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Forest assisted migration

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Forest assisted migration

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Editorial: Forest assisted migration

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Editorial on the Research Topic
Forest assisted migration

Introduction

Recent research indicates that Forest Assisted Migration (FAM) may help mitigate climate change impacts on forests, with nearly 60% of studies supporting its use (Xu and Prescott, 2024). However, FAM poses risks, such as introducing invasive species and maladaptation (Chen et al., 2022), increasing susceptibility to pathogens (Grady et al., 2015), and raising social concerns (Hagerman et al., 2021).

This Research Topic considers the application of assisted migration practices to forest management. We have curated contributions from 65 authors studying 25 species across 11 articles grouped into four subtopics. All articles were published in a special *Frontiers in Forests and Global Change* Research Topic titled "*Forest Assisted Migration*." This Research Topic highlights the interdisciplinary nature of the research. The subtopics include:

1. Genetic and environmental factors influencing plant traits.
2. Assisted migration practices through field trials and silvicultural methods.
3. Social attitudes toward FAM and its implications for forest planning.
4. Models for improving the accuracy of seed transfer and species selection.

Some contributions cross multiple subtopics. Individually and collectively, this Research Topic substantially enhances our understanding of FAM's application.

Genetic and environmental factors

The establishment of provenance trials and common gardens are used to test tree species' responses and performance, often involving transfers across latitudinal or elevational gradients. Moving beneficial alleles may aid populations in adapting to climate change. Lebel Desrosiers et al. showed that acorn provenance (i.e., genetics) and site conditions (i.e., microclimate) can affect *Quercus rubra* survival and growth, with local provenances that are under water stress exhibiting the poorest overall survival. Streit et al. presented a large common garden study that will monitor (over the next 3–5 decades) the intraspecific variability and adaptability of 14 different genera, including 15 native and three non-native species, across a range of colder (and wetter) environments than those found in existing European experiments. Sáenz-Romero et al. found that environmental factors, particularly site climate (e.g., cold temperatures), had a greater impact than genetic factors on the responses of *Abies religiosa* populations, with seedling survival identified as the most critical response variable. Finally, Di Fabio et al. studied phenotypic plasticity and growth stability across species and emphasized the need for choosing stable provenances for assisted migration. They found that long-term climate conditions are more important than climate variability in predicting growth stability.

Field trials and silvicultural methods

Several papers use field studies to examine FAM's efficacy. Pedlar et al., leveraging their long-term experimental results (7–13 years), compared *Quercus* species on former agricultural sites, including seed sources from several hundred kilometers south of their study area, concluding that range expansion of broadleaf species has a good likelihood of success. Streit et al. described the rationale for a new experiment in Switzerland that includes 57 sites, 18 species, and 117 seed sources, emphasizing the need to include a wide range of climate and environmental conditions in common garden studies. Lebel Desrosiers et al. examined local and southern seed sources of *Q. rubra* in Quebec, Canada, finding that southern sources had higher survival and growth than local sources, and that soil moisture may be a limiting factor in range expansion. Nolet et al. presented a silvicultural framework for FAM using a patch-cutting approach that created a range of planting environments and provided replication of FAM at the stand-scale to aid monitoring. A study by Sáenz-Romero et al. examined the transfer of *A. religiosa*, the winter host of the Monarch butterfly, concluding that *A. religiosa* can be established up to 300 m above its current elevation limit, expanding the range of the species.

Social issues and forest planning

Social considerations, including stakeholder perceptions and public involvement, are crucial for successfully implementing assisted migration strategies. In the study by Moreira et al., a series of semi-structured interviews of stakeholders in Quebec, Canada, demonstrated support for assisted migration. However, the stakeholders emphasized the need for a cautious approach and pilot projects to test and verify impacts. Clark et al. also interviewed 33 natural resource managers in the Northeastern USA already engaged in climate change adaptation. The respondents were interested in diversifying current assisted migration approaches but were hesitant to engage with afforestation or the long-distance translocation of exotic species. Nolet et al. proposed that a patch-cut system represents an interesting low-intensity method to integrate assisted migration that could be more socially acceptable than planting after clearcuts. Bower et al. put forward and tested a practical FAM framework for planning assisted migration that should be suitable for all landowners and will aid future learning and implementation. Streit et al. emphasized the critical role of stakeholder collaboration in the Swiss Common Garden network. The stakeholders were consulted throughout the project's development phase, leading to more informed decision-making. Finally, work by Sáenz-Romero et al. exemplifies the need for assisted migration for conservation purposes, as demonstrated by the translocation of *A. religiosa* to higher altitudes for future Monarch butterfly habitat.

Models of seed transfer

Several articles within this Research Topic on FAM use innovative methods for modeling seed transfer and species selection. For example, Richardson et al. presented seed transfer approaches that identified climate analogs for North American biomes using Euclidean distance. In contrast, Adams et al. identified climatically-compatible seedlots for the eastern USA using climate projections based on the sigma (dis)similarity index. These models aim to match the future climate of a target site with the current climate of other locations. Species-independent approaches provide practical tools for identifying suitable planting locations, particularly for species with limited genetic data. These methods use a range of climatic variables, with temperature and moisture emerging as critical factors influencing the success of seed source transfers. Streit et al. established an extensive common garden network across Switzerland for species-specific insights. This network is a model for long-term, large-scale evaluation of multiple species and provenances, providing valuable data for future research and practical applications. Similarly, Sáenz-Romero et al. developed a predictive model based on field studies to assess the growth and survival of *A. religiosa* that offers crucial insights into creating potential future habitats for the Monarch butterfly.

Conclusions

Our Research Topic integrates innovative studies on genetic and environmental factors, field trials, social considerations, forest planning, and modeling techniques for seed transfer and species selection to guide the successful implementation of FAM practices into operational forest management. It highlights the importance of provenance trials and local adaptation for improving species' resilience to climate change. Engaging stakeholders and securing public acceptance are necessary to successfully apply FAM, requiring collaboration among researchers, managers, and communities. By adopting these interdisciplinary and collaborative approaches, we can help ensure sustainable forests that preserve biodiversity and support ecosystem services in a changing climate.

Author contributions

PM: Conceptualization, Writing – original draft, Writing – review & editing. BP: Writing – original draft, Writing – review &

editing. PN: Writing – original draft, Writing – review & editing. AM: Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Generative AI statement

The author(s) declare that Gen AI was used in the creation of this manuscript. Elicit Pro was used for conducting a literature search (Elicit: The AI research assistant; https://elicit.com; accessed November 12, 2024). Grammarly Premium was used to check grammar and conduct plagiarism and AI text checks (Grammarly Premium; https://app.grammarly.com; assessed December 3, 2024).

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A climate analog approach to evaluate seed transfer and vegetation transitions

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Introduction: There is growing recognition that restoring species diversity is crucial to maintaining ecological functions and services. Increasing the diversity of species used in restoration programs has placed greater emphasis on determining the seed transfer needs for a wider array of plants. However, many plants, outside of commercial forestry, lack information that would provide guidance on seed transfer for current or future climates. Generalized seed transfer approaches use climate partitioning to approximate adaptive differentiation among populations and provide an estimation of seed transfer distance for such species.

Methods: Herein, we describe a generalized seed transfer approach that uses Euclidean distance of 19 climate variables within North America (from northern Honduras to the Arctic). Euclidean distances are used to identify climate analogs from vegetation databases of about 685,000 plots, an average density of 1 plot per 32 km^2. Analogs are classified into three thresholds (strong, moderate, and weak) that correspond to altitudinal climate gradients and are guided by the scientific literature of observed adaptive variation of natural tree populations and seed transfer limits.

Results: For strong threshold observations, about 97% of the analogs had climate distances equivalent to $\leq$300 m elevation, whereas for the weak threshold observations, 53% had an elevation equivalence of $\leq$300 m. On average 120, 267, and 293 m elevation separated two points under strong, moderate, and weak thresholds, respectively. In total, threshold classification errors were low at 13.9%.

Discussion: We use examples of plot data identified from a reference period (1961–1990) and mid-century (2056–2065) analogs across North American biomes to compare and illustrate the outcomes of projected vegetation change and seed transfer. These examples showcase that mid-century analogs may be located in any cardinal direction and vary greatly in spatial distance and abundance from no analog to hundreds depending on the site. The projected vegetative transitions will have substantial impacts on conservation programs and ecosystem services. Our approach highlights the complexity that climate change presents to managing ecosystems, and the need for predictive tools in guiding land management decisions to mitigate future impacts caused by climate change.

KEYWORDS

assisted migration, climate change, decision support tool, Euclidean distance, novel climates, reforestation, restoration, vegetative transition

1 Introduction

There is a growing appreciation for restoration that encompasses proactive planning and broadening species diversity (Erickson and Halford, 2020), but genetic information remains scarce for many ecologically important plant species, especially in countries with high biodiversity like México, creating a dilemma for restoration and reforestation programs. On one hand, focusing restoration on well-researched restoration species can limit species diversity and ecological function (Cadotte et al., 2011); on the other hand, expanding the number of restoration species to those that lack genetic information could lead to misguided seed transfer, resulting in maladaptation or outbreeding depression (McKay et al., 2005). Decision support tools that recognize the risks and limitations of seed transfer and broaden the palette of under-utilized species can augment restoration and ecosystem service outcomes by increasing flora and fauna diversity.

Defining the climate space that reflects genetic adaptation is integral to seed transfer and assisted migration. To provide seed transfer guidance for species lacking genetic information, researchers have developed varied approaches using partitioned climate data. One approach defines temperature and aridity thresholds for climatic surfaces to delimit zones for seed transfer (Bower et al., 2014; Castellanos-Acuña et al., 2018; Pike et al., 2020). Another approach uses climate-based Euclidean distance, hereafter referred to as climate distance, to provide a calculation of climate (dis)similarity. Climate distance has been used to identify climate appropriate crops (e.g., Ramírez-Villegas et al., 2011), future refugia (Michalak et al., 2018), and seed transfer zones for wildland restoration (Doherty et al., 2017; Shryock et al., 2018; St Clair et al., 2022). For example, Seedlot Selection Tool (SST, St Clair et al., 2022) is an interactive webtool that calculates climate distance based on user-specified locations. This webtool provides guidance to species seed transfer for which genetic information is not necessarily available, enabling the development of restoration programs for ecologically important species. However, SST requires user-selected climate variables and transfer limits. User-selected variables and limits could lead to either under or over estimation of seed transfer limits depending on the user's knowledge of the species, climate, and climate variation occupied by the species. Because plants can be adapted to seasonal temperature, precipitation, and their interactions (e.g., Putz et al., 2021; Richardson et al., 2021), defining seed transfer limits with a few climate variables can lead to an overestimation of seed transfer limits. More precision in defining climate is needed when considering wide-ranging species and assisted migration due to climate change.

We offer an approach for calculating climate distances to identify future climate analogs—sites with contemporary climate similar to the future climate at a target location. Analogs are drawn from biome and plant inventory databases which provide projections of potential future vegetation for developing strategic seed transfer and proactive restoration plans. The approach is species-independent, operating entirely in climate space, incorporating 19 climate variables, and projections for three Representative Concentration Pathways (RCPs) from three general circulation models (GCMs) for future mid-century climates (IPCC, 2014). We take into consideration a large amount of variation that accompanies future climate projections and simplify the decision process by averaging large climate variability into a single criterion to determine climate analogs. As such, the approach has broad applicability, from land use management to municipal planning. Thus, we hope that our work might contribute to fill an information gap between complex research papers showing the large extent of diverse combinations of GCMs, scenarios of accumulated greenhouse gas emissions and projected climate futures, and on the opposite spectrum, an urgent need for tools to guide practical forest management decisions by foresters and conservationist practitioners. The need to move on from the academic rumination to specific forest management decisions to face climatic change impacts, is becoming more urgent, due to the current acceleration of climatic change (Hansen et al., 2023; Sáenz-Romero, 2023).

We define three analog classes, referred to as thresholds, as an interpretative aid by relating Euclidean climate distances to documented genetic responses to climate. To do this, we note that historic case studies of geographic variation in forest trees, patterns of genetic variation invariably were related to either latitude or elevation, promoting the conclusion that clines in intraspecific genetic effects were largely controlled by temperature (Sorensen, 1992, 1994). Recent climate-based genecological studies (e.g., St Clair et al., 2005; Joyce and Rehfeldt, 2013, 2017; Leites and Benito-Garzón, 2023) have verified this conclusion, although clines occurring along temperature gradients can either be steep (adaptive specialists, Rehfeldt, 1994a,b; St Clair et al., 2005) or shallow (adaptive generalists, Rehfeldt, 1986; Leites and Benito-Garzón, 2023). In specialists, for instance, the interval across which genetic differentiation is first detected can be as small as 300 m elevation, while in generalists, the interval can be 500 m or higher. Indeed, adiabatic effects govern elevation's negative correlation with temperature and positive relationship with precipitation, and these relationships have pronounced effects on ecology (Dobrowski et al., 2009). Therefore, to provide context to Euclidean climate distances, we use elevation to link climate distances, temperature, and genecology. We argue that climate distance thresholds can be defined from the relationship between climate distances and elevation, that is, their equivalence.

Altitudinal clines are well documented, but the interval across which differentiation can be detected varies between specialist and generalist species (e.g., Rehfeldt, 1994a,b). Yet, there are almost no cases where documented clines have been so steep that climate-induced genetic differences could be expected at altitudinal intervals <300 m (e.g., Sorensen, 1992, 1994; Rehfeldt et al., 2020). Adiabatic lapse rates, which are depicted in mean annual temperature estimates from spline surfaces [see Sáenz-Romero et al. (2010)], suggest further that annual temperatures should change by only 1.5°C across a 300 m interval. We reason that climate distances equivalent to an altitudinal difference of 300 m would make a biologically reasonable upper threshold for defining analogous climates. We reason further that a logical upper limit for the strong analog class would be a climate distance equivalent to a 200 m elevation difference, also equivalent roughly to MAT = 1°C. Temporal fluctuations in weather and topographic effects such as aspect seemingly dwarf subtle climate differences at scales less than 200 m (Holden et al., 2011; Rehfeldt et al., 2015) and, therefore, finer resolution of climate distances would be a false precision. For subtending the moderate analog class, we simply use the climate distance midway between that for the strong and weak analog classes.

Our goals are to: (1) present and illustrate a climate distance approach to locating reference period climates (1961–1990) that are climate analogs to projected mid-century climates (decade centered in 2060: 2056–2065) for target locations, (2) define climate analog thresholds by relating climate distances to elevation differences along altitudinal clines at a random selection of geographic points, and (3) infer vegetative changes to plant communities, potential impacts to conservation, and the climatic factors affecting these changes using target locations examples from a wide array of contrasting North American ecosystems.

2 Materials and methods

2.1 Analytic overview

Euclidean distances between a targeted location and reference period climates were calculated with the 'yaImpute' (Crookston and Finley, 2007) and 'gower' (Gower, 1971) packages for R (R Development Core Team, 2021) using 19 climate variables. The yaImpute algorithm calculates nearest neighbor statistics between all observations in the reference period dataframe with each observation in the target dataframe, defined below (see 2.1.1). All climate variables were standardized before analysis to assure that climate distances calculated from disparate databases and disparate geographic localities would be derived from the same statistical distributions and, therefore, be comparable. Because standardization was done prior to analysis, yaImpute's 'raw' option was used to calculate Euclidean distances. Examples of the R code for the methods described here and below can be found at https://github.com/ermilano-fs/ClimDist.

2.1.1 Reference period climates

All climate estimates used herein are from the thin plate splines of Rehfeldt (2006) and Sáenz-Romero et al. (2010), available online at https//charcoal2.cnre.vt.edu/climate/. We use the term 'reference period climate' for 1961–1990 normals from this climate model. The reference period, therefore, is not only incipient to anthropomorphic climate change but also approximates the climate when much of the current plant communities became established. Additionally, the 'target' is the site for which reference period or mid-century climate analogs are desired.

Nearest neighbor climate analogs for target locations are drawn from a pool of locations within five reference period vegetation databases (Table 1). Four of these databases contain ground plot species identifications; one contains North American biomes. Together, these databases contain 1961–1990 climate normals from about 685,000 locations in North America, a density of approximately 1 plot per 32 km^2.

2.1.2 Future target climates

Target dataframes consist of mid-century climate estimates for locations where contemporary analogs are desired. Nearest neighbors are those locations with 1961–1990 climates most similar to the future climate of the target. Future climate estimates of target locations were calculated as the mean of 13 projections of 2060 climates. The projections include five GCMs and 3 RCP scenarios (Supplementary Table S1). See Van Vuuren et al. (2011) for supporting documentation.

2.1.3 Climate variables

Euclidean distances are based on 19 climate variables (Supplementary Table S2) and are of documented utility in studies of plant responses to climate (e.g., Sáenz-Romero et al., 2010; Rehfeldt et al., 2012; Chaney et al., 2017; Worrall and Rehfeldt, 2021). Climate variables include six variables of temperature, seven precipitation variables, and six variables involving temperature-precipitation interactions. Temperature was selected to depict winter cold, summer heat, continentality, and the onset of spring; precipitation variables express the amount and periodicity of precipitation; and temperature-precipitation interactions (e.g., aridity indices) concentrate on the balance between heat and moisture both seasonally and annually.

While collinearity is of no consequence in calculation of the climate distances, surrogates could unduly bias estimates of climate distances. To be sure, on a continental scale, several of our variables show strong simple correlations. Yet, because of this geographic scale, the coefficients are misleading. According to the biome database (Table 1) for instance, the correlation between DD5 and MAT is $r = 0.91$; yet the relationship is pronouncedly non-linear. For D100 and MAT the correlation is $r = -0.94$, but for D100 = 200, MAT can range from −15°C to 3°C. We maintain that the array of climate variables we use refines the climatic breadth of reference and target sites to provide a necessary specificity for choosing analogs.

2.1.4 Standardization

Nearest neighbor analyses frequently employ standardizing procedures to convert variables to a distribution with a mean of zero and a variance of 1, thereby providing equal weights to the variables. Because operative climate variables are not known for most species, we transformed climate variables to standard normal deviates before analysis. First, a climate dataset was built by randomly selecting 988 locations (Figure 1) from the North American biome database between 14° to 60° latitude and 250 m to 3,200 m elevation. Our goal

TABLE 1 Climate databases used as reference period (1961–1990) files.

Database	Basic unit	Species identification	Records (K)	Compiler
North America biomes	Shape file polygons	None	436.5	Rehfeldt et al. (2012)
West USA forest inventory	Ground plots	Forest trees	101.0	Rehfeldt (2006)
East USA and Eastern Canada forest inventory[1]	Ground plots	Selected conifers and hardwoods	104.8	Joyce and Rehfeldt (2017)
Mexico forest Inventory	Ground plots	Conifers	20.7	Sáenz-Romero et al. (2012)
BLM Geospatial	Ground plots	Selected shrubs, forbs and grasses	21.9	Herein[2]

[1]Incomplete south of 35°N. [2]Data source: https://gbp-blm-egis.hub.arcgis.com/pages/aim, accessed November 2022.

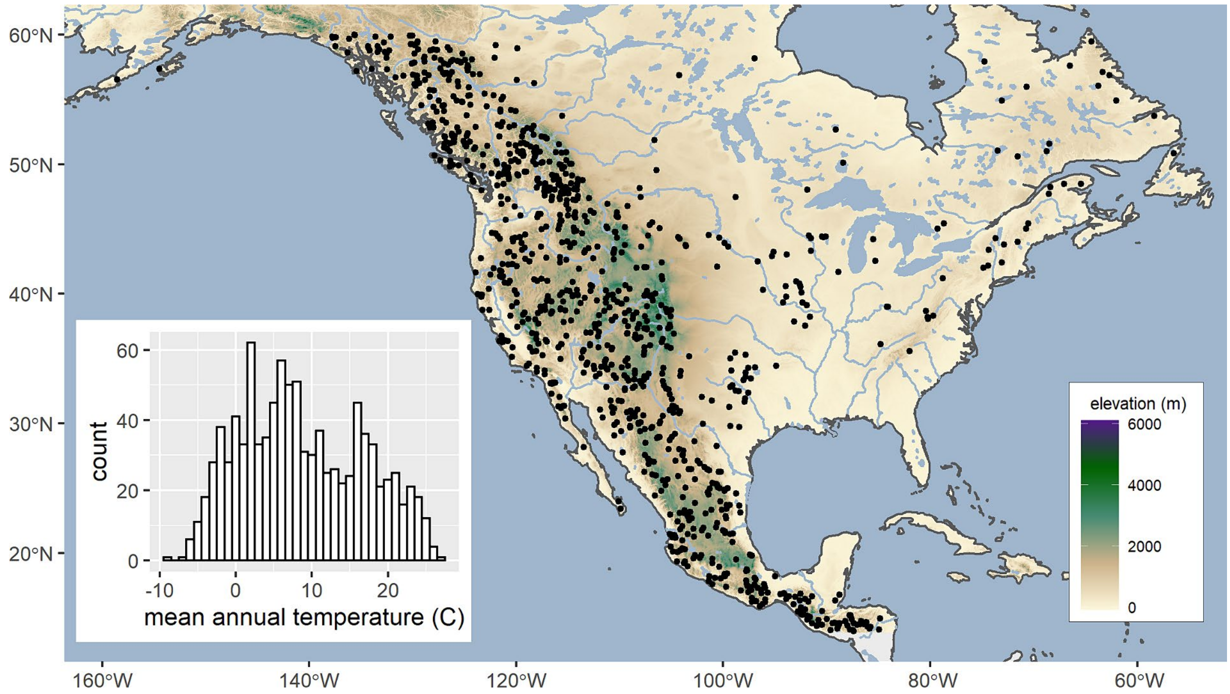

FIGURE 1
Geographic distribution of 988 locations (points) and their mean annual temperature distribution (histogram inset) used to construct a dataset for defining analog thresholds.

was to provide a broad range of climates representative of the continent's vegetation (Figure 1, insert). However, the biome database was built by sampling shapefiles at a rate inversely proportional to their size, so our sample was concentrated in mountainous regions where climate heterogeneity is greatest. Elevation restrictions were imposed to facilitate the definition of climate distance thresholds (see section 2.2). Then, target and reference dataframes were standardized by subtracting the means and dividing by the standard deviations (Supplementary Table S2) for climate of Figure 1 locations. This process assures that Euclidean distance output from our analyses are comparable despite disparate input. Because our calculations occur entirely within climate space, the lack of a quasi-systematic geographic sample is immaterial.

2.2 Thresholds

To calculate thresholds for the Euclidean climate distances, we constructed a series of synthetic altitudinal clines of 500 m centered on each of the 988 locations of Figure 1. Each cline was then sampled at a 10 m interval. Because the spline climate model uses latitude, longitude, and elevation as predictors, climate estimates produced for this dataset consisted of 51 observations with the same coordinates but differing elevations for each of the 988 locations.

Euclidean climate distances were calculated between the 51 observations in the same cline to produce ≈1.25 million climate distances between pairs of observations at known differences in elevation but with the same geographic coordinates. Because the altitudinal clines consisted of 51 data points, the elevation differences within each cline consisted of only 50 unique values with a highly disproportionate number of observations having the same elevation difference. There were, for instance, 48,410 observations in this dataset with an elevation difference of 10 m, but only 988 observations with an elevation difference of 500 m. As a result, the variance in climate distance was directly proportional to the elevation difference (Supplementary Figure S1). Therefore, to relate climate distances to elevation differences, we used the mean climate distance for each value of elevation differences in a linear regression (R base, R Development Core Team, 2021) of climate distance on elevation difference with 48 degrees of freedom. Predicted climate distances at 200 m and 300 m established the upper thresholds for strong and weak analogs, respectively. Moderate analogs were equated to the climate distance midpoint.

To evaluate the effectiveness of these thresholds, we selected at random 25,000 data points from $15^\circ \leq \text{latitude} \leq 60^\circ$ and $-130^\circ \leq \text{longitude} \leq -90^\circ$ from the biome database and calculated climate distances from each point to that of all other data points lying within ±0.025° in latitude and longitude. The maximum geographic distance between observations in this dataset was 3.1 km, assuring low impacts of geographic distance on climatic differences. After discarding all observations with climate distances of zero, the resulting dataset contained about 48,500 observations. However, the observations were highly skewed toward low differences in elevation: nearly 60% involved data points <100 m apart, and about 30% were of locations within 25 m of each other. To create a balanced dataset for verification analyses, we obtained a random sample of about 5,000 observations from each of 4 classes of elevation differences: 0–100, 100–200, 200–300, and >300 m. The sample for the 0–100 class was composed of 25% from 0 to 25 m, 25% from 25 to 50 m; and 50% from 50 to 100 m.

TABLE 2 Confusion matrix showing the error structure when climate distances are classified by analog thresholds and segregated according to elevation differences between pairs of point locations.

Climate distance thresholds	Elevation difference (m)				Row sum
	0–200	200–250	250–300	>300	
Strong analogs	9,279	1,759	753	410 (0.034)	12,201
Moderate analogs	296	427	515	641 (0.341)	1,879
Weak analogs	157	206	287	785 (0.547)	1,435
Dissimilar	268	337	408	3,911	4,924
Column sum	10,000	2,729	1,963	5,747	20,439

The dataset is independent of that used to develop the thresholds. Threshold errors in commission, false positive frequency for elevation differences >300 m, [e.g., 1 – (9,279 + 1,759 + 753/12201)] are shown in parentheses. Error of commission[1] was 0.119; error of omission[2] was 0.069; and the total error[3] was 0.139.

[1] Proportion false positives = (410 + 641 + 785)/(12,201 + 1879 + 1,435). [2] Proportion false negatives = (268 + 337 + 408)/(10,000 + 2,729 + 1963). [3] Proportion total errors = (268 + 337 + 408 + 410 + 641 + 785)/20,439.

We then tallied the number of strong, moderate, and weak climate analogs for the classes of elevation differences to produce a confusion matrix.

2.3 Illustrating climate distance analogs

For mapping, we used the digitized elevation model of the GLOBE Task Team (1999) and R packages 'ggplot2' (Wickham, 2016) and 'terra' (Hijmans et al., 2022) to illustrate for numerous geographic locations (Supplementary Table S3) having applications in restoration or reforestation. In the case studies below, all climate analogs are mapped across geographic window, North America. Rasters of analog predictions used the climate grids at https//charcoal2.cnre.vt.edu/climate/. When compiling potential species composition for contemporary analogs to the contemporary climate of a target, we use ≥30 strong analogs per target location. Species composition for the future climate of a target is dependent on the number of analogs found.

3 Results

3.1 Analog class thresholds

The regression of climate distance on elevation differences had 48 degrees of freedom and produced a fit that was nearly perfect ($R^2 = 0.9999$, Supplementary Figure S1). Predicted values of climate distance for 200 and 300 m of elevation difference produced a threshold of 0.60 for strong analogs and 0.84 for weak analogs with a midpoint of 0.72 for moderate analogs. On average, strong analogs had an elevation equivalency between 0 and 214 m; moderate analogs between 214 and 268 m; and weak analogs between 268 and 302 m.

An empirical assessment of the efficacy of our thresholds is summarized in Supplementary Table S4. Cumulative distributions within analog thresholds showed that for strong analogs, 50% of the analogous pairs fell within 100 m of each other and 98% were within 300 m. Pairs within this class differed in altitude by 120 m on average. For moderate analogs, the average elevation difference between pairs was 267 m, and 68% of the pairs were within 300 m of each other. Weak analogs averaged 293 m separation on average with 53% of pairs being less than 300 m apart (Supplementary Table S4). False positives arise from the variances within classes (Supplementary Figure S1), which are attributable to imperfect relationships between climate model estimates and adiabatic lapse rates, particularly for locations lacking topographic diversity.

The confusion matrix (Table 2) produced from an independent evaluation of classification errors allowed quantification of the risks associated with each threshold. Errors of commission (false positives) are observations classified as analogs but involve elevation differences >300 m. For observations classified as strong analogs, only 410 out of 12,201 (3.4%) involved locations separated by more than 300 m elevation. Therefore, strong analogs at target locations are correctly classified at 96.6% below 300 m elevation and 76% below 200 m. Moderate analog target locations were correctly classified at 65.9% below 300 m, while weak analogs dropped to 45.3% below 300 m. The summaries suggest high confidence in the strong analog classification, but low confidence in weak analogs, as their error was more than 50%. In total, errors of commission amount to 11.8%, and errors of omission (false negatives) are 6.9%. Together, the errors produced by our classification system were 13.9%.

3.2 Focal point climate analogs

We chose two target locations, Moscow Mountain (northern Idaho, United States) and Tiger Mountain (northwestern Washington, United States), to illustrate our approach. First, at Moscow Mountain mapped mid-century analogs (Figure 2A) depict a downward shift in elevation compared to the reference period shown in the elevation profiles (Figure 2B). This example also shows the relationship between climate distance thresholds and elevational breadth. Weak thresholds (dark blue), representing adaptive generalists, span wider ranges of elevation (e.g., 1,000 m under the reference period), whereas strong thresholds (red), representing adaptive specialists, span the narrowest ranges of elevation (e.g., 600 m). At Tiger Mountain our analyses detected numerous climate analogs to this site for the reference period, 164 of which were strong (red dots, Figure 3A). The strong analogs surround the site in both elevation and geographic distance. Only six analogs were found for the mid-century climate, and only one of them was strong (Figure 3B). The strong analog is ~200 km to the south and ~250 m lower in elevation than the target location. In addition to the single strong analog, the algorithm located two moderate analogs (violet dots) and three weak analogs (dark blue dots, Figure 3B). Nearest neighbors with climate distances outside the 0.84 threshold are plotted as white dots, which we use occasionally in subsequent

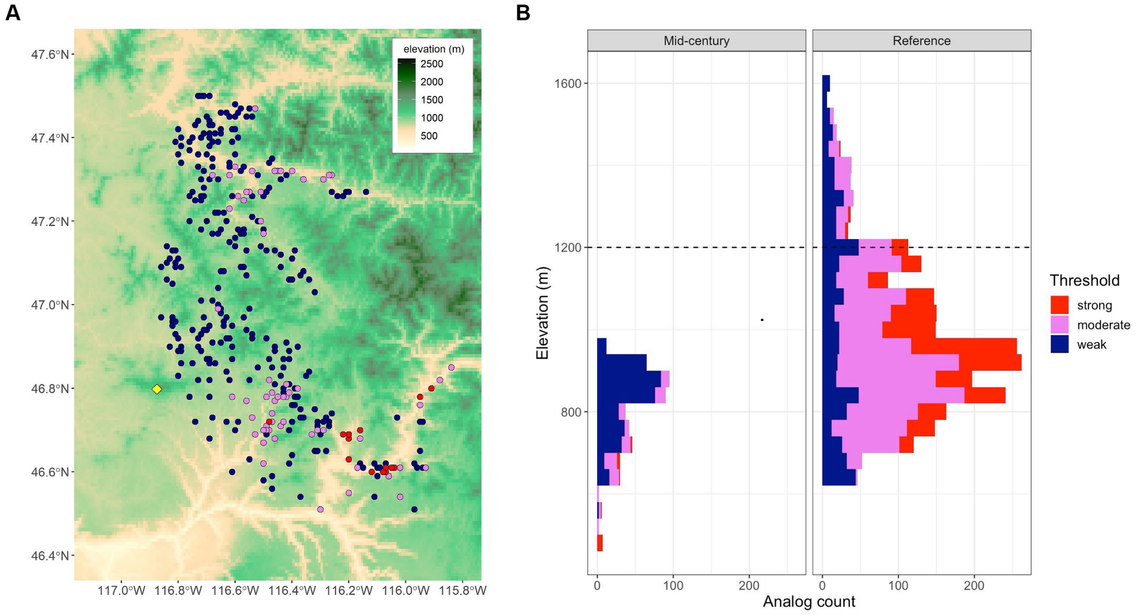

FIGURE 2
(A) Map of mid-century (2055–2065) climate analogs for the Moscow Mountain target location (yellow diamond) in northern Idaho, United States. **(B)** An elevation profile of analog counts for the mid-century (shown in **A**). A reference period (1961–1990) analog elevation profile is shown for comparison. The dashed horizontal line indicates the elevation of the target location.

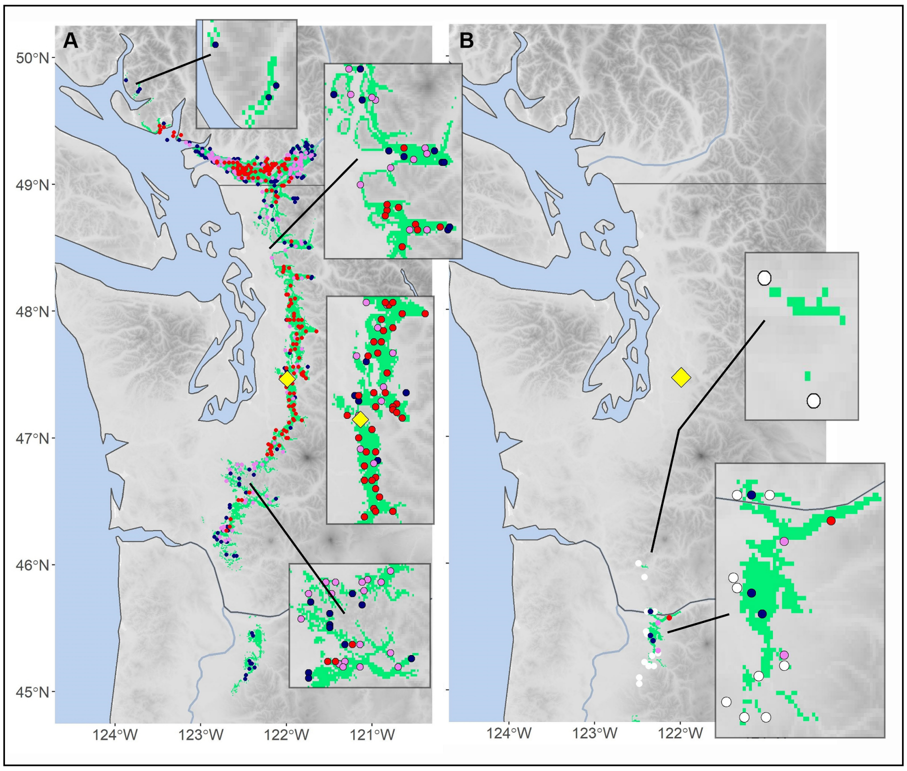

FIGURE 3
(A) Reference period climate (1961–1990) and **(B)** mid-century (2055–2065) analogs (colored circles) for the target location, Tiger Mountain, in the Pacific Northwest (Oregon and Washington, United States). The yellow diamond indicates the target location, with strong, moderate, and weak analogs represented as red, violet, and blue colored circles, respectively. In **(B)**, white circles show nearest neighbors too distant to be considered analogs. The green gridded polygon represents areas under all three classes (i.e., weak to strong threshold).

maps. In addition to mapping analog point locations from plot data, we predict the location of analogs on a 1 km grid of climate variables. In Figure 3, gridded predictions of all three analog classes are colored green. The green encapsulates the plot data supporting the low levels of classification errors.

The single strong analog to the future climate of the Tiger Mountain target offers a glimpse at the internal functioning of the climate distance function. During the reference period, the target had a mean annual temperature (MAT) = 9.7°C and a mean annual precipitation (MAP) = 1,664 mm. According to the mean of 13 GCM climates for 2060, the future climate at this site would have MAT = 12.9°C and MAP = 1,683 mm. Our algorithm locates the strongest climate analog (red dot, Figure 3B) to this site at 211 km to the south and 250 m lower in elevation, having a reference period MAT = 11.7°C and MAP = 1,676 mm. The future climate of the target and the reference period climate of the closest neighbor have a climate distance of 0.591, slightly beneath the strong analog threshold for two sites differing by 1.2°C in MAT and 19 mm in MAP.

By assessing the vegetation components of analog sites, we would conclude that at Tiger Mountain, the reference period vegetation that is dominated by *Pseudotsuga menziesii* and *Thuja plicata* would continue to be suited to the future climate. Yet, it is probable that the most suitable populations for the mid-century climate would originate from the south and lower elevations. Further examples from other biomes with varied analog outputs are provided in the Supplementary Figures S2–S5.

4 Discussion

We present a climate distance–nearest neighbor approach to locating mid-century climate analogs by searching biome and species inventory databases containing climate estimates for point locations. The approach is independent of species genetic information. Populations of all species occurring at the analog site should be suited to the mid-century climate of the target location. This species independence is a distinguishing feature of our approach from trait-based seed transfer approaches (e.g., Rehfeldt et al., 2014; Richardson and Chaney, 2018) and carries advantages and disadvantages for developing seed transfer guidance. The advantage is that the approach can be applied without genetic information, which would benefit many research limited plant species, especially in regions or countries with high biodiversity. The disadvantage is that this approach can potentially be excessively specific to generalists, species that have broad adaptive clines [e.g., *Pinus monticola* (Richardson et al., 2009) and *Thuja plicata* (Rehfeldt et al., 2020)]. For instance, the analogs found for an Ontario, Canada location (Supplementary Figure S4) are closely consistent with results of niche models coupled with genecology estimates made for two species of the region, *Pinus strobus* (Joyce and Rehfeldt, 2013) and *Picea mariana* (Joyce and Rehfeldt, 2017), but the species-specific models provide land managers with greater flexibility in obtaining seed. Nonetheless, our analog approach can be guided using lower thresholds (moderate or weak) for species that are thought to be generalist.

We take the rationale that GCMs and RCPs largely vary in the timing of climate change (Rehfeldt et al., 2012, 2014; Joyce and Rehfeldt, 2013), rather than if climate change will occur. Accordingly, given the variability among climate model projections and carbon emission scenarios, we chose to provide a consensus based on an average of 13 GCMs. Our focus is mid-century, as these projections would have higher certainty than longer timeframes (Fitzpatrick et al., 2018) and are within long-term timeframes of land management planning and lifespans of the organisms that occupy existing ecosystems.

As a basis for discussing our approach, we consider case studies for four themes: management implications for the high latitudes of Canada's boreal forest where climate change is projected to be most pronounced, climate novelty in the Great Basin of western United States, conservation concerns in Mexico's Transvolcanic region, and assisted migration to accommodate shifts in forest composition. Maps contained in the Supplementary Material provide additional natural resource implications for diverse geographic regions.

4.1 High latitude analogs

High latitudes (>58°N) target locations showcase the pronounced and varied vegetation transitions predicted from mid-century climate change. Two target locations that illustrate this variation in spatial distances required to accommodate climate-adapted plant species and populations are found in northern British Columbia (Figure 4)—Muncho Lake and Fort Nelson. These two locations are at similar latitudes and separated by 175 km, but the former is in Canada's Western Cordilleran Physiographic Province, while the latter is in the Interior Plains Province and is 450 m lower in elevation. Our analog analysis, using the biome database (Table 1), suggested that the reference period at Muncho Lake was suited to vegetation from the Canadian taiga tending toward transition with tundra vegetation (Supplementary Table S5). Mid-century strong analogs indicated boreal vegetation without tundra and were found ~150 m lower and ~ 500 km southeast of the site (Figure 4A). At Fort Nelson, reference period analogs were boreal, but mid-century analogs suggested that the vegetation could transition from boreal to northern temperate hardwoods, currently occurring about 1,900 km to the southeast (Figure 4B). Further analyses using the eastern inventory database (Table 1) suggested that eastern species such as *Acer rubra*, *Fraxinus nigra* and *Quercus* species would be suited to the future climate at Fort Nelson. Although boreal species such as *Betula papyrifera, Picea mariana,* and *Abies balsamea* should continue to persist at Fort Nelson, the populations most suited to the mid-century climate currently occur far to the southeast.

4.2 Challenges to restoration in the Great Basin

Sagebrush ecosystems are widespread plant communities in the cold deserts of western North America. Target locations of sagebrush indicated decreasing availability of mid-century analogs with decreasing elevation. Low elevation sites (<1,400 m) trended toward no analogs (e.g., Figures 5A,B), while higher elevation sites (>2,000 m) maintained or gained analogs (Figures 5C,D). Using a broader examination of 60 sagebrush sites, we found that target locations abruptly decreased from abundant analogs to no analogs as summer dryness index (SDI, Supplementary Table S2) increased >0.2 (Figure 6). The relationship between SDI and analog abundance

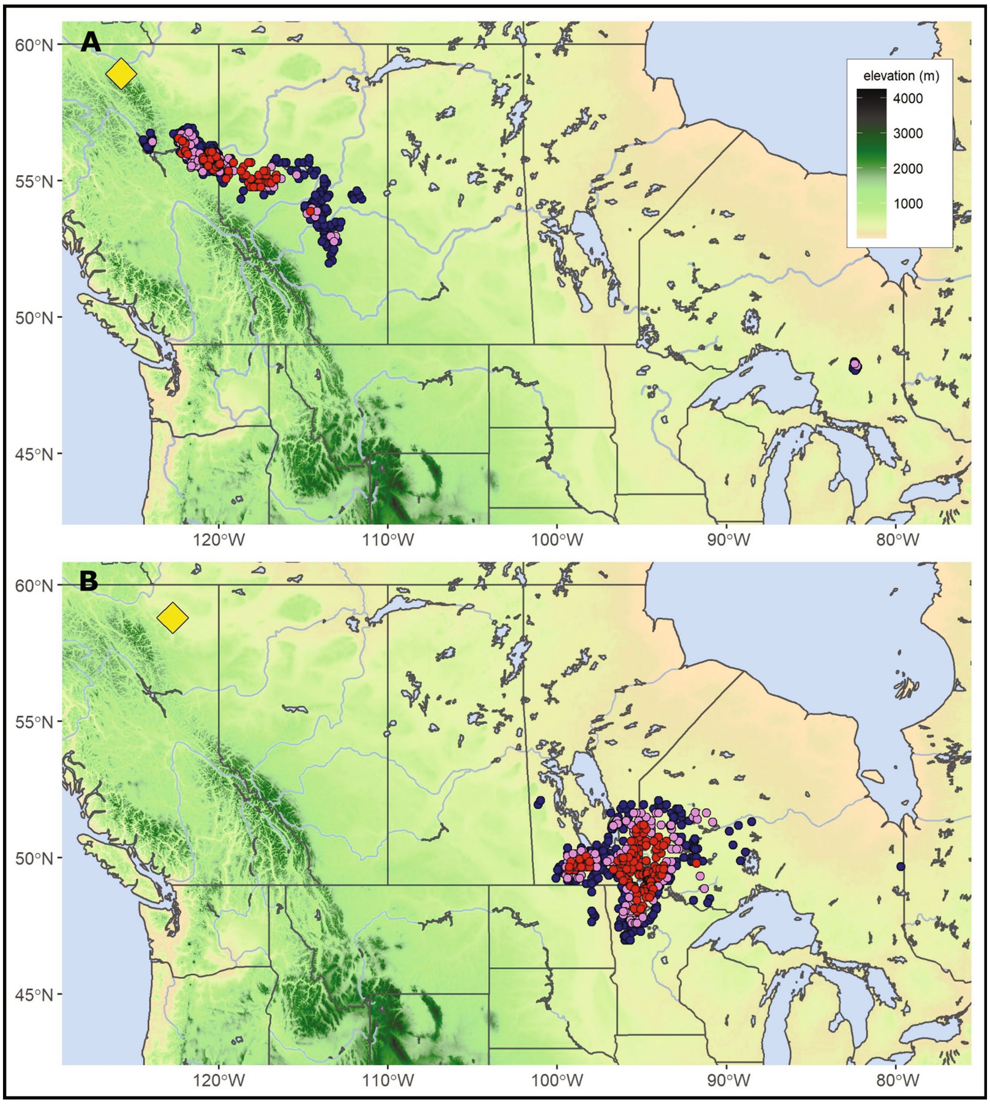

FIGURE 4
A comparison of boreal forest analog variation under mid-century climate. Target locations Muncho Lake **(A)** within the Western Cordilleran Physiographic Province and Fort Nelson **(B)** within the Interior Plains Province are boreal forest sites separated by 175 km and 450 m in elevation. The yellow diamond indicates the target location with mid-century strong, moderate, and weak analogs represented as red, violet, and blue circles, respectively.

suggested that the warmest and driest Great Basin sagebrush sites could have climate novelty by mid-century. Given the general geographic overlap between our predicted climate novelty, regions of low sagebrush resistance and resilience (Chambers et al., 2023), predicted range contraction of big sagebrush (*Artemisia tridentata*, Still and Richardson, 2015), and the occurrence of invasive cheatgrass (*Bromus tectorum*, Bradley and Mustard, 2006), it is plausible that invasive species could be both a predictor and outcome of climate novelty at least in Great Basin. Elsewhere, these trends may be more unpredictable (Bradley et al., 2010). Further examples of locations with varying abundance of mid-century analogs are shown in the Southeast (Supplementary Figure S5) and Pacific Northwest, United States (Supplementary Figure S6). The areas surrounding these no-analog locations have been identified in other studies as regions with novel future climates (Rehfeldt et al., 2012; Mahony et al., 2017).

Management actions suitable for no analog climates are largely unexplored. As shown repeatedly in the paleoecologic record (e.g., Ackerly, 2003), plant associations change as, presumably, competitive interactions among species readjust. Perhaps, therefore, a ‘wait and see’ or ‘let nature take its course’ approach would be the most reasonable. However, these strategies would have to be weighed against risks to threatened and endangered species and ecosystem services. Assisted migration may be a critical component to ecosystem restoration for novel climates, but with no recent historical ecological context to the predicted climates [see Burke et al. (2018)], information is extremely limited to guide management (Mahony et al., 2017).

4.3 Conservation of Mexico’s transvolcanic region

Mexico’s transvolcanic region (an east–west mountain range of high elevations at central Mexico, also known as Trans-Mexican Volcanic Belt) provides examples of analog analyses useful for

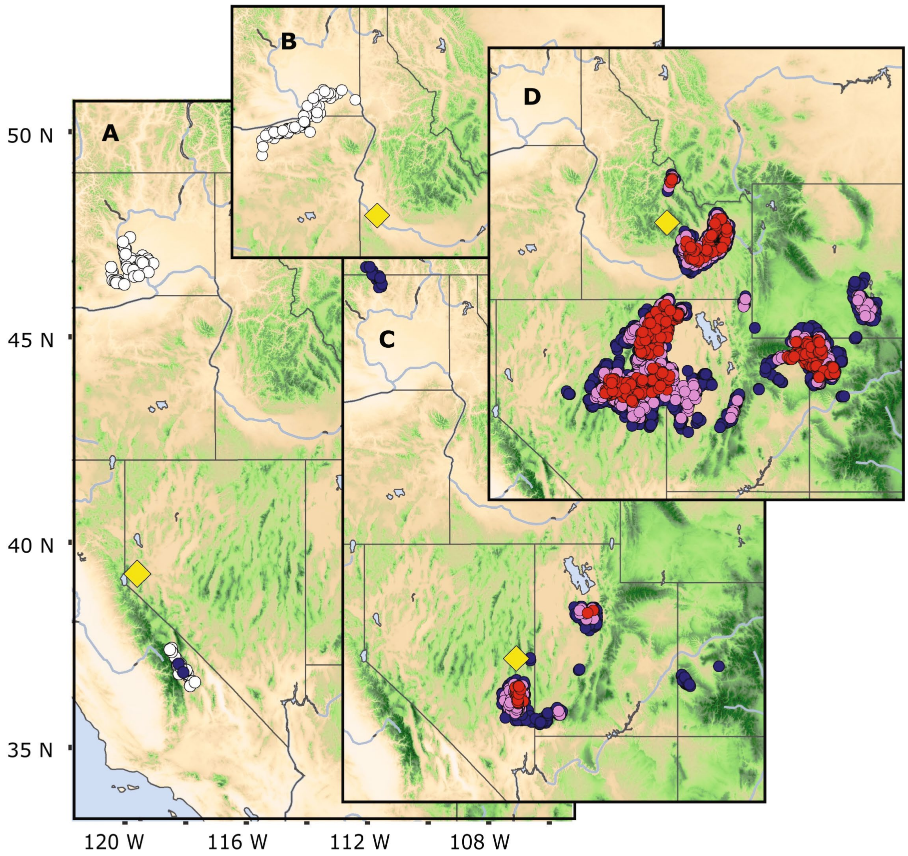

FIGURE 5
Sagebrush target locations, Dayton **(A)**, Birds of Prey **(B)**, Conner Canyon **(C)**, and Trail Creek **(D)** in the USA intermountain region, showing mid-century analogs sites. Lower elevation sagebrush sites, **(A,B)** have few to no analogs, respectively. Higher elevation sagebrush sites, **(C,D)** have numerous analogs during the mid-century. The yellow diamonds indicate the target locations, with strong, moderate, and weak analogs represented as red, violet, and blue colored circles, respectively. White circles show nearest neighbors >0.84 threshold, too distant to be considered analogs.

conservation planning (Figure 7). Forest species, such as *Pinus hartwegii* and *Abies religiosa* that occur near timberline in Mexico's transvolcanic forests, face diminishing opportunities for range expansion, as these species already occur on mountain tops during the reference period. At Nevado de Toluca (examined site at 3,827 m elevation; summit of the volcano at 4,680 m elevation; Figure 7C), the present vegetation is pure *P. hartwegii*. Analogs to the future climate support the decline of *P. hartwegii* dominance from 86 to 50%, while *A. religiosa* and several pine species should be suited to the new climate increases from absent to 67% (Supplementary Table S6).

As the primary host of overwintering migratory Monarch butterfly populations (Sáenz-Romero et al., 2012), *A. religiosa* replacement is of utmost concern at Monera Alta (Figure 7B), which is located within the core area of the Monarch Butterfly Biosphere Reserve, at the border of Michoacán and México states. Mid-century analogs suggest *A. religiosa* will have reduced presence, from 83% occurrence at the reference period to 47% occurrence at mid-century. Suitability of species from warmer habitats, particularly *Pinus pseudostrobus*, will likely increase with the strong analogs 500 m lower in elevation (Supplementary Table S6).

Meanwhile, 98 km to the east, *P. hartwegii* currently inhabits the Nevado de Toluca site at 3,800 m, slightly below the timberline at 4,000 m (Figure 7C). At mid-century this site is expected to provide suitable habitat for the populations of *A. religiosa* currently at Monera Alta (Supplementary Table S6). Transfer of *A. religiosa* from Monera Alta to Nevado de Toluca would be a change in elevation of approximately 400 m (Figure 7C).

Similarly, El Chocolate, Michoacán state, is a tropical dry forest site at low elevation (851 m) supporting a complex mixture of dry tropical forest species. The highly biodiverse forest composition is currently a critical habitat for guacamayas (*Ara militaris*), a migratory macaw. Our analysis shows that mid-century strong analogs are limited in number (78) compared to the reference period (224), are quite local, and average 550 m below the El Chocolate site (Figure 7D), where the species composition is primarily thornscrub species (Supplementary Table S7). Given the endemism of guacamayas to their habitat and the endemic, biodiverse Mexican dry tropical forests (Cué-Bär et al., 2006a,b), a change in composition from dry tropical to thornscrub will likely have considerable and unforeseen effects on guacamayas foraging opportunities and other dependent fauna.

4.4 Vegetation change and assisted migration

Shifts in vegetation observed through climate analogs illustrate the potential downstream effects on ecosystem services. In Mexico,

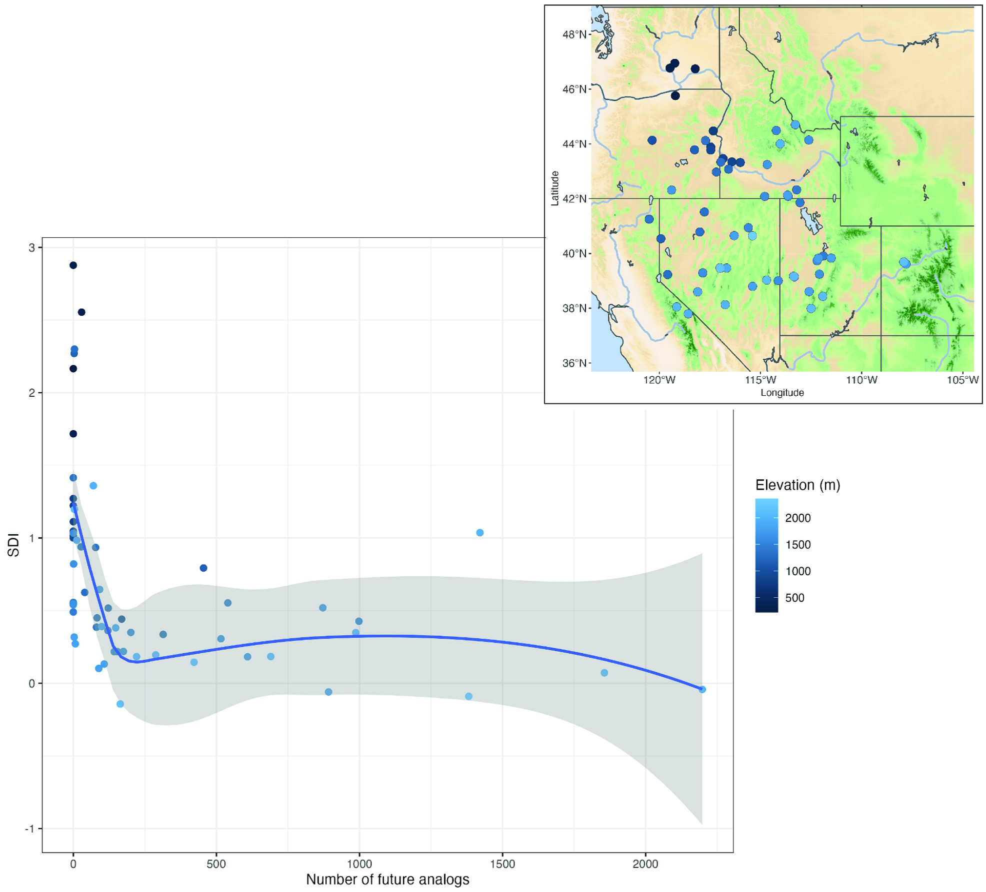

FIGURE 6
Plotted relationship between the number of mid-century analogs (strong, moderate, and weak) at 60 target locations and summer dryness index (SDI, Supplementary Table S2). The grayed area surrounding the fitted line represents the 95% confidence interval. Target locations are displayed in the map inset. Target locations are shown on the map inset and elevations (m) of the targets are shown in a blue gradient.

Pinus pseudostrobus is the dominant and most important commercial pine species in the Trans-Mexican Volcanic Belt. The mid-century analogs for pine forests at Cherán, Michoacán state (Figure 7A) were relatively abundant, with a total of 399 strong analogs (Supplementary Table S7), occurring at lower elevations on the slopes of the surrounding mountains mainly in the volcanic belt but also in the Sierra Madre Occidental and Sierra Madre Oriental (Figure 7A). The vegetation is currently dominated by *Pinus pseudostrobus* with *Pinus montezumae* in the colder sites, which was reflected in the reference period analogs. Mid-century analogs, however, suggest a change in composition to species suited to warmer and drier habitats, such as *Pinus devoniana* and even the nearly tropical *Pinus oocarpa,* and decreased prevalence of *P. pseudostrobus* (Supplementary Table S6).

Forest species composition changes are projected elsewhere in North America. Target locations, Blanca Peak and Uinta River, in the Rocky Mountains, United States, show a shift from cool- to warm-adapted species. At the Blanca Peak site, subalpine species (e.g., *Pinus contorta* and *Picea engelmannii*) are projected to decline or disappear based on the species composition of mid-century analogs. Analogs are found 569 m on average below the target location, supporting an increasing prevalence of species typically occupying warmer habitats (e.g., *Pinus ponderosa, Pinus edulis,* and *Quercus gambelii*; Supplementary Figure S7 and Supplementary Table S8). Along the Uinta River, an elevational transect of four target locations plotted between 1,800 and 2,800 m, similar species shifts emerged (Supplementary Figure S8). A declining presence of mid- and upper-montane species (e.g., *Pinus contorta* and *Abies lasiocarpa*) were projected (Supplementary Table S9), and there was a decline in the abundance of analogs, especially strong analogs (Supplementary Figure S8), at high elevation. The current species are projected to be replaced by juniper woodlands at mid-elevations (Supplementary Table S9).

4.5 Pros, cons and assumptions

Our approach simplifies seed transfer by standardizing a large set climate variables that generalizes plant-climate adaptation. As a result, it is ideally suited to species for which genecological principles are unknown, at least until result of provenance tests on climatically disparate sites would be available. However, it is important to note that generalized approaches cannot provide the species-specific accuracy of genecology studies or species distribution models where particular variables have greater

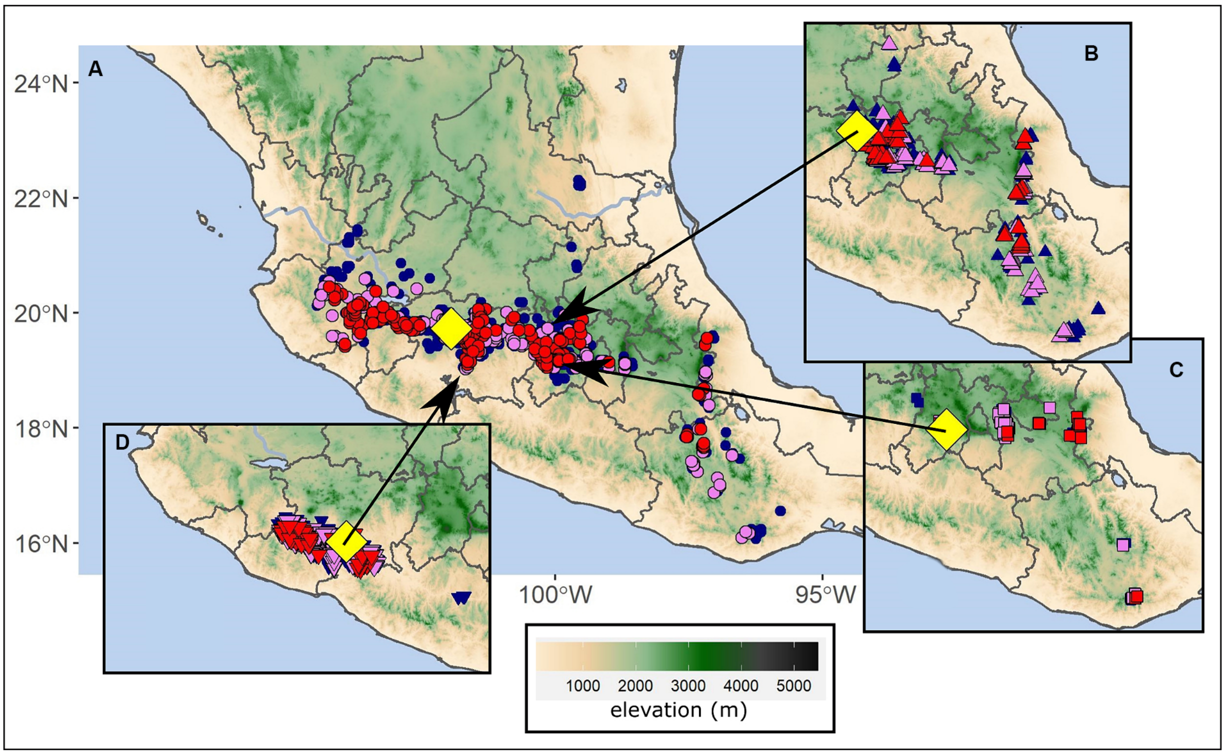

FIGURE 7
Forest commercial **(A)** and conservation **(B–D)** target locations of concern in Mexico. Mid-century analogs are shown for target locations **(A)** Cherán, **(B)** Monera Alta (Monarch Butterfly Biosphere Reserve), **(C)** Nevado de Toluca volcano, and **(D)** El Chocolate. The yellow diamonds indicate the target locations with strong, moderate, and weak analogs represented as red, violet, and blue colored circles, respectively.

importance in defining trait variation in the case of genecology or presence or absence of a species in a particular region. All climate variables have equal weight, making our seed transfer approach broadly applicable to plants, but a degree of species-specific precision is lost. Further study will be needed to assess the nuances between species-specific versus generalized seed transfer. Analogs are defined according to genecological patterns of genetic variation in species with the steepest clines. For many species, therefore, our definitions will be overly conservative which, on the one hand, could unduly handicap managers, but, on the other, greatly reduces the risks associated with seed transfer and assisted migration.

As discussed repeatedly, climate-based research carries two caveats when applied to plant ecology. While climate is the primary driver of plant adaptation, other environmental, evolutionary, and ecological factors can play important roles potentially affecting the persistence or transition of vegetation (e.g., Renne et al., 2019). This means that implementation of practical programs requires personnel intimately familiar with local topography, soils, and ecological requirements of the target species (e.g., Winder et al., 2021). Also, ecological impacts projected from GCMs and their scenarios carry the risks associated with the uncertainty of such predictions (IPCC, 2014). Yet, managers have little recourse but to plow ahead.

5 Conclusion

We demonstrate a climate distance approach that effectively reflects the altitudinal clines that shape adaptive variation in plants. Coupled with biome and plant inventory data, our approach can provide generalized seed transfer guidance for species of restoration concern. Our case studies show that mid-century analogs range from 0 to 825 m lower in elevation and eventually can be found in all cardinal directions from the target location. The case studies illustrate: the varied effects mid-century climates can have on plant populations, that regions and local areas may be prone to novel climates, and the potential broad impacts to conservation and ecosystem services. Our goal is to highlight the dynamic changes that will impact plant communities, develop the analytical components for a decision support tool, and identify species and seed sources needed to mitigate mid-century climates.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary material.

Author contributions

BR: Conceptualization, Funding acquisition, Methodology, Writing – original draft, Writing – review & editing, Formal analysis. GR: Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. CS-R: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing. EM: Data curation, Formal analysis, Methodology, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2024.1325264/full#supplementary-material

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The Swiss common garden network: testing assisted migration of tree species in Europe

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A warmer climate with drier summers will affect the suitability of tree species in their current range in most of Europe. To preserve ecosystem services in the future, many European countries are looking for tree species adapted to the expected future climate and are setting up trials to test them in different environments. In collaboration with forest practitioners and federal and regional authorities, we have established a network of 57 common gardens across large environmental gradients in Switzerland. Over a period of 30 to 50 years, the vitality, growth and survival of 18 tree species from 117 seed sources will be monitored to develop tree species recommendations for forest managers. In this article, we outline the considerations, challenges and trade-offs involved in designing this experiment, as well as the participatory process with a variety of stakeholders, from local foresters to the Federal Office for the Environment. Further, we list experiments testing multiple species on multiple sites in Europe and compare experimental designs, tree species and environmental gradients. The Swiss common garden network complements other European experiments and broadens the potential network by extending the covered environmental gradients to colder and moister conditions. Such targeted assisted migration trials are key to promoting tree species that can cope with the future climate and can help us to foster forest ecosystems that can adapt to rapidly changing climates.

KEYWORDS

assisted migration, climate change adaptation, common garden, experimental plantation, future forest, seed source, tree species

1 Introduction

Global warming combined with more frequent and severe summer droughts and heat spells in large parts of the world, including Europe (Zscheischler et al., 2018; IPCC, 2021), is increasingly affecting forest ecosystems (Chen et al., 2011; McDowell et al., 2020). Changing disturbance regimes will likely result in major declines in forest ecosystem services, such as timber production, protection against natural hazards, biodiversity and recreation (Seidl et al., 2017; Forzieri et al., 2021), and will compromise sustainable forest management (Bolte et al., 2009; Sousa-Silva et al., 2018). Intense climatic drought can impair tree growth and reproduction and increase mortality rates (Allen et al., 2015; Clark et al., 2016; Cailleret et al., 2017; Choat et al., 2018; Brodribb et al., 2020; Schuldt et al., 2020; Senf et al., 2020), ultimately leading to changes in tree species composition and forest structure and to shifts in species distributions (Anderegg et al., 2013; Clark et al., 2016; Brodribb et al., 2020; McDowell et al., 2020; Senf et al., 2021). Since rapid climate change is likely to outpace the ability of many tree species to adapt and survive in their changing habitats (Jump and Peñuelas, 2005), tree species will be forced to colonize new habitats upward in elevation and poleward of their current distribution to track suitable climatic conditions, or they will face local extinction (Parmesan and Yohe, 2003; Aitken et al., 2008; Vitasse et al., 2012; Burrows et al., 2014). Tree species can accomplish part of this migration through natural propagation, but in many cases this process fails to keep pace with the rate of global warming (Zhu et al., 2012). This is especially true in fragmented landscapes, where migration barriers impede range shifts (Saltré et al., 2015).

Assisted migration of tree species (Williams and Dumroese, 2013; Dumroese et al., 2015) and assisted gene flow among populations (Aitken et al., 2008) are management strategies that aim to artificially introduce tree species or tree populations, to locations where growing conditions are expected to be suitable for them in the future climate. This may even save some tree species from extinction (Mc Lachlan et al., 2007). However, assisted migration to areas far outside the current range of a species can also bear some risks: ethical, economical, legal, political and ecological concerns have been brought forward (Spies et al., 2010; Vitt et al., 2010; Aubin et al., 2011; Sansilvestri et al., 2015; Hagerman and Kozak, 2021). Since past relocations have had severe negative ecological implications in some instances, best practices for assisted migration need to be developed (Schwartz et al., 2012; Klein and Arts, 2022). Further, while assisted gene flow has improved growth in certain cases (Aitken and Bemmels, 2016), large environmental distances between seed sources and planting sites have sometimes resulted in lower yield and survival, for example in a provenance trial where *Pseudotsuga menziesii* var. *menziesii* Mirb. (Douglas fir) was established in North America in 1912 (St Clair et al., 2020). In Europe, provenance trials started as early as 1745 (Langlet, 1971), including those with *Abies alba* Mill. (silver fir, Larsen, 1986) *Larix decidua* Mill. (European larch, Weisgerber and Šindelář, 1992), *Picea abies* (L.) Karst. (Norway spruce, Şofletea and Budeanu, 2015), *Pinus sylvestris* L. (Scots pine, Stephan and Liesebach, 1997) and *Quercus petraea* (sessile oak, Sáenz-Romero et al., 2017). In addition, assisted migration experiments in the form of biodiversity trials have been established in major forest types throughout the world to investigate ecosystem functioning with different tree species combinations and various levels of functional diversity (Paquette et al., 2018).

In Switzerland, close-to-nature silviculture is the prevailing forest management system. It favors the natural regeneration of trees (Brang et al., 2014; Brüllhardt et al., 2022), resulting in uneven-aged forests bearing a high species and structural diversity, which are generally more resilient to disturbance and climate change than even-aged forests (Bauhus et al., 2013; Hof et al., 2017). However, natural regeneration does not lead to climate adapted forests *per se*, as tree species presumably adapted to the future climate are often missing in these forests, for example because they are outcompeted by dominant tree species such as beech (Ligot et al., 2013; Dietz et al., 2022) or because they are preferentially consumed by browsing ungulates (Champagne et al., 2021; Angst and Kupferschmid, 2023). Recently, forest managers have started to implement adaptive measures, in particular through the introduction of tree species, i.e., assisted migration (Williams and Dumroese, 2013). Tree species or provenances are often introduced in single pilot plantations (Bürgi and Dietz, 1986; Pretzsch, 2005; Nyssen et al., 2016), which can provide information about tree performance under specific site conditions and the current climate but allow only limited inference to other sites. Therefore, a coordinated plantation approach is needed to generate well-founded tree species recommendations for future forestry practice.

Despite a large body of literature from forest inventories (Mina et al., 2018; Etzold et al., 2019; Abegg et al., 2020; Del Río et al., 2021), provenance studies (Sáenz-Romero et al., 2017), niche modeling (De Rigo et al., 2016), dendroecological studies (Bottero et al., 2021) and experiments (Frank et al., 2017; Fririon et al., 2023), there is still considerable uncertainty regarding the factors that determine the survival, vitality and growth of tree species and provenances under climate change and assisted migration. For over two centuries, scientists have conducted common garden (CG) experiments, also known as experimental plantations, to study the performance of trees from different genetic and/or geographic origins under identical environmental conditions (Langlet, 1971). The majority of early trials were designed to optimize timber production, established due to the growing awareness of the importance of geographic variation, which had earlier repeatedly resulted in plantation failure (Aitken and Bemmels, 2016). In light of the recent and expected climate-change-induced habitat shifts of tree species, the focus of CG experiments changed from provenance studies to networks that systematically incorporate a broad set of tree species along environmental gradients (Alizoti et al., 2022; Fady and Rihm, 2022). Such networks may help to identify species' optima and limits, as well as species and seed sources that can cope with the expected climate of the future, thus enabling forest ecosystems to adapt to rapidly changing conditions. Such information is needed to build a solid scientific foundation for assisted migration.

Large CG networks offer opportunities to investigate research questions over broad environmental gradients. For forest managers, it is more attractive to join coordinated and subsidized CG networks, where they can benefit from insights gained throughout the network, rather than investing in stand-alone pilot plantations. To produce reliable results and use resources effectively, it is important to have a statistically sound and powerful design, as well as coordination with similar initiatives. A particular challenge is that the optimal scientific solution would involve numerous sites over large environmental gradients, ample replication and large tree populations observed over a long timeframe, yet these aspects collide with feasibility constraints, especially regarding available resources. Moreover, such experiments involve many stakeholders, and their planning, establishment and maintenance require major investments in personnel and equipment (Hatfield, 1998). Long-term commitments of the involved stakeholders are essential to secure the success of such experiments. However, reorganizations and financial constraints, which become increasingly likely with the longer duration of projects, can threaten the continuation of an experimental network (Pretzsch, 2005).

New CG networks have been and are currently being established in many places around the globe with the goal of finding tree species and seed sources that are suitable for the future climate (Fady and Rihm, 2022). In North America, similar considerations have resulted in a large number of publications on assisted migration experiments over the last three decades (Palik et al., 2022;

Park and Rodgers, 2023). In Switzerland, we have recently established a CG network testing tree species in forests across a large gradient covering most of the climates that occur in the country and are suitable for tree growth. We planted seedlings grown from seeds of selected tree populations in CGs to improve our understanding of the species' capacities to cope with climate change (Frei et al., 2018). The aim of the project is to derive recommendations that will help forest managers to promote suitable, climate-adapted species, either through natural regeneration or by planting. In this method paper, we present the new Swiss CG network. Specifically, we: (1) describe the participatory planning and decision process employed for designing the Swiss CG network and present its final design, (2) give an overview of the experiments testing multiple tree species on multiple sites in Europe and compare the designs, tree species and environmental gradients to point out the benefits of a European network, and (3) discuss the potential and limits of such trials. We expect this information to benefit others interested in designing similar CG networks and to encourage collaboration, especially across national borders throughout Europe.

2 Methods and comparison

2.1 The Swiss common garden network

2.1.1 Aims and scope

In anticipation of a warmer climate with drier summers, which will affect the climatic suitability of tree species in their current range, scientists, practitioners and authorities in Switzerland have recognized the need to identify suitable tree species that can secure the provisioning of ecosystem services in the future.

Through a joint initiative, involving scientists, federal and regional forest authorities, and forest practitioners from the public and private sectors, a network of 57 CGs has recently been established in forests across large environmental gradients in Switzerland. The network is designed to test and compare 18 tree species. By planting seedlings from seeds of the same populations under different climates, the aim is to improve our understanding of the species' capacities to cope with the expected future climate. The CG network enables a comparison of the performance of different tree species under identical climatic and environmental conditions. Additionally, it makes it possible to study the performance of individual tree species along the environmental gradients. To assess the intraspecific variability of each species in its response to various climates, several seed sources are tested for each species.

The Swiss CG network is designed to serve as an infrastructure for fundamental and applied research in the field of adaptation of forests to future climate conditions over the next 30–50 years. In particular, the network is intended to address the following questions:

Which environmental factors determine the performance of tree species along environmental gradients, and how is their intraspecific variation affected by environmental factors?

How does the performance compare among tree species, how is the interspecific variation affected by environmental factors, and how do the tree species compare regarding intraspecific variation?

2.1.2 The participatory process used to develop the Swiss common garden network

The concept and design for the Swiss CG network were developed through a participatory process involving three main stakeholder groups: (1) the Swiss Federal Office for the Environment (FOEN); (2) the cantonal forest offices, local forest managers and forest owners; and (3) national and international researchers. These stakeholder groups have different roles: FOEN leads the political process toward sustainable forest services under climate change, funds projects that support evidence-based decision-making, and supports the scientific coordination of the Swiss CG network (FOEN, 2020). Land required for the CG sites, as well as the financial and personnel resources to establish and maintain the CGs, is provided by the cantonal forest offices and the forest owners. National and international researchers add value to the CG network by exploring their own research questions based on the CG infrastructure and securing additional third-party funding. They contribute scientific expertise to the development of the experimental design and to evaluations of the results. The Swiss CG network team at WSL coordinates interactions among the stakeholders and is responsible for the implementation of the CG network regarding the interests of the stakeholders.

All stakeholders were consulted throughout the project development phase, i.e., before important design and implementation decisions were made (Figure 1). The experimental design was discussed with all stakeholders in three workshops in 2017 and improved based on their input. The statistical power of the experimental design was validated by Biomathematics and Statistics Scotland (James Hutton Institute, Aberdeen). Statistical power calculations were based on tree height and stem diameter data from experimental forest management sites (Forrester et al., 2021) and from *Abies alba* provenance trials in Switzerland (Commarmot, 1995; Commarmot, 1997). The aim of these evaluations was to guarantee that the experiment has the necessary statistical power to derive inter- and intraspecific differences and relationships between environmental factors and tree performance. The tree species selection was discussed with the cantonal forest authorities via e-mail and in two workshops in 2017, and the seed source selection was discussed with researchers in a workshop in 2018. The experimental sites were selected in close cooperation with the cantonal authorities and the forest owners. The initiation of add-on projects was encouraged during a workshop with the research community in 2019.

2.1.3 Experimental design

To acquire statistically sound data, the experimental design needed to be consistent throughout the network. The statistical power analyses revealed that the most crucial design parameter was the number of sites on which a tree species was to be tested. For a high explanatory power of 80%, the number of sites per species had to exceed 30. In comparison, the number of trees per experimental unit was found to be of lower importance for analyzing growth parameters. However, for mortality analysis, the number of trees needed to be sufficient to be able to estimate the expected mortality at a site. As a minimum difference of 4% in mortality among seed sources on a site was considered relevant, at least 25 seedlings per seed source per site were needed. A block design was used to account for spatial variation within sites (Binkley, 2008). As great attention was paid to finding homogeneous sites, spatial variation within sites was expected to

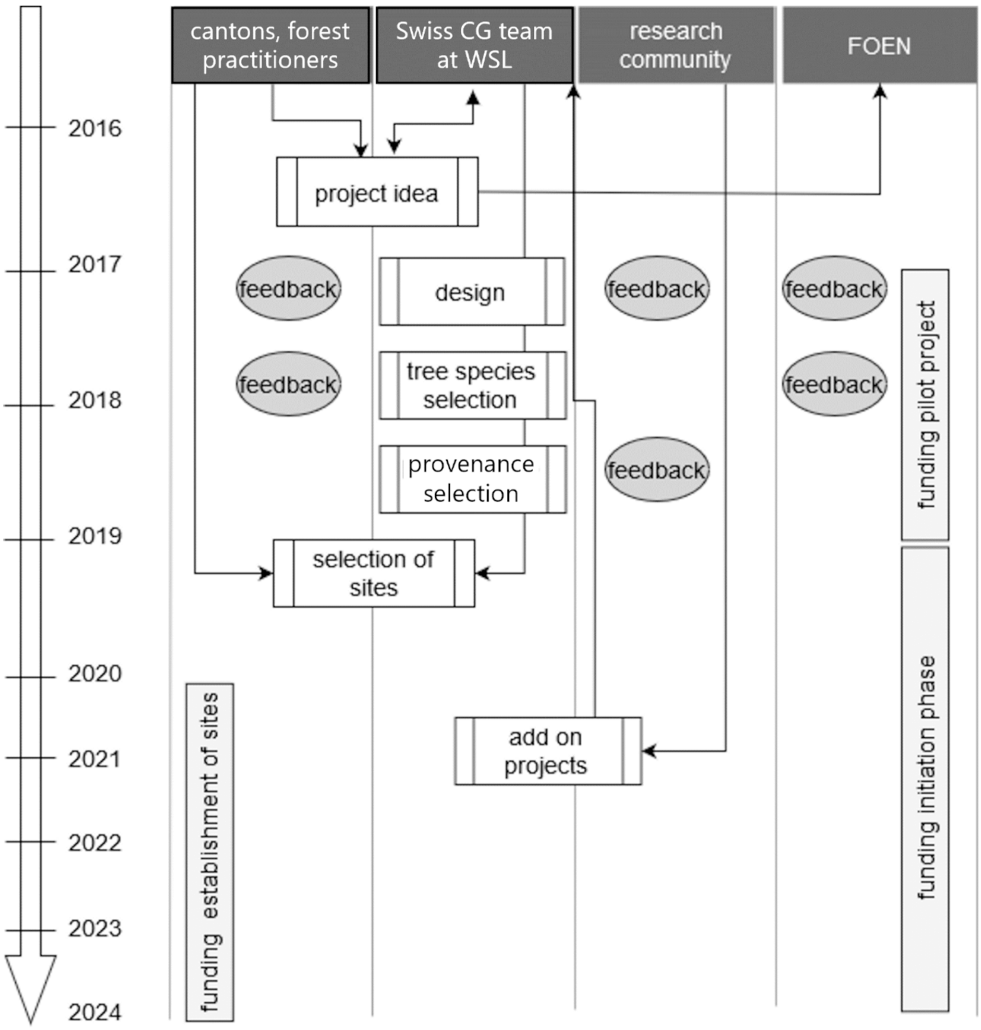

FIGURE 1
Collaboration of stakeholder groups during the project initiation phase of the Swiss common garden (CG) experiment.

be relatively small compared with the site-to-site variation. Therefore, three instead of the initially recommended four blocks per site were ultimately used because of feasibility considerations.

All tree species were planted once in every block (Figure 2). They were grouped into slow- and fast-growing species. These groups were placed in alternating order in the blocks, and the tree species were assigned randomly to plots within each group. Each plot was split into four subplots to which four seed sources of the same tree species were assigned randomly. Nine individual trees were planted in each subplot. The number of seedlings of a specific seed source per site thus amounted to 27 (i.e., 108 seedlings per tree species; Figure 2).

To minimize competition, trees were planted with 2 m spacing between individuals. Between plots, the spacing was doubled to 4 m (Figure 2). The planting zone was protected by a fence to exclude browsing ungulates. Around the fenced planting zone, a buffer zone with a width of approximately half the adjacent stand height was cut clear to reduce shading effects. The available area determined the number of tree species that could be studied at a specific CG site. As an example, the area required for a CG with eight tree species was approximately 1 ha, and nearly half of this area was assigned as buffer zone (47%).

2.1.4 Species selection

The tree species for the experiment were chosen based on several criteria that were considered of importance for future forestry in Switzerland. These included (1) the species' current abundance in Switzerland (i.e., percentages of standing timber volume and basal area in the Swiss National Forest inventory ≥0.1% in at least one of the biogeographical regions; Brändli, 1998); (2) its potential for providing ecosystem services, such as timber production, natural hazard protection, and biodiversity; and (3) the width of its ecological amplitude. Invasive species and those highly susceptible to pathogens or drought were excluded, on the assumption that they will not play a major role in Swiss forestry in the future.

The original set of species included all those with standing timber volume data in the National Forest Inventory. The set was augmented with a number of less abundant species, as well as non-native species, which may have potential on the warmest and driest sites. Initially, 61 candidate tree species were evaluated (Supplementary Table S1). Based on feedback from stakeholders in the participatory process, the decision was made to carry out the experiment with two subsets of tree species (Table 1): a so-called 'core set' of 9 species, each planted

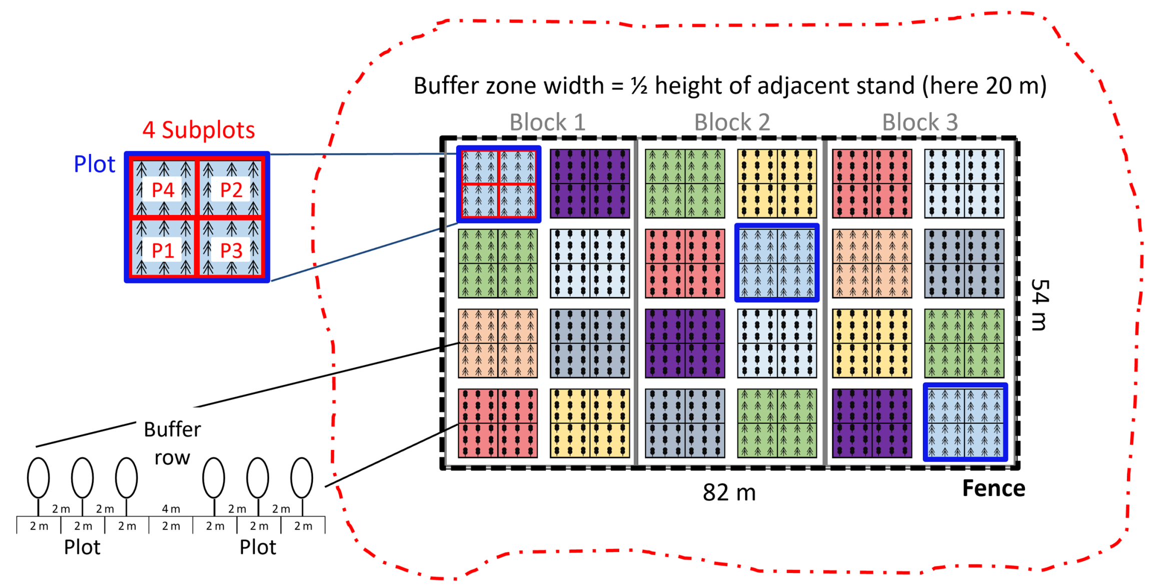

FIGURE 2
Idealized design of a common garden, with 8 tree species repeated in 3 blocks, leading to 24 plots. The plots are split in 4 subplots containing 4 seed sources per species. Each subplot contains 9 individual trees of a given species and seed source. Plots are separated by a buffer row to minimize competition among tree species. To prevent shading effects, the planting zone is surrounded by a buffer zone without trees of approximately half the height of the adjacent stand.

on 35 sites, for which statistically sound data could be obtained; and (2) a so-called 'extension set' of 9 additional species tested on only 15 sites each, mainly at the warm and dry end of the environmental gradient (Figure 3). *Abies alba* was planted on all sites as a reference species.

The Swiss CG network was designed such that tree species are tested in their current range, as well as on sites where the climate is projected and assumed to be suitable for them toward the end of the century, i.e., on sites that are currently colder and/or wetter than their future habitat. To assign tree species to these sites, the following scenario was considered: between the periods 1981–2010 and 2070–2099, the emission scenario RCP 8.5 with the model combination CLMCOM-CCLM5_HADGEM_EUR44 (NCCS 2018) projects an average warming of 4.4°C for Switzerland and a reduction in precipitation of 17% (northern Switzerland) to 25% (southern Switzerland) for the months of April through August, which are considered most relevant for the climatic suitability of trees because this is the main period of growth (Zischg et al., 2021). The anticipated temperature increase of 4.4°C corresponds to an elevational shift of about 800 m considering a lapse rate of 0.55°C/100 m (Fairbridge and Oliver, 2005). The tree species were thus assigned to the sites such that they covered the elevation gradient of their current habitat and elevations up to 800 m higher (Figure 3). Sites below the current warm and dry habitat limit were not included because: (1) the climate will become warmer and drier during the lifetime of the trees, which will lead to a gradually increasing representation of the warm and dry edge over the planned experiment duration; and (2) this project is focused on laying a scientific foundation for assisted migration.

TABLE 1 List of tree species included in the Swiss common garden (CG) experiment.

Core set (9 tree species)	Extension set (9 tree species)
1. *Abies alba* (silver fir)	10. *Acer opalus* (Italian maple)
2. *Acer pseudoplatanus* (sycamore maple)	11. *Acer platanoides* (Norway maple)
3. *Fagus sylvatica* (European beech)	12. *Cedrus atlantica* (Atlas cedar)
4. *Larix decidua* (European larch)	13. *Corylus colurna* (Turkish hazel)
5. *Picea abies* (Norway spruce)	14. *Juglans regia* (Persian walnut)
6. *Pinus sylvestris* (Scots pine)	15. *Prunus avium* (wild cherry)
7. *Pseudotsuga menziesii* (Douglas fir)	16. *Quercus cerris* (Turkey oak)
8. *Quercus petraea* (sessile oak)	17. *Quercus robur* (pedunculate oak)
9. *Tilia cordata* (small-leaved lime)	19. *Sorbus torminalis* (wild service tree)

The 9 species of the core set are planted in at least 35 CGs, whereas the 9 species of the extension set are planted in approximately 15 CGs.

2.1.5 Seed source selection and plant provisioning

With the selected design, four seed sources could be planted per species on each site. However, four seed sources were not considered sufficient to adequately represent the genetic variation within the species (workshop with scientists in 2018, see section 3.2). Therefore, the decision was made to test seven seed sources for each species. One of them is planted as a within-species reference on all sites hosting the respective species, whereas the other six seed sources are planted randomly on half of the sites. This design will allow us to better catch effects of intraspecific variation but not to give recommendations for specific seed sources, because of the small number of seed sources tested per species and the limited number of sites on which individual seed sources are replicated.

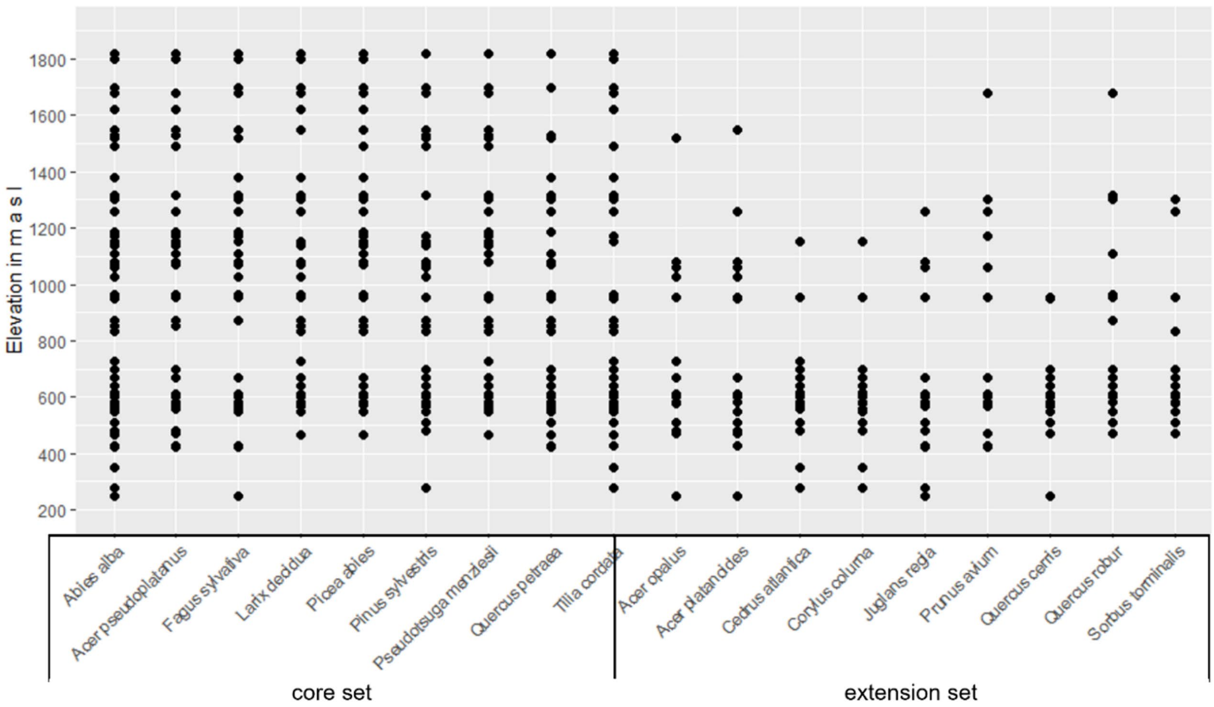

FIGURE 3
Elevations at which the tree species are tested in the Swiss common garden (CG) experiment.

The search for suitable seed sources started in summer 2018, based on the following criteria: (1) seed material should derive from autochthonous stands to ensure that it is adapted to the local climate, (2) seed sources should be OECD-certified (Organization for Economic Co-operation and Development; OECD) to ensure a certain quality level and allow comparisons with other trials, (3) the different seed sources of a species should cover large environmental gradients across the natural habitat and originate from different refugial areas in order to represent the within-species genetic variation, (4) truly marginal populations should be excluded to preclude a potential loss of genetic diversity in isolated populations and (5) sufficient quantities of high-quality seed material should be available. For native species, four to five Swiss seed sources were complemented by two to three seed sources from the warm and dry end of the habitat outside of Switzerland.

In total, planting material was procured from 117 seed sources (for a complete list of seed sources and suppliers, see Supplementary Table S2). For six tree species, the full set of seven seed sources was not found. In these cases, several seed sources were planted on all sites. Most seedlings were raised at the nursery of Emme Forstbaumschule SA in Wyler bei Utzensdorf, Switzerland. However, all seedlings of *Quercus cerris* were grown in Vivaio forestale di Lattecaldo in Morbio Superiore, Switzerland and all seedlings of *Sorbus torminalis* were grown at WSL in Birmensdorf, Switzerland, because these nurseries had specific experience with these two species. In addition, one *Abies alba* seed source, two *Larix decidua* seed sources, and one *Picea abies* seed source were grown at the Forstgarten Rodels nursery in Rodels, Switzerland. One seed source of *Acer platanoides* was grown at the Forstgarten Lobsigen nursery in Lobsigen, Switzerland and one seed source of *Abies alba* was grown at the nursery of Allasia Plant Magna Grecia S.S. in Soveria Mannelli, Italy.

2.1.6 Site selection

Forest sites suitable as potential test sites were suggested by the cantonal forest offices. The proposed sites were evaluated according to the following criteria: (1) homogeneous in aspect, slope and soil properties and (2) area of at least 0.6 ha. A total of 172 sites were proposed, covering 20 of the 26 Swiss cantons. The project team visited 125 sites in 2018, together with representatives of the cantonal forest offices and the local forest managers, to assess the suitability of the sites for the project. Sites that had failed to harbor regeneration for more than 15 years, due to being waterlogged or overgrown with competing vegetation (megaforbs), were excluded. Additional site selection criteria were: (3) interest in participating in the project on the part of the corresponding forest managers and owners and (4) commitment of the cantonal authorities to contributing funding for the establishment of the CG.

Since the gradients over which the species were to be tested varied among the species (Figure 4) and most of the available sites were too small to harbor more than 8–9 tree species, close to 60 sites were required to provide sufficient space for testing all 18 species. The final selection of 57 test sites (Figure 4) represents the major Swiss biogeographic regions, elevation belts, soil types and slope aspects. Six of the 57 sites are large enough to test all 18 tree species. These sites are geographically widespread but are all situated below 1,000 m a.s.l. They have been preselected for intensive monitoring. Currently, additional phytosanitary monitoring is carried out on these sites.

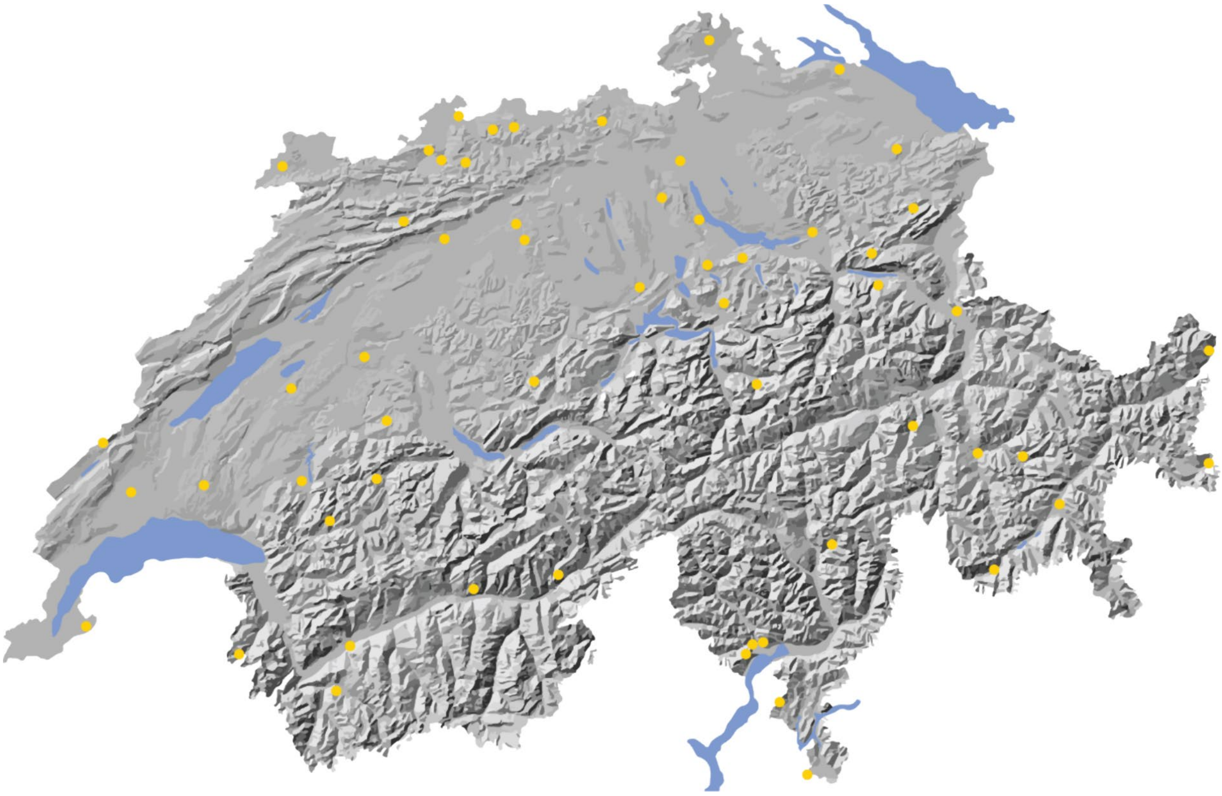

FIGURE 4
Map of Switzerland showing the locations of the 57 experimental sites of the Swiss common garden experiment (yellow dots). For site names, refer to Supplementary Table S3. For site-specific information on the tested tree species and the experimental design, refer to the website: www.testpflanzungen.ch.

2.1.7 Environmental measurements

On all sites, at least one soil profile was dug for detailed soil characterization, including morphology and classification, physical properties, organic matter content, acidity and nutrient availability. Additionally, each site is equipped with an automatic weather station, monitoring air temperature, soil temperature at 15 and 50 cm depth, soil suction at 15 and 50 cm depth, relative humidity, precipitation, wind velocity and direction, solar radiation and barometric pressure, all at 10-min intervals.

2.1.8 Measurements of plant performance

Shortly before planting, seedlings were individually labeled and their initial height (seedling length from root collar to terminal bud) and root collar diameter were measured. Establishment and planting of the 57 sites was distributed over three planting seasons between autumn 2020 and spring 2023. Seedlings that died or disappeared were replaced by replanting new seedlings, up to 2 years after site set-up. Seedling survival and damage were monitored for the first time in the summer after planting. For the 19 sites set up in autumn 2020 and spring 2021, this was done in summer 2021. In summer 2023, seedling survival and damage were monitored on all 57 sites, i.e., on a total of approximately 55,000 plants. Damage was assessed separately for terminal buds, bark and leaves. This survival and damage monitoring will be repeated annually for at least 5 years. Height and length of the seedlings will be measured for the first time after the end of the installation phase in summer 2024. These measurements will be continued annually for at least 5 years, after which the measurement interval will be increased to 2–3 years. The first results on mortality and damage will be published in 2025, whereas an observation time of about a decade is needed to gain valid information on tree growth.

2.2 Overview of common garden experiments in Europe

2.2.1 Approach

In this section, we list experiments conducted in Europe that test multiple tree species on multiple sites, and we acknowledge the potential offered by broadening the CG network. We conducted a systematic literature search using Scopus with the terms 'common gardens', 'trees', 'tree species', 'Europe' and 'assisted migration'. In addition, we contacted colleagues in forest science in Germany, Austria, France, Italy, the Czech Republic and Great Britain to obtain information on more recent, yet unpublished, trials. In addition, we included CG networks in Belgium, France, Germany and Switzerland that are currently in their establishment phase. To ensure a consistent sample, we excluded all single species provenance trials and all experiments conducted on single sites. We further excluded experiments with a focus on the ecosystem functioning of tree species combinations since they offer limited insights on the performance of individual tree species along environmental gradients. Our comparison focuses on the climate space of the planting sites, considering annual mean temperature, annual precipitation sum, and the climatic water balance during the growing season, i.e., the difference between precipitation and potential evapotranspiration for the months with a mean temperature above 5°C. We derived climatic parameters from CHELSA (Climatologies at high resolution for the earth's land surface areas; Karger et al., 2017) and used an approximation for potential evapotranspiration (Turc, 1961). In addition, we compared the sets of tree species tested and the designs of the various CG experiments.

2.2.2 Common garden experiments in Europe

We identified 16 CG experiments with tree species in Europe that matched the criteria defined above (Table 2). Already more than 50 years ago, 8 arboretums were set up in France testing 2,300 seed sources of 70 species (French arboretum; Ducatillion et al., 2022). Although the designs of the arboretums are not consistent, the planting dates are well documented and within-site replication information is available. The fact that the trees in these CGs are at least 50 years old, and were thus planted under different from current climate conditions, makes the data from this experiment very interesting for dendrochronological studies. The arboretums are part of the GEN4X Network (Forest Genetics Network for Research and Experimentation), which includes a total of 1,208 sites installed to study ecosystem functioning or to generate improved reforestation material (only arboretum sites are included in Table 2: Rihm and Fady, 2023).

The Forest Research Institute of Baden-Württemberg (FVA) initiated the establishment of trials involving four non-native *Abies* species in 1972 to compare their performance with that of native *Abies alba* (personal communication, Prof. Dr. Ulrich Kohnle, FVA, April 2022).

In 1985, the Forestry Commission of the United Kingdom initiated a CG trial to find conifers other than *Picea sitchensis* (Bong.) Carrière (Sitka spruce) that could thrive under the climatic conditions in the UK (UK species trials; Mason, 2012). This trial included 11 conifer species (with 25 seed sources) that were planted at 5 sites.

A CG trial was established in France in 1986 to find suitable *Quercus petraea* and *Q. robur* seed sources under a range of climatic conditions. The trial includes 24 European *Quercus* seed sources planted on three sites (French Quercus trial; Bert et al., 2020).

In 2007, an assisted migration trial was started in France, in which three Mediterranean, three cold-adapted and two so-called 'cosmopolitan' tree species were tested on three sites in southern, central and northern France. The objective was to identify whether the projected northward shift of the species could already be observed in this experimental setting (species shift trial; Merlin et al., 2018).

REINFFORCE was the first large-scale European experiment to assess the performance of tree species across a large environmental gradient. The experiment, which was started in 2012, focuses on the climatic suitability of 33 native and non-native tree species (with 114 seed sources) along the Atlantic rim from Portugal to the British Isles (Prieto-Recio et al., 2011; Correia et al., 2018; Reynolds et al., 2021). In the UK, REINFFORCE was complemented by the Forest Research trial. This trial shares the three British REINFFORCE sites and includes two additional sites located further east. The two experiments share 13 species, but the Forest Research trial, which was also started in 2012, included 10 additional species of specific interest to the UK (Reynolds et al., 2021).

At the same time, a trial with eight non-native species (one seed source per species), the so-called 'exotic species trial,' was initiated at five sites spread over Germany, Austria and Switzerland to investigate whether the tested species thrive under central European conditions (Frischbier et al., 2019; Glatthorn et al., 2024).

In 2014, the University of Freiburg initiated a project to find out whether rare and drought-tolerant native tree species could be used for the afforestation of former vineyards in a way that would help preserve the typical cultural landscape structures and increase biodiversity, while serving as a forest genetic reserve for rare species (SILVITI project: Kunz and Bauhus, 2015).

In the same year, the Institute for Applied Plant Biology in Switzerland started a trial with seven native tree species and *Pseudotsuga menziesii* from a total of 35 seed sources on four sites in northern Switzerland, to find out whether seed sources from drier sites in Europe would outperform the native seed sources in the years to come (IAP trial; personal communication, Sabine Braun, October 2017).

The 'climate trials' were installed in Baden Württemberg by the Forest Research Institute of Baden-Württemberg (FVA) in 2018 to test native and non-native tree species and their adaptation to climate change. Further sites testing different seed sources of *Cedrus* species were established in 2020 (personal communication, Andreas Ehring, FVA, June 2022).

With 'Trees for Future,' the Royal Forest Society of Belgium started an innovative project in 2019 to facilitate assisted migration of native and non-native tree species, prevent further degradation of forests due to drought and pest attacks, and increase tree species diversity in forests throughout Belgium (website: www.treesforfutrure.be/en, accessed November 2022).

The aim of the Swiss CG network is to find suitable tree species and seed sources for the future climate along an elevation gradient in all regions of Switzerland. The establishment of the network, testing 117 seed sources of 18 species at 57 experimental sites, started in 2020. (see section 3 for details).

In France, several new CGs have been established recently within the project ESPERENSE with the goal of identifying climate-tolerant tree species. This project started in 2020 with two experiments at eight sites, following an analogue-climate approach, i.e., using four sites that are currently exposed to the climate predicted for the other four sites toward the end of the century. In one of the experiments (ESPERENSE I), the survival of 30 species over 10 years will be studied. In the other experiment (ESPERENSE II), the growth of 8 tree species over approximately 30 years will be tested (Kebli et al., 2019; Kebli et al., 2022; ONF, 2022).

Further experiments are planned across Europe in the framework of the OptForests project (https://www.optforests.eu), which will also include a site in Switzerland managed by the Swiss CG team (planting is planned for autumn 2025). The above list of CG experiments is likely incomplete since many European countries have recently begun to invest into projects to find suitable tree species to ensure important ecosystem services for the future.

2.2.3 Comparison of experiments

The 16 experiments listed in Table 2 show considerable variation in the number of sites (3–57), the number of species (2–70), the number of seed sources or genetic units (4–2,300), the spacing between trees at the time of planting (0.1–3 m), and the

TABLE 2 Overview of common garden experiments in Europe that test the climatic suitability of tree species.

ID	Name of project	Country	# of sites	# of species	# of GUs	Tree spacing [m]	Eyr	Dex	Agencies**	Publication
1	French arboretums	F	8	70*	2,300	various	1969	50+	INRAE, ONF	Ducatillion et al. (2022)
2	Abies trial	D	7	4	4	4 × 1.5	1972–2000	50+	FVA	Personal communication, Prof. Dr. Ulrich Kohnle, FVA, April 2022
3	UK species trials	UK	5	11	25	2	1985	50	Forestry Commission	Mason (2012)
4	French Quercus trial	F	3	2	24	1.75×3	1986	35	INRAE	Bert et al. (2020)
5	Species shift trial	F	3	10	35	0.1	2007	20	CNRS	Merlin et al. (2018)
6	REINFFORCE	F, E, P, UK	38	36	114	3	2012	20+	IEFC & EFIATLANTIC partners	Correia et al. (2018); Reynolds et al. (2021)
7	Forest research trials	UK	5	23	48	2	2012–2013	20+	Forest Research	Reynolds et al. (2021)
8	Exotic species trial	D, A, CH	5	8	8	2	2012	20+	LWF, WSL, Forest Thuringia, BOKU, University of Bayreuth	Frischbier et al. (2019); Glatthorn et al. (2024)
9	SILVITI	D	3	7	na	na	2014	na	University of Freiburg	Kunz and Bauhus (2015)
10	IAP	CH	4	8	35	1.5	2014	20+	IAP	Personal communication, Sabine Braun, October 2017
11	Climate trial	D	12	10	10	3	2018	20+	FVA	Personal communication, Andreas Ehring, FVA, 2/6/2022
12	Trees for future	B	29	30	75	2	2019	20+	SRFB	Website: www.treesforfuture.be/en, accessed June 2024
13	Swiss CG network	CH	57	18	117	2	2020	30–50	WSL, FOEN, 20 cantons	Frei et al. (2018)
14	Cedrus trial	D	3	2	13	3	2020	20+	FVA	Personal communication, Andreas Ehring, FVA, 2/6/2022
15	ESPERENSE I	F	4	33	60	2	2020	10	ONF, INRAE, CNPF, FCBA	Kebli et al. (2022) and ONF (2022)
16	ESPERENSE II	F	4	8	8	2	2020	30	ONF, INRAE, CNPF, FCBA	Kebli et al. (2022) and ONF (2022)

GU: genetic unit, Eyr: year of establishment, Dex: expected duration of the experiment.

*Number of species that are present in at least half of the arboretums.

**BOKU: Universität für Bodenkultur, Vienna, Austria; CNPF: Centre National des Propriété Forestière, France; CNRS: Centre d'Ecologie Fonctionnelle et Evolutive, France; FCBA: L'Institut Technologique Forêt Cellulose Bois-Construction ameublement, France; FOEN: Federal Office for the Environment, Switzerland; Forestry Commission: Bristol, United Kingdom; Forest Research: Farnham, United Kingdom; FVA: Forstliche Versuchs- und Forschungsanstalt Baden Württemberg, Freiburg, Germany; EFIATLANTIC: European Forest Institute of the Atlantic Rim Countries, Barcelona, Spain; IAP: Institute for Applied Plant Biology, Schönbuch, Switzerland; IEFC: Institut Européen de la Forêt Cultivée, Cestas, France; INRAE: Institut national de recherche pour l'agriculture, l'alimentation et l'environnement, France; LWF: Bayerische Landesanstalt für Wald und Forstwirtschaft, Freising, Germany; ONF: Office National des Forêts, France; SRFB: Société Royale Forestière de Belgique, Bruxelles, Belgium; WSL: Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland.

duration of the trials (10–50+ years; Table 2). Overall, the currently running or planned experiments in Europe include about 140 tree species from approximately 2,500 different seed sources on 185 sites. The most frequently selected tree species across all trials are *Quercus petraea, Cedrus atlantica* and *Pseudotsuga menziesii* (all tested in 9 of 16 experiments), followed by *Quercus robur* and *Pinus sylvestris* (both in 7 experiments) and *Cedrus libani*, *Larix decidua* and *Pinus nigra* (in 6 experiments). The 185 experimental sites cover gradients of mean annual temperatures between 3°C and 16°C (median 10°C) and of mean growing season temperatures (months with mean temperatures above 5°C) between 10°C and 16°C (median 13°C). The annual precipitation sums of the experimental sites range from 511 mm to 2,260 mm (median 972 mm), and average monthly precipitation during the growing season ranges from 43 mm to 187 mm (median 80 mm) (Figure 5A). The climatic water balance (CWB) during the growing season at the experimental sites ranges from −46 mm to +158 mm (median + 9 mm). Nearly one-third of the sites (53 of 185) have a negative CWB, meaning that the potential evapotranspiration is higher than the average precipitation sum (sites below the 1:1 line in Figure 5B). In comparison to the other experiments, the Swiss CG network covers the largest gradient of CWB, ranging from −29 mm to +158 mm (median + 26 mm), followed by REINFFORCE, with CWB ranging from −46 mm to +96 mm (median + 3 mm). While the Swiss CG network includes sites with humid and cold climates, REINFFORCE covers humid and warm climates along the European Atlantic coast (Figure 5B). The French *Quercus* trial, the species shift trial, the exotic species trial, SILVITI, and ESPERENSE I and II focus mainly on the dry end of the gradient by including sites with a CWB over the growing season ranging from −42 mm to +7 mm (median − 11 mm).

2.2.4 Filling a niche among European common garden experiments

Most of the currently existing and the planned CG experiments in Europe focus on warm and dry sites (Table 2; Figure 5A) because this is where most countries expect the most severe problems to occur, and hence they are urged to find suitable species for these climates. For Switzerland, however, it is not sufficient to limit trials to the warmest and driest sites, because important ecosystem services, such as the protection against natural hazards, are also required at higher elevations. The climatic suitability of the current tree species is likely to become an issue in these regions as well (Moos et al., 2023). Other tree species already present at lower elevations in Switzerland may be suitable candidates for replacing tree species at higher elevations. However, seed trees of these species are currently mostly absent in these regions.

To identify factors that determine the survival, vitality and growth of tree species, CG networks need to cover broad environmental gradients (Fady and Rihm, 2022). A gradient can be extended by broadening the network, thus meta-analyzing data from multiple European CG experiments together. The REINFFORCE project and the UK species trial offer especially high potential for collaboration, as they contain many sites and cover broad gradients in Atlantic climates (Correia et al., 2018). Whereas REINFFORCE expands to humid and warm climates, the Swiss CG network reaches to humid and cool climates thereby complementing the range covered by REINFFORCE (Figure 5B).

3 Discussion

3.1 The importance of assisted migration experiments for climate change adaptation in forestry

In an evolving climate with more frequent extreme events, forest services are at stake. Assisted migration is recognized as a key strategy for mitigating climate change and maintaining optimum forest health, productivity and ecosystem services (Aitken and Bemmels, 2016). However, to prevent negative ecological implications (Schwartz et al., 2012; Klein and Arts, 2022), assisted migration should be tested in a coordinated network rather than in individual pilot plantations. *In-situ* plantations in a forest environment have many benefits over experiments in controlled environments, such as greenhouses or growth chambers. First, *in-situ* trials can run for several decades, capturing the effects of a combination of hazards and extreme climatic events on trees and providing valuable results regarding mature trees. Second, these mature trees can serve as seed trees for the next generation of trees, providing a head start for forest adaptation.

Since the establishment of *in-situ* trials is labor-intensive, the recombination of existing planting trials created for other reasons, even including pilot plantations of practitioners, may alternatively be used to answer all kinds of research questions (e.g., for dendrochronological, genetic, pest resistance, or biodiversity studies). However, due to differing designs and other experimental variables, which must be accounted for in the analysis, the power to detect the factors that determine the survival, vitality and growth of tree species is lower than in assisted migration experiments with a coherent design. Still, the recombination approach is valuable and followed in several countries, e.g., France (Rihm and Fady, 2023) and Austria (Kristöfel, 2015). In Switzerland, an online application for the documentation of the occurrence of future tree species (from plantations and natural regeneration) was released in April 2024 (www.zukunftsbaumarten.ch, collaboration between the Education Center for Forest BZW in Maienfeld, School of Agricultural, Forest and Food Sciences HAFL and WSL). It will facilitate the exchange between practitioners.

To broaden the potential network of existing planting trials, these approaches should not be restricted to single countries but cover continents. Gaining an overview of experiments testing multiple species on multiple sites in Europe is therefore essential. European initiatives that aim to improve networking across country borders have recently started. The Swiss CG project team contributes expertise, data and research infrastructure to the initiatives OptForest, a Horizon project lead by INRAE, and In-Sylva (proposed for funding), to enlarge the potential network.

3.2 Experiences with the participatory approach for the Swiss common garden network

The objective of the participatory process for planning and designing the Swiss CG network was to ensure that the design of the initiative not only meets scientific requirements, but also integrates the questions and requirements of the various stakeholder groups (Figure 1). While it was not possible to accommodate all expectations

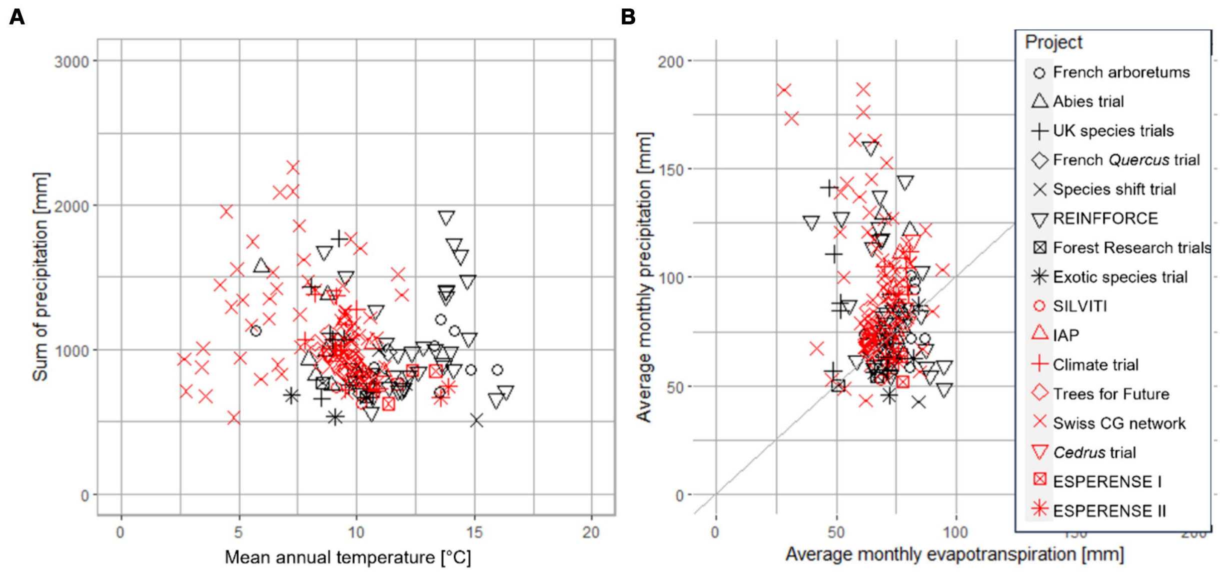

FIGURE 5
Annual precipitation sum [mm] vs. mean annual temperature [°C] at 185 experimental sites in 16 projects **(A)**. Average monthly precipitation [mm] vs. average monthly potential evapotranspiration [mm] after Turc during the growing season at the same sites **(B)**. Sites above the diagonal 1:1 line are wet and sites below are dry.

of the stakeholders, the participatory process increased acceptance of design decisions and enhanced the support for the project. Nevertheless, the scientific team was aware that while stakeholder input was clearly valuable, it was also important not to compromise scientific rigor, in particular regarding the statistical power of the experimental design. An important drawback of the participatory process was that it increased the complexity of the decision processes, particularly when many stakeholders contributed to a discussion, and thus additional time was required to reach final decisions.

3.3 Trade-offs and challenges in designing the Swiss common garden network

When designing a large-scale experiment like the Swiss CG network, some compromises between statistical desirability and practical feasibility are inevitable, given limited resources. During the project planning phase, such conflicts of interest were negotiated between the stakeholders and the project's scientific team. For instance, an important question that arose was the number of CGs in which a tree species should be tested: while it was desirable to test each tree species in many CGs to obtain statistically sound results, the number of suitable sites with the necessary size to establish a CG and the resources available for establishing and maintaining the sites were limited. A power analysis, which was conducted to find the minimum number of sites necessary to answer the research questions with statistical validity, revealed that a species should be tested on at least 30 sites.

Another point of discussion was the number of tree species to be included in the experiment. While the cantons were generally interested in testing a large number of species, a compromise had to be found because both the number and size of sites were limited. For each of the 18 species in the core and extension sets combined, we expect to obtain data on mortality, plant damage and growth performance across the environmental gradient. Where environmental gradients of tree species overlap, interspecific comparisons of species performance will also be possible. For the nine tree species of the core set, statistically sound results can be expected for at least five explanatory variables. The data generated for the species of the extension set are restricted to fewer explanatory variables, to avoid reducing explanatory power.

The number of seed sources to be tested per species presented a similar challenge. The initial intention to include four seed sources per species was discarded because of concerns that this number would not be sufficient to adequately represent the expected within-species genetic variation. Considering the limited size and number of CGs and the fact that reducing the number of species was not a suitable option, the number of seed sources per species was increased to seven, but with the constraint that only four seed sources would be planted per CG. This increased the genetic variation represented in the experiment at the cost of reducing the statistical power to analyze the performance of individual seed sources. However, since the primary aim of the Swiss CG network is to draw conclusions about the species rather than at the seed source level, this compromise was accepted.

For an optimal representation of within-species genetic variation, seed sources should represent large parts of a species' habitat, which also requires taking postglacial migration history into consideration. Due to financial, technical and legal restrictions, it was not possible to harvest seed sources outside of Switzerland specifically for the project. Therefore, mostly commercially available seed sources were procured, but in some cases they were complemented with seed material obtained through research contacts in their respective regions of origin. Forest sanitary concerns also had to be considered. For example, the purchase of native *Pseudotsuga menziesii* seed sources had to be limited to a range from Washington to northern Oregon, while seeds from any more southern seed sources, e.g., California and southern Oregon, could not be imported because of restrictions due to the pathogen *Gibberella circinata* (Gordon et al., 2006), even though these sources might have been interesting for their adaptation to warmer and drier climates.

The cultivation of the reproductive material was challenging in this project. Even after the successful procurement of seeds, seed material from some seed sources did not germinate, or it was impossible to get seeds from the same seed sources again in the following year. Generally, 2020 was a bad seed year, leading to missing seed material from many seed sources in autumn 2021. These restrictions in plant availability from certain seed sources in certain years affected the optimal distribution of the seed sources across the sites and resulted, in some cases, in subplots that had to be left empty.

The selected CG sites in forests cover a large part of the environmental gradient in Switzerland. On average, the Swiss CG network contains one site per 21,000 ha of forested land in Switzerland. In comparison to the forested land area in the different elevation belts (forested land area without shrubs according to the Swiss National Forest Inventory, Abegg et al., 2020), lower sites (below 600 m a.s.l.) are overrepresented (1 site per 12,000 ha of forested land), while higher sites (above 1,000 m a.s.l.) are underrepresented (1 site per 26,000 ha of forested land). The likely reason for the underrepresentation of higher sites is that forests at higher elevations are often less intensively managed because of excessive costs due to difficult terrain and limited accessibility. Further, since the protection against natural hazards is usually the main management target in such forests, this prohibits the creation of larger canopy openings. Therefore, it was usually not possible to establish CG sites in mountain protective forests except in cases where there were pre-existing openings created by natural disturbances, mainly windthrows.

In our experiment, tree species are tested on forest sites under open conditions. Thus, shading and competition between different tree species and between individuals of the same species are excluded as factors influencing tree vitality and growth, leaving only the influence of environmental factors. This setting diminishes, however, the relevance of our results for smaller gaps within forests, where shading and competition play a central role.

3.4 Enhancing the value of the Swiss common garden network

The establishment of the Swiss CG network opens valuable opportunities to study additional research questions beyond the original project goals. The CG team welcomes add-on projects, as long as they do not interfere with the goals of the main project. In a workshop with interested researchers in March 2019, several add-on projects were initiated. In the Swiss Biomass project, the stocked stands on a subset of the experimental sites were investigated before clear-cutting. The data were used to improve the allometric functions, which are important to inform models of carbon storage in forests. The Polytunnel project involves using greenhouses to experimentally extend the climatic gradient beyond the warm and dry range edge of the CG network sites. Specifically, at three CG sites the effects of experimental warming and precipitation reduction on the phenology and growth of a subset of six tree species are being examined. This project was started in 2021 and is planned to run for 10 years. Further, phytopathological monitoring is being conducted on some CG sites to detect the introduction of pathogens, which is an important concern in assisted migration projects. For at least 5 years, this yearly monitoring will be conducted on two sites that each host all 18 tree species and complement each other to host all 117 seed sources. Some of the sites will be used to test new airborne or terrestrial laser-based monitoring techniques. Additional projects on plant–soil interactions and effects of leaf and root biomes on plant mortality are currently being proposed for funding. The initiation of further add-on projects would be desirable. The monitoring of additional parameters could make it possible to answer more questions. For instance, a comprehensive understanding of genetic variation within species and a thorough phenotypic characterization would enhance discussions on intraspecific variation in mortality and growth, as well as phenotypic plasticity. Additionally, the analysis of isotopic variation in leaf matter could shed light on tree species physiological responses to drought.

4 Conclusion

Climate change, with rapidly rising temperatures and an increasing frequency and severity of droughts, may question the continued existence of forests in many regions. Many tree species will cease to be viable in their current habitats. Science-based targeted interventions are therefore urgently needed to promote tree species that can cope with the climate of the future and thus enable forest ecosystems to continue to provide ecosystem services. With these aims, several initiatives have started in recent years across Europe. The recently established Swiss CG network is currently the largest network in Europe dedicated to the search for tree species that can cope with the future climate.

The Swiss CG network lays the foundation for a long-term research program that is tailored to the specific questions and requirements of forest stakeholders in Switzerland, such as the need for protection against natural hazards in mountain forests, but it also fits well within a potential network of European approaches. Therefore, it opens opportunities for common evaluations and meta-analyses. In addition, it offers possibilities for add-on projects, which answer additional research questions. With the findings from the Swiss CG network, we expect to provide politicians, forest authorities and practitioners with scientific evidence to make informed management decisions that secure the future of Swiss forests and the ecosystem services they provide.

Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: We only used approximate site locations as well as species and design information from European common garden networks. Climate data were derived from CHELSA (Karger et al., 2017).

Author contributions

KS: Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Visualization, Writing

– original draft, Writing – review & editing. PB: Conceptualization, Funding acquisition, Methodology, Writing – original draft. EF: Conceptualization, Methodology, Validation, Writing – original draft, Writing – review & editing.

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Conflict of interest

Publisher's note

Supplementary material

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Climatic conditions at provenance origin influence growth stability to changes in climate in two major tree species

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Climate change is expected to outpace the rate at which populations of forest trees can migrate. Hence, in forestry there is growing interest in intervention strategies such as assisted migration to mitigate climate change impacts. However, until now the primary focus when evaluating candidates for assisted migration has been mean or maximum performance. We explore phenotypic plasticity as a potentially new avenue to help maintain the viability of species and populations in the face of climate change. Capitalizing on large, multi-site international provenance trials of four economically and ecologically important forest tree species (*Fagus sylvatica*, *Picea abies*, *Picea engelmannii*, *Pinus contorta*), we quantify growth stability as the width of the response function relating provenance growth performance and trial site climate. We found significant differences in growth stability among species, with *P. engelmannii* being considerably more stable than the other three species. Additionally, we found no relationship between growth performance and growth stability of provenances, indicating that there are fast-growing provenances with a broad climate optimum. In two of the four species, provenances' growth stability showed a significant relationship with the climate of the seed source, the direction of which depends on the species. When taken together with data on growth performance in different climate conditions, a measure of growth stability can improve the choice of species and provenances to minimize future risks in forest restoration and reforestation.

KEYWORDS

growth stability, phenotypic plasticity, provenance trial, common garden, *Fagus sylvatica* (European beech), *Picea engelmannii* (Engelmann spruce), *Pinus contorta* (lodgepole pine), *Picea abies* (Norway spruce)

1 Introduction

High rates of change in future climate projections (IPCC, 2023) will most likely exceed the capacity of long-lived, sessile species such as forest trees to adapt through natural selection (St Clair and Howe, 2007) or migration (Aitken et al., 2008), even if there is a possibility of adaptation in place for some species (Kramer et al., 2010). Phenotypic plasticity will likely play an important role in ensuring the survival of tree species and populations (Leites and Benito

Garzón, 2023), at least in the short term; however, plasticity data for forest trees is relatively scarce, due to amounts of time and resources required for establishing test sites across wide climate ranges. Furthermore, analyses of existing data have been focused on identifying differences in performance in population means. Except for rare examples (Vizcaíno-Palomar et al., 2020), potential differences in plasticity between populations have seldom been studied, despite being important for determining a population's ability to withstand a changing climate (Valladares et al., 2014).

Phenotypic plasticity can be defined in various ways and at different scales, very often employing different terminologies for similar concepts (Nicotra et al., 2010). While research often focuses on plasticity in functional traits such as morphology, phenology, or physiology, we choose to analyze plasticity in growth performance of trees. Growth is a trait of primary interest in forestry, since it directly determines wood production, but it is also of great ecological importance, since growth is closely correlated with fitness and survival in young trees (Moustakas and Evans, 2015; Jiang et al., 2022). We focus on height growth, since it is one of the most important growth traits for trees, and the one for which most data is available.

In this study, we refer to plasticity in functional traits as "phenotypic plasticity" (Ghalambor et al., 2007), and to the lack of plasticity in growth as "growth stability" across different climate conditions (Santini et al., 2010; Alvarez et al., 2020). In our interpretation, growth stability originates from phenotypic plasticity in functional traits (Wright et al., 2016), and we will focus our attention on the differences in growth stability among species and populations, due to the importance of growth stability for forestry interventions. Identifying species or populations with high growth stability across different climate conditions would allow for wider margins of error in estimating the optimal forest tree seed source according to future climate projections. This strategy would help to offset uncertainty in climate models, which dramatically increases when predicting extreme climate events, and have crucial impact on tree growth and survival.

We expect that more generalist species, which are distributed across wider geographical and environmental ranges, have higher growth stability, both on a theoretical basis (Baker, 1974) and based on experimental evidence (Sultan, 2001). In other words, species and populations characterized by broader ecological niches would show more constant growth performance across wider ranges of climate conditions. However, it is also possible that populations with high growth stability might show stable, but low, growth performance, i.e., a trade-off between plasticity and growth performance (Richards et al., 2006; Hendry, 2016). This trade-off, due to the costs associated with maintaining a more flexible genotype or phenotype, has been shown to be particularly relevant under stressful environmental conditions (Van Buskirk and Steiner, 2009). Identifying populations possessing both high growth stability and high growth performance would be of great interest for forest managers and researchers, as they may help buffer increased climate variability and uncertainty associated with climate change.

It is commonly assumed that phenotypic plasticity is an adaptive trait, which might be subject to natural selection, especially in response to highly variable environmental conditions (Alpert and Simms, 2002; Lázaro-Nogal et al., 2015; Carvajal et al., 2017; Vázquez et al., 2017). Under this hypothesis, more unstable climates would select for higher levels of growth stability. For this reason, we investigated the possibility that growth stability of a population might be positively related with climate variability at the seed source. On the other hand, the evidence for a relationship between growth stability and the level of a climate variable itself (not its variability) is more discordant, with some authors arguing that populations at the climate extremes of a species' distribution should show lower levels of phenotypic plasticity. This would be due to genetic drift (Arnaud-Haond et al., 2006) and the costs associated with plasticity being more important in unfavorable environments (Mägi et al., 2011).

In forest science, provenance trials (also called common garden experiments) are a commonly used experimental setup (Langlet, 1971). Growing diverse provenances in a common environment allows genetic (G), environmental (E), and GxE interaction effects to be disentangled if the trials are established in disparate environments (Alberto et al., 2013; Kreyling et al., 2019). Often the genetic structure of the populations and sub-populations used in these trials is not known or well-characterized, and for this reason the term "provenance" is used: a provenance is simply defined as a group of trees originating from a single geographical seed source.

We utilized data originating from established networks of provenance trials of four important tree species (*Fagus sylvatica*, *Picea abies*, *Picea engelmannii*, *Pinus contorta*), allowing us to compare the growth stability of more than 300,000 trees (7–32 years old), originating from numerous seed sources, planted across wide geographic and climate gradients in Europe and North America. By calculating a growth stability index to enable across-species comparisons, we investigated the following hypotheses:

1. There are significant differences in growth stability among different tree species, with species from broader ranges being more stable.
2. There is a negative relationship between provenance growth performance and provenance growth stability.
3. Differences in growth stability among provenances are related to the seed source climate and its inter-annual variability, with provenances from more variable climates having higher growth stability.

2 Materials and methods

2.1 Software

We used R version 4.3.2 (R Core Team, 2023) in RStudio version 2023.09.1 (Posit Team, 2023) for all data preparation, statistical analysis, and figure making.

The "gslnls" (Chau, 2023), "gamlss" (Rigby and Stasinopoulos, 2005), and "emmeans" (Lenth, 2023) packages were used for model fitting and testing. Data manipulation employed functions from the "tidyverse" (Wickham et al., 2019) package collection, and from the "janitor" (Firke, 2023) and "broom" (Robinson et al., 2023) packages. RMSE values were calculated with the function "rmse()" from package "performance" (Lüdecke et al., 2021), while MAE values were obtained with the function "mae()" from package "Metrics" (Hamner and Frasco, 2018). Climate range coverage percentages were calculated using the functions "grDevices::chull()" and the "areapl()" function from the "splancs" package (Rowlingson and Diggle, 2024). PCA was conducted using the package "FactoMineR" (Lê et al., 2008). *p*-values were formatted using functions "p_format()" and "add_significance()" from package "rstatix" (Kassambara, 2023). Geospatial data was manipulated using the packages "terra" (Hijmans, 2023) and "tidyterra" (Hernangómez, 2023).

2.2 Provenance trials

We used provenance trial growth data of four major temperate and boreal forest tree species of North America and Europe with high economic and ecological importance (Figure 1) and large natural distributions, both geographically and climatically. These provenance trials are noteworthy for the breadth of climate conditions covered, especially with respect to the species' ranges, and the number of trial sites and provenances tested (Figure 2). As a confirmation, we calculated the percentage of the climate range of each species covered by the seed sources/trial sites, finding relatively high coverage percents (respectively 48% ± 18% for the seed sources and 19% ± 3% for the trial sites). More in detail, we calculated the percentage climate range as the ratio between the areas of the polygons defined by each species' occurrences and seed sources (or trial sites, respectively) in the MAT × MAP climate space.

2.2.1 *Fagus sylvatica*

Fagus sylvatica L. is a deciduous temperate forest tree. Due to its juvenile shade tolerance and tall growth with a dense canopy, it is the dominant native forest tree in Central Europe (Leuschner and Ellenberg, 2017) found in a wide range of climate and environmental conditions (Fang and Lechowicz, 2006). It is considered highly sensitive to climate change and its persistence and potential role under future climate conditions is debated (Gessler et al., 2006; Saltré et al., 2015; Engel et al., 2023). Population persistence, however, is potentially higher than anticipated due to high phenotypic plasticity in important functional traits such as phenology and leaf morphology (Gárate-Escamilla et al., 2019; Schmeddes et al., 2023).

We utilized data from Robson et al. (2018), which reports on a Europe-wide network of *Fagus sylvatica* provenance trials, established between 1995 and 1998. This dataset comprised more than 174,000 individuals from 194 provenances and 38 trial sites. However, measurement ages differed among trial sites, with at least some trial sites being measured each year from age 1 to 13.

2.2.2 *Picea abies*

Picea abies (L.) H. Karst. is a conifer native to northern and eastern Europe. It has been planted for timber production and became the most economically important tree species in central Europe,

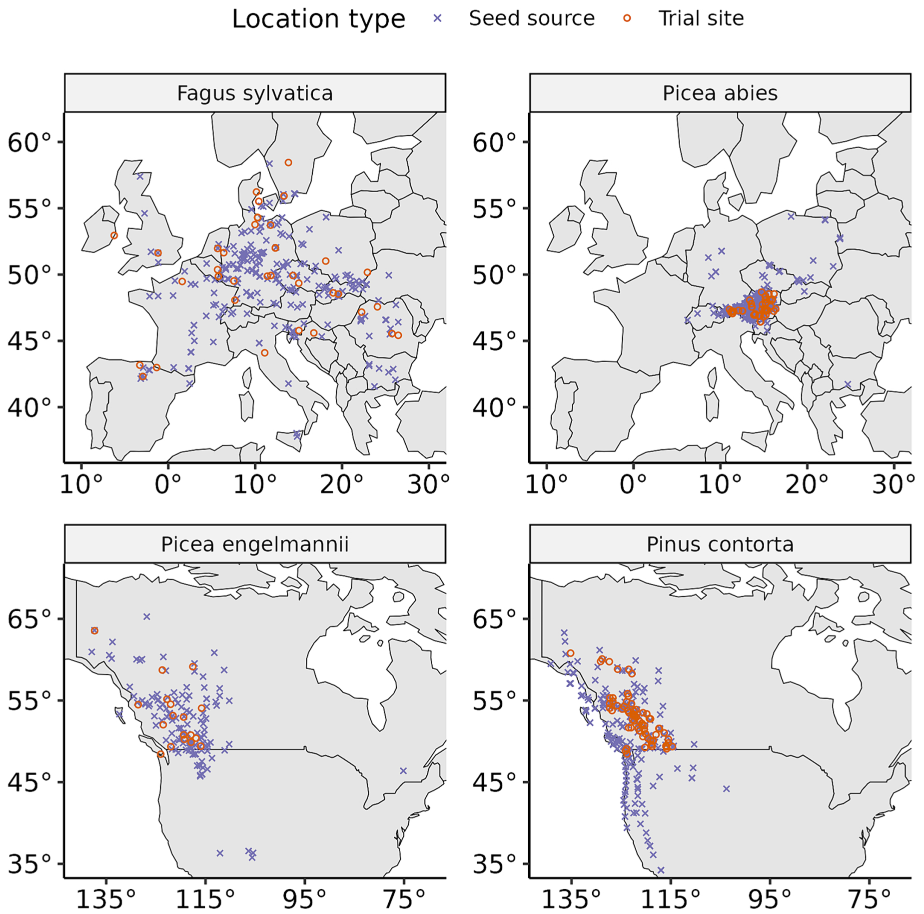

FIGURE 1
Location of the experimental trial sites and of the seed sources in Europe (top row) and North America (bottom row), for the four tree species examined in this study.

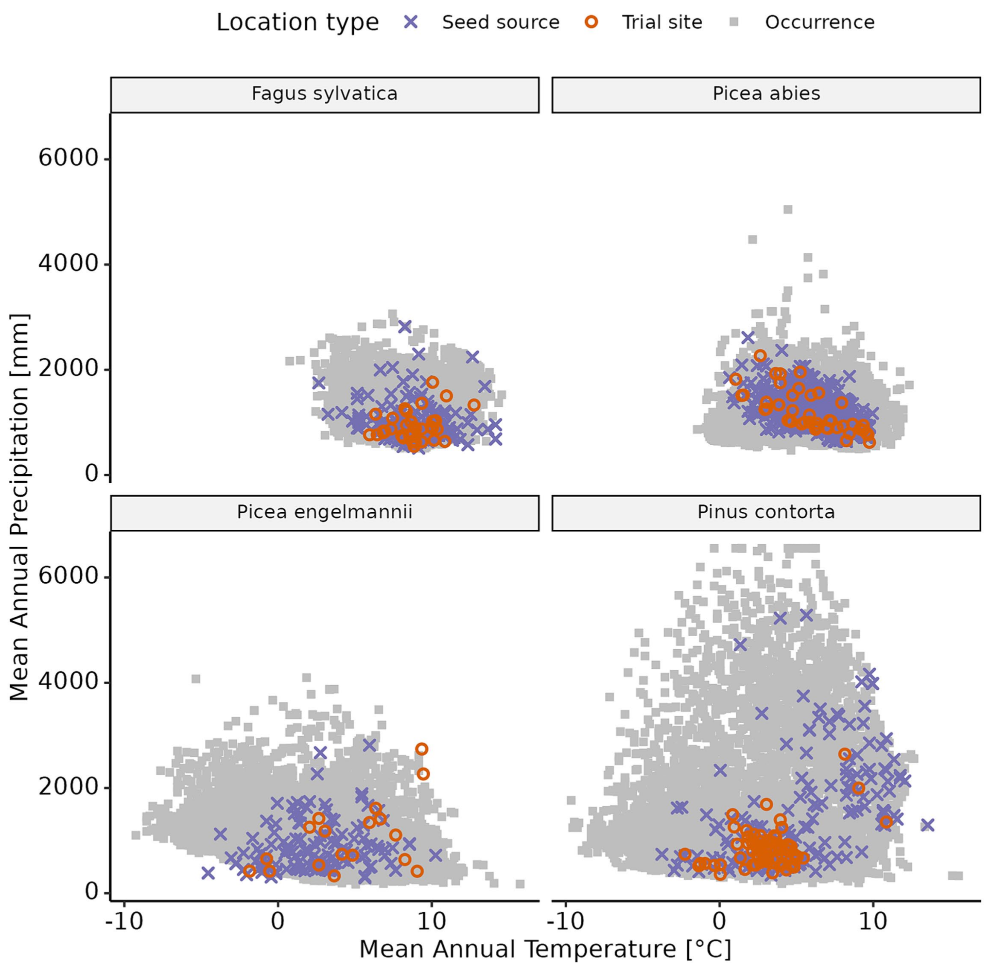

FIGURE 2
Climate distribution of each of the provenance trial sites, seed sources, and the four tree species examined in this study. Species' occurrence data was sourced from the EU-Forest database (Mauri et al., 2017) for *Fagus sylvatica* and *Picea abies*, and from the databasin.org database (Little, 1971; Comendant et al., 2009) for *Picea engelmannii* and *Pinus contorta*.

despite large parts of central Europe being outside its natural range (Leuschner and Ellenberg, 2017). Vast areas of these plantations are currently dying back due to climate-change induced drought and warming in combination with bark beetle attacks (Schuldt et al., 2020), fueling ongoing attempts to diversify monocultural stands and replace the species in the long term (Vacek et al., 2019).

Seedlings from 540 provenances of *Picea abies* were planted at 44 trial sites across Austria in 1978. While the geographic range covered by these trial sites is relatively small (Figure 1), they span a wide proportion of the species' climate range (Figure 2). See Nather and Holzer (1979) and Kapeller et al. (2012) for details regarding the materials, sites and design. Height was recorded at ages 7, 8, 9, 10, and 15.

2.2.3 *Picea engelmannii*

Picea engelmannii and *Picea glauca* are sympatric in across large portions of British Columbia and in the Rocky Mountains of Alberta where they readily hybridize. (For simplicity, we refer to the two species and their hybrids as *P. engelmannii*.) Suitable climate ranges of *P. engelmannii*, the most widely planted species in British Columbia, are expected to shift northward and decline substantially in extent in British Columbia in coming decades due to climate change (MacKenzie and Mahony, 2021).

127 provenances of *Picea engelmannii*, *Picea glauca* and their natural hybrids from western North America were planted at 18 (17 extant) trial sites in British Columbia, Alberta, and the Yukon in 2005. See O'Neill et al. (2014) and Grubinger et al. (2023) for details regarding the materials, sites and design. Height was recorded at ages 3, 6, 10 and 16.

2.2.4 *Pinus contorta*

The most widely distributed and second most widely planted tree species in British Columbia, *Pinus contorta* was heavily impacted by mountain pine beetle in the last 2 decades. Being one of the most strongly locally adapted of the widely distributed tree species of western North America (Rehfeldt, 1994), its productivity is expected to decline substantially as the climate warms (O'Neill et al., 2008). Its climate niche is expected to shift northward and decline substantially in extent in British Columbia in coming decades due to climate change (MacKenzie and Mahony, 2021).

140 provenances of *Pinus contorta* from throughout the species' range in western North America were planted at 60 trial sites in British Columbia and two sites in the Yukon in 1974. See O'Neill et al. (2008)

for details regarding the materials, sites and design. Height was recorded at ages 6, 10, 15, 20, and 32.

2.2.5 Data cleaning

The data was cleaned by identifying outlier trial-years (years in which a trial has a more than 5-fold increase or decrease in height compared to the previous and following year), and correcting the units of measurement where obviously wrongly reported (e.g., meters to centimeters), otherwise discarding the measures for the outlier trial-year. Additionally, individual trees that at any point presented a yearly decrease in height of more than 25 centimeters were removed from the dataset. Overall, 18,165 of 1,214,008 individual measures were discarded.

We chose not to remove extremely short individuals from the analysis (e.g., by removing individuals with height < 1 m at age 10). Such growth rates, while very low, are not overly surprising considering the harsh climate conditions at some trial sites, and the very long climate transfer distances experienced by some provenances. In fact, removing such short individuals would discard valuable information on the climate-growth relationships, flattening and distorting the climate response functions.

Following the clean-up steps described above, our final database comprised more than 1 million records, more than 350,000 individual trees, 760 provenances, and 139 trial sites (Table 1).

2.3 Growth data harmonization

The trial sites were established at different times, and the ages at which height was recorded differed among species and among sites within species; therefore, it was necessary to identify a common age for height assessment, i.e., to harmonize height ages among sites and species. For each tree we fitted tree height to a logistic regression model using age as the independent variable, and extracted height at age 10 (HT10) from the fitted model. We chose to harmonize at age 10, before canopy closure and inter-plot competition could accentuate and bias population differences, masking the purely genetic and climatic effects.

For each individual, the model has the form:

$$Height(age) = \frac{a}{1 + e^{-b \times (age - c)}}$$

Where:

a is one asymptote of the curve (the other being 0).

$a \times b / 4$ is the slope at the midpoint.

c is the location of the midpoint (where $Height(c) = a/2$).

The models were fitted using the function "gsl_nls()" from package "gslnls." Compared to most non-linear fitting functions, gsl_nls() has the advantage of being much less sensitive to the choice of starting parameters, and of being able to converge rapidly and reliably in most cases (Hickernell and Yuan, 1997).

We removed unsuccessful model fits, and regressions for which the estimated parameters were outside the following boundaries: $0 < a < 50; 0 < b; 5 < c$. These boundaries were selected to remove unrealistic model fits, such as those predicting negative height, negative growth, or no growth. Additionally, we ensured the quality of the fitted models by calculating the Root Mean Square Error (RMSE) and Mean Absolute Error (MAE) for each individual model, and aggregating them at the species level (Table 2), calculating their mean and standard deviation separately for each species. RMSE and MAE are commonly used measures of error for regression models, and among their advantages is the fact that they are expressed in the same units as the original response variable (Chai and Draxler, 2014). The formulas for the two error measures are as follow:

$$RMSE = \sqrt{\frac{\sum_1^n \left(predicted_i - observed_i\right)^2}{n}}$$

$$MAE = \frac{\sum_1^n \left|predicted_i - observed_i\right|}{n}$$

The mean model error was quite low, as it was in all cases smaller than 6% of the mean predicted HT10, with the highest values found for *P. contorta*. Furthermore, we ran a linear regression between the values predicted by the individual models and the observed data, obtaining in all cases very high r^2 values and highly significant regressions, signifying that the models can predict very well the patterns found in the data (Table 2). Finally, we removed individual models that did not fit the data well, by calculating for each model the proportion of residuals falling outside a 2 standard deviation range from the mean residual, and removing the individual if this proportion was higher than 0.05.

2.4 Climate data

We employed the CHELSA dataset (Karger et al., 2017, 2020) as the source of the climate data for the present study. The CHELSA database contains very high-resolution (30 arc sec, ~1 km) rasters

TABLE 1 Summary of the cleaned-up dataset.

Species	Total records	Total individuals	Total trial sites (median per seed source)	Total seed sources (median per trial site)	Median age at last measurement
Fagus sylvatica	452,537	174,038	38 (6)	194 (34)	7
Picea abies	300,218	65,481	24 (2)	299 (26)	10
P. engelmannii	205,195	61,778	17 (17)	127 (127)	16
Pinus contorta	237,893	57,973	60 (24.5)	140 (60)	32
Total	1,195,843	359,270	139	760	

TABLE 2 Summary of errors and goodness of fit for the growth data harmonization models.

Species	RMSE meters (percent)		MAE meters (percent)		HT10 meters		Predicted × observed	
	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.	r^2	*p*-value
Fagus sylvatica	0.09 (2)	0.07 (2)	0.07 (2)	0.06 (2)	3.71	1.27	0.998	<0.0001
Picea abies	0.02 (1)	0.02 (1)	0.02 (1)	0.01 (1)	2.38	1.33	1	<0.0001
Picea engelmannii	0.03 (1)	0.04 (2)	0.03 (1)	0.03 (2)	2.08	0.85	0.999	<0.0001
Pinus contorta	0.17 (6)	0.12 (4)	0.14 (5)	0.1 (4)	2.8	0.97	0.999	<0.0001

RMSE, MAE, and HT10 are expressed in meters. Between parentheses is the percent relative to the mean HT10 for the species. RMSE, Root Mean Square Error; MAE, Mean Absolute Error; HT10, Harmonized height at age 10.

covering the entire land surface of the Earth. It contains interpolated estimates of many climatic and derived bioclimatic variables. For each trial site and seed source, we extracted the average values of all 19 available climate variables for the period 1981–2010, as these years best represent the HT10 growth period of the trial sites.

2.4.1 Inter-annual climate variability

Additionally, to quantify the inter-annual climate variability of the trial sites, we extracted monthly precipitation and mean surface temperatures for each trial site location. We then aggregated the data to calculate Annual Precipitation (AP) and Mean Annual Temperature (MAT) for each year at each trial site, from which we calculated the coefficient of variation for AP (AP CV), and the standard deviation of MAT (MAT SD) over the 30-year interval. We calculated the SD of MAT, instead of the CV, because the CV is not defined for a scale without a natural zero point (Dunn and Clark, 2009).

2.4.2 Principal component analysis

To reduce collinearity and the number of climate variables (19 long-term bioclimatic variables and 2 variables for the inter-annual variability, see Supplementary Table S1), we carried out a Principal component analysis (PCA). PCA is an approach commonly used in environmental science/species distribution modeling to simplify complex datasets of correlated variables into a smaller number of variables, which can be more easily employed in modeling (Lever et al., 2017).

We chose not to calculate separate PCAs on different timeframes for each species, or separately for trials sites and seed sources. In the first place, because the differences across time periods in the climate conditions at each trial site/seed source are expected to be relatively small in the time range covered by the present study. Furthermore, these differences should not be so large as to cause significant shifts in long-term climate patterns across the study locations, and therefore we expect that differentiating timeframes would have a minimal impact on the analysis' results. In the second place, the PCA methodology requires using an uniform dataset, to ensure comparability of the Principal Components (PCs). Taken together, these two considerations support our choice of running a single PCA on the entire dataset.

We used the function "PCA()" from the "FactoMineR" package to calculate the PCA on the climate data for all species, seed sources, and trial sites. We then selected the first two PCs for subsequent analyses. All climate variables were centered and scaled, to give each variable equal weight in the analysis, and to aid in subsequent model fitting. The first two PCs accounted, respectively, for 38 and 23% of the variance in the climate variables. In broad terms, higher values of PC 1 indicate higher precipitation amounts, more constant (both within the year and across years) mean temperatures, and warmer and wetter winters. It might be interpreted as a measure of continentality, with increasing values of PC1 associated with a more maritime climate. Higher values of PC 2 indicate colder and rainier conditions in general, and particularly in summer (Figure 3; Supplementary Table S1; Supplementary Figure S1).

2.5 Growth stability index

Since the experimental designs were not fully factorial, i.e., not all provenances were grown in all trial sites, it was necessary to calculate an index to enable the comparison of growth stability among species and among provenances. To this end, we utilize the width of the peak of each provenance's climate response function, referring to it as Growth Stability Index (GSI) in subsequent analyses. Calculating such an index avoids the problem posed by the fact that the provenances were planted in unequal ranges of climate conditions, which would otherwise introduce differences associated with the ranges of growth performance, even in the absence of genetic effects.

We aggregated the individual-tree age-10 data obtained as described in section 2.3, by calculating the median height for each provenance x trial site combination, excluding provenances planted at fewer than four trial sites. We then fit response functions for each provenance, relating provenance HT10 (dependent variable) to trial site climate (independent variable). The Cauchy function, often used in genecology because it is bell-shaped and has parameters with a clear biological interpretation (i.e., width, height and position of the maximum, see Figure 4; Raymond and Lindgren, 1990; Lindgren and Ying, 2000; Thomson et al., 2009), was used to fit the response functions. Importantly, the *c* parameter represents the width of the fitted function at 80% of the maximum fitted response value. Another useful property of the *c* parameter is that it is independent of the growth rate, which allows to directly compare it across species and provenances (more precisely, the *c* parameter is invariant to multiplication of the response values by a constant number). Two response functions were fitted for each provenance – one for each of PC 1 and PC 2.

The response function model had the form:

$$HT10\left(PC_i\right) = \frac{a}{1+\left(\frac{PC_i - b}{c}\right)^2}$$

Where:

a is the maximum value of the curve.

b is the location of the maximum (where $HT10\left(b\right) = a$).

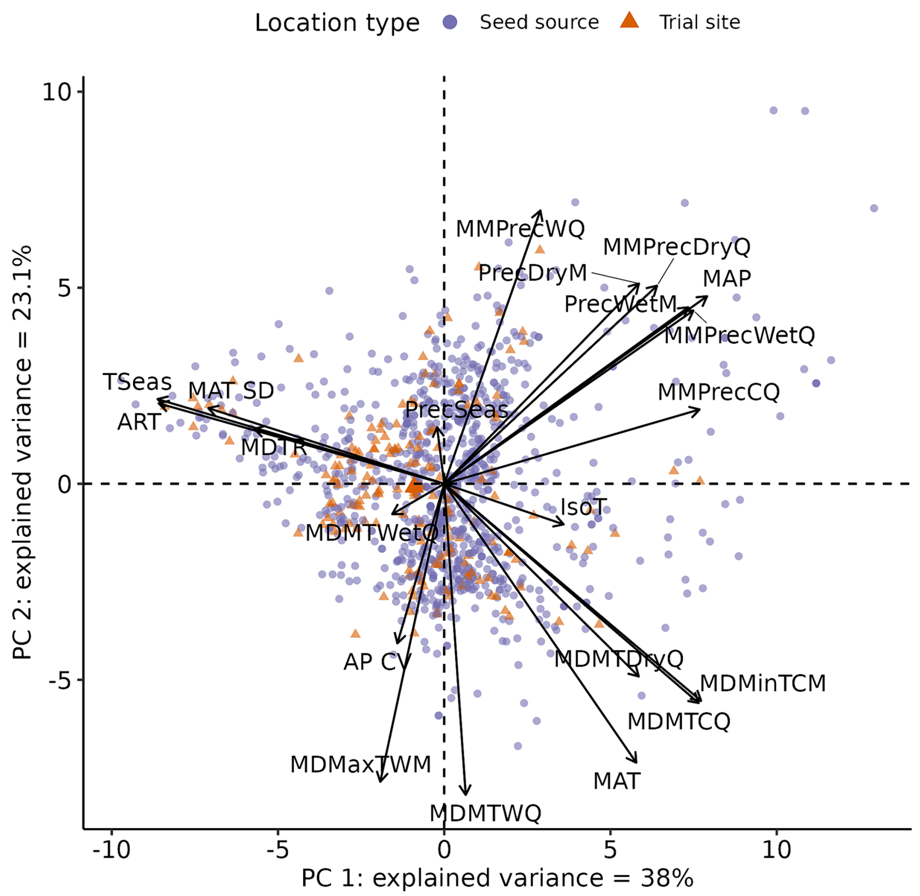

FIGURE 3
Graphical summary of the principal component analysis. The arrows show the loadings of each climate variable along the first two Principal Component axes. The points represent each seed source and trial site in the PC climate space. Each PC axis is labeled with the respective amount of variance explained in the original dataset. See Supplementary Table S1 for abbreviations.

c is the range, centered on b, where $Height\left(PC_i\right) > a \times 0.8$.

The models were fitted using the function "gsl_nls()," described in section 2.3.

We removed unsuccessful model fits, and regressions for which the estimated parameters were outside the following boundaries: $0 < a < \max\left(HT10\right) \times 10; \min\left(PC_i\right) - \frac{range\left(PC_i\right)}{2} < b < \max\left(PC_i\right) + \frac{range\left(PC_i\right)}{2}$. These boundaries were selected to remove unrealistic model fits, such as those predicting negative or extremely high tree heights, and to remove fits where the maximum was too far outside the range of available data.

In a similar way as described in section 2.3, we ensured the quality of the fitted models by calculating the RMSE and MAE for each provenance's model, and aggregating them at the species × PC level (Table 3), calculating their mean and standard deviation separately for each combination of species and PC. The mean model error was higher, with a maximum of 36% relative to the mean predicted HT10 for PC 2 in *P. engelmannii*. Nonetheless, a linear regression between the values predicted by the models and the observed data yielded in most cases high r^2 values (only one under 0.9), and highly significant regressions. We observed the presence of some non-linearity in the predicted x observed plots. As explained above in section 2.3, we removed models which had a high proportion of residuals outside a range of 2 standard deviations from the mean residual.

Since the response functions use the climate at the trial site as the predictor variable, a broader peak implies that there is a wider range of climates where the provenance performs close to the maximum. For this reason, we extracted the c parameter from the fitted functions, to use as a quantifier of the growth stability (hereafter, Growth Stability Index—GSI) of each provenance. As specified above, a separate GSI was calculated for each of the climate variables. When writing about the GSI calculated for a specific climate variable, we refer to it as $\mathrm{GSI}_{\mathrm{variable}}$ (e.g., $\mathrm{GSI}_{\mathrm{PC\ 1}}$).

2.5.1 GSI—species relationship

We tested for differences in GSI among species for each of the climate variables by fitting a full linear mixed effects model including: GSI as response variable; species and PC (with an interaction term) as fixed effect predictors; and provenance as random effect predictor. Additionally, the full model included a dependency of the scale, skewness and kurtosis parameters on the species x climate variable combination.

The model was fitted using the function "gamlss()" from the "gamlss" package, using the "BCPEo" (Box-Cox Power

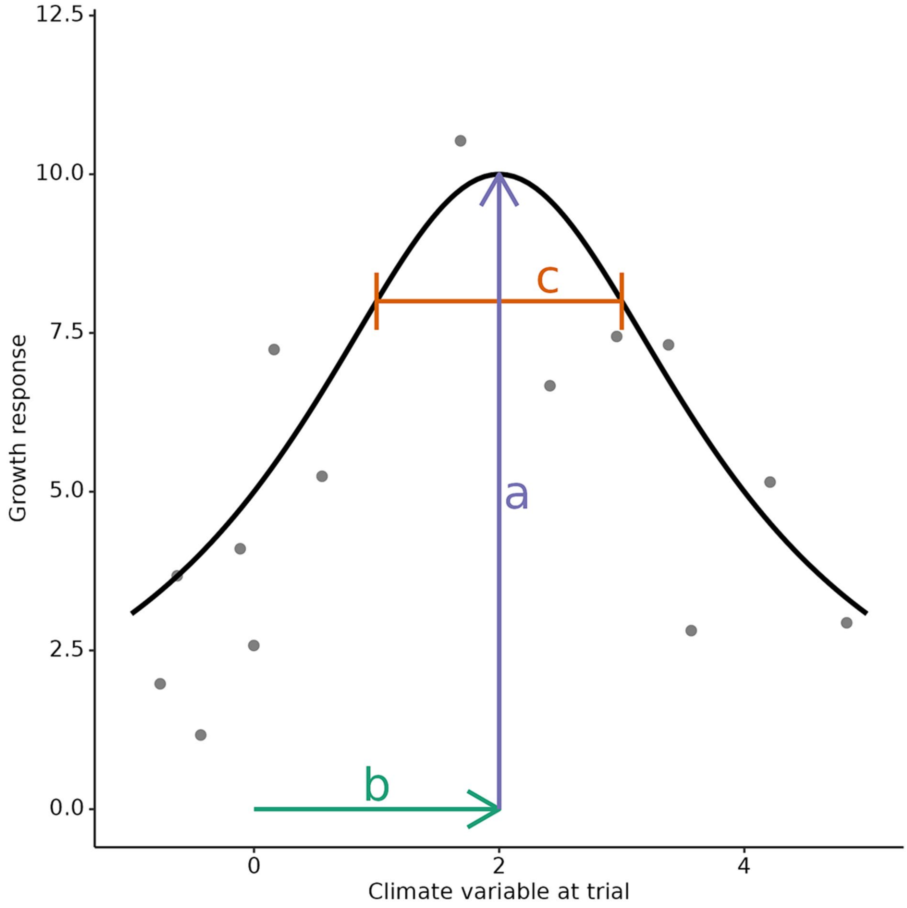

FIGURE 4
Example of Cauchy response function, fitted on simulated data. The provenance's growth response is characterized by the three parameters shown: a represents the maximum growth, at optimal site climate; b represents the position of the optimal site climate; c represents the width of the response function's peak, where growth performance is at least 80% of the maximum.

TABLE 3 **Summary of errors and goodness of fit for the Cauchy growth response models.**

Species	PC	RMSE meters (percent)		MAE meters (percent)		Predicted × observed	
		Mean	Std. dev.	Mean	Std. dev.	r^2	*p*-value
Fagus sylvatica	1	0.46 (14)	0.24 (7)	0.37 (11)	0.19 (6)	0.975	<0.0001
	2	0.21 (7)	0.2 (6)	0.18 (6)	0.17 (5)	0.991	<0.0001
Picea abies	1	0.46 (20)	0.33 (14)	0.36 (15)	0.24 (10)	0.954	<0.0001
	2	0.39 (20)	0.29 (15)	0.3 (16)	0.22 (11)	0.931	<0.0001
Picea engelmannii	1	0.58 (31)	0.11 (6)	0.48 (26)	0.1 (5)	0.912	<0.0001
	2	0.68 (36)	0.12 (6)	0.56 (30)	0.11 (6)	0.884	<0.0001
Pinus contorta	1	0.54 (21)	0.17 (7)	0.43 (17)	0.13 (5)	0.954	<0.0001
	2	0.59 (23)	0.19 (8)	0.47 (18)	0.15 (6)	0.945	<0.0001

RMSE and MAE are expressed in meters. Between parentheses is the percent relative to the mean HT10 for the species. PC, Principal Component; RMSE, Root Mean Square Error; MAE, Mean Absolute Error.

Exponential) error family, employing a log-link for the response variable (Rigby and Stasinopoulos, 2004). This is appropriate for the GSI values, since they are strictly positive real numbers, and is useful because it reduces the skewness of the data and reduces the influence of outliers on the subsequent significance test.

We employed a systematic approach to model term selection, aiming to strike a balance between model complexity and goodness of fit. Our strategy involved iterative cycles of submodel creation, ranking based on the Akaike Information Criterion (AIC), and evaluation of model fit. Starting from the full model, we systematically generated submodels by excluding one term at a time. We ranked the submodels (including the starting model) according to AIC, and inspected them for goodness of fit using the "plot.gamlss()" and "wp()" functions from "gamlss" package. We chose the model with lowest AIC that still fitted the available data well without signs of overfitting. We then repeated this procedure, starting from the selected submodel. More details about the discarded submodels can be found in Supplementary Table S4.

After applying the iterative term removal process described above, we settled on a final model ($r^2 = 0.70$) of the form:

$$GSI_{ij} \sim BCPE\left(\mu_{ij}, \sigma, \nu, \tau\right)$$

$$\log\left(\mu_{ij}\right) = \beta_0 + \beta_1 species_i + \beta_2 PC_j + \beta_3 species_i PC_j$$

$$\log\left(\sigma\right) = \beta_4$$

$$\nu = \beta_5$$

$$\log\left(\tau\right) = \beta_6$$

where μ is the location parameter, σ is the scale parameter, ν is the skewness parameter, and τ is the kurtosis parameter.

We passed the fitted final model to the functions "emmeans()" and "cld.emmGrid()" from the package "emmeans" to calculate the *p*-values for the pairwise differences (alpha = 0.05) in mean GSI across different species, correcting the p-values for multiple testing with Tukey's method.

2.5.2 GSI—growth relationship

We investigated a possible relationship between GSI and HT10 of the provenances with a linear mixed effect model. We used the "gamlss()" function to fit a full model including: HT10 as response variable; species, climate variable, and GSI (with all possible interaction terms) as fixed effect predictors; provenance and trial as random effect predictors.

After applying the iterative term removal process described in section 2.5.1, we settled on a final random intercepts model ($r^2 = 0.79$) of the form:

$$HT10 \sim BCPE\left(\mu_i, \sigma, \nu, \tau\right)$$

$$\log\left(\mu_i\right) = \beta_{trial[i]}$$

$$\beta_k \sim Normal\left(\bar{\mu}, \bar{\sigma}\right)$$

$$\log\left(\sigma\right) = \beta_1$$

$$\nu = \beta_2$$

$$\log\left(\tau\right) = \beta_3$$

where μ is the location parameter, σ is the scale parameter, ν is the skewness parameter, τ is the kurtosis parameter, and $\bar{\mu}$ and $\bar{\sigma}$ are the mean and standard deviation of the random effect distribution.

2.5.3 GSI—seed source climate relationship

We investigated the relationship between climate at the seed source and GSI using a linear mixed effect model. For each PC, we regressed the GSI of each provenance on the PC value of the seed source.

We used the "gamlss()" function to fit a full linear mixed effects model including: GSI as response variable; species, PC, and PC value at seed source (with all possible interaction terms) as fixed effect predictors; provenance as random effect predictor. We once again employed the "BCPEo" error family with a log-link. Additionally, the full model included a dependency of the scale, skewness and kurtosis parameters on the species x climate variable combination.

After applying the iterative term removal process described in section 2.5.1, we settled on a final model ($r^2 = 0.79$) of the form:

$$GSI \sim BCPE\left(\mu_{ijk}, \sigma_{ij}, \nu_i, \tau\right)$$

$$\log\left(\mu_{ij}\right) = \beta_0 + \beta_1 species_i + \beta_2 variable_j + \beta_3 species_i PC_j + \beta_4 species_i PC_j \times PC_{value\,at\,source}$$

$$\log\left(\sigma_{ij}\right) = \beta_5 + \beta_6 species_i + \beta_7 variable_j$$

$$\nu_i = \beta_8 + \beta_9 species_i$$

$$\log\left(\tau\right) = \beta_{10}$$

where μ is the location parameter, σ is the scale parameter, ν is the skewness parameter, and τ is the kurtosis parameter.

We passed the fitted final model to the functions "emtrends()" and "test()" from the package "emmeans," to test if the regression slope was significantly different from zero (alpha = 0.05), across each combination of species and PC, and corrected the p-values for multiple tests with Sidak's method.

3 Results

3.1 Growth stability index

3.1.1 Growth stability differs among species

Growth stability differed markedly among the studied species for all PCs (Figure 5; Supplementary Table S2), but nonetheless, species rankings of GSI values were remarkably consistent across PCs. In particular, *P. engelmannii* showed a significantly higher mean GSI than the other species for both PCs. This difference was large, as in some cases there was an almost 8-fold difference between the species (e.g., difference between *P. engelmannii* and *P. abies* in $GSI_{PC\ 1}$). *Pinus*

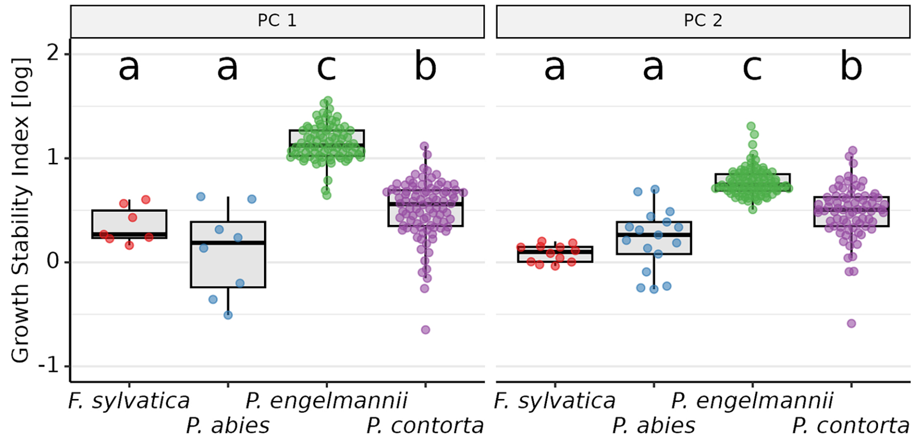

FIGURE 5
Inter-specific differences in growth stability (GSI). Each point corresponds to the GSI for one provenance, overlaid on the corresponding box-plots for each species (median, first and third quartiles, last point less distant than 1.5 times the inter-quartile-range). The GSI values were log10-transformed. Data-points have been jittered for clarity, using the function "geom_quasirandom()" from package "ggbeeswarm." Species sharing a lower-case letter do not differ significantly in their mean GSI. PC 1, Principal Component 1; PC 2, Principal Component 2.

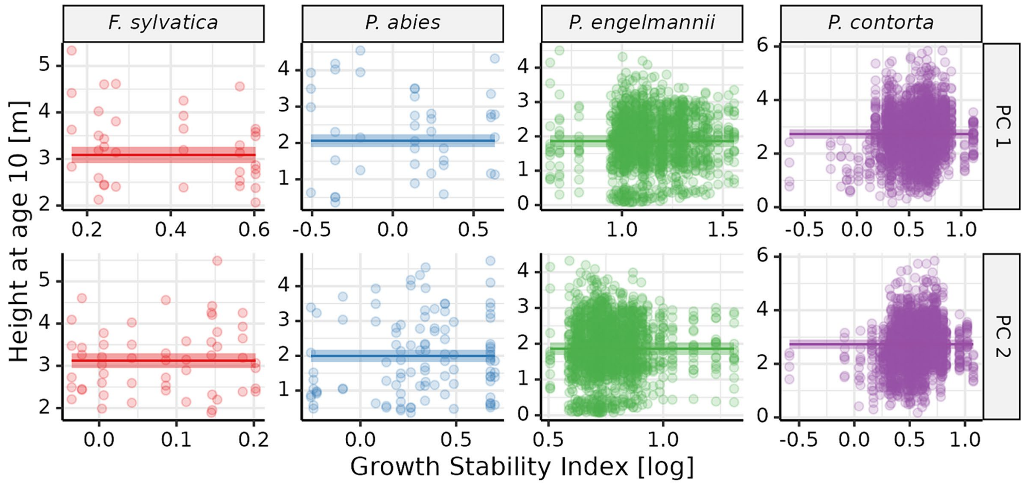

FIGURE 6
Relationship between height at age 10 (HT10) and growth stability (GSI). Each point corresponds to one provenance × trial site combination. The GSI values were log10-transformed. Lines representing the regression between GSI and the corresponding climate variable are overlaid on the raw data. Only fixed effects are shown (i.e., no trial random effect). The shaded bands correspond to the 95% confidence interval of the regression. PC 1, Principal Component 1; PC 2, Principal Component 2.

contorta showed the second-highest growth stability; *F. sylvatica* and *P. abies* both showed the smallest GSI.

3.1.2 Growth stability is not related with growth performance

GSI and growth performance were not significantly related, as indicated by the absence of GSI as an explanatory variable in the final model, which corrected for trial site effects in its mixed effect structure. Likewise, climate at seed source did not affect growth performance consistently across all species and provenances. The final model, which included just the trial random effect, still had a relatively high r^2 value ($r^2 = 0.79$). In summary, growth performance depended strongly on the specific conditions of the trial sites, but not on GSI or source climates for the four studied species. In fact, it was possible to observe in the dataset all combination of growth stability and growth performance (Figure 6). For example, *P. engelmannii* provenance "745" had a stable, but low, growth performance; provenance "693" showed a relatively low growth performance at optimal climate, and a high sensitivity to variations from this optimum; provenance "759" had high growth in optimal conditions, but was also sensitive to changes in climate; while provenance "713" showed good growth performance across a wide range of climate conditions (Figure 7).

3.1.3 Growth stability is linked to source climate

Growth stability was significantly related with climate at the seed source in two of the four studied species (Figure 8; Supplementary Table S3). We observed a highly significant inverse relationship between PC 1 at seed source and GSI in *P. engelmannii*.

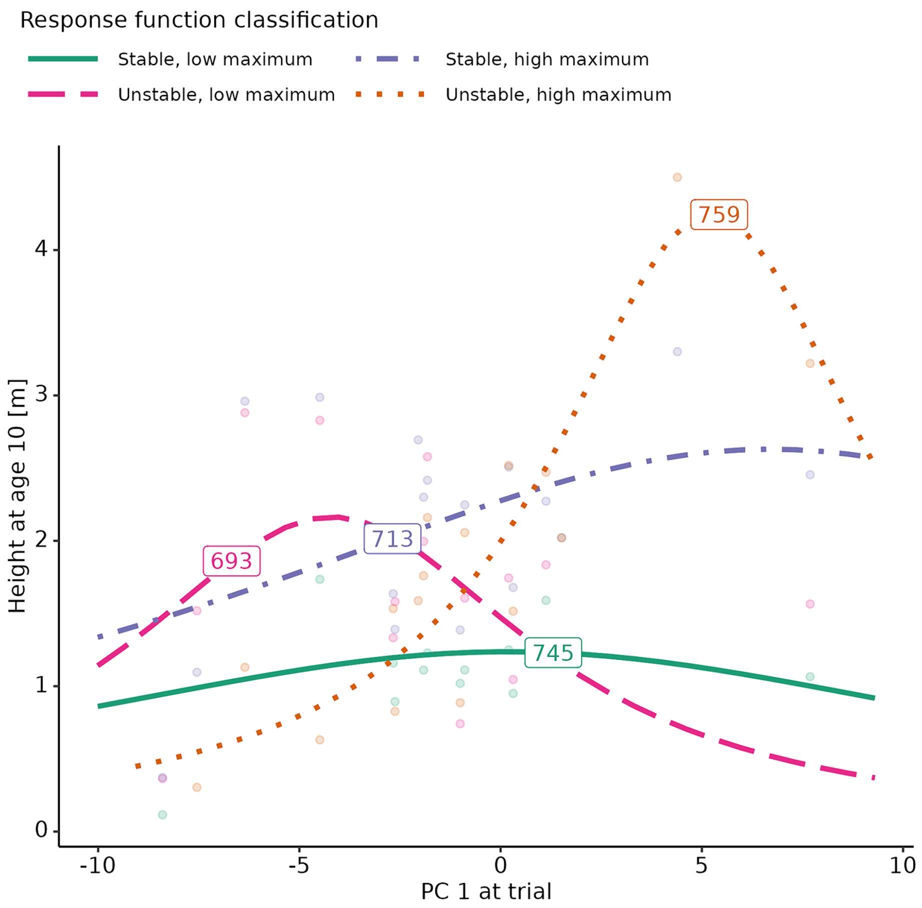

FIGURE 7
Example growth response functions for four *Picea engelmannii* provenances. Fitted Cauchy response functions are superimposed on the raw data-points. The functions are labeled with the corresponding provenance identification code. PC 1, Principal Component 1.

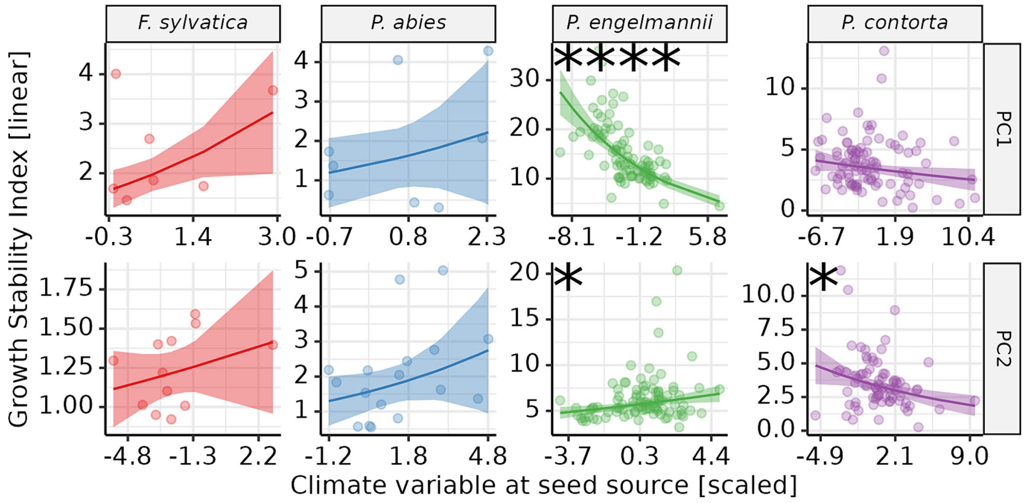

FIGURE 8
Relationship between growth stability (GSI) and climate at the seed source of the provenances. Each point corresponds to the GSI for one provenance. GSI values are on a linear scale. Lines overlaid on the raw data represent the regression between GSI and the corresponding PC. Shaded bands correspond to the 95% confidence interval of the regression. Asterisks indicate the significance level of the regression: empty = $p > 0.05$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ****$p < 0.0001$. PC 1, Principal Component 1; PC 2, Principal Component 2.

This implies that provenances from seed sources which are drier, with colder winters, and with more variable temperatures (both within years and across years) possessed higher growth stability. Missing coordinates for several provenances resulted in fewer data-points for *F. sylvatica* and *P. abies* compared to the GSI – species regression (Figure 5). The scarcity of data-points may have contributed to the absence of significant regressions for these two species.

On the other hand, the direction of the relationship between PC 2 and GSI was not consistent across species, as it was positive for *P. engelmannii* and negative for *P. contorta*. This indicates that provenances of *P. engelmannii* originating from colder sources, and with colder and wetter summers have higher growth stability. The situation seems to be the opposite in regards to *P. contorta*: higher levels of GSI are found in provenances from seed sources which are warmer in general, and in particular drier and warmer in summer.

4 Discussion

Growth stability has been widely studied and applied in the development of crop varieties in agriculture and seed orchard populations in forestry (Li et al., 2017). However, for most species and jurisdictions where reforestation is achieved with natural stand populations, selection of stable provenances has received little discussion, particularly as a climate change adaptation strategy. Prioritizing stable species and provenances for reforestation or afforestation is readily accomplished using existing provenance trial data, and is compatible with other strategies such as assisted migration (Pedlar et al., 2012) and increasing species and seedlot diversity (Hof et al., 2017; Looney et al., 2023). Furthermore, the use of the most stable species and provenances should not impact reforestation costs where a diversity of seed source options exists.

Growth stability differed substantially among the four studied species, corroborating previous reports of species differences in phenotypic plasticity (Gianoli and Valladares, 2012; Stotz et al., 2021), performance stability (Sultan, 2001) and, more generally, niche breadth as quantified for instance by species distribution models (Thomas et al., 2004). Nonetheless, the absolute differences in growth stability among the four species, which all show broad climate niches under which they become dominant, are remarkable. In fact, median GSI values of the four species differed by a factor of as much as eight. The consistency in the ranking of the species across climate variables suggests that the observed differences in growth stability might be due to intrinsic properties of the species, which carry over in a consistent way across different climate variables. In our data, species covering a broader climate range (*P. contorta* and *P. engelmannii*, Figure 2) also showed a higher growth stability. This observation can be linked to the basic ecological assumption of narrow niche width in specialist species vs. wide niche in generalist species (Ma and Levin, 2006), where generalists that occupy more heterogeneous environments also show higher adaptive plasticity (Sultan, 2001; Griffith and Sultan, 2012).

Growth stability also varied strongly among provenances within all four studied species. Interestingly, no association between growth stability and growth performance was observed (Figures 6, 7), with the variation in growth performance in the dataset being explained well with just the effect of the trial sites. For basic research, this finding supports the view that there is no consistent pattern between plasticity and performance, i.e., plasticity can be adaptive, maladaptive, or neutral (Nicotra et al., 2010; Kreyling et al., 2019). This multitude of potential links is probably due to evolutionary costs and limits of phenotypic plasticity (Van Kleunen and Fischer, 2005). This finding is even more interesting for forest management, though, as it suggests that there are certain provenances that combine high growth performance with high growth stability, i.e., the ability to perform well under a wider range of climate conditions. Identifying these provenances seems a promising opportunity in the face of continued rapid climate change and uncertainty in local climate projections.

The fit of response functions is commonly weak where climate is the sole predictor variable (O'Neill et al., 2007), as in the present study. Nonetheless, that we observed significant relationships between GSI and several predictor variables (Figure 8) attests to the extent to which climate drives the evolution of plasticity. Even so, accounting for non-climatic trial site factors that influence growth was found to strengthen response functions (Ford et al., 2017; Hill and Ex, 2020) and models of species distribution (Rehfeldt et al., 2015), site productivity (Fiandino et al., 2020) and floral composition (Vennetier et al., 2008) and could potentially strengthen these genecological models. For example, in Norway spruce, soil conditions were found to have a similar effect on growth as climate (Chakraborty et al., 2019).

In general, we did not find a consistent pattern in the relationship between climate at seed source and growth stability across the species. The scarcity of data-points for *F. sylvatica* and *P. abies* may be one of the causes for the absence of more significant regressions. Having trial locations covering the full climate range of the species (and even beyond it) would probably result in more successful Cauchy model fits, and also in a better understanding of limits of acclimation. The absence of consistent patterns between climate and growth stability across the species, however, could also be due to the absence of selection for different levels of phenotypic plasticity, for example due to similar climate variability across the seed sources, as was concluded regarding a soil specialist herb (Matesanz et al., 2020). The significant relationships we found for *P. engelmannii* imply that provenances from the colder, more continental extremes of the species' climate distribution grow well across a broader range of climate conditions. This may reflect an evolutionary trade-off between plasticity and specialization for milder climates. From the forest planning point of view, this insight might be valuable when looking for provenances to test: more stable provenances are more likely to be found closer to the colder, continental edge of the species' climate distribution, whereas assisted migration frameworks currently focus on the opposite, targeting warmer source climates based on the presumption that they would be pre-adapted to continuous climate warming (Williams and Dumroese, 2013). On the other hand, the inverse relationship between GSI and PC 2 we found for *P. contorta* seems to imply that such a strategy would be a good fit for this species: selecting provenances from warmer and drier seed sources would also indirectly select for climate-stable provenances.

We also did not find a strong pattern in the relationship between inter-annual climate variability at seed source and growth stability. Firstly, the locations studied differed relatively little in their precipitation variability, and as a consequence the AP CV climate variable contributed very little to the two PCs in exam. As for the other measure of inter-annual climate variability, MAT SD, it contributed mostly to PC 1, where it was clustered with ART and TSeas, two measures of within-year temperature variability. For this reason, we cannot separate the effects of adaptation to inter-annual temperature variability from an adaptation to seasonal variations in temperature. Nonetheless, in the case of *P. engelmannii*, the inverse relationship between GSI and PC 1 suggests that provenances from more variable climates are indeed more stable in respect to changes in trial site temperature, in agreement with the expectation that highly variable environments may select for increased phenotypic plasticity (Vázquez et al., 2017).

Overall, it appears that, in our data, differences in long-term climate conditions are more important for predicting differences in growth stability, compared to differences in climate variability. This finding is surprising as several studies suggest that climate variability would select for increased phenotypic plasticity (Alpert and Simms, 2002; Lázaro-Nogal et al., 2015; Carvajal et al., 2017; Vázquez et al., 2017). Meta-analyses differentiating between different aspects of plasticity, however, found a positive link between climate variability and plasticity only for allocation, but not for leaf traits, physiological traits, and, corresponding with our results, growth (Stotz et al., 2021).

In conclusion, we observed among-species and among-provenance differences in their capacity to grow well across a wide climate range, and that these differences in some cases can be explained by the climate conditions at the seed source. The direction of this relationship, however, depends on the species considered. We did not find any relationship between growth performance and growth stability, implying that provenances with both high performance and high growth stability to climate change exist. The results presented here give valuable insights on the growth stability of some important tree species, and point to a new perspective under which to study climate change adaptation in planted forests. They suggest the importance of incorporating insights from the study of growth stability in the selection of species and provenances for forestry interventions, with the objective of increasing forests' resilience to the uncertainties posed by climate change.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

AF: Conceptualization, Formal analysis, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. VB: Formal analysis, Methodology, Writing – review & editing. DC: Data curation, Writing – review & editing. GO'N: Data curation, Methodology, Writing – review & editing. SS: Data curation, Writing – review & editing. JK: Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2024.1422165/full#supplementary-material

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Assisted migration outcomes for oak species and seed sources in southern Ontario, Canada

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Introduction: Forest assisted migration has been proposed as a means to align tree populations with shifting climate habitats under climate change. Here we report on the growth and survival of oak species and seed sources at five assisted migration trials in southern Ontario – an important transition zone between boreal and temperate ecosystems.

Methods: Each trial featured one or more oak species – including red oak (*Quercus rubra*), white oak (*Q. alba*), burr oak (*Q. macrocarpa*), and swamp white oak (*Q. bicolor*) – and seed sources from Ontario, Pennsylvania, and/or Tennessee. The trials were measured for survival and height at between 7 and 13 years after planting.

Results: For several trials and species, southern seed sources performed nearly as well as local sources. However, southern seed sources of burr oak performed significantly worse than local sources at 2 trials in eastern Ontario. These outcomes may have been influenced by reduced quality of southern seed source planting stock at these trials.

Discussion: Our findings generally support previous work that suggests northward movements of seed sources of several hundred kilometers may be safe for assisted migration efforts involving broadleaf tree species. Notably, the trial sites were located at the northern range limits of two oak species in this study (*Q. alba and Q. bicolor*), suggesting the potential for modest range expansions in this boreal-temperate transition zone. These findings help forest managers to better understand potential assisted migration outcomes under climate change.

KEYWORDS

climate change, tree, oak, growth, survival, assisted migration

1 Introduction

Climate change is impacting forests in a variety of ways, including both direct impacts on tree growth (Wang et al., 2023; Girardin et al., 2016) and mortality (Hartmann et al., 2022), and indirect impacts on forest disturbance agents such as insects (Johnson and Haynes, 2023) and fire (Hanes et al., 2019). Given these many drivers of forest change, it is not surprising that global forests are starting to show signs of declining health and resilience (Hammond et al., 2022; Forzieri et al., 2022). Consequently, forest managers are increasingly tasked with adopting policies and practices to help maintain healthy and productive forests – and associated ecosystem functions – as climate change unfolds over the coming decades (Janowiak et al., 2014).

A variety of climate change adaptation techniques have been proposed in the forest management context (Williamson et al., 2019; Peterson et al., 2011). One such approach is assisted migration, wherein planting materials are moved (typically poleward or upslope) to climatically appropriate locations within and/or beyond existing range limits (McLachlan et al., 2007). The goal of such movements is to maintain a reasonable match between the climate at the planting site and the climate to which planting materials are adapted. Several types of assisted migration have been distinguished along a gradient of movement distance (Ste-Marie et al., 2011; Williams and Dumroese, 2013), including: (1) assisted population migration (movement of populations within existing range limits); (2) assisted range expansion (movement of species just beyond existing range limits); and (3) assisted species migration (movement of species far outside existing range limits – typically on the scale of hundreds to thousands of kilometers).

While the concept of assisted migration has existed for some time, empirical examples have been slower to emerge. In the context of commercial forestry, the movement of seed sources within existing range limits has become standard practice in some regions (e.g., O'Neill et al., 2017; van Kerkhof et al., 2022). Modest range expansions have also been proposed for a number of tree species in both forestry (O'Neill et al., 2008) and conservation (McLane and Aitken, 2012) settings. Results from assisted migration field trials have recently started to be reported for a number of species and locations (Pedlar et al., 2023; Wang et al., 2019; Sáenz-Romero et al., 2020; Etterson et al., 2020), but further information is needed to better understand the implications of these movements.

Oaks contribute significant economic and ecological benefits to forest ecosystems in North America (Pedlar et al., 2020). Genetic studies have shown high, range-wide genetic variation and modest population differentiation in oaks (Borkowski et al., 2017). Kriebel (1993) summarized early provenance results and reported potential growth gains associated with seed source movements of several hundred kilometers for a variety of oak species. Furthermore, drought tolerance is widely associated with oaks due to traits such as deep roots and thick leaves (Abrams, 1990; Kaproth and Cavender-Bares, 2016). This combination of features makes various oak species reasonable candidates for assisted migration efforts.

Southern Ontario is an important ecological transition zone between the boreal and temperate forest ecosystems. In this region, characteristic boreal species can be found in remnant populations at their southern range limits, while Carolinian broadleaf tree species reach their northern range limits. As such, this region provides an ideal setting for studying the northward expansion of southern tree species.

Here we report on the early growth and survival of several species of oak at assisted migration trials in southern Ontario, Canada. These trials were established to better understand assisted migration outcomes for these species, several of which are at – or beyond – their northern range limits at the study site locations. Ultimately, this work aims to assist forest managers with climate change adaptation efforts in an era of rapid climate change.

2 Materials and methods

2.1 Seed origins

Our aim was to incorporate provenances that would be reasonable selections for assisted migration efforts. Selection of planting stock origin (seed sources) was guided by a climate similarity analysis using Seedwhere (McKenney et al., 1999; https://cfs.cloud.nrcan.gc.ca/seedwhere/), which identified candidate seed source locations with recent historical climate that is projected to be similar to future climate at each planting site. We employed 1961–1990 as the recent historical climate period because it coincides with peak weather station numbers in Canada and precedes recent, rapid changes in climate. For future climate, we employed a composite of 4 climate models for the 2041–2070 period under the RCP4.5 and 8.5 scenarios [see McKenney et al. (2011) for details on the climate models]. Based on this approach and using a Seedwhere climatic similarity threshold of 0.9, stock at each trial was sourced from two or more locations along a temperature/latitudinal gradient, including: (1) Ontario (ON) seed zones 32, 36, 37, and 38, (2) Indiana County, Pennsylvania (PA), and (3) Warren County, Tennessee (TN) (Figure 1). All planting stock was derived from bulk seed collections in Ontario seed zones or US counties.

2.2 Trial sites

All trials were located in southern Ontario (Figure 1). Temperatures in this region average approximately 7.1°C, with cool winters (−6.0°C on average) and warm summers (19.3°C on average). Annual precipitation averages 886 mm, with similar amounts in summer (222 mm) and winter (210 mm). A significant amount of precipitation in winter falls as snow, with accumulations commonly

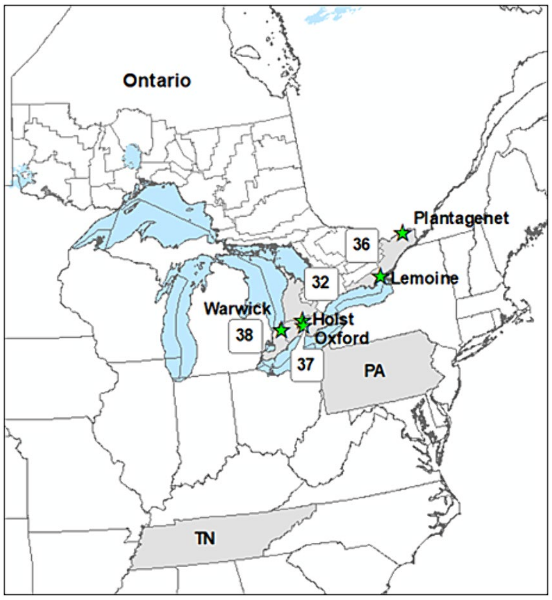

FIGURE 1
Location of seed sources (shaded Ontario seed zones and U.S. states) planted in various combinations at five assisted migration trials (green stars) in southern Ontario.

TABLE 1 Details of assisted migration trials included in the current study.

Trial name	Location	Species planted	Seed sources	Year Est.	Year Meas.	N Planted	Trial notes
Oxford	43.0010°N, 80.8016°W	*Quercus macrocarpa**	SZ37, PA, TN	2011	2023	1,296	No thinning; no predator control.
Holst	43.1935°N, 80.8121°W	*Q. alba*†, *Q. rubra**	SZ37, PA, TN	2010	2019, 2023	648, 648	Thinned 2019; No predator control; *Q. mariliandica* planted at site by mistake.
Warwick	42.9948°N, 81.9445°W	*Q. rubra**, *Q. bicolor*†	SZ37, PA, TN	2016	2023	648, 432	No thinning; no predator control; PA seed source for *Q. bicolor* was *Q. velutina* by mistake.
Lemoine point	44.2200°N, 76.6077°W	*Q. macrocarpa**	SZ36, SZ38, PA, TN	2016	2023	1908	No thinning; fence for deer control
Plantagenet	45.5394°N, 74.9868°W	*Q. macrocarpa**	SZ32, SZ36, SZ37, PA, TN	2014	2022	972	No thinning; no predator control; heavy vole damage

*Trial site is well within species' range limits; movements qualify as assisted population migration.
†Trial site is at, or beyond, species' northern range limits; movements qualify as assisted range expansion.

reaching >20 cm. A summary of key trial site features is provided in Table 1 and maps are provided that show trial locations in relation to each species' distribution (Supplementary Figures S1–S5).

2.2.1 Oxford County

This trial is located on Municipal property southeast of Ingersoll, Ontario at 43.001°N and − 80.8016°W. The site was previously used for agricultural cropping and is classified as moist, with silty texture. Microtopography within the site resulted in variable moisture conditions, which appeared to impact seedling performance throughout. The site was hand planted in April 2011 with 2 + 0 bareroot seedlings. Several hardwood species were planted at the site, but results reported here are limited to three seed sources (Ontario Seedzone 37, Pennsylvania, and Tennessee) of *Q. macrocarpa* – a test of assisted population migration (Supplementary Figure S1). The trial employed a randomized complete block design, consisting of: 12 blocks, each of which contained 4 plots (one for each of the *Q. macrocarpa* seed sources, plus one for the remaining hardwood species not presented here); which in turn contained 36 seedlings planted in a 6 × 6 layout at a 1.8 m x 3.6 m spacing (for a total of 1,296 *Q. macrocarpa* trees). Competing vegetation was controlled by a combination of plastic mulch and mowing between rows. Height and survival measurements for the current study were carried out in winter 2023, 12 growing seasons after planting. No thinning had been carried out at time of measurement.

2.2.2 Holst site

This trial is located on private property northwest of Woodstock Ontario at 43.1935°N and − 80.8121°W. The site is classified as prime agricultural land, with well-drained soils predominantly comprised of glacial deposits (till). Soil textures are predominantly Clay-Loam. The site was disced in fall 2009 and hand planted in April 2010 with 2 + 0 bareroot seedlings. The trial included 2 species (*Q. alba* and *Q. rubra*) and 3 seed sources (Ontario Seedzone 37, Pennsylvania, and Tennessee). Note that the test site is at the northern range limit for *Q. alba* (i.e., assisted range expansion; Supplementary Figure S2), but is well south of the northern limits for *Q. rubra* (Supplementary Figure S3). The two species were planted on adjoining plots of land following identical randomized complete block designs, consisting of: 6 blocks, each of which contained 3 plots (one for each seed source), which in turn contained 36 seedlings planted in a 6 × 6 layout at a 1.7 m x 3.7 m spacing (for a total of 648 trees per species). Competing vegetation was controlled by a combination of plastic mulch and mowing between rows. Tree densities in each plot were thinned by approximately 50% in summer 2019. Height and survival measurements for the current study were carried out in winter 2019 for *Q. rubra* and winter 2023 for *Q. alba*, 9 and 13 growing seasons after planting, respectively. Note that, at time of measurement, it was determined that approximately 33% of the *Q. alba* stock from TN was actually blackjack oak (*Quercus marilandica*) and/or hybrids of this species. Measurements of these trees were not included as part of the formal analysis for this trial but are summarized in the results to indicate how well this species performed at the site, which is located approximately 500 km north of the contiguous northern range limit for *Q. marilandica* (Supplementary Figure S4).

2.2.3 Warwick conservation area

This trial is located on Conservation Area land approximately 40 km east of Sarnia, Ontario at 42.9948°N and − 81.9445°W. The site was previously used for agricultural cropping and is classified as moist, with coarse loamy textured soils. Three seed sources (Ontario Seedzone 37, Pennsylvania, and Tennessee) of two oak species, *Q. rubra* (assisted population migration; Supplementary Figure S3) and *Q. bicolor* (assisted range expansion; Supplementary Figure S5), were hand planted at the site in April 2016. For both species, seedlings from Tennessee were 1 + 0 bareroot seedlings, while those from ON and PA were 2 + 0 bareroot seedlings. The two species were planted on adjoining plots of land following identical randomized complete block designs, consisting of: 6 blocks, each of which contained 3 plots (one for each seed source), which in turn contained 36 seedlings planted in a 6 × 6 layout at a 1.8 m x 3.6 m spacing (for a total of 648 trees per species). Competing vegetation was controlled by mowing between rows. Height and survival measurements for the current study were carried out in winter 2023, 7 growing seasons after planting. At time of measurement, it was determined that all *Q. bicolor* seedlings from Pennsylvania were actually black oak (*Q. velutina*); thus, results reported here for *Q. bicolor* are limited to the Ontario and Tennessee seed sources. No thinning had been carried out at time of measurement.

2.2.4 Lemoine point conservation area

This trial is located on Conservation Area land near Kingston, Ontario at 44.220041°N and − 76.607709°W. The site was previously used for hay production but had been fallow for several years prior to planting. It is classified as a wet site, with heavy clay soils. The site was originally planted in 2012, but due to high levels of mortality, was replanted in April 2016, at which time four *Q. macrocarpa* (assisted population migration; Supplementary Figure S1) seed sources (Ontario Seedzones 36 and 38, Pennsylvania, and Tennessee) were hand planted using 2 + 0 bareroot seedlings. The trial employed a randomized block design, consisting of: 7 blocks, each containing 4 plots (one for each seed source), a further 7 blocks containing 3 plots (one for each seed source except Pennsylvania), and a final block containing 2 plots (one for each of the Ontario seed sources). All plots contained 36 seedlings planted in a 6 × 6 layout at a 1.8 m x 3.6 m spacing (for a total of 1908 trees). Competing vegetation was controlled by mowing between rows, and a fence was installed to reduce deer predation. Height and survival measurements for the current study were carried out in winter 2023, 7 growing seasons after replanting.

2.2.5 Plantagenet

This trial is located on Municipal property in the town of Plantagenet, approximately 50 km east of Ottawa, Ontario at 45.539372°N and − 74.986774°W. The site was previously used for agricultural cropping but had been fallow for several years prior to planting. It is classified as a moist site, with clay textured soils. Five *Q. macrocarpa* (assisted population migration; Supplementary Figure S1) seed sources (Ontario Seedzones 32, 36, and 37, Pennsylvania, and Tennessee) were hand planted at the site in May 2014. Seedlings from Ontario were 1 + 0 bareroot seedlings, while those from Pennsylvania and Tennessee were 2 + 0 bareroot seedlings. The trial employed a randomized block design, consisting of: 3 blocks, each containing 5 plots (one for each seed source), and 3 further blocks, each containing 4 plots (one for each seed source except Ontario Seedzone 36). All plots contained 36 seedlings planted in a 6 × 6 layout at a 1.8 m x 3.6 m spacing (for a total of 972 trees). Competing vegetation was controlled by a combination of mulch mats (1-m diameter) and mowing between rows. Height and survival measurements for the current study were carried out in winter 2022, 8 growing seasons after planting. There was significant vole damage to seedlings during the first few years after establishment, which impacted survival and growth at the trial.

2.3 Climate data

Climate estimates were obtained by interrogating spatial climate models covering Canada and the United States (McKenney et al., 2011). These thin-plate spline-based models are spatially continuous, allowing them to be queried at any location for which geographic coordinates and elevations are known. Specifically, climate values were generated at seed source origins for each year over the 1961–1990 period – a period prior to rapid climate change that may approximate conditions to which the seed sources are adapted – and at each planting site for each year between establishment and measurement (see Table 1). Climate variables selected for comparison included growing season average temperature and precipitation, and annual climate moisture index, which measures the balance between precipitation and potential evapotranspiration (Hogg, 1994). Variables associated with extreme climate events, which can greatly impact young plantation success, are also provided, including annual minimum and maximum temperatures and growing season start date. Due to space limitations, summaries of these variables are provided as supplementary material.

2.4 Statistical approach

Two sample t-tests (R Core Team, 2021) were used to test for differences between the historical climate at a given seed source and the climate experienced at each trial site where it was planted. A bonferroni correction was used to adjust the initial significance cutoff (i.e., $p < 0.05$) to account for multiple comparisons at each test site.

Given that, at certain sites, the age and size of planting stock was not entirely consistent across seed sources, we recognize that calculating relative growth rates (*sensu* Hunt, 1982) would provide a more accurate measure of growth performance. However, immediate post-planting height measurements were not available for these trials, so such an analysis was not possible. Thus, we analyzed tree heights at each site using a mixed effects model:

$$Y_{ijkl} = \mu + \alpha_i + \gamma_j + \delta_{l(k)} + \epsilon_{ijk} \tag{1}$$

where, μ is the overall mean, α_i is the (fixed) effect of seed origin, γ_j is the (random) effect of block, $\delta_{k(j)}$ is the (random) effect of plot nested within block, and ϵ_{ijk} is the model error. The analysis was performed in SAS 9.4 (SAS Institute Inc., 2013) using PROC GLIMMIX, with a residual pseudo-likelihood estimation method and Kenward-Roger correction to the denominator degrees of freedom. The model specified in equation 1 was also used to analyze tree survival, but in this case the logit link and binary distribution were specified in the call to PROC GLIMMIX. Note that, at sites with multiple species (i.e., the Holst and Warwick sites), separate analyses were carried out for each species as the experiments were not designed to incorporate species as an analysis factor.

The R^2 metric, which is a well-known estimate of the proportion of variance explained by normal linear models, is not typically provided for the generalized linear mixed models used here. Thus, we employed a published SAS Macro routine (Jaeger et al., 2017) to obtain R^2 values for the fixed effects in each of our models.

3 Results

3.1 Climate comparisons

For the US seed sources, historical growing season temperatures in Tennessee were significantly warmer than recent temperatures at all trial sites, while those in Pennsylvania did not differ signficantly from temperatures experienced at the trial sites (Figure 2). For the Ontario seed sources, historical growing season temperatures were significantly lower than recent temperatures experienced at the trial sites where they were planted (Figure 2). Historical growing season precipitation was higher at the two US seed sources than at any of the trial sites, but did not differ significantly between Ontario seed sources and trial sites (Figure 2). Annual climate moisture index (CMI) did not vary greatly between seed sources and trial sites, though historical CMI at seed zones 36 and 37 was significantly lower than CMI experienced at the Plantagenet site, while seed zone 38 was historically drier than the Lemoine Point site (Figure 2).

Extreme minimum and maximum temperatures were significantly warmer, and growing seasons started significantly earlier, at the Tennessee and Pennsylvania seed sources relative to the trial sites (Supplementary Figure S6). These metrics were not significantly different between many of the Ontario seed sources and trial sites, though seed zone 32 had lower temperature extremes and later growing season start dates than those experienced at the Plantagenet

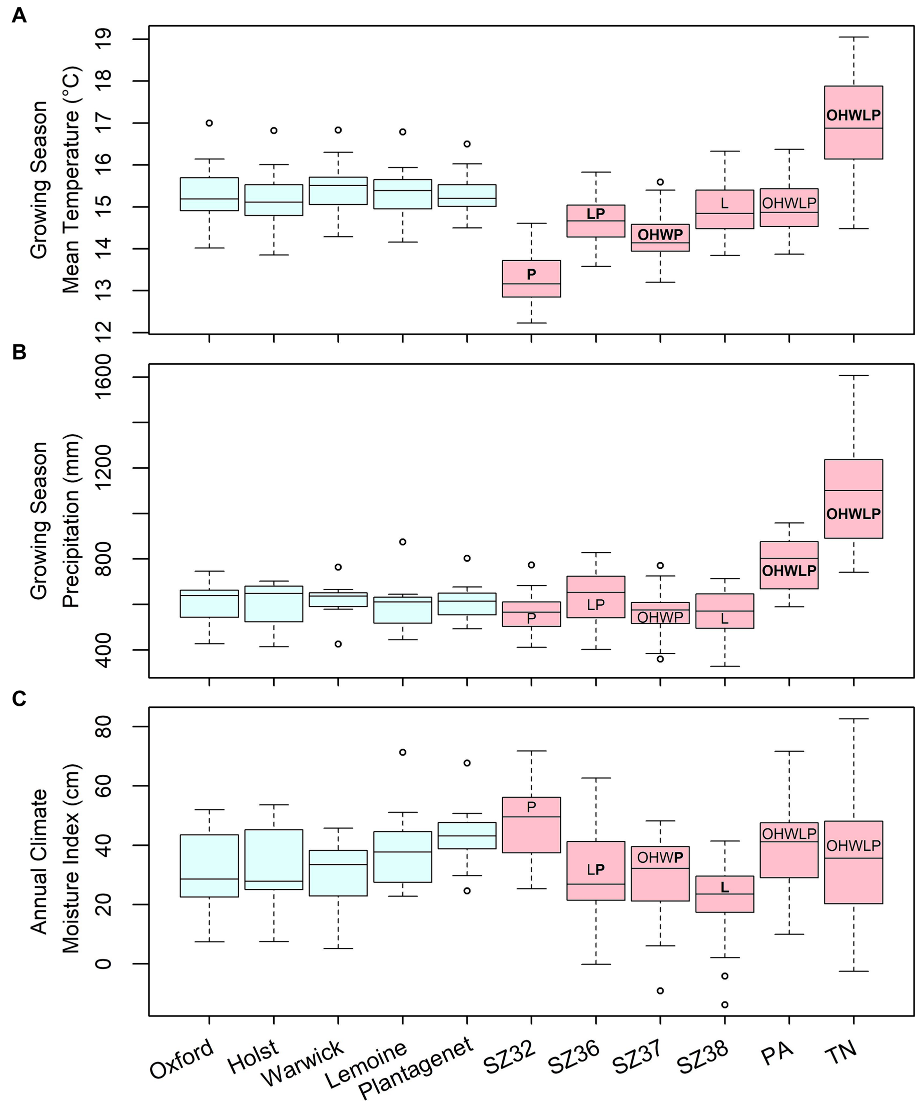

FIGURE 2
Summaries of **(A)** growing season mean temperature, **(B)** growing season precipitation, and **(C)** annual climate moisture index at assisted migration test sites (blue boxes) and seed origins (red boxes) used in the current study. Seed source climate values are for an historical period (1961–1990) that precedes recent rapid climate change; test site values are for the period between planting and measurement (see Table 1 for details). Letters on the seed source boxes indicate the first initial of the trial sites at which they were planted; bold letters indicate significant differences between seed source and trial site climates.

site, while seed zone 38 historically had warmer temperatures and a longer growing season than the Lemoine Point site where it was planted (Supplementary Figure S6).

3.2 Plantation performance

Due to inconsistencies across trials (e.g., different species, provenances, establishment and measurement dates, and site conditions), we present results separately for each assisted migration trial below, but attempt to identify emergent patterns across trials to support key findings from the work.

After 12 growing seasons at the Oxford County site, *Q. macrocarpa* heights averaged 3.68 ± 0.99 m and survival averaged 95.5 ± 5.1%. Neither metric varied significantly across the three seed sources (TN, PA, and ON seed zone 37) planted at the site (Table 2; Figure 3).

After 9 growing seasons at the Holst site, height of *Q. rubra* trees averaged 6.01 ± 1.43 m, with the Ontario seed source growing significantly better than both U.S. seed sources (Table 2; Figure 4A). Survival of *Q. rubra* trees averaged 95.2 ± 4.9%, with no significant differences between seed sources (Table 2; Figure 4B). For *Q. alba*, at 13 growing seasons after planting, height averaged 5.95 ± 1.34 m and survival averaged 75.9 ± 15.2%; there were no significant differences between seed sources for either of these response variables (Table 2; Figure 4).

Approximately 70 suspected *Q. marilandica* seedlings were unintentionally planted at the Holst site along with the *Q. alba* stock from Tennessee. Though not included in the statistical analysis reported above, these trees were measured in 2023 and averaged 3.36 ± 1.12 m in height and survived at a rate of 63.9 ± 20.3%. It is noteworthy that, following cold events in fall 2020/spring 2021, many of these trees exhibited at least modest dieback (e.g., death of branch tips and buds), with about 14% exhibiting severe dieback (e.g., death of 2–5 cm diameter branches). Many of these trees, including those that experienced severe dieback, managed to survive and grow well in future years. None of the other species/seed sources at this site exhibited comparable levels of dieback in relation to these climatic events.

After 7 growing seasons at the Warwick site, height of *Q. rubra* trees averaged 1.97 ± 1.09 m, with no significant differences between seed sources (Table 2; Figure 5A), despite noticeably lower growth associated with the Tennessee seed source. The lack of statistical significance in this case likely reflects the relatively high within-group variation in growth at the site and modest power of the test. Survival of *Q. rubra* trees averaged 68.5 ± 17.6% and the Tennessee seed source exhibited significantly lower survival than the Pennsylvania source, with the Ontario source intermediate between the two (Figure 5B). For *Q. bicolor*, height averaged 2.47 ± 0.79 m and survival averaged 94.0 ± 2.7%; there were no significant differences between seed sources for either of these response variables (Table 2; Figure 5).

At the Lemoine Point site, after seven growing seasons, height of *Q. macrocarpa* trees averaged 1.78 ± 0 0.69 m, with the two Ontario seed sources growing significantly better than the two U.S. sources (Table 2; Figure 6A). Survival averaged 68.1 ± 30.5%, with the Pennsylvania seed source exhibiting the lowest survival, the Tennessee source intermediate, and the two Ontario sources highest (Table 2; Figure 6B).

After 8 growing seasons at the Plantagenet site, height of *Q. macrocarpa* trees averaged 2.43 ± 0.89 m, with the Seed Zone 37 source growing best and the two U.S. sources growing worst (Table 2; Figure 7A). Survival averaged 72.8 ± 26.5%, with the US seed sources exhibiting significantly lower survival than the three Ontario sources (Table 2; Figure 7B).

4 Discussion

This study examines growth and survival of various oak species and seed sources at five trial sites across southern Ontario. Seed sources were selected to cover a range of (primarily northward)

TABLE 2 Significance tests for mixed models relating height and survival of various oak species to seed origin at five assisted migration trials in southern Ontario.

Trial	Species	Response	DF†	*F*	Pr > F	R^2
Oxford county	*Q. macrocarpa*	Height	2, 33.0	0.45	0.6401	0.018
		Survival	2, 36.8	3.2	0.0545	0.146
Holst site	*Q. alba*	Height	2, 11.3	3.44	0.0683	0.324
		Survival	2, 13.7	2.63	0.1079	0.164
	Q. rubra	Height	2, 14.9	13.65	0.0004	0.658
		Survival	2, 23.1	3.29	0.0554	0.210
Warwick Conservation area	*Q. rubra*	Height	2, 15.2	1.76	0.2048	0.188
		Survival	2, 14.4	4.36	0.0330	0.226
	Q. bicolor	Height	1, 9.6	0.47	0.5104	0.047
		Survival	1, 13.9	1.48	0.2443	0.094
Lemoine point Conservation area	*Q. macrocarpa*	Height	3, 56.5	22.55	<0.0001	0.567
		Survival	3, 45.0	53.63	<0.0001	0.781
Plantagenet	*Q. macrocarpa*	Height	4, 38.3	69.99	<0.0001	0.879
		Survival	4, 48.3	26.06	<0.0001	0.797

†Numerator and denominator degrees of freedom for *F*-test.

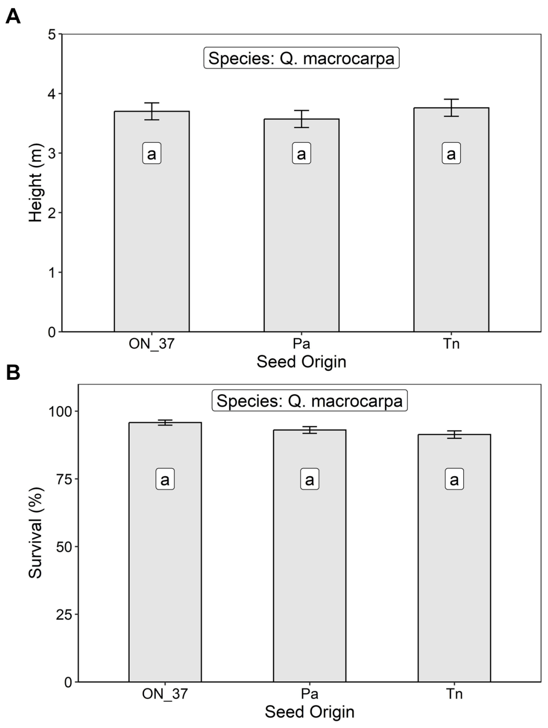

FIGURE 3
Least squares mean **(A)** height and **(B)** survival at age 12 (± S.E.) of *Q. macropcarpa* trees at an assisted migration trial in Oxford County, Ontario in relation to seed origin (ON_37, Ontario Seed Zone 37, Pa, Pennsylvania, and Tn, Tennessee). Differences between seed origins not sharing the same letter are statistically significant (i.e., $p < 0.05$).

movement distances to simulate assisted migration activities under climate change – including movements of some species to locations at, or beyond, northern range limits. Growing season temperatures experienced by trees at the trial sites were warmer than historical conditions associated with many of the Ontario seed sources, but were similar to historical temperatures in Pennsylvania and cooler than those in Tennessee. Extreme temperature conditions followed similar patterns, but in this case, extremes experienced at the planting sites were significantly cooler than historical values in both Pennsylvania and Tennessee. Growing seasons typically started 2–3 weeks earlier in Tennessee and Pennsylvania relative to the planting sites, which indicates potential for frost damage at these northern planting sites. Growing season precipitation at the trial sites was similar to historical precipitation at the various Ontario seed sources, but was lower than historical precipitation in Pennsylvania and Tennessee. Finally, moisture balance was relatively consistent across trial sites and historical seed source conditions. Overall, these findings confirm that a significant range of climate conditions, including climate extremes, was sampled by the seed sources and planting sites included in the study.

Despite evidence that mismatches may already be developing between temperatures at the trial sites and those to which the local seed sources are adapted, the Ontario sources exhibited high growth and survival at all trial sites. There are several potential reasons for this result. First, the magnitude of temperature change, which was approximately 1°C for mean annual temperature in the southern Ontario region over the 1948–2016 period (Bush and Lemmen, 2019), may not yet be large enough to negatively impact growth and survival as trees have been shown to have high levels of phenotypic plasticity (Benito-Garzón et al., 2019). For example, response curves, which plot seed source performance (e.g., height or survival) as a function of climate at a range of planting sites, typically show good performance across a range of conditions (Wang et al., 2006, 2010). Furthermore, previous work has shown that populations in the northern portion of a species' range (which includes all the Ontario seed sources in the current study) typically benefit from a modest amount of climate warming (Pedlar and McKenney, 2017). Finally, the trials are still relatively young, so extreme weather events that impact survival and growth (e.g., late frosts, droughts) may have not yet materialized at the sites.

Seed sources from the U.S. presented mixed results when moved northward to southern Ontario planting sites. At the Oxford, Holst, and Warwick trials, differences between U.S. and local seed sources were relatively minor, though there was some evidence for reduced performance of Tennessee seed sources at the Holst and Warwick sites. Previous efforts have reported similarly modest impacts associated with seed movements of several hundred km (or approximately 5°C of mean annual temperature) for both hardwood (Pedlar et al., 2023) and conifer (Pedlar et al., 2021) species. Conversely, the two U.S. sources exhibited significantly lower growth and survival rates at the Lemoine Point and Plantagenet trials. Given the significant differences in precipitation and extreme temperatures between these seed sources and planting sites, it is possible that these results were climate driven; however, we note a number of caveats associated with these findings. First, there were challenges with obtaining planting stock from the U.S. that was entirely comparable to that of the local Ontario seed sources; concerns regarding the quality of U.S. stock were noted at time of planting for both trials in question. Second, there was significant mortality at the Plantagenet site due to vole damage, which may have, by chance, disproportionately affected the U.S. seed sources. There was also high mortality at the Lemoine Point trial due to wet soil conditions, which may have exacerbated any climate-related impacts at the site.

Two species – *Q. bicolor* and *Q. alba* – achieved high growth and survival rates at trials located near their northern range limits. These results suggest that there is potential for species to survive and grow well when moved to locations at, or beyond, their current northern range limits (i.e., assisted range expansion) – supporting previous studies that have reported successful northward range expansions in forestry (Etterson et al., 2020), restoration (Truax et al., 2018), and horticultural (van der Veken et al., 2008) settings. While there has been considerable debate regarding the appropriate use of assisted migration as a climate change adaptation tool (McLachlan et al., 2007; Hewitt et al., 2011), modest movements of tree species beyond northern range limits, such as those undertaken here, represent a relatively low risk approach that may facilitate northward shifts to track climate change – particularly in landscapes that have been extensively fragmented by human development. The inadvertent planting of *Q. marilandica* oak at the Holst site provided some insight into longer-distance range expansions. While this species has persisted at the site, it exhibited lower rates of survival and growth than the other (native) oak species planted there and was adversely affected by extreme cold events in fall 2020/spring 2021 – and potentially during winter as evidenced by the significantly lower annual extreme minimum temperatures at the Holst site relative to those typically

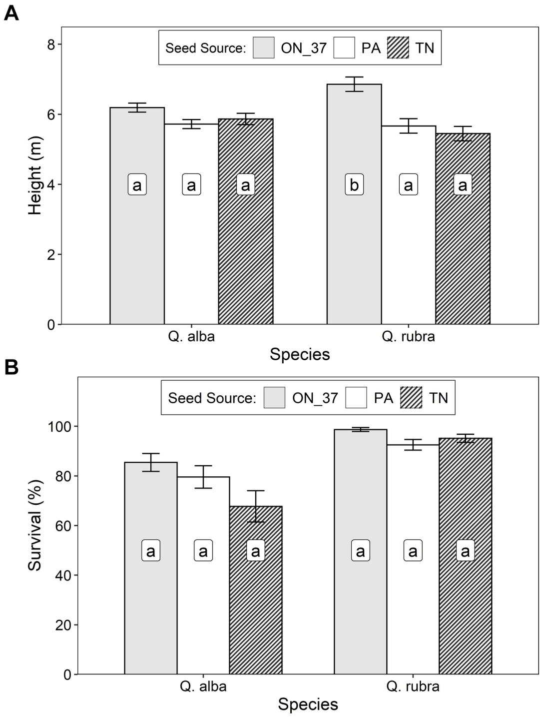

FIGURE 4
Least squares mean (± S.E.) **(A)** height and **(B)** survival of *Q. rubra* and *Q. alba* trees – at age 9 and 13 years, respectively – for 3 seed sources (ON_37, Ontario Seed Zone 37, Pa, Pennsylvania, and Tn, Tennessee) at an assisted migration trial near Woodstock, Ontario. Differences between seed origins not sharing the same letter are statistically significant (i.e., $p < 0.05$).

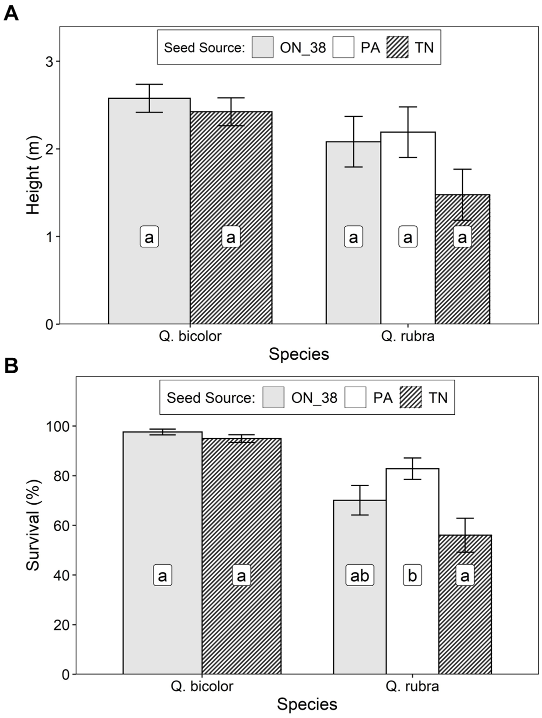

FIGURE 5
Least squares mean (± S.E.) **(A)** height and **(B)** survival of *Q. rubra* and *Q. bicolor* trees at age 7 for 3 seed sources (ON_38 = Ontario Seed Zone 38, Pa, Pennsylvania, and Tn, Tennessee) at an assisted migration trial at the Warwick Conservation Area near Sarnia, Ontario. Differences between seed origins not sharing the same letter are statistically significant (i.e., $p < 0.05$).

experienced at the Tennessee seed source (Supplementary Figure S1). This evidence indicates that, for this species at least, movements upwards of 500 km beyond northern range limits involve significant risk to the survival and growth of the resulting plantation. Comparable within-range movement distances for the other species in the study did not produce similar levels of damage, suggesting modest levels of local climate adaptation across populations, with relatively strong climatic controls at the species level – a pattern that has been reported for numerous species (see review in Copenhaver-Parry et al., 2017).

A growing number of studies are reporting outcomes from assisted migration trials. Similar to the current study, Pedlar et al. (2023) reported that seed sources of several hardwood species (including several oaks) could be moved hundreds of kilometers northward with little impact on resulting growth and survival. Etterson et al. (2020) examined the growth of southern and northern seed sources for two oak species in northern Minnesota and found that the southern seed sources generally outperformed the local northern sources. Similarly, Toledo-Aceves et al. (2023) reported that, in Mexico's Veracruz state, populations of the endangered oak, *Quercus insignis,* could be moved to locations up to 3°C cooler with no negative impacts. Sáenz-Romero et al. (2020) reviewed three different assisted migration trials in Canada and Mexico and reported the following general insights: (1) populations of *Picea glauca* × *P. engelmannii* may be safely planted at locations that are 3°C cooler than local (in terms of mean coldest month temperature); (2) *Pinus albicaulis* can be established outside of its current natural distribution at sites that have climates that are within the species' modeled historic climatic niche; and (3) *Abies religiosa* performs well when moved 400 m upward in elevation. Finally, Gómez-Ruiz et al. (2020) translocated two tropical broadleaf species in Mexico and recommended that movements be limited to within 400 m of elevational range limits. These findings generally support those presented here regarding the suitability of seed sources for northward/upslope movements and the potential for range expansion under climate change.

Pike and O'Connor (2024) recommended northward transfer distances for *Q. rubra* of approximately 300–400 km based on a review of provenance trials and genetic studies. Though not incorporating an extensive range of seed sources, our findings generally support this recommendation for the sample of oak species considered here. Interestingly, Kriebel (1993) reviewed early provenance studies, and concluded that optimal growth of *Q. rubra* at mid-latitudes in the US could be achieved by moving northern seed sources southward by 250–500 km. Though not tested explicitly here, we did not find strong support for the notion of superior performance by northern provenances of *Q. rubra* [see also Leites et al. (2019)].

We recognize several caveats related to the current work. The strength of our findings could be improved by the establishment of control plantations at seed source locations as this was not evaluated in the current study. As noted, it was challenging to obtain planting material that was entirely comparable across seed sources. In particular, seedlings from PA and TN were of lower quality than the

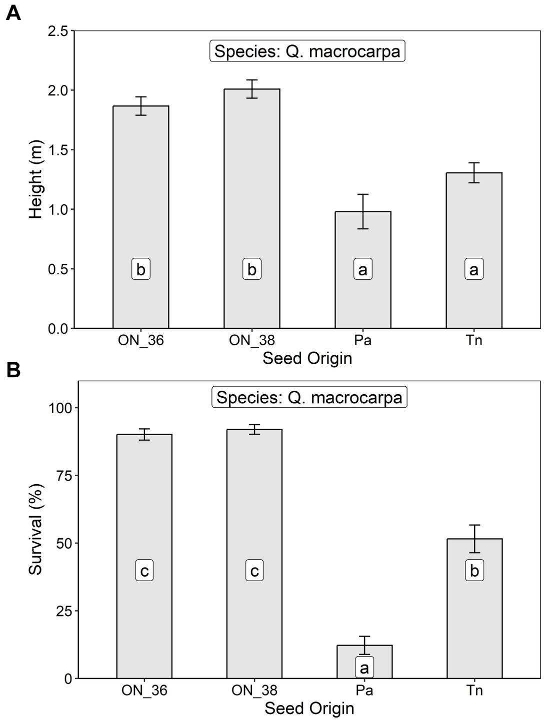

FIGURE 6
Least squares mean **(A)** height and **(B)** survival at age 7 (± S.E.) of *Q. macrocarpa* trees in relation to seed origin (ON_36, Ontario Seed Zone 36, ON_38, Ontario Seed Zone 38, Pa, Pennsylvania, and Tn, Tennessee) at an assisted migration trial in the Lemoine Point Conservation Area near Kingston, Ontario. Differences between seed origins not sharing the same letter are statistically significant (i.e., $p < 0.05$).

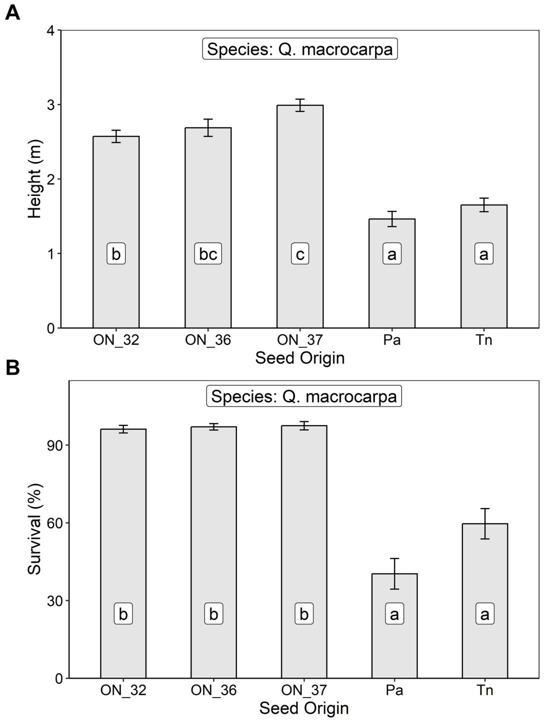

FIGURE 7
Least squares mean **(A)** height and **(B)** survival at age 8 (± S.E.) of *Q. macrocarpa* trees in relation to seed origin (ON_32, Ontario Seed Zone 32, ON_36, Ontario Seed Zone 36, ON_37 = Ontario Seed Zone 37, Pa, Pennsylvania, and Tn, Tennessee) at an assisted migration trial near Plantagenet, Ontario. Differences between seed origins not sharing the same letter are statistically significant (i.e., $p < 0.05$).

local seed sources at the Lemoine Point and Plantagenet trials, which likely contributed to the poor performance of these seed sources at these sites. Furthermore, at several of the sites, seedlings for non-target species were mistakenly included in the seedling order. It was several years before trees were large enough to identify these errors, at which point it was too late to replant; thus, replicates were incomplete for certain seed sources at certain sites. Given the relatively young age of the plantations examined here, our findings should be considered preliminary in nature. Provenance studies have reported changes in the ranking of seed source performance over time, which can impact key study outcomes (Rweyongeza, 2016; Kriebel, 1993). Nonetheless, the early years of a plantation are recognized as being critical for tree survival (Lutz and Halpern, 2006), suggesting that important performance metrics may be measured over this period. Finally, we recognize that survival and growth are but two of a suite of metrics that could be measured to assess performance at these trial sites. Phenological measures are particularly important for assisted migration outcomes and may be assessed at these sites in the future.

5 Conclusion

Our findings suggest that oak trees can be moved significant distances (e.g., hundreds of kilometres poleward/hundreds of meters upslope) for assisted migration efforts, which generally supports previous work on this topic. Poor performance by U.S. seed sources at two trial sites was likely due to lower quality planting stock as opposed to climate-related impacts. However, given the potential impacts of extreme weather events such as droughts and late frosts on young plantations, more restrained transfer distances are recommended. This work adds to a growing literature base concerning assisted migration outcomes for oaks. Future efforts at these sites will examine longer-term differences in growth and survival between seed sources and the response of migrated seed sources to extreme climate events.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

JP: Conceptualization, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. DM: Conceptualization, Funding acquisition, Project administration, Supervision, Writing – original draft, Writing – review & editing. KS: Conceptualization, Data curation, Investigation, Writing – original draft, Writing – review & editing. HZ: Funding acquisition, Project administration, Supervision, Writing – original draft, Writing – review & editing. KM: Conceptualization, Funding acquisition, Project administration, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2024.1445029/full#supplementary-material

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Public perception of forest assisted migration (FAM): a useful approach which requires cautious implementation?

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Forest Assisted Migration (FAM) emerges as a promising strategy of adaptation to climate change (CC) in the forestry sector. This method integrates various sources of knowledge to identify optimal locations for future tree species establishment through human intervention. As climate change presents numerous challenges to Quebec's forests, including shifts in suitable habitats for tree species, the FAM recommends a proactive approach to adapt to these changes. Recognizing the importance of addressing risks and following international resolutions, such as the Paris Agreement on Climate Change (COP21) and Convention on Biological Diversity (CBD), social perception becomes a critical consideration in the decision-making process regarding FAM. To investigate this issue, we conducted semi-structured interviews with 18 key stakeholders in Quebec, including officials from the Ministry of Natural Resources and Forestry, employees of private forestry technical companies, forestry researchers, private forest owners, non-governmental organizations (NGO) members, and other forest stakeholders. We analyzed the data collected in this phase through thematic discrimination, focusing on (i) acceptability (ii) risk perception (iii) feasibility, and (iv) purpose. Then, we compared the discourses with data from other publications addressing the social aspects of FAM. To develop this reflection, we found it important to use a conceptual framework that encompasses the articulation among some concepts of intervention through FAM vs. non-intervention, public trust in government authorities, risk perception and scientific knowledge. The interviews revealed a general inclination among stakeholders to support FAM, dependent upon cautious implementation with pilot projects and studies serving as references for future large-scale applications. Concerns raised by stakeholders included seed production, adequate experimental monitoring, and careful species selection. While some stakeholders were more knowledgeable about current FAM research, others emphasized the importance of economic viability, public participation in decision-making, and transparency in forestry processes. We identified communication and public involvement as fundamental aspects for advancing the perspective of FAM implementation in Quebec; it is crucial to recognize the presence of humans in FAM target areas and their potential contributions to implementation. Moving forward, forest authorities responsible for FAM should prioritize stakeholder engagement at all levels to ensure a socially inclusive strategy of adaptation that respects a wide range of considerations.

KEYWORDS

forest assisted migration, social forest, social acceptance, social perception, qualitative research

Introduction

Among the strategies for responding to climate change, Forest Assisted Migration (FAM) has gained prominence in the past decade. Being more specific than the Assisted Migration (AM) concept, FAM seeks to intentionally move individuals or populations of trees to more suitable areas according to expected future climate conditions (Aitken and Whitlock, 2013; Royo et al., 2023).

The FAM strategy presupposes proactive human action to facilitate ecological transition and forest adaptation. However, this raises a set of questions about the relationship between humans and nature because this relationship varies depending on the values held by different social groups, thereby raising ethical considerations (Aubin et al., 2011). This research is conducted in the areas of social forestry and human geography to better understand the perceived potential and shortcomings of FAM. FAM is considered an emerging approach to adaptation to climate change that raises complex concerns and hopes that require interdisciplinary attention between natural and social sciences.

Amidst this discussion, it is important to emphasize the concept of three intensities of displacement models in FAM that are already addressed in the scientific literature. The first model, Assisted Population Migration is defined as the tree movement within the distribution area of a species (Benomar et al., 2016), which is the least intensive modality, presenting a low risk of maladaptation, forest disease spread, and other undesirable situations for forest health (Ste-Marie, 2011). In addition, studies indicate greater social tolerance for this modality (Pelai et al., 2021a; St-Laurent et al., 2018).

The second model, Assisted Range Expansion, is considered riskier than the Assisted Population Migration. In this case, the movement of species outside and around the current zone of occupancy facilitates natural expansion (Ste-Marie et al., 2011). In this situation, scientists seek to stimulate natural migration to limit the risks of maladaptation because favorable climatic niches are expected to migrate much faster than plant species (Champagne et al., 2021; Iverson et al., 2008; Périé et al., 2014).

The third model, Assisted Species Migration/Exotic Translocation, is the most dangerous modality because it involves the movement of species outside their natural range over distances greater than those accessible by natural dispersal (Charles and Stehlik, 2021). In this case, the use of exotic species would be possible.

Although not typically cited as a model for FAM intensity, Assisted Genetic Migration is an important strategy to highlight. This method facilitates the movement of organisms between populations within a species' existing range to preserve genetic diversity. It also involves the movement of species beyond their historical distribution, bringing individuals from other sources (McLaughlin et al., 2022), such as the white spruce (*Picea glauca*) brought from the United States to Quebec (Benomar et al., 2022a). This approach aims to introduce genetic diversity and resilience into populations of native species, improving their adaptation to changing environmental conditions.

In this way, our study argues that exploring perceptions about forests is essential to better understand the potential use of FAM in forest management strategies in the context of climate change (Foladori and Taks, 2004; Hicks et al., 2010). This would deepen the understanding of the complex human relationship with forests (Moshofsky et al., 2019). This study specifically targeted tree migration in forest environments. To avoid any confusion with the migration of animal species or the planting of exotic species on a small scale, for ornamental or personal use, we opted to include the term "forest" in the designation of this strategy.

The emergence and proliferation of strategies such as FAM can be justified by the current state of climate change, which jeopardizes the reproduction and thus the sustainability of certain tree species. Forest ecosystems may consequently face threats to their composition and structure. The inadequacy of measures implemented in recent decades to mitigate climate change at the global scale, coupled with forecasts of its acceleration (IPCC, 2022), has motivated the formulation of more ambitious projects in Canada, such as FAM (Williams and Dumroese, 2013).

From this perspective, studies in the field of social sciences are crucial for the effectiveness of socioecological management projects, as they provide vital support for cooperation and exchange with populations (Bernard et al., 2020; Lambini et al., 2019). Understanding the perceptions of the actors involved is fundamental and essential according to the principles of participatory democracy that guide the management and development of natural environments (Hajjar and Kozak, 2015).

Therefore, broadening decision-making processes related to the environment to encompass all sectors of society is crucial for incorporating diverse areas of knowledge and epistemological perspectives (IPBES, 2019; Lenoir, 1995). Consequently, it can be affirmed that expanding public participation to include various actors (such as environmental organizations, engaged citizen groups, and indigenous communities) in democratic societies has yielded beneficial effects (Bouthillier and Roberge, 2007; IPBES, 2019; Tardif et al., 2017).

Along these lines, the growing interest in FAM has generated a series of ethical reflections due to the distinct values that are challenged by this forest management approach to CC (Aubin et al., 2011). Thus, from a broad perspective, studies often present biocentric, ecocentric or anthropocentric positions as determining factors in the choices of the actors involved (Hajjar and Kozak, 2015; Mcfarlane and Boxall, 2003). In essence, ecocentrism emphasizes the importance of entire ecological systems, recognizing the interdependence of all life forms, while biocentrism focuses on the intrinsic value of individual organisms beyond humans. Despite these differences, both views stand in contrast to the anthropocentric perspective, which prioritizes the utilization and alteration of nature and forests to meet human needs and improve well-being (Hajjar and Kozak, 2015; Sena, 2019).

The difficulty of accurately predicting the outcomes of forestry interventions such as FAM poses a dilemma that is the subject of discussion (Park and Talbot, 2012). Decision-makers are faced with two situations: wait or act. "Acting" would imply risks of poor adaptation or "maladaptation" of species that are artificially migrated, which would thus increase exposure to epidemics, competition and stress (Hewitt et al., 2011). However, the alternative of "waiting" presents its own set of challenges. Delaying action may lead to missed opportunities for intervention, potentially exacerbating existing issues within forestry ecosystems (Davidson and Simkanin, 2008). Additionally, the longer the delay, the more uncertain decision-makers become about the effectiveness of future interventions (Park and Talbot, 2012). This means that they face not only the immediate risks of taking action but also the potential downsides of waiting, including missed opportunities and heightened uncertainty (Park and Talbot, 2012; Schlaepfer et al., 2009).

Ultimately, FAM is a social and political project that is based on a particular conception of the potential of forest science and human capacities for forest management. A treatment of the subject within the field of social sciences renders it possible to identify more specific aspects not covered by the natural sciences (Guan et al., 2019). This leads to the following question: what are the main values and beliefs that determine the perceptions of social actors toward FAM? The values and beliefs associated to FAM are often formulated as specific considerations, caveats, or proposals associated with a person's own experience with forest management. In summary, the term "perception" involves understanding how people read various aspects of the environment. However, for this study, we define "values" as beliefs in ideas that influence the attitudes and behaviors of the concerned social actors (Batellier, 2016).

As key elements in perception studies, we highlight (i) public cognizance, reflecting the level of knowledge about assisted tree migration; (ii) public opinions, encompassing attitudes, feelings, and behaviors regarding assisted tree migration; and (iii) social acceptance measured by the degree of community support for assisted tree migration.

FAM has been the subject of scientific debate for three decades, generally reflecting the risks (competition, maladaptation, epidemics, fires, etc.) and benefits of its use in the environment (Keel, 2007; McLachlan et al., 2007; Peters and Darling, 1985; Royo et al., 2023). Despite the favorable development of tree species in certain experiments carried out in recent decades in Canada (Klenk, 2015), there is still no consensus in the scientific literature regarding the adoption of FAM as an adaptation strategy against large-scale climate change impacts (Park and Talbot, 2012; St-Laurent et al., 2018). Additionally, there is some uncertainty regarding the ability to implement this strategy on a large scale, given the limitations in nursery production capacity, the scarcity of seeds, the large size of the territory, and the lack of labor (Palik et al., 2022).

In Canada, research on social perceptions of forest management strategies, such as FAM, is limited, with a dozen studies published (Hajjar and Kozak, 2015; Pelai et al., 2021a; St-Laurent et al., 2018). In Quebec specifically, this scarcity is particularly evident. In the context of social participation, this is alarming, especially considering that approximately 92% of Quebec's forests are publicly owned and administered by government bodies (Boulanger et al., 2023).

Materials and methods

Ethical procedures and authorizations

This study was approved by the Ethics Committee for Research with Human Subjects at Laval University (approval number 2021-187).

Study area

The focal region of the studies is the province of Quebec in Canada. Thus, all interviewees were based in Quebec, albeit from different regions (e.g., Capitale-Nationale, Abitibi-Témiscamingue, Outaouais, Estrie, and Maurice). The selection of individuals presented some challenges, first given the specificity of the subject. As very few people are aware of the application of FAM, the recruitment of participants was complex and limited.

Participants were recruited in different areas, from boreal forests in the north to temperate forests in the south. The extensive boreal forest is crucial for carbon storage and biodiversity and the temperate forest is located closer to urban areas. The chosen regions have significant water resources, including numerous rivers and lakes. In turn, climate change threatens Quebec's forests with more frequent forest fires, pest outbreaks and changes in weather patterns that affect forest health and productivity. In the socioeconomic sphere, Quebec is strongly associated with natural resource industries such as forestry, mining and agriculture. Industrial logging is significant, economically vital for some communities and heavily subsidized. However, there is a growing demand for conservation and sustainable practices. This dynamic creates a scenario of challenges and opportunities for the application of FAM.

Interview selection

In this study, semi-structured interviews were essential for identifying nuances and clarifying details regarding the way in which the groups (researchers, stakeholders, forestry workers and private forestry owners) treat the potential of FAM today.

Survey participants were recruited using the snowball sampling method (Audemard, 2020; Leighton et al., 1995), where university or government researchers previously nominated potential interviewees. Additionally, purposive sampling was based on survey profiles of organizations and individuals and their supposed knowledge about forest management. For this second method, 12 organizations involved in forest management, public park management, forest research, representatives of private owners, the timber industry, and non-governmental organizations were included.

Considering the limited number of researchers specializing in the topic, we chose not to specify their region when presenting the results, to guarantee confidentiality and anonymity. The selection of interviewees prioritized subject specialists, particularly those affiliated with government ministries and forestry research institutions. However, we also conducted interviews with forest managers, private landowners, and ecologists. For this latter group, the criterion was a fundamental grasp of the subject matter, though not necessarily an advanced level of expertise in the current research.

During the research preparation phase, we identified a list that pointed out the main organizations and profiles of interviewees that we should contact. The preparation of this list included the participation of professors at Laval University and discussions with researchers associated with the Quebec government. On the other hand, members of the industrial sector, some managers of forestry companies and NGOs were contacted, but did not express interest in discussing the project.

To ensure the rigor, validity, and relevance of the research, sociological principles were integrated throughout all stages of the study. These principles included reflexivity, contextualization, interaction, interpretation of meanings, consideration of subjectivity, theorization, and generalization (Lune and Berg, 2016; Reed et al., 2018). Given that the production of knowledge on social perceptions are subject to change over time and sensitive to the social and cultural context, we examined other studies already carried out in Canada to validate our methodology (e.g., Findlater et al., 2022; Hajjar and Kozak, 2015; Pelai et al., 2021a; St-Laurent et al., 2019). These procedures were crucial to correspond to the principles of qualitative research in social sciences (Baribeau and Royer, 2012; Bertrand et al., 2006).

One advantage of the semi-structured interviews was the possibility of greater proximity and greater interaction with the interviewees (Savoie-Zajc, 2021). This made it possible to address more precise subjects, referring to the actors interviewed and their areas of intervention. In this way, we were able to spontaneously guide the course of the research, producing the best analysis of the responses of research participants.

The interviews encompassed a diverse group of respondents, totaling 18 individuals categorized into five distinct groups, with 29 categories of respondents, as one individual may belong to more than one category. These groups included three (3) private forestry company staff (PFC), five (5) private forest owners (PFO), eleven (11) forestry researchers (FR), four (4) members of NGOs/other forestry stakeholders (FS), and six (6) members of a government ministry (MM). This approach ensured a comprehensive representation of perspectives and expertise within the forestry sector, enriching the insights gathered from the interviews (see Table 1 for details).

TABLE 1 Category and quantity of actors interviewed.

Category of respondent	Number of people per category
Staff of private forestry companies (PFC)	3
Private forest owners (PFO)	5
Forestry researchers (FR)	11
Ministry employees or government institutions (MM)	6
Members of NGOs (FS)	4
Total	29

Development of the interviews

The interviews took place between June 2021 and May 2023. Each respondent received both written and verbal versions of the questions and was allowed 4 to 5 min to respond to each question. Approximately 15 questions were addressed during the interviews. Additionally, follow-up questions were posed to delve deeper into specific aspects based on the responses or to provide further elucidation of certain topics, which is a common strategy in semi-structured interviews (Savoie-Zajc, 2021). The interviews were conducted in French and translated to English by the main author for the purpose of this article.

To validate the collected data during the research period, we employed triangulation by gathering data through various methods and sources. This included observations, inquiries, and specific concerns that were thoroughly discussed not only with fellow students, researchers, and university professors but also through interactions during regular meetings, conferences, symposiums, and field visits. Our engagement extended to on-site experiences, such as visits to the Berthier nursery and two excursions to experimental FAM plantations in Portneuf, Quebec. These plantations were developed as part of the DREAM project (Desired REgeneration Through Assisted Migration), which has been ongoing since 2018 (Royo et al., 2023).

Data analysis

Given that this study adopts an inductive approach, we examined local data to derive references, draw inferences, and gain relevant perceptions in association with other studies. This data collection technique enables an interpretive and constructivist research perspective. It was selected because such an epistemological stance aims to gain a comprehensive understanding of a phenomenon while exploring the perspectives and meanings that social actors attribute to their reality (Savoie-Zajc, 2021). In essence, engaging in joint reflection on FAM through interviews with individuals who are interested or curious about its implementation fosters a dynamic of co-constructing meaning between the researcher and the participants. Consequently, this methodology facilitates the emergence of new discourse and insights into the studied phenomenon (Gauthier, 2009).

The interviews were recorded in both video and audio formats, and a transcription was produced with editing. This editing process aimed to maintain the essence of the recorded narrations and speech while improving readability and understanding. It included grammatical corrections, the elimination of repetitions, and the removal of non-essential elements. Next, contextualized thematic analysis (de Souza, 2019) was conducted to examine the qualitative data. This process was carried out manually. During the analysis, we focused on extracts that highlighted four key concepts: (i) Social participation and acceptance; (ii) Trust in government authorities; (iii) Intervention through FAM vs. non-intervention; (iv) Technical capacity and scientific feasibility of FAM.

Results

Different degrees of FAM and acceptability

Exploring different intensities of FAM and its acceptability sheds light on crucial considerations in this field. Assisted population migration, involving movements within the species' range, has gained general support as a relatively safe and practical approach. On the other hand, the assisted expansion of distribution, which involves the movement of species beyond their current zone of occupation, was considered more daring and appropriate in specific circumstances. Assisted species migration, although emblematic, has faced skepticism due to its higher risk and logistical challenges.

According to these models, most interviewees expressed a preference for the first model, which involves migration within the distribution area using native species. However, some mentioned that they support the second model in specific cases. The third option was deemed unfeasible due to the high level of risk and impracticality, especially when considering systemic issues.

> The discussion about acceptability was extensive, with interviewees expressing optimism about the proposal's chances of acceptance. However, many stakeholders emphasized that the process must continually account for public perceptions of the species involved. I believe that assisted migration is a necessary and inevitable strategy given that climate change is occurring rapidly and that forest ecosystems must adapt quickly. However, the importation of species must be managed carefully to minimize impacts on local ecosystems (FR 1).

Hence, the evolution of acceptability could be attributed to the transparency exhibited in projects. Several interviewees raised concerns regarding the opacity surrounding projects and the heightened centralization, as some interviewees stated, "It is super important to be truly honest when it comes to the level of knowledge we have, the degree of certainty we have. We must accept, we have to say, there are many things we do not know" (FS3).

The discourse surrounding acceptability is highlighted a nuanced picture, where FAM is generally favored but requires an ongoing dialogue between public perception and the species being introduced. Project transparency emerged as a key factor influencing acceptability, as interviewees expressed concerns about opacity and centralization of decision-making.

Finally, although assisted migration is seen as an inevitable strategy in the face of rapid climate change and the urgent need to adapt ecosystems, careful management and transparency are key. The balance between innovation and risk mitigation must be carefully explored to ensure the long-term sustainability of forest ecosystems amid evolving environmental challenges.

Operability and indigenous participation

During several interviews, two themes were raised by the interviewees while assessing the forestry sector's situation, even before we posed specific questions: (i) the risk of a scarcity of technical conditions for large-scale forestry interventions and (ii) indigenous participation in decision-making within this sector. Although this topic extends beyond our focus, these elements play a crucial role in social dialog regarding FAM.

Nearly all the interviewee reports highlighted at least one type of worker shortage in the forestry sector, such as in logging, planting, seedling management, processing, handling, and transportation of materials, along with the subsequent aging of the current workforce. "We are struggling to attract students; their numbers are decreasing. During the summer, there used to be a large workforce. Why are students interested in working in the forest decreasing annually?" (PFO 4). This decline in young people's involvement in forest management activities, particularly students, is considered critical during the planting period. Numerous interviewees expressed concerns about this tendency, emphasizing its potential impact on the viability of FAM, as it would require more workers, especially in northern Quebec, the region far from urban centers and services.

However, even in more southern regions, this issue is highlighted. In connection with this, the requirements extend to the operational absence of studies and workers in nurseries.

> There is a need for considerable knowledge to set it up [FAM], but there is no longer anyone who works in tree nurseries; it is not very interesting for people who prefer to work in ecology, in development software, artificial intelligence, etc. However, the concrete, the ground, there is no one left (MM 2).

Another argument was the importance of integrating native communities into the decision-making process. Among the stakeholders consulted, there was a strong understanding of the unique circumstances of First Nations, with a consensus in favor of collaborative efforts.

> It is certain that it would require consultation specifically to indigenous people; then, the consultations must be consultations where there is a certain power of recommendations (PFO 2).

> If these indigenous populations are not only consulted but also integrated into the process, it is better. We see projects such as

> "Paix des Braves" [territorial agreement signed in 2002 between Quebec and the Cree nation] or successful partnerships with other First Nations; these are projects where they are integrated and allies, and the same should be true for private landowners. They must be in the game, they need to (PFO 1).

Given the historical process of territorial occupation in Quebec, indigenous status is officially recognized by the State (Teitelbaum, 2015). This scenario was constructed through a reinterpretation of the role of the First Nations in the development of Quebec and a new understanding of the presence of different indigenous nations in the province (Dabin, 2022). Due to this shared vision about the importance of First Nations and their role in the province's environmental debate, the importance of indigenous participation in the decision-making process was highlighted by several interviewees (PFO 5; FS 3; PFC 1, 3; FR 1, 2, 4, 7, 10, 11).

Risk perception: intervention vs. non-intervention

Risk perceptions were discussed along with examples, such as the intensity of FAM (inside or outside the distribution area), as well as biological factors (species competition, epidemics and uncontrolled fires) and social factors (economic interest, social participation and technical-scientific capacity). The imperative to intervene in forests amidst climate change was upheld by all parties consulted in our study. Nevertheless, there is broad acknowledgment of the risks inherent in large-scale forest interventions.

The divergences among the actors occurred in the type of intervention to be carried out, with FAM being the subject of discussion and recognized as an option, although not exclusive or a priority for the majority. "The big problem is uncertainty (...). That is why we cannot just depend on FAM; we're not going to replant 100% of our forests in Quebec; we must put a lot of effort into natural regeneration" (FR 2).

All respondents were in favor of implementing pilot projects in the province, and they emphasized that this would mitigate risks if large-scale interventions were necessary in the future (PFC1; FR 11). "I think these are technologies that deserve to be analyzed with pilot projects, which we try on a smaller scale to see a little how they behave" (FS 1).

> For me, invasive species are something that I worry about, competition, particularly with global warming, so that worries me and assisted migration. The secret risk revealed by the migration of an exotic species is a significant topic for discussion in the scientific community (PFO 4).

The reduced large-scale quantitative experience of FAM and the uncertainties about the viability of the strategy (FS 2) contribute to a skeptical view of this strategy. At the technical level, we identified greater uncertainties regarding seed production, adequate knowledge and the choice of species. Regarding seed production, one researcher highlighted the potential difficulty in providing seedlings for assisted migration.

> (. . .) in the boreal forest, we mainly have species that we can dehydrate and preserve in a seed bank. However, the target species for Quebec-assisted migration into temperate forests are species that generally produce seeds that do not survive well or have a short shelf life. These are seeds that do not grow well, which is why we harvested them in the fall. We do not sow them in the spring. Therefore, this difficulty in supply due to the non-conservation of seeds will also influence the choice of essences to be used in migration because if seeds cannot be collected, crops cannot be planted (MM 5).

Therefore, even though they advocate field trials with FAM, some researchers highlight that these probable obstacles need to be carefully analyzed.

In the social sphere, the most recurring reservation pointed to the objectives of FAM in the province. Many interviewees criticized the current utilitarian perspective on forests. In this scenario, ecological priorities might be sidelined, while financial considerations heavily influence decisions about natural environments (FR 4, 5, 9, 10; FS 3, 1). This viewpoint suggests that the ongoing FAM strategy might overshadow alternative reforestation proposals or divert focus from pressing issues related to forest regeneration.

> (...) I have difficulty considering assisted migration in restoration. We invest a lot in economic value. However, we're not doing as much for ecological restoration, which is why I think assisted migration is currently sold as insurance, an insurance policy for timber yield (FR 9).

> The problem is that we always want to provide the same amount of wood supply, when we must at some point find a way to slow down, and for that, I think diversified strategies are needed. (. . .) maybe we should also find a way for the next few decades to slow down harvesting and try to find diversification (FS 1).

Finally, the interviews highlighted that challenges such as uncertainties in the production of seeds for assisted migration, the risks of invasive species and the utilitarian perspective of forests point to the need for careful consideration and diversified strategies in forest management. Balancing economic value with ecological restoration is a significant concern among actors, emphasizing the importance of finding sustainable solutions that prioritize the long-term health and resilience of forests.

Trust and transparency

Regarding trust in the Quebec government, questions were raised regarding current management in the face of climate change and the possibilities for managing assisted migration. Despite occasional criticisms from certain respondents, the majority are optimistic about the possibility of public organizations in Quebec promoting the implementation of FAM (MM 2, 6; PFC 1; PFO 1; FS 2, 4). Among the criticisms, some interviewees questioned the lack of transparency of projects and excessive centralization because "(...) a small group of people should not be responsible for the final decision without consulting other experts" (FS 1).

The interviews revealed that centralization is linked to the extent of decision-making authority and the transparency of the process. Participants frequently expressed a desire for increased social participation, emphasizing the need for transparency and trust in decision-making. While a few suggested that Quebec's current structure requires radical changes (FS 1, 3; FR 8; MM 2, 4), the consensus was that only minor adjustments are needed (FS 2, 4; PFO 2, 3; MM 2, 5).

Another interviewee expressed distrust regarding the way in which the proposal has spread, perhaps without due precautions: "So we replant based on economic profitability, but which does not consider the risks. Therefore, it's a big project that's underway, but it's happening very quickly" (MM 5).

Thus, the concept of transparency was emphasized in all the groups that were interviewed, with unanimous support for clear procedures as a means of upholding acceptance, engagement, and democracy in decision-making.

> It is super important to be honest regarding the level of knowledge we have, the degree of certainty we have. We must accept, we have to say, there are many things we do not know (. . .). I believe that stakeholders can collaborate more effectively, but concrete plans are needed. As mentioned earlier, transparency is key. If the plan is clearly outlined and communicated well, stating exactly what actions will be taken and where they will occur, for example, "We plan to implement this strategy across 25% or 2% of the territory," stakeholders will be more receptive. (FR 4).

In line with statements against centralization, interviewees highlighted that trust is proportional to different actors in the forestry environment when discussing FAM. In other words, the actors understand that there is a direct relationship between communication, participation and trust that must be discussed in the FAM development process in the province.

> (. . .) When engaging in direct dialog with those on the ground, such as professionals, the conversation becomes much more interesting, rich, and complex, fostering a greater level of trust. Professionals often have more influence over individuals than politicians do. It is easier to communicate directly with the people who will be doing the work, such as fixing the roof of your house. If you express a dislike for the color of the roof, it is a straightforward conversation. However, when the government dictates all roof colors, this becomes a different matter altogether. (PFO 5).

Discussions surrounding trust in the Quebec government in relation to forest management, especially in the context of climate change and assisted migration, have led to the need for a deeper assessment. Although there is optimism about the potential of public organizations to implement FAM, there are specific concerns related to the implementation of the strategy.

Overall, trust in government initiatives such as FAM depends on transparent communication, inclusive participation and collaborative efforts among diverse stakeholders, ensuring a balance between ecological priorities, economic interests and public trust in forest management strategies.

Purpose and values in a multifaceted context

In the final segment of our interviews, we asked participants to reflect on the purpose of FAM, considering the key factors discussed earlier, with emphasis on uncertainties, participation, trust in government, and operability. Reflecting on the core purpose of FAM provided some specific insights.

Consequently, the analysis of the interviews showed that despite the different experiences and particular roles of the actors in the forestry sector, the interviewees were similar in terms of priorities, needs and expectations. As we shall see, the understanding of how much the short-term effects of climate change echo in the sector and determine almost the entirety of action plans "Climate change is directly affecting the survival and growth of trees, making them more susceptible to pests and diseases" (FS 6).

The most cited concern is that the strong economic and financial interests in the sector could suggest an inappropriate purpose for FAM. While all interviewees acknowledged the forest's importance to the province's economy, they also emphasized the social and environmental values that serve as pillars of contemporary sustainability (Purvis et al., 2019):

> The companies' interest is now this: they want cheap wood, which, when processed, brings good dividends and provides good value to the shares. Reducing costs would mean having more cheap wood in the factory, and that does not match my vision of sustainable forest management (PFO 1).

With respect to the purposes of the FAM and other measures for adaptation to climate change, the actors noted that another plan must be developed to address the challenges of climate change, prioritizing the protection of biodiversity and social participation.

> More biodiverse ecosystems tend to be more resistant to disease, climate change and even fires. (. . .) I see this [CC strategies] as a proposal that is still in the early stages of study and discussion, especially regarding the possibility of assisted migration to trees. (. . .) However, for me, the most crucial aspect is the semantics of the discussion and the diversity of policies that promote popular participation, democratize knowledge and encourage open debates on how to improve and preserve our forests. This is vital not only for the economy but also for the health of local communities and forest ecosystems (FS 1).

The discourse in favor of biodiversity was frequently highlighted. Some recalled the importance of considering biodiversity studies in line with assisted migration research. In

TABLE 2 Attitudes toward FAM.

Favorable values	Values against
Benefits greater than impacts	Uncertainties
Risk of inaction	Natural resilience
Scientific capacity	Overly favorable to the forest industry
Biodiversity conservation	Precautionary principle

TABLE 3 Behavior toward FAM.

Support	Skepticism/rejection
Participation in pilot projects	Support for other measures
Trust in government	Disbelief in government
Participation and dissemination of studies	Disbelief in current science

short, many actors believe that FAM can be important for forest sustainability if the selection of species is not based solely on commercial factors.

Discussion

When carrying out this study, we identified common concerns among the actors, despite their functioning in different environments. In fact, it was possible to identify different degrees of knowledge among some, but everyone who was willing to talk to us already had a good basic knowledge about FAM. The greatest difference was the deeper level of knowledge of the ministry members, which allowed them to analyze the subject in more detail.

To understand the values derived, we outline in Tables 2 and 3 below the key differences between attitudes and behaviors concerning the topic. In this context, attitude signifies the inclination to act among the relevant stakeholders, whereas behavior pertains to the actual actions carried out. Essentially, attitudes influence behaviors (Batellier, 2016).

While there is variation in the interpretation of the assigned values, they can be either favorable or unfavorable to the FAM depending on the context. However, we have distinguished here how certain terms and values emerged in the interviews.

Despite the tables presenting the values fairly, the discussion does not seem polarized, meaning there are no extreme views on either side. Overall, there is a favorable inclination toward adopting the strategy, as long as it is performed cautiously and without neglecting other potential projects related to climate change adaptation.

We observed that the FAM in this study is associated with reflections regarding the notion of caution and the precautionary principle, crucial themes in environmental studies (Reed et al., 2018). In our approach, we consider risk management through the lens of the precautionary principle and caution, advocating for preventive actions in the face of scientific uncertainties, especially when there is the potential for serious or irreversible environmental damage (Myers, 2002; Newton and Oldfield, 2012).

Throughout the development of this study, we identified scientific uncertainty in environmental studies, including FAM, as a crucial factor in guiding public policies. This observation was consistently highlighted by interviewees, scientific literature (e.g., Pelai et al., 2021b; St-Laurent et al., 2018), and government publications. In the qualitative data collected, the precautionary principle was frequently mentioned, particularly in the context of associated risks and the challenges of controlling long-term effects.

Challenges in terminology and communication

The challenges surrounding terminology and communication in the context of assisted migration strategies are multifaceted and require careful consideration. One of the primary issues identified in this study is the lack of universally accepted and clear terminology for assisted migration. This absence of standardized terms and scientific concepts has led to conceptual confusion and misunderstandings among both experts and stakeholders (Ste-Marie et al., 2011). Despite efforts over several decades to establish a cohesive terminology, variations persist. In this study, we adopted the term FAM, but there are other terms in use, such as “assisted tree migration,” “assisted colonization,” “managed relocation,” and “assisted gene flow” (Benomar et al., 2022b). This lack of unity in presenting the strategy complicates communication efforts and can impede effective dialogue among researchers, policymakers and the public.

Moreover, communication challenges in Quebec are exacerbated by linguistic barriers between anglophone and francophone provinces (Sansilvestri et al., 2016). These linguistic differences can lead to misunderstandings and hinder the dissemination of information about assisted migration strategies. Additionally, weak intergovernmental relations among administrative authorities in forest management further complicate communication and decision-making processes (Gauvin, 2017).

> (. . .) the federal government does not truly have any influence on how provinces manage their forests [legally, in Canada the forest management is an area of provincial jurisdiction]. It is therefore more a matter of pressure exerted by different actors on the provincial government” (MM 5).

An important observation from our study is the limited participation of certain groups and associations, particularly among NGOs and representatives of private forest owners, due to their unfamiliarity with the FAM strategy. This highlights the critical need for enhanced communication efforts and social relations to bridge gaps in understanding and foster inclusivity in discussions about assisted migration.

Moving forward, we propose that addressing these challenges will require dedicated studies in the field of communication and social participation. By consolidating the terminology related to FAM and improving communication strategies, we can reduce barriers to public understanding, promote greater clarity, and facilitate successful dialogue regarding the objectives and implications of assisted migration strategies in Quebec and beyond.

The implementation of the FAM in Quebec

The implementation of FAM in Quebec is a topic that elicits mixed feelings among stakeholders. While there is a general trust in the capabilities of public authorities to carry out initiatives like this, it is not without reservations. Our studies have revealed that, overall, stakeholders appreciate the government's mobilization capacity, efficient organization, and access to technical resources, seen as crucial elements for the successful execution of intervention projects. However, these positive perceptions are accompanied by concerns regarding certain technical aspects of FAM implementation, such as seed production, proper species selection, and workforce availability.

Another concern involves uncertainties and hesitations regarding public participation in decision-making, raising questions about the effectiveness and social acceptance of the strategy. Although our study did not cover a large sample of stakeholders, the results align with broader trends observed in related topics (Yelle, 2013). Ultimately, for the success of the relationship between the state and society, it is crucial to address technical concerns, involve the interested population, and popularize the topic.

Comparative perceptions, Quebec vs. other Canadian provinces

Species assisted migration, the most intensive modality, which involves long-distance migration, was rejected by most of the respondents we interviewed. This situation aligns with several studies published in British Columbia (Hajjar and Kozak, 2015; St-Laurent et al., 2018). The reason could be associated with the greatest risk of a radical change in forest ecosystems. Thus, the use of native species is safer given prior knowledge and the possibility of resilience.

Among the groups studied, the differences in discourse between (i) researchers and members of ministries and (ii) private sector representatives, members of NGOs and private forest owners were highlighted. The former were much more certain potentials, risks, and implementation processes of FAM, while the latter were aware of how the strategy worked but uncertain of its necessity in the face of other available options. Thus, the degree of knowledge of FAM studies in the province increases the acceptability of and confidence in the relevance of the FAM strategy.

One element that appears underdeveloped in thinking about FAM is broadening the discussion with relevant organizations within and outside the province. Despite the impact of researcher networks and data sharing in the academic field (Benomar et al., 2022b), the analyzed discourses show the absence or lack of relationships in the forestry sector among Canadian provinces or among ministries in Quebec, such as the *Ministère de l'Environnement, de la Lutte contre les changements climatiques, de la Faune et des Parcs* (MELCCFP) and the *Ministère des Ressources Naturelles et des Forêts* (MRNF), in the technical field. However, FAM turns out to be an interesting strategy for provoking reflections from different institutional and informal authorities. As it is a controversial strategy, it works as an invitation to debate human action, as well as the management of uncertainty (Lidskog and Löfmarck, 2015; Millar et al., 2007).

According to the semi-structured interviews, in response to the problem raised, we noticed that the main determining values of the social perceptions of actors regarding FAM are trust in the government, public participation and good communication. However, a lack of interest in participating in the interviews was identified on the part of representatives of the forestry industry (large forestry companies). Despite initial contacts, we also encountered difficulties in conducting interviews with indigenous groups in Quebec.

Conclusion

This study aimed to provide a critical reflection on the perceptions of professionals and researchers in the forestry sector about FAM. Although conducted in Quebec, we believe this qualitative research can serve as a reference for similar studies in other regions. Our interview model and the topics discussed—such as governance, level of social participation, social communication, and uncertainty forestry management—are relevant and have been addressed in other recent studies on FAM.

Given its interdisciplinary nature, encompassing social geography, sociology, and environmental sciences, this research offers a broad spectrum of assessments. This breadth can pave the way for more specific studies in the future, enriching the understanding of FAM and its implications across different contexts. In summary, our discussion on the values associated with the Quebec Forest has highlighted fertile ground for future social science research concerning the forest environment. It is imperative to expand studies among indigenous communities and conduct quantitative assessments covering the general population to gain a comprehensive understanding of stakeholders' perspectives.

The interviews provided valuable insights into the perception of FAM in Quebec, showcasing broad acceptance among the consulted groups while also revealing significant concerns related to FAM and forest management. However, nuanced perspectives and considerations emerged during these discussions. While there is a general acknowledgment of the risks associated with large-scale forest interventions, divergent views on the most appropriate types and intensities of interventions were evident, with FAM being one option among others but not universally favored or prioritized.

A key takeaway is the necessity of balancing economic interests with ecological restoration efforts, underlining the importance of a holistic approach to forest management. Concerns raised about the utilitarian perspective on forests underscore the need for integrating environmental sustainability with economic considerations.

In the field of governance, this study proves highly relevant for comparison in broader contexts. We identified several similarities with other environmental studies, not only in FAM but also in forest restoration (e.g., Derak et al., 2018), mining, and the management of protected areas. The findings emphasize key debates regarding decision-making, including challenges related to centralization, transparency, trust in authorities, and the expansion of social participation. Although specific studies in the socio-environmental field may present varied situations, they are likely to encounter similar debates.

In summary, FAM is considered beneficial, but many uncertainties remain about the ability to implement the FAM strategy on a large scale. Additionally, challenges such as uncertainties in seed production for assisted migration, risks of invasive species, and the need for diversified strategies in forest management were identified, highlighting the complexity of managing forest ecosystems in a changing climate.

The study also revealed specific challenges in disseminating knowledge about FAM in the forestry sector, with many potential participants expressing a lack of confidence due to insufficient knowledge. Addressing these challenges requires strategic knowledge dissemination efforts, such as providing educational resources and conducting outreach programs.

Moving forward, collaborative efforts among policymakers, scientists, stakeholders, and local communities will be essential in developing and implementing sustainable solutions that prioritize the long-term health and resilience of forests. Continued research and evaluation of intervention strategies, including FAM, while addressing broader societal and environmental implications, are crucial for effective forest management.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The studies involving humans were approved by the Comités d'éthique de la recherche avec des êtres humains de l'Université Laval. The studies were conducted in accordance with the local legislation and institutional requirements. Written informed consent for participation was not required from the participants or the participants' legal guardians/next of kin because many interviews were carried out remotely. Consent was tacit after the interviewee's rights were explained via email and subsequently recorded during the interviews.

Author contributions

FM: Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review and editing, Validation. J-FB: Methodology, Supervision, Writing – review and editing. PR: Funding acquisition, Supervision, Writing – review and editing. AM: Funding acquisition, Supervision, Writing – review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Adapting the patch-cut system to implement forest assisted migration

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As the Anthropocene tightens its grip on the world, forests are facing escalating disturbance rates, tree mortality, degradation and risks of catastrophic collapses. A popular and controversial proposition is to enhance forests' response diversity by adding novel tree species with missing functional traits through forest assisted migration (FAM). Beyond tests of the survival and growth of southern species or provenances in colder regions and studies of the socio-ecological challenges facing FAM, little interest has been paid to the silvicultural system for FAM implementation. Yet, the topic could influence its biological success, social acceptability, and economic feasibility. For example, southern light-intolerant tree species introduced into northern uneven-aged forests may experience a lack of light availability. Likewise, implementing FAM in clearcuts raises social acceptability issues. The patch-cut system combines advantages of even- and uneven-aged systems useful for FAM; however, perhaps due to the difficulty of its operationalization, it is rarely used. We propose a new way to implement the patch-cut system, enabling from the get-go to plan the location and timing of treatment of each patch in a stand. We discuss the advantages that this revisited patch-cut system presents for FAM: (i) the testing of various planting environments, (ii) easy monitoring in an adaptative management context where each patch is a replicate of a repeated-measure experiment and (iii) low intensity planting for efficient future dispersion of species adapted to a changing climate. We end with a call for the development of an international network of FAM trials within the revised patch-cut system.

KEYWORDS

assisted colonization, assisted migration, global change, adaptation, silviculture, gap, forest management, regeneration method

1 Introduction

As the Anthropocene tightens its grip on the world, our natural ecosystems are facing escalating disturbance rates (Ellis, 2011; Worm and Paine, 2016; Nyström et al., 2019; Folke et al., 2021; Anderegg et al., 2022). Forest health and functioning are particularly affected by the rapidly mounting direct and indirect impacts of climate change along with invasive pests, diseases, and exotic species. Numerous scientific papers indicate rising levels of tree mortality, forest degradation and forest disturbances around the world (Trumbore et al., 2015; Seidl et al., 2017; Hartmann et al., 2022; Patacca et al., 2023). Others report increasing risks of catastrophic collapses of forest ecosystems and functions (Lindenmayer et al., 2016; Silva Junior et al., 2020; Canadell and Jackson, 2021; Forzieri et al., 2022; Parisien et al., 2023).

An increasingly popular and controversial proposition is to enhance the overall response diversity of natural ecosystems such as forests (Mori et al., 2013; Walker et al., 2023) by adding novel tree species with specific key missing functional traits (Mouillot et al., 2013; Messier et al., 2019) to the ecosystem to bolster the forest's resilience and adaptation to future novel climates and other biotic threats. Forest assisted migration (FAM) is such a tool and has emerged as a burgeoning field of study. FAM consists of favoring the establishment of new species in forests within or at varying distance from their current range (Williams and Dumroese, 2013).

While the concept of FAM has been scrutinized (Neff and Larson, 2014; Michalet et al., 2023; Refsland et al., 2023; Argüelles-Moyao and Galicia, 2024), Xu and Prescott (2024) found that 60% of recent papers on FAM express a positive stance toward FAM. They advocate for a holistic approach to its implementation.

Examples of FAM implementation are relatively scarce (Palik et al., 2022). For example, Messier et al. (2019) proposed using functional complex networks as an approach to favor connectivity among stands in a landscape in which FAM was suggested as a tool to increase functional diversity, but without silvicultural strategies ensuring FAM success. Similarly, (Royer-Tardif et al., 2021) suggested a new zoning strategy using FAM in stands with high vulnerability to global change. Royo et al. (2023) present the Desired REgeneration through Assisted Migration (DREAM) network where they focus more on species provenance and physiology than on silvicultural systems. While considerations for connectivity, vulnerability, and species provenance are important, we believe that it is equally important to develop/adapt silvicultural systems that favor FAM success; silvicultural systems could significantly impact the biological success, social acceptability, and economic feasibility of FAM. For instance, introducing temperate light-intolerant tree species into uneven-aged forests managed under the single-tree selection system presents limited chances of success due to lack of light availability. Although the use of even-aged treatments (e.g., clearcuts) could be used to implement FAM, it is likely to raise social acceptability issues (Arnberger et al., 2022).

We believe that there is a silvicultural system which combines the best of both even- and uneven-aged systems — the patch-cut system (Box 1). We believe its advantages of promoting the regeneration of forest tree species that are moderately to highly shade tolerant (Schnake et al., 2023) and maintaining old-growth attributes (Bauhus et al., 2009) would both be very useful when implementing FAM.

While the patch cut system concept relies on solid bases (e.g., improving structural and tree species diversity) (Runkle, 1992; Coates and Burton, 1997), its operational implementation remains underdeveloped. Much of the literature on patch cuts focuses on tree species regeneration (Béland and Chicoine, 2013; Gauthier et al., 2016) and determining the optimal size and positioning of the patches during the initial harvest to promote this regeneration (Coates and Burton, 1997; Parish and Antos, 2005; Bolibok and Szeligowski, 2011; Kern et al., 2017). However, even when patches or gaps have been implemented in a FAM context (Palik et al., 2022), there is a lack of long-term planning regarding how and where subsequent patches (in subsequent entries or harvests) should be located without disrupting the regeneration established in earlier patches.

BOX 1 The patch-cut system in the silvicultural literature.
While the concept of patch cutting, involving selective cutting of parts of a stand larger than a tree or small groups of trees, is not new, it is often not formally classified as a distinct regeneration method but rather considered a variant of selection cutting (Leak and Filip, 1975; Nyland et al., 2016; Ashton and Kelty, 2018), irregular shelterwood (Raymond et al., 2009) or clearcutting (Ministry of Natural Resources and Forestry, 2008). Many silvicultural textbooks do not explicitly mention the patch-cut system (Daniel et al., 1979; Schütz, 1990, 2002; Matthews, 1991; Lanier, 1994; Bailey et al., 2015; Savill, 2019). The definitions of the silvicultural systems are highly variable among jurisdictions and authors, and the way the patch-cut system fits in theses definitions reflects this variability. Despite the patch-cut system's potential benefit in integrating aspects of both even- and uneven-aged approaches, its practical application remains limited. This is revealed by its disproportionately low occurrence in the scientific literature; a search in Google Scholar using the phrases "forest and patch cut," "forest and single-tree selection," and "forest and clear-cut," yielded 261,000, 1,300,000, and 1,610,000 results, respectively. It is even possible that the patch-cut approach is over-represented in scientific studies compared to forest practices used in real-world forest management.

In this paper, we propose a new way to implement the patch-cut system, enabling forest practitioners to plan from the very beginning the location and timing of treatment of each patch and corresponding forwarding trails in a stand for the whole rotation. We hereafter refer to this new implementation as the STEP (Spatially and Temporally Explicit Patch-cut) system. After describing the basics of the STEP system, we delve into the numerous advantages as well as some disadvantages and limitations that this revisited patch-cut system presents for FAM. Afterward we discuss its flexibility and the contexts most suitable to its application. We end with a call for the development of an international network of assisted migration trials using the STEP system.

2 Basics of the STEP system

When planning the STEP system, a stand is subdivided into multiple patches. I. The subdivisions are based on a planned permanent network of forwarding trails adapted to the terrain; these trails are designed in such way that they allow a continued and direct access to each patch (Figure 1A). This is essential to enable the implementation of treatments beyond the primary harvesting operation, such as commercial thinning or a cleaning treatment to release regeneration. Direct access ensures that movement between patches does not disturb regeneration within them. Otherwise, moving through the second patch could harm the regeneration. This planned permanent network of trails is a fundamental distinction between the STEP system and the irregular shelterwood approach proposed by Saunders et al. (2014). II. Each subdivision is large enough (e.g., 0.1 ha) to ensure that most trees will have competition from trees of the same cohort during their whole lifespan, as in even-aged silviculture, thus limiting treatments on a given subdivision to a single development stage. In a FAM context, the patch size is particularly important so as not to restrict our species choice to only light-tolerant species. III.

Each subdivision is small enough (e.g., no more than 0.2 ha) to avoid leading to some negative impacts of clear-cutting. e.g., social acceptance or soil erosion (see Nolet et al., 2018). IV. No more than 1/4 of the subdivisions are harvested successively over the whole rotation, providing at least 4 cohort of patches in the stand and a constant area harvested each time. For example, a stand with 100 subdivisions (of similar sizes) and an 80-year rotation could experience a harvest in 20% of its subdivisions (no adjacent subdivisions) every 16 years (Figure 1A). The relationship between number of cohorts of patches (NCP), age at maturity or rotation age (RA) and cutting cycle (CC) is NCP = RA/CC (Nyland et al., 2016). Of course, productivity could vary among patches and the forest practitioner may choose to modify the harvest schedule during the course of the rotation.

In the stand example presented in Figure 1, the network of trails and mosaic of patches have been sketched manually using a GIS software. This process was time-consuming and would not be efficient on an operational basis. Hence, the implementation of the STEP system on a large scale would require the development of a GIS-based tool to locate the trail network and the patches. Such a tool could first use LiDAR-based elevation model to identify potential trails that avoid terrain obstacles (e.g., steep slopes) for forest operations. Second, the patches could be located and delineated through an optimization algorithm that would consider the potential trails, and the number, size and shape of gaps. Afterward during forest operations, high-accuracy GPS would allow the implementation of both trails and patches that accurately reflects their localisation planned through the GIS based-tool.

3 Advantages of the STEP system for forest assisted migration

In a FAM context, the goal is to utilize as many species as possible to adapt to future climates. In regions where forests are primarily managed through uneven-aged or irregular silviculture, such as single-tree selection cutting or continuous-cover irregular shelterwood, the light-tolerance of dominant species and social pressures often limit the introduction of light-intolerant or mid-tolerant species for FAM. The STEP system enables the use of more light-intolerant species in an environment resembling uneven-aged or irregular structure. This is achieved through larger canopy openings that allow for higher light levels compared to single-tree selection, group selection, or continuous cover irregular shelterwood. Additionally, it involves enhanced care for seedlings and saplings, which can be accessed via a permanent trail network and permanent patch locations. This approach contrasts with current suggestions for group selection or expanding-gap irregular shelterwood. In essence, the STEP system facilitates more efficient implementation of FAM in uneven-aged stands.

Another advantage of the STEP system is that it allows for a gradual introduction of new species into an ecosystem. First, the patches are not harvested and regenerated all at the same time; while FAM is implemented in a patch, there are other patches in which regeneration is naturally established. Second, even within a patch, it is possible to promote both natural regeneration and assisted migration. Hence, if one method fails, the other can step in. In other words, natural regeneration and FAM can co-habit; it is not one or the other. The gradual aspect of FAM implementation in the STEP system is also in line with the gradualness of the effects of global warming. For example, a given southern species may not yet be suitable for a northern site and regenerating a patch with this species may fail. However, the climate may eventually become suitable for that species, and regenerating a patch with this species 10 or 20 years later might have greater chances of success (Nabel et al., 2013). The gradual introduction of species through assisted migration in patches contributes to maximize the dispersion of assisted migrants where patches can act as nuclei for dispersion (Corbin and Holl, 2012). This approach could potentially achieve FAM more efficiently compared to area-wide planting in clearcuts, irregular shelterwood or selection systems.

We argue that the STEP system is inherently a suitable silvicultural approach for implementing forest assisted migration. When implementing FAM, foresters must acknowledge that they are venturing into the unknown underscoring the importance of learning from both successes and failures (Achim et al., 2022). Each patch within a stand managed using the STEP system can be viewed as a replicate of an experiment at the stand level. Implementing the STEP system in a stand aligns with principles of active adaptative management (Walters and Hilborn, 1978), since it can be designed explicitly for continuous learning. For example, if a stand is managed through the STEP system, patches could be planted using various species potentially interesting in a FAM context and compared to patches where indigenous species (natural and/or artificial) are favored (Figure 1B). Enough patches of species (or species assemblies) should be replicated to obtain valuable scientific results. As the knowledge improves with the monitoring of the results from the first cohort of patches, more sound management decisions can be made for the following cohorts of patches. Afterward, the following cohorts should be utilized with the same learning and replication principles in mind. Moreover, as there should be several stands managed through the STEP system in a landscape, the experience could be repeated in time and space in other stands or other questions could be tested in other stands (e.g., the effect of the size of the gaps). When applied within the framework of active adaptive management, the STEP system facilitates the evaluation of concerns related to FAM and influences its associated regulations. This ensures that management practices are based on rigorous scientific knowledge.

Numerous studies have shown that there are segments of society that are reluctant to implement FAM for various reasons including, risks of displacement of indigenous species, potential maladaptation of planted species and risks of pest introduction (Neff and Larson, 2014). Of course, the use of the STEP system cannot completely alleviate these concerns. However, if the STEP system is used in the context of an active adaptive management framework (as it should be), these risks will be monitored, and modifications can be made, if needed. Also, to some extent the STEP system can be considered as an uneven-aged system. As such, the residual trees surrounding a patch can (i) provide propagules for regeneration into the patches and (ii) act as a barrier to potential invading species. Finally, uneven-aged silviculture is generally much more accepted socially than even-aged management. Even though the patches represent small clear-cuts, they are unlikely to raise major esthetics concerns with the public as their visual effects are limited, as illustrated through this landscape visual simulation (Figure 2).

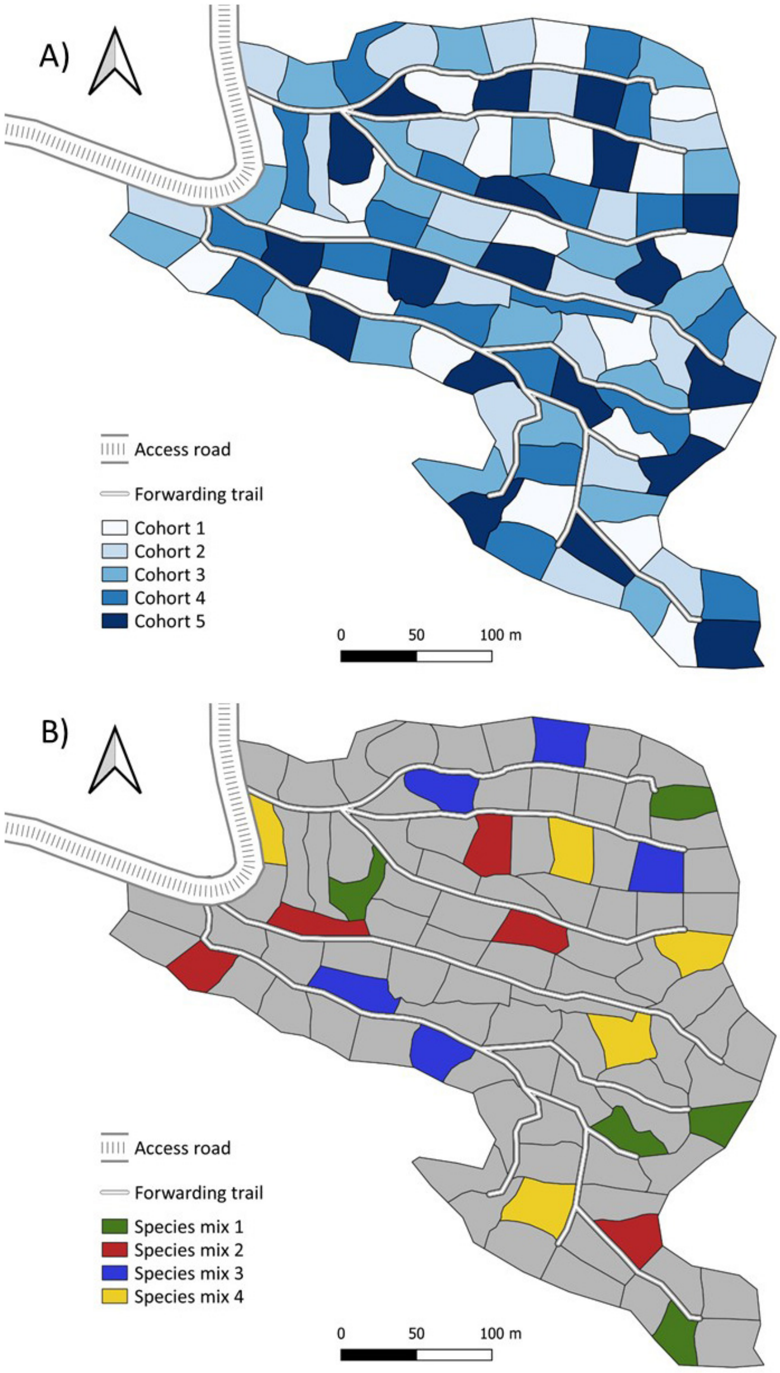

FIGURE 1
To-scale 2D rendering of the layout of trails and 97 patches for the spatially and temporally explicit patch-cut (STEP) system applied to a shade-tolerant hardwood stand with five cohorts. In this example, the average patch size is 0.097 ha and the total area of the stand is 9.43 ha. **(A)** Patches of the same color belong to the same cohort, **(B)** Test of different forest assisted migration species mixtures in one of the cohorts of patches within the spatially and temporally explicit patch-cut (STEP) system.

4 Flexibility of the STEP system

The patch-cut system offers inherent flexibility and variability, as heterogeneity in light conditions within patches favors a diversity of species (Lu et al., 2021). The STEP system allows this flexibility to be more efficiently implement. While a number of examples are provided here, we recognize that foresters would use their knowledge, experience, and imagination to adapt the STEP system to their specific needs. For example, when harvesting the patches, residual trees could be left behind for regeneration, ecological (variable retention) or societal reasons. These trees could either be harvested later when other patches are harvested or could be left permanently. A patch that is to be harvested in a defined year could benefit from a commercial thinning treatment or seedcut 10

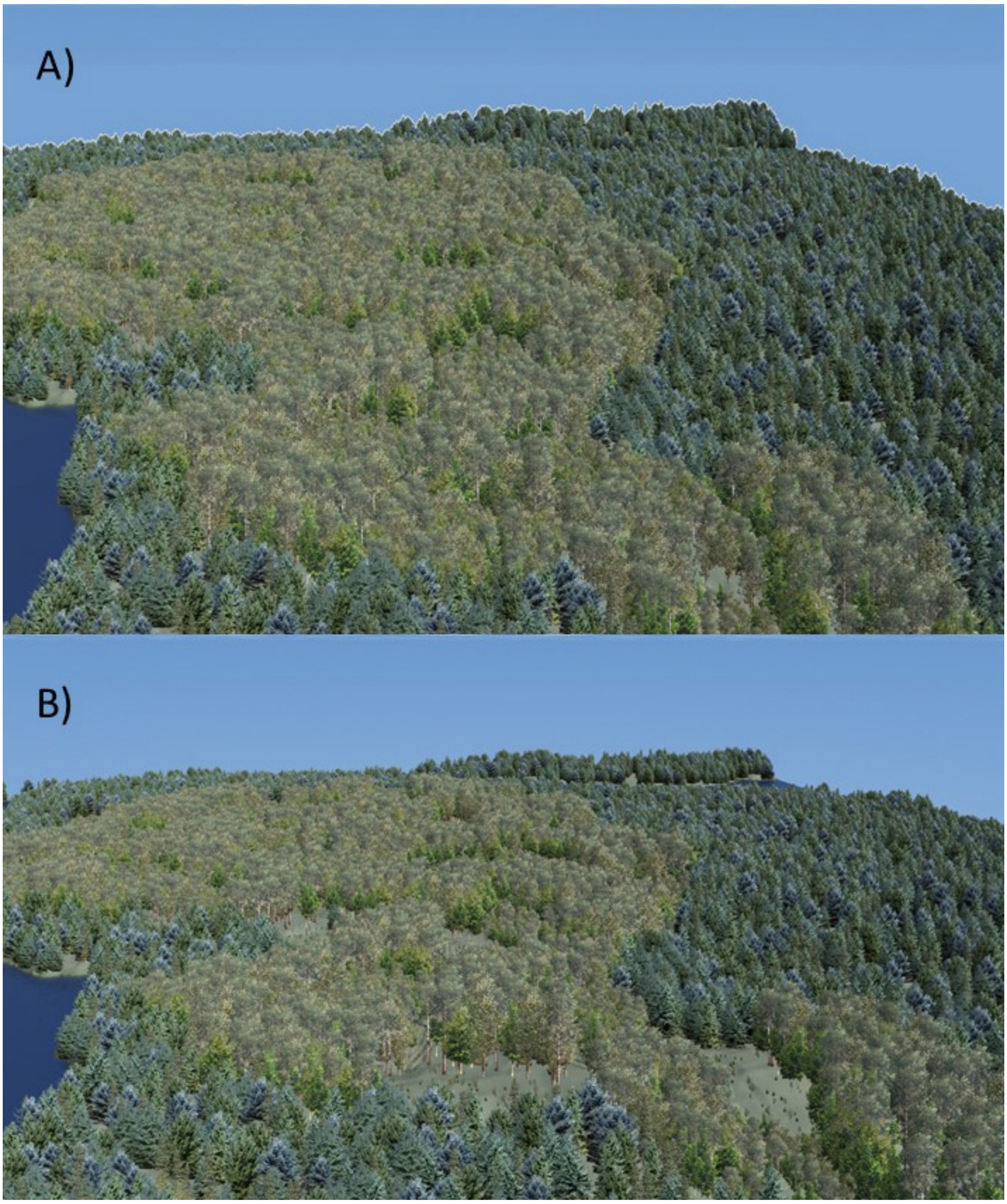

FIGURE 2
Visual effect of implementing the spatially and temporally explicit patch-cut (STEP) system simulated with Visual Nature Studio 3, **(A)** before cutting; **(B)** after cutting the first cohort of patches. The appearance of patches will vary depending on colors of the soil in patches, view angle and distance. All these factors can be modeled according to local conditions.

to 20 years before the harvest. This commercial thinning could be synchronized with the harvesting of other patches, using the permanent trails to provide access to the patches. Likewise, a patch that had been harvested 10–20 years previously could benefit from a non-commercial treatment (e.g., removal of competing vegetation) to promote the growth of seedlings/saplings of desired species. While we usually consider a stand as homogeneous, there is often small-scale heterogeneity within a stand. Hence, patches within the same stand may show abiotic variability especially for soil thickness, slope, moisture regime and aspect. Hence with the STEP system, tree species adapted to the specific conditions of the patches or tree species already present as advanced growth can be favored in given patches. In order to favor the establishment of natural regeneration, the creation of patches can be synchronized with seed years. The size of the patches can also be adjusted to local tree height and to shade tolerance of the desired species. Also, patch size can be adjusted as a function of biodiversity (Schall et al., 2018) or social acceptability concerns. Finally, some patches (clustered or not) could even remain free of harvesting to develop old-growth forest legacies structures (Ezquerro et al., 2019).

5 Contexts appropriate for the application of the STEP system

Minimally, as for any partial harvest silvicultural system, stands appropriate for the application of the STEP system should meet a number of criteria: (i) have a sufficient level of maturity to sustain a financially viable harvest, (ii) not be overmature with short-lived species unable to remain standing until the entire stand is harvested, (iii) be in areas accessible by a regularly maintained road network to facilitate frequent entries, and (iv) present few obstacles hindering the configuration of regularly spaced skidding trails leading to each patch.

More specific to the STEP system, cutting a stand using patches implies either adapting to the current spatial configuration of age classes or imposing a regular configuration. The STEP system advocates for the latter, which implies transforming the natural horizontal structure of the stand and acknowledging that the current state of an untreated stand will never naturally align with this configuration. Consequently, patches where interventions are needed may contain trees that are either younger or older than optimal maturity, potentially leading to sacrifices in wood production during the conversion to the STEP system.

Opting to implement the STEP system in stands of long-lived species could reduce the production sacrifices mentioned earlier, given that these species encompass a wide range of ages suitable for commercial wood volume extraction. Likewise, stands with an irregular or uneven age structure and shade-tolerant species are ideal candidates for the STEP system. These stands typically have enough volume to justify cutting operations, along with advanced growth ready to be promoted into the canopy within newly cut patches.

Despite the above limitations mainly pertaining to the conversion period of the stand into the STEP system, assuming acceptance of production sacrifices, and implementation of artificial regeneration, the STEP system could in theory be applied in stands of any species composition, shade tolerance, longevity or stand structure. Success is however not guaranteed and may vary depending on herbivory, the presence of advanced growth or microsite quality (Kern et al., 2017).

Other considerations, specific to the context of adaptation to climate change, include a strategy promoted by Royer-Tardif et al. (2021) which suggests focusing the effort devoted to assisted migration in portions of the forest that are highly vulnerable to forest ecosystem loss and where wood production is a priority. Similarly, Aquilué et al. (2021) suggested planting novel tree species with specific functional traits that were missing in the forest in centrally located and highly vulnerable stands having low functional diversity. One may assume that in these areas, the current horizontal structure would also be very vulnerable so there would be less wood production sacrifices from converting to the STEP system.

Moreover, in the context of using the STEP system for assisted migration, choosing stands that have many species which are at the northern limit of their distribution could be a good opportunity for introducing these species or provenances or increasing their abundance. Assisted migration of the kind that extends natural distribution has higher social acceptability than assisted migration of species far outside of their current range.

6 The STEP system and forest assisted migration: a call for the development of an international network of experiments

As the interest and number of FAM experiments are increasing worldwide, it is becoming important to start implementing them using appropriate silvicultural systems. We have argued in this paper that the STEP system is one of them, given its advantages for FAM, especially its flexibility and capacity to be designed for continuous learning. This is especially important because we have to keep in mind that using FAM may produce profound changes in ecosystem functioning. Forest scientists thus have the burden of proof to show that they do not play the “sorcerer’s apprentice.” Therefore, we are calling for the establishment of an international network of STEP system assisted migration experiments in different forest biomes and forest types in close collaboration with both researchers and forest managers. We also suggest pairing this network with other FAM experiments and networks already established using other silvicultural systems for comparison (DREAM: Palik et al., 2022; ASCC: Royo et al., 2023).

The main objectives of this paired network should be the following. First, to undertake a world inventory of experimental and commercial FAM tests set up in various biomes to determine which tree species could be tested using different silvicultural approaches. Second, to coordinate the establishment of different silvicultural experiments, ideally but no exclusively based on the STEP system, to address a set of important socio-ecological questions that are directly relevant to policy makers, stakeholders, and the public regarding FAM. Third, to encourage the writing of scientific papers and technical reports to help establish the silvicultural basis on which FAM could successfully be established in various forest biomes, forest types, silvicultural systems and socio-political conditions. The successful implementation of such a novel silvicultural system as STEP could be crucial in transitioning forest management into the integral role of adapting our world forests to global change.

We invite researchers and practitioners to contact us to report on any assisted migration silvicultural experiments or to express their interest in establishing STEP-based trials. Both old and new assisted migration silvicultural experiments will be registered within DIVERSE[1] as a new global research initiative.

Data availability statement

The original contributions presented in this study are included in this article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

PN: Conceptualization, Visualization, Writing – original draft, Writing – review & editing. MB: Writing – original draft, Writing –

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[1] https://diverseproject.uqo.ca/

review & editing. CM: Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Establishing monarch butterfly overwintering sites for future climates: *Abies religiosa* upper altitudinal limit expansion by assisted migration

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Climate change projections suggest a precarious future for the Monarch butterfly (*Danaus plexippus*) as the suitable climatic habitat of its exclusive overwintering host *Abies religiosa* (oyamel, Sacred fir, a conifer endemic to Mexico) inside the Monarch Butterfly Biosphere Reserve (MBBR) is expected to disappear by 2090. Since the upper elevation limit of *A. religiosa* is approximately 3,500m and the summits of mountains within the MBBR are *ca.* 3,550m, we tested the feasibility of establishing *A. religiosa* at four locations outside its current geographic range in the MBBR, on a geographically close volcano, Nevado de Toluca at 4000 (timberline, an extreme site), 3,800, and 3,600m (to test species range expansion upward in elevation), and at 3400m (a reference site, slightly lower than the upper elevation limit of *A. religiosa*). Using existing shrubs as nurse plants to protect the seedlings from extreme temperatures, at each site we planted five to eight populations, originating between 3,100 and 3,500m within the MBBR. After three growing seasons in the field (6years after sowing), we found that: (a) survival and height increment declined steeply with test site elevation; (b) even at the highest sites (3,800 and 4,000m), survival was acceptable, at 68 and 44%, respectively, although the growth was very poor at 4000m; (c) populations responded similarly to transfer; (d) transfer effects were best accounted for by annual dryness index; (e) to compensate for the expected 2.3°C increase in mean annual temperature or 0.009 $\sqrt{{}^{\circ}\mathrm{C}}\,\mathrm{mm}^{-1}$ increase of annual dryness index from the reference period (1961–1990) to the decade centered in 2060, it would be necessary to shift populations approximately 500m to higher elevations; and (f) upward transfers to compensate for the 2.3°C increase in mean annual temperature are expected to result in height increment and survival that are approximately 47 and 21% lower, respectively, than values expected at zero transfer distance. We conclude that the establishment of *A. religiosa* at 3600 and 3,800m is feasible and that planted stands could eventually serve as overwintering sites for the Monarch butterfly under projected future climates.

KEYWORDS

assisted migration, species range expansion, climate change, *Abies religiosa*, Monarch Butterfly Biosphere Reserve, Nevado de Toluca, mixed model, response curve

1 Introduction

Unusual tree mortality linked to anthropogenic climate change (Allen et al., 2010) likely places temperate forests at or near a tipping point. This is because droughts are now more frequent, intense, longer (Munson et al., 2018; Ritchie et al., 2021), and hotter (Hammond et al., 2022). The ongoing acceleration of climate change, driven by the synergic combination of the 2023–2024 El Niño (warm Pacific Ocean Equatorial current; also known as El Niño-Southern Oscillation cycle, ENSO) and other factors (reduction of suspended particles and upper atmospheric sulfur particles; Hansen et al., 2023), is making it increasingly evident that temperate forests around the world may reach and even surpass a tipping point for forest decline (Sáenz-Romero, 2024).

Some forests face a challenge to recover after recent disturbances linked to climate change, such as the 18 million hectares burned by forest fires in Canada in 2023 (Natural Resources Canada, 2023). Fires also risk converting the iconic temperate and boreal forests of Canada from a carbon source to a carbon sink (Council of Canadian Academies, 2022). Boreal Eurasian *Larix decidua* forests are also approaching a tipping point, due to increasing maximum temperatures (Rao et al., 2023).

Abies religiosa (Kunth) Schltdl. and Cham. (oyamel, Sacred fir) is a conifer endemic to Mexico, distributed mainly on moist (mean annual precipitation 900 to 1,500 mm) and cold sites (mean annual temperature 9 to 14°C), at high elevations (2,800 to 3,500 m), mostly along the central-Mexico Trans-Mexican Volcanic Belt, an East–West mountain range between 19° and 20° north latitude, with the highest volcanoes in México (De Rzedowski and Rzedowski, 2005; Benavides-Meza et al., 2011; Sáenz-Romero et al., 2012; Gómez-Pineda et al., 2020). It is a shade-tolerant species, found mainly on northern aspects and in deep soils (Sanchez-Velasquez et al., 1991; Rzedowski, 2006). A map of its contemporary suitable habitat and locations of the natural populations identified in the Mexican National Forest Inventory is available in Sáenz-Romero et al. (2012).

High elevation (3,000 to 3,500 m), pure, and dense stands of *Abies religiosa* within the Monarch Butterfly Biosphere Reserve (MBBR; with an area of 56,259 ha) in central Mexico (see Figure 1) act as an over-wintering host for migratory populations of the Monarch butterfly (*Danaus plexippus*) from November to March each year. The Monarch butterfly migratory populations overwinter exclusively on the crowns and stems of large, mature, *A. religiosa* trees, historically inside of the MBBR, because the dense crown of this species protects the butterfly from extreme temperatures and precipitation (Anderson and Brower, 1996). Rain followed by freezing temperatures in thinned stands of *A. religiosa* sites has been associated with significant Monarch mortality events, suggesting the need for fully occupied stands to protect migratory overwintering colonies.

The size of the Monarch butterfly migratory populations has been decreasing, with the winter 2023–2024 population count being the second lowest in history (Comisión Nacional de Áreas Naturales Protegidas, 2024). Migratory populations were recently identified as endangered on the IUCN list (Walker et al., 2022), despite the MBBR being an example of relatively successful (at least in the Mexican socio-ecological context) *in situ* conservation, having almost completely stopped illegal logging while developing controlled ecotourism (Rendón-Salinas et al., 2023).

Climatic niche modeling under future climate change scenarios suggests that the suitable climatic habitat for *A. religiosa* inside the MBBR will move upward in elevation, before disappearing entirely by the end of the century (Sáenz-Romero et al., 2012). Loss of climatic niche is exacerbated by increased bark beetle outbreaks in *A. religiosa* stands (Gómez-Pineda et al., 2023) linked to drought stress (Sáenz-Romero et al., 2023). Unfortunately, such projected decoupling between the sites occupied by native *A. religiosa* populations and locations where their suitable climate will occur is associated with extreme drought stress, particularly at the xeric limit (low altitude) of the contemporary natural range distribution. Dendrochronological analysis and recent measurements using the Normalized Difference Vegetation Index (NDVI), indicate that *A. religiosa* stands are highly dependent on winter–spring precipitation (Vivar-Vivar et al., 2021) and very sensitive to drought stress. This appraisal seems to be confirmed by recent field observations of rapid defoliation and decay of natural stands due to the now warmer and drier springs (Flores-Nieves et al., 2011; Sáenz-Romero et al., 2012). Also, induced drought stress experiments on *A. religiosa* provenances in nursery and common garden tests, suggest that genetic differentiation among populations for drought tolerance is not statistically significant (Cruzado-Vargas, 2017; Zamora-Sánchez, 2019).

The projected disappearance of the suitable climatic habitat of *A. religiosa* due to climate change (a predicted loss of 96.5% of its suitable climatic habitat nationwide by the end of the century; Sáenz-Romero et al., 2012) is not a problem exclusive to this species. It is a trait shared by many high-elevation forest tree species, for which their proximity to their respective mountain summits represents a risk of population extirpation, as natural migration to higher elevations might not be an option. Such is the case for the Mexican timberline species *Pinus hartwegii* (Gómez-Pineda et al., 2020), the western United States and Canada timberline species *Pinus albicaulis* (McLane and Aitken, 2012), the highly endangered *Picea mexicana* and *Picea martinezii* (Ledig et al., 2010; Mendoza-Maya et al., 2022), among several other North America forest tree species (Seliger et al., 2021).

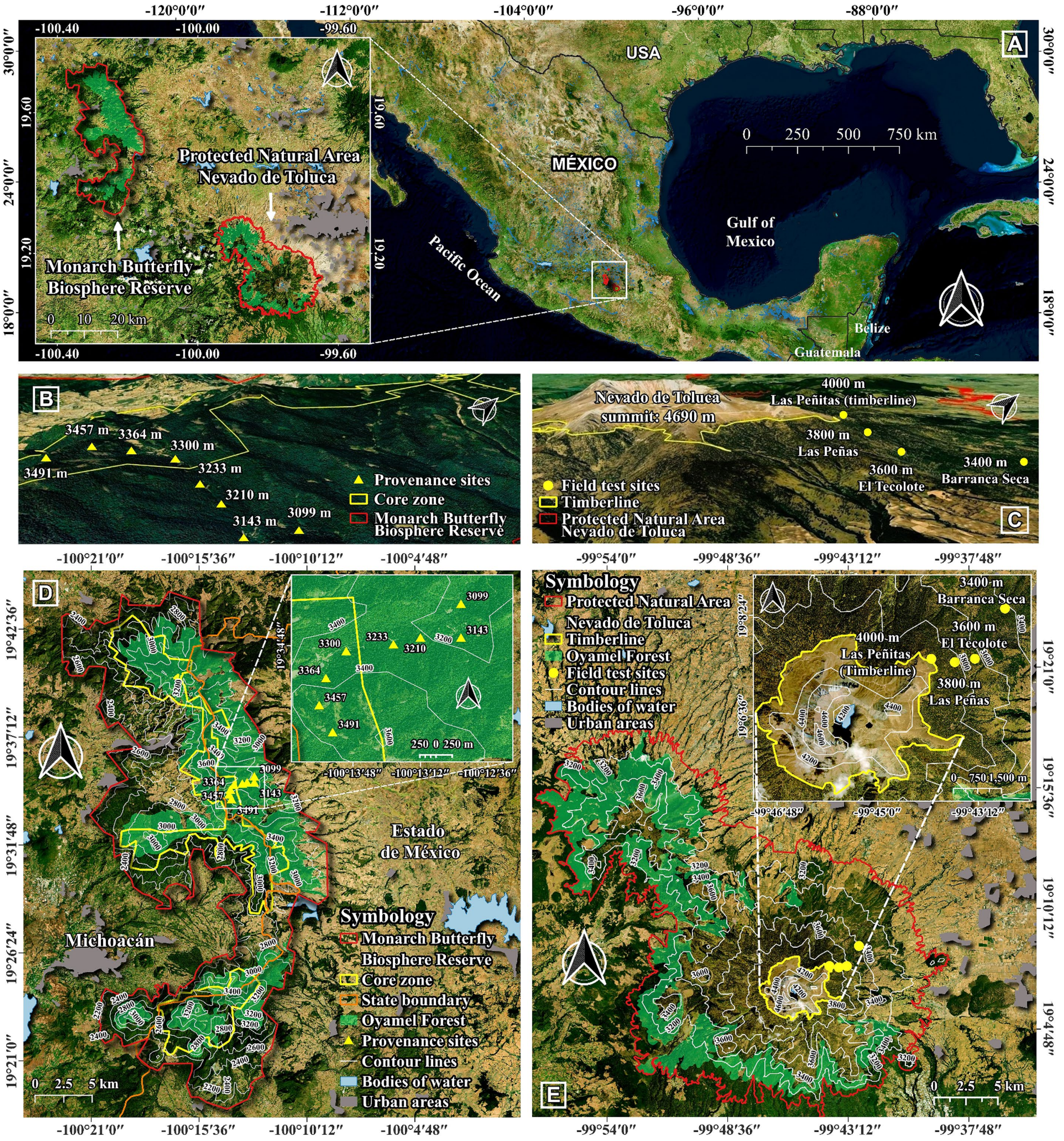

FIGURE 1
(A) Geographic location of the Monarch Butterfly Biosphere Reserve (MBBR) where *A. religiosa* is found, and the Protected Natural Area Nevado de Toluca where the provenance trials were established, in central Mexico. In the left inserted panel, Protected Area limits are indicated with a red contour line. **(B–E)** The core zones of both Protected Natural Areas (coincidental with the timberline at Nevado de Toluca) are indicated with yellow contour lines. **(B,D)** Provenance locations and elevations along an elevational transect in the MBBR (yellow triangles), where seed was collected. **(C,E)** Provenance test site locations (yellow circle symbols) and elevations in the Nevado de Toluca Protected Natural Area, including at the timberline (4,000 m elevation). **(D,E)** Actual distribution of *Abies religiosa* (layer colored in light green) based on Comisión Nacional Forestal (2018). Note that *A. religiosa* is absent above approximately 3,500 m **(E)**.

High-elevation and tree-line tree species are not alone in being challenged to find suitable habitats at elevations higher than their upper elevation range limit. Rare microendemic alpine plant species found above the timberline—*Arenaria bryoides*, *Chionolaena lavandulifolia*, *Castilleja tolucensis*, *Draba nivicola*, and *Plantago tolucensis*—are also expected to lose significant proportions or their entire realized niche due to lack of habitat at higher elevations as climate warms (Ramírez-Amezcua et al., 2016).

Under such grim future scenarios, forest management must adapt. *In situ* conservation measures are insufficient. Pro-active *ex situ* conservation is urgently required, including exploring the establishment of stands of *Abies religiosa* at locations above its upper elevation limit in the Mexican Transvolcanic Belt (MTVB) to recouple the species with its historic climate. Movement of the species beyond its current natural distribution is referred to as "assisted range expansion," one form of assisted migration of the forest – the intentional establishment of forest plantations with seed sources (provenances) from climates slightly warmer than that of the planting site to help maintain forest productivity, health, and ecosystem services in the face of rapid climate change (Winder et al., 2011).

Recoupling could be achieved by planting seedlings grown from seeds taken from the MBBR in locations where MBBR-like climates are expected to occur in the near future (Sáenz-Romero et al., 2016; Richardson et al., 2024). Assisted migration is used throughout British Columbia, Canada (O'Neill et al., 2017) and is proposed as an effective conservation measure for endangered timberline species such as *Pinus albicaulis* (McLane and Aitken, 2012; Sáenz-Romero et al., 2021) or the extremely rare *Picea mexicana* (Ledig et al., 2010; Mendoza-Maya et al., 2022).

The success of assisted migration efforts can be significantly impacted by the magnitude of climatic distance that the populations are moved (i.e., by the migration distance: the difference between the site climate minus the seed source climate): short migration distances may be ineffective, while long migration distances may result in early mortality due to frost damage. Selection of suitable migration distances can be achieved by establishing plantations with populations whose historic climate matches that of the plantation climate expected at some future date (O'Neill and Degner, 2024). However, the lack of empirical evidence of optimum future plantation climate and historic population climate represents a knowledge gap in assisted migration initiatives. Field tests, particularly, those with elevational reciprocal transplants, may provide insight into this issue.

The mountain summits within the MBBR are approximately coincidental with the upper elevation of the natural distribution of *A. religiosa*. It is therefore necessary to establish the species outside the MBBR. Even if such an enterprise were to succeed, there is no guarantee that the Monarch butterfly migratory population would overwinter in the new host plantation sites. This is due to an astonishing phenomenon: the descendants of a fourth generation of the monarchs that stayed in Mexican overwintering sites can return to approximately the same sites every winter. However, we consider inaction not to be an option and prefer to explore novel adaptive forest management options that could offer an opportunity for the survival of the migratory Monarch butterfly populations under future climates. Although the challenges associated with *A. religiosa* establishment are well known, recent evidence suggests that planting under the shade of a nurse shrub can significantly increase the probability of survival (Carbajal-Navarro et al., 2019).

The objective of this study was to assess the ability of *Abies religiosa* to establish and grow at elevations higher than its upper elevation natural range limit outside the MBBR. We hypothesize that acceptable seedling survival and growth rate of *A. religiosa* populations can be achieved in locations higher (and thus colder) than the species' current upper elevation distribution limit. We therefore initiated a species trial of *A. religiosa* using populations from disparate seed source elevations within the MBBR and planted them under nurse shrubs at locations outside the MBBR and at elevations higher than the natural range limit of the species.

2 Materials and methods

2.1 Seed sources

Cones were collected in December 2017 from eight stands of *A. religiosa*, at 50 m intervals along an elevation transect from 3,100 to 3,500 m within the MBBR (Table 1). In each stand, cones were collected from 10 randomly selected open-pollinated mother trees located at least 30 m apart to reduce the possibility of inbreeding.

We use the term 'population' to represent the genotypes represented by these stand samples and 'provenance' to refer to the geographic origin of the populations. However, in the tree breeding domain, populations and provenances are sometimes used interchangeably.

2.2 Seedling production

After exposing the cones to sunlight, seeds were extracted manually and stratified at 4°C for 14 days. Equal numbers of seeds from each of the 10 mother trees were bulked to form each seed lot (population). Seedlings were grown for 2 years in a shade-house (35% shade mesh) in 380 cm^3 rigid containers at the Instituto de Investigaciones sobre los Recursos Naturales (INIRENA), in Morelia (1900 m), Michoacán, Mexico. (Additional seedling production details in Cruzado-Vargas et al., 2021). Seedlings were then transplanted to larger rigid containers (1,000 mL) and transferred to a communal nursery at 3000 m at the Ejido La Mesa, San José del Rincón, Estado de México, near the MBBR where they remained for 1 year to harden before planting.

2.3 Test sites and experimental design

The populations were planted at four field provenance test sites along an elevational gradient on the northeast slope of Nevado de Toluca, an extinct volcano and Protected Natural Area (officially named Flora and Fauna Protection Area Nevado de Toluca), in July 2021 at the start of the rainy season. The test site location was selected because it is the closest mountain to the MBBR with a summit (4,680 m) substantially higher than the *Abies religiosa* upper elevation limit in the MBBR (3,550 m) and because *Abies religiosa* is found most frequently on the same aspect. Furthermore, we chose to situate the provenance test sites within a forest owned by the indigenous community of Calimaya, of the Matlatzincas ethnic group, due to their exceptional forest management. Experience has shown that collaboration with local communities provides site surveillance, capitalizes on traditional ecological knowledge, and engages participants in a way that leads to more effective outcomes, such as the eventual adoption of novel forest management practices.

The four test sites were located at the following elevations: (a) a reference site at 3400 m, an elevation close to that of the upper natural distribution of *A. religiosa* populations at both Nevado de Toluca and the MBBR; (b) 3,600 m, located just above the upper elevation limit of *A. religiosa*, which is around 3,550 m; (c) 3,800 m, to test the feasibility of a significant upward shift beyond the natural upper limit of *A. religiosa*. This shift of about 300 m upward in elevation could compensate for a mean annual temperature increase of 1.5°C, considering the lapse rate of -0.5°C for each 100 m increase in elevation (Sáenz-Romero et al., 2010); and (d) 4,000 m (at the timberline), to test at an extreme cold site to identify the upper elevation limit of the species' fundamental niche. At all four sites, the surrounding forest is dominated by *Pinus hartwegii*, although the site at 3400 m also strongly features *Alnus jorullensis*. More detail of the test site locations is presented in Table 1 and Figure 1.

TABLE 1 Geographic coordinates, elevation, mean annual temperature (MAT), mean annual precipitation (MAP), and annual dryness index (ADI) of *Abies religiosa* provenances and test sites.

Code	Elevation (m)	Lat. N	Long. W	MAT (°C)	MAP (mm)	ADI ($\sqrt{^\circ C}mm^{-1}$)
Provenances from Monarch Butterfly Biosphere Reserve						
2	3,491	19.567	−100.233	8.8	1,094	0.035
3	3,457	19.571	−100.235	9.0	1,089	0.036
5	3,364	19.575	−100.234	9.5	1,065	0.039
6	3,300	19.579	−100.231	9.9	1,048	0.041
7	3,233	19.580	−100.224	10.2	1,029	0.043
8	3,210	19.581	−100.220	10.3	1,022	0.044
9	3,143	19.581	−100.214	10.6	1,001	0.046
10	3,099	19.586	−100.214	10.8	987	0.047
Field test sites at Nevado de Toluca						
Las Peñitas	4,000	19.126	−99.734	5.5	991	0.026
Las Peñas	3,800	19.125	−99.727	6.5	1,012	0.030
El Tecolote	3,600	19.127	−99.721	6.9	1,054	0.031
Barranca Seca	3,400	19.142	−99.712	8.1	1,038	0.035

The climate of the provenances is the average of the reference period 1961–1990, while the climate of the test sites is the average of the period in which the seedlings were growing (2021–2023). The climatic values are only presented here to characterize the provenances and planting sites; climatic variables used in the analysis are as in Table 2.

TABLE 2 Climatic variables estimated for each provenance and for each test site, and climatic transfer distance variables retained as candidate variables for the analysis with the final mixed model.

Code	Unit	Definition
Climatic variables for provenances and test sites		
MAT	°C	Mean annual temperature
MAP	mm	Mean annual precipitation
GSP	mm	Growing season precipitation (total precipitation from April–September)
MTCM	°C	Mean temperature in the coldest month
MMIN	°C	Mean minimum temperature in the coldest month
MTWM	°C	Mean temperature in the warmest month
MMAX	°C	Mean maximum temperature in the warmest month
DD5	°C	Degree-days >5°C
ADI	$\sqrt{^\circ C}mm^{-1}$	Annual dryness index ($\sqrt{DD5}$ / MAP)
Climatic transfer distance variables retained for the analysis		
MAT_{Transfer}	°C	$MAT_{\text{Test Site}} - MAT_{\text{Provenance}}$
$MTCM_{\text{Transfer}}$	°C	$MTCM_{\text{Test Site}} - MTCM_{\text{Provenance}}$
$MTWM_{\text{Transfer}}$	°C	$MTWM_{\text{Test Site}} - MWCM_{\text{Provenance}}$
$MMAX_{\text{Transfer}}$	°C	$MMAX_{\text{Test Site}} - MMAX_{\text{Provenance}}$
ADI_{Transfer}	$\sqrt{^\circ C}mm^{-1}$	$ADI_{\text{Test Site}} - ADI_{\text{Provenance}}$

The experimental design consisted of eight populations planted at each of the four test sites in a randomized complete block design with 30 blocks per site, and a single seedling per population per block. Due to insufficient numbers of seedlings, only 5, 7, and 5 populations were planted at the 3,400, 3,600, and 4,000 m sites, respectively. Thus, we gave priority to the site at 3800 m located 300 m higher than the species' upper elevation limit (equivalent to a coldward shift of approximately 1.5°C in mean annual temperature) where we planted 30 blocks in each site, except at the 4,000 m site, where we planted only 16 blocks. Where a population was absent in an incomplete block, it was replaced by a surplus seedling of another population to ensure that all blocks contained eight seedlings (except for site at 4000 m, where blocks had five seedlings).

To enable trial seedlings to be shaded, shrubs with crowns large enough to provide shade to all eight seedlings were identified. Seedlings were planted in a circle around the main stem, 50 cm from the stem (Figure 2), based on a previous positive experience of using pre-existing shrubs as nurse plants (see Carbajal-Navarro et al., 2019). The 30 blocks at each test site were positioned in a non-contiguous manner since the nurse plants were distributed in an irregular pattern. At the 3,400, 3,600, and 3,800 m sites, the dominant shrub available, *Senecio cinerarioides*, was used as the nurse plant. At the 4,000 m site, where *S. cinerarioides* was nearly absent, the dominant shrub, *Lupinus montanus*, and in a few cases small *P. hartwegii* trees, were used as nurse plants.

2.4 Field measurements

Seedling height (HT) and survival (SURV) were assessed bimonthly (from September 2021) during the growing season and basal diameter was recorded every 6 months. Final measurements were taken in December 2023 at the end of the third field growth season, nearly 6 years after sowing. Plant height was measured to ±1 mm from ground level to the tip of the apical bud. Basal diameter (DIAM; also known as root-collar diameter) was measured at the base of the stem with a digital vernier (KNOVA®, Cupertino, CA, United States) to ±0.1 mm.

Seedling height increment (HTincr) was obtained by subtracting the first measurement from the final measurement. Aerial biomass

FIGURE 2
Abies religiosa seedlings planted in a circle consisting of eight seedlings (one seedling per population) under the shade of pre-existing shrubs (*Senecio cinerarioides*), with the latter serving as a protective nurse plant. The group of eight *A. religiosa* seedlings constitute a block. **(A)** *A. religiosa* seedlings just after planting at the 3,800 m test site. **(B)** *A. religiosa* seedlings at the 3,400 m test site 2 years after planting.

(BIOMASS) of each tree was estimated from final HT and DIAM using a relationship developed through destructive sampling of seedlings of the populations used in the current project (Equation 1; Cruzado-Vargas et al., 2021):

$$\text{BIOMASS} = 1.62490 + \left(0.03538^{*}\ \text{HT}\right) + \left(0.77238^{*}\ \text{DIAM}\right) \quad (1)$$

Where: BIOMASS is the aerial dry biomass (g), HT is the total seedling height (cm), and DIAM is the basal diameter (mm).

As SURV was scored as a binary trait, and blocks contained (in general) a single seedling per population, mean SURV was calculated as proportion of seedlings alive per population per site; consequently, the term 'block' was omitted from the model when analyzing SURV.

As the primary goal of this initiative is conservation, not timber production, we considered survival to be the most important response variable. However, seedling height and aerial biomass (the latter often reflects the growth capacity when considering the abundance of foliage) were also recorded since competition of seedlings with grasses and shrubs at high elevation can eventually compromise success.

2.5 Climate data

Climate data of the seed provenances were obtained for the reference period (1961–1990, i.e., the recent historic climate) from climate spline models (Rehfeldt, 2006; Rehfeldt et al., 2006; Sáenz-Romero et al., 2010; Crookston and Rehfeldt, 2024).[1] The recent historic climate of the provenances is considered the climate to which the populations have evolved and are adapted (Sáenz-Romero et al., 2015).

The climate experienced by the seedlings while in the field (2021–2023) was used to represent the test site climate. Two HOBO data loggers located at each site (Onset Computer Corporation®, Bourne, MA, United States) recorded ambient temperature every 30 min. Monthly precipitation was measured by capturing rainwater in two rainwater traps per site (20 L buried containers with an exterior funnel). The two temperature and precipitation observations at each site were averaged and monthly mean (maximum, average, and minimum) temperatures as well as precipitation were calculated and used to derive nine climatic variables of relevance to plant growth (Rehfeldt et al., 2006; Table 2).

To estimate the impact of a climatic transfer distance on seedling growth and survival, future climatic values were obtained using an ensemble of global climate models with an intermediate level of climate forcing (6.0 Watts/m^3) in https://charcoal2.cnre.vt.edu/climate/ (Crookston and Rehfeldt, 2024).

2.6 Statistical analysis

For each population at each test site, transfer distances (site minus provenance) were calculated for each of the nine climatic variables (the ones from Table 2). Data from the four test sites were pooled and transfer functions relating transfer distances to each derived response trait (HTincr, BIOMASS and SURV) were then developed with a quadratic function to assess the effect of the climatic or elevational transfer.

A mixed model was used in Procedure Mixed of SAS Institute (2014) to account for both the random design and fixed climatic factors (Cruzado-Vargas et al., 2021). The fixed effects considered

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[1] Available at https://charcoal2.cnre.vt.edu/climate/

three components of the effect of climate as a selective force that produces genetic differentiation among populations, or phenotypic plasticity (also considered genotype × environment interaction; Sáenz-Romero et al., 2017): the climate of the provenance (C); the climatic transfer distance (T), and the interaction between the climate of the provenance and climatic transfer distance (C * T). Random effects include factors associated with the experimental design: site, population, block, and the interaction between the site and the population. Details regarding the rationale behind this model are described in Leites et al. (2012a), Leites et al. (2012b), and Sáenz-Romero et al. (2017).

The following mixed model (Equation 2) was initially fitted with the data from all four sites:

$$Y_{ijkl} = \mu + \beta_0 + \beta_1 \mathrm{T_{ij}} + \beta_2 \mathrm{T_{ij}^2} + \beta_3 \mathrm{C_j} + \beta_4 \left(\mathrm{T_{ij}xC_j}\right) + \beta_5 S_i + \beta_6 P_j + \beta_7 B_k\left(S_i\right) + \beta_8\left(S_i \mathrm{x} P_j\right) + e_{ijkl} \tag{2}$$

where Y_{ijkl} is the value of the response variable corresponding to the l^{th} tree for the j^{th} provenance in the k^{th} block in the i^{th} test site. β_0 is the intercept. $\mathrm{T_{ij}}$ is the climatic transfer distance of the j^{th} provenance at the i^{th} test site. $\mathrm{C_j}$ is the value of the climatic variable of the j^{th} provenance. $\mathrm{T_{ij}} * \mathrm{C_j}$ is the interaction between the climatic transfer distance for the j^{th} provenance at the i^{th} test site and the climatic variable of the j^{th} provenance. S_i is the effect of the i^{th} test site; P_j is the effect of the j^{th} provenance; $B_k\left(S_i\right)$ is the effect of the k^{th} block nested within the i^{th} test site; and e_{ijkl} is the error term.

Before developing the full model above, nine reduced models (one for each climatic transfer distance variable) were developed for each response trait (HTincr, BIOMASS, and SURV) to identify the most influential climatic transfer distance variables for use in selecting the strongest full model (Leites et al., 2012a; Sáenz-Romero et al., 2017). The reduced model omitted the terms for C_j and $\mathrm{T_{ij}} * \mathrm{C_j}$ from the full model. For each response variable, the five climatic transfer distance variables with the lowest Akaike Information Criterion (AIC) value were identified and included in the subsequent full models. Models that produced a positive quadratic term coefficient (β_2) were omitted to ensure the biological validity of the models (Rehfeldt et al., 2001; Leites et al., 2012a).

Subsequently, for each response variable, 9 × 5 = 45 full "competing" models were run, which included all possible combinations of the nine provenance climatic variables (those listed in Table 2) and the five climatic transfer distance variables selected in the previous step [after selecting the best climatic transfer distance variables with the reduced model (the model without climate of the provenance explained above); also enlisted in Table 2]. For each response variable, the best model was selected based on AIC value (the smallest the AIC the better) and the significance of the climatic variables (with a F tests, using the option "Solution" of Procedure Mixed; SAS Institute, 2014).

After selecting the best full model for each response variable, we dropped non-significant terms. We then ran all the competing models again to confirm that the final model with non-significant terms removed remained superior to the competing models. Thus, the final model was simplified, retaining only the climate of the provenance and climatic transfer distance as fixed terms, as well as their interaction (Equation 3):

$$Y_{ijkl} = \mu + \beta_0 + \beta_1 \mathrm{T_{ij}} + \beta_2 \mathrm{C_j} + \beta_3\left(\mathrm{T_{ij}xC_j}\right) + \beta_4 S_i + \beta_5 B_k\left(S_i\right) + e_{ijkl} \tag{3}$$

Fitted curves were estimated for each response variable from regression parameter coefficients to visualize the effect of climatic transfer distance and seed source climate on the responses. Finally, the impact of using assisted migration (i.e., the migration distance or climatic transfer distance) on each response variable was estimated by substituting the migration distance and seed source climate into the final fitted equation. To balance the need for adaptation at the time of plantation establishment and at plantation maturity, the migration distance used in these calculations considered the decade centered on the year 2060 as the date to which we expect the plantation climate to match the seed source historic climate (1961–1990). Furthermore, by 2060, the trees would be around 40 years old (from germination), likely providing a minimum acceptable crown size for the overwintering Monarch butterfly. Impacts were expressed relative to the height increment or aerial biomass expected at the zero transfer distance, or at a site with 100% expected survival (projected by the fitted model).

3 Results

Annual Dryness Index (ADI) emerged as the transfer distance variable that produced the strongest final full model for HTincr ($p = 0.0064$) and BIOMASS ($p = 0.0595$; Table 3). Although ADI was not significant (at the $p > 0.05$ level) as a climatic transfer distance term for SURV ($p = 0.4327$), it was still the variable that yielded the best fit in the full model (Table 3).

The fitted climatic transfer curves indicated that seedling performance decreases as transfer distance increases. Specifically, HTincr, SURV, and BIOMASS decreased as the populations were transferred to colder (higher elevation) environments (Figure 3). Although the quadratic response curve had a slightly stronger fit than a linear regression model, we dropped the quadratic term because it was not significant in analyses involving any the climatic variables fitted to the three response variables examined ($p > 0.05$). Thus, the final model was simplified, retaining only the climate of the provenance and climatic transfer distance as fixed terms, as well as their interaction (Equation 3).

Of the competing models, mean minimum temperature in the coldest month (MMIN) was the seed source climatic variable that accounted for the most variation in both HTincr ($p < 0.0001$) and BIOMASS ($p = 0.0023$) in the final model, while ADI was the seed source climatic variable that accounted for the most variation in the final model for SURV ($p = 0.0094$; Table 3). The random term 'population' (resulting from non-climatic factors) was not significant ($p > 0.05$) for any response variable and was therefore dropped from the final model. In contrast, block was significant for all response variables except SURV, for which the term was absent.

Population responses to climatic transfer were relatively weak within each site (Figure 3). In contrast, site climate had a strong effect on the responses, and was the main factor shaping the overall trend of the results, as illustrated in a scatterplot of test site mean annual temperature (MAT) versus population HTincr means at each site (R^2 adjusted = 0.88; $p < 0.0001$; Figure 4). Notably, at the 4,000 m elevation site, the average HTincr approached zero and numerous seedlings

TABLE 3 Mixed model analysis [using the terms of the final model (Equation 3)] for increment in seedling height, aerial biomass, and survival.

Parameter or source of variation	Height increment	Aerial biomass	Survival
Akaike Inf. Criterion (AIC)	6279.1	2110.6	−72.1
Δ AIC*	22.6	0.7	21.4

Fixed effects	Estimate	*p*-value	Estimate	*p*-value	Estimate	*p*-value
Intercept	−188.32	0.1047	1.85	0.3023	−1.35	0.1555
Climate at seed source						
Mean minimum temperature in the coldest month (MMIN)	213.36	<0.0001	2.43	0.0023	–	–
Annual dryness index (ADI)	–	–	–	–	63.23	0.0094
Climatic transfer distance						
Annual dryness index (ADI)	31,530	0.0064	396.61	0.0595	34.60	0.4327
Interaction Climatic at seed source x climatic transfer distance	−33304.6	0.3299	−52.63	0.3843	551.40	0.5701

Random effects	Variance	%	*p*-value	Variance	%	*p*-value	Variance	%	*p*-value
Site	823.35	6.3	0.2378	0.34	8.3	0.1939	0.012	70.6	0.1744
Block (Site)	2121.08	16.1	0.0002	0.59	14.4	0.0007	–	–	–
Error	10,210	77.6	–	3.17	77.3	–	0.005	29.4	–

*Difference between the AIC value of the selected best (shown here) and second best models. Akaike Information Criterion [AIC; Akaike, 1973], estimated parameters, contribution to total variance (of random terms only), and significance for the best full mixed model for each trait (approximately 2.5 years after planting; 6 years after germination). Note that the climatic variables for the provenances differ for some traits (those resulting from the selection of the best climatic variables for each trait among the 45 "competing" models analyzed).

displayed frost damage. In contrast, at the 3,400 m site, HTincr was large and no frost damage was observed (Figures 3A, 4).

The ADI of the seed sources is expected to increase by 0.009 $\sqrt{^{\circ}C}mm^{-1}$ (a warmer and dryer climate) by 2060, relative to the historic (1961–1990) mean ADI. Therefore, to ensure that planted *A. religiosa* populations will experience their historic ADI in 2060, it is necessary to establish plantations on sites that currently have an ADI that is 0.009 units smaller (colder and moister) than the historic climates of the seed sources. In other words, planted seedlings should originate from provenances that are slightly warmer and dryer than the plantation sites. Such a climatic transfer distance would result in seedlings with approximately 54% slower growth rate (Figure 3A), 27% less aerial biomass (Figure 3B), or 27% lower survival compared to that expected in a population at zero climatic transfer distance (Figure 3C).

To translate these results to a more intuitive climatic variable, the response to the assisted migration is more easily appreciated when plotting the response variables against MAT transfer distance (Figure 5). When establishing plantations with seed sources from climates 2.3°C in MAT warmer than the plantation site to compensate for warming between the reference period (1961–1990) and the climate matching the target date (2060), the projected loss is 47% in HTincr (Figure 5A) and 21% in SURV (Figure 5B).

Our fitted elevation transfer functions suggested that a 500 m upward elevation transfer would yield seedlings having a HTincr that is half that of a local seed source (R^2 adjusted = 0.65; $p < 0.0001$; Figure 6).

Only two populations (those from 3,457 m and 3,491 m; Table 1) were moved downward in elevation at the 3,400 m test site (Figure 6). Despite being moved downward by only 60 m, these populations showed a -1.0 MAT transfer distance (Figure 5), suggesting that Nevado de Toluca is slightly colder than the MBBR at the same elevation (see Table 1).

4 Discussion

4.1 Relevance of climatic transfer distance variables

The annual aridity index (ADI), reflecting both annual degree day heat sums and annual precipitation, was the climatic variable that most strongly governs the impact of seed transfer or climate change on the growth (seedling height and aerial biomass) and survival of *Abies religiosa* populations. It was also the climatic variable selected to delineate and match contemporary and future climate seed zones for Mexico (Castellanos-Acuña et al., 2018) and proved to be a critical climatic variable governing the response of *Quercus petraea* provenances in large multi-site provenance tests (Sáenz-Romero et al., 2017).

The mean minimum temperature of the coldest month (MMIN) was identified as the seed source climatic variable that best accounted for variation in response traits, thus corroborating studies in more controlled provenance test environments (Ortiz-Bibian et al., 2017). Nevertheless, the impact of the colder temperatures at the test sites at Nevado de Toluca appeared to override the expression of genetic differentiation among populations.

The lack of significance of population and site as random variables in the full model could be the result of most of the response trait variation being accounted for by the fixed terms related to seed source climate and climatic transfer distance (Table 3). Thus, the

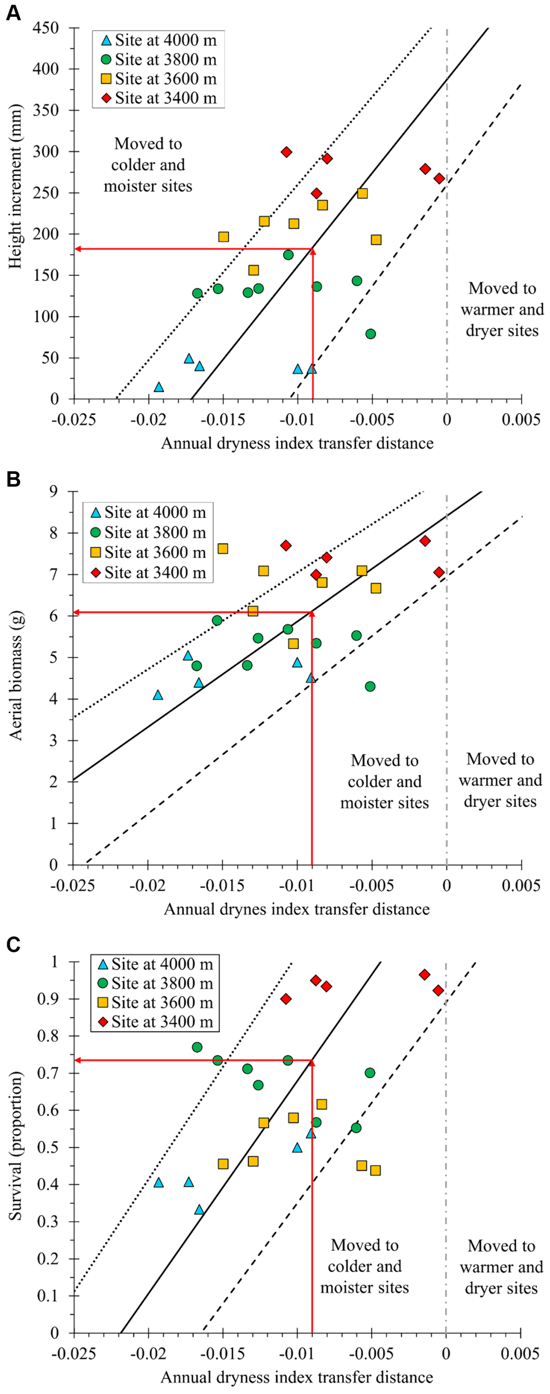

FIGURE 3
Observed response of increment in seedling height **(A)**, aerial biomass **(B)**, and survival proportion **(C)** to the transfer distance for Annual Dryness Index (ADI). On the *X*-axis, more negative values signify moving the seed sources toward colder and moister sites, while a value of zero (vertical gray dashed line) indicates transfer to a test site with a climate similar to that of the seed source (the provenance). Symbols are averages per population per site. Predicted response curves were constructed using the parameters of the fixed terms after fitting the best mixed model (Table 3). The solid curve was estimated using the average climate at the seed sources; the dashed line used the climate of the coldest provenance and the dotted line used that of the warmest provenance. Red arrows indicate the impact on the response variable when the transfer distance is 0.009 $\sqrt{}$°Cmm^{-1} ADI transfer difference, the value required to compensate for the amount of climate change expected by year 2060 at the seed source locations.

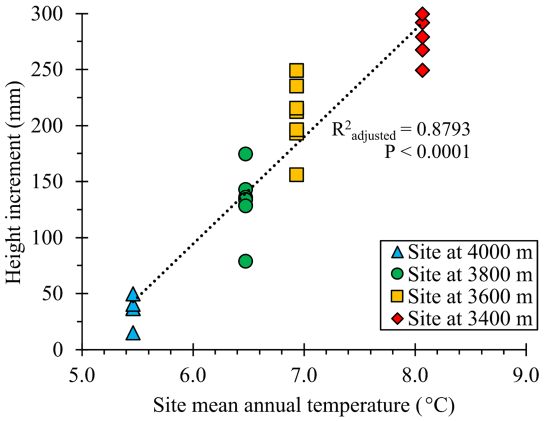

FIGURE 4
Regression of population mean height increment at each test site as a function of test site mean annual temperature (MAT, °C; average 2021–2023). The number of populations tested at the 3,400, 3,600, 3,800, and 4,000 m test sites were 5, 7, 8, and 5, respectively.

selective force of climate to shape genetic differentiation among populations, and the response of these populations at different sites, appears to be more important than gene flow, demographic history, colonization events, or non-climatic factors of the site, including soil edaphics or topography. However, with only four test sites, and only a single test site at each elevation, site climatic and non-climatic (such as soil fertility, drainage, or aspect) factors are confounded. Thus, it would be advisable to establish future assisted migration experiments with more than one site at each elevation.

4.2 Implications for forest management

Our findings suggest that the establishment of *A. religiosa* under pre-existing nurse shrubs is feasible above its upper elevation distribution limit (at sites as high as 3,800 m) and outside its geographic range. Coldward transfer to planting sites with an MAT that is 2.3°C colder than the seed source climate, is required to match seed source historic climates with plantation climates projected for 2060 in central Mexico, and is within the range of 2 to 3°C MAT transfer distance suggested by other assisted migration field experiments (Castellanos-Acuña et al., 2015; St Clair et al., 2020; Cruzado-Vargas et al., 2021; Sáenz-Romero et al., 2021). These findings provide a new opportunity to mitigate climate change impacts on *A. religiosa* and its dependent organism – the Monarch butterfly. As the climate continues to warm, the migration distance required to match the historic climate of seed sources with plantation future climate will increase. Consequently, seed transfer systems developed to implement assisted migration will need to be modified periodically.

In practice, the climatic transfer value selected will depend on how stakeholders and conservation agencies perceive the risk of plantation failure (from over-transfer) versus that of local extirpation (from under-transfer); where local extirpation of the species is anticipated, as is the case with *Abies religiosa*, up to 47% loss of growth and 21% of loss in survival (impacts expected with 500 m upward elevation transfer) may be perceived as acceptable by stakeholders and conservation agencies.

In our view, the most critical response variable is seedling survival, and a survival rate of 78.6% when transferring to sites 2.3°C colder

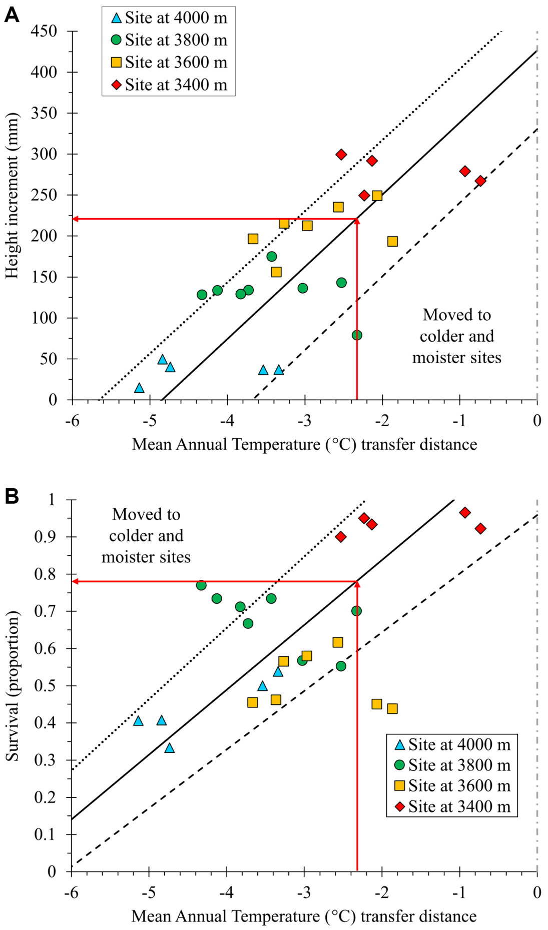

FIGURE 5
Transfer function relating height increment **(A)** and survival **(B)** of *Abies religiosa* populations to mean annual temperature (MAT, °C) climatic transfer distance. Negative transfer values indicate seed source movement toward colder sites (higher altitudes). A transfer distance of zero indicates transfer to a test site with a climate similar to that of the seed source (dashed gray vertical line). Predicted relationships were constructed using the parameters of the fixed terms of the final full model (Equation 3). Solid, dotted, and dashed curves were estimated using the mean, minimum, and maximum MAT of the seed source, respectively. Red arrows indicate the impact on the response variable when populations are transferred by 2.3°C MAT, the amount required to account for expected climatic change by year 2060 at the seed source locations.

can be considered very acceptable. Growth rate can also be important when there exists significant vegetative competition at the recipient site. However, as climate change progresses, the planting sites will become more favorable for the translocated populations and growth rates will improve in the future; in contrast, local native populations might be increasingly maladapted to the future warmer climate. Thus, what is absolutely critical for the translocated populations is to survive the cold climate in the early stages after plantation.

It appears feasible to establish *A. religiosa* at 3800 m on the Nevado de Toluca volcano. Above that elevation, mortality and especially loss of growth become pronounced. Such an appraisal needs to be considered in the context of the fact that Nevado de Toluca has a colder climate than the MBBR at the same elevations, as shown by the lack of populations presenting positive climatic transfer distances (Figure 5), even among the populations that were transferred to lower elevations (those that originating from above 3,400 m; Table 1).

Since *Senecio cinerarioides* has a very shallow crown, it would be desirable to test the feasibility of upward elevation transfer of other shrub species that have wide crowns. The pre-existing shrub *Baccharis conferta* has been used successfully as a nurse plant at lower elevations at the MBBR because it has a very dense crown that provides effective protection against an excess of insolation and extreme cold (Carbajal-Navarro et al., 2019). However, *B. conferta* is nearly absent at 3800 m and completely absent at 4000 m on Nevado de Toluca.

Even if the operational establishment of *A. religiosa* stands at elevations higher than the upper distribution limit of the species (3,550 m) were successful, there is no guarantee that Monarch butterfly migratory populations would shift their overwintering sites by around 75 km to the southeast. However, the fact that Nevado de Toluca, a historically marginal overwintering site (Pérez-Miranda et al., 2020), became the site with the largest Monarch butterfly colony during the 2023–2024 winter season (Comisión Nacional de Áreas Naturales Protegidas, 2024) is reassuring, particularly given that the new site was at a relatively high elevation (3,400 m) and the Nevado de Toluca sites are colder than sites at the same elevations in the MBBR. The migratory Monarch butterfly populations may now be seeking new overwintering sites with climates similar to the historic climate of their usual overwintering sites, which are becoming warmer.

Seedlings planted today would be approximately 40 years of age (from seed germination) by the year 2060 and should have a crown size acceptable for overwintering Monarch colonies, based on the observation that trees 50 years old are common on the overwintering stands (Sáenz-Ceja and Pérez-Salicrup, 2020; Sáenz-Ceja et al., 2022; Carlón-Allende et al., 2018). Obviously, this trial simply demonstrates the feasibility of establishing *Abies religiosa* at higher elevations and outside its current natural distribution. A much greater planting effort, including local participation by forest managers and securing of support resources, would be required to provide dense future stands that could serve as suitable overwintering sites. Thus, in this era of the Anthropocene, it may be possible to establish high-elevation *A. religiosa* stands that can successfully provide overwintering sites for migratory Monarch butterflies in the context of a warmer world.

It is extremely important to note that attempts to provide new colonization areas for the Monarch butterfly and efforts to conserve its current habitat are not mutually exclusive. The eventual establishment of future overwintering sites at higher elevations does not imply that efforts to maintain contemporary stands of *A. religiosa* would cease or diminish. Reforestation within the MBBR with seedlings originating from seeds collected at lower elevations and planted under the protective shade of nurse plants should continue for ecological restoration of sites perturbed by phytosanitary clear-cuts, forest fires, and illegal logging (Carbajal-Navarro et al., 2019) until climate change precludes such efforts. In other words, promoting healthy *A. religiosa* stands to be used by Monarch butterfly migratory populations, both inside and outside of the MBBR, should be parallel tasks of maximum priority.

5 Conclusion

We successfully established *A. religiosa* outside, and at higher elevations, than its current natural distribution limits using pre-existing shrubs as nurse plants. Survival of 68% across all populations at 3800 m, well beyond the natural *A. religiosa* upper limit

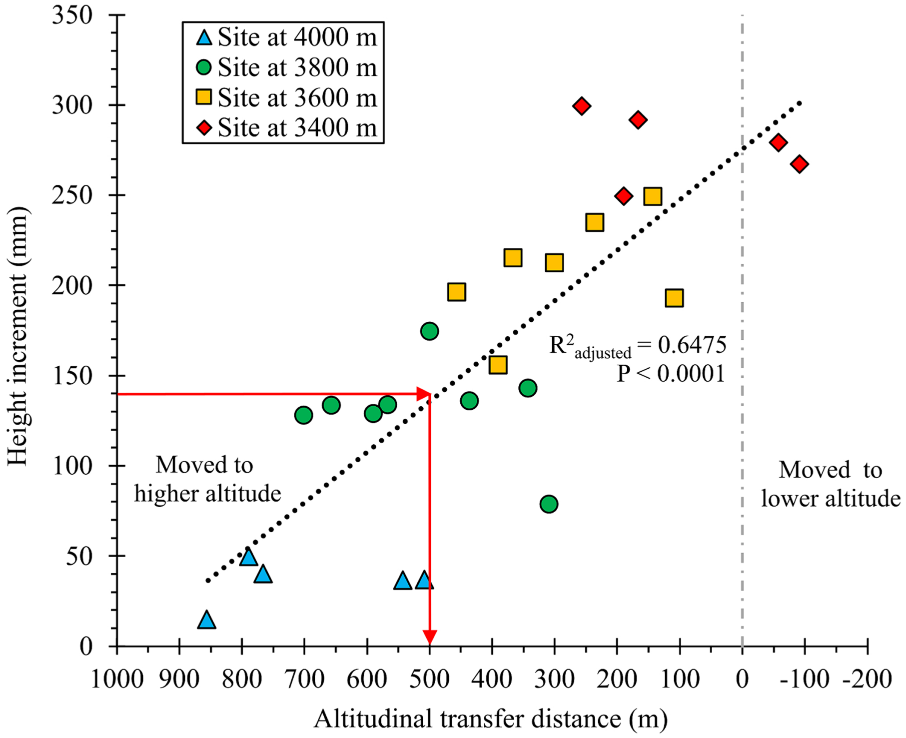

FIGURE 6
Transfer function relating height increment to elevation transfer distance for populations of *Abies religiosa* planted at four test sites. Red arrows indicate the maximum safe seed transfer distance – the elevational transfer associated with height increment that is 50% of the expected height increment of a local population. The number of populations tested at the sites at 3400, 3600, 3,800, and 4,000 m in elevation, were 5, 7, 8, and 5, respectively. The adjusted R^2 was estimated with a linear regression.

distribution of 3,550 m, is an encouraging result. To compensate for an expected warming of 2.3°C of Mean Annual Temperature by the decade centered in 2060 would require an upward shift in elevation of 500 m for each *A. religiosa* provenance, resulting in a survival of 71% and approximately half the growth rate compared to a zero climatic transfer distance. Thus, it may be possible and highly warranted to establish high-elevation *A. religiosa* stands to provide overwintering sites to host migratory Monarch butterflies in a future climate change scenario by the year 2060.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

CS-R: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing. VO-V: Data curation, Investigation, Writing – review & editing. PH-C: Conceptualization, Data curation, Investigation, Writing – review & editing. LP-C: Data curation, Investigation, Writing – review & editing. MJ-J: Data curation, Writing – review & editing, Investigation. AC-V: Data curation, Formal analysis, Investigation, Visualization, Writing – review & editing. GO'N: Formal analysis, Funding acquisition, Visualization, Writing – review & editing. AZ-C: Investigation, Writing – review & editing. GM-Q: Visualization, Investigation, Writing – review & editing. RL-C: Conceptualization, Funding acquisition, Writing – review & editing. AB-G: Conceptualization, Funding acquisition, Methodology, Writing – review & editing. ÁE-A: Conceptualization, Writing – review & editing. LL-T: Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Factors affecting early red oak (*Quercus rubra* L.) regeneration near its northern distribution limit in Quebec

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Red oak is an important species within the North American landscape, with climate change projections indicating a potential northward shift in its distribution. However, understanding the factors influencing its regeneration success at the northern limit remains limited. Site conditions and seed provenance adaptability may play critical roles. To bridge this knowledge gap, we conducted a seed transfer study in two northern red oak stands in Quebec. We firstly investigated stand regeneration history through dendrochronological characterization. Then, we monitored the survival and growth of saplings for four red oak provenances across a south-to-north gradient in field and greenhouse settings, with varying soil nutrient levels due to fertilization, and with or without protection from large herbivores. Results indicated that stands have similar age structures with red oak establishment coinciding with the last major fire disturbance in the early 1920s. However, tree species composition and density differed, suggesting differences in fire disturbance regime or ecological succession status prior to fire. Site had the largest influence on red oak regeneration, with the highest tree density and soil water availability site exhibiting a 29% higher survival rate. Protection against large herbivores also significantly impacted red oak seedling performance, leading to a 16% higher survival rate. Germination, survival and growth also significantly differed between provenances. The local (northernmost) provenance exhibited the poorest overall performance with 28 to 42% lower germination, survival and growth rates, while the two southernmost provenances exhibited superior germination and sprout survival. An increase in soil nutrient availability was beneficial to red oak in the greenhouse, but only marginally benefited survival and growth in the field, suggesting that this factor is of less importance than other factors (e.g., water and light availability) for red oak early regeneration. The findings of this study suggest that silvicultural efforts to favor red oak should focus on site and provenance selection, and that water availability is currently limiting red oak regeneration success at acorn and early seedling life stages (i.e., 1 year old seedlings) near its northern distribution limit.

KEYWORDS

red oak, natural regeneration, ecological factors, provenance, fire disturbance, distribution area, assisted migration

1 Introduction

Red oak (*Quercus rubra* L.) is native of North America and is characterized by a wide distribution, ranging from the upper midwestern United States (Minnesota) to the Canadian Maritimes (Nova Scotia) to the southeastern (Mississippi) and south-central (Oklahoma) states. Its establishment was mostly attributed to the warmer and dryer climate of the early Holocene (Abrams, 1992) and was also likely favored by First Nations and European settlements (Dey and Guyette, 2000; Munoz and Gajewski, 2010) and fire disturbance (Shumway et al., 2001; Brose et al., 2014). Prescribed burning studies suggest that fire can enhance red oak regeneration, although fire frequency and severity determine red oak regeneration success or failure (Signell et al., 2005; Knapp et al., 2015; Greenler et al., 2020). Red oak has fire-resistant physiological adaptations such as post-fire sprouting (Perala, 1974; Sander, 1990), bark thickness (Crow, 1988, Dey and Schweitzer, 2018) and wood compartmentalization after fire injury (Shigo and Shortle, 1979; Brose et al., 2014). These adaptations lead to the idea that fire is a primary driver of red oak regeneration. The benefits of fire disturbance on red oak regeneration include the suppression of late-successional, shade tolerant competing species (Brose et al., 1998; Dey and Guyette, 2000) and soil amendments with wood ash and charcoal, but this may also benefit other species such as red maple (*Acer rubrum* L.) (Green et al., 2010; Granger et al., 2018).

The production of wood ash during a fire improves the acid–base status of the forest floor, e.g., pH and exchangeable Ca, Mg and K, whereas the effects of ash on the mineral soil appear several years or decades after deposition, and the amplitude of its effect varies as a function of the amount of ash produced and soil types, among other factors (Thiffault et al., 2007; Reid and Watmough, 2014). By increasing soil pH, wood ash can also affect N mineralization, thus generating overall improved soil conditions for plant growth (Raison, 1979; Brais et al., 2015). Additionally, with its high surface area, charcoal can improve soil conditions for plant growth by adsorbing allelopathic compounds such as tannins and phenols, which have been recognized as adversely impacting red oak acorn germination and seedling radicle growth (Lodhi, 1978; Hanson and Dixon, 1987). This effect varies with the types and sources of allelopathic substances (Nilsen et al., 1999). Adsorption of phenols can also increase soil microbial activity and nitrification (DeLuca et al., 2006; Lehmann et al., 2011) and thus further improve soil nutrient availability (Jacoby et al., 2017; Zhou et al., 2020). However, fire can negatively impact soils by decreasing organic matter levels and increasing bulk density of surface soil (Phillips et al., 2000).

While red oak regeneration has been limited in its native North American distribution in the last century (Dey et al., 2008; Loftis and McGee, 1993), the species has been highly competitive and has established many areas very successfully in Europe since its introduction in the 18th century (Major et al., 2013; Nicolescu et al., 2020). The fast expansion in Europe where fire disturbance is not prevalent suggests that red oak regeneration is not entirely dependent of fire disturbance, and that other factors (e.g., climate) may play a large role in its failure to regenerate in North America. Other important factors affecting red oak regeneration include its 2–5 years masting cycle (Sander, 1990; Abrams and Johnson, 2013), acorn predation (Schnurr et al., 2004; Lombardo and McCarthy, 2009), herbivory (Ward et al., 2000; Blossey et al., 2019), acorn size and quality, e.g., free of infections (Kormanik et al., 1998; Yi et al., 2015), genotypes with highly specific adaptations (McGee, 1974; Kriebel et al., 1988; Sork et al., 1993; Aldrich et al., 2005) and site intrinsic conditions including soil physicochemical properties as well as light and water availability (Phares, 1971; Kolb et al., 1990; Bauweraerts et al., 2013). This study tested the effect of multiple factors on red oak regeneration of four northern provenances, including fire and site-specific effects along with fertilization with ash and biochar as well as large herbivores. Furthermore, this study combines two experiments, i.e., in the greenhouse and in the field under red oak stands, to more fully elucidate the potential role of each of these factors under both controlled and uncontrolled environments.

Red oak is an important tree species to maintain in the North American landscape as it is a source of high-value lumber and is a significant food source and shelter for fauna (Sork et al., 1983; Pekins and Mautz, 1988). Models project that climate change should be beneficial to the expansion of red oak in northeastern North America and a northern shift in the distribution of the species is expected (Iverson et al., 2019; Prasad et al., 2020). However, such models are generic and they generally overlook specific conditions and environmental factors that control regeneration at finer spatial scales. As such, studies on the regeneration dynamics of red oak at its northern distribution limit have value because this environment is likely to become more prevalent for red oak under climate change. A better understanding of the early ecology of the species at these latitudes will guide management strategies to maintain the species locally and perhaps to increase its distribution northward under climate change.

Two mature red oak stands were studied at the northern distribution limit of the species in Quebec, a rare occurrence at these latitudes at present. The first objective of this study was to assess tree species composition and age structure as a means to assess red oak regeneration history in the stands. We hypothesized that both stands exhibited similar age structure and that their occurrence closely matches the last major fire event in the area (early 1920s, Savage, 2001). The second objective was to assess the influence of seed provenance on seedling regeneration and growth, in a controlled environment (greenhouse) and in the two red oak stands, to isolate and test critical factors such as site intrinsic conditions, herbivory and soil fertility. We hypothesized that (1) intrinsic site conditions and provenances significantly affect germination, survival and growth of red oak, (2) large herbivores have important adverse impacts, and (3) increasing soil nutrient availability by adding wood ash and biochar has benefits.

2 Materials and methods

2.1 Study site

The study was conducted at the Station de Biologie des Laurentides (SBL) of Université de Montréal in St. Hippolyte, Quebec (45°98′93″ N and 74°00′61″ W, Figure 1). The site is at the northern limit of the maple-yellow birch (*Betula alleghaniensis* Britt.) bioclimatic domain of the lower Laurentians. It is mostly composed of maple stands under mesic conditions and coniferous stands [*Abies balsamea* (L.) Mill. or *Thuja occidentalis* L.] under hydric and sub hydric conditions (Savage, 2001). The site is characterized by a warm and humid summer. The

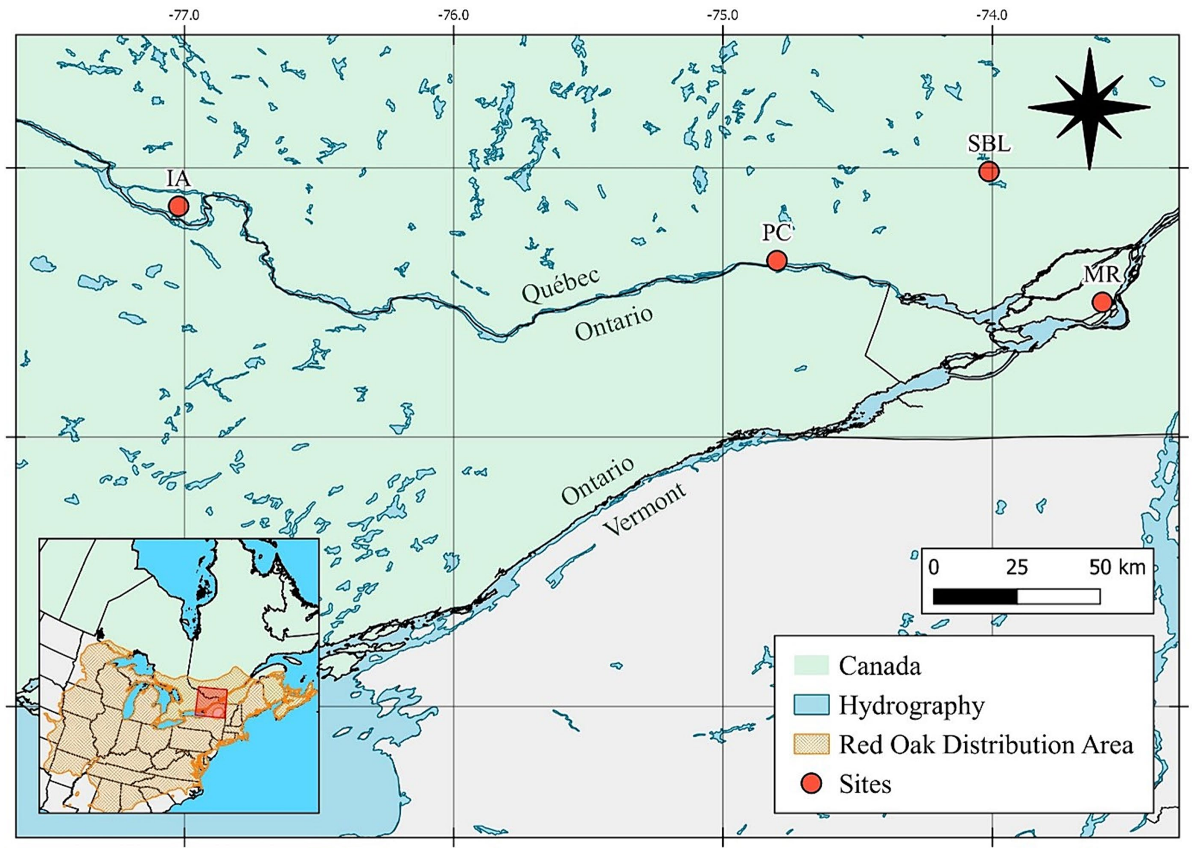

FIGURE 1
Site locations of red oak acorn provenances used for the 2019 field experiment at Station de biologie des Laurentides (SBL). IA is Isle-aux-Allumettes, PC is Pointe-au-Chêne and MR is Mont-Royal. Data was gathered from Government of Quebec (2019) and map projection is NAD Quebec Albers (EPSG:6624).

mean annual temperature, precipitation, days without frost and degree-days simulated with the BioSIM model (Régnière and Bolstad, 1994) between 2003 and 2013 were, respectively, 4.9°C, 1270 mm (with 30% falling as snow), 153 and 2,845 (Bélanger et al., 2021a). Soils are sandy and developed from glacial till made up of anorthosite (Morin series) and felsic rocks (Bélanger et al., 2012) and are classified as Orthic Ferro-Humic and Humo-Ferric Podzols (Soil Classification Working Group, 1998). The site is part of the Grenville geological province, which is in turn part of the Canadian Precambrian Shield.

The only two red oak stands at SBL, i.e., Lac en Coeur (site 1; 45°58′20″ N and 73°59′51″ W) and Lac Corriveau (site 2; 45°58′52″ N and 73°59′29″ W) were selected for this study. They present mature and dominant red oak trees, are situated on well-drained hilltops with south-southeast facing slope aspects and exhibit limited red oak regeneration. They also offer diversity in terms of species composition (Table 1). Both sites are characterized by the dominance of red oak and sugar maple. The tree species composition in site 1 is less diversified than site 2. In site 1, red oak and sugar maple have an identical relative abundance and make up for 92.8% of the sampled trees, whereas only 3 other species were inventoried. Site 2 exhibits a more diversified composition as 11 species were inventoried in the stand. Red oak and sugar maple also make up the bulk of the trees in site 2 (i.e., relative abundance of 89%), but in contrast to site 1, red oak trees are substantially less abundant than sugar maple trees. Red oak and sugar maple trees have an average DBH of 54.7 cm and 32.6 cm in site 1 and of 37.9 cm and 23.1 cm in site 2, respectively (Supplementary material A). Due to their larger diameters, basal area of red oak at sites 1 and 2 is, respectively, about 25 and 5 m^2 ha-1 greater than that of sugar maple. Tree density is higher at site 2 than site 1, with an average of 566 and 382 trees per hectare, respectively (results not shown). Many red oak trees show fused stems within the first 100 cm, which is characteristic of a post-fire regeneration pattern, i.e., multiple stems growing from the same stool. Fire scars on these main bases are often visible, but they were not investigated further to assess the year of fire occurrence more precisely.

2.2 Site dendroecological characterization

Data were obtained from four and five 452 m^2 circular plots (12 m radius) randomly selected in sites 1 and 2, respectively, in the fall of 2018 (Supplementary material G). Within each plot, all trees with a diameter at breast height (DBH) > 10 cm were identified by species and cored using a Haglof 5.1 mm diameter increment borer. For each plot, the percent contribution of each tree species to the total number of trees (abundance) was computed. Collected tree cores were prepared and sanded using standard methods (Payette and Filion, 2018) before counting growth rings under a M80 binocular microscope (Leica, Germany).

TABLE 1 **Tree species frequencies, relative abundances and average age in the two study sites.**

Species	Frequency		Abundance (%)		Mean age (years)	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
Red oak (*Quercus rubra* L.)	32	29	46.4	22.7	95.2	79.0
Sugar maple (*Acer saccharum*)	32	60	46.4	46.9	78.3	86.2
American beech (*Fagus grandifolia*)	1	5	1.5	3.9	25	68.2
White spruce (*Picea glauca*)	–	6	–	4.7	–	62.1
Balsam Fir (*Abies balsamea*)	–	9	–	7.0	–	63.2
White birch (*Betula papyrifera*)	–	10	–	7.8	–	77.8
American basswood (*Tilia americana*)	–	3	–	2.3	–	72.5
Red maple (*Acer rubrum*)	–	2	–	1.6	–	–
Striped maple (*Acer pensylvanicum*)	–	2	–	1.6	–	43.0
Eastern cottonwood (*Populus deltoides*)	–	1	–	0.8	–	61
Yellow birch (*Betula alleghaniensis*)	–	1	–	0.8	–	44
American hophornbeam (*Ostrya virginiana*)	3	–	4.3	–	58.5	–
Black ash (*Fraxinus nigra*)	1	–	1.4	–	90	–

Values for age are means and standard errors (±) of all tree cores. The abbreviations presented here are used in Supplementary Table S1.

2.3 Acorn collection and preparation

Red oak acorns were directly collected in pristine forests at three different sites in the fall of 2017. Acorn collection sites included SBL as well as Mont-Royal (MR) and Pointe-au-Chêne (PC), all within the province of Quebec (Figure 1). Acorns of a fourth provenance, i.e., Isle-aux-Allumettes (IA) were obtained in winter of 2018 from a nursery operated by the *ministère des Forêts, de la Faune et des Parcs* of the Quebec Government. For the SBL provenance, acorns were specifically collected at the two surveyed sites (1 and 2). The sites were selected to capture a latitudinal gradient that mainly encompassed differences in climate, but it also holds differences in stand compositions, geology and soils. The MR provenance is the most southern (45°30′23″ N), followed by the IA provenance (45°51′24″ N), the PC provenance (45°65′45″ N) and the SBL (local) provenance (45°98′93″ N). The MR, PC, and IA sites are warmer and have less precipitation than SBL. The MR, PC, IA, and SBL, respectively, present a 6.8, 6.1, 5.0, and 4.3°C mean annual temperature and 1,000, 1,009, 853, and 1,193 mm mean annual precipitation (1981–2010 period, Government of Canada, 2020). The MR site is within the sugar maple-bitternut hickory bioclimatic domain, whereas the PC and IA sites are located near the northern limit of the sugar maple-bitternut hickory bioclimatic domain, with sugar maple-basswood and sugar maple-yellow birch just north of the PC and IA sites, respectively (Saucier et al., 2009). Like SBL, the PC site belongs to the Grenville geological province, and its soils were developed from glacial till composed of gneiss and marble (Ministère de l'Énergie et des Ressources naturelles, 2020). The MR site is part of the Monteregian Hills complex and is characterized by a magmatic intrusion formed during the late Mesozoic (~125 Ma), unearthed by the differential erosion of the glaciers' over the last 2 million years. Soils are mostly formed from melanocratic and leucocratic gabbro (Amórtegui et al., 2010). The soils at the AI site are derived from alkaline sedimentary rocks of the Trenton group, including shale, limestone and dolomite (Thériault and Beauséjour, 2012). The upper mineral soil (B horizon) was sampled at five locations at all sites and analyzed for pH, total C and N as well as bulk geochemical composition (see Soil analysis section below for details). As a whole, soils at the MR and PC sites are of greater quality (i.e., higher pH and levels of nitrogen, calcium, magnesium and phosphorus) than the SBL and IA sites (Supplementary material B).

Acorn stratification was completed following the protocol described by Nature-Action Québec (2015). The acorns were first washed with a diluted NaClO solution (5%) of the original concentrated bleach solution (3%). This allowed to kill pathogens and/or mold, thus maximizing the conservation of seeds from the start-to-end of the stratification process throughout the winter period. Acorns were then selected based on the criterion of non-viable vs. viable acorns. More specifically, acorns that presented visible outside damages (mold, fissures, holes, etc.) were discarded as non-viable. Also, acorns that floated during the bleaching process were assumed to have an affected core (e.g., weevil, *Curculo glandium* M.) and were thus also discarded. Sorting of the acorns was done to allow optimal quality and germination rates. Selected acorns were then stored in the refrigerator at 2°C for 3 months in large plastic bags prepared with a vermiculite bed to absorb the excess initial moisture. Distilled water was sprayed in each bag on a weekly basis to maintain relative humidity at about 25% to prevent drying. Bags were also opened each week to oxygenate acorns and prevent mold development. Finally, acorns were soaked in water for 24 h one day prior to transplantation in the pots or field plots.

2.4 Greenhouse experiment

A first experiment was carried out for 10 weeks in a greenhouse during summer 2018 with the objective of characterizing germination rates, growth and survival of the red oak provenances under a soil richness gradient. One acorn was planted at the soil surface in 100 cm^3 pot. A total of 170 acorns were planted for SBL and 230 acorns were planted for MR and PC each. The IA provenance was not tested as seeds were not yet available. The pots were placed in 21 rows containing 30 pots each (Supplementary material H). Each row was comprised of three sets of 10 pots of each provenance, placed randomly along the rows. Soil richness treatments were randomly distributed along the rows in series of three pots. This ensured that both the provenances and treatments were distributed throughout the room, thus reducing possible bias induced by unaccounted environmental variations in the greenhouse.

The potting soils were prepared from a base of sand mixed with rich Agro Mix® N7 organic soil (Fafard, Canada). The soil richness treatments were produced from mixing the sand and organic soils in varying proportions. The sand and organic soil mixture corresponded to 9:1, 5:5, and 1:9 volume ratio for the low, average and high soil richness treatments, respectively. The sand and organic soil mixtures were prepared in a concrete mixer, which we ran for 10 min to obtain a fully homogenized soil. Salifu and Jacobs (2006) studied red oak seedling growth under different fertilization treatments and suggested that a fertilization of 15 N-15P-15 K of 25 mg N plant-1 season-1 maximized dry mass production, 100 mg N plant-1 season-1 led to optimum N and P uptake, and 150 mg N plant-1 season-1 induced N and P toxicities. Based on this information, we applied a water soluble 20 N-20P-20 K fertilizer (Miracle-Gro™, Scotts, Canada) to the pots to enhance differences between the soil richness treatments. The low soil richness treatment received a total 3.75 mg N of fertilizer season-1, while the average soil richness treatment received 15 mg N season-1 and the high soil richness treatment received 75 mg N season-1. Equivalents using a 15 N-15P-15 K fertilizer would be 5 mg, 20 mg, and 100 mg N for the low, average and high soil richness treatments, respectively. Air temperature was set at 24°C during the day and 20°C at night, whereas light was provided for 16 h d-1. Pots were watered using a tubing system with individual outlets planted in each pot. The watering system was activated two times per week for a duration of 1 min (equivalent to 300 mL of water per pot). This kept the soil evenly moist but not saturated. Excess water could easily drain at the bottom of the perforated pots.

To assess the performance of red oak provenances as a function of soil richness, growth stages were measured throughout the experiment. Stage 1 corresponded to a successful germination, stage 2 to stem development, stage 3 to the onset of leaf development, and stage 4 to multiple/full leaf development. Germination and sprout survival rates were also monitored. Further total mortality rate per provenance was calculated. This number corresponded to the number of dead sprouts as well as the seeds that did not germinate. A subsample of seedlings ($n = 32$, 40, and 36 for SBL, MR and PC, respectively) was selected at end of the experiment for destructive measurements. Response variables measured were stem height (cm), stem mass (g), number of leaves, dry leaf mass (g), leaf area (cm^2), support root mass (g), and fine root mass (g). Specifically, leaf area was assessed by scanning leaves as .tiff files on a white paper sheet as background and then estimating leaf area with the LeafArea R package (Katabuchi, 2015), which acts as an interface for the image processing program “ImageJ.” All mass measurements were carried out on dried samples (40°C for 48 h), except for leaf area which was measured on air-dried leaves. Other variables derived from direct measurements were mean leaf mass (g leaf-1), mean leaf foliar area (cm^2 leaf-1), aboveground biomass (g), belowground biomass (g), total biomass (g), and root:shoot mass ratio.

Potting soils from the three soil richness treatments were sampled at the beginning and end of the experiment (i.e., weeks 0 and 10). Soils were representative of substrates without and with the weekly addition of a fertilizer. Three replicates were sampled for each treatment, for a total of 18 soil samples to be processed in the laboratory for chemical analysis.

2.5 Field experiment

A second experiment was carried out in the field at SBL. The experimental split-split-plot design included ten blocks distributed evenly among sites. Each block contained twenty-four 900 cm^2 micro-plots separated by 10 cm wide buffers. Micro-plots were identified with stake flags. Half of the micro-plots were set up within a 1.83 m high galvanized metal fence (exclosures) in order to protect red oak seedlings from large herbivores (e.g., deer). The other half of the micro-plots was left unprotected from large herbivores. Each half-block was subdivided randomly into 3 provenances and 4 soil fertilization treatments. The layout was randomly distributed based on the protection from large herbivores (factor 1), followed by the soil fertilization treatments (factor 2), and finally by the random distribution of the 3 provenances within a soil fertilization treatment (factor 3). The soil fertilization treatments included a control, wood ash, biochar, and a combination of ash and biochar. The factor hierarchy is shown in Supplementary material I, whereas an example of an established experimental block is available in Supplementary material J. Wood ash and biochar extractible cations concentrations were estimated via the Mehlich-III acid extraction method. They, respectively, yielded 3,574 and 21.1 mg Ca/L, 150 and 10.5 mg Mg/L, 1,557 and 32.4 mg K/L and 322 and 7.60 mg Na/L. In the fall of 2017, biochar and wood ash were applied at the soil surface at a rate of 1 Mg (dry) ha-1 each, i.e., the lowest rate of biochar at which plant growth (maize) was observed (Glaser et al., 2014) and wood ash at which the acid–base status of the soil was significantly (positively) affected (Brais et al., 2015). The soil treatments are thus believed to be conservative, whereas the combination of wood ash and biochar was used to more completely emulate the expected effect of forest fires on soils. Leaf litter was removed before applying the material and then placed back. Wood ash has a water content of 40%, a pH of approximately 12.3 and a neutralizing capacity of 52%, whereas the biochar was prepared from coarsely grinding wood charcoal prepared from eastern hardwoods using a leaf grinder. Wood ash was sieved at 2 mm before being applied, whereas biochar was applied without sieving. Fertilization was done prior to the next growing season for the soil to react before red oak acorns were planted.

During the last week of May 2018, 12 acorns per micro-plot were planted in the first 5 cm of forest floor. Again, to do so, leaf litter was removed and placed back. The saplings from the greenhouse experiment were then placed in dormancy in the fall of 2018 by progressively reducing photoperiod and temperatures in the greenhouse. As a whole, seedlings had 4 months of growth. These were later transferred and buried under snow in early December 2018 at SBL. Micro-plots were re-fertilized at the same rate prior to the snow. The saplings were then transplanted in the micro-plots in early June of 2019. The IA provenance was also added to the experiment. The acorns were stratified from December 2018 to April 2019 (as described in the previous sections), germinated in pots in May 2019 and then transplanted on the sites in June 2019. The seedlings were transplanted mid-June. Three SBL, four MR, and five PC and IA provenances were transplanted in the micro-plot. In the end, the 3 original provenances were planted in one block in site 1 and one block in site 2, for a total of 48 plots (16 micro-plots per provenance) and 48 SBL seedlings, 64 MR seedlings and 80 PC seedlings, whereas the IA seedlings were planted in two blocks in site 1 and two blocks in site 2, for a total of 32 plots and 160 seedlings.

The effect of provenances and soil fertilization treatments on germination, survival and growth rates were assessed following a schedule with decreasing frequency (from 2 times a week, to once a week and to twice in August). We also monitored herbivory from any signs of browsing damage and activity/movement of small animals within the blocks using a high-resolution bird-watching camera equipped with a motion detection sensor (Wingscapes Birdcam Pro, Moultrie, United States). Measured response variables were survival (%), growth stage, number of leaves and leaf area (cm^2). Seedling survival was estimated from the presence/absence of leaves and buds and the stem dryness level. Growth stage was estimated based on the size of the largest leaf of the seedling, ranging from 1 to 5 cm^2 (e.g., stage 5 corresponded to the largest leaf at 5 cm^2). Number of leaves and total leaf area of each seedling were estimated once in mid-July. Leaf size was assessed using the same template as for the greenhouse experiment. Other response variables derived from data were longevity (i.e., number of weeks alive), mean leaf area (cm^2 leaf-1), maximum growth stage, final growth stage and growth stage regression (i.e., difference between maximum and final growth stages).

To better characterize growing conditions during the study period, soil temperature was measured using type-K thermocouples that were manufactured in our laboratory. Six thermocouples were placed within each block (3 in the unprotected area and 3 in the high-fenced exclosures) at a 12 cm depth within the buffers. Temperature was recorded using a thermocouple digital thermometer (Treacable®, Cole-Palmer, United States). Soil volumetric water content (VWC) was measured with time-domain reflectrometry using a FieldScout TDR 300 Soil Moisture Meter (Spectrum Technologies, United States) equipped with 12.2 cm probe. Measurements were repeated 3 times around each thermocouple. Leaf area index (LAI) was measured during full canopy in July to characterize the light environment within each block using a CI-110 Plant Canopy Imager (CID Bio-Science, United States). Measurements were conducted at 1.5 m above the soil surface.

To avoid soil disturbance where acorns and seedlings were planted, side plots with and without fertilization were established as a means to sample soils, i.e., forest floor and upper podzolic B horizon, and thus assess the effects of ash and biochar on soil chemical composition. These side plots were established as one pair of the control, wood ash, biochar and wood ash+biochar treatments beside each experimental block. Forest floor and upper podzolic B samples were collected from each treatment, for a total of 8 soil samples in each block or 80 samples in total.

2.6 Soil analysis

Soil samples collected in the field were quickly brought back to the laboratory where they were immediately dried in an oven at 50°C over 48 h. A portion of the dried samples was used for measuring pH and exchangeable Ca, Mg, K and P, whereas the rest was ground to <60 μm (PM 400 Planetary Ball Mill, Retsch, Germany) for analyzing the bulk chemical composition, including total C and N. Soil pH in water was measured using soil:water ratio of 1:10 for the forest floor and 1:5 for the mineral soil (Hendershot et al., 2008). Exchangeable Ca, Mg, K and P were measured following a Mehlich 3 extraction (Ziadi and Tran, 2007). Calcium, Mg and K concentrations were measured by atomic absorption spectroscopy (55 AA analyzer, Agilent Technologies, United States), whereas P concentrations were measured using the molybdenum blue colorimetric method (SmartChem 200 Discrete Analyzer, AMS Alliance, United States). Total C and N concentrations were measured by combustion at 1040°C and infrared and thermal conductivity detection, respectively (EA 1108 CHNS-O Elemental Analyzer, Thermo Fisons, United States). Ground samples were also pressed in pellets (13 mm diameter × 10 mm thickness) using a 25 tons hydraulic press (Reflex Instruments, Australia).

Plant Root Simulator (PRS) probes (Western Ag Innovations, Canada) were used to assess solution ionic activity of the different soil richness levels in the greenhouse experiment pots following a paste preparation protocol for which the sample paste was placed on the probes for 3 h (Qian et al., 2008). Four pairs of cation and anion probes were prepared for each soil richness level. The paste was then removed and the probes were cleaned with deionized H_2O and stored in the fridge in zipseal bags until analysis. Elution of the probes was done for 1 h with 0.5 M HCl. NH4-N and NO3-N were determined colorimetrically by continuous flow analysis (Autoanalyser III, Bran & Luebbe, United States), whereas other ions (H_2PO_4-, Ca^{2+}, Mg^{2+}, K^+, Al3+, Fe^{3+}, and Mn^{2+}) were determined by inductively coupled plasma atomic emission spectroscopy (Optima 3,000-DV, PerkinElmer, United States).

Bulk chemical composition of the upper B horizons collected at the PC, MR, IA and SBL was assessed using a X-ray fluorescence spectrometer (Vanta M series, Olympus, Japan) equipped with a rhodium tube of 50 kV and a silica drift detector. Results are reported using the Geochem calibration mode, with one built-in beam filter operating at 40 kV for heavier elements and another operating at 10 kV for lighter elements. Scanning time was set to 30 s per beam such that one whole scan was completed in 60 s. Analyzer drift was verified every 25 pellets with a silica blank. Soil pH in water and total C and N were also assessed on these samples using the methods indicated above.

2.7 Statistical analysis

All statistical tests were performed in the R environment (R Core Team, 2019). Parametric analysis of variance (ANOVA) tests and multiple regression trees (MRT) were used to test the effects of various factors on response variables. For the field experiment, response variables were converted into percent values due to unbalanced number of individuals between plots. For the greenhouse experiment, parametric ANOVAs and permutational ANOVAs were used to categorize the effects of provenances and soil richness. For the field experiment, ANOVAs were used on the four nested factor levels, i.e., site, protection from large herbivores (with or without high-fenced exclosures), soil fertilization and provenances. In the ANOVA, both provenance and soil richness/fertilization were used as the fixed factors. For the field study, repeated-measures ANOVA was used to compare measured soil temperature and volumetric water content (VWC) between sites in the field study. A Tukey post-hoc test was used to identify factor level differences at an alpha significance threshold of 0.05 for the greenhouse experiment and 0.1 for the field experiment. In the latter case, a higher alpha level was preferred because of the low number of denominator degrees of freedom. We proceeded in this manner by keeping in mind that the consequence of failing to detect a difference which did occur in nature (type II error), which is necessarily bound to the alpha level, is likely more serious than the consequence of detecting a difference which did not occur (type I error) (Peterman, 1990). When the conditions of independence of the observations, normality of the residuals and homoscedasticity were not met, data were transformed with square root or natural logarithm.

In ecology, MRT are used to describe and predict relationships between species data and environmental parameters (De'ath, 2002). In this research, the specific MRT approach that was used is the conditional inference trees variant, which is a non-parametric class of regression trees embedding tree-structured regression models into a well-defined theory of conditional inference procedures (Hothorn et al., 2006). The MRT were produced by the *ctree* function within the *party* package (Hothorn et al., 2006) in R. Other R packages used to compute results or produce graphical representations included *dplyr* (Wickham et al., 2020), *ggplot2* (Wickham, 2016), gridExtra (Auguie, 2017), *multcomp* (Hothorn et al., 2008), and *splines* (R Core Team, 2019).

3 Results

3.1 Age structure

Red oak and sugar maple were the oldest tree species at both sites (Table 1). One *Fraxinus nigra* M. tree was the exception in site 1, with a similar age (90 years) to the red oak. Many *F. nigra* trees were found near the south edge of site 1 (at a lower position on the hillslope) and the old *F. nigra* tree may thus originate from another stand with a similar disturbance history and composition that borders the southern limit of site 1. Our results suggests that red oak trees in site 1 established sooner than sugar maple trees by an average of 18 years. Conversely, red oak trees at site 2 are on average 7 years younger than sugar maple trees. As a whole, our results suggests that red oak is relatively close in age to sugar maple, and perhaps older at site 1, but our data do not account for possible prolonged suppression of sugar maple seedlings in the understory.

Very few trees were older than 1906. At that point in time, there was a substantial increase in tree recruitment rates at both sites. Tree recruitment at site 1 mainly occurred during two periods, i.e., 1910 to 1924 and 1951 to 1965. At site 2, recruitment dynamics were not as well defined in time. Recruitment rates were highly variable between 1907 and 1980, shifting from high to low, and they were nearly zero thereafter. Red oak recruitment occurred mainly between 1910 and 1933 at site 1, with a record year in 1918. Sugar maple recruitment was high between 1918 and 1930 and it was irregular and more largely spaced in time between 1930 and 1978. No more recruitment of sugar maple occurred thereafter at site 1. There was steady but small recruitment of red oak at site 2 between 1900 and 1931, whereas high recruitment occurred between 1947 and 1960. Sugar maple recruitment at site 2 mostly occurred between 1907 and 1947. Recruitment of sugar maple was negligible thereafter and completely absent from 1970 and onward.

3.2 Greenhouse experiment

Ionic activities of the soil substrates as measured by paste extracts on PRS probes confirm a strong increase in the availability of macronutrients for red oak seedlings from the low to average to high soil richness treatments (Supplementary material C). The only exception was for NH4-N which suggests relatively homogeneous supply rates between the 3 treatments (Figure 2).

Germination rates of all red oak acorns increased by about 12% from the low soil to the high soil richness treatments (Table 2). Germination rates also increased by provenance in the following order: SBL < MR < PC (Table 2). Sprout survival rates of all red oak provenances were highest under average soil richness and lowest under low soil richness. Sprout survival rates were similar between SBL and MR, whereas PC showed higher rates (Table 2). The MR and PC provenances showed an increase in germination rates with increasing soil richness. On the other hand, the SBL provenance exhibited the greatest germination rate under low soil richness (i.e., 50%), which was a lower germination rates than that observed for the MR and PC provenances under low soil richness. The total mortality rate for the SBL provenance was highest under high soil richness, whereas mortality rates for the MR and PC provenances were highest under low soil richness and lowest under high soil richness. The only provenance that did not suffer post-germination mortality up to the 10th week of experimentation was PC within the average treatment (Table 2). The MR provenance also displayed the largest differences in germination, sprout survival and total mortality rates between the low and high soil richness treatments.

The MRT analysis on germination rates suggests a first partition within the provenance factor, with the SBL provenance being separated from the MR and PC provenances (Figure 3). A second partition is suggested within the treatment factor for the MR and PC provenances, with the low soil richness treatment being separated from the average and high soil richness treatments. A third partition separates the MR provenance from the PC provenance, whereas a final partition separates the average soil richness treatment from the high soil richness treatment for the MR provenance (Figure 3). From the resulting MRT analysis, it can be assessed that SBL differs most from MR and PC, regardless of fertility treatments, and that the difference between low and average soil richness treatments had a higher impact on MR and PC survival than the difference between average and high soil richness treatments. The final partitions show that PC survival is mostly unaffected by an increase in soil nutrient availability beyond the average treatment, while MR shows a slightly improved survival rate.

Morphological variables are presented in Supplementary material D. As a whole, the high soil richness was associated with greater height, foliar surface and leaf, stem and root mass, whereas the low soil richness treatment exhibited the lowest values. The average soil richness treatment did exhibit slightly higher stem mass than the high soil richness treatment. Root/shoot ratio were about 0.8 under low and average soil richness, while the ration was about 0.7 under high soil richness. Two-way parametric and permutational ANOVA tests suggest that total leaf area and mass as well as stem mass were significantly different among soil richness treatments, among provenances, and that there was a significant interaction between the two factors (Supplementary material E). Boxplot analysis of these variables (Figure 4) indicate that this interaction is the result of the SBL provenance. While performance of the MR and PC provenances generally increased with soil richness, the SBL provenance performed at its maximum under average soil richness and performance substantially decreased under high soil richness. ANOVA tests also suggest a significant difference in stem height between provenances, in

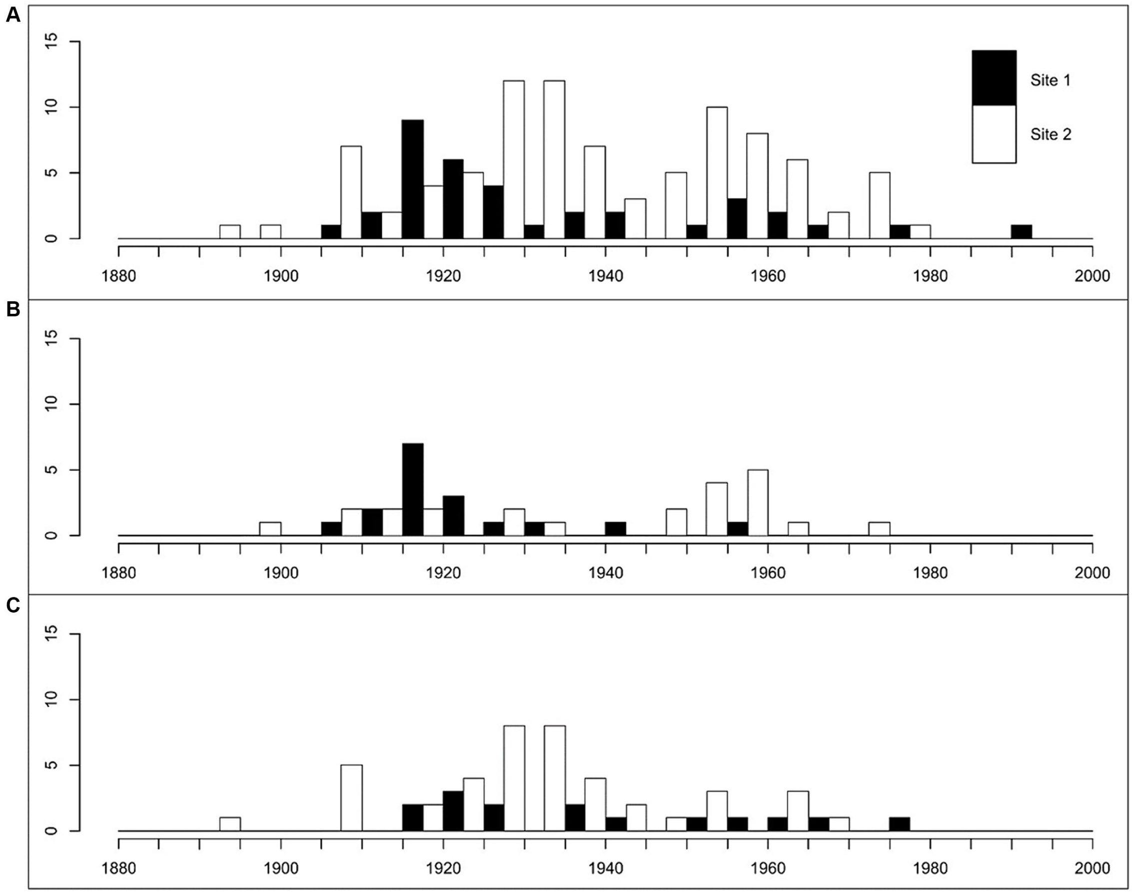

FIGURE 2
Age structure of all cored trees **(A)**, red oak **(B)** and sugar maple **(C)** at the two study sites. Data are only accounting trees for which growth rings could be counted in whole. Trees with rotten or empty cores are not accounted for.

support root mass between soil richness treatments and between provenances, and in ratio of fine roots mass/support roots mass and fine roots mass/leaf mass between treatments (Supplementary material E).

3.3 Field experiment

For the 2018 field experiment, we observed 100% mortality of planted acorns after a two-week period. Mostly heavy rodent predation (mainly eastern chipmunk, *Tamias striatus* L.) but also very dry conditions were fatal to all planted red oak acorns. No other testing/results are thus reported here.

Chemical analyses show that forest floor composition is generally similar between the sites (Supplementary material B). However, site 1 has higher mineral soil total C and N concentrations as well as higher extractible Ca, Mg and K concentrations, whereas soil pH is lower. Ash and biochar fertilization treatments had a substantial positive effect on forest floor Ca, Mg and K concentrations and pH but had no detectable effect on the mineral soil. Wood ash application led to a substantial increase in forest floor pH and Ca, Mg and K concentrations. Biochar only slightly increased forest floor pH and Ca, Mg and K, whereas the combination of ash and biochar showed the largest increase (Supplementary material B). There is an inverse relationship between soil VWC and temperature, i.e., VWC decreasing with an increase in temperature (Supplementary material F). Soil temperature and VWC were, respectively, highest and lowest in August. Site 1 showed slightly higher soil temperatures and lower soil VWC than site 2 throughout most of the summer. Leaf area index averaged 1.9 and 2.4 at sites 1 and 2, respectively. This difference is likely associated with variation in tree density (as expressed in basal area) between the sites (Supplementary material A).

For the 2019 field experiment, there was a large difference in the overall (i.e., all provenances) planted seedling survival rate between the two sites throughout the experiment (Figure 5A). At the last survey, seedling survival rate was 45% in site 1 and 74% in site 2. The difference in survival rate widened between the two sites as early as June 16th and averaged 30.5% for the remainder of the survey. Seedling survival rate also displayed a similar overall pattern at both sites. Independent of sites, seedlings planted in high-fenced exclosures (protected) showed a final survival rate of 65.8% while unprotected seedlings showed a survival rate of 53.2% (Figure 5B). The difference between the protected and unprotected seedlings widened on June 20th but it stabilized at the next survey, i.e., June 26th. Thereafter, survival rate between protected and unprotected seedlings followed a similar pattern and the difference between the two averaged 11.9% for the remainder of the survey.

Seedling survival rate largely varied as a function of acorn provenances (Figure 5C). At the end of the survey, seedling survival

TABLE 2 Germination, sprout survival and total mortality rates (%) of red oak provenances as a function of soil richness over 10 weeks in the greenhouse.

Factor level		Response variable					
Acorn prov.	Soil richness	*n*	Germination	*n*	Sprout survival	*n*	Total mortality
SBL	Low	60	50.0	30	93.3	60	53.4
	Average	50	38.0	19	89.5	50	66.0
	High	60	41.7	25	80.0	60	66.6
MR	Low	70	60.0	42	73.8	70	55.7
	Average	80	70.0	56	98.2	80	31.3
	High	80	85.0	68	94.1	80	20.0
PC	Low	80	73.6	59	86.4	80	36.4
	Average	80	87.5	70	100.0	80	12.5
	High	70	94.3	66	95.5	70	9.9
Soil richness total	Low	210	61.2	131	84.5	210	48.3
	Average	210	65.2	145	96	210	37.4
	High	210	73.7	159	90	210	33.7
Provenances total	SBL	170	43.2	74	87.6	170	62.2
	MR	230	71.7	166	88.7	230	36.4
	PC	230	85.1	195	94.0	230	20.0

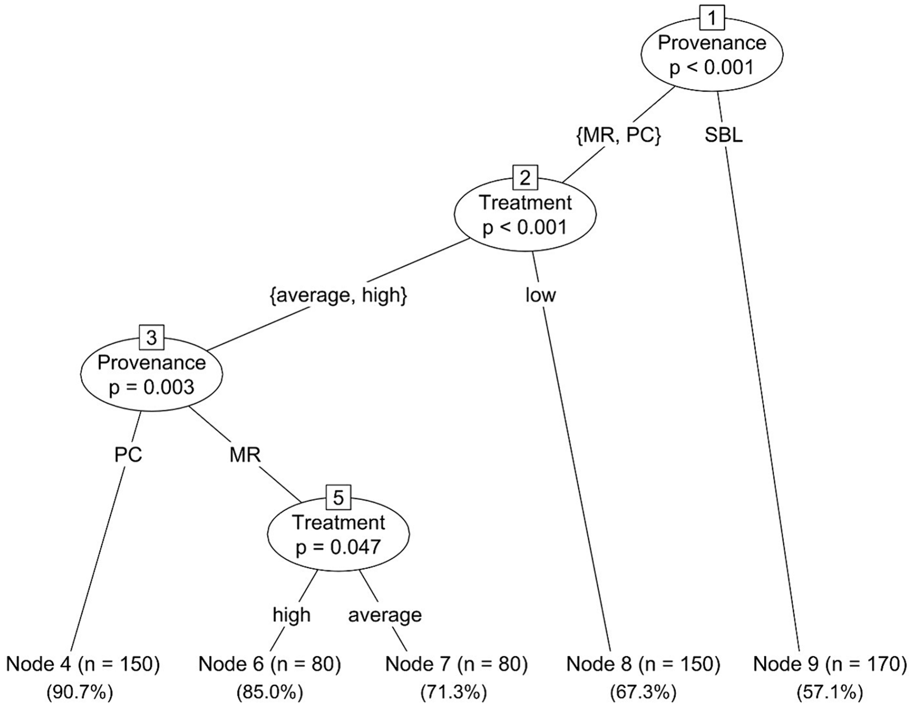

FIGURE 3
Multiple regression tree of red oak germination rates (as a yes/no binary variable) as function of soil richness and acorn provenance over 10 weeks of greenhouse experimentation. Associated germination rates are specified under each node.

rate was highest for the MR provenance (79.2%), followed by IA (59.7%), PC (55.0%), and SBL (43.8%). Survival rate of the MR, PC, and SBL provenances widened early in the survey (between June 14th and 16th) and differences were then maintained for the rest of the survey. While seedling survival rates stabilized by July 4th, survival rate of the IA provenance decreased steadily throughout the survey. However, a short respite in mortality was observed between July 24th and August 2nd. Seedling survival rates displayed smaller variation

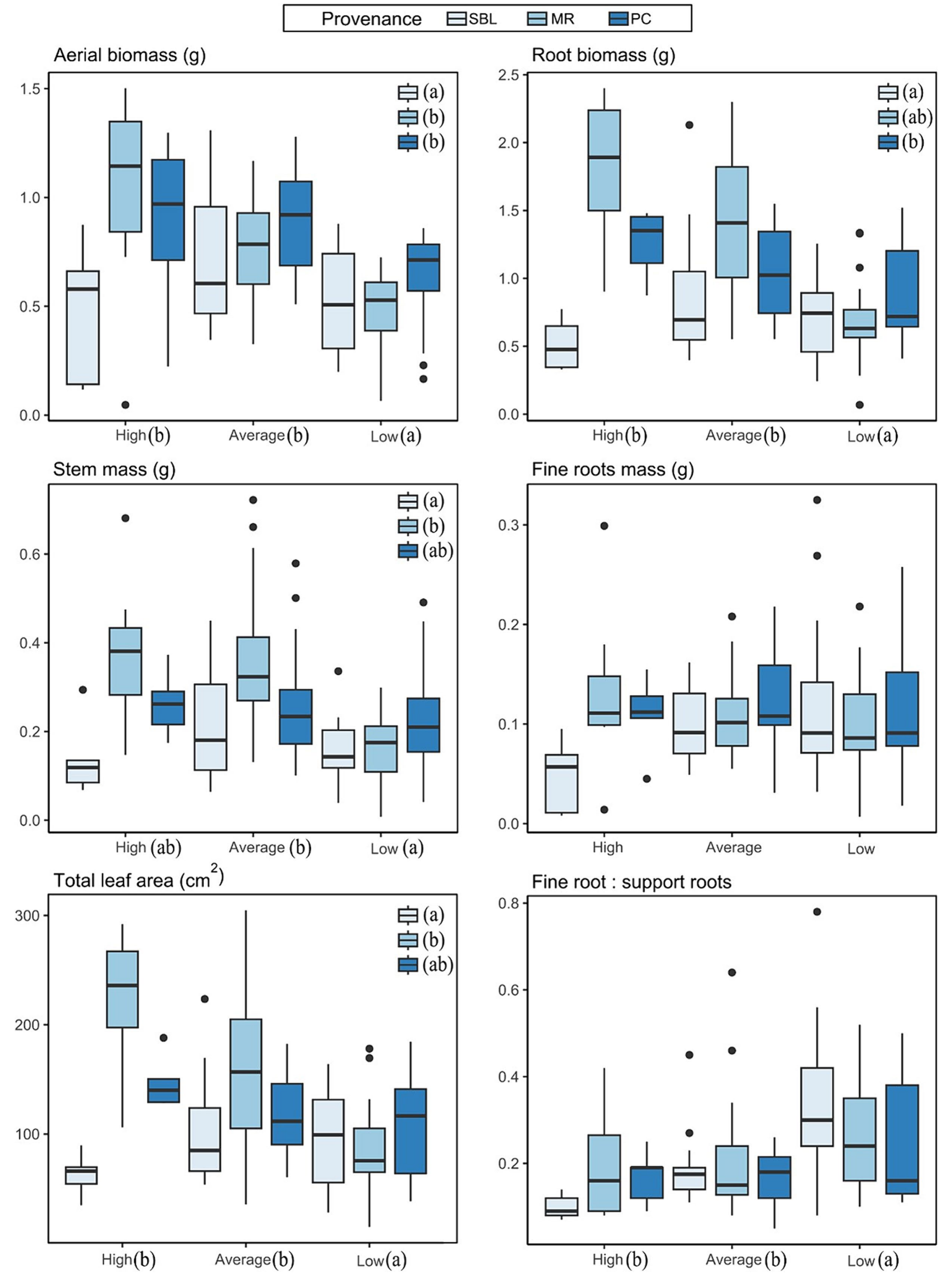

FIGURE 4
Boxplots of response variables measured in the greenhouse (see Supplementary material D for full data table). Letters indicate significant differences ($p < 0.05$) between treatments and between provenances.

among soil fertilization treatments (Figure 5D). The highest survival rate was observed under the ash + biochar treatment at 63.6%, followed by the biochar treatment at 61.6%, the control treatment at 58.8% and the ash treatment at 54%. Overall, seedling survival patterns were similar among fertilization treatments. Although the wood ash treatment initially performed strongly, i.e., 84.1% survival rate between June 16th and 20th, it underperformed relative to the other treatments thereafter. Conversely, the ash + biochar treatment exhibited the lowest survival rate early in the survey, but it was ultimately the treatment with the highest survival rate at the end of the experiment.

The one-factor ANOVA tests show that site had a significant effect on the seedling survival of the SBL, MR, and PC provenances as well

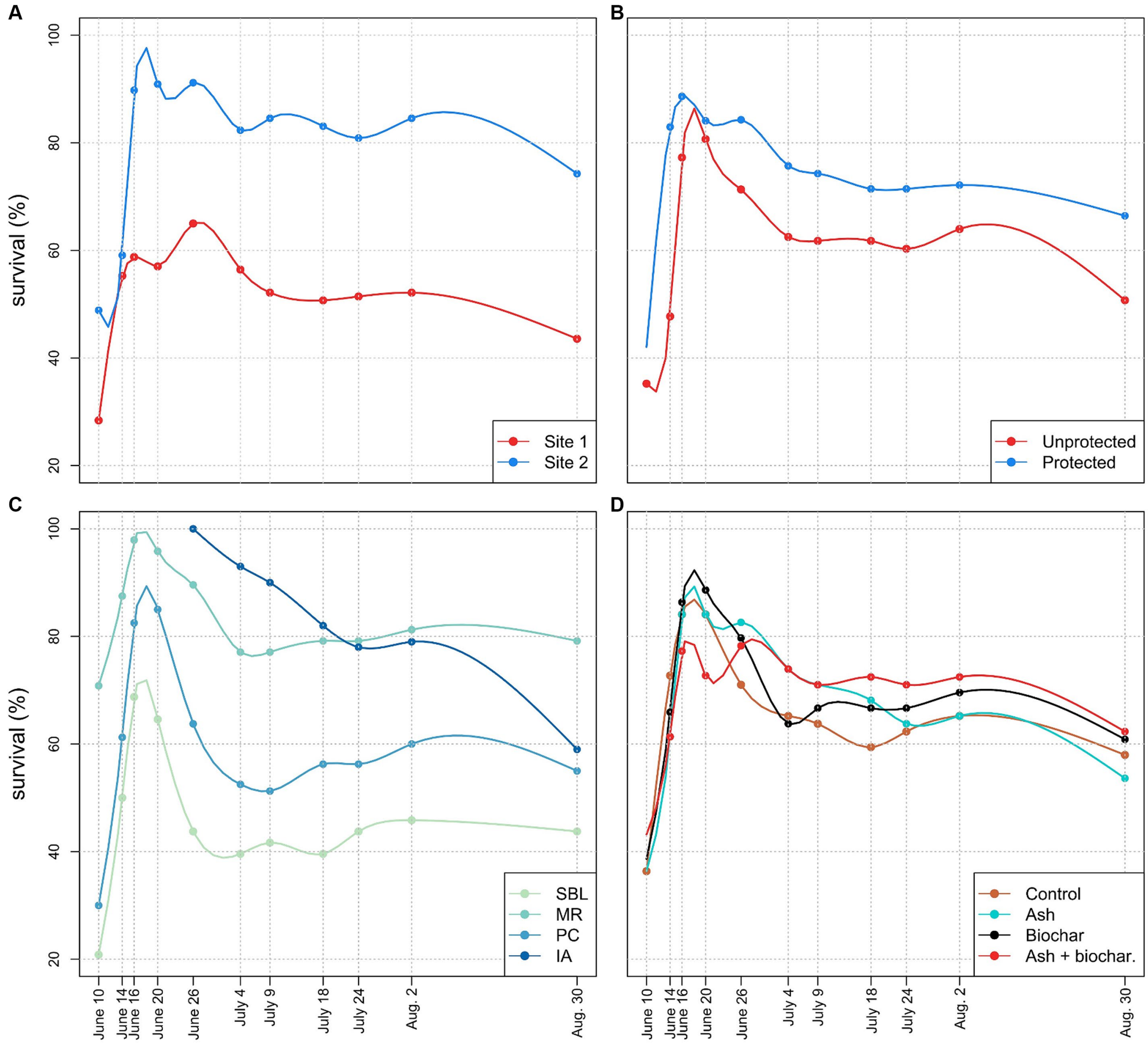

FIGURE 5
Red oak seedling survival rates in the experimental plots at SBL during the 2019 survey as a function of site **(A)**, protection against large herbivores **(B)**, acorn provenance **(C)** and soil fertilization **(D)**. The initial rise in survival rates is the result of some seedlings showing vitality (i.e., leaf development) several days after transplantation.

as all other growth development variables measured (Tables 3, 4). All data indicate that seedlings at site 2 outperformed seedlings at site 1 in regard to survival and growth development. Protection against large herbivores led to higher seedling survival, mean area per leaf and stage regression. A higher stage regression was observed for protected seedlings, which means that seedlings exhibit a larger difference between the maximum and final growth stage achieved. The IA seedlings at site 2 also outperformed seedlings at site 1 in regard to mean area per leaf, final growth stage reached and survival time (Tables 3, 4). Seedling survival rate was marginally significant at $p = 0.1$ (i.e., 14.0% higher at site 2 vs. site 1). The IA provenance showed higher but non-significant survival rates in protected plots than in unprotected ones, while significantly higher maximum and final stages reached highlight the effectiveness of the high-fenced exclosures for IA seedling growth. Seedling protection against large herbivores led to significantly lower maximum and final growth stages reached, which is contrary to SBL, MR, and PC seedlings.

The SBL seedlings exhibited the lowest values for most response variables (e.g., survival rate, number of leaves, final growth stage reached and relative survival time) measured compared to the other provenances (Table 3). The MR provenance exhibited greater performance than the SBL and PC provenances in terms of survival, number of leaves, total leaf area, final and maximum stage reached, survival time and relative survival time, but only survival time and relative survival time were significantly higher than the SBL and PC provenances (Table 3). The IA provenance exhibited a relative survival time similar to the MR provenance, whereas survival rate was 59.7% and not statistically different from the SBL and PC provenances. An increase in mortality of the IA provenance occurred near the end of the survey (Figure 5C). Yet, the IA seedlings exhibited significantly greater total leaf area and final and maximum growth stage reached (Table 3).

Soil fertilization significantly affected the maximum stage achieved by the SBL, MR, and PC seedlings, with an average of 2.37 under the

TABLE 3 Mean ± standard errors of seedling survival and growth development variables measured as a function of site, protection against large herbivores and soil fertilization.

Provenance	Response variable	Site		Protection		Fertilization			
		1	2	No_ fence	Fence	Control	Ash	Biochar	Ash + biochar
SBL, MR, and PC	Survival (%)	40.0 ± 6.66a	78.8 ± 4.27b	51.2 ± 6.79a	67.5 ± 6.58b	55.7 ± 11.5	62.8 ± 7.16	53.9 ± 10.6	65.0 ± 9.71
	Number of leaves	2.59 ± 0.44a	3.59 ± 0.22b	3.29 ± 0.33	2.89 ± 0.39	2.83 ± 0.57	3.63 ± 0.50	2.43 ± 0.42	3.46 ± 0.50
	Total leaf area (cm^2)	5.57 ± 0.99a	9.90 ± 0.81b	7.49 ± 0.90	7.98 ± 1.11	6.00 ± 1.35	9.23 ± 1.41	6.3 ± 1.16	9.41 ± 1.57
	Mean area/leaf (cm^2)	2.24 ± 0.17a	2.72 ± 0.13b	2.28 ± 0.14a	2.80 ± 0.15b	2.09 ± 0.20	2.61 ± 0.23	2.60 ± 0.16	2.70 ± 0.25
	Final stage reached	2.04 ± 0.32a	3.26 ± 0.16b	2.86 ± 0.27	2.44 ± 0.30	2.09 ± 0.43	2.93 ± 0.33	2.46 ± 0.41	3.12 ± 0.41
	Max. stage reached	2.62 ± 0.35a	3.68 ± 0.18b	3.07 ± 0.26	3.23 ± 0.32	2.37 ± 0.45a	3.44 ± 0.30ab	2.98 ± 0.38ab	3.81 ± 0.42b
	Stage regression	1.03 ± 0.18a	0.66 ± 0.09b	0.63 ± 0.09a	1.04 ± 0.16b	0.82 ± 0.18	0.71 ± 0.16	0.77 ± 0.13	0.97 ± 0.26
	Survival time (weeks)	5.34 ± 0.75a	8.73 ± 0.34b	6.95 ± 0.53	7.12 ± 0.81	6.30 ± 1.22	7.14 ± 0.84	6.43 ± 1.00	8.28 ± 0.69
	Relative survival time (%)	48.5 ± 6.83a	79 ± 3.09b	63.2 ± 4.78	64.7 ± 7.34	57.2 ± 11.1	64.9 ± 7.61	58.4 ± 9.08	75.3 ± 6.27
IA	Survival (%)	52.7 ± 6.34	66.8 ± 7.47	56.3 ± 6.65	63.1 ± 7.54	63.6 ± 7.76ab	40.8 ± 10.7a	78.1 ± 11.5b	56.4 ± 5.51ab
	Number of leaves	4.05 ± 0.30	3.34 ± 0.21	3.96 ± 0.27	3.44 ± 0.26	3.77 ± 0.28	4.02 ± 0.41	3.42 ± 0.18	3.58 ± 0.57
	Total leaf area (cm^2)	14.3 ± 1.14	14.8 ± 1.41	15.8 ± 1.18	13.3 ± 1.30	14.2 ± 1.48	16.5 ± 2.11	14.9 ± 1.90	12.7 ± 1.68
	Mean area / leaf (cm^2)	3.62 ± 0.22a	4.39 ± 0.30b	4.20 ± 0.37	3.81 ± 0.15	3.86 ± 0.47	4.16 ± 0.43	4.27 ± 0.36	3.73 ± 0.35
	Final stage reached	2.78 ± 0.38a	4.12 ± 0.50b	4.02 ± 0.45a	2.88 ± 0.46b	3.90 ± 0.49	2.56 ± 0.79	4.40 ± 0.82	2.94 ± 0.31
	Max. stage reached	5.41 ± 0.30	5.85 ± 0.39	6.05 ± 0.38a	5.21 ± 0.29b	5.77 ± 0.51	5.67 ± 0.52	6.07 ± 0.47	5.02 ± 0.50
	Stage regression	2.64 ± 0.40	1.73 ± 0.27	2.03 ± 0.25	2.33 ± 0.43	1.87 ± 0.40	3.10 ± 0.66	1.67 ± 0.47	2.08 ± 0.33
	Survival time (weeks)	5.51 ± 0.26a	6.23 ± 0.24b	6.02 ± 0.25	5.71 ± 0.72	5.73 ± 0.41	5.42 ± 0.37	6.27 ± 0.36	6.05 ± 0.31
	Relative survival time (%)	78.6 ± 3.69a	89.0 ± 3.36b	86 ± 3.57	81.6 ± 3.89	81.8 ± 5.83	77.4 ± 5.38	89.6 ± 5.21	86.5 ± 4.45

Letters indicate significant differences for each variable tested with one-factor ANOVA (see Table 4).

control, 3.44 under ash, 2.98 under biochar and 3.81 under ash + biochar (Tables 3, 4). Soil fertilization had a significant effect on survival rates of IA seedlings, with lower (40.8%) and higher (78.1%) survival under the ash and biochar treatments, respectively (Tables 3, 4).

The MRT analyses captured survival and growth development stages of all four provenances simultaneously (Figure 6). The regression tree of survival rate highlights the effects of site and provenance (Figure 6A). A first separation was made between sites, with site 2 exhibiting higher survival rate than site 1. A second separation was made at site 1 between the provenance groups of MR–IA and SBL–PC. The MR–IA groups had higher survival rate than the SBL–PC group. The regression tree of relative survival time also displays the effects of site and provenance (Figure 6B). However, a first separation was made between the acorn provenance groups of IA–MR and SBL–PC. The IA–MR group exhibited higher relative survival time than the SBL–PC group. A second separation distinguished the two groups into site 1 and site 2. Relative survival time was higher for both groups at site 2. The regression tree of maximum growth stage reached (Figure 6C) and total leaf area (Figure 6D) led to a first separation between the IA provenance and the provenance group SBL–MR–PC. The SBL–MR–PC group was then subdivided into site 1 and site 2. The IA provenance exhibited the highest maximum stage reached and total leaf area. For the SBL–MR–PC group, maximum growth stage reached and total leaf area were higher at site 2.

4 Discussion

The series of experiments conducted in this study have helped portray the main factors responsible for red oak regeneration at SBL. Based on the age of red oaks that match the last known fire

TABLE 4 Mean ± standard errors of seedling survival and growth development variables measured as a function of acorn provenance.

Response variable	Acorn provenance			
	SBL	MR	PC	IA
Survival (%)	43.8 ± 6.66b	79.2 ± 5.99a	55.0 ± 9.75ab	59.7 ± 4.98ab
Number of leaves	2.53 ± 0.44a	3.69 ± 0.37ab	3.05 ± 0.47ab	3.70 ± 0.19b
Total leaf area (cm²)	6.34 ± 1.14a	9.38 ± 1.08a	7.49 ± 1.40a	14.6 ± 0.89b
Mean area/leaf (cm²)	2.59 ± 0.22a	2.58 ± 0.19a	2.38 ± 0.18a	4.01 ± 0.20b
Final stage reached	2.22 ± 0.39a	3.10 ± 0.24ab	2.63 ± 0.40ab	3.45 ± 0.33b
Max. stage reached	2.91 ± 0.42a	3.56 ± 0.22a	2.98 ± 0.40a	5.63 ± 0.25b
Stage regression	0.90 ± 0.16a	0.83 ± 0.16a	0.71 ± 0.16a	2.18 ± 0.25b
Survival time (weeks)	5.67 ± 0.92b	9.10 ± 0.30a	6.34 ± 0.87b	5.87 ± 0.18b
Relative survival time (%)	51.5 ± 8.37b	82.8 ± 2.69a	57.6 ± 7.93b	83.8 ± 2.63a

Letters indicate significant differences for each variable tested with one-factor ANOVA. Note that the IA seedlings were younger and planted a few weeks after the other three provenances and thus, comparison of variables should be done with care, notably survival time and relative survival time.

occurrence, its seems likely that fire has played a significant role on oak regeneration in the past. Fire suppression from the landscape in the last 50 years may also have led to a series of regeneration failures of red oak. The oldest trees at sites 1 and 2 date back to 1920, which points to a wildfire affecting much of the SBL area (Savage, 2001; Bélanger et al., 2004). While both red oak and sugar maple are the dominant tree species at the sites, the cohort recruitment pattern at each site are different. On the one hand, site 1 shows a greater dominance in red oak, mostly established between 1920 and 1940, with some subsequent regeneration from competing sugar maple and greater overall red oak biomass. On the other hand, site 2 exhibits a more concurrent and longer establishment period of red oak and sugar maple trees, the former showing a lower frequency but demonstrating a clear growth advantage from the initial cohort establishment. The red oak trees are, however, smaller in size in comparison to site 1, thus also resulting in lower biomass. Fire disturbance severity, frequency and timing may have played a role in the resulting tree species composition and age structure of these red oak stands (Crow, 1988; Abrams, 1992). Brose (2010) suggested that red oak regeneration is dominant after a medium or high intensity burn applied during either spring or summer, while red maple and yellow poplar regeneration dominate plots after low intensity burns, regardless of timing. In this regard, observed differences in stand tree species composition and density between sites 1 and 2 are likely the result of a divergence in fire severity. This is also in alignment with the idea that the regenerative strategy of red oak is mainly derived from its sprouting ability (Sander, 1990) rather than a physical resistance to fire (in comparison to other oak and hardwood species), with higher fire severity advantaging red oak regeneration because it eliminates mature trees of competing species.

Establishment success of red oak in Europe in the absence of fire as well as situations where the species is considered invasive (Riepšas and Straigytė, 2008; Langmaier and Lapin, 2020) suggest that many other factors govern red oak regeneration. Explanations for this include lower predation from local fauna and higher shade tolerance than indigenous oak species (Major et al., 2013; Nicolescu et al., 2020). In the prolonged absence of fire at SBL, our study highlights that site conditions, namely water availability, genetics (provenance) and control of herbivory are key factors governing (in confounding ways) germination, survival and early growth of red oak.

4.1 Site characteristics

Site was found to be the most significant factor controlling planted red oak seedlings survival and growth differences in the field experiment. Seedlings at site 2 performed better than site 1 for all response variables tested. In this respect, stand characteristics may well provide insights as to the main drivers of red oak regeneration at the sites. Site 2 exhibits much greater tree species diversity and density but lower basal area. Fei et al. (2003) found a strong relationship between cover species and density of red oak regeneration, with a steep decrease under any other species than itself. This somewhat differs from this study's results. As such, it could be argued that the diversified canopy cover at site 2 was beneficial to red oak seedling survival and growth during periods of low water availability.

Although red oak saplings and mature trees are resistant to water stress, seedlings are still vulnerable to such pressures, especially prior to extensive root system development (Kolb et al., 1990; Bauweraerts et al., 2013). For the most part of the 2019 summer, soils at site 1 were warmer and drier than soils at site 2. This difference may be explained by higher density of American beech regeneration at site 2, which is associated with lower light transmission (Collin et al., 2017, 2018), resulting in lower soil temperature and higher soil moisture (Bélanger et al., 2021a). During field measurements, symptoms of water stress such as dried leaves were often observed on experimental seedlings before their death, notably at site 1, which concurs with the explanation of red oak seedling mortality due to water constraints. Kleiner et al. (1992) have also proposed that red oak seedling shoot growth can be negatively impacted by water stress. The 2019 summer at SBL was slightly warmer and drier than normal, especially in May and June (Ministère de l'Environnement et de la Lutte contre les changements climatiques, 2021a), suggesting that water stress may have affected survival and growth that specific year. Germination and seedling establishment will likely be a critical phase under climate change, but red oak seedlings should become less vulnerable to water stress as they develop their root system (Crow, 1988; Sander, 1990). Repeated measures ANOVA suggest that soil temperatures and water volumetric contents measured in 2019 changed significantly throughout the whole season, although no significant difference was detected between sites. In this respect, it is not possible to conclude

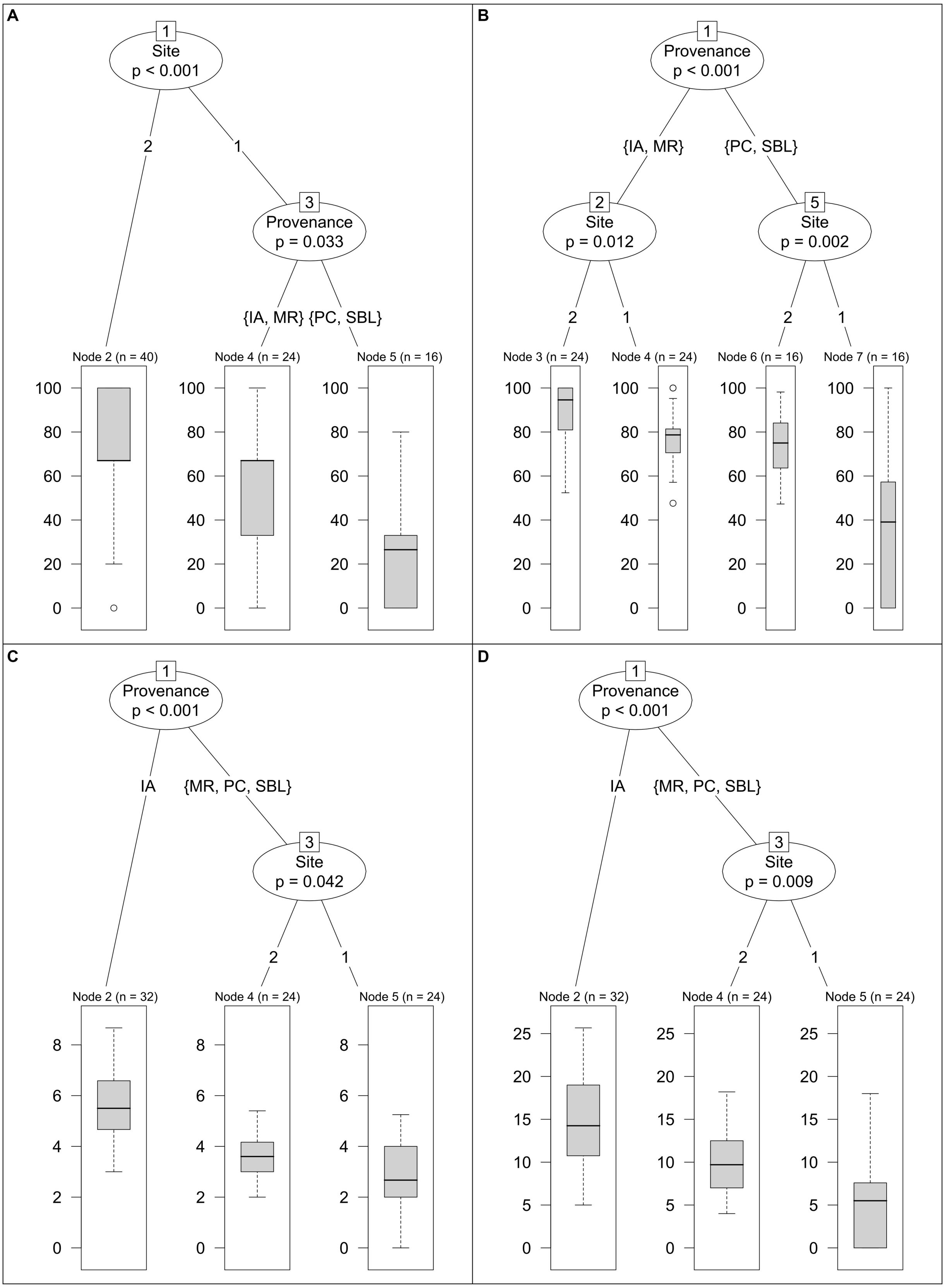

FIGURE 6
Multiple regression tree of red oak survival rate (**A**, in %), relative survival time (**B**, in %), maximum stage reached (**C**, classes 1–8) and total leaf area (**D**, in cm^2) as function of site and acorn provenance. Other factors tested such as protection against large herbivores, soil fertilization and blocking within site were not significant at $p < 0.05$ and were thus excluded from the analyses.

with high certainty that water stress was responsible for the differences in seedling performance between sites 1 and 2. Other overstory effects could also have been important and acting in interaction with soil water availability.

Measurements of LAI suggest 20.6% more leaf surface area in site 2. We suspect tree species composition, notably higher American beech regeneration, is responsible for this difference. Messier and Bellefleur (1988) have shown that spectral irradiance of the forest floor (W/m^2) is lower under American beech than under sugar maple and yellow birch at climax stage. Similar results were reported by Collin et al. (2018) at SBL. Furthermore, Canham et al. (1994) found that light is at <2% of full sun under American beech canopy, while it is at >5% under red oak canopy. Our results at site 2 thus suggest that lower light availability does not negatively impact the performance of red oak seedlings. Conversely, Phares (1971) observed that while red oak seedlings accumulate nutrients under heavy shade (e.g., 10% of light availability), height growth is triggered only at a light availability threshold of 30% light or more, and the highest biomass increments were measured at full sunlight. Brose and Rebbeck (2017) showed similar red oak seedling survival rates (15–75% from lowest to highest available sunlight), although height growth and root collar development were substantially impaired below 40% available sunlight. This implies that higher light availability at site 1 is most likely not responsible for poor seedling performance and corroborates the idea that soil water availability or other overstory effects on microclimate may have played a more significant role in early seedling survival and growth.

4.2 Genetic adaptation

Provenance had a significant impact on germination and growth in the greenhouse as well as seedling survival and growth in the field. This is especially important to highlight as acorn and seedling stock quality are significant factors to consider for red oak seedling development (Ward et al., 2000; Lombardo and McCarthy, 2009).

Contrary to the MR and PC provenances, the SBL provenance underperformed under the higher soil richness level in the greenhouse. Interestingly, the SBL provenance also underperformed in the field experiment compared to the other provenances, whether fertilized or not. McGee (1974) found that seed source elevation can affect seedling budbreak, bud and leaf development and height. Furthermore, Abrams (1994) found that adjacent red oak stands can exhibit distinct genotypes as a result of contrasting microenvironments. Notably, they observed that differences in water availability and drought effects within a limited geographical range created differences in net photosynthetic rates and leaf water potential within the red oak provenances studied.

Two explanations are thus proposed for the poor performance of the SBL provenance. First, of the acorns collected for the germination and seedling studies, acorn infection rates by curculio weevils were highest for the SBL provenance at 77%, whereas the MR and PC provenances had much lower infection rates at 25 and 22%, respectively. Furthermore, damage to the cotyledon was shown to negatively impact red oak acorn germination rate and seedling performance (Yi et al., 2019) because germination and early growth of red oak seedlings are highly dependent on acorn nutrient reserves (Yi and Wang, 2015) since SBL had the smallest average acorn size (3.29 ± 0.07 cm^3 for SBL, 3.47 ± 0.06 cm^3 for PC and 4.10 ± 0.06 cm^3 for MR). It is thus possible that a lower performance of the SBL provenance seedlings in the experiments could be due to an overall lower quality. Second, the poor performance of SBL acorns in the greenhouse could indicate that this provenance was genetically selected to perform better under more acidic and nutrient-poor soil conditions. Acorn collection sites for MR and PC red oaks show higher overall soil nutrient richness (N, P, Ca, Mg) and pH in comparison to SBL and IA, which corroborates with the idea that provenances adapt to specific soil conditions.

In addition, the MR provenance, which is the southernmost provenance, exhibited the highest survival rate in the field experiment by as much as 33% in comparison to the other provenances. For one, the MR provenance has performed better possibly because of greater acorn nutrient reserves that would have been inherited from the highest soil quality at that site. Also, southern provenances are expected to grow sooner in the spring, and this timing would have corresponded to more suitable growing conditions at SBL (e.g., cooler and wetter). Its better performance may also have been favored compared to other provenances by the specific meteorological conditions prevailing during the 2019 summer (i.e., warmer and drier than normal, Ministère de l'Environnement et de la Lutte contre les changements climatiques, 2021a). Specifically, the MR provenance was possibly able to deal better with water stress despite limited root development. Our results in respect to the MR provenance are in support with the general idea that there will be a northern shift in the distribution of red oak in northeastern North America (Iverson et al., 2019; Prasad et al., 2020).

Red oaks, despite spanning a vast geographic range in North American forest landscapes, experience habitat fragmentation due to increasing selection pressures driven by climate change (Iverson and Prasad, 2002). As a result, this species may benefit from assisted migration to mitigate the negative effects of population fragmentation and regeneration failure on certain sites (Rauschendorfer et al., 2022). In a study investigating the effectiveness of assisted migration at the northern edge of red oak distribution, Etterson et al. (2020) found that southern ecotypes exhibited both greater survival and growth compared to their northern counterparts. This finding aligns with the results of our study, which also support the concept of selecting appropriate provenances based on climate analogs (Dessai et al., 2005; Salinger et al., 2005) within the context of assisted migration (Pedlar et al., 2012; Williams and Dumroese, 2013). However, conducting similar research over multiple planting years will still be necessary to further elucidate and understand how ecotypes will cope in the long term under future climate conditions.

4.3 Predation and herbivory

Acorn predation and leaf herbivory had significant impacts on red oak regeneration. The most severe impact was with acorn predation. We believe the failed germination study in 2018 was mostly due to high predation. Regardless of provenance, acorns were almost entirely consumed by local fauna, mainly chipmunks (*Tamias striatus*), when planted in May 2018 as we observed an abundance of empty acorn residues on the ground. Many pictures of eastern chipmunks, white-tailed deer (*Odocoileus virginianus* Zimm.), squirrels (*Sciurus* spp. and *Glaucomys* spp.) and North American porcupine (*Erethizon dorsatum*

L.) foraging red oak acorns and seedlings were captured in the plots (Lebel-Desrosiers, 2021). The 2018 summer was also one of the warmest in record (Ministère de l'Environnement et de la Lutte contre les changements climatiques, 2021b), and this has likely participated in the desiccation of acorns. Second, browsing impacted seedling survival for SBL, MR and PC provenances, but only affected overall growth marginally. Blossey et al. (2019) showed a substantial difference in red oak seedling growth rate induced by browsing, whereas Buckley et al. (1998) found that the removal of plant competitors can enhance the pressure from deer browsing on red oak seedlings. Thus, browsing can be of significant importance for red oak regeneration, and its apparent effect on growth may increase after several growing seasons. This idea is also corroborated by Long et al. (2012) who observed a positive and increasing effect of deer browsing protection on height and root collar development of red oak seedlings over 5 years.

4.4 Soil nutrient availability

Soils are often identified as a main descriptor of site quality and suitability for given species (Hulshof et al., 2020) and red oak specifically (Nowacki et al., 1990; Nowacki and Abrams, 1992). The literature regarding red oak describes the species as thriving on nutrient poor, acidic, uphill mesic sites (Crow, 1988; Sander, 1990), a description that suits both study sites at SBL. As a whole, sites 1 and 2 exhibited similar acid–base status in the forest floor, but the mineral soil at site 1 showed slightly higher total N and exchangeable base cation concentrations. These results suggest that soil nutrients had minimal effect on red oak seedling metrics measured in the field experiment, which may be explained by the presence of too many confounding factors that hold greater limiting effects on its regeneration. For one, water limitations in 2019 likely overshadowed the effect of soil nutrient supply and fertilization on red oak seedlings. The fact that ash and biochar fertilization have, for the most part, not shown a significant increase in seedling survival and growth at either site reinforces the idea that soils with higher pH and nutrient availability, as seen for the forest floor at both sites following ash and biochar application, are not more conducive to red oak survival and growth. This is opposite to the results of the greenhouse experiment that show a positive effect of soil nutrient availability on germination, growth and survival of red oak seedlings. However, the greenhouse experiment was conducted under ideal growing conditions regarding light and water availability as well as air temperature, and without predation and disease.

It should be considered, however, that the absence of a response of red oak seedlings to ash and biochar fertilization could be due to a delay for nutrients to be absorbed by the roots. Several studies show a delayed response of plants to ash fertilization (Reid and Watmough, 2014; Bélanger et al., 2021b). Root length and radius, or more specifically total root surface area, influence plant nutrient uptake (Barber and Silberbush, 1984). As such, the underdeveloped root system of the planted seedlings likely had a low capacity for absorbing the nutrients added from the ash. This could also stem from the fact that while the benefits of ash fertilization on the forest floor occurs quickly, the response of the mineral soil is slower as it takes more time for the nutrients to migrate further down and react with soil exchangeable surfaces (Reid and Watmough, 2014, Brais et al., 2015). Schuler and Robison (2010) showed that fertilization had very little positive effects on red oak seedling survival and growth, even in the case where trees competed with other plants for nutrients and other resources. Furthermore, Kolb et al. (1990) showed that, at higher soil fertility and in the absence of light or water stress, yellow poplar performs better than red oak. Thus, since red oak is outpaced by late-successional or more shade-tolerant competing species, regeneration of the species may not benefit much from higher soil nutrient availability if other resources are limited. Fertilization may provide more benefits in soils with marginal fertility where competing plant species are potentially suppressed by the intrinsically low nutrient supply.

5 Conclusion

This study of red oak at the northern limit of its distribution showed that the species remained dominant in the two studied stands throughout the 20th century but is now showing regeneration failure. Stands appear to be shifting toward more shade-tolerant, late successional species such as American beech. Results also suggest that fire played a role in the establishment of red oak and succession of sugar maple, with red oak stand age structure dating to the last known fire disturbance occurrence. Although red oak trees were dominant in both stands, variability in tree species composition and density between stands suggests that regeneration dynamics differed substantially. This result may be due to differences in pre-fire species composition, fire frequency/severity and site physical characteristics such as slope direction and aspect. The study also displayed the importance of other factors in the regeneration process of red oak trees at this latitude. Site was found to have a significant impact on germination, survival and growth of seedlings. The site with higher LAI showed greater regeneration success, although more research is needed to assess if this was solely a result of lower water stress or other overstory effects on understory microclimate. Acorn provenance was also another important factor affecting red oak regeneration. The findings of this research therefore display the need to better characterize the response of red oak to site quality while considering the genetic signatures for optimizing success at early regeneration stages. Furthermore, parasites such as weevils and borers and foraging by small mammals, mostly rodents, were found to have large effects on regeneration at the acorn stage, while deer browsing was found to significantly affect survival, and growth to some extent, at the seedling stage. Finally, soil nutrient availability affected germination, survival and growth positively only when other factors (e.g., water and light) were not limiting. As a whole, this study highlights the need to select sites with adequate water availability, use provenances with proper future climate analogs, and protect seedlings against herbivory to maximize regeneration success, though further testing is required to fully assess the effect of water availability and associated thresholds for red oak seedling and sapling survival and growth. Fertilization with wood ash will likely only be beneficial if other conditions are met.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because observations were made using a camera only.

Author contributions

SL: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Visualization, Writing – original draft, Writing – review & editing. AC: Methodology, Validation, Writing – review & editing, Data curation, Investigation, Software, Visualization. NB: Methodology, Validation, Writing – review & editing, Conceptualization, Formal analysis, Funding acquisition, Project administration, Resources, Supervision.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2024.1451161/full#supplementary-material

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Forest assisted migration and adaptation plantings in the Northeastern US: perspectives and applications from early adopters

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Threats to the future function of forested ecosystems and stability of ecosystem service provisioning due to global change have motivated climate-adaptive forest management strategies that include various forms of tree planting termed "adaptation plantings". Despite the emergence of these strategies, less is known as to how foresters and other natural resource managers perceive or are engaged with adaptation plantings like forest assisted migration (FAM). This knowledge gap is most pronounced in regions like New England and the North Central US (hereafter, the Northeastern US) where tree planting is less common but expected to be an important forest management tool for adaptation. To address this, we surveyed 33 natural resource managers in this region actively engaged in climate change adaptation (i.e., early adopters of the practice) to assess how tree planting for adaptation is currently being pursued against the perceived barriers, opportunities, and potential future engagement with the strategy. Survey respondents overwhelmingly (93.5%) forecast increases in the future use of adaptation plantings in their work in the region, attributed to increased awareness, acceptance, and interest in the practice. Respondents expressed notable interest in strategies related to diversification and most types of FAM (e.g., assisted population expansion and assisted range expansion), but hesitancy to engage with more contentious planting types like afforestation or FAM linked to the long-distance translocation of exotic species (e.g., assisted species migration). Although examples of local enrichment plantings (i.e., non-FAM) proliferate, nineteen of the top twenty most common tree genera planted contain at least one example of FAM in the study region. The most notable barriers reported were themed as 1) biotic and abiotic, 2) information and material, and 3) policy, social, and economic factors. While most respondents report difficulty obtaining adequate planting material from nurseries (i.e., seedlings), over 80% placed orders shortly before planting ($<$ 1 year) which likely generates difficulty in sourcing seedlings suited for a specific site and future range of environmental conditions. Although this study is limited by focusing on subset of natural resource managers who are early adopters of climate change adaptation within the region, valuable inferences into the barriers and trends are possible from this population serving on the front lines of forest adaptation. Together, these results from early adopters suggest a potentially growing need for allocating resources that engage forest stewards in adaptation planning and serve to refine policy, financing, and management practices to support this adaptation strategy in this region and beyond.

KEYWORDS

assisted migration, managed relocation, silviculture, forestry, assisted colonization, climate adaptation

1 Introduction

Global climate change is expected to affect forested ecosystems worldwide, with impacts to community structure, composition, and ecosystem function (Dale et al., 2001). Consequently, these challenges have given rise to forest management strategies that emphasize ecological maintenance and restoration (Palik and D'Amato, 2023), climate change adaptation (Millar et al., 2007; Bowditch et al., 2020), and greenhouse gas mitigation (i.e., natural climate solutions; (Griscom et al., 2017). Understanding how to implement these strategies, along with associated barriers and opportunities, will be important for moving towards operational implementation of climate-smart and adaptive management strategies in the face of global change (Nagel et al., 2017; Verkerk et al., 2020).

Among a suite of climate-smart and adaptive forest management strategies, artificial regeneration (i.e., tree planting) has increasingly become viewed as a critical tool for global change adaptation (Verdone and Seidl, 2017; Domke et al., 2020; Holl and Brancalion, 2020). Termed here as "adaptation plantings", these tree planting strategies differ from traditional artificial regeneration techniques that largely prioritize commodity and timber production and focus on a limited set of commercially valuable species (Bennett, 2015; Martin et al., 2021). In contrast, adaptation plantings emphasize one or several aspects linked to global change adaptation and correspondingly often involve a greater variety of species and genotypes (see Table 1 for detailed descriptions of adaptation planting types). For instance, adaptation plantings may include strategies aimed at a) promoting the adaptive capacity of ecosystems by diversifying, restoring, and/or sustaining ecologically and culturally important foundational species or ecosystem functions (Stanturf et al., 2014; D'Amato et al., 2023), b) encouraging the functional replacement of species degraded by disturbances (D'Amato et al., 2018), c) mitigating greenhouse gas emissions through increased carbon stocks (Domke et al., 2020; Lefebvre et al., 2021), or d) the use of forest assisted migration (FAM) to adaptively respond to shifting habitat conditions caused by climate change (Pedlar et al., 2012; Palik et al., 2022). Notably, forest assisted migration aims to intentionally augment genotypes or introduce tree species from warmer (e.g. southern latitudes, lower elevation) or otherwise future climate-adapted regions to offset lags in natural migration rates relative to the pace of climate change (Sittaro et al., 2017; Iverson et al., 2019). Despite a long legacy of planting being used in forest management globally as a means of achieving various regeneration objectives (Bennett, 2015), less is known about how natural resource managers are engaged with adaptation planting as part of various forest management strategies (McGann et al., 2022; Himes et al., 2023; Schattman et al., 2024). This is particularly apparent for more "novel" adaptation planting strategies like forest assisted migration that have long been perceived as risky (Hewitt et al., 2011; Findlater et al., 2022) but potentially timely and necessary in some forests where the risk of inaction may lead to greater ecosystem vulnerability (Palik et al., 2022).

Artificial regeneration is commonplace globally and employed in many regions of the United States, such as the southeastern and western states, where tree planting is either a primary silvicultural activity, such as in plantation forestry or complementary to reliance on natural regeneration as part of different silvicultural systems (Nyland, 2007). In other regions like New England and the North Central US (hereafter, the Northeastern US, in accordance with the USDA Forest Service region 9), artificial regeneration has traditionally been of lesser importance due in part to the silvicultural practices and dominant forest types that support abundant natural regeneration of ecologically and economically desired species. Nevertheless, recent interest and a growing recognition for practices that transition beyond "business as usual" approaches have led to growth of adaptation plantings in this region (Muller et al., 2019; Etterson et al., 2020; Clark et al., 2021; Palik et al., 2021). In fact, in 2022 forest nurseries in this region produced over 52 million seedlings supporting reforestation efforts on approximately 16,000 hectares of forest lands (Pike et al., 2022). Moreover, given the high species richness of forests in the Northeastern US, this region is expected to be fertile grounds for forest assisted migration where over 40 tree species are forecast to either decline or increase in habitat suitability due to climate change over the next century (Peters et al., 2020; Prasad et al., 2020). Yet, adaptation plantings like forest assisted migration are not a mainstream practice with few, but a growing number of examples of practice. Therefore, generating an understanding as to how and why natural resource managers in the Northeastern US are engaged with adaptation plantings, including but not limited to assisted migration, will be critical in refining policy, attracting financing, and improving best management practices in this region and beyond (Clark et al., 2023). Lastly, given the need for actionable, translational research during a time of unprecedented change

TABLE 1 A list of planting terms (e.g., types), grouped among commonly associated climate adaptation objectives, along with definition of terms in the context of global change applications and examples of their use.

Adaptation objective	Adaptation planting term	Definitions and examples
Diversity, restoration, and resilience	Species and ecosystem restoration	*Reestablish or diversify native species and ecosystems to historical conditions and/or conditions that are expected to persist.* • Efforts to reestablish *Picea rubens* (www.restoreredspruce.org) and *Castanea dentata*; www.acf.org) populations, two keystone species threatened or functionality extirpated due anthropogenic disturbances and disease, respectively. • Restoration and diversification of upland and riparian forests to support ecosystem resilience (e.g., supporting riparian area function and flood mitigation potential: www.uppersusquehanna.org/usc/) or restoring native habitat impacted by disturbance where natural regeneration would lead to insufficient recovery targets.
	Functional replacement	*Replacement of threatened or otherwise degraded species with new species that confer similar functional traits.* • The replacement of *Fraxinus nigra* lost due to invasive species with species that may maintain wetland habitat function (Palik et al., 2021). • The Civilian Conservation Corps efforts in the 1930s to plant *Pinus resinosa* in anticipation of declines in *P. strobus*.
Forest Assisted Migration (FAM)	Assisted population expansion (aka assisted population migration)	*Population augmentation of a species currently onsite or within its range using climate-adapted genotypes, commonly from southern or lower elevation seed sources. May also be used to confer disease resistance.* • Supplementary planting of southern genotypes (Palik et al., 2022). • Pine blister rust resistant five-needle pines planted through North America (Schoettle and Sniezko, 2007).
	Assisted range expansion	*Movement of a species outside of its historical range and expanded into adjacent areas in anticipation of increased habitat suitability in the near term, but to territory that the species could realistically establish in via natural dispersal over long timescales.* • Range expansion of *Quercus-Carya* species into northern hardwoods (Clark et al., 2021). • Indigenous North Americans promoted the northward expansion of fruit and mast species (Abrams and Nowacki, 2008).
	Assisted species migration	*Movement of at-risk species or the long-distance relocation (e.g., interregional, intercontinental) of a species beyond areas ever accessible via natural dispersal, necessitating deliberate intervention to establish.* • The movement of *Torreya taxifolia*, an endangered glacial relict species (ww.torreyguardians.org). • Asian *Fraxinus mandshurica* planted in Minnesota as a replacement species for *Fraxinus nigra* (Palik et al., 2021).
Greenhouse gas mitigation	Reforestation	*Increase stocking on low density sites and marginal lands (e.g., under or non-stocked cover types suitable for tree species).* • The Nature Conservancy's Plant a Billion Trees campaign and the Minnesota Million (www.nature.org). • Spatially explicit reforestation decision support tools (www.reforestationhub.org).
	Afforestation	*Establish forests on historically unforested lands to increase forest cover.* • Bottomland afforestation systems with multiple species (Gardiner et al., 2004). • Afforestation on agricultural lands taken out of row crop production.
	Reclamation	*Return degraded sites to forested state.* • Tree planting abandoned mines to increase above and belowground carbon stores (Fox et al., 2020). • Reforestation of degraded forests due to wildfire or human activities (Lefebvre et al., 2021).

Although presented within discrete associated climate adaptation strategies, the grouping only serves to differentiate outcomes as many adaptation planting types may achieve one or multiple objectives related to global change. Moreover, objectives unrelated to global change are also available (e.g., timber) but are intentionally omitted for clarity.

(Enquist et al., 2017), it is particularly important to assess the activities of early adopters of practices, as this population can serve as a critical litmus test on the front lines of application, perception, and knowledge transfer (Rosenzweig and Solecki, 2014; Storbjörk et al., 2024).

With these needs in mind, the objectives of this study are to assess current perspectives, practices, and limitations associated with tree planting for adaptation, principally forest assisted migration, in the Northeastern US. To achieve this, we used a survey tool to solicit responses from regional foresters and natural resource managers actively engaged or interested in climate adaptation (i.e., "early adopters" of these practices) to answer the following questions:

1. *What is the current and anticipated future level of engagement with adaptation plantings among early adopters?*

2. *How and why is tree planting being employed for climate change adaptation?*
3. *What species are favored for assisted migration?*
4. *What factors are most limiting decisions to pursue adaptation planting?*

Our overall goal is to provide a critical baseline of knowledge for informing adaptation plantings and broad reforestation practices, seedling production and capacity building, and the barriers limiting the application of these strategies to address diverse adaptation objectives across the region. Given the apparent novelty of some of these practices (i.e., FAM), we specifically targeted a population of early adopters to gauge the state of the practice among this population and have subsequently constrained inferences within this subset of foresters and natural resource managers.

2 Materials and methods

2.1 Survey design and administration

To gather insights into the perspectives and applications of adaptation planting in the region, we conducted an online survey using the Qualtrics survey tool in the spring of 2022. Survey questions were broadly focused on capturing insights into the practices, levels of experience, and barriers facing natural resource managers related to adaptation plantings (see Supplementary Appendix 1 for complete version of the survey administered). The survey was targeted towards natural resource managers and other professionals (e.g., foresters, conservation professionals, researchers) actively engaged with climate change adaptation. Although we recognize the value of querying a broad sample of forest stewards, we were specifically focused on respondents who are interested in or have engaged with climate change adaptation in forest management for our research purposes of characterizing, assessing, and clarifying the challenges and practices of this subgroup of early adopters.

The survey was tested prior to deployment with three forestry professionals familiar with the topic area and revised according to their feedback. Surveys were designed to be completed in less than 30 minutes. No compensation was offered to participants. We used purposeful informant sampling (Patton, 2002) targeting individuals in the twenty-state Northeastern United States, namely New England and North Central regions (Iverson et al., 2008). To achieve this, we solicited participation through email membership lists and online regional newsletters for the Northern Institute of Applied Climate Science (NIACS; 4,326 potential subscribers) as well as via the National Council for Air and Stream Improvement, Inc (NCASI; unknown number of subscribers). Human subject protection approval was issued by the University of Vermont Institutional Review Board (STUDY00002004).

2.2 Analysis

A total of 44 surveys were returned, but we discarded those responses in which the participant completed less than 50% of survey questions and one respondent from outside of the focal region. This process resulted in 33 valid surveys from natural resource managers working in the Northeastern US and engaged with climate change adaptation. Using these data, we generated summaries of results using numerical, rank ordinal, or proportion of responses and examined differences among populations using ANOVAs followed by Tukey Honesty Significance (HSD) as well as Pearson's correlation coefficient. A significance threshold was set for all tests at $\alpha = 0.05$ and each statistical test was assessed and diagnosed to pass test assumptions including those of linearity and normality of residuals. For written essay responses (one question), we report raw responses as well as coded common themes, informed by grounded theory (Charmaz, 2014). Given the limited sample size, we elected not to employ higher-level multivariate models to assess the role of participant demography (e.g., geography, employment, training, etc.), rather focusing on the outcomes of the overall sample population of early adopters engaged in climate change adaptation.

3 Results

Respondents most frequently reported working in New York (33.3%), Massachusetts (21.2%), New Hampshire (12.1%), Vermont (12.1%), and Wisconsin (6.1%). The remaining respondents were from Maine, Maryland, Minnesota, Pennsylvania, and Rhode Island (3.0% each). Participants self-identified to be among various roles engaged in forest stewardship including forester (42.9%), conservation professional (28.6%), landowner (11.9%), researcher (9.5%), and other (7%). Most were employed within conservation agencies (40.5%) while the remaining were employed within state agencies (18.9%), research institutions (13.5%), municipalities (10.8%), federal agencies (8.1%), or in private consulting (8.1%). Respondents reportedly managed varying amounts of forest land, where most oversaw larger land holdings including land exceeding 10,000 hectares (43.3%), 2,000–9,000 hectares (26.7%), and 400–1,999 hectares (13.3%). In terms of forest types, the majority of respondents reported to work in Northern Hardwoods (*Acer-Fagus-Betula*; 26.5%), followed by Oak-Pine (*Quercus-Pinus*; 17.6%), Oak-Hickory (*Quercus-Carya*; 15.7%), Spruce-Fir (*Picea-Abies*; 9.8%), Riparian hardwood (*Ulmus-Fraxinus-Populus; 8.8%*), Aspen-Birch (*Populus-Betula*; 7.8%), and White-Red-Jack Pine (*Pinus strobus-P. resinosa-P. banksiana*; 5.8%).

When asked about their level of experience with tree planting, the majority reported high levels of expertise, with 21.9 and 37.5% self-identified as "very experienced" or "experienced", respectively. The remaining respondents identified as "slightly experienced" (28.1%) or "not at all experienced" (12.5%).

3.1 What is the current and anticipated future level of engagement with adaptation plantings among early adopters?

When respondents were asked if they had used tree planting aimed at global change adaptation, nearly all respondents answered in the affirmative (96.7%), with 54.5% responding "Yes, I have implemented" (*n* = 18), 9.1% responding "No, but I am planning to implement" (*n* = 3), and 33.3% responding "No, but I would consider implementing" (*n* = 11). Only one respondent replied "No, I haven't and don't plan to implement". Of those respondents in the affirmative, the majority (63.6%) reported to have engaged with two – four adaptation planting projects in the last ten years, while 18.2% reported one project, 13.6% reported greater than ten projects, and 4.5% reported five – nine projects.

When respondents were asked how the number of adaptation planting projects that they were engaged with are expected to change over the next 10 years, nearly all reported that relative to present day they expected the number to increase (93.5%) or stay the same (2%). None forecasted a decrease in the number of adaptation planting projects in the future. Among those respondents who provided an optional written response outlining why they expected the amount of adaptation planting projects to change in the future (Figure 1), the most common themes reported were a) *awareness, acceptance, and interest* (*n* = 12, 26%), b) *adaptation and climate resilience* (*n* = 8, 17%), and c) *restoration of species and ecosystems* (*n* = 5, 11%). Only 4% (*n* = 2) explicitly use the term (or related terms) d) *forest assisted migration* as a driver for increasing future adaptation projects, although there are arguably links to the "adaptation and climate resilience" theme noted above. Other themes reported included e) *biotic and abiotic disturbance and stressors*, f) *logistics and best management practices*, g) *research*, h) *invasives, pests and pathogens*, i) *information and resources*, j) *reforestation*, k) *carbon mitigation*, and l) *markets, demand, and forest products*.

3.2 How and why is tree planting being employed for climate change adaptation?

Survey respondents were asked to rank various forest management objectives as to how important they are related to adaptation planting efforts, where very important = 2, important = 1, neutral = 0, unimportant = −1, and very unimportant = −2. In order of mean ranking from most to least important, objectives included a) *to diversify current conditions* (1.4 ± 0.2 SE), b) *to change forest conditions to align with future climate (e.g., FAM;* 1.1 ± 0.2), c) *to change forest conditions to adapt to disturbances (e.g., invasives;* 1.1 ± 0.2), and d) *to store more carbon and greenhouse gasses* (0.9 ± 0.2). Ranked importance among these four strategies did not differ significantly ($p \geq 0.05$ Tukey HSD); however, e) *to maintain historical/existing conditions* (0.2 ± 0.2) ranked significantly lower in terms of importance ($p < 0.05$) compared to all other objectives.

To better understand how different adaptation planting strategies were applied in this region, respondents were asked to rank their level of interest and engagement with ten planting types aimed at global change (Figure 2). Relative to all other levels of strategies, most respondents reported that they have already implemented strategies that included "reforestation of native species", "reforestation to maintain ecosystem functions", and "rehabilitation of degraded sites" (mean proportion of respondents = 43.9%). Additionally, on average 43.5% of respondents reported being interested in the "restoration of historically important [e.g., foundational or keystone] species", "replacing species threatened by disturbance with new species", or "reforestation to increase carbon for climate mitigation" but lack plans or experience in these practices. In terms of assisted migration, 55.6% of respondents report actively having plans or have already implemented assisted population expansion of "climate-adapted genotypes from species currently found onsite" and assisted range expansion of "climate-adapted species not onsite but with ranges found nearby" that would migrate into the region over long timescales (see Table 1 for clarification around terms). On the other hand, most respondents report that they don't plan to implement "afforestation planting on historically unforested lands" (38.7%) or "assisted species migration in the form of long-distance introduction of novel species tolerant of future climate/disturbances" (58.1%).

3.3 What species are favored for assisted migration?

We compared what species were favored for FAM relative to those commonly favored under other non-FAM applications (e.g., local enrichment plantings). Respondents were asked to report which species they plant (or intend to plant), as well as codify each based on three terms relative to seed source location or two FAM types: a) local enrichment of native genotypes (non-FAM), b) assisted population expansion (FAM type 1), or c) assisted range expansion (FAM type 2; Figure 3). Based on responses collected, the most frequently reported deciduous genera were *Quercus* and *Carya* while the most frequently reported coniferous genera were *Pinus* and *Picea*. Overwhelmingly, most plantings are classified as non-FAM local enrichment plantings (71.6% ± 2.7), with only 14.2% (± 1.7) reporting to plant (or intending to plant) under conditions classified as FAM (either assisted population or range expansion). When FAM types are compared, assisted population expansion remains more popular than assisted range expansion strategies (19.6% ± 2.0 versus 8.8% ± 2.1, respectively). In terms of the proportion of plantings coded as FAM, the most common species reported to be planted using FAM (combined assisted population expansion and range expansion) include *Picea* (proportion of plantings reported as FAM = 47%, ranked order of all genera = 9, total number of plantings reported by genera N = 17), *Juglans* (FAM = 46%, rank = 7, N = 18), *Pinus* (FAM = 44%, rank = 2, N = 57), and *Quercus* (FAM = 41%, rank = 1, N = 135). In terms of *Picea*, it is important to note that half of the examples of FAM reported refer to *P. abies* which is non-native to the US (of European origin) and represents the only example of assisted species migration reported in the study.

Among the most frequently reported deciduous and coniferous genera (*Quercus*, *Carya*, *Pinus* and *Picea*), 62 species were reported to be planted, of which a subset of 27 are included in Figure 4 (species list truncated to those with at least ≥ 3 observations). Each species in the subset included at least one observation classified as FAM. Nearly all species include plantings classified as assisted population expansion (89.3% of observations), where the only exceptions that lacked examples are *C. alba*, *P. abies*, and *Q. prinoides*. None of the most common species planted among

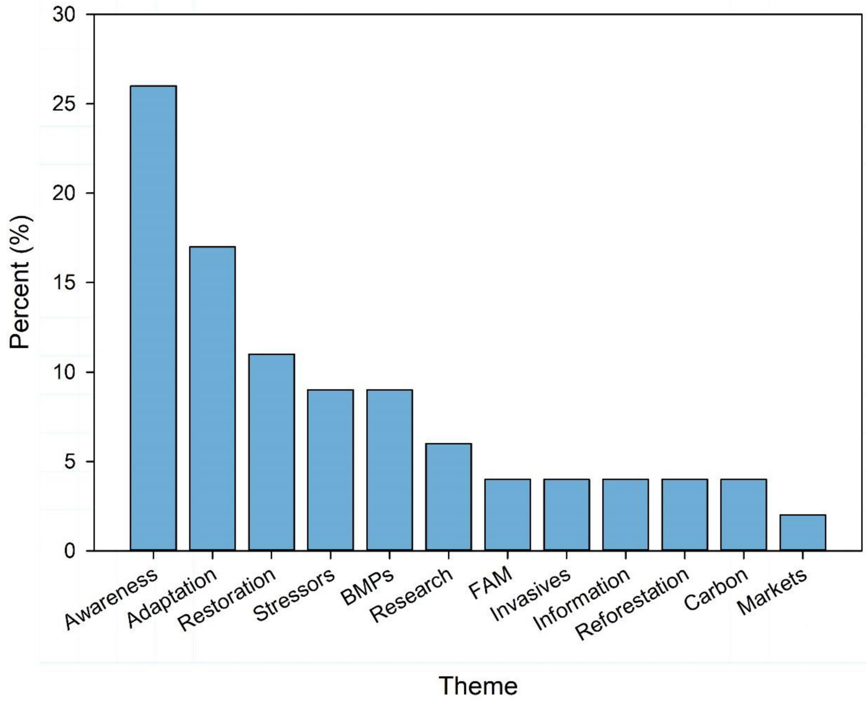

FIGURE 1
Optional text-based responses to the prompt "How do you expect the number of adaptation planting projects that you are engaged with to change over the next 10 years? Why?" Responses are coded by common themes: *Awareness* = awareness, acceptance, and interest, *Adaptation* = adaptation and climate resilience, *Restoration* = restoration of species and ecosystems, *Stressors* = biotic and abiotic disturbance and stressors, *BMPs* = logistics and best management practices, *Research* = Research, *FAM* = forest assisted migration, *Invasives* = invasives, pests and pathogens, *Information* = information and resources, *Reforestation* = reforestation, *Carbon* = carbon mitigation, *Markets* = markets, demand, and forest products. See Supplementary Appendix 2 for raw text-based responses and thematic coding.

each genus were classified as assisted range expansion, including *Q. rubra*, *P. strobus*, *C. ovata*, and *P. glauca*. In fact, species ranked order based on the total number of plantings is inversely correlated with the ranked order of the proportion of assisted range expansion plantings reported per species (mean $r = -0.86 \pm 0.1$, $p \leq 0.01$).

3.4 What factors are most limiting decisions to pursue adaption planting?

Given the important role of species, seedlots, and stock selection in FAM and adaptation plantings, we asked two questions targeted at seedling procurement strategies and availability at forest nurseries. When asked which approach best describes the typical strategy for procuring planting stock, the vast majority (82%) operated on short timelines (< 1 year), electing to place orders several months before planting, based on availability (50%), purchase seedling material immediately before planting (13%), or employ no set strategy (6%). Some respondents did report that they do work with nurseries months to years in advance to grow ideal species, seed sources, or stock types for projects (13%), while 6% employed "other" approaches to procure seedlings. When asked how they would describe their ability to obtain diverse seedlings from forest nurseries (e.g., species, seedlots, and stock types/ages), 66.7% reported to have some or much difficulty in obtaining seedlings. Omitting those who responded that they were unsure to the following prompts, few respondents report having no difficulty obtaining diverse species selection (16.0%), various seed sources (e.g. provenances, genotypes; 4.7%), and different seedling stock (e.g., size/age, containerized vs bare root; 4.2%) in forest nurseries. All remaining respondents reported having some or much difficulty in procuring diverse seedlings (e.g., species, seedlots, and stock types).

Survey respondents ranked seven factors deemed influential in determining adaptation planting decisions, associated with a) biotic and abiotic factors, b) information and material resources, and c) policy, social, and economic considerations (Figure 5). The most important factors in terms of rank order were determined to be related to a) biotic and abiotic (1: *future climate change, disturbances, and novel conditions* and 2: *present-day conditions (e.g., competition, browse, soils, climate)*, then b) information and material resources (3: *access to appropriate planting material (e.g., species, seed sources, stock*) and 5: *information, training, and resources*), followed by c) policy, social, and economic considerations (4: *risk of failure (e.g., maladaptation)*, 6: *economics and labor*, and 7: *policy, regulation, other's perceptions*).

Among the three groups listed above, respondents reported how influential various subcategories are towards informing decisions to plant for climate change adaptation, including eight subcategories linked to biotic and abiotic factors, six associated with information and material resources, and nine related to policy, social, and economic considerations (Figure 6). The most limiting biotic and abiotic factors ranked included *vegetative competition, browse, predation* > *post-planting*

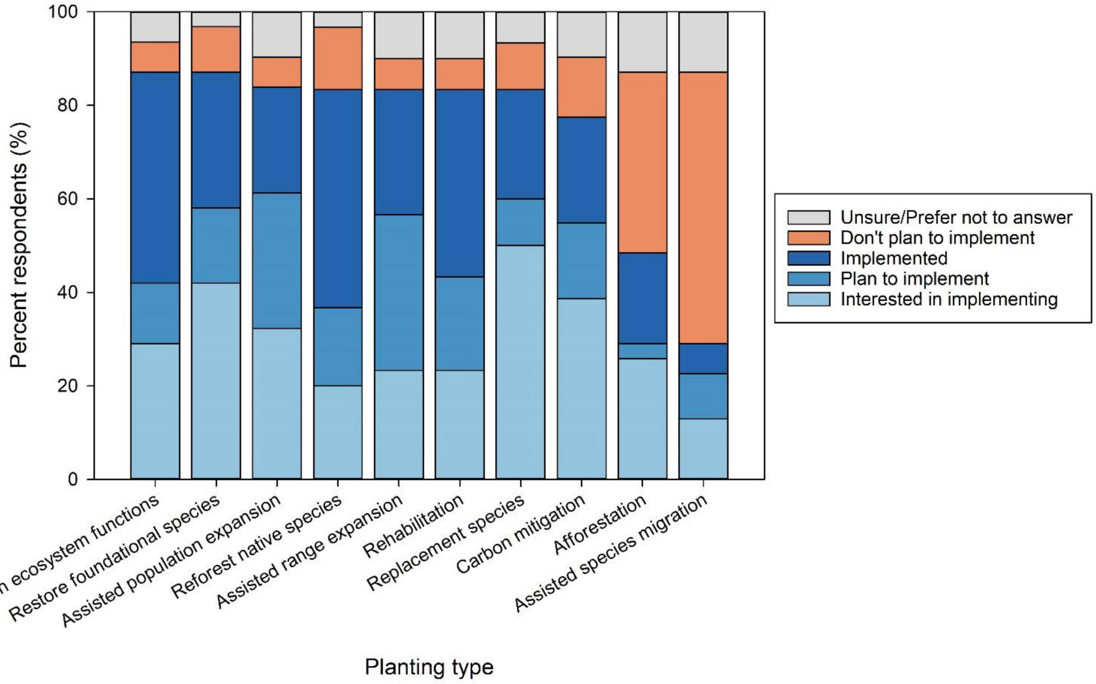

FIGURE 2
Respondent engagement among various adaptation planting types for global change. Planting types are presented from left to right in terms of level of implementation. Given the emphasis on understanding forest assisted migration (FAM) in this work, the three types are FAM are presented here: assisted population expansion, assisted range expansion, and assisted species migration.

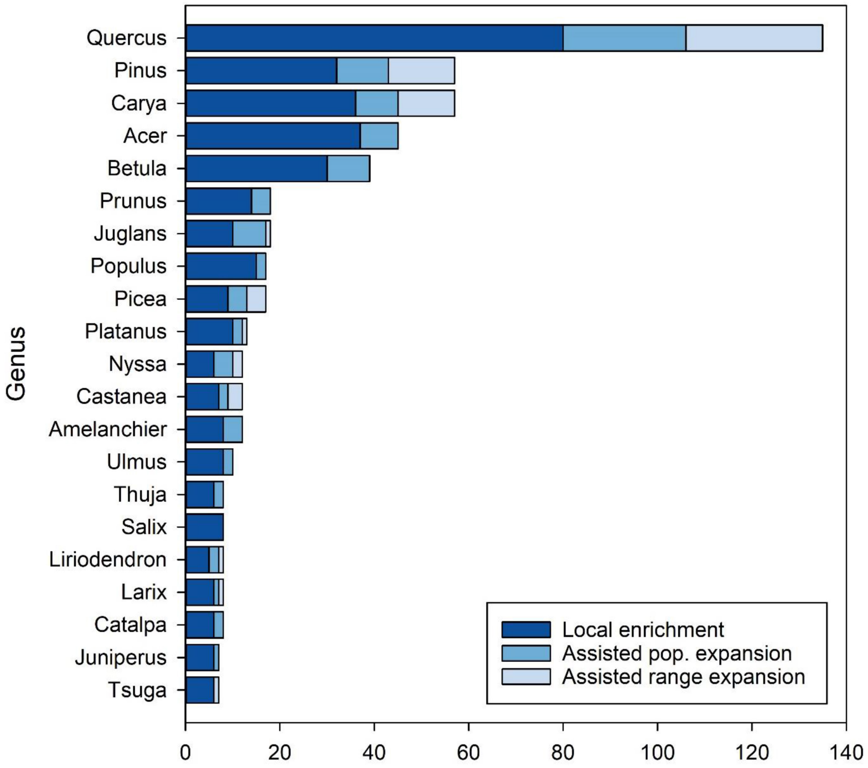

FIGURE 3
Top twenty genera of trees reported or forecasted to be planted by survey respondents. Planting types are presented in terms of the number of plantings binned by (a) local enrichment (non-FAM) and the most common forest assisted migration (FAM) types, (b) assisted population expansion, and (c) assisted range expansion.

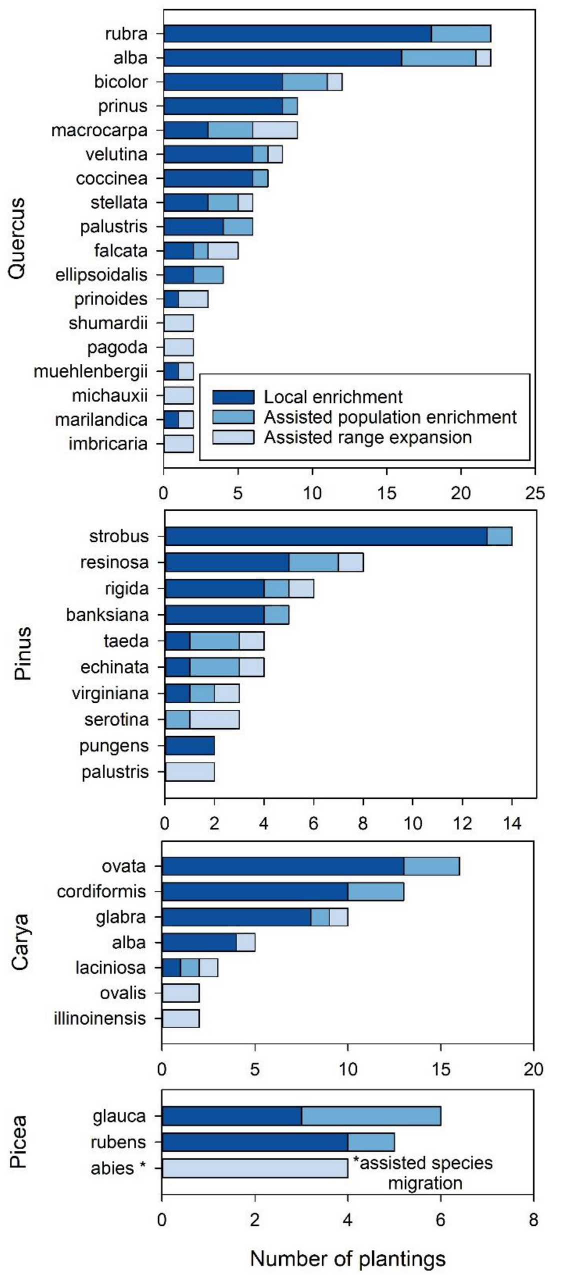

FIGURE 4
The most common species reported (or intended) to be planted among the top two deciduous and coniferous genera. Planting types are presented in terms of the number and percent by (a) local enrichment, and the most common forest assisted migration types, (b) assisted population expansion, and (c) assisted range expansion. Note that *Picea abies* is non-native to the United States and is an example of assisted species migration, but for clarity the figure is coded as assisted range expansion.

management > *invasive plants, pests, and pathogens* > *future projections for climate* > *projected shifts in species habitat* > *site preparation management*, while the least important (based on Tukey HSD tests) were *new, novel, or changes in disturbances* > *current climate (e.g., temperature, precipitation).* The most limiting information and material resources ranked included *stock type availability at nurseries* > *obtaining enough seedlings from nurseries* > *species availability at nurseries* > *seed source availability at nurseries* > *resources for planting climate-adapted species* while the least important was the respondent's *experience with planting.* The most limiting policy, social, and economic considerations ranked included *planting failure occurring* > *funding the practice* > *labor* > *risk of biological invasion,* while the least important were *public perceptions* > *supervisors/landowner directives* > *peers/other manager perceptions* > *policy/regulations* > *economic returns.*

4 Discussion

The capacity of forest ecosystems to respond to global climate change may be driven in part by the forest management decisions made today. For instance, the intentional movement of species and genotypes to match shifting ranges (i.e. FAM), the replacement of threated species, or maintenance and restoration of culturally and ecologically important species (and genotypes) are likely to be necessary if not critical tactics in supporting future levels of ecosystem service delivery that are within a socially acceptable range of variability (Seidl et al., 2016). Yet, to date, little is known about how natural resource managers are engaged in these practices, particularly those more novel adaptation strategies like forest assisted migration. The results from this study largely support the limited but growing body of literature that outline the role of operational scale adaptation planting work in the Northeastern US, particularly those emphasizing FAM (Palik et al., 2022; Royo et al., 2023). Moreover, our study further suggests how and why interest in adaptation plantings may be growing, albeit based on a small, subset population of early adopters actively engaged in climate change adaptation and despite the persistence of external factors that influence its application, including adaptation and FAM objectives, biophysical influences, and logistical barriers.

4.1 Perspectives of adaptation plantings

Results from our survey appear to suggest a growing interest and level of application of tree planting for adaptation. Based on results generated from a population of early adopters actively engaged in climate change adaptation, nearly all respondents in our survey (93%) reported that they expect the number of adaptation planting projects that they are engaged with to increase over the following decade. Although many aspects likely contribute to why interest appears to be increasing, factors such as awareness and acceptance of climate change and invasive species impacts, and interest in adaptation and climate resilience (i.e. FAM) are the most common themes reported among the survey population. These results generally point to factors related to knowledge, perceptions, and peer-to-peer influence that have been shown to influence the adoption of some adaptation practices among foresters (McGann et al., 2022; Schattman et al., 2024), but refine these findings in the context of adaptation planting. This pattern is likely most apparent for more "novel" practices related to adaptation, such as FAM, which historically have been perceived as riskier but may now becoming a more fundamental tactic in the adaptation toolbox (Palik et al., 2022). Although our survey was

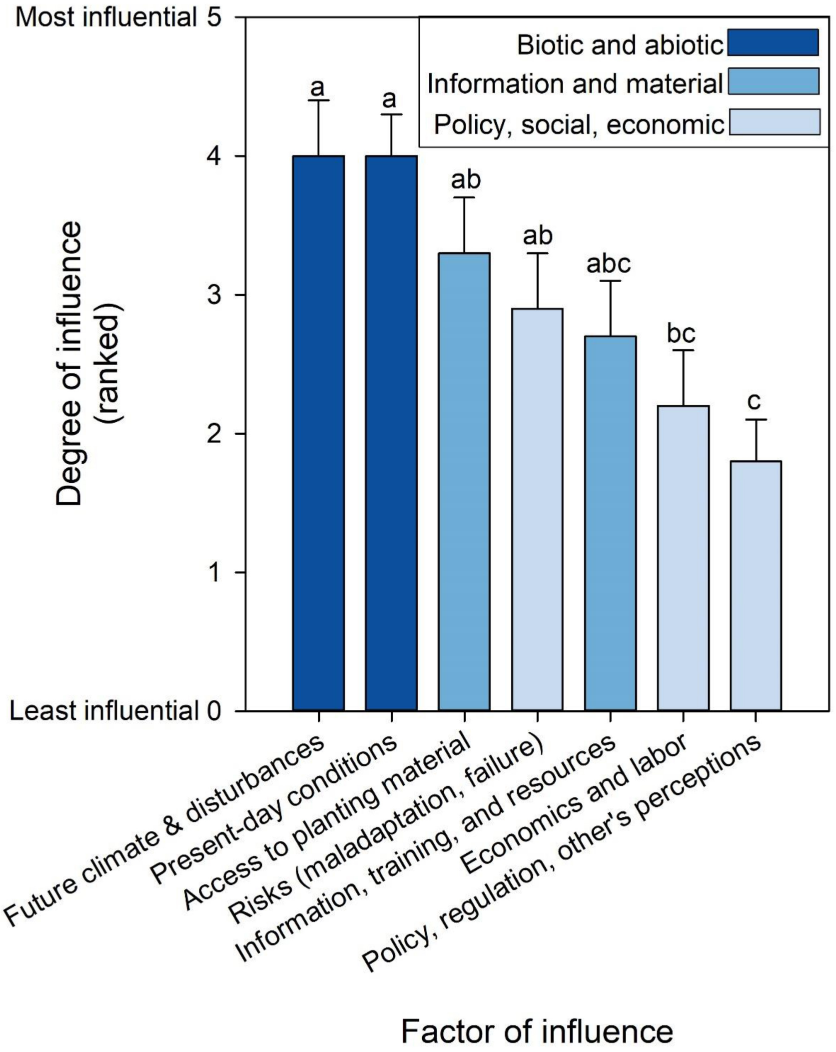

FIGURE 5
Ranked responses to the survey prompt, "What are the greatest influences for your decision to plant for climate change adaptation?", where 5 = *most influential* and 0 = *least influential*. Letters denote groups that are significant different where $p \leq 0.05$.

limited in the number of respondents and focused on a sample population of forest stewards already engaged with adaptation work (i.e., early adopters), the trends in these survey results illustrate that adaptation plantings and FAM may be a key tactic employed in adaptive forest management planning in the future (Himes et al., 2023).

In terms of how adaptation plantings are being pursued, most respondents (over 80%) anticipated the use of planting projects augmented by FAM, specifically assisted population expansion and range expansion. In fact, respondents were twice as likely to report having plans in place to implement FAM in the future relative to all other adaptation planting types queried. One interpretation of this trend is a potential expansion of the application of FAM compared to other adaptation planting types, although more information may be necessary to ascertain directionality. Still, other adaptation planting strategies related to diversifying forest conditions (e.g., restoration of foundational species, the use of replacement species) or carbon mitigation remain important with high levels of interest in future engagement. Although many respondents reported to have had experience implementing strategies related to maintaining historical conditions (e.g., reforestation of native species, maintenance of ecosystem function, rehabilitation of degraded sites), fewer anticipate future projects solely focused on these objectives. This trend is supported by other results in our study that illustrate the population of forest managers sampled here underemphasize strategies aimed at resisting the effects of global change (e.g., planting to maintain historical/existing conditions), rather, they exhibit a preference for planting strategies related to promoting adaptation, resilience, or ecological transition (e.g., to diversify current conditions, to change forest conditions to align with future climate, to change forest conditions to adapt to disturbances, and to store more carbon and greenhouse gasses; (Millar et al., 2007; Palik et al., 2022).

Our survey points to hesitancy among the sampled population to engage with two planting types, afforestation and assisted species migration, which are likely the most controversial and debated planting strategies presented within the scope of our survey (Pedlar et al., 2012; Di Sacco et al., 2021). Criticism of afforestation in this

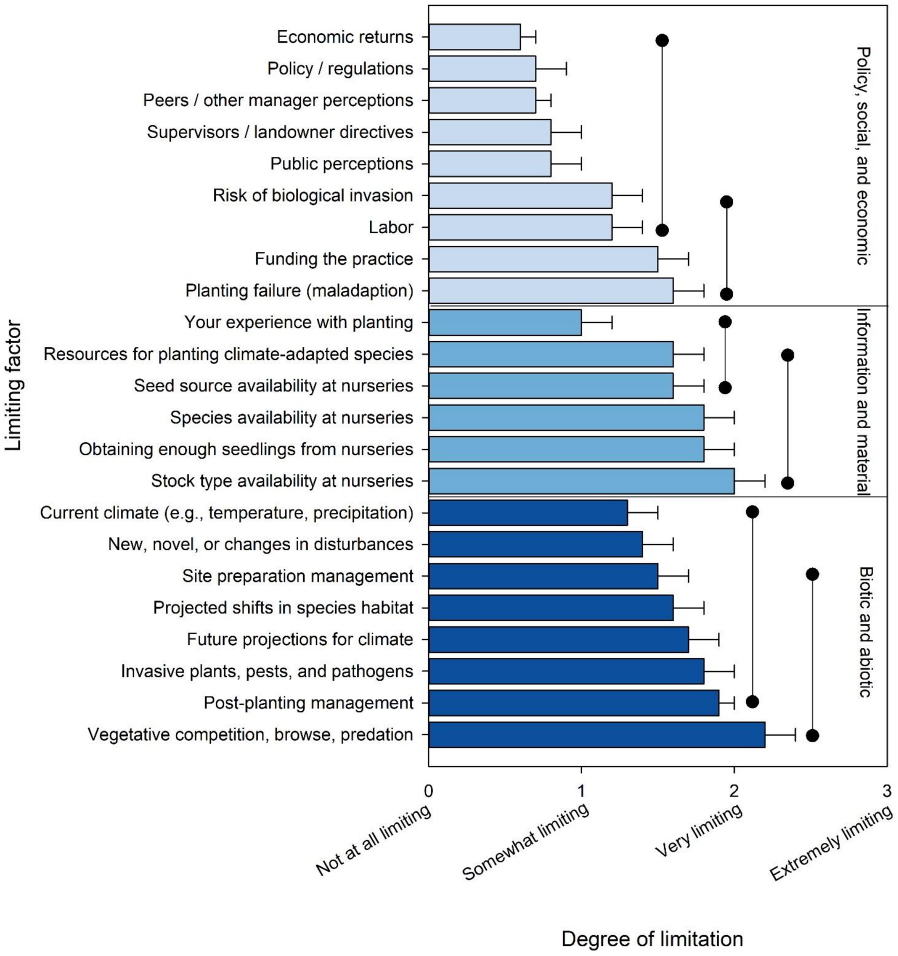

FIGURE 6
Responses to the prompt, "How limiting/influential are the following factors for your decisions to plant for climate change adaptation?". Responses are binned by (a) biotic and abiotic, (b) information and material, and (c) policy, social and economic factors. Horizontal bars denote factors that are not significantly different at $p \leq 0.05$.

region is likely centered around the loss of important herbaceous plant and wildlife habitat as well as ecosystem qualities of fields, meadows, and other historically unforested lands. Additionally, hesitancy to engage with assisted species migration is likely linked to a risk aversion to invasion or other unintended consequences of moving novel or exotic species. Relative to other FAM types like assisted population or range expansion which are regarded more favorably in our survey, manager sentiment toward assisted species migration is much less favorable. Given that adaptation planting types like afforestation and assisted species migration strategies are strongly associated with substantial shifts in ecosystem state, it is likely this generates uncertainty among natural resource managers tasked with sustaining ecosystem functions and services. Yet, as the consequences of global change are increasingly realized and/or uncertainty is minimized through research and implementation, it is possible that adaptation planting types like assisted species migration may become more necessary to adapt, functionally replace, and/or sustain forested ecosystems in the future. Lastly, it is important to note that adaptation planting strategies are not necessarily discrete or isolated from one another and may (or should) be paired to create complementary desired future conditions, such as timber productivity and FAM (Royo et al., 2023), restoration and FAM (Clark et al., 2022), or functional replacement and FAM (Palik et al., 2021). Taken together, the results from this work underscore that tree planting for adaptation appears to be growing in interest and implementation among natural resource managers actively engaged in climate change adaptation, although levels of engagement vary among planting types and objectives.

4.2 Application of forest assisted migration (FAM)

Within the subset population of early adopters sampled, interest in and the application of FAM differs among tree genera and species planted in the Northeastern US. The most commonly planted genera reported in our survey were *Quercus* and *Pinus* (26 and 16 species, respectively), which are highly valued for timber products but also support many critical cultural and ecological functions in the region. Moreover, these genera are some of the most commonly propagated in many forest nurseries in the region (Pike et al., 2018; Clark et al., 2023), likely resulting in relatively abundant inventory and source selection for planting projects. Given the role that these species have historically played in planting practices in the region, it is perhaps unsurprising that they are frequently planted to enrich local populations with native genotypes. This trend is consistent across all genera reported in the study, such that most plantings are classified as local enrichment. Nevertheless, even though engagement (or plans to engage) with FAM is subordinate to plantings for native population enrichment, which is unsurprising given the nascent stage of the practice, FAM still apparently represents up to one quarter of planting efforts reported among the sample population's work.

Among the sample population of early adopters, applications of assisted population expansion appear to be more common compared to assisted range expansion, and with very few examples of assisted species migration. For instance, on average twice as many planting projects reported in this study are coded as assisted population expansion versus those coded as assisted range expansion. Moreover, most genera contain at least one example of assisted population expansion (95%) while fewer genera contain an example of assisted range expansion (55%). One interpretation as to why natural resource managers may be more comfortable with assisted population expansion is that it allows for the accomplishment of multiple goals with more controlled, incremental changes and fewer perceived risks, relative to the other FAM types. For example, the inclusion of a future-climate adapted genotype of a species currently onsite may be considered safer (in terms of maladaptation) while simultaneously promoting climate adaptation and diversification (genotypic). In addition, these applications may be consistent with broader restoration goals to support historical forest and ecological conditions when the species planted represent those that were historically more formerly common in a given landscape (e.g., *Pinus strobus, Picea rubens*). Compared to an assisted range expansion planting, which may carry elevated risks (in terms of maladaptation) given that the target species does not already have a demonstrated site affinity beyond those projected by species distribution models (Iverson et al., 2019), assisted population expansion is more consistent with historical traditions in forest management surrounding matching species to a site based on past experience and current ecological conditions. Still, we only report one species used for assisted species migration, *Picea abies*, a species of European origin having been planted throughout the eastern US since the mid-1800s. Given the long history of planting *P. abies* in the region, it is likely natural resource managers are more comfortable with species as the risks of invasion or other unforeseen consequences of its introduction have been demonstrated to be minimal or unapparent. As threats from global change increase, it is possible that other examples of assisted species migration species like *P. abies* may be applied in broader adaptation context. For example, *P. abies* has been considered to be a candidate species to potentially functionally replace *Tsuga canadensis* in an effort to sustain the critical ecosystem benefits of the ecological keystone species threatened by an invasive pest (Ritter et al., 2023).

It is also possible that species employed under assisted population expansion (or other FAM types) were done so somewhat unintentionally. In our study, many foresters report that one of the greatest challenges related to implementing adaptation plantings is the availability of adequate, diverse planting stock (e.g., species, seed sources) from forestry nurseries, findings consistent with (Clark et al., 2023). Forest nurseries operate on narrow margins and respond to market signals. Given that it can take 1–5 years to grow seedlings for sale, inventories may not change unless buyers work with growers years in advance (see the Target Plant Concept; (Dumroese et al., 2016). Yet, most respondents in our survey report seeking out stock merely months before planting, which likely hinders the ability to refine choices in terms of seed source, species, or stock to match site and climate needs. Under these conditions, if a forester is unable to obtain seedlings from a local nursery or native seed source, it is possible that seedlings may inadvertently come from seed sources outside of the local region but that happen to be representative of a future climate zone.

Although this scenario illustrates the potential for "unintentional" assisted population expansion, it is possible that this may be applied under an assisted range expansion scenario, too. For instance, we had no respondents reporting use of geographically widespread species like *Quercus rubra* and *Pinus strobus* for assisted range expansion, likely attributed to the broad ecological amplitude and breadth of their ranges throughout the study region. Yet, we show an inverse relationship between the frequency a species is planted relative to proportion that the species is planted for assisted range expansion. In other words, uncommon species tended to be planted more frequently under applications termed assisted range expansion. These same species more likely originate from narrower geographic distributions and may be scarcer in forest nursery inventories. Although many factors may contribute to this trend, it is possible that due to a limited nursery inventory and/or failure to place seedling orders early enough, a forester may elect to plant "secondary" species that inadvertently result in the application of assisted range expansion.

4.3 Barriers and limitations of adaptation plantings

Understanding the barriers and limitations that managers face with adaptation plantings, including FAM, has increasingly become an important research focus. Although the perceptions of natural resource managers have been more generally assessed regionally and globally to determine engagement among a broad suite of climate change adaptation strategies in forests (Findlater et al., 2022; McGann et al., 2022; Himes et al., 2023; Schattman et al., 2024), here we illustrate these challenges more specifically in the context of adaptation planting (albeit in a narrower geographic region), which has received considerably less attention. This is particularly timely given the growing interest in the role of tree planting as a natural climate solution (e.g., the World Economic Forum's One Trillion Trees Initiative: https://www.1t.org/; the REPLANT Act as part of the Infrastructure Investment and Jobs Act, 117th US (Congress The 117th U.S., 2021). Some authors report that factors related to policy, social, and economic considerations can be key drivers linked to hesitancy to engage with adaptation practices but find that other factors related to present day threats to forest health may override this hesitancy (McGann et al., 2022; Schattman et al., 2024).

Our findings generally support these assertions such that survey respondents report that factors associated with present and future biotic and abiotic stressors are more important in terms of decision making relative to other facets like policy, social, or economic consideration. More specifically, factors linked to present-day conditions (e.g., vegetative competition and predation or pre/post-planting maintenance activities) or future threats and climate conditions (e.g., invasive pests and pathogens, projected shifts in species habitat) are reportedly the most influential factors in decision making. Still, limitations in funding and labor are also highly ranked in terms of importance under the policy, social, or economic group. Notwithstanding, factors like informational and material resources such as access to planting material (e.g., enough diverse planting stock from forest nurseries) and information, training, and resources (e.g., what and how to select climate-adapted species or genotypes for current and future conditions) rank highly among limiting factors reported among our respondents. Together, these results may narrow the focus as to how to allocate resources that engage forest stewards in adaptation planning. To advance the practice of adaptation plantings and reduce uncertainty under global change, emphasis may need to be placed on developing best practices to address biotic and abiotic factors, increasing research and educational resources to advance to knowledge transfer, expanding forest nursery capacity and ecological diversity, and improving funding and policies available to advance more novel adaptation planting practices like FAM.

4.4 Study limitations

Although climate adaptive management and the potential need for adaptation plantings, including FAM, are a global issue, we were only able to survey the perspectives from foresters and other practitioners from a narrow, albeit critical forest region, the Northeastern US. Moreover, our study is limited by a small number of valid survey respondents, limiting broader inference related to the perceptions and applications of adaptation plantings in the region and beyond. While this work would benefit from a larger sample size, including respondents who are not engaged or interested in climate change adaptation and associated planting activities, many of these perspectives have been captured elsewhere (McGann et al., 2022, 2023; Himes et al., 2023). Moreover, given that many of these planting practices are somewhat new or novel to the study region and associated forest management activities, there are understandably fewer foresters actively engaged with the practice. Nevertheless, despite the small sample size, evidence from adaptation science, technology transfer, public health, and other fields (Gollust et al., 2011; Hardman et al., 2016; Storbjörk et al., 2024) point to the value of assessing the perspectives early adopters who can serve as important litmus tests to understand and refine the state of the practice.

5 Conclusion

In conclusion, interest in tree planting for restoration, FAM, and as a natural climate solution appears to be growing across a diversity of forest stewards. Despite limitations in our study (i.e., a limited number of respondents) which constrain higher level inference, the general trends in the survey population of early adopters of the practice point to an increasing emphasis on adaptation planting as a tool employed by foresters already actively engaged in climate change adaptation in the study region. Further work remains to assess how this population of early adopters compares to other foresters and natural resource professionals not actively engaged in climate change adaptation. While apprehensions remain as to how to best apply adaptation plantings such as FAM, the results from this survey highlight that many forest stewards surveyed have already implemented adaptation plantings, including FAM, or have plans to do so in the near term. Our results also illustrate planting preferences in terms of species used for FAM, potentially serving to inform and refine seedling production needs for future plantings. To ensure success in the future development of adaptation planting projects, emphasis should be placed on developing tools, informational resources, research, and funding to inform best practices. Given the growing importance of these practices in shaping future forest development under climate change, increasing prioritization of training and capacity building to support adaptation planting activities in forest management agencies and organizations across the Northeastern US may need to be considered.

Data availability statement

The datasets presented in this study can be found in online repositories via FigShare.com. See Clark et al. (2023).

Ethics statement

The studies involving humans were approved by the Human subject protection approval was issued by the University of Vermont Institutional Review Board (STUDY00002004). The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study. Written informed consent was obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

Author contributions

PC: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review and editing. AD: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – original draft, Writing – review and editing. LF: Conceptualization, Methodology, Writing – review and editing. MJ: Conceptualization, Resources, Writing – review and editing. RM: Conceptualization, Funding acquisition, Methodology, Writing – review and editing. BP: Conceptualization, Funding acquisition, Methodology, Writing – review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2024.1386211/full#supplementary-material

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A practical framework for applied forestry assisted migration

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Recent and projected changes in climate over this century pose an unprecedented threat to the health, diversity, and productivity of forest ecosystems. Forests have migrated and adapted to long-term changes in climate over thousands to millions of years; however, natural migration rates and adaptive responses of tree populations cannot match the rapid pace of current climate change. Consequently, more climate-informed approaches to reforestation are needed as current reforestation strategies using local seed sources may no longer be adequate to meet forest management objectives. Assisted migration is a climate change adaptation technique that can help maintain the ecosystem services and economic value that forests provide. Forestry assisted migration (FAM) focusses on the movement of populations of widespread, commercially, or ecologically important forest tree species within or just beyond their current ranges as a way to maintain forest productivity and health in the face of climate change. Although the forestry community recognizes FAM as a reforestation tool, guidance for planning and implementation of FAM is lacking and a framework that provides this guidance can prove useful to land managers with limited time and resources available who want to undertake FAM. We developed a practical framework (the FAM Framework) to provide a structured approach to ensure the most important considerations and best available science are utilized by land managers wanting to implement FAM on their land base. The FAM Framework incorporates multiple factors for the application of FAM in four sequential phases: assessment and analysis, climate-based plant material selection, seed procurement and deployment, and documentation and monitoring. The FAM Framework was tested by developing an assisted migration plan for the Superior National Forest, Minnesota (MN), and lessons learned from the development of this specific plan were used to revise and improve the FAM Framework for suitability across all lands.

While originally designed to meet the needs of National Forest System land managers, it is relevant and applicable across the spectrum of land ownership because it incorporates consideration of critical elements in planning and implementing FAM on any landscape while facilitating adaptive management for active learning and future implementation.

KEYWORDS

assisted migration, forest management, reforestation, climate change, climate adaptation, managed relocation

1 Introduction

There is overwhelming evidence that the earth's climate is changing at a rate unprecedented in the last 2,000 years (USGCRP, 2023). Mean global surface temperatures have increased by ∼1.1°C from 1850–1900 to 2011–2020 and are projected to increase by 1.4 to 4.4°C by 2100 (IPCC, 2023). The rapid rate and magnitude of these climatic shifts may exceed both the adaptive capacity of local tree populations and rates of natural seed and pollen dispersal to more climatically appropriate regions (Aitken et al., 2008). As tree populations become increasingly stranded in unsuitable climates, forest health and the sustained provisioning of ecosystem services are at risk (Allen et al., 2010; van Mantgem et al., 2009). The harmful impacts of climate change on forest ecosystems are already evident in forest health declines and tree mortality episodes (Anderegg et al., 2012; Betzen et al., 2021; Breshears et al., 2005; Fettig et al., 2019; Hartmann et al., 2022; Hennon et al., 2016; Mohan et al., 2009; van Mantgem et al., 2009). Moreover, in some locations long-term forest inventory data and modeling exercises both suggest seedling recruitment at range margins lags behind climatically suitable habitat shifts, further constraining the ability of forests to adapt and shift in response to climatic changes (Boisvert-Marsh et al., 2022; Dobrowski et al., 2015; Woodall et al., 2018; Zhu et al., 2012).

Tree planting is the primary tool for re-aligning populations and species with shifting climatic conditions on the landscape to sustain healthy and productive forest ecosystems. In the face of climate change, conventional regeneration strategies, including a reliance on natural regeneration or locally sourced seedlings grown as nursery stock, may no longer be adequate, (Hancock et al., 2023). Forest geneticists have recognized the need to adapt reforestation and seed movement guidelines in the face of changing climates for over 30 years (Ledig and Kitzmiller, 1992). Because natural selection reduces the prevalence of genotypes that are poorly adapted to their local environment, most plant populations, especially those of long-lived trees, are usually considered to be locally adapted (Linhart and Grant, 1996). Foresters recognized this early on after plantation failures with non-local seed and developed seed movement guidelines and seed zones to ensure the use of local seed sources—operating under a "local is best" paradigm (Buck et al., 1970; Cunningham, 1975; Fowells, 1946; McCall, 1939; Pike et al., 2020; Randall, 1996; Randall and Berrang, 2002; Rudolph, 1956; Schmidtling, 2001; Schubert and Pitcher, 1973.).

Increasing evidence suggests that the rate of climate change relative to the long lifespan of trees imparts an intergenerational adaptation lag where individuals are better adapted to the climate in which they germinated, decades to centuries in the past, than contemporary climatic conditions (Rehfeldt et al., 2012). For example, Gray and Hamann (2013) found that due to climate change that has occurred since the reference period of 1961–1990, climatic niches for 15 tree species of major commercial value in western North America, lagged behind their optimum by an average of 130 km or approximately 1.5°C. They projected that this lag would more than double before the mid-21st century. The assumption that local is best may still be conceptually valid but interpreting "local" in the wide-sense rather than the strict sense (Alía et al., 2022). This means using materials from locations with similar climates even if they are geographically distant, rather than using materials only from at or near the deployment site. Therefore, climate change creates an opportunity to reevaluate and potentially decouple seed collection zones and seed deployment zones through the use of assisted migration.

Assisted migration is a general term for the deliberate movement of genotypes, populations, or species to locations or areas outside of their current ranges to maintain biological diversity or ecosystem function in response to climate change (Richardson et al., 2009; Schwartz et al., 2012). Assisted migration actions can be divided into three broad categories: assisted *population* migration (APM), assisted *range expansion* (ARE), and assisted *species* migration (ASM) (Williams and Dumroese, 2013; Figure 1). Contemporary forestry assisted migration (FAM) (Pedlar et al., 2012), focusses on APM and ARE, whereas ASM moves species well outside of their native ranges (Figure 1). Although ASM may be used in targeted circumstances, [for example in a research context (Nagel et al., 2017; Palik et al., 2022; Royo et al., 2023) or for the conservation of a rare, threatened, or endangered species (USFWS, 2024)], it is generally not under broad consideration by the United States Forest Service (USFS) at the landscape scale because it is the most controversial of the three assisted migration types with the highest possible risks (Figure 1). However, it should be noted that due to the lack of standardized terminology for assisted migration the distinction between range expansion and species migration is not clear-cut due to uncertainty on locations of species range limits and varying opinions on what constitutes a natural migration barrier for a given species, or what distance is great enough to make an action ASM. The focus of the framework presented here is on APM and ARE, but this does not necessarily preclude movements that are bordering on species migration when appropriate.

Discussions of the various potential benefits and risks of assisted migration are covered in depth elsewhere both generally (Hunter, 2007; McLachlan et al., 2007; Ricciardi and Simberloff, 2009a,b; Stanturf et al., 2024; Vitt et al., 2009; Vitt et al., 2010; Xu and Prescott, 2024) and specific to FAM (Palik et al., 2022; Pedlar et al., 2012). In brief, by utilizing seed sources pre-adapted

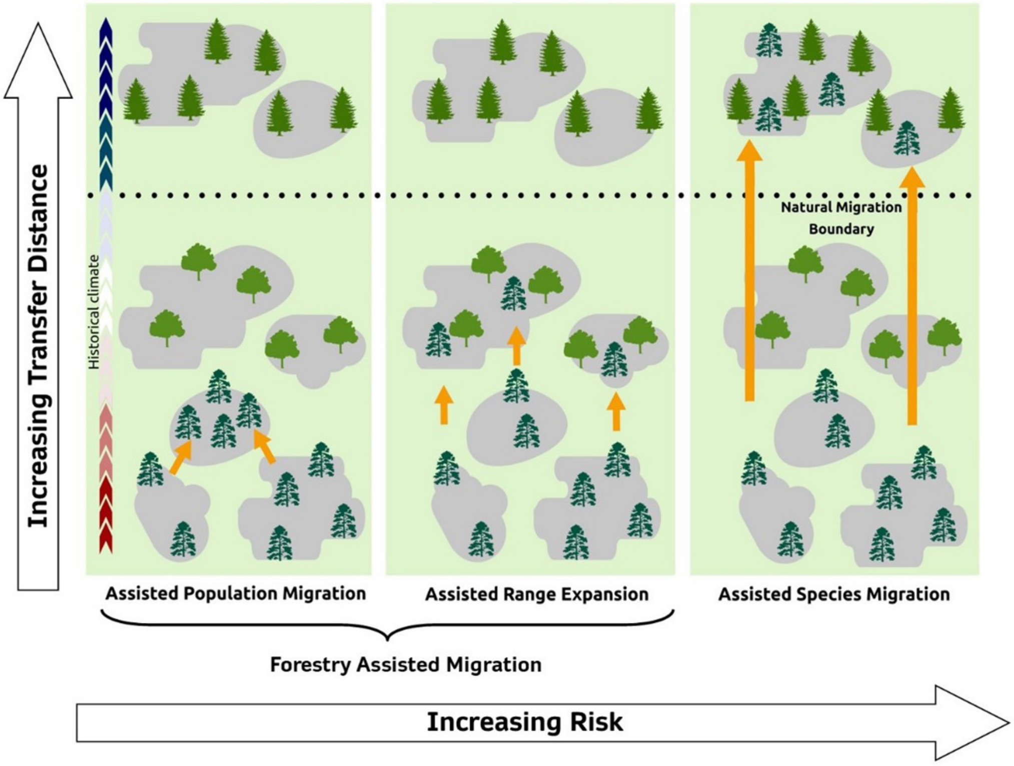

FIGURE 1
Three types of assisted migration where different tree symbols represent different species ranges with historical climates ranging from warm (red) to cool (blue). Gray areas represent tree populations and colored arrows indicate human assisted movement of plant materials. Risks associated with assisted migration generally increases with transfer distance (from USDA Climate Hubs, 2024a).

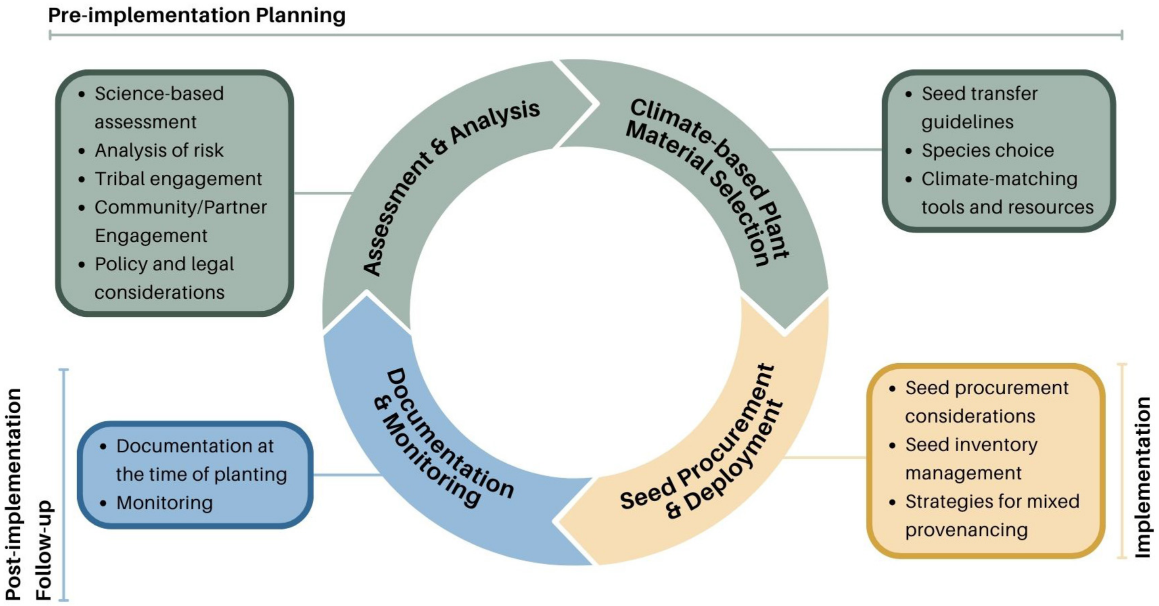

FIGURE 2
Practical FAM framework for applied forest assisted migration.

to projected future climates, FAM seeks to maintain forest health and productivity in the face of climate change. This is accomplished by reducing the likelihood of maladaptation and thereby sustaining the full range of ecosystem services that forests provide such as wildlife habitat, erosion prevention, and carbon uptake and storage (Pedlar et al., 2012; Xu and Prescott, 2024). Healthy forests also take up and store more carbon than unhealthy forests and, thus, are a powerful tool counteracting atmospheric carbon dioxide (CO_2) increases that cause climate change (Bastin et al., 2019). Therefore, it is important that tree planting campaigns are conducted in a climate-informed manner. *Climate-informed reforestation* explicitly incorporates the best available science to plan for, monitor, tend, and adaptively manage naturally seeded or planted tree seedlings so they successfully establish under current climates and persist under a range of projected future climates (USDA Forest Service, 2024a). It considers both challenges and opportunities to foster resilient, healthy, and productive forests that sustain ecosystem services into the future. FAM is one element of climate-informed reforestation that can help to ensure that the right tree (both source population and species) is planted in the right place at the right time. Assisted migration is not without risks, however, with the type and degree of risk varying among the three types of assisted migration (Figure 1). There is also an inherent risk in doing nothing resulting in maladaptation and reduced forest health, diversity, and productivity; so there are risks on all sides of the assisted migration debate.

There is a growing literature on FAM covering its potential benefits, risks, and implementation in large-scale forest management operations and in research (Benomar et al., 2022; Twardek et al., 2023; Xu and Prescott, 2024). Previous frameworks have been developed to address various aspects of assisted migration, including the need for and type of assisted migration (Hällfors et al., 2017 and McLachlan et al., 2007) and the threats and vulnerabilities to species posed by climate change (Potter et al., 2017, Thomas et al., 2010), but often these frameworks are in the context of conservation (Chen et al., 2022, USFWS, 2024). Palik et al. (2022) present a *conceptual* framework for FAM intended to examine its role in the context of a range of climate adaptation strategies, and they identify a range of institutional barriers to its wide-scale adoption. Royo et al. (2023) present a *research* framework designed to address some of the uncertainties that likewise limit the implementation of FAM through the use of modeling to identify seed sources, experimentally testing these sources in greenhouses and growth chambers as well as silvicultural field tests, and then using these results in forest dynamics models to forecast the long-term outcomes of FAM. However, what is lacking is an *applied* framework designed to directly translate the principles of FAM into practice to assist land managers. The focus of this paper is to build upon the recommendations of Palik et al. (2022) and provide a practical framework to facilitate the planning and routine implementation of FAM on a landscape scale.

Our practical approach, the FAM Framework, a process model by which to implement management is comprised of four phases, each incorporating multiple factors: (1) assessment and analysis, (2) climate-based plant material selection, (3) seed procurement and deployment, and (4) documentation and monitoring (Figure 2). The benefit of the FAM framework is that it is science-based and utilizes a structured approach to ensure the most important considerations are utilized by land managers wanting to implement FAM. Use of the FAM Framework should lead to scientifically defensible planning and socially acceptable implementation of FAM as a climate adaptation technique. This is important because as pointed out by Palik et al. (2022) and Royo et al. (2023), FAM is still in its infancy, and many questions, uncertainties, and barriers exist to its application at the landscape scale. To maintain forest health and productivity, changes to the status quo are needed now, and this will require planning prior to implementation and monitoring after implementation in order to enable adaptive management in the future.

The Superior National Forest (SNF) in Minnesota, USA, used the FAM Framework in the development of an assisted migration plan for their forest, the first such plan developed for a national forest. The insights gained from this pilot effort were used to refine the final version of the FAM Framework presented here. We present the FAM Framework through this case study and provide details for how the SNF implemented each phase below.

2 Case study—Superior National Forest

The Superior National Forest is in northeastern Minnesota, along and to the west of Lake Superior and within the 1854 Ceded Territory of the Grand Portage Band of Lake Superior Chippewa, the Fond du Lac Band of Lake Superior Chippewa, and the Bois Forte Band of Chippewa (Figure 3). It has a mix of boreal and temperate forest ecosystems and associated tree species. The SNF encompasses a transition zone between boreal and temperate ecological regions, where several important tree species are near their southern range limits, including white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*), along with significant boreal wildlife species that are rare in other Great Lakes states, such as the moose (*Alces alces*). Other trees are at the northern extent of their current natural distribution on the SNF, such as sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and northern red oak (*Quercus rubra*). The SNF uses tree planting on a large scale (approximately 1 million seedlings across > 1,200 hectares per year) to meet forest management objectives. Climate change is expected to have significant effects on growing conditions on the SNF (Handler et al., 2014) and will likely cause shifts in species composition across its landscape (Iverson et al., 2019). Aware of these projected changes and the unique value of the SNF's boreal characteristics for diverse communities that use the forest, the forest leadership team requested that the SNF become the first national forest within the United States Department of Agriculture (USDA) Forest Service to pilot the FAM Framework (Frerker et al., 2023; Handler et al., 2022).

To develop the plan, the SNF formed an initial core team. This core team engaged a broad group of over 20 partner organizations and 100 individuals from state and local governments, local Tribal Nations, academic researchers, and private industry. Nine working groups contributed to various components of the plan (Table 1). The final plan was published in November of 2023 (Frerker et al., 2023) and an Implementation Guide was developed for SNF use that will be updated as needed as knowledge is gained through experience with FAM implementation (see Supplementary material).

2.1 Phase 1—Assessment and analysis

The assessment and analysis phase of the FAM Framework is an appropriate starting point for developing a plan for

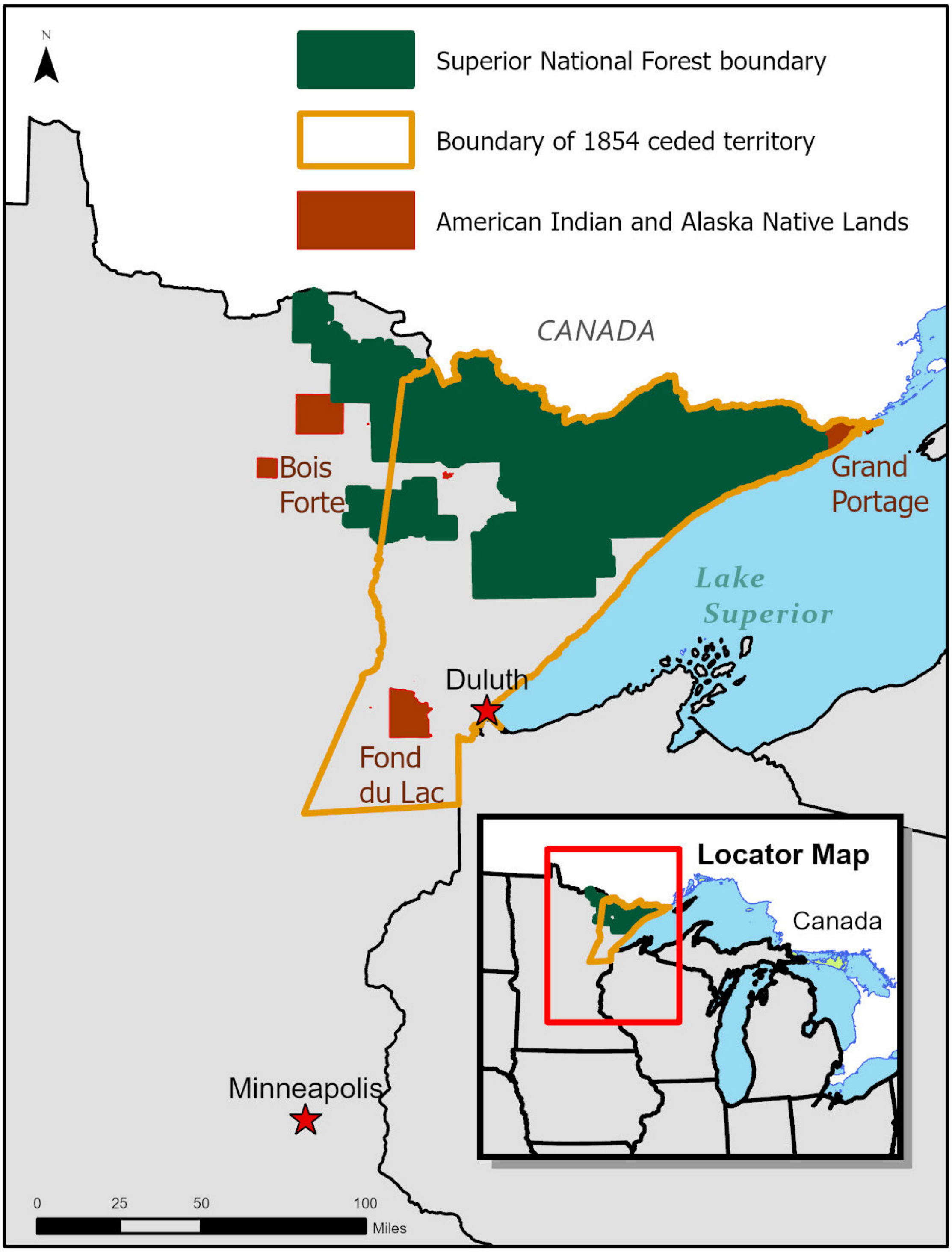

FIGURE 3
Superior National Forest (in green) and ceded territories (yellow line).

FAM and helps determine *where*, *when*, and *what type* of FAM is appropriate. This phase comprises (1) a science-based assessment of the need for FAM, (2) analysis of risk to determine the most appropriate type of FAM, (3) Tribal engagement to understand Tribal priorities and perspectives, (4) community/partner engagement, (5) and policy and legal considerations.

2.1.1 Science-based assessment

An important first step is to evaluate the past, current, and projected future climate to determine whether the use of local seed sources based on current seed zones or seed movement guidelines is likely to result in a forest that is maladapted to its future climate. Mature trees that produce the seed used for reforestation germinated from seeds in the past, and survived because they

TABLE 1 SNF assisted migration plan working groups.

Working group	Representation	Responsibilities
Scientific background	USDA FS (NFS, R&D, SPTF)	Provide background information on assisted migration
Tribal treaty rights and cultural resources	USDA FS (R&D), Fond du Lac Band of Lake Superior Chippewa, Grand Portage Band of Lake Superior Chippewa, Bois Forte Band of Chippewa; GLIFWC, 1854 Treaty Authority, UMN, BIA	Organizing roundtables to gather Tribal input on assisted migration
Genetic considerations	USDA FS (NFS, R&D, SPTF), UMN, UMD, MSU, MN-DNR, MTIC	Gather and summarize species specific information to inform seed transfer and range expansion potential
Logistics for seed sourcing	USDA FS (NFS, SPTF), UMD, MTIC, TNC, Fond du Lac Band of Lake Superior Chippewa, MN-DNR, MI-DNR	Compile information relevant to seed sourcing and collection best practices
Implementation guidelines	USDA FS (NFS, R&D), TNC, BIA, MN-DNR, Private Industry, UMN, Grand Portage Band of Lake Superior Chippewa, GLIFWC	Developed guidance on when, where, and how to use different types of AM. Developed companion Implementation Guide (see Supplementary material)
Monitoring	USDA FS (NFS)	Developed a monitoring protocol to track survival and condition of assisted migration plantings
Research needs	USDA FS (NFS, R&D), Fond du Lac Band of Lake Superior Chippewa, UMN, MN-DNR, TNC	Compile a list of key research topics and questions related to assisted migration on the SNF
Communication	USDA FS (NFS)	Developed outreach materials associated with assisted migration education and plan rollout
Internal program logistics	USDA FS (Superior NF staff)	Developed tools and protocols for the tracking and implementation of assisted migration within Superior NF silviculture program

USDA FS, USDA Forest Service; NFS, National Forest System; R&D, Research and Development; SPTF, State, Private, and Tribal Forestry; GLFWIC, Great Lakes Indian Fish and Wildlife Commission; UMN, University of Minnesota; MSU, Michigan State University; MN-DNR, Minnesota Department of Natural Resources; MTIC, Minnesota Tree Improvement Cooperative; MI-DNR, Michigan Department of Natural Resources; BIA, Bureau of Indian Affairs; UMD, University of Minnesota, Duluth.

were adapted to the climatic conditions at that time. However, the current climate where a particular tree is growing may have measurably changed from the climate at the time when the seed first germinated and began to grow. Online tools such as ClimateNA[1] (Wang et al., 2016) can be used to determine how much the current climate at a given location departs from its historical climate. These comparisons between the past and current climate can indicate the extent to which local seed sources are suitable for use in reforestation. For example, on the SNF from the 1961–1990 to the 1991–2020 time period mean annual temperature has increased nearly 0.5°C and mean coldest month (winter) temperature has increased > 1°C. This analysis can be extended to projected future climate of the intended planting site (see "2.2.3 Climate-matching tools and resources" below). In addition to climate, other factors are important when assessing the suitability of FAM, including stand management history; protected areas and land classification; physiography; ecological, social/cultural values, and edaphic factors; biological interactions, including insect and disease threats and wildlife issues; fire history and future fire risk; and economic values.

Decision support tools such as flowcharts, checklists, or decision trees can be useful to assist land managers in asking the right questions and incorporating the necessary information to determine when, where, and what type of FAM to use. For example, the SNF used USDA Forest Service Forest Inventory and Analysis (FIA) plot data to determine tree species abundance for the suite of species they commonly plant to determine which type of FAM would be applicable to which species. Using Hierarchy of Ecological Units Sections and Subsections as the geographic boundary and FIA abundance values as summarized in the Climate Change Tree Atlas (Peters et al., 2020), a species was determined to be abundant, common, rare, or absent in the Section or Subsection where the planting site is located. If a species was abundant or common, APM of that species was considered. If the species is absent, this was considered ARE or ASM depending on how far away the seed source is located. If a species is "rare" on the landscape, the SNF agreed to coordinate with Tribal Nations to ensure planting of the species considers Tribal priorities. The SNF then developed decision trees that considered site conditions (e.g., land classification, soil and slope parameters, tree species vulnerability, past management), insect and disease issues, and wildlife and other species of interest to help guide which type of FAM to implement on a given planting site (see Supplementary material). These decision trees referenced geospatial data in a mapping exercise that factored in forest type, soil characteristics, and slope together as a tool to assess how climate change risk is distributed across the landscape. In addition, there are other post-fire restoration tools that can be used to prioritize areas for tree planting and inform the choices involved in FAM implementation such as the Southern Rockies Regeneration Tool (Rodman et al., 2022), Regen Mapper (Holden et al., 2022), and the Postfire Conifer Reforestation Planning Tool (Stewart et al., 2021).

2.1.2 Analysis of risk

Assessing the risk of various assisted migration strategies and predicting how well each addresses the desired land management objectives will help managers determine what approach may be appropriate in terms of implementing FAM. Risk can be considered as the probability of a less-than-desired outcome and the severity of

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[1] https://climatena.ca/mapversion

the associated impact (USFWS, 2024). A risk assessment identifies relevant risk factors for a variety of risk types (see Karasov-Olson et al., 2021), whether those factors are present or not, and the potential consequences or impact of that risk. A risk assessment also considers ways to reduce the risk of undesirable outcomes and describes the uncertainty associated with various alternatives being assessed, including not implementing FAM (USFWS, 2024). The extent and level of detail of the risk assessment will depend on both the context and the level of identified risk considering all management alternatives. A risk assessment can be done either using a formal quantitative approach (Karasov-Olson et al., 2021) or using a more informal qualitative guide or checklist to ensure that all types of risks are addressed appropriately (National Invasive Species Council [NISC], 2024). In addition to assessing the potential risks associated with FAM, the risk posed by not implementing FAM is an important consideration. A key risk of not implementing FAM is "adaptation lag" or maladaptation as local adaptation is decoupled from the selective pressures of the environment to which a population is adapted (Jordan et al., 2024) resulting in continued, and potentially irreversible, decline in forest health and productivity. As the earth's climate continues to change, the risk of not implementing FAM has the potential to outweigh the risks its use may pose (Palik et al., 2022).

The SNF did not do a formal risk analysis but did analyze risk through the development of the flow charts and mapping climate change risk (see Supplementary material) combined with a series of Tribal roundtables described in section "2.1.3 Tribal engagement". Ultimately the SNF determined there was a need to be proactive in their approach to implementing assisted migration because of the vulnerability of the forest's boreal ecosystems to climate change (Handler et al., 2014). The map, flowcharts, and roundtable information led them to develop an overall approach of pursuing APM where possible and implementing ARE and ASM with caution, and only after careful consideration of risk categories and formal consultation with Tribal Nations.

2.1.3 Tribal engagement

An important step in the assessment and analysis phase of FAM projects is to understand Tribal perspectives and priorities. Land management decisions on public lands have the potential to affect Tribal sovereignty, treaty rights, and cultural values of local or removed/relocated Indigenous communities including the relationships between plants, animals, water, and people. Tribal engagement can occur through formal government to government consultation and/or more informal collaboration. The SNF developed a model for engaging local Tribal Nations to hear their perspectives on FAM before drafting their plan. To do this, a series of roundtable discussions were convened with a network of Tribal staff and community members. Each roundtable focused on a set of discussion questions/topics (Box 1) and information from these sessions ultimately informed the type and depth of Tribal consultation that would be required for FAM actions (see section "3.2.1 - Consider tribal perspectives early"). An additional resource that provides a framework to integrate Tribal perspectives in FAM planning is *Dibaginjigaadeg Anishinaabe Ezhitwaad*–A Tribal Climate Adaptation Menu (Tribal Adaptation Menu Team, 2019). This resource provides some guiding principles for Tribal engagement and contains an organized collection of general climate change adaptation actions that reflect Indigenous perspectives which may be applicable for FAM.

BOX 1 Sample questions and discussion topics for Tribal engagement.
Some suggested questions and topics include:

- What climate impacts are you most concerned with and why?
- What are our best opportunities for collaboration?
- What are the climate change effects to culturally important species?
- What are the concerns about AM regarding culturally important species?
- What are some potential effects of AM on these species? (positive or negative)
- How should we be mindful of relationships between these species and other beings or other values?
- Are you already doing, or planning, other or other complementary climate adaptation action(s) for these species?

2.1.4 Community/partner engagement

Regardless of land ownership, there are potentially multiple relevant community groups and partners that may have an interest in FAM. Forest management projects of any size on public lands require engagement with the public to elicit ideas, gain support, and ultimately be implemented. This may be especially true for FAM, which is an emerging issue. Key interest groups could include adjacent public and/or private/industry landowners and local communities that use forest lands that could potentially be impacted by FAM. The successful implementation of FAM may benefit from collaboration or partnership with other landowners and all activities on public lands require appropriate environmental analyses and public scoping. Community engagement and partnerships from the earliest stages of planning can help to build support and approval proactively rather than responding to objections at later stages of planning. The SNF actively engaged many partners from the onset of the development of their AM Plan by inviting these stakeholders to provide input and participate in the core team and be active participants in the development of the plan (Table 1).

2.1.5 Policy and legal considerations

Policy regarding use of FAM likely differs among land ownership and land management organizations, and potential restrictions on using non-local seed need to be considered during planning. There may be policies restricting the use of non-local seed sources that organizations may need to revise before FAM can be implemented operationally. Moreover, it is important to consider how any implementation of FAM aligns with land management goals even if it may not be explicitly addressed in existing planning documents. For example, the SNF Land Management Plan (LMP) states that desired conditions include native vegetation communities that are diverse, productive, healthy, and resilient, and that ecological conditions are maintained or restored at multiple landscape scales (USDA Forest Service, 2004). The SNF determined that that there was no language in their LMP that would prohibit them from implementing FAM and its use is consistent both with current and proposed Agency policy and is in alignment with achieving their LMP's desired future conditions.

2.2 Phase 2–Climate-based plant material selection

The success of reforestation is determined by a variety of biotic and abiotic factors at the planting site and hinges on the ability for seedlings to synchronize their growth to the local climate. This phase of the FAM Framework comprises the selection of plant materials that will be needed to ensure seedlings will be adapted to their planting site under a changing climate, including: (1) considering transfer limits and seed transfer guidelines, (2) assessing species choice, and (3) utilizing tools and resources to identify climate-matched seed source locations.

2.2.1 Seed transfer guidelines

Many tree species of commercial value have been extensively studied in common gardens replicated across different environments to develop seed transfer guidelines (Bower and Aitken, 2008; Rehfeldt, 1994; Rehfeldt and Jaquish, 2010; Savva et al., 2007; Schmidtling, 2001; Sorensen, 1992, 1994; St. Clair et al., 2005). These transfer limits and guidelines indicate whether a species is a climatic specialist or generalist and how adaptive genetic diversity is distributed throughout a species' range. For species where species-specific seed zones based on empirical research are not available, provisional seed zones can be used (Bower et al., 2014; Pike et al., 2020). Provisional seed zones are delineated based on areas with climatic conditions that fall within set thresholds. The assumption is that because individuals are adapted to the climate within their local seed zone they can be transferred to planting sites within that zone with limited risk of maladaptation (Bower et al., 2014). However, when implementing FAM, seed will likely need to be moved outside its local seed zone because of mismatches with the projected future climate. For example, seed zones for the SNF were originally developed in 1970 (USDA Forest Service, 2006), and seed for reforestation was collected solely from local stands. Those seed collection zones were updated in 2019 to account for climate change (Berrang, 2019), and climate-matched seed collection areas for future reforestation are in areas to the south of the forest with almost no overlap with SNF forest boundaries (Frerker et al., 2023).

2.2.2 Species choice

Although implementation of FAM involves lower risk movement of populations within or just beyond their current species ranges, species choice will still be a consideration if FAM is employed. Tree species vary in their vulnerability to the impacts of climate change (Potter et al., 2017) and nearly all forest tree species are projected to experience changes in their distribution (Iverson et al., 2019; Peters et al., 2020). If a planting site is near a contracting (i.e., warmer, in most cases lower latitude or elevation) range margin, it may mean that this species, even if currently abundant, may not be well suited to projected future climates at that location (Aitken et al., 2008). In these cases, it may be desirable to focus reforestation efforts on other species present at the site that are not at the potentially contracting edge of their distribution. Conversely, populations of tree species that are near the edge of a distribution projected to expand under climate change may be good candidates for ARE as new suitable habitat becomes available. Populations of trees that exist within the core area of their species range are likely the best candidates for APM (Aitken et al., 2008).

In addition to climate change impacts, some tree species also have important disease or insect considerations that may need to be taken into account when selecting seed sources [e.g., white pines (*Pinus* spp. subgenus *Strobus*) (Keane et al., 2022), Port-Orford-cedar (*Chamaecyparis lawsoniana*) (Sniezko et al., 2020), and eastern hemlock (*Tsuga canadensis*) (Evans et al., 2011)]. For some species where disease or insect resistant seed sources are available these may be the best-adapted even if they are at a higher risk of climate maladaptation. For other species, the presence of insects or diseases in some parts of the range may preclude or complicate seed and seedling movement. Additional resources are available that may be helpful to assess potential future risks from insect and disease incidence increases due to climate change, for example the National Insect & Disease Risk Map (USDA Forest Service, 2018).

The SNF is in a unique ecological position at the transition between the boreal forest to the north and temperate hardwood forest to the south. Depending on the species, any of the three types of assisted migration could potentially be appropriate in this kind of situation. The SNF used species abundance values calculated from FIA data, predicted species distribution maps from the Climate Change Tree Atlas (Peters et al., 2020), as well as feedback from Tribal engagement sessions to choose species for FAM planning. In addition, they also incorporated other considerations such as insect and disease issues {e.g., emerald ash borer (*Agrilus planipennis*) and spruce budworm (*Choristoneura fumiferana*) as well as culturally significant species [e.g., moose, northern white cedar (*Thuja occidentalis*), sugar maple, and paper birch (*Betula papyrifera*)]} in their species choice decisions.

2.2.3 Climate-matching tools and resources

One of the primary justifications of implementing FAM is to prevent a decrease in forest health and productivity due to maladaptation. Global circulation models can project the values of a large suite of climate variables for future time periods and online tools such as ClimateNA (Wang et al., 2016), CHELSA (Karger et al., 2021), and Climate Toolbox (Hegewisch and Abatzoglou, 2024) are available to obtain past, current, and future climate data for the site to be planted and the seed source locations. Simple calculations of the difference between the climate of the seed source location and the planting site provide the climatic transfer distance (St. Clair et al., 2022) and can be used to evaluate the risk of climatic maladaptation. Under the assumption associated with clinal genetic variation that fitness gradually decreases as climatic transfer distance increases, climatic transfer distances that exceed a pre-selected threshold would indicate that this seed would likely be maladapted for a future projected climate. Beyond calculating climatic transfer distance, several climate-matching tools have been developed to assist in matching seed sources with planting sites (e.g., the Seedlot Selection Tool and Climate Adapted Seed Tool) (St. Clair et al., 2022; Stewart et al., 2023). These tools are powerful and can be extremely useful, but they also require varying levels of user input.

When using modeled future climate data, it is important to select the appropriate future time period in order to assess the magnitude of climatic differences and potential maladaptation. Time periods in the near future (e.g., through 2040) may lead to selection of seed sources that will still become maladapted as the climate continues to change beyond that timeframe. Time periods too far into the future (e.g., 2071–2100) may lead to selection of seed sources that are maladapted to current conditions (Aitken and Bemmels, 2016). For example, if seed sources are chosen for much warmer future climates projected at the end of the century, they could suffer frost damage during the critical establishment phase because they are poorly adapted to current temperatures. Mid-century (2041–2070) time period balances the risks of under- or over-estimating future projected climate change (Aitken and Bemmels, 2016). For example, British Columbia uses a climatic transfer that matches the seed source climate prior to significant anthropogenic climate change (1931–1960) with the climate projected for the planting site at a quarter of the rotation age or approximately 15 years after planting (O'Neill and Degner, 2024). This accounts for climate change that has already occurred with a conservative buffer for expected future projected climate change.

It is also important to choose climatic variables carefully, considering local and/or specialized knowledge of the planting site and species of interest. Plant distributions are generally driven by the annual supply of energy (temperature) and water (precipitation) (Stephenson, 1990) and for many temperate forest trees, past research has shown that temperature (both mean annual temperature and winter temperature) is a driving force in local adaptation of populations (Aitken and Bemmels, 2016; Bower and Aitken, 2008; St. Clair et al., 2005). Both mean annual temperature and winter temperature are projected to increase to varying degrees in most locations (IPCC, 2023; Marvel et al., 2023). Projections of precipitation have greater uncertainty both annually and seasonally. However, when precipitation is combined with increased temperatures, it is projected that moisture deficit (either annual or summer) is likely to increase in many locations. Additionally, more extreme events are projected, and many areas may experience both an increase in heavy rain events and dry periods (IPCC, 2023; Marvel et al., 2023). Therefore, it is important to include a measure of precipitation or aridity when determining climate analogs.

The SNF used seed collection zones mapped to climate analogs based on the Seedlot Selection Tool (SST) to identify climate-matched seed collection locations before 2040 and from 2041 to 2070. They combined this information with species-specific transfer distance recommendations to determine the best location for future seed collection. For example, the SNF assisted migration plan includes shifting seed sourcing of some species (e.g., white spruce) to existing orchards that roughly match the Forest's climate analog zone as identified by the SST, while identifying new collection areas within climate-adapted seed zones for species that need to be collected every year [e.g., bur oak (*Quercus macrocarpa*)].

2.3 Phase 3—Seed procurement, management, and deployment

Tree seed is a critical resource of reforestation efforts. Insufficient seed availability is creating constraints for reforestation as well as for implementing FAM. This phase comprises the suite of considerations relevant to the reforestation pipeline including: (1) considerations for seed use planning and seed procurement, (2) seed inventory management, and (3) considering various strategies for mixed provenancing of seed sources during deployment.

2.3.1 Seed procurement considerations

Implementation of FAM will require seed sourced from geographic areas that match the future climate analog, which may mean procuring non-local seed or seedlings from seed zones matched to the climate of the target project area. These non-local sources may, in some cases, include adjacent lands under different jurisdictions or ownership. Land managers that plan to implement FAM will benefit from developing a multi-year seed planning effort to identify locations of appropriate non-local sources to procure sufficient seed ahead of time. Surplus seeds collected for most conifers and hardwood tree species with seeds that can be dried and frozen can be stored for years or decades. Tree species with large seeds that cannot survive drying and freezing, however, would require seed collection areas or seed orchards to ensure dependable annual seed inventories. Several geospatial products are currently available to estimate future seed needs based on forestland risk to disturbances and future climates including the LANDFIRE Fire Return Interval (La Puma, 2023), the USDA Forest Service Climate Risk Viewer (USDA Forest Service, 2024b) and Climate Change Vulnerability Assessments (USDA Forest Service, 2024c), among others.

In the case of the SNF, a portion of the plan is dedicated to identifying seed sourcing cooperators in the event that climate-matched seed is not available from within the boundaries of the forest. The list identifies other national forests, Tribal Nations, state, and private cooperators and information such as species available, the cooperator's ability to collect seed and point-of-contact for seed collection are listed.

2.3.2 Seed inventory management

Climate-informed reforestation requires precise knowledge of seed origin to match the projected climate with a planting site. Where collections are identified only at a coarse scale level (e.g., seed zone, breeding zone, county), an average value (e.g., the climatic center, median value) for climatic variables is used but at the expense of climatic accuracy compared to more precise location identification (e.g., GPS acquired latitude and longitude). This may be especially problematic in areas with steep elevational gradients. Information on seed source location is most useful when conserved at the most descriptive level available so that seed can be deployed in the most precise manner possible. Seed sources that reside in storage but are designated using imprecise source location information from older or improper documentation methods create a challenge for geneticists to align current seed inventory with climate models, making it difficult to provide fine-scale guidance for AM deployment by managers. If source location information is not tracked for a seedlot, this could preclude the use of that seed for FAM because the source climate cannot be determined.

New accessions would benefit from being labeled with the most refined location information available (latitude, longitude, and elevation). This information is also necessary to understand the potential factors affecting planting outcomes (e.g., seedling survival) over time for both FAM projects and reforestation more broadly. In the western US, because of the complex topography, seed collection for FAM will only be useful if collections are separated into accessions that represent relatively small geographic areas, recording the latitude and longitude of the stand of origin. In the eastern US, such as the SNF, tracking seed to the county or counties of origin may provide enough information in many areas for assisted migration where the seed is bulked by state and seed collection zone. Currently, standards for defining seed accessions vary depending on the collector and requirements set by the nursery or other buyer. Improved communication of seed-source identification standards, including seed origin labeling, between seed collectors and nurseries or buyers will help improve the availability of source-identified seed for FAM use on all lands.

2.3.3 Strategies for mixed provenancing

There are benefits and risks to mixing seed sources (e.g., increasing genetic diversity vs. potential outbreeding depression) (Bucharova et al., 2019). The proportion of seedlings that will be from local vs. non-local sources is a consideration when planning FAM. This mixing of seed sources employs portfolio theory (Crowe and Parker, 2008) to minimize risk by increasing genetic diversity to buffer against the impacts of climate change. There are different strategies that have been developed for determining how to mix various seed sources based on planning and land management objectives (Figure 4). A variety of different provenancing strategies have been described elsewhere (Figure 4A), including *composite provenancing*, which aims to mimic natural patterns of gene flow by mixing seed from multiple source locations, but with a larger proportion of local seed, and progressively smaller amounts of seed as the distance of the collection site from the planting site increases (Broadhurst et al., 2008); *admixture provenancing* which also mixes seed source locations, but aims to maintain a wide genetic base, without regard to the location of the source population relative to the planting site (Breed et al., 2013); *predictive provenancing* where seed from areas where the current climate matches a future predicted climate of the planting site (Sgrò et al., 2011); and *climate-adjusted provenancing* where the seed sources are biased in the direction of projected future climates (Byrne et al., 2013). Both predictive provenancing and climate-adjusted provenancing account for just a single projected future climate at a time. Prober et al. (2015) state that although future climates cannot be predicted without uncertainty the general trend is robustly predicted and the climate-adjusted provenancing approach incorporates a mix of seed sources from a climatic gradient biased toward the direction of predicted climate change. However, it is important to consider a diverse range of potential future climates based on a suite of models and climate scenarios to account for uncertainty. Managing for specific future climates, even if based on ensemble projections may be easier operationally, but this can provide a false sense of certainty and security. *Portfolio climate-adjusted provenancing* is a variation that simultaneously considers a diverse range of plausible future climates (Figure 4B). This approach can be used in a practical manner to bracket the range of plausible futures considering different representative concentration pathways (RCPs), climate models, time-periods, and climate variables. It establishes sideboards on the range for which seed sources can be collected and/or used, but also ensures the entire range is considered. Managing for the range of potential future climates is more complicated but intentionally and purposefully provides for designing seed mixes to be robust to the range of future climates. This will require land managers to use professional judgement to select the sources to include in seed mixes.

The SNF decided on a staggered process of FAM implementation that combines provenancing strategies outlined above. The SNF will gradually use up local seed caches while new protocols are developed for collecting seeds in climate analog zones. Full conversion of the reforestation program to APM stock is anticipated by 2050. ARE will be implemented on a case-by-case basis only after formal Tribal Consultation.

2.4 Phase 4—Documentation and monitoring

In the US, tens of millions of hectares of both public and private land are in need of reforestation (Fargione et al., 2021) and the increasing size and severity of wildfires is increasing the number of hectares in need of reforestation through planting (Fargione et al., 2021; USDA Forest Service, 2022). As public land managers strive to scale up and optimize climate-informed reforestation to meet land management goals (e.g., Executive Order 14072), it will be critical to establish clear protocols and guidelines to ensure that the necessary data are collected to determine the outcomes of management work. Only monitoring can ascertain when FAM approaches are working and when they are not, to ensure forests continue to provide the ecological benefits on which Tribes, communities, and stakeholders rely. The final phase of the FAM Framework comprises (1) documentation of activities at the time of planting and (2) monitoring of plantings to guide adaptive management.

2.4.1 Documentation at the time of planting

Planting is a critical time to ensure robust documentation and data archiving because of that information's importance to tracking the success of FAM over time. It is helpful to plan and track information about the seedlings and how seedlings are planted as well as identify information needs about the planting site to inform future monitoring. During FAM plantings, the design of the physical layout of the planting may require tradeoffs between achieving silvicultural objectives and the ease of future monitoring. It is important to track the seedling sources to compare growth and survival among different seed sources, especially when multiple seed sources are planted on a single site. Comparisons of growth and survival rates can help managers identify which seed sources are performing well and can highlight under which circumstances the local (i.e., *status quo*) seed source is showing maladaptation or performing poorly relative to a FAM source. It typically is easiest to track seed sources if blocks are planted from a single seed source. The risk from this layout is that if a seed source proves to be unsuitable for a location, the whole block is more likely to fail. To buffer against having large areas with failed establishment or poor survival, seedlings from different seed sources could be intermixed in a planting. However, with multiple sources, unless seedlings are labeled by source at the time of planting, it will be impossible to track seed source over time. With a modest amount

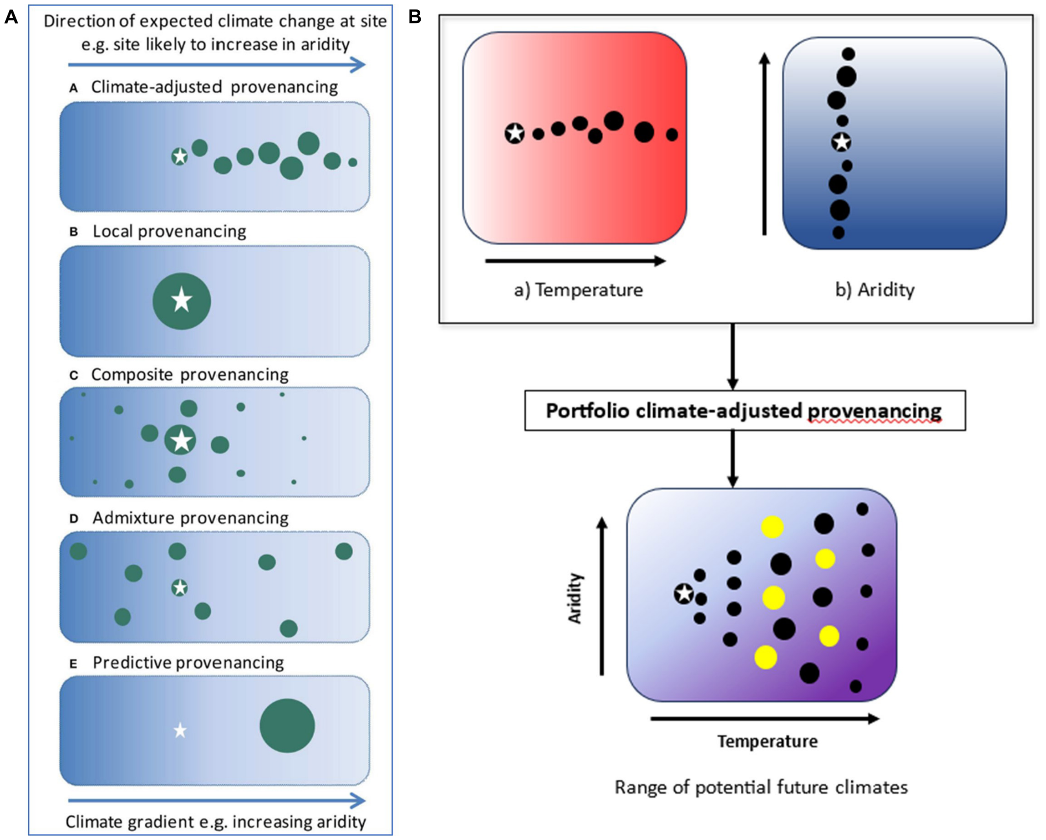

FIGURE 4
(A) From Prober et al. (2015) (used with permission). The star indicates the planting site and the green circles represent seed sources used for reforestation. The size of the circles indicates the relative quantities of each seed source used at the planting site. **(B)** Portfolio climate-adjusted provenancing. In this example climatic variables are **(a)** temperature, which increases from left to right, and **(b)** aridity which increases from bottom to top. When using portfolio climate-adjusted provenancing, multiple future climates (RCPs and time-periods) are considered to identify a diverse range of potentially adapted seedlots. Yellow colored circles indicate a potential set of seed sources for a seed mix designed to be robust to a range of possible future climates.

of pre-planning, it is possible to incorporate a small monitoring plot within operational plantings where seedlings are labeled by source location. Ideally, the plot is representative of the broader planting site so that it can be utilized for monitoring throughout the lifespan of the stand and reliably inform future management decisions.

When implementing FAM, it will be important to not only plan for the layout of the planting, but also to determine the information to be collected and recorded at the time of planting and where to store that information for future use. Data standards and stewardship are critical for future use of the data to inform adaptive management of the stand and future seed selection and procurement across the ecological region. Data can be maintained in both spatial and tabular databases, and in operational use, it is important to develop minimum data requirement guidelines and distinguish any optional elements. It is critical that the protocol captures data and information necessary to determine the success of FAM while simultaneously minimizing the impact on the field-going staff. A minimum standard set of core data for FAM will require components related to seed sources, planting, and initial survival. When possible, FAM efforts can leverage existing systems and practices to streamline adoption and determine what augmentations to those systems are needed to ensure FAM can be identified and tracked. For example, the SNF identified places in an existing agency database, the Forest Service Activity Tracking System, that could record when and where FAM took place at the time of planting, and developed protocols for properly monumenting FAM seedlings in the field.

2.4.2 Monitoring

Monitoring provides feedback and forms the critical link to close the loop in our FAM Framework to inform adaptive management so that based on lessons learned as FAM is implemented, future implementation can be adjusted. The data gathered through monitoring provides the information to initiate the Assessment and Analysis phase for future FAM projects and ensure (if not improve) their success.

A monitoring protocol will help ensure that relevant information is collected at appropriate intervals to inform future analyses. Important monitoring information for FAM plantings is data related to survival and health for each seed source, and land managers may also wish to collect climate data (e.g., temperature, precipitation, occurrence of extreme events) for additional analysis. Depending on the planting site's location, local weather stations may be sufficient, or this information could be supplemented with local meteorological data collection in remote locations or when additional precision is needed. The seedling stage is when trees are most vulnerable to abiotic stressors such as cold injury or drought stress (Aitken and Bemmels, 2016), and collecting data on survival at frequent intervals can be particularly informative during early years of stand development. One-year and three-year post planting assessments are suggested to detect potential impacts of planting technique and to respond in the event of failure. After initial establishment, seedlings should be free-to-grow, and monitoring of both growth and survival could shift to longer intervals (e.g., every five years). The number of trees monitored is an important consideration in the monitoring protocol. If FAM is implemented over hundreds or thousands of hectares, it will be impractical or even impossible to monitor all trees or even all stands. This is where monitoring plots established at the time of planting may be most efficient, effective, and valuable. An additional consideration is who will be responsible for carrying out monitoring over time. When local staff and technicians are unable to accommodate the increased workload, it is worth considering collaboration with external partners to provide staff and/or contracting capacity for monitoring. In some instances, researchers may want to partner with managers where FAM provides opportunities to address outstanding research questions [e.g., The Experimental Network for Assisted Migration and Establishment Silviculture (USDA Forest Service, 2023)]. No matter who is assigned the role and responsibility for monitoring, it will also be important to ensure any data collected during monitoring be incorporated into appropriate databases so that it can be linked back to the planting information and be queried for future planning analyses and to inform future management decisions. For example, the Superior NF devised a monitoring protocol that built on established protocols, modifying the existing survey techniques to be conducted at a higher intensity and with additional information collected on tree condition and competition from surrounding vegetation. In addition to monitoring survival and condition of seedlings, climate conditions from the nearest weather station will be monitored to help determine potential causes of seedling mortality.

3 Discussion

Applying an early draft of the FAM Framework in the development of the first Assisted Migration Plan for a national forest, the SNF gained considerable insights into each of the four phases of the FAM Framework. These insights helped to refine the final FAM Framework presented here. During each phase of the FAM Framework, it became apparent that a one-size-fits-all approach for planning and implementing FAM is not possible, but rather, the broad FAM Framework can be adapted and tailored to suit local needs. A key outcome of implementing the FAM Framework was interpersonal networking between SNF staff, the Minnesota Department of Natural Resources, county governments, and others who will have important roles in procuring climate-adapted tree seed for the SNF. The roundtables that were conducted also fostered relationship building and provided key information to the Core Team on what Tribal community members and natural resources staff did and did not want to see from the SNF's FAM efforts. Following are some key insights gained from the development of the SNF Assisted Migration Plan.

3.1 Key insights - assessment and analysis

3.1.1 Consider Tribal perspectives early

Climate change impacts and decisions related to FAM implementation will undoubtedly affect the ability of Tribal citizens to fully exercise their formal treaty rights within the 1854 Ceded Territory within which the SNF is located. Utilizing the FAM Framework, the SNF engaged with local Tribal Bands at the onset of the Assessment and Analysis phase to ensure FAM would be considered in a respectful manner. It immediately became apparent that there was a difference in opinion on how proactive the SNF should be with FAM on the landscape. The SNF felt a great urgency to begin shifting species compositions on the landscape in order to adapt to future climates and was initially pushing for an aggressive approach that considered both APM and ARE strategies. However, Tribal engagement via the roundtables revealed that there was discomfort from the Tribal Nations around these aggressive types of FAM because of the cultural value that current species and species assemblages on the landscape hold. As a result of these early dialogs, the final approach to FAM outlined in the SNF plan is more conservative, focusing on APM of the entire planting stock (∼1 million seedlings annually) by 2050. The SNF plan outlines requirements to receive consent for ARE and ASM actions through formal consultation meetings. APM actions, by contrast, may proceed with informal Tribal collaboration.

3.1.2 Define a process for distinguishing between the three FAM types—scale matters

When considering FAM for different tree species, it is important to acknowledge the different risk levels associated with each type of AM (Figure 1). However, distinguishing between APM, ARE, and ASM in practice and on the ground is less clear-cut than the definitions on paper. Through Tribal roundtable discussions, it became apparent that there was comfort with implementation of APM on the SNF but discomfort with ARE and ASM on the landscape. Further conversation revealed that it can be hard to distinguish where a particular species range begins or ends on the edge of species distribution limits like on the SNF. For example, a SNF staff member may consider moving a species from a neighboring state onto the forest a form of ARE, a Tribal Band member may consider ARE to be moving a species from a neighboring *county*. To resolve this difference in perception of scale and develop a way to clearly articulate when each type of FAM was being implemented, the SNF developed a process for distinguishing between the three types, based on species abundance at the planting site location.

3.2 Key insights - climate-based plant material selection

3.2.1 Consider species genetics

In order to select the appropriate species and populations within species for use in FAM, it was important to review information regarding genetic diversity, population structure, and any existing seed zones and/or seed transfer guidelines developed for species commonly used in reforestation. This information is critical to ensuring the appropriate choice of seed source. It is helpful to consult information available on these topics for the species of interest when planning FAM. The SNF provided a team of geneticists with a list of 16 tree species of interest (most commonly planted or ones they were interested in introducing in the future) and asked them to provide recommendations on transfer distances (Pike and Haase, 2024). This information can be found for many commercially important species in the published literature and will be included in the forthcoming update to the Silvics of North America (USDA Climate Hubs, 2024b).

3.3 Key insights - seed procurement and deployment

3.3.1 Partnerships are critical

Based on climate-matching analyses and established seed transfer guidelines, a series of maps of analog zones were produced for potential future seed collection locations for the SNF. It was immediately apparent that none of these locations were located within the SNF boundary. Some collection zones before 2040 overlapped other national forest boundaries in the area, but by mid-century the analog zones have little to no overlap with USDA Forest Service National Forest Systems lands (Berrang, 2019). This means that partnerships will be critical to the SNF for obtaining FAM seed, emphasizing the importance of collaboration with state, county, Tribal, private, and non-profit organizations to gather and obtain seed. Obtaining seed for FAM on national forests in the Eastern US poses additional challenges because of the varied land ownership. Administrative boundaries likely will be a consideration when identifying suitable seed sources regardless of whether neighboring lands are other national forests or under a different jurisdiction. Therefore, establishing partnerships to ensure the species of interest are available and accessible in off-site locations and establishing a mechanism for obtaining the seed (SNF seed collections crews or purchasing of seed from the landowner) are logistics that are important to address in the near-term.

3.4 Key insights - documentation and monitoring

3.4.1 Timing and communication of FAM seed availability are critical

FAM implementation is only beginning on the SNF, however, it is apparent that detailed documentation and continuous communication are necessary for success. There are many unknowns related to when a stand will be harvested and ready for planting and when the desired seed stock will be ready for deployment in the field. Because of this unpredictability related to timing, continual feedback on the process is critical to make sure the proper FAM stock is available for planting when the SNF needs it and that it is tracked and recorded once it is placed in the ground to allow for future monitoring.

4 Conclusion–toward national-scale implementation

Land managers on the SNF and elsewhere are eager to implement FAM on the ground, but thoughtful planning is important to ensure this adaptation technique is implemented in a climate-informed and a culturally and ecologically respectful manner. Before implementing FAM at the landscape scale, it is important to consider each of the elements in the FAM Framework so that managers can work in a consistent and coordinated approach that fully accounts for cultural (Tribal, wildlife, and other social values), ecological (species ranges, genetic diversity and structure, and climate change) and operational factors specific to their local landscape. Further, the burden of figuring out the logistics for selecting, procuring, deploying, and monitoring FAM seedlings cannot be placed on one individual land manager, and local policy and management guidelines for the landowner/manager will also be important to consider. Also, FAM is one just tool in the climate adaptation toolbox and can be employed alongside other climate adaptation treatments and practices that can be selected and combined to fit local challenges, concerns, and situations (Halofsky et al., 2018; Janowiak et al., 2014; Nagel et al., 2017; Ontl et al., 2018).

In a time of rapid climate change, there is no clear guidebook on how to implement FAM and professional judgement will be critical. The FAM framework is a structured approach to ensure the most important considerations and best available science are utilized in the planning and implementation of FAM. The practical FAM Framework developed here follows a logical cycle from planning, to implementation, to follow-up monitoring that is intended to facilitate the application of FAM in a scientifically, culturally, and ecologically defensible way. The piloting of the FAM Framework by the SNF provided valuable insights and helped to refine the final version presented here, and in addition, the SNF developed some useful tools and resources to accompany the FAM Framework. Using lessons learned from this pilot, it is hoped that this framework can be applied to other national forests and public lands more generally.

As Aitken and Bemmels (2016) state: “it’s time to get moving.” Over three decades ago Ledig and Kitzmiller (1992) predicted the need for deploying non-local seed and promoted the idea of broader deployment of species, seed sources, and families. Today, FAM is still not widely implemented outside the context of research. Given the current rapid pace of change, land managers do not have the luxury of waiting another 30 years to implement these practices. Land managers can use the FAM Framework to apply FAM and learn as we go. Documentation and monitoring will be crucial to allow adaptive management as we learn from our collective experience. Every instance of reforestation using FAM will have its own nuances, but our FAM Framework seeks to overcome some of the institutional barriers to wide-scale adoption of FAM identified by Palik et al. (2022). Ultimately, our FAM Framework is relevant and applicable across the spectrum of land ownership because it incorporates consideration of critical elements in planning and implementing FAM on any landscape while facilitating adaptive management for active learning and future implementation.

Author contributions

AB: Conceptualization, Writing – original draft, Writing – review & editing. KF: Writing – original draft, Writing – review & editing. CP: Writing – original draft, Writing – review & editing.

NL: Writing – original draft, Writing – review & editing. BP: Writing – original draft, Writing – review & editing. AR: Writing – original draft, Writing – review & editing. SA: Writing – original draft, Writing – review & editing. AF: Writing – review & editing. LB: Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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Identifying climatically-compatible seedlots for the eastern US: building the predictive tools and knowledge to enable forest assisted migration

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Introduction: Global climate change and associated stressors threaten forest ecosystems due to the rapid pace of climate change, which could exceed the natural migration rate of some tree species. In response, there is growing interest to research and implement forest assisted migration (FAM). Here, we used a species-independent indicator based on climate analogy, according to the sigma (dis)similarity (σ_d) index, to match planting sites across the eastern US with (future) climatically-compatible seedlots (CCS).

Methods: We developed CCS for a grid composed of 1 × 1° of latitude and longitude. CCS were based on future climate analogs with $\leq 2\sigma_d$ analogy to ensure CCS were representative of future climate change. CCS were located for three time periods, 2030's, 2050's, and 2090's and three emissions scenarios (SSP2-4.5, SSP3-7.0, and SSP5-8.5) from the Coupled Model Intercomparison Project phase 6 database, using 12 climate variables.

Results: CCS were identified for the majority of 1 × 1° grids based on the SSP3-7.0 scenario. Approximately 28% of 1 × 1° grid's 2090's projections included future climate novelty. The 2030's, 2050's, and 2090's CCS were located on average 222, 358, and 662 km or 1, 2, and 3 eastern seed zones away from the 1 × 1° grids, respectively. CCS were also located further south-southwest (188–197°). In addition, the average forest cover of CCS was approximately 2%, 5%, and 10% less than that of the 1 × 1° grids.

Discussion: Our development and synthesis of CCS emphasized four key results: (i) average distances to 2030's and 2050's CCS were similar to seed-transfer guidelines for some tree species, but 2090's CCS exceeded current recommendations; (ii) south-southwesterly locations of CCS aligned with tree species habitat distribution dynamics; (iii) future climate novelty potentially challenges the conceptual basis of FAM if tree species are not adapted to climate change; and (iv) variation in forest cover among CCS presents potential opportunities and challenges due the presence or absence of forestland to source seed. Ultimately, our goal was to locate and synthesize CCS that could enable FAM decision support.

KEYWORDS

forest assisted migration, climatically-compatible seedlot, climate analog, adaptive silviculture, climate change

1 Introduction

Global climate change and associated stressors represent some of the greatest challenges facing forest ecosystems today (Parmesan et al., 2022; Domke et al., 2023). This is exemplified by the rapid pace of climate change, which could exceed the natural migration rate of some species, leading to maladaptation and ecological and economic losses (Aitken et al., 2008; Mckenney et al., 2011; Price et al., 2013; Etterson et al., 2020; Prasad et al., 2020; Bisbing et al., 2021). One adaptation strategy increasingly discussed is Forest Assisted Migration (FAM), usually as a mechanism to accelerate natural species or genotype migration to compensate for anticipated ecological, economic, and cultural losses (Millar et al., 2007; Pedlar et al., 2012; Williams and Dumroese, 2013; Nagel et al., 2017; Palik et al., 2022). The emerging consensus is that as forest vulnerability to climate change increases, FAM will likely become an increasingly important strategy in forest conservation and management.

The anticipated prevalence of climate-driven migration lags and variety of FAM forms can be illustrated through the United States Forest Service (USFS) Climate Change Tree Atlas (https://www.fs.usda.gov/nrs/atlas/tree/) (Iverson et al., 2019a,b). The Tree Atlas quantifies potential distribution dynamics of current and projected future habitat of 125 eastern US tree species. For example, within the Northeast region, 65 of these species are expected to experience regional habitat increases by 2100 (under a very high emissions scenario), of which 24 are non-endemic to the Northeast and only seven may naturally migrate into the region by 2100, despite expected habitat outfilling. Specifically, whether tree species or genotypes are sourced and transplanted within their current range, just outside their range, or far from their range refers to *assisted population expansion*, *assisted range expansion*, or *assisted species migration*, respectively—exemplifying different levels of FAM intensity, endemism, and associated risk. However, practitioners in the eastern US lack the resources and confidence identifying the precise optimal seed sources for these species—a topic described in recent FAM literature (Park and Talbot, 2018; Palik et al., 2022; Royo et al., 2023)—because resources such as the Tree Atlas do not currently account for intraspecies variation (Leites et al., 2019; Prasad and Leites, 2022) and guidelines for selecting the best genetic sources are unavailable for most species (Pike et al., 2020), including recently developed universal response functions that integrate both genetic and environmental information (Wang et al., 2010; Chakraborty et al., 2015).

Implementing FAM inherently involves a degree of risk due to many interacting factors (Dumroese et al., 2015; Park and Talbot, 2018). Perceived short- and long-term challenges with respect to local vs. non-local seed source optimality to potentially novel environmental and changing climate conditions threaten the potential success of FAM. From a climate standpoint, local seed sources are expected to progressively respond negatively to intensifying climate change. On the other hand, non-local seed sources identified for their future adaptation are expected to increasingly respond favorably to climate change. However, non-local seed sources must survive current climate conditions in which they may be less adapted due to phenological mismatches. In addition to short-term responses to climate, non-local seed sources must also adapt to potentially novel plant-soil feedbacks (Refsland et al., 2023), browsing pressure (Champagne et al., 2021a), and moisture regimes (Champagne et al., 2021b) that local seed sources may be better adapted. Thus, early seedling survival is key to FAM success (Corlett and Westcott, 2013). Provenance tests have historically been critical to providing information on short-term acclimatization of non-local seed sources and the development of seed transfer distances for a select number of tree species. Recent provenance trials and early results from FAM studies have shown that non-local seed sources can be successful and even outperform local seed sources during this crucial period (Lu et al., 2014; Palik et al., 2022). Hence, identifying appropriate seed sources is key to developing practical knowledge on how to guide FAM efforts.

Researchers have instead developed generalizable, sometimes species-independent, approaches to identifying appropriate seed sources or seed-transfer guidelines when optimum species or genetic information is unavailable. For example, tree seed zones may be based on climatic thresholds related to drought or cold hardiness (Bower et al., 2014; Erickson and Halford, 2020; Pike et al., 2020). The US Eastern Seed Zone Forum, for example, identifies current eastern seed zones as a combination of cold hardiness zones and ecoregions that are intended to delineate key adaptive responses in which native seed may be collected and planted without deleterious effects due to phenological mismatches (http://www.easternseedzones.com/) (Pike et al., 2020). To facilitate FAM when species or genotypes have not been field tested or when genetic information is unavailable, the Seed Zone Forum recommends seed transfers within or between adjacent seed zones, i.e., ∼1–2 seed zones, to enable adaptation to future climate change as a general rule (Pike et al., 2020). Transfer distances >2 seed zones, however, are thought to pose risk of genetic maladaptation, especially in the near term before the climate has changed in favor of individuals from warmer regions. Nonetheless, these recommendations recognize that accelerating climate change may warrant transfers exceeding conservative movements between adjacent seed zones (Pike et al., 2020).

Alternatively, researchers may identify optimal seed sources using climate distances between two points in a fixed area, in which seed may be sourced from locations where climates are most similar, i.e., climatic distances are minimized (Doherty et al., 2017; Shryock et al., 2018; St.Clair et al., 2022; Royo et al., 2023). As opposed to *ad hoc* migration prescriptions, which may be comprised of indiscriminately-sourced seed from more southern locations, climate-distance approaches offer a more geographically- and thus climatically-precise approach that researchers are increasingly advocating (Young et al., 2020; Royo et al., 2023). In addition, collections across fixed seed zones may be compromised if zones are too large, increasing maladaptation across large distances, vs. too small, necessitating unwarranted or excessive collections (O'Neill et al., 2014). Similarly, more climatically-precise methods in the eastern US are expected to better capture a greater range (besides temperature-related variables) of key climatic responses, e.g., moisture, in the adaptive profile of selected seed sources, such that climatically-compatible seedlots may also be located further west or east, e.g., drier or wetter, of a planting site, as observed in the distribution dynamics of tree species habitat in the Tree Atlas (Iverson et al., 2019a).

Here, we used a standardized climate-distance and species-independent index, sigma (dis)similarity (σ_d) (Mahony et al., 2017), to identify climate analogs—contemporary locations with climates similar to the anticipated future climate of a planting site (Williams et al., 2007; Grenier et al., 2013). We refer to these new locations as (future) climatically-compatible seedlots (CCS). The general premise of this approach is that CCS located within future climate analogs are expected to better minimize risk and maximize seedling adaptation potential because they originated from similar climates to the planting site's anticipated future climate (Young et al., 2020; St.Clair et al., 2022; Royo et al., 2023). Thus, the expectation is that they are pre-adapted to the anticipated future climate of a planting site. Climate analog modeling within a FAM context is growing in popularity. However, broad syntheses for regions such as the eastern US are lacking. The eastern US is an ideal candidate for such a synthesis because it contains some of the most forested regions in the US, coincides with existing adaptive resources, i.e., Tree Atlas and eastern seed zones, and is where FAM is actively being used in support of climate-adaptive forestry (Nagel et al., 2017; Palik et al., 2022).

Climate analogy and σ_d also provides a basis for the identification of future climate novelty. Novel climates are emerging conditions with no analog in the observational record. Future climate novelty could challenge the conceptual basis of FAM because FAM is partially dependent on the premise that successful seedling establishment of future-climate-adapted tree species or genotypes is based on the complementarity of their fundamental niche to the anticipated future climate space (Williams and Jackson, 2007). However, if no reference conditions exist for a future climate, FAM may be less reliable due to climate change exceeding the adaptive potential of prospective seed sources. Some estimates suggest 10%−40% of Earth's terrestrial surface, including portions of the eastern US, are expected to experience climate novelty by 2100 (Mahony et al., 2017). Identifying the emergence and locations at risk of developing future climate novelty may be an important consideration in FAM adaptive planning and risk assessment.

Our objectives were to use climate analogy according to σ_d to quantify potential CCS for the eastern US and provide a broad synthesis on CCS patterns that may enable FAM decision support. We used a grid of 1 × 1° latitude and longitude as our frame of reference. Our work synthesizes geographic patterns in CCS: (i) climate analogy of CCS, i.e., (dis)similarity of future climates; (ii) distance to CCS (both in geographic distance and minimum number of seed zones and plant hardiness zones between CCS and planting sites); (iii) direction to CCS (as degrees bearing); (iv) emergence of future climate novelty; and (v) variation in forest cover between 1 × 1° grid planting sites and CCS as an examination of potential socio-environmental opportunities or challenges due to the presence or absence of forestlands at desired, i.e., most-climatically matched, locations. We used climate models based on 2030's, i.e., current (2021–2040), 2050's, i.e., mid-century (2041–2060), and 2090's, i.e., late-century (2081–2100) periods, according to three emissions scenarios, SSP2-4.5, SSP3-7.0, and SSP5-8.5, derived from the Coupled Model Intercomparison Project phase 6 (CMIP6) database (IPCC, 2022).

2 Materials and methods

2.1 Study area

We quantified CCS for a series of 494, 1 × 1° grids located in the eastern US (east of the 100th Meridian) developed as part of the USFS Climate Change Tree Atlas (Figure 1a). The geographic footprint provided a coarsely-summarized continuous grid of representative sites permitting sufficient climate observations from historical weather stations. In addition, the 1 × 1° grid focus complements the Tree Atlas, delivering a single information point enabling FAM decision support. Forest cover averaged 31.21 ± 2.14% (±95% CI) and ranged from 0.03 to 86.25% across the grid (NALC, 2020). CCS were located within a larger study domain encompassing the extent of the western hemisphere north of the equator as defined by the input climate data. The region was also partitioned into five geographic regions and 92 eastern US seed zones to assist in our synthesis (Iverson et al., 2008; Pike et al., 2020) (Figures 1b, c).

2.2 Sigma (dis)similarity (σ_d)

We used climate analogy according to σ_d to locate CCS for each 1 × 1° grid (Mahony et al., 2017). This approach produces σ_d surfaces that depict geographic areas where current climate conditions are most similar, i.e., analogous, to each 1 × 1° grid's forecasted climate. σ_d is derived from standardized Mahalanobis distances and interpreted as a multivariate *z*-score metric (Mahony et al., 2017; Fitzpatrick and Dunn, 2019). The use of Mahalanobis distances reduces limitations in variable scaling, e.g., °C vs. mm, and variance inflation due to correlations. Mahalanobis distances were standardized with respect to local 1 × 1° grid climate variability and scaled according to the half-normal percentile of the associated chi distribution, where *n df* equaled the number

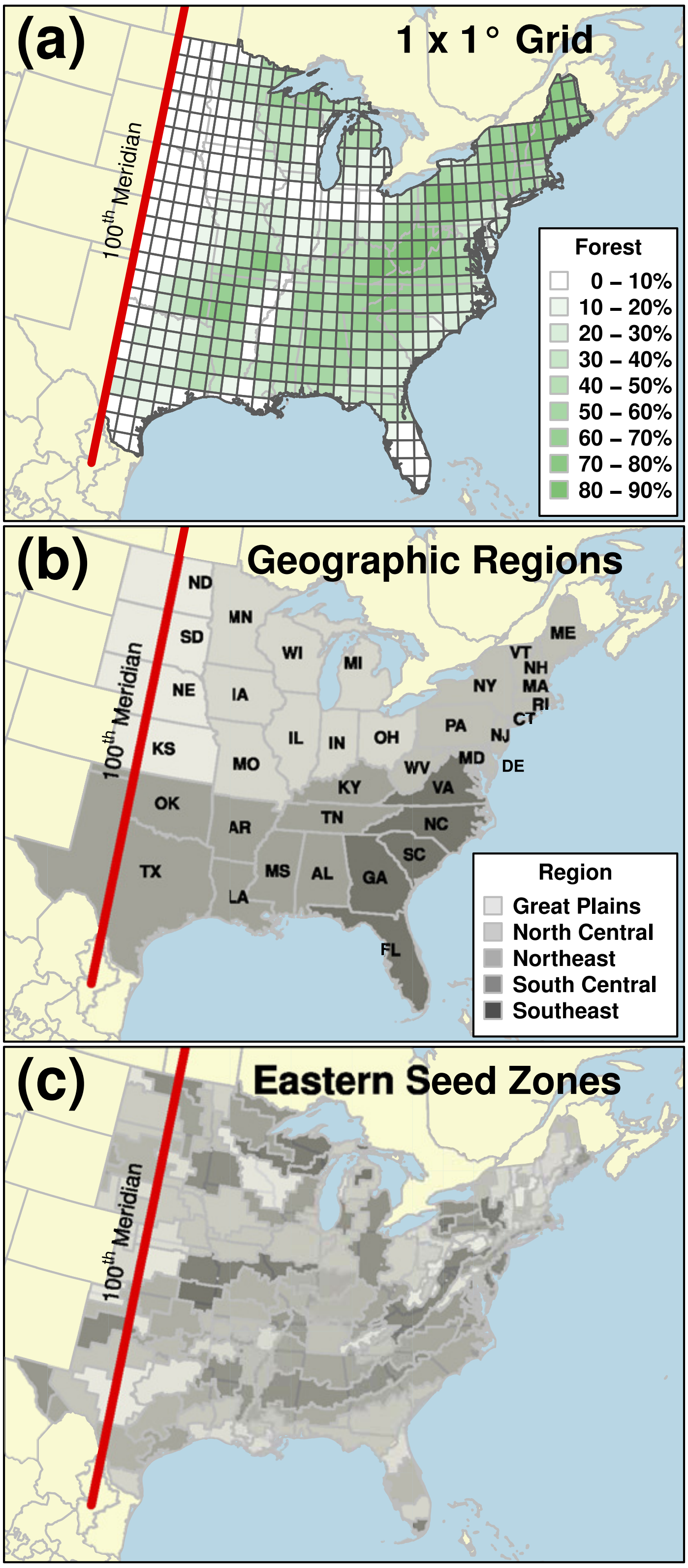


FIGURE 1
The eastern US 1 × 1° grid where we located (future) climatically-compatible seedlots (CCS) **(a)**, including five geographic regions **(b)** and 92 eastern US seed zones **(c)**. Note 1 × 1° grids are referenced by their southeastern corner, i.e., a coordinate of 45.89, −88.46 occurs in the S45_E88 1 × 1° grid.

of dimensions, i.e., climate variables, and $1\sigma_d$, $2\sigma_d$, and $4\sigma_d$ corresponded to the 68th, 95th, and 99.9th normal percentiles, respectively. A $0\sigma_d$ indicates identical climates, i.e., a 1 × 1° grid's future climate and its closest-matched contemporary climate analog are a perfect match. σ_d is both a measure of the strength of climate analogy and an indicator of future climate novelty. Hence, σ_d may serve as a proxy for seedling adaptation potential to future climate change, i.e., where analogy is strongest (σ_d lowest) seedling adaptation, e.g., survival, productivity, reproduction, may be greatest. Thus, we defined an upper threshold of $2\sigma_d$ (95th percentile), in which we confidently assigned CCS to each 1 × 1° grid's σ_d surface. This is because values $>2\sigma_d$ generally indicate future climate novelty (Mahony et al., 2017). In other words, values $>2\sigma_d$ indicate a 1 × 1° grid's future climate is dissimilar to any contemporary climate in the study domain, which we interpret as there being no CCS for that 1 × 1° grid's anticipated future climate.

2.3 Climate data

We used 12 climate variables and three datasets to map σ_d values and locate CCS for each 1 × 1° grid. The 12 climate variables consisted of mean minimum and maximum temperature (°C) and total precipitation (mm) for each of the four climatological seasons; winter (December, January, and February), spring (March, April, and May), summer (June, July, and August), and autumn (September, October, and November). The variables were selected because we considered them to represent fundamental elements of future climate change and because they have been supported in previous climate analog mapping applications (Mahony et al., 2017; Fitzpatrick and Dunn, 2019).

2.3.1 Contemporary climate data [A]

The first dataset was a contemporary climate surface [A] that we converted into the σ_d surfaces, serving as the regional climate pool and potential CCS. We used gridded 1-km resolution climate data for North America provided by the AdaptWest Project and generated using ClimateNA v7.3 software (AdaptWestProject, 2022). The geographic extent of [A] defined the larger study domain across North America. These data were based on downscaled PRISM (PRISMClimateGroup, 2022) and WordClim data (Fick and Hijmans, 2017), estimated over a 30-year period from 1981–2010.

2.3.2 Future climate data [B]

The second group of datasets were projections of each 1 × 1° grid's future climate [B], we spatially related to [A]. Future climate data in [B] were averaged within the extent of each 1 × 1° grid for the 12 climate variables. We used climate models derived from the Coupled Model Intercomparison Project phase 6 (CMIP6) database (corresponding to the 6th IPCC Assessment Report) (IPCC, 2022) and the 8-model general-purpose ensemble selected by Mahony et al. (2022). The raster surfaces were provided by the AdaptWest Project and included ensemble-mean projections from models ACCESS-ESM1.5, CNRM-ESM2-1, EC-Earth3, GFDL-ESM4, GISS-E2-1-G, MIROC6, MPI-ESM1.2-HR, and MRI-ESM2.0 (see AdaptWestProject, 2022, for details on these projections).

Future climate projections were provided in 20-year averages for the time periods of 2021–2040, 2041–2060, and 2081–2100 to accommodate a spectrum of climate-adaptation options in [B]. We refer to these temporal projections as enabling "adaptation" to 2030's, 2050's, and 2090's predicted climates or current, mid-century, and late-century, respectively. We also included Shared Socioeconomic Pathways, SSP2-4.5 (intermediate warming limited to <3°C), SSP3-7.0 (high warming limited to <4°C), and SSP5-8.5 (very high warming exceeding >4°C), to assess a range of emissions scenarios. We focused our results on SSP3-7.0 here as our objectives were to provide a general pattern of CCS representative of potential challenges for FAM, while acknowledging the likelihood of a given scenario is challenging (Hausfather and Peters, 2020; Schwalm et al., 2020; Hausfather et al., 2022). In addition, we found similarities in the geographic locations of CCS across emissions scenarios, e.g., 72% of all 2050's CCS were located <100 km from one another across SSP2-4.5, SSP3-7.0, and SSP5-8.5 (though these similarities declined in 2090's projections). We provided results for all three emissions scenarios in the Supplementary material, using tables and interactive web maps created with the *leaflet* R package (Cheng et al., 2024).

2.3.3 Historical interannual climate data [C]

The third and final dataset was developed from NOAA weather station records to estimate historical interannual climate variability [C] within each 1 × 1° grid. σ_d standardizes climatic distances with respect to historical climate data. We estimated [C] for the 12 climate variables using the Global Summary of the Month (GSOM) dataset (Lawrimore et al., 2016). The GSOM dataset contains meteorological events at monthly resolution from 1763, composed primarily of daily Global Historical Climatology Network observations. We located all weather stations within each 1 × 1° grid that contained ≥20 years of observations over a reference period of 1961–2010 using the *rnoaa* R package (Chamberlain, 2020). We used the 50-year reference period and required a minimum of five unique weather stations per 1 × 1° grid to estimate [C] in order to ensure sufficient climate observations for calculating σ_d. Station records were averaged using inverse distance weighting to the center of each 1 × 1° grid and monthly records were aggregated to the four climatological seasons to match the climate data in [A] and [B]. For 1 × 1° grids (mostly located along coastlines with limited land area) without five weather stations or ≤20 years of observations, we searched outwards from the cell's centroid incorporating the nearest five weather stations with these criteria into the analyses, similarly using inverse distance weighting to calculate the 12 climate variables.

2.4 Statistical analyses

We located CCS for each 1 × 1° grid by converting [A] into surfaces of σ_d using future climate projections in [B] and scaling climatic distances with respect to local historical climate

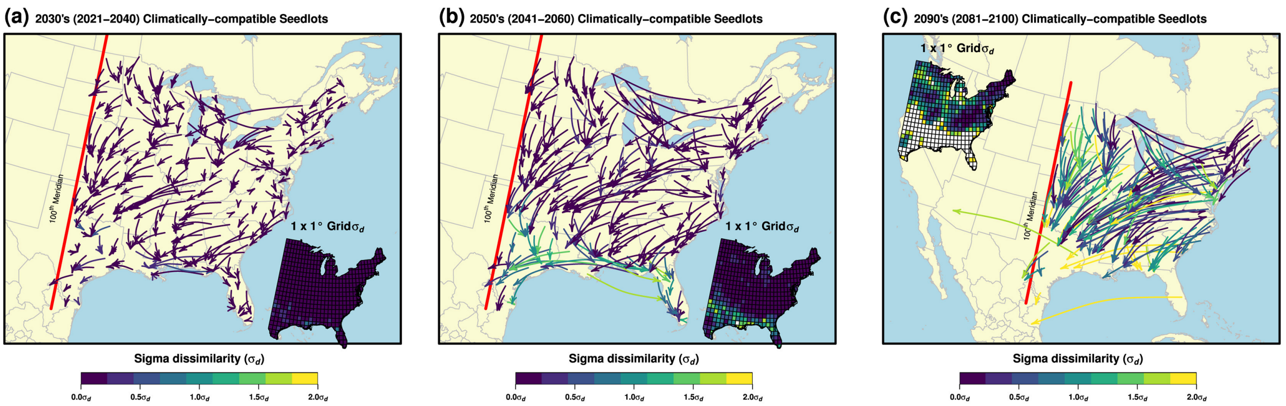


FIGURE 2
Locations of (future) climatically-compatible seedlots (CCS) $\leq 2\sigma_d$ analogy for the eastern US 1 × 1° grid under the SSP3-7.0 emissions scenario and three adaptation planning periods: 2030's (2021–2040) **(a)**, 2050's (2041–2060) **(b)**, and 2090's (2081–2100) **(c)**. Arrows point each 1 × 1° grid's CCS, omitting $>2\sigma_d$ novelty (note only 50% of CCS in each period are shown for display purposes). The analogy (or novelty) of each 1 × 1° grid's future climate projection to its CCS is shown in color on each arrow and in inset maps (1 × 1° grids $>2\sigma_d$ novelty are displayed in white color).

variability in [C]. All analyses were conducted in R (https://www.r-project.org/) and we adapted methods and R scripts provided in Mahony et al. (2017). We considered CCS to include $\leq 2\sigma_d$ analogy between [A] and [B] (in each 1 × 1° grid). We summarized the strength of analogy (or novelty), i.e., σ_d value, distance (km), and bearing (°) to the pixel with the least σ_d value. We provided summaries for 37 eastern US states and five geographic regions. The 1 × 1° grid cells were assigned to individual states, regions, seed zones, and plant hardiness zones using majority rule, i.e., the geographic feature with the greatest areal extent within a 1 × 1° grid was used. We used eastern seed zones version 2.2 and plant hardiness zones version 2023 (Pike et al., 2020; USDA Agricultural Research Service, 2023). The granularity and resolution of these maps can lead to over- or under-counting zones (from 1 × 1° grid to CCS) if they are spatially-disjoined and/or overly-small. For our purposes, we snapped the original maps to US counties to force small, spatially-disjoined sections of zones to be absorbed into larger zones (particularly in the case of plant hardiness zones) or be separated into individual zones (eastern seed zones). Finally, we estimated percent forest cover amount within each 1 × 1° grid and the landscape surrounding each CCS within a 50-km buffer radius (an area roughly similar in size to the average 1 × 1° grid). Forest cover was estimated with the 2020 North American Land Cover dataset provided in 30 m resolution, based on Landsat satellite imagery of Canada, Mexico, and the US (NALC, 2020).

3 Results

3.1 Distinguishing climatically-compatible seedlots (CCS)

We located CCS $\leq 2\sigma_d$ analogy for all ($n = 494$) of the 1 × 1° grids for the 2030's, i.e., current (2021–2040) period, all but one ($n = 493$) of the 1 × 1° grids for the 2050's, i.e., mid-century (2041–2060) period, and 356 (~72%) of the 1 × 1° grids for the 2090's, i.e., late-century (2081–2100) period, under the SSP3-7.0 emissions scenario (Figure 2, Table 1). In other words, 28% of 1 × 1° grids displayed emerging climate novelty under 2090's climate projections. Supplementary Tables S1–S9 and interactive web maps (Supplementary Figures S1–S3) summarize results for all three emissions scenarios (SSP2-4.5, SSP3-7.0, and SSP5-8.5). The fewer number of 2090's CCS resulted from accentuated $>2\sigma_d$ novelty emerging throughout the southern portion of the eastern US, attributed to accelerated climate change and deficient land area further south, e.g., the Gulf of Mexico, to draw representative analogs.

3.2 Analogy of climatically-compatible seedlots (CCS)

The σ_d value, as a potential measure of CCS adaptation to climate change, was on average 0.03 ± 0.01 (±95% CI) σ_d (~2nd percentile) for the 2030's, $0.20 \pm 0.03\ \sigma_d$ (~16th percentile) for the 2050's, and $0.71 \pm 0.06\ \sigma_d$ (~52nd percentile) for the 2090's periods (noting that $0\sigma_d$ is a perfect match, $\leq 2\sigma_d$ is up to a moderate level of (dis)similarity, and $>2\sigma_d$ is indicative of future climate novelty) (Mahony et al., 2017) (Table 1). Altogether, the total area representing $\leq 2\sigma_d$ analogy for each CCS was on average 451-, 351-, and 177-thousand km^2 for the 2030's, 2050's, and 2090's planning periods, respectively (Supplementary Tables S2, S5, S8).

3.3 Distance to climatically-compatible seedlots (CCS)

The geographic distance to CCS (from 1 × 1° grid planting cell's centroid to the pixel with the lowest σ_d value) was on average 222 ± 12 km for the 2030's, 358 ± 20 km for the 2050's, and 662 ± 35 km for the 2090's adaptation planning periods (Table 1). Regionally, 1 × 1° grids located in the Southeast and South Central regions

TABLE 1 Regional and US state-level statistics of (future) climatically-compatible seedlots (CCS) ≤2σ_d analogy for the three adaptation periods, 2030's (2021–2040), 2050's (2041–2060), and 2090's (2081–2100), and SSP3-7.0 emissions scenario, including the number (n) of CCS, i.e., 1 × 1° grids with CCS, and the mean (±95% CI) σ_d value, distance to CCS (km), bearing to CCS (°), number of seed zones from 1 × 1° grid to CCS, and difference (Δ) in forest cover (%) between 1 × 1° grid and CCS (note, only CCS located within established eastern US seed zones could be used in calculating the number of seed zones to CCS, generally excluding CCS west of the 100th Meridian).

Region	n 1 × 1° grids	n CCS	σ_d	km	°	n seed zones to CCS	ΔCCS forest cover (%)
2030's (2021–2040)							
Eastern Region	494	494	0.03 ± 0.01	222 ± 12	188 ± 4	1.19 ± 0.09	−2.27 ± 1.31
Great Plains	46	46	0.01 ± 0.00	206 ± 22	196 ± 9	1.17 ± 0.16	−0.89 ± 0.95
North Central	159	159	0.01 ± 0.00	227 ± 17	184 ± 6	1.37 ± 0.18	−2.01 ± 2.78
Northeast	81	81	0.00 ± 0.00	202 ± 41	182 ± 15	1.41 ± 0.28	−4.05 ± 3.21
South Central	132	132	0.07 ± 0.02	226 ± 23	196 ± 9	1.20 ± 0.16	−2.51 ± 2.55
Southeast	76	76	0.02 ± 0.02	234 ± 41	187 ± 12	0.57 ± 0.19	−1.32 ± 2.82
Alabama	12	12	0.03 ± 0.04	267 ± 63	216 ± 27	0.83 ± 0.25	−10.70 ± 5.42
Arkansas	10	10	0.02 ± 0.02	265 ± 38	191 ± 28	1.70 ± 0.48	4.31 ± 10.92
Connecticut	2	2	0.00 ± 0.00	104 ± 823	224 ± 52	0.50 ± 6.35	−15.75 ± 134.25
Delaware	1	1	0.01	123	236	3	37.09
Florida	23	23	0.06 ± 0.06	160 ± 60	165 ± 23	0.43 ± 0.22	−2.19 ± 4.06
Georgia	15	15	0.03 ± 0.04	312 ± 94	219 ± 17	0.33 ± 0.27	−2.30 ± 7.82
Illinois	16	16	0.01 ± 0.01	216 ± 62	193 ± 18	1.12 ± 0.43	12.31 ± 5.00
Indiana	11	11	0.01 ± 0.00	340 ± 172	199 ± 26	1.73 ± 0.61	11.39 ± 7.69
Iowa	18	18	0.01 ± 0.00	234 ± 35	198 ± 19	1.06 ± 0.40	3.72 ± 6.20
Kansas	15	15	0.01 ± 0.01	214 ± 32	190 ± 16	1.00 ± 0.21	−2.93 ± 2.59
Kentucky	8	8	0.00 ± 0.00	409 ± 218	230 ± 14	1.25 ± 0.59	−1.48 ± 13.76
Louisiana	15	15	0.17 ± 0.10	214 ± 91	189 ± 48	1.07 ± 0.64	5.25 ± 7.61
Maine	17	17	0.00 ± 0.00	249 ± 84	180 ± 30	1.08 ± 0.69	−1.93 ± 8.24
Maryland	3	3	0.00 ± 0.00	131 ± 87	136 ± 94	2.00 ± 2.48	−9.46 ± 42.62
Massachusetts	5	5	0.00 ± 0.00	214 ± 165	214 ± 14	2.40 ± 2.99	−1.69 ± 8.84
Michigan	29	29	0.01 ± 0.01	220 ± 41	149 ± 14	2.25 ± 0.74	−17.55 ± 6.48
Minnesota	31	31	0.01 ± 0.01	207 ± 25	172 ± 12	1.10 ± 0.22	0.39 ± 6.38
Mississippi	14	14	0.07 ± 0.07	258 ± 76	161 ± 32	1.00 ± 0.39	−0.40 ± 9.19
Missouri	22	22	0.00 ± 0.00	259 ± 33	222 ± 7	1.59 ± 0.30	−6.44 ± 6.59
Nebraska	11	11	0.00 ± 0.00	217 ± 38	184 ± 10	1.45 ± 0.35	0.34 ± 1.09
New Hampshire	3	3	0.00 ± 0.00	138 ± 108	216 ± 27	1.00 ± 2.48	−8.13 ± 23.48
New Jersey	4	4	0.00 ± 0.00	93 ± 54	180 ± 10	0.75 ± 0.80	−1.50 ± 19.04
New York	21	21	0.00 ± 0.00	195 ± 68	184 ± 38	1.48 ± 0.42	−2.58 ± 6.57
North Carolina	20	20	0.00 ± 0.00	194 ± 52	195 ± 19	0.50 ± 0.24	1.04 ± 6.62
North Dakota	9	9	0.00 ± 0.00	193 ± 42	189 ± 26	0.89 ± 0.26	−0.71 ± 0.59
Ohio	13	13	0.01 ± 0.01	193 ± 44	188 ± 23	0.92 ± 0.58	3.86 ± 7.89
Oklahoma	18	18	0.05 ± 0.04	201 ± 36	202 ± 9	1.67 ± 0.34	−10.36 ± 8.63
Pennsylvania	13	13	0.00 ± 0.01	239 ± 115	144 ± 41	1.54 ± 0.47	−11.72 ± 7.99
Rhode Island	1	1	0	118	231	0	3.03
South Carolina	10	10	0.00 ± 0.00	456 ± 173	222 ± 11	0.60 ± 0.37	4.00 ± 7.87
South Dakota	11	11	0.01 ± 0.02	197 ± 81	222 ± 19	1.36 ± 0.45	0.49 ± 0.99
Tennessee	13	13	0.00 ± 0.00	296 ± 89	226 ± 15	1.85 ± 0.73	−1.00 ± 8.69

(Continued)

TABLE 1 (Continued)

Region	*n* 1 × 1° grids	*n* CCS	σ_d	km	°	*n* seed zones to CCS	ΔCCS forest cover (%)
Texas	42	42	0.10 ± 0.03	154 ± 21	186 ± 15	0.82 ± 0.23	−2.55 ± 4.09
Vermont	4	4	0.01 ± 0.02	406 ± 862	194 ± 59	2.50 ± 3.79	−1.62 ± 24.43
Virginia	8	8	0.00 ± 0.00	121 ± 36	127 ± 40	1.50 ± 1.61	−9.54 ± 9.19
West Virginia	7	7	0.00 ± 0.00	90 ± 74	200 ± 97	0.71 ± 0.70	−3.39 ± 12.41
Wisconsin	19	19	0.01 ± 0.00	198 ± 40	181 ± 21	0.84 ± 0.29	−6.30 ± 8.96
2050’s (2041–2060)							
Eastern Region	494	493	0.20 ± 0.03	358 ± 20	189 ± 4	1.71 ± 0.10	−4.77 ± 1.51
Great Plains	46	46	0.05 ± 0.02	293 ± 25	190 ± 6	1.65 ± 0.19	−0.45 ± 1.15
North Central	159	159	0.06 ± 0.01	375 ± 26	184 ± 6	1.96 ± 0.20	−3.42 ± 2.99
Northeast	81	81	0.02 ± 0.01	321 ± 50	190 ± 12	1.85 ± 0.26	−9.94 ± 3.87
South Central	132	131	0.49 ± 0.09	353 ± 30	193 ± 8	1.74 ± 0.15	−5.93 ± 2.90
Southeast	76	76	0.26 ± 0.09	408 ± 87	191 ± 10	1.07 ± 0.19	−2.67 ± 3.74
Alabama	12	12	0.32 ± 0.30	355 ± 67	197 ± 37	1.00 ± 0.27	−9.01 ± 4.50
Arkansas	10	10	0.23 ± 0.15	339 ± 60	173 ± 22	2.50 ± 0.51	0.86 ± 16.58
Connecticut	2	2	0.01 ± 0.06	168 ± 104	210 ± 133	0.50 ± 6.35	−27.81 ± 44.13
Delaware	1	1	0.15	239	180	4	−2.07
Florida	23	23	0.64 ± 0.18	397 ± 235	177 ± 23	1.00 ± 0.31	−2.31 ± 7.95
Georgia	15	15	0.31 ± 0.25	368 ± 120	202 ± 21	0.87 ± 0.19	−3.57 ± 9.25
Illinois	16	16	0.08 ± 0.03	362 ± 52	205 ± 13	2.00 ± 0.48	15.01 ± 8.75
Indiana	11	11	0.05 ± 0.04	395 ± 153	215 ± 11	1.73 ± 0.61	11.13 ± 7.00
Iowa	18	18	0.03 ± 0.02	357 ± 38	204 ± 11	2.00 ± 0.34	0.79 ± 3.80
Kansas	15	15	0.08 ± 0.04	311 ± 44	193 ± 10	1.60 ± 0.35	−2.81 ± 2.99
Kentucky	8	8	0.01 ± 0.01	624 ± 170	212 ± 45	2.38 ± 0.62	−5.24 ± 20.61
Louisiana	15	14	1.05 ± 0.27	509 ± 147	201 ± 43	1.79 ± 0.61	−4.56 ± 11.32
Maine	17	17	0.00 ± 0.00	322 ± 58	205 ± 7	1.33 ± 0.40	−2.99 ± 9.01
Maryland	3	3	0.08 ± 0.18	464 ± 1,117	182 ± 136	3.00 ± 2.48	−6.04 ± 37.03
Massachusetts	5	5	0.01 ± 0.02	290 ± 107	214 ± 9	2.60 ± 2.26	−11.28 ± 8.58
Michigan	29	29	0.08 ± 0.04	437 ± 98	142 ± 14	2.65 ± 0.93	−17.65 ± 7.90
Minnesota	31	31	0.06 ± 0.03	328 ± 51	166 ± 10	1.73 ± 0.31	−3.30 ± 6.80
Mississippi	14	14	0.51 ± 0.33	383 ± 119	174 ± 32	1.43 ± 0.37	−2.65 ± 9.40
Missouri	22	22	0.01 ± 0.01	418 ± 44	220 ± 7	2.32 ± 0.29	−9.34 ± 5.05
Nebraska	11	11	0.01 ± 0.01	306 ± 37	183 ± 6	1.91 ± 0.36	−0.12 ± 0.96
New Hampshire	3	3	0.00 ± 0.00	148 ± 112	220 ± 56	1.50 ± 6.35	−13.92 ± 28.14
New Jersey	4	4	0.04 ± 0.07	169 ± 64	189 ± 19	1.25 ± 0.80	−6.70 ± 17.69
New York	21	21	0.04 ± 0.03	290 ± 90	166 ± 30	1.76 ± 0.52	−4.64 ± 7.60
North Carolina	20	20	0.01 ± 0.00	427 ± 127	199 ± 19	0.95 ± 0.18	0.90 ± 6.95
North Dakota	9	9	0.03 ± 0.03	279 ± 52	197 ± 22	1.44 ± 0.56	−0.68 ± 0.86
Ohio	13	13	0.11 ± 0.06	370 ± 67	188 ± 32	1.62 ± 0.63	3.82 ± 12.41
Oklahoma	18	18	0.39 ± 0.19	283 ± 34	187 ± 10	2.06 ± 0.32	−10.70 ± 9.46
Pennsylvania	13	13	0.02 ± 0.02	449 ± 178	180 ± 44	2.08 ± 0.52	−22.09 ± 10.70
Rhode Island	1	1	0	280	213	1	−22.83

(Continued)

TABLE 1 (Continued)

Region	*n* 1 × 1° grids	*n* CCS	σ_d	km	°	*n* seed zones to CCS	ΔCCS forest cover (%)
South Carolina	10	10	0.02 ± 0.01	527 ± 208	217 ± 12	0.90 ± 0.23	0.49 ± 10.21
South Dakota	11	11	0.07 ± 0.04	268 ± 79	190 ± 17	1.64 ± 0.45	2.62 ± 1.57
Tennessee	13	13	0.01 ± 0.01	411 ± 82	221 ± 15	2.23 ± 0.44	−9.47 ± 5.18
Texas	42	42	0.69 ± 0.14	254 ± 29	190 ± 12	1.31 ± 0.25	−5.22 ± 4.90
Vermont	4	4	0.01 ± 0.02	397 ± 851	217 ± 52	2.50 ± 3.79	−3.15 ± 25.96
Virginia	8	8	0.00 ± 0.00	314 ± 340	155 ± 40	2.12 ± 1.51	−14.91 ± 10.70
West Virginia	7	7	0.01 ± 0.01	315 ± 143	194 ± 67	2.00 ± 0.76	−19.09 ± 21.10
Wisconsin	19	19	0.06 ± 0.04	327 ± 86	176 ± 20	1.22 ± 0.44	−7.98 ± 8.42
2090's (2081–2100)							
Eastern Region	494	356	0.71 ± 0.06	662 ± 35	197 ± 4	2.94 ± 0.13	−9.56 ± 2.16
Great Plains	46	41	1.00 ± 0.16	504 ± 28	181 ± 5	2.59 ± 0.27	0.48 ± 1.23
North Central	159	146	0.75 ± 0.08	616 ± 28	190 ± 5	3.17 ± 0.21	−6.81 ± 3.82
Northeast	81	81	0.39 ± 0.11	742 ± 100	203 ± 9	3.32 ± 0.27	−17.86 ± 4.13
South Central	132	46	0.91 ± 0.20	589 ± 84	209 ± 8	2.61 ± 0.31	−14.29 ± 5.96
Southeast	76	42	0.71 ± 0.19	902 ± 156	214 ± 12	2.00 ± 0.37	−7.69 ± 6.00
Alabama	12	5	1.19 ± 0.82	386 ± 80	172 ± 33	1.60 ± 0.68	−17.81 ± 19.00
Arkansas	10	2	0.92 ± 1.87	438 ± 263	202 ± 256	2.50 ± 6.35	−34.48 ± 279.94
Connecticut	2	2	0.40 ± 0.44	1,665 ± 2,666	236 ± 5	3.50 ± 6.35	−5.34 ± 97.76
Delaware	1	1	1.25	1,755	241	5	23.33
Florida	23	2	1.87 ± 0.08	1,894 ± 544	248 ± 3	NA	28.52 ± 72.83
Georgia	15	4	0.67 ± 1.05	507 ± 202	209 ± 28	1.75 ± 0.80	−20.27 ± 15.14
Illinois	16	15	1.20 ± 0.17	661 ± 93	201 ± 18	3.33 ± 0.40	14.50 ± 10.34
Indiana	11	10	0.92 ± 0.27	664 ± 140	211 ± 13	3.50 ± 0.38	15.55 ± 16.00
Iowa	18	18	0.67 ± 0.21	597 ± 52	204 ± 5	3.22 ± 0.32	0.55 ± 4.31
Kansas	15	10	1.41 ± 0.29	557 ± 59	194 ± 7	3.60 ± 0.37	−3.44 ± 3.86
Kentucky	8	8	0.34 ± 0.21	779 ± 100	221 ± 9	3.12 ± 0.54	−12.60 ± 23.11
Louisiana	15	0	NA	NA	NA	NA	NA
Maine	17	17	0.03 ± 0.02	495 ± 52	205 ± 3	2.76 ± 0.43	−10.26 ± 8.57
Maryland	3	3	1.10 ± 1.35	1,584 ± 808	241 ± 5	4.33 ± 3.79	−8.29 ± 71.19
Massachusetts	5	5	0.16 ± 0.09	670 ± 355	212 ± 15	3.80 ± 2.04	−19.77 ± 6.34
Michigan	29	23	0.70 ± 0.21	602 ± 48	159 ± 14	3.19 ± 0.80	−21.34 ± 9.98
Minnesota	31	29	0.65 ± 0.19	570 ± 80	167 ± 10	3.28 ± 0.71	−9.16 ± 7.73
Mississippi	14	3	1.58 ± 1.12	520 ± 271	199 ± 110	2.67 ± 1.43	5.43 ± 38.90
Missouri	22	21	0.53 ± 0.17	636 ± 40	214 ± 3	3.48 ± 0.23	−17.49 ± 9.06
Nebraska	11	11	0.57 ± 0.18	504 ± 44	181 ± 6	2.45 ± 0.35	0.99 ± 1.58
New Hampshire	3	3	0.07 ± 0.19	334 ± 241	195 ± 41	2.00 ± 0.00	−32.58 ± 35.70
New Jersey	4	4	1.06 ± 1.04	1,118 ± 823	223 ± 52	3.75 ± 0.80	−4.95 ± 30.01
New York	21	21	0.48 ± 0.23	658 ± 203	177 ± 21	3.76 ± 0.63	−20.41 ± 8.51
North Carolina	20	20	0.45 ± 0.15	842 ± 164	216 ± 17	1.60 ± 0.28	−4.15 ± 8.37
North Dakota	9	9	1.03 ± 0.38	441 ± 73	179 ± 12	1.56 ± 0.41	0.97 ± 1.50
Ohio	13	12	0.93 ± 0.32	802 ± 177	207 ± 31	2.83 ± 0.81	5.38 ± 12.73

(Continued)

TABLE 1 (Continued)

Region	*n* 1 × 1° grids	*n* CCS	σ_d	km	°	*n* seed zones to CCS	ΔCCS forest cover (%)
Oklahoma	18	3	1.43 ± 1.81	493 ± 116	206 ± 19	2.00 ± 2.48	−23.89 ± 34.81
Pennsylvania	13	13	0.60 ± 0.34	773 ± 206	207 ± 30	3.15 ± 0.48	−25.84 ± 13.89
Rhode Island	1	1	0.29	483	215	1	−29.72
South Carolina	10	8	1.52 ± 0.33	1,061 ± 434	227 ± 19	1.75 ± 0.87	−5.82 ± 10.79
South Dakota	11	11	1.04 ± 0.30	507 ± 57	170 ± 9	2.64 ± 0.34	3.13 ± 1.02
Tennessee	13	13	0.48 ± 0.35	604 ± 63	208 ± 12	3.00 ± 0.49	−7.33 ± 11.61
Texas	42	12	1.34 ± 0.32	596 ± 317	221 ± 22	1.50 ± 6.35	−20.66 ± 8.79
Vermont	4	4	0.28 ± 0.58	633 ± 873	194 ± 41	3.50 ± 3.79	−16.86 ± 20.64
Virginia	8	8	0.31 ± 0.23	843 ± 563	188 ± 48	3.38 ± 1.34	−21.14 ± 16.22
West Virginia	7	7	0.13 ± 0.12	879 ± 379	227 ± 35	3.14 ± 0.83	−26.02 ± 4.13
Wisconsin	19	18	0.75 ± 0.25	513 ± 51	192 ± 10	2.50 ± 0.52	−17.68 ± 11.25

generally displayed the greatest distances to CCS across the three adaptation periods, e.g., 353 ± 30 and 408 ± 87 for 2050's South Central and Southeast CCS, respectively, whereas 1 × 1° grids of the Great Plains region largely displayed the smallest distances to CCS, e.g., 293 ± 25 for 2050's CCS (Table 1).

Geographic distances to CCS, on average, roughly corresponded to 1, 2, and 3 seed zones (specifically 1.19 ± 0.09, 1.71 ± 0.10, and 2.94 ± 0.13 seed zones) from the 1 × 1° grid's native seed zone to the seed zone of its CCS for the 2030's, 2050's, and 2090's periods, respectively (Table 1). The distance to CCS also averaged 1–2 plant hardiness zones (specifically 0.92 ± 0.08, 1.27 ± 0.08, and 2.24 ± 0.10 plant hardiness zones) for the 2030's, 2050's, and 2090's periods, respectively (Supplementary Tables S2, S5, S8). In addition, CCS were located on average 2.18 ± 0.15, 3.41 ± 0.21, and 6.05 ± 0.39 1 × 1° grid cells from the 1 × 1° grid planting site for the 2030's, 2050's, and 2090's periods, respectively (Supplementary Tables S2, S5, S8). The CCS were also located 0.73 ± 0.07, 1.02 ± 0.08, and 1.83 ± 0.11 US states from the 1 × 1° grid planting site (based on majority feature) for the 2030's, 2050's, and 2090's periods, respectively (Supplementary Tables S2, S5, S8). This is important to note if statutes preclude the selling or procuring of seedlings from other jurisdictions, i.e., non-local sources.

3.4 Direction to climatically-compatible seedlots (CCS)

The bearing (representing the angle in degrees measured clockwise from north) to CCS was on average 191 ± 2°, indicating that CCS were generally located south-southwest of each 1 × 1° grid, with an increasing tendency for more southwesterly locations over extended planning periods, e.g., 2090's (Table 1). Specifically, CCS were located on average 188 ± 4°, 189 ± 4°, and 197 ± 4° from each 1 × 1° grid's centroid for the 2030's, 2050's, and 2090's periods, respectively. Some regional patterns were also apparent; CCS (across 2030's, 2050's, and 2090's projections) for the North Central region were located on average 184° to 190° to the southwest of each 1 × 1° grid, whereas CCS of the Northeast averaged 182° to 203°.

3.5 Forest cover of climatically-compatible seedlots (CCS)

The amount of CCS forest cover (based on % forest within a 50-km buffer radius) was on average −2.27 ± 1.31%, −4.77 ± 1.51%, and −9.56 ± 2.16% less than that of their associated 1 × 1° grid for the 2030s, 2050's, and 2090's periods, respectively (Table 1, Figure 3). The Northeast region displayed the greatest average difference in forest cover amount between 1 × 1° grids and CCS, e.g., −17.86 ± 4.13 for 2090's CCS. In contrast, the Great Plains region displayed the smallest average difference in forest cover amount between 1 × 1° grids and CCS, e.g., 0.48 ± 1.23 for 2090's CCS.

3.6 Regional comparisons

The majority of CCS (~96%−98%) $\leq 2\sigma_d$ analogy across the three adaptation periods were located within the eastern US (east of the 100th Meridian), whereas non-representative analogs ($>2\sigma_d$ novelty) were more often located outside the eastern US (west of the 100th Meridian, including Mexico) (Figure 2); some of this is attributed to anticipated $>2\sigma_d$ novelty observed in the southern US. CCS among the 2030's and 2050's periods were also generally located within the same geographic region as the 1 × 1° grid in which they represent, e.g., 75 and 70% of the Northeast region's CCS for the 2030's and 2050's planning periods were located within the Northeast, respectively (Figures 4a, b). However, only 54% of the Northeast region's 2090's CCS remained in the Northeast (Figure 4c). The majority (~30%) of the Northeast region's other 2090's CCS were located in the South Central region. This pattern is apparent for much of the 1 × 1° grid, especially in the Northeast and North Central regions, i.e., USFS Region 9. The South Central region is the only region to host CCS for all other geographic

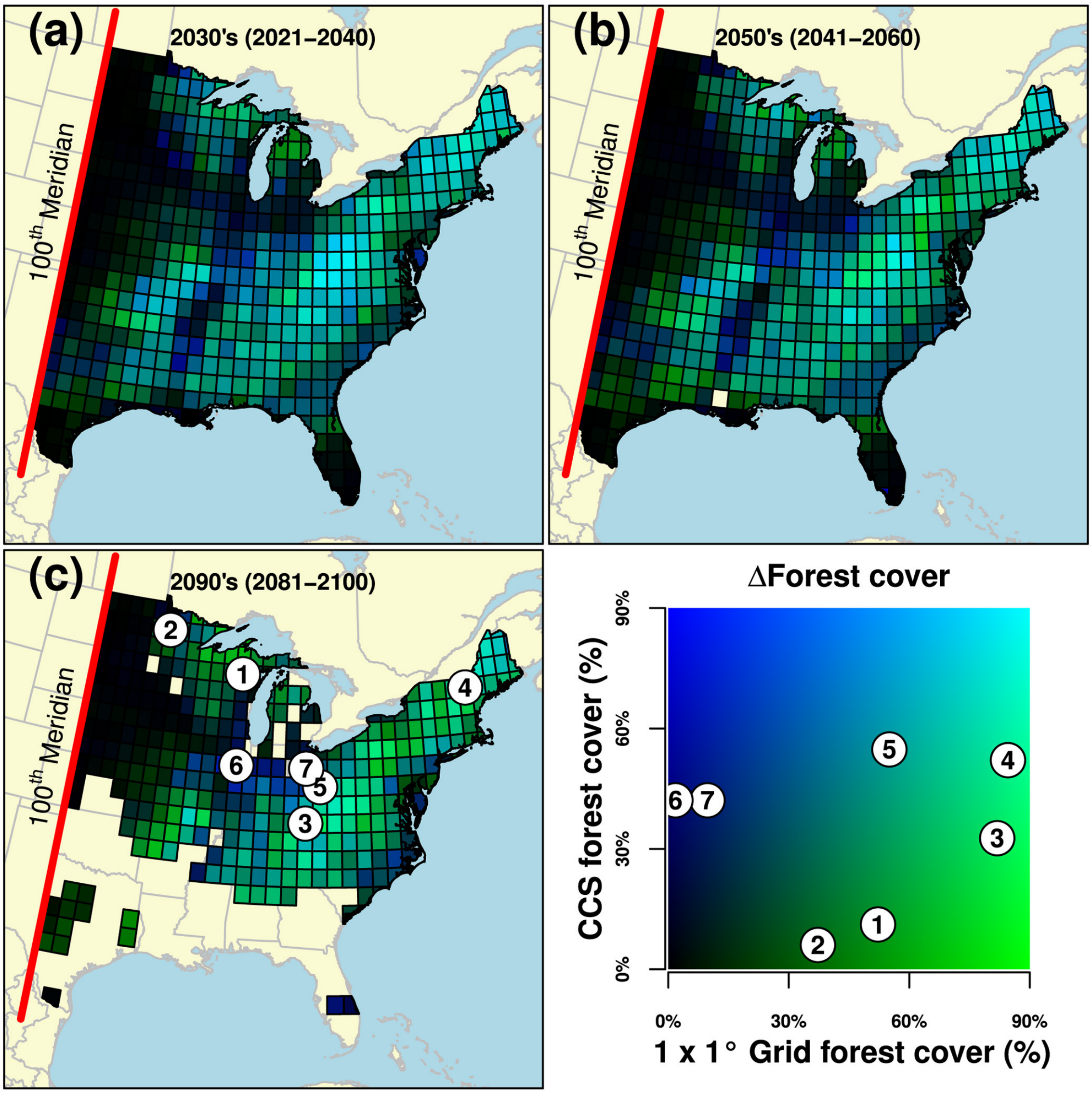
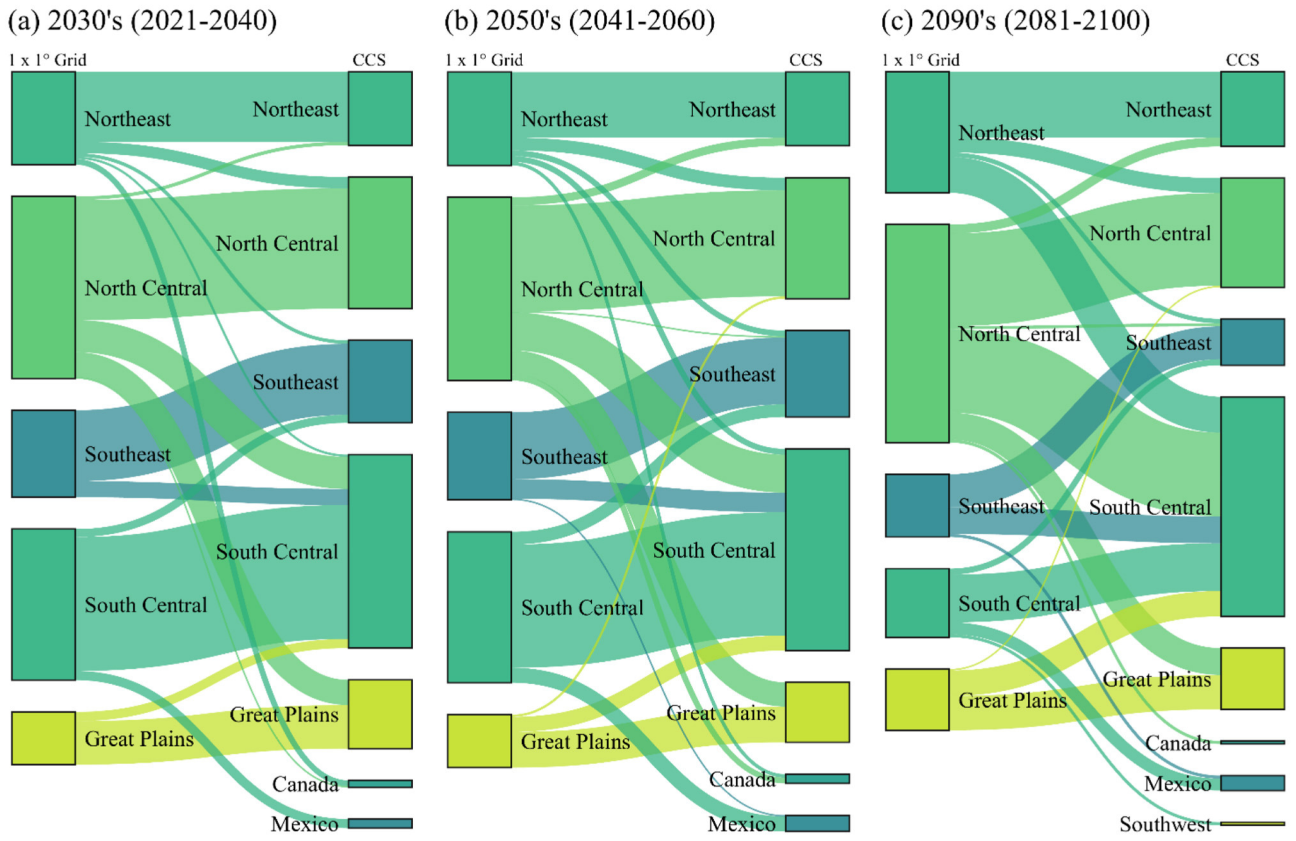


FIGURE 3
Color composite visualizing variation in forest cover (%) difference (ΔForest cover) between eastern US 1 × 1° grids and their (future) climatically-compatible seedlots (CCS) for the 2030's (2021–2040) **(a)**, 2050's (2041–2060) **(b)**, and 2090's (2081–2100) **(c)** periods. Forest cover values were transformed into channels of color in which 1 × 1° grid forest cover represented the green axis, CCS forest cover the blue axis, and a default value of 0 was set for the red axis. We provide seven examples for the 2090's period. Examples 1–2 (located in the greener color space) highlight potential challenges due the absence of forest cover (to source seed) at CCS (y axis in legend) relative to 1 × 1° grid (x axis). Examples 3–4 highlight dramatic differences in forest cover but still including CCS with >30% forest cover. Example 5 is neutral (1 × 1° grid and CCS both including >50% forest cover). Finally, examples 6–7 (in bluer color space) highlight potential opportunities for some 1 × 1° grids to source from regions with greater forest cover. Note 1 × 1° grids $>2\sigma_d$ novelty are not displayed.

regions across each period, e.g., 37% of 2090's CCS (excluding the South Central region) were located within the South Central region (Figure 4c).

4 Discussion

There is a growing need to manage for climate-driven range shifts (Bonebrake et al., 2018). Novel strategies and frameworks aimed to conserve ecosystem integrity under climate change, including FAM, are being increasingly researched and implemented (Millar et al., 2007; Pedlar et al., 2012; Nagel et al., 2017; Palik et al., 2022; Royo et al., 2023). Challenges implementing FAM include identifying optimal seed sources and estimating seed-transfer guidelines when relevant genetic information is unavailable. However, due to the need to implement these strategies under a rapidly changing climate, researchers must develop fast and efficient approaches to guide targeted collections, such as with the use of climate data. Here, we used climate analogy according to σ_d, a species-independent and climate-distance approach, to locate CCS for the eastern US that may serve as a surrogate for genetic information. The goal of this work was to provide a broad synthesis of CCS patterns that may enable greater FAM decision support across the eastern US.


(a) 2030's (2021-2040)

(b) 2050's (2041-2060)

(c) 2090's (2081-2100)

FIGURE 4
A flow diagram depicting the geographic region where 1 × 1° grids and their (future) climatically-compatible seedlots (CCS) are located under the SSP3-7.0 emissions scenario for the 2030's (2021–2040) **(a)**, 2050's (2041–2060) **(b)**, and 2090's (2081–2100) **(c)** periods. The size of the vertical bars represents the number of individual 1 × 1° grid cells (left) or CCS (right) and the width of the flows (left to right) indicates the number of connections.

4.1 Distance to climatically-compatible seedlots (CCS)

Average distances to CCS $\leq 2\sigma_d$ analogy were expectedly large (under the SSP3-7.0 emissions scenario), yet similar to maximum transfer distances (to avoid phenological mismatches) recommended for some species, as derived from provenance trials, common gardens, and other published resources (Pike and Haase, 2024). For example, maximum seed transfers of 100–200 miles (161–322 km) are commonly recommended for some species, e.g., sugar maple (*Acer saccharum*), and upwards of 300 miles (483 km) for others, e.g., red pine (*Pinus resinosa*), depending on the species (LaBonte, 2022; Pike and Bloese, 2022). These distances are similar to average distances to 2030's and 2050's CCS (222 and 358 km, respectively). Average distances across seed zones to 2030's and 2050's CCS (1 and 2 seed zones, respectively) were also similar to recommendations by the Eastern Seed Zone Forum (Pike et al., 2020). It is important to note that seed-transfer guidelines are different from CCS developed here—CCS show where to source seed and seed-transfer guidelines define the expected maximum distance seed may be moved before deleterious effects, which may help validate CCS or enable selection among species with least risk of maladaptation (see Tree Atlas section below).

In addition, recent studies in the eastern US show support for seed transfers and/or distances to assisted-migrated tree species' northern range termini of 100–200 km, including early survival results nearing 100% in one study (Muller et al., 2019). As a potential proxy to transfer distance, comparisons in survival among *assisted population expansion* vs. *assisted range expansion* plantings have also been examined, but results have been mixed (Muller et al., 2019; Palik et al., 2021, 2022; Clark et al., 2022)—likely because species vary in their tolerance to seed transfer (Leites et al., 2019). Nonetheless, these studies seemingly support seed transfers among CCS representative of adaptation to the next ∼1.5–2 decades and ∼200 km or 1–2 seed zones in distance, based on early survival results.

However, 2090's CCS average distances (662 km, ≥3 seed zones, and ≥2 plant hardiness zones) exceeded current seed transfer recommendations. It is important to note that geographic distance alone can sometimes be a poor correlate of adaptation to novel planting environments (Leimu and Fischer, 2008). Rather, it is the underlying differences in the abiotic, e.g., climate and soils, and biotic, e.g., competitors or pests or pathogens, environment that affects survival, which geographic distance may not always integrate because environmental gradients transition more gradually or sharply than expected, e.g., floristic tension zones between boreal and temperate forest types (Joyce and Rehfeldt, 2013). Some site-level differences may also be partially mediated by appropriately matching tree species to finer-scale habitat at the planting site (see below). Nonetheless, researchers are recognizing that more intense seed movements, strategies, and risk acceptance are needed to avoid the potential opportunity cost of FAM, which may include moving species or genotypes beyond current transfer recommendations—especially to enable adaptation to 2100 climate change, the risk of inaction may exceed FAM risks (Palik et al., 2022; Royo et al., 2023).

4.2 Direction to climatically-compatible seedlots (CCS)

Second, CCS were located on average south-southwest of the 1 × 1° grid planting sites—a pattern generally resembling drier, continental climates. This is important because it likely associates with longitudinally-aligned traits influenced by precipitation, such that moving genotypes south-to-north may not necessarily minimize maladaptation nor maximize resiliency goals under FAM (Zhu et al., 2012; Fei et al., 2017; Gougherty et al., 2021). These subtle shifts in degrees bearing relative to orientation north can produce different patterns in CCS geographies relative to 1 × 1° grid origin, especially as distances increase. For example, a shift in bearing from 190° to 203° would result in the movement of a CCS by 150 km (or 143 km west and 42 km north) using an average geographic distance of 662 km. It is difficult to disentangle how specific climate features contribute to the joint distribution of (dis)similarity change. However, these results generally reflect the nature of climate change within the eastern US (Dobrowski et al., 2013). In addition, these results are similar to anticipated range shifts in the mean centers of suitable habitat of many eastern US tree species that are expected to shift in a northeast direction and originate from more southwestern locations (Iverson et al., 2019a).

4.3 Future climate novelty

Third, we also detected large areas of emergent climate novelty $>2\sigma_{\mathrm{d}}$ across the eastern US, particularly in the Southeast and South Central regions and for later-century projections, e.g., ∼28% of 1 × 1° grids may experience climate novelty during the 2090's period. This is partially attributed to deficient land area further south at southern latitudes at the extent of terrestrial habitat along the Gulf of Mexico. In contrast, areas along the Appalachian range, e.g., state of Vermont in the Northeast, may be buffered from $>2\sigma_{\mathrm{d}}$ novelty due to increased topographic heterogeneity, enabling CCS to be drawn from lower elevations throughout the study domain. However, other regions may experience future climate novelty, including ∼9% of 1 × 1° grids in the North Central region. The only region expected to not experience future climate novelty (at the 1 × 1° grid scale) under the SSP3-7.0 emissions scenario was the Northeast. It is important to note that results emphasized in our study were based on the high SSP3-7.0 emissions scenario, according to global warming trends limited to <4°C. For the unmitigated, very-high SSP5-8.5 emissions scenario exceeding >4°C, 46% of 1 × 1° grids in the eastern US may experience future climate novelty (at the 1 × 1° grid scale) (Supplementary Table S9).

Future studies might examine the influence of climate novelty on FAM outcomes. We currently cannot predict how seed sources collected across a range of analogies, i.e., σ_{d} values, will respond to climate change. For example, what impacts (if any) to short- or long-term survival may occur if CCS with moderate levels of (dis)similarity, e.g., $0.5\sigma_{\mathrm{d}}$, vs. CCS with perfect alignment to climate change, i.e., $0\sigma_{\mathrm{d}}$, are used? Similarly, at the other end of the gradient and from a local climate change perspective, understanding tree species and genotype response across a range of σ_{d} values could assist in whether or not to pursue FAM and perhaps even FAM timing. In other words, it may be that local seed sources are better than non-local seed sources up to a minimum threshold, i.e., σ_{dmin}, in which local climate change has exceeded historical variability and the tolerance of local tree species and genotypes. This could function as a means to trigger FAM consideration and enhance confidence in non-local seed source establishment because the climate now aligns better with the CCS in which seed were sourced. It is important to note that even for the 2030's earliest planning period, the most closely-matched climate analogs and subsequent CCS were located 222 km on average from the 1 × 1° grid planting sites. Because of these distances, it likely indicates we have already met a minimum threshold to begin engaging in FAM practices, emphasizing a need to consider non-local seed sources in forest management planning sooner than later.

It is also possible that survival and productivity are less influenced by subtle differences in analogy, local climate departure, or even possibly moderate levels of climate novelty because slightly missing the optimal habitat of seed sources may not be that serious (Gray et al., 2011). In addition, some tree species show levels of plasticity that could suggest an ability to respond to climate novelty (Hamrick, 2004; Leimu and Fischer, 2008; Copenheaver et al., 2020). Short-term responses of seedlings sourced along gradients of (dis)similarity may be tested in common gardens, greenhouses, or other controlled environments (Bronson and Gower, 2010). Identifying key demographic parameters along these gradients could help (i) refine the selection of CCS, (ii) determine how much of the optimal climatic habitat may be missed (Gray et al., 2011), (iii) whether subtle (≤100 km) differences among emissions scenarios affect future adaptation potential (at least from a FAM decision standpoint in selecting among emissions scenarios to inform collections), and (iv) enable identification of population structures that facilitate climate change adaptation within species. Ultimately, from an operational standpoint, some level of moderate climate analog mismatch would need to be incorporated into the decision-making process due to the presence of seed sources and nursery practice (see below).

4.4 Forest cover of climatically-compatible seedlots (CCS)

Fourth, we detected variation in forest cover amount among 1 × 1° grids and their CCS. Specifically, CCS were on average comprised of less (current) forest cover than that of the associated 1 × 1° grid. This is important because it may overestimate FAM confidence if seed sources are unavailable at CCS. In the provided examples, target 1 × 1° grids among the upper North Central region were comprised of 37 and 52% forest cover while their CCS were comprised of only 6 and 11% forest cover, respectively (Figure 3's examples 1–2). These differences were even more dramatic in other examples (3–4 highlight 1 × 1° grids comprised of >80% forest cover but with CCS comprised of at least 30%—50%

forest cover) but neutral in another (example 5 highlights a 1 × 1° grid and CCS that were both comprised of 55% forest cover). Still, CCS may be located in landscapes with greater levels of forest cover (examples 6–7), presenting potential opportunities with increased area to locate seed sources. Our intention here was to highlight potential challenges and opportunities when identifying seed sources within CCS due to the presence or absence of forestlands, including the likelihood of missing ecologically, economically, or culturally important species.

4.5 Complementarity to species models and seed zones

The regional focus of our work was selected to coincide with the USFS Climate Change Tree Atlas. The CCS being located primarily within the eastern US and within the extent of the Tree Atlas allows for complementary information to be shared that either the Tree Atlas or CCS in this article do not provide individually (similar to seed-transfer guidelines). For example, the Tree Atlas predicts that post oak (*Quercus stellata*) and black hickory (*Carya texana*) may experience increasing habitat suitability within southeastern Ohio by 2100 (Peters et al., 2020). Here, CCS for this time period under the SSP3-7.0 emissions scenario were largely located across parts of the Ozarks in the state of Arkansas, also where these species occur likewise—though representing a large seed transfer of ∼1,100 km. Hence, tree lists provided by the Tree Atlas support identification of future-climate-adapted tree species whereas CCS identify locations where these species may be sourced. Further refinement in FAM decision making may also incorporate seed-transfer guidelines (if available) or other information including seed zone or plant hardiness zone maps. In addition, the intersection of where within a species range climate analogs are located can provide more geographically-specific information to inform application of climate adaptation as well as a basic understanding to identify gradients of within species heterogeneity (Prasad and Potter, 2017; Gougherty et al., 2021).

4.6 Limitations and assumptions

Environmental data, particularly on soils, topography, and microbial communities and their interactions, are not currently incorporated directly into climate analog mapping, but these abiotic and biotic characteristics are known to impact the ability of tree species to adapt to new habitats (Leimu and Fischer, 2008; Lafleur et al., 2010; Refsland et al., 2023). Post-mapping environmental filters may be used to refine the selection of CCS where environmental conditions are agreeable to the planting site. In addition, FAM practitioners have the ability seek out suitable planting environments for specific tree species within the larger landscape, e.g., dry ridgetop vs. mesic bottomland (Iverson et al., 1997). Extreme weather events, particularly intense precipitation, that are expected to increase in frequency are also not easily incorporated into climate projections (Rastogi et al., 2020). Other challenges emerge if species currently occupy suboptimal habitat and are in climatic disequilibrium (Rehfeldt et al., 2018); this is particularly acute among species with narrow ranges (Seliger et al., 2021) and could affect FAM outcomes if species assemblages do not adequately reflect contemporary climate conditions. It is also unlikely to distinguish a species' pure climatic equilibrium because anthropogenic-climate forcing has been present throughout the observational record and tree species have been adapting to global change for a millennia (Davis, 1983; Hamrick, 2004; Prasad et al., 2024).

The selection of climate variables may also influence the location of CCS. However, our use of 12 seasonal climate variables, spanning a broad range of climate variation across the annual cycle, is likely to be applicable to most situations in a general way. In addition, these variables are fundamental, first-order variables that serve as the basis of more derived bioclimatic variables. Nonetheless, future work examining the effect of CCS analogy (or novelty) could also test a range of variables on seedling response because tree species are expected to respond independently to different climate features, including within-species variation (Joyce and Rehfeldt, 2013; Leites et al., 2019; Prasad and Leites, 2022). Species- or even population-specific CCS could be introduced through increased knowledge of inter- and intra-specific responses to different climate variables. In such a way, climate analog models could be tuned to the precise selection of species-relevant climate characteristics. While doing so may increase FAM confidence in enabling more species-specific CCS, the models do lose generality to be quickly applied across forest communities to rapidly enable fast and efficient seed collections. Still though, genetic information and field trials of provenance testing remain a critical step, including integration of genetic and environmental information into universal response functions (Wang et al., 2010; Chakraborty et al., 2015) to enhance basic understanding of physiological responses and inform management implementation. In addition, the coarse grain of the 1 × 1° grid likely masks fine-scale climate variation (within future climate projections) along topographic gradients or supplemental warming due to heat island effects. On the other hand, examining CCS at too a fine resolution could necessitate unwarranted or excessive collections (O'Neill et al., 2014), but may be useful in identifying terrain features or refugia that buffer against the most severe of anticipated impacts (Morelli et al., 2016; Stralberg et al., 2020). Our 1 × 1° grid focus ultimately balances some of these scale-based constraints by providing a discrete set 494 representative sites across the eastern US.

4.7 Potential barriers to assisted migration implementation

Climate-distance models offer a geographically- and thus climatically-precise approach to match CCS to planting sites. However, there is tension between current nursery practice and the desire to know the precise geographic origin of seed sources as this is not currently a common practice (Palik et al., 2022; Clark et al., 2023). In fact, it is unlikely that when the geographic origins of seed sources are known, it will match the precision of CCS in this study at 1 km resolution. Rather, climate-distance approaches may be treated as providing a general pattern in which CCS may be identified. The recent development of the eastern seed zone map is meant to in part define the origin of seed sources, i.e., "collections zones." However, CCS may occur within smaller subsections of a seed zone, i.e., seed zones may be too large, or CCS may be distributed across more than one seed zone, providing opportunities to possibly blend these approaches in the future (see Supplementary Figures S1–S3). In addition to the challenges outlined throughout, nursery production and access is also broadly considered a potential key barrier to forest restoration and FAM operationalization (Fargione et al., 2021; Clark et al., 2023). It is also apparent that broad interregional cooperation is needed. For example, CCS were located on average ∼1–2 US states away from the 1 × 1° grids across the three climate periods. As FAM increases, practitioners are expected to increasingly rely on CCS in other jurisdictions, potentially far from their region of comfort or within disallowed areas due to statutes that preclude selling seedlings from non-local sources. Of particular note is USFS Region 9's (North Central and Northeast) anticipated reliance on CCS located within Region 8 (Southeast and South Central).

5 Conclusion

Our development of (future) climatically-compatible seedlots (CCS) for the eastern US 1 × 1° grid and following synthesis emphasized four key results: (i) Average distances to 2030's and 2050's CCS were expectedly large, yet within range of maximum transfer distances recommended for some tree species. These distances also seemingly validate the Eastern Seed Zone Forum's recommendations of moving seed across 1–2 seed zones (as a general rule when species or genotype information is unavailable) to support adaptation to climate change (within this time frame). In contrast, average 2090's CCS' distances were larger than recommended, highlighting the magnitude of climate change and need for forest assisted migration (FAM) research that examines seed transfers this large. (ii) CCS were located south-southwest—not directly south—resembling the nature of climate change projections and mean centers of habitat shifts anticipated for eastern US tree species. (iii) Future climate novelty was present in future climate projections, potentially challenging the conceptual basis of FAM if tree species are not adapted to these changes. (iv) CCS typically occurred in areas with dissimilar levels of forest cover as the planting sites, presenting potential opportunities or challenges due to the presence or absence of forestlands at CCS. This also implies potential differences in forest assemblages between sites and future work may consider examining associated impacts to sourcing ecologically, economically, or culturally important species. The overall goal of this work was to provide a set of outputs that may enable FAM decision support. The need to implement forest climate change adaptation strategies designed to manage for tree species habitat redistribution under climate change is exceeding the knowledge base needed to inform management guidance. Climate-based and species-independent approaches can help bridge this gap and enable identification of CCS to support FAM.

Data availability statement

Publicly available datasets were analyzed in this study. This data can be found at: https://adaptwest.databasin.org/.

Author contributions

BA: Conceptualization, Formal analysis, Funding acquisition, Writing – original draft, Writing – review & editing. AR: Conceptualization, Funding acquisition, Writing – review & editing. CK: Conceptualization, Funding acquisition, Writing – review & editing. DB: Conceptualization, Funding acquisition, Writing – review & editing. SM: Methodology, Resources, Writing – review & editing. AG: Writing – review & editing. AP: Methodology, Resources, Writing – review & editing. LI: Methodology, Resources, Writing – review & editing. ER: Writing – review & editing. PR: Writing – review & editing. CP: Writing – review & editing. JM: Writing – review & editing. AM: Writing – review & editing.

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Conflict of interest

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2024.1449340/full#supplementary-material

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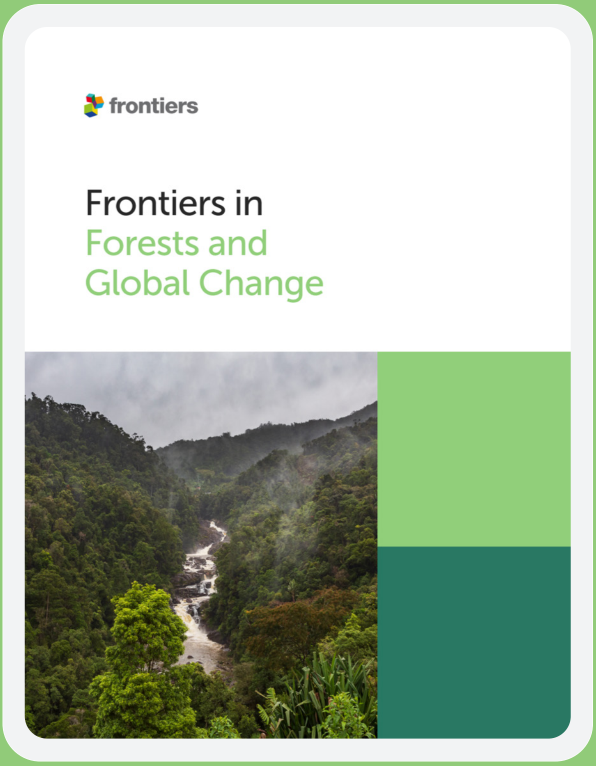

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