

HOW WELL CAN EXISTING FORESTS WITHSTAND CLIMATE CHANGE?

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Introduction

There is widespread concern that forest tree species may not be able to cope with future environmental changes. Such concern arises from the discrepancy between the generation period of trees and the time span of climate change, in addition to the general assumption that, according to palaeoecological data, the rate of evolution is slower than the rate of present climate change (Davis et al. 2005). Expected temperature increases are far higher than those that occurred during the interglacial periods of the Quaternary. The concern also stems from the growing body of papers predicting extinctions in plants and animals as a result of climate change (Thomas et al. 2004; Thuiller et al. 2005). This debate was further strengthened by the publication of forecast distribution maps for forest trees at the end of the current century that clearly indicate that major changes, if not local extinction, may be expected (Thuiller 2003; Badeau et al. 2005). However, none of these papers have considered the various responses that tree species may adopt and the evolutionary changes that populations may

undergo. For example, the niche-based models that are used to predict future distribution of species are based on the conservation of species' climatic envelopes, ignoring the capacity of populations to modify their ecological niche (Thuiller et al. 2006). In this paper, I will challenge these views by confronting these perspectives with recent results obtained in population genetics of forest trees, and expectations based on evolutionary processes.

'How fast will a tree population respond to climate change?' remains one of the main questions. Monitoring evolutionary changes in trees is a challenging task, as only diachronic approaches can be used; hence, there is a dramatic lack of experimental data to answer this question. There are, however, various sources of information that can be assembled to provide arguments as to how trees may be able to cope with the ongoing climate change: results of provenance tests, quaternary palaeoecological records of evolutionary changes, and artificial transfer of populations from cool to milder climates.

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I will review the results from these sources and proceed in four steps. The first part will be devoted to the description of the genetic mechanisms that are likely to promote evolutionary changes in response to climate change. These mechanisms will be described at individual, population and species level. I will then examine the time scales at which these mechanisms are acting. The third part addresses the essential argument concerning evolutionary rates in trees: 'How fast do trees evolve?' and 'What records of evolutionary change are available?' The final part tackles the potential responses of tree populations in terms of risks of extinction, local adaptation and migration.

Evolutionary mechanisms

Evolutionary mechanisms contributing to the adaptation of a given species may be acting at different levels: individuals, populations and species. I will review some of these processes, and concentrate on those that have been at least partly documented in the forestry literature.

Evolutionary mechanisms at the individual level

Adaptive mechanisms of individual trees have been gathered under the generic term *plasticity*, but they may actually cover different processes, acting separately or in combination.

Individual heterozygosity

There is a wide body of literature on the distribution of individual heterozygosity

in tree populations, based on isozyme investigations (see Bush and Smouse (1992) for a review). Older stands exhibit usually higher heterozygosity than younger stands. Interpretation of these results is still controversial, as some authors advocate that increased heterozygosity was the mechanistic consequence of elimination of inbred genotypes, due to correlation between homozygosity and inbreeding depression (Ledig 1986). Others have claimed that heterozygosity at the specific study loci (overdominance) contributes to higher fitness (Mitton and Grant 1984) or that heterozygous individuals exhibit greater buffering capacity towards environmental change (Mitton 1997). Whatever the evolutionary significance of heterozygosity might be, there are examples where individual heterozygosity has been correlated (surrogate or cause?) to adaptation to strong environmental changes. This is illustrated by the comparative analysis of heterozygosity in sensitive versus tolerant beech populations in heavily polluted areas during the late 1970s in Germany (Müller-Starck 1988). In this example, the observed heterozygosity of each tolerant beech population was greater than the heterozygosity of sensitive populations wherever the comparison was made, and the difference was larger at higher altitudes where pollution was stronger.

Acclimation

Acclimation is the phenotypic change of a single individual to gradual environ-

mental modification, i.e. it is a reversible process. The premature leaf fall of some trees during dry summers is an example of rapid acclimation. A well illustrated case of acclimation response over the lifetime of a tree is the gradual decrease of leaf stomatal density on a single birch tree that was observed over 50 years (Wagner et al. 1997) as a response to the steadily increasing atmospheric CO₂ concentration. The genetic basis of such phenotypic response has not been elucidated, and to date it is considered to probably be a physiological adaptation to environmental change. However, a recent investigation in quantitative trait loci (QTL) detection of ecophysiological traits in seedlings of forest trees has indicated that the number and contributions of QTLs might vary substantially according to the CO₂ concentration (Torti 2005).

Epigenetic response

Many epigenetic responses have been documented in plants as a response to temporary, severe environmental or biotic stresses (Madlung and Comai 2004). This review indicates that changes in gene expression may be generated by structural changes (e.g. quantitative modification of repetitive DNA; insertion or deletion of transposable elements) or by change in DNA methylation. Epigenetic effects under milder environmental changes have not received as much experimental support, with the exception of the modifications in chromatin of target loci on vernalization in plants (Sung and Amasino 2005).

In a series of repeated experiments on offspring originating from the same parents but with the mothers raised under different weather conditions, it has been shown that the climate during sexual reproduction influences the development of seedlings (Skrøppa et al. 1994; Johnsen and Skrøppa 1997). It has been clearly shown that the timing of bud break in spring, leader shoot cessation in summer, bud set in autumn and the lignification of the annual ring are all processes that will be advanced or delayed according to temperature during female reproduction. Temperature-induced regulation of the level of gene expression (through methylation) in the developing embryos is supposed to last in the progenies as an 'epigenetic memory' (Johnsen et al. 2005).

Evolutionary mechanisms at the population level

Natural selection has driven population differentiation throughout the natural distribution of forest trees. The response is a continuous shift in gene frequencies or phenotypic values of traits. There is ample evidence of the efficiency of natural selection shown by the large body of literature on provenance tests (see Wright (1976) and Morgenstern (1996) for reviews in North American species, and König (2005) for a review in European species). In almost any tree species for which provenance tests have been established, significant variation between populations has been observed for fitness-related traits. There are sev-

eral clinal patterns of geographical variation that are congruent across species living in different continents, suggesting that these patterns result more probably from directional selection pressures than from stochastic, demographic or historical effects. For example, bud burst shows a clear latitudinal variation in all conifers, with northern provenances flushing earlier and setting bud earlier than southern populations (Wright 1976). Other evidence that selection is the most likely evolutionary force responsible for provenance variation is given by the comparative analysis of 'historical' versus 'geographical' factors of variation. In oaks, it was shown that extant populations stemming from the same source (refugial) of glacial origin but growing today in different ecological sites exhibit strong phenotypic differentiation for fitness-related traits, while the populations are not differentiated for neutral genetic markers (Le Corre et al. 1997; Kremer et al. 2002).

Evolutionary mechanisms at the species level

Besides the processes acting at the individual or population level, there are also important processes acting at the metapopulation level of a species. These may contribute to increasing the fitness of a given population that encounters severe selective pressures. Migration of alien genes through gene flow will change the genetic composition of the receiving population. Subsequent changes might be unfavour-

able or favourable, depending on the source population (Lenormand 2002). If the migrating gene has a positive effect on fitness, it will rapidly increase its frequency in the receiving population. The dynamics of migrating genes (migration rates, subsequent frequency variation and change in population fitness) have never been monitored in forest tree populations, but deserve to receive more attention within the focus of climate change. Clearly, a species that has a continuous distribution across contrasting ecological sites might be able to 'import' genes contributing to higher fitness in areas exposed to severe stress. However, a species having a scattered and disrupted distribution may not be able to benefit from alien genes. Extensive research has been done on gene flow in forest trees at a rather narrow spatial scale (Smouse and Sork 2004; Austerlitz et al. 2004). Most of these theoretical and experimental studies have shown that gene dispersion has both local and large-distance components, as revealed by the existence of the 'fat tails' of the dispersion curve. The second component is, of course, more relevant in the context of climate change, as drier sites where potentially favourable genes are likely to exist, may be separated by rather long distances from the sink population that would benefit from the imported gene. Dispersion from the source to the sink populations may take one or more generations, depending on the spatial connectivity between the two.

Time scales of evolutionary mechanisms

The time scales where these mechanisms may act should be separated into two components (single or multiple generations), depending on whether their effects are cumulative over generations or not.

Mechanisms acting at the individual level will of course take place during the lifetime of a tree. However, they may not be cumulative over successive generations in a directional pattern. Individual heterozygosity would be cancelled out after each generation as meiosis and random mating will disrupt allelic associations in diploid organisms. Acclimation or epigenetic responses may also be erased when passing to the next generation, depending on their inheritance. The genetic basis of methylation or other epigenetic sources of change is not fully understood, and their inheritance remains speculative at this stage.

Natural selection would induce recurrent and cumulative directional evolutionary change over successive generations. Significant effects can already be expected within one single generation. Genetic change within one generation depends on the level of genetic variation (selection differential), and the further cumulative change over generations results from the combined effects of genetic variation and heritability (selection response) (Falconer 1989; Conner and Hartl 2004). Investigations in quantitative genetics of forest trees have shown

that there is large genetic (additive) variance for most traits studied so far (e.g. growth, form, wood quality) but rather low heritability (except for wood physical properties and phenology) (Cornelius 1994; Kremer 1994). Hence, genetic variation, rather than heritability, is the most important driving factor of evolutionary change. Unfortunately, fitness-related traits have not been studied in such detail and the amount of genetic variation for these traits is less known. Nevertheless, based on the data on other traits and the additional results obtained with gene markers, one might also expect a high level of genetic variation. Significant evolutionary changes can therefore be expected within one generation, as a result of the predominant role of genetic variation versus heritability. These speculations are actually supported by the results observed in artificial selection programmes. They show that rather moderate selection rates can lead to important genetic change in the very early generations of selection (Anonymous 2005).

Migration over long distances connecting source populations where genes of interest exist and sink population where they might increase fitness may require a few generations to take place. This remains to be investigated in more detail. Gene flow studies have usually been undertaken at two extreme time scales: (1) instantaneous gene dispersion within one generation, conducted by parentage analysis; and (2) cumulative estima-

tions over long historical time scales, derived from genetic differentiation measures. The research that is required in the frame of climate change is the estimation of dispersion distances over a very few successive generations at the landscape scale.

Evolutionary rates due to environmental change

Evolutionary rates measure the genetic change of a population over time. Change is monitored from the 'ancestral' source population to the extant population (allochronic monitoring, Hendry and Kinnison 1999) and this requires three sources of information: source population, time period and extant population. Allochronic approaches cannot be implemented in trees, as the source population can hardly be accessible. Therefore synchronic approaches have been preferred, which consist of comparing different extant populations that have diverged from a common source population. While allochronic approaches measure evolutionary rates, synchronic approaches measure differentiation rates. Even if there can be strong discrepancies between both rates (Hendry and Kinnison 1999), large differentiation among existing populations bears witness of past evolution. Focusing on differentiation for obtaining indirect estimates of evolutionary rates makes provenance tests of forest trees very attractive. However, an important component lacking in provenance re-

search is the time scale that separated the ancestral from the extant provenances. An additional difficulty in using provenance tests is that our interest in evolutionary rates related to global change is to address only directional changes generated by environmental modifications. However, differentiation results from the contribution of very different evolutionary factors. In addition to the processes mentioned in the previous paragraph, additional demographic and historical trajectories may have influenced population differentiation.

Below, I will provide a few examples where indirect estimates of evolutionary rates were available in forest trees. The results are extracted from provenance tests that were screened for two additional criteria: (1) indication of time scales separating extant provenances from the source populations, and (2) indirect evidence that population differentiation is only due to directional selection generated by environmental change.

Differentiation between 'recently' established populations in Europe

Norway spruce (*Picea abies*) has colonized southern Scandinavia during the last 2000 years by natural spreading or through human-mediated dispersion (Bradshaw et al. 2000; Bradshaw and Lindbladh 2005). This is probably the most recent documented spreading of a European tree species. Provenance tests established with seeds originating from

Scandinavia or North Baltic regions (Hannerz and Westin 2000; Danusevicius and Gabrilavicius 2001) showed evidence of population differentiation for all traits investigated, and particularly for phenological traits. Moreover, the trend of geographic variation follows a clinal latitudinal pattern in each study, suggesting that natural selection occurring during the past 2000 years was the main evolutionary driver of population divergence.

For other European tree species, where colonization was achieved over a longer period, population differentiation is of less interest because the time scale for divergence was expanded over much longer periods. For example, pedunculate oak (*Quercus robur*) and sessile oak (*Q. petraea*) have occupied their extant range in Central Europe since 8000–6000 years ago (Brewer et al. 2002), and they have also diverged extensively for phenological traits (Ducouso et al. 1996). It was further demonstrated that the observed provenance variation in a provenance test was generated by diversifying selection due to different environmental conditions occurring at the original sites of the provenances (Kremer et al. 2002) rather than historical factors.

Differentiation between source and transferred populations (European species)

Seed of forest trees have been transferred by man in many different directions in Europe. In a very few cases, the geo-

graphical origin of an introduced population is documented, and today's comparisons of the source and transferred population offers an interesting opportunity to estimate evolutionary rates. As an example, Norway spruce has been transferred from the Harz Mountains in Germany (latitude 52°N) to central Norway (64°N), and provenance tests were established with three sources of material: seeds collected from the native stands (in the Harz Mountains); the introduced stands in Norway; and Norwegian local populations grown at the same latitude as the introduced stands (Skrøppa and Kohlmann 1997; Saxe et al. 2001). The results showed that offspring of the introduced stands set bud at the same time as offspring of the local autochthonous populations and earlier than offspring of the native source population from Harz (Skrøppa and Kohlmann 1997). The time scales for population divergence is, in this example, one generation. Significant shifts in one generation were also found for frost resistance in Maritime pine (*Pinus pinaster*), in which provenances from the Atlantic coast were transferred inland to the Massif Central of France. After one generation, seedlings originating from the Massif Central stands exhibited higher frost resistance than provenances from the Atlantic coast (Bouvarel 1960).

Differentiation between source and transferred populations (exotic tree species)

Exotic tree species, mainly originating from North America, have been widely

introduced to Europe during the past centuries. Lodgepole pine (*Pinus contorta*) and Sitka spruce (*Picea sitchensis*) in Nordic countries and Douglas fir (*Pseudotsuga menziesii*) and red oaks (*Quercus* spp.) in central Europe are among the well known introduction success stories. Interestingly, in some cases the change in distribution corresponded to a change of climate, mimicking the future predicted climate change in Europe. Similarly to autochthonous tree species that were transferred to other regions, exotic tree species offer unique case studies permitting evaluation of their divergence since their introduction. Northern red oak (*Q. rubra*) is a well documented case. The species was introduced shortly after the French revolution (Timbal et al. 1984) and today it is widespread in Europe. A genetic survey based on cpDNA (chloroplast DNA) showed that introduced populations harbour the same haplotypes as populations from the natural distribution, suggesting that the introduced gene pool is a representative sample of the original germplasm (Magni Diaz 2004). A large-scale provenance test was established in south-western France, and the collection included progenies collected from introduced European stands. Interestingly, the introduced populations, as a whole, exhibited a clear shift in bud burst and leaf coloration from the populations of the natural range (Daubree and Kremer 1993). As the time scale is at most 200 years, these results also provide clear evidence for rapid evolution in Northern red oak.

Other examples illustrating the divergence of exotic species have been reported in Saxe et al. (2001), and are best known by practitioners for formation of landraces in forest trees. The differentiation of landraces might, however, originate from three different causes: (1) directional shifts due to different selection pressures existing in the natural and introduced range; (2) changes in the genetic structures of introduced and natural stands; (3) stochastic shifts due to foundation events or genetic drift effects due to the limited amount of seed introduced. Results should therefore be interpreted with caution, as our focus (in relation to global change) is mainly on directional shifts generated by new selection pressures.

These examples clearly suggest that evolutionary rates might be quite substantial, despite the long generation intervals of trees. Forest tree populations may exhibit significant differentiation in a very few generations. Rapid evolution may result from the contribution of different evolutionary processes acting at the individual, population or species level. An important motor of evolution is obviously the level of diversity that resides within tree populations. There is also a more mechanistic interpretation that derives from the complex genetic architecture of adaptive traits. For a trait that is controlled by a large number of genes, differentiation builds up not only from the differences in allelic frequencies at the different genes, but also from

the complementary contribution of alleles at different genes. As the number of genes increases, so will the number of favourable associations, and they will be captured right at the beginning by diversifying selection (Le Corre and Kremer 2003).

Expected responses to environmental change

Climatic projections for the end of the 21st century predict that today's climatic envelopes of forest tree species will be shifted northwards and eastwards, on average, by a few hundred kilometres (Thuiller 2003; Badeau et al. 2005). In these predictions, the future tree distributions are projected on the assumption that current envelopes reflect species' environmental preferences, which are assumed to remain the same under climate change. To illustrate these predictions in the case of sessile oak and beech (*Fagus sylvatica*), France will be out of their new climatic envelope, whereas central Finland is likely to be included within the envelope. Although strictly based on a 'copy-and-paste' approach of constant climatic envelopes, these projections raise in concrete terms the issues that forest trees are facing. What will happen at the western and southern limits that are likely to be out of the climatic envelope? Will there be a progressive decline of the species and extinctions? Will local populations adapt to the new conditions? What will happen at the eastern and northern limit, where new

areas will be included in the climatic envelope? Will trees be able to migrate at such distances to cope with the shift of the climatic envelope? Species will most likely respond differently to these challenges, depending on their ecology, demographic and genetic structures, and biotic interactions with other species. Additional reasoning on how trees will respond should take into account evolutionary processes leading to changes in their climatic envelope over time. We are lacking experiments to answer these questions, as evolutionary change would need to be monitored over successive generations. However, two sources of information can help to understand and predict future responses:

- lessons of past evolution of trees in response to climate change occurring over longer time scales; and
- results from multi-site provenance tests.

By assembling elements from these sources of information, one can make some speculations on the risks of extinction, migration potential of the species to cope with the shift of the climatic envelope, and adaptation to environmental change.

Risks of extinction

During the past two million years (Quaternary era), forest trees have been confronted with successive glacial periods (lasting from 70 000 to 100 000 years), alternating with interglacial periods (lasting from 10 000 to 20 000 years). More

than fifteen periods generated by orbital oscillations of Earth (so called Milankovitch oscillations) occurred successively during the entire Quaternary era (Hays et al. 1976). These repeated drastic environmental changes were followed by important alternating retractions and expansions of tree species distributions, placing them in different habitats over time and space, and preventing them from specialization. It is thought that repeated climatic oscillations selected species for their dispersability and low specialization (Dynesius and Jansson 2000). Indeed, extinctions of European forest trees occurred between 2.4 to 1.7 million years ago, during the early severe glacial cycles of Quaternary. Many species that existed in Europe at the end of Tertiary, based on fossil evidence, disappeared and are nowadays only present in North America and Asia (e.g. species belonging to *Magnolia*, *Liriodendron*, *Nissa*, *Taxodium* and *Sequoia*) (Skelton 1993). Periodic climate changes during the Quaternary period resulted in important extinction rates during the earlier oscillations, but selected species with reduced specialization and efficient dispersability, mitigating extinction in the long term. It is intriguing to notice that there has been no tree species extinction during the most recent periods, despite the occurrence of very rapid climate changes (Dansgaard-Oeschger events). Indeed, rapid warming episodes occurred during the last glacial periods every 1500 years, followed by gradual cooling over longer periods (Alley 2000). During Dansgaard-Oeschger

events temperature increased by from 5° to 10°C over a few decades. These rates are of the same magnitude as the future predicted changes, but the warming occurred during the glacial periods. No extinction of tree species has been reported from the investigations of those periods. Quaternary evolutionary history suggests that past climate changes have selected species able to prevent extinction, thanks to their rapid dispersion and colonization of contrasting habitats. Natural selection induced by climate changes therefore produced, in particular, species with large distributions in northern latitudes (Dynesius and Jansson 2000). One might conclude from these speculations that extinction risks under the present climate change are lower for those species, whereas highly specialized species occurring at lower latitudes may be exposed to higher risks.

Migration potential

Postglacial history of forest trees provides additional information on the dispersal capacity of trees. Since trees were major components of past European landscapes, they produced large quantities of pollen that survive in fossil remains (Huntley and Birks 1983). Migration rates were inferred from historical species ranges reconstructed using pollen fossil data for several European tree species (Birks 1989) in the British Isles and on a continental scale in oaks (Brewer et al. 2002) and beech (Magri et al. 2006). The average rate of spreading

varied between 100 and 700 metres per year, depending on species and the periods of colonization. Earlier dispersion rates (11 000 to 9000 BP) were usually higher and strongly correlated with climate change, whereas more recent rates (6000 to 4000 BP) were lower, as competition between species constrained their spread (Birks 1989). Despite the limitation of migration rates derived from pollen data (McLachlan and Clark 2004), these figures could be used to provide some rough estimates predicting future natural dispersion. At maximum, trees would be able to shift their range from 10 to 70 km during the next coming hundred years, not taking into account that land fragmentation and agriculture would actually reduce migration. This is far less than the shifts of range predicted for oak or beech based on the climatic envelope projections, which amounts to a few hundred kilometres (Thuiller 2003; Badaeu et al. 2005). Hence, natural dispersion would need to be assisted by artificial seed transfer to cope with the shifting climatic envelopes.

Short-term adaptation

Predictions of the potential adaptation of trees to climate change can be made from provenance tests that were established under various environmental conditions. When a given provenance is planted in many different environments, the response function of a measured trait can be constructed if the mean value of trait is plotted as a function of any en-

vironmental variable of the testing site. Unfortunately, most provenance tests were established on a limited number of sites and thus do not allow the construction of these functions. There are, however, a few cases where large scale provenance test were established (Rehfeldt et al. 2002 for Scots pine (*Pinus sylvestris*); Rehfeldt et al. 1999 for Lodgepole pine). Rehfeldt and co-workers constructed response curves for two surrogates of tree fitness: survival and height growth as a function of mean temperature of the testing site. These two case studies provided convergent results that can be summarized in three points:

The response curve usually follows a parabolic function, although the maximum of the function is not a peak. The curve reaches a plateau extending over a few Celsius degrees. The plateau indicates, therefore, substantial plasticity in the provenances.

When compared to the temperature where the provenance reaches the maximum value for the fitness surrogate, the temperature of the site where the provenance originates is, on average, lower. The difference being on average 2.8°C in Lodgepole pine (Table 8 in Rehfeldt et al. 1999) and 2.6°C in Scots pine (Page 921 in Rehfeldt et al. 2002) for height growth.

The temperature difference between the inhabited climate and the optimum climate is related to population latitude. Northern provenances tend to be native

to cooler climates than their optimum whereas southern provenances tend to originate from climates near their optimum (Figure 6 in Rehfeldt et al. 2002 for Scots pine; Figure 10 in Rehfeldt et al. 1999 for Lodgepole pine).

These observations suggest that the predicted temperature increase for the next century would still fall within the optimal region of the response curve. These preliminary optimistic results should, however, be taken with caution as they rely only on surrogates of fitness (height growth and survival). Secondly, they concern widespread tree species of northern latitude, which have actually been selected for generalism and plasticity, as described earlier (Dynesius and Jansson 2000). Responses of other tree species of southern latitude and with scattered distributions or highly specific habitats also need to be studied.

Conclusion and recommendations

There is a growing body of evidence stemming from different sources of information (Quaternary evolutionary history; lessons from population and species transfers; provenance experiments) that trees may have resources and mechanisms to respond to climate change. Overall, the pieces of evidence are fragmentary and refer to separate case studies in different time and space settings. It remains an open research field as to how strong and how prevalent these mechanisms will be in the evolutionary setting

of future climate change. Unfortunately, such investigations would need long-term experiments and would not be able to answer short-term concerns. In the meantime, however, a few recommendations can be made for further research that could lead to practical short-term implementations.

Construction of response functions in provenance tests

Provenance tests have been widely established during the past 50 years in Europe, either through national or international initiatives. For most economically important species, the data sets are, however, scattered among different research institutions, limiting their compilation for the construction of response curves. In-depth exploitation of the data—in a similar manner to the Rehfeldt studies—requires assembling the different data sets, and remains undone. Full exploitation may be limited by the heterogeneity of sampling strategies or experimental designs used. Nevertheless, the results of these investigations would provide some clues regarding the transferability of forest reproductive material. A strong recommendation is the assessment of different complementary surrogates of fitness, and particularly sexual reproduction.

Monitoring of evolutionary change in transferred tree populations

There are many historical examples of artificial transfers of tree populations or

species (in the case of exotics). In some cases, these transfers mimicked climate change, e.g. transfer from cooler to milder climate. A review of these scenarios and their final outcome (success or failure) should be made. Of particular interest is the estimation of the evolutionary changes –and particularly adaptation— that was associated with these transfers. Introduction scenarios, including tracking of source populations by molecular fingerprints, could be reconstructed and evolutionary change monitored. These investigations would ideally complement the provenance test analysis, as a few generations have usually elapsed since introduction, whereas provenance tests only reveal changes after one generation. Additionally, transferred populations or species have usually been implemented over larger areas than provenance tests and the transferred material has been tested in a real forestry context, rather than an experimental plantation.

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