Article (refereed) - postprint

Fady, Bruno; Aravanopoulos, Filippos A.; Alizoti, Paraskevi; Mátyás, Csaba; von Wühlisch, Georg; Westergren, Marjana; Belletti, Piero; Cvjetkovic, Branislav; Ducci, Fulvio; Huber, Gerhard; Kelleher, Colin T.; Khaldi, Abdelhamid; Kharrat, Magda Bou Dagher; Kraigher, Hojka; Kramer, Koen; Mühlethaler, Urs; Peric, Sanja; Perry, Annika; Rousi, Matti; Sbay, Hassan; Stojnic, Srdjan; Tijardovic, Martina; Tsvetkov, Ivaylo; Varela, Maria Carolina; Vendramin, Giovanni G.; Zlatanov, Tzvetan. 2016. Evolution-based approach needed for the conservation and silviculture of peripheral forest tree populations. *Forest Ecology and Management*, 375. 66-75. 10.1016/j.foreco.2016.05.015

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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, Holiday 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).
The fate of peripheral populations is indeed of particular interest in the context of climate change (Mátyás et al. 2009, Valladarès et al. 2014, Allen et al. 2015). These populations may (i) be where the most significant evolutionary changes will occur within the distribution range, (ii) face increasing extinction risk, or (iii) be the source of migrants for the colonization of new areas at leading edges or (iv) of genetic novelty for reinforcing standing genetic variation throughout the distribution range (Alleaume-Benharira et al. 2006). Deciding which strategy to implement for conserving and sustainably using the genetic resources of peripheral populations is a challenge with substantial future consequences. Additionally, conservation, on the one hand, and, on the other, sustainable use of forest tree species and of their genetic resources are often driven by different societal goals (Fady et al. 2016). Both approaches need to be reconciled and harmonized for managing peripheral populations.

Here, we first review the genetic and ecological processes acting on different types of peripheral populations and discuss why these processes may be needed for adapting forests and for forest management under climate change. We particularly focus on peripheral populations at the rear edge of species distributions where environmental changes are or will become most acute. We then discuss and suggest silvicultural and conservation approaches and principles, which may be used for the management of these valuable populations, in order to maintain active the genetic and ecological processes that have sustained them over time.

We conclude by highlighting that peripheral populations should be a research priority and their genetic resources protected and used.

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

Peripheral populations can be defined as those at the edge of the geographic distribution of a species (e.g. Channell and Lomolino 2000, Lira-Noriega and Manthey 2014). With climate change shifting many distribution ranges poleward, peripheral populations can be viewed in a dynamic context. At the expanding periphery, “leading edge” populations are typically the result of relatively recent long distance dispersal and demographic expansion and exhibit tolerance to winter cold or late frost. They also contribute to the poleward expansion mostly via long distance dispersal and demographic expansion (Hampe and Petit 2005).
Rear edge populations, conversely, are situated at the retreating edge of a poleward shifting range. They are typically small and characterized by long term persistence in suitable but restricted habitats such as those of the glacial cycles of the Pleistocene (e.g. Liepelt et al. 2009 for *Abies alba*). It is likely that selection favors local adaptation in rear edge populations, particularly tolerance to drought. Their genetic distinctiveness is high and although their genetic diversity may be rather variable, it has not hampered their persistence and driven them to extinction (Fady and Conord 2010, Hampe and Petit 2005, Petit et al. 2003).

Demographic and evolutionary processes shape peripheral populations differently compared to populations at the core of the distribution, depending on their situation in the geographic space (Figure 1).

![Diagram of demographic and genetic processes affecting populations across their distribution range. Here, the species range is shown as being fragmented and divided into two](image-url)
geographic entities, separated by a mountain. Geography can influence genetic and demographic processes in variable ways across the species distribution range, as depicted by the grey shapes (source: Alleaume-Benharira et al. 2006, Hampe and Petit 2005, Ohsawa and Ide 2008).

Whether leading edge populations are diverse enough to efficiently contribute to colonization will depend on the amount of gene flow from core populations and among leading edge populations (Alleaume-Benharira et al. 2006). Disjunct populations at the leading edge establish via long distance seed dispersal and may suffer from founder effect and reduced fitness because of genetic drift and inbreeding depression due to limited mate availability (Restoux et al. 2008). However, they may have increased adaptation to long distance dispersal (Cwynar and MacDonald 1987). In contrast, non-disjunct leading edge populations connected to core populations or other leading edge populations by moderate levels of gene flow may have increased fitness while the same populations can show reduced fitness under high levels of gene flow (gene swamping, Alleaume-Benharira et al. 2006).

Because of their persistence over long periods of geological time in isolated, locally suitable habitats (for example, by shifting their distribution along mountainsides), disjunct rear edge populations receive low levels of potentially maladaptive asymmetric gene flow from core populations. If disjunct rear edge populations can track their local habitat shifts fast enough, their persistence may be assured. Non-disjunct rear edge populations, by contrast, receive significant amounts of maladaptive asymmetric gene flow from core populations, which may hamper their persistence, particularly at low elevation where ecological conditions strongly limit habitat suitability (Borovics and Mátys 2013, Lenormand 2002). Overall, rear edge peripheral populations are particularly and increasingly at risk under current and predicted global warming conditions (Figure 2).
Figure 2. Beaumont-de-Ventoux in the southeastern French Alps is a rear edge, *Abies alba* (Mill.) population growing under sub-Mediterranean climate conditions between 950 and 1550 m above sea level. Evidence of dieback (grey trees) is widespread since the summer heat wave of 2003 (Cailleret et al. 2014). This population demonstrates adaptation to winter drought but not summer drought (Roschanski et al. 2016) and may not be able to track or adapt to its habitat change fast enough, raising concern for its persistence under climate change.

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

Whether or not peripheral populations are adaptable to changing conditions remains debatable and evidence from short- or long-lived plant and animal data is often conflicting (Kawecki 2008). The idea that peripheral populations are less genetically diverse than core populations derives from the “abundant center theory” where population size and abundance decreases toward range margins as habitat becomes less suitable (Sagarin and Gaines 2002). However, peripheral habitats are not necessarily sub-optimal and range edges may in fact harbor high quality habitats (Channell and Lomolino 2000, Lira-Noriega and Manthey 2014). In fact, genetic diversity does not systematically decrease from core to periphery (Eckert et al. 2008).
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).
The increased occurrence of extreme climatic events coupled with high intensity and frequent ecological stress, increases vulnerability and limits adaptive capacity (Davis and Shaw 2001). At the rear edge and at low elevation margins, drought and heat waves interacting with invasive pests and diseases will be major constraining factors (Allen et al. 2010). At the leading edge and at high elevation margins, persisting cold events and photoperiod limitations as well as pests and diseases spreading from the core distribution or from lower elevations may remain strong challenges for adaptation and hence slow down colonization of suitable areas (Rehm et al. 2015).

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

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

III. SILVICULTURE IN PERIPHERAL POPULATIONS

1. Principles of management of peripheral populations: maintaining stability and increasing resilience

Living organisms are adapted to the disturbance regimes under which they have evolved (Alfaro et al. 2014). Therefore, forest ecosystem management based on an understanding of natural disturbance regimes is a sound silvicultural approach in both core and peripheral populations (Bergeron et al. 1999). However, novel forms of disturbance, or combinations of disturbances, may soon emerge (Allen et al. 2015, Lindenmayer and McCarthy 2002) and seriously impact peripheral more than core forest populations. Part of the solution at least for maintaining peripheral populations and increasing their resilience is a type of silviculture that can simultaneously preserve genetic diversity as a main source of adaptability to disturbance
and accelerate genetic adaptation so as for tree populations to track environmental changes locally (evolution-oriented forestry, Lefèvre et al. 2014).

Peripheral populations, as well as their genetic resources, need to be identified and their conservation status prioritized in national forest strategies and climate adaptation plans where they could serve as “climate change” in-situ conservation units (Kelleher et al. 2015). They need to be recognized as specific management units in forest management plans and identified as high conservation value stands. Maintaining stable, variably structured forest stands, mixed where possible, while supporting and protecting long-term natural regeneration (Sagnard et al. 2011), safeguarding healthy, isolated trees either at the fore-front of colonization or at the rear limits, are all desirable goals for peripheral populations. In specific cases, unconventional interventions must be developed to protect the survival of these populations, e.g. partial removal of competing shrubs, or planting a provisory nursing stand. Box 1 provides an example of management practices in central Europe. In the Mediterranean where most rear edge populations of European tree species are located, a fire prevention strategy should also be an integral part of management plans.

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

Using over 30 year-long regeneration periods with as many seed trees as possible is standard practice at the upper tree limit and on steep slopes in beech forest of the Dinaric region and in the northern Alps in Bavaria. Long-term regeneration periods involving many seed trees are particularly suitable to create mosaic- and uneven-aged structures, increasing genetic diversity and thus the adaptability of the future stand. If necessary because of successive low seed crop years, genetic diversity can be increased by supplementing natural regeneration with stored seeds collected in-situ. Removal of trees that have reached harvest size is usually postponed until these trees have regenerated naturally. Regeneration aimed at group structure is small-scaled using an irregular shelterwood method and performed over several cutting periods. This guarantees minimal impact on soils as these populations often grow on steep, erosion-prone slopes. In the Dinaric region, overstory removal is avoided as it negatively influences soil stability and seedling vigor and quantity (Matić et al. 2003). During regeneration, strong measures are taken to avoid overgrowing weeds, soil degradation, forest fires and grazing. At the rear edge of its distribution in the Dinaric Alps, beech becomes ecologically marginal and is found in mixed stands with pedunculate oak (*Quercus robur* L.). There, groups or
individually admixed beech trees are favored to promote fruiting and improve their vitality (Klepac et al. 1996). Overall, forest management operates at the level of trees and groups of trees, particularly because securing regeneration is a major concern in these often seriously degraded populations (Zlatanov 2006).

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
and increased abundance of mycorrhiza (Smith and Read 2008) and (iv) fostering and increasing flowering and seed set (Box 2). In view of declining seed yields, the damage to seed crops caused by foraging game and, in some regions by grazing, should be curtailed.

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

**Leading edge:** Flowering and seed production are annually highly variable in most tree species. However, insufficient flowering and low seed set are of particular concern at the leading edge, for example in Scots pine (*Pinus sylvestris* L.) and birch (*Betula pendula* Roth.). While trees in plantations successfully acclimate to colder conditions, seed production and migration probably limit northward expansion, as several consecutive warm years are needed for successful regeneration. In addition, only a small proportion of trees is responsible for most of the seed production. As experiments in Finland show no clear genetic correlation between flowering, growth and acclimation capacity, the only guideline for management of peripheral birch populations is to favor individuals showing highest capacity for seed production so as to even out seed production, thereby increasing effective population size (Rousi et al. 2011).

**Rear edge:** In Portugal, rear edge populations of cork oak (*Quercus suber* L.) and holm oak (*Quercus ilex* L. / *Q. rotundifolia* Lam.) demonstrate low and highly variable flower and seed production, as well as a declining number of reproductive trees over the years. On suitable sites, with deep soil that can compensate for lack of rainfall, the proportion of fruiting cork oak trees varies between 40-80% depending on mast year, while on a poor site it varies between 10-20%. Such deep soil stands with reduced drought stress constitute excellent candidates for in-situ conservation as well as quality habitats for assisted migration schemes when threatened populations need to be transferred to safer places (sensu Richardson et al. 2009). In holm oak stands that have been declining for a prolonged period of time, density decreases to less than 15 trees per ha. At such low density and with declining flowering and fruiting, the quantity and genetic diversity of seedlings can be seriously jeopardized (see simulations in Sagnard et al. 2011).

3. **Peripheral populations: valuable resources as planting material**

   Economic, ecological and/or conservation interests justify active silvicultural intervention in peripheral populations to support their survival and regeneration. The genetic resources of peripheral populations may also be a valuable contribution for securing the stability or resilience of threatened core distribution populations under assisted gene flow schemes (see below). Although still debated, genetic resources of these populations could be directly used
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
of the population at risk. Dynamic in-situ conservation of forest genetic resources occurs within a natural system in which the evolutionary forces, which give rise to and maintain genetic diversity, are allowed to act and modify allele and gene frequencies (Lefèvre et al. 2013).

With ex-situ conservation, populations and individuals are conserved as copies outside of their natural habitat, in the field, in storage vaults or cryopreserved collections. Ex-situ collections are at the root of breeding activities, although they fall short of conserving all genotypes that may be of importance as their primary goal is the selection of a few individuals with desired phenotypes or of known pedigrees. Field collections of individuals allowing spontaneous mating and reproduction (dynamic ex-situ conservation; Eriksson et al. 1993) may provide conditions in which evolutionary forces are allowed to act and modify allele and gene frequencies (Lefèvre et al. 2013) and offer an alternative to standard in-situ and ex-situ strategies.

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

In Europe, several legal frameworks and programs deal with the identification and monitoring of components of biological diversity (as defined by the 1992 Convention on Biological Diversity) and can be used to support the conservation of peripheral populations.

• FOREST EUROPE (former Ministerial Conferences on the Protection of Forests in Europe, MCPFE);
• The Council Directive Nr. 92/43/EEC on the conservation of natural habitats and of wild fauna and flora (Habitats Directive);
• The European Forest Genetic Resources Programme (EUFORGEN).

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

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

Conservation of all levels of diversity, from genes to species and communities, can be implemented simultaneously on the same site if target species for gene conservation are also keystone species in a particular habitat, ensuring similar conservation objectives, and if some level of silviculture or habitat management is allowed (Box 4). Protected habitats must be
sufficiently large and include significant landscape heterogeneity to maintain evolutionary
processes in different target species (Fady et al. 2016). When this is not the case, specific gene
conservation measures, such as in-situ conservation units or dynamic ex-situ collections, need
to be adopted and decoupled from other species conservation measures (Koskela et al. 2013).

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.

At the rear edge, peripheral populations often harbor a keystone species of interest for
habitat conservation (e.g. sub-Mediterranean endemic *Pinus nigra Salzmannii* (Dunal) Franco
habitats in southern France). Thus, they may be particularly suited for simultaneous in-situ
conservation combined with habitat preservation (Fady et al. 2016). However, many of these
populations will risk extirpation and may thus become prime candidates for managed
relocation (“the intentional movement of biological units from current areas of occupancy to
locations where the probability of future persistence is predicted to be higher”, Richardson et
al. 2009). This form of climate change related ex-situ conservation is perfectly compatible
with ex-situ gene conservation (see below) but the local decline of the target species warrants
silvicultural interventions for gene conservation that may be incompatible with some forms of
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.
Figure 3. Example of a decision cascade process for selecting genetic conservation actions in peripheral populations. The first step of the process is to identify threats to peripheral populations, i.e. using monitoring, particularly ‘target (or focused) monitoring’, which is based on existing hypotheses and associated models of system responses to management (adapted from Nichols and Williams 2006).

Genetic monitoring is an efficient tool to check how peripheral populations are adapting to changes in the environment. It provides an early warning system for supporting management decisions regarding silvicultural practices, securing the stability of peripheral populations and safeguarding an undisrupted supply of FRM (Paul, et al. 2000). An assessment of peripheral populations will enable the identification of the most valuable peripheral populations for production of FRM and for their conservation. Priority should be given to populations showing significant adaptation to specific environmental conditions likely to become more widespread under climate change. At the leading edge, the likelihood that populations can contribute to the colonization of new habitats should be assessed (e.g. growth plasticity, sufficient fecundity, high dispersal). At the rear edge, populations displaying long term
persistence (Hampe and Petit 2005) or showing growth plasticity and tolerance to drought should be prime candidates.

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

3. Deciding when peripheral populations need to be conserved ex-situ

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

In some fortunate instances, ex-situ conservation efforts may be shared with the aims of forest tree breeding (Yanchuk 2001). A form of dynamic ex-situ conservation has long been practiced by forest tree breeders and the archived material may be an irreplaceable element of conservation (e.g. in case of European black poplar, wild cherry and some conifers).
However, breeders’ archives rarely include material from peripheral populations, although, with breeding programs now required to consider climate change, this is starting to change (Fady et al. 2015).

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

Geographically peripheral forest tree populations provide multiple ecosystem services, from provisioning, regulating to cultural as well as a habitat for numerous species. Global environmental change, particularly climate change, is increasingly putting peripheral populations at risk. This is particularly true at the rear edge 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). Rear edge peripheral populations may contain traits of high potential value for adapting forests and forest management to new environmental conditions, locally as well as range-wide (Holliday et al. 2012). Without proper management, this unique and potentially useful genetic diversity is likely to erode under climate change (Mátyás et al. 2009). Comparatively, climate change threats may appear less severe at the leading edges of species distributions where peripheral populations benefit from pre-adapted gene flow to warmer temperatures (Lenormand 2002).

Uncertainty in future environmental conditions due to global climate change is a major issue for developing sound, long-term forest management strategies (Lasch et al. 2005, Garcia-Gonzalo et al. 2007, Lefèvre et al. 2014, Lindner et al. 2014). In peripheral populations where environmental and, consequently, demographic and genetic stochasticity is generally high, the stakes are raised even higher. Peripheral populations can be the theatre of large evolutionary change, face increasing extinction risk, be the source of migrants to colonize new areas at expanding margins and constitute a unique reservoir of genetic resources for assisted gene flow. It is our opinion that habitat conservation, gene conservation and forest management strategies, which are often carried out separately, uncoordinatedly, or in conflict with one another (Fady et al. 2016) should be reconciled when dealing with peripheral populations, particularly at the rear edge.

Further, we propose that peripheral forest tree populations should be managed under an evolution-oriented forestry (Lefèvre et al. 2014). Under exceptional circumstances, either 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
dge 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).

VI. ACKNOWLEDGEMENTS

We wish to thank COST Action FP1202 “Strengthening conservation: a key issue for
adaptation of marginal/peripheral populations of forest trees to climate change in Europe
(MaP-FGR)” for financial support and the members of its management committee for very
constructive comments while the manuscript was being drafted. BF also acknowledges the
financial support of projects AMTools (ANR-11-AGRO-005-04) and ERA-NET BiodivERsA
2011-2012 “TipTree” (ANR-12-EBID-0003). The manuscript was collectively written and
edited by the first 6 authors in the authorship list, while all other authors contributed ideas and
text. All authors read and approved the final version of the manuscript. BF took the
responsibility of the final editing of the submitted manuscript.

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