



Seeing the trees as well as the forest: The importance of managing forest genetic resources



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ABSTRACT

Reliable data on the status and trends of forest genetic resources are essential for their sustainable management. The reviews presented in this special edition of *Forest Ecology and Management* on forest genetic resources complement the first ever synthesis of the State of the World's Forest Genetic Resources (SOW-FGR) that has just been published by the Food and Agriculture Organization. In this editorial, we present some of the key findings of the SOW-FGR and introduce the seven reviews presented in this special edition on: (1) tree genetic resources and livelihoods; (2) the benefits and dangers of international germplasm transfers; (3) genetic indicators for monitoring threats to populations and the effectiveness of ameliorative actions; (4) the genetic impacts of timber management practices; (5) genetic considerations in forest ecosystem restoration projects using native trees; (6) genetic-level responses to climate change; and (7) *ex situ* conservation approaches and their integration with *in situ* methods. Recommendations for action arising from the SOW-FGR, which are captured in the first Global Plan of Action for the Conservation, Sustainable Use and Development of Forest Genetic Resources, and the above articles are discussed. These include: increasing the awareness of the importance of and threats to forest genetic resources and the mainstreaming of genetic considerations into forest management and restoration; establishing common garden provenance trials to support restoration and climate change initiatives that extend to currently little-researched tree species; streamlining processes for germplasm exchange internationally for research and development; and the intelligent use of modern molecular marker methods as genetic indicators in management and for improvement purposes.

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1. Introduction

Reliable data on the status and trends of tree genetic resources of present or potential benefit to humans are required to support the sustainable management of perhaps as many as 100,000 tree species found globally inside and outside forests (Oldfield et al., 1998). Recognising the importance of these resources and the need for information, the first ever synthesis of the State of the World's Forest Genetic Resources (SOW-FGR), which focuses on the 'tree' component of forests, has just been published by the Food and Agriculture Organization (FAO, 2014a). The production of this report – which involved synthesising information collected in a common format by 86 countries that together account for over 85% of global forest cover – represents a milestone in assembling

the knowledge needed to better manage forest genetic resources nationally and internationally.

To accompany the SOW-FGR, a series of expert-led thematic studies on tree genetic resources was commissioned by the FAO. These were the starting point from which the reviews that make up this special issue of *Forest Ecology and Management* were developed. In this editorial, we first present some of the key findings of the SOW-FGR, before introducing the content of the reviews. We conclude with recommended priorities for future action, which generally coincide with the Strategic Priorities of the first Global Plan of Action for the Conservation, Sustainable Use and Development of Forest Genetic Resources (FAO, 2014b), based on the findings of the SOW-FGR. The series of articles in this special issue celebrates the heightened recognition – especially through the publication of the SOW-FGR – of the value of forest genetic resources globally, resources that previously received scant attention despite their importance. The articles presented here are also a lament, however, for the ongoing often unnoticed loss of

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these resources, which erodes the opportunities for developing new tree products, and limits the evolutionary potential of forests to respond to environmental change and other global challenges. Geburek and Konrad (2008) discussed reasons why the conservation of forest genetic resources has not worked, including difficulties in assessment, in assigning value and in coordinating management. This series of articles lays out some reasons why such conservation is imperative and recommends actions towards resolving some of the challenges.

Starting with the SOW-FGR itself: of the approximately 8,000 taxa of trees, shrubs, palms and bamboo cited as useful in the individual Country Reports compiled to produce the global report – which represent around a quarter of all the woody perennials estimated to be used regularly by humans (FAO, 2014a) – 42% are indicated to be used for timber and 41% for non-wood forest products (NWFPs). The SOW-FGR indicates that around 30% of these species are actively managed for their products and services, while about half of the 8,000 are indicated to be threatened in some way. Despite their importance and notwithstanding the level of active management indicated by Country Reports, only about 700 of these tree species were recorded to be subject to tree improvement programmes, while the SOW-FGR indicates that genetic parameters have been described for only approximately 1% of all tree species.

Country Reports listed almost 2,300 tree species as national priorities for conservation and management, with economic value in the formal economy a major factor in prioritisation. Country Reports indicated that relatively little attention is given by national compilers of use data to the value of tree products and services in the informal economy, despite their high importance here (as related by Dawson et al., 2014, this special issue). Of the above species, approximately 500 were nominated as priorities for management at least in part for negative reasons related to their invasiveness potential (explored in this special issue by Koskela et al., 2014). The most common priority species globally was teak (*Tectona grandis*), followed by river red gum (*Eucalyptus camaldulensis*), white poplar (*Populus alba*), Norway spruce (*Picea abies*) and common leucaena (*Leucaena leucocephala*) (mentioned by 21, 19, 15, 14 and 14 individual Country Reports, respectively). Taking these five tree species as examples, many of the countries assigning them as priorities for action did not have them occurring naturally, which indicates a strong need for international coordination in conservation and management efforts, something that is indicated by a number of authors in this special issue (e.g., Dawson et al., 2014; Koskela et al., 2014). Four of the five are also mentioned as invasive species in at least one country, hence part of the reason for the overall priority ranking is negative considerations, indicating the necessity for caution in transferring even the most highly valued germplasm among countries.

Country Reports also listed approximately 1,800 tree species conserved *ex situ* in seed banks, botanic gardens and elsewhere, with approximately 600 of these belonging to the aforementioned category of priority species. Without doubt, this significantly underrepresents the number of tree species stored *ex situ*, however, as illustrated by the large number of entries in the Tree Seed Suppliers Directory (TSSD), a database that lists more than 5,800 woody perennial species available globally through seed suppliers' active collections (Dawson et al., 2013; TSSD, 2014). Furthermore, the Millennium Seed Bank (MSB, Kew, UK) currently holds seed of over 10% of the world's wild plant species in long-term storage – including a very wide range of trees – and by 2020 aims to hold 25% (MSB, 2014). A significant problem remains, however, in the limited genetic representation of these collections due to narrow sampling and the lack of passport data that accompanies accessions (Dawson et al., 2013). More data and better coordination of collections are clearly required. Better coordination is also needed

between *ex situ* and *in situ* efforts. Although it is generally agreed that *in situ* conservation is the first line of defence, it is only in Europe that reserves known as dynamic gene conservation units are established systematically to conserve tree genetic resources (Lefèvre et al., 2013).

2. Trees and livelihoods

The first review by Dawson et al. (2014) in this special issue of Forest Ecology and Management considers the value of tree genetic resources for tropical rural communities. What is known and what is assumed about value for different tree products and services? Actual benefits are often not well quantified as exemplified by the Country Reports of the SOW-FGR, where little quantitative information is given. Reasons for this gap in knowledge include ubiquity of use and an absence of appreciation of the benefits of trees and their genetic resources (Byron and Arnold, 1997; Dawson et al., 2009; de Foresta et al., 2013). For example, while Dawson et al. (2014) indicate that there are many citations in the literature to the importance of NTFPs, until a decade ago few of these studies were designed in a way to allow well-thought through development interventions (Belcher and Schreckenberg, 2007). The situation has much improved in the last decade, however, with a number of wide-ranging systematic reviews and meta-analyses being undertaken, culminating recently in the work of the Poverty Environment Network (Angelsen et al., 2014; PEN, 2014). Even today, however, in most cases of NTFP extraction the importance of considering genetic factors in management – such as the breeding system and the effective population size of the source plants – are not given much consideration (Ticktin, 2004).

Agroforestry practices have been widely adopted globally (Zomer et al., 2009) and farm landscapes contain many planted and retained forest trees (AFTD, 2014; Dawson et al., 2013). Although some attention has been paid to the genetic improvement of trees for timber and food production in smallholder agroforestry systems, little attention has been given to trees used for soil fertility replenishment and animal fodder production, despite potential benefits for productivity and green house gas emission reductions (Fisher and Gordon, 2007; Ray, 2002). Further attention to the genetic improvement of indigenous fruit trees, which harbour high intraspecific variation in production traits, has also been recognised as an important intervention for smallholders' livelihoods (Leakey et al., 2012). Notwithstanding the livelihood and environmental benefits, some authors have argued that further tree domestication in farmland should not be promoted because it could have negative impacts for inter- and intra-specific genetic diversity in agricultural landscapes; however, without improvements in yield and quality, farmers may choose not to plant trees at all, which would likely result in a worse situation (Sunderland, 2011).

The major tree commodity crops have all been subject to a degree of formal breeding (Mohan Jain and Priyadarshan, 2009), and landrace and wild populations – often still found in forests – have an important role to play in tree crop development. There are limited mechanisms for production to support the conservation of these latter stands, however, and more attention is required in developing approaches that share costs and benefits. A good illustration Dawson et al. (2014) quote is that of coffee (*Coffea* spp.) production. In this case, Brazil is the largest global producer, but wild forest coffee (*Coffea arabica*) is found in the threatened forests of the Ethiopian highlands: how, then, can Brazil support coffee conservation in Africa (Labouisse et al., 2008)? Another case is apple (*Malus domestica*), which is grown globally but whose centre of origin is Central Asia, where populations of the principal progenitor, *Malus sieversii*, are vulnerable to loss (Williams, 2009). Deter-

mining the potential economic value for breeding purposes of wild and landrace stands of tree commodities is essential for presenting a case for conservation to producers and their governments (Geburek and Konrad, 2008). As Dawson et al. (2014) state, a rare example where such an analysis has been undertaken to date showed the significant potential benefits of conserving wild coffee genetic resources (Hein and Gatzweiler, 2006), and more such analyses for other tree products are required.

3. Transfers of trees

Tree germplasm transfers are deeply integrated into the story of human movement and trade, probably beginning with the introduction of fruit trees, along the Asian ‘Silk Road’ for example, in a timeframe that spans millennia. In the second review of this special issue, Koskela et al. (2014) explore the history of human-mediated tree germplasm transfers since the beginning of provenance research, in particular for the global wood production industry. Benefits and risks of such transfers are discussed as well as the uncertainties around whether the ease enjoyed by researchers and others when importing reproductive material in previous decades will continue. Are potentially cumbersome mechanisms really necessary to ensure equitable sharing of benefits or do the public benefits of unencumbered movement outweigh any losses or risks? This discussion is particularly timely with the coming into force of the Nagoya Protocol that Koskela et al. (2014) discuss.

Germplasm transfers have supported production directly and have led to genetic characterisation through multi-locational provenance trials and molecular marker studies, research that has supported provenance selection and breeding (e.g., König, 2005; Magri et al., 2006; Petit et al., 2002). In the past 60 years, for example, tree improvement has capitalised on the range-wide capture and exchange of genetic diversity of valuable tree species to significantly increase wood yields. In spite of advances in molecular genetics and genomics, provenance and progeny trials are still needed to understand trait variation and their establishment will continue to require the transfer of germplasm.

At the same time, however, as Koskela et al. (2014) indicate, wide germplasm exchange has raised concerns about pest and disease spread and tree invasiveness in natural and anthropogenic ecosystems (as well as the ‘genetic pollution’ of natural stands of the transferred species, when exchange is within native distributions, see Wickneswari et al., 2014 and Thomas et al., 2014, both this special issue). These concerns must be weighed carefully against the benefits of exchange (Carruthers et al., 2011; Richardson et al., 2011; also highlighted in the Introduction above based on the Country Reports of the SOW-FGR). In Europe, for example, invasion by alien forest pathogens has increased exponentially over the last three decades, with living plants (often transferred for ornamental purposes) and soil the main transfer substrates (Santini et al., 2013). The negative effects of such transferred pests and diseases can be exacerbated by climate change, as reviewed by Alfaro et al. (2014, this special issue).

Koskela et al. (2014) note that with the coming into force of the Nagoya Protocol on access to genetic resources and benefit sharing (Nagoya Protocol, 2014), the transaction costs for sourcing tree germplasm (and other plant materials such as leaves and bark) for international research purposes may increase, especially for trees whose natural distributions cover a large number of countries. The danger is that this will slow down international research just at the time when its importance to respond to anthropogenic climate change and other global challenges is increasing (Alfaro et al., 2014, this special issue), and just when new research tools such as advanced genomic methods could support major breakthroughs in production (Neale and Kremer, 2011).

4. Indicators for tree genetic resources

The third review of the series directly addresses the first of the reasons discussed by Geburek and Konrad (2008) for the failure of conservation of forest genetic resources – the lack of appropriate indicators for assessing and monitoring genetic erosion. Such indicators are needed to better understand the potential negative consequences of genetic diversity losses – and to develop ameliorative actions for conservation and sustainable use. Geburek and Konrad (2008) noted that although a variety of molecular markers were available as indicators to assess the status of neutral genetic diversity they do not provide measures of adaptive potential. In the six intervening years since their overview, molecular markers for adaptive traits have received more attention but are still more prototypes than for regular use, and Graudal et al. (2014) recommend using a combination of ecological and demographic surrogates along with molecular markers as the best available solution.

In spite of myriad processes and dozens of measures proposed over the past two decades, Graudal et al. (2014) relate how and why genetic indicators are currently absent from most biodiversity monitoring schemes, and they describe ongoing attempts to fill this gap. Current absence appears to reflect a number of factors, including difficulties (both perceived and real) in the measurement of genetic diversity for many species and a lack of knowledge of the importance of intraspecific variation (Aravanopoulos, 2011; Dawson et al., 2009). As a result, the few available indicators that are concerned with tree genetic diversity are primarily ‘response’ ones, even though – as Graudal et al. (2014) point out – ‘response’ indicators cannot be used independently of ‘state’ ones. A compilation of data by Graudal et al. (2014) from 84 of the Country Reports that inform the SOW-FGR also confirms a general absence of genetic diversity indicator information.

By considering past and current biodiversity indicator initiatives (e.g., CI-SFM, 2014; Sparks et al., 2011; UNEP/CBD/AHTEG, 2011), Graudal et al. (2014) provide a refined framework for a set of genetic-level indicators. The proposed indicators cover multiple geographic scales and diversity, productivity, knowledge and management elements; are based on a genecological approach; and can be embedded within current indicator initiatives. According to the authors, the state of *diversity* should be based on changes in species’ population distributions and diversity patterns for selected taxa, while trends in the *productivity* of the genetic resources under use reflect the potential for further mobilisation. Trends in *knowledge*, including in education and communication, underpin the capacity for further development, while trends in *management* reveal where improvements in current practice are required. With regard to knowledge and management elements, Graudal et al. (2014) relate how loss of competence globally in taxonomy and applied genetic resource management (e.g., in tree seed handling) are therefore particularly serious concerns (Drew, 2011; Graudal and Lillesø, 2007).

5. Forest management impacts

Do we really know how harvesting trees for timber affects genetic diversity? The question is more complex than often imagined and is addressed by Wickneswari et al. (2014) in the fourth review of this special issue. The authors review the effects of timber management practices on tree genetic resources in boreal, temperate and tropical forests. At one end of the silvicultural spectrum, clear-cutting may have similar effects genetically to those caused by significant pest outbreaks, fires and storms (see Alfaro et al., 2014, this special issue) by decreasing population size and connectivity and increasing genetic differentiation and inbreeding. At the other end of the spectrum with close-to-nature forestry, the effects

are closer to those of localised dieback and browsing. Genetic responses for the same silvicultural practice may differ among species and populations, however, depending on the biological attributes of the tree and its ecological status. Important factors include: spatial distribution and density; shade tolerance, mating system and growth rate; past range expansions and contractions (e.g., due to natural climate oscillations); and the overall extent of forest. As Wickneswari et al. (2014) indicate, the length of application of a particular management system is also an important factor.

Controlled harvesting and regeneration experiments in North America include the Ecosystem Management Emulating Natural Disturbance project (EMEND), which began in 1998. This project seeks to determine how forest harvest and regenerative practices can best maintain biotic communities, spatial patterns of structure and ecosystem integrity, compared with mixed-wood landscapes originating through natural disturbances (EMEND, 2014). In another landmark project, the Eco-Gene model (Degen et al., 1996) was used to elucidate the long-term consequences of logging and forest fragmentation in seven Amazonian timber species in the DendroGene initiative, which incorporated data on genetic structure and gene flow collected before and after logging had taken place (e.g., Sebbenn et al., 2008; Vinson et al., 2014).

As Wickneswari et al. (2014) indicate, plantations for wood production may provide corridors and habitat for flora and fauna that support the maintenance of genetic diversity, but they may also have negative effects, such as increasing the pest and disease load. In addition, gene flow from alien (exotic or 'locally exotic', cf. Barbour et al., 2008) provenances may through hybridisation and introgression eventually swamp locally adapted genotypes in natural forests, if plantation areas are large (Fady et al., 2010; see also Thomas et al., 2014, this special issue). Such introgression may, however, not be universally bad, as indicated by Alfaro et al. (2014, this special issue); it is sometimes advocated as a means to generate new evolutionary potential to respond to climate change and other adaptive challenges.

6. Genetic diversity and forest restoration

Why do so many restoration efforts fail? Undoubtedly there are many reasons, but one that has been under-appreciated is a persistent lack of attention to matching species and seed source to the planting site (Bozzano et al., 2014). In the fifth review of this special issue, Thomas et al. (2014) address this topic by focusing on important genetic considerations in ecosystem restoration programmes based on native tree species. The scale of importance of such work is indicated by the revised Strategic Plan of the Convention on Biological Diversity for 2011–2020, one aim of which is to restore 15% of degraded ecosystems globally by the end of the current decade (ABT, 2014). Since it is estimated that two billion hectares of land could benefit from restoration, this would imply successful restoration efforts on an area of 300 million hectares in the next six years.

While currently applied measures of success are often not informative for determining the long-term sustainability of restored ecosystems, as noted by Thomas et al. (2014), many current restoration projects fail to reach their objectives by any measure (Cao et al., 2011; Wuethrich, 2007). Although the reasons for failure are sometimes complex (as illustrated by examples in China; Zhai et al., 2014), inadequate attention to the genetic composition of the planting material used is a contributing factor (Bozzano et al., 2014) that has often not been well recognised or studied, with a few exceptions (e.g., Broadhurst, 2011; Kettle et al., 2008; Sinclair et al., 2006).

Based on their review of current practices, Thomas et al. (2014) recommend measures to increase the potential for success in restoration projects. To reduce the dependence on better-studied – but sometimes not particularly well-suited – exotic species in restoration programmes, more knowledge is required on the reproductive biology, phenology and propagation of indigenous trees. Although locally sourced germplasm may be best adapted to restoration site conditions and therefore be the priority for planting and reseeded, it is important to note that this is not always the case (Breed et al., 2013; McKay et al., 2005). Restoration sites may be particularly harsh and not similar to the environment under which local sources evolved. It is also important to plan for future conditions which may differ significantly from current ones. Local genetic resources may not be sufficiently diverse; those that remain after habitat degradation may, for example, be genetically eroded and suffer from inbreeding depression, due to forest fragmentation and related factors (Lowe et al., 2005; Vranckx et al., 2012). These issues have been explored most extensively as part of the SEEDSOURCE initiative, designed to develop best practice for tree germplasm sourcing in degraded neotropical landscapes (e.g., Breed et al., 2012; Rymer et al., 2014). As Thomas et al. (2014) point out, even when local genetic resources are adequate, it is common practice to collect seed from only a few trees, limiting long-term sustainability of the restored forest.

7. Responding to climate change

The intraspecific diversity of many tree species has facilitated their survival and adaptation to diverse environments including climatic variability over hundreds of millennia. What role can this rich evolutionary potential play in maintaining adapted populations of trees under the rapid changes now experienced in many forested regions? Alfaro et al. (2014) explore this question in the sixth review of this special issue. They relate the mounting evidence for the negative effects of climate change on forests, both through direct (temperature, rainfall, etc., effects on trees themselves) and indirect (e.g., increased pest, disease and fire incidence) pressures. Greater climate-related pest and disease attacks are particularly problematic due to the short generation intervals of most pests and diseases compared to trees. This means that pests and diseases can evolve and spread more quickly under new environmental conditions than their hosts (Raffa et al., 2013; Smith et al., 2008). The devastating attacks of mountain pine beetle (*Dendroctonus ponderosae*) on lodgepole pine (*Pinus contorta*) forests in North America in the last decade, apparently caused by a series of climate-related events including unusually warm winters that allowed overwintering of the beetle, provide a good example (Creeden et al., 2014; Safranyik and Carroll, 2006).

As Alfaro et al. (2014) relate, phenotypic plasticity (the capacity of a genotype to express different phenotypes in different environments; de Jong, 2005), the ability to adapt genetically, and seed and pollen mobility, are all important attributes in responding to climate change events as well as to other human environmental impacts such as pollution (Aitken et al., 2008; Karnosky et al., 1998). High extant genetic diversity and the enormous quantity of seed (each potentially a different genotype) produced by outcrossed parent trees support adaptive responses to change (Petit and Hampe, 2006). The speed at which environments alter in some geographic regions may however be greater than the ability of trees to cope (Jump and Penuelas, 2005). Then, human-mediated responses such as the facilitated translocation of germplasm and breeding may be required, supported by the high genetic diversity in adaptive traits that is often found within trees' range-wide distributions (Aitken and Whitlock, 2013; Rehfeldt et al., 2014).

Although the need for forest management practices to adjust to climate change may seem clear to scientists, practical foresters sometimes question this (Milad et al., 2013). Of more concern to practitioners, for example, may be forest loss due to commercial agriculture and illegal (or otherwise unplanned) logging (Guariguata et al., 2012). In this context, more effective than ‘stand alone’ climate-related measures will be management interventions that are good practice under ‘business as usual’ scenarios. To convince forest managers to engage more actively, they need to be presented with good science-based and economically-costed estimates of the risks and benefits of inaction versus action (Joyce and Rehfeldt, 2013). Alfaro et al.’s review calls for greater recognition of the role of genetic diversity in promoting resilience (e.g., the economic value of composite provenancing; Bosselmann et al., 2008), moves to improve our understanding of the underlying mechanisms and role of epigenetic effects in responding to climate change; and the development and application of straightforward guidelines for germplasm transfers, where appropriate (Rehfeldt et al., 2014).

8. *Ex situ* conservation and integration with *in situ* methods

In the seventh and final review of this special issue, Pritchard et al. (2014) discuss *ex situ* conservation measures for trees, their integration with *in situ* approaches, and the particular roles of botanic gardens in conservation. Botanic gardens have participated widely in the collection and storage of tree seed, pollen and herbarium specimens, and in the establishment of living collections *in vitro* and in arboreta (BGCI, 2014; MSB, 2014). They have, however, moved far beyond their traditional role in *ex situ* conservation and have been widely involved in forest inventory, biological characterisation and threat mapping initiatives that support *in situ* conservation, as well as in the design of *in situ* reserves. From an *ex situ* collection perspective, of concern is the limited representativeness in collections of total intraspecific variation, as botanic gardens have traditionally been more interested in ‘capturing’ species than the genetic variation within them (Kozłowski et al., 2012; Oldfield, 2009). Difficulties in the regeneration of stored tree seed – such as the long period to maturity after planting, large growth form and the outbreeding reproductive system of most species – are also of concern, once seed viability under storage has decayed to the level at which regeneration is required (Dawson et al., 2013). Significant efforts are therefore being made to minimise the need for regeneration by ensuring optimal seed processing before storage and the maintenance of seed in the best possible storage conditions.

As Pritchard et al. (2014) relate, the diagnosis of tree seed storage behaviour is an important undertaking (Sacandé et al., 2004), as it helps to develop predictive biological models to indicate the risks associated with handling seeds with particular features (Daws et al., 2006; Hong and Ellis, 1998). The limited data that are available on tree seed half-lives indicate great variation across species, but it is sometimes measured in hundreds of years (RBG, 2014). Exceptionally, a seed from the date palm ‘tree’ (*Phoenix dactylifera*) germinated 2,000 years after it was first collected (seed found during archaeological excavations at the Herodian fortress of Masada, Israel; Sallon et al., 2008).

In contrast to orthodox seed, the recalcitrant seed of many tree species, which cannot be stored conventionally, apparently lack the ability to ‘switch-off’ metabolically late in development or to undergo intracellular dedifferentiation (Berjak and Pammenter, 2013). Alternative conservation solutions to dry seed storage for trees with recalcitrant seed – such as cryopreservation of shoot tips and embryonic tissue followed by *in vitro* recovery (Li and Pritchard, 2009) – are the subject of research, where the main pro-

gress in recent years has been in vitrification methods (Sakai and Engelmann, 2007). The continuous improvement in knowledge of specific seed storage protocols as well as cryopreservation techniques means that there is growing optimism for many species for which storage of reproductive material had been considered to be impossible.

Until recently, *ex situ* and *in situ* conservation have been undertaken independently with little coordination. Continuing efforts are needed to ensure complementarity between the approaches (and, indeed, with other intermediate, such as *circa situm*, methods; Dawson et al., 2013). This article describes some initial steps in that direction. One central aspect of coordination is gap analysis to identify where deficiencies in *ex situ* collections correspond with areas of high forest lost and threat: such areas may then be priorities for new germplasm collections (Maxted et al., 2008).

9. Outlook

In their analysis of the problems of forest genetic resource conservation, Geburek and Konrad (2008) indicated that one difficulty is the lack of a coordinated approach to effect management. A Global Plan of Action for the Conservation, Sustainable Use and Development of Forest Genetic Resources, devised from the findings of the SOW-FGR (FAO, 2014b), is one important means to address this gap. The Global Plan of Action has four main areas: (1) increasing availability of information on forest genetic resources to facilitate and enable better decision making on sustainable use and management; (2) strengthening and harmonisation of conservation methods to support forest genetic resources and evolutionary processes both inside and outside forests; (3) enhancing approaches to sustainably use and develop forest genetic resources to support livelihoods; and (4) developing more appropriate policies, institutions and capacity-building approaches to support successful planning in the forestry sector. The recommendations of the articles in this special issue are largely in accordance with these priorities, with specific areas for action highlighted below.

Dawson et al. (2014) indicate that to improve the management of tree genetic resources for livelihoods requires a greater understanding of genetic processes in NTFP production (e.g., Baldauf et al., 2013) and more attention to genetic quality in the provision of tree planting material to small-scale farmers. In addition, more work is required to exploit genetic variation in wild and landrace stands of tree commodity crops to develop cultivars that perform better in more resilient and sustainable mixed-species smallholder production systems. Dawson et al. (2014) reinforce the position of Geburek and Konrad (2008) that more attention needs to be given to the proper valuation of tree genetic variation for breeding and production, in order to provide a stronger case for conservation. In the last decade, the field of community genetics has massively grown, with the importance of genetic diversity in sustaining ecosystem services more widely recognised (Moore et al., 2014; Wymore et al., 2014), but this work also requires quantification in monetary terms of the value of genetic diversity, for example, when it is considered in restoration initiatives (Bozzano et al., 2014).

Both Thomas et al. (2014) and Alfaro et al. (2014) stress the need for more provenance trials on tree species, especially on little-researched species that are important not only for the plantation-based wood fibre industry but more generally (e.g., Ræbild et al., 2011). Thomas et al. (2014) indicate that new trials are needed that pay more attention to how restoration sites are different from original habitats and that use less traditional planting formats (e.g., uneven-aged stands, in mixes with other species) to mimic natural regeneration. Alfaro et al. (2014) highlight that further multi-environment common garden field trials are required to provide a better understanding of climate-adaptive variation

within tree species, including in drought, pest, disease and fire tolerance and resistance traits.

For such trials to take place and to further support the characterisation of genetic variation, Koskela et al. (2014) indicate the importance of streamlining the international processes of germplasm exchange for research purposes, in the light of the implementation of the Nagoya Protocol. Such research will also be supported by studies to advance developments in seed and *in vitro* storage technology as advocated by Pritchard et al. (2014), investigations which need to proceed beyond the species level to study intraspecific variation in storage characteristics (Daws and Pritchard, 2008).

Graudal et al. (2014) are positive about the potential to develop appropriate indicators to monitor tree genetic variation. This is because a range of 'state' indicators considered unrealistic only two decades ago can now be proposed for immediate implementation due to advances in geographic information systems, in high throughput molecular genotyping and in bioinformatics. Molecular markers, for example, are now much cheaper to generate and use, and, importantly, can be associated directly with adaptive variation (e.g., Funk et al., 2012; Hansen et al., 2012; Neale and Kremer, 2011). Careful experimental design is however still required if the current disappointingly low level of application of molecular genetic data to on-the-ground forest management is to be increased (FAO, 2004; Jannadass et al., 2009).

Wickneswari et al. (2014) stress that the monitoring of genetic variation at genes that directly relate to productivity and fitness is required to further explore the consequences of selective timber cutting in forests. This is because actual data on how changes in the genetic structure of logged tree populations influence production volumes, timber quality and economic value are surprisingly limited, representing a major gap that must be filled. Graudal et al. (2014) note that the establishment of 'Sentinel Landscapes' in Africa, Asia and Latin America by the CGIAR Consortium Research Programme on Forests, Trees and Agroforestry (FTA, 2014), with each landscape spanning national boundaries and land use systems, provides a new opportunity for testing the validity of indicator methods.

Advances in molecular genetic characterisation that include methods such as next-generation high-throughput DNA and RNA sequencing mean that the low percentage of tree species analysed genetically to date should increase rapidly in the next decade (Russell et al., 2014). An interesting dawning application is in tracking timber origins and species. This is needed to reduce the serious problem of illegal trade in many commercially important timbers, which leads to losses of billions of USD in the formal economy, as well as environmental and social concerns (Degen et al., 2013; Lowe and Cross, 2011). Species that are difficult to distinguish by their wood anatomy can be identified using so-called barcodes – DNA sequences that vary among species but are invariant within (Lahaye et al., 2008). In addition, since geographically-proximate timber trees are (typically) more similar than those farther apart, even trees not individually fingerprinted before harvesting can be tracked based on reference samples, allowing discrimination between legal concessions and illegal harvest zones (see, e.g., GTTN, 2014).

To respond to climate change, Alfaro et al. (2014) indicate the importance of new breeding approaches (e.g., El-Kassaby et al., 2012). This is because current methods are often too slow to respond adequately due to long generation times in breeding cycles (Yanchuk and Allard, 2009). Such approaches are facilitated by advances in genomics, but the importance of participatory domestication, working with local communities, also has much to offer (Dawson et al., 2014; Leakey et al., 2012). Another important issue to address is the role of epigenetic buffering in climate change responses (Aitken et al., 2008). The most well known exam-

ple of epigenetic effects in trees is variation in the phenology of bud set in Norway spruce (*Picea abies*; Johnsen et al., 2009), but similar effects have been observed in other species (e.g., Greenwood and Hutchison, 1996; Webber et al., 2005). There is, however, a general lack of information on epigenetic effects in angiosperm trees (Rohde and Junntila, 2008).

Finally, further studies on geographic patterns of molecular genetic variation in trees in combination with more advanced ensemble methods of past-, present- and predicted future-climate ecological niche modelling are required to understand climate impacts on species and forests, and prioritise geographic regions for conservation (Cavers and Dick, 2013; Lefèvre et al., 2013; Thomas et al., 2012). Because data on tree species distributions are often deficient, the utility of vegetation maps as proxies for distributions is also an important area of research (VECEA, 2014).

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References

- ABT, 2014. Aichi Biodiversity Targets. <www.cbd.int/sp/targets/> (accessed 07.07.14).
- AFTD, 2014. The Agroforestry Database. <www.worldagroforestry.org/resources/databases/agroforestry> (accessed 30.06.14).
- Aitken, S.N., Whitlock, M.C., 2013. Assisted gene flow to facilitate local adaptation to climate change. *Annu. Rev. Ecol. Syst.* 44, 367–388.
- Aitken, S.N., Yeaman, S., Holliday, J., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol. Appl.* 1, 95–111.
- Alfaro, R.I., Fady, B., Vendramin, G.G., Dawson, I.K., Fleming, R.A., Sáenz-Romero, C., Lindig-Cisneros, R.A., Murdock, T., Vinceti, B., Navarro, C.M., Skråpaa, T., Baldinelli, G., El-Kassaby, Y.A., Loo, J., 2014. The role of forest genetic resources in responding to biotic and abiotic factors in the context of anthropogenic climate change. *For. Ecol. Manage.* 333, 76–87.
- Angelsen, A., Jagger, P., Babigumira, R., Belcher, B., Hogarth, N.J., Bauch, S., Borner, J., Smith-Hall, C., Wunder, S., 2014. Environmental income and rural livelihoods: a global-comparative analysis. *Global Development* (in press). <http://dx.doi.org/10.1016/j.worlddev.2014.03.006>.
- Aravanopoulos, F.A., 2011. Genetic monitoring in natural perennial plant populations. *Botany* 89, 75–81.
- Baldauf, C., Ciampi-Guillardi, M., dos Santos, F.A.M., Pereira de Souza, A., Sebbenn, A.M., 2013. Tapping latex and alleles? The impacts of latex and bark harvesting on the genetic diversity of *Himatanthus drasticus* (Apocynaceae). *For. Ecol. Manage.* 310, 434–441.
- Barbour, R.C., Crawford, A.C., Henson, M., Lee, D.J., Potts, B.M., Shepherd, M., 2008. The risk of pollen-mediated gene flow from exotic *Corymbia* plantations into native *Corymbia* populations in Australia. *For. Ecol. Manage.* 256, 1–19.
- Belcher, B., Schreckenberg, K., 2007. Commercialisation of non-timber forest products: a reality check. *Dev. Policy Rev.* 25, 355–377.
- Berjak, P., Pammenter, N.W., 2013. Implications of the lack of desiccation tolerance in recalcitrant seeds. *Frontiers in Plant Science* 4, article 478 <www.frontiersin.org/Plant_Science>.
- BGCI, 2014. Plants for the Planet – Five Year Plan 2013–2018. Botanic Gardens Conservation International. <www.bgci.org/> (accessed 02.07.14).
- Bosselmann, A.S., Jacobsen, J.B., Kjær, E.D., Thorsen, B., 2008. Climate Change, Uncertainty and the Economic Value of Genetic Diversity: A Pilot Study on Methodologies. Forest and Landscape Denmark, Hørsholm, Denmark.
- Bozzano, M., Jalonen, R., Thomas, E., Boshier, D., Gallo, L., Cavers, S., Bordács, S., Smith, P., Loo J. (Eds.), 2014. Genetic considerations in ecosystem restoration using native tree species. State of the World's Forest Genetic Resources – Thematic Study. United Nations Food and Agriculture Organization, Rome, Italy and Biodiversity International, Rome, Italy.
- Breed, M.F., Gardner, M.G., Ottewill, K.M., Navarro, C.M., Lowe, A.J., 2012. Shifts in reproductive assurance strategies and inbreeding costs associated with habitat fragmentation in Central American mahogany. *Ecol. Lett.* 15, 444–452.
- Breed, M.F., Stead, M.G., Ottewill, K.M., Gardner, M.G., Lowe, A.J., 2013. Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conserv. Genet.* 14, 1–10.

- Broadhurst, L.M., 2011. Genetic diversity and population genetic structure in fragmented *Allocasuarina verticillata* (Allocasuarinaceae) – implications for restoration. *Aust. J. Bot.* 59, 770–780.
- Byron, N., Arnold, M., 1997. What Futures for the People of the Tropical Forests? CIFOR Working Paper No. 19. Center for International Forestry Research, Bogor, Indonesia.
- Cao, S., Chen, L., Shankman, D., Wang, C., Wang, X., Zhang, H., 2011. Excessive reliance on afforestation in China's arid and semi-arid regions: lessons in ecological restoration. *Earth Sci. Rev.* 104, 240–245.
- Carruthers, J., Robin, L., Hattingh, J.P., Kull, C.A., Rangan, H., Wilgen, B.W.V., 2011. A native at home and abroad: the history, politics, ethics and aesthetics of acacias. *Divers. Distrib.* 17, 810–821.
- Cavers, S., Dick, C.W., 2013. Phylogeography of neotropical trees. *J. Biogeogr.* 40, 615–617.
- CI-SFM, 2014. Implementing Criteria and Indicators for Sustainable Forest Management in Europe. <www.ci-sfm.org/> (accessed 28.07.14).
- Creeden, E.P., Hicke, J.A., Buiute, P.C., 2014. Climate, weather, and recent mountain pine beetle outbreaks in the western United States. *For. Ecol. Manage.* 312, 239–251.
- Daws, M.I., Pritchard, H.W., 2008. The development and limits of freezing tolerance in *Acer pseudoplatanus* fruits across Europe is dependent on provenance. *CryoLetters* 29, 189–198.
- Daws, M.I., Garwood, N., Pritchard, H.W., 2006. Predicting desiccation sensitivity in seeds of woody species: a probabilistic model based on two seed traits and 104 species. *Ann. Bot.* 97, 667–674.
- Dawson, I.K., Lengkeek, A., Weber, J.C., Jamnadass, R., 2009. Managing genetic variation in tropical trees: linking knowledge with action in agroforestry ecosystems for improved conservation and enhanced livelihoods. *Biodivers. Conserv.* 18, 969–986.
- Dawson, I.K., Guariguata, M.R., Loo, J., Weber, J.C., Lengkeek, A., Bush, D., Cornelius, J., Guarino, L., Kindt, R., Orwa, C., et al., 2013. What is the relevance of smallholders' agroforestry systems for conserving tropical tree species and genetic diversity in *in situ* and *ex situ* settings? A review. *Biodivers. Conserv.* 22, 301–324.
- Dawson, I.K., Leakey, R., Clement, C.R., Weber, J.C., Cornelius, J.P., Roshetko, J.M., Vinceti, B., Kalinganire, A., Masters, E., Jamnadass, R., 2014. The management of tree genetic resources and the livelihoods of rural communities in the tropics: non-timber forest products, smallholder agroforestry practices and tree commodity crops. *For. Ecol. Manage.* 333, 9–12.
- de Foresta, H., Somarrriba, E., Temu, A., Boulanger, D., Feuilly, H., Gauthier, M., 2013. Towards the assessment of trees outside forests. Resources Assessment Working Paper No. 183. Food and Agriculture Organization of the United Nations, Rome, Italy.
- de Jong, G., 2005. Evolution of phenotypic plasticity: patterns of plasticity and the emergence of ecotypes. *New Phytol.* 166, 101–117.
- Degen, B., Gregorius, H.-R., Scholz, F., 1996. ECO-GENE: a model for simulation studies on the spatial and temporal dynamics of genetic structures of tree populations. *Silvae Genetica* 45, 323–329.
- Degen, B., Ward, S.E., Lemes, M.R., Navarro, C., Cavers, S., Sebbenn, A.M., 2013. Verifying the geographic origin of mahogany (*Swietenia macrophylla* King) with DNA-fingerprints. *Forensic Sci. Int. Genet.* 7, 55–62.
- Drew, L.W., 2011. Are we losing the science of taxonomy? As need grows, numbers and training are failing to keep up. *Bioscience* 61, 942–946.
- El-Kassaby, Y.A., Klapšt, J., Guy, R.D., 2012. Breeding without breeding: selection using the genomic best linear unbiased predictor method (GBLUP). *New Forest.* 43, 631–637.
- EMEND, 2014. Ecosystem Management Emulating Natural Disturbance. <www.emendproject.org/> (accessed 30.06.14).
- Fady, B., Brahic, P., Cambon, D., Gilg, O., Rei, F., Roig, A., Royer, J., Thévenet, J., Turion, N., 2010. Valoriser et conserver le Pin de Salzmann en France. *Forêt Méditerranéenne* 31, 3–14.
- FAO, 2004. Preliminary review of biotechnology in forestry, including genetic modification. Forest Genetic Resources Working Paper FGR/59E. Food and Agriculture Organization of the United Nations, Rome, Italy.
- FAO, 2014a. The State of the World's Forest Genetic Resources. Commission on Genetic Resources for Food and Agriculture, Food and Agriculture Organization of the United Nations, Rome, Italy.
- FAO, 2014b. Global Plan of Action for the Conservation, Sustainable Use and Development of Forest Genetic Resources, Food and Agriculture Organization of the United Nations, Rome, Italy.
- Fisher, H., Gordon, J., 2007. Improved Australian tree species for Vietnam. ACIAR Impact Assessment Series Report No. 47. The Australian Centre for International Agricultural Research, Canberra, Australia.
- FTA, 2014. Forests, Trees and agroforestry. Livelihoods, Landscapes and Governance. <www.foreststreesagroforestry.org/> (accessed 30.06.14).
- Funk, C.W., McKay, J.K., Hohenlohe, P.A., Allendorf, F.W., 2012. Harnessing genomics for delineating conservation units. *Trends Ecol. Evol.* 27, 489–496.
- Geburek, T., Konrad, H., 2008. Why the conservation of forest genetic resources has not worked. *Conserv. Biol.* 22, 267–274.
- Graudal, L., Lillesø, J.-P.B., 2007. Experiences and Future Prospects for Tree Seed Supply in Agricultural Development Support: Based on Lessons Learnt in Danida Supported Programmes 1965–2005. Ministry of Foreign Affairs, Danida, Copenhagen, Denmark.
- Graudal, L., Aravanopoulos, F., Bennadi, Z., Changtragoon, S., Fady, B., Kjær, E.D., Loo, J., Ramamonjisoa, L., Vendramin, G.G., 2014. Global to local genetic diversity indicators of evolutionary potential in tree species within and outside forests. *For. Ecol. Manage.* 333, 35–51.
- Greenwood, M.S., Hutchison, K.W., 1996. Genetic after-effects of increased temperature in *Larix*. In: Hom, J., Birdsey, R., O'Brian, K. (Eds.), Proceedings of the 1995 Meeting of the Northern Global Change Program. USDA Forest Service, Radnor, USA, pp. 56–62.
- GTTN, 2014. The Global Timber Tracking Network. <www.globaltimbertrackingnetwork.org/> (accessed 30.06.14).
- Guariguata, M.R., Locatelli, B., Haupt, F., 2012. Adapting tropical production forests to global climate change: risk perceptions and actions. *Int. Forestry Rev.* 14, 27–38.
- Hansen, M.M., Olivieri, I., Waller, D.M., Nielsen, E.E., The GeM Working Group, 2012. Monitoring adaptive genetic responses to environmental change. *Mol. Ecol.* 21, 1311–1329.
- Hein, L., Gatzweiler, F., 2006. The economic value of coffee (*Coffea arabica*) genetic resources. *Ecol. Econ.* 60, 176–185.
- Hong, T.D., Ellis, R.H., 1998. Contrasting seed storage behaviour among different species of *Meliaceae*. *Seed Sci. Technol.* 26, 77–95.
- Jamnadass, R., Lowe, A., Dawson, I.K., 2009. Molecular markers and the management of tropical trees: the case of indigenous fruit. *Trop. Plant Biol.* 2, 1–12.
- Johnsen, Ø., Kvaalen, H., Yakovlev, I.A., Dæhlen, O.G., Fossdal, C.G., Skrøppa, T., 2009. An epigenetic memory from time of embryo development affects climatic adaptation in Norway spruce. In: Gusta, L.V., Wisniewski, M.E., Tanino, K.K. (Eds.), Plant Cold Hardiness. From the Laboratory to the Field, CABI, Wallingford, UK, pp. 99–107.
- Joyce, D.G., Rehfeldt, G.E., 2013. Climatic niche, ecological genetics, and impact of climate change on eastern white pine (*Pinus strobus* L.): guidelines for land managers. *For. Ecol. Manage.* 295, 173–192.
- Jump, A.S., Penuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol. Lett.* 8, 1010–1020.
- Karnosky, D.F., Podila, G.K., Gagnon, Z., Pechter, P., Akkapeddi, A., Coleman, M., Dickson, R.E., Isebrands, J.G., 1998. Genetic control of responses to interacting O₃ and CO₂ in *Populus tremuloides*. *Chemosphere* 36, 807–812.
- Kettle, C.J., Ennos, R.A., Jaffre, T., Gardner, M., Hollingsworth, P.M., 2008. Cryptic genetic bottlenecks during restoration of an endangered tropical conifer. *Biol. Conserv.* 141, 1953–1961.
- König, A.O., 2005. Provenance research: evaluating the spatial pattern of genetic variation. In: Geburek, T., Turok, J. (Eds.), Conservation and Management of Forest Genetic Resources in Europe. Arbor Publishers, Zvolen, Slovakia, pp. 275–333.
- Koskela, J., Vinceti, B., Dvorak, W., Bush, D., Dawson, I.K., Loo, J., Kjaer, E.D., Navarro, C., Padolina, C., Bordács, S., et al., 2014. Utilization and transfer of forest genetic resources: a global review. *For. Ecol. Manage.* 333, 22–34.
- Kozłowski, G., Gibbs, D., Huan, F., Frey, D., Gratzfeld, J., 2012. Conservation of threatened relict trees through living *ex situ* collections: lessons from the global survey of the genus *Zelkova* (Ulmaceae). *Biodivers. Conserv.* 21, 671–685.
- Labouisse, J., Bellachew, B., Kotecha, S., Bertrand, B., 2008. Current status of coffee (*Coffea arabica* L.) genetic resources in Ethiopia: implications for conservation. *Genet. Resour. Crop Evol.* 55, 1079–1093.
- Lahaye, R., van der Bank, M., Bogarin, D., Warner, J., Pupulin, F., Gigot, G., Maurin, O., Duthoit, S., Barracough, T.G., Savolainen, V., 2008. DNA barcoding the floras of biodiversity hotspots. *Proc. Natl. Acad. Sci. USA* 105, 2923–2928.
- Leakey, R.R.B., Weber, J.C., Page, T., Cornelius, J.P., Akinnifesi, F.K., Roshetko, J.M., Tchoundjeu, Z., Jamnadass, R., 2012. Tree domestication in agroforestry: progress in the second decade (2003–2012). In: Nair, P.K.R., Garrity, D. (Eds.), Agroforestry: the Future of Global Land Use. Advances in Agroforestry, vol. 9. Springer Science+Business Media, New York, USA, pp. 145–173.
- Lefèvre, F., Koskela, J., Hubert, J., Kraigher, H., Longauer, R., Olrik, D.C., Schüller, S., Bozzano, M., Alizoti, P., Bakys, R., et al., 2013. Dynamic conservation of forest genetic resources in 33 European countries. *Conserv. Biol.* 27, 373–384.
- Li, D.-Z., Pritchard, H.W., 2009. The science and economics of *ex situ* plant conservation. *Trends Plant Sci.* 14, 614–621.
- Lowe, A., Cross, H.B., 2011. The application of DNA methods to timber tracking and origin verification. *IAWA J.* 32, 251–262.
- Lowe, A.J., Boshier, D., Ward, M., Bacles, C.F.E., Navarro, C., 2005. Genetic resource impacts of habitat loss and degradation; reconciling empirical evidence and predicted theory for neotropical trees. *Heredity* 95, 255–273.
- Magri, D., Vendramin, G.G., Comps, B., Dupanloup, I., Geburek, T., Gömöry, D., Latałowa, M., Litt, T., Paule, L., Roure, J.M., et al., 2006. A new scenario for the quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytol.* 171, 199–221.
- Maxted, N., Dulloo, M.E., Ford-Lloyd, B.V., Iriondo, J.M., Jarvis, A., 2008. Gap analysis: a tool for complementary genetic conservation assessment. *Divers. Distrib.* 14, 1018–1030.
- McKay, J.K., Christian, C.E., Harrison, S., Rice, K.J., 2005. "How local is local?" – A review of practical and conceptual issues in the genetics of restoration. *Restor. Ecol.* 13, 432–440.
- Milad, M., Schaich, H., Konold, W., 2013. How is adaptation to climate change reflected in current practice of forest management and conservation? A case study from Germany. *Biodivers. Conserv.* 22, 1181–1202.
- Mohan Jain, S., Priyadarshan, P.M. (Eds.), 2009. Breeding Plantation Tree Crops. Tropical Species. Springer Science+Business Media, New York, USA.
- Moore, B.D., Andrew, R.L., Kulheim, C., Foley, W.J., 2014. Explaining intraspecific diversity in plant secondary metabolites in an ecological context. *New Phytol.* 201, 733–750.

- MSB, 2014. The Millennium Seed Bank project. <www.kew.org/science-conservation/millennium-seed-bank> (accessed 30.06.14)..
- Nagoya Protocol, 2014. The Nagoya Protocol on Access and Benefit-sharing. <www.cbd.int/abs/> (accessed 30.06.14)..
- Neale, D.B., Kremer, A., 2011. Forest tree genomics: growing resources and applications. *Nat. Rev. Genet.* 12, 111–122.
- Oldfield, S.F., 2009. Botanic gardens and the conservation of tree species. *Trends Plant Sci.* 14, 581–583.
- Oldfield, S., Lusty, C., MacKinven, A., 1998. *The World List of Threatened Trees*. World Conservation Press, Cambridge, UK.
- PEN, 2014. The Poverty Environment Network. <www.cifor.org/pen/> (accessed 30.06.14)..
- Petit, R.J., Hampe, A., 2006. Some evolutionary consequences of being a tree. *Annu. Rev. Ecol. Evol. Syst.* 37, 187–214.
- Petit, R.J., Csaikl, U.M., Bordacs, S., Burg, K., Coart, E., Cottrell, J., van Dam, B., Deans, J.D., Dumolin-Lapègue, S., Fineschi, S., et al., 2002. Chloroplast DNA variation in European white oaks: phylogeography and patterns of diversity based on data from over 2600 populations. *For. Ecol. Manage.* 156, 5–26.
- Pritchard, H.W., Moat, J., Ferraz, J.B.S., Marks, T.R., Camargo, J.L.C., Nadarajan, J., Ferraz, I.D.K., 2014. Innovative approaches to the preservation of forest trees. *For. Ecol. Manage.* 333, 88–98.
- Ræbild, A., Larsen, A.S., Jensen, J.S., Ouedraogo, M., Groot, S., Damme, P., Bayala, J., 2011. Advances in domestication of indigenous fruit trees in the West African Sahel. *New Forest.* 41, 297–315.
- Raffa, K.F., Powell, E.N., Townsend, P.A., 2013. Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. *Proc. Natl. Acad. Sci. USA* 110, 2193–2198.
- Ray, P.K., 2002. *Breeding Tropical and Subtropical fruits*. Springer-Verlag, Berlin, Germany.
- RBG, 2014. Royal Botanic Gardens, Kew. Seed Information Database. <<http://data.kew.org/sid/>> (accessed 02.07.14)..
- Rehfeldt, G.E., Jaquish, B.C., Saenz-Romero, C., Joyce, D.G., Leites, L.P., St Clair, J.B., Lopez-Upton, J., 2014. Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: reforestation. *For. Ecol. Manage.* 324, 147–157.
- Richardson, D.M., Carruthers, J., Hui, C., Impson, F.A.C., Miller, J.T., Robertson, M.P., Rouget, M., Le Roux, J.J., Wilson, J.R.U., 2011. Human-mediated introductions of Australian acacias – a global experiment in biogeography. *Divers. Distrib.* 17, 771–787.
- Rohde, A., Junttila, O., 2008. Remembrances of an embryo: long-term effects on phenology traits in spruce. *New Phytol.* 177, 2–5.
- Russell, J.R., Hedley, P.E., Cardle, L., Dancey, S., Morris, J., Booth, A., Odee, D., Mwaura, L., Omondi, W., Angaine, P., et al., 2014. tropiTree: An NGS-based EST-SSR Resource for 24 Tropical Tree Species. *Public Library of Science One (PLoS ONE)* 9, e102502 <www.plosone.org/>..
- Rymer, P.D., Sandiford, M., Harris, S.A., Billingham, M.R., Boshier, D.H., 2014. Remnant *Pachira quinata* pasture trees have greater opportunities to self and suffer reduced reproductive success due to inbreeding depression. *Heredity* (in press). <http://dx.doi.org/10.1038/hdy.2013.73>..
- Sacandé, M., Jøker, D., Dulloo, M.E., Thomsen, K.A. (Eds.), 2004. *Comparative Storage Biology of Tropical Tree Seeds*. International Plant Genetic Resources Institute, Rome, Italy.
- Safranyik, L., Carroll, A., 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In: Safranyik, L., Wilson, B. (Eds.), *The Mountain Pine Beetle: a Synthesis of Biology, Management and Impacts on Lodgepole Pine*. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, Canada, pp. 3–66.
- Sakai, A., Engelmann, F., 2007. Vitrification, encapsulation–vitrification and droplet-vitrification: a review. *CryoLetters* 28, 151–172.
- Sallon, S., Soloway, E., Cohen, Y., Korchinsky, R., Egli, M., Woodhatch, I., Simchoni, O., Kislev, M., 2008. Germination, genetics, and growth of an ancient date seed. *Science* 320, 1464.
- Santini, A., Ghelardini, L., De Pace, C., Desprez-Loustau, M.L., Capretti, P., Chandelier, A., Cech, T., Chira, D., Diamandis, S., Gaitniekis, T., 2013. Biogeographical patterns and determinants of invasion by forest pathogens in Europe. *New Phytol.* 197, 238–250.
- Sebbenn, A.M., Degen, B., Azevedo, V.C.R., Silva, M.B., de Lacerda, A.E.B., Ciampi, A.Y., Kanashiro, M., da Carneiro, F.S., Thompson, I., Loveless, M.D., 2008. Modelling the long-term impacts of selective logging on genetic diversity and demographic structure of four tropical tree species in the Amazon forest. *For. Ecol. Manage.* 254, 335–349.
- Sinclair, E.A., Bussell, J.D., Krauss, S.L., Hobbs, R., Dixon, K.W., 2006. Molecular markers detect multiple origins of *Agonis flexuosa* (Myrtaceae) plants used in urban bushland restoration. *Ecol. Manage. Restor.* 7, 234–235.
- Smith, C.M., Wilson, B., Rasheed, S., Walker, R.C., Carolin, T., Shepherd, B., 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. *Can. J. For. Res.* 38, 982–995.
- Sparks, T.H., Butchart, S.H.M., Balmford, A., Bennun, L., Stanwell-Smith, D., Walpole, M., Bates, N.R., Bomhard, B., Buchanan, G.M., Chener, A.M., et al., 2011. Linked indicator sets for addressing biodiversity loss. *Oryx* 45, 411–419.
- Sunderland, T.C.H., 2011. Food security: why is biodiversity important?. *Int. Forestry Rev.* 13, 265–274.
- Thomas, E., van Zonneveld, M., Loo, J., Hodgkin, T., Galluzzi, G., van Etten, J., 2012. Present spatial diversity patterns of *Theobroma cacao* L. in the neotropics reflect genetic differentiation in Pleistocene refugia followed by human-influenced dispersal. *Public Library of Science One (PLoS ONE)* 7, e47676 <www.plosone.org/>..
- Thomas, E., Jalonen, R., Loo, J., Boshier, D., Gallo, L., Cavers, S., Bordacs, S., Smith, P., Bozzano, M., 2014. Genetic considerations in ecosystem restoration using native tree species. *For. Ecol. Manage.* 333, 66–75.
- Ticktin, T., 2004. The ecological implications of harvesting non-timber forest products. *J. Appl. Ecol.* 41, 11–21.
- TSSD, 2014. The Tree Seed Suppliers Directory. <www.worldagroforestry.org/our_products/databases/tssd> (accessed 30.06.14)..
- UNEP/CBD/AHTEG, 2011. Report of the Ad Hoc Technical Expert Group on Indicators for the Strategic Plan for Biodiversity 2011–2020. The United Nations Environment Programme, the Convention on Biological Diversity and the Ad Hoc Technical Expert Group, Meeting at High Wycombe, UK, 20–24 June 2011. The Secretariat of the Convention on Biological Diversity, Montreal, Canada..
- VECEA, 2014. A Potential Natural Vegetation Map for Eastern Africa. <<http://www.vegetationmap4africa.org/>> (accessed 28.07.14)..
- Vinson, C.C., Kanashiro, M., Sebbenn, A.M., Williams, T.C.R., Harris, S.A., Boshier, D.H., 2014. Long term impacts of selective logging on two Amazonian tree species with contrasting ecological and reproductive characteristics: inferences from Eco-gene model simulations. *Heredity* (in press). <http://dx.doi.org/10.1038/hdy.2013.146>..
- Vranckx, G., Jacquemyn, H., Muys, B., Honnay, O., 2012. Meta-analysis of susceptibility of woody plants to loss of genetic diversity through habitat fragmentation. *Conserv. Biol.* 26, 228–237.
- Webber, J., Ott, P., Owens, J., Binder, W., 2005. Elevated temperature during reproductive development affects cone traits and progeny performance in *Picea glauca* x *engelmannii* complex. *Tree Physiol.* 25, 1219–1227.
- Wickneswari, R., Rajora, O.P., Finkeldey, R., Aravanopoulos, F., Bouvet, J.-M., Vaillancourt, R.E., Kanashiro, M., Fady, B., Tomita, M., Vinson, C., 2014. Genetic effects of forest management practices: global synthesis and perspectives. *For. Ecol. Manage.* 333, 52–65.
- Williams, N., 2009. Fruit heartland threatened. *Curr. Biol.* 19, R431–R432.
- Wuethrich, B., 2007. Reconstructing Brazil's Atlantic rainforest. *Science* 315, 1070–1072.
- Wymore, A.S., Bothwell, H.M., Compson, Z.G., Lamit, L.J., Walker, F.M., Woolbright, S.A., Whitham, T.G., 2014. Community genetics applications for forest biodiversity and policy: planning for the future. In: Fenning, T. (Ed.), *Challenges and Opportunities for the World's Forests in the 21st Century*. Forestry Sciences, vol. 81. Springer Science+Business Media, New York, USA, pp. 707–725.
- Yanchuk, A., Allard, G., 2009. Tree improvement programmes for forest health – can they keep pace with climate changes?. *Unsylva* 60, 50–56.
- Zhai, D.-L., Xu, J.-C., Dai, Z.-C., Cannon, C.H., Grumbine, R.E., 2014. Increasing tree cover while losing diverse natural forests in tropical Hainan, China. *Reg. Environ. Change* 14, 611–621.
- Zomer, R.J., Trabucco, A., Coe, R., Place, F., 2009. *Trees on Farm: Analysis of Global Extent and Geographical Patterns of Agroforestry*. Working Paper No. 89. The World Agroforestry Centre, Nairobi, Kenya..