

Perspective

Desired REgeneration through Assisted Migration (DREAM): Implementing a research framework for climate-adaptive silviculture

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ABSTRACT

Global change is reshaping climatic conditions at a tempo that exceeds natural migration rates for most tree species. As climate change amplifies the disparity between species' adaptive capacity and local climates, tree populations risk becoming geographically stranded in increasingly unsuitable conditions. This mismatch may cause catastrophic losses of key forest ecosystem services such as carbon sequestration, habitat provisioning, and forest products. In response, forest managers and researchers are developing a suite of climate-adaptive strategies designed to sustain forest diversity and function. Among these, forest assisted migration (FAM) involves the movement of planting stock from source populations to locations either within or beyond their current ranges. The goal is to establish forests that can survive in today's climate and expected to thrive in future conditions, thereby sustaining ecosystem goods and services. Because FAM is still in its infancy, implementation is limited by many uncertainties. Climatically derived seed sourcing is needed to ensure that planting stock possesses the ecophysiological amplitude to withstand both current and future climatic conditions at the destination site. Additionally, more knowledge about the impacts of local herbivores and intraspecific competition are needed because these drivers will co-regulate seedling success along with climate. Practically, these uncertainties must be addressed to instill in managers sufficient confidence that FAM investments will fulfill long-term management and societal goals relative to other silvicultural approaches.

The Desired REgeneration through Assisted Migration (DREAM) framework is an international collaboration that uses basic and applied research to reduce these uncertainties and derive climate-informed planting approaches. DREAM is self-reinforcing in that each step in the process informs and strengthens subsequent phases. Namely, it sources seed in a climatically informed manner, experimentally tests this sourced stock to probe for physiological maladaptation under controlled settings, grows the stock in the field under a range of silvicultural scenarios, and finally forecasts long-term outcomes using models parameterized from the controlled- and field-tests. In this paper, we describe the DREAM framework and illustrate aspects of its implementation drawing from two experimental sites: one in Québec, Canada and one in Wisconsin, USA. Moreover, we place the DREAM study into the broader FAM context by briefly contrasting it with other operational examples throughout North America. Knowledge gained from this research-management collaboration will expand current reforestation

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paradigms to include future climate-adaptive ones that aim to use the *right seed*, planted in the *right places*, under the *right conditions*.

1. Introduction

1.1. Climate change and climate-adaptive forestry

Despite growing global commitment to limiting climate change, current greenhouse gas emission trajectories and socioeconomic constraints make it probable that we will surpass the 1.5 °C increase in temperature from pre-industrial baseline established by the Paris Agreement by 2030 (Matthews and Wyness, 2022). This unrelenting and rapid tempo of change is beginning to outpace the adaptive capacity and carbon storage potential of natural and managed forests worldwide and may ultimately diminish terrestrial plant diversity and ecosystem function (Harrison, 2020; Messier et al., 2022). This issue is particularly acute in the diverse temperate forests of eastern North America where exceptionally high warming trends and relatively limited topographic relief contribute to century-scale predicted climatic conditions resembling contemporary climates found hundreds of kilometers away (Giorgi, 2006; Veloz et al., 2012; Mahony et al., 2017; Karmalkar and Horton, 2021). The temporal and spatial scale of these shifts far surpasses natural migration rates for many tree species (Aitken et al., 2008; Loarie et al., 2009), likely resulting in species distributions that fail to track their shifting climate optima (Zhu et al., 2012; Sittaro et al., 2017; Woodall et al., 2018). Thus, forests, particularly at ecotones, risk becoming “zombie communities” (sensu Decker et al., 2021) as reproductive individuals become geographically stranded in increasingly unsuitable and volatile climates, unable to regenerate locally. Ultimately, these changes may lead to catastrophic losses of key forest ecosystem services such as carbon sequestration, habitat provisioning, and forest products, among others.

The mounting pressures of climate change on forest ecosystems compel managers to modify current practices and develop new approaches to sustain and promote resilient forests adapted to future conditions in order to ensure long-term production of forest goods and services (Nagel et al., 2017). Such climate-adaptive silvicultural strategies often focus on practices that combat or mitigate the more short-term changes to forest sustainability caused by a changing climate (Millar et al., 2007). Examples of these include fuel reduction treatments to decrease wildfire and insect outbreak risk or manipulations of stand density to reduce drought impacts (e.g., Long et al., 2018; Moreau et al., 2022; reviewed by Keenan, 2015). Although these management actions may help limit the severity of anticipated impacts from climate change, over time, the accumulation of climate-driven stressors may limit their effectiveness, ultimately surpassing a tipping point beyond which forests may suffer abrupt – and currently unpredictable – permanent shifts in composition and structure (Millar et al., 2007; Trumbore et al., 2015, reviewed by Turner et al., 2020).

Alternatively, managers may opt to address rapidly shifting habitat conditions by pro-actively altering community composition and population genetic structure in ways that may better align with anticipated future climates. This approach, broadly known as forest assisted migration (hereafter, FAM, *sensu* Pedlar et al., 2012) refers to the deliberate movement of individuals or genetic material from native seed sources (i.e., provenance) to locations either within or beyond their current ranges. Forest assisted migration encompasses three variants of that span various levels of increasing intensity (and associated increasing uncertainty) ranging from moving provenances i) *within* their current range (assisted population migration [APM]), ii) *slightly beyond* their current range (assisted range expansion [ARE]), or iii) *far beyond* their current range boundaries (assisted species migration [ASM]; Williams and Dumroese, 2013). The concepts, operational feasibility, and ecological and social considerations of FAM are reviewed and discussed

elsewhere (e.g., Vitt et al., 2010; Hewitt et al., 2011; Pedlar et al., 2012; Dumroese et al., 2015; Sáenz-Romero et al., 2016; Palik et al., 2022). The consensus that has emerged from these discussions is that FAM is increasingly considered an option for forest management, despite the uncertainties surrounding its implementation (Klenk and Larson, 2015; Pelai et al., 2021; Handler et al., 2022).

On a fundamental level, the success of FAM requires confidence that such management actions will not only succeed, but also confer benefits to ecosystem health and productivity beyond those provided from business-as-usual silvicultural approaches that focus only on retaining the species and genotypes currently present on the landscape (Duveneck and Scheller, 2015; Gustafson et al., 2020; Nevins et al., 2021). A key concern for managers is that the ecological and operational challenges associated with these decisions are complex and the science available to guide decisions remains new, incomplete, and uncertain (Park and Talbot, 2018). In general, managers lack i) access to decision-support tools for sourcing seed for many regions and locations, ii) confidence in the ecophysiological tolerances of putatively future-adapted stock, iii) knowledge about the silvicultural strategies necessary to maximize growth and survival yet minimize invasion risk of individuals transferred to sites with novel conditions relative to their source geographic locations, and iv) tools to assess the long-term effectiveness of FAM in conserving ecosystem goods and services at ecosystem and landscape scales.

The juxtaposition of these knowledge gaps and/or guidance with the demands of a rapidly changing climate creates a dilemma for land managers (Park et al., 2014). Namely, rather than operating under the well-established current regeneration, climate, and disturbance dynamics of their region, managers must make decisions in the face of considerable uncertainty in climate forecasting, anticipated and future ecological dynamics, and selection of suitable source individuals for FAM (Gray et al., 2011; Park et al., 2014; Keenan, 2015; Sáenz-Romero et al., 2021). The combination of these uncertainties complicates forest policy and management decisions because establishment of potentially maladapted source individuals for FAM, combined with silvicultural strategies that may be unsuited to actual future climate, poses risks to investments in climate-adaptive forest management and possible rejection of FAM for some forest users (Pelai et al., 2021).

2. The DREAM framework

The Desired REgeneration through Assisted Migration (DREAM) framework was developed to reduce these uncertainties by providing a structured approach for designing, testing, and implementing FAM with an end goal of reducing risk and increasing confidence in climate-adaptive management actions. DREAM leverages expertise from three research disciplines with applications to climate adaptation science: modelling, physiology, and silviculture, integrating insights from all three in a structured and self-strengthening manner to ensure success in assisted migration plantings (Fig. 1). Specifically, DREAM responds to Park and Talbot's (2018) appeal that assisted migration research should explore responses to both climate change and possibly novel abiotic and biotic conditions and their interactions. DREAM is self-reinforcing in that each step in the process informs and strengthens subsequent phases. First, advanced climate modelling is used to source seed in a geographically and climatically informed manner. Second, this putative future-adapted stock is experimentally tested to identify any maladaptation to expected climates. Third, stress-tested stock is planted in an operational silvicultural experiment with factorial manipulations of understory microenvironment, browsing pressure, and intraspecific plant competitors to derive appropriate planting strategies that optimize

seedling growth and survival at the destination site. Finally, long-term outcomes of FAM are forecasted using forest dynamics models calibrated using the physiological and demographic data from prior experiments. Moreover, the design and delivery of multiple facets of the DREAM framework are meant to be conducted in full collaboration with land managers to support an end goal of delivering actionable knowledge. Through these steps, the DREAM approach specifically addresses knowledge gaps necessary to plan and execute successful FAM plantings.

In this paper, we describe the four-part conceptual framework of DREAM and illustrate how it is implemented in collaboration with land managers. We draw from two operational studies: one located in Québec, Canada and a second in Wisconsin, USA, and explain how each step addresses known gaps in FAM knowledge. Finally, we provide an overview of a selection of existing operational approaches to FAM in North America with a brief discussion of their development and their relative advantages and disadvantages for advancing climate-adaptive forest management. For the purpose of this paper, we follow Palik and colleagues' (2022) definition of 'operational' as studies applied in a forest management context, rather than a strictly research setting.

2.1. Sourcing planting stock under forest assisted migration

Sourcing planting stock in the context of FAM is an inherently challenging step to achieving desired resiliency goals under climate change. To achieve desired success, source material should be optimally matched to the future conditions of a target destination site. Locating suitable planting stock may benefit from the premise that future climate conditions of an intended planting site are suitably represented elsewhere on the landscape today (typically warmer climates, e.g., in the Northern Hemisphere usually further south or at lower elevations). Accordingly, plant material collected from such locations should be better poised to adjusting to climate change than local sources located at a target destination site (Etterson et al., 2020; see Glossary of Terms, Appendix S1). A technique referred to as climate analogue modelling provides a basis for determining the similarity of climates from different geographical locations and times (Mahony et al., 2017; Williams and Jackson, 2007). Thus, the climate analogue approach is the basis for climate-based selection of precisely sourced plant material in the DREAM experiment. In this context, a climate analogue is a geographic location that has a contemporary climate similar to that of the projected climate at a target destination site and a geographic location to source seeds for FAM. Climate analogy has already been used for seed source

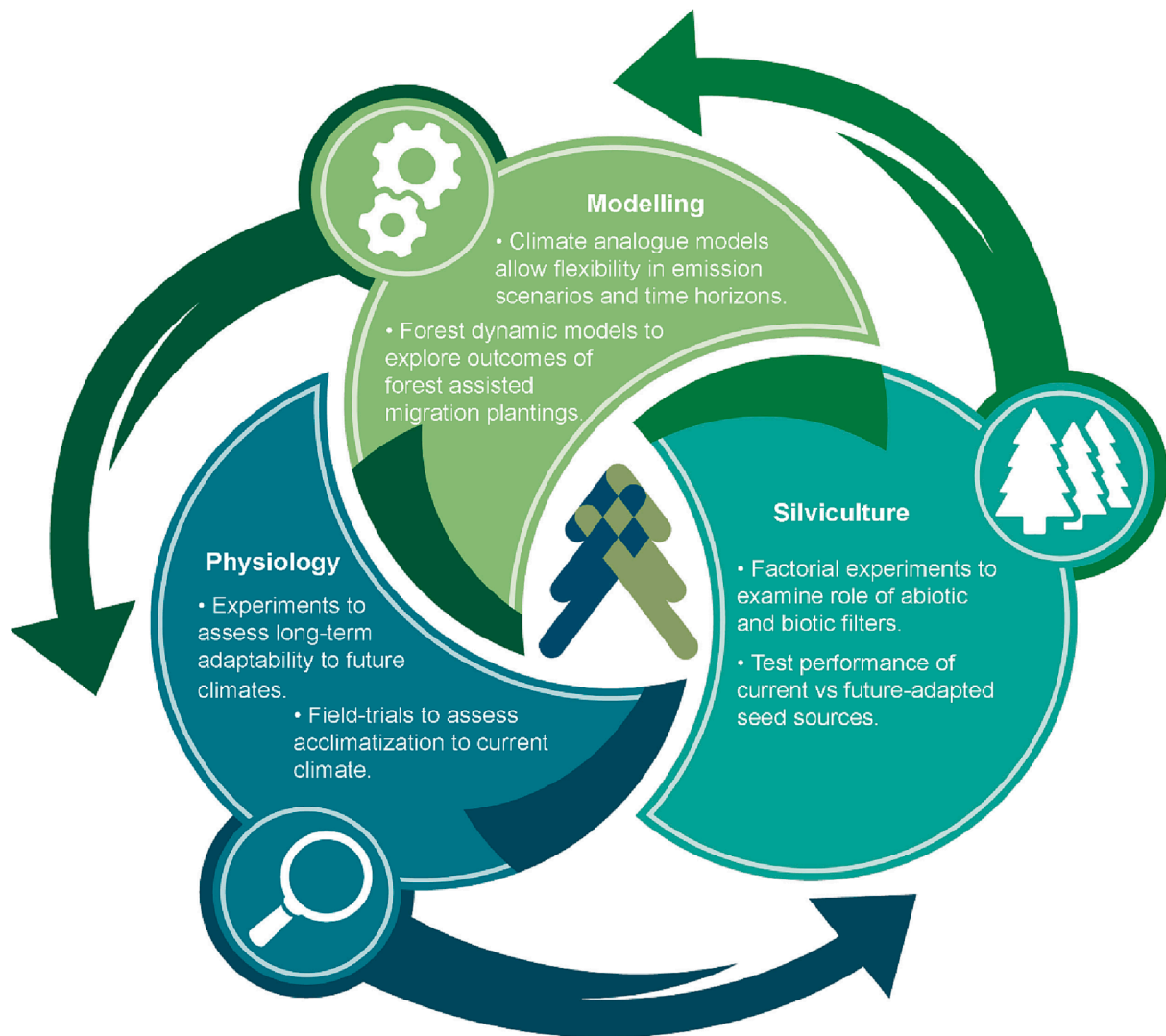


Fig. 1. Conceptual model of how the Desired REgeneration through Assisted Migration (DREAM) framework incorporates approaches climate and forest dynamics modelling, plant physiology, and silviculture in a structured, complementary, and self-strengthening manner.

selection, such as in the web-based Seedlot Selection Tool (St.Clair et al., 2022). Climate analogue models provide geographical surfaces of climate dissimilarity between contemporary climates and two future climate projections (Representative Concentration Pathways (RCP) 4.5 and 8.5 Wm^{-2}) for two time periods: a mid-century (2041–2070) and an end-century (2071–2100) horizons, and locations with the least dissimilar climates may guide the sourcing of seed or other planting material (see Fig. 2). For instance, for a DREAM study in Québec, climate variables used to find analogues were the mean annual daily temperature, the daily minimum temperature in May, the mean annual precipitation, whereas, in a Wisconsin DREAM study, 12 climate variables composed of mean minimum and maximum temperature ($^{\circ}\text{C}$) and total precipitation (mm) among the four climatological seasons (winter (DJF), spring (MAM), summer (JJA), and autumn (SON)) were used. In application, attention must be given to interpreting analogue surfaces, because, under extreme scenarios, the future climate is too different from current climate analogues. In such cases, managers may assign threshold dissimilarity values to ensure optimally-matched seed sources and be willing to accept that there may not be an appropriate analogue for their destination planting site. Furthermore, in some regions, climate projections, such as RCP, may mischaracterize precipitation or other climate variables important to plant growth and survival.

Optimal seed sources closely matched to future climates under extreme scenarios (e.g., late-century, geographically distant to destination sites) may be less likely to tolerate local climatic conditions, at least

in the short term (e.g., risk of late or early frost in early spring or late autumn, respectively) before the climate has changed enough for the species to thrive. For example, the USA Eastern Seed Zone Forum recommends transferring seed no further than one or two seed zones, while recognizing that greater distances may be necessary under climate change (Pike et al., 2020). Seed zones are defined as the geographic areas within which seeds can be harvested and planted (see Glossary; Appendix S1). These areas are typically large enough to permit commercial collections but small enough to delineate key adaptation differences in plant taxa (Pike et al., 2020). As opposed to *ad hoc* seed collections, researchers are increasingly advocating for greater geographic precision (and thus climatic precision) in seed collection for climate resiliency purposes (Young et al., 2020).

2.2. Ecophysiological concerns in the context of forest assisted migration

The success of FAM depends on early seedling survival, primarily determined by the adaptive capacity of the introduced individuals to current conditions at the destination site (Corlett and Westcott, 2013). Such conditions include many factors, such as climatic (e.g., moisture; Champagne et al., 2021c), biotic (e.g., herbivory; Champagne et al., 2021a), and edaphic (e.g., plant-soil feedbacks; Refsland et al., 2023). Although potentially able to survive, normal functioning and growth of introduced plant material could be impeded or altered by these conditions to such an extent that productivity would be negatively affected,

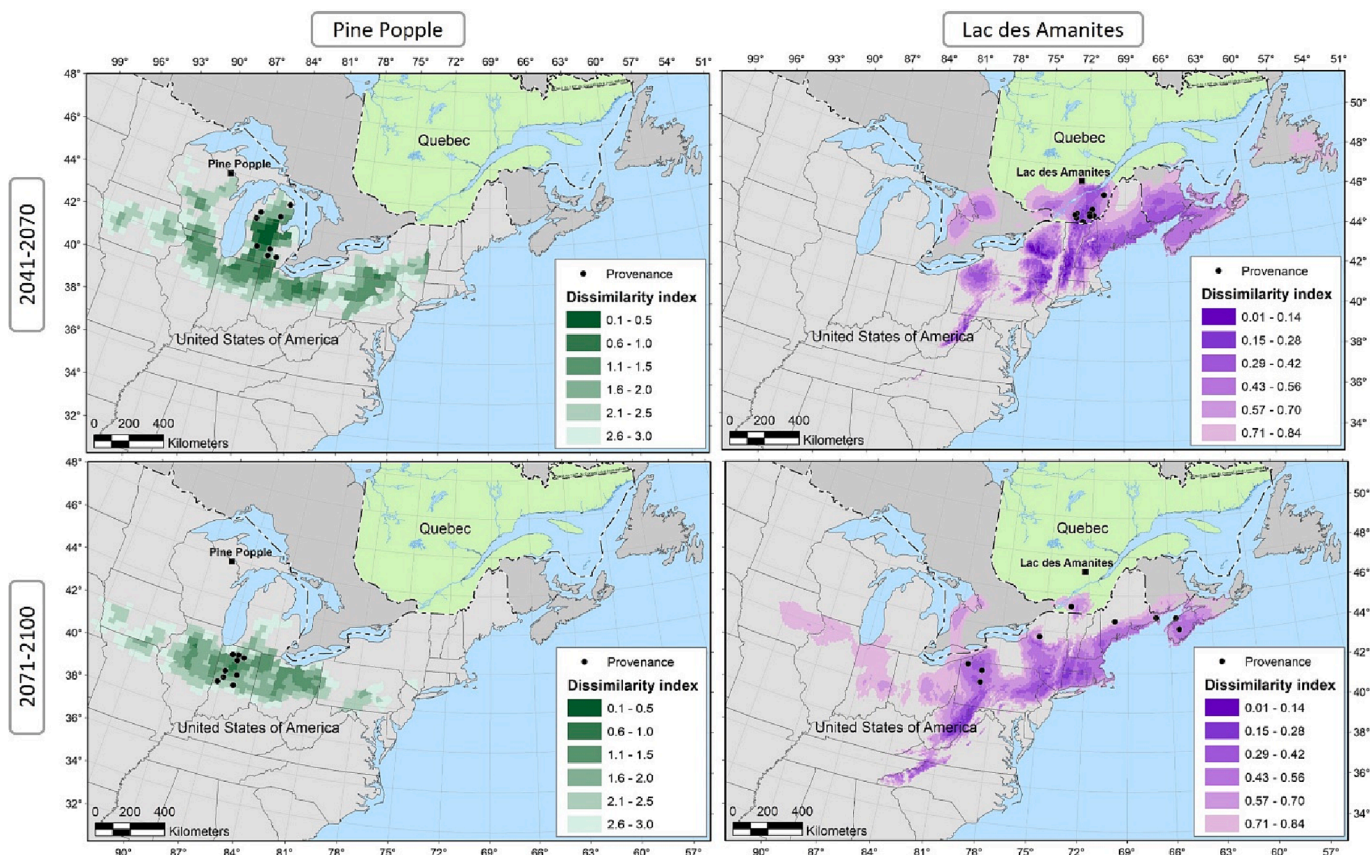


Fig. 2. Contemporary climate analogues corresponding to the expected future climate of two experimental sites (indicated by square symbols): Pine Popple (PP, left column) and Lac des Amanites (LA, right column). Climate analogues were quantified for both mid (2041–2070) and late century (2071–2100) for each site. Shading on the maps represents the relative dissimilarity index value for each site, in which a low dissimilarity index value indicates a contemporary climate analogue for a FAM planting destination's expected future climate. Both sites used climate projections according to RCP 8.5 and the Coupled Model Intercomparison Project phase 5 (CMIP5) database. The PP site used statistically downscaled (1-km resolution) projections according to a 13-model ensemble, including 12 climate variables (mean minimum and maximum temperature and total precipitation) aggregated to the four climatological seasons (winter, spring, summer, autumn). The LA site used statistically downscaled (10-km resolution) projections according to a 11-model ensemble, including three variables (mean annual daily temperature, daily minimum temperature in May and mean annual precipitation). Further details are provided in Section 2.1. Black dots indicate seed collection areas (i.e., provenances) within the climate analogue.

and the tree would be considered maladapted to the site (O'Neill et al., 2008). On the other hand, some individuals might exhibit adaptive plasticity (e.g., adjustment of specific leaf area to maintain photosynthesis efficiency) to acclimate to a destination site. However, it may be difficult to select such individuals without prior ecophysiological studies and related modelling.

Provenance tests can provide critical information on short-term acclimatization and critical seed transfer distances. For example, Lu et al. (2014) reported that the adaptive plasticity and growth potential of white spruce (*Picea glauca* [Moench] Voss) varied considerably among 245 range-wide genotypes sampled across North America, and that local provenances could be outperformed by nonlocal ones. According to Thomson and Parker (2008) and Thomson and colleagues (2009), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Miller) B. S.P.) seed sources in southern Ontario (Canada) may benefit from transfer from current to cooler environments. Recent research in an operational FAM context has documented the short-term acclimatization (based on survival and growth variables) of planted seedlings. For example, in Minnesota, Palik et al. (2022) reported early FAM planting results including high (~100%) survival for assisted population migration and assisted range expansion hardwood plantings and low survival for assisted species migration plantings (*Pinus ponderosa* Dougl. ex Laws.; ~45% survival).

While FAM studies can test short-term responses to current climate and intra- and interspecific competition at the destination site, there are limitations to these types of studies. One limitation of such *in situ* planting studies is that they can test only the abiotic conditions that are present during the specific years of testing at the location of study (a limitation of provenance studies as well). Further, trying to untangle the specific abiotic causes for success or failure can be difficult. DREAM not only incorporates *in situ* testing, but also uses controlled experiments in growth chambers or greenhouses to explore ecophysiological responses and tolerances to expected future temperature or moisture conditions at destination sites (e.g., Champagne et al., 2021c). Such environmental manipulations allow for testing of multiple abiotic factors, alone or in interaction, across a range of both current and future climates. Testing along a gradient of abiotic conditions is vital to reduce the chance for cryptic maladaptation. Cryptic maladaptation occurs when maladaptation is only detected many years after the FAM planting, when an extreme abiotic event occurs (Benito-Garzón et al., 2013). Controlled experiments will not include the intra- and interspecific competition associated with *in situ* testing, but they do provide robust evidence of acclimatization on shorter timescales and for lower cost than field-based studies, thereby increasing confidence that FAM plantings are a sound investment (Aitken and Whitlock, 2013). Finally, the measured ecophysiological responses to these experiments are powerful not only to better describe *in situ* outcomes, but to improve simulation of tree growth, competition, and succession in models that use ecophysiological first principles (see 2.4, below).

2.3. Experimentation through silvicultural studies

A growing body of evidence reveals that the physiologically-mediated potential of seedlings to establish and grow in a specific climatic regime is determined by the soils, microbial communities, browsers, and plant competitive neighborhoods found at that site (i.e., fundamental vs realized niche, Hutchinson, 1957, see also Post, 2013; Vandvik et al., 2020; Champagne et al., 2021a; Winder et al., 2021; Refsland et al., 2023). Although ecophysiological stress tests determining the limits of adaptability can reduce the uncertainty of assisted migration planting success, an understanding of how the multiple and often interacting drivers at the destination site will impact the seedlings is ultimately required (e.g., Fisichelli et al., 2013; Park et al., 2014; Parnesan and Hanley, 2015; Bucharova, 2017). Additionally, variation in forest overstory composition and structure may dictate understory plant dynamics directly by altering light, temperature, and moisture

(reviewed by De Frenne et al., 2021) or indirectly by mediating the strength of plant-plant competition (Royo and Carson, 2006), modulating herbivory risk (Champagne et al., 2021a), and altering plant-soil feedbacks (Marshall, 2000).

DREAM tackles multiple context dependencies through studies of operational FAM trials that establish a diverse, mixed-species forest community planted with seed of both current and future adapted seed sources using a fully-factorial manipulation of overstory shading, cervid (e.g., deer) browsing, and understory competition (Fig. 3a). The study design is a split-split-split block, where an overstory density treatment represents the whole plot, with a cervid treatment as a split plot, a competing vegetation control treatment as the split-split plot, and with three seed sources (i.e. climate analogues) producing the third split or experimental unit. Each experimental block contains varying overstory density treatments created through timber harvests. The experimental blocks are separated by an untreated area acting as a control (or reference area). The cervid treatment is implemented by fencing half of each overstory treatment to eliminate browsing, leaving the other half open to ambient browsing. The competing vegetation treatment removes neighboring and overtopping understory vegetation in half of each cervid treatment, whereas the other half of each cervid treatment leaves understory vegetation in place. Although the experimental manipulations of overstory trees, cervids, and competing vegetation are requisite to the design, the form and implementation of these treatments (e.g., clearcut vs patch cut; mechanical vs chemical competitor control) is determined by regional ecological context, site history, and local land management practice. Hence, the realized design is intended to produce science relevant at a local to regional scale.

Each overstory × cervid × competing vegetation treatment contains three FAM planting approaches based on climate analogues (Fig. 3b). The climate analogues represent geographic regions that currently have climate similar to each of the three distinct climate periods (current climate and modeled mid-century and end-of-century climates) projected for the study sites (see 2.1, above). The same species are used in the climate analogues across the experiment. The species selected for study were based on several factors, including predicted habitat suitability shifts (i.e., 'winners' vs 'losers'; Iverson et al., 2019) and ecological traits (Table 1) as well as socio-economic considerations. Selected species also varied in both shade-tolerance and browse susceptibility, the two traits assumed to mediate the responses to the treatments within the experimental design. Equally important in selecting species is the knowledge, experience, and interest of forest land managers. For example, managers and their agencies may opt for a more conservative approach that moves seed sources within their range or a less conservative approach that explores the performance of species not currently found at the destination site.

Each of the selected species is planted randomly within a row to create a mixed species stand in which competitive neighborhoods vary at the individual seedling scale (Fig. 3b). Overall, the experimental design allows a robust evaluation of the independent and interactive effects among climate-adaptability and key abiotic (e.g., light, temperature, moisture) and biotic (i.e., browsing, competition) factors known to influence forest renewal, yet that can be shaped and modified through silviculture. Moreover, the inclusion of both current and future-adapted seed sources allows us to discern whether translocated sources outperform local ones under a range of abiotic and biotic conditions (Benito-Garzón et al., 2013; Park and Talbot, 2018).

2.4. Forecast modelling

A critical step to implementing the DREAM framework is understanding the distant future. Specifically, implementing climate-adaptive FAM strategies will depend, in part, on perceptions of their potential long-term success. Long-term emergent properties of stands established through FAM plantings will not be known for decades or more and not soon enough for near-term management decisions. Traditionally, real-

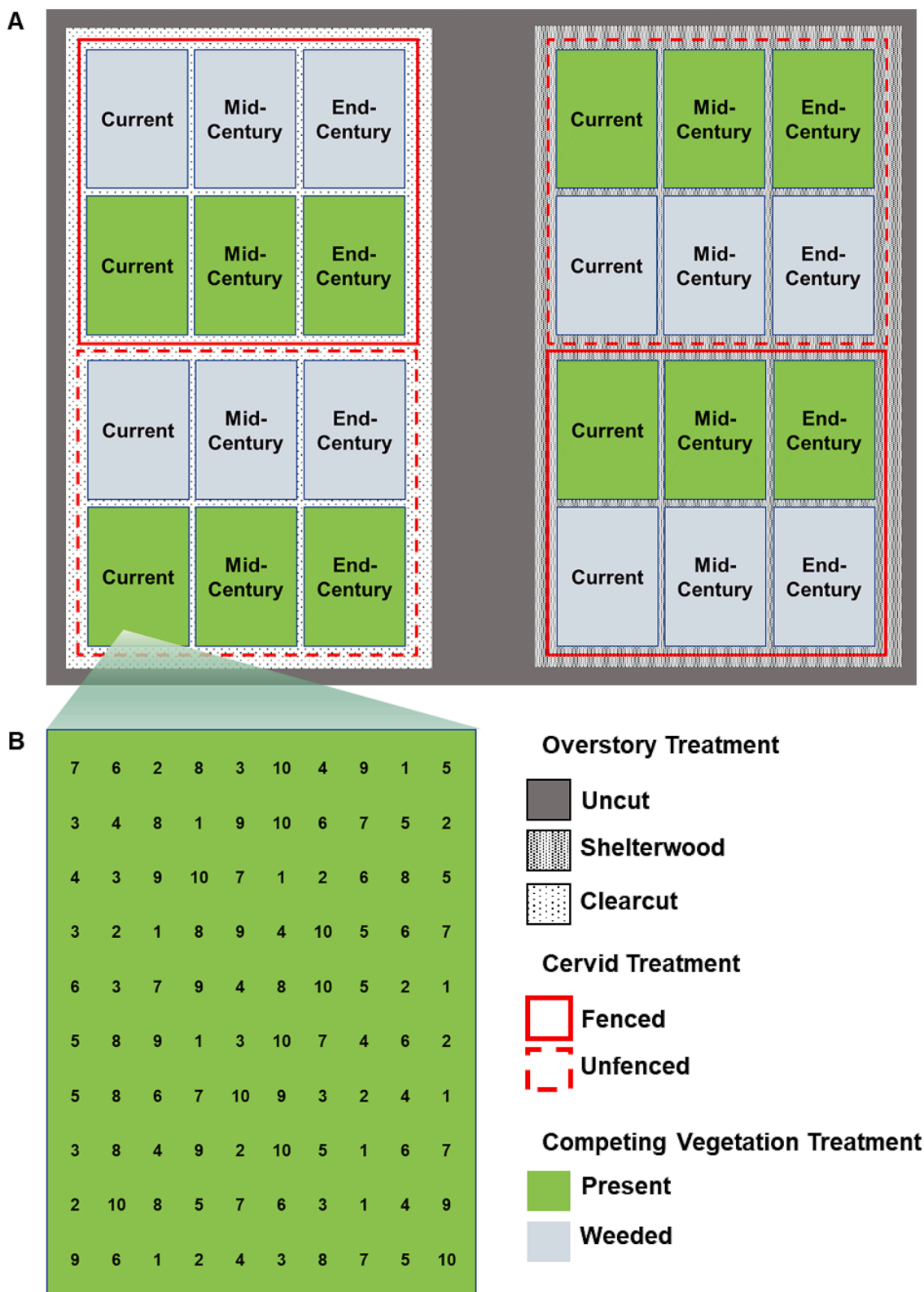


Fig. 3. Representation of one block (replication) of the DREAM silviculture experimental design. A) In this example, the experimental block contains two overstory treatment plots (1.2 ha each): clearcut (white stippled) and 50% shelterwood cut (light gray). The two treatments are separated by an uncut forest buffer that serves as a reference area (dark grey) to observe stand dynamics without any intervention. Within an experimental site, there are multiple blocks wherein each block contains a full split-split-split factorial design with the experimental units of FAM mixed species plantings representing three climate analogues (current climate and modeled mid-century and end-of-century climates) nested within a cervid treatment (solid red vs dashed red lines) and nested within competing vegetation treatments (green vs gray). B) A more detailed example of the experimental unit (616 m² within the unfenced, clearcut portion of the block) where each species (#1–#10) within a FAM climate analogue is planted randomly within a row and replicated across multiple rows.

Table 1

Species selected for planting at the Lac des Amanites (Québec, Canada) and Pine Popple (Wisconsin, USA) DREAM experimental sites. For each site, we note whether the site falls within the species' current range and if the species is expected to experience declining (↓) or improving (↑) habitat suitability by end of century. Species noted by a star (*) are those whose current range does not include these northerly, cold site locations but are predicted to have increasingly suitable habitat at these locations as climate changes^{1,2}. For each species, we also summarize its shade tolerance³ and susceptibility to cervid browsers^{4,5}.

Common Name	Latin name	Lac des Amanites ^a	Pine Popple ^b	Shade Tolerance ^c	Browse Susceptibility ^{c,d}
White Spruce	<i>Picea glauca</i>	↓	↓	Tolerant	Low
Black Walnut	<i>Juglans nigra</i>		*	Intolerant	Low
Shagbark Hickory	<i>Carya ovata</i>	*	*	Moderately-Tolerant	Low-Moderate
White Pine	<i>Pinus strobus</i>	↑	↑	Moderately-Tolerant	Low-Moderate
Northern White-Cedar	<i>Thuja occidentalis</i>	↓	↓	Moderately-Tolerant	Low-Moderate
Eastern Hemlock	<i>Tsuga canadensis</i>		↓	Very Tolerant	Low-Moderate
Sugar Maple	<i>Acer saccharum</i>	↑	↓	Very Tolerant	High
White Oak	<i>Quercus alba</i>		↑	Moderately-Tolerant	Moderate
Black Cherry	<i>Prunus serotina</i>	*		Intolerant	Moderate
Northern Red Oak	<i>Quercus rubra</i>	*		Moderately-Tolerant	Moderate-High
American Basswood	<i>Tilia americana</i>		↓	Tolerant	High
Tulip Poplar	<i>Liriodendron tulipifera</i>		*	Intolerant	High
Red Spruce	<i>Picea rubens</i>	↓		Tolerant	Low
Red Pine	<i>Pinus resinosa</i>	↑		Intolerant	Moderate

^aPérié et al. (2014).

^bPeters et al. (2020).

^cNiinemets and Valladares (2006). Five-level scale of shade tolerance (very intolerant to very tolerant) corresponds approximately to the following light availabilities expressed as percentage of full sunlight: 1, >50%; 2, 25–50%; 3, 10–25%; 4, 5–10%; 5, 2–5%.

^dChampagne et al. (2021b). e. Latham et al. (2005).

time forest monitoring over decades has allowed tests of extensive processes such as stand development and succession following silvicultural treatments (Barrette et al., 2022). However, the long-term tree responses and stand dynamics of novel forest mixtures have rarely been studied, and FAM studies will not provide clear results for decades or centuries.

Therefore, forecasted outcomes of the DREAM framework are needed to provide some assurance of long-term success to justify current efforts to implement FAM. Forest landscape models represent one approach to project long-term tree responses and stand dynamics of novel forest mixtures under climate futures. However, few such studies have been attempted, so obtaining forecasted outcomes of FAM are limited in scope (Duveneck and Scheller, 2015; Gustafson et al., 2020; Nevins et al., 2021; Gustafson et al., 2023; Soubeyrand et al., 2023).

Recently, a forest landscape model (LANDIS-II) was used to model FAM approaches that varied transfer distance of seed sources for FAM planting sites in Wisconsin. The model projected that ecosystem goods and services were maintained when the migrated species were each selected for a specific forest good or service, but those decisions sometimes had unintended consequences on other goods and services (Gustafson et al., 2023). Because only a limited number of goods and services were evaluated, questions remain about the ability of FAM to maintain other priority ecosystem goods and services in the study landscape. The study also revealed that the data available to parameterize seed sources as transfer distances increase are limited.

Forest landscape modelling helps to bridge several key knowledge gaps in FAM. First, models can predict likely outcomes of planted stands created through FAM within the context of a management plan, regional natural disturbance drivers, and a range of future potential climate scenarios. For instance, the LANDIS-II (Scheller et al., 2007) forest landscape model uses tree-level ecophysiology attributes to simulate growth and competition, formalized rule sets to simulate landscape-scale disturbance (including timber harvest prescriptions and plantings), and monthly climate projections to forecast forest dynamics (composition, living and dead biomass, spatial pattern) over large (10⁵–10⁷ ha) landscapes and long (centuries) timescales (Scheller et al., 2007). Second, the data generated from DREAM physiological testing of seedlings sourced from various climate analogues (see Section 2.3) can be used to calibrate such models and improve the accuracy of tree-level life history and physiological parameters by seed source, especially within the FAM context (see Section 2.2). Finally, forest landscape models can be used to produce objective comparisons between

management scenarios that ignore climate change (i.e., “business as usual”) and various climate-adaptive management strategies for FAM. Ultimately, forecast modelling can help managers evaluate the expected long-term outcomes of forests regenerated using alternative assisted migration strategies in the context of anticipated climate change, disturbance regimes, and management strategies.

3. Case studies

DREAM represents an international collaboration, implemented in a site-specific context. There are various DREAM projects at different developmental stages. Two are furthest along in implementation: Lac des Amanites in Québec, Canada and Pine Popple in Wisconsin, USA (Fig. 4). These two sites were jointly conceptualized using the same base protocols and thus share many characteristics (Table 2). With respect to DREAM guiding principle of increasing confidence in climate-adaptive management actions, it was important that the study be designed in such a way to provide useful, actionable information. Thus, we collaborated closely with forest managers from the outset to ensure we were operating at meaningful scales and selecting species of management interest. These efforts were not without significant logistical challenges, which are discussed herein.

3.1. Forest managers and operational aspects of experimental planning

In both jurisdictions, FAM was proposed as a way to account for climate change in the rehabilitation of stands degraded by past forestry practices such as diameter-limit cutting, or threatened by novel ecological stressors (e.g., high-browsing pressure, invasive earthworms, recalcitrant understory layers), or both. Forest managers were involved in the planning of the experiment at both sites and, given initial stand conditions, two silvicultural strategies were deemed appropriate for establishing a fully-stocked, new age class with mixed-species: 1) planting in open conditions (i.e. clearcut) or 2) planting in a partial cut (uniform shelterwood) to moderate microclimatic conditions (e.g., temperature) in the understory before final overstory removal.

The Québec site was the first to be established, and decisions regarding site selection were made by a multi-disciplinary team of researchers with expertise in silviculture, ecology, and physiology, in close collaboration with regional forest managers. This team selected fertile sites with the highest growth potential to help sustain the southern species proposed for range expansion planting (see Table 1). Site criteria

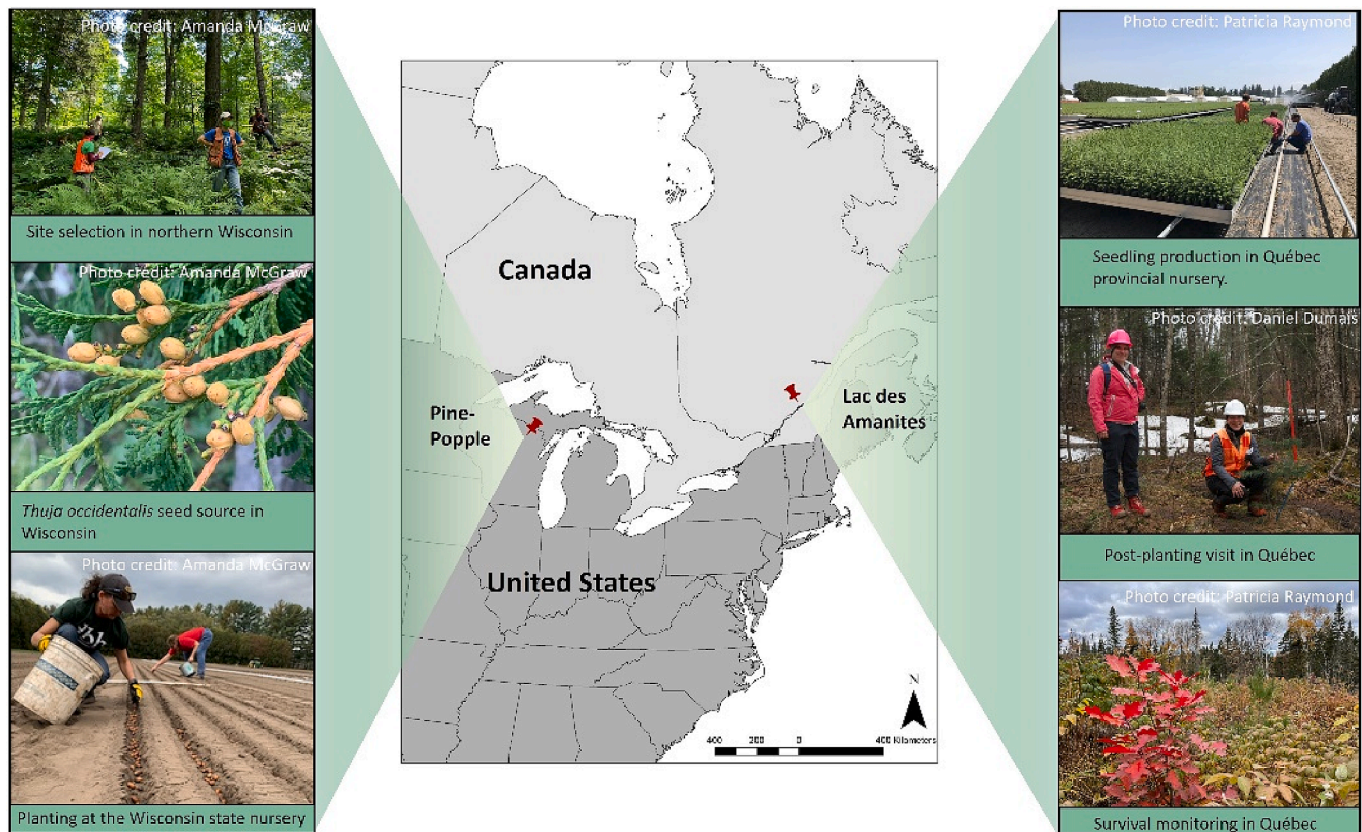


Fig. 4. Locations of the DREAM experimental site in Québec (Lac des Amanites) established in 2018 (right column), and the second DREAM experimental site in Wisconsin (Pine Popple) established in 2021 (left column). The Québec site photos show, in descending order, seedling production at the provincial nursery, a site visit after planting, and the planted stand in year 4. The Pine Popple site photos show, in descending order, an early site visit to finalize its selection, Northern white cedar cones ripening before collection, and hand-sowing seed at the state nursery.

also included stands with histories of exploitive cutting for timber value but also with high enough densities to conduct a partial harvest (e.g., $>20 \text{ m}^2/\text{ha}$). In Wisconsin, a team of research scientists along with state government foresters and silviculturists were recruited to develop site criteria (e.g., site productivity, stand characteristics, assisted migration management recommendation). The team conducted site visits to evaluate potential research sites using those criteria. Additional site criteria common to Lac des Amanites and Pine Popple were ease of access, gentle slope, and sufficient size to accommodate a harvest and large-scale experiment.

Similarly, species selected for planting resulted from a combination of scientific considerations and operational aspects (Table 1). The goal was to generate a list of species to plant that included a mix of commercial coniferous and broadleaf species with ecological value, and a list of species with both increasing and decreasing habitat suitability by the end of this century for each site. In addition, the list of species to plant would have some species common and some unique to each site. Lastly, the list of species to plant was vetted by local nursery staff and forest managers to ensure that they could be produced by local nurseries and expected to add value for the local wood products industry.

3.2. Seed procurement and seedling production

Seed procurement to populate the experimental units of three climate analogues, based on model predictions (Section 2.1), proved challenging. Climate analogue models indicated that for the Lac des Amanites site, current climate was represented in the areas surrounding the study location (Mauricie and Capitale-Nationale regions), mid-century was represented in the Estrie region and end-century was represented in Nova Scotia and Northeastern United-States. For Pine

Popple, the current climate was best represented by seed from Wisconsin, while climate analogue models indicated that mid-century seed should be collected from lower Michigan and end-century seed should be collected from northern Indiana (Fig. 2). In Lac des Amanites, the scientific team used provincial and national seed collections to identify appropriate seed sources from known origins (i.e., seedlots; Tables 1 & 2 and Fig. 2). While these sources provided most of the seeds for the coniferous species, provincial government employees and private contractors collected seed for northern red oak (*Quercus rubra* L.) and shagbark hickory (*Carya ovata* (Miller) K. Koch). The remaining seeds were purchased through commercial seed companies. Seed acquisition beyond the Canadian borders was difficult because of administrative constraints and low availability. For the Pine Popple site, state and federal government employees and private contractors collected all seeds because there were no extensive government seed collections available. For seed sources identified within Wisconsin, state government foresters and nursery staff assisted with seed collection. Similar to Québec, collecting seed outside state jurisdictional boundaries was challenging and required significant networking and coordination among natural resources staff from several states, federal employees, and independent seed collectors.

Seed sources in each climate analog were collected from wild trees rather than seed orchard or seed production areas. Collecting from wild sources presented additional challenges, because the species of interest were not always found or abundant in each climate analog, seed collectors with local knowledge of species occurrence and origin were difficult to find, and, in the same year, seed crops were poor for some species and good for others. As reforestation efforts (including FAM) ramp up substantially in the coming years to meet the goals of management and various ecological restoration pledges (Haase and Davis,

Table 2

Comparison of two DREAM experimental sites, including landscape and pre-planting conditions, as well as applied treatments.

Characteristics	Québec–Lac des Amanites	Wisconsin–Pine Popple
Location	Lat. 47.128 N, Long. –72.409 W	Lat. 45.885 N, Long. –88.452 W
Management history	- Public land (Provincial forest management) - Frequent partial cuts, including high grading before the 1990's	- Public land (State management since 2006) - Frequent, partial cuts over ~80 years by previous industrial landowner
Landscape context	- Balsam fir – yellow birch bioclimatic domain^a - Managed forest landscape in a wildlife reserve with hunting activities of 774 km, surrounded by controlled hunting zones (Zones d'Exploitation Contrôllées, ZEC). - Other activities in the region include recreation, agriculture and stone extraction (quarry).	- Ecological landscape^b second-growth forest – predominately northern hardwoods forest type - The site is a Wisconsin Wild Rivers property^c. Hunting occurs. The surrounding landscape is heavily forested and few activities unrelated to outdoor recreation and forestry exist.
Climate		
• Normals	1981–2010 ^d - Mean annual daily temperature: 4 °C (S.D. 1.3) - Daily minimum temperature in May: 4.3 °C (S.D. X) - Mean annual precipitation: 1133.2 mm - Mean annual snowfall: 230.3 cm	1997–2022 ^e - Mean annual daily temperature: 4.6 °C (S.D. 0.9 °C) - Daily minimum temperature in May: 4.5 °C (S.D. 1.3 °C) - Mean annual precipitation: 772.2 mm - Mean annual snowfall: 136.7 cm
Pre-harvest attributes		
• Stand type and state	<i>Betula alleghaniensis</i> – conifer forest type, mesic and nutrient rich, impoverished in species composition and tree quality	Northern hardwood forest type, mesic and nutrient rich, with simplified overstory dominated by <i>Acer saccharum</i> , limited structural diversity
• Understory	Limited regeneration attributed to seed bearer removal and browsing; abundant non-tree competition	Limited regeneration attributed to browsing and invasive earthworms
• Cervid abundance	- White-tailed deer (per hunting area): 2.2/km² in 2008, 4.02/km² in 2018^f - Moose (in the reserve): 7.3/10 km² in 2009^g	White-tailed deer^h: 10 ± 2/km², with county (deer management unit) objective to increase populations
• Other biotic perturbators	- Snowshoe hares - Spruce budworm epidemics	- Snowshoe hares - Invasive earthworms
Harvest		
• Harvest treatments	- Partial cut: 40% removal establishment cut, uniform shelterwood - Clearcut: 100% removal 2016: Harvest 2017: Disk trenching scarification in clearcuts (June) Exclosure installation (July) August–September 2018: Tree planting	- Partial cut: 50% removal establishment cut, uniform shelterwood - Clearcut: 100% removal 2024/2025: Anticipated harvest 2025: Post-harvest site prep (mowing, exclosure installation) 2025: Tree planting
• Sequence of treatments		
Seedling production		

Table 2 (continued)

Characteristics	Québec–Lac des Amanites	Wisconsin–Pine Popple
• Source	- Provincial and national seed centre (Centre de semences forestières de Berthier, Berthier, Qc and National Tree Seed Centre, Fredericton, NB) - Private seed providers - Collection by Ministry of Natural Resources and Forestry employees and private contractors	- Collection by state and federal employees and private contractors - Seed collection from natural origin trees where possible - Seed could come from unknown origin trees if natural origin could not be located
• Production	- Provincial government nursery (Berthier, Qc) - Coniferous seeds sown in 2017, deciduous seeds in 2018 (containers) <i>Carya ovata</i> sown in Fall 2017 (bare root)	- Wisconsin Department of Natural Resources State Nursery (Boscobel, WI) - Deciduous and some coniferous seeds sown in fall 2022, remaining coniferous seeds sown in spring 2023

^a Saucier et al. (2009).

^b Wisconsin Department of Natural Resources (2015).

^c Wisconsin Department of Natural Resources (2023).

^d Environment Canada (2019).

^e Midwestern Regional Climate Center (2023).

^f Lebel and De Bellefeuille (2021).

^g Lefort and Massé (2015).

^h Wisconsin Department of Natural Resources (2022).

2017), demand for source-identified seed will increase. This heightened demand can only be met by increasing the pool of trained seed collectors, developing new orchard and seed production areas, and improving communication with commercial seed collectors (Fargione et al., 2021). Continued documentation of seed procurement challenges associated with applied, operational-scale research studies will also provide important insights to improve seed procurement programs.

Nursery capacity and the ability to handle various seedlots are also challenges for operationalizing assisted migration in the USA (Palik et al., 2022) and for increasing seedling production globally (Bannister et al., 2018; Graudal et al., 2022). However, both Québec and Wisconsin have government-run nurseries that were able to produce seedlings for the DREAM experiment. Collaboration with nursery staff was pivotal, and in some cases, affected the selection of species to plant by considering their knowledge and capacity to propagate species. We chose to grow all seedlings for the Québec and Wisconsin study sites at their respective government-run nurseries, rather than growing seedlings at the nursery nearest the climate analogue from which they were sourced. This alleviated costs for transport and additional permitting and coordination efforts. As a result, we were able to ensure consistency in seed processing, storing, and other nursery cultural practices (Grossnickle et al., 2020). However, this did increase the burden on those government-run nurseries, especially when introducing species that are not normally grown. Nursery program leaders in Wisconsin are confident that they can overcome the knowledge gap where new species are concerned by outreaching with other professionals in their network. One of the larger concerns among nurseries is a lack of adequate staffing, training, and infrastructure, especially to meet the increasing demands of reforestation efforts and other management programs that rely on planting rather than natural regeneration or direct seeding (Fargione et al., 2021). State and tribal forest nurseries and seed partnerships in the USA are eligible for 10 million dollars in support (additional \$35 million for federal nurseries) as part of the Bipartisan Infrastructure Law (U.S. Public Law 117–58), which is anticipated to help increase seedling production.

3.3. Experiment current status

As of 2022, the Lac des Amanites experimental site was fully established with seedlings planted in August–September 2018, except for shagbark hickory, that required two growing seasons in the nursery and was planted in May 2020. The planted seedlings were censused for growth, survival, and status in the autumns of 2018, 2019, 2020 and 2021. Survival was also assessed in the spring of 2019, 2020, 2021. Three-year survival was high among most species, and remained high after three growing seasons, ranging from 93% for white spruce (*Picea glauca* (Moench) Voss) to 81% for black cherry (*Prunus serotina* (Erhr.)). In contrast, shagbark hickory seedlings showed only 78% survival after two growing seasons; this species may have been disadvantaged by the different planting year and initial condition. For seedlings planted in 2018, three-year growth rates averaged between a low of 8.7 cm·yr⁻¹ for shade-tolerant sugar maple (*Acer saccharum* Marshall) to 60.1 cm·yr⁻¹ for mid-tolerant white pine (*Pinus strobus* L.). However, all species suffered from a variety of disturbances. Of particular interest is the recurrence of spring frost damage on northern red oak, and to a smaller extent on sugar maple and black cherry, and the arrival of white pine blister rust that affected eastern white pine (*Pinus strobus* L.). For the Pine Popple site experiment, seedling propagation is currently underway and outplanting is scheduled for spring 2025.

4. Forest assisted migration in practice

Forest assisted migration research and operations are still in their infancy. Given that such studies are limited, relatively new, and require long-term assessment, it remains impossible to conduct a thorough review of FAM practice. Nevertheless, in Table 3 we summarize a few ongoing operational FAM studies (*sensu* Palik et al., 2022) – some published and some in progress – that capture a range of approaches currently underway in North America.

The diversity in the approaches taken by these FAM studies speaks to the variety of challenges and opportunities found across various forest types and project goals. One striking difference observed among the selection of FAM projects in Table 3 is the tradeoff between spatial

replication and design complexity within a site. At one end of the spectrum are studies that are constrained in species selection and experimental treatments within a site yet have expansive replication at a dozen or more sites sometimes distributed across hundreds of kilometers. Such broad geographic scope is possible when focusing on specific hypotheses (e.g., fixed vs flexible seed sourcing guidelines; Ertterson et al., 2020) or when implemented in a particular sociological and ecological context that enables generality. Such conditions are met in FAM studies located in the western USA (e.g., ENAMES, California Post-Fire Restoration) where forest cover is extensive and contiguous, fire is the predominant management challenge, and desired taxa are few, yet geographically widespread (chiefly, *Pseudotsuga menziesii* (Mirb.) Franco and *Pinus ponderosa* Lawson and C. Lawson). In contrast, in the eastern USA, land ownership patterns are smaller and patchier, interfering with regional tree migrations. Further, ecological stressors are more varied (e.g., fire, windthrow, pest outbreaks, overbrowsing), and tree diversity is greater at both local (i.e., alpha) and landscape (i.e., gamma) scales (Marks et al., 2016). In addition, phenology and seed production are cold-climate sensitive (i.e., late frosts), which may delay seed dispersal to more favorable habitats at the northern edge of their distributions (Sharma et al., 2022). Given this context, existing FAM studies in this region typically fall at the opposite end of the experimental design spectrum such that studies have greater complexity, but are limited in their spatial replication. These studies, including DREAM and the eastern USA Adaptive Silviculture for Climate Change sites (i.e., Cutfoot, Second College Grant), test several species, multiple assisted migration approaches (e.g., APM vs ASM), and explore the role of interacting environmental stressors. In this regard, DREAM is noteworthy in that it addresses Park and Talbot's (2018) recommendations to test several species in mixture, from multiple climate analogues obtained through bioclimatically precise sourcing (e.g., Champagne et al., 2021b) and planted under conditions designed to assess interactions among factors such as cervid browsing, competing vegetation, and microenvironment controlled by overstory manipulation.

Common among all operational studies is the relatively low number of seed sources tested. Several of the surveyed studies included both current and putatively future-adapted seed sources to allow testing of

Table 3

Summary of various characteristics of select forest assisted migration (FAM) studies in North America and how these respond to assisted migration research needs identified by Park and Talbot (2018). Sites listed include both the Desired REgeneration through Assisted Migration (DREAM) in Lac des Amanites, Québec, Canada and Pine Popple, Wisconsin, USA; the Adaptive Silviculture for Climate Change sites at the Cutfoot and Second College Grant (Minnesota and New Hampshire, USA respectively; see Muller et al. 2019; Clark et al. 2022), post-fire assisted migrations plantings in California, USA (Young et al. 2020), the Adaptation Forestry Study in Minnesota, USA; see Ertterson et al. 2020), and the Experimental Network of Assisted Migration and Establishment Silviculture (ENAMES; see Slesak, 2023).

	DREAM QC & PP	ASCC SCG	ASCC Cutfoot	CA Post Fire Restoration	MN Adaptation Forestry	ENAMES
N sites	1	1	1	3	16	25+
N species per site	9–10 ^a	8	8	6	2	1–4 ^d
Type of FAM	APM/ARE/ASM	APM/ARE	APM/ARE/ASM	APM	APM	APM
N Seed Sources	3	1	1–4 ^b	2–3 ^c	2	4
Mixed vs Monoculture	Mixed	Mixed	Mixed	Monoculture	Monoculture	Monoculture
Climate analogue informed seed sourcing	Yes	No	No	No	No	Yes
Cervid Access	Unfenced/Fenced	Unfenced/Fenced	Unfenced ^b	Unfenced	Fenced	Varies ^d
Competing Vegetation	Present/Weeded	Present/Weeded	Weeded	Weeded	Weeded	Varies ^d
Overstory Conditions	Multiple: Clearcut vs 40–50% Uniform Shelterwood	Irregular Shelterwood with 0.1–0.4 ha gaps in 20% of area	Expanding gap, irregular shelterwood initially with 20% of area in 0.2 ha gaps	Restoration plantings following fire	Clearcut	Generally post-fire with either dead overstory or following salvage harvest

^a The Lac des Amanites site in Québec, Canada has nine species whereas the Pine Popple site in Wisconsin, USA has 10 species.

^b Each species is represented by one seedlot except for *Pinus ponderosa* Lawson C. Lawson which contains four seed sources ranging from Nebraska to Montana. Conifers were bud-capped to protect from herbivory. See Muller et al. (2019)

^c *Pinus jeffreyi* Balf., *Calocedrus decurrens* (Torr) Florin, and *P. lambertiana* Douglas represented by two seedlots and *Pseudotsuga menziesii* (Mirb.) Franco and *P. ponderosa* Dougl. ex Laws by three seedlots.

^d Generally only one species is planted per site. By design, a variety of establishment practices are crossed with APM treatments depending on landowner preference, including vegetation or browse control, and treatments that test stock types.

whether FAM plantings produced a meaningful benefit over locally sourced seed. However, restricted climate-adapted seed sourcing invariably limits generality and risks failure as geographically precise climate-adapted seed source selection may, inadvertently, be maladapted to the specific conditions at the destination site (Breed et al., 2013; Bucharova, 2017). In contrast, common garden provenance studies often comprise a greater number of provenances for detecting genetic controls on specific traits (e.g., Ukrainetz et al., 2011; Benomar et al., 2016). Of particular note is the Assisted Migration Adaptation Trial (AMAT) which tested 15 different species with up to 10 seed sources at 48 sites throughout the Pacific Northwest in Canada and the USA (O'Neill, 2022). Unlike operational FAM studies, however, provenance trials seek to explore variation in tree performance (e.g., growth survival) across environmental clines and thus are largely open-grown monocultures in which competing vegetation and browsing is controlled. Thus, they provide crucial evidence on acclimatization and critical seed transfer distances (Pedlar et al., 2021), which can inform FAM practices, but are not sufficient to operationalize FAM practices. In contrast, DREAM is innovative in that it is explicitly designed to test transplanted seedling performance under a range of potentially interacting conditions (Park and Rodgers, 2023, this issue).

5. Conclusions

The various DREAM projects provide a unique framework that can be upscaled and tested in multiple environments. For all experimental sites, it was important to have considerable input from local land managers to help select sites, to define silvicultural scenarios, while also considering the feasibility of local seedling production. Seed procurement, especially for climate adapted seed sources, is likely to remain a significant challenge for FAM; therefore, operationalization will require increased capacity for seed procurement and seedling production, and innovation for producing species either never or rarely produced locally (Haase and Davis, 2017; Fargione et al., 2021). A current important challenge for FAM is the precise choice of seed sources for future climates. In the short term, seedlings may be maladapted to the destination environment, placing the experiments at risk for loss of planted stock. Prior controlled environment experiments before field establishment may reduce this risk of maladaptation, while permitting an improved understanding of the mechanisms of acclimation and adaptability. Data from these preliminary studies could also feed into site-level physiological models, or landscape-level simulation models, to give managers a glimpse of future scenarios of stand development and to account for spatial processes within the landscape. The choice of silvicultural system applied will ultimately influence abiotic and biotic conditions and their potential interactions to determine seedling establishment and long-term survival of trees.

Operationally, the DREAM framework responds to multiple, realistic challenges of FAM on the ground. The species mixtures promote resilience and multiple climate analogues permit the testing of responses to several climate scenarios, while variable experimental factors contribute to evaluating pertinent local abiotic and biotic conditions and interactions. This framework was conceived in the context of eastern North America, but very different approaches may exist (or are currently being tested) in different social, economic, and ecological contexts. Operationalized FAM studies, including DREAM, provide unique testing grounds to examine a myriad of important questions that may determine the success and impact of FAM. These studies may range from examining how species interactions, both within and among trophic levels, play out when novel tree communities are created (Refsland et al., 2023; Champagne et al., 2021a), to the social and cultural acceptability of these practices. Indeed, engaging with the public and Indigenous communities to enhance FAM literacy using a participatory process that is respectful of their views and values is among the key steps needed for wide-scale implementation of FAM (Peterson St-Laurent et al., 2018; Matson et al. 2021).

CRediT authorship contribution statement

Alejandro A. Royo: Conceptualization, Methodology, Writing – original draft. **Patricia Raymond:** Conceptualization, Methodology, Writing – original draft. **Christel C. Kern:** Conceptualization, Methodology, Writing – original draft. **Bryce T. Adams:** Methodology, Visualization, Writing – original draft. **Dustin Bronson:** Methodology, Visualization, Writing – original draft. **Emilie Champagne:** Methodology, Visualization, Writing – original draft. **Daniel Dumais:** Methodology, Visualization, Writing – original draft. **Eric Gustafson:** Methodology, Visualization, Writing – original draft. **Paula E. Marquardt:** Methodology, Visualization, Writing – original draft. **Amanda M. McGraw:** Methodology, Visualization, Writing – original draft. **Jessica Miesel:** Methodology, Visualization, Writing – original draft. **Alison D. Munson:** Methodology, Visualization, Writing – original draft. **Catherine Périé:** Methodology, Visualization, Writing – original draft. **Felipe J. Tavares Moreira:** Writing – review & editing. **Anne Ola:** Writing – review & editing. **Mathieu Bouchard:** Writing – review & editing. **Jean-François Bissonnette:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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