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Contact CEH NORA team at
noraceh@ceh.ac.uk

1 Evolution-based approach needed for the conservation and silviculture of peripheral 2 forest tree populations

3 Bruno Fady*(1), Filippos A. Aravanopoulos *(2), Paraskevi Alizoti (2)*, Csaba Mátyás
4 (3)*, Georg von Wühlisch (4)*, Marjana Westergren (5)*, Piero Belletti (6), Branislav
5 Cvjetkovic (7), Fulvio Ducci (8), Gerhard Huber (9), Colin T. Kelleher(10), Abdelhamid
6 Khaldi (11), Magda Bou Dagher Kharrat (12), Hojka Kraigher (5), Koen Kramer (13), Urs
7 Mühlethaler (14), Sanja Peric (15), Annika Perry (16), Matti Rousi (17), Hassan Sbay (18),
8 Srdjan Stojnic (19), Martina Tijardovic (15), Ivaylo Tsvetkov (20), Maria Carolina Varela
9 (21), Giovanni G. Vendramin (22), Tzvetan Zlatanov (23).

10
11 (1) INRA, UR629, Ecologie des forêts méditerranéennes (URFM), Avignon, France (author
12 for correspondence). Tel: +33 (0)43272 2908. E-mail: bruno.fady@avignon.inra.fr.

13 (2) Faculty of Agriculture, Forest Science & Natural Environment, Aristotle University of
14 Thessaloniki, Thessaloniki, Greece

15 (3) University of West Hungary, Inst. of Environmental and Earth Sciences, Sopron, ,
16 Hungary

17 (4) Johann Heinrich von Thünen Institute, Institute of Forest Genetics, Großhansdorf,
18 Germany

19 (5) Slovenian Forestry Institute, Ljubljana, Slovenia

20 (6) University of Torino, DISAFA Agricultural Genetics, Grugliasco, Italy

21 (7) University of Banja Luka, Faculty of Forestry, Banja Luka, Bosnia and Herzegovina

22 (8) CREA SEL, Consiglio per la ricerca in agricoltura e l'analisi dell'economia agraria,
23 Forestry research centre, Arezzo. Italy

24 (9) Bavarian Institute for Forest Seeding and Planting, Teisendorf, Germany

25 (10) DBN Plant Molecular Laboratory, National Botanic Gardens of Ireland, Dublin, Ireland

26 (11) National Research Institute of Rural Engineering, Water and Forests (INRGREF),
27 University of Carthage, Tunis, Tunisia

28 (12) Laboratoire Caractérisation Génomique des Plantes, Faculty of Science, Saint Joseph
29 University, Beirut, Lebanon

30 (13) Alterra – Green World Research, Vegetation, Forest, and Landscape Ecology, and
31 Wageningen University, Wageningen, The Netherlands

32 (14) Burgersriedstrasse 11, Bruegg, Switzerland

33 (15) Croatian Forest Research Institute, Jastrebarsko, Croatia

34 (16) Centre for Ecology and Hydrology, Penicuik, United Kingdom

35 (17) Natural Resources Institute Finland (Luke), Vantaa, Finland

36 (18) Forest Research Centre, Agdal Rabat, Morocco

37 (19) University of Novi Sad, Institute of Lowland Forestry and Environment, Novi Sad, Serbia

38 (20) Forest Research Institute, Sofia, Bulgaria

39 (21) Instituto Nacional de Investigação Agrária e Veterinária, Oeiras, Portugal

40 (22) Institute of Biosciences and Bioresources, National Research Council, Sesto Fiorentino
41 (FI), Italy

42 *: equal contribution

43

44 | **ABSTRACT:**

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

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

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

68

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

71

72 | I. INTRODUCTION

73 Geographically peripheral populations have regularly attracted the attention of ecologists
74 and geneticists who have sought to understand processes that limit geographical ranges
75 (Gaston 2009, Kawecki 2008, Lenormand 2002). Because they are found at the edge of
76 distribution areas and may represent ecologically marginal habitats, peripheral populations are
77 “natural laboratories” for understanding how demography and genetic processes such as
78 natural selection shape local adaptation and either prevent or facilitate colonization of new
79 habitats. Whether peripheral populations can evolve depends on complex interactions between
80 gene flow, selection, genetic drift, immigration and intrinsic population growth rate. The
81 relative contribution of each process, depends on local and historic conditions as well as on
82 life-history traits (Abeli et al. 2014, Alberto et al. 2013, Alleaume-Benharira et al. 2006,
83 Benavides et al. 2013, Eckert et al. 2008, Lira-Noriega and Manthey 2014, Peterman et al.
84 2013, Ursenbacher et al. 2015).

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

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

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

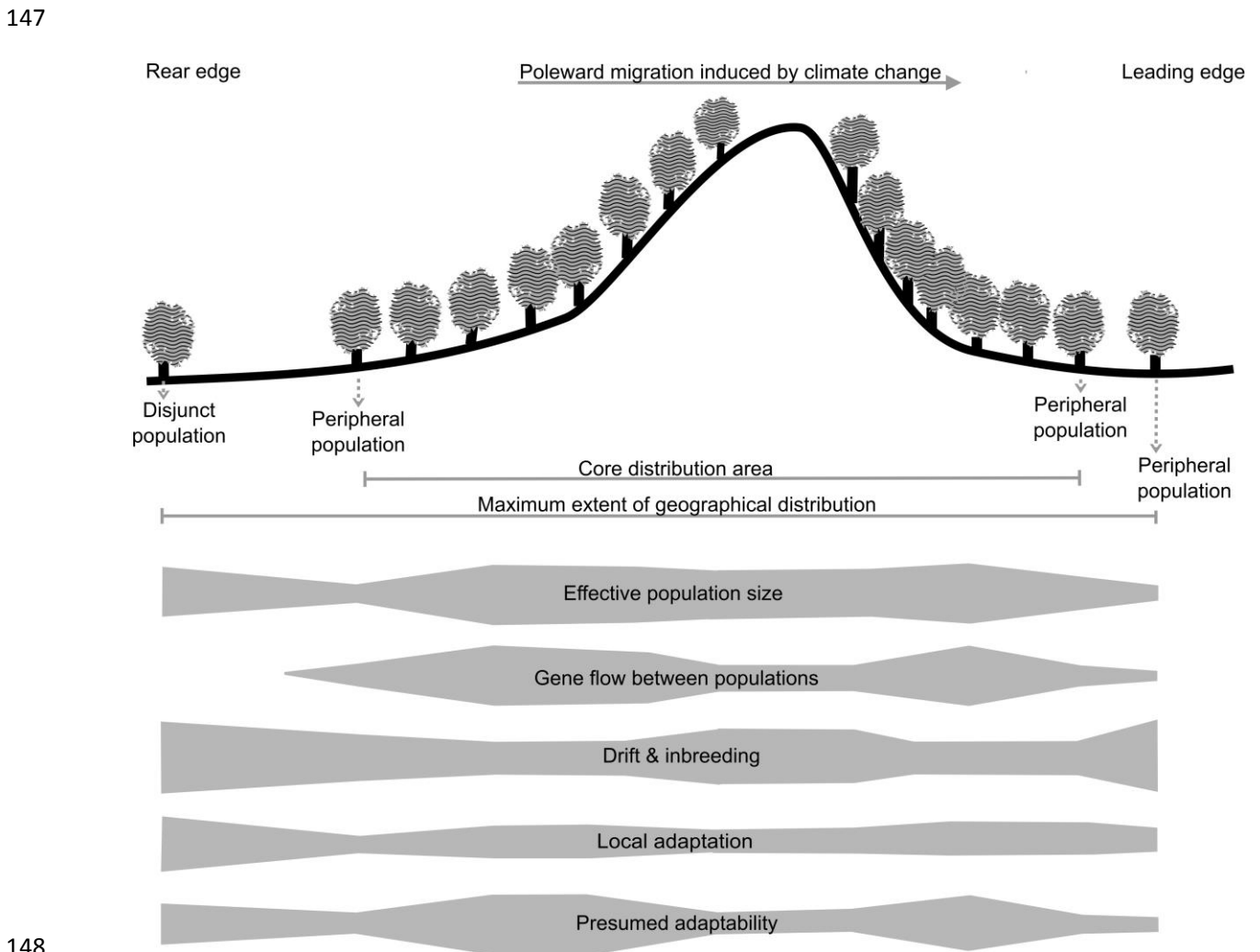
124 **II. THE EVOLUTIONARY POTENTIAL OF PERIPHERAL FOREST TREE** 125 **POPULATIONS AND THEIR VALUE FOR ADAPTING FORESTS TO** 126 **CLIMATE CHANGE**

127 **1. The evolutionary potential of peripheral populations is driven by unique** 128 **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).



148
 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

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).



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).

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

211 Other evidence from both simulation and experimental works demonstrate that the fitness
212 of peripheral populations can remain high in their own environment (Alleaume-Benharira et
213 al. 2006, Ganopoulos et al. 2011, Restoux et al. 2008) as well as in alien environments
214 (Kreyling et al. 2014, Thiel et al. 2013). This is when population size and gene flow levels
215 remain high enough and genetic diversity does not decrease too strongly. Rear edge
216 populations where environmental conditions have remained somewhat stable throughout the
217 Pleistocene provide a good example of high fitness and adaptive potential (Hampe and Petit
218 2005).

219

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

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

298 **2. Regeneration is a critical process in peripheral populations**

299 At the leading edge of species distributions, low dispersal rate, inbreeding due to small
300 population size, heavy browsing and unsuitable soils may hamper regeneration and population
301 establishment and persistence, particularly under climate change. For example, browsing
302 heavily affects peripheral populations of English yew (*Taxus baccata* L.) at high latitudes,
303 further reducing the regeneration success of these partially inbred populations (Myking et al.
304 2009). Management options for facilitating and securing population expansion at the leading
305 edge include the use of genetically diverse reproductive material, herbivore deterrents and,
306 potentially, assisted gene flow (Aitken and Whitlock 2013, see below for a discussion on
307 assisted gene flow).

308 At the rear edge of species distributions, climate may become increasingly unfavorable
309 and thus many populations will become ecologically marginal, with drastic consequences for
310 their survival. Rising temperatures and land use change were found to be responsible, despite
311 some evidence of an adaptive response, for the gradual extinction over the last half-century of
312 low elevation, rear edge populations of European beech in the Catalan mountains (Jump et al.
313 2006, Peñuelas et al. 2007). Rising temperatures will also affect natural regeneration in many
314 rear edge peripheral populations, possibly leading to complete failure. The negative effect of
315 climatic extremes on flowering and seed set in populations at the rear edge may become a
316 serious obstacle. For example, with mean temperatures increasing globally, the dormancy
317 requirements of many broadleaved tree species may not be met (e.g. Afroze and O'Reilly
318 2013 for *Sorbus aucuparia*, and Doody and O'Reilly 2011 for *Fraxinus excelsior*), which may
319 prevent germination as demonstrated for beech (Krawiarz and Szczotka 2008). However,
320 beyond sporadic reports, there are yet insufficient investigations on this subject.

321 Management options available to prevent the decline of natural regeneration, the reduction
322 of genetic diversity and eventually the extirpation of rear edge peripheral populations, depend
323 on prevailing local ecological conditions and may include: (i) partial removal of herbaceous
324 species to reduce competition with natural regeneration; (ii) retention of shrubs as facilitators
325 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.

329

330

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

332

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* Richardson 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

358 **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

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

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

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

385 **IV. CONSERVATION OF THE GENETIC RESOURCES OF PERIPHERAL** 386 **POPULATIONS**

387 Conserving within-population genetic diversity, i.e. genetic resources, should be the
388 cornerstone of any conservation strategy aiming at ensuring long-term persistence of species
389 and habitats (Laikre 2010). *In-situ* and *ex-situ* conservation are the main strategies used for
390 conserving genetic resources worldwide. Both strategies have been well defined by
391 international regulatory bodies such as the United Nations Convention on Biological Diversity
392 (CBD) and the International Treaty on Plant Genetic Resources for Food and Agriculture
393 (ITPGRFA). *In-situ* conservation, traditionally meaning conserving individuals in species'
394 natural environment, builds on the idea that changing environmental conditions are key for
395 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

426 **1. Habitat conservation and genetic conservation: not necessarily incompatible** 427 **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

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

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

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

468 At the leading edge, migrant seeds and pollen may modify the genetic and species
469 composition of local ecosystems and bring about conflicting views between habitat
470 conservation, species conservation and gene conservation strategies. A strategy not
471 prioritizing evolutionary processes would be detrimental to gene conservation (Lefèvre et al.
472 2014, Fady et al. 2016). The same conflicting views may arise if mortality increases in
473 populations at the core of the geographical range. Whereas high adult tree mortality may be
474 acceptable for dynamic *in-situ* conservation if gene flow is significant (as an efficient way to
475 speed up evolutionary processes, Lefèvre et al. 2014), it might not be so for habitat
476 conservation, recreational activities or species conservation. Guidelines are urgently needed
477 on when and where habitat, species and genetic resource conservation can be compatible and
478 desirable, particularly at range edges.

479

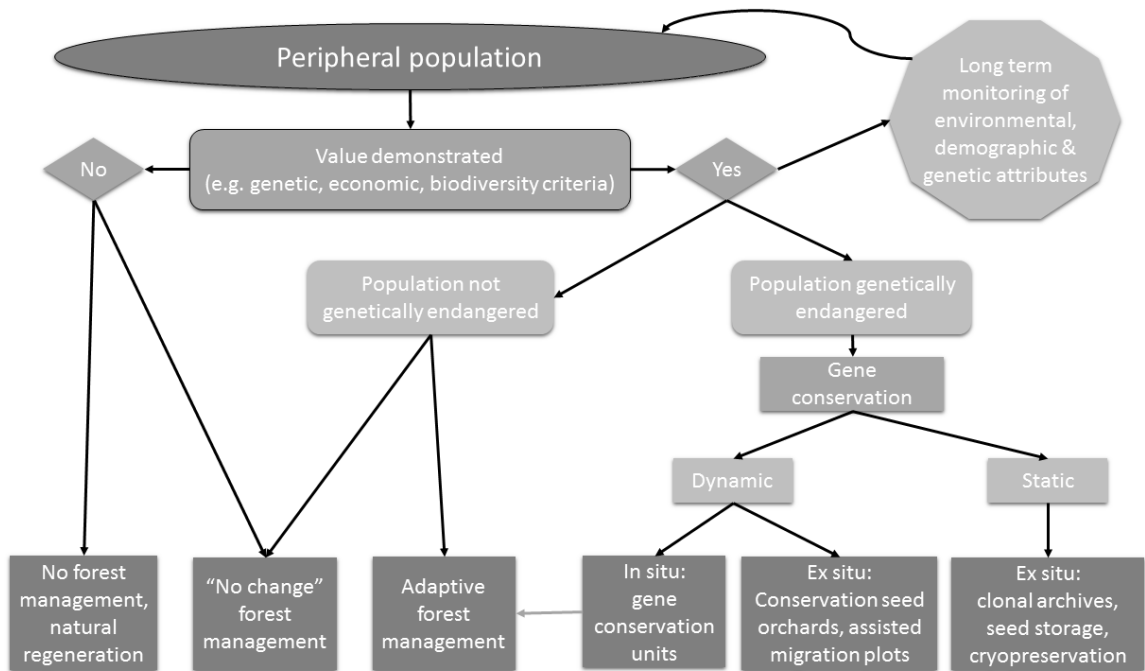
480 **2. Using genetic planning and monitoring for conservation in peripheral populations**

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

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

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

501
502



503
504

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

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 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).

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

557 **V. CONCLUSIONS AND PERSPECTIVES: PERIPHERAL POPULATIONS** 558 **- 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

585 habitat conservation and the forest management communities. Without this option, many rear
586 edge peripheral populations will face extirpation and their unique genetic resources will be
587 lost. Their adaptive potential needed to strengthen declining forests elsewhere in their range
588 will also vanish. Under uncertain climate conditions, peripheral populations, particularly at
589 the rear edge, have an option value that no forest and habitat manager should want to lose. In
590 this context, they are key assets for adaptive forestry (i.e. the ability of forestry as a system to
591 adapt to changes in climate, Lindner et al. 2010) and are recognized as a strategic priority by
592 the Global Plan of Action for the Conservation, Sustainable Use and Development of Forest
593 Genetic Resources of the Food and Agriculture Organization of the United Nations (FAO
594 2014).

595 We would also like to draw attention to the importance of regular monitoring. Peripheral
596 populations, including those planted artificially, constitute early warning sentinels for dieback
597 that should be recognized as outstandingly useful. An inventory of both natural and
598 planted/naturalized peripheral populations must be a priority, in order to implement
599 meaningful long-term genetic monitoring.

600 Whether genetic adaptation will be sufficient to allow the long-term persistence of forest
601 trees within their current distribution and how changes in biotic interactions will affect this
602 process, is currently one of the research priorities for forest management and conservation. In
603 this area of research, peripheral populations (particularly at the rear-edge) are “natural
604 laboratories” that have a particular role to play. Given the complexity of ecological and
605 demographic conditions found in peripheral populations, and how they interplay, complex
606 models that consider demographic, genetic and ecophysiological processes jointly in forest
607 dynamics are necessary (Kramer et al. 2015, Oddou-Muratorio and Davi 2014).

608

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619

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