

INTRODUCTION

Banking on the future: progress, challenges and opportunities for the genetic conservation of forest trees

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Abstract Genetic diversity provides the essential basis for the adaptation and resilience of tree species to environmental stress and change. The genetic conservation of tree species is an urgent global necessity as forest conversion and fragmentation continue apace, damaging insects and pathogens are transported between continents, and climate change alters local habitat suitability. Effective and efficient genetic conservation of tree species presents a substantial challenge because of the lack of basic information about many species, inadequate resources, and a historical lack of coordination within and between conservation sectors. Several cooperative efforts are already under way and are achieving conservation success, but much work remains. The *Gene Conservation of Tree Species—Banking on the Future* workshop in 2016 enabled the exchange of information and the creation of collaborations among tree conservation stakeholders. Several key themes emerged during the meeting's presentations and dialogue, which are further explored in this paper. In situ conservation of species is the long-term goal and is often the most efficient approach for preserving the genetic diversity of many forest tree species. Whether existing reserves adequately protect species and are sufficient for future conservation needs is uncertain. Ex situ conservation is an important complement to in situ efforts, acting as an

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insurance measure against extinction, providing material for restoration, enabling additional research opportunities, and educating the public. Networks of botanic gardens, government agencies, and non-governmental organizations must continue to coordinate ex situ and in situ efforts to improve the efficiency and effectiveness of tree conservation efforts. Assessing and prioritizing which species and populations require genetic conservation and prioritizing among them is a critical need. Two key tree restoration needs are for wider dissemination of planting stock, particularly stock with resistance to insects and pathogens, and for specific silvicultural prescriptions that facilitate restoration efforts. Effective genetic conservation of forest trees will require ongoing cooperation among widely diverse groups of scientists, managers, and policymakers from the public and private sectors.

Keywords Ex situ conservation · Forest management · Genetic diversity · Global change · In situ conservation · Restoration

Genetic conservation challenges and workshop purpose

The challenge of adequately conserving the genetic diversity of tree species is underscored by the fact that, until very recently, we had no reliable estimate of the total number of existing tree species, despite their crucial ecological and economic importance. A comprehensive analysis of published data sources and expert input now counts at least 60,065 tree species currently known to science (Beech et al. 2017), perhaps 20% of the approximately 380,000 plant species in the world (Kew 2012). These numerous tree species provide extensive economic value and essential ecosystem functions; provide many social, cultural, medicinal, and scientific benefits; and offer vital options for future development and adaptation (FAO 2014b; Millennium Ecosystem Assessment 2005). The threats they face, however, are myriad, extensive and persistent. These include pest and pathogen infestations (Dukes et al. 2009; Ramsfield et al. 2016), drought (Millar and Stephenson 2015), climate change (van Mantgem et al. 2009; Fettig et al. 2013), land conversion and fragmentation (Riitters et al. 2016; Wade et al. 2003), and unsustainable use and exploitation (Shearman et al. 2012; Asner et al. 2009).

Genetic conservation is clearly in order for many tree species. The Global Strategy for Plant Conservation (GSPC), originally approved in 2002 in association with the international Convention on Biological Diversity, recognized this reality by outlining 16 outcome-oriented global targets for 2020 that focus on plant diversity, including halting its loss and effectively securing its conservation and sustainable use (Sharrock 2012). The GSPC is an ambitious undertaking: About 20% of all the world's plant species are threatened (Kew 2012). If we assume this ratio holds for trees, then 12,000 to 20,000 tree species may be in need of some sort of protection. Recently, the compiled list of threatened trees encompassed 9641 species, of which 1894 were critically endangered, 3436 were endangered, and 4311 were vulnerable (Rivers et al. 2015). Only about one-third of tree species, however, have had comprehensive conservation status assessments (Beech et al. 2017), so the magnitudes of the decline and loss of tree species are mostly unknown. This lack of understanding of conservation needs is particularly acute in tropical and semi-tropical developing areas of the world, since most tree-oriented genetic conservation research has focused on temperate and boreal species. These areas, however, host extraordinary tree

diversity: 8715 species in Brazil, 5776 in Columbia, and 5142 in Indonesia, for example (Beech et al. 2017). As Peter Crane (2015) notes, the effective conservation of all tree species is an even greater challenge than assessing the conservation status of the world's tree species, given the absence of basic information about many species, the lack of adequate resources and will, and the decentralized nature of plant conservation science. Still, he asserts: "The charismatic megaflores are a gift to the whole of humanity bequeathed to us by millions of years of evolution. It is important that we act now to ensure their future."

It was in this context of tree genetic conservation needs and challenges that more than 120 scientists and managers from six countries met at the *Gene Conservation of Tree Species—Banking on the Future* workshop in Chicago, Illinois, United States, in May 2016, organized by the United States Department of Agriculture (USDA) Forest Service and The Morton Arboretum, the Chicago Botanic Garden, Botanic Gardens Conservation International, the USDA Agricultural Research Service, the Western Forestry and Conservation Association, the American Public Gardens Association, and the Global Trees Campaign. The purpose of the workshop was to facilitate the exchange of the latest information, research, and action on the genetic conservation of tree species, especially those at risk from stressors such as insects, pathogens, drought, exploitation, and habitat loss. During five plenary talks, 84 contributed oral presentations, 24 poster presentations, and six working sessions, the workshop highlighted major studies and actions undertaken by organizations for the long-term conservation of trees as well as risk assessments that help to inform and prioritize genetic conservation strategies. Participants used this information during the meeting to develop a set of recommended action items that can be used to form and strengthen partnerships, fostering collaboration to accelerate genetic conservation efforts. The workshop included a field tour of natural habitats at Fermilab and at The Morton Arboretum outside Chicago, as well as an address by Crane, former director of the Royal Botanic Gardens, Kew, and former dean of the Yale School of Forestry and Environmental Studies.

The meeting was organized around the four following general topics, with key challenges, opportunities and action items emerging from each: In situ conservation, ex situ conservation, identification of species and populations to be conserved, and restoration of species and ecosystems of conservation concern. Each is explored below following an overview of the importance of genetic diversity.

The importance of genetic diversity

Genetic diversity is essential for forest tree species because it provides a basis for adaptation and resilience to environmental stress and change. The loss of the option value conveyed by genetic variation could be particularly detrimental to the future survival of tree species in the face of numerous severe stresses (Schaberg et al. 2008; Jump et al. 2009). Nations in temperate parts of the world recognized the fundamental importance of forest tree genetic variation by incorporating three genetic diversity indicators outlined in the Montreal Process Criteria and Indicators for the Conservation and Sustainable Management of Temperate and Boreal Forests (Montréal Process Working Group 2009). In the United States, the USDA Forest Service incorporates these indicators in its periodic forest sustainability assessment framework (United States Department of Agriculture Forest Service 2011; Nelson et al. 2015).

As long-lived, immobile, and often widespread life forms, tree species need high levels of genetic diversity to adapt to changing environmental influences (FAO 2014b). In fact, tree species maintain significantly more genetic variation within rather than among their populations compared to other groups of plants, perhaps enough in many cases—when combined with their capacity for long-distance pollen dispersal—to allow species to adapt to changing environmental conditions (Hamrick 2004). A central objective of genetic conservation, therefore, is to maintain genetic integrity and natural levels of genetic diversity, and to enhance genetic diversity in populations and species where it has been eroded (Rajora and Mosseler 2001), an objective that is particularly important in plant species and populations that are threatened by extirpation (Maunder et al. 2004b). A major threat to forest tree genetic resources is human-induced climate change, through which populations may be rendered unfit for new environmental conditions and for existing biotic and abiotic disturbances occurring outside their historic distribution, frequency and intensity ranges (Alfaro et al. 2014). Other, more immediate, threats to forest tree genetic diversity include (1) exotic insect and pathogen infestation, which have had the best documented and possibly greatest impact on forest tree genetic structure, and (2) deforestation, which directly eliminates locally adapted populations (Ledig 1992).

Beyond preserving existing levels and patterns of variation, an additional goal of genetic conservation efforts should be to support the continued evolution of species and populations (Eriksson et al. 1993), with the aim of enhancing adaptive genetic variation by increasing the probability that new alleles will be saved and that genetic variance in quantitative traits will be increased (Namkoong 1997). Such efforts may require the integration of both in situ (on site) and ex situ (off site) conservation efforts to ensure that best practices in forestry and horticulture are combined to enhance genetic diversity, especially in high-value species and those with small and vulnerable populations (Pritchard et al. 2014). A recent example is that of Rocky Mountain bristlecone pine (*Pinus aristata* Engelm.), for which a range-wide ex situ seed collection was combined with assessments of the health and ecological conditions of 61 distinct stands across the species range and of the relationship between stand and regeneration characteristics and environmental factors. The results will inform proactive management actions to increase population resilience in the face of a non-native pathogen, climate change, and altered disturbance regimes (Schoettle and Coop 2017).

Adaptive genetic diversity is a primary focus of conservation genetics because of its importance over the long-term, during which it allows for the maintenance of adaptive evolutionary potential, and over the short-term, during which it is associated with the maintenance of reproductive fitness (Frankham et al. 2002). Quantifying adaptive genetic diversity within and across the ranges of tree species is therefore critical for achieving the objectives of both in situ and ex situ conservation. Without spatially explicit information about the distribution of within-population genetic diversity and between-population differentiation, it is not possible to effectively and efficiently preserve the genetic resources of tree species, either in reserves or in seed collections. Ideally, the most important information for guiding genetic conservation decision-making would come from quantitative phenotypic traits associated with the fitness of an organism to its local environmental conditions and its ability to adapt to environmental changes, but this is difficult to measure (sensu Frankham et al. 2002). Adaptive traits are usually quantified in field trials, but such studies are expensive and time-consuming (Graudal et al. 2014). As a result, aside from a few economically important tree species (e.g., Rehfeldt et al. 2014; Tripana et al. 2007), we understand very little about patterns of adaptive variation across the distributions of most species. Provenance trials for the relatively few tree species of high economic value

may not be entirely relevant to conservation and restoration, however, because they are generally designed to focus on traits of interest to production forestry and include an inherent sampling bias toward trees with high values for those traits (Boshier and Boyle 2000). Because it is not generally possible to directly measure adaptive traits, selectively neutral molecular genetic markers like microsatellites are an important tool for estimating adaptive potential across populations because molecular genetic diversity is the most rapidly and easily accessible measure of genetic diversity in natural populations (Jump et al. 2009), even though these markers usually are not associated with adaptive trait variation in tree species (Reed and Frankham 2001). Studies based on a variety of marker types are decreasing in cost and are more economical than evaluations of adaptive traits (Morales-Hidalgo et al. 2015), and have the ability to generate large amounts of genetic data that can easily be combined with environmental information (Graudal et al. 2014).

Genetic diversity analyses using molecular markers are particularly important for rare, endemic, and threatened tree species (Pautasso 2009). For these species, small population size and population isolation are of particular concern because they may result in susceptibility to genetic drift and inbreeding (Jaramillo-Correa et al. 2009), reducing the fitness of populations (Reed and Frankham 2003) and their capacity to adapt to changing environmental conditions (Willi et al. 2006). There have been numerous recent investigations of the genetic diversity of imperiled tree species consisting mainly of small and isolated populations (e.g., Schoettle et al. 2012; Tamaki et al. 2016; Boraks and Broders 2016; Quiñones-Pérez et al. 2017), with implications for both in situ and ex situ conservation efforts, including establishing the degree of inbreeding and identifying populations with lower and higher levels of genetic diversity.

In situ conservation is more relevant to the management of widespread tree species, many of which include populations containing unique, rare and unusual genetic variation and complex genetic structures that necessitate preservation of a hierarchy of stands, populations and races (Millar and Libby 1991). Range-wide studies using molecular markers (e.g., Potter et al. 2012; Wei et al. 2011; de Lafontaine et al. 2013; Kimura et al. 2014) can identify populations harboring relatively high or low levels of genetic variation and offer insights into the existence of intra-species evolutionary lineages that may have undergone differential natural selection and thus may possess unique adaptive traits. This information should be highly applicable to conservation planning and management decision-making. The power of these studies has increased and their cost has decreased in recent years with the improvement of high-throughput methods and the ability to identify large numbers of markers, such as single nucleotide polymorphisms (SNPs) and simple sequence repeats (SSRs, or microsatellites) across the genomes of trees (Porth and El-Kassaby 2014). These marker systems have made formerly difficult and expensive analyses more accessible for gene conservation applications. Because most genetic diversity and differentiation analyses focus on temperate and boreal tree species, more knowledge is needed for tropical and semi-tropical tree species, including patterns of inbreeding and the degree of gene flow within species ranges (Pautasso 2009). Additionally, while neutral genetic marker data are better than no information at all, long term conservation of rare species will be more successful when informed by results of quantitative genetic analyses. A renewed focus on quantitative genetics and genomics is therefore needed to understand whether and how species will adapt to changing conditions (Kramer and Havens 2009). It is worth noting that molecular geneticists are increasingly able to develop and apply techniques such as next-generation sequencing, novel genotyping methods, and gene expression strategies, that facilitate cost-effective, large-scale analyses of neutral and non-neutral markers (Kirk and Freeland 2011). These new methods, often called ecological

genomics, can produce more precise estimates of adaptive genetic potential and population genetic parameters (Aravanopoulos 2016). Ecological genomics is already being applied to tree species (Eckert et al. 2013), including across broad scales (Pais et al. 2017; Liu et al. 2016).

In situ conservation

Efforts to conserve gene pools of forest tree species in situ are generally considered the long-term goal and the most efficient conservation approach for preserving genetic diversity (Fig. 1). In situ forest genetic resource conservation encompasses a wide variety of activities including identifying species and areas to protect, the actual protection of an area containing priority species, population monitoring and reinforcement, preparing management plans for species or forests, and outreach and education regarding the appropriate use of forest genetic resources (FAO 2014b). In situ conservation, through networks of protected and/or restored areas, typically represents a more evolutionarily dynamic approach than ex situ methods because the target species or population can maintain its full range of evolutionary and ecological functions and processes, and can track the environmental changes to which it must adapt (Rajora and Mosseler 2001). In situ conservation also permits the maintenance of ecological, aesthetic, ethical and cultural values of tree species, with the additional benefit that genetic resources of multiple species can be conserved simultaneously (FAO 2014b). Finally, in situ conservation measures may also be less expensive than collecting and managing genetic resources in seed banks or through other ex situ conservation mechanisms (Ledig et al. 1998), although in situ conservation also encompasses the costs of population monitoring and habitat management, often in remote areas. Because in situ conservation is the preferred approach for ensuring the dynamic maintenance of genetic diversity and evolutionary processes within forest tree species, the Food and Agricultural Organization (FAO) of the United Nations included the strengthening of the contribution of primary forests and protected areas to in situ conservation as a strategic priority in its Global Plan of Action for the Conservation, Sustainable Use and Development of Forest Genetic Resources (FAO 2014a). The Global Strategy for Plant Conservation (GSPC) for 2020 includes a target of conserving at least 75% of threatened plant species in situ (Sharrock 2012).

Species, and more directly their populations and individuals, are the outcome of entwined genetic and ecological processes, so in situ conservation of species needs to take into consideration communities and ecosystems in which the plants exist (Rolston 2004). Specifically, effective in situ conservation requires that ecosystem functions and processes, as well as population genetic processes within tree species, be maintained within a network of sites that comprehensively represent all levels of genetic organization (genes, populations, species) (Kanowski 2000).

A strict definition of in situ conservation focuses on the establishment and management of reserves explicitly for the conservation of forest tree biodiversity. Forest genetic resources are more likely to be adequately and efficiently preserved when reserve establishment and design follow biogeographic guidelines as much as possible given constraints such as existing human land use. These guidelines include ensuring reserves are as large as possible, have biologically meaningful boundaries, are connected with other protected areas, and encompass a range of successional stages and habitats (Given 1994). Within ecological regions, these forest preserves should be (1) comprehensive, by representing all

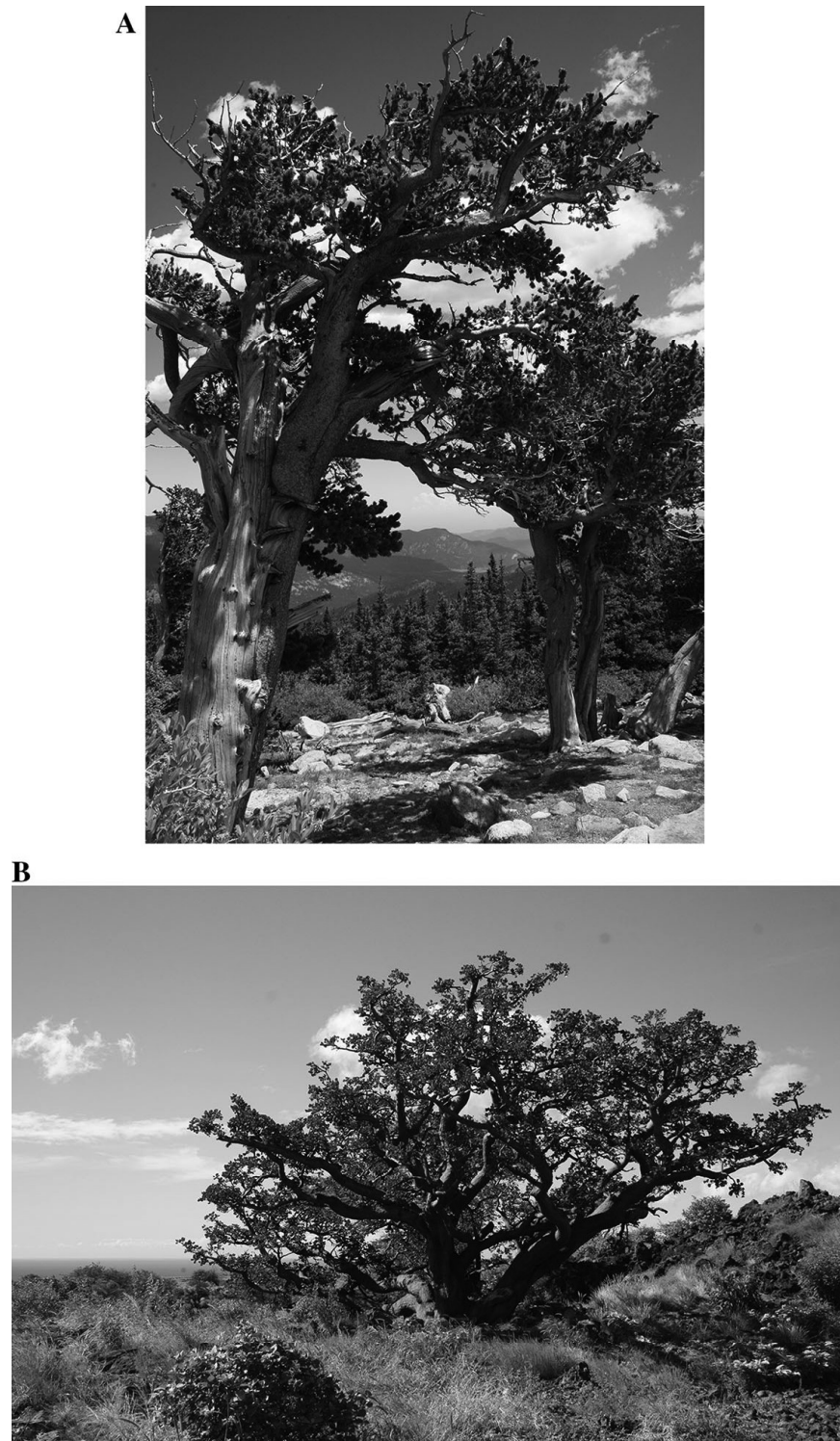


Fig. 1 In situ conservation of rare tree species. **a** Rocky Mountain bristlecone pine (*Pinus aristata* Engelm.) grows in a set of relatively small, high-elevation populations in Colorado, New Mexico, and Arizona, USA; many of these occur within government-owned protected areas, including the Mount Goliath Natural Area in Arapaho National Forest of central Colorado. **b** Wiliwili (*Erythrina sandwicensis* O. Deg.) is endemic to low-elevation tropical dry forests on leeward sides of the Hawaiian Islands, such as at a Waikoloa Dry Forest Preserve on the Big Island, Hawai‘i, USA, managed by a nonprofit organization. Photo: Kevin M. Potter

forest ecosystems; (2) adequate, in that they are able to maintain the viability and integrity of populations, species and communities; (3) representative, in the sense that diversity within ecosystems is replicated across the ecological region; and (4) efficient, in relation to encompassing ecological, economic and social objectives (Kanowski 2000). These are broad-scale goals so achieving them requires improved coordination across multiple stakeholders, including private land owners, local municipalities, state and provincial divisions, native peoples, and federal agencies. Such cooperation may even transcend national boundaries, as in one case in Europe where 33 countries have agreed to a dynamic forest genetic resources conservation framework that aims to preserve genetic diversity of trees within an evolutionary context while allowing generational turnover in the forest (Lefevre et al. 2013). Finally, active management may be necessary for in situ reserves to be able to continue to conserve forest genetic resources in light of rapid climate change. Management includes silvicultural treatments such as thinning and prescribed fire to increase resistance to threats (Jacobs 2007), and the use of assisted colonization to increase genetic diversity by establishing populations adapted to future climates within or adjacent to reserves (St Clair and Howe 2011). Other innovative management strategies may be applied, including using in situ conservation of seedling banks to maintain a large number of young plants in a relatively small area, especially for species with recalcitrant seeds (Pritchard et al. 2014). As expressed during the 2016 gene conservation workshop in Chicago, future research is needed to determine whether existing reserves adequately protect species and are sufficient for future conservation given ongoing threats to tree species, including habitat loss and changing climate.

The GSPC calls for securing at least 15% of the area of each ecological region or vegetation type globally through effective management and/or restoration by 2020 (Sharrock 2012). The percent of protected forestland in the world actually exceeded this threshold by 2015, having increased to 16.3% from 7.7% in 1990. This percentage varied by climatic domain, however, and did not reflect a 2.5% global decline in primary forest area and a 10% decline in the tropics during the same timeframe (Morales-Hidalgo et al. 2015). In this context, relying on strict reserves alone for in situ conservation is unlikely to accomplish complete and efficient conservation of imperiled forest tree species, particularly in parts of the world where deforestation levels are high and where reserved status may not confer protection from forest conversion, selective harvesting, grazing, and other threats. In fact, most in situ conservation of forest genetic resources happens outside protected areas on lands in a range of public, private and traditional ownerships, especially in multiple-use forests and those used primarily for wood production. The conservation of forest genetic resources should be integrated into the land-use designations of these forests and the regulations governing their use and management (FAO 2014b).

The management of forest species outside of strict in situ reserves (sometimes called *circa situ* or near site conservation) should incorporate principles of landscape ecology and adaptive management, including (1) maintenance or restoration of connectivity between protected areas, (2) maintenance of heterogeneity across forest landscapes, (3) maintenance of structural complexity and floristic diversity within forest stands, and (4) use of a variety of management strategies implemented at different scales (Kanowski and Boshier 1997). Additionally, on a smaller scale, silvicultural and other management practices should take the population size, reproductive biology, and growth rate of a species into account to ensure that genetic diversity and evolutionary processes are maintained in forest populations (Ratnam et al. 2014; Schaberg et al. 2008).

Long-distance movement of genes by both pollen and seed can alleviate the effects of inbreeding depression and genetic drift in small populations, and can help maintain or

increase genetic variation in recipient populations, facilitating adaptation to new environmental conditions (Alfaro et al. 2014; Aravanopoulos 2016). Because of the greater potential mobility of their seeds and pollen, trees are expected to have higher rates of interpopulation gene flow than herbaceous plants with the same dispersal mechanisms; among trees, gymnosperms should experience more gene flow than angiosperms because of their modes of pollination and seed dispersal, and trees with wind-dispersed pollen tend to have greater gene flow and less among-population differentiation than those with other breeding systems (Hamrick and Nason 2000). Advances in our understanding of the capacity of pollen, particularly from pines, to be transported over very long distances is requiring conservation geneticists to rethink long-held hypotheses about pollen dispersal gradients, the limitations of gene flow, and even the degree to which small populations are isolated by distance from their neighbors (Williams 2017).

Despite the advantages of in situ conservation of forest genetic resources, there are important constraints to its ability to protect forest genetic resources, including high rates of deforestation in certain regions, the uncertain impacts of climate change, insufficient knowledge about the importance of genetic diversity and genetic processes, and inadequate enforcement of policies and regulations enacted to conserve forest genetic resources (FAO 2014b). Thus, it may be necessary to apply additional or alternate conservation strategies such as ex situ approaches and restoration efforts.

Ex situ conservation

Ex situ conservation strategies are those that preserve plants or plant germplasm away from their areas of natural occurrence (Given 1994). These methods can include seed, pollen, and tissue banks; clonal and seedling orchards; botanic gardens; and arboreta (Maunder et al. 2004b), but may also encompass any collection or planting of material not established or managed specifically to regenerate itself naturally, such as provenance and progeny tests (Yanchuk and Lester 1996). Governments and non-governmental organizations around the world have made strong commitments to ex situ conservation, conserving about 1800 tree species in dedicated ex situ conservation collections, mostly in botanic gardens; many of these species are from economically important genera such as *Pinus*, *Eucalyptus*, and *Albizia* (FAO 2014b). The GSPC acknowledged the important role of ex situ conservation by calling for representation of at least 75% of threatened plant species in ex situ collections, preferably in the country of origin, with at least 20% available for recovery and restoration efforts (Sharrock 2012). Much work remains before this goal is achieved, however. Of 5330 endangered and critically endangered tree species globally, only 26% (1389) are represented in ex situ collections (Rivers et al. 2015).

Ex situ conservation is an important complement to in situ conservation efforts, especially for very rare or threatened species, or when in situ conservation is not a viable option, or as a safety duplication measure (FAO 2014b; Cavender et al. 2015). At the most basic level, ex situ conservation collections can safeguard valuable samples of wild plant diversity, but under more strategic and coordinated initiatives can play a critical role as part of an integrated conservation response supporting the retention and restoration of wild plant diversity (Maunder et al. 2004b). In practice, ex situ conservation collections are generally static rather than dynamic, in that they do not often allow for continued genetic change in species (i.e., sexual reproduction). Increasingly, however, botanic gardens and other ex situ collection managers are pursuing coordinated germplasm exchange and even

captive breeding efforts across institutions to improve genetic diversity and generate more individuals of very rare species, such as efforts with dawn redwood (*Metasequoia glyptostroboides* Hu and W. C. Cheng) at the Dawes Arboretum (Payton 2010).

Seed banking, the long-term storage of seed at low moisture and temperature, has the capacity to effectively conserve high levels of variation at a low relative cost per individual (Oldfield and Newton 2012; Li and Pritchard 2009), and is the most widely applied ex situ conservation strategy for plants (Fig. 2). Seed banks therefore have the dual purpose of providing a long-term safeguard against the loss of biodiversity through storage that lasts decades or even centuries, while providing a supply chain for shorter term restoration or research efforts (Guerrant et al. 2014). Examples in North America include extensive seed collections from whitebark pine (*Pinus albicaulis* Engelm.) and foxtail pine (*P. balfouriana* Balf.) (Snieszko et al. 2017), eastern hemlock (*Tsuga canadensis* [L.] Carr.) and Carolina hemlock (*T. caroliniana* Engelm.) (Jetton et al. 2013), and ash (*Fraxinus*) (https://www.nsl.fs.fed.us/geneticconservation_ash.html).

The length of seed viability is largely unknown for many species, however, despite the need for information about expected viability following different lengths of time in storage (Snieszko et al. 2017), making it necessary to regularly assess germination rates. Additional seed collections over time may also be required, depending on how long seed remains viable. To improve the effectiveness of seed banking, researchers should focus on improving proper post-harvest handling and storage, which will allow the development of species-specific strategies for conservation based on storage behavior (FAO 2014b). The development of species-specific protocols for seed handling and storage is often a challenge, given the time required and the variety of storage, stratification and germination protocols employed even for a single species, but is essential given that long-term seed storage complements components of both in situ and ex situ conservation (Snieszko et al. 2017). Additionally, researchers need to identify appropriate post-storage stratification and germination protocols for many tree species. The seed banking approach, however, works only for species having orthodox seed storage behavior, that is, seeds that remain viable for long periods of time at low temperatures and moisture levels. For recalcitrant species, such as oaks and magnolias, other more expensive alternatives are needed, including cryopreservation in liquid nitrogen, tissue culture, field and greenhouse plantings, and cultivation in living collections such as botanic gardens and arboreta (Oldfield and Newton 2012; FAO 2014b). Recent advances have occurred in many of these areas, including the expansion of living collections to conserve threatened tree species in sufficient numbers to ensure broad genetic diversity in their progeny (Pritchard et al. 2014; Cavender et al. 2015). For example, a collaboration between the American Public Gardens Association (APGA) and the USDA Forest Service focuses on collecting, propagating, and distributing propagules (for ex situ collections) from tree species with recalcitrant or unorthodox seed including sweetbay (*Magnolia virginiana* L.), Oglethorpe oak (*Quercus oglethorpensis* W. H. Duncan), and coastal sage scrub oak (*Q. dumosa* Nutt.) (<https://publicgardens.org/programs/plant-collections-network/tree-gene-conservation-partnership>).

The choices of which species and populations to collect and the methods with which the germplasm is maintained for long periods of time may determine which species survive into the next century in ex situ collections that otherwise would not (Guerrant et al. 2014). Unfortunately, ex situ collections face many of the same genetic hazards as small populations in the wild, such as genetic drift, mutation accumulation, and inbreeding depression, as well as some unique ones, such as artificial selection (for conditions in the ex situ collection) and outbreeding depression (the result of crossing among previously reproductively isolated populations of a species) (Schaal and Leverich 2004). Ex situ collections

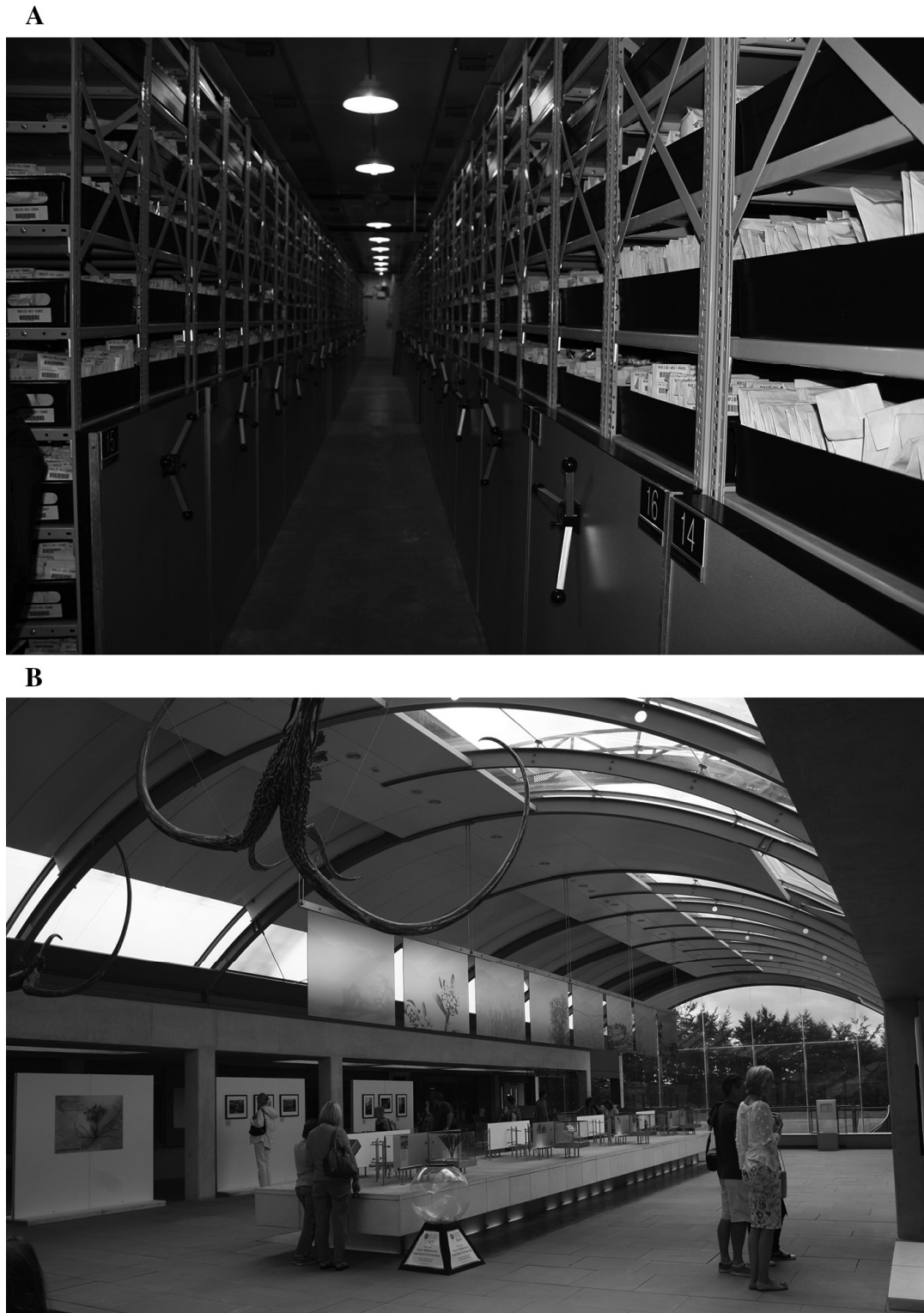


Fig. 2 Long-term genetic resource preservation facilities. **a** Conventional seed storage collections (at -18°C) at the National Center for Genetic Resources Preservation in Fort Collins, Colorado, USA, which stores approximately 890,000 accessions from 9300 plant species, including trees. **b** The Millennium Seed Bank of the Royal Botanical Gardens Kew, United Kingdom, with more than 2 billion seeds in storage from approximately 37,400 plant species, and an extensive public outreach program. Photo: Kevin M. Potter

need to be maintained to preserve representative levels of genetic diversity, to minimize deleterious genetic change, and to reduce genetic risk (Havens et al. 2004). Similarly, the initial propagule sampling itself (Fig. 3) should represent the extent of adaptive genetic variation across the range of a given tree species. How this is accomplished depends on several factors, including the purposes for which the collection is made (long-term storage or restoration), the nature of the material available (e.g., number of populations, orthodox vs. recalcitrant seed), and whether the benefit of the collection is worth the cost to have enough material for use when needed (Guerrant et al. 2004). In general, sampling should encompass between five and 50 populations across the species distribution, potentially stratified by important geographic or environmental gradients; should include at least 50 individuals within each population; and should be collected and accessioned within maternal lines (with seed from each individual plant kept separately) rather than bulked (Guerrant et al. 2014). Uniform ex situ sampling guidelines, however, do not apply equally well to all species, and spatial sampling strategies and sample sizes produce different outcomes when species differ in population size, genetic connectivity, or mode of pollination (Hoban and Schlarbaum 2014). For example, some species have been successfully conserved ex situ by sampling fewer populations and individuals per population (Dvorak et al. 1999). On the other hand, species with high levels of self-fertilization or low levels of dispersal will require many more samples than are commonly recommended to reach genetic diversity targets. Allele capture is almost always higher by sampling fewer seeds from more plants than by sampling more seeds from fewer plants (Hoban and Strand

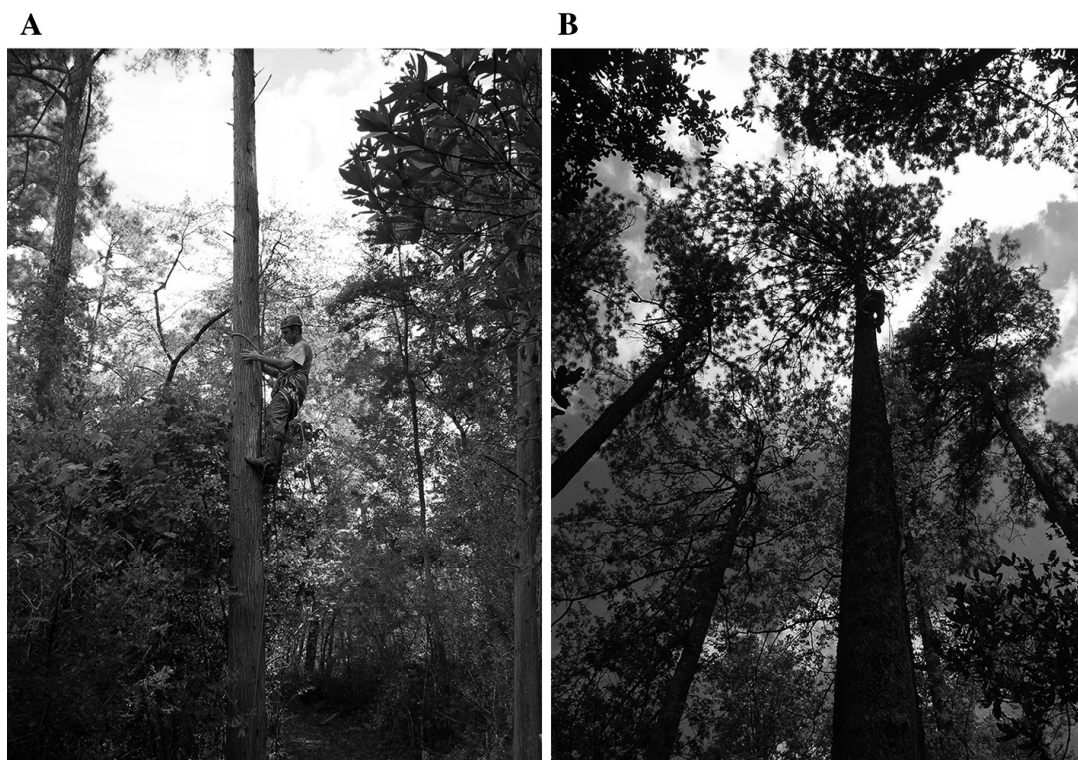


Fig. 3 Ex situ gene conservation collection efforts. **a** Seed collection from Atlantic whitecedar (*Chamaecyparis thyoides* (L.) Britton, Sterns & Poggenb.) from Jones Lake State Park in North Carolina, USA. **b** Pollen collection from tecunuman pine (*Pinus tecunumanii* Eguiluz & Perry) near San Jeronimo, Guatemala. **a** Photo: Robert M. Jetton; **b** Photo: Kevin M. Potter

2015). In the case of species with non-continuous distributions, it is critical that sampling cover the total spatial extent of the species because omitting areas of occurrence will lead to either under-estimating or over-estimating the degree of genetic differentiation (Rico 2017). Finally, while these principles should help guide the efficient sampling of genetic variation for tree species, proceeding with a somewhat imperfect sampling plan as soon as practicable may be a better approach in some cases than waiting until all the recommendations can be followed. It may be possible to fill sampling gaps later, and at least a portion of the representative genetic variation will have been conserved.

Botanic gardens and arboreta play a critical role in the development of ex situ collections of threatened plant species (Fig. 4a), both in seed banking efforts and in living collections of many exceptional species that either do not produce seeds or produce seeds that are recalcitrant (Fant et al. 2016). Indeed, a few extremely imperiled tree species, such as the Franklin tree (*Franklinia alata* W. Bartram ex Marshall) of the southeastern United States (Fig. 4b), Wood's cycad (*Encephalartos woodii* Sander) of KwaZulu-Natal in South Africa, and the Saint Helena redwood (*Trochetiopsis erythroxylon* [Forst.] Marais) on the South Atlantic island for which it is named, exist only in cultivation, most importantly in botanic gardens and arboreta. These institutions are in a position to make important contributions to tree conservation because they maintain extensive collections of living trees, as well as seeds and other germplasm, which can be valuable in supporting both ex situ and in situ conservation efforts, and they support the skills and ability to



Fig. 4 Ex situ conservation in botanic gardens and cultivation. **a** The imperiled Gowen cypress [*Hesperocyparis goveniana* (Gordon) Bartel], limited to two small natural populations on the Monterey Peninsula of California, here planted in the Jardin des Plantes de Montpellier, France. **b** The Franklin tree (*Franklinia alata* W. Bartram ex Marshall), extinct in the wild but persisting in horticultural collections, including this one in North Carolina, USA. Photo: Kevin M. Potter

identify, cultivate and propagate a wide range of tree species (Oldfield and Newton 2012). They also are in a unique position to play a significant role in ex situ conservation because they have the land and the facilities, such as breeding nurseries, tissue culture laboratories and seed banks, necessary to maintain genetically diverse tree collections (Cavender et al. 2015). Finally, as facilities visited by many millions of people each year, botanic gardens and arboreta can be innovative leaders in educating the public about the need for plant conservation (Given 1994). In all cases, partners in government agencies and non-governmental organizations also play an important complementary role.

At the same time, there are challenges to effective tree conservation by botanic gardens and arboreta, such as an insufficient strategic focus on conservation in some of these institutions, an historical emphasis on collecting a very small number of individuals from many different species (“stamp collecting”), and a lack of global coordination among botanic gardens and arboreta (Cavender et al. 2015). To ensure botanic gardens, arboreta and seed banks fulfil their conservation role as stewards for threatened plants, they should adopt a stronger focus on including threatened trees in their collections, as well as on diversifying their collections to better represent taxa currently reported as absent from collections (Rivers et al. 2015). Fant et al. (2016) proposes that these institutions build on approaches used by the zoological community to manage metapopulations of threatened plants across networks of gardens and to coordinate germplasm exchange. Finally, it is worth noting that the enormous number of trees in general cultivation could serve as a diffuse ex situ conservation population, especially in cases where using locally sourced seed for restoration is not possible, or in areas where the genetic diversity of natural populations has been reduced by inbreeding (LaBonte et al. 2017).

Despite advances in ex situ conservation practices, these methods alone typically cannot conserve the same range of genetic diversity that can be preserved by in situ conservation, and ex situ populations—whether seed banks, progeny tests, or conservation plantings—are still subject to natural selection forces that can further reduce their genetic variability (Yanchuk and Lester 1996). Conservation geneticists, therefore, do not suggest that ex situ collections can or should replace natural populations. Instead, these methods are often implemented as part of an integrated management portfolio of conservation efforts, and serve as an insurance policy against extinction and as a source of material for reintroduction and research (Holsinger and Vitt 1997; Oldfield and Newton 2012). Participants at the *Gene Conservation of Tree Species—Banking on the Future* workshop underscored the need for increased coordination between ex situ and in situ efforts to improve the efficiency and effectiveness of tree conservation programs. One such coordinated effort is the Global Trees Campaign, a joint initiative of Botanic Gardens Conservation International (BGCI) and Fauna & Flora International which aims to save globally threatened trees and their habitats through coordinated in situ and ex situ conservation, restoration of natural habitats, and sustainable forest management (Oldfield 2008; Oldfield and Newton 2012). Additionally, horticultural skills necessary for ex situ conservation methods, such as handling highly recalcitrant seeds, could be applied in attempts to restore tree populations in situ, while the collection of wildlings from natural stands could augment ex situ collections (Pritchard et al. 2014).

Participants at the Chicago workshop underscored the need for improved networks of botanic gardens, arboreta and seed collection organizations to better coordinate conservation efforts, particularly in the tropics. Along those lines, four collaborative networks (the American Public Gardens Association; Botanic Gardens Conservation International, U.S.; The Center for Plant Conservation; and the Plant Conservation Alliance Non-Federal Cooperators Committee) recently created the North American Plant Conservation Initiative,

a joint effort to engage botanic gardens working actively in plant conservation to achieve the goals of the North American Botanic Garden Strategy for Plant Conservation, as well as goals of local and global plant conservation strategies (BGCI 2016). It is possible, however, that such international collaborative networks may be affected by the implementation of the 2010 Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization, which may significantly alter international germplasm transfer practices by increasing transaction costs and the time needed to lawfully obtain forest genetic resources (Koskela et al. 2014). On the other hand, the Nagoya Protocol creates incentives for nations to conserve and sustainably use genetic resources by helping to ensure that those nations share in the benefits of their resources (Oldfield and Newton 2012).

Collaborative tree conservation actions will have a greater impact if they are supported by efforts to create global databases so that data, knowledge and collections are more available to the research, conservation, and forestry communities (Pritchard et al. 2014). Examples include BGCI's PlantSearch database, the only such global information source about plants in cultivation, which relies on collection holders to upload up-to-date taxa lists annually (Rivers et al. 2015), and GlobalTreeSearch, a complete list of tree species occurrences, georeferenced to the country level (Beech et al. 2017), that will provide the foundation for the Global Tree Assessment (see below).

Identification of species and populations to be conserved

Two organized sessions at the workshop focused on the identification and prioritization of tree species and populations in need of genetic conservation intervention. One of the 16 targets of the GSPC is a completed assessment of the conservation status of all known plant species to guide conservation action (Sharrock 2012). The completion of a conservation assessment for all plant species is urgent given the scientific consensus that the world has entered an era of mass extinctions in which the current extinction rate is at least three orders of magnitude higher than Earth's average across biological and geological history (Pimm and Brooks 1999). The longstanding and alarmingly high rate of forest cover loss is a particular concern for the conservation of forest genetic resources, as are unsustainable tree harvesting, climate change, the international movement of insects and pathogens, catastrophic fires, and invasive plant competitors (FAO 2014b). As an important effort toward achieving the GSPC target, a comprehensive Global Tree Assessment is under way to assess the conservation status of all tree species. Organized by BGCI and the International Union for Conservation of Nature (IUCN) Species Survival Commission's Global Tree Specialist Group, its goal is to complete the assessment by 2020. The Global Tree Assessment will be a major challenge, requiring the international coordination of numerous organizations and individuals, and a comprehensive list of the world's tree species along with their country-level distributions, GlobalTreeSearch (Beech et al. 2017), but success will improve targeting of conservation resources to tree species at greatest risk; improve the design of forest conservation, restoration and management efforts; and strengthen capacity for sustainable forest management and land planning (Newton et al. 2015).

The Global Tree Assessment will contribute to the development of the IUCN Red List (<http://www.iucnredlist.org/>), which aims to provide objective and scientifically based information on the current status of globally threatened biodiversity (Mace et al. 2008). Within the Red List framework, quantitative criteria referring to fundamental biological

processes underlying population decline and extinction are applied so that species are listed appropriately as critically endangered, endangered, or vulnerable. The IUCN system is designed to increase the consistency, transparency and validity of its categorization, but it is not intended to provide robust predictions about the fate of individual species or to quantify factors such as rarity, ecological role, or economic importance (Mace et al. 2008). NatureServe and its partners evaluate the conservation status of North American species using an approach similar to the IUCN Red List, while incorporating a broader set of species characteristics that encompasses rarity, threats and trends (Faber-Langendoen et al. 2012). NatureServe ranks species on a five-point conservation status scale (G1–G5) from most to least imperiled (<http://explorer.natureserve.org>); this assessment can be conducted globally, nationally, or within subnational units such as states or provinces.

Priority-setting is particularly important when the conservation need exceeds the capacity to respond to those needs (Millar et al. 2007). To efficiently allocate limited resources, it is necessary to apply rational, systematic, and defensible methods to prioritize species and populations for conservation (Bottrill et al. 2008). The USDA Forest Service, therefore, has coordinated tree species conservation assessments specific to the United States or to regions of the country. Project CAPTURE, for example, is a data- and expert-opinion-driven hierarchical framework that categorizes species into vulnerability classes associated with strategies for maintaining adaptive genetic variation through monitoring, management, and conservation (Potter et al. 2017). Conceptually (Foden et al. 2013), Project CAPTURE categorizes species based on the three dimensions of vulnerability: threat exposure, threat sensitivity, and adaptive capacity relative to the threat. It builds on previous regional National Forest System efforts to assess the vulnerability of forest tree species to climate change and other threats (Devine et al. 2012; Potter and Crane 2012). Other efforts also have been directed at prioritizing, for genetic conservation and breeding purposes, the wild relatives of tree species that are important food, forage, medicinal, ornamental or industrial crops. Specifically, these projects compare the potential geographic and ecological diversity of the wild crop species with resources currently accessible in gene banks to identify taxa and geographic areas of particular conservation concern (Castaneda-Alvarez et al. 2016). Such species-level analyses should prioritize those that experience a rapid decline in conservation status, as with ash species in North America, which are being decimated by the nonnative emerald ash borer (*Agrilus planipennis* Fairmaire). Ongoing and regular monitoring of trends in tree species population sizes is therefore a necessity.

Most conservation assessment platforms operate at the species level, but a need also exists to identify populations within the distributions of tree species most in need of genetic conservation actions. Gap analyses may assess the degree to which genetic units of a forest tree species, defined by breeding zones and ecoregion boundaries, exist within protected areas (Lipow et al. 2004). They may also focus on the fact that locally adapted populations of wide-ranging species may lag behind their optimal climate conditions under climate change, and therefore use bioclimate envelope models to identify which individual populations are most likely to experience adaptational lags in coming decades (Gray and Hamann 2013). Another strategy to prioritize occurrence locations for conservation applies a novel combinatorial method to incorporate multiple dissimilar georeferenced data sets—such as genetic diversity metrics, previous seed sampling efforts, and climate change projections—into a geographic prioritization of areas for the most effective and efficient conservation of genetic diversity (Hastings et al. 2017). This approach integrates geographic information systems (GIS) with the multi-attribute frontier method (Yemshanov et al. 2013) to identify locations most in need of conservation actions. Rather than

requiring prior information or judgment about the relative importance of the criteria, it instead ranks each area of interest objectively against the other areas by considering values for all of the criteria simultaneously.

Clearly, numerous conservation assessment approaches currently exist that can be applied to assist in efforts to evaluate the degree of imperilment for tree species and their populations, particularly in North America. Opportunities exist to apply these frameworks cooperatively to achieve a more thorough understanding of what species are most in need of genetic conservation action. Collaborative efforts are under way to create a complete checklist of North American tree species, and to apply aspects of different conservation assessment platforms to develop a comprehensive Red List for tree species in a region. These lists can then be incorporated in the Global Tree Assessment and into efforts to meet the 2020 targets of the Global Strategy for Plant Conservation.

Restoration of species and ecosystems of conservation concern

When in situ efforts are not sufficient to effectively conserve the genetic diversity of tree species, but ex situ actions have preserved a representative sample of that species' variation, the logical next step is to consider the restoration of that species into a natural forest setting. The Global Strategy for Plant Conservation (GSPC) for 2020 includes two targets directly relevant to the restoration of forest trees: at least 15% of each ecological region or vegetation type secured through effective management or restoration, and at least 75% of threatened plant species in ex situ collections, with at least 20% available for recovery and restoration efforts (Sharrock 2012). While as much as 13 million hectares of natural forest are lost annually worldwide, as many as 300 million hectares of forest may be planted by 2020 (FAO 2010). Exotic species for commercial production are the predominant source of reforestation material, particularly in the tropics. At the same time, increasing the use of native species in restoration activities contributes to the conservation of these species and of their genetic diversity, particularly if the seed sources are appropriate to the planting site (Thomas et al. 2014a). One developing example is Malawi's national tree, the Mulanje cedar (*Widdringtonia whytei* Rendle), which is a high-value timber species that occurs naturally only in the Mulanje Mountain Biosphere Reserve and is critically endangered because of over-exploitation and fire (Bayliss et al. 2007) (Fig. 5a). Attempts to restore cedar forests and to grow the species more widely have been limited by its poorly understood ecology, pathology and horticulture, so BGCI, the Mulanje Mountain Conservation Trust and the Forestry Research Institute of Malawi are leading a project to define optimal growing conditions and to improve horticultural protocols for cedar restoration on Mulanje Mountain and for wider cultivation in Malawi. The objective is to deliver both biodiversity benefits and livelihood benefits by restoring populations of the cedar and generating alternative sources of sustainable income for local people currently relying on harvesting cedar timber. Through a partnership established at the 2016 genetic conservation workshop in Chicago, BGCI has engaged the U.S. Forest Service to study the genetics of Mulanje Cedar to help ensure that reforestation activities maintain natural levels of genetic diversity.

Forest restoration is a relatively young and complex science, so the theoretical underpinnings of the discipline are still evolving (Jacobs et al. 2015). Forest restoration has the potential to conserve the genetic resources of tree species and the persistence and functionality of forest ecosystems, but there is a high risk that restoration efforts could fail.

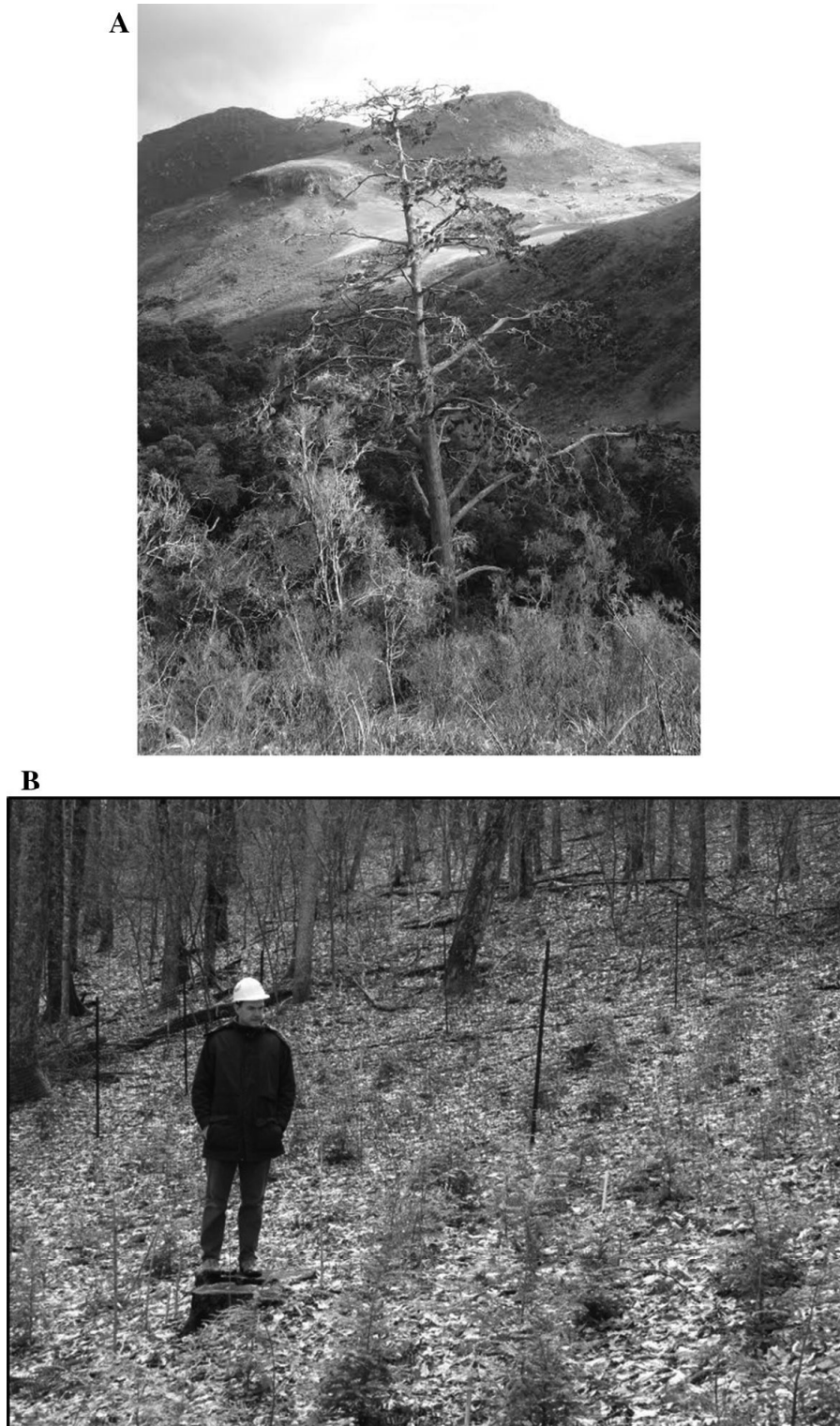


Fig. 5 Restoration of imperiled tree species. **a** Malawi's critically endangered national tree, Mulanje cedar (*Widdringtonia whytei* Rendle), which is the focus of restoration efforts on Mulanje Mountain as cedar forest cover has declined more than 90% in the last 30 years. **b** A restoration study, in Haywood County, North Carolina, USA, testing the effects of canopy structure, deer exclusion, fertilization and competition control on the establishment and early survival of eastern hemlock (*Tsuga canadensis* (L.) Carrière) in areas where it has been eliminated by the exotic hemlock woolly adelgid (*Adelges tsugae* Annand). **a** Photo: Andrew Bower; **b** Photo: Robert M. Jetton

Forest restoration decision-support tools are therefore needed to (1) guide the collection and propagation of germplasm to ensure a broad genetic base of restored tree populations, (2) match species and provenances to restoration sites where they are likely to be adapted based on current and future site conditions, and (3) enable landscape-level planning in restoration objectives (Thomas et al. 2014b).

To ensure that restored plant species will survive and be able to produce viable offspring, which is necessary for a restored ecosystem to be both functional and resilient, it is crucial that the planting material represents a certain minimum level of intraspecific diversity (Thomas et al. 2014a). Insufficient, inconsistent, and uncoordinated seed supplies, however, can be a significant limiting factor in forest restoration at the local scale, and even more so at the landscape scale (Merritt and Dixon 2014). Many ex situ seed collections, for example, are unlikely to be sufficient in size to be able to support landscape level restoration, but could be used to establish small stands of trees that would be the parent trees for more extensive seed collections in the future (Snieszko et al. 2017). Increased conservation demand will require better coordination between germplasm collection, ex situ propagation, and restoration efforts (Maunder et al. 2004a). Improved dissemination of two items, especially between public and private land owners and seed sources, were identified at the Chicago workshop as important needs for genetic-conservation-oriented restoration: (1) germplasm resources, both in terms of increased production capacity and more strategic and coordinated methods for dissemination, and (2) species-specific management information. Efforts to address these needs in the United States would build upon existing conservation collections coordinated by the USDA Agricultural Research Service's National Plant Germplasm System, the U.S. Department of Interior Bureau of Land Management's Seeds of Success program (Haidet and Olwell 2015), the USDA Forest Service and its partners, and the Center for Plant Conservation. Currently, focused breeding and restoration programs in the United States represent more than 100 species of trees and shrubs, mostly maintained by federal agencies and universities (FAO 2012). For example, Camcore, an international tree breeding and conservation program at North Carolina State University and funded by the USDA Forest Service, maintains seed collection and research projects for 10 imperiled U.S. tree species including eastern hemlock and Carolina hemlock (Hodge et al. 2017). Both hemlock species have been decimated by the exotic hemlock woolly adelgid insect (*Adelges tsugae* Annand) (Fig. 5b). To address this threat, more than 2000 seedlings of these species have been established in seed orchards in three countries, with an objective of making genetically diverse germplasm available for in situ breeding and restoration once successful adelgid management is accomplished (Jetton et al. 2013; Oten et al. 2014). Camcore also has collected seed from two dozen pine species in Mexico and South America, with 86% of provenances and 70% of families established in genetic trials and gene banks, and with seeds supplied to eight pine restoration studies in Mexico and Guatemala (J. L. Lopez, personal communication).

Participants in the tree genetic conservation workshop also identified the need for increased availability of pest- and pathogen-resistant planting stock to facilitate tree restoration activities. This need is likely to be intense in coming years given the many ongoing invasions by insects and pathogens that have large impacts on native tree species. These invasions alter ecosystem functions such as productivity, nutrient cycling and wildlife habitat (Lovett et al. 2016). Classical breeding methods can produce genetically diverse and resistant populations for restoration and reforestation, if a low frequency of resistance is present in the host species or one of its relatives, although the development of resistant populations is typically slow because most tree species have relatively long generation times (Snieszko 2006). Examples of species bred for pathogen resistance for

restoration include American chestnut (*Castanea dentata* [Marsh.] Borkh.) for chestnut blight, caused by *Cryphonectria parasitica* (Murrill) Barr (Steiner et al. 2017); and whitebark pine for white pine blister rust, caused by *Cronartium ribicola* J.C.Fisch. (Schoettle and Snieszko 2007). Transgenic approaches, such as incorporating genes from pathogen-resistant organisms, also may play a role in the restoration of threatened tree species, sometimes as part of an integrated approach that includes conventional breeding (Merkle et al. 2007; Steiner et al. 2017).

A topic that emerged repeatedly at the workshop was the need for better guidance on matching restoration locations with the proper tree seed source, particularly in light of changing climatic conditions. This has always been a challenge in ecological restoration, but it is becoming more so as changing climatic conditions mean that locally sourced seeds are not always an appropriate (or best) option as was assumed in the past (Havens et al. 2015). Given the many uncertainties associated with climate change, reforestation strategies should emphasize the conservation, diversification, and broader deployment of species, seed sources, and families, with planting programs potentially deploying non-local seed sources from further south or from lower elevations (Ledig and Kitzmiller 1992). Because appropriately sourced germplasm is necessary to ensure that new populations become self-sustaining and resilient (Broadhurst et al. 2008), the development of seed transfer zones for species restoration needs significant focus, particularly in light of rapid climate change (Kramer and Havens 2009; Harris et al. 2006). Ideally, species-specific seed transfer zones should be generated using information from common garden studies that can relate adaptive genetic variation to geographic and climatic variables (Ying and Yanchuk 2006), but this approach is not possible for most tree species, other than those of commercial importance, because of the extensive resources required (Vogel et al. 2005). Instead, generalized seed zones for restoration can be based on historical and current range distributions (Dalglish et al. 2016), ecoregion delineations (Miller et al. 2010), and/or relevant geospatial environmental data (Bower et al. 2014), which may be projected into the future to reflect potential changing conditions (Potter and Hargrove 2012). Such seed zones, along with disturbance models and species distribution projections, would be helpful in guiding the assisted migration of genetic material (Alfaro et al. 2014), although assisted migration for “species rescue” purposes is difficult and has been rarely implemented (Pedlar et al. 2012). Both assisted species migration and assisted population migration have relevance for conservation restoration, and should be implemented in a framework that assesses species or population vulnerability to climate change, sets priorities and management targets, and emphasizes long-term monitoring (Dumroese et al. 2015).

Integration of societal influences lags far behind progress in the development of restoration technologies and the ecological knowledge base needed to effectively restore threatened species (Jacobs et al. 2013). Multiple restoration paradigms exist, based on restoration goals that are social choices subject to open debate in a democratic society; these include revegetation, ecological restoration, functional restoration, and forest landscape restoration (Stanturf et al. 2014). Defining the objectives of the restoration project and setting realistic goals, therefore, is a critical step toward ensuring its long-term sustainability (Jacobs et al. 2015). For example, restoration efforts focused on species and populations (falling under IUCN’s definition of “conservation translocation”) have different objectives than those focused on recovering degraded ecosystems (Corlett 2016), although ecosystem restoration projects could have potential genetic conservation components or consequences (e.g., DeWald and Kolanoski 2017). Science should fulfill the role of informing and framing the debate about restoration goals by providing objective

descriptions of feasibility and probable consequences (Stanturf et al. 2014), including when genetic conservation is a potential restoration objective.

Key conclusions and meeting outcomes

The job of effectively and efficiently conserving the world's forest genetic resources is a large and complicated one, perhaps even overwhelming to some (Crane 2015), but it is imperative given the ecological, economic and cultural importance of forest tree species. Fortunately, we know how to start working toward achieving our tree conservation goals. We will need additional research, management, education and training capacity to understand and mitigate the threats to species; better information about species distributions; more policy and funding support for research and conservation; and a public that better understands the importance of plants and why they need to be conserved (Havens et al. 2014). These will all require cooperation among widely diverse groups of scientists, managers, and policymakers from the public and private sectors around the world. The *Gene Conservation of Tree Species—Banking on the Future* workshop was designed to encourage the exchange of information and the creation of collaborations among these stakeholders.

Several key themes emerged from the meeting's presentations and dialogue, which were further explored in this paper:

1. Several international organizations and policy frameworks have recognized the need for tree genetic conservation and have set ambitious targets for in situ conservation, ex situ conservation, and restoration of tree species. *Governments and non-governmental organizations around the world have made significant progress* toward meeting these goals.
2. *Basic information about many tree species is greatly lacking*, complicating efforts to meet global conservation targets. The Global Tree Assessment represents an example of an important step forward by evaluating the conservation status of all of the world's tree species, while GlobalTreeSearch, a complete and georeferenced country-level list of tree species, provides the foundation for the assessment.
3. *Partnerships are essential* to accomplish the effective genetic conservation of tree species. Better coordination is needed among government agencies, botanic gardens, arboreta, plant and seed collection groups, and other non-governmental organizations.
4. Researchers need to *evaluate whether existing in situ reserves adequately protect species* and are sufficient for future conservation needs in context of ongoing threats to tree species, including habitat loss and changing climate. Additionally, genetic conservation of tree species should be better integrated into the management of protected areas, particularly in light of pests and pathogens, climate change, and other threats.
5. Research must *address key knowledge gaps* about the most effective and efficient approaches to conserve tree species using ex situ methods, and to restore them to natural environments.
6. *Botanic gardens and arboreta can and should play a critical role* in the ex situ and in situ conservation of tree species, both in seed collection and banking efforts and in living collections of species that do not produce seeds easily stored using standard seed banking methods. They also are uniquely positioned to educate the public about the importance of tree species genetic diversity and the need to preserve it.

7. *Better coordination is needed* between in situ and ex situ conservation efforts to improve the efficiency and effectiveness of tree conservation programs.
8. Critical needs exist for *increased production of planting stock* for restoration purposes, particularly stock that is resistant to important pests and pathogens, for more strategic dissemination of this germplasm, and for guidance about how to match restoration locations with the proper seed sources.
9. Much of the world's tree genetic conservation efforts have focused on temperate and boreal tree species, so *a greater emphasis is required for tropical and semi-tropical tree species*, particularly given their high diversity.
10. Conservation needs exceed the capacity to respond to them, so *scientifically sound priority-setting efforts are required* to identify tree species and populations in greatest need of conservation action. Successful forest tree gene conservation efforts must anticipate future needs relating to the threats faced by tree species and the resources required to protect their genetic resources.

In addition to the scores of research presentations describing cutting-edge science in forest tree genetic conservation (with corresponding papers published in this special issue and in a conference proceedings document by the USDA Forest Service's Pacific Northwest Research Station), participants readily shared information and worked to develop partnerships and to advance existing collaborations. A highlight of the workshop, for example, was the signing of a memorandum of understanding between the North American Plant Conservation Initiative (see "Ex situ conservation", above) and the USDA Forest Service, setting a framework for these partners to work more closely to further plant genetic conservation. At the conclusion of the workshop, participants committed to pursuing this and other actions to improve the global understanding of tree genetic conservation needs and best practices. As Crane (2015) reminded those interested in the future of tree diversity, "There is plenty to be done, there is no time to lose, and as opportunities arise they need to be seized with vigour." Participants at the *Gene Conservation of Tree Species—Banking on the Future* workshop did their best to follow his advice, and planned to continue doing so.

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References

- Alfaro RI, Fady B, Vendramin GG, Dawson IK, Fleming RA, Saenz-Romero C, Lindig-Cisneros RA, Murdock T, Vinceti B, Navarro CM, Skroppa T, Baldinelli G, El-Kassaby YA, Loo J (2014) The role of forest genetic resources in responding to biotic and abiotic factors in the context of anthropogenic climate change. *Forest Ecol Manag* 333:76–87. doi:10.1016/j.foreco.2014.04.006
- Aravanopoulos FA (2016) Conservation and monitoring of tree genetic resources in temperate forests. *Curr Rep Rep* 2(2):119–129. doi:10.1007/s40725-016-0038-8

- Asner GP, Rudel TK, Aide TM, Defries R, Emerson R (2009) A contemporary assessment of change in humid tropical forests. *Conserv Biol* 23(6):1386–1395. doi:10.1111/j.1523-1739.2009.01333.x
- Bayliss J, Makungwa S, Hecht J, Nangoma D, Bruessow C (2007) Saving the island in the sky: the plight of the Mount Mulanje cedar *Widdringtonia whytei* in Malawi. *Oryx* 41(1):64–69. doi:10.1017/s0030605307001548
- Beech E, Rivers M, Oldfield S, Smith P (2017) GlobalTreeSearch: the first complete global database of tree species and country distributions. *J Sustain For*. doi:10.1080/10549811.2017.1310049
- BGCI (2016) North American botanic garden strategy for plant conservation, 2016–2020. Botanic Gardens Conservation International, Chicago
- Boraks A, Broders KD (2016) Population genetic diversity of the rare hardwood butternut (*Juglans cinerea*) in the northeastern USA. *Tree Genet Genomes* 12(3):10. doi:10.1007/s11295-016-1002-2
- Boshier DH, Boyle TJ (2000) Forest conservation genetics: limitations and future directions. In: Young AG, Boshier D, Boyle TJ (eds) *Forest conservation genetics: principles and practice*. CSIRO Publishing, Collingwood, pp 289–297
- Bottrill MC, Joseph LN, Carwardine J, Bode M, Cook C, Game ET, Grantham H, Kark S, Linke S, McDonald-Madden E, Pressey RL, Walker S, Wilson KA, Possingham HP (2008) Is conservation triage just smart decision making? *Trends Ecol Evol* 23(12):649–654. doi:10.1016/j.tree.2008.07.007
- Bower AD, St Clair B, Erickson V (2014) Generalized provisional seed zones for native plants. *Ecol Appl* 24(5):913–919
- Broadhurst LM, Lowe A, Coates DJ, Cunningham SA, McDonald M, Vesk PA, Yates C (2008) Seed supply for broadscale restoration: maximizing evolutionary potential. *Evol Appl* 1(4):587–597. doi:10.1111/j.1752-4571.2008.00045.x
- Castaneda-Alvarez NP, Khoury CK, Achicanoy HA, Bernau V, Dempewolf H, Eastwood RJ, Guarino L, Harker RH, Jarvis A, Maxted N, Muller JV, Ramirez-Villegas J, Sosa CC, Struik PC, Vincent H, Toll J (2016) Global conservation priorities for crop wild relatives. *Nat Plants* 2(4):6. doi:10.1038/nplants.2016.22
- Cavender N, Westwood M, Bechtoldt C, Donnelly G, Oldfield S, Gardner M, Rae D, McNamara W (2015) Strengthening the conservation value of ex situ tree collections. *Oryx* 49(3):416–424
- Corlett RT (2016) Restoration, reintroduction, and rewilding in a changing world. *Trends Ecol Evol* 31(6):453–462. doi:10.1016/j.tree.2016.02.017
- Crane P (2015) Can we save the charismatic megaflores? *Oryx* 49(3):377–378. doi:10.1017/s0030605315000708
- Dalgleish HJ, Nelson CD, Scrivani JA, Jacobs DF (2016) Consequences of shifts in abundance and distribution of American Chestnut for restoration of a foundation forest tree. *Forests* 7(1):9. doi:10.3390/f7010004
- de Lafontaine G, Ducousso A, Lefevre S, Magnanou E, Petit RJ (2013) Stronger spatial genetic structure in recolonized areas than in refugia in the European beech. *Mol Ecol* 22(17):4397–4412. doi:10.1111/mec.12403
- Devine W, Aubry C, Miller J, Potter KM, Bower AD (2012) *Climate change and forest trees in the Pacific Northwest: Guide to vulnerability assessment methodology*. USDA Forest Service, Pacific Northwest Region, Olympia
- DeWald LE, Kolanoski KM (2017) Conserving genetic diversity in ecological restoration: a case study with ponderosa pine in northern Arizona. *New Forest, USA*. doi:10.1007/s11056-016-9565-1
- Dukes JS, Pontius J, Orwig D, Garnas JR, Rodgers VL, Brazee N, Cooke B, Theoharides KA, Stange EE, Harrington R, Ehrenfeld J, Gurevitch J, Lerdau M, Stinson K, Wick R, Ayres M (2009) Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: what can we predict? *Can J For Res Revue* 39(2):231–248. doi:10.1139/x08-171
- Dumroese RK, Williams MI, Stanturf JA, Clair JBS (2015) Considerations for restoring temperate forests of tomorrow: forest restoration, assisted migration, and bioengineering. *New Forest* 46(5–6):947–964. doi:10.1007/s11056-015-9504-6
- Dvorak WS, Hamrick JL, Hodge GP (1999) Assessing the sampling efficiency of ex situ gene conservation efforts in natural pine populations in Central America. *For Genet* 6(1):21–28
- Eckert AJ, Wegrzyn JL, Liechty JD, Lee JM, Cumbie WP, Davis JM, Goldfarb B, Loopstra CA, Palle SR, Quesada T, Langley CH, Neale DB (2013) The evolutionary genetics of the genes underlying phenotypic associations for loblolly pine (*Pinus taeda*, Pinaceae). *Genetics* 195(4):1353–1372. doi:10.1534/genetics.113.157198
- Eriksson G, Namkoong G, Roberds JH (1993) Dynamic gene conservation for uncertain futures. *Forest Ecol Manag* 62(1–4):15–37

- Faber-Langendoen D, Nichols J, Master L, Snow K, Tomaino A, Bittman R, Hammerson G, Heidel B, Ramsay L, Teucher A, Young B (2012) NatureServe conservation status assessments: methodology for assigning ranks. NatureServe, Arlington
- Fant JB, Havens K, Kramer AT, Walsh SK, Callicrate T, Lacy RC, Maunder M, Meyer AH, Smith PP (2016) What to do when we can't bank on seeds: what botanic gardens can learn from the zoo community about conserving plants in living collections. *Am J Bot* 103(9):1541–1543. doi:10.3732/ajb.1600247
- FAO (2010) Global forest resources assessment. Main report. Commission on Genetic Resources for Food and Agriculture, Food and Agriculture Organization of the United Nations, Rome
- FAO (2012) The state of the world's forest genetic resources: country report—United States of America. Commission on Genetic Resources for Food and Agriculture, Food and Agriculture Organization of the United Nations, Rome
- FAO (2014a) Global plan of action for the conservation, sustainable use and development of Forest Genetic Resources. Commission on Genetic Resources for Food and Agriculture, Food and Agriculture Organization of the United Nations, Rome
- FAO (2014b) 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
- Fettig CJ, Reid ML, Bentz BJ, Sevanto S, Spittlehouse DL, Wang TL (2013) Changing climates, changing forests: A Western North American perspective. *J Forest* 111(3):214–228. doi:10.5849/jof.12-085
- Foden WB, Butchart SHM, Stuart SN, Vie JC, Akcakaya HR, Angulo A, DeVantier LM, Gutsche A, Turak E, Cao L, Donner SD, Katariya V, Bernard R, Holland RA, Hughes AF, O'Hanlon SE, Garnett ST, Sekercioğlu CH, Mace GM (2013) Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS ONE* 8 (6). doi:10.1371/journal.pone.0065427
- Frankham R, Ballou JD, Briscoe DA (2002) Introduction to conservation genetics. Cambridge University Press, Cambridge
- Given DR (1994) Principles and practice of plant conservation. Timber Press, Portland
- Graudal L, Aravanopoulos F, Bennadji Z, Changtragoon S, Fady B, Kjaer ED, Loo J, Ramamonjisoa L, Vendramin GG (2014) Global to local genetic diversity indicators of evolutionary potential in tree species within and outside forests. *Forest Ecol Manag* 333:35–51. doi:10.1016/j.foreco.2014.05.002
- Gray LK, Hamann A (2013) Tracking suitable habitat for tree populations under climate change in western North America. *Clim Change* 117(1–2):289–303. doi:10.1007/s10584-012-0548-8
- Guerrant EOJ, Fiedler PL, Havens K, Maunder M (2004) Revised genetic sampling guidelines for conservation collections of rare and endangered plants. In: Guerrant EOJ, Havens K, Maunder M (eds) *Ex situ plant conservation: supporting species survival in the wild*. Island Press, Washington, pp 419–438
- Guerrant EO, Havens K, Vitt P (2014) Sampling for effective ex situ plant conservation. *Int J Plant Sci* 175(1):11–20. doi:10.1086/674131
- Haidet M, Olwell P (2015) Seeds of success: a national seed banking program working to achieve long-term conservation goals. *Nat Areas J* 35(1):165–173
- Hamrick JL (2004) Response of forest trees to global environmental changes. *Forest Ecol Manag* 197(1–3):323–335. doi:10.1016/j.foreco.2004.05.023
- Hamrick JL, Nason JD (2000) Gene flow in forest trees. In: Young AG, Boshier D, Boyle TJ (eds) *Forest conservation genetics: principles and practice*. CSIRO Publishing, Collingwood, pp 81–90
- Harris JA, Hobbs RJ, Higgs E, Aronson J (2006) Ecological restoration and global climate change. *Restor Ecol* 14(2):170–176. doi:10.1111/j.1526-100X.2006.00136.x
- Hastings JM, Potter KM, Koch FH, Megalos M, Jetton RM (2017) Prioritizing conservation seed banking locations for imperiled hemlock species using multi-attribute frontier mapping. *N Forest*. doi:10.1007/s11056-017-9575-7
- Havens K, Guerrant EOJ, Maunder M, Vitt P (2004) Guidelines for ex situ conservation collection management: minimizing risks. In: Guerrant EOJ, Havens K, Maunder M (eds) *Ex situ plant conservation: supporting species survival in the wild*. Island Press, Washington, pp 454–473
- Havens K, Kramer AT, Guerrant EO (2014) Getting plant conservation right (or not): the case of the United States. *Int J Plant Sci* 175(1):3–10. doi:10.1086/674103
- Havens K, Vitt P, Still S, Kramer AT, Fant JB, Schatz K (2015) Seed sourcing for restoration in an era of climate change. *Nat Areas J* 35(1):122–133
- Hoban S, Schlarbaum S (2014) Optimal sampling of seeds from plant populations for ex situ conservation of genetic biodiversity, considering realistic population structure. *Biol Conserv* 177:90–99. doi:10.1016/j.biocon.2014.06.014
- Hoban S, Strand A (2015) *Ex situ* seed collections will benefit from considering spatial sampling design and species' reproductive biology. *Biol Conserv* 187:182–191. doi:10.1016/j.biocon.2015.04.023

- Hodge GR, Lopez JL, Acosta JJ, Woodbridge WC, Jump R, Jetton RM, Whittier WA, McGee JR, Gutierrez E (2017) Camcore 2016 annual report. North Carolina State University, Raleigh
- Holsinger KE, Vitt P (1997) The future of conservation biology: what's a geneticist to do? In: Pickett STA, Ostfeld RS, Shachak M, Likens GE (eds) The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity. Chapman and Hall, New York, pp 202–217
- Jacobs DF (2007) Toward development of silvical strategies for forest restoration of American chestnut (*Castanea dentata*) using blight-resistant hybrids. *Biol Conserv* 137(4):497–506. doi:10.1016/j.biocon.2007.03.013
- Jacobs DF, Dalglish HJ, Nelson CD (2013) A conceptual framework for restoration of threatened plants: the effective model of American chestnut (*Castanea dentata*) reintroduction. *New Phytol* 197(2):378–393. doi:10.1111/nph.12020
- Jacobs DF, Olie JA, Aronson J, Bolte A, Bullock JM, Donoso PJ, Landhausser SM, Madsen P, Peng SL, Rey-Benayas JM, Weber JC (2015) Restoring forests: what constitutes success in the twenty-first century? *New Forest* 46(5–6):601–614. doi:10.1007/s11056-015-9513-5
- Jaramillo-Correa JP, Beaulieu J, Khasa DP, Bousquet J (2009) Inferring the past from the present phylogeographic structure of North American forest trees: seeing the forest for the genes. *Can J For Res* 39(2):286–307. doi:10.1139/x08-181
- Jetton RM, Whittier WA, Dvorak WS, Rhea JR (2013) Conserved ex situ genetic resources of eastern and Carolina hemlock: eastern North American conifers threatened by the hemlock woolly adelgid. *Tree Planters' Notes* 70:59–71
- Jump AS, Marchant R, Penuelas J (2009) Environmental change and the option value of genetic diversity. *Trends Plant Sci* 14(1):51–58. doi:10.1016/j.tplants.2008.10.002
- Kanowski PJ (2000) Politics, policies and the conservation of forest genetic diversity. In: Young AG, Boshier D, Boyle TJ (eds) *Forest conservation genetics: principles and practice*. CSIRO Publishing, Collingwood, pp 275–287
- Kanowski PJ, Boshier DH (1997) Conserving the genetic resources of trees in situ. In: Maxted N, Ford-Lloyd BV, Hawkes JG (eds) *Plant conservation: the in situ approach*. Chapman and Hall, London, pp 207–219
- Kew (2012) Plants under pressure—a global assessment. The first report of the sampled red index list for plants. Royal Botanic Gardens, Kew. http://www.kew.org/sites/default/files/kppcont_027304.pdf. Accessed 9 Feb 2017
- Kimura MK, Uchiyama K, Nakao K, Moriguchi Y, San Jose-Maldia L, Tsumura Y (2014) Evidence for cryptic northern refugia in the last glacial period in *Cryptomeria japonica*. *Ann Bot* 114(8):1687–1700. doi:10.1093/aob/mcu197
- Kirk H, Freeland JR (2011) Applications and implications of neutral versus non-neutral markers in molecular ecology. *Int J Mol Sci* 12(6):3966–3988. doi:10.3390/ijms12063966
- Koskela J, Vinceti B, Dvorak W, Bush D, Dawson IK, Loo J, Kjaer ED, Navarro C, Padolina C, Bordacs S, Jamnadass R, Graudal L, Ramamonjisoa L (2014) Utilization and transfer of forest genetic resources: a global review. *Forest Ecol Manag* 333:22–34. doi:10.1016/j.foreco.2014.07.017
- Kramer AT, Havens K (2009) Plant conservation genetics in a changing world. *Trends Plant Sci* 14(11):599–607. doi:10.1016/j.tplants.2009.08.005
- LaBonte N, Tonos J, Hartel C, Woeste KE (2017) Genetic diversity and differentiation of yellowwood [*Cladrastis kentukea* (Dum.Cours.) Rudd] growing in the wild and in planted populations outside the natural range. *N For*. doi:10.1007/s11056-017-9566-8
- Ledig FT (1992) Human impacts on genetic diversity in forest ecosystems. *Oikos* 63(1):87–108. doi:10.2307/3545518
- Ledig FT, Kitzmiller JH (1992) Genetic strategies for reforestation in the face of global climate change. *Forest Ecol Manag* 50(1–2):153–169
- Ledig FT, Vargas-Hernandez JJ, Johnsen KH (1998) The conservation of forest genetic resources: Case histories from Canada, Mexico, and the United States. *J Forest* 96(1):32–41
- Lefevre F, Koskela J, Hubert J, Kraigher H, Longauer R, Olrik DC, Schueler S, Bozzano M, Alizoti P, Bakys R, Baldwin C, Ballian D, Black-Samuelsson S, Bednarova D, Bordacs S, Collin E, De Cuyper B, De Vries SMG, Eysteinnsson T, Frydl J, Haverkamp M, Ivankovic M, Konrad H, Koziol C, Maaten T, Paino EN, Ozturk H, Pandeva ID, Parnuta G, Pilipovic A, Postolache D, Ryan C, Steffenrem A, Varela MC, Vessella F, Volosyanchuk RT, Westergren M, Wolter F, Yrjana L, Zarina I (2013) Dynamic conservation of forest genetic resources in 33 European Countries. *Conserv Biol* 27(2):373–384. doi:10.1111/j.1523-1739.2012.01961.x
- Li DZ, Pritchard HW (2009) The science and economics of ex situ plant conservation. *Trends Plant Sci* 14(11):614–621. doi:10.1016/j.tplants.2009.09.005

- Lipow SR, Vance-Borland K, St Clair JB, Henderson J, McCain C (2004) Gap analysis of conserved genetic resources for forest trees. *Conserv Biol* 18(2):412–423
- Liu JJ, Snieszko R, Murray M, Wang N, Chen H, Zamany A, Sturrock RN, Savin D, Kegley A (2016) Genetic diversity and population structure of Whitebark Pine (*Pinus albicaulis* Engelm.) in Western North America. *PLoS ONE* 11 (12). doi:10.1371/journal.pone.0167986
- Lovett GM, Weiss M, Liebhold AM, Holmes TP, Leung B, Lambert KF, Orwig DA, Campbell FT, Rosenthal J, McCullough DG, Wildova R, Ayres MP, Canham CD, Foster DR, LaDeau SL, Weldy T (2016) Nonnative forest insects and pathogens in the United States: impacts and policy options. *Ecol Appl* 26(5):1437–1455
- Mace GM, Collar NJ, Gaston KJ, Hilton-Taylor C, Akcakaya HR, Leader-Williams N, Milner-Gulland EJ, Stuart SN (2008) Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv Biol* 22(6):1424–1442. doi:10.1111/j.1523-1739.2008.01044.x
- Maunder M, Guerrant EOJ, Havens K, Dixon KW (2004a) Realizing the full potential of ex situ contributions to global plant conservation. In: Guerrant EOJ, Havens K, Maunder M (eds) *Ex situ plant conservation: supporting species survival in the wild*. Island Press, Washington, pp 389–418
- Maunder M, Havens K, Guerrant EOJ, Falk DA (2004b) *Ex situ* methods: a vital but underused set of conservation resources. In: Guerrant EOJ, Havens K, Maunder M (eds) *Ex Situ plant conservation: supporting species survival in the wild*. Island Press, Washington, pp 3–20
- Merkle SA, Andrade GM, Nairn CJ, Powell WA, Maynard CA (2007) Restoration of threatened species: a noble cause for transgenic trees. *Tree Genet Genomes* 3(2):111–118. doi:10.1007/s11295-006-0050-4
- Merritt DJ, Dixon KW (2014) Seed availability for restoration. In: Bozzano M, Jalonen R, Thomas E et al. (eds) *The state of the world's forest genetic resources—thematic study. Genetic Considerations in Ecosystem Restoration Using Native Tree Species*. Commission on Genetic Resources for Food and Agriculture, Food and Agriculture Organization of the United Nations, Rome, pp 97–104
- Millar CI, Libby WJ (1991) Strategies for conserving clinal, ecotypic and disjunct population diversity in widespread species. In: Falk DA, Holsinger KE (eds) *Genetics and conservation of rare plants*. Oxford University Press, New York, pp 149–170
- Millar CI, Stephenson NL (2015) Temperate forest health in an era of emerging megadisturbance. *Science* 349(6250):823–826. doi:10.1126/science.aaa9933
- Millar CI, Stephenson NL, Stephens SL (2007) Climate change and forests of the future: managing in the face of uncertainty. *Ecol Appl* 17(8):2145–2151. doi:10.1890/06-1715.1
- Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: synthesis*. Island Press, Washington
- Miller SA, Bartow A, Gisler M, Ward K, Young AS, Kaye TN (2010) Can an ecoregion serve as a seed transfer zone? Evidence from a common garden study with five native species. *Restor Ecol* 19:268–276. doi:10.1111/j.1526-100X.2010.00702.x
- Montréal Process Working Group (2009) Technical notes on implementation of the Montréal process criteria and indicators, Criteria 1-7, 3rd edn. Montréal Process Liaison Office. http://www.montrealprocess.org/Resources/Criteria_and_Indicators/index.shtml
- Morales-Hidalgo D, Oswalt SN, Somanathan E (2015) Status and trends in global primary forest, protected areas, and areas designated for conservation of biodiversity from the Global Forest Resources Assessment 2015. *Forest Ecol Manag* 352:68–77. doi:10.1016/j.foreco.2015.06.011
- Namkoong G (1997) A gene conservation plan for loblolly pine. *Can J For Res* 27(3):433–437
- Nelson MD, Flather CH, Riitters KH, Sieg C, Garner JD (2015) National report on sustainable forests—2015: conservation of biological diversity. In: Stanton SM, Christensen GA (eds) *Pushing boundaries: new directions in inventory techniques and applications: Forest Inventory and Analysis (FIA) symposium 2015*, vol Gen. Tech. Rep. PNW-GTR-931. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland
- Newton A, Oldfield S, Rivers M, Mark J, Schatz G, Garavito NT, Cantarello E, Golicher D, Cayuela L, Miles L (2015) Towards a global tree assessment. *Oryx* 49(3):410–415. doi:10.1017/s0030605315000137
- Oldfield S (2008) Choices for tree conservation. *Oryx* 42(2):159–160
- Oldfield S, Newton AC (2012) *Integrated conservation of tree species by botanic gardens: a reference manual*. Botanic Gardens Conservation International, Richmond
- Oten K, Merkle SA, Jetton RM, Smith BC, Talley ME, Hain FP (2014) Understanding and developing resistance in hemlocks to the hemlock woolly adelgid. *Southeast Nat* 13:147–167
- Pais AL, Whetten RW, Xiang QY (2017) Ecological genomics of local adaptation in *Cornus florida* L. by genotyping by sequencing. *Ecol Evol* 7(1):441–465. doi:10.1002/ece3.2623
- Pautasso M (2009) Geographical genetics and the conservation of forest trees. *Perspect Plant Ecol Evol Syst* 11(3):157–189. doi:10.1016/j.ppees.2009.01.003

- Payton G (2010) Conserving the Dawn Redwood: the *Ex Situ* collection at the Dawes Arboretum. *Arnoldia* 68(1):26–33
- Pedlar JH, McKenney DW, Aubin I, Beardmore T, Beaulieu J, Iverson L, O'Neill GA, Winder RS, Ste-Marie C (2012) Placing forestry in the assisted migration debate. *Bioscience* 62(9):835–842. doi:10.1525/bio.2012.62.9.10
- Pimm SL, Brooks TM (1999) The sixth extinction: how large, how soon, and where? In: Raven P (ed) *Nature and human society: the quest for a sustainable world*. National Academy Press, Washington
- Porth I, El-Kassaby YA (2014) Assessment of the genetic diversity in forest tree populations using molecular markers. *Diversity* 6:283–295
- Potter KM, Crane BS (2012) Silviculture and the assessment of climate change genetic risk for southern Appalachian Forest Tree Species. In: Butnor JR (ed) *Proceedings of the 16th Biennial southern silvicultural research conference (BSSRC), general technical report SRS-156*. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, pp 257–258
- Potter KM, Hargrove WW (2012) Determining suitable locations for seed transfer under climate change: a global quantitative model. *New Forest* 43(5–6):581–599. doi:10.1007/s11056-012-9322-z
- Potter KM, Jetton RM, Dvorak WS, Hipkins VD, Rhea R, Whittier WA (2012) Widespread inbreeding and unexpected geographic patterns of genetic variation in eastern hemlock (*Tsuga canadensis*), an imperiled North American conifer. *Conserv Genet* 13(2):475–498. doi:10.1007/s10592-011-0301-2
- Potter KM, Crane BS, Hargrove WW (2017) A United States national prioritization framework of tree species threatened by climate change. *N Forest*. doi:10.1007/s11056-017-9569-5
- Pritchard HW, Moat JF, Ferraz JBS, Marks TR, Camargo JLC, Nadarajan J, Ferraz IDK (2014) Innovative approaches to the preservation of forest trees. *Forest Ecol Manag* 333:88–98. doi:10.1016/j.foreco.2014.08.012
- Quiñones-Pérez CZ, González-Elizondo MdS, Wehenkel C (2017) Ruling out genetic erosion in *Picea chihuahuana* Martínez. *N Forest*. doi:10.1007/s11056-017-9581-9
- Rajora OP, Mosseler A (2001) Challenges and opportunities for conservation of forest genetic resources. *Euphytica* 118(2):197–212
- Ramsfield TD, Bentz BJ, Faccoli M, Jactel H, Brockerhoff EG (2016) Forest health in a changing world: effects of globalization and climate change on forest insect and pathogen impacts. *Forestry* 89(3):245–252. doi:10.1093/forestry/cpw018
- Ratnam W, Rajora OP, Finkeldey R, Aravanopoulos F, Bouvet JM, Vaillancourt RE, Kanashiro M, Fady B, Tomita M, Vinson C (2014) Genetic effects of forest management practices: global synthesis and perspectives. *Forest Ecol Manag* 333:52–65. doi:10.1016/j.foreco.2014.06.008
- Reed DH, Frankham R (2001) How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. *Evolution* 55(6):1095–1103. doi:10.1554/0014-3820(2001)055[1095:HCCAMA]2.0.CO;2
- Reed DH, Frankham R (2003) Correlation between fitness and genetic diversity. *Conserv Biol* 17(1):230–237
- Rehfeldt GE, Leites LP, St Clair JB, Jaquish BC, Saenz-Romero C, Lopez-Upton J, Joyce DG (2014) Comparative responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: clines in growth potential. *Forest Ecol Manag* 324:138–146
- Rico Y (2017) Using computer simulations to assess sampling effects on spatial genetic structure in forest tree species. *N Forest*. doi:10.1007/s11056-017-9571-y
- Riitters KH, Wickham J, Costanza JK, Vogt P (2016) A global evaluation of forest interior area dynamics using tree cover data from 2000 to 2012. *Landscape Ecol* 31(1):137–148. doi:10.1007/s10980-015-0270-9
- Rivers M, Shaw K, Beech E, Jones M (2015) *Conserving the world's most threatened trees: a global survey of ex situ collections*. Botanic Gardens Conservation International, Richmond
- Rolston H (2004) In situ and ex situ conservation: Philosophical and ethical concerns. In: Guerrant EOJ, Havens K, Maunder M (eds) *Ex situ plant conservation: supporting species survival in the wild*. Island Press, Washington, pp 21–39
- Schaal B, Leverich WJ (2004) Population genetic issues in ex situ plant conservation. In: Guerrant EOJ, Havens K, Maunder M (eds) *Ex situ plant conservation: supporting species survival in the wild*. Island Press, Washington, pp 267–285
- Schaberg PG, DeHayes DH, Hawley GJ, Nijensohn SE (2008) Anthropogenic alterations of genetic diversity within tree populations: implications for forest ecosystem resilience. *Forest Ecol Manag* 256(5):855–862. doi:10.1016/j.foreco.2008.06.038
- Schoettle AW, Coop JD (2017) Range-wide conservation of *Pinus aristata*: a genetic collection with ecological context for proactive management today and resources for tomorrow. *N Forest*. doi:10.1007/s11056-017-9570-z

- Schoettle AW, Snieszko RA (2007) Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. *J For Res* 12(5):327–336. doi:10.1007/s10310-007-0024-x
- Schoettle AW, Goodrich BA, Hipkins V, Richards C, Kray J (2012) Geographic patterns of genetic variation and population structure in *Pinus aristata*, Rocky Mountain bristlecone pine. *Can J For Res Revue* 42(1):23–37. doi:10.1139/x11-152
- Sharrock S (2012) Global strategy for plant conservation: a guide to the GSPC, All the Targets, Objectives and Facts. Botanic Gardens Conservation International, Richmond
- Shearman P, Bryan J, Laurance WF (2012) Are we approaching ‘peak timber’ in the tropics? *Biol Conserv* 151(1):17–21. doi:10.1016/j.biocon.2011.10.036
- Snieszko RA (2006) Resistance breeding against nonnative pathogens in forest trees—current successes in North America. *Can J Plant Pathol-Rev Can Phytopathol* 28:S270–S279
- Snieszko RA, Kegley A, Savin DP (2017) Ex situ genetic conservation potential of seeds of two high elevation white pines. *N Forest*. doi:10.1007/s11056-017-9579-3
- St Clair JB, Howe GT (2011) Strategies for conserving forest genetic resources in the face of climate change. *Turk J Bot* 35(4):403–409. doi:10.3906/bot-1012-98
- Stanturf JA, Palik BJ, Williams MI, Dumroese RK, Madsen P (2014) Forest restoration paradigms. *J Sustain For* 33:S161–S194. doi:10.1080/10549811.2014.884004
- Steiner KC, Westbrook JW, Hebard FV, Georgi LL, Powell WA, Fitzsimmons SF (2017) Rescue of American chestnut with extraspecific genes following its destruction by a naturalized pathogen. *N Forest*. doi:10.1007/s11056-016-9561-5
- Tamaki I, Setsuko S, Tomaru N (2016) Genetic diversity and structure of remnant *Magnolia stellata* populations affected by anthropogenic pressures and a conservation strategy for maintaining their current genetic diversity. *Conserv Genet* 17(3):715–725. doi:10.1007/s10592-016-0817-6
- Thomas E, Jalonen R, Gallo L, Boshier D, Loo J (2014a) Introduction. In: Bozzano M, Jalonen R, Thomas E et al. (eds) The state of the world’s forest genetic resources—thematic study. Genetic considerations in ecosystem restoration using native tree species. Commission on Genetic Resources for Food and Agriculture, Food and Agriculture Organization of the United Nations, Rome, pp 3–12
- Thomas E, Jalonen R, Loo J, Boshier D, Gallo L, Cavers S, Bordacs S, Smith P, Bozzano M (2014b) Genetic considerations in ecosystem restoration using native tree species. *Forest Ecol Manag* 333:66–75. doi:10.1016/j.foreco.2014.07.015
- Tripana V, Bourgeois M, Verhaegen D, Vigneron P, Bouvet JM (2007) Combining microsatellites, growth, and adaptive traits for managing in situ genetic resources of *Eucalyptus urophylla*. *Can J For Res Revue* 37(4):773–785. doi:10.1139/x06-260
- United States Department of Agriculture Forest Service (2011) National Report on Sustainable Forests—2010. U.S. Department of Agriculture Forest Service, Washington
- van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fule PZ, Harmon ME, Larson AJ, Smith JM, Taylor AH, Veblen TT (2009) Widespread increase of tree mortality rates in the Western United States. *Science* 323(5913):521–524. doi:10.1126/science.1165000
- Vogel KP, Schmer MR, Mitchell RB (2005) Plant adaptation regions: ecological and climatic classification of plant materials. *Rangel Ecol Manag* 58(3):315–319. doi:10.2111/1551-5028(2005)58[315: PAREAC]2.0.CO;2
- Wade TG, Riitters KH, Wickham JD, Jones KB (2003) Distribution and causes of global forest fragmentation. *Conserv Ecol* 7(2):16
- Wei XX, Beaulieu J, Khasa DP, Vargas-Hernandez J, Lopez-Upton J, Jaquish B, Bousquet J (2011) Range-wide chloroplast and mitochondrial DNA imprints reveal multiple lineages and complex biogeographic history for Douglas-fir. *Tree Genet Genomes* 7(5):1025–1040. doi:10.1007/s11295-011-0392-4
- Willi Y, Van Buskirk J, Hoffmann AA (2006) Limits to the adaptive potential of small populations. *Annu Rev Ecol Evol Syst* 37:433–458
- Williams CG (2017) How meso-scale pollen dispersal and its gene flow shape gene conservation decisions. *N Forest*. doi:10.1007/s11056-017-9574-8
- Yanchuk AD, Lester DT (1996) Setting priorities for conservation of the conifer genetic resources of British Columbia. *Forest Chron* 72(4):406–415
- Yemshanov D, Koch FH, Ben-Haim Y, Downing M, Sapio F, Siltanen M (2013) A new multicriteria risk mapping approach based on a multiattribute frontier concept. *Risk Anal* 33(9):1694–1709. doi:10.1111/risa.12013
- Ying CC, Yanchuk AD (2006) The development of British Columbia’s tree seed transfer guidelines: purpose, concept, methodology, and implementation. *Forest Ecol Manag* 227(1–2):1–13