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Forests and global change: what can genetics contribute to the major forest management and policy challenges of the twenty-first century?

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1 **Forests and global change: what can genetics**
2 **contribute to the major forest management and**
3 **policy challenges of the 21st century?**
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7 *Running title: Genetics and sustainable forest management and policy*
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51

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54

55 **Abstract**

56

57

58 The conservation and sustainable use of forests in the 21st century pose huge
59 challenges for forest management and policy. Society demands that forests provide a
60 wide range of ecosystem services, from timber products, raw materials and renewable
61 energy to socio-cultural amenities and habitats for nature conservation. Innovative
62 management and policy approaches need to be developed to meet these often
63 conflicting demands in a context of environmental change of uncertain magnitude and
64 scale. Genetic diversity is a key component of resilience and adaptability. Overall,
65 forest tree populations are genetically very diverse, conferring them an enormous
66 potential for genetic adaptation via the processes of gene flow and natural selection.
67 Here, we review the main challenges facing our forests in the coming century and
68 focus on how recent progress in genetics can contribute to the development of
69 appropriate practical actions that forest managers and policy makers can adopt to
70 promote forest resilience to climate change. Emerging knowledge will inform and
71 clarify current controversies relating to the choice of appropriate genetic resources for
72 planting, the effect of silvicultural systems and stand tending on adaptive potential
73 and the best ways to harness genetic diversity in breeding and conservation programs.
74 Gaps in our knowledge remain and we identify where additional information is
75 needed (e.g. the adaptive value of peripheral populations or the genetic determinism
76 of key adaptive traits) and the types of studies that are required to provide this key
77 understanding.

78

79

80 **Keywords:** sustainable forestry; assisted migration; climate change; adaptation;
81 genetic diversity; gene conservation.

82

83

84 **Introduction**

85 The development of appropriate and informed policy for the conservation and
86 sustainable use of forests worldwide, during the 21st century and beyond, presents
87 several challenges. The long life-span of trees makes them susceptible to both short
88 and long term environmental disturbances (Alberto et al. 2013). The natural cycles of
89 environmental disturbances are being modified by human activities and this is
90 predicted to intensify in the future with major effects on biodiversity (Alfaro et al.
91 2014, Sala et al. 2000). Thus, policies that guide forest management decisions must be
92 amenable to both short and long term assessment. Innovative forest management and
93 policy approaches are necessary to meet the often conflicting demands of a changing
94 society and the need to deliver an array of provisioning, regulating and socio-cultural
95 ecosystem services (MEA 2005, TEEB 2012). To ensure effective implementation in
96 practice, these new approaches need to be more responsive to the future needs of
97 society in general, more amenable to cross-sectorial cooperation and more evidence-
98 based than is currently the case (Vanhanen et al. 2007).

100 Because of the incomplete scientific evidence on the effect of silviculture on long
101 term forest sustainability and because forests provide a wide range of goods and
102 services for society, forest-related societal challenges can result in controversy,
103 polarization of views, stalemates and deadlocks (van Eeten 1999). While some of the
104 controversies are philosophical in nature, others could be resolved by further scientific
105 research. For example, it is debatable whether management based on natural
106 regeneration is more sustainable than planting in reforestation programs (Espelta et al.
107 2003, Morrissey et al. 2010) because the outcome will depend on a number of factors,
108 including availability of sufficient appropriate seed sources for natural regeneration,
109 ecological traits of the planted trees species, etc. Similarly, there is lack of clarity
110 regarding the relative merits of gradual tree selection versus clear-felling as a
111 harvesting strategy for timber production in commercial forests (Lundqvist et al.
112 2013). Other controversies relate to the relative benefits of stand conversion compared
113 to ecological restoration; the use of exotic species (or non-autochthonous parent
114 material of native species) instead of native material of local origin as a source of
115 forest reproductive material in plantation forests; the use of multiple versus single
116 species forest plantations; the acceptance and application of clonal forestry and the
117 use of genetically-modified trees in intensive forestry; among others (MCPFE 2008).

118

119 In addition to these uncertainties and societal controversies, there is the recognition
120 that climate change will have an impact and should therefore be included in these
121 longstanding debates (Noss 2001). The realization that many local habitats will cease
122 to offer the same potential for forest cover and production as they have in the past
123 represents a serious paradigm shift for forestry. The uncertainty regarding the
124 magnitude of the change at different spatial scales presents yet another difficulty for
125 the development of appropriate forestry policy. For example, due to their location at
126 the rear-edge of species distributions, countries in the Mediterranean region are
127 generally expected to experience the consequences of climate change more abruptly
128 than the more northerly countries of Europe (Hampe & Petit 2005). Nevertheless,
129 habitat changes are also expected to be severe at high latitudes and generally greater
130 in the lowlands than at high elevations (Loarie et al. 2009). There is therefore, a need
131 for sound, informed policy development that is tailored to both local and regional
132 scales to ensure that the most appropriate forest management strategies are
133 implemented. The recognition that there is no single approach underlines the
134 importance of selecting appropriate practices that fit the conditions and objectives of
135 each particular situation (Millar et al. 2007).

136

137 The term adaptation (see Annex 1 for definitions of this and other terms used
138 throughout the paper) is commonly used to cover a range of purposes in the context of
139 global, and particularly climate, change (Biesbroek et al. 2010). In forestry, the term
140 is generally used to encompass all aspects of forest management that need to be
141 modified to prepare forests so that they can continue to provide their usual ecosystem
142 services under (the uncertainties of) global change (Bernier & Schoene 2009), as in
143 “adapting forests to climate change” or “adaptive forestry”. However, from a genetic
144 perspective, adaptation has a different, more restrictive meaning, i.e. the evolutionary
145 capacity of a population to cope with a changing environment through genetic
146 changes. The ability of forests to adapt in a genetic way, i.e. genetic adaptation, to the
147 new environments that will result from climate change depends on: (i) the speed and
148 intensity of climate change across species ranges, (ii) the existence of genetic

149 diversity among individuals in natural populations and (iii) the ability of this diversity
150 to migrate between populations through pollen and seed movement, i.e. gene flow
151 (Savolainen et al. 2007; Kremer et al. 2012). Populations with high genetic diversity
152 for adaptive traits (i.e. rich in genetic resources) are more likely to be able to respond
153 via natural selection to the challenges posed by climate change (Jump et al. 2008).
154 The adaptive potential (Scotti 2010) of forests worldwide thus depends on the genetic
155 resources found both within populations and among forest stands that are connected
156 via effective gene flow.

157

158 In 1994, in recognition of the importance of genetic diversity for forest sustainability,
159 FOREST EUROPE (the pan-European political process for the sustainable
160 management of the continent's forests, <http://www.foresteuropa.org/>) created
161 EUFORGEN (<http://www.euforgen.org/>), a collaborative network of European
162 countries whose remit is to promote the conservation and sustainable use of forest
163 genetic resources. However, despite this high level recognition of the importance of
164 forest genetic diversity, the National and European forest policy agencies frequently
165 ignore this aspect when developing indicators and guidelines on how forest
166 management should prepare for and react to climate change (Koskela et al. 2007).
167 Similarly, the role of forest genetic resources is often omitted from the
168 recommendations (Graudal et al. 2014) issued by habitat and species conservation
169 agencies and non-governmental organizations, such as those within the framework of
170 the European Habitat directive (Council Directive 92/43/EEC). This is despite the
171 consideration that forest genetic resources in forest management strategies are key in
172 ensuring that forests can adapt to climate change (Lefèvre et al. 2013). The overall
173 lack of attention given to the genetic dimension of forest adaptation is probably due to
174 a general lack of knowledge of the recent advances in forest genetics among forest
175 managers and policy makers.

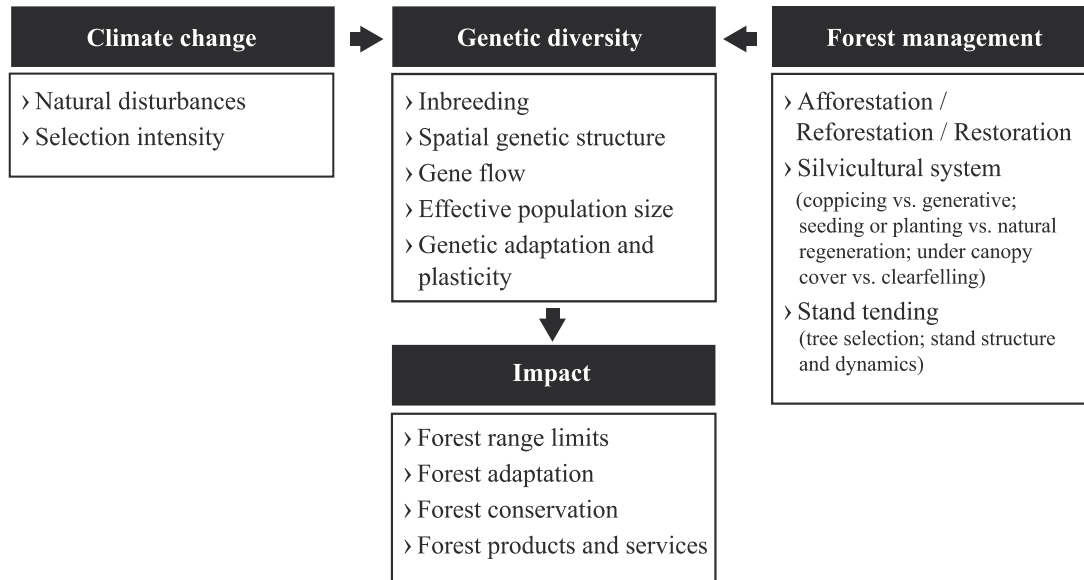
176

177 In this article, we review the major challenges faced by forest managers and policy
178 makers in temperate Europe in the 21st century for which recent progress in genetics
179 can contribute to the development of appropriate practical solutions. We deliberately
180 focus on the practical issues that arise from these forest challenges, listing them as
181 they are perceived in a management context. Seven major challenges emerged from
182 discussions between the stakeholders of the Linktree project who had direct roles in
183 developing policy and appropriate management to prepare forests for climate change.
184 These range from natural regeneration to assisted migration and from conservation to
185 breeding. We address naturally regenerated and plantation forests but exclude
186 genetically modified organisms from our report as they are not currently available for
187 most species of interest to European forestry. We present examples where uncertainty
188 adds complexity to management decisions. For these examples, we provide insights
189 into how science, and particularly an understanding of genetics, can help to inform
190 policy directions. In doing so, we aim at bridging the gaps between science,
191 management and policy which typically operate within different spheres of influence
192 and across different time frames and are not always driven by the same concerns.

193

194 We also aim to demonstrate that some key forest management and policy questions
195 can be resolved by genetic studies, in particular those using new generation
196 technology that is now increasingly becoming accessible and of practical use for
197 forest trees. These studies give insights into the current and future consequences of
198 particular management strategies on the evolutionary response of tree populations

199 and, in turn, can guide how management strategies should be adapted to foster the
 200 evolutionary potential of forests under changing conditions. Figure 1 shows a
 201 summary of the processes affecting the genetic diversity of forest trees and how
 202 management can use and modify these processes to prepare forests for climate
 203 change.
 204



205
 206

207 Figure 1. Processes affecting the genetic diversity of forest trees and how
 208 management can harness these processes to prepare forests for climate change. The
 209 pressure applied by forest management on the state of genetic diversity has impacts
 210 that affects the forest as a whole. Climate change drives the system and the selection
 211 pressure it imposes can be reduced by management practices.
 212
 213

214 **Challenge 1: Will the genetic resources available in natural forests remain**
 215 **appropriate and be sufficient under climate change?**
 216

217 *This question relates to the adaptive potential of forest tree populations and their*
 218 *reaction to climate change. Depending on the management goal (e.g. production,*
 219 *protection or recreation), phenotypic traits of interest to managers will be wood*
 220 *quantity and quality or survival and health. Standing genetic variation and the*
 221 *phenotypic plasticity found in forest tree populations provide the means to cope with*
 222 *the new conditions.*
 223

224 Climate envelope modelling shows that species distribution ranges and the species
 225 composition of forests are likely to change considerably over the coming decades (e.g.
 226 Thuiller et al. 2005). However, this modelling approach, based on correlation of
 227 geographic distribution with a range of climate variables, cannot accurately predict
 228 the future distribution of species because it does not take into account important
 229 ecological and evolutionary processes such as competition at the community level,
 230 dispersal, phenotypic plasticity and adaptive potential. In the few studies in which
 231 genetic diversity has been included in the modelling frameworks, it has been found to
 232 modify the predicted range of forest tree species under climate change considerably
 233 (Benito-Garzón et al. 2011, Oney et al. 2013). This highlights the urgent need for

234 appropriate genetic methods and data to determine the adaptive potential of existing
235 material.

236

237 Currently, the best available source of genetic data on phenotypic traits of importance
238 for local genetic adaptation comes from “common garden” trials which contain
239 material sourced from a range of origins, called provenances in the forestry literature.
240 Published results from such trials show that adaptive genetic diversity is large in most
241 forest tree species, mainly within but also among populations (Ducouso et al. 1996),
242 although there are remarkable exceptions (e.g. *Pinus pinea*, Mutke et al. 2010). These
243 trials also provide evidence of local genetic adaptation across the range of species and
244 demonstrate that most tested provenances display large phenotypic plasticity for key
245 adaptive traits when grown under different climatic conditions (Rehfeldt et al. 2002).
246 These findings are important because they indicate that, provided climate shifts are
247 not too steep and some degree of growth yield reductions are acceptable for
248 management objectives, current genetic resources of many tree species are likely to
249 remain appropriate in many of their current habitats, particularly within the core of
250 geographic distribution ranges.

251

252 Unfortunately, common garden trials are only available for a restricted number of
253 commercially important forestry species, they rarely include representatives of all the
254 ecologically relevant seed sources and in many cases the trials are insufficiently
255 replicated across the distribution range of the target species. Notably, peripheral
256 populations (i.e. coming from the ecological and geographical distribution margins)
257 are under-represented in existing field trials. There is therefore an urgent need for the
258 establishment of pan-European and range-wide species and provenance trials of novel
259 and native species (see for example the REINFFORCE initiative,
260 <http://reinfforce.iefc.net/>). These should be established using provenances from across
261 the distribution range grown at multiple sites which include locations within the
262 current distribution ranges as well as those that are beyond the current range but are
263 predicted to become suitable in the future for the target species.

264

265 When field trials already exist, their analysis at a national or range-wide scale could
266 provide immediate answers to some of the questions raised by managers regarding the
267 potential of their populations to adapt to climate change (see for example
268 www.treedivnet.ugent.be, an international network of common garden experiments
269 where monocultures are compared with mixed species or mixed provenance
270 treatments, and EU funded initiatives, such as Trees4Future,
271 <http://www.trees4future.eu/>, and the COST action FP1202, <http://map-fgr.entecra.it/>),
272 The measurement of meaningful adaptive traits in these trials is recognized to be
273 challenging in terms of the time and expertise required to obtain them (e.g. drought
274 tolerance, phenology, seed production, and other life history traits, Chambel et al.
275 2007) and rapid and cost-effective phenotyping methods of many hundreds of
276 individuals need to be developed if the full benefit of these expensive trials is to be
277 secured (Neale & Kremer, 2011). Progress in fast phenotyping approaches is being
278 made with modern methods such as terrestrial Lidar scanning for measurement of tree
279 size and form (Eysn et al. 2013), chlorophyll fluorescence for estimating stress via
280 photosynthetic efficiency (Salmela et al. 2011) and others (Alia & Majada 2013)
281 becoming available. Greenhouse trials, in which treatments such as drought and pests
282 and diseases can be imposed, represent a useful and sometimes alternative strategy to
283 expose and assess standing genetic variation and phenotypic plasticity in key traits for

284 seedlings and young trees (Sagnard et al. 2002, Chambel et al. 2007). Results from
285 these trials will provide an understanding of variation in adaptive traits and how it is
286 distributed across the landscape. This knowledge will form a framework with which
287 to guide advice on the scale of current and future movement of planting material can
288 be practiced without the fear of maladaptation. It will also contribute to models which
289 aim to determine the evolutionary potential of our forests to cope with climate change.

290

291 Advances in molecular approaches are beginning to make it possible to link
292 phenotypes to variation in genetic markers (González-Martínez et al. 2006). For
293 example, such approaches have already been used to explore cold and drought
294 resistance in several conifers (Neale & Kremer 2011, Eveno et al. 2008, Grivet et al.
295 2011). By taking advantage of new cost-effective genotyping-by-sequencing (GbS)
296 methods it is now possible to adopt a genome scanning approach to generate millions
297 of data points across the genome. In one of the first such studies in forest trees it was
298 shown that extensive variation exists within natural populations of pines for genes
299 linked to ecologically-relevant traits (Parchman et al. 2012). Ultimately, it is
300 anticipated that these approaches will provide managers with the practical tools to
301 determine whether their targeted trees and stands have the capacity to adapt to climate
302 change, at low cost even in non-commercial species.

303

304 *In conclusion, most genetic studies to date indicate that there is a large amount of*
305 *heritable adaptive variation available in tree species on which natural selection can*
306 *operate. Thus, the rather dramatic predictions made by climate envelope models of*
307 *large scale changes in forest distribution within the coming decades require*
308 *reassessment and refinement to include genetic processes. However, adaptive*
309 *potential depends on the species and local ecological conditions and demographic*
310 *constraints could severely limit the capacity of populations to evolve under the most*
311 *severe climate changes. Thus, although usually appropriate, management scenarios*
312 *based solely on locally existing forest material and genetic resources may be*
313 *hazardous particularly at range and ecological edges.*

314

315

316 **Challenge 2: What should be monitored to determine whether the native species**
317 **in natural woodlands are currently at risk under climate change?**

318

319 *Both a lack of genetic adaptation and demographic collapse can drive populations to*
320 *extinction. Determining which genetic and demographic thresholds will lead to*
321 *maladaptation is crucial to make informed management decisions, particularly in*
322 *forests where, despite predictions, evidence of decline due to climate change is not yet*
323 *strong. This can be achieved by genetic monitoring.*

324

325 Although forest monitoring is often carried out by countries to assess the state of their
326 forests and the social, economic and environmental benefits they derive from them, it
327 rarely includes any assessment of genetic resources (Graudal et al. 2014).

328 Aravanopoulos (2011) defines genetic monitoring as “the quantification of temporal
329 changes in population genetic variation and structure”. He suggests that genetic
330 monitoring should focus on ecologically and economically important forest tree
331 species and on four key genetic processes: (1) natural selection, (2) genetic drift and
332 (3) gene flow and one demographic process linked to gene flow: the mating system.
333 Carried out at regular intervals, genetic monitoring will provide much needed

334 information on adaptive potential. Protected areas where there is less human mediated
335 interference and management practices are carried out with a lighter touch than in
336 other forest types constitute excellent sentinels of the effects of climate change and
337 are thus also appropriate candidates for genetic monitoring.

338 Neutral molecular markers can now be used with relative technical and financial ease
339 to monitor genetic drift, gene flow and the mating system. The relationship between
340 neutral genetic diversity and standing genetic variation at fitness related genes in large
341 populations is not straightforward (Le Corre & Kremer 2013) and genomic
342 approaches are not yet sufficiently generally accessible to be applied to clarify the
343 relationship. There is therefore a need to determine the most efficient ecological
344 proxies that could be used instead to assess the adaptive potential of forest
345 populations by forester. Aravanopoulos (2011) suggests that several demographic
346 indicators, such as: age class structure, filled seed set and seedling density can be used
347 as these proxies. A system of genetic monitoring for forest tree species broadly based
348 on the concepts discussed here, was proposed and successfully tested in Germany for
349 providing early warning signs of environmental changes affecting forests (Konnert et
350 al. 2011).

351
352 Studies using novel approaches will be needed to assess standing genetic variation
353 and adaptive potential directly. General information can come from progeny tests in
354 common gardens (Houle 1992) or *in situ* experimentation (e.g. reciprocal
355 transplantation schemes), where heritability and genetic variance can be measured.
356 Sophisticated association and genome-wide ecological studies will increasingly
357 provide information on standing genetic variation available for adapting to changing
358 environments (see references above in Challenge 1). It is expected that genes involved
359 in genetic adaptation will vary along the geographical range of species (see Hancock
360 et al. 2011 for the model plant species *Arabidopsis thaliana* and Prunier et al. 2012
361 for an example in forest trees), thus the establishment of an inventory of such
362 adaptively important genes (and their allelic variants) across the full species range is a
363 priority for current and future applied genetics research.

364
365 *In conclusion, monitoring the potential of forests to adapt genetically under climate is*
366 *necessary over broad areas to inform management. Monitoring based on parameters*
367 *used in classical forest management (such as adult age classes, seedling density and*
368 *presence of pests) can now be coupled with molecular genetics assessment methods to*
369 *provide early warning signs of maladaptation risks. Incorporating genetic monitoring*
370 *as a component of the current pan-European forest monitoring efforts would provide*
371 *key indicators of evolutionary and adaptive potential.*

372

373

374 **Challenge 3: Is assisted migration the answer for managing forests and their** 375 **habitats under climate change?**

376

377 *This question typically arises when sound evidence suggests that current genetic*
378 *resources at a site will cease to offer an appropriate option under future climate*
379 *(Challenge 1) and introduction of non-local resources is being considered. Assisted*
380 *migration concerns the sourcing of seed and planting stock and can take two forms:*
381 *the use of exotic species (i.e. species that do not naturally occur at the planting*
382 *location or, more generally, within the country) or the use of non-local genetic*
383 *resources (i.e. populations of naturally occurring species which originate from other*

384 *parts of the species distribution range). In management plans, the definition of*
385 *assisted migration is often restricted to the use of exotic species and the option to use*
386 *conspecific material from a different origin is frequently overlooked.*
387

388 The use of exotics has been practiced in forestry for centuries, often with great
389 success in terms of sustaining wood production (e.g. *Pseudotsuga menziesii*, *Pinus*
390 *radiata*, *Abies grandis*, *Picea sitchensis*, etc introduced in Europe). Such successful
391 introductions are often the culmination of extensive trials and on the basis of their
392 results, the elimination of many species from the candidate list. Although there are
393 numerous examples of successful introductions (e.g. mountain habitat restoration in
394 France in the 19th century (Charry 1996, Bartoli & Musch 2003), there are also
395 notable instances of spectacular failures. A classic example is eastern white pine,
396 *Pinus strobus* L., a five-needle pine which was introduced into France from North
397 America in the mid-16th century, and into England and Germany 150 and 300 years
398 later, respectively. In the mid-19th century the European plantations were colonized by
399 the pathogenic fungus *Cronartium ribicola* of Asian origin, with catastrophic results
400 due to lack of resistance to the disease (Karlman 2001). Consequently, this species is
401 now rarely used in European forestry. Also, some of the successfully introduced
402 species in Europe have become invasive (e.g. *Robinia pseudoacacia* and *Quercus*
403 *rubra*), causing habitat management problems on a massive scale.
404

405 The translocation of genetic resources from one region of the species distribution to
406 another is also a form of assisted migration (*sensu* Richardson et al. 2009), i.e. within-
407 species assisted migration or “assisted gene flow” *sensu* Aitken and Whitlock (2013).
408 Again, foresters have used this management option extensively at least since the 19th
409 century, very often as a strategy for planning large scale reforestation programs when
410 local seed supplies were insufficient or thought to be less productive than non-local
411 resources (Bartoli & Musch 2003) or to overcome budget limitations: for example
412 4000 tons of oak seed were brought into Germany for planting from south-eastern
413 Europe (Kleinschmit, 1993); cherry seedlings were sold in Europe from seeds
414 obtained in jam factories (Kleinschmit & Kleinschmit, 2009). Here again, despite
415 some general success, maladaptation of the planting stock has also resulted in severe
416 economic lost (see for example the massive dieback of Portuguese seed sources of
417 maritime pine planted in South West France after the 1984-1985 severe winter frost,
418 Timbal et al. 2005).
419

420 It is now well recognized that assisted gene flow is neither risk-free for the target
421 species themselves nor for their associated communities (see for example Aitken &
422 Whitlock 2013). This understanding underpins the European Council Directive
423 1999/105/EC on the marketing of forest reproductive material which requires seed
424 companies to attach clear passport data to traded resources. This traceability allows
425 forest managers to make informed decisions regarding the likelihood of maladaptation
426 of purchased planting stock and the potential ecological consequences of using it.
427 Some managers have attempted to reduce the risk of planting failure under climate
428 change by mixing seed lots within and among regions of provenance and among years
429 (i.e. ‘composite provenancing’). However, according to Ennos et al. (1998) the use of
430 assisted gene flow for such insurance purposes should only be considered if levels of
431 variation within indigenous populations are so low that they are unlikely to be able to
432 adapt to future conditions by themselves and if the imported material is considered to

433 be better adapted to future climatic conditions than the indigenous populations, which
434 are both difficult to ascertain (see Challenge 2).

435

436 Thus, assisted gene flow could offer a reasonable solution for situations in which local
437 resources are declining, adult tree mortality is above a set threshold and natural
438 regeneration is low or absent despite supplementation efforts using locally sourced
439 seed (Ledig & Kitzmiller 1992, Hubert & Cottrell 2007, CRGF 2008). This is a form
440 of genetic rescue where hybridizing local resources with genetically unrelated
441 resources could restore fitness (Hedrick et al. 2011). It requires seed material to come
442 from stands “preadapted” to a future (and uncertain) climate and it is not free of risk
443 as it could also result in outbreeding depression (i.e. lower overall fitness because of
444 disruption of co-adapted gene complexes). Ecological risks, such as within-species
445 introgression or modification of biotic interactions, although somehow attenuated
446 compared to those from exotics, are also present with assisted gene flow (Aitken &
447 Whitlock 2013). Broad scale analyses such as those of Rehfeldt et al. (2002) for *Pinus*
448 *sylvestris*, where the fitness of exotic provenances is compared to that of the local
449 provenances at a trial site, enable the appropriateness of local resources to be
450 evaluated and the need for transfer across seed zones to be assessed.

451

452 *In conclusion, assisted migration programs can disrupt local genetic adaptation and*
453 *affect the present and future dynamics of forest genetic resources. We can take*
454 *advantage of past experiences in the introduction of species and provenances, but*
455 *these are not real experiments to test the effectiveness of present-day assisted*
456 *migration programs. Caution is needed in the use of extensive assisted migration as*
457 *the responses will likely affect not only trees but also the whole forest community in*
458 *which they are established.*

459

460

461 **Challenge 4: Is natural regeneration the most appropriate management**
462 **technique for promoting the adaptation of natural forests to climate change?**

463

464 *Natural regeneration is being promoted in a European context of close-to-nature*
465 *forest management for several reasons including those that relate to cost reduction,*
466 *decreased disturbance, better selection potential due to larger seedling density and*
467 *conservation and continuous evolution of the local gene pool. It is thus generally*
468 *considered to be the most appropriate management method in protected habitats.*
469 *However, the success of natural regeneration is variable and factors such as soil type,*
470 *abundance of competing weeds, herbivore pressure, species light requirements and*
471 *availability of seed sources may force management to consider other regeneration*
472 *approaches.*

473

474 Whether natural regeneration is a better strategy for regenerating forests than
475 plantation remains an open question (Espelta et al. 2003, Morrissey et al. 2010), but it
476 is clear that within this debate, genetic considerations are rarely given the importance
477 they deserve (except when the management goal is to use the local gene pool or
478 GMOs are involved). This is unfortunate as genetic diversity considerations can be an
479 important basis for preferring one strategy over the other (Ledig & Kitzmiller 1992),
480 particularly in small forest stands (Vranckx et al. 2014) and their relevance is central
481 to climate change related issues (Koskela et al. 2007, Alfaro et al. 2014).

482

483 The question geneticists must address to help management in this context is whether
484 the level of genetic diversity (and the amount of seedlings) available from natural
485 regeneration is sufficient (Vranckx et al. 2014). Decisions regarding whether natural
486 regeneration is more appropriate than planting for the maintenance of genetic
487 diversity (and ultimately adaptive potential) can be informed by some level of genetic
488 monitoring based on appropriate methods (Aravanopoulos 2011 and see Challenge 2).
489 If the stand to be regenerated is genetically of average or above average diversity for
490 the species, and if seedlings are abundant, then natural regeneration is likely to be the
491 most appropriate option. When using natural regeneration, managers should make
492 sure that: i) adult trees contributing to natural regeneration are plentiful and not too
493 similar phenotypically (see minimum requirements for conservation of genetic
494 diversity in Koskela et al. 2013), ii) varied silvicultural treatments are implemented at
495 the landscape scale (see the effect of structure and density on the spatial genetic
496 diversity of seedlings in Sagnard et al. 2011) and iii) enough time is left for natural
497 regeneration to be thinned by varying levels and forms of natural or silviculture-based
498 selection (competition for light and water, resistance to herbivores, pests and
499 diseases).

500

501 If natural regeneration is scarce and/or a species in the stand has significantly lower
502 than average genetic diversity which may result in detrimental effects such as fixation
503 of deleterious alleles at adaptive loci (see how to monitor in Challenge 2), then a
504 strategy based on planting is likely to be beneficial. Managers who adopt this
505 approach should ensure that there is high genetic diversity in their planting stock by
506 insisting that seed lots used for plantation are based on equal contributions from at
507 least 30 to 50 seed trees (legal standards of most countries do not include this
508 requirement). They should also give careful consideration to the geographic origin of
509 the stock and chose the source that is most likely to be adapted to the conditions at
510 planting site.

511

512 Greater mortality (and thus potential for selecting advantageous phenotypic traits) is
513 expected under a natural regeneration regime than one based on planting. A plantation
514 will typically install 1200 to 2500 seedlings/ha, whereas this number increases by one
515 or two orders of magnitude with natural regeneration. Amm et al. (2012), for
516 example, show that selection intensity could be as high as 0.0001 between the seed
517 production and the recruitment stage in *Abies alba* Mill. For any given heritable
518 phenotypic trait of importance to forestry, it would be necessary to increase initial
519 densities of plantations dramatically to reach the same level of selection intensity as
520 that of natural regeneration, and these are unlikely to be acceptable under current
521 operational conditions.

522

523 *In conclusion, to provide sufficient material on which natural selection can operate to*
524 *bring about evolutionary change, the option of natural regeneration is likely to be*
525 *most appropriate as it typically provides a much larger base population than is the*
526 *case for plantations. Forestry will need to rethink its strategies for long rotation*
527 *species to make it possible for selection to occur in those areas where climate change*
528 *is expected to have its strongest impacts.*

529

530

531 **Challenge 5: Should/can the conservation of genetic diversity be included as a**
532 **component of habitat and species conservation strategies?**

533

534 *Managers tend to give much less consideration to the conservation of the genetic*
535 *resource (gene conservation) than to that of the species and habitat. Habitat*
536 *conservation usually aims to protect a set of particular ecological processes that*
537 *sustain a defined range of species, often rare or endangered, or are particular to an*
538 *ecosystem. In contrast, the in situ conservation of a genetic resource aims to maintain*
539 *the process of genetic adaptation under natural selection and demographic shifts so*
540 *that the individuals of a target species which are best adapted to current conditions*
541 *survive and breed to produce the next generation. Thus, a holistic biodiversity*
542 *conservation strategy consists of several different strands, the aims and approaches of*
543 *which are not necessarily compatible.*

544

545 Management of protected areas is mostly directed towards the conservation of rare
546 and endangered species and habitats (Peterken 1977, Klein et al. 2009) and there is
547 little direct focus on gene conservation. In contrast, *in situ* gene conservation is
548 generally practiced in large plots consisting of the major forest tree species in
549 common habitats where genetic processes can occur. The networks of gene
550 conservation units for forest tree species in Europe follow a set of minimum
551 requirements, including range-wide genetic diversity representativeness and their
552 management procedures aim to shield conservation units from maladaptive gene flow
553 (see Koskela et al. 2013 for a full description). Thus, networks of gene conservation
554 units provide a level of protection of biodiversity that is seldom considered in
555 protected areas that, we believe, warrants worldwide recognition such as
556 categorization as IUCN protected areas. Gene conservation units are also useful for
557 demonstrating that the integration of genetic principles into management does not
558 hinder silviculture and forest planning and instead, can significantly contribute to
559 adaptive forest management by introducing evolutionary considerations into everyday
560 practice (Lefèvre et al. 2013, Koskela et al. 2013).

561

562 The application of the greenway or ecological corridor approach used by planners to
563 establish a network of linked land and water habitats in the landscape (Ignatieva et al.
564 2011) may in some cases reconcile habitat, species and gene conservation strategies.
565 Corridors can facilitate both migration and gene flow which are key processes in the
566 maintenance of adaptive potential (Savolainen et al. 2007). Gene flow is generally
567 predicted to make a strong contribution to genetic adaptation (as it maintains the
568 overall genetic diversity, on which natural selection operates) in most forest tree
569 species (Kremer et al. 2012). However, large gaps of knowledge still exist. For
570 example, the effects of different forest landscape components on the rates of long-
571 distance gene flow are currently poorly understood. Although studies tend to
572 demonstrate that fragmentation indeed increases genetic drift and loss of fitness
573 (Vranckx et al. 2011) and the presence of woodland corridors and hedges generally
574 improve genetic connectivity, the distance that native forests have to be apart to
575 experience significantly reduced genetic connectivity is species specific and depends
576 on pollen and seed dispersal. Monitoring whether ecological corridors really do
577 promote gene flow, evolutionary processes and migration to more suitable habitats, as
578 well as identifying which species are most at risk by fragmentation, remain a
579 necessity.

580

581 The role of habitat connectivity is particularly controversial for the maintenance of
582 evolutionary potential for populations from the periphery of the distribution range and

583 this is particularly relevant in the context of climate change. Models have shown that
584 pollen flow may in fact decrease genetic adaptation rate in some instances (Kuparinen
585 et al. 2010). Leading edge peripheral (as well as numerous small) populations in
586 northern Europe do not always demonstrate local genetic adaptation (Leimu &
587 Fischer 2008). For these, pollen flow from the core of the distribution area may be
588 beneficial, particularly from a climate change perspective as core populations are
589 better adapted to the future conditions that are predicted at the leading edge. In this
590 case, connectivity will reduce inbreeding and drift at the leading edge (Willi &
591 Fischer 2005). Conversely, disjunct populations at the rear edge, with a long history
592 of demographic stability (Hampe & Petit 2005), will suffer from maladaptive gene
593 flow from core populations (Lenormand 2002). Rear edge populations, geographically
594 or ecologically disjunct from species distribution ranges, may constitute hotspots of
595 evolutionary potential provided their census size is not too small (Lesica & Allendorf
596 1995). Plans to reconnect these to other populations within the main distribution range
597 of the species should therefore be resisted to maintain their genetic distinctiveness.
598 However, on the other hand, gene flow from these rear edge populations could be
599 helpful for the adaptive evolution of core and leading edge populations in of the to
600 climate change.

601

602 *In conclusion, gene conservation of forest tree species should be viewed as an*
603 *integral part of biodiversity conservation, alongside that for species and habitats. As*
604 *each conservation focus has discrete objectives that may require different*
605 *management strategies, it is important to run them in parallel and non-exclusively*
606 *over the landscape at national and regional levels. However, protected forest areas in*
607 *which there is little or no active management can sometimes directly contribute the*
608 *conservation of forest genetic resources and genetic diversity monitoring (Challenge*
609 *2) should become a priority concern there for the most relevant species.*

610

611

612 **Challenge 6: Do the current objectives of tree breeding programs address**
613 **climate change sufficiently? Does the current usage of forest reproductive**
614 **material represent the best practice in preparation for climate change?**

615

616 *Tree breeding involves selecting individuals that have particularly desirable traits*
617 *and crossing these individuals to improve the trait or traits of interest within*
618 *populations. Breeding programs can therefore produce genetic resources which are*
619 *valuable in enabling forests to adapt to climate change and to provide more and/or*
620 *better ecosystem services. Historically, selection in these breeding programs has*
621 *targeted commercially important traits such as growth, wood density, stem*
622 *straightness and complete resistance to particular pathogens in clonal forestry (e.g.*
623 *poplars), with the goal of marketing the desired product within a minimum time span.*
624 *This breeding paradigm only makes sense if the environment remains constant during*
625 *the entire production rotation.*

626

627 Despite risks related to climate change in the forest sector, many European countries
628 continue to subsidize and support the use of a limited set of clones or varieties
629 produced by breeding programs established long ago, and this for a limited set of
630 commercial tree species (Alia & Majada 2013). Many species of interest in the 1970s
631 have dropped out of financial support schemes and seed orchards (mostly for conifers)
632 have been neglected or even destroyed and are no longer used to provide seed.

633 Moreover, new breeding efforts are scarce outside a few dominant commercial
634 species. Both practice and breeding efforts are thus too limited and inadequate for the
635 challenges of the 21st century (which is recognized by the community and has led, for
636 example, to the EU initiative Trees4Future, see Challenge 1). A few breeding
637 programs, however, are now incorporating in their objectives functional traits of
638 relevance to adaptive potential (e.g. water use efficiency, phenology along with the
639 more traditional traits of growth and wood quality, e.g. the Maritime Pine breeding
640 programs in France and Spain, Bouffier et al. 2013), providing an example to follow
641 in other species.

642
643 Modern breeding methods based on genomic selection offer great potential for
644 multipurpose breeding programs. Genomic selection has the potential to accelerate
645 breeding in long-generation species, substantially increasing genetic gains while also
646 providing a flexible framework to incorporate changes in breeding targets. It is
647 already widely used in animal and crop selection but has only recently started to be
648 applied to forest trees in species such as eucalypts. Advances are also being made
649 rapidly towards implementation in conifers and other broadleaves such as poplar
650 (Plomion et al. 2015). By genotyping at regular intervals across the genome with a
651 large number of markers (classically over 10 markers/cM, i.e. over 15,000-30,000
652 markers in forest trees), genomic selection approaches are able to predict phenotypes
653 with variable degrees of accuracy, depending on the effective population size of the
654 base population, linkage disequilibrium, heritability and the genetic architecture of the
655 desired trait (Grattapaglia & Resende 2010).

656
657 There are calls from the research community for breeding programs to consider more
658 seriously genetic resources outside the current very few commercial species, to form
659 links with conservation programs and to address traits and uses that have not yet been
660 considered (Fins et al. 2006). For assisted gene flow and ecological restoration for
661 example, breeding for increased genetic diversity and evolvability alone might be a
662 reasonable goal in itself (Alia & Majada 2013, Lefèvre et al. 2013). Benefits from
663 state-of-the-art selection theory and practice can be down-scaled and used in so called
664 low-input breeding programs. Low-input breeding carries both the ideas of selection
665 towards rusticity and a highly cost-effective selection process in terms of direct
666 benefits to users (Dawson et al. 2008). Low input breeding is based on a breeding
667 cycle that ceases early in the selection process, uses information from both wild
668 populations and common gardens, and relies heavily on molecular markers to
669 delineate meaningful geographic zones, track candidate genes and maintain a high
670 effective population size (Lindgren & Wei 2006, El-Kassaby & Lstiburek 2009). Such
671 breeding strategies represent flexible and viable alternatives to complicated and costly
672 (high-input) breeding programs that are designed for high yield situations (Wang et al.
673 2010).

674
675 *In conclusion, policy-makers should be aware that breeding programs need to adapt*
676 *quickly to the challenges of the 21st century while existing ex situ collections and past*
677 *selection efforts should be rescued and conserved. Whether based on a high or a low*
678 *input strategy, breeding programs should include the assessment of phenotypic traits*
679 *that are likely to be important in conferring genetic adaptation to climate change*
680 *(which may well be found outside usually investigated resources and will require*
681 *well-organized international collaboration). Low-input breeding strategies represent*
682 *an opportunity to do so for species that are traditionally under-represented in*

683 *breeding programs because of their low market value. This may be useful, as in the*
684 *future such species (e.g. Mediterranean trees) may become increasingly important*
685 *under climate change.*

686

687

688 **Challenge 7: What are the socio-economic benefits of genetic conservation and**
689 **breeding under global change scenarios?**

690

691 *In addition to changing perceptions of the importance of genetic resources for better*
692 *coping with increased disturbances, the views of society are also shifting regarding*
693 *the role of genetic resources in meeting the demands for forest goods and services.*
694 *The two main current drivers of this shifting perception are climate change and*
695 *expected future demands by end-users.*

696

697 Future demands by European end-users are anticipated to focus on an increase in
698 renewable energy and materials, both to mitigate climate change and to promote trade
699 and economic growth (Farizo et al. 2014, Soliño et al. 2012). This will be
700 accompanied by a need to produce more product per unit of land area as the demands
701 for urbanization, recreation, nature conservation and food production should reduce
702 the amount of land that is available to forestry. There will be pressure to improve the
703 quality of timber (e.g. by increasing stiffness in solid wood or by lowering the lignin
704 content). According to Vanhanen et al. (2007), the maturing forest product markets in
705 Europe will place pressure on the forest sector to restructure through development and
706 adoption of technical and social innovations. At the same time, the demand for
707 recreation and nature conservation is also increasing, and the desirability of a uniform
708 product (which can be more easily achieved via clonal forestry) for the bio-economy
709 has to be balanced against the need to maintain high levels of biodiversity.

710

711 Forest trees are characterized by a low level of domestication in comparison to other
712 organisms, and consequently, the high levels of intra-specific genetic variation
713 (among and within populations) that most tree species naturally contain has largely
714 been maintained. This variation is essential for the long term adaptability of the tree
715 species themselves as well as the associated species that depend on them. It is also
716 crucial because it serves as the reservoir for breeding resources in the future.
717 However, overall social perceptions of the benefits of biodiversity conservation to
718 forest ecosystem services are usually based on species richness and the importance of
719 intra-specific genetic diversity is generally not accorded the consideration it deserves.
720 This is possibly because genetic diversity is a component of biodiversity that is not
721 easily visible or accessible to most people. Also, the perceived importance of
722 biodiversity varies with the socio-economic environment (Dominguez-Terrero and
723 Soliño, 2011). Intra-specific genetic diversity has an intrinsic economic value which,
724 despite its importance, is unfortunately poorly recognized in economic valuation
725 scenarios (Thorsen & Kjaer 2007). Highly-diverse forests are also better prepared to
726 response to societal demands for new specialized forest products and increased
727 productivity under climate change.

728

729 *In conclusion, increasing the societal perception of the value of genetic diversity in*
730 *managed forest ecosystems should be a priority. New methodological developments in*
731 *forest and landscape genetics could help to assess the socio-economic importance of*
732 *conservation or breeding activities. Raising awareness in forest managers, policy*

733 *makers and conservationists of the essential role of genetic diversity on biodiversity*
734 *dynamics and adaptability of forests to future conditions is urgently needed.*
735 *Improvements in knowledge transfer beyond academia are required.*

736

737

738 **Conclusion**

739

740 Climate change will impact natural forests forcing trees, their keystone species, to
741 move, adapt or disappear locally. Climate change is also likely to alter the health of
742 forest trees worldwide. The speed and extent to which these alterations are likely to
743 occur remain difficult to predict accurately. Ultimately, the decision to adopt one
744 management strategy over another is in the hands of managers and policy makers who
745 should be able to make “no regret” decisions. We have shown that genetic diversity
746 will play a vital role in determining the resilience and adaptability of forest tree
747 populations to climate change whatever the management objectives chosen
748 (production, protection or recreation).. Genetic knowledge will help managers and
749 policy makers make informed, science-based decisions for prioritizing strategies and
750 it is essential that practitioners keep abreast of scientific advances in this field. Of
751 course, much uncertainty remains and we expect that results from common gardens
752 and the rapid advances that are being made in genomics will soon contribute much
753 needed information for critical issues such as assisted migration and assisted gene
754 flow. This developing understanding will also help tree breeders to apply multi-trait
755 selection approaches to produce the most appropriate phenotypes needed under
756 changed climate conditions. Managing forests and other natural landscapes to
757 conserve and sustainably use genetic diversity is a sensible, practical and risk-
758 reducing strategy under uncertain environmental conditions, that can be applied in
759 production, protection and recreation forests alike.

760

761

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