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# Moving up north: How do translocated seedlings perform in mixed-species plantings at the boreal-temperate interface?

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## ARTICLE INFO

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## ABSTRACT

Climate change is forcing us to find innovative solutions to help managed forests cope with rapidly shifting environmental conditions. One of these tools is assisted forest migration, the deliberate movement of individuals or genetic material from native sources (i.e. provenance) to locations within or beyond their current ranges. This study aims to assess the climate analogue concept as seed sourcing method in an assisted migration field trial. We evaluated the five-year survival and growth of nine species in mixedwood plantings established in 2018 in Quebec, Canada. The factorial experimental design comprised cutting treatments (1.2 ha patch clearcut vs. 40 % uniform shelterwood), cervid exclusion (excluded vs. non-excluded) and competing vegetation (brushcut vs. control) treatments. Seedlings were grown from seeds of locations associated to three climate analogues: current climate, projected climate for mid-century (2041–2070) and end-of-century (2071–2100). Five-year survival averaged 84 %, ranging from 69 % for *Carya ovata* to 90 % for *Quercus rubra*. End-of-century analogue performed less well than others for relocations > 500 km. All species grew larger in patch clearcut than in shelterwood, especially *Pinus, Picea* and *Thuja* spp. (3–4× diameters, 2–3× heights). To a lesser extent, brushing slightly improved diameter growth of *Carya ovata*, *Quercus rubra* and *Thuja occidentalis*, but only in patch clearcuts for *Prunus serotina*, *Pinus* and *Picea* spp. Impact of cervid was minimal likely due to snowpack protection. We observed limited effects of climatic mismatch on translocated seedlings, which supports the climate analogue approach as seed sourcing method. Longer-term monitoring will be required to confirm trends.

## 1. Introduction

Forests have long been adapted to the local climates in which they have evolved, but climate change now threatens their health, productivity, and the essential ecological and social benefits they provide globally (Stanke et al., 2021; Hartmann et al., 2022; Altman et al., 2024). As temperatures rise, shifts in the geographic ranges of woody species are already occurring, driven by both expansion through colonization at the colder margins (Boisvert-Marsh et al., 2019; Chakraborty et al., 2021) and retraction through local extinctions at the warmer margins (Berner and Goetz, 2022; Gougherty et al., 2024). Ecotones, such as the temperate-boreal zone in North America, could experience range contractions, as boreal conifer species are expected to adapt poorly to future climatic conditions (Reich et al., 2015). Temperate hardwood species could also have difficulties migrating naturally further north due to dispersal limitations, environmental tolerance limits, and positive or negative biotic interactions (Lafleur et al., 2010; Frelich et al., 2012; Walker et al., 2024). Given these constraints to species dispersal and establishment, forest assisted migration (hereafter “assisted migration”), the deliberate movement of individuals or genetic material from native seed sources (i.e., provenance) to locations within or beyond their current ranges, is proposed as a tool to maintain tree populations, forest ecosystem functions and to facilitate ecological transition (Dumroese et al., 2015; O’Neil and Gómez-Pineda 2021; Chakraborty et al., 2024).

Assisted migration is one of the adaptive strategies recommended in

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a portfolio of approaches to face of climate change uncertainty in forest management (i.e., "Resistance", "Resilience", "Transition", *sensu* Millar et al., 2007; Nagel et al., 2017). This tool is however relatively new and still has many knowledge gaps (Park and Talbot, 2018), technical difficulties (Palik et al., 2022; Clark et al., 2023) and risks (Vitt et al., 2010; Aubin et al., 2011; Pedlar et al., 2012; Champagne et al., 2021a; Findlater et al., 2022) that limits its large-scale operational implementation. A major challenge is to identify seed sources that confer long-term growth and survival advantages under climate change, while minimizing losses due to near-term weather events (Park and Talbot, 2018). These risks increase with tree species or genotype translocation distance, also represented by the gradient of assisted migration intensity (*sensu* Dumroese et al., 2015), i.e. whether they are within their current range (assisted population migration), just outside their range (assisted range expansion) or far from their range (assisted species migration).

To limit maladaptation risks, tools like hardiness zones and provenance trials have been used to provide guidance on safe translocation distances, e.g., a maximum of two seed zones (Pike et al., 2020; Pedlar et al., 2021). Climate-distance index such as climate analogues, i.e. contemporary locations with climates similar to the anticipated future climate of a planting site, are also being tested as a decision-making tool (Grenier et al., 2013; Adams et al., 2024). Climate analogues are especially pertinent for species for which we have little genetic information, for example without defined seed zones (McKenney et al., 1999). This concept, however, still needs to be tested with robust field trials (Royo et al., 2023; Adams et al., 2024).

During the establishment phase, seedlings can be affected by abiotic and biotic stressors (e.g. microclimate, interspecific competition, cervid browsing), which can hinder their survival and development (Champagne et al., 2021a; Clark et al., 2022); these stressors may be more important for translocated seedlings. Manipulating microenvironmental conditions with silvicultural treatments, for example by maintaining a partial canopy cover that limits temperature extremes, may help attenuate those stresses (Royo et al., 2023; Dumais et al., 2025). Yet, our ability to develop assisted migration strategies is constrained by our limited knowledge on survival, growth and acclimatization capacity of southern tree species and provenances in response to biotic and abiotic stressors at higher latitudes (Park and Talbot, 2018). Furthermore, species diversity and structural diversity should also be considered in planning for assisted migration, given their role in fostering resistance and resilience to stresses (Alfaro et al., 2014; Felton et al., 2016; Messier et al., 2019; Guignabert et al., 2024). For example, using species mixtures with complementary traits is recommended to promote forest adaptive capacity and carbon storage (Messier et al., 2019; Aquilué et al. 2021; Urgoiti et al., 2022; Warner et al., 2023), however, validation under field conditions remains limited.

Translocating resource-demanding species such as temperate hardwood species into northern forests requires selecting fertile sites, but the latter can also constitute resilient and high-quality late-successional forest habitats. Selecting poorly regenerated high-graded stands (e.g., by diameter-limit cutting) growing on fertile sites for assisted migration plantings could contribute to enhance stand composition, quality, productivity (Kenefic et al., 2014; Raymond et al., 2020, 2024), diversity and resilience (Aquilué et al. 2021; Messier et al., 2021), with potentially climate-adapted species and genotypes (Royo et al., 2023). This study is set within the context of forest rehabilitation, where we aimed to evaluate the climate analogue approach as a tool for guiding seed sourcing for assisted migration in a field experiment. We also manipulated forest cover, cervid access and understory vegetation to test the effects of abiotic and biotic constraints on seedling survival and growth. We hypothesized that climatic mismatch increases with translocation distance, thus resulting in declines in survival and growth along the climate analogue gradient. We predict that southern species (i.e. non-local deciduous species) and southern provenances (i.e. mid-century and end-of-century climate analogues) are affected disproportionately relative to local species and provenances. We also predict that by reducing microclimate variation, partial overstory cover may mitigate reductions in survival experienced by non-local species and southern populations of local species in their new environment. However, their growth response will be higher where resources are more abundant (e.g., in open areas with competing vegetation control).

## 2. Methods

### 2.1. *Study area*

The experiment is located approximately 95 km northwest of Quebec City, near the Lac des Amanites in the Réserve faunique de Portneuf (Québec, Canada; lat. 47.128° N, long. −72.409° W). Two cervid species co-occur at light to moderate density in the area: white-tailed deer (*Odocoileus virginianus*) estimated at density of 4.0 individuals/km$^2$ in 2018 (Lebel and De Bellefeuille, 2021) and moose (*Alces alces*) at 7.3 individuals/10 km$^2$ in 2009 (Lefort and Massé 2015). We established this study in the balsam fir (*Abies balsamea* (L.) Mill.) – yellow birch (*Betula alleghaniensis* Britt.) bioclimatic domain, ecoregion 4c-M, hills of the middle Saint-Maurice (Saucier et al., 2009). A high hill topography with rounded summits (altitude 365 m) characterize the landscape. Humo-ferric podzols have developed on deep glacial tills and are moderately well-drained sandy loams (Soil Classification Working Group, 1998). Mean annual daily temperature and total precipitation (1981–2010) are respectively 4.0°C and 1133 mm, including a mean annual snow fall of 230 cm (Environment Canada, 2019). During the study period, the mean annual daily temperature values measured at the study site averaged 4.3°C (VP-4 Sensor, Part #40,023, 1.3 m above ground, see Dumais et al., 2025 for more information).

Selected stands belong to the yellow birch – balsam fir ecotype and were harvested at least once by diameter limit cutting prior to the 1990's. In 2017, these irregular uneven-aged stands had a mean precut merchantable basal area (BA) of 25.7 m$^2$/ha and were composed of 41 % *Betula alleghaniensis*, 26 % *Abies balsamea*, 11 % *Acer rubrum* (L.), 10 % *Acer saccharum* (Marsh.), 6 % *Picea rubens* (Sarg.) and a minor component of *Picea glauca* ([Moench] Voss), *Betula papyrifera* (Marsh.), *Fraxina nigra* (Marsh.) and *Populus tremuloides* (Michx). Main understory non-tree woody species comprised *Acer spicatum* (Lamb.), *Viburnum lantanoides* (Michx), *Corylus cornuta* (Marsh.) *Dryopteris carthusiana* ([Villars] H. P. Fuchs*)* and *Taxus canadensis* (Marsh.).

#### 2.1.1. *Experimental design*

The Lac-des-Amanites experiment is the first site of the international network DREAM (Desired REgeneration through Assisted Migration), as described in Royo et al. (2023). It follows a split-split-split-plot factorial design, structured within four complete randomized blocks. Blocking was performed prior to the cut to account for the variability caused by the hilly topography, where slopes varied from gentle to moderate (4–30 %). The experiment tests two overstory cutting treatments, 100 % in patch clearcut and 40 % uniform shelterwood, which are applied to 140 × 86 m main plots (1.2 ha with a >20 m buffer). Each main plot is divided into subplots measuring 56 × 66 m to test the effect of cervid exclusion, with one half designated as an exclosure (2.4 m high woven galvanized fences) and the other as a non-exclosure. Within each subplot, sub-subplots of 28 × 66 m are used to examine understory vegetation control, with one half undergoing brushcutting while the other remains untreated. These sub-subplots are further divided into sub-sub-subplots of 28 × 22 m to assess the influence of climate analogues, representing current, mid-century, and end-of-century climates.

This factorial design comprises 24 experimental units, representing all combinations of two cutting treatments (Cut: patch clearcut vs. uniform shelterwood), two cervid exclusion treatments (Herbivore: exclosure vs. non-exclosure), two vegetation control treatments (Vegetation: brushcut vs. control), and three climate analogue treatments (Analogue: current, mid-century, and end-of-century). Each experimental unit contains 12 seedlings per species across all species except

*Carya ovata,* totaling 288 seedlings per species per block. Due to technical constraints, we were unable to collect sufficient seeds to complete the current climate analogue of *Carya ovata*. As a result, for this species only, the factorial design includes 16 experimental units, totaling 192 seedlings of *Carya ovata* per block (12 seedlings × 2 analogues × 2 vegetation treatments × 2 herbivore treatments × 2 cutting treatments).

### 2.1.2. Species and seed selection

We selected nine species representing a diversity of traits and resistance to abiotic and biotic stresses, while being ecologically and economically important (Table 1). Among them three are non-local deciduous species: *Carya ovata* ([Miller] K. Koch), *Prunus serotina* (Erhr.) and *Quercus rubra* (L.). The other deciduous is local: *Acer saccharum.* The five coniferous species are local: *Picea glauca, Picea rubens, Pinus resinosa* (Ait.), *Pinus strobus* (L.) and *Thuja occidentalis* (L.).

Based on assisted migration classifications defined by Dumroese et al. (2015), the planting of *Quercus rubra* at Lac-des-Amanites falls under "assisted range expansion", as it involves moving a species just beyond its established range. In contrast, the planting of *Prunus serotina* and *Carya ovata* corresponds to "assisted species migration", which refers to the movement of species to suitable habitats far outside their current range (i.e., not present in the next bioclimatic domain). The planting of the six local species falls under “assisted population migration”, which involves the movement of southern provenances within a species’ existing range limits to enhance adaptation to changing climatic conditions.

We selected seedlots that could fit with the climate analogue maps modeled for two emission scenarios (4.5 and 8.5 RCP). We calculated two sets of climate analogues (one for 4.5 and one for 8.5 RCP) based on the method developed by Grenier et al. (2013) using data from the 5th IPCC (The Intergovernmental Panel on Climate Change) report and scaled (10 km × 10 km) for North America. These two scenarios equate to SSP2–4.6 and SSP3–7.0 shared socio-economic pathways of CMIP6, respectively (Wotherspoon et al., 2023). We calculated the climatic distances using the Zech–Aslan Energy (ZAE) statistic (Grenier et al., 2013), a multivariate measure that integrates multiple climate variables into a single dissimilarity value. We used three variables (mean annual temperature, mean annual precipitation and minimum temperature in May) and two future periods: 2041–2070 (mid-century) and 2071–2100 (end-of-century) (Royo et al., 2023). Cold tolerance correlates with temperature heterogeneity across species ranges, with minimum winter temperatures for conifers and hardwoods in the Northern Hemisphere (Kreyling et al., 2015). We also accounted for spring minimum temperature, a factor especially limiting for hardwood species, because temperature fluctuation during dehardening puts vulnerable flowers and expanding leaves at risk (Jönsson et al., 2004; Kollas et al., 2014; Mura et al., 2022). Annual precipitation was included in the model given its influence on species distribution (Prasad et al., 2024).

For each species, seeds were collected from locations (provenances) within each of the three climate analogue zones: current (80 ± 14 km), mid-century (195 ± 81 km), and end-of-century (584 ± 78 km). Seed collection was conducted independently for each species. To account for genetic diversity within each climate analogue zone, we ensured that seeds were sourced from multiple seed-bearing trees. For non-local species, we used the closest available seedlots at their current northern range as proxy of the local source (current climate). As a result, the selected provenances originate from a latitudinal gradient ranging from 41.0°N to 47.8°N, covering a geographical span from Pennsylvania (USA) to Quebec (Canada) (Table 1, Fig. 1).

### 2.1.3. Nursery seedling production

All seedlings were grown at the provincial government nursery in Berthierville (QC, Canada). Conifer seeds were stratified, except for *Pinus resinosa* and *Thuja occidentalis* (end-of-century) lots. *Quercus rubra* acorns were pre-soaked before planting to initiate germination. Conifers were sown in micro-cells containers in May 2017 and then transplanted in June 2017 to containers (IPL® [Saint-Damien, QC, Canada] 25–310: 25 cells, 310 cm$^3$ each) for a large-stock seedlings production (2 growing seasons). Hardwood species (except for *Cary ovata*) were sown in the spring of 2018 and container-grown (IPL 28–340: 28 cells, 340 cm$^3$

**Table 1**
Coordinates of seed sources (provenances) based on climate analogue modelling and distance from the planting site (47.128°N, −72.409°W). For each species, we noted the end-of-century habitat suitability, and the forest assisted migration type (FAM).

| Species | Habitat suitability[a] | FAM[b] | Climate analogue | Latitude (°N) | Longitude (°W) | Distance (km) |
|---|---|---|---|---|---|---|
| *Picea glauca*<br>White spruce | ↓ | APE | Current | 47.800 | −72.917 | 83 |
| | | | Mid-cent. | 45.750 | −71.417 | 172 |
| | | | End-cent. | 44.850 | −66.980 | 486 |
| *Picea rubens*<br>Red spruce | ↓ | APE | Current | 47.167 | −72.717 | 31 |
| | | | Mid-cent. | 45.433 | −71.300 | 208 |
| | | | End-cent. | 44.660 | −69.990 | 332 |
| *Thuja occidentalis*<br>Northern-white cedar | ↓ | APE | Current | 47.157 | −71.824 | 36 |
| | | | Mid-cent. | 46.504 | −70.597 | 150 |
| | | | End-cent. | 44.806 | −65.552 | 585 |
| *Pinus strobus*<br>Eastern white pine | ↑ | APE | Current | 47.117 | −73.250 | 72 |
| | | | Mid-cent. | 45.083 | −72.083 | 233 |
| | | | End-cent. | 43.675 | −75.307 | 455 |
| *Pinus resinosa*<br>Red pine | ↑ | APE | Current | 46.867 | −72.333 | 34 |
| | | | Mid-cent. | 45.267 | −72.567 | 213 |
| | | | End-cent. | 44.233 | −65.333 | 634 |
| *Acer saccharum*<br>Sugar maple | ↑ | APE | Current | 46.980 | −70.550 | 135 |
| | | | Mid-cent. | 45.518 | −71.605 | 192 |
| | | | End-cent. | 41.000 | −79.000 | 874 |
| *Quercus rubra*<br>Northern red oak | * | ARE | Current | 46.910 | −71.210 | 88 |
| | | | Mid-cent. | 45.499 | −72.529 | 187 |
| | | | End-cent. | 41.600 | −79.000 | 820 |
| *Prunus serotina*<br>Black cherry | * | ASM | Current | 46.974 | −70.417 | 145 |
| | | | Mid-cent. | 45.384 | −71.598 | 206 |
| | | | End-cent. | 41.825 | −80.003 | 855 |
| *Carya ovata*<br>Shagbark hickory | * | ASM | Current | 46.351 | −72.578 | 94 |
| | | | Mid-cent. | 45.414 | −72.686 | 198 |
| | | | End-cent. | 45.343 | −73.181 | 214 |

[a] Périé et al. (2014). Habitat suitability projected for the end of the century (2071–2100): ↓=unfavorable; ↑=favorable; *new habitat.

[b] Dumroese et al. (2015). APE=assisted population expansion; ARE=assisted range expansion; ASM=assisted species migration.

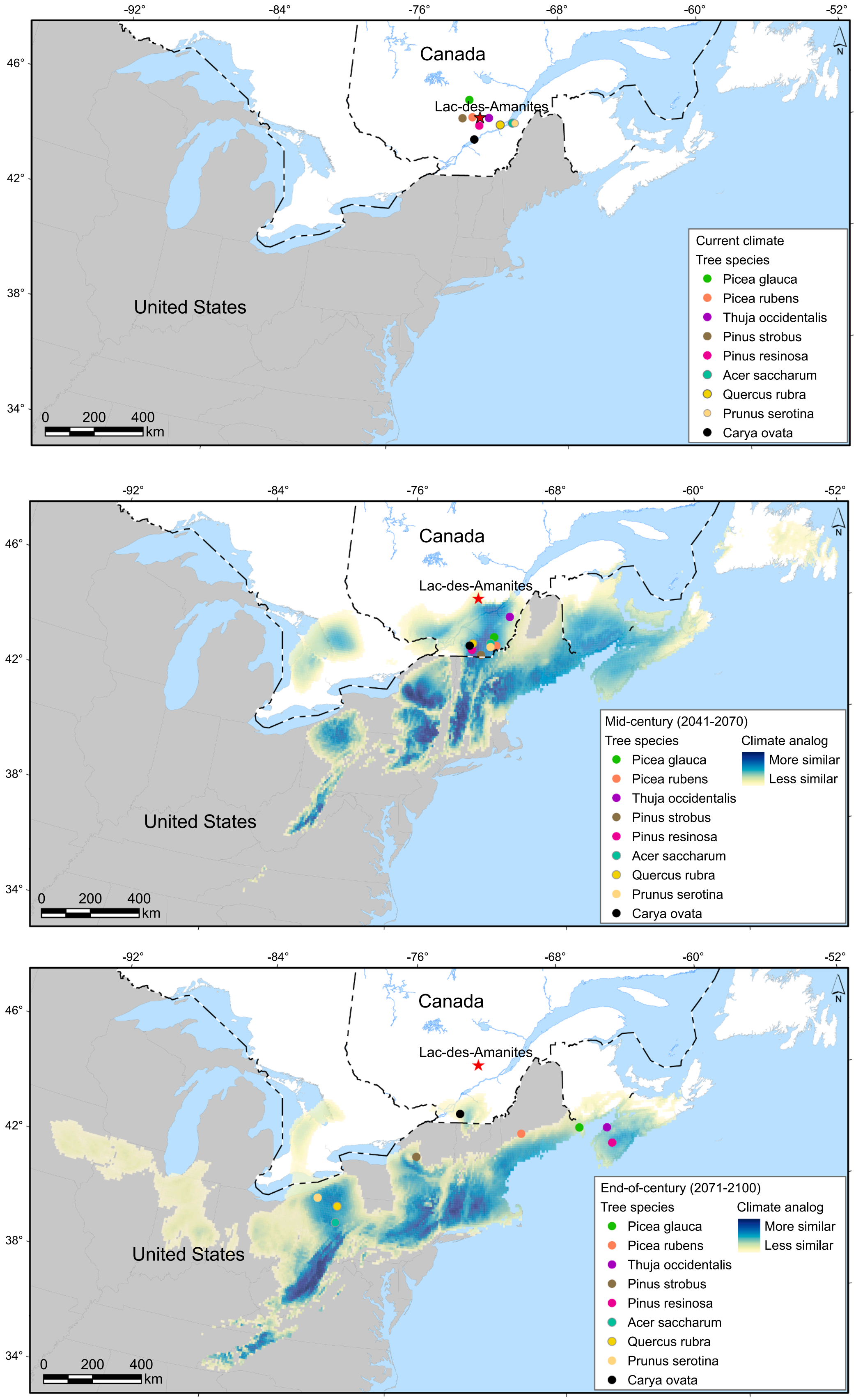

**Fig. 1.** Distribution of seed sources (provenances) used for seedling production for the three climate analogue treatments: current climate, mid-century (2041–2070) and end-of-century (2071–2100), based on the 8.5 RCP emission scenario.

each) until August 2018 so that they could be planted in the field after one growing season. *Carya ovata* was grown bare root (sown in November 2017) and required 2 complete growing seasons before planting.

#### 2.1.4. *Field application of treatments*

Prior to harvesting, we marked trees to remove in the shelterwood treatment (40 % of merchantable basal area [MBA, trees dbh >90 mm]) with priority to weak trees, poor form and short-lived species such as balsam fir. We initially aimed a 50 % establishment cut and planned a tree marking of 30 % MBA, given we expected that skidding trails (approx. 6 m wide) would harvest another 20 %. The operators, however, disturbed less than expected and felling operations only harvested 40 % of MBA. The mid-story vegetation was not further removed beyond the establishment cut; approximately 50 % of full sunlight was transmitted at 1,30 m height (Dumais et al., 2025). Three blocks were logged with a feller-buncher (Tiger Cat 822 C) and hauled with a grapple skidder (Tiger Cat 635D) in July 2017. Due to operational constraints and machinery availability, the last block was treated in June 2018 with a multifunctional harvester (Tiger Cat 845B mounted with a Log max 7000 felling head) and a forwarder (Ponsse Elk). In late June 2018, soil was prepared for planting in each patch clearcut by disk trenching using a Timberjack 560D mounted with a TTS scarifier. There was no site preparation in the shelterwood cutovers to avoid root damage on residual trees. In July 2018, we built fences (56 m × 66 m × 2.4 m) made of woven galvanized wire to exclude cervids on half of planted areas. In an effort to exclude snowshoe hare (*Lepus americanus*), we added finer woven wire (2.5 cm openings) on the first 1.20 m lower section to fill the openings caused by the uneven ground surface.

We planted the Lac-des-Amanites experiment with 9216 seedlings of eight species in August-September 2018 and 664 seedlings of *Carya ovata* in May 2020 (one growing season later) because of the different seedling nursery technique required. Each experimental unit received 12 rows (2 m apart) containing one seedling of each of the nine species, which were randomly assigned within the row and spaced by 2 m. We measured the diameter (1 cm above root collar) and height of each seedling at the time of planting. Survival, diameter (mm), and height (cm) were re-assessed in 2023. During the second growing season (July-August 2020), we cut all the competing vegetation between the planted seedlings using mechanical brushsaws (Stihl FS 410 C) in the sub-subplots planned for vegetation control. At the time of the 5-yr assessment (2023), competing vegetation had regrown in the brushcut treatment, but were still lower in height and density than the untreated vegetation in the control treatment areas (pers. obs.).

### 2.2. *Statistical analyses*

We evaluated the effect of four treatments on three response variables: survival rate (%), mean annual diameter growth (mm/yr), and mean annual height growth (cm/yr). These three variables were analyzed separately for each species, using the full-factorial combination of treatments (Cut × Herbivore × Vegetation × Analogue) as explanatory variables, resulting in a total of 27 models (9 species × 3 response variables). We used general linear mixed models and checked visually for normality and heteroscedasticity of residuals. To properly model the random effect (multiple levels of split-plots), we used a stepwise approach. We first computed the model with the most nested level of error, i.e. the sampling error (Block × Cut × Herbivore ×Vegetation × Analogue) and then verified that this model converged properly and that random effects could be estimated. We then sequentially added additional levels of errors associated with the split-plots until all levels were included or that the model could not converge. For each combination of species and response variable, we used the model with the most complete structure that could converge. All models were computed with the GLIMMIX procedure (SAS 9.4, SAS Institute Inc., Cary, NC, USA), using a binomial distribution for survival, and a gaussian distribution for diameter and height annual growth. Statistical significance of the selected model was assessed with a Type III ANOVA table using Kenward-Roger's methods of estimation for degrees of freedom, with α set at 0.05. For statistically significant explanatory variables with more than two levels, we used least-squares means differences, with Kenward-Roger degrees of freedom, using the LSMeans function. Estimates presented are back transformed (when required) with 95 % confidence intervals.

### 2.3. *Results*

#### 2.3.1. *Seedling survival after 5 years*

Overall, 84 % of seedlings survived after 5 years, with averages ranging from 69 % for *Carya ovata* to 90 % for *Quercus rubra* (Table 2). Survival rates of *Prunus serotina*, *Acer saccharum* and *Carya ovata* differed among climate analogues (Tables S1-S3). *Prunus serotina* of the mid-century analogue survived better (88 %) than those associated with the current climate (78 %) and the end-of-century (75 %). *Acer saccharum* survival was also greater for seedlings of the mid-century analogue (89 %) than those of the end-of-century analogue (80 %), but without differing from those of current climate (85 %). *Carya ovata* survival was higher for the end-of-century analogue (86 %) than for the mid-century analogue (53 %).

Survival in response to other treatments varied among species. *Thuja occidentalis*, *Pinus resinosa,* and *Carya ovata* all exhibited slightly higher survival in the open area of patch clearcuts than under the partial cover of shelterwood cuts with respective increases of 6 %, 8 % and 15 % in mean survival (Tables S3, S5-S6). Additionally, in absence of brushcutting, *Carya ovata* survived better in the patch clearcut than in the shelterwood (82 % vs 62 %; significant Cut × Vegetation interaction, Table S3 and S10). Within the shelterwood treatment, *Acer saccharum* survived better outside than inside the exclosures (89 vs 80 %; significant Cut × Herbivore interaction, Table S2 and S10). For the other species, survival was not affected by treatments. There was no difference

**Table 2**
Overall five-year survival rate (%) by species extracted from raw data and survival rate estimates by species and climate analogue evaluated by a least-squares means.

| Species | Overall survival | Climate analogue | | |
|---|---|---|---|---|
| | | Current | Mid-cent. | End-cent. |
| *Picea glauca* | 88.8 (1.0) | 89.7 (1.7) | 89.7 (1.8) | 89.2 (1.7) |
| *Picea rubens* | 82.8 (1.4) | 85.4 (2.7) | 83.5 (2.9) | 84.2 (2.8) |
| *Thuja occidentalis* | 87.0 (1.3) | 91.1 (1.8) | 89.0 (2.1) | 85.3 (2.5) |
| *Pinus strobus* | 81.9 (1.2) | 82.9 (3.0) | 84.4 (2.8) | 81.1 (3.1) |
| *Pinus resinosa* | 82.7 (1.6) | 84.8 (2.6) | 87.3 (2.8) | 83.0 (2.8) |
| *Acer saccharum* | 83.5 (1.5) | **84.9 (3.3)ab** | **89.4 (2.7)a** | **80.4 (3.8)b** |
| *Quercus rubra* | 90.0 (1.0) | 91.6 (1.8) | 91.0 (1.9) | 91.3 (2.0) |
| *Prunus serotina* | 79.8 (1.4) | **78.2 (2.6)a** | **88.4 (1.9)b** | **75.1 (2.8)a** |
| *Carya ovata* | 69.2 (3.2) | N/A | **53.3 (4.9)a** | **86.0 (2.4)b** |

Notes: Standard error is presented in parenthesis. Differing letters indicate significant differences among climate analogues (main effect). One Analogue treatment (Current) was removed from the analysis because of the lack of seedlings at planting for *Carya ovata*.

among treatments and their interactions for *Pinus strobus* and *Picea glauca* (Tables S7 and S8). A triple interaction (Cut × Vegetation × Analogue, Tables S4 and S9) was detected for *Quercus rubra* and *Picea rubens*, but further statistical tests revealed no significant difference among treatment levels.

### 2.3.2. Seedling annual growth after 5 years

Seedlings responded positively to the greater resource availability in the open areas of patch clearcuts compared to the partially shaded environment of shelterwood cuts. This was reflected in greater diameter growth for all species (Fig. 2) and greater height growth for *Prunus serotina, Thuja occidentalis, Picea* and *Pinus* species in patch clearcuts (Fig. 3, Tables S1 to S9). Conifers exhibited the strongest response to cutting treatments, with diameter growth 3–4 times higher and height growth 2–3 times greater in patch clearcuts compared to the shelterwood cuts.

To a smaller extent, and mostly in interaction with other treatments, competing vegetation controlled by brushcutting influenced seedling growth, especially in terms of diameter growth. The vegetation control treatment increased diameter for *Carya ovata* (28 %), *Quercus rubra* (35 %) and *Thuja occidentalis* (24 %) (Fig. 2). Diameter growth after vegetation control only increased in patch clearcuts for all other species (except for *Acer saccharum*): *Prunus serotina* (41 %), *Pinus strobus* (28 %), *Pinus resinosa* (33 %), *Picea glauca* (32 %) and *Picea rubens* (35 %) (significant Cut × Vegetation interaction, Fig. 2). The positive effect of vegetation control on diameter growth decreased with translocation distance (from north to south) for *Pinus strobus* (increases: current climate 52 %, mid-century 27 %, end-of-century 10 %) and *Picea glauca* (increases: current climate 50 %, mid-century 26 %, end-of-century 20 %) (significant Vegetation × Analogue interactions, Tables S7, S8 and S11).

The effect size of the climate analogue, when present, was small. Growth variables varied with climate analogue (main effect) for *Quercus rubra* (height), *Acer saccharum* (diameter and height), *Thuja occidentalis* (height) and *Pinus strobus* (diameter and height). Response differed among species, with smaller seedlings for end-of-century analogues in *Acer saccharum, Quercus rubra* and *Thuja occidentalis*, and larger end-of-century seedlings for *Pinus strobus* (Figs. 4 and 5).

Cervid exclusion influenced growth variables, but only on a few species and in interaction with other treatments. *Thuja occidentalis* had greater diameter and height growth when both cervid herbivory and understory vegetation were controlled (significant Cut × Herbivore × Vegetation × Analogue (diameter) and Herbivore × Vegetation (height) interactions, Tables S5 and S12). *Acer saccharum* diameter growth responded positively to the vegetation control treatment when they were located outside the exclosures in patch clearcuts (significant Cut × Herbivore × Vegetation interaction, Tables S2 and S13). *Picea glauca* seedlings of the current climate grew higher inside the exclosures than outside (significant Herbivore × Analogue interaction, Tables S8 and S12). *Picea rubens*' growth response in diameter and height outside the exclosures was greater when the vegetation was controlled (significant Herbivore × Vegetation interactions, Tables S9 and S12).

## 3. Discussion

While most recent knowledge on assisted migration is derived from provenance tests implemented under optimal conditions, e.g, open grown and well-tended plantations, few studies have integrated the effects of abiotic and biotic constraints on seedling survival and growth (Park and Talbot, 2018; Champagne et al., 2021a). Our study assessed some of these factors and their interactions in field conditions. Five-year results showed a predominant effect of cutting treatments on growth, thus highlighting the importance of light as a limiting resource for seedlings at high latitude (Lieffers et al., 1999; Messier et al., 1999). To a lesser extent, and mostly in the patch clearcuts, competing vegetation control also improved growth of conifer species and of *Prunus serotina*, as reported by other studies in temperate forest (e.g., Paquette et al., 2006; Dumais et al., 2020). Impacts of cervid were limited and mainly observed on highly selected *Thuja occidentalis* and *Acer saccharum* (Champagne et al., 2021b), in interaction with other treatments. During the first five-years after planting, most seedlings were covered by snow during the winter (230 cm mean annual snowfall in the area), which protected them from browsing (Potvin, 1995). Twigs of woody plants are a staple element of cervid diet in winter (Dumont et al., 2005).

### 3.1. Species response to climate analogues treatments (provenances)

Survival and growth response to the climate analogue treatments was variable across species. Results only partially supported the hypothesis of the increasing climatic mismatch with translocation distance. As predicted, species with the longest translocation distance presented differences in growth and survival among climate analogue treatments, non-local species in assisted species migration (*Prunus serotina, Carya ovata*) and assisted range expansion (*Quercus rubra*). For instance, we observed that seedlings from location further south had a slightly lower survival (*Prunus* – end-of-century, *Carya ovata* – mid-century) or growth (*Quercus rubra* – end-of-century). Nevertheless, three local species in assisted population migration (*Acer saccharum, Pinus strobus, Thuja occidentalis*), also showed differences among climate analogues, either smaller survival and growth (*Acer saccharum* – end-of-century), smaller growth, (*Thuja occidentalis* – end-of-century) or larger growth (*Pinus strobus* – end-of-century) with more southern provenances. There was no difference among climate analogues for the three other local species (*Picea glauca, Picea rubens, Pinus resinosa*).

It is possible that other factors influenced species' response, such as the species evolutionary strategy (i.e., specialist vs. generalist) related to the intraspecific genetic variability and phenotypic plasticity (Leites and Benito Garzón, 2023). It could be the case for our study located at high latitude (47°N), where there is evidence for a trade-off between investment in growth and cold tolerance for both conifers and deciduous species (Aitken and Bemmels, 2016; Leites et al., 2019). Species considered as specialists such as *Prunus serotina*, *Pinus strobus* and *Picea glauca* experience high intra-specific variability and can exhibit strong growth clines along temperature gradients (Leites et al., 2019; Leites and Benito Garzón, 2023). Translocations far beyond the range of the local conditions for which they are adapted can thus lead to maladaptation, such as slower growth and higher mortality. In the present study, it was only the case for *Prunus serotina*, the specialist that was translocated on the greatest distance (855 km). Species considered as generalist like *Quercus rubra, Acer saccharum* and *Thuja occidentalis* usually experience little intraspecific genetic variation to climate; their phenotypic plasticity can allow them to cope better with local conditions (Solarik et al., 2018; Leites et al., 2019; Leites and Benito Garzón, 2023; Mura et al., 2025). In our study, however, we observed slightly lower performances with the end-of-century analogues for these species (>500 km translocations).

Yet, the main trend in the observed responses to the climate analogue treatments was a slightly lower survival or growth performance of the southernmost provenance (end-of-century) compared to the local provenances, especially for seed sources translocated further than 500 km. This distance was beyond the recommended limits in current seed transfer guidelines (e.g. <300–400 km, Adams et al., 2024; Pike and Haase, 2024), and could explain the results obtained for *Prunus serotina, Quercus rubra, Acer saccharum* and *Thuja occidentalis* (Table 1). *Carya ovata* and *Pinus strobus* contrasted in their response to climate analogues, with a higher performance of end-of-century seedlings. This could be explained by the smaller difference in their translocation distance (Table 1), where mid-century and end-of-century models overlapped (Fig. 1). This was also reflected in the climatic distances for these two species (Table S14). Mid-century and end-of-century analogues were rather climatically similar for *Pinus strobus* (0.60 in climatic distance index). The range of climatic distances among analogues was also

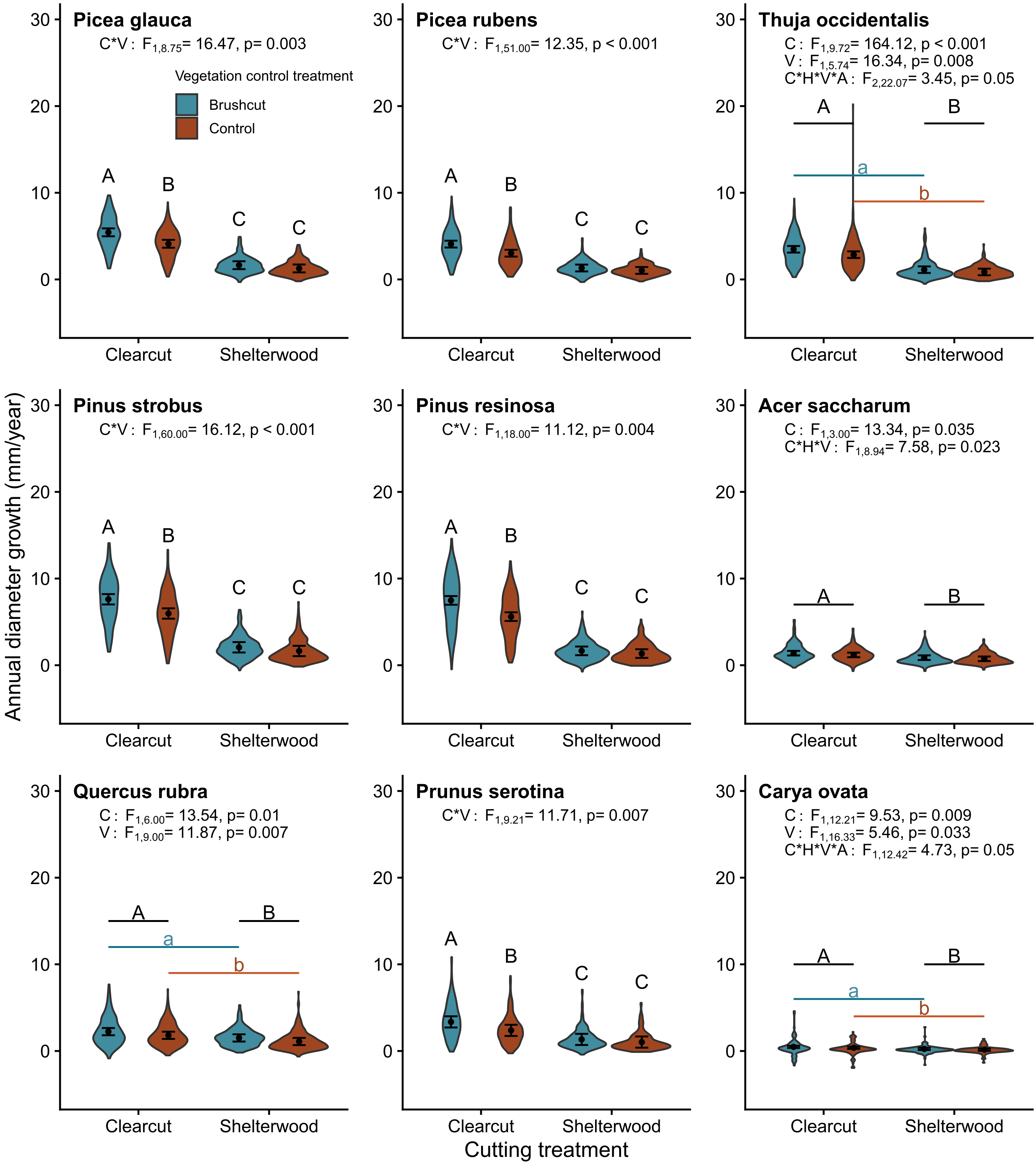

**Fig. 2.** Effects of cutting and vegetation control treatments on annual diameter growth (all species but *Carya ovata*: Diam$_{5th\ year}$ – Diam$_{Plantation}$/5; *Carya ovata*: Diam$_{4th\ year}$ – Diam$_{Plantation}$/4;) for the nine species planted in the assisted migration experiment. Violin shapes present the data distribution, while the dots and lines are model estimates and confidence intervals (95 %). When significant, mixed model factor effects are noted on the panel, C=Cut, V=Vegetation, H=Herbivore, and A=Analogue. Letters represent statistically significant differences among treatments, as evaluated by least-squares means for statistically significant interactions or treatments ($\alpha = 0.05$). Capital letters represent effect of the interaction between treatments, or effects of the cutting treatment when the interaction was not significant. Lowercase letters represent effects of vegetation control treatment.

small for *Carya ovata* (0.75–1.39), so the results should be interpreted with caution for these two species.

In the specific case of *Carya ovata*, the lower survival and slower growth, as well as the apical shoot damage observed in the field, hints that this species might not be the best candidate for assisted species migration (Table 2 and Figs. 4–5). Hence, climatic conditions could have

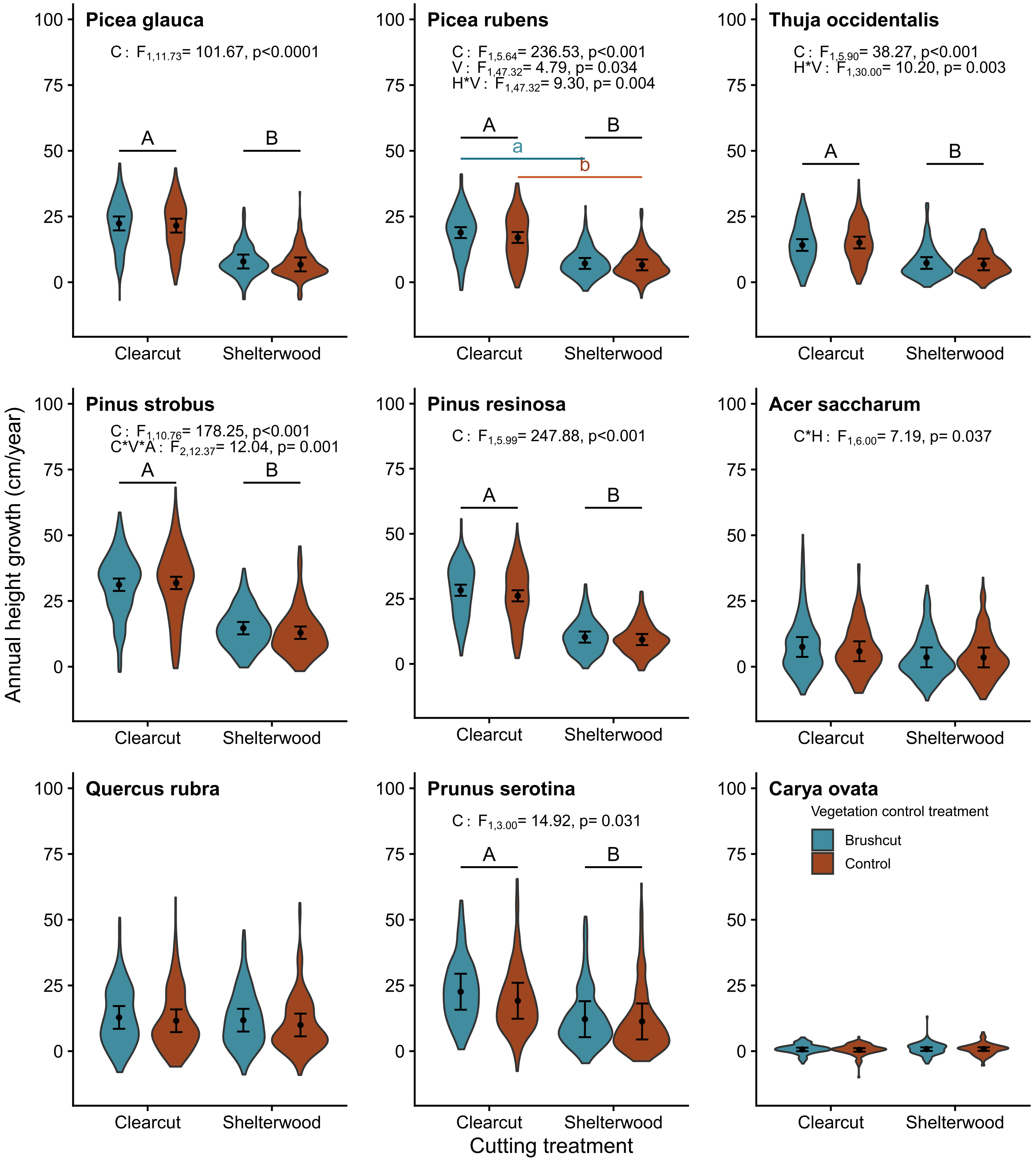

**Fig. 3.** Effects of cutting and vegetation control treatments on annual height growth (all species but *Carya ovata*: $\text{Height}_{5\text{th year}} - \text{Height}_{\text{Planting}}/5$; *Carya ovata*: $\text{Height}_{4\text{th year}} - \text{Height}_{\text{Planting}}/4$;) for the nine species planted in the assisted migration experiment. Violin shapes present the data distribution, while the dots and lines are model estimates and confidence intervals (95 %). When significant, mixed model factor effects are noted on the panel, C=Cut, V=Vegetation, H=Herbivore, and A=Analogue. Letters represent statistically significant differences among cutting treatment, as evaluated by least-squares means for statistically significant interactions or treatments (α = 0.05).

been too harsh at 47°N, as indicated by important apical shoot damage in the first years (also observed for *Carya cordiformis*, Clark et al., 2022). Our data logger recorded the winter minimum temperature reaching –40 °C and late frost events during leaf flush during years 2 and 3 (Dumais et al., 2025). In addition, this species prioritizes investing its resources in the pivotal root system during the first years and little in height growth, which makes it vulnerable to competing vegetation during the establishment phase (Graney, 1990). Repeated damage to seedlings during the first years can be determinant to its early survival. The other non-local species *Prunus serotina* and *Quercus rubra* grew well in their

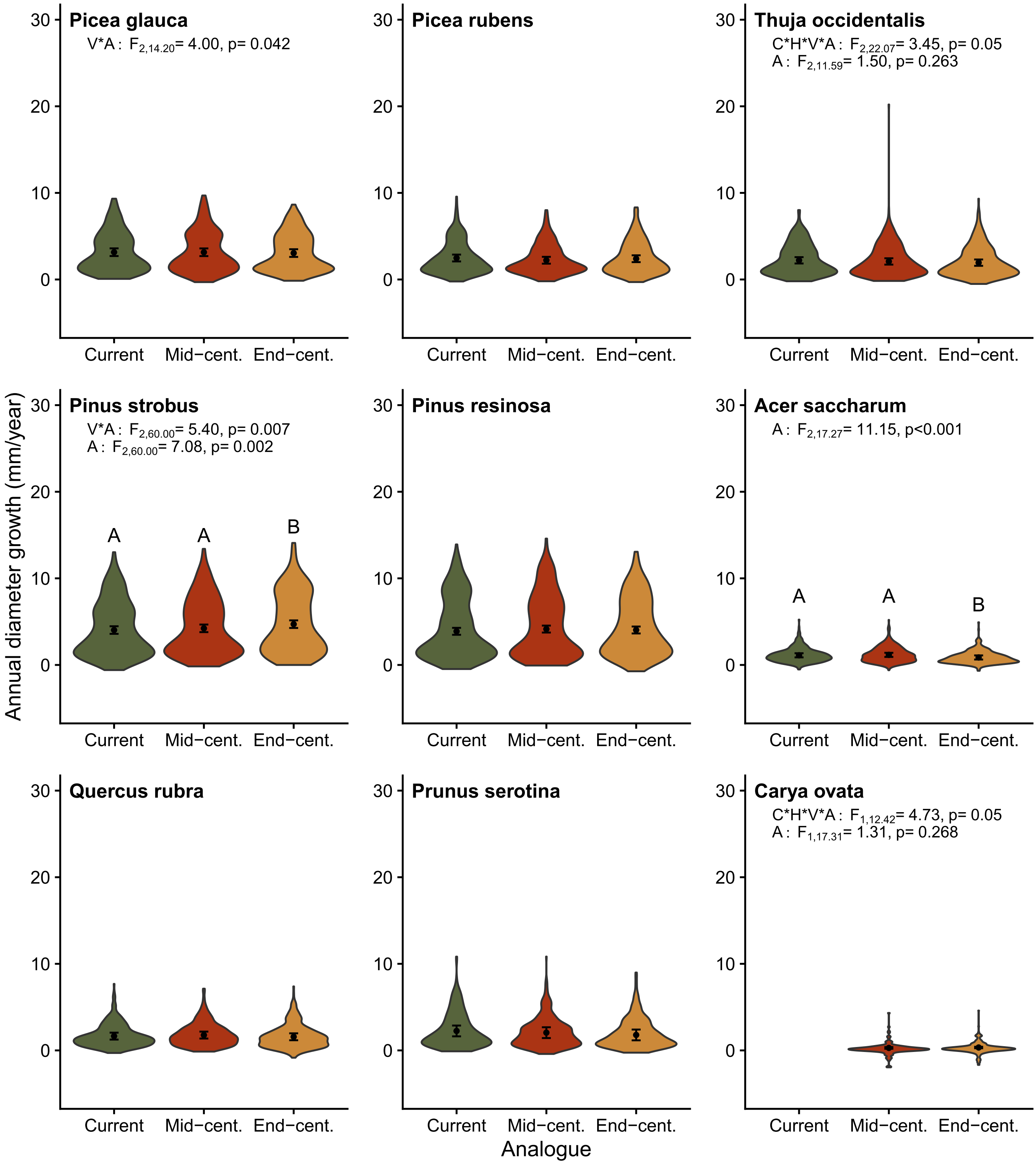

**Fig. 4.** Effects of climate analogue on annual diameter growth (all species but *Carya ovata*: $\text{Diam}_{5\text{th year}} - \text{Diam}_{\text{Planting}}/5$; *Carya ovata*: $\text{Diam}_{4\text{th year}} - \text{Diam}_{\text{Planting}}/4$;) for the nine species planted in the assisted migration experiment. Violin shapes present the data distribution, while the dots and lines are model estimates and confidence intervals (95 %). When significant, mixed model factor effects are noted on the panel, C=Cut, V=Vegetation, H=Herbivore, and A=Analogue. Letters represent statistically significant differences among treatments, as evaluated by least-squares means for statistically significant interactions or treatments ($\alpha = 0.05$). For *Carya ovata*, one analogue treatment was removed from the analysis because of the lack of seedlings at planting.

new environment. These two species behave as pioneer species and can experience rapid growth after early establishment, even at higher latitude (Etterson et al., 2020; Paquette et al., 2006; Clark et al., 2022). The slightly lower survival and growth observed for end-of-century *Acer saccharum, Quercus rubra* and *Prunus serotina* could be counterbalanced by a better drought tolerance compared to seedlings grown from local

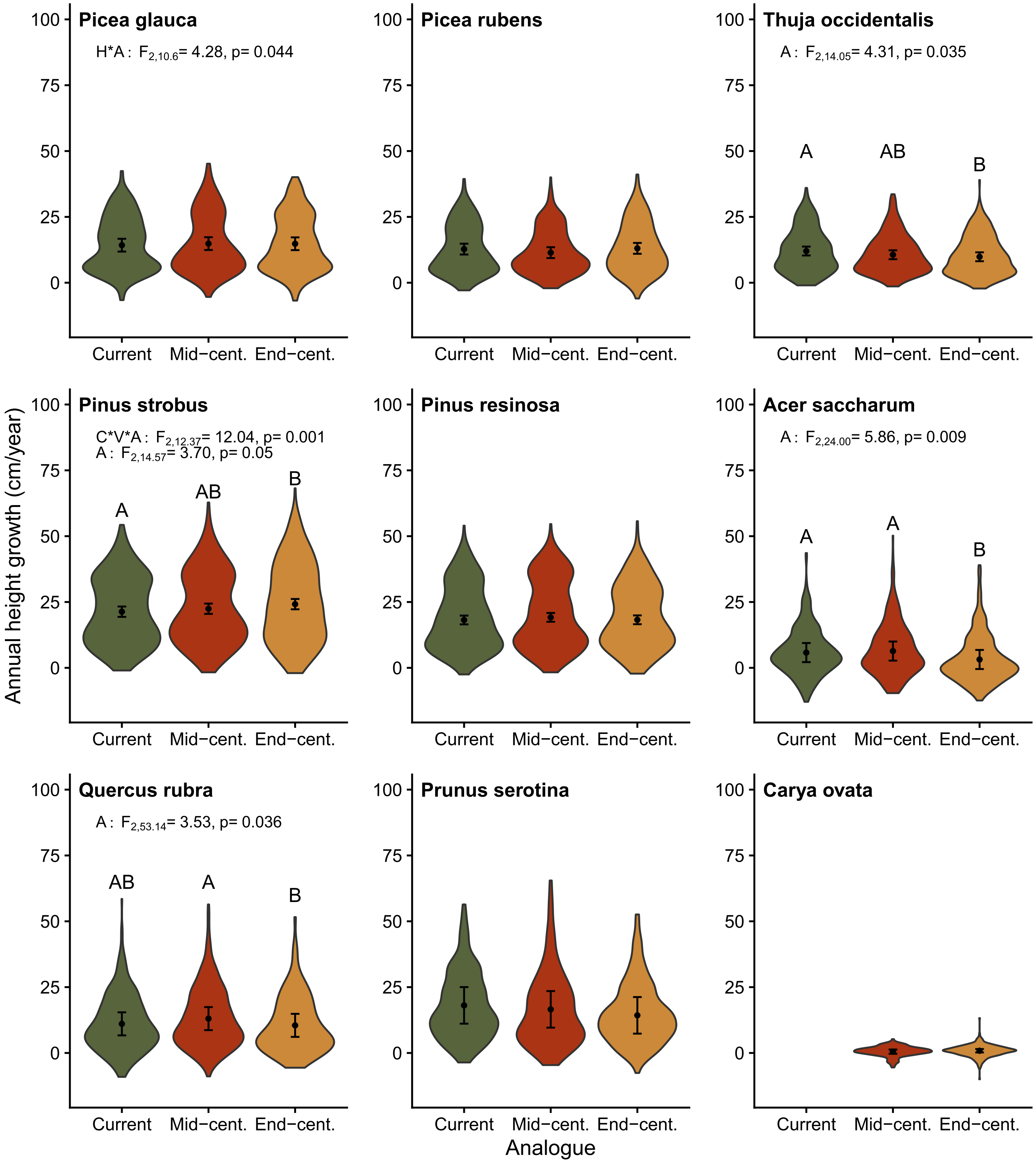

**Fig. 5.** Effects of climate analogue on annual height growth (all species but *Carya ovata*: Height$_{5th\ year}$ – Height$_{Planting}$/5; *Carya ovata*: Height$_{4th\ year}$ – Height$_{Planting}$/4;) for the nine species planted in the assisted migration experiment. Violin shapes present the data distribution, while the dots and lines are model estimates and confidence intervals (95 %). When significant, mixed model factor effects are noted on the panel, C=Cut, V=Vegetation, H=Herbivore, and A=Analogue. Letters represent statistically significant differences among treatments, as evaluated by least-squares means for statistically significant interactions or treatments (α = 0.05). For *Carya ovata*, one Analogue treatment was removed from the analysis because of the lack of seedlings at planting.

source, current populations (Dumais et al., 2025). As for *Picea* species and *Pinus resinosa,* they could be good candidates for assisted population migration; their performance was similar across provenances.

Overall, significant differences in survival and growth across climate analogues were limited, implying a certain flexibility for assisting migration of the studied species. Further, our results indicate that local is not necessarily 'local' anymore, because the climate has shifted already since the seed-bearing trees were established in past decades (O'Neill and Gómez-Pineda, 2021). In many cases, the moderately translocated (mid-century) seedlings performed as well or better than local sources, which could suggest that reforestation efforts might be using relatively high proportions of seed associated to a mid-century analogue. These results also align with the conservative recommendations of moderate seed zone transfers ~2 seed zones, ≤ 400 km (Adams et al., 2024; Pike and Haase, 2024).

#### 3.1.1. Role of the shelterwood for southern species and provenances

We expected that by reducing microclimate variability, the partial cover in the shelterwood treatment would facilitate seedling survival of southern species and provenances, but our first five-year results did not support this prediction. In fact, survival rates were either not influenced by the overstory cutting treatments or were slightly greater in the patch clearcut (*Carya ovata*, *Thuja occidentalis* and *Pinus resinosa)*, where light availability was two times higher than in the shelterwood understory (Dumais et al., 2025). The absence of an interaction between cutting treatments and climate analogues confirmed that there was no positive effect of the shelterwood cover on growth and survival rate for southern provenances. In fact, the foliage of seedlings produced in the open-grown tree nursery conditions could allow these to benefit from full light conditions, even if species are shade-tolerant (e.g., Dumais et al., 2019, 2020). These enhanced light conditions could profit our seedlings planted at high latitudes, where light is limited because of shorter growing seasons and lower solar angle (Lieffers et al., 1999; Messier et al., 1999). In our study, seedlings of all species planted in patch clearcuts improved their diameter growth, while seedlings of conifers and *Prunus serotina* also increased their height growth compared to the shelterwood. These growth results are consistent with higher gas exchange performance that we previously observed for *Picea glauca*, *Thuja occidentalis* and *Prunus serotina* in patch clearcuts (Dumais et al., 2025). The absence of significant gain in height growth for *Quercus rubra, Acer saccharum* and *Carya ovata* compared to the shelterwood can be partly explained by the late frost damage to the apical stem occurring during leaf flush in year 2 and 3 (Parent, 2022, unpublished data collected at this study site, Champagne et al., 2025). Even though the partial cover is not necessary to ensure survival of southern deciduous species, it can facilitate seedling acclimation during the first years (Paquette et al., 2006; Truax et al., 2018).

### 3.2. Implications for management

This study aimed to assess the climate analogue concept as seed sourcing method in an operational assisted migration field trial. Our first five-year results with high survival rates (84 %) tend to demonstrate that it is an appropriate approach. There were only slight differences in survival and growth among climate analogues, suggesting that we have options based on climate-based indices to guide us in seed sourcing. Although encouraging, these results are short-term and should be interpreted with caution, particularly because the seedlings were protected by a deep snow layer during their first winters, reducing their exposure to harsh microclimate conditions and cervid browsing. Up to now, assisted population expansion appears as a possibility to conserve local species in ecosystems, at least for boreal conifers growing at the southern part of their range (e.g., *Picea* and *Thuja* spp.). The option of introducing non-local species through mixtures with local species (Muller et al., 2019) also appears feasible, especially in case of assisted range expansion (e.g. *Quercus rubra*). Results can be more variable for assisted species migration (e.g. good performance of *Prunus serotina vs* poor for *Carya ovata*) and not all species appear equal candidates. Because factors other than translocation distance can be as important, such as the capacity to tolerate shade and competition, species with wide ecological amplitude are better candidates for assisted species migration (Muller et al., 2019; Clark et al., 2022).

We conducted this study in a context of silvical rehabilitation with the goal to enhance the resilience and adaptive capacity of mixedwood stands altered by past diameter-limit cutting. All species including the shade-tolerant ones grew better in open conditions of small patch clearcut with ground scarification, suggesting the use of this silvicultural scenario for assisted migration plantings. Where patch clearcut is not possible because of aesthetic or social acceptability, or because the stand structure is not appropriate for clearcuts, planting in harvest gaps through a selection or a shelterwood system would be sound (Muller et al., 2019; Clark et al., 2022). One-time brushcutting around the planted seedlings in the first five years resulted in limited growth increase. More frequent or longer-term brushcutting management could be necessary in the future (Dumais et al., 2025). Long term monitoring of these assisted migration plantings will be important to assess the capacity of seedlings to eventually develop as mature trees to provide wood products, seeds, and other ecosystem services.

## CRediT authorship contribution statement

**Alejandro A. Royo:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Jean-Pierre Tremblay:** Writing – review & editing, Methodology. **Alison D. Munson:** Writing – original draft, Methodology, Funding acquisition. **Catherine Périé:** Writing – review & editing, Validation, Formal analysis. **Christel C. Kern:** Writing – review & editing, Methodology, Conceptualization. **Daniel Dumais:** Writing – review & editing, Methodology, Conceptualization. **Emilie Champagne:** Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Conceptualization. **Patricia Raymond:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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## Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Given her role as Associate Editor, Christel C. Kern had no involvement in the peer review of this article and had no access to information regarding its peer review. Full responsibility for the editorial process for this article was delegated to another journal editor. Other authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123179.

## Data availability

Seedlings survival and growth data from an assisted migration trial in temperate mixedwood forest, Québec, Canada (DFDR)

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