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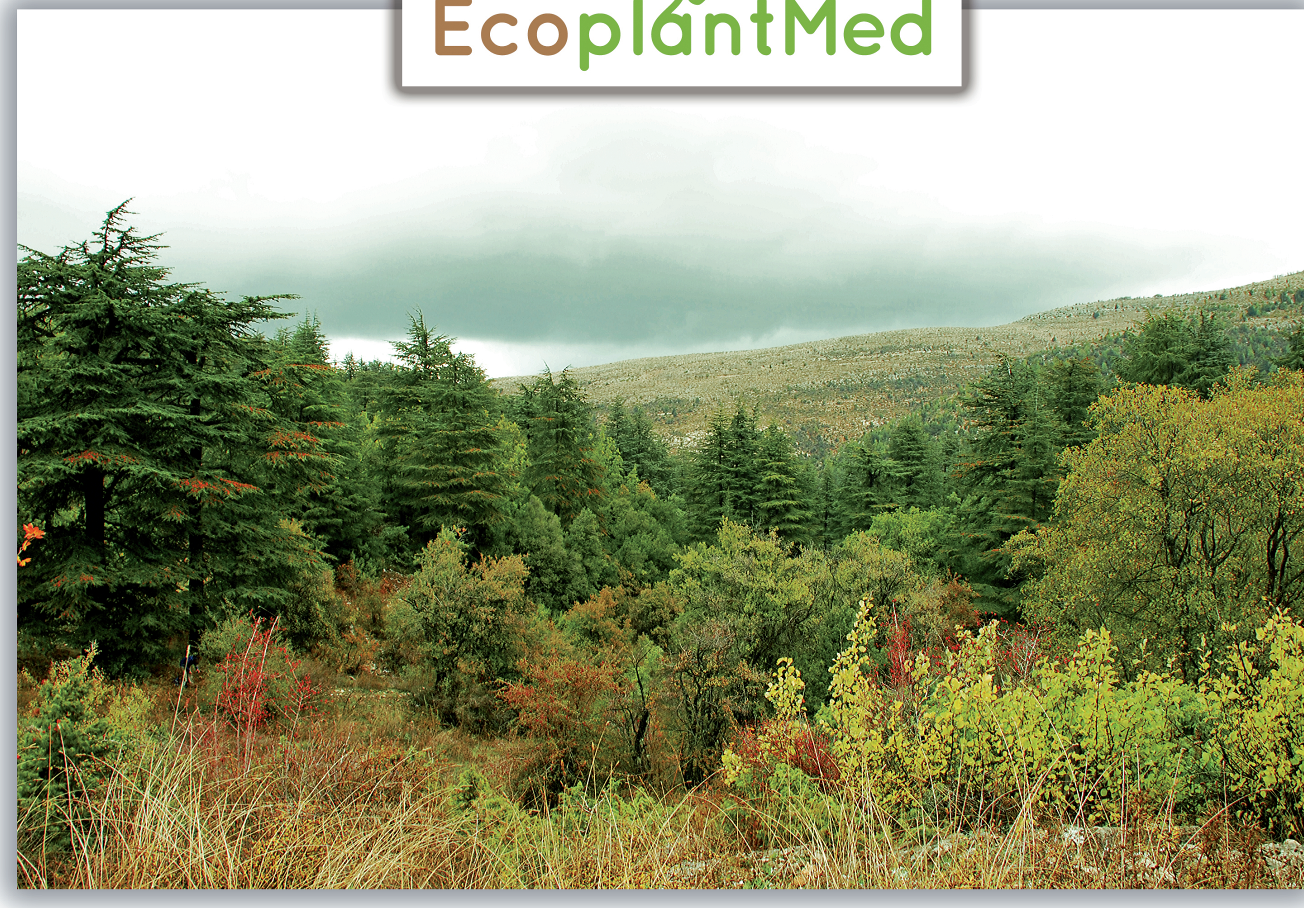

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The relevance of genetic considerations to ensure effective forest restoration

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Abstract
Forest restoration could play a crucial role in ensuring the ecological stability of very fragile ecosystems in the Mediterranean, where rural populations still depend on the environment. Many past restoration efforts did not achieve their expected impacts for a variety of reasons, this paper focuses on one of these: the lack of attention to the genetic diversity of forest reproductive material (FRM) initially used. This paper presents the main factors to be considered, namely (i) the genetic suitability of FRM to the site, (ii) the nature and size of the genetic pool used to supply FRM and (iii) the regeneration potential of the restored forest. In addition, it presents the rationale for a longer timeframe during which key decisions and practical activities in the restoration process take place as crucial for successful ecosystem restoration. The scale of restoration envisaged by many recent international targets would vastly increase the ecological and economic value of currently degraded lands. However, in order to be successful in creating adaptable, self-sustaining ecosystems, it is essential that forest restoration pays more attention to the genetic composition and provenance of the forest reproductive material used. In order to improve the likelihood of success, the paper concludes by presenting some key policy recommendations for the use of forest genetic resources in forest ecosystem restoration.

Key words: adaptive capacity, ecosystem restoration, forest reproductive material, FRM, forest restoration, genetic diversity, resilience, seed selection.

Introduction

In the Mediterranean Basin, only about 5% of the original extent of forest cover remains today, mainly as a result of human activities affecting this hot spot of biodiversity. Restoration in the Mediterranean could play a crucial role in ensuring the ecological stability of very fragile ecosystems, where rural populations still depend on the environment. The most recent strategy of the UN Convention on Biological Diversity, through the Aichi Biodiversity Targets, adopted the aspirational target of restoring 15% of the world's degraded ecosystems. This goal, one of many, to which countries have committed themselves, while apparently extremely ambitious, could be achieved by doubling current rates of afforestation, forest regeneration and expansion of silvipasture and agroforestry.

Unfortunately, many past restoration efforts failed to some extent or completely (Wuethrich, 2007). Furthermore, past successes and failures have been poorly documented, robbing future efforts of the opportunity to learn and adopt better practices.

One of the main technical causes of non-performance, and one of the most neglected, has been a failure to give the genetic diversity of forest reproductive material (FRM) due to weight. In a meta-analysis of almost 250 plant species reintroductions worldwide, Godefroid *et al.*, (2011) found that knowledge of the genetic diversity of the species introduced, and integrating that knowledge in seed sourcing, enhanced significantly the survival rate from the first year after reintroduction, and that this effect increased over time.

With the importance of genetic diversity in mind, a group of forestry scientists coordinated the preparation of a book-length report on *Genetic Considerations in Ecosystem Restoration Using Native Tree Species* (Bozzano *et al.*, 2014) as an input to the first report on *The State of the World's Forest Genetic Resources*. That book presents the scientific basis and evidence for the importance of genetics in forest ecosystem restoration. This paper summarizes its arguments and recommendations by reviewing the role of genetic considerations in a wide range of ecosystem restoration activities that involve trees. This paper also presents some of the recommendations of the EUFORGEN study on "Use and transfer of forest reproductive material in Europe in the context of climate change" (Konnert *et al.*, 2015).

The scale of restoration envisaged by many recent targets would vastly increase the ecological and economic value of currently degraded lands. However, in order to be successful in creating adaptable, self-sustaining ecosystems, it is essential that forest restoration (especially large scale restoration) pays more attention to planting material, and in particular to genetic considerations. The main factors to consider are: the genetic suitability of FRM to the site, the quality and quantity of the genetic pool used to supply FRM and the regeneration potential of the restored forest. It is also crucial for successful ecosystem restoration to

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understand the timeframe in which key decisions and practical activities in the restoration process take place. Without greater attention to these concerns, rehabilitation and restoration efforts may produce a short-term increase in forest cover, but that cover will not be self-sustaining.

Selection of species and seed

In sites that are not very degraded, where a reasonable population of adult trees is present in the surroundings, and the soil is in reasonable condition, natural regeneration may be the best option, provided that the drivers of degradation can be identified and halted. In all other cases, it will be necessary to bring FRM, in the form of seeds or seedlings, to the restoration site. This requires three decisions that take place during a rather long timeframe and that are often taken by different actors, who unfortunately are frequently guided more by economic constraints than by ecological constraints.

Selection of species

Native species are generally favoured because they will be better adapted to local biotic and abiotic conditions and thus, able to support the biodiversity essential to a functioning ecosystem. In some cases, unfortunately, an absence of local FRM of native species induces practitioners to substitute them with exotic species. While the use of exotic species may be acceptable from a purely production perspective, in line with the ecosystem restoration process, the use of exotic species is generally a bad idea, because exotic species will not occupy the missing niches in the ecosystem. In the absence of local, native FRM, it is better to change provenances rather than species (see below). Nevertheless, in certain cases, exotic species may be useful or even essential to help as nurse crops in order to improve the microenvironment on much degraded sites before planting native species.

Selection of seed

There are certainly cases where better performances of local sources are reported in the literature. For example, among provenances of *Pseudotsuga menziesii* introduced into Oregon, USA, local sources survived an unusual and prolonged period of cold, whereas more distant provenances were badly damaged or killed (Johnson *et al*., 2004). In France, 30,000 ha of *Pinus pinaster* established with frost-sensitive material from the Iberian Peninsula succumbed during the bad winter of 1984-5 (Timbal *et al*., 2005). Experiences such as these, and the fear of damage or loss of the local autochthonous material, have convinced many practitioners that local seed sources are always preferable. However, especially when considering changing climate, it may be better to look further afield.

A working group of the European Forest Genetic Resources Programme (EUFORGEN) recently published a report on *Use and transfer of forest reproductive material in Europe in the context of climate change* that contains several recommendations on the selection of FRM (Konnert *et al*., 2015). Three of the critical recommendations are:

- FRM transfer is a valuable option for adapting forests to climate change;
- Local is not always best;
- Change provenances instead of species when local species show decline.

In essence, these recommendations and others in the report, are urging those responsible for planning and implementing forest restoration schemes to consider a wider impact and longer time-frame than is currently prevalent. The ability of the restored forest to reproduce itself without further intervention, and to be part of a whole, functioning ecosystem capable of delivering a full range of ecosystem services, ought to be the goal of restoration.

One reason to consider non-local provenances is that the assumption that FRM from local sources is well adapted to local conditions, is not always correct. In declining and fragmenting populations, for example, local adaptation may be lower as a result of reduced gene flow and genetic drift. Soil conditions in degraded sites may be quite different from those present when the remaining trees were established. Even reasonably intact forest patches may not be a good source of genetically diverse FRM if they have been subject to intensive management practices, which can modify the breeding patterns of the remaining reproductive trees and result in increasingly inbred seeds.

Inbred seeds often do not establish as well as more heterozygous material. Even when establishment is good, however, the effects of inbreeding may not become manifest until planted trees reach maturity, which can take 30 years or more. Reduced genetic diversity results in a reduced ability to adapt to changing conditions, either through plasticity or through natural selection. Under such conditions, there is a strong possibility that the restored ecosystem will not be self-sustaining, and another restoration effort will be needed. Incorporating more genetic diversity at the outset will avoid such waste. In such cases, it may be advisable to seek seed from locations that are distant in space but closer in current and predicted environmental conditions.

One argument against the use of very distinct genotypes of FRM concerns the deleterious effects of outbreeding depression, when the FRM reaches maturity and mates. While such outbreeding depression, caused by the break-up of linked adaptive complexes, has been discussed as a theoretical counterpoint to inbreeding depression, there is little hard evidence for or against it in trees. As long as some uncertainty remains, and with it the need for focused research on outbreeding depression in restoration activities, practitioners should nevertheless give strong consideration to sourcing non-local FRM.

In seeking non-local FRM, it is essential to consider the ability of FRM to survive any predicted environmental changes. While precise predictions of future conditions are impossible, one can predict that greater genetic diversity in the FRM will allow natural selection to favour some individuals as conditions – biotic and abiotic – change. Genetic diversity is positively related to both the fitness of tree populations and the functioning and resilience of the ecosystems of which the trees are a part. Sufficiently, large diversity is thus necessary to ensure the survival of restored forests.

Diversity of forest reproductive material sources

One key recommendation is that seed for FRM must be collected from a large enough sample (20-60 individuals per source population for each species, depending on reproductive biology and other factors), to ensure that there is sufficient genetic diversity to permit adaptation and thus, the long-term survival of the restored forest. Several general guidelines for tree seed collection exist, and they aim to ensure a minimum level of genetic diversity (for example, 95% of the alleles in a population) with the least amount of effort. Unfortunately, a survey of restoration practitioners suggests that these rules are often unknown or unused (Bozzano *et al*., 2014). This is probably because following the guidelines correctly involves a greater expenditure of effort now, while the effects of lack of genetic diversity are not seen for some considerable time. Incentives to encourage the collection of more representative seed samples would help to ensure the success of restoration projects. The ability to quickly assess the genetic diversity of a seed collection, before accepting them into a restoration effort and investing in, for example, growing them on, would be very helpful.

Perhaps the most difficult factor to include in the selection of sources for suitable FRM is the impact of climate change, which is currently often not considered at all (Bozzano *et al*., 2014). As noted, degraded sites offer less than optimal conditions for seedling establishment and growth. If, at the same time, climate is becoming harsher, that adds further selection pressure. Intuitively, trees in sites that are already affected by climate change could be better adapted to harsh conditions and thus, a good source of FRM. However, one needs to be guided also by a firm understanding of the interactions between genetic and environmental (G x E) effects. Such studies of G x E interactions require multi-location progeny and provenance trials and climate modelling, but while many such trials have been established over the past decades as part of efforts to improve production, data are not readily available in a form that can be analysed to guide the selection of sources of FRM. A concerted effort to locate such information and make it available to restoration practitioners would improve future restoration. Furthermore, the existence of some provenance trials does not diminish the need for new trials to be established in order to inform future restoration efforts. The EUFORGEN report on FRM and climate change cited earlier (Konnert *et al*., 2015) recognises the need for better documentation and for continued provenance research to cope with climate change.

Uncertainty about both the extent of climate change and of potential G x E interactions can pose a risk to restoration. If neither climate change nor genetic suitability can be accurately estimated, one potential solution may be to use seed from mixed sources. Such composite provenance – mixing a large amount of local material from diverse environmental conditions with a medium amount of material from intermediate distances that is ecologically matched to predicted future conditions and a small amount of distant, ecologically diverse populations – could simulate natural gene flow and offer a best bet to secure the necessary genetic diversity and adaptability to ensure successful establishment of a self-sustaining ecosystem (Thomas *et al*., 2014). In the same vein, admixture provenance ignores adaptability and genetic suitability. Instead, seed collection focuses on capturing a wide selection of genotypes from large populations in various different environments; with no bias towards the restoration site (Breed *et al*., 2013). Admixture provenances aims to create a large, highly diverse gene pool that allows natural selection to choose the best-adapted genotypes. For both approaches, decision support tools could assist practitioners to select the best available sources of FRM and to create mixtures of FRM that offer the greatest likelihood of establishing successfully. However, there will always remain a need for researchers who can personally verify the suggestions made by decision support tools on the basis of their actual knowledge of the specific details of the restoration project.

Timeframe

Planning for genetic adaptability 30 years in the future is just one aspect of forest restoration that requires long-term thinking. It takes time to plan for a successful restoration, starting with the need to choose seed sources. Having identified the seed sources, time is needed to identify and collect from sufficient parents and in years of good seed production. Producing seedlings suitable for planting out also takes time, and nursery seedlings are often favoured in restoration projects because they establish more readily. However, genetically ideal material may not be available, especially in commercial nurseries. For that reason, restoration projects may need to enter into dialogue with commercial nurseries to ensure that the nurseries have time both to collect and propagate material to the project's specifications. Failing that, projects may need to establish their own specific nurseries near the restoration site to ensure a ready supply of genetically diverse seedlings from carefully selected sources. In both cases, it is important that nurseries should not discard slow-growing individuals, as these will constitute part of the genetic diversity that ensures future adaptability.

Increasing adaptive capacity

Restored tree populations, like natural populations, may persist if environmental changes are within their range of plasticity or if they can track suitable ecological niches by migration. They may also persist through differential survival and adaptation to new environmental conditions or may go extinct. Avoiding the third fate requires imbuing restoration projects with as much adaptive capacity or resilience, as it is often referred to, as possible. Several approaches are possible.

Large population size, as long as it includes sufficient genetic diversity, is probably the most effective contribution to resilience, by allowing the population to persist in the long term and to undergo evolutionary adaptation. The larger the population, the more likely it is to survive pests and diseases, and environmental extremes such as drought or fire, and the less likely to suffer genetic erosion. Godefroid *et al.* (2011) reviewed several plant introductions and found a positive relationship between the number of reintroduced individuals and their survival rate. Another element in adaptation is the rate of generation turnover. For this reason, it may be a good idea deliberately to create gaps to enable the establishment of a new generation of trees and to use management techniques to rejuvenate tree populations. Connecting restored areas to remaining forests, where possible, will also probably promote long-term survival and adaptation, by enabling gene flow. Mating systems, pollen and seed dispersal distances and mechanisms and landscape aspects of gene flow, such as topography, all need to be considered during the planning phase of restoration projects. In addition, the survival of pollinators and seed dispersers also needs to be a part of project planning, as do other aspects of the surrounding biota, including herbivores and symbionts such as mycorrhizal fungi and nitrogen-fixing bacteria. Finally, rather than focusing on a single tree species for restoration, consideration should be given to restoring a forest of mixed species. As Thomas *et al.* (2014) note:

> Restoration should, as far as possible, create appropriate conditions to foster re-establishment of the interactions and associations between species and genotypes. This should improve success rates for restoration, and promote associated biodiversity benefits. Overall, higher species and genetic diversity are known to improve ecosystem stability, resilience, productivity and recovery from climate extremes, which is of increasing importance under environmental change.

Measuring success

Monitoring the success of restoration needs to take place over a longer period than is conventional, essentially long enough, such that evolutionary fitness can start to be assessed. An extended monitoring phase is important because it may reveal the need for corrective action well after the initial planting. An even more important aspect of monitoring is that short-term monitoring is usually capable of looking only at the wrong, or at least unhelpful, measures. Number of hectares covered and number of seedlings planted, say almost nothing about the future prospects of the restoration. Even short-term seedling survival rates give very little indication of success.

A thorough evaluation of a restoration project needs to cover a long period of time, from establishment through growth to maturity and succession. Such assessments, while necessary, are expensive and extend well beyond the original restoration phase. Nevertheless, continuous or periodic monitoring over a long time span should be built into restoration efforts, not least because the results of such monitoring may guide adaptive management of the restoration to keep it on track.

Currently, very few restoration efforts make any attempt to include genetic indicators in their evaluations. This probably reflects the general lack of awareness of the importance of genetic considerations in restoration efforts (Bozzano *et al.*, 2014). The few positive examples, such as a thorough study of Banksia attenuata in Australia by Ritchie and Krauss (2012), suggest that these restorations were successful, in that there were few differences among the populations studied. In general, however, there is an absence of evidence. It is therefore crucial to further develop user-friendly guidelines and protocols to assist emerging restoration practitioners with the choice of tree species and sources of FRM (Thomas *et al.*, 2015).

Long-term monitoring may require the development of new techniques, for example to measure changes in the genetic diversity of the surviving trees. Ideally, evaluation of different projects would adopt a standard set of techniques and measures, especially for molecular genetic measurements, in order to ensure that datasets are comparable. In this context, the rapid development of techniques poses challenges to standardization, but they could be overcome by establishing baselines of, for example, genetic heterogeneity in thriving populations. Comparisons with such baseline data could indicate how well the restoration is doing. Ideally, practitioners also need better surrogate measurements for genetic diversity for cases in which it may not be possible to obtain molecular data directly.

Conclusion

Giving full weight to genetic considerations in planning forest restorations, greatly increases the probability that restored forest ecosystems, will thrive and continue to provide ecological and economic services into an uncertain future. Thomas *et al*. (2014) offer sets of recommendations (distilled from Bozzano *et al*. 2014) for research and for practice. From these, one overarching recommendation is to establish stronger links between research and practice, because restoration projects have untapped potential to generate scientific knowledge that will improve future restoration. Breed *et al*. (2013) point out that more restoration projects could deliberately incorporate an experimental component, and that doing so would create a virtuous cycle of increased collaboration, reciprocal exchange of information and potentially a more useful presentation of research findings that in turn leads to better uptake and enhanced restoration projects. The need for improved knowledge and practical advice will become even more urgent in future in view of the limited restoration experience of the many new actors likely to emerge in response to major international commitments to restoration goals.

Policy recommendations

Perhaps the most important recommendations, concern the policy background against which restoration efforts take place. Changes here could be a significant driver of improved restoration. Furthermore, the importance of using appropriate and suitable FRM has been highlighted by a decision of the 12th meeting of the Conference of the Parties to the Convention on Biological Diversity in 2014[1], which called for “due attention to both native species and genetic diversity in ecosystem conservation and restoration activities…”.

The key recommendations for the policy are to:

1. Put in place supportive national strategies that create demand for good quality FRM of native tree species. Such frameworks should explicitly address the importance of adequate selection of sufficiently diverse genetics in ecosystem restoration.
2. Identify appropriate incentives and financing mechanisms that will encourage the evaluation of restoration success in a more holistic way. Such evaluation should include assessments of how well genetic integrity and connectivity is maintained and restored.
3. Ensure that existing information relevant for restoration practitioners and researchers, including information hidden in grey literature and local and traditional knowledge, is freely accessible and easily searchable, particularly in local languages.
4. Broaden education and training curricula to promote greater understanding of the importance of genetic considerations in restoration projects. This training and associated material must be targeted at the variety of actors active in restoration, including local nurseries and seed collectors who are an important part of FRM production chains for restoration purposes, but who need training and support to optimize genetic diversity and adaptive potential in FRM.

In many countries, large-scale projects receive subsidies from the government, which offers an ideal opportunity for governments to implement incentive schemes to encourage better use of diverse and adapted germplasm.

[1]Decision XII/19, 2014). https://www.cbd.int/doc/decisions/cop-12/full/cop-12-dec-en.pdf

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