

## RESEARCH ARTICLE

# Ecological memory and regional context influence performance of adaptation plantings in northeastern US temperate forests

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**Abstract**

1. Species distribution models predict shifts in forest habitat in response to warming temperatures associated with climate change, yet tree migration rates lag climate change, leading to misalignment of current species assemblages with future climate conditions. Forest adaptation strategies have been proposed to deliberately adjust species composition by planting climate-suitable species. Practical evaluations of adaptation plantings are limited, especially in the context of ecological memory or extreme climate events.
2. In this study, we examined the 3-year survival and growth response of future climate-adapted seedling transplants within operational-scale silvicultural trials across temperate forests in the northeastern US. Nine species were selected for evaluation based on projected future importance under climate change and potential functional redundancy with species currently found in these ecosystems. We investigated how adaptation planting type ('population enrichment' vs. 'assisted range expansion') and local site conditions reinforce interference interactions with existing vegetation at filtering adaptation strategies focused on transitioning forest composition.
3. Our results show the performance of seedling transplants is based on species (e.g. functional attributes and size), the strength of local competition (e.g. ecological memory) and adaptation planting type, a proxy for source distance. These findings were consistent across regional forests but modified by site-specific conditions such as browse pressure and extreme climate events, namely drought and spring frost events.
4. *Synthesis and applications.* Our results highlight that managing forests for shifts in future composition represents a promising adaptation strategy for incorporating new species and functional traits into contemporary forests. Yet, important barriers remain for the establishment of future climate-adapted forests that will most likely require management intervention. Nonetheless, the broader applicability of our findings demonstrates the potential for adaptation plantings to serve as strategic source nodes for the establishment of future climate-adapted species across functionally connected landscapes.

**KEYWORDS**

assisted migration, climate change, forestry, reforestation, regeneration, seedlings, silviculture, survival

## 1 | INTRODUCTION

Climate change is expected to impact the function, health and adaptive processes of forest ecosystems around the globe (McDowell et al., 2020). The uncertainty of these impacts represents one of the greatest challenges facing resource managers seeking to maintain the delivery of ecosystem services while adapting to new or changing conditions. Despite projected shifts from species distribution models (Peters et al., 2020), tree migration rates currently lag behind climate change (Sittaro et al., 2017) creating misalignment of current assemblages with future climate conditions (Aitken et al., 2008). These lags have generated a need for adaptive management strategies, such as the deliberate establishment of species projected as future climate adapted in localized plantings to serve as future propagule sources for sustaining forest ecosystem function (Etterson et al., 2020; Messier et al., 2019; Pedlar et al., 2012).

Forest management strategies have been broadly proposed to promote ecological adaptation for global change (Millar et al., 2007; Nagel et al., 2017). Of the least understood and contentious approaches are transitional strategies, which promote compositional or structural shifts representative of forecasted habitats, notably through the adjustment of species composition through adaptation plantings of tree seedlings (also referred to as 'assisted migration'; Aubin et al., 2011; Pedlar et al., 2012; Williams & Dumroese, 2013). Although various classifications of adaptation plantings may be employed differing in terms of species novelty and risk (e.g. biological viability, economic input, social acceptance), two commonly proposed types are as follows: population enrichment (PE) aimed at augmenting regeneration pools of future climate-adapted species already onsite (lowest novelty and risk, already practiced by foresters) and assisted range expansion (ARE) of species from a nearby climate range not found onsite but expected to be adapted to future habitats (moderate novelty and risk; Williams & Dumroese, 2013).

While interest in adaptation plantings has grown, including incorporation into forest policy considerations (Spies et al., 2010) and decision support tools (Swanston et al., 2016), their ecological outcomes have primarily been evaluated based on landscape simulation models (Duveneck & Scheller, 2015) with few field-based experiments to determine the operational feasibility and effectiveness of adaptation plantings in a given region or ecosystem type. As such, key uncertainties remain, including how site-level factors such as ecosystem memory that persist after a disturbance may interact with transplants and limit the degree to which composition can be transitioned (Bengtsson et al., 2003; Johnstone et al., 2016). Moreover, increased variation in extreme climate conditions during seedling establishment could limit operational feasibility and further influence the efficacy of adaptation plantings (Park & Talbot, 2018).

Forest managers and scientists have long experimented with provenance to examine adaptation in plantations and common gardens

(Aitken et al., 2008; Savolainen et al., 2007; Vilmorin, 1862), yet fewer experiments are executed in a silvicultural context. Additionally, experiments often focus on commercially valuable species and traits associated with volume production, highlighting a need to evaluate adaptation plantings representing diverse functional traits that complement those forecasted to decline to maintain ecosystem functions and assemblages. Prior investigations of adaptation plantings as part of silvicultural experiments have focused on monospecific or fire-dependent conifer-dominated ecosystems in central and western North America (Etterson et al., 2020; Gray et al., 2011; Muller et al., 2019), yet key knowledge gaps remain as to the efficacy of adaptation plantings in other globally important systems such as multi-species forests of northeastern North America, where historic disturbance regimes and abundant natural regeneration may strengthen ecological memory and persistence of forest types despite forecasted shifts in function (Johnstone et al., 2016; Seymour et al., 2002).

Ecological memory has been used to describe ecosystem responses in the form of informational (e.g. adaptive traits) and material legacies (e.g. individuals, propagules) that persist after a disturbance that shape ecosystem responses, and has been viewed in terms of ecological resilience to abrupt transitions (Bengtsson et al., 2003; Johnstone et al., 2016). In the context of forest regeneration, a forest may be evolutionarily conditioned by a given disturbance, climatic or biophysical regime to contain a suite of regeneration traits that provide a recruitment advantage over other species or traits maladapted to these conditions (Bellingham & Sparrow, 2000; Keeley et al., 2011). Despite the existence of such dynamics in temperate forests of the northeastern US (Plotkin et al., 2013), recent projections indicate high potential for increases in suitable habitat for future climate-adapted species in the region under climate change, potentially conflating this response. Indeed, while 24–26 species are forecasted to decline in future habitat compatibility (Peters et al., 2020), 11–19 species have already been identified for assisted migration and 1–12 are expected to infill naturally over time (Iverson et al., 2019), highlighting the potential importance of adaptation plantings.

Our study aims were to assess the response of mixed-species future climate-adapted plantings for PE and ARE applied in a silvicultural context in northern hardwood and mixed conifer-hardwood forests in the northeastern US. We capitalize on the Adaptive Silviculture for Climate Change project (ASCC; Nagel et al., 2017) to examine the performance of future climate-adapted seedling transplants in the context of broadly proposed forest adaptation strategies. Our primary objective was to test the role of species and biophysical constraints (e.g. ecological memory, regional forest type) in affecting how adaptation plantings may be employed by managers throughout the most forested region in the United States. We hypothesize that (a) seedling performance will be determined based on the strength of site level ecological memory, in terms of vegetative competition and (b) seedling performance will be variable across sites and among species, particularly between those locally adapted to site (PE) and those requiring assisted migration (ARE).

## 2 | MATERIALS AND METHODS

### 2.1 | Adaptive silviculture for climate change study sites

Adaptation plantings were tested as part of the New England installation of the ASCC project (NEASCC), an international, co-produced operational-scale experiment examining local interpretations of adaptation strategies for climate change (Nagel et al., 2017). Several adaptive silvicultural approaches guide the ASCC experiment (termed Resistance, Resilience, Transition; cf. Millar et al., 2007), yet the focus of our study was the 'Transition' treatment, which aims to alter forest overstorey composition to represent that forecasted under future climate and disturbance conditions. Furthermore, this is the only treatment where planting future climate-adapted species was included in the NEASCC study design (see Table S1). NEASCC was established at Dartmouth College's Second College Grant (SCG), in northern New Hampshire (Figure 1; Table 1). Additional adaptation plantings were tested at the University of Vermont's Wolcott (WOL) and Washington Research Forests (WAS) in northern and central Vermont to provide regional replication.

Second College Grant is dominated by northern hardwood forests located within the Northeastern Highlands biophysical region where soils are predominately coarse-loamy, frigid spodosols, formed typically in dense glacial till (Griffith et al., 2009). WOL is an Acadian mixed conifer-hardwood forest in the Northern Green Mountains biophysical region where soils are shallow and well-drained fine sandy loams derived from acidic metamorphic bedrock (Thompson et al., 2019). WAS is a rich northern hardwood forest in the Northern Vermont Piedmont characterized by rich calcareous soils and bedrock. All sites are second-growth forests naturally regenerated following harvesting in the early 20th century. Regional climate is characterized by cold, long winters and warm, short growing seasons (110–120 days), where mean annual temperature and precipitation is 4.5°C and 1,009.2 mm, respectively (NCDC, 2020), although extreme climate anomalies (e.g. drought, spring frosts) occur and were experienced during this experiment.

### 2.2 | Treatments and experimental design

Silvicultural treatments at SCG were replicated into four blocks, with treatment units approximately 10 ha in size (4 replicates). Treatments at SCG included, but were not limited to, 0.1 and 0.4 ha harvest gaps with retention across 20% of the treatment unit. Gaps sizes were selected to reflect those associated with mesoscale disturbances in the region (Seymour et al., 2002) and to provide adequate light levels to match silvics of future climate-adapted transplants (mean shade tolerance  $3 \pm 0.4$  standard error on a 1–5 scale, where 1 = very intolerant and 5 = very shade tolerant; Paquette & Messier, 2011) relative to dominant species in these forests (mean shade tolerance  $4.5 \pm 0.3$ ; Hanson & Lorimer, 2007; Raymond et al., 2018). Only select harvested gaps were planted at SCG (2 per block,  $n = 8$  per gap size). Due to constraints

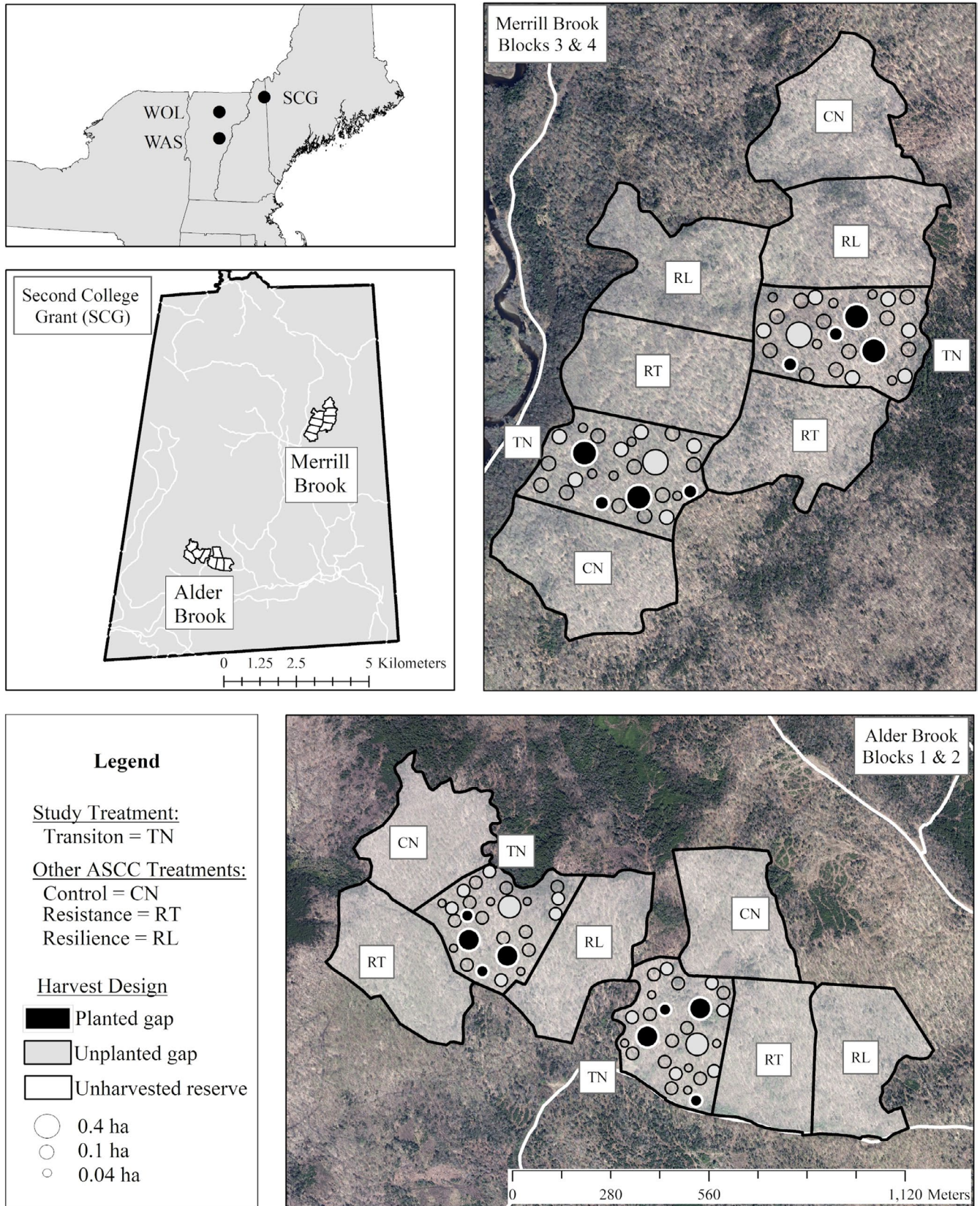
in parcel size and management objectives, only 0.1 ha gaps were installed and planted at WOL and WAS ( $n = 3$  per research forest).

Nine species were selected for testing, informed by species distribution models (Table 2; Janowiak et al., 2018; Peters et al., 2020). Given the coarse scale of projections, regional manager and scientist knowledge helped localize recommendations, including the selection of some species projected to decline in the northeastern US, but with expected climate refugia at study sites (e.g. *Picea rubens*). Emphasis was placed on species with complementary functional traits relative to species currently onsite projected to decline (see Table S2). Bare-root seedlings from eight species were obtained from state and private nurseries. A ninth species, a hybrid *Castanea dentata* bred for tolerance to chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) by The American Chestnut Foundation (Steiner et al., 2017) through controlled pollination between surviving trees and disease-tolerant *C. mollissima* (Blume) was planted as seed following Bonner and Karrfalt (2008). Given the operational nature of the experiment and limited regional nursery capacity (Fargione et al., 2021; Tepe & Meretsky, 2011), we were unable to test specific seed zones within species. Instead, the outcomes of this work represent what managers would encounter if they were to apply like treatments under current nursery capacity and stock availability.

Seedlings were planted in late May–June 2018 as close to leaf-out as possible. In all, 200 seedlings were planted in 0.1 ha gaps ( $n = 20$ /species) and 400 seedlings were planted in 0.4 ha gaps ( $n = 40$ /species) at 2 m spacing. To account for germination failure, *C. dentata* sowing numbers were doubled, but this species was only available for experimentation at SCG. Overall, 4,675 seedlings were planted at SCG, while 471 and 474 were planted at WAS and WOL, respectively. Species locations were randomized and planted at suitable microhabitats within 0.5 m of pre-determined locations. Protective mesh tubes were placed around half of plantings to minimize herbivory, and after the first year, competing vegetation within 1 m radius of half of seedlings was mowed using brush saws, yielding a split-split plot design.

### 2.3 | Field data collected

All seedlings were tracked for three growing seasons (2018–2020). Baseline measurements were collected within 2 weeks of planting and repeated measures were collected biannually at the beginning and end of growing seasons. Survival was recorded every measurement period while root collar diameter (RCD) and stem height were collected after each growing season. Planting site conditions including seedbed (scarified or undisturbed soils) or presence of woody overstorey vegetation (trees forming gap edges, retention trees, mature saplings >6 cm diameter at breast height <2 m from seedlings) were recorded. The relationship of height and crown spread of transplants relative to natural vegetation within a 1 m<sup>2</sup> neighbourhood was recorded after second and third growing seasons, using ordinal competition classes (suppressed, intermediate, co-dominant, free-to-grow). Visual observations of seedling conditions were noted (e.g. presence of browse, frost damage).



**FIGURE 1** Regional study sites in New Hampshire (Dartmouth College's Second College Grant (SCG)) and Vermont (University of Vermont's Washington (WAS) and Wolcott (WOL) Research Forests). SCG is the focal site for the New England Adaptive Silviculture for Climate Change project, with four 10 ha replicated treatments across Alder and Merrill Brook research areas (see Table S1 for all treatment descriptions). Adaptation plantings were tested within a subset of 0.1 and 0.4 ha harvest gaps (black circles) in 'Transition' treatments. Additional plantings were tested within six 0.1 ha gaps at WAS and WOL

TABLE 1 Study site conditions

Spatially explicit characteristics			Climate (normals, observed) <sup>a,d</sup>						Pretreatment stand conditions			
Research Forest	Bedrock	Lat	Long	Elev	EMNT	EMXT	Tmin01	Tmax07	MAT	MAP	BA (m <sup>2</sup> /ha)	Composition (%)
Second College Grant (SCG), New Hampshire	Metapelite and quartzite <sup>b</sup>	44.885	-71.079	550	-42.2, -37.2	32.8, 32.8	-18.3, -16.5	23.5, 23.7	3.5, 4.1	1,196.6, 1,239.1	26.6 ± 1.5	<i>Acer saccharum</i> (34), <i>Fagus grandifolia</i> (24), <i>Betula alleghaniensis</i> (17), <i>Acer rubrum</i> (9), <i>Picea rubens</i> (6), other HW (11), other SW (1)
Washington Research Forest (WAS), Vermont	Carbonaceous phyllite and limestone <sup>c</sup>	44.042	-72.417	600	-37.8, -27.2	35.6, 36.1	-14.5, -13.2	25.2, 27.6	5.2, 7.9	1,003.7, 739.8	33.2 ± 2.6	<i>Acer saccharum</i> (56), <i>Fraxinus americana</i> (20), <i>Acer rubrum</i> (8), <i>Fagus grandifolia</i> (7), other HW (12)
Wolcott Research Forest (WOL), Vermont	Quartzite <sup>c</sup>	44.598	-72.425	370	-39.4, -31.1	34.4, 34.4	-13.6, -13.6	25.3, 27.8	5.0, 7.2	1,072.6, 998.8	37.9 ± 2.2	<i>Acer rubrum</i> (22), <i>Picea rubens</i> (20), <i>Abies balsamea</i> (18), <i>Tsuga canadensis</i> (14), <i>Betula alleghaniensis</i> (10), <i>Prunus serotina</i> (7), <i>Betula papyrifera</i> (7), other HW (4)

Notes: Temperature = °C, precipitation = m, elevation = m, composition = importance values based on basal area and trees per hectare.

Abbreviations: BA, basal area; Elev, Elevation; EMNT, extreme minimum temperature; EMXT, extreme maximum temperature; HW, hardwoods; MAP, mean annual precipitation; MAT, mean annual temperature; SW, softwoods; Tmax07, July mean maximum temperature; Tmin01, January mean minimum temperature.

<sup>a</sup>The first climate values presented are 30-year normals (1991–2020), followed by the observed values during the study period (2018–2020), reported from nearest available meteorological stations.

<sup>b</sup>Lyons et al. (1997).

<sup>c</sup>Ratcliffe et al. (2011).

<sup>d</sup>NCDC (2020).

## 2.4 | Statistical analysis

Cox proportional hazard regression (hereafter: 'Cox models') was used to compare species-specific survival curves within research forests, to test for differences within a single time-constant covariate (Cox, 1972; Martinussen & Scheike, 2006). Due to violations in proportional hazards assumption by multivariate predictors, we limited Cox models to species-only covariate survival models within experimental forests that satisfied assumptions. Cox models were performed using the phreg procedure in the SAS statistical package (SAS Institute Inc, 2013).

Generalized linear mixed models (Bolker et al., 2009) were used to test abiotic and biotic influences affecting seedling survival with a binomial error distribution using the GLMMTMB package (Brooks et al., 2017) in the statistical package R version 3.6.1 (R Core Team, 2019). R was used for all subsequent analyses. Given the experimental scope and higher replication at SCG, survivorship models relied on this site to examine seedling response. Fixed effects evaluated included species, harvest treatment, planting bed conditions, initial seedling size (RCD), proximal woody overstorey vegetation (presence/absence) and their interactions. Block, competition control and browse protection were included as random effects. We also examined regional survivorship in 0.1 ha treatments across research forests and included species, initial seedling size, research forest and their interactions. Plot, competition control and browse protection were included as random effects.

Seedling growth was assessed using relative growth rate (RGR) in above-ground biomass to control for between-species variation in sizes. Given the relative absence of species-specific seedling allometry models for volume, green wood volume was assumed to be conical and calculated as:

$$V_{gw} = 1/3\pi hr^2,$$

where  $h$  is the seedling height (mm) and  $r$  is the radius of RCD (mm). Biomass was calculated using methods modified from Woodall et al. (2011):

$$\text{Biomass} = V_{gw} \times SG_{gw} \times W,$$

where  $SG_{gw}$  is the species' specific gravity in green wood (Miles & Smith, 2009) and  $W$  is the weight of water. RGR is calculated as the difference in seedling sizes between first and last measurements over the 3-year monitoring period (Hunt & Cornelissen, 1997), where  $D$  is the individual seedling biomass:

$$\text{RGR} = \frac{\ln D_2 - \ln D_1}{t_2 - t_1}.$$

The seedling RGR response was tested using linear mixed-effects models with Gaussian error distribution in the lme4 package (Bates et al., 2015). Growth was assessed using live individuals after the 3-year period. Like survival models, SCG was used as the primary experimental site and the same fixed effects were tested,

TABLE 2 Species, initial sizes ( $M (\pm SE)$ ), planting type and silvical characteristics for seedling adaptation plantings tested

Species planted	Seed source location	Initial size		Species silvical characteristics				
		RCD	Height	Planting type	Shade tolerance <sup>b</sup>	Drought tolerance <sup>b</sup>	Growth rate <sup>c</sup>	Leaf habit <sup>c</sup>
Black birch <i>Betula lenta</i> L.	Pennsylvania	6 ( $\pm 0.1$ )	79.8 ( $\pm 1$ )	ARE	3.2	3	Moderate	Deciduous
Bitternut hickory <i>Carya cordiformis</i> (Wangenh.) K. Koch	Illinois	4.9 ( $\pm 0.1$ )	23.8 ( $\pm 0.2$ )	ARE	2.1	4	Slow	Deciduous
American chestnut (hybrid) <i>Castanea dentata</i> (Marshall) Borkh. B3F3	Virginia	3.8 ( $\pm 0.1$ ) <sup>a</sup>	33.6 ( $\pm 0.7$ ) <sup>a</sup>	ARE	3.1	3	Rapid	Deciduous
Red spruce <i>Picea rubens</i> Sarg.	Nova Scotia	6.5 ( $\pm 0.1$ )	54.3 ( $\pm 0.4$ )	PE	4.4	2.5	Moderate	Evergreen
Eastern white pine <i>Pinus strobus</i> L.	New Hampshire	3.8 ( $\pm 0.1$ )	10.9 ( $\pm 0.3$ )	PE	3.1	2.3	Rapid	Evergreen
Bigtooth aspen <i>Populus grandidentata</i> Michx.	Michigan	2.9 ( $\pm 0$ )	22.8 ( $\pm 0.3$ )	PE	1.2	2.5	Rapid	Deciduous
Black cherry <i>Prunus serotina</i> Ehrh.	Pennsylvania	2.6 ( $\pm 0$ )	23.9 ( $\pm 0.3$ )	PE	3.5	3	Rapid	Deciduous
Northern red oak <i>Quercus rubra</i> L.	New Hampshire	4.5 ( $\pm 0.1$ )	24.7 ( $\pm 0.3$ )	PE	2.8	2.9	Moderate	Deciduous
Eastern hemlock <i>Tsuga canadensis</i> (L.) Carrière	Michigan	3.7 ( $\pm 0.1$ )	26.3 ( $\pm 0.2$ )	PE	4.8	1	Slow	Evergreen

Abbreviations: RCD, root collar diameter (mm); Height (cm); Planting type: ARE, assisted range expansion; PE, population enrichment.

<sup>a</sup>*C. dentata* planted as seed. Baseline measurements are from one year of growth.

<sup>b</sup>Niinemets and Valladares (2006).

<sup>c</sup>USDA-NRCS (2021).

except biomass was used for initial seedling size and understory vegetation cover (ordinal) was included since it was only measured during the second and third measurement periods. Models used to examine regional differences in RGR followed the same form as regional survival models.

We examined 23 survival and 46 growth models representing different a priori hypotheses regarding ecological factors affecting seedling response at SCG and 11 survival and 12 growth models to test regional differences (see Table S3). Each model was assessed and diagnosed to pass model assumptions of linearity and normality of residuals. Following inspection of residuals, we determined a log transformation for initial sizes was appropriate. Model selection was performed using Akaike information criterion (AIC; Burnham & Anderson, 2002) to determine the best approximating model in a given candidate set, using the AIC<sub>CMODAVG</sub> package (Mazerolle, 2020). A null model containing solely intercept and error terms and an informed null model that incorporated initial seedling size as a fixed effect were included. Multiple competing models were compared and ranked according to change in AIC ( $\Delta AIC$ ), where top candidate models were considered to have strong support when  $\Delta AIC$  values were  $< 7$  (Burnham & Anderson, 2002).

To further analyse the relationships of covariates tested with adaptation plantings, we isolated predictors from best supported models for post hoc testing. Analysis of variance (ANOVA) was used for factors and Pearson's correlations for linear relationships

(significance threshold  $\alpha = 0.05$ ). Each test was assessed to pass model assumptions of linearity and normality of residuals. We also explored factors not included in models (e.g. adaptation planting type) using ANOVAs.

### 3 | RESULTS

#### 3.1 | Survival

Regionally, 3,152 of 5,620 seedling transplants survived through the third growing season (mean =  $56.7 \pm 1.4\%$ ; Table 3). Mortality decreased between subsequent annual measurements ( $p < 0.001$ ; year 1 =  $29.1 \pm 2.3\%$ , year 2 =  $11.6 \pm 1.54\%$ , year 3 =  $2.6 \pm 0.6\%$ ; *C. dentata* germination failure excluded). First year mortality varied among sites (SCG =  $23.7 \pm 1.6\%$ , WAS =  $29.5 \pm 1.7\%$ , WOL =  $32.9 \pm 3.2\%$ ;  $p = 0.025$ ), but by the third year, only SCG ( $4.0 \pm 0.6\%$ ) differed from WAS and WOL (pooled mean:  $0.8 \pm 0.5\%$ ;  $p = 0.012$ ). Regional survival was best explained by species, initial RCD, research forest and their interactions based on the best approximating model (AIC weight = 0.87; Table 4). The estimated predicted odds for initial RCD increased 2.82 times for every unit of increase in size (see Table S4). The ranked order for species based on predicted odds of survival relative to the reference was *Quercus rubra* (5.73) > *Prunus serotina* (2.51) > *P. rubens* (2.22) > *Pinus strobus* (1.59) > *Betula*

TABLE 3 Summary statistics by research forest and treatment (0.4 and 0.1 ha gaps). Letters denote significant differences based on Tukey HSD (combined 0.1 ha treatments;  $\alpha \leq 0.05$ )

Species	No. planted/no. surviving		Survival (%)						RGR biomass ( $\text{g g}^{-1} \text{ year}^{-1}$ )									
	SCG		WOL		SCG		WAS		WOL		HSD		SCG		WAS		WOL	
	0.4 ha	0.1 ha	0.1 ha	0.1 ha	0.4 ha	0.1 ha	0.1 ha	0.1 ha	0.1 ha	0.1 ha	0.1 ha	0.4 ha	0.1 ha	0.1 ha	0.1 ha	0.1 ha	0.1 ha	0.1 ha
<i>B. lenta</i>	292/136	158/65	56/25	60/34	46.7 ± 2.6	41.3 ± 8	45.4 ± 14	45.4 ± 14	56.7 ± 8.3	b	1.6 ± 0.08	1.9 ± 0.15	1.5 ± 0.11	1.3 ± 0.08	b			
<i>C. cordiformis</i>	319/176	158/82	59/39	60/30	55 ± 5.4	51.9 ± 2.3	66.2 ± 5.7	66.2 ± 5.7	50 ± 5.8	bc	1.1 ± 0.04	1.2 ± 0.05	1.3 ± 0.07	1 ± 0.1	c			
<i>C. dentata</i>	640/315	319/145	–	–	49.2 ± 3.8	45.5 ± 6.8	–	–	–	–	2.3 ± 0.12	2.2 ± 0.14	–	–				
<i>P. rubens</i>	318/255	160/124	59/52	60/39	80.2 ± 3.9	77.5 ± 4.7	88.3 ± 7.3	88.3 ± 7.3	65 ± 5.8	e	1.8 ± 0.03	1.8 ± 0.05	1.9 ± 0.06	1.8 ± 0.07	b			
<i>P. strobus</i>	297/205	155/112	60/39	59/30	68.8 ± 5.5	72.4 ± 3.4	65 ± 2.9	65 ± 2.9	50.9 ± 0.9	cde	3.2 ± 0.11	2.8 ± 0.1	3.5 ± 0.21	3.2 ± 0.23	a			
<i>P. grandidentata</i>	313/147	156/54	41/15	57/12	46.9 ± 4.8	34.4 ± 4.2	36.5 ± 1.5	36.5 ± 1.5	21.1 ± 3	a	4 ± 0.17	3.6 ± 0.23	2.2 ± 0.23	2.3 ± 0.25	a			
<i>P. serotina</i>	312/122	154/61	77/33	60/33	39.1 ± 2.7	39.6 ± 7.4	46.2 ± 8.8	46.2 ± 8.8	55 ± 8.7	ab	3.3 ± 0.16	3.2 ± 0.3	3.8 ± 0.34	2.1 ± 0.17	a			
<i>Q. rubra</i>	303/240	147/116	60/35	58/51	79.1 ± 3.3	79 ± 4.9	58.3 ± 8.8	58.3 ± 8.8	88.1 ± 4.3	e	1.7 ± 0.04	1.7 ± 0.08	1.6 ± 0.1	1.7 ± 0.11	b			
<i>T. canadensis</i>	316/171	158/82	59/39	60/38	54.2 ± 6.4	52 ± 4.6	66.4 ± 11.5	66.4 ± 11.5	63.3 ± 1.7	bcd	2 ± 0.07	1.9 ± 0.1	2.1 ± 0.11	2.2 ± 0.19	b			
Combined	3,110/1,767	1,565/841	471/277	474/267	57.7 ± 2.2	54.8 ± 2.6	60 ± 4.1	60 ± 4.1	56.2 ± 4	–	2.1 ± 0.04	2.1 ± 0.05	2.1 ± 0.08	1.8 ± 0.06	–			

*lenta* (1.44) > *Tsuga canadensis* (1.16) > *Populus grandidentata* (reference) > *Carya cordiformis* (0.45). The predicted odds of survival for WAS and WOL were 0.34 relative to SCG. The interaction terms increased the mean odds between species × research forest (1.28 ± 0.25), initial diameter × research forest (1.5) and species × initial RCD (2.52 ± 0.81).

Mean survival differed by species across regional 0.1 ha treatments, where ranked percent survivorship was *P. rubens* (77.1 ± 3.8), *Q. rubra* (76.5 ± 4.3), *P. strobus* (66.2 ± 3.1), *T. canadensis* (57.5 ± 3.7), *C. cordiformis* (54.5 ± 2.6), *C. dentata* (45.5 ± 6.8), *B. lenta* (45.4 ± 5.6), *P. serotina* (44.3 ± 5.0) and *P. grandidentata* (31.7 ± 3.1). This order was consistent across regional forests with few exceptions (Figure 2), where site-level survivorship differed among *P. grandidentata*, *C. cordiformis*, *P. strobus* and *Q. rubra* ( $p \leq 0.05$ ).

Separate Cox models applied to research forests revealed unique predicted survival curves for each species (Figure 3). All subsequent survival results focus on SCG. Species were tested using maximum likelihood analysis and compared using hazard ratios (HRs; 95% confidence intervals), where HRs < 1 indicate reduced risk of mortality relative to the reference (here, *P. serotina*). HRs ranked lowest-highest are *Q. rubra* (0.27 CI = 0.21–0.33,  $p < 0.001$ ), *P. rubens* (0.27 CI = 0.22–0.34,  $p < 0.001$ ), *P. strobus* (0.4 CI = 0.33–0.49,  $p < 0.001$ ), *C. cordiformis* (0.66 CI = 0.56–0.77,  $p < 0.001$ ), *T. canadensis* (0.7 CI = 0.6–0.83,  $p < 0.001$ ), *B. lenta* (0.79 CI = 0.68–0.91,  $p = 0.001$ ), *P. grandidentata* (0.84 CI = 0.73–0.97,  $p = 0.02$ ) and *C. dentata* (0.92 CI = 0.8–1.06,  $p = 0.2$ ; Table S5).

Survival within 0.1 and 0.4 ha harvest treatments at SCG was best explained by species, initial RCD and presence of woody overstorey vegetation (AIC weight = 0.9). The predicted odds for initial RCD increased 3.63 times for every increase in size. The ranked order for species based on predicted odds of survival relative to the reference was *C. dentata* (4.55) > *Q. rubra* (3.17) > *P. strobus* (2.27) > *P. rubens* (1.85) > *T. canadensis* (1.19) > *P. serotina* (1.00) > *P. grandidentata* (reference) > *C. cordiformis* (0.82) > *B. lenta* (0.42). Presence of woody overstorey vegetation over microsite increased survivorship 1.45 times.

The role of understorey competition was tested on a subset of seedlings, despite its exclusion from models. Suppressed seedlings survivorship was lower (60.4 ± 3.7%,  $p < 0.05$ ) compared to other competition classes, which collectively did not significantly differ (pooled mean survivorship for intermediate, co-dominant, free-to-grow classes: 90.4 ± 1.4%; Figure 4). Intraspecific differences revealed this pattern for all species except *Q. rubra* and *T. canadensis*, where group means were not different. No differences in survival were observed between 0.1 and 0.4 ha harvest gap sizes (see Figure S1). Species classified as PE survived at higher rates (59 ± 2.0%,  $p = 0.007$ ) compared to ARE (49 ± 2.6%).

### 3.2 | Growth

Across sites, mean above-ground biomass RGR was  $2.32 \pm 0.04 \text{ g g}^{-1} \text{ year}^{-1}$ . Regional growth was best explained by

**TABLE 4** Summary of confidence set models (including intercept-only and informed null) for survival and growth across regional planting sites and Second College Grant (SCG), based on the Akaike information criterion ( $\Delta\text{AIC} \leq 7$ ). Parameter estimates accompany main effects and interaction terms, whereas values for logistic generalized linear mixed-effect models (GLMM) are odds ratios and values for Gaussian linear mixed-effects (LME) models are actual estimates. Parameter estimates for categorical variables with  $\geq 3$  factors are presented as mean and SE. For complete parameter estimates, see Table S4

Response and model	Model form	K	AIC	$\Delta\text{AIC}$	AICWt.
Three-year survival (logistic GLMM):					
Regional	$\sim \beta_0[0.18] + iD[2.82] + Rf[0.34 \pm 0.0] + S[9.52 \pm 7.96] + iD \times Rf[2.52 \pm 0.81] + Rf \times S[1.28 \pm 0.25] + iD \times S[1.12 \pm 0.27] + \epsilon_{p,cc,CG}$	37	2,697.64	0	0.87
	$\sim \beta_0[0.15] + iD[3.38] + Rf[0.88 \pm 0.31] + S[6.32 \pm 5.09] + Rf \times S[1.67 \pm 0.27] + iD \times S[1.29 \pm 0.3] + \epsilon_{p,cc,CG}$	35	2,702.5	4.86	0.08
	$\sim \beta_0[0.19] + iD[2.64] + Rf[0.37 \pm 0.04] + S[2.43 \pm 0.58] + Rf \times S[1.36 \pm 0.27] + iD \times Rf[2.26 \pm 0.56] + \epsilon_{p,cc,CG}$	30	2,703.63	5.99	0.04
	$\sim \beta_0[-1.39] + iD[1.22] + \epsilon_{p,cc,CG}$	3	2,845.14	145.12	0
	$\sim \beta_0[0.27] + \epsilon_{p,cc,CG}$	2	2,988.05	288.04	0
SCG	$\sim \beta_0[0.16] + iD[3.63] + S[1.91 \pm 0.49] + Wv[1.45] + \epsilon_{b,cc,CG}$	14	5,047.81	0	0.90
	$\sim \beta_0[0.19] + iD[3.65] + S[1.6 \pm 0.4] + Wv[1.1] + S \times OV[1.43 \pm 0.12] + \epsilon_{b,cc,CG}$	22	5,052.71	4.9	0.08
	$\sim \beta_0[-1.01] + iD[1.09] + \epsilon_{b,cc,CG}$	3	5,480.13	426.99	0
	$\sim \beta_0[0.45] + \epsilon_{b,cc,CG}$	2	5,707.97	654.83	0
Relative growth rate in above-ground biomass (Gaussian LME):					
Regional	$\sim \beta_0[1.37] + iB[-0.18] + S[0.58 \pm 0.7] + Rf[-0.05 \pm 0.17] + S \times Rf[-0.03 \pm 0.07] + \epsilon_{p,cc,CG}$	29	1,187.11	0	1
	$\sim \beta_0[1.94] + iB[-0.20] + \epsilon_{p,cc,CG}$	3	1,533.62	415.5	0
	$\sim \beta_0[0.68] + \epsilon_{p,cc,CG}$	2	1,906.46	788.35	0
SCG	$\sim \beta_0[1.17] + iB[-0.22] + S[0.19 \pm 0.07] + Uc[0.14] + Sb[0.06] + S \times Uc[0.12 \pm 0.03] + \epsilon_{b,cc,CG}$	24	2,637.95	0	0.76
	$\sim \beta_0[1.21] + iB[-0.22] + S[0.19 \pm 0.07] + Uc[0.14] + S \times Uc[0.12 \pm 0.03] + \epsilon_{b,cc,CG}$	23	2,641.79	3.83	0.11
	$\sim \beta_0[1.25] + iB[-0.22] + S[0.19 \pm 0.07] + Uc[0.14] + Wv[-0.05] + S \times Uc[0.12 \pm 0.03] + \epsilon_{b,cc,CG}$	24	2,642.06	4.11	0.1
	$\sim \beta_0[2.07] + iB[-0.21] + \epsilon_{b,cc,CG}$	3	3,804.79	1,193.73	0
	$\sim \beta_0[0.74] + \epsilon_{b,cc,CG}$	2	4,514.91	1,903.85	0

Notes: Parameter codes and reference factors: iD, log initial diameter; iB, log initial biomass; S, species (survival model reference: *P. grandidentata*; RGR model reference: *C. cordiformis*); Uc, understorey competition; Sb, seedbed (reference: unmodified); Wv, woody overstorey vegetation (reference: absence); Rf, research forest (reference: SCG); Tr, treatment (reference: 0.1 ha gap). Error terms: b, block; p, plot; cc, competition control; bp, browse protection. Significance: italic =  $p \leq 0.05$ , bold =  $p \leq 0.01$ , bold italic =  $p \leq 0.001$ .

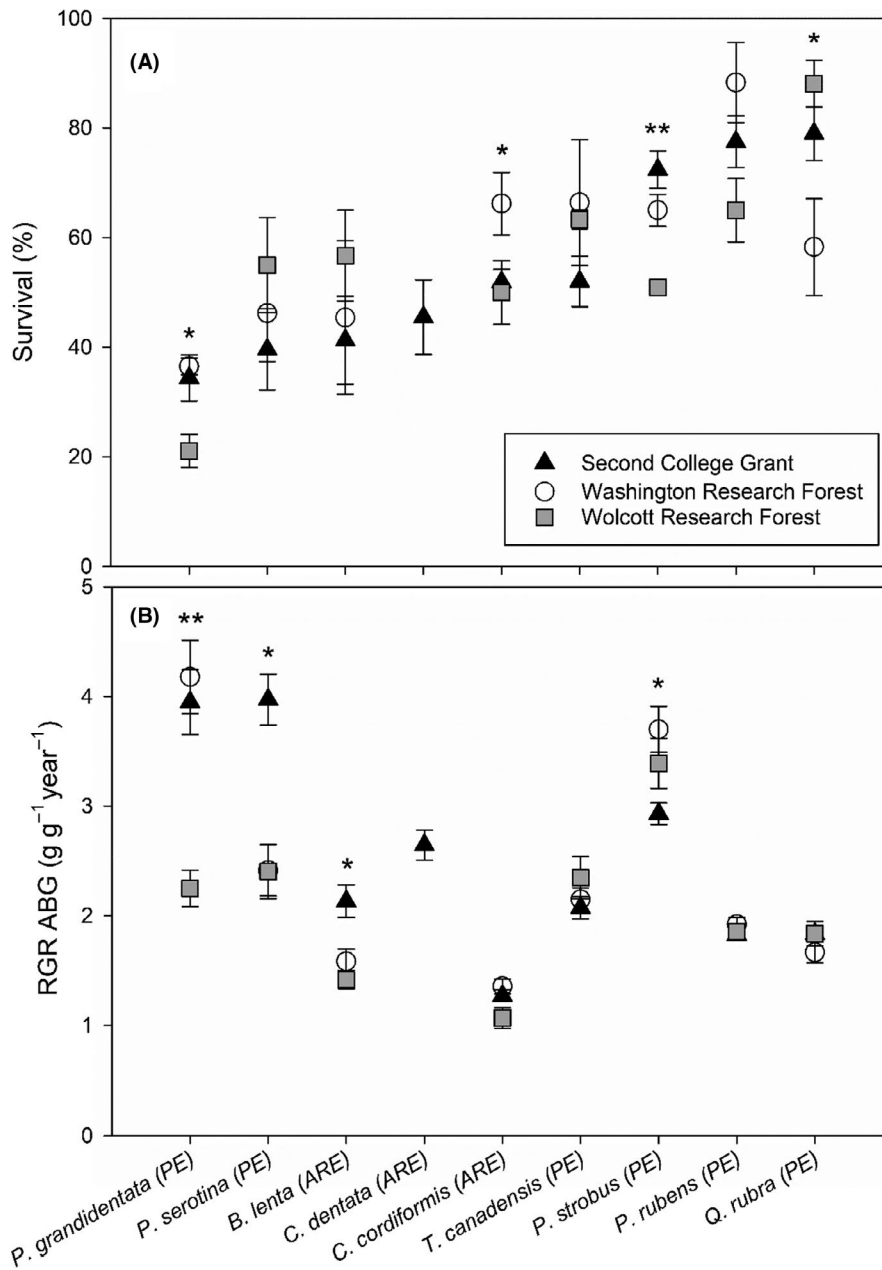
initial seedling biomass, species, research forest, and the interaction between species and research forest (AIC weight = 1). The ranked order for species based on effect size relative to the reference was *P. grandidentata* (0.84) > *B. lenta* (0.72) > *P. serotina* (0.71) > *P. rubens* (0.58) > *P. strobus* (0.55) > *T. canadensis* (0.34) > *Q. rubra* (0.32) > *C. cordiformis* (reference). The initial seedling biomass estimate was -0.18 for every unit of increase in size. Relative to SCG, estimates were positive for WAS (0.12) but negative for WOL (-0.22). Mean effect size for research forest  $\times$  species was  $-0.03 \pm 0.07$ .

Growth differed significantly across regional 0.1 ha harvest treatments, where species ranked by RGR in biomass ( $\text{g g}^{-1} \text{ year}^{-1}$ ) were *C. cordiformis* ( $1.3 \pm 1.25$ ), *Q. rubra* ( $1.8 \pm 0.06$ ), *B. lenta* ( $1.8 \pm 0.09$ ), *P. rubens* ( $1.8 \pm 0.03$ ), *T. canadensis* ( $2.6 \pm 0.07$ ), *C. dentata* ( $2.6 \pm 0.13$ ), *P. strobus* ( $3.2 \pm 0.09$ ), *P. grandidentata* ( $3.5 \pm 0.18$ ) and *P. serotina* ( $3.6 \pm 0.19$ ). This order was regionally consistent, although site-level differences were apparent within *P. strobus*, *P. grandidentata*, *B. lenta* and *P. serotina* ( $p \leq 0.05$ ).

Growth within 0.1 and 0.4 ha harvest treatments at SCG was best explained by species, initial seedling biomass, seedbed, understorey competition and the interaction between species and understorey competition (AIC weight = 0.76). The effect of initial seedling biomass was -0.22 for every increase in biomass. The ranked order for species based on effect size relative to the reference was *P. rubens* (0.59) > *T. canadensis* (0.33) > *P. strobus* (0.29) > *B. lenta* (0.14) > *Q. rubra* (0.10) > *P. grandidentata* (0.09) > *C. dentata* (0.04) > *C. cordiformis* (reference) > *B. lenta* (-0.01). Predicted growth was slightly higher in undisturbed over scarified seedbeds (0.06) and increased with reduced understorey competition (0.14). The mean effect for species  $\times$  understorey competition was  $0.12 \pm 0.3$ , approximately the reverse order compared to the species-only main effect (*P. serotina* > *P. grandidentata* > *B. lenta* > *C. dentata* > *P. strobus* > *Q. rubra* > *P. rubens* > *T. Canadensis* > *C. cordiformis* (reference)).

Initial seedling size was negatively correlated with growth (log-transformed; Pearson's  $r = -0.46$ ,  $p < 0.001$ ). On average,





**FIGURE 2** (A) Three-year survival and (B) relative growth rate in above-ground biomass (RGR) by species across sites. Asterisks indicate differences within species (\* $p \leq 0.05$ , \*\* $p \leq 0.01$ ). Species names along x-axis are coded by population enrichment (PE) and assisted range expansion (ARE) plantings

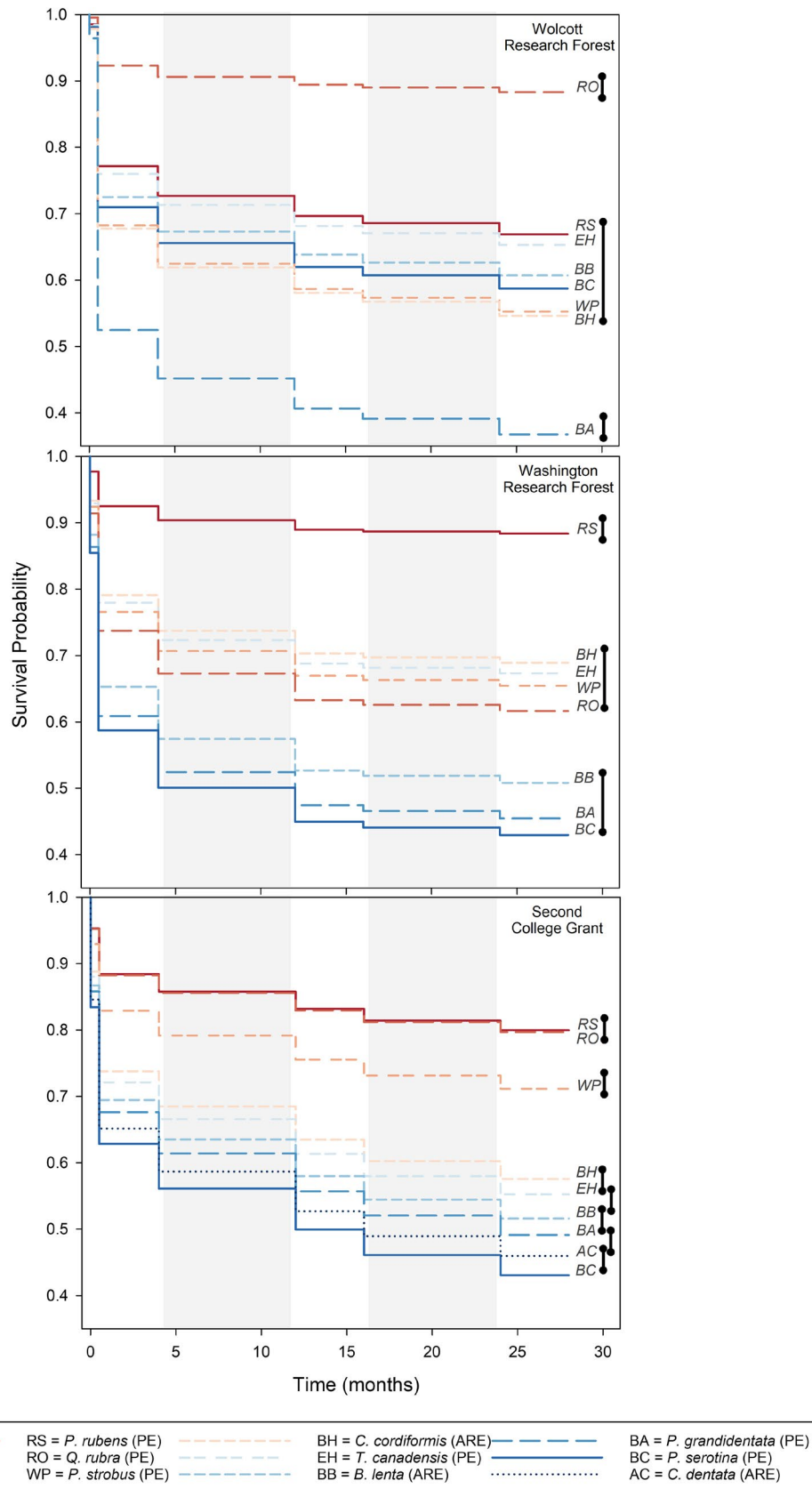
growth increased 23.6% ( $0.45 \pm 0.03 \text{ g g}^{-1} \text{ year}^{-1}$ ,  $p \leq 0.05$ ) between each competition class. Intraspecific differences reveal the same growth pattern across species, although some were insensitive to different degrees of competition (*Q. rubra*, *C. cordiformis*, *T. canadensis*). No differences in growth were observed between 0.1 and 0.4 ha harvest treatments. PE species grew at higher rates ( $2.46 \pm 0.03 \text{ g g}^{-1} \text{ year}^{-1}$ ,  $p = 0.01$ ) compared to ARE ( $2.04 \pm 0.05$ ). Damage from late spring frost was observed at SCG, which disproportionately affected *Q. rubra* (24.2%), *C. dentata* (19.2%) and *C. cordiformis* (6.1%).

Seedling transplants at SCG were browsed less frequently ( $14.0 \pm 1.6\%$ ,  $p = 0.02$ ) compared to WAS and WOL ( $18.1 \pm 1.1\%$  and  $24.3 \pm 4.5\%$ , respectively). The ranked occurrence of browse by species was *B. lenta* ( $45.5 \pm 3.9\%$ , A), *Q. rubra* ( $33.1 \pm 9.4\%$ , AB), *P. serotina* ( $31.8 \pm 6.8\%$ , AB), *P. grandidentata* ( $31.3 \pm 4.5\%$ ,

AB), *C. cordiformis* ( $15.0 \pm 3.6\%$ , BC), *C. dentata* ( $14.9\%$ , BC), *T. canadensis* ( $3.3 \pm 2.6\%$ , C), *P. strobus* ( $1.7 \pm 1.0\%$ , C) and *P. rubens* ( $1.2 \pm 1.1\%$ , C; letters denote group means not significantly different at  $p \leq 0.05$ ).

## 4 | DISCUSSION

The ability of forest ecosystems to respond to climate change may be driven by the capacity for species to adapt to shifting ranges or migrate to new suitable habitats. To date, natural migration rates have failed to track the speed of climate change potentially leading to maladaptation (Aitken et al., 2008; Etterson et al., 2020; Sittaro et al., 2017). Thus, many have called for novel approaches to respond to shifting species ranges and community assemblages,



**FIGURE 3** Predicted species survival curves based on Cox models for each research forest. Grey shading indicates periods of dormancy (winter). Vertical bars indicate groups that are not significantly different (see Table S5). Species names are preceded by a species acronym and followed by coded distinguishing population enrichment (PE) and assisted range expansion (ARE) plantings

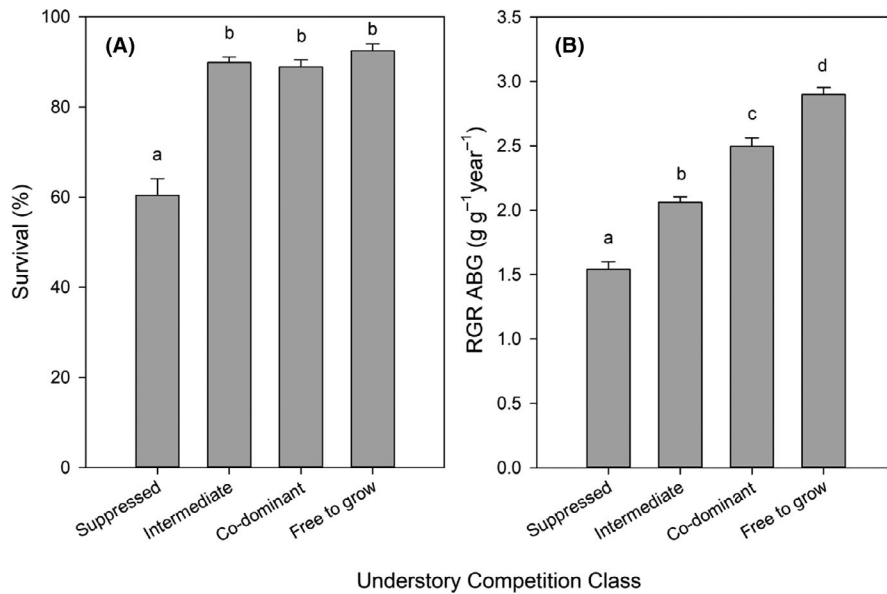


FIGURE 4 (A) Survival and (B) relative growth rate in above-ground biomass (RGR AGB) by competition class at Second College Grant

namely through adaptation plantings (Messier et al., 2019; Pedlar et al., 2012; Williams & Dumroese, 2013). Our findings are consistent with the few existing operational-scale studies in temperate regions that demonstrated variable performance between future climate-adapted species and the influence of ecosystem memory (Etterson et al., 2020; Muller et al., 2019). Our study further highlights the strength of ecological factors that vary in a regional context at controlling the establishment of mixed-species plantings for forest adaptation.

We demonstrate the 3-year response of species planted in novel mixtures is strongly affected by interactions with species currently onsite and local site conditions, supporting our hypothesis that seedling performance is predicated on biophysical factors such as ecological memory in the form of vegetative competition, although pressure from competition varied the site-level response. Ecological memory has been used to describe ecosystem resilience to transitions (Bengtsson et al., 2003; Johnstone et al., 2016). Therefore, in the context of species range shifts, the ecological memory of our experimental sites is adapted to contemporary biophysical conditions (climate, vegetation, geologic attributes), giving locally adapted species a competitive advantage over future climate-adapted transplants aimed at transitioning forest composition. This site-specific inertia is likely to persist until conditions change enough to favour the establishment of future climate-adapted species. Such dynamics may present similar operational challenges for adaptation plantings in other systems, where climate and disturbance regimes favour long-term dominance by shade-tolerant tree species or persistence of understorey vegetation (Brice et al., 2019, 2020; L f et al., 2019).

While the strength of competition response is predicated on factors such as forest developmental stage, seed source and micro-site characteristics, contemporary drivers may erode the strength of ecological memory (Webster et al., 2018). For instance, herbivory, invasive plants or drought may filter natural recruitment inadvertently favouring the establishment of other species (Canham & Murphy, 2016; Champagne et al., 2021; George & Bazzaz, 1999; Royo

& Carson, 2006). In our study, seedling transplants were browsed by ungulates (e.g. deer, moose) nearly twice as frequently at WAS and WOL compared to SCG, and the occurrence of browse was disproportionately higher on deciduous (28.6%) over coniferous seedling transplants (2.1%), likely owing to differences in the size of the harvest operations by site, local population numbers and palatability of certain species transplants over others (cf. Champagne et al., 2021). Furthermore, more seedlings were suppressed by vegetative competition at SCG compared to WAS and WOL ( $20.1 \pm 0.02$ ,  $0.3 \pm 0.0$ , and  $4.1 \pm 0.03$ , respectively,  $p < 0.001$ ), most likely attributed to differences in browse pressure. As such, browse has altered the natural vegetative response to canopy disturbance differently between sites, thereby modifying the strength of ecosystem memory at filtering performance of adaptation plantings.

Clear differences in growth and survival were apparent, supporting our hypothesis that species-level responses are unequal. It is probable that key mechanisms determining species response are influenced by functional attributes. For example, mortality was mediated for deciduous species (e.g. *C. cordiformis*, *Q. rubra*, *C. dentata*), which frequently root-sprouted after whole-stem dieback (24%). The ability to respond to dieback permitted climate-maladapted ARE species such as *C. dentata* and *B. lenta* to persist despite injury to terminal shoots and sensitive plant structures from cold winter conditions, a pattern by which seedling growth forms become increasingly shrub-like over time (Gurney et al., 2011). *P. strobus* performed well across sites, likely due to the species' rapid growth rates combined with intermediate tolerance for competition and light stress, although this species has been shown to be outcompeted by hardwoods on nutrient rich sites, likely requiring subsequent release treatments (Hibbs, 1982; Kenefic et al., 2021). Some species with rapid initial growth such as *P. grandidentata* and *P. serotina* were able to outcompete understorey vegetation, but also had poor survivorship suggesting low vigour individuals succumbed to competition due to shade intolerance. Nevertheless, in some circumstances, shade-intolerant species like *P. serotina* exhibit plasticity

in growth rates, whereby suppressed individuals may survive long periods without growth (Closset-Kopp et al., 2007). This pattern of growth-survivorship trade-off is observable across species where rapid above-ground growth is linked with lower survivorship relative to species with higher survivorship due to preferential allocation to below-ground structures (Canham et al., 1999; Kobe, 1997). Higher below-ground growth coupled with a broad seedling architecture for *Q. rubra* and *C. cordiformis* likely offset slower initial growth rates allowing seedlings to be less affected by competition. Still, it is unclear how this strategy will translate as a competitive advantage given the relative height growth of these species was less than co-occurring species (Dyderski & Jagodziński, 2019; Kuehne et al., 2014). Conversely, the high shade tolerance of *P. rubens* and *T. canadensis* offset slow growth and prolonged survival, a growth strategy that allows these species to persist as suppressed individuals for decades while maintaining photosynthetic capacity under low-light levels (Dumais & Prévost, 2007; Manley & Ledig, 1979).

Seedling transplant stress, a condition that commonly occurs after seedlings are moved from a nursery to forested settings, is typically associated with stress from moisture, nutrients or increased solar exposure and can often lead to elevated levels of mortality in the first growing season (Jacobs et al., 2005; Rietveld, 1989; Struve & Joly, 1992). The first year mortality of seedlings we examined follow this predictable trend, a pattern closely associated with seedling size (Haase, 2008). Nonetheless, it is possible that adaptation plantings are subjected to greater transplant stress given that the current deployment of tree nurseries are not spatially aligned with projected future ranges of species (Tepe & Meretsky, 2011), increasing the likelihood of moisture, temperature or physical stress during storage and handling. Furthermore, during the installation of this experiment, this region was under extreme drought conditions and precipitation was regionally sporadic, whereby rainfall (>1 mm) occurred within 1–4 days of planting at SCG but did not occur for 11 and 15 days after planting at WAS and WOL, respectively. As such, it is probable that the differences among first year mortality rates are linked to increasing drought stress across a regional moisture gradient. Nevertheless, by the final growing season, mortality rates at SCG were highest, most likely attributed to increased vegetative competition relative to lower pressure at other sites.

Given the short duration of this work, it is unclear how slower initial growth rates will translate to long-term forest development, but survival will likely be correlated with shade tolerance, concordant with dominant species found regionally (Hanson & Lorimer, 2007). Although harvest treatment had no effect on 3-year seedling response, it will be important to track seedling performance as forest canopy closure progresses in these systems, as treatment level effects may become more apparent under lower levels of light (0.1 ha gaps) versus higher levels (0.4 ha gaps). Results from a secondary study (not reported here) show reduced survival (–83.7%) and growth (–24.9%) for the most shade-tolerant species tested (*Q. rubra*, *P. rubens*, *P. strobus*, *T. canadensis*) when planted in closed-canopy forests compared to open conditions. The exception was *T. canadensis*, the most shade-tolerant conifer in eastern North America which increased survivorship (19.4%). Since

many regional future climate-adapted species are shade intolerant, it will be critical to evaluate the long-term performance of transplants as canopy closure proceeds in systems.

The importance of initial size on seedling performance is well documented (MacFarlane & Kobe, 2006; Thomas, 1996). Our results demonstrate this, but the direction of the effect was opposite for response variables. Moreover, we observed a slight negative relationship between growth and survival ( $R = -0.2$ ,  $p = 0.025$ ), indicating a multi-way trade-off between initial size, growth and survival. These dynamics are likely attributed to differences in species examined in this study. For example, *B. lenta* was the largest seedling tested and over half (62%) died back from desiccation and sunscald associated with exposure and maintenance of greater transpirational area. Conversely, *P. serotina* was the smallest seedling tested and was observably more susceptible at exposed microsites and to resource competition. Other species had mixed results indicating factors such as functional traits and local site conditions must be considered alongside initial size when determining adaptation planting mixtures.

This study suggests that the most potent driver on seedling response was adaptation planting type, a proxy for source transfer distance, supporting our hypothesis that seedling performance is variable based on adaptation planting type. PE transplants with ranges encompassing experimental sites performed better than ARE transplants outside of current species ranges. The relationship between seed-transfer zones and plant response is well recognized where populations exhibit strong physiological clines with local adaptation (Aitken et al., 2008; Savolainen et al., 2007). In the context of changing global conditions, intraspecific differences in fitness have been observed showing increased climate adaptation for populations from southern over historic seed zones, suggesting lags in local climate adaptation (Etterson et al., 2020). While modifications in seed zones will be required to maintain contemporary assemblages with climate-adapted genotypes, inter-species comparisons offer critical insights into historic and future climate-adapted species relationships and biophysical drivers affecting no-analogue assemblages. This is important for species-rich temperate forested regions like the northeastern US and elsewhere where more future climate-adapted species will require assisted migration (11–19 species) relative to those currently onsite that may infill naturally (1–12 species; Iverson et al., 2019). While it is possible alterations in provenance may improve the climate match for species tested in our investigation, warranting further study, the broader implications of inter-species comparisons better reflect potential changes for mixed-species systems and highlight challenges for assisted migration under current climate conditions.

#### 4.1 | Broader implications for management and policy

Forests in northeastern North America are projected to experience profound increases in suitable habitat for tree species, as such, adaptive silvicultural interventions coupled with adaptation plantings may

be necessary to facilitate establishment. We demonstrate seedlings from a range of functional attributes and adaptation planting types may be introduced during the initial stand establishment stage; however, the strength of ecological memory may filter efforts to transition species composition. To respond to the inertia of competitive natural regeneration, managers may need to incorporate competition controls to reduce pressure on adaptation plantings.

When this experiment was installed, this region experienced a 98th percentile spring drought affecting site-level survivorship along a regional moisture gradient. In two of three subsequent years, late spring frost events damaged sensitive plant structures on maladapted, ring and semi ring-porous deciduous transplants. Increasing extreme weather frequency will have important implications on the establishment and long-term performance of adaptation plantings (Park & Talbot, 2018), and events like these may be future climate analogues for conditions under which managers may be considering the implementation of adaptation plantings in the future (Janowiak et al., 2018). As such, planting at densities above those typically used as benchmarks for successful reforestation efforts may be needed to account for elevated mortality rates during such extreme events.

With increased attention on forests as critical carbon sinks for reforestation efforts (Domke et al., 2020; Fargione et al., 2021), planting seedlings has increasingly been viewed as central elements to climate adaptation and mitigation strategies leading to the development of programmes such as the World Economic Forum's One Trillion Trees Initiative or the United States One Trillion Trees Interagency Council (Federal Register, 2020). In the context of broadly proposed reforestation and afforestation efforts of understocked, non-forested or disturbed lands (Canadell & Raupach, 2008; IPCC, 2014), the performance of diverse adaptation plantings may be increasingly complicated by degraded soils, altered competitive vegetation dynamics (e.g. little or no competition, novel interference interactions with agricultural or invasive species) or exposure under climate extremes. Additionally, another hurdle that managers considering adaptation plantings may face that this study experienced was our ability to source diverse planting stock, where regional nursery capacity was limited and the nearest commercial supplier with adequate inventory necessitated that seedlings be shipped long distances, which influenced stock quality. Moreover, due to the patchwork of land ownerships in this region, some adaptation planting frameworks that rely on forest zonation (e.g. TRIAD; Park et al., 2014) may be met with implementation challenges. Rather than aiming for wholesale transitions in community composition, plantings may be effective when considered within broader landscape functioning. While the focal unit of our experiment was gap portions of stands, these sites are spatially strategic nodes with potential for dispersal in a larger landscape network, consistent with the recommendations from Messier et al. (2019) based on complexity theory (see D'Amato & Palik, 2020). Nevertheless, important ecological barriers remain for the establishment of future climate-adapted species such as the legacy of ecosystem memory of contemporary forests that may be resilient to management efforts to alter species composition.

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## CONFLICT OF INTEREST

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

## AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and methodology and installed the experiment; P.W.C. collected the data; P.W.C. and A.W.D. analysed the data; P.W.C. and A.W.D. led the writing; All contributed to drafts and gave approval for publication.

## DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.br15dvb1> (Clark et al., 2021).

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