

WRAP UP OF THE DYGEN CONFERENCE

Dynamics and conservation of genetic diversity in forest ecosystems

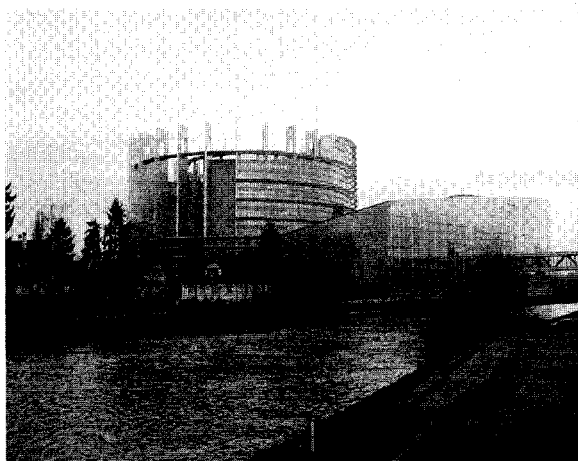
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Background and Objectives

(*Antoine Kremer & Marie Pierre Reviron*)

At the beginning of the nineties, two initiatives emerged that boosted research in population genetics of forest trees in Europe and its application in conservation issues. The first initiative was the launch by the European Commission of successive calls within the 4th Framework programme 94–98 (FAIR, BIOTECH Programme) and the 5th Framework programme 98–02 (Quality of Life and Energy and Environnement Programme). Research on important issues such as the monitoring of genetic diversity and the understanding of the basic mechanisms shaping diversity was supported. At least twenty different projects involving more than 160 labs that addressed the issues of description and evolution of genetic diversity were funded. More than thirty different tree species, ranging from Mediterranean to Alpine ecosystems, were studied. During the same period, European countries agreed to implement actions for the effective conservation and sustainable utilization of forest genetic resources. Following Resolution 2 of the Strasbourg Ministerial Conference for the protection of Forests in Europe, 1990, the European Forest Genetic Resources Programme (EUFORGEN) was established. It operates through networks in which forests geneticists and others specialists analyze needs, exchange experiences and develop conservation objectives and methods for selected species. EUFORGEN has also provided a good platform for disseminating the results from research projects conducted within the EU.

The DYGEN conference was intended to fill the gap



between basic research conducted through R & D research proposals in the area of population, evolutionary and ecological genetics and the implementation of their results in conservation actions.

The first objective of the DYGEN conference was to share and disseminate major achievements obtained in the frame of the R&D projects. The conference focussed on the main genetic, ecological and anthropic processes modifying diversity in forest ecosystems. An overview of the state of the art was provided by sixteen invited speakers. The second objective was to highlight the applicability of the results in conservation issues. Conservation actions and measures were considered for three categories of forest species: endangered and disseminated, widespread and intensively cultivated species. The third objective was to identify gaps and future research needs in the field of “Population and Conservation Genetics in European Forest Trees”.



The DYGEN conference was a joint initiative of the coordinators of the EU supported projects and chairs of the EUFORGEN networks. Results of EU supported projects were presented together with the activities of the EUFORGEN networks. These data and results were confronted to other approaches and investigations conducted in other parts of the world (Asia, Africa, America), and also with other organisms. The conference was introduced by officials of the European Commission, who highlighted the support given during the 4th and the 5th framework and the perspectives within the 6th framework programme.

The conference was attended by 278 participants from 43 countries, and subdivided in 11 different sessions (8 sessions devoted to the dynamics of genetic

regulatory elements may be the key to quantitative variation and provide a unifying framework, (vi) sharing tools openly will unify a community.

Session A4 and A5 – Colonization and climate change

(Csaba Mátyás & Koen Kramer)

Forest trees are well suited for colonization studies; because of (i) well documented range shifts and, (ii) preserved “footprints” both in sediments and in intraspecific genetic structure. The session papers suggest the following state of knowledge on the genetic effect of postglacial colonization on intraspecific variation pattern of temperate forest trees:

- Recent transeuropean studies confirmed strong correlations between intraspecific genetic structure and colonization history. In European trees allelic richness and differentiation is highest in the Mediterranean, the putative refugial area. Genetic diversity increases northwards, with migration distance and/or colonization time.
- Migration by seed (consequently, the reproductive system of species) has played the dominant role in shaping the genetic structure of species as compared to other genetic processes.
- Holocene colonization progressed rather patchy and irregularly, often pulsing, following climatic oscillations on different time scales (geological to interannual level).
- In North America, the survival of small populations close to glacial limits is highly probable. Therefore earlier estimates of relatively high migration speeds (>200 m/yr) should be revised.
- The existence of refugial populations at higher latitudes is less probable in Europe. Still, available paleoecological data have to be further refined. Massive human disturbance in the recent millennia may have had its influence as well on the genetic structure of remaining forests, especially with the beginning of planned forest management (transfer of reproductive material, exotic plantings).
- Refugial lineages preserved in maternally inherited DNA-haplotypes can be conveniently utilized for identification of populations and even wood products. At the same time, the genetic legacy of long lasting separation in glacial refugia is minor in adaptive respect. Historic effects have been obliterated by selection pressure and gene flow. There are indications that these processes might effectively act within relatively few generations.
- Stochasticity in migration and extinction events support earlier views about nonoptimality or adapta-

tional lag in forest tree populations. The non-equilibrium state has its analogy also on species (i.e. association) level (non-analogous associations).

The greatest challenge to forest genetics in the near future is to provide expertise in shaping nature (and gene) conservation strategy and forest policy in view of probable climatic changes, based on joint evaluation of paleoecological and genetic data. Of special interest are genetic and demographic conditions at the retreating edge of distribution areas and in climatically-ecologically sensitive regions, such as the semiarid zone of the Mediterranean, or low-elevation locations on the border of closed forests and woodlands.

Session A6 – Spatial dynamics and natural regeneration

(Paolo Menozzi & Andrew Lowe)

Five oral and 16 poster presentations were contributed in this session. The presentations mainly concentrated on those processes which reinforce or disrupt spatial structure, mostly at the gene level, although species level processes were also examined. Several of the mechanisms that establish spatial structure are closely related to the topics of other sessions (i.e. gene flow, silvicultural regime). The detection of spatial structure has been greatly enhanced by the development of autocorrelation statistics and, in the case of genetic structure, by the availability of highly polymorphic molecular markers, both multiallelic and multilocus. For the purposes of this review, the mechanisms which most influence spatial dynamics are grouped into two categories, gene flow and landscape processes, but some factors could appear in either grouping and are not exclusive.

Gene flow

- Seed dispersal – limited seed dispersal establishes spatial structure, and can lead to isolation by distance (IBD)
- Mating system – inbreeding and clonality increase spatial genetic structure whereas outcrossing disrupts it
- Pollen dispersal – the mode of pollination (e.g. wind or insect) appears important as external factors e.g. wind direction and pollinator behaviour in fragmented landscapes can impact on spatial genetic structure –related to landscape issues
- Fecundity – age and size of individuals may affect an individuals fertility
- Variation – the level of individual and annual variation in the above factors can be huge and needs some quantification.

Landscape

- Density – the density of individuals within a landscape (e.g. dispersed, aggregated) impacts on spatial genetic structure as can other extraneous factors (e.g. logging) which change the overall tree density
- Fragmentation – spatial genetic structure and gene flow may be very different in continuous forest blocks compared to fragmented compartments
- Adaptation – the distribution of genes under selection may be controlled by environmental factors, and a reduction in fitness due to inbreeding depression may be important
- Generational – spatial genetic structure is composed of many different generations, and is a combination of factors acting on all cohorts. Spatial structure within a seedling cohort may be very different from that of the mature tree generation
- Topography – physical landscape features (e.g. mountains) may present barriers to gene flow, whilst others (e.g. valleys) may influence the predominant direction of gene flow (e.g. via wind), and will influence spatial genetic structure.

Key questions arising during discussion

How can we differentiate factors, can we have expectations or null models?

1. What are significant landscape changes affecting gene flow/ structure
2. How resilient are systems, what levels of dynamism/variation

Future developments and take home messages

1. Issues of scale – genetic structure of population/regional scale
2. Landscape – direction of wind, development of new GIS integrated statistics
3. Individual variability – needs quantification
4. Distribution of adapted traits, importance of selection and inbreeding depression

Session A7 – Artificial Seed Transfer

(Phil Aravanopoulos & Gerhard Müller-Starck)

Session A7 included four oral presentations and six posters. In the presentations, the importance of autochthony and delineation of provenances was pinpointed, in particular due to their association with the notion of local adaptiveness. However, it became evident that under conditions of rapid environmental change, the significance of autochthony and provenances may become less relevant. In this respect it is crucial to better understand the genetic consequences of environmental change and corresponding modifications

of a-biotic and/or biotic stress components in order to formulate an adequate strategy regarding artificial seed transfer. This strategy may incorporate enrichment of genetic resources via transfer from areas outside of the target area, particularly when it is estimated that genetic loads of the populations in question are high under the conditions of environmental stress. Therefore the objectives regarding the seed sources to be used in a particular area may have to be revised or differentiated according to the underlying environmental change.

The use of genetic markers is constitutive in revealing population processes; nevertheless the choice of marker, or families of markers to be employed, as well as of genomes to be studied, should be an exhaustive process. Marker properties differ considerably so that in many cases it is recommended to employ different categories of genetic markers, i.e. those which address the nuclear and those which refer to the cytoplasmic genome. The use of a combination of markers and genomes will substantially help in the verification of the dynamics of genetic variation, and may alleviate the problem of compensation of effects. Alterations in the frequencies of rare alleles provide means to assess genetic diversity and future genetic potential of artificial populations. The above approaches may highlight both the potential resemblance of artificial reforestation or plantations in comparison to adjacent autochthonous populations, as well as the determination of the origin of the seed sources used. In this respect they can assist in forest certification practices. Genetic markers were also used efficiently to investigate the transfer of genetic variability that is present in seed stands or orchards, to the progeny populations that are created. A particularly interesting result is that progenies of the same maternal population, originating from different seed years, significantly differed in their set of rare alleles. The potential use of greenhouse seed orchards may result in improved control of the seed crop.

The indicative power of genetic markers was successfully employed in assessing impacts of artificial selection on gene pools. In case that markers do reveal substantial reduction of genetic diversity following artificial selection, questions need to be answered unequivocally concerning criteria for corresponding limitations and floatings. However, even if neutral genetic markers do not seem to provide evidence for genetic erosion, this may not be regarded as proof. Sampling of adaptive diversity and the potential future use of functionally important markers has to be considered as well.

Session A8 – Silvicultural regimes

(Berthold Heinze & Dušan Gömöry)

In this section, there were one introductory plenary lecture, four contributed talks, and one poster; but aspects of silviculture were also mentioned in presentations in other sections. All changes in genetic structures associated with changes in population densities and mating systems have direct implications for silviculture.

A review of studies published to date gives a contrasting picture concerning genetic effects of silvicultural treatments. This was reflected in the diversity of topics and case studies presented, with examples from Europe, Asia, and Africa. Differences are also apparent in the treatment of widespread species that dominate the stands vs. scattered species with low density, and colonizing – extinction behaviour vs. very low density tropical trees. Correspondingly, markers and data analysis methods presented in this section varied widely as well.

A study in *Shorea curtisii*, a tropical Dipterocarpaceae tree in Malaysia, showed the importance of the seedling population on the forest floor for buffering the effects of logging. Demography plays an important role. The study also showed up how difficult it is to design studies with trees of low density due to stochastic effects. A similar study in Cameroon on a Meliaceae species found no effects of logging, which means removal of mature trees, on measures of genetic diversity, and neither on isolation by distance. Only weak small scale spatial structures were present before logging which disappeared afterwards. A similar case may be present in trees of scattered occurrence in Europe. A simulation study of spatial genetic structure, and comparison to *Sorbus torminalis* data, showed that local patterns of colonisation and extinction can explain clusters of related trees and maintenance of genetic diversity in the whole population. A study of the conifer, Scots pine (*Pinus sylvestris*), showed practically no effects of different silvicultural treatments on pollination of remaining trees – continuous forests may buffer any effects effectively. Somewhat higher effects were reported in a poster about beech (*Fagus sylvatica*) in Southern Italy.

The discussion centred around the following themes:

- ‘Silvicultural treatment’ has different meanings in different species and countries or regions.
- Life history traits and distribution patterns of the species may play a role as well (scattered and continuous species, early and late succession).
- It is difficult to define satisfactory standards in such studies – either temporal or spatial. But maybe the intensity and scale of the treatment should be addressed in future studies to define a 'no effect level'

threshold.

- Effects may be stronger first on demography, only then genetic effects may give a sizable impact.
- The patchwork of different measures in the spatial and temporal dimensions taken in larger regions, and the generation overlap across many stands, may buffer individual effects on the local scale
- Problems are more likely and immediate in typical tropical species, especially those actively afforested, sometimes with translocated material.

Session B1-Conservation of rare and disseminated species

(Leonardo Gallo & Mari Rusanen)

Normally, the conservation of the so-called “rare” and of disseminated species implies not only the conservation of its genetic resources but also the restoration and conservation of the threatened habitats where they occur. Immediately actions are necessary since in many cases the effective population size has dramatically decreased. In these cases, research on ecological aspects is usually more important than on genetics and must be accompanied by immediate rescue activities of the remaining material. The presented case of *Vitis vinifera* is one more where human activities degraded the natural habitats so much that a natural recovery of its genetic diversity seems impossible.

In situ conservation measures are evolutionary more important but *ex situ* conservation can not be avoid in urgent cases. In this sense it should be considered that population is not only the evolutionary unit but should be in most cases the conservation unit too. Genetic processes and evolutionary factors such as genetic drift, isolation by distance, gene flow dynamics, adaptation, etc. can be in general better understood through the analysis of rare or disseminated species. This can be seen in some of the presented posters. Some examples on this are the *Austrocedrus chilensis* evidence of genetic drift in North Patagonia, Argentina or the effects of fragmentation in the genetic diversity of *Juniperus communis* in the Netherlands and in the red squirrel population in the United Kingdom. This gives “rare” species and populations an additional scientific value that has to be taken into account when considering the needs for their conservation. Strong selection pressure and restricted gene flow on isolated and small populations can derive in special adaptive forms. This seems to be the case of the presented *Populus nigra* hairy morphotype. Because isolation is generally related to marginal distribution areas, and these to extreme environmental conditions, generally heat and drought, such adaptations should be taken specially into account

in the frame of the probable quick global climatic change that is expected. Conserving adaptedness is one of the peculiarities of conservation of “rare” populations and species.

Since unique and particular genotypes are normally conforming most of these “rare” populations and species (like in the presented case of the Mediterranean *Zelkova* species), special attention should be paid to international co-operation to apply urgent measures in the monitoring, protection and rescue of them. In this sense, the presented EU projects FRAXIGEN and “Conservation of Elm Genetic Resources” are good examples to be imitated. Finally, although it is true that in conservation biology rarity attracts, in most cases this attraction has good fundamental reasons.

Session B2 – Conservation of widespread species (*Florian Scholz & Felix Gugerli*)

The session covered issues in relation to the conservation of widespread forest tree species, a subject which is often overlooked given the concerns for those species that are rare and vulnerable in a short-time perspective. The four oral presentations and the five posters displayed a wide variety of issues and addressed problems of various dimensions. These ranged from local to large-scale focuses and presented different approaches for assessing, monitoring, and attempting to conserve forest tree species and their genetic diversity.

Conservation efforts usually follow a series of sequential actions, which are called for once a threat has been detected. The regionally dramatic situation was illustrated with examples from SE Asia, where large forest areas have been destroyed in the past 30 years. In order to compile the distributional background for the species of concern in British Columbia, a GIS-based approach was presented, which included information obtained from botanical inventories, potential threats, forestry practices, etc. Monitoring strategies for the assessment of the health status in Ukrainian conservation reserves established in the early eighties were exemplified for European beech. Parameters resulting from the analyses of molecular markers nowadays are often part of the characters used for setting priorities in the selection of potential conservation areas. An example from a tropical forest tree species indicated possible conclusions that may be drawn based on the historical information obtained from population genetic information, whereas the case study in the temperate Sitka spruce reminded us of the sampling problems when aiming at conserving either frequent and widespread or rare and local alleles.

It became obvious that conservation efforts not only

need to consider a suite of different criteria, but are also confronted with highly divergent interests. The catalogue of selection criteria applied in Slovenia showed how long a list of considerations may be and how difficult it is to set the relevant priorities. It is evident that different groups of stakeholders may have highly divergent interests leading to opposing priorities. Specific examples for the collaborative approaches used during the implementation of a gene conservation program were given for the case of Switzerland. Needless to say: international co-ordination is mandatory for an effective and reasonable attempt in conserving genetic resources of widespread species, as advocated by a poster from Scandinavia.

There remained three basic questions that arose from the session’s discussion: (i) What are the threats specific for widespread species, (ii) where do we need to set priorities when aiming at the conservation of these species, and (iii) what can we learn from molecular markers and/or phenotypic traits with respect to the relative importance of target areas?

Session B3 – Conservation of domesticated species (*Jaroslav Burczyk & Sven de Vries*)

The impact of human activities on forest ecosystems is continuously increasing. At the same time several forest tree species are being intensively domesticated. From a genetic point of view, the domestication may be broadly considered as all human activities altering genetic diversity of populations, including selection through tree improvement, distant transfers of forest reproductive material (FRM) and environmental changes affecting reproductive patterns and adaptability potential. While most of the temperate forest tree species are subjected to domestication (in a broad sense) there are examples of trees, where this process occurred most intensively influencing the species status.

The session B3 on conservation of domesticated species included one invited presentation, nine voluntary presentations and seven posters. It was shown how domestication affected various forest tree species (eg. black poplar, radiata pine, chestnut, cherry, wild apple, some oak species) and how genetics may be helpful for understanding their current status and future conservation. Several important aspects of domestication have been raised in the presentations, the posters and also in the discussion during this particular session, some of which are summarized below.

The extent of natural populations of highly domesticated species is declining, which potentially may affect their genetic diversity and adaptability. Therefore one of the efforts that needs to be taken is to monitor and

maintain genetic diversity in natural populations, which may serve as a basis for population restorations and for new selection criteria in tree improvement programs. Whenever possible, genetic diversity should be maintained through domestication processes, although so far there is little evidence for large genetic differences between natural and cultivated populations, at least based on neutral genetic markers. Maintaining genetic diversity, however, depends mainly on silvicultural management practices and it is the role of geneticists to show impacts on decision makers and to convince them to implement genetic conservation. Little is known of what the current or potential impacts can be of domesticated populations on natural stands through gene flow and hybridization, and this issue becomes important as more plantations are being established in close proximity to natural populations. It is generally agreed, that we certainly need empirical data obtained from well designed experiments in order to be able to account for gene flow from cultivated to natural populations and for hybridization processes. There is a need to develop genetic tools (markers and protocols) for monitoring the transfer and diversity of forest reproductive material (FRM), which is especially important for intensively domesticated species. Some examples from poplars are already being implemented on a larger scale. Interest-

ingly, there were no reports concerning genetically modified trees (GMO), however, it is anticipated that the development of genomics in forest trees, which will likely affect mostly the domesticated species, may emphasize the importance of GMO issues in the coming decade.

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*Antoine Kremer
Marie Pierre Reviron*