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Evolution-based approach needed for the conservation and silviculture of peripheral forest tree populations

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ABSTRACT:

The fate of peripheral forest tree populations is of particular interest in the context of climate change. These populations may concurrently be those where the most significant evolutionary changes will occur; those most facing increasing extinction risk; the source of migrants for the colonization of new areas at leading edges; or the source of genetic novelty for reinforcing standing genetic variation in various parts of the range. Deciding which strategy to implement for conserving and sustainably using the genetic resources of peripheral forest tree populations is a challenge.

Here, we review the genetic and ecological processes acting on different types of peripheral populations and indicate why these processes may be of general interest for adapting forests and forest management to climate change. We particularly focus on peripheral populations at the rear edge of species distributions where environmental challenges are or will become most acute. We argue that peripheral forest tree populations are "natural laboratories" for resolving priority research questions such as how the complex interaction between demographic processes and natural selection shape local adaptation; and whether genetic adaptation will be sufficient to allow the long-term persistence of species within their current distribution.

Peripheral populations are key assets for adaptive forestry which need specific measures for their preservation. The traditionally opposing views which may exist between conservation planning and sustainable forestry need to be reconciled and harmonized for managing peripheral populations. Based on existing knowledge, we suggest approaches and principles which may be used for the management and conservation of these distinctive and valuable populations, to maintain active genetic and ecological processes that have sustained them over time.

Key words: geographic distribution range; forest tree genetics; ecology; climate change; forest management; conservation.

I.   INTRODUCTION

Geographically peripheral populations have regularly attracted the attention of ecologists and geneticists who have sought to understand processes that limit geographical ranges (Gaston 2009, Kawecki 2008, Lenormand 2002). Because they are found at the edge of distribution areas and may represent ecologically marginal habitats, peripheral populations are "natural laboratories" for understanding how demography and genetic processes such as natural selection shape local adaptation and either prevent or facilitate colonization of new habitats. Whether peripheral populations can evolve depends on complex interactions between gene flow, selection, genetic drift, immigration and intrinsic population growth rate. The relative contribution of each process, depends on local and historic conditions as well as on life-history traits (Abeli et al. 2014, Alberto et al. 2013, Alleaume-Benharira et al. 2006, Benavides et al. 2013, Eckert et al. 2008, Lira-Noriega and Manthey 2014, Peterman et al. 2013, Ursenbacher et al. 2015).

Whereas ecologists and geneticists tend to agree with Lesica and Allendorf (1995) that peripheral populations are valuable for conservation, conservationists and conservation planners often do not put a high value on peripheral populations unless they belong to a species that is itself threatened (e.g. Leppig and White, 2006, Steen and Barrett 2015). Because of their often slower growth, poorer wood quality and lower economic value, peripheral forest tree populations are usually not recognized and managed as valuable forestry assets either (Lindner et al. 2010). This is unfortunate because peripheral populations often contain unique genetic resources, which may ultimately prevent species extinction (Channell and Lomolino 2000, Holliday et al. 2012, Kawecki 2008). This is frequently true at the "rear edge" (*i.e.* the low-latitude limit) of species geographic distributions where populations have often persisted over long periods of geological time and experienced a complex evolutionary history (for Europe, see Hampe and Petit 2005).

The value of peripheral populations is starting to be recognized as global climate change is now being placed at the forefront of many habitat management plans and included in emerging national and international forest adaptation strategies. For example, genetic resources found at low latitude in Europe and around the Mediterranean are currently receiving renewed interest as planting material (forest reproductive material, FRM) for higher latitudes in Europe (Konnert et al. 2015).

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103   The fate of peripheral populations is indeed of particular interest in the context of climate

104   change (Mátyás et al. 2009, Valladarès et al. 2014, Allen et al. 2015). These populations may

105   (i) be where the most significant evolutionary changes will occur within the distribution

106   range, (ii) face increasing extinction risk, or (iii) be the source of migrants for the colonization

107   of new areas at leading edges or (iv) of genetic novelty for reinforcing standing genetic

108   variation throughout the distribution range (Alleaume-Benharira et al. 2006). Deciding which

109   strategy to implement for conserving and sustainably using the genetic resources of peripheral

110   populations is a challenge with substantial future consequences. Additionally, conservation,

111   on the one hand, and, on the other, sustainable use of forest tree species and of their genetic

112   resources are often driven by different societal goals (Fady et al. 2016). Both approaches need

113   to be reconciled and harmonized for managing peripheral populations.

114   Here, we first review the genetic and ecological processes acting on different types of

115   peripheral populations and discuss why these processes may be needed for adapting forests

116   and for forest management under climate change. We particularly focus on peripheral

117   populations at the rear edge of species distributions where environmental changes are or will

118   become most acute. We then discuss and suggest silvicultural and conservation approaches

119   and principles, which may be used for the management of these valuable populations, in order

120   to maintain active the genetic and ecological processes that have sustained them over time.

121   We conclude by highlighting that peripheral populations should be a research priority and

122   their genetic resources protected and used.

123

II.   THE EVOLUTIONARY POTENTIAL OF PERIPHERAL FOREST TREE POPULATIONS AND THEIR VALUE FOR ADAPTING FORESTS TO CLIMATE CHANGE

1.   The evolutionary potential of peripheral populations is driven by unique demographic and genetic processes

129   Peripheral populations can be defined as those at the edge of the geographic distribution

130   of a species (e.g. Channell and Lomolino 2000, Lira-Noriega and Manthey 2014). With

131   climate change shifting many distribution ranges poleward, peripheral populations can be

132   viewed in a dynamic context. At the expanding periphery, "leading edge" populations are

133   typically the result of relatively recent long distance dispersal and demographic expansion and

134   exhibit tolerance to winter cold or late frost. They also contribute to the poleward expansion

135   mostly via long distance dispersal and demographic expansion (Hampe and Petit 2005).

136   Rear edge populations, conversely, are situated at the retreating edge of a poleward

137   shifting range. They are typically small and characterized by long term persistence in suitable

138   but restricted habitats such as those of the glacial cycles of the Pleistocene (e.g. Liepelt et al.

139   2009 for *Abies alba*). It is likely that selection favors local adaptation in rear edge

140   populations, particularly tolerance to drought. Their genetic distinctiveness is high and

141   although their genetic diversity may be rather variable, it has not hampered their persistence

142   and driven them to extinction (Fady and Conord 2010, Hampe and Petit 2005, Petit et al.

143   2003).

144   Demographic and evolutionary processes shape peripheral populations differently

145   compared to populations at the core of the distribution, depending on their situation in the

146   geographic space (Figure 1).

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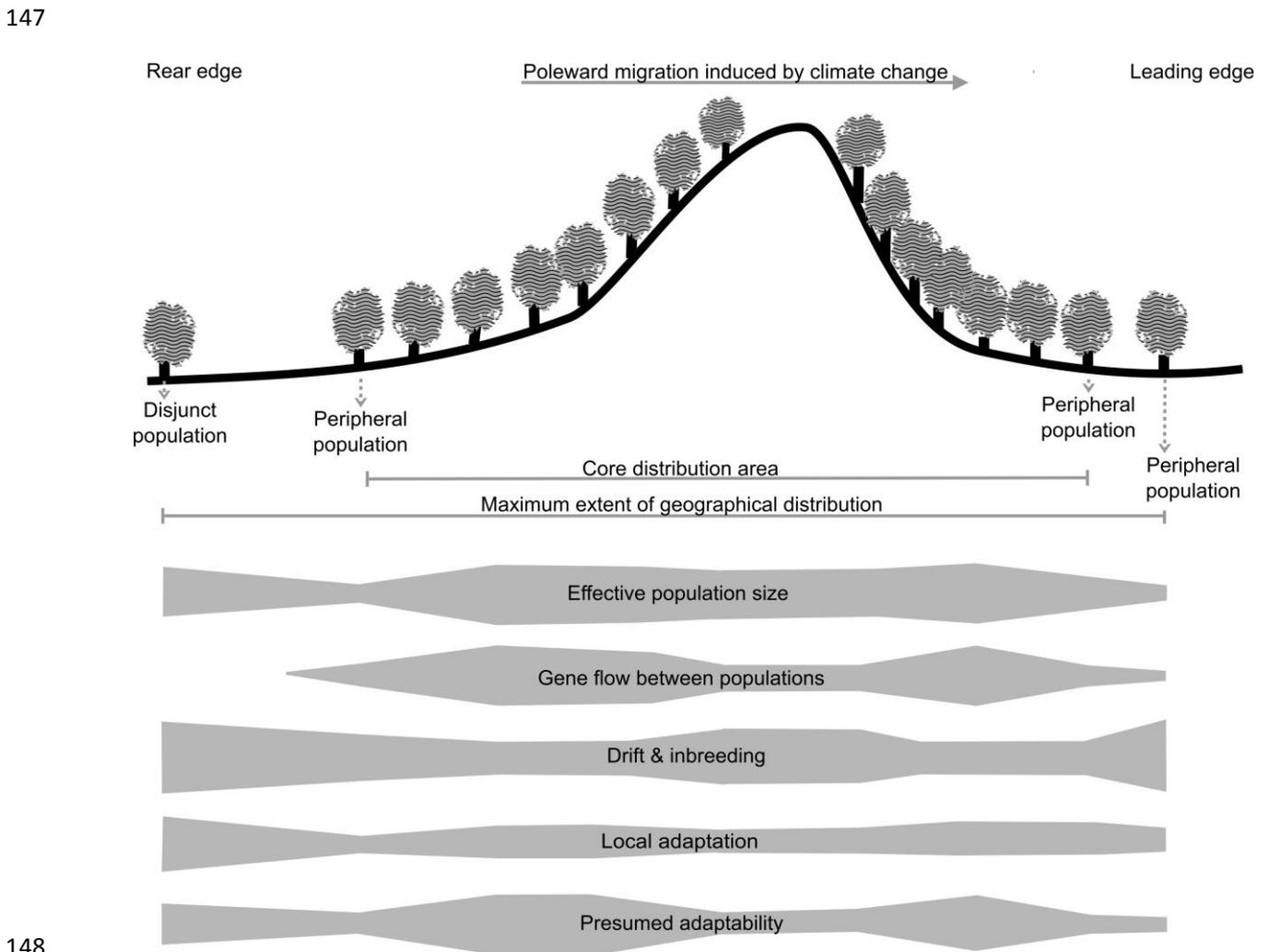
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149   Figure 1. Some demographic and genetic processes affecting populations across their

150   distribution range. Here, the species range is shown as being fragmented and divided into two

5

151 geographic entities, separated by a mountain. Geography can influence genetic and

152 demographic processes in variable ways across the species distribution range, as depicted by

153 the grey shapes (source: Alleaume-Benharira et al. 2006, Hampe and Petit 2005, Ohsawa and

154 Ide 2008).

155

156   Whether leading edge populations are diverse enough to efficiently contribute to

157 colonization will depend on the amount of gene flow from core populations and among

158 leading edge populations (Alleaume-Benharira et al. 2006). Disjunct populations at the

159 leading edge establish via long distance seed dispersal and may suffer from founder effect and

160 reduced fitness because of genetic drift and inbreeding depression due to limited mate

161 availability (Restoux et al. 2008). However, they may have increased adaptation to long

162 distance dispersal (Cwynar and MacDonald 1987). In contrast, non-disjunct leading edge

163 populations connected to core populations or other leading edge populations by moderate

164 levels of gene flow may have increased fitness while the same populations can show reduced

165 fitness under high levels of gene flow (gene swamping, Alleaume-Benharira et al. 2006).

166   Because of their persistence over long periods of geological time in isolated, locally

167 suitable habitats (for example, by shifting their distribution along mountainsides), disjunct

168 rear edge populations receive low levels of potentially maladaptive asymmetric gene flow

169 from core populations. If disjunct rear edge populations can track their local habitat shifts fast

170 enough, their persistence may be assured. Non-disjunct rear edge populations, by contrast,

171 receive significant amounts of maladaptive asymmetric gene flow from core populations,

172 which may hamper their persistence, particularly at low elevation where ecological conditions

173 strongly limit habitat suitability (Borovics and Mátyás 2013, Lenormand 2002). Overall, rear

174 edge peripheral populations are particularly and increasingly at risk under current and

175 predicted global warming conditions (Figure 2).

176

177

178   Figure 2. Beaumont-de-Ventoux in the southeastern French Alps is a rear edge, *Abies alba*

179 (Mill.) population growing under sub-Mediterranean climate conditions between 950 and

180 1550 m above sea level. Evidence of dieback (grey trees) is widespread since the summer heat

181 wave of 2003 (Cailleret et al. 2014). This population demonstrates adaptation to winter

182 drought but not summer drought (Roschanski et al. 2016) and may not be able to track or

183 adapt to its habitat change fast enough, raising concern for its persistence under climate

184 change.

185

186 **2. Peripheral populations are not necessarily evolutionary dead-ends**

187   Whether or not peripheral populations are adaptable to changing conditions remains

188 debatable and evidence from short- or long-lived plant and animal data is often conflicting

189 (Kawecki 2008). The idea that peripheral populations are less genetically diverse than core

190 populations derives from the "abundant center theory" where population size and abundance

191 decreases toward range margins as habitat becomes less suitable (Sagarin and Gaines 2002).

192 However, peripheral habitats are not necessarily sub-optimal and range edges may in fact

193 harbor high quality habitats (Channell and Lomolino 2000, Lira-Noriega and Manthey 2014).

194 In fact, genetic diversity does not systematically decrease from core to periphery (Eckert et al.

195 2008).

7

Few common garden experiments of forest trees actually test peripheral populations and sites. When data are available, peripheral populations demonstrate phenotypic trait values (mean and variance) different from those found in core populations for a limited range of traits usually related to growth (Rehfeldt et al. 2002). Peripheral populations are possibly under much higher selection pressure than others and could thus be well adapted to extreme or fluctuating conditions (Borovics and Mátyás 2013), while their adaptability might be lower than often presumed, possibly because extreme selection pressure can influence plastic responses negatively (Valladarès et al. 2007). Rear edge peripheral populations often display slower growth under more favorable ecological conditions than their native ones. For example, Rehfeldt et al. (2002) and Shutjaev and Giertych (2003) showed that rear edge peripheral populations of Scots pine (*Pinus sylvestris* L.) generally lagged behind core populations in terms of phenotypic plasticity for height growth. Similar results are available for jack pine (*Pinus banksiana* Lamb., Mátyás and Yeatman 1992). At the leading edge, strong selection for resistance to cold and adverse photoperiod may limit the ability of trees to adapt to warming conditions (Savolainen et al. 2011).

Other evidence from both simulation and experimental works demonstrate that the fitness of peripheral populations can remain high in their own environment (Alleaume-Benharira et al. 2006, Ganopoulos et al. 2011, Restoux et al. 2008) as well as in alien environments (Kreyling et al. 2014, Thiel et al. 2013). This is when population size and gene flow levels remain high enough and genetic diversity does not decrease too strongly. Rear edge populations where environmental conditions have remained somewhat stable throughout the Pleistocene provide a good example of high fitness and adaptive potential (Hampe and Petit 2005).

3. Peripheral populations are important for adapting forests to global climate change

Experimental results show the adaptability and phenotypic plasticity of peripheral populations to be variable (see above). However, both niche and process-based modelling approaches including genetic differentiation and plasticity processes demonstrate that peripheral populations (particularly rear edge ones) are important for the persistence of species under climate change (Benito-Garzón et al. 2011, Valladarès et al. 2014; Kramer et al 2010).

227 The increased occurrence of extreme climatic events coupled with high intensity and
228 frequent ecological stress, increases vulnerability and limits adaptive capacity (Davis and
229 Shaw 2001). At the rear edge and at low elevation margins, drought and heat waves
230 interacting with invasive pests and diseases will be major constraining factors (Allen et al.
231 2010). At the leading edge and at high elevation margins, persisting cold events and
232 photoperiod limitations as well as pests and diseases spreading from the core distribution or
233 from lower elevations may remain strong challenges for adaptation and hence slow down
234 colonization of suitable areas (Rehm et al. 2015).

235 Predicting which peripheral populations will be able to resist, survive and evolve under a
236 globally changing climate is a challenge when prioritizing conservation status and adapting
237 management for these populations. For one thing, understanding which biotic and abiotic
238 factors form rear and leading edges is far from trivial (Slaton 2015). Despite some knowledge
239 gaps, many European countries have used ecological and genetic tools (such as provenance
240 tests, niche models, phylogeographic studies) to support such prioritization in forest trees and
241 these efforts need to be continued (Konnert et al. 2015).

242 In the next two sections, principles and examples of management of peripheral forest tree
243 populations are discussed, in view of changing climatic conditions. We discuss silviculture
244 and conservation separately, although in most cases the two are or need to be combined and
245 balanced depending on management priorities.

246

247 II. **SILVICULTURE IN PERIPHERAL POPULATIONS**
248 **1. Principles of management of peripheral populations: maintaining stability and**
249 **increasing resilience**
250 Living organisms are adapted to the disturbance regimes under which they have evolved
251 (Alfaro et al. 2014). Therefore, forest ecosystem management based on an understanding of
252 natural disturbance regimes is a sound silvicultural approach in both core and peripheral
253 populations (Bergeron et al. 1999). However, novel forms of disturbance, or combinations of
254 disturbances, may soon emerge (Allen et al. 2015, Lindenmayer and McCarthy 2002) and
255 seriously impact peripheral more than core forest populations. Part of the solution at least for
256 maintaining peripheral populations and increasing their resilience is a type of silviculture that
257 can simultaneously preserve genetic diversity as a main source of adaptability to disturbance

258 and accelerate genetic adaptation so as for tree populations to track environmental changes

259 locally (evolution-oriented forestry, Lefèvre et al. 2014).

260   Peripheral populations, as well as their genetic resources, need to be identified and their

261 conservation status prioritized in national forest strategies and climate adaptation plans where

262 they could serve as "climate change" *in-situ* conservation units (Kelleher et al. 2015). They

263 need to be recognized as specific management units in forest management plans and identified

264 as high conservation value stands. Maintaining stable, variably structured forest stands, mixed

265 where possible, while supporting and protecting long-term natural regeneration (Sagnard et al.

266 2011), safeguarding healthy, isolated trees either at the fore-front of colonization or at the rear

267 limits, are all desirable goals for peripheral populations. In specific cases, unconventional

268 interventions must be developed to protect the survival of these populations, e.g. partial

269 removal of competing shrubs, or planting a provisory nursing stand. Box 1 provides an

270 example of management practices in central Europe. In the Mediterranean where most rear

271 edge populations of European tree species are located, a fire prevention strategy should also

272 be an integral part of management plans.

273

274 Box 1: Managing high elevation beech (*Fagus sylvatica* L.) populations in central Europe:
275 insights from a close-to-nature silvicultural model that can serve for peripheral forest tree
276 populations.

277

278 Using over 30 year-long regeneration periods with as many seed trees as possible is standard
279 practice at the upper tree limit and on steep slopes in beech forest of the Dinaric region and in
280 the northern Alps in Bavaria. Long-term regeneration periods involving many seed trees are
281 particularly suitable to create mosaic- and uneven-aged structures, increasing genetic diversity
282 and thus the adaptability of the future stand. If necessary because of successive low seed crop
283 years, genetic diversity can be increased by supplementing natural regeneration with stored
284 seeds collected *in-situ*. Removal of trees that have reached harvest size is usually postponed
285 until these trees have regenerated naturally. Regeneration aimed at group structure is small-
286 scaled using an irregular shelterwood method and performed over several cutting periods.
287 This guarantees minimal impact on soils as these populations often grow on steep, erosion-
288 prone slopes. In the Dinaric region, overstory removal is avoided as it negatively influences
289 soil stability and seedling vigor and quantity (Matić et al. 2003). During regeneration, strong
290 measures are taken to avoid overgrowing weeds, soil degradation, forest fires and grazing. At
291 the rear edge of its distribution in the Dinaric Alps, beech becomes ecologically marginal and
292 is found in mixed stands with pedunculate oak (*Quercus robur* L.). There, groups or

293 | individually admixed beech trees are favored to promote fruiting and improve their vitality
294 | (Klepac et al. 1996). Overall, forest management operates at the level of trees and groups of
295 | trees, particularly because securing regeneration is a major concern in these often seriously
296 | degraded populations (Zlatanov 2006).

297

2. Regeneration is a critical process in peripheral populations

At the leading edge of species distributions, low dispersal rate, inbreeding due to small
population size, heavy browsing and unsuitable soils may hamper regeneration and population
establishment and persistence, particularly under climate change. For example, browsing
heavily affects peripheral populations of English yew (*Taxus baccata* L.) at high latitudes,
further reducing the regeneration success of these partially inbred populations (Myking et al.
2009). Management options for facilitating and securing population expansion at the leading
edge include the use of genetically diverse reproductive material, herbivore deterrents and,
potentially, assisted gene flow (Aitken and Whitlock 2013, see below for a discussion on
assisted gene flow).

At the rear edge of species distributions, climate may become increasingly unfavorable
and thus many populations will become ecologically marginal, with drastic consequences for
their survival. Rising temperatures and land use change were found to be responsible, despite
some evidence of an adaptive response, for the gradual extinction over the last half-century of
low elevation, rear edge populations of European beech in the Catalan mountains (Jump et al.
2006, Peñuelas et al. 2007). Rising temperatures will also affect natural regeneration in many
rear edge peripheral populations, possibly leading to complete failure. The negative effect of
climatic extremes on flowering and seed set in populations at the rear edge may become a
serious obstacle. For example, with mean temperatures increasing globally, the dormancy
requirements of many broadleaved tree species may not be met (e.g. Afroze and O'Reilly
2013 for *Sorbus aucuparia*, and Doody and O'Reilly 2011 for *Fraxinus excelsior*), which may
prevent germination as demonstrated for beech (Krawiarz and Szczotka 2008). However,
beyond sporadic reports, there are yet insufficient investigations on this subject.

Management options available to prevent the decline of natural regeneration, the reduction
of genetic diversity and eventually the extirpation of rear edge peripheral populations, depend
on prevailing local ecological conditions and may include: (i) partial removal of herbaceous
species to reduce competition with natural regeneration; (ii) retention of shrubs as facilitators
for provision of shade (Benavides et al. 2013, Castro et al. 2004); (iii) improvement of soil

326 and increased abundance of mycorrhiza (Smith and Read 2008) and (iv) fostering and

327 increasing flowering and seed set (Box 2). In view of declining seed yields, the damage to

328 seed crops caused by foraging game and, in some regions by grazing, should be curtailed.

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330

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331 Box 2: Flowering and seed set at the leading and rear edges of natural distributions

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333 *Leading edge*: Flowering and seed production are annually highly variable in most tree

334 species. However, insufficient flowering and low seed set are of particular concern at the

335 leading edge, for example in Scots pine (*Pinus sylvestris* L.) and birch (*Betula pendula* Roth.).

336 While trees in plantations successfully acclimate to colder conditions, seed production and

337 migration probably limit northward expansion, as several consecutive warm years are needed

338 for successful regeneration. In addition, only a small proportion of trees is responsible for

339 most of the seed production. As experiments in Finland show no clear genetic correlation

340 between flowering, growth and acclimation capacity, the only guideline for management of

341 peripheral birch populations is to favor individuals showing highest capacity for seed

342 production so as to even out seed production, thereby increasing effective population size

343 (Rousi et al. 2011).

344

345 *Rear edge*: In Portugal, rear edge populations of cork oak (*Quercus suber* L.) and holm oak

346 *Quercus ilex* L. / *Q. rotundifolia* Lam.) demonstrate low and highly variable flower and seed

347 production, as well as a declining number of reproductive trees over the years. On suitable

348 sites, with deep soil that can compensate for lack of rainfall, the proportion of fruiting cork

349 oak trees varies between 40-80 % depending on mast year, while on a poor site it varies

350 between 10-20%. Such deep soil stands with reduced drought stress constitute excellent

351 candidates for *in-situ* conservation as well as quality habitats for assisted migration schemes

352 when threatened populations need to be transferred to safer places (*sensu* Richarson et al.

353 2009). In holm oak stands that have been declining for a prolonged period of time, density

354 decreases to less than 15 trees per ha. At such low density and with declining flowering and

355 fruiting, the quantity and genetic diversity of seedlings can be seriously jeopardized (see

356 simulations in Sagnard et al. 2011).

357

3. Peripheral populations: valuable resources as planting material

359 Economic, ecological and/or conservation interests justify active silvicultural intervention

360 in peripheral populations to support their survival and regeneration. The genetic resources of

361 peripheral populations may also be a valuable contribution for securing the stability or

362 resilience of threatened core distribution populations under assisted gene flow schemes (see

363 below). Although still debated, genetic resources of these populations could be directly used

12

as planting material (i.e. forest reproductive material in the European legislation) for enrichment planting and also for tree breeding purposes (Konnert et al. 2015).

Assisted gene flow consists of mixing non-local pre-adapted genotypes into local, potentially threatened populations (Aitken and Whitlock 2013). There are few risks associated with using genotypes from peripheral populations in assisted gene flow schemes: outbreeding depression has rarely been demonstrated in forest trees and, although there is evidence that adaptation to drought is not present in all dry site ecotypes (e.g. for beech, Peuke et al. 2002), several studies have shown that peripheral drought-resistant populations exhibit better drought adaptation than core populations (e.g. for beech, Rose et al. 2009; Ivojević et al. 2012; Robson et al. 2012). Therefore, Thiel et al. (2013) suggest using mixtures of planting material from peripheral drought-adapted populations with local populations, adapted to different environmental factors. Guidelines for using peripheral populations need to be recognized and tested species by species and according to management objectives.

Peripheral populations can thus contribute significantly to facilitating adaptation of more central populations through assisted gene flow. Therefore, the identification of seed stands located at the periphery of distribution areas and the use of their FRM in reforestation when appropriate (i.e. as part of assisted gene flow strategies) and as a source of genetic novelty in breeding and conservation programs should be encouraged. It is worth noting that, for example, the legal framework for the production and marketing of FRM in the European Union (Council Directive 1999/105/EC) does not restrict the commercial use of genetic resources from peripheral populations (Konnert et al. 2015).

IV. CONSERVATION OF THE GENETIC RESOURCES OF PERIPHERAL POPULATIONS

Conserving within-population genetic diversity, i.e. genetic resources, should be the cornerstone of any conservation strategy aiming at ensuring long-term persistence of species and habitats (Laikre 2010). *In-situ* and *ex-situ* conservation are the main strategies used for conserving genetic resources worldwide. Both strategies have been well defined by international regulatory bodies such as the United Nations Convention on Biological Diversity (CBD) and the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA). *In-situ* conservation, traditionally meaning conserving individuals in species' natural environment, builds on the idea that changing environmental conditions are key for evolving new adaptive trait variants in populations while not putting the long-term persistence

396 of the population at risk. Dynamic *in-situ* conservation of forest genetic resources occurs

397 within a natural system in which the evolutionary forces, which give rise to and maintain

398 genetic diversity, are allowed to act and modify allele and gene frequencies (Lefèvre et al.

399 2013).

400   With *ex-situ* conservation, populations and individuals are conserved as copies outside of

401 their natural habitat, in the field, in storage vaults or cryopreserved collections. *Ex-situ*

402 collections are at the root of breeding activities, although they fall short of conserving all

403 genotypes that may be of importance as their primary goal is the selection of a few individuals

404 with desired phenotypes or of known pedigrees. Field collections of individuals allowing

405 spontaneous mating and reproduction (dynamic *ex-situ* conservation; Eriksson et al. 1993)

406 may provide conditions in which evolutionary forces are allowed to act and modify allele and

407 gene frequencies (Lefèvre et al. 2013) and offer an alternative to standard *in-situ* and *ex-situ*

408 strategies.

409

410 | Box 3: Legal aspects linked to the conservation of the genetic resources of peripheral
411 | populations in Europe

412 | In Europe, several legal frameworks and programs deal with the identification and monitoring
413 | of components of biological diversity (as defined by the 1992 Convention on Biological
414 | Diversity) and can be used to support the conservation of peripheral populations.
415 | •   FOREST EUROPE (former Ministerial Conferences on the Protection of Forests in
416 | Europe, MCPFE);
417 | •   The Council Directive Nr. 92/43/EEC on the conservation of natural habitats and of
418 | wild fauna and flora (Habitats Directive);
419 | •   The European Forest Genetic Resources Programme (EUFORGEN).

420 | In particular, the Habitats-Directive and EUFORGEN promote the development and
421 | implementation of dynamic *in-situ* conservation strategies across country borders through
422 | concrete objectives. At the national level, objectives for managing peripheral populations
423 | should be integrated within Forest and Conservation Acts, forest management practices and
424 | silvicultural concepts of each country.

425

**1. Habitat conservation and genetic conservation: not necessarily incompatible
    management targets**

428   Conservation of all levels of diversity, from genes to species and communities, can be

429 implemented simultaneously on the same site if target species for gene conservation are also

430 keystone species in a particular habitat, ensuring similar conservation objectives, and if some

431 level of silviculture or habitat management is allowed (Box 4). Protected habitats must be

432 sufficiently large and include significant landscape heterogeneity to maintain evolutionary

433 processes in different target species (Fady et al. 2016). When this is not the case, specific gene

434 conservation measures, such as *in-situ* conservation units or dynamic *ex-situ* collections, need

435 to be adopted and decoupled from other species conservation measures (Koskela et al. 2013).

436

Box 4: Conserving the genetic resources of cork oak (*Quercus suber* L.) at the rear edge in the Jebel Serj National Park in Tunisia.

In Tunisia, cork oak has seen its range reduced by half over the last 80 years. This reduction is due to different causes, both man-made and natural. Social, climatic and technical constraints are major stumbling blocks to restoration efforts for cork oak forests in Tunisia. Under climate change, drought and pest and disease resistance, such as that found in populations geographically distant from the central cork oak area, offer renewed opportunities for conservation, restoration and breeding.

The peripheral population of Jebel Serj (Siliana), located more than 120 km south of the core area, is an excellent example of successful management. Until 2010, it suffered the same extinction risk as other peripheral populations as it did not benefit from any special protection measures. Following a campaign to raise awareness, forest authorities decided to include this population within the just established Jebel Serj National Park by extending the area of this nature reserve dedicated to the protection of the Montpellier maple (*Acer monspessulanum* L.), another very rare species in Tunisia. This change of status has already improved the visibility of the peripheral population of cork oak of Jebel Serj, has raised conservation awareness among local people and has definitely increased the interest of policymakers. The effectiveness of this conservation measure is well illustrated by the fact that natural regeneration, although absent before 2010, is now beginning to be visible in this population.

456

457   At the rear edge, peripheral populations often harbor a keystone species of interest for

458 habitat conservation (e.g. sub-Mediterranean endemic *Pinus nigra Salzmannii* (Dunal) Franco

459 habitats in southern France). Thus, they may be particularly suited for simultaneous *in-situ*

460 conservation combined with habitat preservation (Fady et al. 2016). However, many of these

461 populations will risk extirpation and may thus become prime candidates for managed

462 relocation ("the intentional movement of biological units from current areas of occupancy to

463 locations where the probability of future persistence is predicted to be higher", Richardson et

464 al. 2009). This form of climate change related *ex-situ* conservation is perfectly compatible

465 with *ex-situ* gene conservation (see below) but the local decline of the target species warrants

466 silvicultural interventions for gene conservation that may be incompatible with some forms of

467 conservation (e.g. in a strict Nature Reserve).

At the leading edge, migrant seeds and pollen may modify the genetic and species composition of local ecosystems and bring about conflicting views between habitat conservation, species conservation and gene conservation strategies. A strategy not prioritizing evolutionary processes would be detrimental to gene conservation (Lefèvre et al. 2014, Fady et al. 2016). The same conflicting views may arise if mortality increases in populations at the core of the geographical range. Whereas high adult tree mortality may be acceptable for dynamic *in-situ* conservation if gene flow is significant (as an efficient way to speed up evolutionary processes, Lefèvre et al. 2014), it might not be so for habitat conservation, recreational activities or species conservation. Guidelines are urgently needed on when and where habitat, species and genetic resource conservation can be compatible and desirable, particularly at range edges.

2. Using genetic planning and monitoring for conservation in peripheral populations

Conservation planners need to recognize the value of peripheral populations of widespread species, not just of rare and endangered ones (Leppig and White 2006, Pressey et al. 2007). Genetic-oriented conservation planning is a process of: (i) recognition of specific targets (delineation of conservation areas), (ii) identification of endangering demographic and genetic processes (iii) instigation of specific measures, for capturing and sustaining a high level of genetic diversity (Paul et al. 2000).

The essence of genetic conservation planning in this context is to avoid extinction of identified and endangered peripheral populations by maintaining their natural reproduction capacity (Koskela et al. 2013). Of specific importance are characteristics of the genetic/reproductive system (first of all mating, dispersal and regeneration features). There are only a few species for which reliable genetic information is available to support the selection of priority populations and to formulate proper measures. In most cases species-level data may serve as proxies: patterns of natural distribution; social status (i.e. stand-forming or scattered), level of threats, tolerance to biotic and abiotic stress, etc. (Graudal et al. 2014).

The maintenance of *in-situ* conservation units needs active management interference, monitoring the results of management and, when these fail, *ex-situ* conservation measures (Figure 3). A decision cascade approach has been suggested as a method of prioritizing and subsequently managing target populations (Kelleher et al. 2015). The decision cascade can include criteria to assess population decline (such as in IUCN 2012) or the risk of genetic depletion (e.g. Potter and Crane 2010), with the subsequent mitigation measures.

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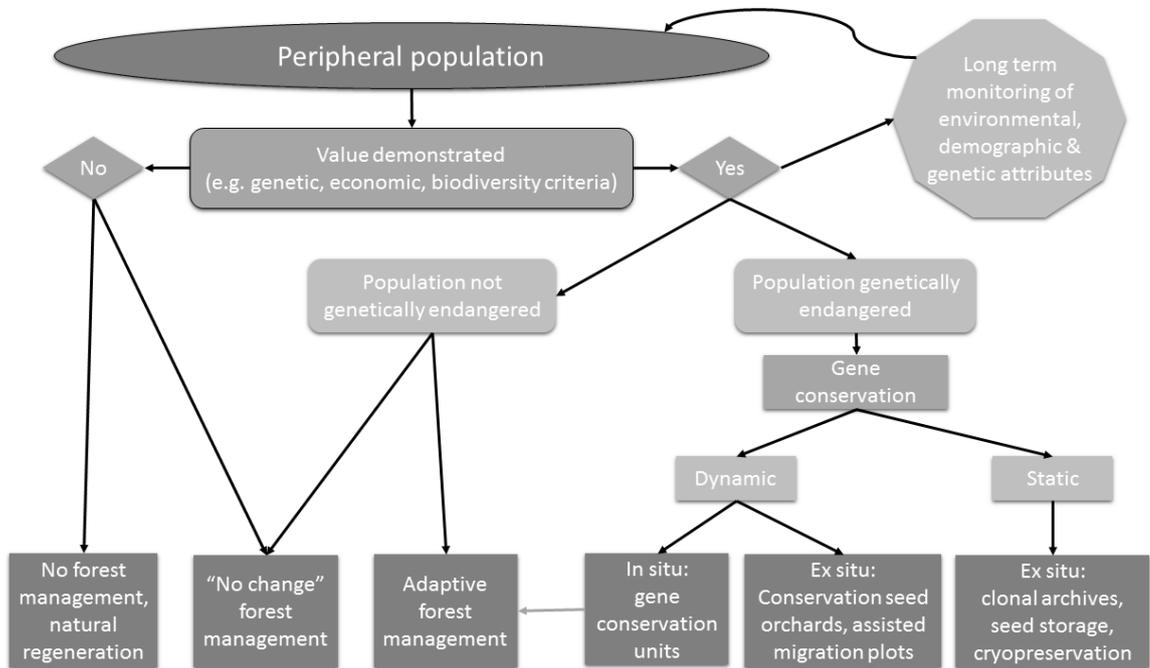
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505   Figure 3. Example of a decision cascade process for selecting genetic conservation actions
506 in peripheral populations. The first step of the process is to identify threats to peripheral
507 populations, i.e. using monitoring, particularly 'target (or focused) monitoring', which is
508 based on existing hypotheses and associated models of system responses to management
509 (adapted from Nichols and Williams 2006).

510

511   Genetic monitoring is an efficient tool to check how peripheral populations are adapting to
512 changes in the environment. It provides an early warning system for supporting management
513 decisions regarding silvicultural practices, securing the stability of peripheral populations and
514 safeguarding an undisrupted supply of FRM (Paul, et al. 2000). An assessment of peripheral
515 populations will enable the identification of the most valuable peripheral populations for
516 production of FRM and for their conservation. Priority should be given to populations
517 showing significant adaptation to specific environmental conditions likely to become more
518 widespread under climate change. At the leading edge, the likelihood that populations can
519 contribute to the colonization of new habitats should be assessed (e.g. growth plasticity,
520 sufficient fecundity, high dispersal). At the rear edge, populations displaying long term

17

521 persistence (Hampe and Petit 2005) or showing growth plasticity and tolerance to drought
522 should be prime candidates.

523   Regular genetic monitoring of ongoing conservation activities (Figure 3) enables the
524 quantification of temporal changes in genetics and dynamics of populations, using appropriate
525 and inexpensive parameters (Frankham 2010, Aravanopoulos 2011). It is based on assessing
526 indicators (genetic diversity, genetic drift, gene flow, selection) stemming from the
527 conceptual framework of the gene-ecological approach, through a set of verifiers (Graudal et
528 al. 2014). Some of these verifiers should be estimated on a regular basis (demographic
529 parameters), while others may be recorded at longer time intervals such as per decade or
530 longer (genetic parameters). This is a species-independent method with a prognostic value
531 applicable to any population of interest in order to enhance the conservation effort
532 (Aravanopoulos 2011). In addition, health conditions, recruitment patterns and environmental
533 parameters of peripheral populations should also be monitored. The intensity of monitoring
534 depends on the features of the genetic/reproductive system of the species, on the actual threats
535 and social interests.

536

537 **3. Deciding when peripheral populations need to be conserved *ex-situ***
538   With habitat quality decline and extinction threats rising worldwide, particularly at rear
539 edges and at low elevations (Hampe and Petit 2005), *in-situ* conservation may no longer be
540 sustainable (Koskela et al. 2013). *Ex-situ* conservation and particularly cryopreservation are
541 increasingly perceived as a necessary complementary system to *in-situ* conservation strategies
542 (Li and Pritchard 2009). However, *ex-situ* collections are typically small-sized populations
543 where genetic diversity is lower than in their *in-situ* counterparts and which cannot undergo
544 adaptation by natural selection. *Ex-situ* conservation is a thus a form of evolutionary dead-end
545 that could be detrimental to peripheral population conservation, particularly in forest trees
546 with very long generation times. (Koskela et al. 2013). *Ex-situ* conservation, therefore, should
547 remain a last resort option to be decided case-by-case, e.g. when specific indicators point to
548 severe extirpation risks (Figure 3) and its dynamic form preferred (Koskela et al. 2013).

549   In some fortunate instances, *ex-situ* conservation efforts may be shared with the aims of
550 forest tree breeding (Yanchuk 2001). A form of dynamic *ex-situ* conservation has long been
551 practiced by forest tree breeders and the archived material may be an irreplaceable element of
552 conservation (e.g. in case of European black poplar, wild cherry and some conifers).

18

553 However, breeders' archives rarely include material from peripheral populations, although,

554 with breeding programs now required to consider climate change, this is starting to change

555 (Fady et al. 2015).

556

V.   CONCLUSIONS AND PERSPECTIVES: PERIPHERAL POPULATIONS - A RESOURCE WORTH PROTECTING AND USING!

559   Geographically peripheral forest tree populations provide multiple ecosystem services,

560 from provisioning, regulating to cultural as well as a habitat for numerous species. Global

561 environmental change, particularly climate change, is increasingly putting peripheral

562 populations at risk. This is particularly true at the rear edge of species geographic distributions

563 where populations have often persisted over long periods of geological time and experienced

564 a complex evolutionary history (for Europe, see Hampe and Petit 2005). Rear edge peripheral

565 populations may contain traits of high potential value for adapting forests and forest

566 management to new environmental conditions, locally as well as range-wide (Holliday et al.

567 2012). Without proper management, this unique and potentially useful genetic diversity is

568 likely to erode under climate change (Mátyás et al. 2009). Comparatively, climate change

569 threats may appear less severe at the leading edges of species distributions where peripheral

570 populations benefit from pre-adapted gene flow to warmer temperatures (Lenormand 2002).

571   Uncertainty in future environmental conditions due to global climate change is a major

572 issue for developing sound, long-term forest management strategies (Lasch et al. 2005,

573 Garcia-Gonzalo et al. 2007, Lefèvre et al. 2014, Lindner et al. 2014). In peripheral

574 populations where environmental and, consequently, demographic and genetic stochasticity is

575 generally high, the stakes are raised even higher. Peripheral populations can be the theatre of

576 large evolutionary change, face increasing extinction risk, be the source of migrants to

577 colonize new areas at expanding margins and constitute a unique reservoir of genetic

578 resources for assisted gene flow. It is our opinion that habitat conservation, gene conservation

579 and forest management strategies, which are often carried out separately, uncoordinatedly, or

580 in conflict with one another (Fady et al. 2016) should be reconciled when dealing with

581 peripheral populations, particularly at the rear edge.

582   Further, we propose that peripheral forest tree populations should be managed under an

583 evolution-oriented forestry (Lefèvre et al. 2014). Under exceptional circumstances, either

584 assisted gene flow or managed relocation should be employed and endorsed by both the

habitat conservation and the forest management communities. Without this option, many rear

edge peripheral populations will face extirpation and their unique genetic resources will be

lost. Their adaptive potential needed to strengthen declining forests elsewhere in their range

will also vanish. Under uncertain climate conditions, peripheral populations, particularly at

the rear edge, have an option value that no forest and habitat manager should want to lose. In

this context, they are key assets for adaptive forestry (i.e. the ability of forestry as a system to

adapt to changes in climate, Lindner et al. 2010) and are recognized as a strategic priority by

the Global Plan of Action for the Conservation, Sustainable Use and Development of Forest

Genetic Resources of the Food and Agriculture Organization of the United Nations (FAO

2014).

We would also like to draw attention to the importance of regular monitoring. Peripheral

populations, including those planted artificially, constitute early warning sentinels for dieback

that should be recognized as outstandingly useful. An inventory of both natural and

planted/naturalized peripheral populations must be a priority, in order to implement

meaningful long-term genetic monitoring.

Whether genetic adaptation will be sufficient to allow the long-term persistence of forest

trees within their current distribution and how changes in biotic interactions will affect this

process, is currently one of the research priorities for forest management and conservation. In

this area of research, peripheral populations (particularly at the rear-edge) are "natural

laboratories" that have a particular role to play. Given the complexity of ecological and

demographic conditions found in peripheral populations, and how they interplay, complex

models that consider demographic, genetic and ecophysiological processes jointly in forest

dynamics are necessary (Kramer et al. 2015, Oddou-Muratorio and Davi 2014).

edited by the first 6 authors in the authorship list, while all other authors contributed ideas and

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responsibility of the final editing of the submitted manuscript.

VII.   REFERENCES

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