OXFORD

BioScience, 2023, **73**, 575–586
https://doi.org/10.1093/biosci/biad049
Advance access publication date: 31 July 2023
Forum

A lack of ecological diversity in forest nurseries limits the achievement of tree-planting objectives in response to global change

Peter W. Clark, Anthony W. D'Amato, Brian J. Palik, Christopher W. Woodall, Paul A. Dubuque, Gregory J. Edge, Jason P. Hartman, Lucia A. Fitts, Maria K. Janowiak, Lucas B. Harris, Rebecca A. Montgomery, Mike R. Reinikainen and Christopher L. Zimmerman

Peter W. Clark (peter.clark@uvm.edu) and Anthony W. D'Amato are affiliated with the Rubenstein School of Environment and Natural Resources, at the University of Vermont, in Burlington, Vermont, in the United States. Brian J. Palik is affiliated with the Northern Research Station, USDA Forest Service, in Grand Rapids, Minnesota, in the United States. Christopher W. Woodall is affiliated with the Northern Research Station, USDA Forest Service, in Durham, New Hampshire, in the United States. Paul A. Dubuque is affiliated with the Minnesota Department of Natural Resources, in Saint Paul, Minnesota, in the United States. Gregory J. Edge is affiliated with the Wisconsin Department of Natural Resources, in La Crosse, Wisconsin, in the United States. Jason P. Hartman is affiliated with the Michigan Department of Natural Resources, in Lansing, Michigan, in the United States. Lucia A. Fitts is affiliated with the Department of Forest Resources at the University of Minnesota, in Saint Paul, Minnesota, in the United States. Maria K. Janowiak is affiliated with the Northern Institute of Applied Climate Science, USDA Northern Research Station, in Houghton, Michigan, in the United States. Lucas B. Harris is affiliated with the Rubenstein School of Environment and Natural Resources, at the University of Vermont, in Burlington, Vermont, in the United States. Rebecca A. Montgomery is affiliated with the Department of Forest Resources at the University of Minnesota, in Saint Paul, Minnesota, in the United States. Mike R. Reinikainen is affiliated with the Minnesota Department of Natural Resources, in, Saint Paul, Minnesota, in the United States. Christopher L. Zimmerman is affiliated with The Nature Conservancy, in Albany, New York, in the United States.

Abstract

Tree planting is increasingly being adopted as a strategy to address global change, including mitigation, adaptation, and restoration. Although reforestation has long been central to forest management, the desired outcomes of traditional and emerging tree-planting strategies face barriers linked to a lack of ecological diversity in forest nurseries. In the present article, we outline how insufficient diversity in nursery seedlings among species, genotypes, and stock types has impeded and will continue to hinder the implementation of diverse ecological or climate-suitable planting targets, now and into the future. To support this, we demonstrate disparities in seedling diversity among nursery inventories, focusing on the northern United States. To overcome these challenges, we recommend avenues for improving policy and financing, informational resources and training, and research and monitoring. Absent these advances, current seedling production and practices will fall short of ambitious tree-planting goals proposed for forest restoration and global change mitigation and adaptation.

Keywords: reforestation, mitigation, adaptation, nursery, forestry, seedlings, seed source, provenance, seedlot, genotype, assisted migration, tree planting

Global climate change is expected to dramatically affect forested ecosystems, presenting challenges for foresters, conservationists, and policymakers worldwide (Dale et al. 2001). In response, forest conservation strategies, including climate adaptation frameworks (Millar et al. 2007, Schuurman et al. 2021), as well as ambitious reforestation and afforestation initiatives emphasizing large-scale tree planting, have been proposed (e.g., the World Economic Forum's One Trillion Trees Initiative; the REPLANT Act as part of the Infrastructure Investment and Jobs Act, 117th US Congress 2022). Such momentum has generated substantial and growing interest in tree planting as a solution for restoration (of species and ecosystems) or adaption and mitigation to the effects of global change. Despite a long history of using tree planting to meet various reforestation and economic goals (Bennett 2015), the lofty desired outcomes of emerging planting strategies are not a simple solution to address the challenges of global change and will be met with several barriers for implementation (Holl and Brancalion 2020, Di Sacco et al. 2021). Although expanding seedling production is widely recognized to be a central challenge to meeting this growing need (see Fargione et al. 2021), enabling tree-planting projects to meet diverse ecological and climate-suitable planting targets will be the greatest barrier to ensuring biologically, economically, and socially just outcomes (Bennett 2015).

Various tree-planting strategies for global change have been proposed (see box 1) to restore or sustain native ecosystem functions (Stanturf et al. 2014, Gann et al. 2019), mitigate climate change through increased carbon stores (Domke et al. 2020), or adaptively respond to nonnative pests and pathogens or changing climatic conditions through biological diversification (e.g., functional replacement, assisted migration; Pedlar et al. 2012, Palik et al. 2022). Although the motivations for traditional reforestation practices aimed at timber production or other commodities remain strong (Martin et al. 2021), these practices are increasingly being complemented by planting decisions in response to a warming climate, shifting species habitats, and natural disturbances (e.g., wildfire, invasive pests, and pathogens) linked to global change (Klenk and Larson 2015). Irrespective of the planting project goals, fundamental economic and logistic issues remain that will limit the implementation of tree-planting initiatives, with calls to greatly expand seed and nursery seedling

Received: February 12, 2023. **Revised:** April 20, 2023. **Accepted:** May 18, 2023

Box 1. Tree-planting strategies for global change.

Tree-planting strategies vary in terms of global change objectives. In the present article, we outline three commonly proposed planting strategies for global change, including a summary of challenges and intended outcomes. Although presented as discrete options, our grouping merely serves to differentiate outcomes, because many can be complementary (or conflicting). Furthermore, although reforestation strategies for timber production or other utilities are not reviewed in the present article, these practices remain important and are not necessarily isolated from the considerations outlined below (Martin et al. 2021).

Mitigative tree-planting strategies aim to increase forest biomass to offset greenhouse gas emissions via enhanced carbon stores (Domke et al. 2020). These strategies largely include reforestation efforts to increase forest stocks (Cook-Patton et al. 2020), reclamation of degraded forests (e.g., mines and other disturbed lands; Fox et al. 2020), or afforestation to establish new forests on lands that, historically, were unforested (IPCC 2014). Although these strategies have long been part of forest management, the carbon mitigation potential of tree planting has generated considerable international attention (e.g., www.1t.org). In fact, some estimates suggest that mitigative planting could sequester an additional 6.1 metric tons of carbon dioxide per hectare per year in the United States (Cook-Patton et al. 2020), or store 205 gigatons of carbon globally (Bastin et al. 2019), although debate exists regarding the on-the-ground realities of these estimates (Veldman et al. 2019). While mitigative planting can offer secondary benefits (e.g., biological diversification, wildlife habitat, flood mitigation), negative consequences involving ecological and societal conflicts (e.g., water use, grassland habitat degradation; Holl and Brancalion 2020) and environmental equity (e.g., displacement of tradititonal uses, land rights; Scheidel and Work 2018) can potentially undermine benefits. Concerns remain that project coordinators may become singularly focused on carbon storage with potential tradeoffs or negative consequences in ecological function and adaptability (e.g., compositional diversity, structural complexity, habitat development).

Restorative tree-planting strategies principally aim to diversify, restore, or replace species, communities, or ecosystem functions that have been threatened or degraded (Stanturf et al. 2014, Gann et al. 2019). Although practiced for decades (Dumroese et al. 2005), restoration plantings may be pursued in response to threats from global change (e.g., invasives, disease, pollution, flooding). Frequently, the aim is to diversify forests on the basis of historical conditions to promote ecological persistence, particularly when onsite seed sources are absent, or forest management regimes fail to recruit target species. This practice may include species reintroductions or restoration of habitats important for climate resilience, such as riparian areas. In addition, restorative plantings may support functional assemblages, especially when the degradation or loss of dominant or keystone species threaten forest functioning. For instance, the anticipated loss of *Fraxinus nigra* (Marshall), a species necessary for hydrologic regulation of lowland forests, has led to evaluations of planting *functional replacement species* to maintain wetland habitat function (D'Amato et al. 2018b). Ultimately, the goals of restorative plantings may vary, but focus on augmenting, maintaining, or restoring forest function in the context of actual and anticipated changes.

Future-climate-suitable planting strategies are a reaction to climate change advancing more rapidly than the pace that tree species can migrate (in the eastern United States and elsewhere; Sittaro et al. 2017), likely modifying habitats and threatening ecosystem functioning. In response, foresters and conservationists may transition forest composition on the basis of anticipated shifts in future habitat (Nagel et al. 2017). Frequently, these efforts are termed *assisted migration*, and they broadly encompass the movement of populations or species to new environments (Pedlar et al. 2012, Williams and Dumroese 2013, Palik et al. 2022). Foresters have long experimented with the movement of genotypes through common garden experiments to inform transfer distances under historical climate. Traditionally more emphasis has been placed on species in support of timber production (Dumroese et al. 2005, Park and Rodgers 2023), rather than sustaining ecosystem services linked to global change. Although few operational-scale forested assisted migration examples exist (see Palik et al. 2022), tensions exist between local ecological adaptation and lags in migration (Etterson et al. 2020, Clark et al. 2021). Concurrently, we lack scientific consensus regarding potential risks and appropriate uses of assisted migration (e.g., maladaptation, invasion, best management practices; Pedlar et al. 2012). Although routine use of assisted migration is not yet widespread, the risk profile of many forests has already fundamentally changed making the pursuit of climate-responsive plantings timely and potentially lower risk than no action (Palik et al. 2022).

volume production in all its various forms (e.g., bare-root, containerized, cuttings, plugs; hereafter called *seedlings*; Merritt and Dixon 2011, Haase and Davis 2017, Fargione et al. 2021). In addition, considerable emphasis has been placed on frameworks outlining seed provenancing strategies emphasizing the need for biological and genetic diversity in tree-planting initiatives for restoration or climate adaptation (Breed et al. 2013, Broadhurst et al. 2015, Jalonen et al. 2018). Despite the ostensible utility of these proposals, less attention has been paid to the capacity of forest nurseries to actually supply a diverse and shifting inventory of seedlings (e.g., species, functional groups, climate-suitable genotypes, seedling sizes, and other stock types) relative to those traditionally favored for timber production (Tepe and Meretsky 2011, Whittet et al. 2016). Failure to diversify seedling production in forest nurseries today will hamper options for meeting an ever-widening spectrum of planting goals for global change, with potential legacy effects expected in future forest demography, ecosystem homogeneity, and vulnerability. For reforestation projects, which overwhelmingly rely on seedlings produced in forest nurseries, the ability of these nurseries to maintain sufficiently diverse inventory will likely be a major bottleneck in supporting ecologically rich, climate-suitable plantings, now and into the future.

Over a decade ago, Tepe and Meretsky (2011) asked whether forest nurseries in the United States were prepared to meet restoration targets in response to climate change. In the present article, we revisit this question by assessing the status of forest nurseries and seedling production, emphasizing the availability of ecologically and climatically diverse inventories in the context of tree-planting efforts for global change. Although the specific

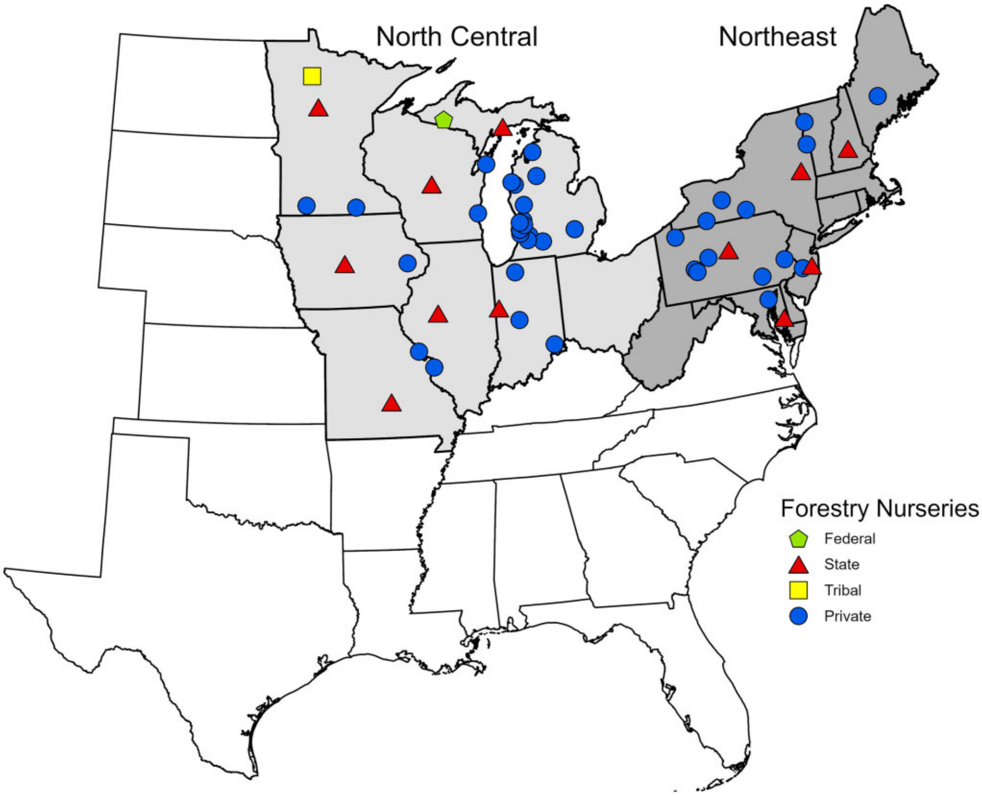

Figure 1. The northern US focal region, which includes the 20 North Central (light gray) and Northeastern states (dark gray), along with the location and ownership type of forestry nurseries.

challenges differ regionally (see Fargione et al. 2021, Martin et al. 2021), the issues we identify are broadly and globally relevant to tree-planting initiatives (Jalonen et al. 2018). As such, we focus on the northern region of the eastern United States, which includes the 20 Northeastern and North Central states (figure 1; Iverson et al. 2008), because this region serves as a useful case with lessons that are broadly translatable for tree planting. For instance, the northern region of the eastern United States is one of the most densely forested and compositionally diverse regions in North America but, by some estimates, supports over 16 million hectares of land area available for reforestation and afforestation, potentially necessitating up to 22.5 billion seedlings (https://www.reforestationhub.org/, Domke et al. 2020). Moreover, this region has the highest concentration of nonnative insects and diseases in North America (Lovett et al. 2016), is already experiencing climate change-induced impacts (Swanston et al. 2018), contains over 40 tree species forecasted to decline from or migrate into this region over the next century because of climate-induced shifts in habitat suitability (Peters et al. 2020), and is where tree planting for global change is already being enlisted in forest ecosystem management (Palik et al. 2022).

Our goal in the present article is to assess the ability of northern US forest nurseries to meet the need to supply sufficiently diverse seedlings (e.g., species, native and climate-adapted genotypes), relative to emerging tree-planting efforts aimed at global change (e.g., mitigation, restoration, adaptation; see box 1). We address this by reviewing forest nursery capacity and seedling inventories (e.g., species, seedlot geography), linking the outcomes to factors that limit effectively operationalizing these strategies into routine practice. Our objectives are to broadly illustrate the barriers associated with species, genotype, and stock type availability that will hinder emerging tree-planting efforts specifically aimed at global change. We conclude by proposing that, to use tree planting as a tool for managing forests in response to global change, forward-looking policy and funding, training and informational resources, and research and monitoring will be needed to support the diversification of forest nurseries and inventories.

Diversifying plant production in forest nurseries

Expanding seedling production in forest nurseries will be central to achieve ambitious tree-planting objectives aimed at addressing global change. In fact, Fargione and colleagues (2021) estimated that a 2.3-fold increase in production will be needed to meet broadly proposed reforestation goals in the contiguous United States, along with refining the seedling supply chain (e.g., labor, nursery capacity, outplanting actions). Forest nurseries are a unique bottleneck for scaling up tree planting in response to global change, but the scope of the challenge reaches far beyond volume production of seedlings.

The novelty of some planting strategies for global change, such as the movement of climate-suitable species and genotypes, likely generates uncertainty among forest nurseries, hampering broad scale investment. This is particularly germane in regions where nurseries have declined and where speculative investment in growing new, future-climate adapted, or traditionally underrepresented (nontimber) species and seedlots may carry high financial risk.

In the following sections, we outline barriers that will limit the success of future tree-planting initiatives specifically related to nursery access, species availability, seedlot diversity, and other seedling characteristics. Although aspects of these have been synthesized elsewhere in terms of broadly proposed strategies and best practices (e.g., Breed et al. 2013, Broadhurst et al. 2015, Jalonen et al. 2018, Di Sacco et al. 2021), we focus in the present article on the current state of forest nursery practices related to diversifying seedling inventory because they are a unique pinch point for seedling procurement and project success. Given that forest nurseries serve as the principal outlet for seedling propagation used for the overwhelming majority of tree-planting efforts, we reveal how current practices will directly and indirectly hinder the expansion and diversification of tree planting for global change, both now and into the future.

Nursery access

On the basis of records obtained from the National Nursery and Seed Directory (https://rngr.net/) and systematic Internet queries, 605 plant nurseries are located in the 20-state northern US region, but only 56 nurseries grow and sell tree seedlings in volumes suitable for conservation, reforestation, or other uses in forestry (as opposed to horticultural purposes; see the supplemental material for detailed methodology; figure 1). Of these, 42 are private nurseries, and 12 are state operated, predominantly in the North Central states. The remaining two are administered by the federal government or Tribal Nations. Government-operated tree nurseries have been on the decline for decades (Dumroese et al. 2005), such that of the 59 nurseries historically operated by the US Department of Agriculture (USDA) Forest Service to supply seedlings for federal lands, six remain today, with only one in the northern US region. In a survey of state-operated nurseries and tree breeding programs, nearly all respondents from the states lacking government-run nurseries reported insufficient inventory, including a lack of diversity among species, seed geographic origin, and stock sizes (NASF 2016). Nursery closures have coincided with declines in funding to support research as well as in tree breeding focused on producing species and genotypes more capable of withstanding the effects of climate change (D'Amato et al. 2018a).

Relative to private nurseries, where the largest demand is commonly from industrial timber-oriented operations that plan years in advance, state-operated nurseries have historically had the flexibility to grow more nontimber species for wildlife or conservation purposes. Theoretically, this could translate into the production of species and sources grown for diversification, restoration, or climate change adaptation. However, most nurseries are typically entirely funded by seedling sales and operate on narrow financial margins. Publicly funded nurseries have frequently come under scrutiny during state budget negotiations and shifting political administrations, resulting in many closures. These legislative actions serve as guardrails that likely motivate seedling inventories in favor of reliable species and stock types (low financial risk, low reward in terms of ecological diversity) relative to the production of species and genotypic diverse, climate-adapted inventories (high financial risk, high reward in terms of ecological diversity). Consequently, nurseries report three major barriers associated with producing seedling inventory in response to climate change: laws or policies that constrain inventory decisions, uncertainty of how the future climate will necessitate the need to adapt, and continued high client demand for traditional species, seed, and stock (Tepe and Meretsky 2011). Given that propagating seedlings can take several years before they reach maturity to be successfully outplanted, it is understandable why nurseries may be wary of speculatively investing in inventory with greater risk portfolios. Without change in policy or a sustained market signal, tree nurseries will remain behind the curve aimed at producing a shifting target of sufficiently diverse, climate-adapted stock in adequate quantities. Moreover, advances in the network of professional development, education, and extension programs may be needed to reduce uncertainties associated with propagation and demand for traditionally underrepresented species.

Between 2012 and 2020, the overall production of seedlings has generally declined (figure 2a). Moreover, the vast majority (80%) of seedlings in the northern focal region are produced in the North Central states rather than in the Northeastern states (figure 2b). Such concentration of production will hinder tree-planting efforts because species and seed sources likely originate from similar geographic or bioclimatic zones (more on this below). In addition, given the sensitivity of seedlings to stress, misalignment between lifting and outplanting times (e.g., a southern nursery may process seedlings weeks to months before northern soils are frost free) or excessive shipping, handling, and storage times increase the likelihood of seedling health problems or mortality.

Species bias in seedling availability

The varied objectives for global change plantings demand a diverse suite of species and functional groups. This will necessitate a change in nursery practices, which have historically been focused on species favored for timber production, although the proportion grown for wildlife and conservation purposes has increased in recent decades (Dumroese et al. 2005). For instance, coniferous species make up more than 97% of the seedlings grown in the United States, with the vast majority (80%) produced in the southeastern states (Haase et al. 2021), largely for plantation forestry operations. In the northern US focal region, coniferous species valued for wood production and nontimber products (e.g., Christmas trees) are also disproportionately represented in inventories and constrained to just a few species—namely, *Pinus* spp. (L.), *Abies* spp. (Mill.), and *Picea glauca* ((Moench) Voss). Likewise, the most common deciduous seedlings are hard mast species (e.g., nut and one-seeded fruit producers) primarily valued for wood production, such as *Quercus* spp. (L.), *Juglans nigra* (L), *Carya illinoinensis* ((Wangenh.) K.Koch), and *Prunus serotina* (Ehrh.; NASF 2016). Although these species are found in diverse habitats and confer valuable functional attributes linked to restoration, adaptive capacity, and biomass production (e.g., carbon sequestration and mitigation), they only represent a small fraction of the diverse species and life history traits present in northern and eastern US forest. The consequence is that tree-planting efforts are frequently biased toward these few core workhorse species that can be reliably propagated and readily sourced from nurseries (Broadhurst et al. 2015). Such homogeneity in species and functional diversity in forest nursery inventory serves as a major barrier for foresters and conservation biologists aiming to generate structurally complex, compositionally diverse, and ecologically resilient future forests (D'Amato and Palik 2020, Palik et al. 2020).

In our review of northern US forest nursery inventories (see the supplemental material for detailed methodology), we found significant disparities in the availability of diverse species sought in the context of global change (figure 3). Although many species may be used among one or several emerging planting strategies to achieve various outcomes to address global change (e.g., species restoration and assisted migration applied simultaneously; cf. Clark et al. 2022), we focus on species that typify these approaches within three discrete categories:

Future-climate-suitable species are those expected to be well adapted to future climatic conditions throughout much of the

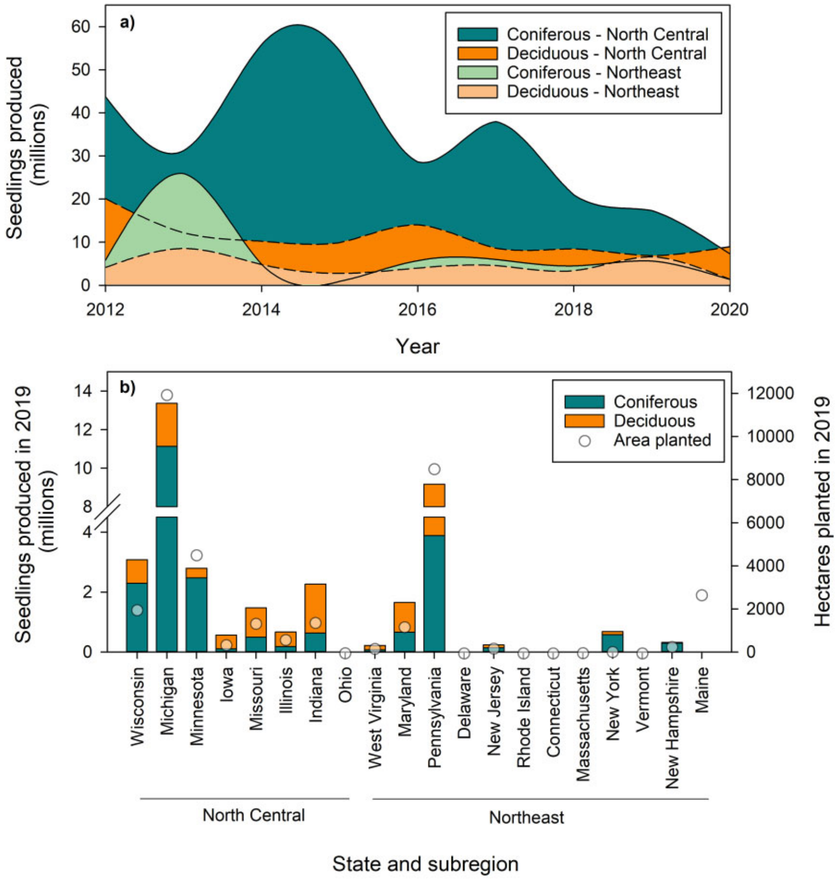

Figure 2. Northern US nursery production of deciduous and coniferous tree seedlings (a) from 2012 to 2020 by region (unstacked, smoothed trends between groups) and (b) in 2019 by state. The year 2019 was used because it was more representative of state-level trends than was 2020 when production was affected by the coronavirus pandemic. Panel (b) also includes the estimated area planted based on USFS Forest Inventory and Analysis estimates of planting densities and state-level ground-plot data. See the supplemental material for details regarding data sourcing.

northern United States because of increases in habitat suitability under projected climate change (Peters et al. 2020), and potentially serve as candidate species employed for assisted migration. Example species include *Quercus rubra* (L.), *Pinus strobus* (L.), and *Acer rubrum* (L.).

Functional replacement species are those being evaluated as a means of replacing species and their functional traits that are at risk of decline because of global change. Example species include *Quercus bicolor* (Willd.), *Carya cordiformis* ((Wangenh.) K.Koch), and *Tsuga canadensis* ((L.) Carrière), which have been identified to replace *Fraxinus nigra* (Marshall), *Fagus grandifolia* (Ehrh.), and *Picea* or *Abies* species, respectively (Palik et al. 2022).

Species restoration includes reintroductions of threatened but ecologically or culturally important keystone species (Costanza et al. 2017), including *Picea rubens* (Sarg.), *Castanea dentata* ((Marsh.) Borkh.), and *Ulmus americana* (L.). Although the latter two remain susceptible to disease, blight-tolerant strains have been developed, are commercially available, and are included within operational-scale planting efforts in anticipation of larger-scale reintroductions (Clark et al. 2021, Palik et al. 2021).

Each species listed above in the three planting strategies was commercially available in our assessment, although major differences exist among species; most are highly limited in terms of availability and regional representation. For example, *Q. rubra* and *P. strobus*, two species predicted to be future-climate suitable are frequently available at forest nurseries, with most states (75%) supporting several nurseries with inventory. This is unsurprising, because these species are highly favored for timber production. On the other hand, ecologically important species such as *C. cordiformis* and *P. rubens* are severely underrepresented, with only seven and two nurseries maintaining inventory, respectively. Although we were unable to assess the number of seedlings available for sale on the basis of nursery inventories, we are aware that, remarkably, only 800 *P. rubens* seedlings were commercially available for purchase in 2022—enough to reforest less than 1 hectare. This number pales in comparison to the potential need to effectively incorporate this species, or any species, into diverse reforestation projects. Although these data represent only 1 year of nursery inventory, the disparities in species availability we observed are likely consistent with other recent years and will continue to be a significant barrier to achieve ecologically diverse tree-planting efforts, now and into the future.

Low genotypic diversity and poor record keeping

The prevailing view in restoration and conservation science has been to prioritize the use of native seed from predefined seed zones, because these sources are considered well adapted to local conditions while maintaining genetic diversity. However, because climate change shifts habitat suitability, seeds will need to be sourced from collection zones that represent one or potentially multiple future climatic conditions expected for the planting site (Pedlar et al. 2012, Breed et al. 2013, Prober et al. 2019). Given the ages attained by trees, determining what timeframe and

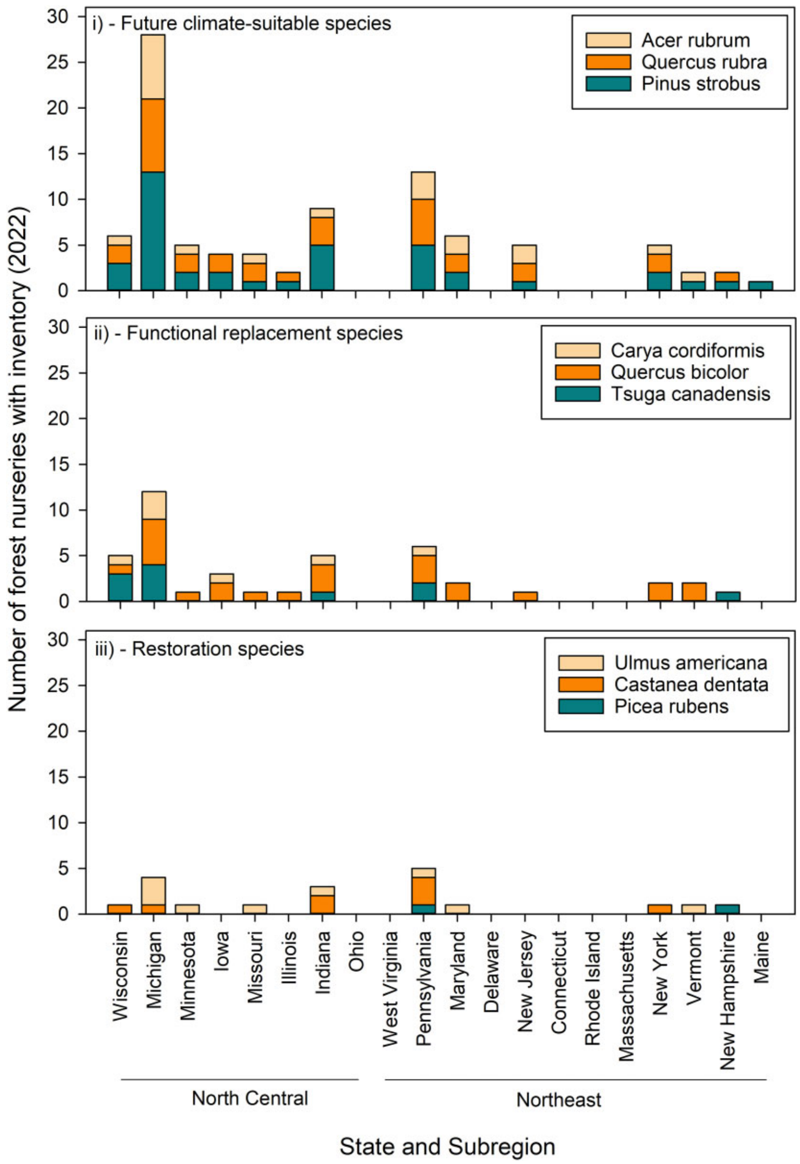

Figure 3. The number of forest nurseries that sold select species in 2022. Although many species may be employed within and across emerging tree-planting strategies for global change, we focus on nine deciduous and coniferous tree species that typify these approaches within three common objectives: future-climate-suitable plantings (e.g., assisted migration), functional replacement (restoration) plantings, and species restoration plantings (see the text and box 1 for details regarding terms). See the supplemental material for methodological details regarding data sourcing

which future climate regime to target when sourcing seeds remains a substantial challenge for nurseries and forest managers. Irrespective of the seed-sourcing strategy employed, we found that current nursery inventories fail to supply sufficiently diverse seedlots within species.

Depending on the species and nursery type (e.g., private, state operated), seed procurement may occur internally by nursery staff or outsourced to a limited number of commercial suppliers or to a declining number of private seed collectors (with mixed levels of training; Haase and Davis 2017). This results in varying levels of genotypic diversity within collections (e.g., one versus numerous parent trees). Moreover, documentation pertaining to source and geographic origin is often lacking. Although seed production orchards have historically been important, particularly for timber species (e.g., *Pinus taeda* (L.)), most seedlings grown in the eastern United States are from wild-seed collections, often of unknown quality and genetic origin (Nevill et al. 2016, Erickson and Halford 2020). During poor seed production years when local sources are depleted, nurseries may obtain seeds from well outside of the region, provided that cold hardiness (Daly et al. 2012), a proxy for climate suitability under historical conditions, is justifiably comparable. Unfortunately, linking performance to cold hardiness is merely one measure of genotypic adaptation, which further restricts the capacity to maintain genetic diversity in tree planting. Taken together, there are few options for seedling buyers to refine orders to match project climate profiles, potentially generating climate misalignment and maladaptation (in both the short and the long term).

Presently, there is overwhelming scarcity of seedlings originating from sufficiently diverse bioclimatic seed zones. To illustrate this, figure 4a depicts the number of seed collection zones (defined by Pike et al. 2020 on the basis of a combination of cold hardiness and ecoregions), where *Q. rubra* seeds were collected for 2022 nursery seedling inventories. Within the focal region, seedlings

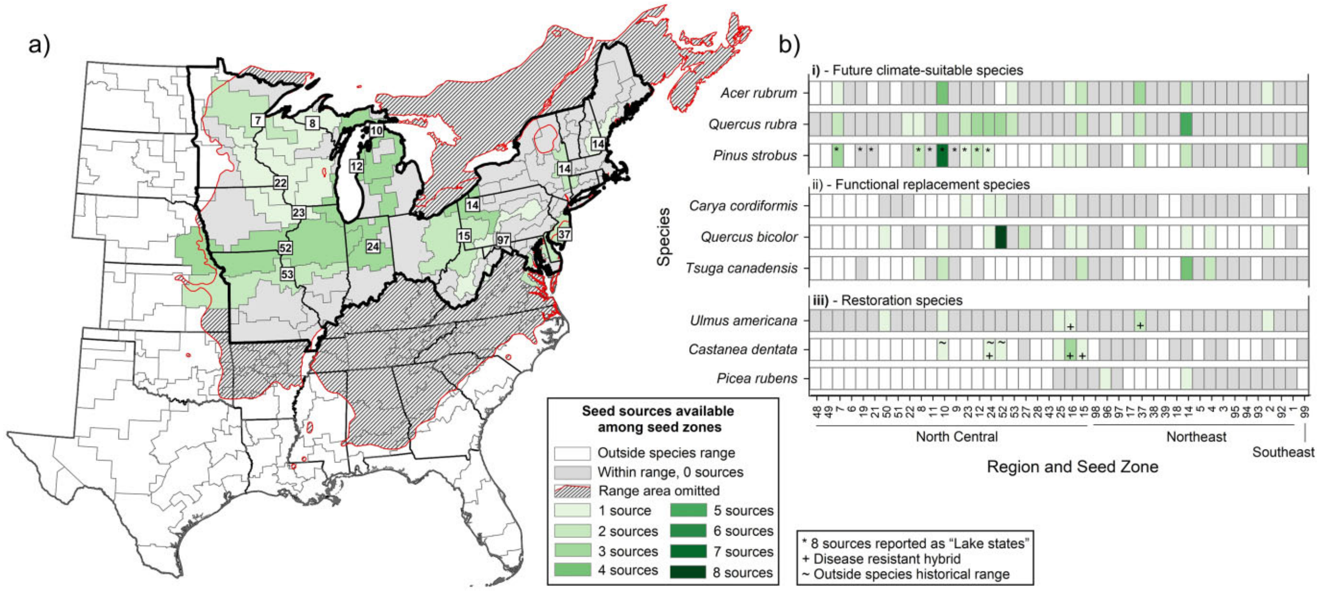

Figure 4. Seed source availability in 2022 seedling inventories from forest nurseries located within the northern US focal region, where panel (a) depicts the number of **Quercus rubra** seed sources available within discrete seed zones throughout the species' range (the hashed area was omitted from the analysis) and panel (b) illustrates source availability among nine target species that typify those commonly used for future-climate-suitable plantings, functional replacement of threatened keystone species, and species restoration efforts where historic ranges have been degraded (see the text and box 1 for details regarding terms). The seed zones were generated by Pike and colleagues (2020) and are derived from a combination of plant cold hardiness zones and Bailey's ecoprovinces. In panel (b), each cell represents a seed zone (the **x**-axis is depicted approximately west to east), where white cells correspond to those in which species were historically absent (Little 1971). The color-coded cells indicate seed zones in which species were historically present and indicates whether a seed source was available for purchase at scale. See the supplemental material for methodological details regarding data sourcing.

originated from only 31% of the seed zones within the species range. This trend is particularly troubling, given that *Q. rubra* is one of the most widely propagated deciduous tree species in the United States. Furthermore, seed source scarcity was exacerbated among all the species examined (figure 4b), where most had very few sources available, typically representing less than 28% of the seed zones within each respective species' ranges. Unlike trees with orthodox seeds (i.e., *A. rubrum, P. strobus*), which survive drying and freezing to allow for preservation in seed storage facilities for years, species with recalcitrant seeds (i.e., *Q. rubra, C. dentata*) are challenging to preserve for long periods and must be collected annually, further complicating the need to expand seed-harvesting practices and infrastructure. Although biological and logistical factors determine where and why seed is collected, such as desirable seed-masting traits and predictability, it is clear from these results that current forest nursery production severely underrepresents seed provenance, genetic diversity, or climate suitability among the species examined. Consequently, tree-planting efforts suffer from restricted, homogenous genotypes and source provenances likely unrepresentative and potentially maladapted to current or future planting sites.

In our assessment, the quality of seed source records maintained by nurseries vary considerably depending on the species, collection type (e.g., wild, seed orchard), or collector (e.g., internal, commercial distributor, hobbyist). Although some nurseries maintained detailed records of seed origin (e.g., latitude, longitude, elevation) and made them readily available on request, in most instances records were not advertised in catalogues, difficult to obtain, exceedingly generalized (e.g., "Lake States" *P. strobus*, a region composed of eight states and more than 30 seed zones, covering 1,040,000 square kilometers), or even of unknown origin. Additionally, less than 25% reported cold hardiness thresholds, a proxy for current or future-climate suitability, and none readily tracked seedlots in accordance with Pike's seed zones. While we were able to obtain some level of seed source information for most (86%) nursery records, the challenges we experienced reflect the barriers a forester or conservation practitioner would encounter when seeking to match seedlots with project needs. This is further compounded when attempting to match other seedling traits, such as species or stock types against inherently dynamic environmental, economic, and operational conditions that can alter or postpone narrow planting windows.

The "right" seedlings

Despite growing interest in tree planting for global change adaptation and restoration, some foresters do not actively employ tree planting as part of management plans. In a survey from the northeastern United States (McGann et al. 2023), foresters report some of the greatest barriers for planting for global change include a lack of resources for selecting climate appropriate seedlings (e.g., species, origin, stock) or uncertainty about best practices for novel planting strategies (e.g., assisted migration, functional replacement). This disconnect may be linked to nurseries and deficient or diminishing institutional knowledge of propagation and planting practices, which are likely exacerbated for novel species and seedling stock types traditionally underrepresented in commercial nursery or timber operations.

One solution is use of seedlot selection tools (e.g., https://seedlotselectiontool.org/sst/, www.easternseedzones.com), species distribution models (e.g., Climate Change Tree Atlas, www.fs.usda.gov/nrs/atlas/tree), and stronger nursery–client partnerships, as was outlined in the Target Plant Concept (Dumroese et al. 2016). Although most buyers have historically had little influence on nursery inventory (except for large industrial forest owners), the target plant concept involves a collaborative process to produce ideal plants for meeting project outcomes.

The result is greater refinement in the development of species, provenances, and stock types while lessening the burden on nurseries to grow speculative inventory. Despite these advantages, the target plant concept is seldom practiced. Although seedlings typically require 2–5 years to grow to be suitable for planting, many foresters commonly place seedling orders only months before outplanting. Moreover, the selection of target species necessitates a keen understanding of present and future climate and the development of best practices for regeneration under novel, more extreme conditions (Benito-Garzón et al. 2013, Clark and D'Amato 2023). Unfortunately, there are few examples to guide this process for emerging planting strategies or in ecosystems such as lowland forests where planting has historically been uncommon, challenging the development of targeted seedling–site combinations.

Advancing future policy, resources, and best practices

Tree-planting strategies for global change vary in scope and objective, including mitigative, restorative, and climate-responsive actions. Increasing calls for expansion of planting will be seriously hindered by several factors associated with seedling availability (e.g., labor or supply shortages, seed procurement; Fargione et al. 2021). Specifically, we highlight deficiencies in regional inventory, species availability, and limited, homogeneous seed sources. To overcome these barriers, we recommend the following efforts be placed on improving policy and financial support, on informational resources and training, and on research development, tracking, and monitoring.

Policy and financial support

Changes in policy and increases in financial support are likely needed to implement and diversify emerging tree-planting initiatives. Presently, government agencies such as the US Forest Service and many US states lack clear policies for the movement of species or genotypes, rather, relying on seed zones delineated in the 1970s on the basis of climate and land use at the time. Although species transfer guidelines under a warming climate exist (e.g., Pike 2021), these are guided by historical climatic conditions and primarily emphasize species for timber production (Palik et al. 2022, Park and Rodgers 2023). Globally, forest nurseries report reluctance to diversify species and climate-adapted seed-sourcing practices—a hesitancy linked to policies and market pressures that constrain inventory decisions (Tepe and Meretsky 2011, Whittet et al. 2016, Bannister et al. 2018). With respect to policy, state and federal legislation that actively promotes the advancement of seedlot diversity and clarifies regulations (or a lack thereof) on the movement of genotypes may help guide growers to increase and diversify nursery inventory. In addition, agreement within the scientific community is needed to support a cohesive strategy to facilitate tree-planting efforts for global change, because current or ambiguous policies hamper the ability to match species and seed sources to a changing climate. For instance, various federal policies outlined in the USDA Forest Service Manual (e.g., Reforestation Policy FSM 2472.03, Native Plant Material Policy FSM 2070.3, Genetic Resources Management FSM 2475.03) prohibit the use of nonnative species and genotypes in tree-planting and forest-management activities on federal lands (USDA 2014). However, the recent US National Forest System Reforestation Strategy points to a shifting sentiment and serves as an important (albeit broad) framework for expanding and modernizing reforestation tactics on federal lands during an era of global change (USDA 2022). The goals outlined by this strategy include expanding seed production for climate-adapted species and genotypes to promote future forest resilience. Still, advances are needed to define these approaches more explicitly such that they translate to action at a federal and state level. At the same time, the European Union recently passed a deforestation-free supply chain policy that seeks to ban the trade of forest and agricultural products originating from a jurisdiction (i.e., county) where there is planting of nonnative tree species in naturally regenerating forests (Council of the European Union 2022). Although the goal is ostensibly to halt the conversion of natural forests into nonnative plantations (frequently in the tropics), an unintended consequence could result in impeding tree planting for climate change adaptation elsewhere in the world, including temperate forests. Finally, policies that tie reforestation to more traditional metrics such as density, seedling survival, and growth and yield may need to be modified to reflect the ever-widening goals for tree planting to sustain ecosystem functions in addition to timber production. To help meet benchmarks for propagating and planting increasingly diverse or future-adapted species and genotypes that carry a heightened degree of speculative investment, legislation that promotes incentive programs in the form of regulation or tax breaks may also help motivate nurseries and buyers to diversify seedling inventory.

Financial incentives will be needed to support sufficient access to nurseries and diverse seed procurement, production, and inventory. Although tree nurseries may naturally respond to market pressures, a sustained market signal is needed to invest in staff and infrastructure, which may take decades without assistance. Presently, ambitious tree-planting targets and short funding cycles result in periodic, intense demand on nurseries. Such pressure can result in buyers selecting seedlings on the basis of availability rather than on the basis of a more refined approach based on project objectives, site conditions, and near- and long-term climatic conditions. Unfortunately, few forest nurseries can risk holding a broad but sufficiently diverse inventory in terms of species, genotypes, and stock types, without substantial financial risk. Such a strategy is simply impractical without a financial buffer. With numerous closures in government funded forest nurseries, it is unclear how private nurseries will respond without a sustained market signal to increase and diversify their inventory. To fill this gap, substantial federal and state-level investment may be needed to bolster the capacity of public nurseries and seed collection efforts. This strategy may stimulate production from private nurseries once a stable demand is apparent. In fact, in 2023, the US federal government made an investment of US$35 million in expanding federal nursery capacity and an additional US$10 million to support state and Tribal nurseries and native seed partnerships (USDA 2023). Likewise, the Canadian government has made similar investments (Department of Finance Canada 2020). However, given the existing (and growing) reforestation backlog, declines in nursery infrastructure, and complex needs for diverse seeds and seedlings, it is likely that substantially more public investment in the form of grants, loans, and cost-share programs will be needed to reinvigorate, diversify, and expand forest nurseries and propagation infrastructure (e.g., seed processing, storage, land area). In addition, funding to support research and tree breeding focused on producing species and genotypes more capable of withstanding the effects of climate change will be needed.

Labor shortages and ageing demographics in nursery trades (seed collectors, nursery employees) have been identified among the biggest limitations for scaling forest seed collection and nursery capacity for global change (Haase and Davis 2017, Fargione et al. 2021). Recruitment of new workers in these fields is needed to fill the skilled-labor gap and to prevent the loss or degradation of institutional knowledge. Unfortunately, efforts to fill this labor gap have fallen short (Haase and Davis 2017). Guest workers on temporary visas (e.g., US H-2B visa program) often play an important role on tree-planting crews, reforesting millions of hectares in the United States annually, but unclear policies and legislation have made it challenging for businesses to participate in this service (Blinn et al. 2021). In the United States, long-term solutions are needed to allow guest workers temporary entry to meet the labor demand from tree planting not fulfilled by US workers. Finally, funding and job-training programs may also serve as economic drivers for job creation while potentially providing renewed access to nurseries in underserved areas. As such, federal and state government programs such as the proposed Civilian Climate Corps (117th US Congress 2022), modeled after historical tree-planting initiatives generated by the US government's New Deal and the 1930s Civilian Conservation Corps could be leveraged to enhance the labor pool, particularly to entice younger workers into a career path and to incentivize the collection and production among sufficiently diverse species, genotypes, and stock types. In addition, it may be necessary to increase wages, improve work conditions, and offer more full-time employment opportunities to entice workers over the short and long term to seek jobs in the nursery and reforestation trades.

Informational resources and training

Improvement in informational resources and training is needed to advance knowledge uptake, develop best management practices, and reduce uncertainties throughout the reforestation pipeline (e.g., seed procurement, nursery production, pre- and postplanting activities; cf. Fargione et al. 2021). As foresters and natural resource managers increasingly look to tree planting as a management strategy for global change, it is important that buyers work with nurseries years in advance to develop project appropriate seedlings (e.g., the target plant concept). Failure to plan well in advance can lead to missing time-sensitive seed production (i.e., masting years) and harvesting windows or other factors such as extreme climate that will likely exacerbate the procurement of the right seedlings for a project's needs.

In the United States, the federal-level interest in reforestation (e.g., the Infrastructure Investment and Jobs Act and the National Forest System Reforestation Strategy; USDA 2022) coupled with growth in the private sector (e.g., The Nature Conservancy's Minnesota Million campaign) demonstrate the need for national and regional reforestation specialists responsible for coordinating seedling production and best practices to match diverse tree-planting initiatives (now and into the future). Examples of these services and infrastructure that already exist are cosupported by the federal government and extension education (see the Reforestation, Nurseries, and Genetic Resources, https://rngr.net), which can serve as a model and nexus for expanding personnel and capacity. Such specialists could reciprocally engage with nurseries and natural resource managers to reduce knowledge gaps and ensure that best practices are adaptive and transferrable. Furthermore, such individuals could help coordinate the development of regionally diverse tree-planting projects across agencies and landowners, informed by how the practice is being pursued across the landscape, rather than an ad hoc stand-by-stand approach in terms of species and genotypes selected.

Information and professional development incentives may be needed to support seed collectors, nurseries, tree planters, and foresters to improve best practices for tree planting under global change. Presently, there are few resources for nurseries and tree-planting project managers to easily assess what to plant or which climate future to target. The novelty of tree-planting strategies for global change will necessitate resources for reducing this uncertainty, by localizing decisions and improving best practices via university extension programs and literature, online decision support tools, or peer to peer adaptation trainings (e.g., Northern Institute of Applied Climate Science Adaptation Workbook, www.adaptationworkbook.org). Under some circumstances, continuing educational credits may be tied to certification or licensing (both new and existing) as a means of evolving and diversifying industry practices. Finally, more explicit integration of regeneration guidelines associated with planting applications, such as the use of future-climate-adapted species or genotypes, into state best management practices and forest certification standards, could further encourage development of communities of practice and capacity around tree planting under global change.

Research development, tracking, and monitoring

Finally, as examples of emerging planting strategies are developed, improvements in research development, tracking seedlots, and monitoring of outcomes will be required to refine target plants and best practices. In a global assessment of tree-planting organizations, only 5% reported pursuing postplanting monitoring outcomes (Martin et al. 2021). To ensure forests are sustainably managed, some US states have adopted policies such as the Oregon Forest Practices Act that tie postharvest reforestation outcomes to requirements in terms of seedling survival and stand establishment. It may be appropriate to apply similar practices to monitor the outcomes of emerging planting projects, assessed against multiple measures of ecological health and adaptation, not just survival or future biomass production. However, unlike postharvest reforestation projects, which are often tied to commercial outcomes, mandating monitoring requirements on planting projects that lack a commercial purpose (e.g., restoration, climate adaptation, or mitigation) could have perverse effects by increasing the cost threshold for doing these kinds of activities. Therefore, financial incentives may be necessary to offset the costs of monitoring some emerging planting projects. Although monitoring efforts need to track the short-term performance of plantings (3–5 years), given the novelty of many planting objectives (e.g., assisted migration of species and climate-suitable genotypes, functional replacement), research and demonstration efforts will also need established to track the outcomes over longer time periods throughout various stages of tree and forest maturation (from 15 to more than 80 years). Research demonstration where business-as-usual treatments (e.g., silvicultural strategies, planting arrangements, species, genotypes) are compared with innovative treatments in side-by-side, operationally established plots may be needed to be established across ecosystem types to reduce knowledge gaps and improve knowledge transfer (see Gardiner et al. 2008, Nagel et al. 2017, Palik et al. 2022). The funding and establishment of permanent monitoring plots specifically stratified among planting projects, similar to the USDA's Forest Inventory and Analysis program or state-level continuous forest inventory plots, will be necessary to ascertain the stand-, ecosystem-, and landscape-level effects of planting initiatives aimed at global change.

To assist forest nurseries and clients in developing ecologically- and climate-appropriate inventory, reciprocal reporting of planting outcomes will be needed. Traditional measures of growth and survival should be the minimum, but in some circumstances, where more novel planting mixtures are used (e.g., assisted migration, functional replacement), finer measures of plant physiological performance or maladaptation such as heat and drought tolerance or winter freezing injury may be useful for future decision-makers. In addition, given the intended goals of emerging tree-planting strategies for global change, it may be necessary to track outcomes in terms of the influence on habitat relationships, the sustenance of ecologically or culturally important forest functions, or ecosystem service outputs (e.g., flood mitigation, greenhouse gas storage). Greater emphasis on outplanting monitoring and information sharing will be needed to assess and refine practices, particularly for emerging planting strategies with only nascent evidence. As such, incentivizing greater participation and information sharing of planting designs, seedlings deployed (species, seedlots, and stock types), and project outcomes exchanged via open-access data repositories, such as the Propagation Protocols Database (https://npn.rngr.net/propagation/protocols) or regional silviculture libraries (e.g., www.uvm.edu/nesl), may be necessary to reduce knowledge gaps and foster broader, landscape-level decision-making.

To match the future need, nurseries will need to ensure that high quality records of seed origin are readily obtainable for buyers to ascertain seedling adaptation potential under rapidly changing climatic conditions. To facilitate this, the development of a national seed-labeling standard and database would greatly improve seedlot selection, with high resolution records of source collections (e.g., latitude, longitude, elevation). Updates to truth-in-labeling laws, such the Federal Seed Act of 1939, which governs interstate commerce and importation of agricultural and vegetable seeds, may be needed to integrate forest seed to stimulate such standards. Likewise, intrastate-level labeling laws may be necessary given that this act does not cover the movement of seeds within state boundaries. Presently, few states maintain seed-labeling laws that include forest seeds, and where applicable, enforcement is not strict (Mangold and Bonner 2008). Although examples of seed certification exist in agricultural sectors or in forestry in some parts of the United States (e.g., the Pacific Northwest), these have historically focused on commercial outcomes. Updating seed-labeling certification and standards may be necessary to ensure the accuracy, development, and availability of diverse species and seed of documented provenance. Furthermore, an accessible database would serve both private and public nurseries to better assess market needs while generating a clearinghouse for seedling buyers to better refine seedling selections to site conditions. Given the growing need to rapidly diversify the species and genotypes used in tree-planting initiatives, such decision support tools are critical to ensure informed practices.

Conclusions

Tree planting represents an exciting natural climate solution by providing an avenue to diversify, adapt, restore, or mitigate the effects of global change (Canadell and Raupach 2008, Griscom et al. 2017). Despite the urgency presented by climate change, it is important that emerging planting strategies consider complex ecosystem functions, because uniform, monocultural plantations can be vulnerable to stressors and devoid of multiple ecosystem benefits (Bennett 2015). Beyond planting trillions of seedlings, emphasis also needs to be placed on diversifying forest nurseries and outplanting practices to allow for the promotion of compositional diversity, structural complexity, and functional connectivity to foster multiple ecological functions, cultural values, and the long-term resilience of forests (Palik et al. 2020). To realize this, we outline tangible improvements to policy and financial incentives, informational resources and training, and research and monitoring that could be used to fill knowledge gaps and meet rapidly expanding tree-planting needs. Without these changes, current seedling capacity and practices may fail to meet the needs of the diverse and ambitious tree-planting goals being pursued, limiting what can be accomplished in adapting to and mitigating global change impacts.

Supplemental Material

Supplemental data are available at *BIOSCI* online.

Acknowledgments

Funding was provided by the Department of Interior Midwest and Northeast Climate Adaptation Science Centers, the National Council for Air and Stream Improvement, the USDA Forest Service Northern Research Station, the USDA National Institute of Food and Agriculture McIntire–Stennis Cooperative Forestry Research Program, the National Science Foundation (grant no. 1920908), the University of Vermont Rubenstein School of Environment and Natural Resources (RSENR), and the Northern Institute of Applied Climate Science, a collaborative partnership led by the USDA Forest Service. An earlier version of the manuscript was improved on the basis of feedback from members of the RSENR Silviculture and Applied Forest Ecology Lab at the University of Vermont.

References

117th US Congress. 2022. HR 3684: Infrastructure Investment and Jobs Act.US Congress. www.congress.gov/bill/117th-congress/house-bill/3684.

Bannister JR, et al. 2018. Major bottlenecks for the restoration of natural forests in Chile. *Restoration Ecology* 26: 1039–1044. doi:10.1111/rec.12880

Bastin JF, et al. 2019. The global tree restoration potential. *Science* 364: 76–79. doi:10.1126/science.aax0848

Benito-Garzón M, et al. 2013. Extreme climate variability should be considered in forestry assisted migration. *BioScience* 63: 317. doi:10.1525/bio.2013.63.5.20

Bennett BM. 2015. *Plantations and Protected Areas: A Global History of Forest Management*. MIT Press.

Blinn CR, O'Hara TJ, Russell MB. 2021. H-2B guest workers and the critical role they play in US forests. *Journal of Forestry* 119: 467–477. doi:10.1093/jofore/fvab022

Breed MF, et al. 2013. Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conservation Genetics* 14: 1–10. doi:10.1007/s10592-012-0425-z

Broadhurst LM, et al. 2015. Maximizing seed resources for restoration in an uncertain future. *BioScience* 66: 73–79. doi:10.1093/biosci/biv155

Canadell JG, Raupach MR. 2008. Managing forests for climate change mitigation. *Science* 320: 1456–1457. doi:10.1126/science.1155458

Clark PW, D'Amato AW. 2023. Seedbed not rescue effect buffer the role of extreme precipitation on temperate forest regeneration. *Ecology 104: e3926*.

Clark PW, et al. 2021. Ecological memory and regional context influence performance of adaptation plantings in northeastern US temperate forests. *Journal of Applied Ecology* 59: 314–329. doi:10.1111/1365-2664.14056

Clark PW, et al. 2022. Restoring a keystone tree species for the future: American chestnut assisted migration plantings in an adaptive silviculture experiment. *Forest Ecology and Management* 523: 120505. doi:10.1016/j.foreco.2022.120505

Clark PW, D'Amato AW, Palik BJ. 2023. Ecological diversity of northern US forest nursery inventories. *FigShare*. doi:10.6084/m9.figshare.22568047

Cook-Patton SC, et al. 2020. Lower cost and more feasible options to restore forest cover in the contiguous United States for climate mitigation. *One Earth* 3: 739–752. doi:10.1016/j.oneear.2020.11.013

Costanza KKL, et al. 2017. The precarious state of a cultural keystone species: Tribal and biological assessments of the role and future of black ash. *Journal of Forestry* 115: 435–446. doi:10.5849/jof.2016-034R1

Council of the European Union. 2022. *Regulation on Deforestation-Free Products*. European Parliament.

Dale V, et al. 2001. Climate change and forest disturbances. *BioScience* 51: 723–734. doi:10.1641/0006-3568(2001)051

Daly C, et al. 2012. Development of a new USDA plant hardiness zone map for the United States. *Journal of Applied Meteorology and Climatology* 51: 242–264. doi:10.1175/2010JAMC2536.1

D'Amato AW, Palik BJ. 2020. Building on the last "new" thing: Exploring the compatibility of ecological and adaptation silviculture. *Canadian Journal of Forest Research* 51: 172–180. doi:10.1139/cjfr-2020-0306

D'Amato AW et al. 2018a. Silviculture in the United States: An amazing period of change over the past 30 years. *Journal of Forestry* 116: 55–67. doi:10.5849/jof-2016-035

D'Amato AW et al. 2018b. Evaluating adaptive management options for black ash forests in the face of emerald ash borer invasion. *Forests* 9: 348. doi:10.3390/f9060348

Department of Finance Canada. 2020. Supporting Canadians and Fighting COVID-19: Fall Economic Statement 2020. Government of Canada. www.budget.canada.ca/fes-eea/2020/report-rapport/toc-tdm-en.html.

Di Sacco A, et al. 2021. Ten golden rules for reforestation to optimize carbon sequestration, biodiversity recovery and livelihood benefits. *Global Change Biology* 27: 1328–1348. doi:10.1111/gcb.15498

Domke GM, et al. 2020. Tree planting has the potential to increase carbon sequestration capacity of forests in the United States. *Proceedings of the National Academy of Science* 117: 24649–24651.

Dumroese RK, et al. 2005. Forest service nurseries: 100 years of ecosystem restoration. *Journal of Forestry* 103: 241–247. doi:10.1093/jof/103.5.241

Dumroese KR, et al. 2016. Meeting forest restoration challenges: Using the target plant concept. *Reforesta* 1: 37–52.

Erickson VJ, Halford A. 2020. Seed planning, sourcing, and procurement. *Restoration Ecology* 28: S216–S224. doi:10.1111/rec.13199

Etterson JR, et al. 2020. Assisted migration across fixed seed zones detects adaptation lags in two major North American tree species. *Ecological Applications* 30: e02092.

Fargione J, et al. 2021. Challenges to the reforestation pipeline in the United States. *Frontiers in Forests and Global Change* 4: 629198.

Fox JF, Campbell JE, Acton PM. 2020. Carbon sequestration by reforesting legacy grasslands on coal mining sites. *Energies* 13: 6340. doi:10.3390/en13236340

Gann G, et al. 2019. International principles and standards for the practice of ecological restoration: Second edition. *Restoration Ecology* 27: S1–S46. doi:10.1111/rec.13035

Gardiner E, et al. 2008. Establishing a research and demonstration area initiated by managers: The Sharkey restoration research and demonstration site. *Journal of Forestry* 106: 363–369.

Griscom BW, et al. 2017. Natural climate solutions. *Proceedings of the National Academy of Sciences* 114: 11645–11650. doi:10.1073/pnas.1710465114

Haase D, Davis A. 2017. Developing and supporting quality nursery facilities and staff are necessary to meet global forest and landscape restoration needs. *Reforesta* 0: 69–93. doi:10.21750/refor.4.06.45

Haase DL, et al. 2021. Forest nursery seedling production in the United States: Fiscal year 2020. *Tree Planter's Notes* 64: 108–114.

Holl KD, Brancalion PHS. 2020. Tree planting is not a simple solution. *Science* 368: 580–581. doi:10.1126/science.aba8232

[IPCC] Intergovernmental Panel on Climate Change. 2014. *Climate Change 2014: Synthesis Report*. IPCC.

Iverson LR, et al. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management* 254: 390–406.

Jalonen R, et al. 2018. Forest and landscape restoration severely constrained by a lack of attention to the quantity and quality of tree seed: Insights from a global survey. *Conservation Letters* 11: e12424. doi:10.1111/conl.12424

Klenk NL, Larson BMH. 2015. The assisted migration of western larch in British Columbia: A signal of institutional change in forestry in Canada?. *Global Environmental Change* 31: 20–27. doi:10.1016/j.gloenvcha.2014.12.002

Little E. 1971. *Atlas of United States Trees, vol. 1: Conifers and Important Hardwoods*. US Department of Agriculture. Miscellaneous publication no. 1146.

Lovett GM, et al. 2016. Nonnative forest insects and pathogens in the United States: Impacts and policy options. *Ecological Applications* 26: 1437–1455. doi:10.1890/15-1176

Mangold RD, Bonner FT. 2008. Certification of tree seeds and other Woody plant materials. Pages 131–139 in Bonner FT, Karrfalt RP, eds. *The Woody Plant Seed Manual*. US Department of Agriculture. Handbook no. 7.

Martin MP, et al. 2021. People plant trees for utility more often than for biodiversity or carbon. *Biological Conservation* 261: 109224. doi:10.1016/j.biocon.2021.109224

McGann TC, et al. 2023. Climate adaptive management in the northeastern United States: Common strategies and motivations of rural and urban foresters. *Journal of Forestry* 121: 182–192.

Merritt DJ, Dixon KW. 2011. Restoration seed banks: A matter of scale. *Science* 332: 21–22.

Millar CI, Stephens N, Stephenson S. 2007. Climate Change and forests of the future: Managing in the face of uncertainty. *Ecological Applications* 17: 2145–2151.

Nagel LM, et al. 2017. Adaptive silviculture for climate change: A national experiment in manager–scientist partnerships to apply an adaptation framework. *Journal of Forestry* 115: 167–178.

[NASF] National Association of State Foresters. 2016. *Nursery and Tree Improvement Program Survey*. NASF. www.stateforesters.org/newsroom/nursery-and-tree-improvement-program-survey.

Nevill PG, et al. 2016. Seed production areas for the global restoration challenge. *Ecology and Evolution* 6: 7490–7497. doi:10.1002/ece3.2455

Palik BJ, et al. 2020. *Ecological Silviculture: Foundations and Applications*. Waveland Press.

Palik BJ, et al. 2021. Eighth-year survival and growth of planted replacement tree species in black ash (Fraxinus nigra) wetlands threatened by emerald ash borer in Minnesota, USA. *Forest Ecology and Management* 484: 118958. doi:10.1016/j.foreco.2021.118958

Palik BJ, et al. 2022. Operationalizing forest assisted migration in the context of climate change adaptation: Examples from the eastern USA. *Ecosphere* 13: 4260.

Park A, Rodgers JL. 2023. Provenance trials in the service of forestry assisted migration: A review of North American field trials and experiments. *Forest Ecology and Management* 537: 120854. doi:10.1016/j.foreco.2023.120854

Pedlar JH, et al. 2012. Placing forestry in the assisted migration debate. *BioScience* 62: 835–842.

Peters MP, et al. 2020. Climate Change Tree Atlas, vers. 4. Climate Change Resource Center, US Forest Service. www.fs.usda.gov/nrs/atlas .

Pike CC. 2021. White spruce: Guidance for seed transfer within the Eastern United States. *Tree Planter's Notes* 64: 19–25.

Pike C, et al. 2020. New seed-collection zones for the eastern United States: The Eastern Seed Zone Forum. *Journal of Forestry* 118: 444–451. doi:10.1093/jofore/fvaa013

Prober SM, et al. 2019. Shifting the conservation paradigm: A synthesis of options for renovating nature under climate change. *Ecological Monographs* 89: e01333. doi:10.1002/ecm.1333

Scheidel A, Work C. 2018. Forest plantations and climate change discourses: New powers of "green" grabbing in Cambodia. *Land Use Policy* 77: 9–18. doi:10.1016/j.landusepol.2018.04.057

Schuurman GW, et al. 2021. Navigating ecological transformation: Resist–accept–direct (RAD) as a path to a new resource management paradigm. *BioScience* 71: 16–29.

Sittaro F, et al. 2017. Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. *Global Change Biology* 23: 3292–3301.

Stanturf JA, Palik BJ, Dumroese RK. 2014. Contemporary forest restoration: A review emphasizing function. *Forest Ecology and Management* 331: 292–323. doi:10.1016/j.foreco.2014.07.029

Swanston C, et al. 2018. Vulnerability of forests of the Midwest and Northeast United States to climate change. *Climatic Change* 146: 103–116. doi:10.1007/s10584-017-2065-2

Tepe TL, Meretsky VJ. 2011. Forward-looking forest restoration under climate change: Are U.S. nurseries ready?. *Restoration Ecology* 19: 295–298. doi:10.1111/j.1526-100X.2010.00748.x

[USDA] US Department of Agriculture. 2014. Timber management. Section 2400 in *Forest Service Manual*. USDA.

[USDA] US Department of Agriculture. 2022. *Strategy Growing and Nurturing Resilient Forests*. USDA.

[USDA] US Department of Agriculture. 2023. Biden–Harris Administration Invests Nearly $10 Million for Reforestation through Forest Nursery and Native Seed Partnerships. USDA. Release no. 0043.23. www.usda.gov/media/press-releases/2023/02/24/biden-harris-administration-invests-nearly-10-million-reforestation.

Veldman JW, et al. 2019. Comment on "the global tree restoration potential." *Science* 366: 7976. doi:10.1126/science.aay7976.

Whittet R, et al. 2016. Supplying trees in an era of environmental uncertainty: Identifying challenges faced by the forest nursery sector in Great Britain. *Land Use Policy* 58: 415–426. doi:10.1016/j.landusepol.2016.07.027

Williams M, Dumroese K. 2013. Preparing for climate change: Forestry and assisted migration. *Journal of Forestry* 111: 287–297.

Received: February 12, 2023. **Revised:** April 20, 2023. **Accepted:** May 18, 2023