Forest tree Marginal Populations in Europe
Report on the state of knowledge on forest tree marginal and peripheral populations in Europe

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Abstract - Marginal/peripheral (MaP) forest populations exist at the edge of species ranges, and may contain unique genetic diversity arising from adaptation to the adverse or unusual conditions within the regions they inhabit. The effects of climatic and other global changes are likely to be increasingly significant, and will affect forest tree species and their marginal populations. Studying adaptive processes in MaP populations is crucial, and of mutual interest for European and non-European countries, to understanding the evolution of species, and for the development of forest genetic resources (FGR) conservation, management strategies, and networks to cope with global change. These populations are threatened not only by global warming, but by various other threats arising from human activities. Because of their millennia-long history of adaptation to environmental changes, FGR growing in Europe may prove invaluable for adapting the forestry sector.

Keywords - Forest genetic resources; forest tree marginal populations; MaPs; marginality; COST Action FP 1202 MaP FGR.

Introduction

Marginal/peripheral (MaP) forest populations exist at the edge of species ranges, and may contain unique genetic diversity arising from adaptation to the adverse conditions in which they live. Because they typically attract less economic interest, peripheral forest tree populations are usually neither recognized nor managed as valuable forest resources (Lindner et al., 2010). Furthermore, conservationists and conservation planners seldon put a high value on peripheral populations, unless they belong to a species that is itself threatened (Leppig and White 2006, Thuiller 2007, Steen and Barrett 2015). Nevertheless, ecologists and geneticists tend to agree with Lesica and Allendorf (1995), that peripheral populations should be considered as valuable for conservation.

Understanding the adaptive processes in MaP populations is crucial and of mutual interest for European and non-European countries in order to safeguard the future of forest ecosystems. Developing conservation and management strategies for the forest genetic resources (FGR) contained within MaP populations is necessary to preserve and adapt European forests to the effects of global change. Because of their millennia-long history of continuous adaptation within rapidly changing environments', FGR extant in MaP populations throughout Europe may prove invaluable for adapting the forestry sector.

However, MaP populations are threatened not only by ongoing climate change but also by disturbances arising from a complex of human activities. Southern Europe represents an ideal region for study, as the effects of climate change on FGR will be greater and occur sooner than in the rest of Europe, and will affect the mesophilic species populations which provided the genetic diversity base of the post-Quaternary recolonisation of the European continent.

It is generally assumed that the present species distribution and genetic variation in Europe derived from Quaternary refuge areas distributed mainly in the southern peninsulas; however, it is likely that other marginal populations survived in central Europe and more northern areas (Tzedakis et al. 2013).

The COST Action FP1202 "*Strengthening conservation: a key issue for adaptation of marginal peripheral populations of forest trees to climate change in Europe (MaP-FGR)*" (http://www.cost.eu/COST_Actions/fps/FP1202) was intended to focus European attention on this particular topic and on

the adaptive potential of genetic resources growing at the edges of the forest tree species distribution. This potential is today endangered by rapid changes to habitats, caused by factors of both natural and human origin, and needs to be better studied, protected, and valorised in view of the implementation of adaptive strategies.

The idea for the Action was conceived within the framework of the activities of FAO Silva Mediterranea, namely Working Group 4 "*Forest Genetic Resources in the Mediterranean Region*" (http://www.fao.org/forestry/silva-mediterranea/88915/en/), comprised of all Mediterranean countries, where genetic resources must cope with rapid climate change as well as significant changes in land-use patterns.

The Action was then proposed and developed with the contribution of nearly all European countries, and was also extended also to non-COST countries in the Maghreb and the Near East. Additional support was provided by international bodies including FAO, CIHEAM, Bioversity International/Euforgen, EFIMED, and IUFRO. In total, researchers and stockholders from 32 COST, and six COST Near Neighbor Countries attended: Algeria, Austria, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, Cyprus, Czech Republic, Denmark, Finland, France, FYR Macedonia, Germany, Greece, Hungary, Ireland, Israel, Italy, Latvia, Lebanon, Lithuania, Montenegro, Morocco, Netherlands, Norway, Poland, Portugal, Romania, Serbia, Slovakia, Slovenia, Spain, Switzerland, Tunisia, Turkey, the United Kingdom, and Ukraine.

The main objective of COST Action FP1202 was to generate relevant knowledge on the role and use of MaP populations in the adaptation of forests to global change via a multidisciplinary approach. In particular, the Action addressed the conservation and management of MaP FGR by: (i) compiling information on climate change impacts upon MaP populations, (ii) making information available for the preparation of national and pan-European forest plans and strategies for adaptation and mitigation, (iii) developing criteria for monitoring and conserving FGR, and (iv) sharing results with forest managers. The main results can be found in several documents produced and downloadable at the MaP-FGR web site: http://map-fgr.entecra.it/, or can be supplied by the national experts of the Action Management Committee.

Not all MaP populations are of equal value for adapting forests to climate change (Lesica and Allendorf 1995). Some, as a consequence of maladaptation, may have little value for conservation. Others, particularly those in Southern Europe, may contain unique combinations of genes of high value for mitigation and adaptation, resulting from long term evolutionary and adaptive processes (Hampe and Petit 2005, Fady et al. 2016).

Prioritizing MaP FGR on the basis of their genetic value was one of the objectives of the Action, as identifying high value populations is of direct relevance to conservation and management practice. direct relevance for conservation and management.

Specific objectives in the Action were also:

- to collect, collate, analyze and synthesize information from past and on-going projects related to genetic diversity and impacts of climate change;
- to record and list existing conservation efforts and status, in order to identify gaps and set conservation priorities;
- to analyze and raise awareness on the role of FGR in the adaptation of MaP populations;
- to perform meta-analysis of collected data to identify common trends on the dynamics of genetic diversity in terms of the response to global change;
- to provide recommendations and guidelines for forest managers and national policy makers to conserve and sustainably use MaP FGR for forest adaptation and mitigation of climate change;
- to highlight the potential of MaP populations for the adaptation to climate change in other networks dealing with FGR conservation.

Objectives were targeted by 4 working groups, namely:

WG1: Gathering of already available data and compilation of ecological, genetic, and global change information, and in particular climate effects, relating to FGR and the distribution of MaP populations (Initially led by Julian Gonzalo, and later by Eduardo Notivol and Ricardo Alia).

WG2: Evaluation and analysis of WG1 information, including the development of genetic diversity maps for each species/population, and of methodology for evaluation of FGR diversity; compilation of databases of relevant institutions, genetic material, trials and networks, and identification of gaps in current knowledge. This group also performed meta-analysis of the data to identify common and divergent trends of FGR responses to global change. (Led by Giovanni Giuseppe Vendramin and Paraskevi Alizoti).

WG3: Mainstreaming genetic diversity into sustainable forest management in the context of global change, considering both conservation and use of FGR. (Led by Bruno Fady and Philippos Aravanopoulos).

WG4: Coordination and organization of all networking, database management, training and communication activities: conferences, workshops, training schools, the web toolbox, open access databases, reports, publications, and Short Term Scientific Missions (STSMs). (Initially led by Christophe Besacier, and later by Nicolas Picard and Valentina Garavaglia)

Results of the Action

The main results of the action are reported here, in the papers of this issue, and are also largely available on the Action web site.

When the Action began, there were many ideas, but a consensus had not yet been reached regarding the defining characteristics of MaP populations. Initially, marginality was discussed in terms of geography, then developing to include genetic characteristics, and ecological traits. It has been necessary to define and reconcile the concepts of geographic, ecological, and genetic marginality for both molecular markers and phenotypic traits. Spatialization of data was another important topic addressed in the final stages.

It was also discovered that:
- it is not straightforward to use information available in literature and existing databases, even if already partially consolidated at EU level;
- models of marginality cannot be generalized by species, type of marginality, or by ecological/geographic level;
- when evaluating climatic scenario and other thematic maps, difficulties arise in reproduction of methodology;
- collating geographic, genetic, and phenotypic data is already difficult at the species level, and becomes more difficult when trying to focus attention toward marginal populations;
- it is ultimately easier to use model species to simplify the work of identifying valuable indexes for defining "marginality".

Information on the distribution and ecology of target species was gathered, and meta-databases constructed for both neutral and adaptive genetic variation. Fifteen countries contributed data for 14 species, resulting in a relatively large dataset at the wider European level. These species were: *Abies alba, Fagus sylvatica, Fraxinus excelsior, Fraxinus sp., Picea abies, Pinus halepensis, P. brutia, Pinus nigra, Pinus pinaster, Pinus pinea, Pinus sylvestris, Taxus baccata, Quercus robur* and *Quercus petraea*.

Maps were constructed based upon data col-

lected from the above databases for species with an adequate number of populations across Europe. A niche model approach was used to define the ecological marginality of the populations, and geographical marginality indexes were then established for each of the different species/populations.

Analyses on the patterns of genetic diversity among environmentally or geographically marginal vs core populations were then performed together with the regression of intra-population phenotypic variation and phenotypic population plasticity against five marginality indexes for quantitative/adaptive traits. Based on data collected from the meta-database, several species were identified for use as models based upon to the availability of information for both adaptive genetic variation and molecular markers: *Fagus sylvatica, Abies* spp., *Picea abies, Pinus halepensis,* and *Pinus brutia*.

Collaborative documents, including an opinion paper (Fady et al. 2016), and a policy brief were produced to reach scientists, policy makers, and other stakeholders. Additional scientific and technical papers were produced by the more than 250 people who had exchanges with the Action initiatives [http://map-fgr.entecra.it/?page_id=74].

Other important outcomes included the compilation of an expert database of marginal and peripheral populations in Europe and in Near Neighbor Countries, along with maps and information describing the state of genetic resources of 24 Mediterranean forest tree species in collaboration with the FAO.

Last but not least, the dissemination of information and training of new scientists has been a concerted effort for all participants: five training schools were provided for PhD students and young researchers in the MaP FGR field, with more than 100 Trainees and 30 Trainers, and more than 60 STSMs funded by the Action.

In terms of gender balance, the majority of participants in the action were female (Figure 1), , from inner to outer ring years considered are 2013, 2015, and 2016.

From the beginning, networking activities have been made available at international level events, including FAO Silva Mediterranea meetings, EFIMED
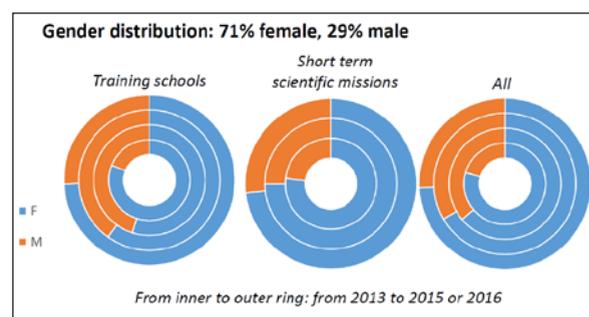
Figure 1 - Gender balance in the Action.

Mediterranean weeks, the Durban World Forestry Congress, FAO COFOs, COP 21, TreeBreedex, Trees-4Future, and IUFRO meetings.

This compilation of a number of national reports represents one of the Action's dissemination routes, and addresses the state of knowledge on conservation and management of MaP FGRs in Europe.

Marginality

Presently, less than 30% of the Earth's land mass is covered by forests. This proportion is steadily decreasing each year, either as a result of active deforestation or due to the effects of global changes.

Table 1 - Forested Areas of the world (https://en.wikipedia.org/wiki/List_of_countries_by_forest_area).

Region	Forested area (km²)	% of land area
World	39,000,000	26.19%
Polar regions (Russia, Scandinavia and North America)	13,800,000	35.38%
Latin America and the Caribbean	9,640,000	45.67%
East Asia and the Pacific	7,332,000	35.18%
Africa	6,500,000	21.80%
Canada and the United States	3,680,000	26.00%
European Union	1,600,000	35.00%
Australia	1,470,832	19.00%
India	778,424	23.68%
West Asia (Middle East and Arabia)	36,600	01.00%

More than 1.6 million km² of forested area lies within the European Union, accounting for around 35% of the European continent's total area, and 4% of the global forest area.

In Europe, due to intense and historical anthropogenic pressure, forested areas have been subject to strong fragmentation, and consequently to a progressive and continuous erosion in terms of surface area as well as species composition and genetic diversity. Nowadays, the complex phenomenon of so-called global change tends to exacerbate the effects of this fragmentation, particularly in terms of climatic effects (Brook et al. 2008). Climatic changes are occurring at such a rapid rate that many tree populations are showing evidence of severe stress.

It has been predicted that alleles from populations adapted to warmer climates, in particular those at the leading edge, may flow toward, and promote adaptation in populations growing in cooler conditions, as a consequence of asymmetric gene flow (Aitken et al. 2008, 2016). According to the same authors, populations growing at the edges where factors are changing dramatically will likely face genetic erosion or, under extreme conditions, extirpation. More widespread species, with larger population sizes, are likely to persist and adapt, but are also likely to suffer adaptation lag for several generations. On account of these adaptation lags, interspecific competition may weaken, allowing species to persist under sub-optimal conditions. Species with small populations, fragmented ranges, low fecundity, or suffering decline as a consequence of invasive insects or disease should be candidates for implementing methods of assisted migration.

A consequence of excessive fragmentation is an overall increase in size of forest boundaries which are exposed to limiting factors in the surrounding environment, leading to a progressive reduction in biodiversity, and within-species genetic erosion. However, having undergone relatively long periods of isolation in the past, these fragmented habitats may contain unique combinations of species as well as distinctive genetic and adaptive variability, that may provide the necessary adaptive capacity to safeguard against future uncertainty arising from global change and the ever-increasing anthropogenic pressures on ecosystems (Muillot et al. 2015).

In the Quaternary age, and in the previous eras, climatic changes have occurred at different intensities and over differing time periods (Pinna 1996). In some, climate changes occurred rapidly, over tens of years, and in others slowly, with average variations of only a few degrees over hundreds of years (Pinna 1977). Faster climatic changes have imposed stronger selective pressure on forest populations, most likely driving epigenetic factors and phenotypic plasticity expression (Schlichting 1986, Pigliucci 2001). Today's climate change rates, coupled with anthropogenic modifications, such as changes to land-use, have altered or may prevent gene flow, and can be expected to interfere with adaptation and migration, and likely with the survival of many populations or species (Davis and Shaw 2001).

Indeed, the responses of tree populations to global changes may be too slow to be viable. Moreover, as the population patches resulting from fragmentation are small, they are at an increased risk of a variety of genetic consequences, such as decreased dispersal, genetic erosion, and inbreeding, which are likely to impact upon long-term survival. Remnant populations often contain only a subset of the genetic diversity found in the previously continuous habitat. Adaptive processes that act upon underlying genetic diversity therefore have a smaller pool of fitness-maintaining alleles to act upon in the face of environmental change.

Marginalization *per se* should not be considered as pathological. It should be instead considered simply as a natural aspect of the evolutionary dynamics of a species in relation to the temporal and spatial variation of environmental factors in its natural

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range. Therefore, a marginal population is part of the species richness. It assumes a pathological meaning when range reduction is excessive, and the speed of change and fragmentation are too high to allow stable adaptive processes.

The COST Action FP1202 effectively summarised some definitions of marginality and marginal tree populations as follows:

- *geographical marginality* is generally used to refer to peripheral populations growing at the edge of their range. Species ranges can shift following environmental, typically climatic changes;

- *ecological marginality* can be observed anywhere within the range of a species, including the core;

- *altitudinally marginal* populations are usually islands of stunted, malformed trees, that with the warming climate could develop into reproductively capable, well-developed individuals, acting as 'nucleus' for further species expansion through seed dispersal;

- geographically marginal populations may themselves be either marginal or disjoint, the former connected to the core population by asymmetric gene flow (Kremer et al. 2012), while the latter are not;

- within the geographically marginal, leading and trailing edge populations can be identified. *Leading edge* populations represent expansion into new territories, their establishment largely determined by long-distance dispersal events. *Trailing edge* populations are those which persist in regions that are becoming unsuitable;

- where unfavourable driving forces occur, the result may be a displacement of the range at the trailing edge; alternatively, a fraction of the populations may persist in locally suitable environments (*stable edges*).

Together with other evolutionary genetic mechanisms, populations can maintain genetic diversity through migration. In continuous habitats, populations encounter few impediments to establishment on suitable sites. In fragmented habitats, suitable sites are separated by barriers and therefore gene flow is inhibited or completely disrupted. Under these circumstances, the capacity of species to integrate the unique genetic information contained within remnant populations is severely limited. Inbreeding increases and the fitness of the population is globally reduced (Hampe and Petit 2005, Fady et al. 2016). However, disrupted habitats and populations can sometimes re-establish connectivity and gene flow, as frequently occurred during the recurrent climate interglacial cycles. These periodically interconnected populations are collectively defined as meta-populations (Hanski 1991).

According to Kremer et al. (2012), theoretical models predict that asymmetric gene flow from larger core populations into those on the periphery may prevent local adaptation in marginal areas. Thus, a large gene flow can homogenize allele frequencies across space, reducing the adaptive divergence of meta-populations.

Following northward postglacial migration of tree species, the remnant forest populations remaining at more southern latitudes have experienced a long period in which to adapt to local conditions, and at the same time have had repeated exchanges with other nearby meta-populations. Because of this, they may have remained sufficiently isolated to fix particular traits while retaining enough variation to be adaptively dynamic. Kremer et al. (2012) provided evidence that, within the life-span of a generation, genes can move over spatial scales larger than the habitat shifts predicted under climate change, and that the northern border of a migrating species, the so-called leading populations, will progressively colonise new available and suitable environments.

Pollen viability and seed dispersal will strongly influence the demographic and genetic structure of leading populations. Austerlitz and Garnier-Géré (2003), modelling migration of outcrossing forest trees, demonstrated the major importance of relatively frequent medium-distance dispersal events over rarer events of much longer distance during the colonization process. In both marginal and leading edges, the survival of species will be dependent on individuals adapted to extreme conditions.

Marginal habitats are also of interest, not only because they may show marked genetic differentiation from populations at the core of a range, but also because of the potential for hybridization among closely related species. Hybridisation can be advantageous for adaptation (Thompson et al. 2009). Differentiated populations of closely related species can produce hybrid individuals of greater fitness than those of the parent species. This has happened in many areas along the Mediterranean peninsulas, which are of high genetic and species diversity. In these areas, the cooler, moister air at high elevation on mountain ranges favoured the survival of mesophilic species throughout the glacial and interglacial periods, and numerous genetic

taxa emerged. Peninsulas became established as important refugia for species survival, and engines of speciation and hybridization (Hewitt 2011).

Preserving MaP populations is fundamental in order to protect sources of unique variation, likely to be of great importance for species adaptation to the rapid global changes occurring in the Anthropocenic era (Crutzen 2006, Steffen et al. 2007).

Common characteristics of marginal populations include their spatial isolation from the core (continuous) population and the reduced suitability of the environment as compared to that in the core population. Marginal populations are also usually smaller in size, and may be more prone to extirpation as a result.

According the centre-periphery hypothesis, peripheral populations exhibit lower genetic diversity and greater genetic differentiation as a consequence of small effective population size and greater isolation relative to geographically central populations as confirmed by Eckert et al. (2008), who reviewed this assertion.

On the ground, it can be complex to define marginal and peripheral (MaP) populations in regions where human influence has been significant for centuries or millennia. To do so, we need to understand the geography, ecology, and genetics of populations, as well as the abiotic and biotic drivers responsible for the direction and speed of range shifts.

Because they grow at the edges of distributions, MaP populations may represent 'natural laboratories' for understanding how demography and genetic processes, such as natural selection, shape local adaptation, and if either prevent or facilitate colonization of new habitats (Fady et al 2016).

Approaches to identify existing MaP populations include the use of geographic distances as thresholds when considering geographically marginal populations, while ecological distances (e.g. based on landscape heterogeneity) may highlight ecologically marginal populations.

MaP populations may be distinguished on the basis of genetic characteristics, if genetically distinct from the core population, and the use of genetic tools together with common garden networks is therefore another key approach in their identification. Integration with common garden networks is vital to understanding and improving information on the adaptive value of marginal populations that may be of value for conservation and use in practice (Màtyàs 2007). Moreover, modelling should also be based upon new experiments outside of the current natural ranges. Integration of these trials with genomic information will allow for better prediction of tree responses to climate change (Kremer et al 2012, Alberto et al. 2013).

The key role of marginal populations for maintenance of biodiversity throughout the Quaternary renders them extremely important for the conservation of intra- and interspecific biodiversity in the face of climate change (Hampe and Petit 2005, Fady et al. 2016). Species may also respond relatively rapidly to change via phenotypic plasticity or invocation of an epigenetic response (Bräutigam et al. 2013, Nicotra et al. 2010 (Eriksson, 1996; Eriksson et al., 1993). These mechanisms are particularly important for plants in marginal environmental conditions where phenotypic traits may be canalised to genetic fixation.

Given the potential vulnerability of MaP populations, the degree and extent of their adaptive plasticity the speed with which they may move or become extinct, and their disproportionate contribution to genetic diversity, it is vitally important that we are able to identify them and understand how they are likely to change in response to future climate change (Eckert et al. 2008).

The use of this information in conservation and sustainable management of forest genetic resources will ensure that MaP populations receive the attention they deserve in terms of genetic conservation under climate change.

Main results from the regional compilations

For practical reasons, the area covered by the COST Action has been subdivided into five regions, mainly on the basis of bioclimatic similarity.

There is of course considerable variation within each region, on account of wide latitudinal ranges, as well as differences in climate, soil, and habitat characteristics. This variability is also due to the presence of important mountain ranges which lie in differing orientations, and are responsible for climate variation at a local level. Of these, the Atlas, Cantabrian, Pyrenees, Pontus, Taurus, and Caucasus mountains are oriented in an east-west direction, while the Scandinavian Alps, Alps, Dinaric Alps, Balkans, and Carpathians are mainly oriented in a north-south direction. It is evident that this orographic structure plays an important role in the wind circulation and characteristics of climatic patterns with a strong influence on species distribution.

Altitude is an important factor in gene pool conservation for mesophilic species in southern areas, which host the mountainous habitats suitable for populations belonging to these species. Most of these populations can be classified as *marginal*, and originated from former glacial refugia. Mountains, together with the larger rivers, are in some cases barriers for species migration, but altitude can

also compensate for the effect of latitude in habitat distribution, allowing, for example, for the survival of mesophilic species at lower latitudes.

In Europe, the effect of oceanic streams such as the Gulf are important, as they influence the occurrence of habitats in nearly all of western Europe. In the interior of Europe, the oceanic conditions give way to a more continental climate. These continental climates are dominated by northern and eastern winds, while in the south the climatic conditions are strongly influenced by subtropical wind circulation which makes frequent incursions into higher latitudes in the three main European peninsulas (Iberian, Italian, and Balkan).

The changes occurring in recent decades have resulted in a progressive shift to higher mean temperatures at higher latitudes and altitudes, and an increase in the intensity and frequency of extreme events which pose serious problems to species distributions.

Consequently, marginal populations can be seriously endangered by the shift of their ecological envelope, by isolation caused by a reduction in habitability in the surrounding area, as well as by human activities (Zhu et al. 2012).

Human impacts

History and socio-economic evolution have played a significant role in shaping the present-day characteristics of European forests.

According to Eurostat, the population of Europe is around 842 million, living within an area of 26.7 million km², in which forests accounted for 1.5 million km² in 1990, and 1.6 million km² today, with an increase evident over the last twenty-five years (World Bank 2015). Several non-European neighboring countries also participated in the COST Action: Turkey, Israel, Lebanon, Tunisia, Algeria, and Morocco. The total estimated forest area for these countries is around 1.4 million km².

According to the World Bank (2006), the rural population in Europe accounts for around 25% of the total, while in the Middle East and North Africa this figure is around 35.5%. Together with the climate, population density is a good indicator of the potential impacts upon habitats and forests. The mean population density in Europe is ~31.6 per km², ranging from 16 per km² in Norway to 393 per km² in the Netherlands. In the Middle East and North Africa, the total population is around 350 million, with an average population density of ~35 per km² (World Bank 2006). As countries in these regions typically contain large regions of desert, it should be understood that local population densities will be substantially higher.

The level of economic development should also be considered with regards to the evaluation of potential impacts. People living in temperate areas experience higher living standards and may view forested areas differently than those in the south, where forests are less productive and ecosystems more fragile, but very often overexploited to meet needs of the local economy. In these regions, it is worth remembering the significant impacts to forests resulting from high wood consumption of ancient civilizations. Humans began impacting upon forested regions at southern latitudes at least some 3,000 years prior to northern latitudes. The effects of these impacts are still evident in areas today regarded as biodiversity hot spots. In most countries, the majority of primary forests were cut back over a few centuries to clear land for agriculture, and were strongly modified by plantations and silviculture. In some, intensive forest tree farming accounts for a significant proportion of the forested area and of wood production. It should be acknowledged that protected areas in the EU today cover a relatively large area, almost 21% of the total (EEA 2012), including most of the marginal populations we consider here.

Geographic barriers to gene flow

Five important hotspots of genetic diversity were determined by the geographic structure of the Mediterranean area: Iberia, Italy, the Balkans, the Middle East, and North Africa. These regions served as refugia during glacial periods, providing sources of genetic material for re-colonization during interglacial periods. Orography, climate, and land-use are the main barriers shaping the present genetic structure of biodiversity and species genetics in Europe following the Quaternary period.

Geographic morphology is the main barrier, modifying micro-climatic conditions both at the local level and wider scale, and interacting with another main factor, the climate distribution. As described above, the orientation of mountain ranges has determined the routes of re-colonization available to tree species.

In western Europe, the Atlantic climate represents a barrier due to the effect of the warm Gulf stream. There, the temperate mild Atlantic climate has allowed the post-glacial colonization of mesophilic tree species.

During glaciations, the lower sea level in some areas allowed gene flow to occur between territories which are today disconnected. This is the case for islands such as the Aegean, Great Britain and Ireland, and other territories such as the Balkans and Apennines.

Altitude related barriers occur due to the isotherm distribution, and populations belonging to species requiring colder climates are often isolated on mountain tops. A similar scenario arises from the phenomenon of thermal inversion in some smaller regions, whereby the bottoms of valleys and canyons are unusually cool. In these areas, mesophilic species usually found at higher altitudes may find suitable habitats and remain isolated (Dinuluca et al. 2016, Saracino 2012).

Climatic differences among sites may result in asynchrony in flowering phenology of populations, which may then inhibit gene flow. Indeed, when population ranges are relatively continuous both in altitude and in latitude, flowering phenology is clinal and synchronized. When the range become fragmented a larger asynchrony can occur, and can be a serious barrier to gene flow among the isolated populations (Fuchs et al. 2003).

Together those typically considered, alternative barriers to gene flow should be evaluated. These can arise from silvicultural activities, the introduction of monoculture across large areas, rather than giving preference to a mixed forest system.

Introduced species can be sufficiently invasive as to impede natural regeneration of local autochthonous species. This is the case for Norway spruce in large areas of Europe, or for beech when it stifles other species in southern areas such as silver fir. The same occurs when silviculture is halted, due to an excess of protectionism, in particular, scenarios where clear cutting or coppicing is recurrently needed to clear the ground in order to favour regeneration of some species.

In Mediterranean regions, fire is a basic limiting factor which in some cases has influenced adaptation i.e. for natural regeneration dynamics. The prevention of fires might be a barrier for serotinous species.

In some cases, the forest nursery system itself can became a bottleneck or a barrier when genetic resources are improperly sampled or managed during the nursery breeding processes (Konnert et al. 2015).

Possible future modifications due to climatic change

According to the IPCC (2011), Europe has been warming faster than the global average over the last 30 years, local conditions varying between 2° C and 4° C on average, this variation being more pronounced in winter and at high latitudes (Holtmeier and Broll 2005). Precipitation is forecast to be reduced by 5-15% in northern areas, and by up to 20% in the south. An increase in extreme events, such as storms, long heat waves, and drought is also anticipated. Consequently, more frequent periods of flooding and drought are expected. Drier conditions may cause an increase in the length of the fire season, resulting in an greater risk of forest fires that have increased in frequency and intensity since the 1970s (Schär et al. 2004).

In southern areas of Europe, the African subtropical anticyclone has shifted in its periodical occurrence some several hundred kilometres northward and contributes to an increase in the intensity and frequency of heat waves, the length of dry periods, and other extreme events. As a consequence, climatic instability will increase in southern Europe, and forest fires in these regions may become fiercer.

Desertification risk in southern regions and possible climate tropicalization is predicted in several areas, from Africa to the Middle East, which would result in an acceleration of the water cycle and increased flood risk.

In contrast, in the Atlantic area and at northern latitudes, a longer growing season could have a positive effect. There, phenological records over the last 30 years show earlier springs and later autumns. In general, budburst has occurred consistently earlier for several northern and mesophilic species. This, however, increases the risk of late frost damage that, already an issue at southern latitudes, is expected to become more frequent in the North.

The Mediterranean will probably suffer major changes, affecting the most vulnerable habitats where MaP populations of the major European species grow. Moreover, water scarcity is likely to affect several Mediterranean countries in the coming years with serious social consequences and probable land degradation. Together with forest fires, the harmful effects from natural hazards such as pests and disease may also increase.

Marginal populations in Europe

The species economically most important and widespread in northern Europe, with continuous distributions are *Pinus sylvestris*, *Picea abies*, and *Betula pendula*, and to an extent *Larix decidua*. These are characterized by extensive gene flow and show clinal variation in adaptive traits. Scattered populations, normally associated with a more Atlantic climate, are also present at high latitude, including *Taxus baccata*, *Fagus sylvatica*, *Fraxinus excelsior*, *Tilia cordata*, *Corylus avellana*, *Ulmus glabra*, *Quercus petraea*, *Q. robur*, and *Ilex aquifolium*.

For most of these species, genetic information on marginality exists, showing a general trend of MaP populations to host less variation and exhibit

greater differentiation than core populations.

Moving progressively towards the southern latitudes, in the Atlantic region, biodiversity increases dramatically, with a higher number of species for which marginal and peripheral populations have been identified. Among them are *Abies alba*, *Acer monspessulanum*, *Arbutus unedo*, *Castanea sativa*, *Fagus sylvatica*, *Fraxinus excelsior*, *Juniperus turbinate*, *Picea abies*, *Pinus halepensis*, *P. nigra*, *P. pinaster*, *P. pinea*, *P. sylvestris*, *Populus nigra*, *P. tremula*, *Quercus pyrenaica*, *Q. robur*, *Q. petraea*, *Q. pubescens*, *Q. cerris*, and *Q. suber*, *Salix phylicifolia*, *Sorbus torminalis*, and *Ulmus laevis*.

Proceeding towards more continental areas in central Europe, the heterogeneity of the landscape has caused fragmentation of some major species ranges. For example, because of the more xeric conditions, the Pannonian lowland forms a gap in the distribution of many tree species such as the mesophilic scattered hardwoods.

Norway spruce attains its southern limits in the Alps and Carpathians (www.euforgen.org/maps), and the species boundaries for more temperate species such as silver fir occur in northern Bavaria and Thuringia, the Vosges in France, and Carpathians in eastern Europe. This boundary also represents the northern limit for more thermophilic species such as *Sorbus domestica* and *Quercus pubescens*, while *Pinus cembra*, *Betula nana*, and *B. humilis* have marginal edges with respect to their core distribution area in the boreal region. These regions represent the northern range for other hardwoods such as *Castanea sativa*, *Pinus cembra*, *Populus nigra*, *Pyrus pyraster*, *Sorbus torminalis*, *Tilia platyphyllos*, *Ulmus laevis* and more.

The southern edges of *Larix decidua*, *P. abies*, and *Pinus cembra* distributions occur at the Alps, while several species such as *Abies alba*, *Fagus sylvatica* and the most noble hardwoods extend their range towards Apennines, with marginal scattered populations.

Finally, southern areas are rich in biodiversity, especially mountainous regions, due to the high levels of endemism represented by different taxa deriving from remnants of genera nowadays considered typically northern. These may be regarded as remnants of past cooler periods. *Pinus sylvestris* reaches its southern limits in Italy, Spain, and Greece. *Quercus petraea* and *Q. robur* have their fragmented edges in Italy and the Iberian Peninsula.

Many groups of closely related species exist in the southern Europe, which have adaptively diverged i.e. *P. halepensis* and *P. brutia*, several *Acer* and *Fraxinus* species, oaks, Mediterranean firs in northern Africa, junipers, and cedars in Middle East. Moreover, many northern species have trailing edges

in the south, and a huge number of marginal habitats occur for more common trees such as *F. sylvatica*, *A. alba*, *Pinus mugo*, *C. sativa*, *P. avium*, *Sorbus* sp., *Populus* sp., *P. abies*, as well as for rarer trees such as *Q. ithaburensis*, *B. pendula*, that exist at their southern limits as marginal populations.

The southernmost area of our network, and the Middle East, represent the northernmost edges of tree species as *Cyperus papyrus* and *Acacia albida*.

P. heldreichii and *Alnus cordata* represent instances of Tertiary species occurring in fragmented populations which are both marginal and isolated at the same time. Unique isolated populations are remnants of ancient ancestral species differentiated, likely as a consequence of isolation, into endemic species such as *A. pinsapo*, *A. numidica*, *A. nebrodensis*, *A. equitrojani*, and *Cupressus dupreziana*.

Current status of protection

In Europe, the majority of the most important legislative initiatives are implemented by individual countries, and a number of protected areas networks already exist that can provide support for identifying, monitoring, and protecting genetic resources growing in MaP populations. In the MCPFE system, as well as according to FOREST EUROPE, UNECE, IUCN, and FAO principia, these protected areas are categorized into "no active intervention", "minimum intervention", and "conservation through active management".

Most European countries have recorded part of their genetic resources into the EUFGIS system database (http://portal.eufgis.org/), and a number of the gene conservation units (GCU) can also be classified as MaP populations. The EUFGIS database contains information on 3,128 units and 102 tree species in 34 countries. These units harbour a total of 3,773 tree populations. EUFGIS can be a useful tool to support countries in the management of MaP FGR as agreed in the context of Forest Europe, the pan-European forest policy process. Similarly, a total of 11,385 sites are recorded into databases of Natura 2000 in the EU territory (https://www.eea.europa.eu/data-and-maps/data/natura-8). However, while Natura 2000 records all habitats, EUFGIS records forest populations.

National Parks and other protected areas (see major information in regional and national reports) encompass the majority of populations defined as marginal. Protection measures and initiatives are typically more consistent among northern European countries than those in the south.

Despite the large human pressure, natural forests have locally been conserved by protected areas networks: these areas vary in size between 0.2% in

Turkey, to 38.2% in Croatia of the total forest area.

In nearly all countries, national registers of forest genetic resources record basic materials including MaP populations. These registers can be a helpful source for the proper use of reproductive materials from MaP populations. Moreover, these registers implement the European rules and the OECD scheme on Forest Reproductive Materials, so that MaP FGR can be of immediate utility when and where needed. Topak (1997) previously prepared a list of basic materials from all Mediterranean basin countries, that can be used as a reference when monitoring the present status of many seed stands, and consequently several MaP populations in the region.

Conclusion

Some authors have shown how fragmentation has been positive for the great endemic diversity that may result, however, fragmentation may also result in isolation, genetic drift, and genetic erosion. Areas of high population density also represent barriers to gene flow, reducing local levels of genetic diversity. Genetic analyses have shown that agricultural land offers ~1,000 times more resistance to gene flow than semi-natural habitats. This indicates that patterns of dispersal are constrained by the spatial configuration of remnant patches of suitable habitat (Ortego et al. 2015). In this context, shifts of isotherms play an important role as they may alter mountain temperate forest ecosystems at too high a rate for adaptation to keep pace, and exacerbate the effects of fragmentation on gene pools.

Forest genetic resources growing in marginal populations can be a valuable source of adapted reproductive materials. Indeed, the use of more adapted genetic materials should be mandatory when selecting species for planting, especially in relation to ecological sustainability and in view of the effects of climate change. In light of this, legislation should be more stringent with regard to certification and traceability, and ensure that the propagation path of material is traceable to the site of plantation.

Providing teaching on MaP forest genetic resources is of primary importance to preserve a genetic heritage which has survived for millennia of natural changes and human pressure. Conserving forest trees genetic resources requires maintaining *in situ* their adaptive potential, their forest community, and their entire forest ecosystem. *Ex situ* methods, such as assisted migration should be used only as the last extreme pragmatic solution.

Scarascia-Mugnozza and Matteucci (2005) listed the following as research priorities for the Mediterranean Forest Research Agenda:

- the impact of climate and land-use change on Mediterranean forest ecosystems' functioning: assessing and monitoring the main physical and biological processes including biodiversity and and the water cycle and the integration of the risk of forest fires in land-use and landscape planning and management;
- policy, economic, and institutional aspects of sustainable provision of forest goods and services;
- forest and woodlands in the context of integrated management of land resources: models and decision systems for optimizing multi-objective and multi-actor management problems;
- monitoring the genetic structure of populations with special attention to the genetic resources of marginal and peripheral populations.

With regards to forestry, the following technical actions would be required, reconciling information on legislation and methods among the Action participants, COST, Neighboring, and Near-Neighboring Countries:

- coordinating actions and strategies among different regions of the pan-European and neighboring regions;
- adaptation measures to be developed combining silviculture with ancillary and more naturalistic measures (e.g. respect for dead biomass and microhabitats in forests);
- pursuing the resilience of the forest ecosystem by strengthening the capacity for natural regeneration;
- implementing forest restoration and restoring the water cycle in degraded habitats and ecosystems;
- maintaining silvipastoral systems where biodiversity could be lost if abandoned;
- extending the due diligence principia and PEFC certification to genetic resources and forest reproductive materials.

These principia are also recognized and adopted as vital by the new ongoing FAO survey of Mediterranean forests.

Genetic variability has to be protected, and in turn, the adaptability of populations to environmental change. Research should be supplemented with data including species inventories, legislation, practical use, and coordination at national and pan-European levels, together with promotion of public awareness on the importance of conservation of the endangered species in forest ecosystems.

Research is called for with an increased emphasis on fine ecophysiology and adaptive traits, genetic variation, and genomics.

Regional reports

The regional reports were assembled as it follows for practical reasons. In some cases the name of a State can be repeated in two different regions. This is due to the occurrence of different climatic features shared by the same country.

Baltic region: Norway, Sweden, Finland, Denmark, Estonia, Latvia, Lithuania, and Poland;

Atlantic region: Belgium, Denmark France, Germany, Ireland, Portugal, Norway, Spain, The Netherlands, and The United Kingdom;

Central Europe region: Austria, Czech republic, Germany, Italy, Poland, Slovakia, Hungary, Ukraine, and Romania;

Southeastern Europe region: Bulgaria, Croatia, Greece; Montenegro, Romania, Serbia, Slovenia, and Ukraine;

Mediterranean region: Croatia, Cyprus, France, Greece, Israel, Italy, Lebanon, Morocco, Portugal, Spain, Tunisia, and Turkey.

References

Aitken SN., Yeaman S., Holliday JA., Wang T., Curtis-McLane S. 2008 - *Adaptation, migration or extirpation: climate change outcomes for tree populations.* Evolutionary Applications 1(1): 95-111. doi:10.1111/j.1752-4571.2007.00013.x.

Alberto FJ., Aitken SN., Alia R., Gonzalez-Martinez SC., Hänninen H., Kremer A., Lefèvre F., Lenormand Th., Yeaman S., Whetten R., Savolainen O. 2013 - *Potential for evolutionary responses to climate change – evidence from tree populations.* Global Change Biology 19: 1645–1661. doi:10.1111/gcb.12181

Austerlitz F., Garnier-Géré PH. 2003 - *Modeling the impact of colonisation on genetic diversity and differentiation of forest trees: interaction of life cycle, pollen flow and seed long-distance dispersal.* Heredity 90: 282–290. doi:10.1038/sj.hdy.6800243

Bräutigam K., Vining KJ., Lafon-Placette C., Fossdal CG., Mirouze M., Marcos JG., Fluch S., Fernández Fraga M., Guevara MA., Abarca D., Johnsen Ø., Maury S., Strauss SH., Campbell MM., Rohde A., Díaz-Sala C., Cervera MT. 2013 - *Epigenetic regulation of adaptive responses of forest tree species to the environment.* Ecology and Evolution 3(2): 399–415. doi:10.1002/ece3.461

Brook BW., Navjot S., Sodhi NS., Corey JA., Bradshaw CJA. 2008 - *Synergies among extinction drivers under global change.* Trends in Ecology and Evolution 23(8): 453–460. doi:10.1016/j.tree.2008.03.011

Crutzen PJ. 2006 - *The Anthropocene: the current human-dominated geological era. Paths of Discovery Pontifical Academy of Sciences,* Acta 18 Vatican City www.pas.va/content/dam/accademia/pdf/acta18/acta18-crutzen.pdf;

Davis MB., Shaw RG. 2001 - *Range Shifts and Adaptive Responses to Quaternary Climate Change.* Science 292 (5517): 673-679. doi:10.1126/science.292.5517.673

Dinulica F., Marcu V., Borz SA., Vasilescu MM., Petritan IC. 2016 - *Wind contribution to yearly silver fir (Abies alba Mill.) compression wood development in the Romanian Carpathians.* iForest 9: 927-936. doi:10.3832/ifor1742-008 [online 2016-10-02]

Eckert CG., Samis KE., Lougheed SC. 2008 - *Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond.* Molecular Ecology. 17: 1170–1188. doi:10.1111/j.1365-294X.2007.03659.x

EEA 2012 - *Protected areas in Europe - an overview.* EEA Report No 5/2012, Copenhagen. ISBN 978-92-9213-329-0, ISSN 1725-9177 doi:10.2800/55955

Eriksson G. 1996 - *Evolutionary genetics and conservation of forest tree genetic resources.* In: Turok J., Eriksson G., Kleinschmit J., Canger S. (eds) Noble Hardwood Network. Report of the first meeting, 24-21 March 1996, Escherode, Germany. IPGRI, Rome:159-167.

Eriksson G. 1998 - *Sampling for genetic resources populations in the absence of genetic knowledge.* In: Turok J., Collin E., Demesure B., Eriksson G., Kleinschmit J., Rusanen M., Stephan R. (eds). Noble Hardwood Network. Report of the second meeting, 22-25 March 1991, Lourizan, Spain. IPGRI, Rome: 61-75.

Eurostat 2007 - *Total Population as of 01.01.06.* http://ec.europa.eu/eurostat/portal/page?_pageid=1996,39140985&_dad=portal&_schema=PORTAL&screen=detailref&language=en&product=Yearlies_new_population&root=Yearlies_new_population/C/C1/C11/caa10000

Fady B., Aravanopoulos FA., Alizoti P., Mátyás C,von Wühlisch G., Westergren M., Belletti P., Cvjetkovic B., Ducci F., Huber G., Kelleher CT., Khaldi A., Dagher Kharrat M., Kraigher H., Kramer K., Mühlethaler U., Peric S., Perry A., Rousi M., Sbay H., Stojnic S., Tijardovic M., Tsvetkov I., Varela MC., Vendramin GG., Zlatanov T. 2016 - *Evolution-based approach needed for the conservation and silviculture of peripheral forest tree populations.* Forest Ecology and Management 375: 66–75.

Fuchs EJ., Lobo JA., Quesada M. 2003 - *Effects of forest fragmentation and flowering phenology on the reproductive success and mating patterns of the tropical dry forest tree Pachira quinata.* Conservation Biology 17: 149–157. doi:10.1046/j.1523-1739.2003.01140.x

Hampe A., Petit RJ. 2005 - *Conserving biodiversity under climate change: the rear edge matters.* 8 (5): 461-7. doi:10.1111/j.1461-0248.2005.00739.x.

Hanski I.1991 - *Single-species metapopulation dynamics: concepts, models and observations.* Biological Journal of the Linnean Society 42: 17–38. doi:10.1111/j.1095-8312.1991.tb00549.x

Hewitt G M, 2011 - *Mediterranean Peninsulas: The Evolution of Hotspots.* In: Zachos F., Habel J. (eds.). Biodiversity Hotspots. Springer, Berlin, Heidelberg: 123 – 147.

Holtmeier FK., Broll G. 2005 - *Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales.* Global Ecology and Biogeography, Global Ecol. Biogeogr. 14: 395—41.

Konnert M., Fady B., Gömöry D., A'Hara S., Wolter F., Ducci F., Koskela J., Bozzano M., Maaten T., Kowalczyk J. 2015 - *European Forest Genetic Resources Programme (EUFORGEN). Use and transfer of forest reproductive material in Europe in the context of climate change.* European Forest Genetic Resources Programme (EUFORGEN), Bioversity International, Rome, Italy (E ISBN 978-92-5-107538-8): xvi and 75 p.

Kremer A., Ronce O., Robledo-Arnuncio JJ., Guillaume F., Bohrer G., Nathan R., Bridle JR., Gomulkiewicz R., Klein EK., Ritland K., Kuparinen A., Gerber S., Schueler S. 2012 - *Long-distance gene flow and adaptation of forest trees to rapid climate change.* Ecology Letters 15: 378–392. doi:10.1111/j.1461-0248.2012.01746.x

Leppig G., White JW. 2006 - *Conservation of peripheral plant populations.* California. Madroño 53(3): 264-274.

Lesica P., Allendorf FW. 1995 - *When Are Peripheral Populations Valuable for Conservation?.* Conservation Biology 9: 753–760. doi:10.1046/j.1523-739.1995.09040753.x

Lindner M., Maroschek M., Netherer S., Kremer A., Barbati A., Garcia-Gonzalo J., Seidl R., Delzon S., Corona P., Kolström M., Lexer MJ., Marchetti M. 2010 - *Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems.* Forest Ecology and Management. 259(4, 5): 698-709. doi:10.1016/j.foreco.2009.09.023

Màtyàs C. 2007 - *What do field trials tell about the future use of forest reproductive material?* In: Koskela J., Buck A., Teissier du Cros E. (eds) "Climate change and forest genetic diversity: implications for sustainable forest management in Europe". Biodiversity International, Rome, Italy: 53-69.

Mouillot D., Bellwood DR., Baraloto C., Chave J., Galzin R. 2013 - *Rare Species Support Vulnerable Functions in High-Diversity Ecosystems.* PLoS Biol 11(5): e1001569. doi:10.1371/journal.pbio.1001569

Myking T., Vakkari P., Skrøppa T. 2009 - *Genetic variation in northern marginal Taxus baccata L. populations. Implications for conservation.* Forestry 82: 5529-539. doi:10.1093/forestry/cpp022

Nicotra AB., Atkin OK., Bonser SP., Davidson AM., Finnegan EJ., Mathesius U., Poot P., Purugganan MD., Richards CL., Valladares F., van Kleunen M. 2010 - *Plant phenotypic plasticity in a changing climate.* Trends in Plant Science, 15, 12: 684-692. doi:10.1016/j.tplants.2010.09.008

Ortego J., Aguirre MP., Noguerales V., Cordero PJ. 2015 - *Consequences of extensive habitat fragmentation in landscape-level patterns of genetic diversity and structure in the Mediterranean esparto grasshopper.* Evol Appl. 8(6): 621–632. doi:10.1111/eva.12273

Pigliucci M. 2001 - *Phenotypic Plasticity: beyond nature and nurture.* The Johns Hopkins Univ. Press, Baltimore and London: 328 pp.

Pinna M. 1977 . *Climatologia. [Climatology].* Ed. UTET, Torino: 442 pp.

Pinna M. 1996 - *Le variazioni del clima : dall'ultima grande glaciazione alle prospettive per il 21° secolo. [The climate changes: since the last glaciation towards persepctives for the 21st century].* Ed. F. Angeli ©, Milano: 214 pp.

Saracino A. 2012 - *Le faggete campane e lucane: gli usi e le tipologie [Beech forests in Campania and Basilicata:uses and types].* In: Sul trattamento delle faggete in Italia: dal metodo scientifico all'empirismo dei nostri giorni *[The silviculture of Beech forests in Italy: from the scientific method to the empiricism of nowadays]* I Georgofili, Quaderni 2012-III, Firenze, Accademia dei Georgofili: 61-72. doi: 10.13140/RG.2.1.2221.7120

Scarascia-Mugnozza G., Matteucci G. 2012 - *Mediterranean forest research: challenges and opportunities in a changing environment.* http://www.enea.it/it/pubblicazioni/pdf-eai/gennaio-febbraio2012/ss-mediterraneanforests.pdf

Schär Ch., Vidale PL., Lüthi D., Frei Ch., Häberli C., Liniger MA., Appenzeller Ch. 2004 -*The role of increasing temperature variability in European summer heatwaves.* Nature 427: 332-336. [www.nature.com/nature]

Schlichting D. 1986 - *The evolution of phenotypic plasticity of Ecology in plants.* Annual Review and Systematic, 17: 667-693.

Steen DA., Barrett K. 2015 - *Should states in the USA value species at the edge of their geographic range?* The Journal of Wildlife Management 79: 872–876. doi:10.1002/jwmg.897

Steffen W., Crutzen PJ., McNeill JR. 2007 - *The Anthropocene: Are Humans Now Overwhelming the Great Forces of Nature.* AMBIO: A Journal of the Human Environment. 36 (8): 614- 621. doi:10.1579/0044-7447(2007)36[614:TAAHNO]2.0.CO;2

Thompson JD., Gaudeul M., Debussche M. 2009 - *Conservation Value of Sites of Hybridization in Peripheral Populations of Rare Plant Species.* Conservation Biology 24 (1): 236-245. doi: 10.1111/j.1523-1739.2009.01304.x

Topak M. 1997 - *Directory of seed sources of the Mediterranean Conifers.* FAO 1997: http://www.fao.org/docrep/006/AD112E/AD112E00.HTM

Tzedakis PC., Emerson BC., Hewitt GM. 2013 - *Cryptic or mystic? Glacial tree refugia in northern Europe.* Trends in Ecology & Evolution 28 (12): 696 -704. http://dx.doi.org/10.1016/j.tree.2013.09.001

World Bank (The), 2006. *Migration and Remittances Factbook-Middle East and North Africa.* http://web.worldbank.org/archive/website01058/WEB/IMAGES/MENA.PDF

World Bank (The), 2015. *The Forest area, European union.* https://data.worldbank.org/indicator/AG.LND.FRST.K2?locations=EU

Zhu K., Woodall CW., James S., Clark JS. 2012 - *Failure to migrate: lack of tree range expansion in response to climate change.* Global Change Biology 18: 1042–1052, doi: 10.1111/j.1365-2486.2011.02571.x