



Genetic considerations in ecosystem restoration using native tree species



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ABSTRACT

Rehabilitation and restoration of forest ecosystems are in growing demand to tackle climate change, biodiversity loss and desertification—major environmental problems of our time. Interest in restoration of ecosystems is increasingly translated into strong political commitment to large-scale tree planting projects. Along with this new impetus and the enormous scale of planned projects come both opportunities and risks: opportunities to significantly increase the use of native species, and risks of failure associated with the use of inadequate or mismatched reproductive material, which though it may provide forest cover in the short term, will not likely establish a self-sustaining ecosystem. The value of using native tree species in ecosystem restoration is receiving growing recognition both among restoration practitioners and policy makers. However, insufficient attention has been given to genetic variation within and among native tree species, their life histories and the consequences of their interactions with each other and with their environment. Also restoration practitioners have often neglected to build in safeguards against the anticipated effects of anthropogenic climate change. Measurement of restoration success has tended to be assessments of hectares covered or seedling survival in a short timeframe, neither of which is an indicator of ecosystem establishment in the long term. In this article, we review current practices in ecosystem restoration using native tree species, with a particular focus on genetic considerations. Our discussion is organised across three themes: (i) species selection and the sourcing of forest reproductive material; (ii) increasing resilience by fostering natural selection, ecological connectivity and species associations; and (iii) measuring the success of restoration activities. We present a number of practical recommendations for researchers, policymakers and restoration practitioners to increase the potential for successful interventions. We recommend the development and adoption of decision-support tools for: (i) collecting and propagating germplasm in a way that ensures a broad genetic base of restored tree populations, including planning the sourcing of propagation material of desired species well before the intended planting time; (ii) matching species and provenances to restoration sites based on current and future site conditions, predicted or known patterns of variation in adaptive traits and availability of seed sources; and (iii) landscape-level planning in restoration projects.

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1. Introduction

Ecosystem restoration is of increasing global interest as part of broader strategies to tackle climate change, loss of biodiversity and

desertification, major environmental problems of our times. This emerging interest was formalized with the adoption of the revised and updated Strategic Plan of the UN Convention on Biological Diversity (CBD) for 2011–2020, which aims for the restoration of at least 15% of degraded ecosystems by 2020 (Aichi Target 15). As approximately 2 billion hectares of land are estimated to have potential to benefit from restoration (GPFLR, 2011; Laestadius et al., 2012), achieving Target 15 would imply the restoration of 300 million hectares, in this time frame.

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Large-scale restoration has been initiated in many parts of the world. In the 1970s, the “Green Wall” was started in China; in early 2000 a similar effort was launched in Africa.¹ Many other large-scale commitments have been made recently, such as: the Bonn Challenge, a core commitment to restore 150 million hectares of lost forests and degraded lands worldwide by 2020; Brazil's Atlantic Forest Restoration Pact (15 million hectares)²; and India's Green Mission (5 million hectares).³ Considering that many restoration projects achieve limited success or fail completely (e.g., Wuethrich, 2007), it is imperative that future projects, representing massive investments, be carried out in such a way as to be sustainable and resilient. The reasons for failures in forest restoration practice are often not well understood but include planting material that is inadequately matched to the environmental conditions at the restoration site and inappropriate silvicultural approaches and techniques (Godefroid et al., 2011; Kettle, 2010; Le et al., 2012; Wenying et al., 2013).

One of the proposed, holistic goals of ecological restoration by lead members of the International Society of Ecological Restoration emphasises “reinstating autogenic ecological processes by which species populations can self-organise into functional and resilient communities that adapt to changing conditions while at the same time delivering vital ecosystem services” (Alexander et al., 2011b). An important consideration in achieving the goal of self-sustaining ecosystem restoration is the genetic composition of reproductive material which affects the success of restoration both in the short and the long term. Genetic diversity is positively related not only to the fitness of tree populations (Breed et al., 2012; Reed and Frankham, 2003; Schaberg et al., 2008) but also to wider ecosystem functioning and resilience (Elmqvist et al., 2003; Gregorius, 1996; Kettenring et al., 2014; Muller-Starck et al., 2005; Sgrò et al., 2011; Thompson et al., 2010). For example, significantly reduced growth was observed in second and third generation seedlings of *Acacia mangium* compared to the mother trees originally introduced to Sabah (Malaysia) from Australia in 1967 which represented genetically reduced sub-samples (Sim, 1984). Self-sustainability of tree populations depends on adaptive genetic variation, combining the potential for survival and good growth and resistance to changing biotic and abiotic stresses (Aitken et al., 2008; Dawson et al., 2009; Pautasso, 2009; Schueler et al., 2012; Tooker and Frank, 2012). Furthermore, the extent of gene flow across landscapes over subsequent generations is important for the successful long-term restoration of ecosystems and tree populations (Céspedes et al., 2003; Cruz Neto et al., 2014; Navascues and Emerson, 2007; Ritchie and Krauss, 2012).

To our knowledge, the success of restoration in terms of establishing tree populations that are genetically diverse and appropriate to the restoration site has rarely been rigorously evaluated. In the few studies we found that were aimed at evaluating the appropriateness of germplasm collection practices in restoration efforts, mismatching of germplasm to site conditions (Krishnan et al., 2013; Liu et al., 2008; Sinclair et al., 2006), and genetic bottlenecks, were common problems. In the case of genetic bottlenecks, source populations for germplasm collection were either declining (Broadhurst et al., 2006; Broadhurst, 2011), or if they were large and presumably diverse, collection practices failed to capture this genetic diversity (Burgarella et al., 2007; Kettle et al., 2008; Krishnan et al., 2013; Li et al., 2012; Navascues and Emerson, 2007; Salas-Leiva et al., 2009).

In this paper we review current practices in ecosystem restoration using native tree species, focusing on the influence of genetics

on long- and short-term success. We build on a thematic study on genetic considerations in forest ecosystem restoration methods that was developed to support the FAO's (2014) State of the World's Forest Genetic Resources report (Bozzano et al., 2014). The importance of genetic considerations in restoration practice is presented in the context of three themes: (i), selecting sources of forest reproductive material among and within species; (ii) increasing resilience by fostering natural selection, ecological connectivity and species associations; and (iii) measuring the success of restoration activities. We identify when and how genetic factors should be considered in the various stages of forest ecosystem restoration, pose key research questions, and conclude by providing practical recommendations for the communities of researchers, policy makers, and restoration practitioners to improve the potential for the long-term success of restoration efforts.

2. Species selection and the sourcing of forest reproductive material (FRM)

2.1. Native vs. exotic and local vs. non-local

In sites with low to intermediate levels of degradation, where soils are largely intact and there are sufficient germplasm sources for the next generation (e.g., mature trees or a soil seed bank), natural regeneration may be the best choice (Chazdon, 2008). This bypasses some of the risks associated with introducing germplasm, by promoting the maintenance of genetic integrity and the recruitment of well-adapted seedlings. However, in sites where: (i) diverse native seed sources are lacking or insufficient, (ii) seed sources suffer from genetic erosion; and/or (iii) active planting is envisaged, the introduction of forest reproductive material from off-site may either be advantageous or the only solution, at least in the short term.

The first decision with respect to planting material concerns species selection. In order to restore self-sustaining ecosystems and their services, native species are generally preferred over exotics, although exotic species may be useful or even necessary in some cases, for example, as nurse crops to ameliorate the microenvironment on very degraded sites (Lamb, 2012; Montagnini and Finney, 2011; Newton, 2011; Thomas, 2014). Native species are expected to be adapted to local biotic and abiotic conditions and thus support native biodiversity and ecosystem function to a greater degree than exotics (Tang et al., 2007). In addition, evidence is growing for the importance of choosing tree species that are representative of different functional groups based on adaptive traits (Aerts and Honnay, 2011; Davis et al., 2011; Laughlin, 2014). However, selecting native species on the basis of functional group requires more knowledge than is currently available about traits associated with their reproductive biology, phenology, and propagation. This knowledge gap may often compromise the optimal selection and use of native species for restoration and result in the selection of better documented, but less suited, exotic species (Boshier et al., 2009; Godefroid et al., 2011; Newton, 2011).

Species choice is followed by the identification of appropriate sources of planting material. If FRM is not adapted to site conditions, there may be severe consequences such as low initial survival or high mortality before reaching reproductive age (Bresnan et al., 1994). Alternatively, and probably more typically, maladaptation to site conditions may be expressed gradually, for example through reduced growth, low competitiveness and poor seed set. Johnson et al. (2004) described another common expression of maladaptation which appeared years after planting. In their example, *Pseudotsuga menziesii* provenances introduced into Oregon, USA, performed well from 1915 to 1955 and then were hit with an unusual and prolonged cold period; local sources survived but

¹ <http://www.fao.org/partnerships/great-green-wall>.

² <http://www.pactomataatlantica.org.br/protocolo.aspx>.

³ <http://www.indiaenvironmentportal.org.in/category/34854/thesaurus/national-mission-for-green-india-gim/>.

off-site sources were either badly damaged or killed. Similarly, 30,000 ha of *Pinus pinaster* Aiton plantations, established in the Landes region of France with non-frost-resistant material from the Iberian Peninsula, were destroyed during the bad winter of 1984 into 1985 (Timbal et al., 2005).

Since the first generation of trees plays a key role in subsequent natural regeneration at a site, if the founder population is established using FRM from a small number of related trees, the consequent low genetic diversity and inbreeding may result in reduced fitness in future generations (McKay et al., 2005; Reed and Frankham, 2003; Stacy, 2001). In particular, if the original planting material is vegetatively propagated and originates from just a few trees, self-pollination can be a problem in the next generation. In a study which compared selfed and outcrossed offspring of clonal *Pseudotsuga menziesii* 33 years after establishment, for example, the average survival of selfed offspring was only 39% of that of the outcrossed trees. Moreover, the average diameter at breast height of the surviving selfed trees was only 59% that of the surviving outcrossed trees (White et al., 2007). When planting material originates from seed collected from a few related trees, inbreeding effects will be less serious, but depending on the amount of mating between close relatives, fitness may be reduced in subsequent generations. Ensuring a minimum level of genetic diversity in founder populations is particularly important in restoration projects, considering that regardless of breeding system, inbreeding depression is more commonly expressed in more stressful environments (Fox and Reed, 2010), such as the degraded soils found at most restoration sites.

There is a general preference in ecosystem restoration efforts for FRM from local sources (Breed et al., 2013; McKay et al., 2005; Sgrò et al., 2011). This is based on the assumption that local FRM has undergone natural selection to become best adapted to the local conditions of a nearby restoration site, an assumption that is not always correct (Bischoff et al., 2010; Hereford, 2009; Kettenring et al., 2014; McKay et al., 2005). Local adaptation may, for example, be hindered by gene flow, genetic drift, and/or a lack of genetic variation. The superiority of non-local genotypes has been demonstrated in reciprocal transplant experiments for some herbaceous plant species (Bischoff et al., 2010), and through provenance trials of some tree species (e.g., *Cordia alliodora*). Excessive emphasis on 'local' germplasm may obscure the fact that geographical proximity to the restoration site is not necessarily the best indicator of the quality or suitability of FRM. In the degraded soils that typify restoration sites, conditions may be very different from those under which local populations originally developed. Environmental mosaics may result in sites far apart having similar ecologies, while closer sites differ.

Where remaining forests near the restoration area are highly fragmented, isolated trees may be inbred, have reduced fitness, or exhibit other negative consequences of small population size, and may not constitute good seed sources (Aguilar et al., 2008; Breed et al., 2012; Eckert et al., 2010; Honnay et al., 2005; Lowe et al., 2005; Szulkin et al., 2010; Vranckx et al., 2012). These conditions can be assumed to be common in many areas where restoration efforts are targeted. The quality of existing local forest patches as sources of FRM must also be carefully evaluated in the light of past or ongoing resource use or disturbance, particularly silvicultural management practices (Lowe et al., 2005; Schaberg et al., 2008; Soldati et al., 2013; Wickneswari et al., 2004). For example, the high intensity of some logging methods may modify breeding patterns in the residual trees and result in increasingly inbred seeds through selfing or crossing between closely related individuals (Ghazoul et al., 1998; Murawski et al., 1994; Ng et al., 2009; Wickneswari et al., 2014, this issue), compromising the population as a seed source. In such cases, sourcing FRM from further away, yet from similar ecological conditions, may be a better option than

resorting to nearby fragmented or intensively logged forests or isolated trees (Breed et al., 2011; Sgrò et al., 2011).

Any introduction of non-local FRM, even of native species, holds risks. If the non-local FRM is of the same species, or closely related to the species remaining on the restoration site, but from genetically distinct sources, there is a risk of genetic contamination of the local populations (Ellstrand and Schierenbeck, 2000; Rogers and Montalvo, 2004; McKay et al., 2005; Millar et al., 2012). Therefore, it is important to try to ensure that FRM is genetically matched to the neighbouring (fragmented) populations of the same species (McKay et al., 2005; Aitken et al., 2008). Gene flow between native resident populations and non-local introduced plants might lead to outbreeding depression. Outbreeding depression occurs when crosses between local and non-local sources produce generations with reduced fitness (Lowe et al., 2005). One theory to explain the occurrence of outbreeding depression is that co-adapted gene complexes are broken up during recombination (Templeton, 1986).

Outbreeding depression is widely discussed, although there is still little hard evidence for or against it in trees (but see Stacy, 2001; Frankham et al., 2011). This might be due to the time required to convincingly demonstrate its effects, which may only emerge after multiple generations (Rogers and Montalvo, 2004), or it may be because many tree species have regular long-distance dispersal events, resulting in sufficient gene flow to avoid complete genetic isolation of populations even when they are geographically distant (Ward et al., 2005; Dick et al., 2008). Outbreeding depression seems most likely to be a risk when high quantities of FRM are introduced from environments that are very different from the local one (Frankham et al., 2011). In light of current uncertainties, it is necessary to carefully weigh the risk of outbreeding depression against the risk that on-going loss of genetic diversity poses to the long-term persistence of populations (McKay et al., 2005; Edmands, 2007; Sgrò et al., 2011). The true risk of outbreeding depression in restoration activities should be tested through experimental research (Breed et al., 2013).

2.2. Climate change considerations in the selection of germplasm

Planning for the expected impacts of climate change complicates the choice of seed sources for restoration. Climate change will have a strong impact on many restoration sites (Hobbs et al., 2009), yet currently few restoration practitioners appear to consider climate predictions in their design (Sgrò et al., 2011; Bozzano et al., 2014). Degraded forest sites typically constitute tough environments for seedling establishment and growth. When the climate simultaneously becomes harsher, natural or planted propagules experience even stronger selection pressure. Tree species generally have high genetic variation in adaptive traits, constituting latent adaptive potential which is expressed only when conditions change (Gamache and Payette 2004; O'Neill et al., 2008; Doi et al., 2009; Thompson et al., 2010; Mata et al., 2012; Alfaro et al., 2014, this issue). Intuitively, the gene pool of surviving trees on sites that are already affected by climate change could provide useful seed sources for sites with conditions that are currently less extreme, but still nearing the edge of a species' tolerance. This is because such residual trees may be better adapted to the extreme conditions.

However, the identification and selection of appropriate sources of FRM for a given restoration site should ideally be guided by the strength of the interaction between genotype performance and current and future environmental conditions (genotype-by-environment, $G \times E$ interactions), which are studied using multi-location progeny or provenance trials and climate modelling, respectively (Sgrò et al., 2011). Globally, some 700 tree species are subject to some level of improvement, including provenance

and/or progeny testing (FAO, 2014). Such tests can help identify planting sources that are adapted to a particular site and the range within which reproductive material of a species can be moved without significant loss of adaptation (ecological tolerance limits). While the oldest provenance trials were of temperate timber species, established both within and outside their natural ranges, more recently there have been more trials of tropical species including those that are important for non-timber forest products. Although many previously established provenance tests were not designed specifically to characterise adaptive traits of a range of provenances across diverse environments, survival and growth are basic measures of adaptation to the site where a trial is planted (Mátyás, 1994). A serious problem, however, is that the results of many provenance trials have not been published and data are not readily available: a concerted effort must be made in support of restoration efforts to locate information and make it available in a form that is relevant to restoration practitioners (see also Koskela et al., 2014, this special issue).

If provenance trials do not exist at the time of planting, it is worthwhile to invest in their establishment, to inform future decisions about the most appropriate seed sources, particularly under climate change. Ideally, provenance trials should cover the range of environments in which the species occurs as well as future environmental conditions where the species may be planted. Often the site conditions in an area to be restored are substantially different from those of surrounding forest; for example, degraded sites may be more prone to drought, include depleted soil or lack other species that would normally be part of a functioning forest ecosystem. Future provenance trials should include such conditions. They should also be established in less traditional plantation formats to mimic natural regeneration, by planting mixed species, at close spacing to encourage early competition, and with minimal intervention (e.g., little weeding), although care must be taken to ensure that the experimental design will lead to robust results. Given the current speed of climate change, it is also becoming more important to factor time into conventional $G \times E$ approaches, which should thus become $G \times E \times T$ assessments (Gallo, 2013).

A growing number of studies recommend the use of seed from mixed sources to anticipate the potential impacts of climate change (Broadhurst et al., 2008; Sgrò et al., 2011; Breed et al., 2013). Depending on the knowledge available and the expected seriousness of climate change, different approaches have been proposed. If both $G \times E$ and climate change are expected to be low for the species of interest, a mix of FRM obtained from local genetically diverse populations may suffice. In cases where either $G \times E$ or climate change are not known, composite provenancing has been proposed as a strategy to increase the adaptive potential of FRM (Broadhurst et al., 2008; Sgrò et al., 2011; Breed et al., 2013). Composite provenancing aims to simulate natural gene flow dynamics by mixing (i) a high proportion of material sourced locally from a range of environmental conditions in the same seed zones, with (ii) a medium proportion of material sourced from intermediate distances (neighbouring seed zones) that is ecologically matched to future predicted conditions (e.g., including FRM from warmer rather than cooler environments) and (iii) a low proportion of FRM from distant populations that are ecologically diverse.

Breed et al. (2013) go one step further by presenting a provenance selection decision tree whereby decisions are based on evidence and confidence limits surrounding climate distribution modelling, and the degree of population genetic and/or environmental difference between populations. They propose an admixture provenancing approach for situations where there is high confidence in substantial climatic change, but where little is known about the $G \times E$ interaction. In admixture provenancing, seed collection is focused on capturing a wide selection of genotypes from large populations occurring in various environments,

with no spatial bias towards the revegetation site and no regard to gene flow dynamics (Breed et al., 2013).

In some cases, habitat conditions will be altered to such an extent by climate change and interacting factors such as land use changes that deliberate movement of FRM along environmental gradients may be necessary (Aitken et al., 2008; Sgrò et al., 2011). In different countries around the world, provenance transfer or assisted migration approaches are already being integrated in restoration and tree planting practices. In Western Canada, for example, a forest regulation has been changed to accommodate new seed transfer rules to better match seedlings to expected future conditions. Ideally FRM transfer decisions should be based on solid field trial data, and provenance transfer planning based purely on climate distribution modelling approaches is still highly controversial (e.g., Seddon, 2010; Sgrò et al., 2011). This is due to the uncertainties associated with both species distribution models and future climate models (for a discussion see Alfaro et al., 2014, this special issue). In situations where no provenance trial data are available, the composite or admixture provenancing described above may be the more prudent approach (Breed et al., 2013).

Species distribution modelling can nonetheless be useful as a first step for guiding the choice of the potential seed sources to be used in the mixtures described above. This is particularly the case when distribution models are used in combination with genetic characterization data, which can provide complementary information about the genetic diversity profiles among and within source populations (Soldati et al., 2013; Azpilicueta et al., 2013). Recent advances in geospatial modelling and the proliferation of ever-cheaper genotyping techniques make it possible to better design restoration efforts at the landscape level, not only for matching FRM to present and/or future site conditions, but also for optimising connectivity of populations (McRae and Beier, 2007).

Although time requirements and the cost of molecular genetic analyses are decreasing rapidly, genetic data is still lacking for many tree species. In the meantime, knowledge about levels and patterns of genetic diversity is often extrapolated to less known species on the basis of similar life history traits (Hamrick and Godt, 1990, 1996), but care must be taken because correlations can be low and experience has shown that patterns of variation for every tree species are different (Rehfeldt, 1994). Among the many potential life history traits that might be expected to correlate with patterns of genetic diversity, Duminil et al. (2007) reported that genetic structure is generally related to mating system (selfing vs. outcrossing) for nuclear markers and seed dispersal mode (gravity vs. other categories) for maternally-inherited markers.

2.3. FRM collection protocols

It is pivotal that germplasm collection missions capture a representative sample of the genetic diversity of the target species that will be used in restoration projects. A number of general guidelines for tree seed collection aim to ensure a minimum level of genetic diversity, such as those published by The Australian Network for Plant Conservation Inc. (Vallee et al., 2004), the University of California (Rogers and Montalvo, 2004), the World Agroforestry Centre⁴ (ICRAF) (Kindt et al., 2006), ENSCONET (2012) and Royal Botanic Gardens, Kew (2003). Today, such guidelines appear to be largely unknown or overlooked by restoration practitioners or those who supply germplasm for restoration (Bozzano et al., 2014; Godefroid et al., 2011). This is probably partly because their

⁴ Also see <http://www.worldagroforestry.org/resources/databases/tree-seeds-for-farmers> for additional manuals and guidelines.

implementation can be time and resource demanding when applied to trees and partly because the negative effects of genetic homogeneity are often not immediately evident but accumulate over time (Rogers and Montalvo, 2004).

Generally accepted rules have been developed for how many samples one should collect to capture at least 95% of genetic variation (measured as alleles) with the least amount of effort. Such rules relate to many factors, such as breeding or pollination system and flowering and seed characteristics (Dvorak et al., 1999; Brown and Hardner, 2000). In general, a smaller number of seeds from many trees is a better sample of the genetic diversity within a population than many seeds from a few trees (Brown and Hardner, 2000). In a completely outcrossing species at least 30 randomly selected trees should be sampled (Rogers and Montalvo, 2004). If there is evidence of substantial self-pollination, a minimum sample of 60 trees is recommended (Brown and Hardner, 2000). Sampling from fewer trees will not capture the range of genetic diversity, whereas collecting more than the minimum sample size is recommended when the main aim is to maintain genetic diversity over generations (Rogers and Montalvo, 2004).

Care should be taken to avoid unintentional selection of traits during seed harvest such as systematically discarding small seed, as this may lead to loss in the germplasm's adaptive capacity to biotic and abiotic stressors such as pests or climate change. Growth rate and timing of flowering and fruiting are other traits that may be subject to unintentional selection. Harvesting seed in a narrow time window can reduce genetic variation in flowering time as well as any correlated traits. Harvesting seed towards the beginning or end of seed maturity may similarly result in genetic shifts in the trait (Rogers and Montalvo, 2004).

2.4. Nurseries

By far the most popular planting material in restoration projects is nursery seedlings, partly because this enhances successful establishment (Godefroid et al., 2011). As a consequence, the possibility of using optimal species combinations and FRM which is both adapted to site conditions and genetically diverse is often limited by what is available in nurseries. Seed collectors and nurseries (private and public) are driven by economic considerations and produce what they expect to sell. Nurseries often minimize the number of species they grow for reasons that may relate to the accessibility and availability of seed sources, strategies to simplify management, to minimize the risk of unsold production or because of a lack of appropriate protocols (e.g., dormancy breaking) (Graudal and Lillesø, 2007; Lillesø et al., 2011). To avoid being subject to the vagaries and practicalities of supply, ideally project-specific nurseries should be set up. Restoration practitioners who plan to obtain FRM from existing nurseries should communicate early on with nursery managers to provide sufficient time for propagation of the desired species and to allow seed collection standards for genetic diversity to be met.

In many large-scale restoration efforts such as in the Xingu, Brazil (Durigan et al., 2013), the Atlantic Forest, Brazil (Rodrigues et al., 2011), and in the water towers of Kenya (Olang and Kundu, 2011), the restoration process often involves large numbers of actors and nurseries, requiring a decentralised approach. In such cases, logistics become extremely important for making quality FRM available to widespread nurseries. Community nursery operators are among the possible actors in decentralised approaches and their involvement can bring additional benefits such as experience with propagation of native trees and knowledge about the locations and distribution of local seed sources. At the same time, it is important to strengthen the capacity of local people in seed collection strategies to ensure the genetic diversity of planting stock (Kindt et al., 2006).

High genetic diversity of reproductive material produced in nurseries can help ensure survival of sufficient numbers of trees that are planted in a degraded ecosystem by allowing for natural selection on site. At the same time, it is important to cull inferior phenotypes and produce plants that are already hardened to the planting conditions, to increase their chances of establishment and survival at the planting site (FORRU, 2006, p. 102).

2.5. Restored populations as future sources of FRM

If properly designed, individual restoration efforts should contribute to the conservation of native tree species and their genetic variation, and can provide FRM for future restoration efforts (Sgrò et al., 2011). The potential of restored forests to become seed sources for future restoration activities should be taken into consideration when planning restoration, especially for rare, endemic or endangered species for which the availability of suitable FRM is often very limited. Efforts should be made to avoid the successive use of seed collections from planted stands with low genetic diversity (e.g., Lengkeek et al., 2005; Pakkad et al., 2008), as this may exacerbate the effects of a narrow genetic base in subsequent populations. Maintaining records of the sources of FRM is essential, as it will inform decisions about future collection and management. Such records will also allow lessons to be learned about the site-adaptability and viability of the original FRM used as the restored forests mature and the fitness of populations can be evaluated (Rogers and Montalvo, 2004; Godefroid et al., 2011; Breed et al., 2013).

3. Increasing resilience by fostering natural selection, ecological connectivity and species associations

Tree populations face three possible fates under changing environmental conditions: (i) they may persist if the changes remain within the range of their plasticity or they are able to track appropriate ecological niches through migration; (ii) they may persist through adaptation to new environmental conditions where they currently grow; or (iii) they may be extirpated (Aitken et al., 2008). These same fates apply to tree-based ecosystems in the process of being restored. Given the uncertainty of future climatic conditions and lack of knowledge of the nature and distribution of adaptive traits in tree species, several measures have been suggested to build resilience to climate change into forest restoration initiatives. Such measures include increasing population sizes, enhancing species and genetic diversity, ensuring the maintenance of tree cover in the landscape for genetic and geographic connectivity between tree populations, and identifying and protecting evolutionary refugia (Ledig and Kitzmiller, 1992; Aitken et al., 2008; Sgrò et al., 2011; Bhagwat et al., 2012; Pauls et al., 2013).

The process of natural selection, necessary for adaptation to occur in place, depends upon population size, amount of variation among individuals, selection pressure and gene flow from neighbouring populations. Thus, the adaptive potential of a tree population in the process of being restored can be expected to correlate positively with its size, at least on the assumption that appropriate reproductive material has been used (i.e. representing sufficient adaptive genetic variation) (Reed and Frankham, 2003; Sgrò et al., 2011). Maintaining evolutionary potential – the ability of populations to both persist over the long term and undergo evolutionary adaptation in response to changing environmental conditions – depends on large, effective population sizes (Sgrò et al., 2011); typically several thousand rather than several hundred breeding individuals (Menges, 1991; Lawrence and Marshall, 1997). Larger population sizes reduce the loss of genetic diversity through drift and buffer against the risk of population loss due to

biotic (e.g. pest or disease) or abiotic stochastic events (e.g. drought, storms or fire) (Alfaro et al., 2014, this issue). It may also be sensible to experiment with planting high densities using highly diverse seed sources and to anticipate relatively high mortality rates that can be expected to result from chronic or acute climatic stress (Ledig and Kitzmiller, 1992; Miyawaki, 2004; Chmura et al., 2011). Based on a review of recent plant reintroductions, Godefroid et al. (2011) found a positive relationship between the number of reintroduced individuals and their survival rate. The rate of generation turnover is key to the capability of tree populations to adapt to changing climate through shifts in trait values from generation to generation. Hence, methods to accelerate turnover rates, such as gap creation, may need to be considered to promote rapid natural selection. Also, the establishment of uneven-aged tree stands is worth exploring for short and long term resilience benefits.

Restored forest should become part of a landscape mosaic, connected to the remaining forest where it exists. Restored areas may often be too small to sustain viable populations of tree species on their own. Therefore, it is important to design restoration projects in a way that effectively connects them to existing tree populations in the landscape or to other restored areas (Cruz Neto et al., 2014), and promotes the migration of tree species, to habitats or micro-habitats within or near restoration sites where environmental conditions best match their requirements for survival, growth and reproduction (Aitken et al., 2008; Newton, 2011).

Connectivity and gene flow are important to foster out-crossing of self-compatible species and sufficient pollen availability for self-incompatible species (Breed et al., 2012). Reduced cross pollination can result in increased selfing and inbreeding depression leading to reduced seed set depending on the species' level of self-incompatibility. Ensuring genetically effective connection requires that mating systems, pollen and seed dispersal distances and landscape permeability to gene flow are taken into account from the planning phase of restoration projects. Although many tree species are capable of high gene flow among populations (Ward et al., 2005; Dick et al., 2008) this varies across species and different types of land use (Vranckx et al., 2012; Breed et al., 2012). To achieve this, special attention should be given to promoting the survival and mobility of pollinators and seed dispersers (Markl et al., 2012), for example, by facilitating their movement across hard edges caused by human infrastructure (this has been done, for example by using bioducts over or under highways).

Historical evidence suggests that the dispersal mode of tree species is an important factor in their persistence under climate change (Bhagwat et al., 2012). Species with high fecundity, small seeds capable of long distance dispersal and short generation times – characteristic of many pioneer tree species – are more likely to both adapt and migrate more quickly (Aitken et al., 2008) than those producing few, large seed. Hence, when designing connectivity networks and strategies, attention needs to be paid to dispersal mode. At a large scale, connectivity between different biotic elements of both natural and cultivated landscapes that cover environmental gradients and in particular steep ecological clines and areas with recent environmental change, will increase the long-term ability to sustain large populations, allow for migration and maximise *in situ* adaptation potential (Alfaro et al., 2014, this issue; Dawson et al., 2013; Sgrò et al., 2011).

Today, most restoration efforts focus explicitly on restoration of the tree component of forest ecosystems, perhaps because trees form the basic habitat matrix, facilitating the occurrence and evolution of other less prominent organisms (cf. Lamit et al., 2011). However, during their growth and development, trees themselves interact with and depend on many other species – pollinators and seed dispersers, as well as herbivores, and symbiotic organisms such as mycorrhizal fungi or nitrogen-fixing bacteria. There is also

increasing evidence that the genetic variation in one species affects that in another species, resulting in complex co-evolutionary processes within entire ecosystems (*community genetics*; cf. Whitham et al., 2003, 2006). In some cases, species and genotype relationships may have significant impacts on successful establishment of a population (Ingleby et al., 2007; Nandakwang et al., 2008), for example, by ameliorating negative impacts of abiotic or biotic stresses such as herbivory (Jactel and Brockerhoff, 2007).

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 (Gregorius, 1996; Elmqvist et al., 2003; Reusch et al., 2005; Thompson et al., 2010; Alexander et al., 2011a; Isbell et al., 2011; Sgrò et al., 2011; Kettenring et al., 2014; Alfaro et al., 2014, this issue).

4. Measuring success

Despite an accumulation of experience of ecosystem restoration over recent decades, it is still common to measure the success of restoration efforts primarily in terms of the number of seedlings planted or their survival in the short term (Menges, 2008; Le et al., 2012). Our review of the literature indicates very few examples of studies that included genetic indicators in evaluations of restoration success for tree populations (e.g., Burgarella et al., 2007; Navascues and Emerson, 2007; Salas-Leiva et al., 2009; Broadhurst, 2011; Ritchie and Krauss, 2012; Li et al., 2012; Cruz Neto et al., 2014). The amount of genetic variation is nonetheless an indicator of functional and resilient ecosystems and hence also the long-term success of restoration activities (Thompson et al., 2010). The omission of approaches that aim to increase resilience through a focus on long-term population viability, even in recent conceptual models that otherwise list extensive success indicators and drivers (Le et al., 2012), is illustrative of a general lack of awareness of the importance of genetics in restoration projects. As a positive example, Ritchie and Krauss (2012) conducted a detailed genetic assessment of restored *Banksia attenuata* populations in Australia, including comparison of genetic diversity, spatial genetic structure, mating systems, pollen dispersal distances and seedling performance between natural and planted populations and their offspring. They found in most cases only negligible differences between the populations, indicating that the case was also one of good restoration practice. In what follows we present, from a theoretical perspective, genetic measures for restoration success in an ideal world.

Successful re-establishment of functional ecosystems can only be truly evaluated in the long term by covering all the main stages in restoration (including forest establishment, growth and maturation; Le et al., 2012). The problem is that such assessments can be expensive and extend substantially outside the time span of most projects. A plan for continuous or periodic monitoring of the progress towards measurable objectives should, however, be an integral part of any restoration effort to allow for adaptive management (Godefroid et al., 2011). Ideally, the baseline for genetic monitoring should include the genetic structure of: (i) remnant trees of the degraded populations in the landscape, (ii) naturally regenerated saplings, (iii) source populations of germplasm used, (iv) seedlings to be used for restoration; and (v) mating patterns in undisturbed and disturbed populations. Such information would allow assessment and a better understanding of the changes in the genetic diversity and structure of populations

throughout the restoration process, the genetic viability of the progeny and, eventually, the success of restoration on timescales over which fitness can be judged. Monitoring changes in genetic diversity must be framed in a biologically meaningful context, to interpret whether any observed changes are within a normal or desirable range, or whether they signal some serious loss that could have negative repercussions (Rogers and Montalvo, 2004; Wickneswari et al., 2014, *this issue*). For example, the loss of selectively neutral traits measured using molecular markers does not necessarily translate into loss of variability in adaptive traits (Holderegger et al., 2006).

The genetic diversity profile of one or more reference natural populations (where possible) from the same seed zone or ecological niche is useful for comparing with the genetic diversity of the developing tree populations under restoration. Use of similar or standardized molecular techniques to assess diversity of restored populations would facilitate comparability and wider applicability of the findings, although the rapid changes in techniques poses problems for standardization. In the long term, databases could be established containing reference levels of genetic diversity per species and for different target areas of restoration. Genetic monitoring of restoration projects could then be limited to measuring the genetic diversity of the restored tree populations and comparing these values with the reference values. In some cases it may be difficult to determine genetic diversity baselines for species used in restoration, for example, when natural populations have been nearly or completely eliminated. In such cases it may be necessary to define a baseline rather than a target to allow assessment of the success of restoration activities. In addition to comparing levels of genetic diversity between restored populations and their natural analogues, where feasible it is also important to compare the genetic connectivity between restored and adjacent populations against a baseline (Ritchie and Krauss, 2012).

A combination of ecological and molecular genetic indicators would provide the best results in genetic monitoring of forested ecosystems (reviewed in Aravanopoulos 2011; Gaudal et al., 2014, *this issue*). However, as many restoration efforts will not immediately include molecular studies to assess levels of genetic diversity, two types of indicators to evaluate genetic composition of restored tree populations are needed: one for situations where molecular studies are feasible and detailed information can be obtained, and another for situations where such studies are not feasible and information must be obtained indirectly (see Dawson et al., 2009), for example, by monitoring the growth and reproductive success of the tree populations established through restoration. However, a more rigorous approach for wider application requires the development of effective surrogates for genetic diversity, the elaboration of which first requires a good understanding of various genetic, biological, ecological and management processes and how they may affect genetic diversity during restoration (Gaudal et al., 2014, *this issue*; Wickneswari et al., 2014, *this issue*). Priority criteria for the selection of species for which to develop surrogate indicators may include existence of baseline genetic data and sensitivity to environmental changes (e.g., based on their life-history traits; Vranckx et al., 2012; Jennings et al., 2001).

A more frequent application of genetic assessments of the success of restoration projects (e.g., Ritchie and Krauss, 2012; Cruz Neto et al., 2014) would permit testing and comparison of the performance of different restoration methods for different species combinations and site contexts. Lastly, while there is an urgent need for better ways to synthesize and distribute knowledge from successful projects for the definition of best practices in ecosystem restoration, it is also important that failures in restoration are reported more systematically to help improve future practice (Godefroid et al., 2011).

5. Conclusions and recommendations

Success in restoring forest ecosystems using native species – as healthy living systems, capable of adaptation and evolution – requires attention to seed selection and sourcing, creating connectivity across landscapes, and building in adaptability for changing climates. Development of measures of successful restoration should include effective indicators of provenance-site matching and genetic diversity. If genetic diversity is not taken into consideration, restored ecosystems are not likely to be self-sustaining as species will have limited ability to adapt to environmental changes and inbreeding which reduces fecundity may become a problem. Embedding genetic considerations into ecosystem restoration protocols will greatly improve the likelihood that the restored forest ecosystems are able to thrive and continue to provide services in the future, especially under progressive climate change. In the following we present a number of recommendations to help fill the main remaining gaps in research, practice and policy that currently hamper the use of native species, as well as the success of restoration projects.

5.1. Future research

1. Strive to establish a stronger link between restoration research and restoration practice. Restoration projects themselves have great potential to generate scientific knowledge, for example, through systematic incorporation of an experimental component (Breed et al., 2013). This may lead to increased collaboration, a reciprocal interchange of information between scientists and practitioners, and hence more practical formulation of research findings that leads to better uptake.
2. Expand knowledge on the factors that currently limit the use of native species, including lack of knowledge on propagation methods, availability of FRM and limits imposed by people's perceptions, and identify ways to overcome these constraints.
3. Study options to safely extrapolate recommendations on genetic issues developed from well-studied species to broader groups of plants with comparable characteristics.
4. Evaluate the impact of different restoration methods on the genetic diversity of restored tree populations depending on species and site contexts, to be able to identify appropriate restoration methods for diverse species and contexts.
5. Identify context-appropriate means for ensuring that restoration projects add value to the landscape in terms of connectivity between populations and habitats, facilitating species migration, as well as complementarity of land uses and livelihoods' of local people. This requires collaboration between natural sciences and social sciences in research projects.

5.2. Restoration practices

1. Strive to increase the variety of native tree species used in restoration activities, and support the establishment of associated species relevant to the re-creation of ecosystem functionality, such as pollinators and seed dispersers.
2. Use FRM that is well matched to the environmental conditions of the restoration site and represents a broad genetic base, and document the origin of FRM.
3. Given the uncertainty of predictions of future climate, aim to promote resilience by maximising species and genetic diversity from sources that are best matched to the site conditions, encouraging gene flow and facilitating species migration to allow natural selection to take place.

4. Plan for the sourcing of adequate propagation material of desired species well before the intended planting time to ensure the identification and production of optimal material for the site and restoration objectives.
5. Consistently plan restoration efforts in the landscape context and seek to integrate them into the surrounding landscape matrix.

5.3. Policies, institutions and capacity building

1. Put in place supportive regulatory frameworks that create demand for good quality FRM of native tree species. Such frameworks should explicitly address the importance of adequate selection of germplasm in ecosystem restoration. For example, mechanisms for the implementation of seed zones for sourcing FRM could be significant for more consistent use of appropriate germplasm in restoration projects (Azpilicueta et al., 2013; Krauss et al., 2013; Sáenz-Romero et al., 2006; Hamann et al., 2011).
2. Identify appropriate incentives and financing mechanisms. These mechanisms should encourage the evaluation of restoration success in a more holistic way that also includes assessments of how well genetic integrity and connectivity is maintained or restored. In many countries, large-scale afforestation projects receive subsidies from the government. Such incentive schemes, as an example, could be used to encourage better use of diverse and adapted germplasm.
3. Existing information relevant for restoration practitioners and researchers, including information hidden in grey literature (Boshier et al., 2009) and that which comes from local and traditional knowledge (Douterlungne et al., 2013), should be made freely accessible and easily searchable, also in local languages.
4. Existing guidelines for the collection of FRM need to be broadened and adjusted to the practicalities of collection and the restoration context, but above all better communicated to and used by restoration practitioners. To achieve this, education and training curricula should be broadened to promote understanding of the importance of using native species and genetically diverse and appropriate FRM, as well as appropriate approaches, in restoration projects. Training and dissemination 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 need training and support to optimise genetic diversity and adaptive potential in FRM.

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