








RESEARCH ARTICLE

Future carbon sequestration potential in a widespread transcontinental boreal tree species: Standing genetic variation matters!

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Funding information

Canadian Wood Fibre Center; Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: RGPIN-2019-06672; Canadian Forest Service; Genomics R&D Initiative; Ministerul Cercetării, Inovării și Digitalizării

Abstract

Climate change (CC) necessitates reforestation/afforestation programs to mitigate its impacts and maximize carbon sequestration. But comprehending how tree growth, a proxy for fitness and resilience, responds to CC is critical to maximize these programs' effectiveness. Variability in tree response to CC across populations can notably be influenced by the standing genetic variation encompassing both neutral and adaptive genetic diversity. Here, a framework is proposed to assess tree growth potential at the population scale while accounting for standing genetic variation. We applied this framework to black spruce (BS, *Picea mariana* [Mill] B.S.P.), with the objectives to (1) determine the key climate variables having impacted BS growth response from 1974 to 2019, (2) examine the relative roles of local adaptation and the phylogeographic structure in this response, and (3) project BS growth under two Shared Socioeconomic Pathways while taking standing genetic variation into account. We modeled growth using a machine learning algorithm trained with dendroecological and genetic data obtained from over 2600 trees (62 populations divided in three genetic clusters) in four 48-year-old common gardens, and simulated growth until year 2100 at the common garden locations. Our study revealed that high summer and autumn temperatures negatively impacted BS growth. As a consequence of warming, this species is projected to experience a decline in growth by the end of the century, suggesting maladaptation to anticipated CC and a potential threat to its carbon sequestration capacity. This being said, we observed a clear difference in response to CC within and among genetic clusters, with the western cluster being more impacted than the central and eastern clusters. Our results show that intraspecific genetic variation, notably associated with the phylogeographic structure, must be considered when estimating the response of widespread species to CC.

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KEYWORDS

boreal tree species, carbon sequestration, climate change, common gardens, dendrochronology, genomics, local adaptation, phylogeographic structure, standing genetic variation

1 | INTRODUCTION

Forests worldwide could help mitigate anthropogenic climate change (CC), notably thanks to their potential as carbon sinks (Griscom et al., 2017). Among the methods that can be deployed to use forests for carbon sequestration, reforestation and afforestation (planting in areas that were not previously forested) are popular due to their relatively low cost and easy implementation (Lemprière et al., 2013). As a result, various global initiatives have set planting goals, exemplified by the 2019 EU Biodiversity strategy targeting 3 billion trees by 2050 or the Canadian government's commitment to planting 2 billion trees in Canada by 2030, in addition to operational reforestation (Messier et al., 2022). However, these initiatives have sparked discussions and differing perspectives within the community concerning their effectiveness and potential drawbacks, calling for new insight on trees as a way to mitigate CC (Di Sacco et al., 2021).

Climate change is already impacting directly and indirectly forest ecosystems (e.g., Mirabel et al., 2023; Price et al., 2013). Boreal and arctic latitudes are expected to see the highest increase in mean annual temperatures in North America (Ranasinghe et al., 2021). As such, there will be a rapid geographic shift of the bioclimatic envelope underlying the distribution of boreal tree species towards the poles (Boisvert-Marsh et al., 2022; McKenney et al., 2014). Even though some species may be able to cope with changing environmental conditions thanks to their phenotypic plasticity and evolutionary potential, the extent of species-specific adaptive capacity remains uncertain and could vary among species (Meester et al., 2018; Royer-Tardif et al., 2021). Maladaptation to climate would impact tree productivity and increase forest vulnerability to abiotic and biotic stress (Charney et al., 2016; Chaste et al., 2019; Girardin, Bouriaud, et al., 2016; Smith et al., 2014). This would likely reduce forest carbon sequestration capabilities (Ma et al., 2012) given that a forest's carbon sequestration capacity is directly dependent on its resilience and the maintenance of good functioning ecosystem processes (Andres et al., 2023; Zalesny et al., 2012). Tipping points could even be reached and change boreal forests from carbon sinks to carbon sources (e.g., Liu et al., 2023; Miquelajauregui et al., 2019).

The selection of climatically suitable seed sources is a standard practice in forestry and will be increasingly important to cope with CC (Aitken & Bemmels, 2016; Pedlar et al., 2012). On the one hand, planting trees from populations likely adapted to a given future climate could avoid, at least partially, the aforementioned maladaptation and, therefore, directly sustain forest resilience and capacity to maintain ecosystem services (Aitken & Whitlock, 2013; Girardin et al., 2021). Furthermore, introducing pre-adapted alleles into local populations could improve their chance to survive and adapt to future conditions (assisted gene flow) (Aitken & Whitlock, 2013). However,

climate is a moving target and identifying the optimal population-climate match requires a nuanced understanding of current population adaptations and a careful assessment of their potential for future growth in anticipated climate scenarios. Yet, a significant hurdle lies in accurately gauging the adaptability of current populations, particularly when forecasting future growth. Growth projections often overlook intraspecific genetic variation, neglecting the intricacies of a species' CC response (Perret et al., 2024; Razgour et al., 2019). This oversight could prove problematic in estimating the adaptive capacity of trees in the face of evolving climates. Quantification of growth responses, which serve as a proxy for fitness (Younginger et al., 2017), becomes instrumental in determining the adaptive trajectory of boreal tree species. This approach is not only valuable in understanding adaptation but also translates into assessing carbon sequestration potential.

Over time, the dynamic interplay of evolutionary (e.g., mutation, natural selection, and gene flow) and demographic processes (e.g., founder effects) has shaped the natural genetic variation within species. Consequently, the standing genetic variation of a species arises not only from contemporary local adaptation but also from past climate events, the genetic history of the species, and the effects of vicariance (De Lafontaine et al., 2018; Gérardi et al., 2010). In species characterized by broad geographic distribution, this may lead to distinct lineages or genetic groups, each harboring a unique reservoir of standing genetic variation available for adaptation (De Lafontaine et al., 2018). Consequently, even when exposed to similar environmental conditions, this can result in divergent and unique adaptive outcomes across populations (Gougherty et al., 2021). For any species, this pool of genetic variation, encompassing conditionally neutral variants, is considered the raw material for coping with future environmental changes (Anderson et al., 2013; Mitchell-Olds et al., 2007). For those reasons, the isolation of transcontinental boreal tree populations in different glacial refugia during the Late Quaternary may have led to genetic differentiation and the development of unique evolutionary backgrounds (e.g., Goessen et al., 2022; Leroy et al., 2020; Prunier et al., 2012). This understanding is important for assessing how these boreal tree species might respond to contemporary and future CCs, as their genetic diversity and unique adaptations can influence their resilience and capacity to thrive in changing environments (Aitken et al., 2008).

Common garden experiments consist in the comparison of populations from distinct geographic locations growing in the same environmental setting. In this setting, it is possible to study the response variability of fitness-related traits amongst populations and to comparatively assess their response to the climate of the experimental site. When the home site of every population is included as an experimental site, local adaptation (i.e., the fitness

advantage of local populations over foreign ones at a given site) can be assessed (Kawecki & Ebert, 2004; Lortie & Hierro, 2022; Savolainen et al., 2007). A correlation between population responses and the climate at their respective origins, may also be interpreted as indicative of local adaptation (Candido-Ribeiro & Aitken, 2024; Gárate-Escamilla et al., 2019; Leites & Benito Garzón, 2023; Savolainen et al., 2013), as relationships between traits, functions and climate potentially indicates climate-driven selection processes (De Villemereuil et al., 2016; Etterson et al., 2016; Schwinning et al., 2022). Therefore, common gardens allow the direct assessment of intraspecific variation in both growth response and potential adaptive response, and the identification of the main underlying environmental factors associated with any observed phenotypic divergence (Aitken & Bemmels, 2016). When replicated in different environments, common gardens also allow the evaluation of the extent of phenotypic plasticity, that is, how individuals adjust their phenotypes across different environments (De Villemereuil et al., 2016; Gárate-Escamilla et al., 2019; Leites & Benito Garzón, 2023; Schwinning et al., 2022). Finally, using space-for-time substitution (Kremer et al., 2014; Marquis et al., 2020), common gardens can also be used to predict population responses to CC (Aitken & Bemmels, 2016).

Black spruce (*Picea mariana* [Mill.] B.S.P., hereafter BS), an important species from an ecological and economical perspective, is the most widespread coniferous tree species in Canada (Viereck & Johnston, 1990). This resource-production species is one of the most planted species in Canada (Mullin et al., 2011) and is included in future carbon sequestration scenarios (Ménard et al., 2022). In this context, it is important to evaluate how the different BS populations across the species range are adapted to current climate and how they may respond to climatic changes in terms of growth. This information will then help to understand how the species' capacity to sequester carbon will be affected by CC, and which seed sources may be the most suitable for plantations. BS typically shows adaptive divergence between populations for adaptive traits such as height, or timing of bud flush and bud set (Beaulieu et al., 2004; Prunier et al., 2011; Silvestro et al., 2023). Over its distribution range, BS is subdivided into three main genetic lineages, hereafter named clusters, as the lingering genetic consequence of the Quaternary ice age (Gérardi et al., 2010; Jaramillo-Correa et al., 2004). Each cluster is carrying distinct standing genetic variation that may influence ongoing and future local adaptation (De Lafontaine et al., 2018; Prunier et al., 2012). Therefore, integrating genomic data into growth models developed from common gardens to account for the intraspecific genetic variation, including the phylogeographic structure (Razgour et al., 2019), of BS should provide less biased estimates of BS growth potential under future climates (Girardin et al., 2021).

In this study, we attempt to characterize BS adaptation to climate at the population level to then predict the impact of CC on its carbon sequestration potential. We expect that this knowledge will provide a more accurate assessment of the species response potential within its range and support the implementation of reforestation

and afforestation strategies. We use a dendroecological approach in BS common garden experiments distributed across Canada to evaluate the adaptation and growth potential of this transcontinental species. The four 48-year-old common gardens comprise 62 populations representative of the species range and its phylogeographic structure. We apply a Random Forest algorithm to develop a growth model that explains annual aboveground biomass increment (ABI) from juvenile growth up to crown closure at the population level. We then use this model to realize projections using ensembles of climate models and Shared Socioeconomic Pathways (SSPs). Our first objective is to identify the predominant climatic factors modulating ABI. Our second objective is to investigate the heterogeneity of population responses to climate related to standing genetic variation linked either to local adaptation or the phylogeographic structure of the species. Our third objective is to predict how BS biomass accumulation could be impacted by CC across experimental sites and populations.

2 | MATERIALS AND METHODS

2.1 | Data

2.1.1 | Common garden/dendroecology

The dendroecological data were obtained from four common gardens in Canada: Peace River (PR, province of Alberta, 56.30°N, 117.30°W), Mont-Laurier (ML, province of Quebec, 46.60°N, 75.80°W), Chibougamau (CH, province of Quebec, 50.20°N, 74.20°W) and Acadia Research Forest (AC, province of New Brunswick, 46.00°N, 66.30°W). The sites have contrasting climates with, for the period 1980–2019, mean annual temperatures of 1.61, 3.74, –0.34 and 5.46°C, and relative % soil volumetric water content of 50%, 95%, 98%, and 94%, respectively (see details in Table 1; Table S1). The AC garden (southernmost) is, therefore, the warmest site, whereas the CH garden is the coldest. The PR garden is the driest while the other gardens are all comparatively wetter, with CH having a slightly higher mean soil moisture content than AC and ML. These common gardens were established as part of the Range-Wide Provenance Study initiated in 1967 by the Petawawa National Forestry Institute of the Canadian Forest Service (Morgenstern, 1978). Throughout this paper, we employ the term “provenance” to denote the geographic and climatic source of a population, and we use the term “population” to describe the trees cultivated from seed collected at the provenance level (one population per provenance). Sixty-two BS provenances representative of the species range from Alaska to Newfoundland and covering more than 20° of latitude, from 44°N to 65°N, were sampled for this study, although not all provenances are present in every garden (see Table S2 for a list of the provenances established in each garden). The seeds were collected from 1967 to 1970 and the different gardens were established in 1974 or 1975. The common gardens were arranged in randomized blocks containing plots of 8–16 trees for

TABLE 1 Means of the climate conditions (1980–2019) at the four common gardens.

Site	$T_{\text{mean winter}} (^{\circ}\text{C})$	$T_{\text{mean spring}} (^{\circ}\text{C})$	$T_{\text{mean summer}} (^{\circ}\text{C})$	$T_{\text{mean fall}} (^{\circ}\text{C})$	SMI spring (%)	SMI summer (%)	SMI fall (%)
Peace River (PR)	-13.95 [2.79]	2.96 [1.92]	15.74 [0.77]	1.72 [1.65]	58.54 [15.96]	48.69 [14.48]	41.37 [15.42]
Mont-Laurier (ML)	-11.47 [2.03]	3.46 [1.53]	17.13 [0.95]	5.88 [1.12]	98.50 [1.12]	92.36 [5.81]	95.16 [5.63]
Chibougamau (CH)	-17.15 [2.12]	-1.48 [1.64]	14.66 [0.86]	2.59 [1.24]	99.31 [0.56]	96.22 [2.99]	98.96 [1.40]
Acadia (AC)	-7.68 [1.52]	4.16 [1.16]	17.73 [0.78]	7.64 [1.02]	98.83 [0.75]	91.30 [4.96]	91.33 [9.11]

Note: T_{mean} is the mean seasonal temperature at the site. SMI stands for the mean seasonal soil moisture index, that is the relative % soil volumetric water content, estimated following Hogg et al. (2013). The standard deviation from the mean is represented in brackets.

each provenance, depending on the garden, and with trees spaced at 1.80m×1.80m at PR, 2.45m×3.05m at ML, 2.40m×2.40m at CH, and 1.80m×1.80m at AC.

More than 2600 trees were sampled between 2014 and 2019 for this study (352 in PR, 752 in ML, 806 in CH, and 717 in Acadia). Three blocks were randomly chosen for each common garden, avoiding pockets of mortality due to windthrow or other external influences. Wood increment cores of 5mm in diameter were collected to the pith at breast height (1.3m) on six to seven trees per provenance in each block (see Table S3 for the number of trees sampled by provenance). Sampling was done starting with the four trees at the center of the plots, with the additional trees sampled being chosen to avoid grazed or suppressed trees. Coring was done on the southern face of the trees. Diameter at breast height and tree height were also measured. Increment cores were frozen until they could be processed and conditioned to 7% moisture content before being sawed in slices of 1.68 mm in width. The width of each growth ring was measured using the software *CooRecorder* (Larsson, 2013). The rings were visually dated, and the dating was statistically validated using *CDendro* and *COFECHA* software (Holmes, 1983; Larsson, 2013). The ring density was measured with a *Quintek X-ray* system at Université Laval and the Laurentian Forestry Center (Québec, Canada) at a 20µm resolution.

2.1.2 | Genetic data and admixture proportion

DNA extraction was performed on needle tissue obtained from a total of 1628 trees representing 67 provenances (refer to table S2 in Girardin et al., 2021). The extraction process utilized the *Nucleospin 96 Plant II* kit (Macherey-Nagel, Bethlehem, PA). Subsequently, genotyping was carried out on the trees using 229 single nucleotide polymorphisms (SNPs), following the methods outlined in Girardin et al. (2021), at the *Génome Québec Innovation Centre* genotyping platform (McGill University, Montréal, Canada), employing the *Sequenom iPLEX Gold* technology (Ehrich et al., 2005). *Structure v.2.3.4* was used, as described in Girardin et al. (2021), to determine the genetic structure and obtain *Q*-values (optimal $K=3$). $K=3$ corresponds to three main glacial lineages (Jaramillo-Correa et al., 2004, 2009). The genetic admixture proportions (*Q*-values) were averaged for trees of the same population to allow generalization.

2.1.3 | Climate data

Historic climate variables (1980–2019) for each of the four common gardens were obtained using the *BioSIM* software (V.11.6; Régnière & Bolstad, 1994). The software produced daily minimum, maximum and mean temperatures, precipitation, relative humidity, solar radiation, and snow water equivalent using *Environment and Climate Change Canada's* historical daily weather observations. Interpolation of daily data was achieved using the four closest weather stations to each of the gardens, adjusting them for elevation and location

differentials with regional gradients, and averaging values using a $1/d^2$ weight, where d is distance. The length of the growing season, frost events, and the soil moisture index (SMI, expressed as relative % soil volumetric water content, Hogg et al., 2013) were then calculated from this data. The seasonal mean for each variable was then obtained by averaging the daily data from December to February for winter, March to May for spring, June to August for summer, and September to November for autumn. The phenology of BS xylogenesis, that ends during the fall (around the day of the year 280 to 290), is of interest for carbon sequestration and likely to be affected by CC (Gallinat et al., 2015), as well as by provenances (Guo et al., 2022; Perrin et al., 2017). As a result, we decided to include the autumn climate in our analyses. Daily data were averaged over the 30 years before seed collection (1930–1969) to obtain the mean annual temperature (MATp), the mean daily precipitation (MDPp), and the growing degree days (GDD5p) for each provenance (Figure 1b–d).

The same climatic variables were generated for the 2022–2100 period at each of the common garden locations. For this, we used

monthly climate normals, made available to the BioSIM downscaling assimilation scheme, from Earth System Models CanESM5, ACCESS-ESM1.5, GFDL-ESM4, MRI-ESM2 and UK-ESM1.5 of the Climate Model Intercomparison Project 6 (O'Neill et al., 2016) and following two SSPs (Chen et al., 2021). Daily time series were then stochastically generated by the BioSIM software for each garden from these monthly normals. One set of daily climate variables for each model, SSP and garden site was produced. Of the two SSPs, SSP2-4.5 is an intermediate scenario following a “middle of the road” narrative. It includes CO₂ emissions remaining constant until the middle of the century before decreasing, producing a radiative forcing of 4.5 W m⁻² and an estimated warming around 2.7°C above 1900s levels by the end of the century. On the other hand, SSP5-8.5 is a high reference scenario that is somewhat unlikely but can serve as a baseline for the worst-case scenario. It is based on a “fossil-fueled development” storyline with no additional climate policy with CO₂ emissions doubling by 2050 and a radiative forcing of 8.5 by 2100 (Chen et al., 2021).

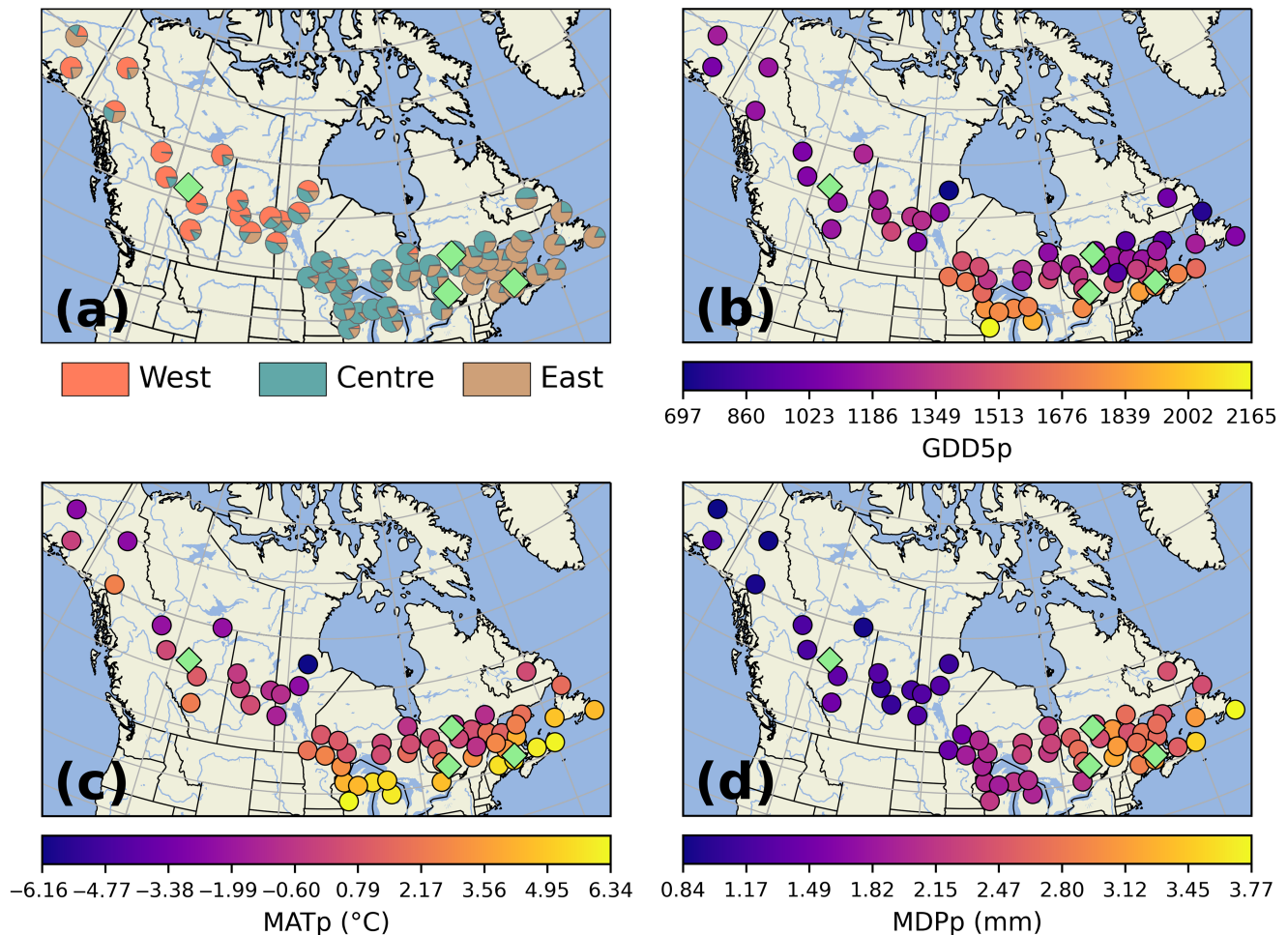


FIGURE 1 (a) Admixture proportion ($k=3$) determined for each population. (b–d) Climate at the provenance origin. GDD5p (b) is the mean annual growing degree days, MATp (c) the mean annual temperature and MDPp (d) is the mean daily precipitation. Common gardens are represented by green diamonds. Map lines delineate study areas and do not necessarily depict accepted national boundaries. GDDp, growing degree days of the provenance; MATp, mean annual temperature of the provenance; MDPp, mean daily precipitation of the provenance.

2.2 | Statistical analysis

2.2.1 | ABI calculation

The ABI was calculated by combining ring width and ring density as proposed by Girardin et al. (2021). In doing so, the ring width was first converted, using an allometric equation, into annual volumetric increment, which was then multiplied by the ring density to obtain the ABI (Kg, see Supporting Information S4 for more details).

2.2.2 | Model building

We modeled the relationship between ABI and annual climate variation in the gardens. Tree age is known to have a strong influence on growth (e.g., Girardin et al., 2011) and, as such, it was included as a covariate. Similarly, climate of the provenances was included to account for local adaptation (Candido-Ribeiro & Aitken, 2024; Gárate-Escamilla et al., 2019). Finally, since it has been shown previously that local adaptation in black spruce populations varies within and among clusters (Prunier et al., 2012), the cluster composition of the populations was included to account for the phylogeographic structure of the species. Plasticity is another important factor to consider as it influences both the growth responses of populations in the garden, and the future response and adaptive potential of those populations (Leites & Benito Garzón, 2023). Our model incorporates plasticity by integrating annual climate variation from several gardens, enabling the response of populations to vary with both temporal and spatial climate variation (Gárate-Escamilla et al., 2019). However, a comprehensive examination of plasticity would require a more targeted and reciprocal experimental design, possibly involving cloned individuals or a series of treatments, which falls beyond the scope of the current study (e.g., Candido-Ribeiro & Aitken, 2024; Cornille et al., 2022).

We employed a Random Forest algorithm for the modelling (Breiman, 2001). This machine learning algorithm enables one to model a large set of variables at once and handle nonlinear relationships as well as multicollinearity between the explanatory variables. Machine learning models are nonparametric and data-driven, and as such do not rely on expert opinion for the specification of their parameters. In general, Random Forest is a good choice for making predictions while still allowing inference (Lucas, 2020). Using Python (V.3.10.2; Van Rossum & Drake, 2009) and the package ScikitLearn (Pedregosa et al., 2011), a Random Forest regression, was trained with annual ABI as the dependent variable and age, climate, and provenance variables as explanatory variables. We performed a random search through the hyperparameter space to tune the maximum number of trees in the forest, the number of variables to consider when splitting a node and the maximum depth of each tree. To determine the optimal number of trees, values between 100 and 1500 were tested and a value around 500 gave the best results. For the number of variables to consider, values between 1 and 11 (total number of variables) were tested and six variables offered good model

performance. Finally, a maximum depth of 20 nodes was an optimal value. The calculations were carried out using the Graham cluster of the Digital Research Alliance of Canada (alliancecan.ca). To assess the accuracy of the model, 10% of the data were randomly selected and set aside for final validation. To assess the capability of the model to generalize to new BS populations, the model was also retrained by setting aside a random selection of six BS populations, and a validation was carried out on these as well (Table S5). This allowed us to ensure that spatial autocorrelation does not skew validation scores (Ploton et al., 2020). We then retrained and tested models using other combinations of variables to determine whether our model was missing any important climatic variables (Table 2). Our aim was to strike a balance between realism and performance, to develop a model capable of exploring the influence of standing genetic variation, that is, local adaptation and the phylogeographic structure, on the heterogeneity of populations' responses to climate. In addition, we sought to ensure the model's reliability for growth projections.

Starting with our base model (A, see Table 3), we retrained the model (model B) adding all of our climatic variables (detailed in Table 2). Indeed, even if temperature and SMI are influential variables (Girardin et al., 2021; Mirabel et al., 2022), other variables, frost for example (Marquis et al., 2020), may also be of importance. We also trained one model without climatic factors (C), one without the genetic clusters and climate of the provenance (D), and a model without the climate of the provenance (E) or without the genetic clusters (F) to see how the omission of those variables would impact our model. We also ensured that the variations in experimental design did not have an influence on our results by testing one model with the sites as categorical variables and observing no change in validation scores (data not shown).

2.2.3 | Variable importance and effect

Random forest models provide a metric of each variable's importance by analyzing the place and recurrence of this variable in the decision trees, and deducing how useful this variable was to reduce Gini impurity during training (Menze et al., 2009). However, it has been shown that this metric is flawed since it misrepresents the importance of categorical variables (Strobl et al., 2008) and of variables with interactions (Wright et al., 2016). To circumvent this issue, we also calculated the importance of each variable in the model by randomly permuting its values in the validation set, essentially replacing it with noise and calculating the loss in the predictive power of the model. The more the model relies on a variable to make a prediction (i.e., the more important the variable is), the more the accuracy of the model should decrease if this variable is replaced by noise (Breiman, 2001; Bureau et al., 2005). We also calculated the accumulated local effects (ALEs, Apley & Zhu, 2020) of the most important variables in the model to further investigate our model. This method allows an unbiased visualization of the effect of a variable in a model, even when variables are correlated (Molnar, 2022). We used the scikit-explain package (Flora et al., 2022) to calculate and plot the ALEs.

TABLE 2 Studied variables.

Variable	Details	Units	Used in models
Age		Years	A, B, C, D, E, F
Cluster composition	Proportion East, West, Centre. Phylogeographic structure	%	A, B, C, E
Air temperature	Four seasons. Climate of the garden	°C	A, B, D, E, F
Soil moisture index	Spring, summer, autumn; SMI. Climate of the garden	%	A, B, D, E, F
Total precipitation	Four seasons; including snow. Climate of the garden	mm	B
Relative humidity	Four seasons. Climate of the garden	%	B
Solar radiation	Four seasons. Climate of the garden	W m ⁻²	B
Snow water equivalent	Winter, spring, autumn. Climate of the garden	mm of water	B
Length growing season	Five consecutive days above 0°C. Climate of the garden	Days	B
Frost events	Four seasons. Climate of the garden	Days	B
Previous year air temperature	Four seasons. Climate of the garden	°C	A, B, D, E, F
Previous year SMI	Spring, summer, autumn. Climate of the garden	%	A, B, D, E, F
Mean annual temperature of the provenance	MATp. Climate of the provenance	°C	A, B, C, F
Mean daily precipitation of the provenance	MDPp. Climate of the provenance	mm	A, B, C, F
Growing Degree Day of the provenance	Baseline temperature of 5°C; GDD5p. Climate of the provenance	GDD	A, B, C, F

TABLE 3 Model comparisons.

Model	Explanatory variables	R ²	MSE	MAE
A	Age + cluster + clim. prov. + temp. + SMI + prev. temp. + prev. SMI	0.472	0.689	0.597
B	A + other climatic factors (see Table 2)	0.473	0.688	0.596
C	Age + cluster + clim. prov.	0.291	0.925	0.710
D	Age + temp. + SMI + prev. temp. + prev. SMI	0.434	0.739	0.619
E	Age + cluster. + temp. + SMI + prev. temp. + prev. SMI	0.470	0.692	0.597
F	Age + clim. prov. + temp. + SMI + prev. temp. + prev. SMI	0.474	0.687	0.596

Note: See Table 2 for definition of variables.

Abbreviations: Clim. prov., climate of the provenance; MAE, mean absolute error; MSE, mean square error; prev. SMI, previous year SMI; prev. temp., previous year temperature; temp., temperature.

2.2.4 | Predictions

Model A was used to predict the growth of the populations under CC. For two populations in particular, the number of surviving trees in some gardens was less than expected and as a result fewer trees were sampled than desired (Table S3). We decided not to exclude those provenances from the projections as the model capacity to generalize to new provenances was assessed and the results obtained for those provenances should still be relevant. We chose to simulate the growth that the trees would have after 40 years if they were planted

in the existing common gardens, either in 1980 (reference baseline), 2023 or in 2060. This corresponds to the locations and range of ages the model was trained on. We used the climatic conditions produced using each Earth System Models to make five sets of projections for SSP5-8.5 and for SSP2-4.5, the mean of these projections was then calculated, and 95% confidence intervals were calculated using bootstrap iterations. The climatic conditions projected under SSP5-8.5 exceeded the range of the data that were used to train model A (Figure S6). Consequently, we will only focus on the growth projections under the SSP2-4.5 in the rest of the article. The result obtained under the SSP5-8.5 will be detailed in Figure S7.

3 | RESULTS

3.1 | Site and population-specific annual biomass growth increments

A total of 88,844 tree rings from 2627 trees, 62 populations representative of the species range and four common gardens, distributed from Alberta to New Brunswick, were evaluated in this study. As of 2015, after 40 years of growth, trees at the ML site were the most productive with a mean observed accumulated biomass of 72 Kg when averaged over all populations. AC was the second most productive site (mean accumulated biomass of 54.5 Kg), then PR (53.1 Kg) and finally CH (49 Kg). Over the period since the establishment of the gardens, ABI followed a similar path at all sites (Figure 2). ABI increased to reach a peak, around 1997 for PR and ML, 1996 for CH and 1992 for AC. It then decreased progressively to reach a plateau around 2005 for PR and ML, or kept decreasing until past 2015 for CH and AC. Generally, populations from

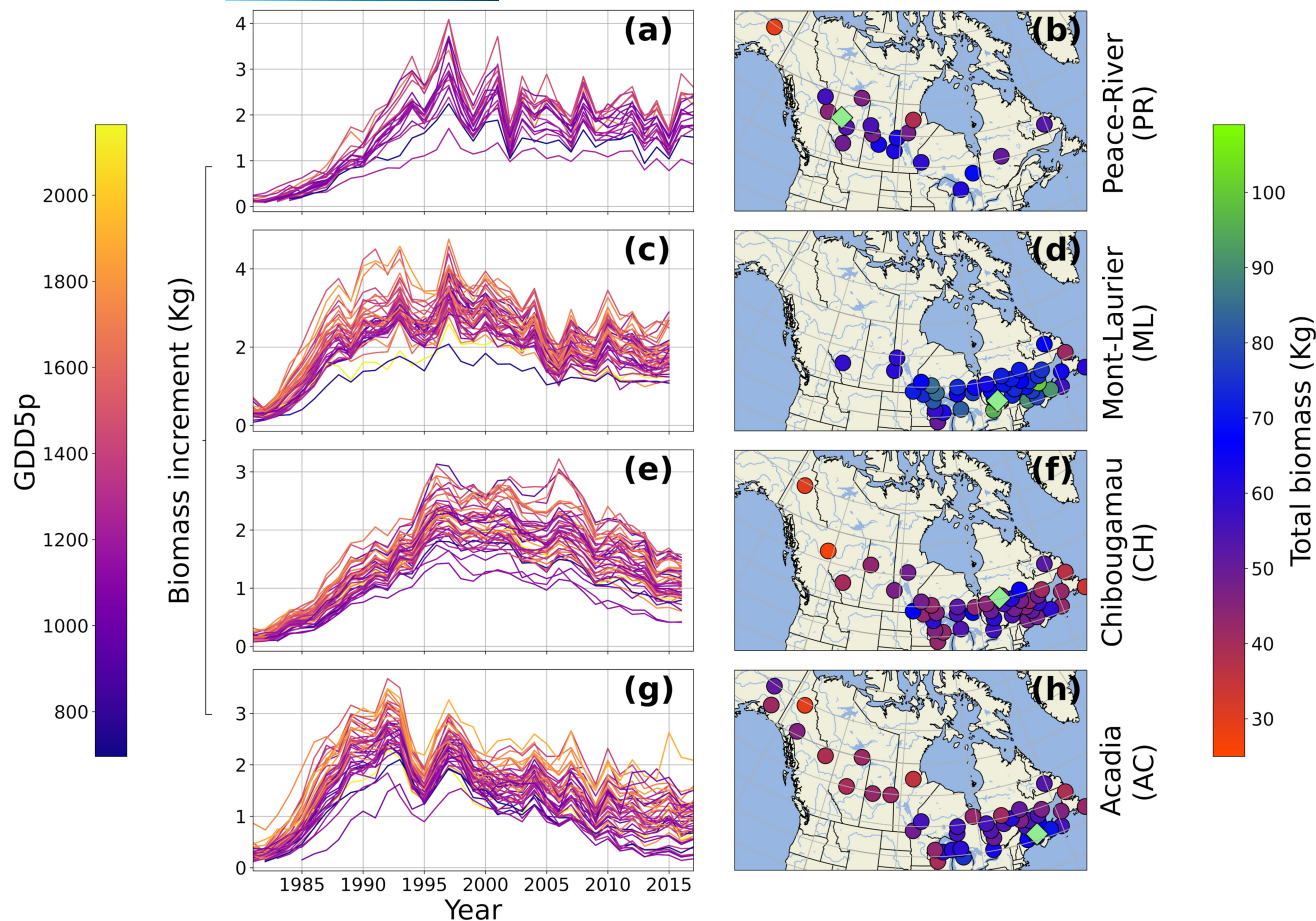


FIGURE 2 (a, c, e, g) Observed annual ABI averaged by population over time. The color gradient represents the mean annual growing degree day above 5°C of the provenance (GDD5p, GDD). (b, d, f, h) Mean total cumulated biomass (in Kg), as of 2015, by population. Each point represents a provenance at its geographic origin and the green diamonds show the location of the common gardens. Map lines delineate study areas and do not necessarily depict accepted national boundaries. ABI, aboveground biomass increment; GDD, growing degree days.

regions with high GDD5 seemed to perform better than the others. Individual performance by population is shown in Figure 2 and summarized in Table S2.

3.2 | Comparative analysis of model performances

The first step of our modelling process was a model comparison aiming to ensure no important climatic variables were left out of the model and to compare the relative importance of the climate of the garden (plasticity), the climate of the provenance (local adaptation) and the phylogeographic structure in the growth response. Table 3 shows the validation R^2 scores of the various models tested compared to the base model (model A). Model A offered good performances and seemed to not lack any important climatic variables among those tested in model B. Model A also accounts for all the factors of interest, namely plasticity, local adaptation, and the phylogeographic structure of the species. In the remainder of the analyses, we will mostly focus on this model.

3.3 | Variables importance

Apart from the age variable, which had a Gini importance of 45% and a permutation importance of 110%, the most important variables in the retained model (A) were the mean autumn temperature of the previous year and the mean autumn and summer temperatures of the current year (Figure 3), ranking second (Gini: 7.5%, permutation: 19.2%), third (Gini: 6%, permutation: 15.6%), and fourth (Gini: 5%, permutation: 15.7%), respectively. Other climatic variables were all $\leq 3\%$ for Gini and $\leq 5.6\%$ for permutation importance.

The ALE plots illustrated in Figure 4 depict the deviation from the mean prediction for a given variable value. This deviation may be due to both the direct effect of the variable or its interaction with other variables. The mean autumnal temperature from the previous and current year had a similar impact on ABI. The effect of these variables oscillated between 0.2 and -0.05 Kg up to around 8°C. Above this temperature, the effect on ABI became negative and reached -0.4 and -0.37 Kg, respectively. Regarding the summer mean temperature, its impact was negative below 16°C (approximately

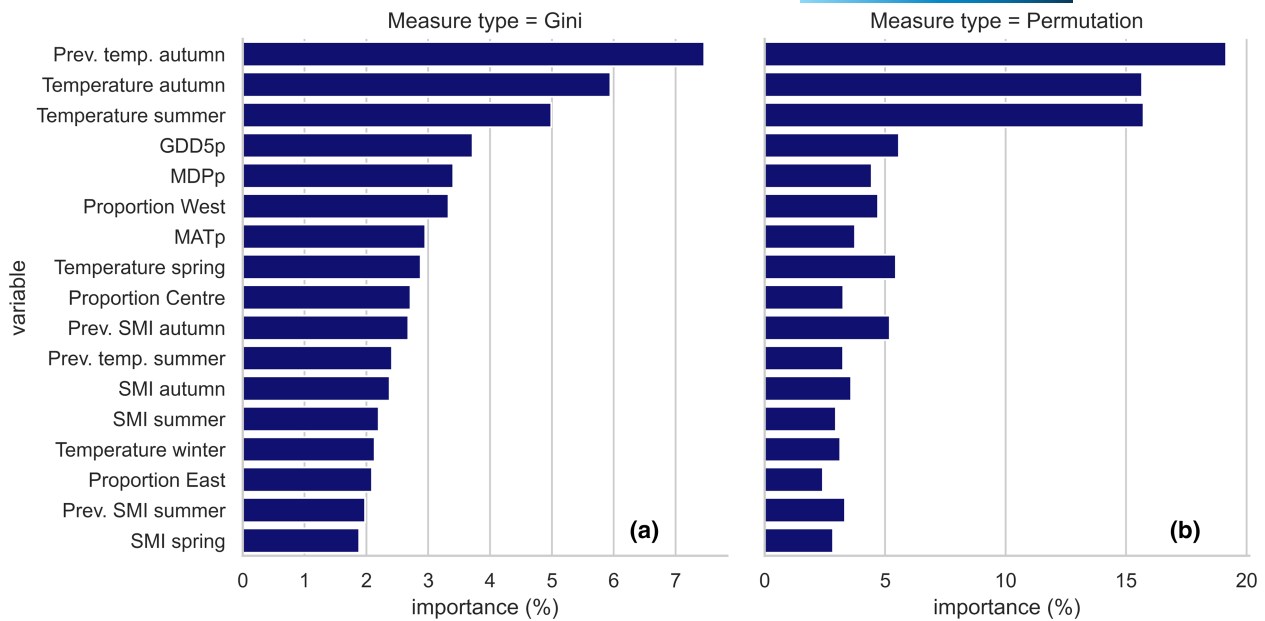


FIGURE 3 Importance of variables in model A. (a) The Gini importance is a measurement of how high and often each variable is present in the decision trees of the Random Forest (how helpful it is to decrease Gini impurity). (b) The permutation impurity is a measurement of the loss of predictive power when a variable is replaced by noise (randomly permuted). Although both are expressed as a percentage, Gini percentage refers to the variable importance relative to other variables, whereas the Permutation percentage refers to the loss of predictive power relative to the base model. GDD5p, MATp, MDPp, Prev. temp. and prev. SMI stand for growing degree days of the provenance, mean annual temperature of the provenance, mean daily precipitation of the provenance, previous year temperature and previous year soil moisture index, respectively.

-0.05 Kg), transitioning to a positive effect up to 18°C, peaking up to 0.15 Kg, and subsequently dropping under -0.1.

Variables related to local adaptation (climate of the provenance) and the phylogeographic structure were comparatively less influential than the climate variables discussed earlier (Figure 3). Notably, the GDD5 of the provenance had a somewhat parabolic effect on the ABI (Figure 4). Populations with lower GDD5p values appeared to have a lower ABI than the mean (-0.1 Kg), with this discrepancy diminishing progressively to become positive and reach 0.15 Kg from 1500 to 1750 GDD. Populations with GDD5p values exceeding 1750 GDD exhibited an ABI similar to the mean. The effect of MDPp was negative for the drier provenances (-0.2 at 1 mm) and then progressively increased to become positive and reach a plateau around 0.1 Kg at 2.5 mm. The effect of MATp was close to the mean expected for a peak above 0.2 Kg at 6°C. Populations containing more than 5% of the western genetic cluster exhibited an ABI between 0.1 and 0.2 Kg lower than the mean (Figure 4). This was mirrored in the effects of the two other genetic clusters, which were close to the mean except for populations with a low proportion of the central cluster. Those had an ABI close to 0.1 Kg lower than average.

3.4 | Projected biomass growth by population and common garden

Trajectories for the accumulated biomass of BS populations after 40 years of growth varied among sites and time horizons (2020,

2063 and 2100) when fitted model A was applied to future climate projections under SSP2-4.5 (Figure 5). For the PR, ML and AC sites, the overall future biomass accumulations were projected to be lower than the baseline levels (up to 53.6% lower, for the mean accumulated biomass at ML by 2100), irrespective of the time horizon. Conversely, at the CH site, an increase in biomass (+17% on average) is projected for the mid-century, followed by a subsequent decrease to a level slightly higher than the baseline (+10.2% on average).

Although less important than climate factors, local adaptation and the phylogeographic structure exert significant influences on biomass growth performance (Figure 6). For all common garden sites, inter-population differentiation in projected biomass growth performance is notable between eastern and western populations, with a clear delineation matching the genetic cluster distribution (compare Figure 1a to Figure 6). Eastern populations generally exhibited superior performance. For example, populations from provenances east of 97°W had a biomass 21.3% higher than the others on average on all sites and time horizons. In particular, the populations from Prince Edward Island, were among the most productive and ranked within the five most productive populations for all sites and time horizons, except PR in 2020 (Figure 6; Table S8). All populations at the ML and AC sites, whether originating from the north or south of the range, displayed a decrease in projected accumulated biomass due to the detrimental impacts of climate factors for the time horizons of 2063 and 2100 (Figure 6). This pattern was also true at the PR site, with the notable exception of one of the northwestern populations, which displayed an increase in biomass for both time

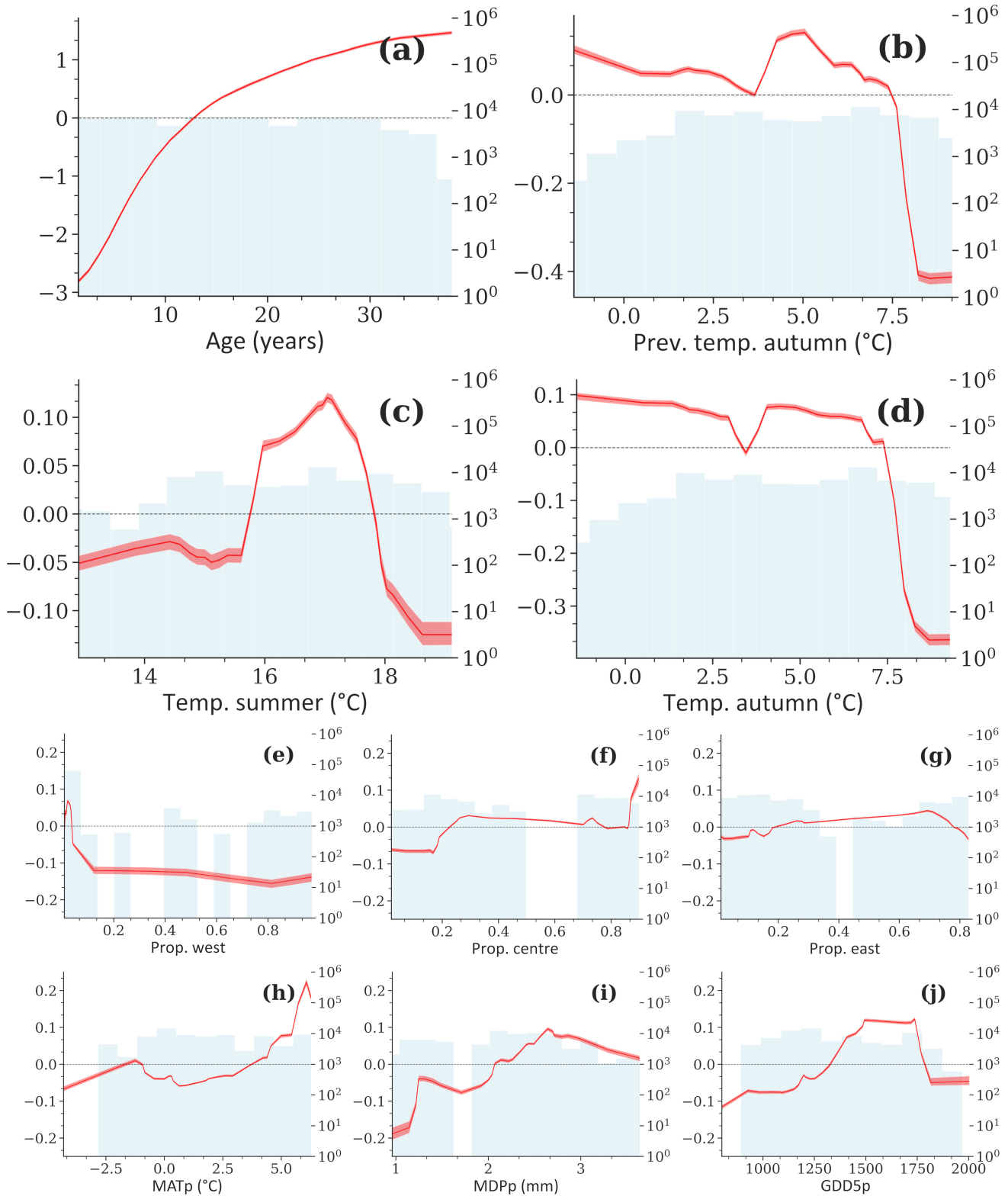


FIGURE 4 Accumulated local effect (ALE) plots of the main effect of the four most important climatic variables (a–d), the climate at the provenance (e–g), and the cluster admixture (h–j). The width of the red areas around the curves represents the bootstrap confidence intervals. The light blue histograms represent the number of observations in each bin on which the ALE was calculated and is represented on a logarithmic scale. GDD5p, MATp, MDPp, Prev. temp., temp., and prop. stand for growing degree days of the provenance, mean annual temperature of the provenance, mean daily precipitation of the provenance, previous year temperature, temperature, and cluster proportion (admixture), respectively.

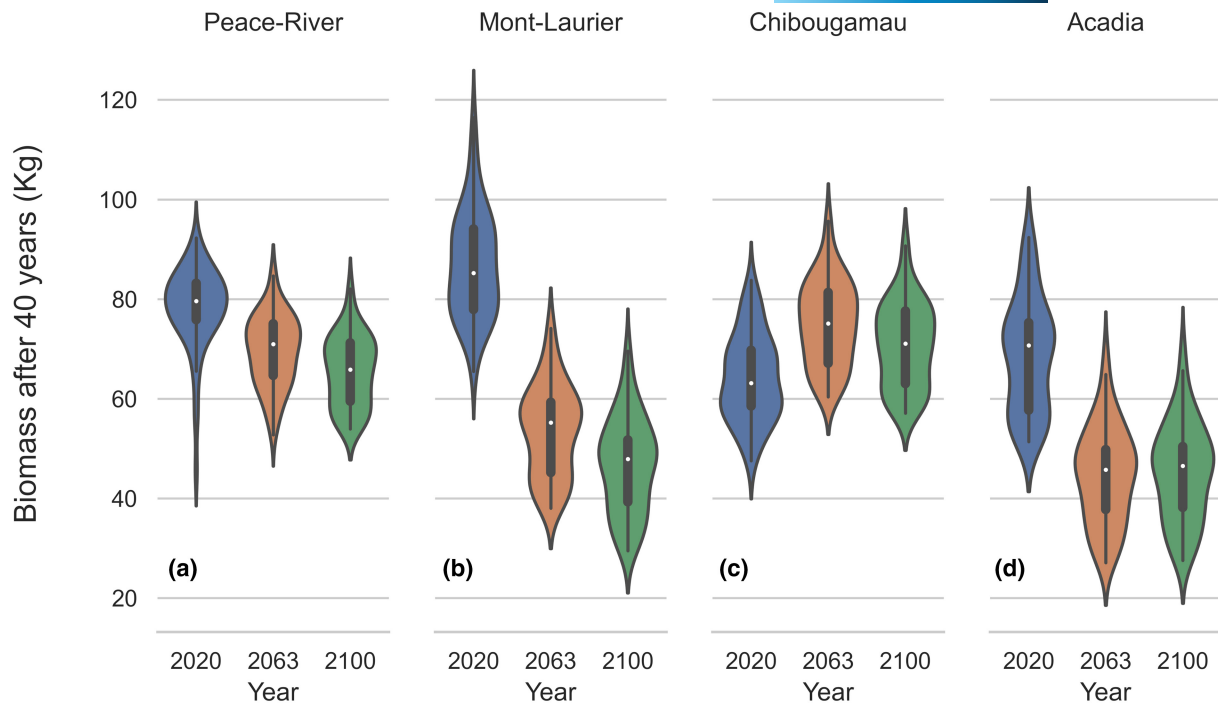


FIGURE 5 Projected mean accumulated biomass after 40 years of growth for all populations at (a) Peace River, (b) Mont Laurier, (c) Chibougamau, and (d) Acadia, in 2020 (baseline), 2063 or 2100 under SSP2-4.5.

horizons (up to +23.1% in 2100). Most populations exhibited an increase in biomass in 2063 compared to the baseline (up to 55.2%) at the CH site. In 2100, although most populations still experienced an increase compared to the baseline, the magnitude of the increase was smaller for some populations, with some even showing no increase or a decrease in biomass (Figure 6).

4 | DISCUSSION

This study characterized 62 BS populations using dendroecology and projected their accumulated aboveground biomass, with the inference of carbon sequestration potential as an underlying purpose. To this end, four 48-year-old common gardens were used to assess BS potential growth response to current and, through time-space substitution, future climates (Leites & Benito Garzón, 2023). The influence of the standing genetic variation encompassing the phylogeographic structure present in this species and local adaptation were also considered. This allowed the assessment of BS growth responses to CC at the population scale.

Variations in annual biomass production of BS in the studied common gardens were primarily driven by autumn and summer temperatures, with autumn temperature influencing growth the following year as well. Our results did not show a strong effect of SMI and other climatic variables on growth, which is consistent with other large-scale analysis of tree-ring data across Canada (Mirabel et al., 2022). Interestingly, lower to medium range temperatures in autumn and summer were positively correlated with ABI as biomass increased with temperature. However, higher temperatures were

associated with lower ABI. The identification of a nonlinear response curve of black spruce ABI with temperature aligns with findings from other studies conducted in both these common gardens and natural forest settings (Girardin et al., 2014; Pedlar & McKenney, 2017). There was a clear threshold around 8°C for mean average autumn temperature and 18°C for summer temperature above which an increase in temperature became detrimental to BS growth. The positive effect of temperature on growth is well-documented and is usually attributed to the promotion of photosynthesis and carbon assimilation (Way & Oren, 2010; Way & Sage, 2008). The negative effect of high temperature on biomass is most likely related to a lack of resources at the end of the growing season. Latewood formation is a more resource-demanding process compared to earlywood formation because of cell wall thickening and secondary wall deposition, and as such, it is mainly regulated by carbon supply (Deslauriers et al., 2016; Verbančič et al., 2018). Beyond an optimum, high temperatures can indirectly reduce photosynthetic rates by increasing air dryness, thus leading to stomatal closure, reduced leaf-level transpiration, and increased dark respiration rates, thereby affecting growth (Girardin, Hogg, et al., 2016; Mirabel et al., 2022; Way & Sage, 2008). Although our model operated at the seasonal scale, these effects are likely driven more specifically by days with extremely high temperatures. Trees are known to increase storage of nonstructural carbohydrates in autumn (Hoch et al., 2003). These reserves are then used in spring when growth resumes (Tixier et al., 2019). High respiration rates in autumn may also consume the carbon resources (i.e., nonstructural carbohydrates) that serve to build reserves for the beginning of the next growing season, thus explaining the effect of previous year autumn temperature. As a

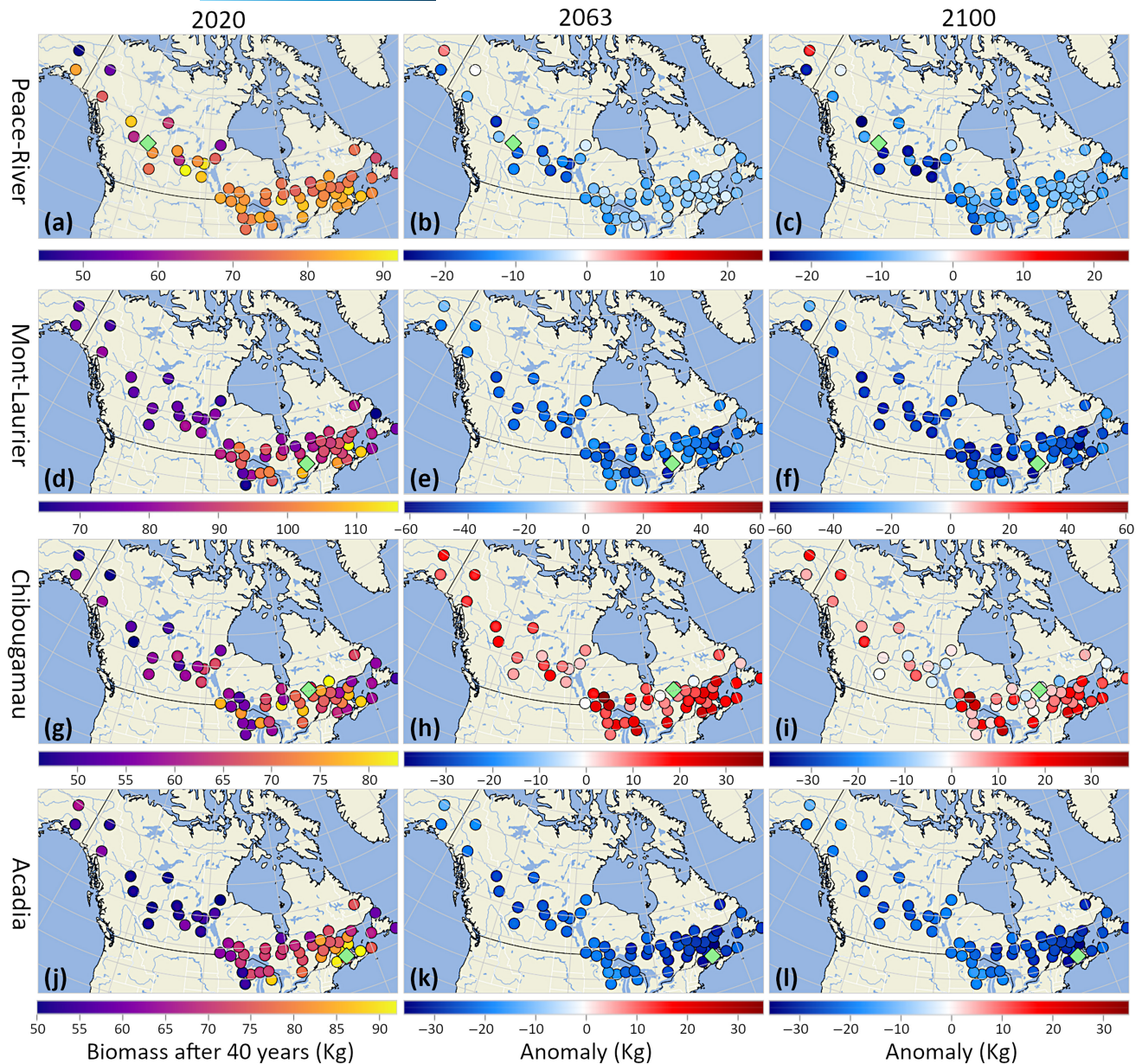


FIGURE 6 Projected baseline (a, d, g, j, 2020) and individual population-specific mean biomass anomalies at each common garden, following 40 years of growth under the SSP2-4.5 scenario (b, e, h, k, 2063 and c, f, i, l, 2100). Biomass anomalies were computed for each population by measuring the difference from their respective baselines. Each data point on the graph corresponds to a specific population and is positioned according to its provenance. The common gardens are symbolized by green diamonds. Map lines delineate study areas and do not necessarily depict accepted national boundaries. Readers are invited to consult [Table S8](#) for absolute growth values.

matter of fact, with the decrease in photoperiod in autumn, low irradiance tends to suppress photosynthesis (Makela et al., 2004; Stangl et al., 2022; Tarvainen et al., 2016). In this case an increase in respiration rates is more likely to pass the point of photosynthetic accumulation. Additionally, certain boreal conifer species show a reduction in photosynthesis when grown under warm autumn conditions compared to cool autumn or warm summer (Barichivich et al., 2013; Piao et al., 2008). On the other hand, for white spruce (Stinziano & Way, 2017) and Norway spruce (Stinziano et al., 2015), studies in growth chambers found that photosynthesis is sustained under a simulated warm autumn despite a decreasing photoperiod. Warming

temperatures, however, cause white spruce to exhibit both increased respiration and suppressed growth (Stinziano & Way, 2017). Overall, the carbon dynamics in autumn are susceptible to CC, and further research is needed, given that autumn physiology is not as well understood as that of other seasons.

This nonlinear temperature effect was reflected in the biomass projections. The coldest site (CH) showed an increase in accumulated biomass compared to the baseline, indicative of a decrease in cold limitation. However, the beneficial effect of a temperature increase at the CH site would probably be transient and short-lived, as the estimated biomass accumulation is projected to decrease during

the second half of the century. This is similar to what was found by D'Orangeville et al. (2018) and Girardin, Hogg, et al. (2016). This suggests that trees growing at this coldest site may be brought past their growth optimum during this period, eventually making them vulnerable to the adverse effects of elevated temperature. The projections for warmer sites were even more pessimistic, indicating that these sites had already exceeded their growth optimum in terms of temperature and were already experiencing a decrease in biomass accumulation, with the decline being faster the warmer the site. The decline appears to slow down in the second half of the century, although it is possible that this is due to the model being trained on a temperature range cooler than the climate during this period, and future growth during this period may be worse than indicated by the model. The Canadian boreal forest is a wide-ranging ecosystem, encompassing a large variety of environments. The sites were chosen to be representative of this diversity, but also of the possible change the boreal landscape may undergo in the future. This implies that, as a whole, BS dominated boreal forests may become negatively affected by CC by the end of the century.

As expected, the results also revealed heterogeneity of growth responses between BS genetic clusters, indicating the influence of standing genetic variation. Notably, there was a clear difference in growth projections between populations from the western cluster and the other clusters, with the former generally exhibiting lower growth. This aligns with ALE plots indicating lower biomass in the western cluster and shows that, although the effect size of the cluster variables is low relative to other variables, it is consistent enough to have a significant impact on growth over the long term, which is concordant with Girardin et al. (2021). Some caution must be applied when interpreting the ALE plot showing the effect of the west cluster as most populations displayed a high or a low admixture of this cluster. The effect for populations with intermediate admixture may be inaccurately extrapolated by the model. Nevertheless, those results illustrate the importance of considering the phylogeographic structure and local adaptation, when projecting the growth of boreal trees. Western populations exhibiting lower biomass may be due to increased sensitivity to temperatures above 18°C in summer or 8°C in autumn, or reduced responsiveness to temperatures below these thresholds. Eastern populations, except at the warmest site (AC), show less susceptibility to CC, though at AC they showed slightly more vulnerability, indicating potential limits to adaptation. However, projections for AC fall outside of our calibration range, warranting caution in interpreting growth projections.

The dichotomy between west and east is less pronounced initially at PR but becomes evident over time, with western populations more affected by CC. This could be attributed partly to PR's drier conditions favoring western populations in a first time, with, in a second time, temperature emerging as the primary driver of biomass as climate changed, particularly impacting western populations. Overall, eastern populations exhibited more variability in their response to CC, except at the PR site. Previous studies have already highlighted differences between western and other populations

(Thomson et al., 2009) and the lower productivity of western Canadian populations (Girardin et al., 2021).

GDD5p emerged as the most relevant factor to consider for local adaptation. ALE plots demonstrated a parabolic relationship between ABI and GDD5p, with populations from the middle of the range exhibiting higher growth than those at the extremes. Populations with a lower GDD5p are typically from higher latitudes and exhibit reduced growth as an adaptation to a shorter growing season, terminating their growth earlier in the year to avoid frost damage since a trade-off exists between growth and frost tolerance (Guo et al., 2022; Johnsen et al., 1996). Conversely, populations from warmer regions tend to have a longer growing season, resulting in higher biomass accumulation. This relationship holds true even when populations are placed in the same environment (Benomar et al., 2016; Sniderhan et al., 2018), as observed in our common garden (Figure 2). There is an exception to this tendency, however, with the populations from the warmest provenances exhibiting the lowest productivity. This phenomenon could be explained by their movement northward to the common garden, thereby exposing them to lower temperatures than those they are adapted to. Interestingly the effect of local adaptation was not straightforward in the projections, as there were no clear trends correlating with GDD5p, MATp, or MDPP.

The influence of adaptation to local climate and phylogeographic structure on growth is congruent with previous works. Indeed, Prunier et al. (2012) found evidence of lineage specific adaptation to temperature and precipitation in BS, as well as parallel adaptation between lineages (i.e., the same adaptation happening independently in each lineage) since postglacial recolonization. The signal linked to these factors is intertwined in our results. This is not surprising as, on one hand, the phylogeographic structure directly influences the standing genetic variation on which natural selection will act in the process leading to local adaptation. On the other hand, the two factors are statistically hard to separate with the method used in this study. The presence of parallel adaptation may obfuscate the role of the phylogeographic structure, and some climatic variables are partly confounded with genetic cluster repartition, like precipitation (Pearson's r of -0.7). More targeted research may be needed to untangle the effects of the phylogeographic structure from adaptation effects, for example using GEA (Prunier et al., 2012) or GWAS (Edwards et al., 2015) with a large SNP dataset (e.g., Lind et al., 2024).

Several studies have attempted to estimate the impact of CC on BS growth, yielding inconsistent results. Some studies have shown a negative effect (D'Orangeville et al., 2018; Girardin, Hogg, et al., 2016; Sharma, 2022), while others report a positive impact (Charney et al., 2016; Chaste et al., 2019; Gaboriau et al., 2023; Hember et al., 2017; Pau et al., 2022; Puchi et al., 2020). These discrepancies can be attributed, in part, to differences in scale and methodology (Marchand et al., 2018). Overall, it appears that warming generally has a negative effect on trees in the southern range but a positive effect on the growth of cold-limited trees in the northern part of the range (Beck et al., 2011; D'Orangeville et al., 2018; Girardin, Hogg, et al., 2016; Moreau et al., 2020). Our results align

with this trend, although they are more pessimistic for trees at northern sites, as even these sites exhibited a projected decline in biomass by the end of the century. The predicted increase in temperature and its potential negative effect on BS growth bodes ill for the capacity of the species to maintain carbon sequestration, especially under high CO₂ emission scenarios (see Figure S7). Although the potential of trees to capture carbon, regardless of their geographic origin, at northern latitudes may increase in the near future, this potential is likely to decrease afterwards. The carbon sequestration potential of trees at southern latitudes will likely only decrease with time. Overall, our results indicate a general maladaptation of the species to future climates in the long term. Alternatively, if the increase in temperature is less than what is projected by SSP2-4.5, it is possible that summer and autumn temperatures remain under the detrimental threshold, resulting in positive effects for BS growth.

It should be noted that our study focused on ABI at the individual tree level. To extrapolate these findings to the ecosystem scale and evaluate the impact of CC on boreal forests, it is necessary to consider extreme climatic events, tree mortality, and overall forest disturbances (Baltzer et al., 2021; Chaste et al., 2019; Gaboriau et al., 2023; Girardin et al., 2021). These factors, which are expected to increase in the future, can directly influence tree growth or mortality, thereby affecting biomass at the forest level (Brecka et al., 2018; Pau et al., 2023). We stress that considering these aspects is crucial when selecting seed sources for reforestation or assisted gene flow. For instance, populations that exhibit potentially high biomass production under future climatic conditions may not necessarily be the most resistant to extreme events or disturbances. Policy makers, modelers, and forest managers should assess the associated risks beforehand, particularly when adopting a productivity-oriented seed sourcing approach for carbon sequestration scenarios.

5 | CONCLUDING REMARKS

Our findings underscore the importance of acknowledging the influence of standing genetic variation, which is the result of local adaptation and evolutionary history, in shaping the response and adaptive potential of populations to future climate. It is erroneous to assume that all populations within a species respond uniformly to environmental changes (Gougherty et al., 2021; Razgour et al., 2019). This is crucial but not always considered when predicting the future of a species, whether in terms of distribution (e.g., species distribution models), biomass production and carbon sequestration potential, or in terms of response to CC in general. For example, space-for-time substitution is often used to extrapolate the future of a species from a handful of populations based on their performance under current climate, without considering that these populations may be adapted to this climate while the rest of the species is not (see Perret et al., 2024), let alone considering the phylogeographic structure. In this context, common gardens are a precious resource in that they allow space-for-time substitution while accounting for adaptation. This principle is true for BS but is also likely applicable to other

boreal species with wide distributions, as research has revealed similar genetic histories and heterogeneity in adaptive responses among many of these species (Cinget et al., 2015; De Lafontaine et al., 2010; Gérardi et al., 2010; Godbout et al., 2005, 2010; Jaramillo-Correa et al., 2004; Napier et al., 2020).

The implications of our findings extend to the selection of populations for effective implementation of assisted gene flow and reforestation efforts. These results challenge the traditional recommendation of “local is best”, which advocates for using seed sources from the immediate vicinity of a plantation site. Additionally, our results cast doubt on the belief that, in the context of assisted gene flow, populations from southern regions would be most suitable for maximizing productivity and growth at a more northern site. For species like BS, historical processes have shaped its geographic distribution and the present-day genetic diversity. Each genetic cluster harbors unique variation that could play a crucial role in ongoing and future local adaptation processes (De Lafontaine et al., 2018; Prunier et al., 2012). In light of these considerations, a comprehensive understanding of population-level adaptation is essential for making informed decisions regarding CC mitigation strategies, seed sourcing, and new adaptive forest management practices. This could be achieved with genomic approaches to predict genetic offsets (Fitzpatrick et al., 2021; Gougherty et al., 2021; Lind et al., 2024) in combination with a new generation of short- and long-term common garden experiments (Leites & Benito Garzón, 2023).

AUTHOR CONTRIBUTIONS

Etienne Robert: Conceptualization; formal analysis; methodology; project administration; supervision; visualization; writing – original draft; writing – review and editing. **Patrick Lenz:** Conceptualization; investigation; methodology; writing – review and editing. **Yves Bergeron:** Conceptualization; supervision; writing – review and editing. **Guillaume de Lafontaine:** Conceptualization; writing – review and editing. **Olivier Bouriaud:** Conceptualization; writing – review and editing. **Nathalie Isabel:** Conceptualization; formal analysis; investigation; methodology; project administration; supervision; writing – original draft; writing – review and editing. **Martin P. Girardin:** Conceptualization; formal analysis; investigation; methodology; project administration; supervision; writing – original draft; writing – review and editing.

ACKNOWLEDGMENTS

This work was made possible thanks to the financial and in-kind support provided by the Canadian Forest Service of Natural Resources Canada (NRCan) for the project T-REX (Tree Rings in common garden Experiments), the Sustainable Fibre Solution program of the Canadian Wood Fibre Centre and the Genomics R&D Initiative. Further financial support was provided by the NSERC Discovery Grant program (RGPIN-2019-06672). OB acknowledges funding from a grant of the Ministry of Research, Innovation and Digitization, CNCS-UEFISCDI, project number PN-III-P4-PCE-2021-1677, within PNCDI III. We thank David Gervais, Christine Simard, Marie-Claude Gros-Louis, Manuel Lamothe, Xiao Jing Guo, Esther Pouliot, Simon Nadeau, Marie Deslauriers, Philippe Labrie, Jean-François Légaré,

Eric Dussault, Daniel Plourde, Jamie Farrell, Jeanne Portier, and Johann Housset, all from NRCan, for field and laboratory work, help with data and planning, and technical advice. Thanks to Deogratias Rweyongeza and colleagues from the Alberta Ministry of Forestry and Parks for providing access to the Peace River site and to Jim Stewart and Jared Salvail from NRCan, for support with fieldwork at this site. Thanks to Dale Simpson and John McMullen for access to and metadata from the Acadia site. We also thank Jean Bousquet from the Canada Research in Chair Forest Genomics (Université Laval) for sharing their black spruce SNP resources. We acknowledge all the people that were involved in seed collection, curation, and plantation establishment during the 1960's and 1970's, as well as colleagues involved in maintenance of sites and data collection and who hence helped to create and foster this important resource over the decades. We are grateful to Carole Coursolle and Benjamin Marquis, both from NRCan, as well as two anonymous reviewers, for reviewing and for helpful feedback.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are available on figshare at (<https://doi.org/10.6084/m9.figshare.25772784.v1>). These data were derived from the following resources available in the public domain: Environment and Climate Change Canada's portal (<https://climate.weather.gc.ca/>) and the BioSIM server (<https://cfs.nrcan.gc.ca/projects/133>).

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How to cite this article: Robert, E., Lenz, P., Bergeron, Y., de Lafontaine, G., Bouriaud, O., Isabel, N., & Girardin, M. P. (2024). Future carbon sequestration potential in a widespread transcontinental boreal tree species: Standing genetic variation matters! *Global Change Biology*, 30, e17347. <https://doi.org/10.1111/gcb.17347>