IRIS AperTO

UNIVERSITÀ DEGLI STUDI DI TORINO

AperTO - Archivio Istituzionale Open Access dell'Università di Torino

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

This is a pre print version of the following article:

Original Citation:

Availability:

This version is available http://hdl.handle.net/2318/1562487 since 2017-05-23T14:19:48Z

Published version:

DOI:doi:10.1016/j.foreco.2016.05.015

Terms of use:

Open Access

Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)

12 October 2024

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

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

(1) INRA, UR629, Ecologie des forêts méditerranéennes (URFM), Avignon, France (author for correspondence)

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

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

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

(5) Slovenian Forestry Institute, Ljubljana, Slovenia

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

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

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

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

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

(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 Kindom

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 Agraria 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 marginal and peripheral forest tree populations is of particular interest in the

46 context of climate change. These populations may concurrently be those where the most

47 significant evolutionary changes will occur; those most facing increasing extinction risk; the

48 source of migrants for the colonization of new areas at leading edges; or the source of genetic

49 novelty for reinforcing standing genetic variation in various parts of the range. Deciding

50 which strategy to implement for conserving and sustainably using the genetic resources of

51 marginal and peripheral forest tree populations is a challenge. Here, we review the genetic

52 and ecological processes acting on different types of marginal and peripheral populations and

53 indicate why these processes may be of general interest for adapting forests and forest

54 management to climate change. We particularly focus on marginal and peripheral populations

at the rear edge of species distributions and at ecological margins therein, where environmental challenges are or will become most acute. We argue that marginal and peripheral forest tree populations are natural laboratories for resolving priority research questions such as how the complex interaction between gene flow, selection, genetic drift, immigration and intrinsic population growth rate shape local adaptation and whether genetic adaptation will be sufficient to allow the long-term persistence of species within their current distribution. Simultaneously, they are key assets for adaptive forestry which need specific measures for their preservation. We suggest approaches and principles which may be used for the management and conservation of these unusual yet valuable populations, in order to maintain active genetic and ecological processes that have sustained them over time. The traditionally opposing views of conservation planning and sustainable forestry need to be reconciled and harmonized for managing marginal and peripheral populations.

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

I. INTRODUCTION

Ecologically marginal and geographically peripheral forest tree populations are at risk, now more than ever. Global environmental change, particularly climate change, challenges the sustainability of these potentially useful populations that also often carry a societal, ethical or recreational value. This is especially 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). There, marginal and 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). Because of local adaptation effects, valuable resources may also be found at ecological margins within the core of species distribution areas, for example at low

elevation along mountain slopes. Without proper management, severe erosion of this unique and potentially useful genetic diversity is likely to occur under climate change (Mátyás et al. 2009). Comparatively, threats may appear less severe at the leading edges of species distributions where marginal and peripheral populations may benefit from gene flow from pre-adapted populations that will replenish their potentially low genetic diversity during migration (Lenormand 2002).

Foresters have often planted economically valuable tree species outside of the natural distribution range at low-latitude or low elevation sites, thereby creating artificial margins. In Europe, these include Scots pine (Pinus sylvestris), black pine (Pinus nigra), silver fir (Abies alba), chestnut (Castanea sativa), wild cherry (Prunus avium), sessile oak (Quercus petraea) and especially Norway spruce (Picea abies). Many of these forests, which have naturalized and expanded (e.g. Pinus nigra in the Apennines in Italy, Piermattei et al. 2012), are today challenged by changing climate and land uses.

Marginal and 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). Marginal and peripheral populations are natural laboratories for understanding how demography and selection shape local adaptation and prevent or facilitate colonization of new habitats. Whether marginal and peripheral populations are evolutionary “dead-ends” or “hot-spots” depends on complex interaction between gene flow, selection, genetic drift, immigration and intrinsic population growth rate. The relative contribution of each depends on local and historic conditions as well as on life history traits (Abeli et al. 104 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 marginal and peripheral populations are valuable for conservation, conservationists and conservation planning often do not put a high value on marginal and peripheral populations unless they belong to species that are themselves threatened (e.g. Leppig and White, 2006,

Steen and Barrett 2015). Because of their often slower growth, poorer wood quality and lower economic value, marginal and peripheral forest populations are usually not recognized and managed as valuable forestry assets either (Lindner et al. 2010). This is unfortunate because marginal and peripheral populations can constitute climate warming refugia and ultimately may prevent species to go extinct altogether (Channell and Lomolino 2000). Also, marginal and peripheral populations may likely contain unique genetic resources (Kawecki 2008), useful in a range of natural and management settings.

The recognition of the value of marginal and peripheral populations is, however, starting to change as global change is now being placed at the forefront of many habitat management plans, while national and international forest adaptation strategies are emerging. For example, genetic resources found at low latitude in Europe and around the Mediterranean are currently receiving renewed interest as forest reproductive material in Europe (Konnert et al. 2015). The fate of marginal and peripheral populations is of particular interest in the context of climate change (Mátyás et al. 2009, Valladarès et al. 2014, Allen et al. 2015). These populations may (a) be the place where the most significant evolutionary change will occur, (b) face increasing extinction risk, or (c) be the source of migrants for the colonization of new areas at leading edges or for reinforcing standing genetic variation in various parts of the range (Alleaume-Benharira et al. 2006). Deciding which strategy to implement for conserving and sustainably using the genetic resources of marginal and peripheral populations is a challenge. 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. Opposing views need to be reconciled and harmonized for managing marginal and peripheral populations.

Here, we review the genetic and ecological processes acting on different types of marginal and peripheral populations and indicate why these processes may be of general interest for adapting forests and forest management to climate c hange. We particularly focus on marginal and peripheral populations at the rear edge of species distributions and at ecological margins therein, where environmental challenges are or will become most acute. We suggest

approaches and principles which may be used for the management and conservation of these unusual yet valuable populations, in order to maintain active genetic and ecological processes that have sustained them over time.

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

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

We make a distinction between marginal and peripheral populations because they arise as a result of different demographic and evolutionary processes and thus, may need to be managed differently. Peripheral populations are those furthest away from the core geographic distribution of a species. The periphery (i.e. edge) of a distribution area is often classified as either a leading (or expanding, or colonizing) or a rear (or trailing) edge, based on Holocene post-glacial migration history. Leading edge populations are situated at the front of presently expanding or advancing distribution areas (e.g. for temperate forests, at high latitudes and altitudes). At the leading edge, the standing genetic variation of marginal and peripheral populations may be currently too low to contribute efficiently to colonization unless there is significant gene flow from core populations.

Rear edge populations, conversely, are situated at the retreating front of a shifting range (e.g. in the Mediterranean region, Hampe and Petit 2005). Isolated populations not connected by gene flow to the core of the distribution area qualify as disjunct irrespective of their situation at the leading or the rear edge.

Ecological margins can be present throughout the geographic range and appear when the species reaches the limits of its ecological niche, thus forming marginal populations. The habitat of species is sub-optimal at ecological margins (Kawecki 2008).

167 Figure 1. Some demographic and genetic processes affecting populations across their
168 distribution range. Here, the species range is shown as being divided into two geographic
169 entities, separated by a mountain. While peripheral populations occur at the edges of the range
170 of the species, ecological margins can be found throughout the range wherever ecological
171 conditions become sub-optimal. Ecological marginality and geography can influence genetic
172 and demographic processes in variable ways across the species distribution range, as depicted
173 by the grey shapes (source: Hampe and Petit 2005, Ohsawa and Ide 2008).
174
175 Demographic and evolutionary processes shape marginal and peripheral populations
176 differently compared to populations at the core of the distribution, depending on their
177 situation in the geographic and ecological space (Figure 1). Leading edge disjunct populations
178 establish via long distance dispersal and may suffer from founder effect, reduced fitness
179 because of genetic drift and inbreeding depression 179 due to reduced mate availability (Restoux
180 et al. 2008). These populations are not necessarily ecologically marginal, as colonization
181 speed of forest trees is much lower than the contemporary climatic shifts, especially on plains
182 (Jump et al. 2009). Leading edge populations may have increased adaptation to long distance
183 dispersal (Cwynar and MacDonald 1987).
184 Rear edge disjunct populations are not necessarily ecologically marginal either, although
185 they might be small and potentially prone to extinction. Their main features may be their
186 persistence over long periods of geological time (for example as climate refugia) and thus
187 their genetic uniqueness results from long-term divergence (e.g. Liepelt et al. 2009 for Abies
188 alba). Non-disjunct leading and rear edge populations are characterized by asymmetric gene
189 flow from the core of the distribution area, which can be either maladaptive (rear edge) or
190 adaptive (leading edge) under climate change range shifts.
191 At ecological margins, throughout the geographic range, selection pressure (with or
192 without the occurrence of maladaptive gene flow) will drive the evolutionary trajectory and
193 ability of populations to persist (Alleaume-Benharira et al. 2006, Borovics and Mátyás 2013,
194 Gaston 2009, Hampe and Petit 2005, Kawecki 2008, Kremer et al. 2012, Kubisch et al. 2014,

195 Lenormand 2002). Under climate change, rear edge peripheral populations and low elevation
196 marginal populations, are particularly and increasingly at risk (Figure 2).
197
198
199 Figure 2. Beaumont-de-Ventoux in the southeastern French Alps is a rear-edge, disjunct
200 Abies alba population growing under sub-Mediterranean climate conditions where evidence
201 of dieback (grey trees) is widespread since the summer heat wave of 2003.
202
203 2. The evolutionary potential of marginal and peripheral populations
204 Whether or not marginal populations are adaptable to changing conditions remains
205 theoretically debatable and evidence from short- or long-lived plant and animal data is often
206 conflicting (Kawecki 2008). Local adaptation is not as widespread as commonly thought and
207 that small populations, particularly, rarely demonstrate evidence of local adaptation (Leimu
208 and Fischer 2008, and, for forest trees, see St Clair and Howe 2007).
209 Few common garden experiments of forest trees actually test marginal and peripheral
210 populations and sites. When data are available, marginal populations demonstrate phenotypic
211 trait values (mean and variance) different from those found in core populations for a range of
212 traits (Rehfeldt et al. 2002). Marginal and peripheral populations are possibly under much
213 higher selection pressure than others and could thus be well adapted to extreme or fluctuating
214 conditions (Borovics and Mátyás 2013), while their adaptability might be lower than often
215 presumed. Populations from the trailing or xeric limit often display slower growth in more
216 favorable ecological conditions. For example, Rehfeldt et al. (2002) showed that xeric margin
217 populations generally lagged behind core populations in terms of phenotypic plasticity for
218 height growth. Similar results are available 218 for jack pine (Pinus banksiana; Mátyás and
219 Yeatman 1992) and Scots pine (Pinus sylvestris; Shutjaev and Giertych 2003). At the leading
220 edge, strong selection for resistance to cold and photoperiod may limit the ability of trees to
221 adapt to warming conditions (Savolainen et al. 2011).
222 These results do not support the hypothesis that marginal populations always have high

223 adaptability and phenotypic stability because extreme selection can negatively influence
224 plastic responses (Valladarès et al. 2007). The importance of genetic diversity and phenotypic
225 plasticity in determining adaptive potential has been shown to be a key issue when predicting
226 species distributions using climate envelop modelling (Benito-Garzón et al. 2011).
227 Much experimental evidence (e.g. part of the studies in Eckert et al. 2008) challenges the
228 idea that there is a decrease of genetic diversity from core to periphery (Lenormand 2002,
229 Kawecki 2008) and thus the reality of the "abundant center theory" (Sagarin and Gaines
230 2002) which states that core populations are more abundant than marginal and peripheral
231 populations where the balance between gene flow and selection limits population adaptation
232 and thus, species range. First, and from a methodological perspective, geographical margins
233 are not necessarily ecological margins, which can confuse issues (Lira-Noriega and Manthey
234 2014). All peripheral habitats are not sub-optimal and range edges may in fact harbor high
235 quality habitats (Channell and Lomolino 2000). Also, marginal and peripheral populations are
236 not necessarily evolutionary dead-ends. Given sufficient population size and/or high enough
237 levels of gene flow (which is not exceptional in forest trees, e.g. Kremer et al. 2012), their
238 fitness can be high in their own environment (Alleaume-Benharira et al. 2006, Ganopoulos et
239 al. 2011, Restoux et al. 2008) as well as in alien environments (Kreyling et al. 2014, Thiel et
240 al. 2013). This is particularly the case of rear edge populations with a complex evolutionary
241 history (Hampe and Petit 2005).
242
243 3. The importance of marginal and peripheral populations for adapting forests to
244 global change
245 The occurrence of extreme climatic events coupled with high intensity and frequent
246 ecological stress, likely increases vulnerability and limits adaptive capacity. At the rear edge
247 and at low elevation margins, drought and heat waves in interaction with the spread of new
248 and invasive pests and diseases will be major constraining factors. At the leading edge and at
249 high elevation margins, persisting cold events and photoperiod limitations as well as pests and
250 diseases spreading from the core 250 distribution or from lower elevations may remain strong

251 challenges for adaptation and hence reduce the geographic extent of suitable areas at leading
252 edges (Rehm et al. 2015).
253 Deciding which peripheral and marginal populations will be able to resist, survive and
254 evolve is a challenge when prioritizing and adapting management for these populations. For
255 one thing, understanding which biotic and abiotic factors form rear- and leading-edges is far
256 from trivial (Slaton 2015). Despite some knowledge gaps, innovative ecological and genetic
257 tools have been developed to support such prioritization in forest trees and these efforts need
258 to be continued (Konnert et al. 2015).
259 In the next two chapters, principles and examples of management of marginal and
260 peripheral forest tree populations are discussed, in view of changing climatic conditions. We
261 discuss silviculture and conservation separately, although in most cases the two are or need to
262 be combined and balanced depending on management priorities.
263
264 III. SILVICULTURE IN MARGINAL AND PERIPHERAL POPULATIONS
265
266 1. Principles of management of marginal and peripheral populations: maintaining the
267 stability and increasing the resilience
268 Forest tree species are best adapted to the disturbance regimes under which they have
269 evolved (Bergeron et al. 1999). Therefore, forest ecosystem management based on an
270 understanding of natural disturbance regimes is also a sound silvicultural approach in
271 marginal and peripheral populations (Alfaro et al. 2014, Allen et al. 2015). However, novel
272 forms of disturbance, or combinations of disturbances, may soon emerge (Lindenmayer and
273 McCarthy, 2002) and seriously impact marginal and peripheral forest populations. Therefore,
274 management methods should be adjusted to take into account the effect of silvicultural
275 interventions on genetic diversity and, consequently, on adaptability. This type of
276 management simultaneously accelerates genetic adaptation by facilitating tree populations to
277 track environmental changes and preserves genetic diversity as a main source of adaptability
278 to unknown disturbance cycles (evolution-oriented forestry, Lefèvre et al. 2014).

Marginal and peripheral populations, as well as their genetic resources, need to be identified and included as a priority 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 282 management units in forest management plans and identified as high conservation value stands. Maintaining stable, mixed, variably structured forest stands, as well as supporting and protecting long-term natural regeneration (Sagnard et al. 2011), safeguarding vital, isolated trees either at the fore-front of colonization or at the rear limits, are all desirable goals for marginal and peripheral populations. In specific cases, unconventional interventions must be developed to protect the survival of populations, e.g. partial removal of competing shrubs, or planting a provisory nursing stand. Box 1 provides an example for 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: Examples of management practices adapted to ecologically marginal beech (Fagus sylvatica) populations in central Europe.

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 marginal beech forest of the Dinaric region and in the northern Alps in Bavaria. Long-term regeneration periods are particularly suitable to create mosaic- and uneven-aged structures, increasing the future stability of these marginal stands. 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 several carefully applied regeneration cuts. This guarantees minimal impact on soils as these marginal populations often grow on steep slopes. In the Dinaric region, overstory removal is avoided as it negatively influences stability and quality of regeneration (Matic et al. 2003). If necessary during low seed crop years, natural regeneration is supplemented by stored seeds collected in- situ to strengthen local adaptation

307 as local genetic diversity is considered large enough. During regeneration, strong measures
308 are taken to avoid overgrowing weeds, soil degradation, forest fires and grazing. At the lower
309 limit of its distribution in the Dinaric Alps, beech becomes ecologically marginal and is found
310 in mixed stands with pedunculate oak (Quercus robur). There, groups or individually
311 admixed beech trees are favored to promote fructification and improve their vitality (Klepac
312 et al. 1996). Overall, forest management operates at the level of trees and groups of trees,
313 particularly because securing regeneration is a major concern in these often overly degraded
314 marginal populations (Zlatanov 2006).
315
316 Regeneration, a specific silvicultural task in marginal an 316 d peripheral populations
317 At the leading edge of species distributions, low dispersal rate, inbreeding due to small
318 population size, increased browsing and unsuitable soils may hamper regeneration and
319 population establishment and persistence under climate change. For example, browsing
320 hinders the regeneration of partially inbred marginal populations of English yew at high
321 latitudes (Myking et al. 2009). Management options for facilitating and securing population
322 expansion at the leading edge include the use of genetically diverse reproductive material and
323 assisted gene flow (Aitken and Whitlock 2013, see below for a discussion on assisted gene
324 flow), and, more than elsewhere, herbivore deterrents.
325 At the rear edge of species distributions, climate may become increasingly unfavorable
326 and thus many populations will become ecologically marginal, with drastic consequences for
327 their survival. Rising temperatures and land use change were found to be responsible, despite
328 some evidence of an adaptive response, to the gradual extinction over the last half-century of
329 low elevation, rear edge populations of European beech in the Catalan mountains (Jump et al.
330 2006, Peñuelas et al. 2007). Rising temperatures will also affect natural regeneration in many
331 rear edge marginal populations. The negative effect of climatic extremes on flowering and
332 seed set in populations at the rear edge may become a serious obstacle. For example,
333 dormancy requirements of many broadleaved tree species may be not met by increased
334 temperatures (e.g. Afroze and O'Reilly 2013 for Sorbus aucuparia, and Doody and O'Reilly

335 2011 for Fraxinus excelsior), which may stop germination altogether as demonstrated for
336 beech (Krawiarz and Szczotka 2008). However, beyond sporadic reports, there are yet
337 insufficient investigations on this subject.
338 Management options available to counteract extinction, decline of natural regeneration
339 and reduction of genetic diversity in rear-edge marginal populations, depend on prevailing
340 local ecological conditions and may include: (i) partial removal of herbaceous species to
341 reduce competition with natural regeneration; (ii) retention of shrubs as facilitators for
342 provision of shade (Benavides et al. 2013, Castro et al. 2004); (iii) soil and mycorrhiza
343 abundance improvement (Smith and Read 2008) and (iv) fostering and increasing flowering
344 and seed set (Box 2). In view of declining seed yields, the damage to seed crops caused by
345 foraging game and, in some regions by grazing, should be curtailed.
346
347
348 Box 2: Flowering and seed set at the leading- and 348 rear-edges of natural distributions
349
350 Leading edge: Flowering and seed production are annually highly variable in most tree
351 species. However, insufficient or lacking flowering and low seed set are of particular concern
352 at the leading edge, for example in Scots pine (Pinus sylvestris) and birch (Betula pendula).
353 While trees in plantations successfully acclimate to colder conditions, seed production and
354 migration are probably limiting the northward expansion, as several consecutive warm years
355 are needed for successful regeneration. In addition, only a small proportion of trees is
356 responsible for most of the seed production. As experiments in Finland show no clear genetic
357 correlation between flowering, growth and acclimation capacity, the only guideline for
358 management of marginal birch populations is to favor individuals showing highest capacity
359 for seed production (Rousi et al. 2011).
360
361 Rear edge: In Portugal, rear edge populations of Quercus suber and Quercus ilex /
362 rotundifolia demonstrate low and highly variable flower and seed production, as well as a

363 declining number of reproductive trees over the years. On suitable sites, with deep soil that
364 can compensate for lack of rainfall, the proportion of fruiting cork oak trees varies between
365 40-80 % depending on mast year, while on a poor site it varies between 10-20%. Such deep
366 soil stands with reduced drought stress constitute excellent candidates for in-situ conservation
367 as well as quality habitats for assisted migration schemes when threatened populations need to
368 be transferred to safer places (sensu Richarson et al. 2009). In holm oak (Quercus ilex) stands
369 that have been declining for a prolonged period of time, density decreases to less than 15 trees
370 per ha. At such low density and with declining flowering and fructification, the quantity and
371 the genetic quality of seedlings can be seriously jeopardized (see simulations in Sagnard et al.
372 2011).
373
374 3. Marginal and peripheral populations: valuable resources for forest reproductive
375 material
376 Economic, ecological and/or conservation interests justify active silvicultural intervention
377 in marginal and peripheral populations to support their own survival and regeneration. The
378 genetic resources of marginal and peripheral populations may also be a valuable contribution
379 for securing the stability or resilience of threatened core distribution populations under
380 assisted gene flow schemes. Although still debated, the forest reproductive material (FRM) of
381 these populations could be directly used for enrichment planting and also for tree breeding
382 purposes.
383 Assisted gene flow consists of mixing non-native pre-adapted genotypes into local,
384 potentially threatened populations (Aitken and Whitlock 2013). There are few risks associated
385 with using marginal and peripheral in assisted gene flow schemes: outbreeding depression has
386 rarely been demonstrated in forest trees 386 and, although there is evidence that adaptation to
387 drought is not present in all dry site ecotypes (e.g. for beech, Peuke et al. 2002), several
388 studies have shown that marginal drought-resistant populations exhibit better drought
389 adaptation than core populations (e.g. for beech, Rose et al. 2009; Ivojevic et al. 2012;
390 Robson et al. 2012). Therefore, Thiel et al. (2013) suggest to use intermixtures of marginal

391 and drought-adapted populations with local populations, adapted to different environmental
392 factors. Suggestions for using marginal populations need to be recognized as general
393 guidelines and tested species by species and according to management objectives.
394 Marginal and peripheral populations can thus contribute significantly to assisted gene
395 flow. The legal framework in the European Union for the production and marketing of FRM
396 (Council Directive 1999/105/EC) does not restrict the commercial use of genetic resources
397 from marginal and peripheral populations (Konnert et al. 2015). Identification of seed stands
398 located in marginal environments and the use of their FRM in reforestations when appropriate
399 (i.e. as part of assisted gene flow strategies) and as a source of genetic novelty in breeding and
400 conservation programs (and ex-situ collections) should be encouraged.

401 IV. CONSERVATION OF THE GENETIC RESOURCES OF MARGINAL
402 AND PERIPHERAL POPULATIONS

403 The in-situ and ex-situ conservation of genetic resources has been well defined by
404 international regulatory bodies such as the United Nations Convention on Biological Diversity
405 (CBD) and the International Treaty on Plant Genetic Resource for Food and Agriculture
406 (ITPGRFA). In-situ conservation builds on the idea that changing environmental conditions
407 are key for evolving new adaptive traits in populations while not putting the long-term
408 persistence of the population at risk. Dynamic in-situ conservation of forest genetic resources
409 involves a natural system in which the evolutionary forces which give rise to genetic
410 diversity, are allowed to act and modify allele and gene frequencies (Lefèvre et al. 2013).
411 With ex-situ conservation, populations and individuals are conserved as copies in field,
412 storage vault or cryopreserved collections. Ex-situ collections are at the root of breeding
413 activities, although they are far from containing all genotypes that may be of importance to
414 conservation as their primary goal is the selection of a few individuals with desired
415 phenotypes or of known pedigrees. Field collections allowing spontaneous mating and
416 reproduction (dynamic ex-situ conservation; Eriksson et al. 1993) may provide conditions in
417 which evolutionary forces are allowed to act and modify allele and gene frequencies (Lefèvre
418 et al. 2013) and offer an alternative to standard in-situ and 418 ex-situ strategies. With raising

419 extinction threats worldwide, particularly at rear edges and at low elevations (Hampe and
420 Petit 2005), cryopreservation is increasingly perceived as a complementary system to
421 conservation strategies (Li and Pritchard 2009). However, its advantages are doubtful for
422 forest trees and their highly complex genetic system and long life cycle.
423
424 Box 3: Legal aspects linked to the conservation of the genetic resources of marginal and
425 peripheral populations in Europe
426 In Europe, several legal frameworks and programs deal with the identification and the
427 monitoring of components of biological diversity (as defined by the 1992 Convention on
428 Biological Diversity) and can be used to support the conservation of marginal and peripheral
429 populations.
430 • FOREST EUROPE (former Ministerial Conferences on the Protection of Forests in
431 Europe, MCPFE);
432 • The Council Directive Nr. 92/43/EEC on the conservation of natural habitats and of
433 wild fauna and flora (Habitats Directive);
434 • The European Forest Genetic Resources Programme (EUFORGEN).
435 In particular, the Habitats-Directive and EUFORGEN promote the development and
436 implementation of dynamic in-situ conservation strategies across country borders through
437 concrete objectives. At the national level, objectives for marginal and peripheral populations
438 should be integrated within Forest and Conservation Acts, forest management practices and
439 silvicultural concepts of each country.
440
441 1. Habitat conservation and genetic conservation: not necessarily incompatible
442 management targets
443 Conservation of all levels of diversity, from genes to species and communities, can be
444 implemented simultaneously on the same site if target species for gene conservation are also
445 keystone species in a particular habitat, ensuring similar conservation objectives, and if some
446 level of silviculture or habitat management is allowed (Box 4). Protected habitats must be

447 sufficiently large and include significant landscape heterogeneity to maintain evolutionary
448 processes in different target species (Fady et al. 2015). When this is not the case, specific gene
449 conservation measures, such as dynamic in-situ conservation units or ex-situ collections, need
450 to be adopted and decoupled from other species conservation measures (Koskela et al. 2013).
451
452
453 Box 4: Conserving the genetic resources of cork o 453 ak at the rear edge in a National Park in
454 Tunisia.
455 In Tunisia, cork oak has seen its range reduced by half over the last 80 years. This reduction is
456 due to different causes, both man-made and not. Social, climatic and technical constraints are
457 major stumbling blocks to restoration efforts of cork oak forests in Tunisia. Under climate
458 change, drought and pest and disease resistance, such as that found in marginal populations
459 geographically distant from the central cork oak area, offer renewed opportunities for
460 conservation, restoration and breeding.
461 The marginal population of Jebel Serj (Siliana), located more than 120 km south of the core
462 area, is an excellent example of successful management. Until 2010, it suffered the same
463 extinction risk as other marginal populations as it did not benefit from any special protection
464 measures. Following a campaign to raise awareness, forest authorities decided to include this
465 population within the just established Jebel Serj National Park by extending the area of this
466 nature reserve dedicated to the protection of the Montpellier maple (Acer monspessulanum
467 L.), another very rare species in Tunisia. This change of status has already provided better
468 visibility to the marginal cork oak of Jebel Serj, has raised conservation awareness among
469 local people and has definitely increased the interest of policymakers. The effectiveness of
470 this conservation measure is well illustrated by the fact that natural regeneration, although
471 absent before 2010, is now beginning to be visible in this population.
472
473 At the rear edge, marginal and peripheral populations often harbor a keystone species of
474 interest for habitat conservation (e.g. sub-Mediterranean endemic Pinus nigra Salzmanni pine

habitats in southern France). Thus, they may be particularly suited for simultaneous in-situ conservation combined with habitat preservation. However, many of these populations will risk extirpation and may also 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) and ex480 situ conservation under climate change. At the leading edge, migrants may modify the composition of local keystone and dominant species and bring about conflicting views between habitat conservation and gene conservation strategies. 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.

Conservation at high elevation ecological margins in the core of the distribution range may have similarities with that proposed for leading edge populations. The availability of sites necessary for potential population expansion 489 is vital, if an endangered population has reached mountain ridges or peaks, or if soil, moisture or vegetation cover conditions above the present distribution limit are unsuitable for colonization; then ex-situ conservation will be the only option. This calls for a timely and careful examination of the site conditions beyond present leading edges.

2. Planning and monitoring conservation in marginal and peripheral populations

Conservation planning needs to recognize the value of marginal and 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.

The essence of genetic conservation planning is to avoid extinction of identified and

503 endangered marginal and peripheral populations by maintaining their natural reproduction
504 capacity. Of specific importance are characteristics of the genetic/reproductive system (first of
505 all mating, dispersal and regeneration features). There are only few species where reliable
506 genetic information is available to support the selection of priority populations and to
507 formulate proper measures. In most cases species level data may serve as proxies (pattern of
508 natural distribution; social status, i.e. stand-forming/scattered; level of threats; tolerance to
509 biotic and abiotic stress etc.).
510 The maintenance of conservation units needs active management interference, monitoring
511 of results of management and, when these fail, ex-situ conservation measures (Figure 3). A
512 decision cascade approach has been suggested as a method of prioritizing and subsequently
513 managing target populations (Kelleher et al. 2015). The decision cascade can include criteria
514 to assess population decline (such as in IUCN 2012) or the risk of genetic depletion (e.g.
515 Potter and Crane 2010), with the subsequent mitigation measures.
516
517
518 Figure 3. Example of a decision cascade process for selecting genetic conservation actions
519 in marginal and peripheral populations. The first step of the process is to identify threats to
520 marginal and peripheral populations, i.e. using monitoring, particularly 'target (or focused)
521 monitoring', which is based on existing hypotheses and associated models of system
522 responses to management (adapted from Nichols and Williams 2006).
523
524 Genetic monitoring is an efficient tool to control how marginal and peripheral populations
525 are adapting to changes in the environment. It provides an early warning system for
526 supporting management decisions regarding silvicultural practices, securing the stability of
527 marginal and peripheral populations and safeguarding an undisrupted supply of FRM. An
528 assessment of the status of marginal and peripheral populations will: (i) make possible the
529 identification of marginal and peripheral populations most valuable for production of FRM
530 and for conservation and (ii) enable focusing available resources on their management and

531 monitoring. Priority should be given to populations showing significant adaptation to one or
532 more desirable traits. At the leading edge, the likelihood that populations can contribute to the
533 colonization of new habitats should be assessed (e.g. growth plasticity, sufficient fecundity,
534 high dispersal). At the rear edge, populations displaying long term persistence (Hampe and
535 Petit 2005) or showing growth plasticity and tolerance to drought should be prime candidates.
536 Regular genetic monitoring of ongoing conservation 536 activities (Figure 3) enables the
537 quantification of temporal changes in genetics and dynamics of populations, using appropriate
538 and inexpensive parameters (Frankham 2010, Aravanopoulos 2011). It is based on assessing
539 indicators (genetic diversity, genetic drift, gene flow, selection) stemming from the
540 conceptual framework of the gene-ecological approach, through a set of verifiers (Graudal et
541 al. 2014). Some of these verifiers should be estimated on a regular basis (demographic
542 parameters), while others may be recorded at longer time intervals such as per decade or
543 longer (genetic parameters). This is a species-independent method with a prognostic value
544 applicable to any population of interest in order to enhance the conservation effort
545 (Aravanopoulos 2011). In addition, health conditions, recruitment patterns and environmental
546 parameters of marginal and peripheral populations should also be monitored. The intensity of
547 monitoring depends on the features of the genetic/reproductive system of the species, on the
548 actual threats and social interests.
549
550 3. Deciding when marginal and peripheral populations need to be conserved ex-situ
551 With the decline of the ecological quality of the habitat in which the species of interest is
552 growing, in-situ conservation may no longer be sustainable. However, ex-situ conservation
553 may form an evolutionary dead-end that could be detrimental to marginal and peripheral
554 population conservation, particularly in forest trees with very long generation times. Dynamic
555 ex-situ conservation, therefore, should remain a last resort option to be decided case-by-case,
556 e.g. when specific indicators point to severe extirpation risks (Figure 3).
557 In some fortunate instances, ex-situ conservation efforts may be shared with the aims of
558 forest tree breeding. Ex-situ conservation has long been practiced by forest tree breeders and

559 the archived material may be an irreplaceable element of conservation (e.g. in case of
560 European black poplar, wild cherry and some conifers). However, breeders' archives rarely
561 include material from marginal and peripheral populations, although, with breeding programs
562 required to consider climate change, this is starting to change (Fady et al. 2015).
563
564 V. CONCLUSIONS AND PERSPECTIVES: 564 MARGINAL AND
565 PERIPHERAL POPULATIONS - A RESOURCE WORTH PROTECTING
566 AND USING!
567 Future uncertainty in environmental conditions due to global climate change is a major
568 issue for developing sound, long-term forest management strategies (Lasch et al. 2005,
569 Garcia-Gonzalo et al. 2007, Lefèvre et al. 2014, Lindner et al. 2014). This uncertainty needs
570 to be taken into consideration even more for marginal and peripheral populations where
571 environmental and, consequently, demographic and genetic stochasticity is high compared to
572 core populations.
573 Marginal and peripheral populations contain very valuable genetic resources for the
574 maintenance of the adaptive potential of species. Habitat conservation and gene conservation
575 strategies, especially in marginal and peripheral populations, are often carried out separately,
576 uncoordinatedly, or in conflict with one another (Fady et al. 2015). However, both are
577 concerned with threats, such as environmental change, habitat fragmentation, land use change,
578 inappropriate forest management, and others, which simultaneously impact species,
579 populations and gene diversity. It is our opinion that the different resource management views
580 and strategies, concerning conservation on the one hand and utilization on the other, need to
581 be reconciled in marginal and peripheral populations, particularly at the rear edge and at
582 ecological margins.
583 We propose that sustainable forestry practices encompass conservation aspects in a more
584 comprehensive manner by endorsing an evolution-oriented forestry (Lefèvre et al. 2014),
585 especially in regions where marginal and peripheral populations are found. Conservation
586 practices include the need to manage via silvicultural techniques when keystone species are

declining. We believe that in exceptional circumstances, either assisted gene flow or managed relocation of certain marginal and peripheral populations should be employed and endorsed by both the habitat conservation and the forest management communities. Without this option, many rear-edge populations will face extinction and their pre-adapted genetic resources will be lost. Their ability to strengthen potentially declining forests elsewhere in their range will also vanish. Under uncertain environmental conditions, marginal and peripheral populations, particularly at the rear-edge and at ecological margins, have an option value that no forest and habitat manager should want to see disappear. They are one of the key assets for adaptive forestry (i.e. the ability of forestry 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 F 597 orest 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, for which we propose solutions. Particularly, marginal and peripheral populations, including those planted artificially, constitute early warning signals for dieback that should be recognized as outstandingly useful. An inventory of both natural and planted/naturalized marginal and 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, marginal and peripheral populations (particularly at the rear-edge and at ecological margins) are “natural laboratories” that have a particular role to play. Given the complexity of ecological and demographic conditions found in marginal and peripheral populations, and how they interplay, using complex models that consider demographic, genetic and ecophysiological processes jointly in forest dynamics are needed (Kramer et al. 2015, Oddou-Muratorio and Davi, 2014).

In the words of Alleaume-Benharira et al. (2006): “The fate of such marginal populations

615 is also very important in the context of climatic change as they might be the theatre of

616 evolutionary change, face increasing extinction risk, or be the source of migrants to colonize

617 new areas at expanding margins. It is therefore critical to identify the different sources of

618 maladaptation in such populations and to propose efficient conservation measures".

619

620 VI. ACKNOWLEDGEMENTS

621 We wish to thank COST Action FP1202 "Strengthening conservation: a key issue for

622 adaptation of marginal/peripheral populations of forest trees to climate change in Europe

623 (MaP-FGR)" for financial support and the members of its management committee for very

624 constructive comments while the manuscript was being drafted. BF also acknowledges the

625 financial support of projects AMTools (ANR-11-AGRO-005-04) and ERA-NET BiodivERsA

626 2011-2012 "TipTree" (ANR-12-EBID-0003). The manuscript was collectively written and

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

628 text. All author 628 s read and approved the final version of the manuscript. BF took the

629 responsibility of the final editing of the submitted manuscript.

630

631 VII. REFERENCES

632

633 Abeli T, Gentili R, Mondoni A, Orsenigo S, Rossi G, 2014. Effects of marginality on plant

634 population performance. Journal of Biogeography 41, 239-249.

635 Alberto FJ, Aitken SN, Alía R, González-Martínez SC, Hänninen H, Kremer A, Lefèvre F,

636 Lenormand T, Yeaman S, Whetten R, Savolainen O, 2013. Potential for evolutionary

637 responses to climate change – evidence from tree populations. Global Change Biololy 19,

638 1645–1661

639 Afroze F, O'Reilly C, 2013. Breaking seed dormancy in European rowan seeds and its

640 implications for regeneration. New Forests 44, 547–557.

641 Aitken SN, Whitlock MC, 2013. Assisted gene flow to facilitate local adaptation to climate

642 change. Annual Review of Ecology Evolution and Systematics 44, 367 -388.

643 Alfaro RI, Fady B, Vendramin GG, Dawson IK, Fleming RA, Sáenz-Romero C, Lindig-
644 Cisneros RA, Murdock T, Vinceti B, Navarro CM, Skrøppa T, Baldinelli G, El-Kassaby
645 YA, Loo J, 2014. The role of forest genetic resources in responding to biotic and abiotic
646 factors in the context of anthropogenic climate change. Forest Ecology and Management
647 333, 76-87.
648 Alleaume-Benharira M, Pen IR, Ronce O, 2006. Geographical patterns of adaptation within a
649 species' range: interactions between drift and gene flow. Journal of Evolutionary Biology
650 19, 203–215.
651 Allen CD, Breshears DD, McDowell NG, 2015. On underestimation of global vulnerability to
652 tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6:
653 art129
654 Aravanopoulos FA, 2011. Genetic monitoring in natural perennial plant populations. Botany
655 89, 75-81.
656 Benavides R, Rabasa SG, Granda E, Escudero A, Hódar JA, et al., 2013. Direct and indirect
657 effects of climate on demography and early growth of Pinus sylvestris at the rear edge:
658 changing roles of biotic and abiotic factors. PLoS ONE 8, e59824.
659 Benito-Garzón M, Alía R, Robson TM, Zavala MA, 2011. Intra-specific variability and
660 plasticity influence potential tree species distributions under climate change. Global
661 Ecology and Biogeography 20, 766–778.
662 Bergeron Y, Harvey B, Leduc A, Gauthier S, 1999. Forest management guidelines based on
663 natural disturbance dynamics: stand- and forest-level considerations. Forestry Chronicle
664 75, 49–54.
665 Borovics A, Mátyás C, 2013. Decline of genetic diversity of sessile oak at the retracting
666 (xeric) limits. Annals of Forest Science 70, 835-844.
667 Castro J, Zamora R, Hodar JA, Gomez JM. 2004. 667 Seedling establishment of a boreal tree
668 species (Pinus sylvestris) at its southernmost distribution limit: consequences of being in a
669 marginal Mediterranean habitat. Journal of Ecology 92(2), 266-277.
670 Channell R, Lomolino MV, 2000. Dynamic biogeography and conservation of endangered

671 species. Nature 403,84–86.

672 Cwynar LC, MacDonald GM. 1987 . Geographical variation of lodgepole pine in relation to

673 population history. American Naturalist 129, 463 – 469

674 Doody CN, O'Reilly C, 2011. Effect of long-phase stratification treatments on seed

675 germination in ash. Annals of Forest Science 68, 139–147.

676 Eckert CG, Samis KE, Lougheed SC, 2008. Genetic variation across species' geographical

677 ranges: the central–marginal hypothesis and beyond. Molecular Ecology 17, 1170-1188.

678 Eriksson G, Namkoong G, Roberds JH, 1993. Dynamic gene conservation for uncertain

679 futures. Forest Ecology and Management 62, 15-37.

680 Fady B, Cottrell J, Ackzell L, Alía R, Muys B, Prada A, González-Martínez SC, 2015. Forests

681 and global change: what can genetics contribute to the major forest management and

682 policy challenges of the twenty-first century? Regional Environmental Change 15, On line

683 first. doi: 10.1007/s10113-015-0843-9.

684 FAO, 2014. Global plan of action for the conservation, sustainable use and development of

685 forest genetic resources (GPA FGR). Commission on genetic resources for food and

686 agriculture, Rome, Italy (http://www.fao.org/3/a-i3849e.pdf).

687 Frankham R, 2010. Challenges and opportunities of genetic approaches to biological

688 conservation. Biological Conservation 143, 1919-1937.

689 Ganopoulos I, Aravanopoulos FA, Argiriou A, Kalivas A, Tsaftaris A, 2011. Is the genetic

690 diversity of small scattered forest tree populations at the southern limits of their range

691 more prone to stochastic events? A wild cherry case study by microsatellite-based

692 markers. Tree Genetics & Genomes 7, 1299-1313.

693 Garcia-Gonzalo J, Peltola H, Briceno-Elizondo E, Kellomaeki S, 2007. Changed thinning

694 regimes may increase carbon stock under climate change: a case study from a Finnish

695 boreal forest. Climatic Change 81, 431–454.

696 Gaston KJ, 2009. Geographic range limits: achieving synthesis. Proceedings of the Royal

697 Society B-Biological Sciences 276, 1395-1406.

698 Graudal L, Aravanopoulos F, Bennadji Z, Changtragoon S, Fady B, Kjær ED, Loo J,

699 Ramamonjisoa L, Vendramin GG, 2014. Global to local genetic diversity indicators of
700 evolutionary potential in tree species within and outside forests. Forest Ecology &
701 Management, 333, 35-51.
702 Hampe A, Petit RJ, 2005. Conserving biodiversity under climate change: the rear edge
703 matters. Ecology Letters 8, 461-467.
704 Holliday JA, Suren H, Aitken SN, 2012. Divergent selection and heterogeneous migration
705 rates across the range of Sitka spruce (Picea sitchensis). Proceedings of the Royal Society
706 B-Biological Sciences 279, 1675-1683
707 IUCN, 2012. International Union for the Conservation of Nature (IUCN) - Red List
708 Categories and Criteria: Version 3.1. Second edition. Gland, Switzerland and Cambridge,
709 UK. IUCN. Iv + 32 p.
710 Ivojevic S, Višnjic C, Mekic F, 2012. Drought resistance 710 of various provenances of beech
711 (Fagus sylvatica L.) from parts of its natural range in Bosnia and Herzegovina. . Works of
712 the Faculty of Forestry University of Sarajevo 1, 19 – 28.
713 Jump AS, Hunt JM, Peñuelas J, 2006. Rapid climate change-related growth decline at the
714 southern range edge of Fagus sylvatica. Global Change Biology 12, 2163–2174.
715 Jump A, Mátyás C, Peñuelas J, 2009, The altitude-for-latitude disparity in the range
716 retractions of woody species. Trends in Ecology and Evolution 24:(12) pp. 694-701.
717 Kawecki TJ, 2008. Adaptation to Marginal Habitats. Annual Review of Ecology, Evolution,
718 and Systematics 39, 321–42
719 Kelleher CT, de Vries SMG, Baliuckas V, Bozzano M, Frýdl J, Gonzalez Goicoechea P,
720 Ivankovic M, Kandemir G, Koskela J, Koziol C, Liesebach M, Rudow A, Vietto L,
721 Zhelev Stoyanov P, 2015. European Forest Genetic Resources Programme
722 (EUFORGEN): Developing approaches to the conservation of forest genetic resources in
723 Europe in the context of climate change. Bioversity International, Rome, Italy. 57 p.
724 Klepac D, Dundovic J, Gracan J, 1996. Hrast luznjak (Quercus robur L.) u Hrvatskoj
725 (Pedunculate oak (Quercus robur L.) in Croatia). Hrvatske sume, Zagreb, 560 p. (in
726 Croatian, with detailed English summaries).

727 Konnert M, Fady B, Gömöry D, A'Hara S, Wolter F, Ducci F, Koskela J, Bozzano M, Maaten
728 T, Kowalczyk J, 2015. European Forest Genetic Resources Programme (EUFORGEN):
729 Use and transfer of forest reproductive material in Europe in the context of climate
730 change. Bioversity International, Rome, Italy. 77 p
731 Koskela J, Lefèvre F, Schüler S, Kraigher H, Olrik DC, Hubert J, Longauer R, Bozzano M,
732 Yrjänä L, Alizoti P, Rotach P, Vietto L, Bordács S, Myking T, Eysteinsson T,
733 Souvannavong O, Fady B, De Cuyper B, Heinze B, von Wühlisch G, Ducousso A,
734 Ditlevsen B, 2013. Translating conservation genetics into management: pan-European
735 minimum requirements for dynamic conservation units of forest tree genetic diversity.
736 Biological Conservation 157, 39–49.
737 Kramer K, van der Werf B, Schelhaas M-J, 2015. Bring in the genes: genetic
738 ecophysiological modeling of the adaptive response of trees to environmental change.
739 With application to the annual cycle. Frontiers in Plant Science, 5.
740 Krawiarz K, Szczotka Z, 2008. Influence of temperature and abscisic and gibberellic acids on
741 polyamine biosynthesis in European beech (Fagus sylvatica L.) seeds during dormancy
742 breaking. Acta Biologica Cracoviensia, Series Botanica 50/1, 73–78.
743 Kremer A, Ronce O, Robledo-Arnuncio JJ, Guillaume F, Bohrer G, Nathan R, Bridle JR,
744 Gomulkiewicz R, Klein EK, Ritland K, Kuparinen A, Gerber S, Schueler S, 2012. Long
745 distance gene flow and adaptation of forest trees to rapid climate change. Ecology Letters
746 15, 378–392.
747 Kreyling J, Buhk C, Backhaus S, Hallinger M, Huber G, Huber L, Jentsch A, Konnert M,
748 Thiel D, Wilmking M, Beierkuhnlein C, 2014. Local adaptations to frost in marginal and
749 central populations of the dominant forest tree Fagus sylvatica L. as affected by
750 temperature and extreme drought in common garden experiments. Ecology and Evolution
751 4, 594-605.
752 Kubisch A, Holt RD, Poethke HJ, Fronhofer EA, 2014. Where am I and why? Synthesizing
753 range biology and the eco-evolutionary dynamics of dispersal. Oikos 123, 5-22.
754 Lasch P, Badeck FW, Suckow F, 2005. Model-based analysis 754 of management alternatives at

755 stand and regional level in Brandenburg (Germany). Forest Ecology and Management
756 207, 59–74.
757 Lefèvre F, Koskela J, Hubert J, et al., 2013. Dynamic Conservation of Forest Genetic
758 Resources in 33 European Countries. Conservation Biology 27, 373-384.
759 Lefèvre F, Boivin T, Bontemps A, Courbet F, Davi H, Durand-Gillmann M, Fady B, Gaüzere
760 J, Gidoin C, Karam MJ, Lalagüe H, Oddou-Muratorio S, Pichot C, 2014. Considering
761 evolutionary processes in adaptive forestry. Annals of Forest Science 71, 723-739.
762 Leimu R, Fischer M, 2008. A meta-analysis of local adaptation in plants. PLoS One 3, 12.
763 Lenormand T, 2002. Gene flow and the limits to natural selection. Trends in Ecology and
764 Evolution. 17, 183-189.
765 Leppig G, White J, 2006. Conservation of peripheral plant populations in California. Madroño
766 53, 264–274
767 Lesica P, Allendorf FW, 1995. When are peripheral populations valuable for conservation?
768 Conservation Biology 9, 753–760.
769 Li DZ, Pritchard HW, 2009. The science and economics of ex situ plant conservation. Trends
770 in Plant Science 14, 614 – 621
771 Liepelt S, Cheddadi R, de Beaulieu JL, Fady B, Gömöry D, Hussendörfer E, Konnert M, Litt
772 T, Longauer R, Terhürne-Berson R, Ziegenhagen B, 2009. Postglacial range expansion
773 and its genetic imprints in Abies alba (Mill.) - a synthesis from paleobotanic and genetic
774 data. Review of Palaeobotany and Palynology, 153, 139-149.
775 Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R,
776 Delzon S, Corona P, Kolstro M, Lexer J, Marchetti M, 2010. Climate change impacts,
777 adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology and
778 Management 259 (2010): 698–709.
779 Lindner M, Fitzgerald JB, Zimmermann NE, Reyer C, Delzon S, van der Maaten E, Schelhaas
780 MJ, Lasch P, Eggers J, van der Maaten-Theunissen M, Suckow F, Psomas A, Benjamin P,
781 Hanewinkel M, 2014. Climate change and European forests: What do we know, what are
782 the uncertainties, and what are the implications for forest management? Journal of

Environmental Management 146, 69-83.

Lindenmayer D, McCarthy M, 2002. Congruence between natural and human forest disturbance – an Australian perspective. Forest Ecology and Management 155, 319–335.

Lira-Noriega A, Manthey JD, 2014. Relationship of genetic diversity and niche centrality: a survey and analysis. Evolution, 68(4), 1082-93.

Matic S., I. Anic, M. Oršanic, 2003. Silvicultural practices in beech forests. In: Obicna bukva u Hrvatskoj (European beech in Croatia), Matic S., Ž. Ledinski, J. Janeš (eds.), Zagreb, 370 – 391 (in Croatian, with detailed English summary).

Mátyás C, Vendramin GG, Fady B, 2009. Forests at the limit: evolutionary-genetic consequences of environmental changes at the receding (xeric) edge of distribution. Annals of Forest Science 66, 800-803.

Mátyás C, Yeatman CW. 1992. Effect of geographical transfer on growth and survival of jack pine (Pinus banksiana Lamb) populations. Silvae Genetica 43, 370-376.

Myking T, Vakkari P, Skrøppa T, 2009. Genetic 796 variation in northern marginal Taxus baccata L. populations. Implications for conservation. Forestry 82, 529-539.

Nichols JD, Williams BK, 2006. Monitoring for conservation. Trends in Ecology and Evolution 21, 668-673.

Oddou-Muratorio S, Davi H, 2014. Simulating local adaptation to climate of forest trees with a Physio-Demo-Genetics model. Evolutionary Applications 7, 453–467.

Ohsawa T, Ide Y, 2008. Global patterns of genetic variation in plant species along vertical and horizontal gradients on mountains. Global Ecology and Biogeography 17, 152–163.

Peñuelas J, Oyaga R, Boada M, Jump AS, 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). Ecography 30, 830-838.

Peterman WE, Feist SM, Semlitsch RD, Eggert LS, 2013. Conservation and management of peripheral populations: Spatial and temporal influences on the genetic structure of wood frog (Rana sylvatica) populations. Biological Conservation 158, 351-358.

Peuke AD, Schraml C, Hartung W, Rennenberg H, 2002. Identification of drought-sensitive

811 beech ecotypes by physiological parameters. New Phytologist 154, 373–387.

812 Piermattei A, Renzaglia F, Urbinati C, 2012. Recent expansion of Pinus nigra Arn. above the

813 timberline in the central Apennines, Italy. Annals of Forest Science 69, 509-517.

814 Potter KM, Crane BS, 2010. Forest Tree Genetic Risk Assessment System: A Tool for

815 Conservation Decision-Making in Changing Times. User Guide Version 1.2, USDA

816 Forest Service, 47 p.

817 Pressey RL, Cabeza M, Matts ME, Cowling RM, Wilson KA, 2007. Conservation planning in

818 a changing world. Trends in Ecology and Evolution 22, 583-592.

819 Rehfeldt GE, Tchebakova NM, Parfenova YI, Wykoff WR, Kuzmina NA, Milyutin LI, 2002.

820 Intraspecific responses to climate in Pinus sylvestris. Global Change Biology 8, 912–929.

821 Rehm E, Olivas P, Stroud J, Feelez K, 2015. Losing your edge. climate change and the

822 conservation value of range-edge populations. Ecology and Evolution 5, 4315–4326.

823 Restoux G, E Silva D, Sagnard F, Torre F, Klein EK, Fady B, 2008. Life at the margin: the

824 mating system of Mediterranean conifers. Web Ecology 8, 94–102.

825 Richardson DM, Hellmann JJ, McLachlan JS, et al., 2009. Multidimensional evaluation of

826 managed relocation. Proceedings of the National Academy of Sciences of the United

827 States of America 106, 9721-9724.

828 Robson MT, Sánchez-Gómez D, Cano FJ, Aranda I, 2012. Variation in functional leaf traits

829 among beech provenances during a Spanish summer reflects the differences in their

830 origin. Tree Genetics & Genomes 8, 1111-1121.

831 Rose L, Leuchner C, Köckemann B, Buschmann H, 2009. Are marginal beech (Fagus

832 sylvatica L.) provenances a source for drought tolerant ecotypes. European Journal of

833 Forest Research 128, 335-343.

834 Rousi M, Heinonen J, Neuvonen S, 2011. Intrapopulation variation in flowering phenology

835 and fecundity of silver birch, implications for adaptability to changing climate. Forest

836 Ecology and Management 262, 2378-2385.

837 Sagarin RD, Gaines SD, 2002. The ‘abundant center' 837 distribution: to what extent is it a

838 biogeographical rule? Ecology Letters 5, 137–147.

839 Sagnard F, Oddou-Muratorio S, Pichot C, Vendramin GG, Fady B, 2011. Effect of seed
840 dispersal, adult tree and seedling density on the spatial genetic structure of regeneration at
841 fine temporal and spatial scales. Tree Genetics & Genomes 7, 37-48.
842 Savolainen O, Kujala ST, Sokol C, Pyhäjärvi T, Avia K, Knürr T, Kärkkäinen K, Hicks S,
843 2011. Adaptive potential of northernmost tree populations to climate change, with
844 emphasis on Scots pine (Pinus sylvestris L.). Journal of Heredity 102, 526–536.
845 Shutjaev AM, Giertych M, 2003. Scots pine (Pinus sylvestris L.) in Eurasia – a map album of
846 provenance site interactions. Polish Academy of Sciences, Kórnik, 266 p.
847 Slaton MR, 2015. The roles of disturbance, topography and climate in determining the leading
848 and rear edges of population range limits. Journal of Biogeography 42, 255–266.
849 Smith SE, Read DJ, 2008. Mycorrhizal Symbiosis, Elsevier, New York, NY, USA.
850 St. Clair BJ, Howe GT, 2007. Genetic maladaptation of coastal Douglas fir seedlings to future
851 climates. Global Change Biology 13, 1441–1454.
852 Steen DA, Barrett K, 2015. Should states in the USA value species at the edge of their
853 geographic range? Journal of Wildlife Management 79, 872-876.
854 Thiel D, Kreyling J, Backhaus S, Beierkuhnlein C, Buhk C, Egen K, Huber G, Konnert M,
855 Nagy L, Jentsch A, 2013. Different reactions of central and marginal provenances of
856 Fagus sylvatica to experimental drought. European Journal of Forest Research 133, 247-
857 260.
858 Ursenbacher S, Guillon M, Cubizolle H, Dupoue A, Blouin-Demers G, Lourdais O, 2015.
859 Postglacial recolonization in a cold climate specialist in western Europe: patterns of
860 genetic diversity in the adder (Vipera berus) support the central-marginal hypothesis.
861 Molecular Ecology 24, 3639-3651.
862 Valladarès F, Gianoli E, Gómez JM, 2007. Ecological limits to plant phenotypic plasticity.
863 New Phytologist 176, 749-763.
864 Valladarès F, Matesanz S, Guilhanmon F, Aranjo MB, Balaguer L, Benito-Garzon M, et al.,
865 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species
866 range shifts under climate. Ecology Letters 17, 1351–1364.

Zlatanov T, 2006. Perspectives for sustainable management of the forests in Lesnovska river basin. Journal of Balkan Ecology 9, 125–130.