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Operationalizing forest-assisted migration in the context of climate change adaptation: Examples from the eastern USA

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Abstract

There is increasing momentum to implement conservation and management approaches that adapt forests to climate change so as to sustain ecosystem functions. These range from actions designed to increase the resistance of current composition and structure to negative impacts to those designed to transition forests to substantially different characteristics. A component of many adaptation approaches will likely include assisted migration of future climate-adapted tree species or genotypes. While forest-assisted migration (FAM) has been discussed conceptually and examined experimentally for almost a decade, operationalizing FAM (i.e., routine use in forest conservation and management projects) lags behind the acceptance of the need for climate adaptation. As the vulnerability of forest ecosystems in climate change increases, FAM may need to become an integral management tool to reduce long-term risks to ecosystem function, despite real and perceived barriers for its implementation. Here we discuss the concept of operational-scale FAM and why it remains a controversial, not yet widely adopted component of climate adaptation. We present three case studies of operational-scale FAM to illustrate how the practice can be approached pragmatically within an adaptation framework despite the barriers to acceptance. Finally, we discuss a path toward advancing the wide use of operational-scale FAM.

KEYWORDS
ecosystem function, operational scale, regeneration, resilience, resistance, silviculture, transition

INTRODUCTION

Climate change may represent the greatest challenge ever faced by forest managers, conservation biologists, and ecologists, with already realized and projected impacts that include changes in forest productivity (Bottero et al., 2017) and tree habitat suitability (Peters et al., 2020), catastrophic tree mortality, and altered pest behavior (Bentz et al., 2010). Concerns over these impacts are reflected by an ever-increasing focus on developing strategies to increase the adaptive capacity of forests (Nagel et al., 2017; Rissman et al., 2018).

One potential component of forest adaptation strategies that remains controversial is assisted migration of future-adapted genotypes and species of trees (Aubin et al., 2011), often done to compensate for projected loss of habitat and decline of native species of commercial, cultural, and ecological values. Debates in the literature often hinge upon the nuances of assisted migration terminology relative to the potential conservation and management goals (Dumroese et al., 2015). For instance, to distinguish it from species-rescue-assisted migration, which primarily aims to avoid extinction of species of conservation concern (e.g., McLane & Aitken, 2012), forest-assisted migration (FAM) has been used in the context of forests to broadly maintain function, productivity, and ecosystem services (Pedlar et al., 2012). Although both carry elements of uncertainty, FAM may be entrained with less of the assisted migration controversy (Aubin et al., 2011; Ricciardi & Simberloff, 2009) because it fits within broader climate change adaptation approaches aimed at maintaining ecosystems at larger scales (Swanston et al., 2016).

Concepts, policies, and decision-making frameworks for use of FAM have been reviewed extensively over the last decade (e.g., Park & Talbot, 2018; Pedlar et al., 2012; Williams & Dumroese, 2013), with potential outcomes of FAM primarily explored with modeling (e.g., Duveneck & Scheller, 2015; Gray & Hamann, 2013), or inferred from examinations of provenance trials spanning a range of climate conditions (e.g., Aitken et al., 2008). Until recently, however, there have been few published examples that illustrate how to incorporate FAM into climate change adaptation strategies at sufficiently large, operational scales that are translatable to forest conservation and management strategies (Clark et al., 2021; Etterson et al., 2020; Muller et al., 2019; Young et al., 2020). A lack of operational-scale implementation of FAM, where we define operational as the practice being applied in actual forest management projects, rather than strictly in a research setting, likely reflects the inexperience of forest managers and conservation biologists with the concept, a belief that FAM carries too high a risk (Findlater et al., 2021), a perceived lack of social license to pursue FAM broadly (Neff & Larson, 2014), and strong adherence to the precautionary principle (Ricciardi & Simberloff, 2009). Given that many forests are at risk or have already fundamentally changed (e.g., Allen et al., 2010), FAM may nevertheless be an essential tool for climate adaptation to insure against change and with lower long-term risk to ecosystem vulnerability.

Despite uncertainty that may be limiting widespread, operational use of FAM, there is at the same time a growing urgency to evaluate, demonstrate, and implement climate change adaptation strategies in forests (Schmitt et al., 2021). There is also a growing recognition that climate adaptation in forests must expand beyond a focus on maintaining timber production capacity to be inclusive of maintaining a broad range of ecosystem services (e.g., D'Amato, Jokela, et al., 2018; Rissman et al., 2018). It is therefore unlikely that these objectives can be met without greatly increasing the use of FAM, which likely will also require increased communication and cooperation between research scientists and forest managers to achieve the desired aims for FAM.

Yet the devil is in the details regarding operational-scale use of FAM; there are different forms of FAM applicable to different adaptation approaches that carry varying degrees of risk (Dumroese et al., 2015). Increased understanding of how FAM can be incorporated into climate change adaptation strategies in ways that can satisfy different levels of experience and risk acceptance may lead to wider use.

Our goal in this article is to show how FAM can be incorporated into climate change adaptation strategies in managed forests in ways that will facilitate informed use and generation of best practices by foresters and conservation biologists. Our specific objectives include (1) examining the role of FAM in the context of a range of climate change adaptation strategies and (2) highlighting examples of operational-scale use of FAM in adaptation demonstrations in the eastern United States, specifically in the Northwoods of Minnesota and in New England. We focus on this region as it represents the most forested region in United States and is already experiencing the impacts caused by climate change (Swanston et al., 2018). Additionally, well over 40 tree species are forecasted to decline from or migrate into this region (Iverson et al., 2019), further underscoring the potential need for best practices in FAM to be developed and operationalized. The concepts we discuss may be applicable to the western United States, but distinctly different forest ownership patterns and climate trends warrant a dedicated review of western considerations and examples that are beyond the scope of this discussion.

FAM IN THE CONTEXT OF CLIMATE CHANGE ADAPTATION STRATEGIES

Climate change adaptation strategies are commonly addressed in the literature in a general way (e.g., Mawdsley et al., 2009), but those that apply adaptation concepts to forest management practices in an organized, actionable fashion are more limited and often related (Cross et al., 2012; Janowiak et al., 2014; Millar et al., 2007; Nagel et al., 2017; Peterson St-Laurent et al., 2021; Schuurman et al., 2020; Stein et al., 2014; Swanston et al., 2016).

One seminal article (Millar et al., 2007) provided a conceptual framework for adaptation that could be incorporated into forest conservation and management strategies. Millar et al. (2007) categorized adaptation approaches into resistance, resilience, and response (now often referred to as transition; Nagel et al., 2017). Generally, these represent increasing degrees of novelty, effort, and risk, as well as a lengthening of the temporal perspective for assessing success. As we discuss below, the strategies also reflect a gradient of incorporation of FAM (Figure 1).

Briefly, resistance strategies generally seek to prevent change to some highly valued, core aspects of a system, where the values may be economic, social, or ecological. These strategies are often considered high risk in the long term and may focus on adapting a forest to expected nearer-term climate changes, such as more frequent or severe growing season drought (Nagel et al., 2017). As commonly conceived, resistance strategies focus on manipulating components of forest structure (e.g., the arrangement and distribution of tree sizes), but less on changing composition, thus FAM may have limited application in achieving this strategy.

A resilience strategy works within a broader range of ecological outcomes, typically defined by the ecosystem's range of natural variability. The presumption is that a forest can be adapted to future climate by emphasizing diversity within native species and structures that have greater future adaptability. Even with a focus on use of native species, a resilience strategy may include FAM by establishing genotypes of these species from areas within their range that have a current climate similar to the projected climate of the area of interest (Nagel et al., 2017). FAM used in this way is an example of assisted population expansion, which is the movement of species or genotypes over relatively short distances, with the expansion occurring contiguously within the current distribution (Leech et al., 2011; Williams & Dumroese, 2013).

It should be noted that foresters have been practicing assisted population expansion for decades by planting seed sources from within a range of a species that are, for instance, more disease resistant than the local population, for example, blister rust resistant five-needle pines in North America (Schoettle & Sniezko, 2007). In the context of a resilience adaptation strategy, a forester might plant seedlings from a population that comes from a warmer part of the range, although still within the natural distribution.

Finally, a transition strategy greatly increases the potential for use of FAM. This strategy assumes that habitat for at least some native tree species has, or will, become unsuitable and actions should consequently be taken to alter forest composition to increase the

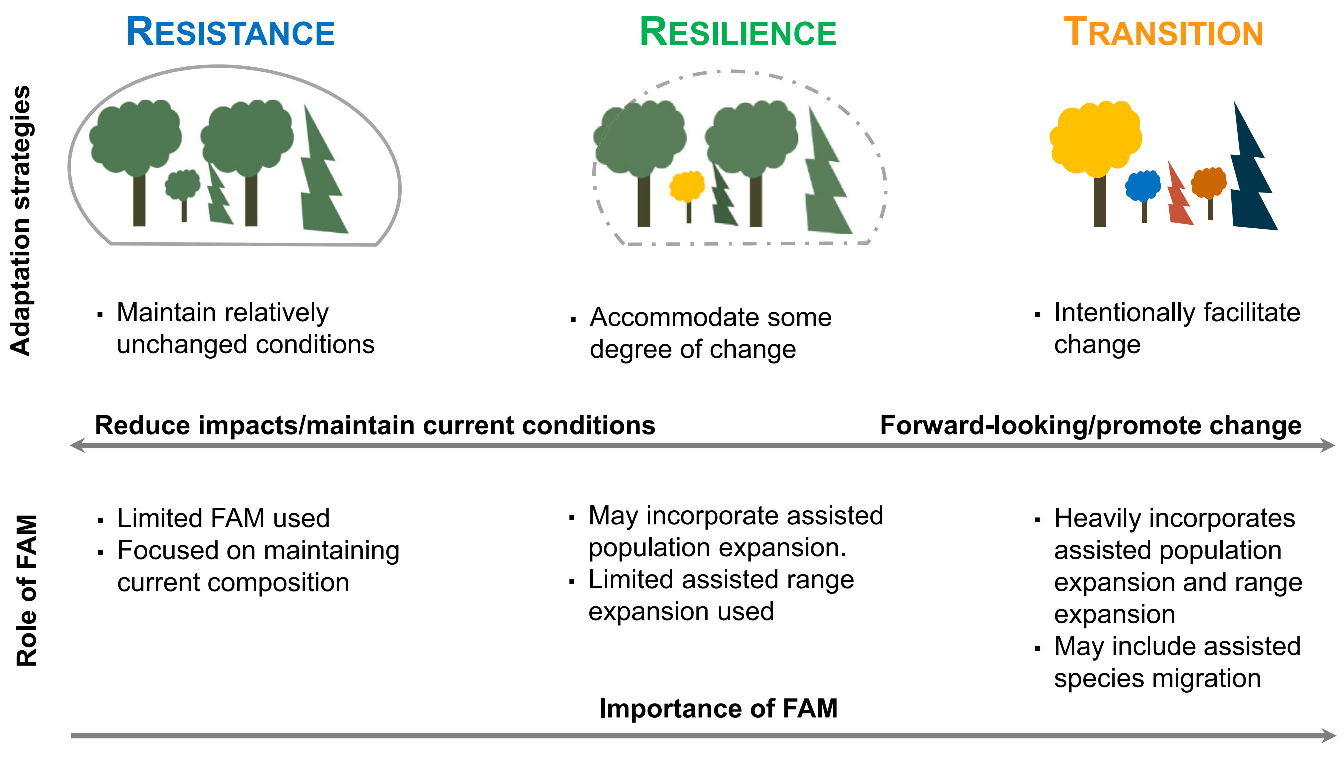

FIGURE 1 Forest-assisted migration (FAM) as part of climate adaptation strategies. The role of FAM increases with degree of change in forest conditions. Redrawn and adapted from Millar et al. (2007), Swanston et al. (2016), and Nagel et al. (2017).

proportion of species better adapted to future climate. While assisted population expansion may be part of a transition strategy, transition is more likely to include the addition of novel species using assisted range expansion, which moves species to suitable locations adjacent to (but outside of) the current range, most often done to keep pace with changing conditions (e.g., warmer climates; Williams & Dumroese, 2013). Like assisted population expansion, the use of assisted range expansion has been practiced for decades or longer. For example, pine (*Pinus* L.) seed sources in the southeastern United States have occasionally been moved northward by one seed zone (Schmidtling, 2001); however, the primary motivation for this historic FAM has been the increase in growth for production forestry, with less emphasis on ecological function. Additionally, Indigenous people of North America likely promoted the expansion of mast and fruit species, such as the assisted movement of oak (*Quercus* L.), along the northern extent of its range (Abrams & Nowacki, 2008).

Although not always framed within FAM (see Pedlar et al., 2012), the role of long-distance translocation of exotic species may also fit a forest transition strategy (Leech et al., 2011). This is often treated in the literature as assisted species migration (Williams & Dumroese, 2013); however, rather than focusing on the prevention of species extinction, in the context of assisted migration, this refers to the assisted long-distance migration (e.g., interregional, transcontinental, and intercontinental) of a species beyond areas accessible via natural dispersal (Dumroese et al., 2015). The risks and uncertainties of exotic forest transplants are not without concern, with examples of invasive colonization (e.g., black cherry [*Prunus serotina* Ehrh.] in Europe; Starfinger et al., 2003) and is central to debates surrounding the implementation of assisted migration. As such, extreme caution is warranted, as the routine use of assisted species migration will be unlikely and rapid learning will be correspondingly limited. Still, in the context of FAM, examples of this practice are starting to be discussed, for example, replacing eastern hemlock (*Tsuga canadensis* [L.] Carrière) with Norway spruce (*Picea abies* [L.] Karsten) to sustain wildlife benefits (Ritter, 2020; https://www.nrs.fs.fed.us/sustaining_forests/conserve_enhance/wildlife_fish/norway-spruce-bird-habitat/) or to replace native black ash (*Faxinus nigra* Marsh.) with emerald ash borer (EAB)-resistant Manchurian ash (*Fraxinus mandshurica* Rupr.) (see *Case Study 2: FAM in black ash wetlands*).

OPERATIONALIZING FAM

There are several overarching causes for limited operational-scale implementation of FAM, including: (1) forest managers and conservation biologists may lack on-the-ground experience with implementation of climate change adaptation strategies, particularly practices that include FAM; (2) there are overriding concerns about perceptions, risk, and maladaptation; and (3) a focus on the immediate timber resources, operational capacity, and guidance, rather than longer-term ecosystem function, leads to less urgency to operationalize FAM as an adaptation tool.

Forest manager experience with climate change adaptation and artificial regeneration

The extent to which an organization is operationalizing FAM may reflect the level of experience forest managers have with climate change adaptation strategies in general, although this experience is growing due in large part to comprehensive training and planning tools such as the Climate Change Response Framework (Swanston et al., 2016). The success of the Response Framework is reflected in the growing number of on-the-ground adaptation examples in North America (Box 1). FAM can be part of these adaptation approaches, but its routine use lags behind implementation of the adaptation approaches themselves, due in part to the perceived risks and unfamiliarity with FAM by managers (Ontl et al., 2018).

The inexperience that forest managers have with FAM as part of adaptation strategies likely serve as a barrier that contributes to the nascent few operational examples. For instance, despite profound interest in adaptation strategies to facilitate community transitions toward future-adapted species, the routine practice of tree planting for artificial regeneration is highly variable by ecoregion and land ownership (Ontl et al., 2018), especially in forests with abundant natural regeneration. This lack of routine use of artificial regeneration is reflected in the declining number of tree nurseries (NASF, 2016) and number of seedlings planted as part of broader reforestation efforts (Haase et al., 2021). With a forthcoming need to incorporate FAM into forest management and conservation practices, anemic budgets for forest management coupled with unfamiliarity with reforestation best practices may hinder routine use of FAM. In a survey from the northeastern United States, foresters report that some of the greatest barriers for tree planting, including FAM, are (1) available information and resourcing (e.g., nurseries), (2) economics, (3) labor, (4) public perceptions, (5) governmental policy, and (6) the need to balance multiple objectives (McGann, 2022). Therefore, the decline in institutional knowledge and resources for artificial regeneration may further foster

BOX 1 Forest-assisted migration (FAM) in the Climate Change Response Framework.

The Climate Change Response Framework (www.forestadaptation.org) is a collaborative effort to operationalize climate adaptation in ecosystem management. The framework fosters science–management partnerships that generate ecoregional forest vulnerability assessments and numerous climate adaptation strategies menus. The adaptation menus build on the foundational concepts of resistance, resilience, and transition developed by Millar et al. (2007) with tiered strategies, approaches, and tactics that describe more specific adaptation pathways leading from on-the-ground actions. The menus are further tailored to resource areas, so that relevant strategies and familiar terminology more readily enable practitioners to use the menus as planning and communications tools. All menus include strategies that involve FAM, often with associated case studies that illustrate how FAM helps meet operational goals.

Adaptation strategies menus with case studies have been published for forestry (Brandt et al., 2016; Janowiak et al., 2014; Swanston et al., 2016), watershed management (Shannon et al., 2019), carbon stewardship (Ontl et al., 2020), wildlife management (LeDee et al., 2021), and from tribal perspectives (Tribal Adaptation Menu Team, 2019). Hundreds of real-world projects have used the menu-workbook process, most often relying on resilience strategies, but also frequently using transition strategies to maintain or restore ecosystem function (Ontl et al., 2018). In cases of transition, managers have commonly chosen to favor or restore native species that are better adapted to the projected climate, sometimes including FAM as a minor component of planting (e.g., Janowiak et al., 2014). Notable exceptions occur in cases of realignment, where the existing species are projected to lose habitat and are already rapidly declining. In such cases, investments in continued attempts to maintain the existing ecosystem may be viewed as higher risk than shifting to non-native or nonlocal species that are better adapted to emerging and projected conditions. This is particularly true when the most highly valued ecosystem services are not linked to specific species but can instead be realized more generally, for example, through forest cover and structure (e.g., for watershed values and habitat), and stem form (e.g., for timber). Examples can be found at https://forestadaptation.org/adapt/demonstration-projects, searching by the keyword "assisted migration."

inexperience, having a lasting impact on the efficacy of FAM in adaptation strategies. Frameworks such as the Target Plant Concept serve as useful resources for best practices aimed at determining "ideal" planting material and practices for a site (Dumroese et al., 2016).

Historical growing practices have largely prioritized species for timber production (Dumroese et al., 2005) and climate at the time of planting, with declining resources to support forest adaptation or explicit consideration of selecting species for a future climate (D'Amato, Palik, et al., 2018). Therefore, the novelty and need for FAM species and genotypes planted for conservation, timber, and ecosystem services across multiple ecoregions offer few tangible examples, further highlighting knowledge gaps for forest managers. This is further exacerbated since artificial regeneration in many forest types has historically been uncommon, such as lowland forest ecosystems.

Perceptions and risks of FAM

The risks of assisted migration and FAM have been well described and debated in the literature (Aubin et al., 2011; Karasov-Olson et al., 2021; McLachlan et al., 2007; Pedlar et al., 2012). For instance, the potential for genetic maladaptation is considered a key barrier to the widespread use of FAM. The concern is that species or genotypes selected for their future climate suitability will be maladapted to the current climate. This concern is not unique to FAM, as contemporary tree improvement programs use seed transfer functions developed from provenance trials to establish safe transfer distances, as well as the boundaries of seed zones, to avoid maladaptation (McKenney et al., 2009).

The problem with using current seed zones to guide transfer in the context of climate change is that the zones may be overly small and potentially not reflective of changes that have already occurred. In many regions, transfers that have adaptation advantages are already at low risk because the climate is now suitable for species from more southerly latitudes or lower elevations. Lags have even been detected in current seed zone delineations that do not align with changing climate conditions (Etterson et al., 2020). As such, transfers of up to 200 km north or 100 m in elevation are likely safe (Gray & Hamann, 2013; Pedlar et al., 2012). It is also possible that vigorously growing FAM species or provenances could outcompete local material maladapted to future climates, only to succumb to environmental stress later (Whittet et al., 2019). Nevertheless, given the long generation times of most tree species, it may be difficult to select species and genotypes that have a low risk of maladaptation in both the near and long term.

Decisions around FAM combine technical evidence, policy, and value-based considerations of conservation, and ethics. Disentangling these makes decision-making challenging, such that assisted migration may not be evaluated exclusively based upon scientific considerations (Findlater et al., 2021; Neff & Larson, 2014), but will also, for example, be judged on the degree to which society is comfortable (or not) with greatly altering nature. Yet, an alternative perspective is that the risk profile in many forests has already fundamentally changed, with documented habitat shifts, increased pest outbreaks, and loss of ecosystem services, such that pursuit of FAM in an operational setting is actually timely and involves lower long-term risk (e.g., Allen et al., 2010; Kurz et al., 2008).

Effectively addressing uncertain but variable future environmental conditions will require embracing flexible management strategies. Climate adaptive strategies are inherently characterized by some degree of risk-taking, frequent reassessment of goals and conditions, and a capacity to modify outcomes as conditions change. Considering this iterative process is central to adaptive management (Millar et al., 2007), placing FAM within a climate adaptation framework strengthens the desired outcomes of FAM and reduces the likelihood of unforeseen risks.

FAM and ecosystem function

Much of the historical application of FAM, largely in a non-climate change context, has been within a narrow timber focus in the establishment of plantations of commercially valuable species. By contrast, contemporary applications of FAM, although still likely to account for future commodity outputs, will largely be motivated by objectives of sustaining ecosystem functions, requiring a reframing of how FAM is operationalized. Ecological silviculture systems, which pattern forest management practices on natural models (Palik et al., 2020), is one framework for intentionally moving FAM into wider practice as a means of restoring and maintaining ecosystem services in forests managed for wood given uncertain and changing conditions.

Ecological silviculture emphasizes structural and compositional heterogeneity. Silviculture that generates heterogeneity in environmental conditions, resources, and structure can provide multiple pathways for adaptation to future stressors and disturbances, while also sustaining a wider range of ecosystem services than timber-focused models (Palik et al., 2020). This may also be the key to successful use of FAM. For example, many of the tree species projected to be future-adapted in northeastern North America are intolerant or mid-tolerant of shade (Peters et al., 2020). As such, use of forest management methods aimed at seedling regeneration that emulate ecological processes such as heavy partial canopy disturbances like microbursts or moderate-severity fires may be appropriate for introducing these species into current ecosystems (D'Amato & Palik, 2020). Although future disturbance dynamics in these forests will likely shift with climate change, recognizing the role of these historical recruitment events may enhance FAM success in the near term (cf. D'Amato, Palik, et al., 2018).

As species ranges change with climate conditions, the outcomes may lead to new species assemblages. Similarly, as species transition or decline in their abundance, the repercussions associated with the loss of functional traits may be detrimental to forested ecosystems. Modifications in the functional profile of forests may have broad sweeping consequences on ecosystem function, including changes in carbon dynamics, wildlife, productivity, hydrology, and cultural values. Perhaps most concerning is the potential loss of important or keystone species that possess functional attributes that shape their respective ecosystem (e.g., black ash wetlands, shaded eastern hemlock groves, and longleaf pine [*Pinus palustris* Mill.] woodlands). In these cases, species loss can lead to fundamental shifts in ecosystem function. Therefore, with respect to FAM, special attention may need to be placed on promoting the functional redundancy of forests to ensure ecosystem function is maintained.

CASE STUDIES OF OPERATIONAL-SCALE FAM

In this section, we present some case studies of operational-scale adaptation experiments that incorporate FAM. This is done in the context of providing guidance on how FAM can be used more routinely with applications justified by a desire to manage risk. We highlight three case studies of FAM that were implemented in ways to address and overcome, to varying degrees, the barriers of inexperience, perceptions of risk, and a narrow focus on timber resources. These examples were implemented as part of large, codeveloped, management-inspired projects focused on climate change adaptation and threat reduction. Each is operational in scale and sufficient in scope such that the management organizations involved counted them as part of their targets of annual harvest and planting. They are representative of a range of forest adaptation strategies and are translatable to on-the-ground practices by way of having comprehensive forest management prescriptions that are inclusive of harvesting, site-preparation, regeneration, and intermediate tending activities. We acknowledge that the management entities involved in the case studies likely leveraged research involvement to justify accepting a degree of risk by using FAM that may not be available to all management entities.

The case studies are located in the eastern forest region of the United States. Broadly, this region has been identified as highly vulnerable to climate change and has already experienced significant climate warming over the last century. In particular, this densely forested region is likely subject to changes in tree population- and landscape-level compositional shifts, due to the prevalence of non-native insects and diseases, as well as projected shifts in species habitat associated with climate change (e.g., Janowiak et al., 2014). In fact, declines in suitable tree habitat are forecasted for over 20 species, while a dozen species are expected to benefit from assisted population expansion and up to 20 species would require assisted range expansion to keep pace with habitat shifts (Iverson et al., 2019). For each case study, we summarize the ecological and forest management context, the forest adaptation strategies being used, and how FAM is factored in the treatments to achieve the desired future conditions.

Case Study 1: FAM in red pine forests in northern Minnesota, USA

The iconic Great Lakes pine forest is an important component of the landscape on dryer sites in the western Great Lakes region of North America, including Minnesota, Wisconsin, and Michigan in the United States and southern Ontario in Canada. Broadly dry forests are vulnerable to climate change (Swanston et al., 2018), and pine forests in Minnesota are at risk due to geographic juxtaposition adjacent to prairie to the west.

Red pine (*Pinus resinosa* Ait.) and eastern white pine (*Pinus strobus* L.) are the dominant tree species in these forests, but other species are cumulatively abundant, including balsam fir (*Abies balsamea* [L.] Mill.), white spruce (*Picea glauca* [Moench] Voss), jack pine (*Pinus banksiana* Lamb.), trembling and bigtooth aspen (*Populus tremuloides* Michx. and *P. grandidentata* Michx.), red maple (*Acer rubrum* L.), northern red oak (*Quercus rubra* L.), bur oak (*Quercus macrocarpa* Michx.), and paper birch (*Betula papyrifera* Marsh.). Most species are commercially important for wood and many, including red pine, are at risk from climate change induced growth declines (Bottero et al., 2017) or declines in habitat (Nagel et al., 2017).

Recognizing the urgency to address climate adaptation operationally, managers in the Chippewa National Forest (CNF) in northern Minnesota, USA implemented a 200-ha application of FAM in red pine forests as part of the Adaptive Silviculture for Climate Change (ASCC) network (Box 2; Nagel et al., 2017). The CNF-ASCC installation includes a passive control, along with resistance, resilience, and transition treatments (as described previously); the former two treatments do not include FAM, while the latter two are inclusive of it in different forms (Muller et al., 2019). Tree species choices for FAM were facilitated by discussions at workshops, model predictions (Peters et al., 2020), and native plant and suitability guidelines for the region.

FAM in the resilience treatment involves planting future climate-adapted native species in 0.2-ha canopy gaps, including eastern white pine, northern red oak, bur oak, and red maple. The seed source for eastern white pine is from northeastern Wisconsin, USA, and is blister rust resistant and likely adaptable to future climate, while seed sources for the hardwood species are from approximately 100–200 km south of CNF-ASCC in east-central Minnesota. As all species are native to the ecosystem and region, but genetically distinct from local populations, their inclusion is an example of assisted population expansion.

Transition treatment not only includes assisted population expansion by using the same species as resilience but also includes both assisted range expansion and species migration (Muller et al., 2019). FAM species are planted across entire stands, after a partial-harvest treatment that created spatial variability in microclimate and resources. The additional species in the transition treatment include white oak (*Quercus alba* L.), bitternut hickory (*Carya cordiformis* [Wangenh.] K. Koch), and black cherry (Figure 2). These species have established populations within 120–160 km south of the forest, with outlier populations farther north; thus, inclusion is an example of assisted range expansion. The treatment also includes four seed sources of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) from the most eastern, lowest elevation portions of its range in the western United States. While the species is occasionally planted in northern Minnesota, its nearest established population is 200 km west of the study area. Its use is an example of assisted species migration and reflects stakeholder desire to examine a potential ecological and cultural replacement for red pine.

Early results from the transition treatment show that the survival of assisted population and range expansion species is near 100% (Figure 3). Ponderosa pine

BOX 2 Forest-assisted migration (FAM) in the Adaptive Silviculture for Climate Change (ASCC) network.

The ASCC (www.adaptivesilviculture.org/) provides examples of ecosystem-specific climate-adaptive silviculture, inclusive of resistance, resilience, and transition approaches. The forest management prescriptions were codeveloped for each ASCC site through a partnership of scientists, managers, and stakeholders to align with overarching management goals and real-world policy, social, and operational constraints. Each is of sufficient scale and scope to be operationally relevant and most include FAM in some form.

Here we highlight the role of FAM in four additional ASCC examples, including: (1) mixed conifer forest on Flathead National Forest (FNF), Montana, USA; (2) pine–hardwood woodlands at the Jones Ecological Research Center (JRC), Georgia, USA; (3) high-elevation spruce–fir forests at the Colorado State Forest (CSF), Colorado, USA; and (4) mixed pine–hardwood forests of the Petawawa Research Forest (PRF), Ontario, Canada. Each includes tree regeneration as part of the resilience and transition treatments, often achieved through artificial methods including planting seedlings. The forest management approaches used to promote new tree recruitment emphasize the creation of structural heterogeneity (e.g., harvests that generate complexity among overstory tree sizes and distributions) and microsites for the establishment of a diversity of future climate-adapted tree species.

The FNF utilizes assisted population expansion in both the resilience and transition treatments by planting mid- and high-elevation seed sources of western larch (*Larix occidentalis* Nutt.) and blister rust resistant western white pine (*Pinus monticola* Dougl. ex D. Don). Ponderosa pine, also from mid- and high-elevation seed sources, is utilized in the transition treatment, with this bordering on assisted range expansion since the species is not found at the study site, although the latter is located within its geographic range (Crotteau et al., 2019).

The JRC utilizes assisted population expansion in the transition treatment, focusing on a single species. To transition this pine–hardwood woodland ecosystem, forest harvests reduced the density of longleaf pine and removed mesic oak species. Mesic oaks are replaced with planted turkey oak (*Quescus laevis* Walt.), using seed sources collected from a nearby sandhill ecosystem and selected because of its drought and fire tolerance (Bigelow et al., 2021).

The CSF utilizes assisted population expansion in the transition treatment to favor future-adapted species that tolerate variable environmental conditions and disturbances (e.g., drought, mixed-severity fire, and insects), with emphasis on southern genotypes. Specifically, this site includes Douglas fir in canopy gaps and low density stands, ponderosa pine on drier microsites in canopy gaps, limber pine (*Pinus flexilis* James) and blister rust resistant bristlecone pine (*Pinus longeava* D.K. Bailey) particularly on ridgetops, and blue spruce (*Picea pungens* Engelm.) on wetter microsites within low density stands.

The PRF includes FAM in each adaptation strategy. In the resistance strategy, plantings of eastern white pine from local seed sources are augmented with assisted population expansion plantings from three southern seed sources approximately 200, 500, and 1000 km away. In the resilience strategy, plantings of local eastern white pine, red pine, and northern red oak are augmented with 50% assisted population expansion from southern seed sources. Lastly, the transition treatment includes assisted population expansion of pitch pine (*Pinus rigida* Mill.), northern red oak (southern source), white oak (southern source), and assisted range expansion of species, including American chestnut (*Castenea dentata* [Marsh.] Borkh.).

(assisted species migration) survival was moderate, but where it survives, growth is two to three times that of other species (Muller et al., 2019).

Case Study 2: FAM in black ash wetlands

Forests containing ash (*Fraxinus* L.) in eastern North America are threatened by the EAB (*Agrilus plannipenis* Fairmaire), an insect that feeds on phloem and functionally eliminates ash trees across the region (Herms & McCullough, 2014). Black ash wetlands in northern Minnesota, USA, are particularly at risk from EAB invasion, as the region contains nearly 500,000 ha of black ash wetlands (Youngquist et al., 2017), with a warming winter climate likely lead to increased survival of larvae (Christianson & Venette, 2018).

EAB has created a unique context for FAM in this setting, as black ash often constitutes 70%–95% of overstory trees and plays a central role in regulating ecosystem

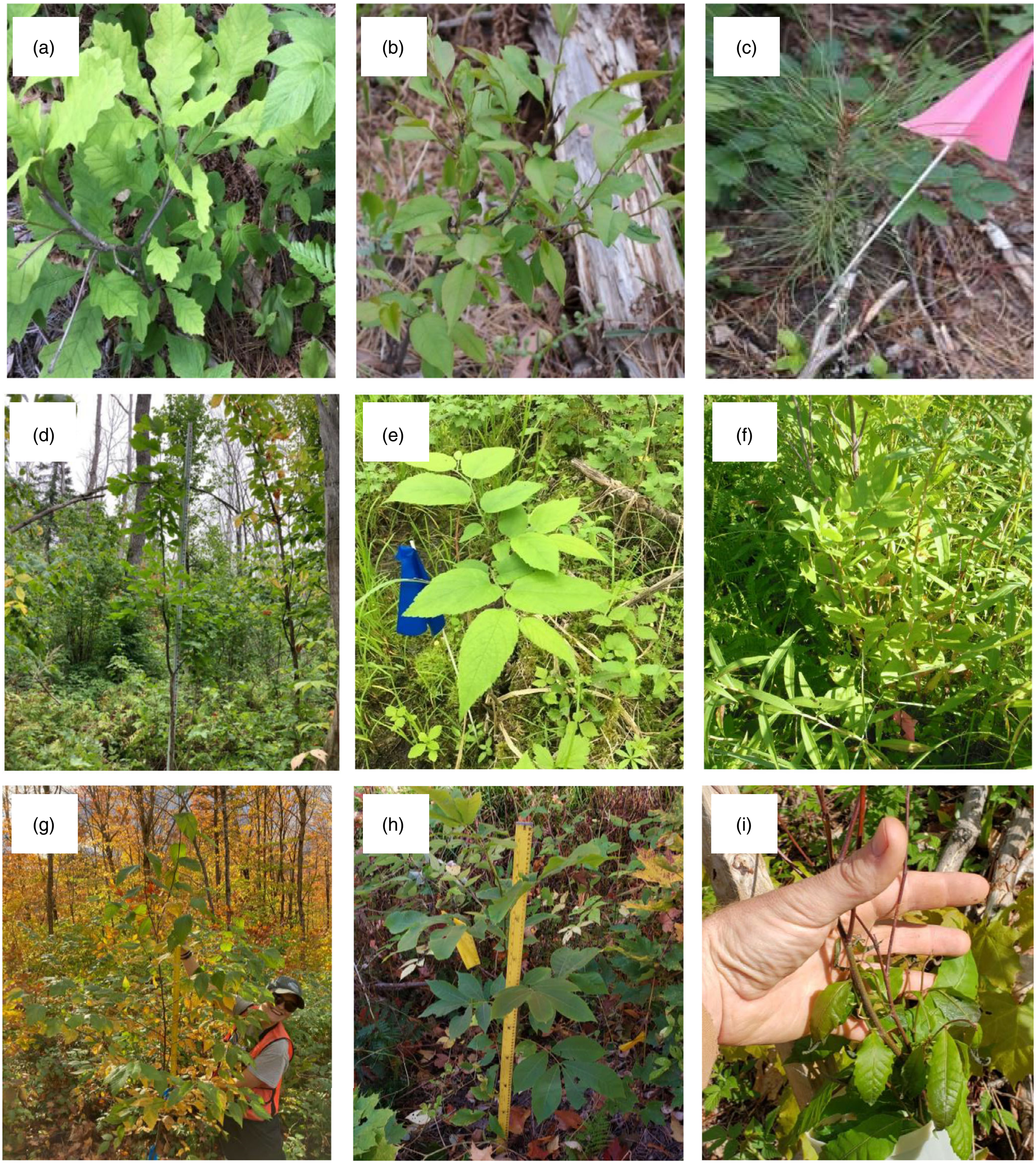

FIGURE 2 Examples of assisted range expansion (RE) and species migration (SM) in the field. Images (a)–(c) are planted in a red pine forest in northern Minnesota, USA, as part of the Chippewa National Forest-Adaptive Silviculture for Climate Change experiment (CNF-ASCC); images (d)–(f) are planted in a black ash dominated wetland in northern Minnesota, USA, as part of the Chippewa National Forest-Emerald Ash Borer experiment (CNF-EAB); images (g)–(i) are planted in northern hardwood and spruce–hardwood mixedwood forests in New England, USA, as part of the Second College Grant-Adaptive Silviculture for Climate Change experiment (SCG-ASCC). Panels (a) white oak (RE), (b) black cherry (RE), (c) ponderosa pine seedling from a Black Hills, South Dakota seed source (SM), (d) 8-year-old swamp white oak (RE), (e) hackberry (RE), (f) Manchurian ash (SM), (g) black birch (RE), (h) bitternut hickory (RE), and (i) American chestnut (RE) exhibiting winter injury maladaptation to extreme cold temperatures.

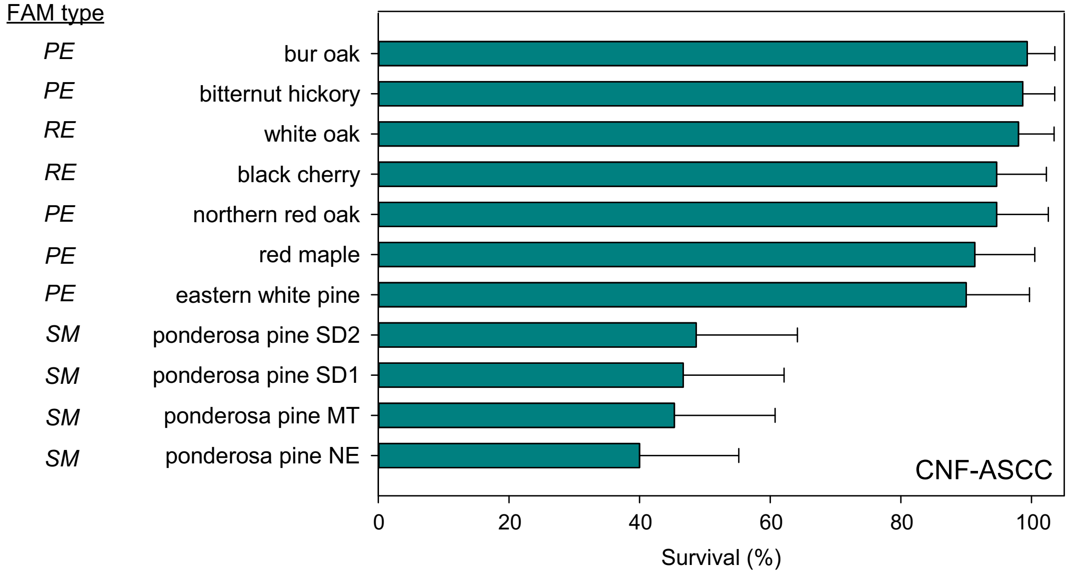

FIGURE 3 Three-year survival of species planted in a Minnesota, USA, pine forest as part of the Chippewa National Forest-Adaptive Silviculture for Climate Change project (CNF-ASCC). Forest-assisted migration (FAM) types include assisted population expansion (PE), assisted range expansion (RE), and assisted species migration (SM). Values are means ± 1 SE (from Muller et al., 2019). Ponderosa pine seed sources are South Dakota (SD1, SD2), Montana (MT), and Nebraska (NE), USA.

function (Youngquist et al., 2017). Forest managers and conservation biologists are increasingly interested in the application of FAM in black ash wetlands to increase the probability of maintaining a forested condition with nonhost species that are also future climate adapted (D'Amato, Palik, et al., 2018).

An operational-scale case study of this is located in the Chippewa National Forest (CNF-EAB) and includes four harvest treatments, including a passive control, the creation of small gaps, total canopy removal, and emulation of EAB through the intentional girdling of all black ash. In treatment of each stand, 12 potential replacement tree species were planted after considering the tolerance of saturated soils and projected future climate adaptability.

Eight species, including red maple, balsam poplar (*Populus balsamifera* L.), eastern cottonwood (*P. deltoides* Bartr. ex Marsh.), trembling aspen, black spruce (*Picea mariana* [Mill.] B. S. P.), eastern larch (*Larix laricina* [Du Roi] K. Koch), northern white cedar (*Thuja occidentalis* L.), and yellow birch (*Betula alleghaniensis* Britton), while native, occur in very low abundance, such that their inclusion was considered to assist population expansion. A hybrid assisted population expansion/range expansion approach was used to introduce Dutch elm disease tolerant American elm (*Ulmus americana* L.), with planting material derived from a cross between the resistant Valley Forge strain and a local tolerant tree. True assisted range expansion was used by introducing swamp white oak (*Quercus bicolor* Willd.) and hackberry (*Celtis occidentalis* L.) (see Figure 2), species whose northern range termini are expected to expand into the area with climate change (Peters et al., 2020). Finally, assisted species migration was used to introduce Manchurian ash (*F. mandshurica* Rupr.), an EAB-resistant Asian species. This species is native to northeastern Asia but is occasionally cultivated as an ornamental in parts of North America. It was selected as a potential ecological replacement for black ash, but also a cultural replacement, as the wood splints derived from annual growth rings of black ash are used for basket making by Indigenous people throughout the Great Lakes region and northeastern North America (Looney et al., 2017).

Selection of some of these species carries a considerable risk of failure since forest managers and conservationists have little experience with artificial regeneration in black ash wetlands. The loss of black ash at these sites can lead to increases in the water table (Slesak et al., 2014), endangering the likelihood of the establishment of future forest and leading to fundamental shifts in ecosystem state (e.g., a transition from forested to persistent non-forested state). The inclusion of species that may serve as functional and cultural replacements to maintain these wetland forests was considered a primary goal. Therefore, their use was justified by the magnitude of threat EAB and climate change pose to the ecosystem and associated cultural values.

To date, the highest levels of survival have been in treatments where at least some residual black ash were retained (unharvested stands, girdled areas, and small gap cutting; Palik et al., 2021). Under these conditions, residual trees likely facilitate new cohort development by ameliorating increases in saturated conditions associated with tree mortality (Slesak et al., 2014). Of the species with highest survival, the majority are those introduced with FAM: American elm, swamp white oak, hackberry, and Manchurian ash (Figure 4).

Case Study 3: FAM in northern hardwoods and mixedwood forests of New England, USA

The mixed deciduous and coniferous forest of northern New England, USA, constitute 10.8 milion ha, of which over two-thirds are held in private ownership (i.e., noncorporate or family forest owners). This mixed species, densely forested region is shaped by a legacy of land use, often resulting in simplified forest composition and structural characteristics. The Second College Grant ASCC site (SCG-ASCC) in New Hampshire encompasses 200 ha and represents the largest replicated, operational-scale experiment of its kind in the northeastern United States. Unlike other ASCC network sites located within fire-dominated systems, the SCG-ASCC is in mesic northern hardwood forests where small canopy gap forming events (e.g., wind, insects, senescence) are the primary ecosystem disturbance. Dominant tree species include sugar maple (*Acer saccharum* Marsh.), yellow birch, and American beech (*Fagus americana* Ehrh.), with lesser components of red maple, red spruce (*Picea rubens* Sarg.), and other species. The primary climate change impacts are expected to result from increasing wind and ice events, moisture stress, native and invasive pests and diseases, and the loss of key species or functional groups. Moreover, this region is expected to experience large shifts in future species assemblages, with many new species requiring assisted migration (Iverson et al., 2019).

The natural disturbance regime in these forests has historically favored shade-tolerant species via small canopy gaps, yet most future climate-adapted species forecasted for this region require higher light conditions (Peters et al., 2020). Therefore, forest management techniques aimed at transitioning composition emphasized the creation of higher light microclimates via canopy gaps (0.1 and 0.4 ha), conditions near the upper limit of historical variability. This strategy aims to facilitate the natural establishment of future-adapted species on site, plus the use of planted FAM. Although not part of the ASCC framework, FAM species were tested in replicate forest sites in Vermont characterized by spruce–fir–northern hardwoods (red spruce, balsam fir, and red maple) and nutrient-rich northern hardwoods (sugar maple and white ash).

Of nine FAM species tested, six were locally present but make up a minor proportion of current forest composition, including northern red oak, eastern white pine, eastern hemlock, black cherry, bigtooth aspen, and red spruce. No attempts were made to obtain specific seed

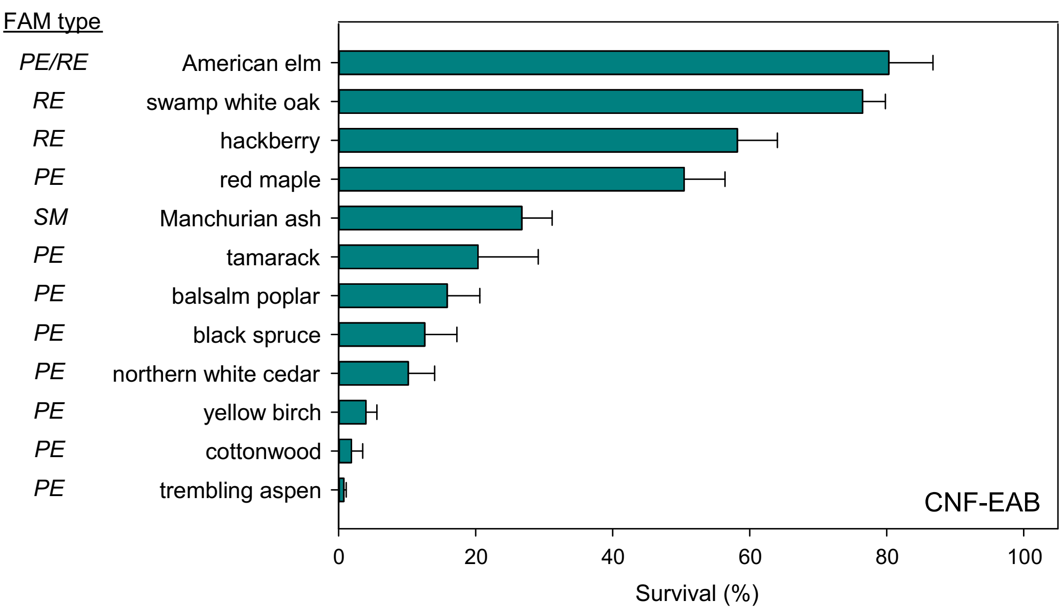

FIGURE 4 Eighth-year survival of species (in a "group-selection" harvest treatment) planted in the Chippewa National Forests to increase the resilience of lowland black ash forests to impacts of emerald ash borer (CNF-EAB) and climate change (Palik et al., 2021). Forest-assisted migration (FAM) types include assisted population expansion (PE), assisted range expansion (RE), and assisted species migration (SM). Values are means ± 1 SE.

sources for these species, although all were from southerly or maritime parent material, and thus are considered assisted population expansion. Additionally, three species not currently on site were tested as an assisted range expansion approach, including bitternut hickory, black birch, and a hybrid American chestnut bred for disease resistance. Species were selected using input from regional natural resource managers and scientists, model projections, and site characteristics. Emphasis was placed on the functional redundancy of traits, such that FAM may functionally replace tree species forecasted to decline (e.g., deep shaded conifers and hard mast producing species). Given the limited number of tree nurseries and inventory, this experiment was unable to control for seed source; however, this lack of control represents the current state of regional nursery capacity, which will likely continue to influence operationalized FAM.

Although differences in survivorship are apparent (Figure 5), one of the primary controls on seedling performance was vegetative competition (Clark et al., 2021). While climate models suggest that many species in this region will require FAM, clear biological barriers still inhibit efforts to transition forest composition. These results were particularly pronounced for assisted range expansion species, which performed poorly relative to assisted population expansion species. Regionally, species response was variable, due to other factors such as drought during planting, browse pressure, species-specific traits, seedling quality, and extreme winter temperatures leading to dieback and maladaptation for some FAM species (see American chestnut; Figure 2i).

Lessons from case studies

Taken together, these operational-scale case studies offer lessons that may clarify the challenges, risks, and opportunities for the routine use of FAM. Overall, we observed no consistent trends in all three case studies in FAM performance (here, seedling survival) between types (assisted population expansion, range expansion, and species migration) among sites (Figure 6). Although examples exist where more locally adapted assisted population expansion plantings performed better than assisted range expansion (e.g., SCG-ASCC), the opposite is also true when novel assisted range expansion species performed similarly (e.g., CNF-ASCC) or better (e.g., CNF-EAB). These results not only demonstrate the viability of FAM in climate adaptation planning, but also illustrate how climate adaptive FAM may resolve the challenges of forester inexperience, perceptions of risk, and ability to maintain ecosystem function. Although barriers remain for the routine use of assisted species migration, its incorporation will likely become increasingly warranted, especially in cases where ecosystem function is at risk.

A central dictum of uncertain climate futures is that no singular approach will meet the needs of all scenarios (Millar et al., 2007). Therefore, a toolbox approach that utilizes a combination of options for adaptation may be the most effective approach. In terms of FAM, this may mean that more conservative approaches that promote ecosystem resistance or resilience may employ assisted population expansion or in some instances range expansion from nearby species. As the risk profile of global forests continues to increase and undesirable thresholds are reached, actions to transition ecosystems that employ longer distance transfers of assisted range expansions, or under select circumstances, assisted species migration, will become increasingly warranted. In the case studies detailed above, various types of FAM were incorporated into each forest aimed at various climate scenarios, both near and longer term. This approach recognizes that one size may not fit all and that trade-offs may exist with increasing transfer distance. Simultaneously, this approach acknowledges that uncertainties remain in favoring FAM based on current climate conditions (assisted population expansion) versus more extreme shifts under future conditions (assisted range expansion).

Despite the challenges of FAM, best practices and tools exist, which may be built upon to increase favorable outcomes (e.g., seed transfer guidelines, model projections, and the Target Plant Concept). Still, the novelty of FAM may not match previous knowledge, such that a flexible and adaptive approach may be better suited for practice. To further integrate the principles learned from our review and generated from the case studies, we have developed a conceptual framework for operationalizing FAM (Figure 7). This framework is suitable as a standalone adaptive management cycle or can be nested within a climate adaptation process such as the Adaptation Workbook (Swanston et al., 2016) or other planning processes (Cross et al., 2012; Stein et al., 2014). The purpose of this is to provide a flexible foundation to help forest managers, conservation biologists, and decision-makers engage with tools and strategies needed to make informed decisions to effectively operationalize FAM. When used within a broader adaptation planning process, it provides prompts for deeper consideration, when FAM has been identified as a potential adaptation action. Essentially, this process revolves around (1) planning for uncertainty by considering how the use of FAM within the climate adaptive strategies of resistance, resilience, and transition may support management goals, (2) assessing the specific application of FAM within a

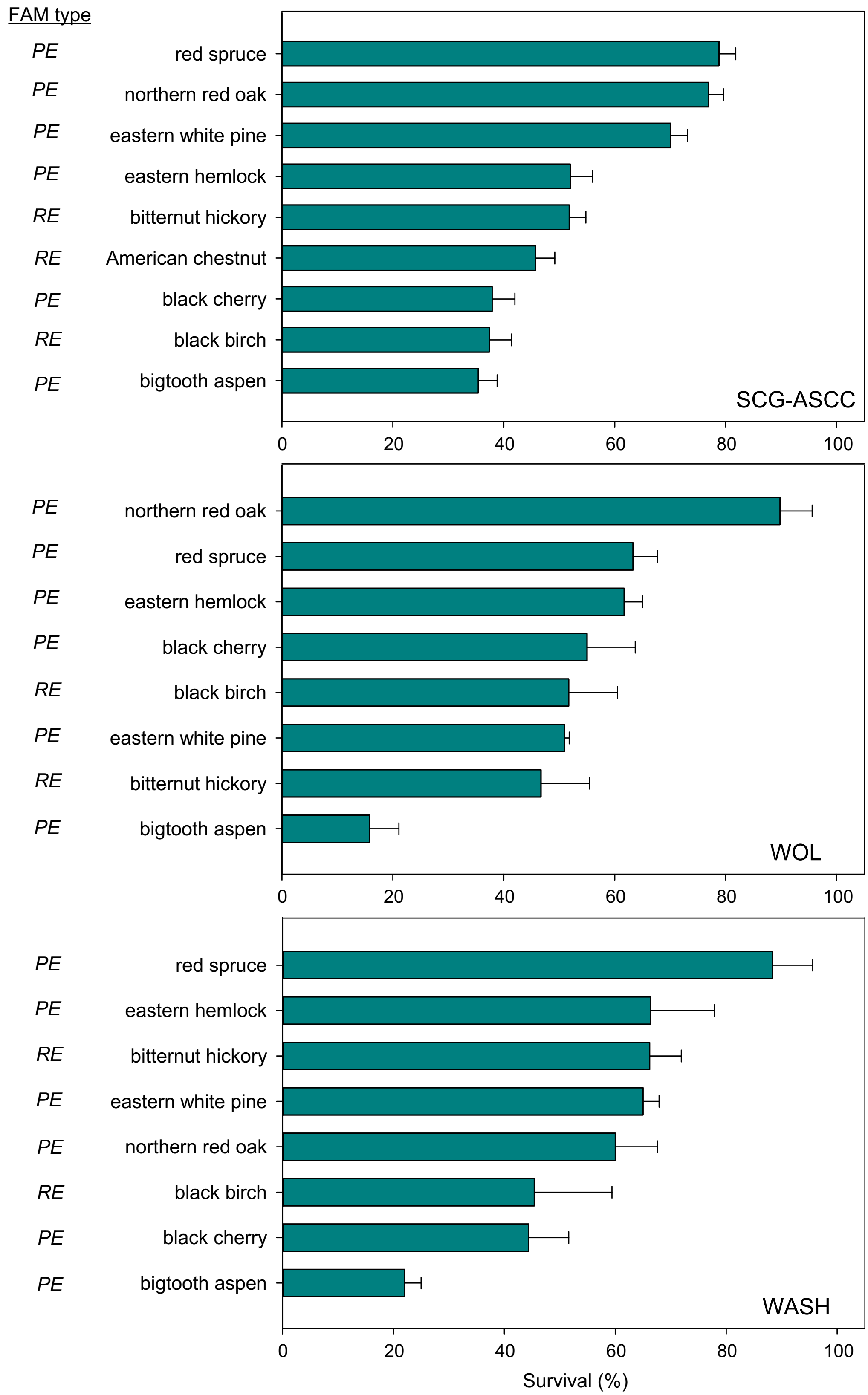

FIGURE 5 Four-year survival of species planted in gaps (0.1 and 0.4 ha, combined results) to transition the composition of three forest types in New England, USA, to future conditions. The northern hardwood site is located on the Second College Grant (SCG), NH as part of the Adaptive Silviculture for Climate Change (ASCC) (Clark et al., 2021). Additional forest-assisted migration (FAM) replicates include a spruce–fir–northern hardwood forest in Wolcott, VT (WOL) and a rich northern hardwoods forest in Washington, VT (WASH), USA. FAM types include assisted population expansion (PE) and assisted range expansion (RE). Values are means ± 1 SE (unpublished data).

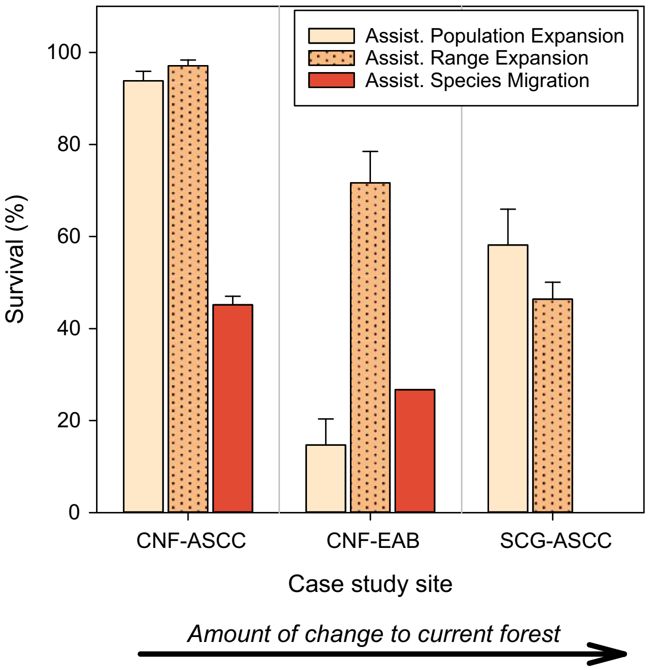

FIGURE 6 Survivorship for each case study site presented by forest-assisted migration (FAM) type: Chippewa National Forest-Adaptive Silviculture for Climate Change experiment (CNF-ASCC); Chippewa National Forest-emerald ash borer experiment (CNF-EAB); and Second College Grant-Adaptive Silviculture for Climate Change experiment (SCG-ASCC). Values are means ± 1 SE.

forested landscape by localizing threats and desired future conditions, (3) implementation of best available practices while maintaining contingency, (4) monitoring and adaptively responding to FAM outcomes, and (5) a process of sharing and reporting to reduce uncertainties and knowledge transfer for routine use of FAM. By employing FAM within this adaptation framework, the case studies presented are examples of successfully overcoming barriers of experience, risk, and practice employed within an ecosystem context to actualize FAM at operational scales.

ADVANCING OPERATIONAL FAM

Routine use of FAM at operational scales is beginning to gain momentum. The slow trend toward operationalizing FAM is in contrast to the more rapid advancement and promotion of climate change adaptation approaches in general (Swanston et al., 2016). But, as we have pointed out, the two are intimately linked—FAM is an integral component of several adaptation approaches. Hesitancy to engage in FAM operationally reflects constraints, uncertainty about the practice, and unwillingness to assume the risk of failure. Other factors that may contribute include limited nursery capacity, difficulty prioritizing budgets to facilitate FAM, and policy constraints on its use.

We have outlined approaches to minimize risk of failure through an adaptation framework, which contain a range of adaptation strategies that incorporate FAM to varying degrees. These include (1) a resistance strategy, which largely defers consideration of regeneration and compositional shifts, including FAM, to a future date, (2) a resilience strategy, which may include an assisted population expansion, and (3) a transition strategy, which may incorporate multiple forms of FAM, including assisted range expansion and occasionally assisted species migration. Although the latter presents considerable challenges to conservation theory, value perceptions, and barriers under policy, we have shown its application under limited circumstances to be warranted. Forest managers and conservation biologists pursuing adaptation strategies can vary the level of risk depending on project objectives, forest conditions, and stakeholder concerns. Moreover, as they become more experienced with FAM, their willingness to assume some risk is likely to increase.

Despite some constraints, an increasing number of organizations are adjusting guidelines and tools to allow or encourage the use of FAM. For instance, some seed use guidelines, which historically dictated that seed sources come from locally defined collection zones, have been updated to integrate climate change scenarios allowing for FAM to be incorporated into selections (e.g., http://easternseedzones.com/; Pike et al., 2020). Additionally, the United States Department of Agriculture (USDA) Forest Service has tools to help managers with seed source selection in the context of climate change (www.seedlotselectiontool.org). Concurrently, the province of British Columbia's (Canada) Ministry of Forests adopted a Climate Based Seed Transfer approach that matches the climate and latitude of a seed source with near-future climate of the planting location (www.gov.bc.ca/climatebasedseedtransfer; O'Neill et al., 2017). Adoption of such tools and policy will reduce barriers for FAM; as such, organizational-level policy that clearly outlines expectations and guidelines is likely needed if FAM is to become routinely operational.

Another practical constraint to widespread operational-scale FAM is lack of capacity by nurseries to produce sufficient numbers of seedlings from various species and genotypes, especially for those species not traditionally grown for commercial purposes (Fargione et al., 2021; Whittet et al., 2016). While there are many nurseries that supply forest management organizations and companies with seedlings, these may in fact be produced using seed that the latter supply from their own seed orchards or suppliers. In the short term, these sources may be hard pressed to acquire sufficient seed

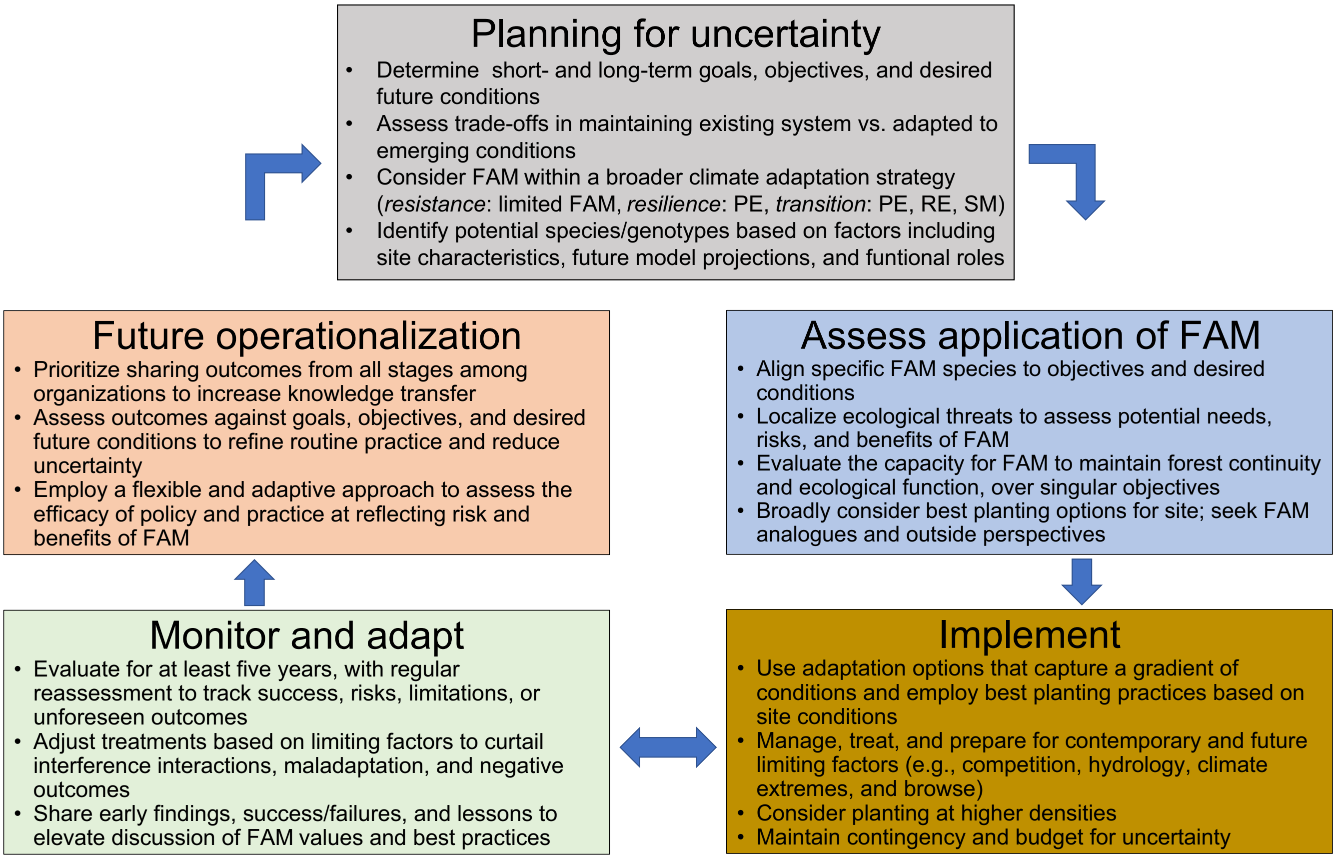

FIGURE 7 Conceptual framework for operationalized forest-assisted migration (FAM), developed with practitioners in mind and suitable as a standalone adaptive management cycle or nested within a climate adaptation process such as the Adaptation Workbook. PE, assisted population expansion; RE, assisted range expansion; SM, assisted species migration.

from desired seed zones and species, oftentimes relying on wild collections of unknown genetics. Therefore, it is likely that suppliers will be unable to accommodate requests for various species and genotypes desired for FAM in large enough numbers to meet demand.

In the end, significant strides forward in advancing operational-scale FAM will only occur once management organizations and agencies take steps to remove institutional barriers to the practice. Moreover, training of personnel in the fundamentals of FAM, within the context of climate change adaptation approaches and risk management, will increase technical proficiency. Forest managers who choose to budget and implement FAM within their project areas would ideally receive continued technical support as a follow-up to this training. A few principles that may be helpful while prioritizing and communicating the use of FAM are outlined in Box 3. Finally, at the organizational level, FAM can be advanced to operational scales by dedicating funding to the practice as clearly delineated components of reforestation budgets.

CONSERVATION, MANAGEMENT, AND POLICY IMPLICATIONS

Conservation and forest management approaches for adapting forests to anticipated climate change impacts are increasingly being discussed and implemented. FAM of novel genotypes and species of trees is likely to be an important component of some adaptation strategies in order to sustain ecosystem functions including hydrology, tree productivity, carbon storage, and wildlife habitat. The pursuit of FAM is timely, especially as the risk to many forests increases or has already changed such that investments to maintain existing ecosystems may pose a higher risk than shifting to non-native or nonlocal species better adapted to emerging conditions. Employing FAM within an adaptation framework like the one presented here will improve knowledge transfer and reduce uncertainty for routine use. Additionally, achieving routine operational-scale use of FAM in managed forests depends on (1) continued training of forest managers, conservationists, and ecologists in use of climate change adaptation approaches, (2) willingness to

BOX 3 A checklist for prioritization and communication of operational forest-assisted migration (FAM).

1. Consider FAM within the context of silvicultural approaches aimed at climate adaptation, including resistance, resilience, and transition approaches. Depending on the approach, FAM will have more or less relevance.
2. Take an ecosystem perspective when considering FAM; ecosystem function in addition to timber production needs to be sustained. Considerations for wildlife habitat, watershed function, carbon storage, and so forth, are increasingly important in the discussion.
3. When undertaking FAM, consider the use of native, future climate-adapted species first. Depending on the forest type, there likely will be one or more native species that are predicted to have stable or increased habitat suitability.
4. Be aware of the potential for complex interactions among climate change, tree species, and forest pests. Climate change may be contributing to unique pest behavior, necessitating the establishment of nonhost species, even if the host species itself is not directly being impacted by climate change.
5. Ultimately, establishment of novel tree species may be required to maintain ecosystem functions and meet societal expectations in the future. Still, foresters should be pragmatic in their choice of species to translocate. First, consider species with nearby outlier populations and avoid large latitudinal shifts.

assume some risk of failure in the near term due to maladaptation, and (3) adopting an ecosystem focus for management that is not dependent on any particular tree species.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Palik et al., 2022) used to derive Figures 3–6 are available from Figshare: https://doi.org/10.6084/m9.figshare.20085296.v1.

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REFERENCES

Abrams, M. D., and G. J. Nowacki. 2008. "Native Americans as Active and Passive Promoters of Mast and Fruit Trees in the Eastern USA." *Holocene* 18: 1123–37. https://doi.org/10.1177/0959683608095581.

Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. "Adaptation, Migration or Extirpation: Climate Change Outcomes for Tree Populations." *Evolutionary Applications* 1: 95–111.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, and N. Cobb. 2010. "A Global Overview of Drought and Heat-Induced Tree Mortality Reveals Emerging Climate Change Risks for Forest." *Forest Ecology and Management* 259: 660–84.

Aubin, I., C. M. Garbe, S. Colombo, C. R. Drever, D. W. Mckenney, C. Messier, J. Pedlar, and M. A. Saner. 2011. "Why We Disagree about Assisted Migration: Ethical Implications of a Key Debate Regarding the Future of Canada's Forests." *The Forestry Chronicle* 87: 755–65.

Bentz, B. J., J. Rgnire, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negron, and S. J. Seybold. 2010. "Climate Change and Bark Beetles of the Western United States and Canada: Direct and Indirect Effects." *Bioscience* 60: 602–13. https://doi.org/10.1525/bio.2010.60.8.6.

Bigelow, S. W., C. E. Looney, and J. B. Cannon. 2021. "Hurricane Effects on Climate-Adaptive Silviculture Treatments to Longleaf Pine Woodland in Southwestern Georgia, USA." *Forestry: An International Journal of Forest Research* 94: 395–406. https://doi.org/10.1093/forestry/cpaa042.

Bottero, A., A. W. D'Amato, B. J. Palik, J. B. Bradford, S. Fraver, M. A. Battaglia, and L. A. Asherin. 2017. "Density-Dependent Vulnerability of Forest Ecosystems to Drought." *Journal of Applied Ecology* 54: 1605–14. https://doi.org/10.1111/1365-2664.12847.

Brandt, L., A. Derby Lewis, R. Fahey, L. Scott, L. Darling, and C. Swanston. 2016. "A Framework for Adapting Urban Forests to Climate Change." *Environmental Science and Policy* 66: 393–402. https://doi.org/10.1016/j.envsci.2016.06.005.

Christianson, L. D. E., and R. C. Venette. 2018. "Modest Effects of Host on the Cold Hardiness of Emerald Ash Borer." *Forests* 9: 1–15. https://doi.org/10.3390/f9060346.

Clark, P., A. W. D'Amato, K. S. Evans, P. G. Schaberg, and C. W. Woodall. 2021. "Ecological Memory and Regional Context Influence Performance of Adaptation Plantings in Northeastern US Temperate Forests." *Journal of Applied Ecology* 59: 314–29. https://doi.org/10.1111/1365-2664.14056.

Cross, M. S., E. S. Zavaleta, D. Bachelet, M. L. Brooks, C. A. F. Enquist, E. Fleishman, L. J. Graumlich, et al. 2012. "The Adaptation for Conservation Targets (ACT) Framework: A Tool for Incorporating Climate Change into Natural Resource Management." *Environmental Management* 50: 341–51. https://doi.org/10.1007/s00267-012-9893-7.

Crotteau, J. S., E. K. Sutherland, T. B. Jain, D. K. Wright, M. M. Jenkins, C. R. Keyes, and L. M. Nagel. 2019. "Initiating Climate Adaptation in a Western Larch Forest." *Forest Science* 65: 528–36. https://doi.org/10.1093/forsci/fxz024.

D'Amato, A. W., E. J. Jokela, K. L. O'Hara, and J. N. Long. 2018. "Silviculture in the United States: An Amazing Period of Change over the Past 30 Years." *Journal of Forestry* 116: 55–67. https://doi.org/10.5849/jof-2016-035.

D'Amato, A. W., and B. J. Palik. 2020. "Building on the Last "New" Thing: Exploring the Compatibility of Ecological and Adaptation Silviculture." *Canadian Journal of Forest Research* 51: 172–80. https://doi.org/10.1139/cjfr-2020-0306.

D'Amato, A. W., B. J. Palik, R. A. Slesak, G. Edge, C. Matula, and D. R. Bronson. 2018. "Evaluating Adaptive Management Options for Black Ash Forests in the Face of Emerald Ash Borer Invasion." *Forests* 9: 348. https://doi.org/10.3390/f9060348.

Dumroese, K. R., T. D. Landis, J. R. Pinto, D. L. Haase, K. W. Wilkinson, A. S. Davis, T. Alberg, J. Beck, and S. Grossnickle. 2016. "Meeting Forest Restoration Challenges: Using the Target Plant Concept." *Reforesta* 1: 37–52.

Dumroese, R. K., T. D. Landis, J. P. Barnett, and F. Burch. 2005. "Forest Service Nurseries: 100 Years of Ecosystem Restoration." *Journal of Forestry* 103: 241–7. https://doi.org/10.1093/jof/103.5.241.

Dumroese, R. K., M. I. Williams, J. A. Stanturf, and J. B. S. Clair. 2015. "Considerations for Restoring Temperate Forests of Tomorrow: Forest Restoration, Assisted Migration, and Bioengineering." *New Forests* 46: 947–64. https://doi.org/10.1007/s11056-015-9504-6.

Duveneck, M. J., and R. M. Scheller. 2015. "Climate-Suitable Planting as a Strategy for Maintaining Forest Productivity and Functional Diversity." *Ecological Applications* 25: 1653–68.

Etterson, J. R., M. W. Cornett, M. A. White, and L. C. Kavajecz. 2020. "Assisted Migration across Fixed Seed Zones Detects Adaptation Lags in Two Major North American Tree Species." *Ecological Applications* 30: 1–20.

Fargione, J., D. L. Haase, O. T. Burney, O. A. Kildisheva, G. Edge, S. C. Cook-Patton, T. Chapman, et al. 2021. "Challenges to the Reforestation Pipeline in the United States." *Frontiers in Forests and Global Change* 4: 629198.

Findlater, K., S. Hagerman, R. Zozak, and V. Gukova. 2021. "Redefining Climate Change Maladaptation Using a Values-Based Approach in Forests." *People and Nature* 4: 231–42. https://doi.org/10.1002/pan3.10278.

Gray, L. K., and A. Hamann. 2013. "Tracking Suitable Habitat for Tree Populations under Climate Change in Western North America." *Climatic Change* 117: 289–303. https://doi.org/10.1007/s10584-012-0548-8.

Haase, D. L., C. Pike, S. Enebak, L. Mackey, Z. Ma, C. Silva, and J. Warren. 2021. "Forest Nursery Seedling Production in the United States—Fiscal Year 2020." *Tree Planter's Notes* 64: 108–14.

Herms, D. A., and D. G. McCullough. 2014. "Emerald Ash Borer Invasion of North America: History, Biology, Ecology, Impacts, and Management." *Annual Review of Entomology* 59: 13–30. https://doi.org/10.1146/annurev-ento-011613-162051.

Iverson, L. R., A. M. Prasad, M. P. Peters, and S. N. Matthews. 2019. "Facilitating Adaptive Forest Management under Climate Change: A Spatially Specific Synthesis of 125 Species for Habitat Changes and Assisted Migration over the Eastern United States." *Forests* 10: 989.

Janowiak, M. K., C. W. Swanston, L. M. Nagel, L. A. Brandt, P. R. Butler, S. D. Handler, P. Danielle Shannon, et al. 2014. "A Practical Approach for Translating Climate Change Adaptation Principles into Forest Management Actions." *Journal of Forestry* 112: 424–33. https://doi.org/10.5849/jof.13-094.

Karasov-Olson, A., M. W. Schwartz, S. A. Skikne, J. J. Hellmann, J. D. Olden, D. J. Lawrence, J. T. Morisette, et al. 2021. "Co-Development of a Risk Assessment Strategy for Managed Relocation." *Ecological Solutions and Evidence* 2: e12092.

Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. "Mountain Pine Beetle and Forest Carbon Feedback to Climate Change." *Nature* 452: 987–90. https://doi.org/10.1038/nature06777.

LeDee, O. E., S. D. Handler, C. L. Hoving, C. W. Swanston, and B. Zuckerberg. 2021. "Preparing Wildlife for Climate Change: How Far Have We Come?" *The Journal of Wildlife Management* 85: 7–16.

Leech, S. M., P. L. Almuedo, and G. O. Neill. 2011. "Assisted Migration: Adapting Forest Management to a Changing Climate." *BC Journal of Ecosystems and Management* 12: 18–34.

Looney, C. E., A. W. D'Amato, B. J. Palik, and R. A. Slesak. 2017. "Overstory Treatment Influences Growth of Replacement Tree Species in *Fraxinus nigra* Forests Threatened by the Emerald Ash Borer in Minnesota, USA." *Canadian Journal of Forest Research* 47: 183–92. https://doi.org/10.1139/cjfr-2016-0369.

Mawdsley, J. R., R. O'Malley, and D. S. Ojima. 2009. "A Review of Climate-Change Adaptation Strategies for Wildlife Management and Biodiversity Conservation." *Conservation Biology* 23: 1080–9. https://doi.org/10.1111/j.1523-1739.2009.01264.x.

McGann, T. 2022. "Climate Adaptive Forest Management in the Northeastern US: Social and Ecological Motivations, Barriers, and Responses of Rural and Urban Foresters." Graduate College Dissertations and Theses, University of Vermont. https://scholarworks.uvm.edu/graddis/1562.

McKenney, D., J. Pedlar, and G. O'Neill. 2009. "Climate Change and Forest Seed Zones: Past Trends, Future Prospects and

Challenges to Ponder." *Forestry Chronicle* 85: 258–66. https://doi.org/10.5558/tfc85258-2.

McLachlan, J. S., J. J. Hellmann, and M. W. Schwartz. 2007. "A Framework for Debate of Assisted Migration in an Era of Climate Change." *Conservation Biology* 21: 297–302. https://doi.org/10.1111/j.1523-1739.2007.00676.x.

McLane, S. C., and S. N. Aitken. 2012. "Whitebark Pine (*Pinus albicaulis*) Assisted Migration Potential: Testing Establishment North of the Species Range." *Ecological Applications* 22: 142–53. https://doi.org/10.1890/11-0329.1.

Millar, C. I., N. Stephens, and S. Stephenson. 2007. "Climate Change and Forests of the Future: Managing in the Face of Uncertainty." *Ecological Applications* 17: 2145–51.

Muller, J. J., L. M. Nagel, and B. J. Palik. 2019. "Forest Adaptation Strategies Aimed at Climate Change: Assessing the Performance of Future Climate-Adapted Tree Species in a Northern Minnesota Pine Ecosystem." *Forest Ecology and Management* 451: 117539.

Nagel, L. M., B. J. Palik, M. A. Battaglia, A. W. D'Amato, J. M. Guldin, C. W. Swanston, M. K. Janowiak, et al. 2017. "Adaptive Silviculture for Climate Change: A National Experiment in Manager-Scientist Partnerships to Apply an Adaptation Framework." *Journal of Forestry* 115: 167–78.

NASF. 2016. "National Survey of State Operated Tree Seedling Nurseries and Tree Improvement Programs." https://www.stateforesters.org/newsroom/nursery-and-tree-improvement-program-survey/.

Neff, M. W., and B. M. H. Larson. 2014. "Scientists, Managers, and Assisted Colonization: Four Contrasting Perspectives Entangle Science and Policy." *Biological Conservation* 172: 1–7. https://doi.org/10.1016/j.biocon.2014.02.001.

O'Neill, G., T. Wang, N. Ukrainetz, L. Charleson, L. McAuley, A. Yanchuk, and S. Zedel. 2017. "A Proposed Climate-Based Seed Transfer System for British Columbia." Technical Report, Ministry of Forests and Range. https://www.for.gov.bc.ca/hfd/pubs/docs/TR/TR099.pdf.

Ontl, T. A., M. K. Janowiak, C. W. Swanston, J. Daley, S. Handler, M. Cornett, S. Hagenbuch, C. Handrick, L. McCarthy, and N. Patch. 2020. "Forest Management for Carbon Sequestration and Climate Adaptation." *Journal of Forestry* 118: 86–101. https://doi.org/10.1093/jofore/fvz062.

Ontl, T. A., C. Swanston, L. A. Brandt, P. R. Butler, A. W. D'Amato, S. D. Handler, M. K. Janowiak, and P. D. Shannon. 2018. "Adaptation Pathways: Ecoregion and Land Ownership Influences on Climate Adaptation Decision-Making in Forest Management." *Climatic Change* 146: 75–88. https://doi.org/10.1007/s10584-017-1983-3.

Palik, B. J., P. W. Clark, and A. W. D'Amato. 2022. "Planted Seedling Survival Data from Three Climate Adaptation and Assisted Migration Experiments in the Eastern USA." Figshare. Dataset. https://doi.org/10.6084/m9.figshare.20085296.v1.

Palik, B. J., A. W. D'Amato, J. F. Franklin, and K. N. Johnson. 2020. *Ecological Silviculture: Foundations and Applications*. Long Grove, IL: Waveland Press, Inc.

Palik, B. J., A. W. D'Amato, R. A. Slesak, D. Kastendick, C. Looney, and J. Kragthorpe. 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. https://doi.org/10.1016/j.foreco.2021.118958.

Park, A., and C. Talbot. 2018. "Information Underload: Ecological Complexity, Incomplete Knowledge, and Data Deficits Create Challenges for the Assisted Migration of Forest Trees." *Bioscience* 68: 251–63.

Pedlar, J. H., D. W. M. Kenney, I. Aubin, T. Beardmore, J. Beaulieu, L. Iverson, G. A. O. Neill, R. S. Winder, and C. Ste-marie. 2012. "Placing Forestry in the Assisted Migration Debate." *Bioscience* 62: 835–42.

Peters, M. P., A. M. Prasad, S. N. Matthews, and L. R. Iverson. 2020. *Climate Change Tree Atlas (Version 4)*. Delaware, OH: USFS, NRS & NIACS. https://www.nrs.fs.fed.us/atlas.

Peterson St-Laurent, G., L. E. Oakes, M. Cross, and S. Hagerman. 2021. "R–R–T (Resistance–Resilience–Transformation) Typology Reveals Differential Conservation Approaches across Ecosystems and Time." *Communications Biology* 4: 1–9.

Pike, C., K. M. Potter, P. Berrang, B. Crane, J. Baggs, L. Leites, and T. Luther. 2020. "New Seed-Collection Zones for the Eastern United States: The Eastern Seed Zone Forum." *Journal of Forestry* 118: 444–51. https://doi.org/10.1093/jofore/fvaa013.

Ricciardi, A., and D. Simberloff. 2009. "Assisted Colonization Is Not a Viable Conservation Strategy." *Trends in Ecology and Evolution* 24: 248–53. https://doi.org/10.1016/j.tree.2008.12.006.

Rissman, A. R., K. D. Burke, H. A. C. Kramer, V. C. Radeloff, P. R. Schilke, O. A. Selles, R. H. Toczydlowski, et al. 2018. "Forest Management for Novelty, Persistence, and Restoration Influenced by Policy and Society." *Frontiers in Ecology and the Environment* 16: 454–62. https://doi.org/10.1002/fee.1818.

Ritter, C. 2020. "The Ecological Value of Spruce Plantations in Massachusetts." Masters Theses 904, University Massachusetts. https://doi.org/10.7275/17383805.

Schmidtling, R. C. 2001. "Southern Pine Seed Sources." General Technical Report SRS-44. http://www.srs.fs.usda.gov/pubs/2797.

Schmitt, K. M., T. A. Ontl, S. D. Handler, M. K. Janowiak, L. A. Brandt, P. R. Butler-Leopold, P. D. Shannon, C. L. Peterson, and C. W. Swanston. 2021. "Beyond Planning Tools: Experiential Learning in Climate Adaptation Planning and Practices." *Climate* 9: 1–16. https://doi.org/10.3390/cli9050076.

Schoettle, A. W., and R. A. Sniezko. 2007. "Proactive Intervention to Sustain High-Elevation Pine Ecosystems Threatened by White Pine Blister Rust." *Journal of Forest Research* 12: 327–36. https://doi.org/10.1007/s10310-007-0024-x.

Schuurman, G. W., C. H. Hoffman, D. N. Cole, D. J. Lawrence, J. M. Morton, D. R. Magness, A. E. Cravens, S. Covington, R. O'Malley, and N. A. Fisichelli. 2020. "Resist-Accept-Direct (RAD)—A Framework for the 21st-Century Natural Resource Manager (No. 2020/2213)." USDI National Park Service.

Shannon, P. D., C. W. Swanston, M. K. Janowiak, S. D. Handler, K. M. Schmitt, L. A. Brandt, P. R. Butler-Leopold, and T. Ontl. 2019. "Adaptation Strategies and Approaches for Forested Watersheds." *Climate Services* 13: 51–64. https://doi.org/10.1016/j.cliser.2019.01.005.

Slesak, R. A., C. F. Lenhart, K. N. Brooks, A. W. D'Amato, and B. J. Palik. 2014. "Water Table Response to Harvesting and Simulated Emerald Ash Borer Mortality in Black Ash Wetlands in Minnesota, USA." *Canadian Journal of Forest Research* 44: 961–8. https://doi.org/10.1139/cjfr-2014-0111.

Starfinger, U., I. Kowarik, M. Rode, and H. Schepker. 2003. "From Desirable Ornamental Plant to Pest to Accepted Addition to the Flora? – The Perception of an Alien Tree Species through the Centuries." *Biological Invasions* 5: 323–35. https://doi.org/10.1023/B:BINV.0000005573.14800.07.

Stein, B. A., P. Glick, N. Edelson, and A. Staudt. 2014. *Climate-Smart Conservation: Putting Adaption Principles into Practice*. Washington, DC: National Wildlife Federation.

Swanston, C., L. A. Brandt, M. K. Janowiak, S. D. Handler, P. Butler-Leopold, L. Iverson, F. R. Thompson, T. A. Ontl, and P. D. Shannon. 2018. "Vulnerability of Forests of the Midwest and Northeast United States to Climate Change." *Climatic Change* 146: 103–16. https://doi.org/10.1007/s10584-017-2065-2.

Swanston, C., M. Janowiak, L. A. Brandt, P. R. Butler, S. D. Handler, P. D. Shannon, A. D. Lewis, et al. 2016. *Forest Adaptation Resources: Climate Change Tools and Approaches for Land Managers*, 2nd ed. Washington, DC: USDA Forest Service, General Technical Report NRS-87-2.

Tribal Adaptation Menu Team. 2019. *Dibaginjigaadeg Anishinaabe Ezhitwaad: A Tribal Climate Adaptation Menu*. Odanah, WI: Great Lakes Indian Fish and Wildlife Commission. 54 pp.

Whittet, R., S. Cavers, R. Ennos, and J. Cottrell. 2019. "Genetic Considerations for Provenance Choice of Native Trees under Climate Change in England." Forestry Commission Research Report (Issue March).

Whittet, R., J. Cottrell, S. Cavers, M. Pecurul, and R. Ennos. 2016. "Supplying Trees in an Era of Environmental Uncertainty: Identifying Challenges Faced by the Forest Nursery Sector in Great Britain." *Land Use Policy* 58: 415–26. https://doi.org/10.1016/j.landusepol.2016.07.027.

Williams, M., and K. Dumroese. 2013. "Preparing for Climate Change: Forestry and Assisted Migration." *Journal of Forestry* 111: 287–97.

Young, D. J. N., T. D. Blush, M. Landram, J. W. Wright, A. M. Latimer, and H. D. Safford. 2020. "Assisted Gene Flow in the Context of Large-Scale Forest Management in California, USA." *Ecosphere* 11: 03001. https://doi.org/10.1002/ecs2.3001.

Youngquist, M. B., S. L. Eggert, A. W. D'Amato, B. J. Palik, and R. A. Slesak. 2017. "Potential Effects of Foundation Species Loss on Wetland Communities: A Case Study of Black Ash Wetlands Threatened by Emerald Ash Borer." *Wetlands* 37: 787–99. https://doi.org/10.1007/s13157-017-0908-2.

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