

Forests at the limit: evolutionary – genetic consequences of environmental changes at the receding (xeric) edge of distribution.

Report from a researcher workshop

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In view of expected climatic changes, the adaptive potential of forest ecosystems and the future risks of diversity loss and extinction have received much attention. The behaviour of a species and of a population under changing conditions depends on their adaptive potential (genetic diversity, persistence, plasticity).

In ecology, judging of adaptability is based on the concept that presence of species (distributional patterns) depend – among other factors – on the physiological tolerance limits to climatic effects. This concept has to be extended, however, by the assertion that physiological tolerance is unquestionably determined by genetics. Limits of tolerance are therefore genetically set and will determine the presence or absence of species. Thus, adaptive response to environmental stress is to a large extent a genetic issue, especially at the limits of distribution where shifts are expected.

Publications on climate change-triggered vegetation shifts in the temperate belt are abundant. Studies and analyses deal however mostly with the shift of the thermal (“upper” or “front”) limits of distribution. Migration at the front or forward colonisation is the most visible and illustrative response to climate change. On the other hand, retreat at the rear and xeric limits is insufficiently studied in spite of its ecological importance. Xeric species margins may be defined as low altitude and low latitude limits of species distribution along a moisture balance gradient. In the northern hemisphere, xeric distribution limits of forests and forest tree species extend across the woodland ecotones of the Mediterranean, Southeast Europe, South Siberia and North America. The forest cover in these densely populated regions bear high ecological and social values, it is therefore an imperative to evaluate available knowledge with the objective to mitigate effects triggered by rapidly changing conditions. At the xeric limit, selection pressure may narrow genetic variation and the increase in frequency of extreme events may result in growth decline and mortality.

What makes the problem of climatic selection at the xeric margin so special? Processes are there fuzzy, more difficult to follow than at the front limits, and changes cannot be coped by spontaneous processes alone. Human effects are omnipresent and ecological-socioeconomic consequences serious. Therefore additional efforts are necessary to properly

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understand the heritable background of ecosystem responses, to involve research communities active in related fields, and to make results understandable for stakeholders.

With the support of the European Network of Excellence „EVOLTREE”, a researcher workshop was organised in Sopron (Hungary) by Prof. Csaba Mátyás (University of West Hungary) to provide a forum for discussions and to support the surfacing of new concepts. The aim of the meeting was to present the state of the knowledge and to identify future research needs with the objective of finding ways to mitigate climate selection pressure effects at the receding edge of distributions of forest tree species. The intention of the organizer was to broaden both the geographic and disciplinary scope of the theme to reveal the global character of the problem and to raise awareness for the issue of the xeric (lower) limits of forests. The location in Sopron was selected because it is situated at the receding (xeric) edge of closed temperate European forests and of main stand-forming species, where predicted effects of climate change are most threatening.

The consultation took place May 11-15, 2009. More than 40 invited scientists from Europe and North America took part in the sessions and discussions which covered three thematic areas:

1. Ecological, demographic and evolutionary perspectives of marginal and receding populations,
2. Genetic implications of extreme selection events: genomics of adaptation, genetic background of tolerance and plasticity,
3. Experiences from field trials, tasks for human intervention and research gaps at the receding edge of ranges.

Two excursions presented symptoms of dieback and pest damages caused by climatic extremes, experiences with human-aided migration (species introductions) and currently applied silvicultural countermeasures in three state forest companies. During the closing discussion, conclusions and recommendations were formulated, the edited version of which is presented here.

MAIN CONCLUSIONS AND RECOMMENDATIONS OF THE RESEARCHER WORKSHOP DISCUSSIONS

Some definitions about range limits

Range limits of species follow the shift of environmental conditions. Receding limits appear at the rear of species ranges moving in one direction. Rear edge margins contain populations that have remained roughly in place for a very long time (usually in favourable topographic situations), at least since the Last Glacial Maximum, and their evolutionary trajectory has been largely independent of population dynamics across the main range. Trailing edge populations are left behind the contiguous range shift.

Xeric species margins may be defined as low altitude and low latitude limits of species distribution areas along a moisture balance gradient. Although determined primarily by climatic factors, xeric receding edges may also be influenced by interspecific interactions, edaphic conditions, anthropogenic effects etc.

Xeric receding species margins are affected by climate change

Receding edges, especially xeric limits are seldom addressed in the literature. This may come from the fact that they are not perceived as endangered because marginal populations often belong to widespread species. Also, no major shifts are noticeable there (although there are documented reports of increased dieback due to climate change and including insect

outbreaks triggered by increased drought). Xeric range margins often occur in areas where species do not currently raise economic or conservation concerns. Although all climate models predict an increase in frequency, duration and intensity of drought, there is great uncertainty not only in species distribution models (effects of socio-economical and political decisions, lack of ecological variables, spatial resolution) but also in predicted climate scenarios themselves. This may have a disproportional impact on our ability to predict the fate of marginal populations. Current bioclimatic envelope models, set at species level are not accurate for determining the fate of xeric as well as of other edge populations.

SOME QUESTIONS THAT NEED URGENT ANSWERS

1 Where are xeric range margins?

Current xeric range limits of species (external limits) are often not well defined and difficult to assess for at least four reasons: (1) species range margins are ecologically very heterogeneous and fuzzy, especially where orography is complex (Mediterranean, Balkans) and soil is very heterogeneous; (2) low elevation / low latitude land has mostly been converted to agriculture, often leading to local extinction of marginal occurrences; (3) forest management is often artificially influencing survival and regeneration, thus obscuring natural processes; (4) lack of coordinated research. Without this information, processes affecting local population persistence at range margins will not be properly understood. Delineating xeric range margins will also help improve climate envelope models.

2 Can changes at the receding edge be predicted reliably?

On ecosystem level, climatic change triggers alteration of competitiveness and brings manifold risks. The response of populations to climatic extreme events at the xeric limit will be decided on the one hand by species-specific response set by the genetic system, and on the other hand by difficult-to-forecast interactions and calamities, caused by known and/or newly emerging pests and diseases. There is a need for long term monitoring using for example remote sensing, permanent field plots, multi-species (community level) age class spatial structures and reproductive success measurements, dendroecology, etc, to assess past and future changes at range limits.

3 Are xeric edge populations valuable for conservation and future adaptation?

Populations at range margins are often perceived as not valuable for conservation assuming that they may contain less genetic diversity. However, many ancient lineages may persist in edge populations. Because of selection and drift (among other factors), these may also contain divergent genetic resources and unique adaptations. Under climate change, sites of xeric edge populations will undergo strong ecological changes. Purifying selection may be strong, in spite of potentially significant gene flow.

Extreme events may cause population extirpation and ancient lineages may disappear, along with their original genetic make-up. On the other hand, populations have strong ecological resilience, reasons of which clearly need to be better understood, such as evolutionary history, genetic system of species, epigenetics and phenotypic plasticity, or community dynamics. Basic information on genetic (neutral and adaptive) and phenotypic diversity of populations is still needed at xeric range margins.

4 What are the adaptation processes involved at xeric range margins?

Xeric margins are areas where populations face significant genetic adaptation challenges under any type of environmental change, but particularly under climate change. Several cutting edge tools and approaches are relevant to address adaptation at the xeric edge. Molecular genetic methods allow for the identification of selection signatures, clinal variation of adaptive traits and association between marker loci, genotypes and related adaptive traits (e.g. genes related to stress tolerance, to phenology, to hydraulic conductance, etc). Association mapping is particularly promising for trees. Also, epigenetic processes, their duration and the species they are expressed in should be better understood, as they could contribute to explain phenotypic plasticity, and can counteract maladaptive gene flow. Hybridization is another process that need to be more deeply investigated (e.g. in species complexes such as *Quercus*, *Pinus*, *Abies*, etc) and may be exploited for genetic rescue. As a tool, provenance tests (and reciprocal transplants) are very valuable although new tests are needed that include marginal populations as well as marginal test sites (and possibly also species mixtures). More generally, a better understanding of the relative importance of gene flow, drift, selection and genetic buffering (plasticity, epigenetics) processes, locally at range margins as well as range-wide, is definitely needed.

5 A combined genetic and ecological (demographic) approach is needed

General models and investigations, including demographic (mating system, seed production, dispersal, recruitment dynamics) and genetic processes, possibly set at the community level (e. g. including at least insects) and including population level information, are needed to describe, understand and then simulate receding edge population dynamics under climate change. Functionally meaningful phenotypic traits that are easy to monitor, need to be measured over large sample sizes and over long time.

IMPLICATIONS FOR FOREST MANAGEMENT AND CONSERVATION

Research findings have to gain access to long-term management and conservation strategies. This includes principles of selection and maintenance of conservation areas, rules for reproductive material use (seed zone delineation, seed/plant transfer) and adjustment of silvicultural methods (regeneration techniques, regulation of stand structure) of managing ecosystems at the receding edge of distributions. Compared to spontaneous natural processes, shifts triggered by current and future climatic changes are too fast. Therefore human support for persistence and resilience of ecosystems seems to be inevitable, including human-aided migration (introduction, transfer) of species which bears additional risks.

These alternative approaches, with all the uncertainties they may contain, need to be tested very soon.