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Considerations for restoring temperate forests of tomorrow: forest restoration, assisted migration, and bioengineering

R. Kasten Dumroese[1] · Mary I. Williams[2] · John A. Stanturf[3] · J. Bradley St. Clair[4]

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Abstract Tomorrow's forests face extreme pressures from contemporary climate change, invasive pests, and anthropogenic demands for other land uses. These pressures, collectively, demand land managers to reassess current and potential forest management practices. We discuss three considerations, functional restoration, assisted migration, and bioengineering, which are currently being debated in the literature and have the potential to be applied independently or concurrently across a variety of scales. The emphasis of functional restoration is to reestablish or maintain functions provided by the forest ecosystem, such as water quality, wildlife habitat, or carbon sequestration. Maintaining function may call upon actions such as assisted migration—moving tree populations within a species current range to aid adaptation to climate change or moving a species far outside its current range to avoid extinction—and we attempt to synthesize an array of assisted migration terminology. In addition, maintenance of species and the functions they provide may also require new technologies, such as genetic engineering, which, compared with traditional approaches to breeding for pest resistance, may be accomplished more rapidly to meet and overcome the challenges of invasive insect and disease pests. As managers develop holistic adaptive strategies to current and future anthropogenic stresses, functional restoration, assisted migration, and bioengineering, either separately or in combinations, deserve consideration, but must be addressed within the context of the restoration goal.

✉ R. Kasten Dumroese
kdumroese@fs.fed.us

[1] Grassland, Shrubland, and Desert Ecosystems, Rocky Mountain Research Station, U.S. Forest Service, Moscow, ID, USA

[2] School of Forest Resources and Environmental Sciences, Michigan Technological University, Houghton, MI, USA

[3] Center for Forest Disturbance Science, Southern Research Station, U.S. Forest Service, Athens, GA, USA

[4] Land and Watershed Management, Pacific Northwest Research Station, U.S. Forest Service, Corvallis, OR, USA

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Introduction

Tomorrow's forests are under extreme pressures from anthropogenic activities. Anticipated (and unanticipated) changes to forested landscapes will require land managers to consider a broad range of management options, some of which are perceived controversial by some because they often challenge current forest restoration paradigms (Stanturf et al. 2014a). In this paper, our objective is to present some of the challenges that managers of temperate forests are facing and examine three potential management actions (functional restoration, assisted migration, bioengineering) that have been the recent focus of reviews (functional restoration: Stanturf et al. 2014a; assisted migration: Williams and Dumroese 2013) or restoration models (Jacobs et al. 2013) and that managers may possibly use to mitigate these adverse effects on tomorrow's forests. We discuss how they are justified and how they might be applied depending on the context of the restoration, either independently or concurrently at the same or different scales. In addition, we provide an example of how these concepts could be considered and applied within a contemporary restoration scenario.

Challenges

During the past three centuries, the planet has undergone dramatic anthropogenic changes (Ellis 2011) and this trend continues. The current annual rate of forest conversion (deforestation) is estimated at 13 million ha per year (FAO 2010). Perhaps more insidious, however, is the chronic degradation of forests, where the addition of new disturbances leads to loss of biodiversity that reduces ecosystem response to perturbations, destabilizes the system, and ultimately leads to a loss of function (Hooper et al. 2005). Therefore, a chief challenge to forestland managers is conserving genetic resources within and among species (St. Clair and Howe 2011) on the world's 2 billion ha of degraded forests (Minnemayer et al. 2011).

Forest degradation has causes that vary by biome and social governance structures. In the tropics, exploitive logging and agricultural encroachment are primary drivers whereas in temperate forests many biotic and abiotic stressors are involved, including fire suppression and invasive pests. Climate change, in terms of higher temperatures, altered precipitation, and more frequent extreme events are global threats to forests. Projections that estimate the world population will increase from its current 7 billion to between 9.7 and 12.5 billion by the end of this century (Fig. 1) indicate the largest population gains will be coincidental where forests are abundant (United Nations 2012). Commensurate with population growth is the expansion of international trade, which has increased 27-fold during the past 65 years (WTO 2014). Globally, areas with high human activity and international trade tend to host more invasive forest pests (Roy et al. 2014). Indeed, the numbers of nonindigenous insects and diseases introduced into forests in North America and Europe have increased dramatically during the past century (Fig. 1) and some pests have caused considerable damage to tree species (Aukema et al. 2010; Santini et al. 2013). In the temperate forests of southwest Australia, a single introduced species, *Phytophthora*

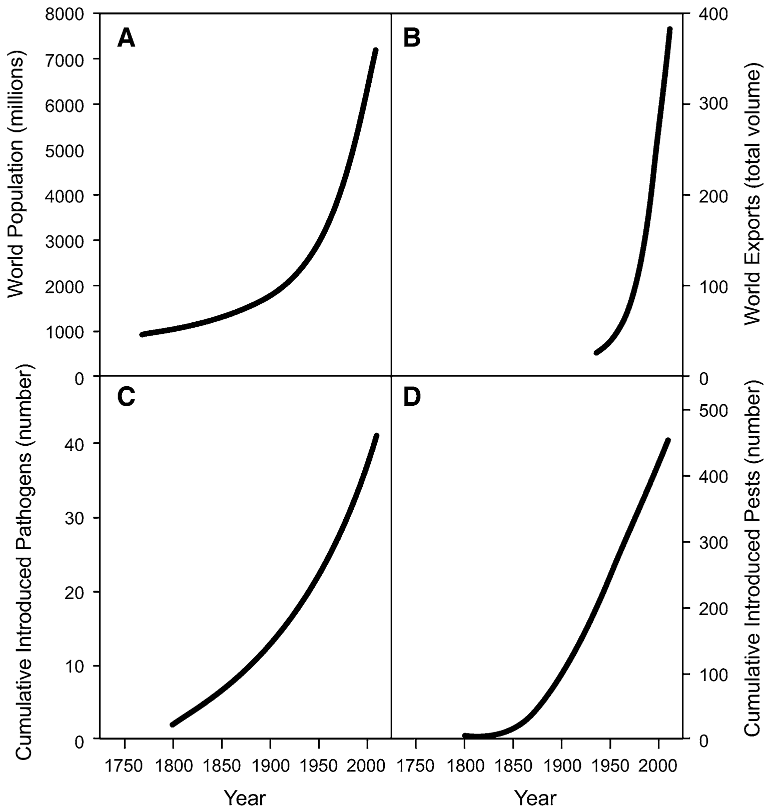

Fig. 1 Since 1880, global population (**a** Goldewijk 2005), world trade (**b** WTO 2014), and the number of introductions of fungal pathogens into Europe (**c** Santini et al. 2013) and insects and diseases into the U.S.A. (**d** Aukema et al. 2010) have all increased exponentially, putting extreme pressure on the world's forests

cinnamomi, is infesting native trees, causing significant direct and indirect changes to the ecosystem and pushing several rare taxa to extinction (Shearer et al. 2007). This same pathogen, introduced into southern Europe, is responsible for the decline of *Quercus* species (Brasier 1996). In the U.S., an average of 2.5 new pests arrives annually, with a high impact pest arriving every other year (Aukema et al. 2010). Worldwide, the number of such introductions is expected to climb (Fisher et al. 2012).

Changes in climate are increasing the likelihood, frequency, and intensity of extreme weather events, such as heat waves, cold snaps, floods, and drought (Walsh et al. 2013). Where forests remain, many tree species and populations may not be able to adapt or migrate fast enough to changes in climate (Zhu et al. 2012; Gray and Hamann 2013). Climate projections indicate trees must migrate more than 3000 m per year, far exceeding their observed annual rates of less than 500 m (Davis and Shaw 2001; Aitken et al. 2008). In North America, populations are already lagging 130 km in latitude, or 60 m in elevation, behind their optimal climate niche (Gray and Hamann 2013). Although less fragmented forests are thought to have an advantage in keeping pace with climate change (Loarie et al. 2009), climate change-induced forest mortality caused by heat and drought may already be a global phenomenon (Allen et al. 2010). Heat waves will be a common occurrence (Karl et al. 2008) contributing to drought and wildfires (Trenberth 2011). Planting the standard species in regions highly sensitive to climate change may be unwarranted (Hebda 2008), given that reductions in fire frequency from 100–300 years to 30 years, for example, have the potential to quickly shift some North American forest systems to woodlands and grasslands (Westerling et al. 2011), thereby reducing the availability of genetic resources needed to adapt or move. Furthermore, forest pests may be encouraged by shifts in climate (both by more favorable conditions for the pest and less favorable conditions for tree growth) resulting in landscape-scale tree mortality (Logan et al. 2003; Lindner et al. 2010). By 2100, an estimated 55 % of landscapes in the western U.S. may exhibit climates that are incompatible with vegetation occurring there today (Rehfeldt et al. 2006); similar scenarios are possible for Europe (Lindner et al. 2010) and these changes are projected to have severe economic consequences (Hanewinkel et al. 2013).

Climate change effects might be so abrupt that management options will be limited, even within a species' current range. Notwithstanding, plant survival may be determined more by availability of suitable recipient ecosystems (Aubin et al. 2011), the existence of landscape connections needed for plants to move (Hannah 2008), and the intensity of insect outbreaks (Logan et al. 2003; Bentz et al. 2010). Outbreaks of *Dendroctonus ponderosae* (Coleoptera: Curculiondae) in *Pinus contorta* forests, for example, are accelerated by warm temperatures and low precipitation to such an extent that even changes in management cannot curtail its impact (Regniere and Bentz 2008). Similarly, increases in the activity of insects and diseases are predicted for Europe's temperate mountain ranges (Lindner et al. 2010). Even for forests projected to have increased productivity under future climate (Lindner et al. 2010), anthropogenic disturbance is expected to increase (Ellis 2011).

Meeting the challenges

Functional restoration strives to bring back or improve a condition in which the regular function(s) that contribute to a forested system are present (see review by Stanturf et al. 2014a). A defining feature of functional restoration is its focus on what a forest provides rather than on what particular species compositions and structures formerly were present. This may involve redirecting existing human-altered forests to a more useful composition or structure through typical silvicultural treatments (e.g., thinning, reintroducing natural fire regimes, or interplanting desired species), or more strident treatments, such as those found on drastically altered sites resulting from resource extraction (e.g., mining or petroleum production). Although a late seral, complex structure and its functions are often the restoration goal (Stanturf et al. 2014b), maintaining specific functions may require maintaining or moving a forest toward an earlier, open, seral structure. The emphasis of functional restoration is that a change in condition to ensure function is more important than matching an historical reference condition—function, rather than legacy or integrity of a former forest stand condition defines success. And the value of each function, and the restoration effort to achieve it, is driven by societal as well as biological criteria (Stanturf et al. 2014a).

Strategies used to address functional restoration can be rehabilitation, reconstruction, reclamation, or replacement (Stanturf et al. 2014b). Reviewed in Stanturf et al. (2014b), these terms, while not used with consensus, logically reflect the level of restoration required across a continuum from low to severe degradation. Functional restoration can be achieved using a variety of silvicultural treatments at various scales.

Although restoring to a legacy or reference condition is not a tenet of functional restoration, restoring ecosystem function based on an understanding of contemporary reference conditions is a viable starting point for maintaining response options that facilitate the transition of forests to future climate conditions (Millar et al. 2007). On one hand, it may be that minor species in the forest may become more prominent. For example, *Acer rubrum* occurs in many current forest ecosystems of the Great Lakes region in North America, but generally at low abundance (e.g., Seymour 1992); climate niche-models, however, predict increasing habitat suitability and importance under even the most extreme emissions scenarios (Iverson et al. 2004). Thus, employing silvicultural treatments that ensure a currently minor species such as *A. rubrum* continues to be present in ecosystems where it occurs naturally can help transition forests to future conditions. On the other hand, maintaining forest function may require replacement of the native genotypes of a species with those more adapted to the future climate (e.g., assisted population migration; see Fig. 3; see Williams and Dumroese 2013; Stanturf et al. 2014a). Classic silvicultural methods and assisted migration build on the dynamic properties of forest ecosystems to maintain function and provide capacity to adapt favorably to future climates. Clearly, forest species change locations and in their abundance on the landscape in response to changing climate; movement can be long distance (Ohlemüller et al. 2012) or relative to aspect (Millar et al. 2006) and may occur in unfamiliar ways in the future, highlighting the ever-important need for management strategies that are not founded on maintaining the status quo (Moritz and Agudo 2013).

Assisted migration, the intentional movement of species or populations in response to observed or anticipated climate change (Fig. 2) (Ste-Marie et al. 2011), might be a valuable tool for rare, long-lived, and locally adapted species and populations, especially those threatened by fragmentation and pathogens and with limited adaptation and migration capacities (St. Clair and Howe 2011; Erickson et al. 2012). As discussed earlier, native populations adapted to sites under current climate may become maladapted as changes in climate occur. Assisted migration may be used to ensure adapted populations by countering two limitations of tree migration: long generation cycles and reduced dispersal ability (Potter and Hargrove 2012). Assisted migration can be applied at different scales, including moving populations within a species' current range, beyond a species' range proximate a current distribution, or long distances outside its current range (Fig. 3) (Ste-Marie et al. 2011; Winder et al. 2011; Williams and Dumroese 2013). In addition, movements can be geographic (e.g., distance along an elevation gradient), climatic (e.g., change in number of frost-free days along an elevation gradient), and/or temporal (e.g., date when the current climate of the migrated population equals the future climate of the outplanting site) (Fig. 4).

By introducing adapted plant materials, assisted migration has potential to promote resilience to change and/or ease habitat transitions already occurring and realigning systems where resources are severely degraded or fragmented (Millar 2014). Assisted migration is beginning to find its way into climate change adaptation plans (e.g., IPCC 2014) although consensus about its implementation is hampered by research and conservation challenges, existing management policies, uncertainty about future conditions, and non-standardized terminology (Hewitt et al. 2011). Assisted migration terminology, like that of restoration (see Stanturf et al. 2014a) becomes unwieldy because universalism in definitions is trumped by historical use within various disciplines and creation of context-

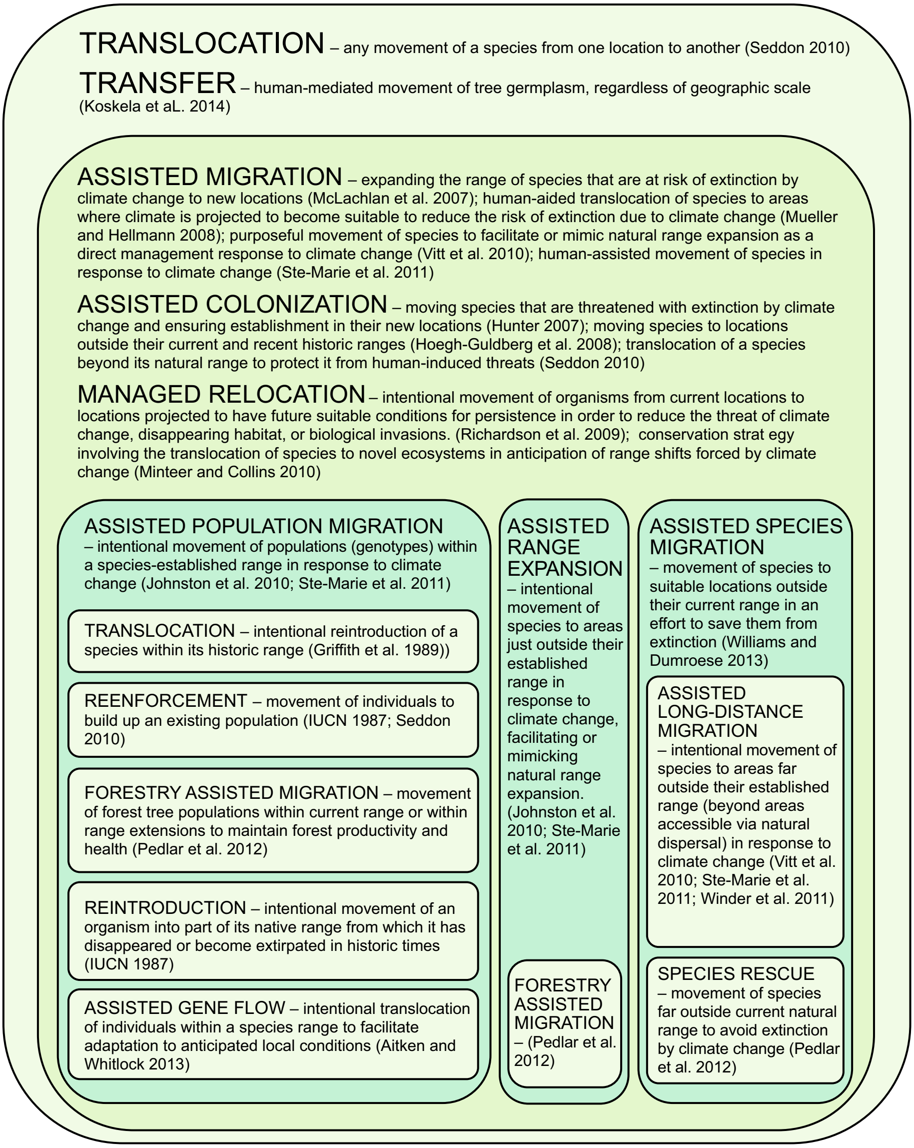

Fig. 2 The movement of plants has been defined many ways depending on context, from very broad to very narrow applications. The terms “transfer” and “translocation” may be the broadest terms. “Assisted migration,” “assisted colonization,” and “managed relocation” all essentially describe human movement of plants in response to climate change. These three terms can be further subdivided into three additional categories defined by the scale of movement: within the current range (i.e., assisted population migration and similar terms), proximate the current range (i.e., assisted range expansion), and long-distance (i.e., assisted species migration and similar terms)

base descriptions (Fig. 2). Although no explicit solution exists for this, remaining mindful to discuss assisted migration within the context of the restoration goal should support better communication among scientists and among scientists, land managers, and the public.

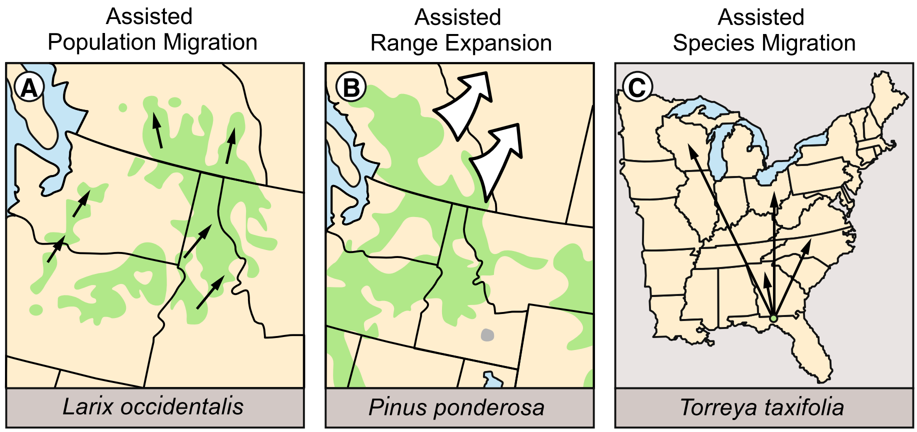

Fig. 3 Seed migration can occur as assisted population migration in which seed sources are moved climatically or geographically within their current ranges (*shaded*), even across seed transfer zones; e.g., moving *Larix occidentalis* 200 km north within its current range (**a**). Seed sources can also be moved climatically or geographically from current ranges to suitable areas just outside the range to assist range expansion, such as moving seed sources of *Pinus ponderosa* from British Columbia into Alberta, Canada (**b**). For assisted species migration, species could be moved far outside current ranges to prevent extinction, such as planting *Torreya taxifolia* in states north of Florida where it naturally occurs (**c**). (Terms from Ste-Marie et al. 2011; Winder et al. 2011; Williams and Dumroese 2013; maps adapted from Petrides and Petrides 1998; Torreya Guardians 2015)

Seed sources will need to remain matched to the climates of the next decade or two in order to ensure survival and growth. Such movements are within current management practices for movements within seed zones in the U.S.; for example, average transfer distances within *Pseudotsuga menziesii* seed zones in western Oregon and Washington are 2.2 °C (Kilkenny and St. Clair personal communication). Such short-scale movements could be employed to buffer uncertainty regarding the amount of climate change in an area by improving gene flow among populations through planting more diverse seed sources, both within and among forest stands (O'Neill et al. 2008; St. Clair and Howe 2011), realizing that an understanding of levels and distances of gene flow and the structure of genetic variation across the landscape is necessary so that promoting future adaptation through outplanting is balanced with potential loss of genetic variants and existing genetic variation within nearby stands (St. Clair and Howe 2011; Aitken and Whitlock 2013). Eventually, shifting climates may render current species or populations maladapted, as predicted, for example, for *Picea abies* in the southwestern portion of its current European range (Sykes and Prentice 1996) and for broadleaved species moving northward from temperate European forests to the current boreal forests (Thuiller et al. 2006). This may force managers to plant to increase genetic diversity and the adaptive potential of existing forests (St. Clair and Howe 2011). These interplantings within the landscape matrix of existing forest may be most efficiently established after management or natural stochastic events. Depending on the level of maladaptation, outplanted seedlings could include a mixture of local seed sources and non-local seed sources identified to be better adapted under future climates (on-set of maladaptation) or entirely distant seed sources (well-manifested maladaptation). Given the uncertainty of future climates, combinations of current and future seed sources would provide a "no-regrets" approach (sensu Kates et al. 2012) for land managers; poor performers would be lost through natural selection or

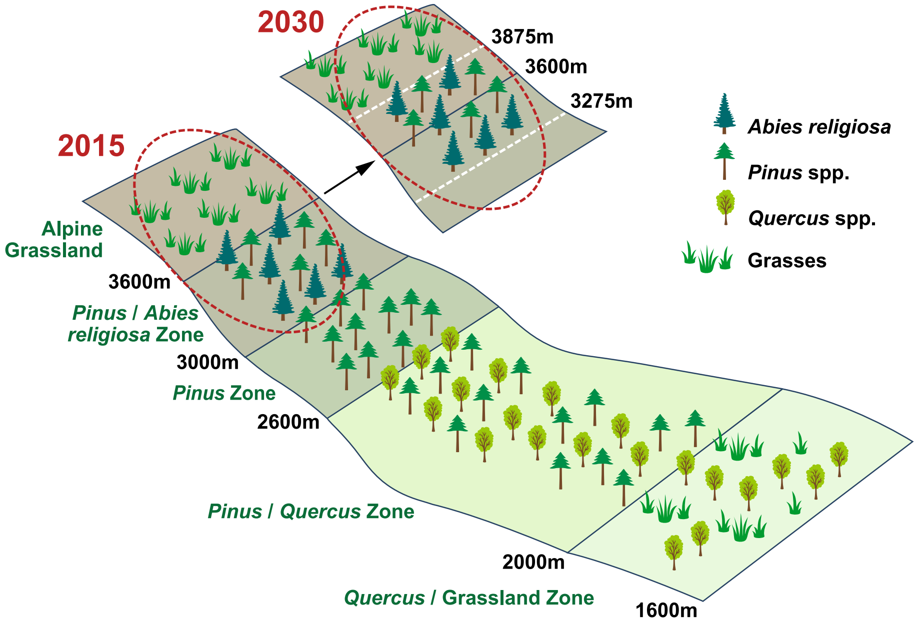

Fig. 4 Assisted migration can be performed along an elevation gradient. In this example, assisted migration of *Abies religiosa* 275 m upwards in altitude may be necessary to mitigate changes in climate so that this species can continue to provide its function as an overwintering host for *Danaus plexippus*. Adapted from Sáenz-Romero et al. (2006)

silvicultural activities such as thinning. The challenge will be monitoring for maladaptation, defining a threshold for action, identifying the source of new materials, and obtaining appropriate balance in deployed genetic resources.

The approval for testing and conducting assisted migration is likely to be case and region specific. In Canada, assisted migration is being tested and considered for *Abies albicaulis* (McLane and Aitken 2012) and *Larix occidentalis* (NRC 2013), both foundation species of commercial importance and hosts to many other plants and animals. In southern Mexico, it has been suggested that seed sources of *Abies religiosa* be moved 275 m upwards in altitude in order that populations growing 15 years from now would still experience today's climate (Fig. 4) (Sáenz-Romero et al. 2012) and continue to provide essential overwintering habitat for the charismatic, threatened, international migrant *Danaus plexippus* (Lepidoptera: Nymphalidae). Similar recommendations are being made for *Pinus oocarpa* (Sáenz-Romero et al. 2006) and *Pinus hartwegii* (Viveros-Viveros et al. 2009) in Mexico and Central America. In the U.S., a citizen-driven initiative to save *Torreya taxifolia*, a southeastern evergreen conifer, from extinction is by planting it well north of its current and historic range (McLachlan et al. 2007; Barlow 2011).

Although early provenance tests were not designed to answer climate change questions *per se*, they can be reassessed to more effectively deploy provenances on the landscape in response to climate change (Isaac-Renton et al. 2014) and test new concepts, such as central-peripheral gene flow, that may provide another tool for determining proper movement of plant materials (Yang et al. 2015). Climate niche modeling that couples genetic information from provenance tests and common garden studies with climate information in a GIS can be used to identify current and projected distributions (McLane and Aitken 2012; Notaro et al. 2012; Isaac-Renton et al. 2014; Rehfeldt et al. 2014a). Although modeled projections have some uncertainty in future climate predictions and are limited to species for which we have genetic and/or occurrence data along with environmental and climatic information (Park and Talbot 2012), they provide an indication of how climatic conditions will change for a particular site.

Assisted migration undoubtedly disrupts established understandings of natural resource management and long-held views in conservation biology, therefore it must be implemented in a framework that assesses species and population vulnerability to climate change, sets priorities, selects options and management targets, emphasizes long-term monitoring, and adjusts as needed. Adoption requires land managers to balance species conservation against risks posed by introduced species (Schwartz 1994), although this risk may be overstated as few forestry tree species have become invasive (see Koskela et al. 2014). Assisted population migration and assisted range expansion are more likely scenarios than assisted species movement, and the risk of spreading pathogens from transferring seeds is relatively low compared to moving live plants (Pedlar et al. 2012; Santini et al. 2013). Assisted migration should consider the critical, in situ preservation of adapted species and populations at the trailing edges of changing ranges because, compared to leading edge populations, they have unique features that were important for maintenance of biodiversity during previous shifts in climate (Hampe and Petit 2005). Indeed, refugia (i.e., phylogeographical hotspots), areas of “significant reservoirs of unique genetic diversity favorable to the evolutionary process,” have already persisted through repeated episodes of rapid and major environmental change (Médail and Diadema 2009). Although not all current refugia remaining from the Last Glacial Maximum may serve as refugia under contemporary climate change, their persistence on the landscape due to unique circumstances and characteristics of past warming and cooling events makes their identification valuable (Keppel et al. 2012). Indeed, understanding the process likely to produce refugia to contemporary climate change would be a powerful tool in preserving genetic diversity (Keppel et al. 2012).

Biotechnology, a broad and controversial discipline in which biological resources are used to develop products that serve a specific purpose or value, may help to maintain tree species and populations and the functions they provide. In forestry, biotechnology can be designed to meet the needs for a particular species, population, or landscape, for example, to enhance forest regeneration by improving tree population performance (e.g., seedling growth and wood production), conserve genetic resources (e.g., seed, gene, and DNA banks), save foundation species from extinction (e.g., *Pinus albicaulis*), develop pest-resistant seedlings (e.g., *Cronartium ribicola* resistance), increase adaptability (e.g., select drought-tolerant seed sources), and identify suitable seed sources via molecular markers. Although traditional breeding and use of biocontrol agents fit broadly into the bioengineering category, we will instead focus in the succeeding paragraphs on a few innovative tools, discuss their potential for addressing tomorrow’s forests, and provide some examples.

In situ and ex situ are two basic strategies for conserving forest genetic resources. In situ conservation of ecosystems and habitats occurs in their natural settings (e.g., protected areas and public and private lands) and ex situ conservation of components (seeds, vegetative materials, and genetic materials) happens outside of their habitat in seed collections or banks (Engelmann 2012). Advances in ex situ technologies make it possible to isolate and store DNA collected from nonviable seed lots and plant parts stored in herbaria and store plant tissues, such as somatic embryos (asexual vegetative tissue) (Ford-Lloyd and

Jackson 1991). Slow-growth storage and cryopreservation technologies have opened the door for conserving a variety of plant materials and tree species, including those that do not produce seeds every year, vegetatively propagate, or require long-term storage (Ford-Lloyd and Jackson 1991; Engelmann 2012). Cryopreservation, storage at ultra-low temperatures (−196 °C with liquid nitrogen), may be the only conservation approach for long-term storage of some forest tree species although genetic stability and viral contamination of such materials are a concern (Engelmann 2012). Slow-growth storage and cryopreservation of shoot cultures and buds are being tested for *Sequoia sempervirens* because it primarily reproduces asexually through shoots and roots (Barbour et al. 2001) and the only existing conserving strategies are in situ (Ozudogru et al. 2012). Cryopreservation also offers the ability to store tissue cultures and clones grown from somatic embryos while testing is performed for the selection of desired traits (e.g., growth and drought-tolerance). Such operations have been established for the commercial testing and production of interior spruce (*Picea glauca* × *Picea engelmannii*) in British Columbia (Grossnickle and Sutton 1999). Thus, cryopreservation offers opportunity to store germplasm until it can be used to restore species. For example, in the case of the invasive *Agrilus planipennis* (Coleoptera: Buprestidae) and its decimation of *Fraxinus* in North America, cryopreservation is underway to conserve germplasm until sufficient resources become available for traditional or transgenic breeding (see below), and/or biological control of *A. planipennis* becomes effective.

Biotechnology offers options beyond traditional breeding methods for the conservation and restoration of forest species and populations, such as the use of molecular markers and genetic engineering. Genetic engineering involves the direct manipulation of an organism's genome, where its DNA has been modified to include a new trait (e.g., pest resistance). Although not yet approved for commercial forest trees in the U.S. (or even conservation and restoration use), genetic engineering techniques are being considered and tested. Applications are under review by regulatory agencies for the release of frost-tolerant *Eucalyptus* that can sustainably address society's need for wood in southeastern U.S. (Hinchee et al. 2011). Government approval, however, may first come only for species threatened by pests and pathogens (Adams et al. 2002). Cisgenic (using genes from closely-related or same species) and transgenic (using genes from sexually incompatible organisms) are viable options in a large-scale restoration program to create *Castanea dentata* trees resistant to *Cryphonectria parasitica* (Jacobs et al. 2013). The reintroduction of resistant *C. dentata* may help restore a variety of functions in eastern North American forests absent since its demise, including large and consistent mast crops consumed by humans and wildlife, durable, rot-resistant wood products, and unique decomposition and nutrient cycling traits (see Jacobs et al. 2013). Scientists are using a myriad of complimentary tools including intra- and inter-species breeding for resistance, identification of genes that provide resistance and using them to increase resistance in planting stock, and employing new, large-scale genomic mapping techniques to identify resistance genes in the Asian *C. mollissima* that can be introduced to *C. dentata* through traditional backcross breeding techniques. Success has already been noted for a backcrossed resistant hybrid of *C. dentata* (Bauman et al. 2014). Molecular techniques including the use of genetic markers, mapping, and genomics have proven useful in understanding the epidemiology of *Cronartium ribicola* in five-needled pines (e.g., *P. albicaulis*, *P. flexilis*, and *P. monitcola*) (Richardson et al. 2010; Kim et al. 2011) and are an important part of the restoration strategy that includes outplanting resistant seedlings (Keane and Schoettle 2011).

In light of increasing pressures on forest ecosystems, reliance on and advancement of ex situ conservation strategies, molecular genetics, genomic studies, and genetically engineered forest materials may increase. Indeed, for tree species and genera disappearing from large extents of eastern North America (e.g., *Juglans cinerea*, *Fraxinus* spp., *Persea* spp.) or narrowly-distributed, critically-endangered species in Australia (e.g., *Eucalyptus recurva* and *Lambertia fairallii*), effects of introduced pests may render biotechnology as the only viable method for preserving these species and the ecosystem functions they provide. It is unlikely, however, that biotechnological tools will completely replace traditional silvicultural techniques, breeding methods, and conservation strategies in forest management. For example, for *Pseudotsuga menziesii* populations in Mexico that are projected to face unfavorable climate conditions for growth by 2060 (Rehfeldt et al. 2014a), long-term conservation options, such as slow-growth storage and cryopreservation might be options, but efforts to protect refugia, locate suitable growing sites and seed sources, and collect and store genetic resources should also be in place (Rehfeldt et al. 2014b).

An illustration

Fraxinus nigra can be used to illustrate how these three considerations may be used in a forest management scenario. This species grows in the northern portions of the eastern and central U.S. and southeastern portions of Canada (Wright and Rauscher 1990). Currently, North American *Fraxinus* are threatened by *Agrilus planipennis* (Colepoptera: Buprestidae). So, how might functional restoration, assisted migration, and biotechnology be discussed, individually and in concert, as part of a strategy to maintain the function of forests in which *F. nigra* is an important member?

In addition to timber products, two important functions provided by *F. nigra* are its role in regulating the hydrology of wetland forests (see Slesak et al. 2014) and its use in basketry by indigenous people (Diamond and Emery 2011). Use of traditional silvicultural practices to maintain function, such as group selection followed by artificial regeneration of other species native to those sites, would increase site biodiversity and subsequent resilience to ensure hydrological function. During treatment, silvicultural practices that maintain sustainable development of size classes and form desired by indigenous people for their basket making craft would have merit as well. Silvicultural treatments would be monitored and assessed for success.

Although a good first step, the success of the above application of functional restoration might be enhanced by combining it with assisted migration. When engaging in artificial regeneration, species and seed sources anticipated to be adapted to future climate scenarios would be deployed; this could be either population migration and/or assisted range expansion. More southerly seed sources of species already occurring with *F. nigra*, such as *Acer rubrum*, *Betula alleghaniensis*, *Populus tremuloides*, and *Ulmus* spp. (Iverson et al. 2011), could be moved northward in anticipation of future climate (i.e., population migration) and species, such as *Liquidambar styraciflua* or *Taxodium distichum*, not growing in the current range of *F. nigra* might similarly be moved from the northern limits of their current range and introduced into the southern portions of the range of *F. nigra* to help fulfil the hydrological role of *F. nigra* (i.e., assisted range expansion). Unfortunately, none of these species augment or replace the function of *F. nigra* as a source of traditional basket material.

Despite the best efforts of functional restoration and assisted migration, the rapid expansion of *A. planipennis* and nearly complete decimation of *Fraxinus* in invaded stands indicate it would be prudent to immediately collect and store seeds of diverse populations across the range of *F. nigra*, especially from individual trees showing potential tolerance or resistance (Simpson 2010). This material could be used now, once biocontrol agents become widespread and efficacious, and/or for traditional or transgenic breeding for *A. planipennis* resistance. The scope of such breeding would be dependent on stakeholder priorities, societal and legal acceptance of GMOs (in the case of transgenic work with resistant Chinese *Fraxinus* (Rebek et al. 2008) or cisgenic work with *Bacillus thuringiensis* (Pijut et al. 2010)), available funding, and/or the success of deployed biological control agents (another form of biotechnology) to reduce *A. planipennis* effects. Resistant material could eventually be deployed to the landscape via functional restoration, perhaps with the movement of southerly sources northward to account for changes in climate (assisted population migration) or northerly sources moved further north into new suitable habitat (assisted range expansion). Together, functional restoration, assisted migration, and biotechnology may offer a more holistic approach to forest management.

Context is important

The appropriate use of functional restoration, assisted migration, biotechnology, and their combinations must be determined within a relevant context. Concerns about invasive species, lack of research, ecological risks, community support, and uncertainty in climate models and with forest tree plasticity in response to climate are not unique to any one approach; all of them have advantages and disadvantages (Table 1), but their relevance, suitability, and applicability should be evaluated within the context of the restoration goal. Our best available tools may not guard against future pests or be of use in novel conditions, and the risk of creating an invasive species through restoration efforts, assisted migration, or reintroduction of native species may occur. The risk of invasion, however, is subject to debate because the definition itself depends upon human perception (Mueller and Hellmann 2008). Some degree of "invasiveness" in an assisted migration effort might be necessary for establishment. Further, the "nativity" of replacement species or germplasm will become increasingly blurred given that the current definition can be vague and dependent on many factors (see Smith and Winslow 2001), including distance from its home range. Therefore, future working definitions of ''native'' will need to be "scientifically grounded, dynamic, flexible, project specific, realistic," and, we add, contextual (Shackelford et al. 2013; Stanturf et al. 2014a).

The complex, multi-faceted decisions on how land managers tend tomorrow's forests will ultimately be driven by societal values (Ciccarese et al. 2012; Stanturf et al. 2014a). Citizens can be reluctant to accept management strategies involving the manipulation of plant materials through breeding programs, using nonlocal seed sources, genetic modification, and moving seeds outside a species' range (Hajjar et al. 2014). Further, the current willingness of forestland managers to employ climate change adaptation strategies is contingent upon their confidence that climate change is anthropogenic (Lenart and Jones 2014). Land managers who agree are more likely to undertake less traditional silvicultural aspects of functional restoration (e.g., functional species composition versus legacy species composition) and, for any aspect of assisted migration, they are only somewhat confident in knowing what specific actions to take. For widespread application of any new approach to silviculture in response to climate change, scientists will need to provide managers more definitive, contextually-based evidence of potential benefits and risks (Lenart and Jones

Table 1 Some general advantages and disadvantages of functional restoration, assisted migration, and biotechnology

	Advantages	Disadvantages
Functional restoration	Focuses on desired functions provided by forests Applicable across all levels of degradation Relies mainly on established silvicultural treatments May more realistically align societal goals with resources available for restoration Applicable across multiple scales and in combinations with other management options, such as assisted migration and biotechnology Mandates public involvement in decision making	Reference condition or legacy characteristics may not be final goal Potential poor public perception when species introductions are needed to achieve function Potential conflicts/disagreements among the public in defining desired functions
Assisted migration	Assisted population migration can be implemented as part of current artificial reforestation programs; relatively low cost; low risk of unintended consequences; no drastic changes to contemporary forest composition Assisted range expansion can replace declining species due to climate change with different species anticipated to have better adaptation that are already proximate Assisted species migration may be only viable method to prevent species extinction; historical long-distance transfers of trees have provided significant increases in productivity	Rapid changes in climate may negate short distance migration efforts Uncertainty about future climate hampers determining target migration distances; potential unintended consequences to recipient ecosystem, such as adverse effects on other species in the receiving location Will require significant changes to policy, law, perception before implementation
Biotechnology	Traditional breeding a proven technique; low risk of unintended consequences; often multiple genes in play Transgenic breeding may significantly reduce time to produce improved material; could work on multiple stressors concurrently Cisgenic breeding may significantly reduce time to produce improved material; could work on multiple stressors concurrently; potential to modify species for traits not currently residing in them, such as tolerance to drought, salts, herbicides, and pests	May take decades because of slow reproduction of trees Poor public perception of genetically modified organisms; trans- and cis-genic trees may have less resilience than traditionally bred trees because fewer genes may be involved Cryopreservation may not work for all species of concern

2014); this most likely applies to functional restoration and biotechnology as well. So, while our considerations may be viable options for conserving and restoring some forest tree species and populations, it may be difficult to implement any program without first improving technology transfer, increasing dialogue, and determining which societal values and services forests are to be managed for (Friedman and Foster 1997). After learning more about management strategies and options, the public may be more amendable to alternatives (Hajjar et al. 2014).

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