles with a frequency of 0.05 and stated that this
395 requires 59 unrelated gametes. Taking into consideration differences in the breeding systems of
396 trees, Brown and Hardner (2000) recommended that a sample should include a minimum of 50
397 random and unrelated trees. As a worst-case scenario, Brown and Hardner (2000) concluded that
398 open-pollinated seed collected from a minimum of 15 maternal trees would sample a large part of
399 genetic diversity within a population.

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401 4.2.2. Dynamic perspective

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403 Applications of MVP and ESU to improve the genetic management of conservation populations

404 have been debated extensively during the past 30 years (see Traill et al. (2010) and Flather et al.

405 (2011) for MVP; Fraser and Bernatchez (2001) for ESU). Various MVP and ESU approaches have

406 been defined using different criteria but they all have a common goal, i.e. long-term conservation

407 of evolutionary processes and adaptive diversity. However, no single ESU approach is the best one

408 for all situations (Fraser and Bernatchez, 2001) and there is no universal threshold for MVP either

409 (Flather et al., 2011). MVP also depends on context-specific factors (Traill et al., 2007).

410

411 The minimum size of a genetically viable population is commonly defined using effective

412 population size (N_e), which is a parameter measuring the intensity of random genetic drift in the

413 Wright-Fisher model population (e.g. Hartl and Clark, 1997). Based on theoretical studies,

414 recommendations for the minimum population size range from $N_e=500$ (Franklin, 1980; Soulé,

415 1980; Lande and Barrowclough, 1987) to $N_e=5000$ (Lande, 1995) when the goal is to maintain

416 evolutionary potential. A meta-analysis by Traill et al. (2007) found a median, standardized MVP

417 estimate of 4169 individuals based on published studies on 212 species (mainly animals). If the

418 goal is to maintain reproductive fitness in the short term (over a few generations), the minimum

419 population size of $N_e=50$ has been suggested by many studies (see Frankham et al., 2002).

420

421 The question of how many individuals should be included in a conservation unit has also been

422 studied extensively in forest trees. However, as N_e is extremely difficult to determine accurately in

423 tree populations, it is frequently approximated by the number of reproducing trees (N_r), i.e. the

424 effective size of an observed biological population instead of a model one (e.g. Hattermer, 2005a).

425 The recommendations for N_r range from 50 (e.g. Brown and Hardner, 2000) to 500 (e.g. Hattermer,

426 2005b) and 1000 (Lynch, 1996).

427

428 Franklin (1980) and many other theoretical studies on MVP are based on the assumption that

429 additive genetic variance (V_a) rather than allelic diversity determines evolutionary potential, and

430 that its level depends on the balance between random genetic drift and mutation. The change in

431 additive genetic variance (ΔV_a) is calculated as the difference between the increase in genetic

432 variation per generation due to mutation (V_m) and the loss of additive genetic variation per

433 generation due genetic drift ($V_a/2N_e$) (e.g. Frankham et al., 2002). At mutation-drift equilibrium

434 ($\Delta V_a=0$), N_e equals $V_a/2V_m$. Various theoretical studies have estimated V_m differently and this

435 explains the large variation in the recommended minimum population sizes. These

436 recommendations can thus be debated until it is better known which mutations are always

437 deleterious, and which ones are deleterious in some conditions and beneficial in others (Frankham

438 et al., 2002).

439

440 Expected heterozygosity (H_e) and V_a are expected to decline in a population by a factor of $1-1/2N_e$

441 per generation (e.g. Hartl and Clark, 1997). The assumptions of this model include equal sex ration,

442 random mating and non-overlapping generations, and that no selection, mutation or migration

443 take place. However, these assumptions do not often hold in case of tree populations.

444 Furthermore, this model probably over-estimates the decrease of V_a because they do not take into

445 account the role of linkage disequilibrium and interactions among loci (Carter et al., 2005; Kremer

446 and Le Corre, 2012).

447

448 *4.2.3. Recommendations for the sizes of the dynamic conservation units of forest trees*

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473

474 However, assuming that the average generation time of a European tree species is 50 years, a
475 model population with $N_e=500$ would maintain 99.8% of its original genetic diversity after 100
476 years. Smaller populations with $N_e=50$, 15 or 5 would maintain 98.0%, 93.4% and 81.9% of their
477 genetic diversity, respectively. These calculations do not take into account any outside gene flow
478 which is likely to offset some part of the loss of in genetic diversity, nor bi-parental inbreeding
479 that, on the contrary, can reduce the diversity. Furthermore, spatial genetic structure is not
480 considered. Using a simulation approach and the most realistic seed dispersal functions for a
481 model population, Sagnard et al. (2011) showed that a spatial genetic structure (non-random
482 distribution of related genotypes in space) could result from a single mating event when $N_e < 16$.
483
484 Migration can play a significant role in maintaining genetic diversity in tree populations. Long-
485 distance gene flow via seed and pollen dispersal increases genetic variation in tree populations in
486 two ways (Kremer et al., 2012). Firstly, long-distance effective pollen dispersal increases the
487 genetic diversity in seeds produced by the current tree generation. Secondly, migrant seeds can
488 accumulate in a population over many years, increasing the number genotypes in the next tree
489 generation. This suggests that long-distance gene flow can compensate partly or fully the loss of
490 genetic diversity due to genetic drift in small tree populations or even increase their genetic
491 diversity, depending on the situation.
492
493 Based on the theoretical considerations and practical aspects, we propose that the minimum size
494 of a genetic conservation unit should be either 500, 50 or 15 reproducing individuals depending on
495 tree species and conservation objectives (Table 1). As some tree species are capable of vegetative
496 reproduction (through root sprouts or partially buried shoots), efforts should be made to check if

497 there are identical genotypes (clones) of such tree species present within a unit and take this into
498 consideration when estimating the number of reproducing genotypes.

499
500 In Cases 1 ($N_r=500$) and 2 ($N_r=50$) (Table 1), the minimum number of reproducing trees can be
501 temporarily lower than what is indicated if it is necessary to create gaps to promote natural
502 regeneration, for example. The prerequisite is that the minimum number of reproducing trees has
503 contributed to mating (and seeding depending on the species) before the regeneration process
504 has been initiated with silvicultural measures. Furthermore, N_r should recover to the minimum
505 level or above in the near future after a management intervention. We consider Case 3 ($N_r=15$) as
506 an exceptional case. All units with such a low number of reproducing trees should be subjected to
507 appropriate measures to increase their population size. Furthermore, seed or other reproductive
508 material from these units should be collected urgently for ex situ conservation.

509

510 *4.3. Management of dynamic conservation units*

511

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

521 quantity and genetic quality. In some particular cases, such as riparian pioneer tree species,
522 ecological engineering may be needed to ensure natural regeneration (Lefèvre et al., 2001).
523
524 Under the first objective, management efforts should aim to protect the units against natural or
525 man-made catastrophes. Obviously, the units can never be fully protected against these stochastic
526 events but management can increase the resilience of the tree populations so that they can persist
527 during a catastrophe and recover from it. In the absence of any catastrophe, successional
528 development may also threaten the existence of tree populations and management efforts are
529 needed to halt or reverse this natural process, depending on the target species.
530
531 Under the second objective, silvicultural techniques, such as thinning, are often needed to
532 maintain the vitality of the target tree populations and to avoid stands becoming too dense with
533 reduced health, vigour and seed production. Thinning typically removes out-competed individuals
534 or it can be applied in a systematic way but as long as stand density remains above a certain
535 threshold, thinning usually has limited genetic consequences (El-Kassaby and Benowicz, 2000;
536 Lefèvre, 2004). After thinning, target tree populations should still have a sufficient number of
537 effectively mating and reproducing trees to prevent reduction of genetic diversity through
538 demographic bottlenecks and consanguineous mating, and to maintain genetic diversity.
539 Furthermore, the spatial distribution of trees should be such that it is reasonable to assume that
540 sexual reproduction takes place randomly, and that the level of relatedness among the next
541 generation of trees, or spatial genetic structure, is as low as possible (Sagnard et al, 2011).
542
543 Silvicultural techniques should be applied in such a way that they support reproductive processes
544 and result in adequate regeneration of the target tree species. Natural regeneration should be

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

552

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

563

564 Detailed guidelines for field-level management of the units are already available (e.g. Koski et al.,
565 1997; FAO, DFSC, IPGRI, 2001; Lefèvre et al., 2001; Rotach, 2005) so we do not discuss them here.
566 However, we want to highlight the importance of relevant practices and policies in supporting
567 management of the units. As countries are ultimately responsible for conserving genetic resources
568 within their territory, management of the units needs overall coordination at the national level.

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

576

577 *4.4. Monitoring of dynamic conservation units*

578

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

583

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

591

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

603

604 Development of a more operational genetic monitoring system for forest trees is a necessary and
605 urgent task as problems in the genetic processes of tree populations are usually not immediately
606 observable by measuring natural regeneration or vitality of seeds (Konnert et al., 2011).

607 Aravanopoulos (2011) proposed a simplified genetic monitoring approach which includes only
608 three indicators (natural selection, genetic drift and a gene flow-mating system), to be evaluated
609 based on three demographic (age and size class distribution, reproductive fitness and regeneration
610 abundance) and four genetic (effective population size, allelic richness, latent genetic potential
611 and outcrossing/actual inbreeding rate) verifiers. This new scheme is a useful step towards making
612 genetic monitoring more feasible and cost-effective in terms of field and laboratory work, but it
613 does not solve all the problems (e.g. multiple indicators may still give conflicting results) and it still
614 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).

620

4.5. Deployment of the pan-European minimum requirements

622

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.

636

5. Conclusions

638

639 The pan-European minimum requirements for genetic conservation units of forest trees presented
640 in this paper constitute a major step in improving genetic management of forest trees in a large
641 geographical scale. They provide managers, forest owners and policy makers with practical,
642 science-based recommendations for implementing dynamic conservation of forest trees in a
643 coordinated manner across different countries and situations. The presented requirements were
644 developed for the European tree species and conditions so they cannot be applied to other
645 regions without modifications. However, we believe that they provide other regions with a useful
646 example on how such requirements can be developed through regional collaboration.
647 Furthermore, as range-wide genetic studies and mapping of valuable populations are increasingly
648 carried out also for tropical and sub-tropical tree species (e.g. Kadu et al., 2011; van Zonneveld et
649 al., 2012), countries in other regions would also benefit from having common requirements for
650 genetic conservation units of forest trees modified for their conditions.
651
652 In addition to secured regeneration and adequate number of reproducing trees within a
653 conservation unit, it is crucial that a network of the units has a sufficient coverage of the spatial
654 genetic variation present in a given species (Koski et al., 1997; Crandall et al., 2000). As it is very
655 difficult to define a universal minimum number of units for a conservation network that could be
656 justified for all tree species (Brown and Hardner, 2000), we did not include this aspect to the
657 minimum requirements. Instead, we argue that the minimum number of units for conservation
658 networks of forest trees should be defined species by species using available data on the existing
659 conservation units, species distribution, range-wide genetic diversity studies and results of
660 common garden tests or other information on adaptive traits. This would also allow assessment of
661 duplication in conservation efforts between countries and, considering the level of threats for a

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688 Legends

689

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

692

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

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Comment citer ce document :

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

Requirement group	Detailed requirements
Basic requirements	<p>The unit has</p> <ol style="list-style-type: none"> 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. <p>One or more tree species have been recognized as target tree species for genetic conservation in the management plan.</p> <p>One of the following conservation objectives has been clearly stated for each target tree species within a unit:</p> <ol style="list-style-type: none"> 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	<p>The minimum population size depends on the conservation objective as follows:</p> <p>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 consist of 500 or more reproducing trees.</p> <p>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.</p> <p>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.</p>
Management	<p>Silvicultural interventions are allowed within the unit and they are actively applied, as needed, to:</p> <ol style="list-style-type: none"> 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	<p>Field inventories are carried out every five or ten years to assess regeneration success and the population size, and to update the management plan.</p> <p>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.</p>