Interactions between climate, soil and competition drive tree growth in Quebec forests

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A B S T R A C T

Climate, soil, and competition factors jointly drive tree growth variability at local and regional scale. However, the comprehensive interaction of these factors and their combined effects on tree responses within their environment remains poorly explored in current research. Using a detailed forest inventory dataset in Québec, we examined tree growth of balsam fir (*Abies balsamea* Mill), black spruce (*Picea mariana* Mill), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marshall), white birch (*Betula papyrifera* Marshall), and yellow birch (*Betula alleghaniensis* Britton), as a function of competition for light and space with neighboring trees, climate and soil-related variables. Interactions between all these variables were considered in a Bayesian model predicting tree growth. The amount of light received by trees was the main variables explaining tree growth except for coniferous tree species which was influenced mostly by climate variables. Among the studied species, only red maple and white birch exhibited increased growth under warmer conditions. Intraspecific competition had strong species-specific impacts, varying from negative effects for balsam fir, to positive for red maple and yellow birch. Interactions between climate, soil, and competition played a crucial role in shaping growth patterns, especially for sugar maple, and black spruce that strongly responded to a combination of climate and competition factors. In general, tree growth also increased with the soil cation-exchange capacity (CEC), especially when higher CEC is coupled with higher temperatures and precipitation, except for black spruce. While anticipated climate conditions in Quebec, even under the most optimistic scenarios, will have a strong negative impact on the tree growth of most tree species, management can mitigate this impact by promoting tree diversity with more complex stand structures.

1. Introduction

Forest management and biodiversity will face multiple challenges in the coming decades due to the climate-change-related rise in temperature and increase in droughts (Molina et al., 2022; Girona et al., 2023). Forecasting how forests will respond to these changes requires a good understanding of the factors affecting tree distribution and growth. At global scale, tree distribution and growth are closely linked to climate and soil properties as they influence the length of the growing season and, nutrient and water availability (Goldblum and Rigg, 2005; Lafleur et al., 2010). At local scale, such as the stand level, tree growth also depends on competition with other trees for light, soil nutrients and water (Zhang et al., 2015; Aussenac et al., 2019; Boakye et al., 2021). The influence of competition, climate and soil on tree growth is frequently studied, but we lack understanding on how these factors interact to influence tree responses in their environment (Henneb et al., 2020; Oboite and Comeau, 2020).

Climate has an important effect on tree growth, especially at higher latitude in temperate and boreal forests (Doblas-Reyes et al., 2021). In the boreal forest, tree growth is primarily limited by a short growing

season due to cold temperatures and frozen soils in the dormant season (Gennaretti et al., 2017; J. Wang et al., 2023). However, as the climate warms, the growing season in the boreal zone may become longer and tree growth may increase (Loehle and Solarik, 2019; Moreau, Chagnon et al., 2020). In temperate forests, water limitations are more important than those linked to direct effect of temperature, and climate change may imply reduced tree growth due to more frequent droughts (Loehle and Solarik, 2019; Moreau, Achim et al., 2020).

Tree survival and growth also tightly depend on soil quality determined by properties such as soil texture, pH, structure or nutrient content. Soil texture, for example, is associated with soil porosity, which regulates the water holding capacity and gaseous diffusion (Upadhyay and Raghubanshi, 2020). Tree responses to soil properties are highly species-specific. In the boreal zone, jack pine performs well on sandy soil with low water retention, whereas spruce trees prefer silty or clay textures (Ste-Marie et al., 2007). Soil pH is also important because it influences the availability of nutrients to the trees. Trees tend to grow well in slightly acidic soil, with a pH between 6 and 7. If the soil pH is too acidic or too alkaline, it can limit the ability of trees to absorb nutrients. Only some tree species are specialized for more acidic soils such as red maple in the temperate zone (Burns and Honkala, 1991). In addition, strong interactions exist between climate and soil properties. For example, lower temperature and higher precipitation can be coupled with soil paludification, resulting in reduced stand productivity (Simard et al., 2007; Paré et al., 2011).

In addition to the above abiotic factors, shade from surrounding trees and the number of surrounding trees determine resource availability and are important to predict tree-scale growth responses (Canham et al., 2004). Competition between trees can be enhanced or mitigated by soil properties (Cavard et al., 2011). Poor quality soils can reduce the availability of nutrients, which can make competition between trees more intense (Coates et al., 2013). In the boreal forest, competition for nutrients is often high due to low soil nutrient availability (Ghotsa Mekontchou et al., 2020). Understanding these intricate interactions is crucial for predicting how the forest ecosystem may respond in the future, especially considering the rising of temperature due to climate change. Accurately determining the growth responses of tree species of the Quebec forest would enable the development of site-specific management strategies aiming to ensure the long-term health and resilience of forest ecosystems.

In this study, we analyzed tree growth in a variety of temperate and boreal mixed forest stands in Quebec (Canada) covering a large soil fertility and climate gradient and considering competition of neighbouring trees. We selected Quebec as our study area because of its ecological significance as a region that experiences a wide range of soil and climate conditions. Furthermore, Quebec's forests are particularly vulnerable to climate change, as these changes are more pronounced in higher latitudes, potentially impacting forest management practices. In Quebec some temperate tree species find their northernmost distributional range, while boreal tree species have their southern range in the south of the province. Our focus is on the interaction between soil, climate, and competition factors to understand which conditions may especially decrease tree growth. We used data from the RESEF dataset ("Réseau d'Étude et de Surveillance des Ecosystèmes Forestiers") which includes 45 forest stands in Quebec. These stands undergo successive inventories, where tree diameters and positions were tracked through successive inventories every 5 years since the 1980 s. We selected 33 sites with a minimum of two inventories to extract tree growth information. Soil chemistry and texture were available at the sites. The specific objectives of this study were: (a) determine how competition, soil fertility and climate affect the growth of common tree species in Quebec, (b) determine which interaction effects are more deleterious for the growth of specific tree species in Quebec forests (e.g., low soil fertility combined to high competition; high climate stress combined to high competition) (c) identify future vulnerabilities with climate change for the studied tree species.

2. Methods

2.1. Study area and study material

The study area encompassed the major vegetation zones of Quebec, ranging from pure deciduous forests in southern Quebec, to temperate and boreal mixedwood stands, and boreal coniferous forests above the northern limit of the commercial forest zone (Fig. 1, supporting information Figure B.1, Table B.1 and B.2). The mean annual temperature within the study area varies from 6 °C to − 1 °C, while annual precipitation exhibited a gradient from east to west Quebec, ranging from 1381 mm to 871 mm per years (supporting information Table B.1). The major perturbations affecting these forests are fire events and insect outbreaks (Aakala et al., 2023). Variations in temperature and precipitation as well as disturbances play a crucial role in shaping the composition and dynamics of the study stands (Brice et al., 2020).

Our study focuses on dominant tree species of Quebec forests, including balsam fir (*Abies balsamea* Mill), black spruce (*Picea mariana* Mill), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marshall), white birch (*Betula papyrifera* Marshall) and yellow birch (*Betula alleghaniensis* Britton). Red maple, sugar maple, and yellow birch are deciduous trees adapted to well-drained, organic-rich soils. They are commonly found in mature temperate forests and exhibit shade tolerance. These species are also frequently encountered in transitional zones between deciduous and coniferous forests (Burns and Honkala, 1991). White birch is less shade tolerant, has greater tolerance to colder climates and is typically found further north in the boreal forest compared to the previous hardwoods. Balsam fir is a coniferous species well-adapted to acidic and humid soils and is frequently observed in Quebec's boreal and sub-boreal forests. Black spruce is a cold-adapted conifer that thrives in peatlands and nutrient-poor soils.

The used data come from the RESEF dataset ("Réseau d'Étude et de Surveillance des Ecosystèmes Forestiers"), which was established in the 1980 s to provide fundamental data for comparative analysis, track long-term ecosystem dynamics, evaluate the impact of climate change on forest ecosystems, and analyze the relationships between ecological factors and natural or anthropic perturbations (Fig. 1, supporting
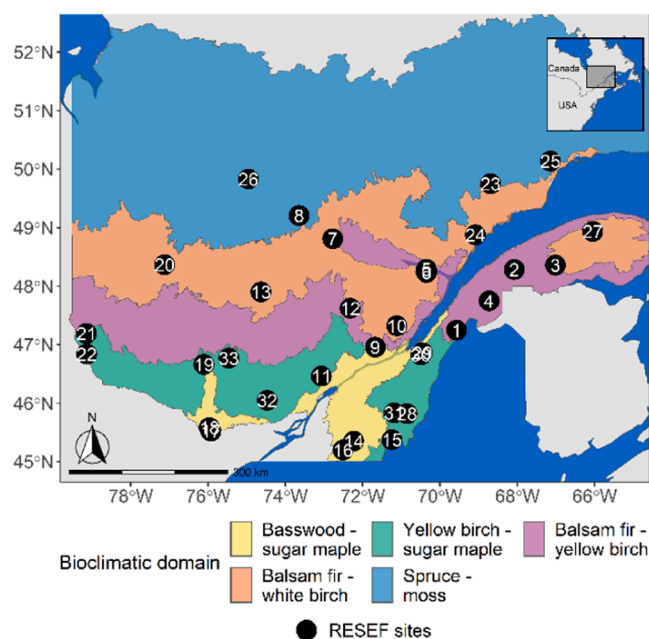

Fig. 1. Map of the location of the selected RESEF sites and main bioclimatic domains of Quebec (Canada). Numbers in points correspond to the site identity in supporting information Figure B.1, Table B.1 and Table B.2, which present site characteristics and species composition.

information Figure B.1, Table B.1 and B.2). In each stand, tree diameters and positions of trees with a DBH (Diameter at Breast Height) greater than 1 cm are measured through successive inventories every 5 years from 1986 to 2020. Stand size range from 0.5 ha in deciduous stands to 0.25 ha squared area in mixed and boreal stands. Diametrical tree growth (mm.y^{-1}) data was computed by subtracting the DBH between two inventories and dividing by the number of growing seasons between the two inventories. This was the response variable of our models once transformed to logarithm. After selection of the species of interest, we only retained healthy trees, trees with a diameter of at least 9.1 cm corresponding to trees of commercial interest, and sites where soils samples were available. The final dataset includes 45 forest stands spread across all major forested vegetation zones of Quebec but 33 was selected for this study based on the presence of at least two inventories per sites (latitude from 45.20 to 49.83 and longitude from −79.14 to −67.01; Fig. 1) with 149 different yearly inventories and 30568 computed growth data (mm.y^{-1}; black spruce: 12158; sugar maple: 11356; balsam fir: 4861; yellow birch: 963; white birch: 713 and red maple: 517).

From the RESEF dataset, we also computed the level of neighbourhood competition experienced by each tree with the following Neighborhood Competition Index (NCI):

$$NCI_i = \sum_{j=1}^{N} \left(\frac{DBH_j^{\alpha}}{dist_{ij}^{\beta}} \right), \tag{1}$$

where NCI_i is the effect of competition on the tree i, DBH_j is the diameter at breast height in cm of the neighbor j, α is a parameter expressing the exponential effect of DBH of the neighboring trees, $dist_{ij}$ is the distance in meter between the tree i and the neighbor j, and β is a parameter expressing the exponential effect of distance on the NCI. We selected neighbouring trees within 10 m from focal trees. NCI_i was computed with individuals of the same species (NCI_{intra}), conifer trees of different species ($NCI_{conifer}$) and deciduous trees of different species ($NCI_{deciduous}$). We used specific α and β parameter values for each study species from Soubeyrand et al. (2023). For trees located at the edge of the plot, where the circle with a radius of 10 m from the focal trees extends beyond the plot, we weighted the NCI value based on the area of the circle included within the plot.

At each RESEF site, soil properties were measured at most inventory dates, including soil nutrients and texture. From the measured properties, we used the pH, the cation exchange capacity (CEC) and the percentage of clay in the B horizon, which are three variables that may well summarize soil fertility (Duchesne et al., 2002; Collin et al., 2016, 2018; Hansson et al., 2020; Ouimet et al., 2021). For inventories with missing soil samples, we used the mean variable value of all other inventories at the same site.

Light available for each tree at each inventory date was computed with the SORTIE-ND model (Pacala et al., 1996; Murphy, 2011). SORTIE-ND is a spatially explicit, individual-based model that simulates stand dynamics by modeling the whole life cycle of trees within a stand (i.e., seedling, sapling, adult and snag). SORTIE-ND is based on the tree growth calculation including a shading module (GLI light module) that computes the proportion of light received by each tree in the stand according to the height and the crown dimension of the neighboring trees. SORTIE-ND requires tree allometric parameters to compute tree crown dimension and height from tree DBH. We used parameters from Poulin et al. (2008) and Soubeyrand et al. (2023)). When tree species parameters were not available, i.e., neighboring trees out of our target tree species, we used available tree parameters from species with similar biological traits. We provided to SORTIE-ND tree DBH, position and whether trees were dead or alive to create stem maps of all inventories at the RESEF sites. We then ran SORTIE-ND one single timestep to extract the proportion of shadow received by the target trees ranging from 0 (full sun) to 100 (no sun).

2.2. Climate data

We obtained historical climate data for each RESEF site using the ClimateNA software (T. Wang et al., 2016) and extracting data from the first to the last inventory by providing GPS coordinates and elevation. We only used two humidity-related and two temperature-related climate variables known to have high impact on tree growth (Hogg, 1997; St. Clair et al., 2008): the average vapour pressure deficit (VPD), the precipitation sum (PPT), the average temperature (TAVE), and the growing degree days of the summer season (DD5), i.e., June, July and August. To each inventory and corresponding tree growth period, we assigned the average values of the climate variables starting from the previous inventory year.

2.3. Bayesian models of tree growth

We modeled tree growth increment (in mm.year^{-1}) as:

$$\begin{aligned} \text{logGrowth} = {} & \alpha + \beta \text{ size effect} + \gamma \text{ shading effect} + \theta \text{ crowding effect} + \\ & \rho \text{ soil effect} + \varphi \text{ climate effect} + \text{interactions} + \text{random effect} \end{aligned} \tag{2}$$

In this model, α represents the intercept. β size effect captures the tree size effect modelled as β size effect $= \beta_1$ DBH^2 + β_2 DBH. γ shading effect captures the influence of the shadows created by neighboring trees. θ crowding effect accounts for the crowding effect including intra-species competition (NCI_{intra}), conifer competition ($NCI_{conifer}$), and deciduous competition ($NCI_{deciduous}$) with the following equation θ crowding effect $= \theta_1 NCI_{intra} + \theta_2$ $NCI_{conifer} + \theta_3$ $NCI_{deciduous}$. The soil effect is described by ρ soil effect $= \rho_1$ CEC^2 + ρ_2 CEC + ρ_3 pH$_{water}^2$ + ρ_4 pH$_{water}$ + ρ_5 PC$_{clay}^2$ + ρ_6 PC$_{clay}$. Finally, the climate effect is described by φ climate effect $= \varphi_1$ PPT^2 + φ_2 PPT + φ_3 VPD^2 + φ_4 VPD + φ_5 T$_{AVE}^2$ + φ_6 T$_{AVE}$ + φ_7 DD5^2 + φ_8 DD5. Interactions terms are included between climate and soil, soil and competition as well as climate and competition. A random effect of the site on the intercept is also included. We executed the models using the brms package (Bürkner, 2021) using 2 chains and 2000 iterations on the R software (version 4.2.3; R Core Team, 2023).

The combination of variables used in model 1 was selected by removing iteratively variables of the same group at once, i.e., climate, soil, competition and shade variables. We also tested potential interactions between variables. We finally fitted 34 models per species. Models were compared based on a leave-one-out cross-validation approach (LOO Information Criterion; Vehtari et al., 2020). We thus selected the model with the lowest LOO information Criterion (supporting information C).

We utilized R^2 as a measure to assess the model's calibration and we determined the ability of the models to capture the underlying patterns in tree growth responses in terms of R2 using the R package performance (Gelman et al., 2019). Furthermore, we conducted a visual comparative analysis between the model predictions and observed data to identify any discrepancies, overfittings, underfittings, or misalignments, thereby providing an evaluation of the overall parameterization performance.

We also compared the LOO Information Criterion of specific leave-one-out models (i.e., full model without soil constraints, full model without competition, full model without climate, full model without light) and using the full model as a reference baseline to evaluate the relative importance of the 4 groups of variables in explaining tree growth of each species. The larger the difference between one tested model and the full model, the more important the corresponding group of variables was for explaining tree growth of that species.

2.4. A priori distribution of the parameters

The a priori distributions of the model parameters needed in a Bayesian framework were determined for soils and climate parameters with independent datasets spanning larger geographical regions

(determination of priors for climate variables) or including additional sites (determination of priors for soil variables). It was important to get accurate *a priori* distribution for these parameters because only one value per RESEF inventory was available relative to the much higher number of observations for the DBH, the competition and the shading effects corresponding to one observation per tree per inventory. Conversely, for the DBH, shading and competition parameters, we set a scale-centered normal distribution as an uninformative prior.

For the *a priori* distributions of the climate parameters, we used data from an extensive network of government plots in the northeastern United States and the Canadian provinces of Ontario, Quebec and New Brunswick covering most of the distribution range of the studied tree species. This network comprises 42090 DBH measurements in 3757 plots (10685 for balsam fir; 8229 for red maple; 6789 for white birch; 4488 for sugar maple; 3876 for black spruce; 1981 for yellow birch). Using this data, we modeled in a Bayesian framework tree growth per each species as a function of VPD, PPT, TAVE, and DD5. Historical climate values were extracted using climateNA providing GPS coordinates and elevation per each site. The models used scale-centered climate variables and tree DBH and used various combinations of the following explanatory variables, $\log growth = \beta_1\ DBH^2 + \beta_2 DBH + \varphi_1\ PPT^2 + \varphi_2 PPT + \varphi_3\ VPD^2 + \varphi_4 CMI + \varphi_5\ TAVE^2 + \varphi_6\ TAVE + \varphi_7\ DD5^2 + \varphi_8 DD5$. Model selection proceeded with the following rules: (a) the simple and quadratic effect of DBH were necessarily selected, (b) only one between VPD and PPT, and one between TAVE and DD5 could be selected because of their high cross-correlation, and (c) when quadratic term was selected also the linear term was necessarily selected. We selected the model with the lowest LOO Information Criterion. The prior distribution for all parameters followed a standard normal distribution. The posterior distributions of the retained model parameters were used as priors for the model of Eq.1.

For a more exact determination of the priors of the soil parameters, we used decadal dendrometric and edaphic data from the Quebec government's permanent inventory plots distributed in the commercial forest of Quebec. We extracted tree growth of the study species where the same soil variables used for the model of Eq.1 were available. This represented 17021 tree growth measurement in 961 sites. We scale-centered all soil variables and used the posteriors of the DBH parameters obtained with the preceding climate model. The *priors* for the soil model were also set as normal distributions. We then selected the best combination of the following full model based on the LOO Information Criterion: $\log growth = \beta_1\ DBH^2 + \beta_2 DBH + \rho_1\ CEC^2 + \rho_2 CEC + \rho_3\ pH_{water}^2 + \rho_4\ pH_{water} + \rho_5\ PC_{clay}^2 + \rho_6\ PC_{clay}$. Model selection proceeded with the following rules: (a) the simple and quadratic effect of DBH were necessarily selected, and (2) when the quadratic effects were selected, the related linear effect was necessarily selected. Similarly to the retained climate variables, the posterior distributions of the retained soil model parameters were used as priors for the model of Eq.1.

2.5. Analysis of tree growth responses

For each species, we showed on plots the effects of the retained climate and soil variables on tree growth, including interactions with the competition terms. This procedure allowed for visualizing the influence of the significant variables, while displaying the potential impact of climate change and understanding how forest management may contribute to reduce such impact by modulating competition between trees. For the climate variables, we also extracted the mean climate conditions for the 2100 horizon at all RESEF sites where one species was present and displayed such values on the plots to analyze potential future species-specific responses. We used four different Shared Socio-economic Pathways (SSP) climate scenario from the IPCC Sixth Assessment Report (SSP1: A future with strong global cooperation, ambitious sustainability policies, and low greenhouse gas emissions; SSP2: Socio-economic development continues along current trends, with moderate efforts to address climate change; SSP3: Limited global cooperation, high inequality, and fragmented climate change efforts; SSP5: Heavy reliance on fossil fuels, rapid economic growth, and limited climate action; IPCC, 2023). The mean of 13 simulations from models contributing to the Coupled Model Intercomparison Project was used (T. Wang et al., 2016). For the soil variables, we extracted values from the permanent inventory plots of the Quebec government where one species was present. We displayed the resulting frequency distribution on plots of that species, highlighting the potential future responses of each tree species within its respective edaphic distribution ranges.

3. Results

3.1. Model selection

The selection of the climate variables differed for the different species. The model for yellow birch only retained VPD, while the other models always retained one temperature-related (TAVE or DD5) and one humidity-related (PPT or VPD) variable (Table 1). Among the soil variables, CEC has been consistently selected, but not necessarily with a quadratic effect. Therefore, CEC appeared to be a good indicator of the growth for all the study species. For all species growth increased with CEC, except for black spruce. Maples and conifer trees were also linked to the clay content, and to pH in the case of the two conifer tree species (Table 1).

The final models (see Eq. 1) for sugar maple, balsam fir, black spruce and balsam fir retained all group of variables whereas for red maple and white birch, interactions related with competition have not been selected, and for yellow birch none of the terms related with climate were selected (Table 2).

For sugar maple and yellow birch, shade from surrounding trees and competition for space, water and nutrients were identified as the most influential factors (Fig. 2). For the remaining species, the relative importance of the groups of variables is more shared. Nonetheless, shade emerges as a significant factor for white birch growth. Climate appeared to be particularly important for black spruce and balsam fir.

3.2. Quality of model fit

The predicted growth curves generally aligned with the actual growth rates for each species, with better performance for balsam fir, black spruce, and white birch (Fig. 3, Table 2). However, it is important to note that the models fitted better for high growth rates than for low growth rates and that the model uncertainties were large.

3.3. Impact of explanatory variables and of their interactions on tree growth

The model coefficients can be analyzed to interpret tree-growth trends according to ontogenic and environmental conditions. The coefficient of the DBH squared was found to be negative, except for red

Table 1

Climate and soil variables selected with the preliminary analysis on independent datasets.

Species	Selected climate variables	Selected soil properties
Balsam fir	VPD + TAVE + TAVE^2	CEC + CEC^2 + pH + pH^2 + PC$_{CLAY}$ + PC$_{CLAY}$^{2}
Black spruce	VPD + VPD^2 + TAVE + TAVE^2	CEC + CEC^2 + pH + PC$_{CLAY}$ + PC$_{CLAY}$^{2}
Red maple	PPT + PPT^2 + DD5 + DD5^2	CEC + PC$_{CLAY}$
Sugar maple	DD5 + VPD + VPD^2	CEC + CEC^2 + PC$_{CLAY}$
White birch	VPD + VPD^2 + TAVE + TAVE^2	CEC
Yellow birch	VPD + VPD^2	CEC

Table 2

Group of variables retained in the final models (Eq. 1) explaining the radial growth of the tree species and explained variance. The random effect of the site is included in the R^2.

Species	Model selected with LOO	R^2
Balsam fir	Size effect + competition + soil + climate + shading + soil:competition + climate:competition + soil:climate (full model)	0.49
Black spruce	Size effect + competition + soil + climate + shading + soil:competition + climate:competition + soil:climate (full model)	0.34
Red maple	Size effect + competition + soil + climate + shading + soil:climate	0.30
Sugar maple	Size effect + competition + soil + climate + shading + soil:competition + climate:competition + soil:climate (full model)	0.22
White birch	Size effect + competition + soil + climate + shading + soil:climate	0.35
Yellow birch	Size effect + competition + soil + shading + sol:competition	0.22

maple, indicating an increase in growth until an optimal DBH followed by a decrease in growth as DBH increases. The red maple's slightly positive DBH square coefficient indicates the presence of a DBH value where unexplained constrains by our model are maximal (Fig. 4). For all species, lower light availability corresponded to lower tree growth. Intraspecific competition had a positive impact on red maple, yellow birch, and white birch but had a negative effect on balsam fir, sugar maple, and black spruce. Especially for balsam fir, intraspecific competition was more detrimental than interspecific competition. Competition from coniferous species had a detrimental effect on red maple, sugar maple, and yellow birch. Black spruce and white birch were instead not significantly affected by any kind of competition. It is important to emphasize that even when the simple of competition effect doesn't have a direct impact on tree growth (see Fig. 4), it can significantly modulate the effect of other environmental variables by interaction (see below).

Only red maple and white birch showed increased growth under warmer climate, other species showed a decline in growth. However, several interactions between climate, soil, and competition may modulated tree growth (Fig. 5 and Fig. 6). The growth trends of balsam fir trees appeared to increase with warmer temperatures, but high uncertainties are noted, also considering a potential decline in growth. For sugar maple, growth decreased with increasing DD5, an effect amplified under high intraspecific competition (Fig. 5). Similar findings were found for black spruce, where higher TAVE values leaded to decrease growth, especially under high intraspecific competition. Tree growth of red maple and yellow birch increased with higher intra-specific competition (NCI intra).

By 2100, tree species will face climate conditions much different than the current ones in Quebec even in the most optimistic climate scenario. These changes may profoundly affect tree growth. For example, black spruce growth in Québec will be limited by the rise in temperatures even under the most optimistic scenario (Fig. 5).

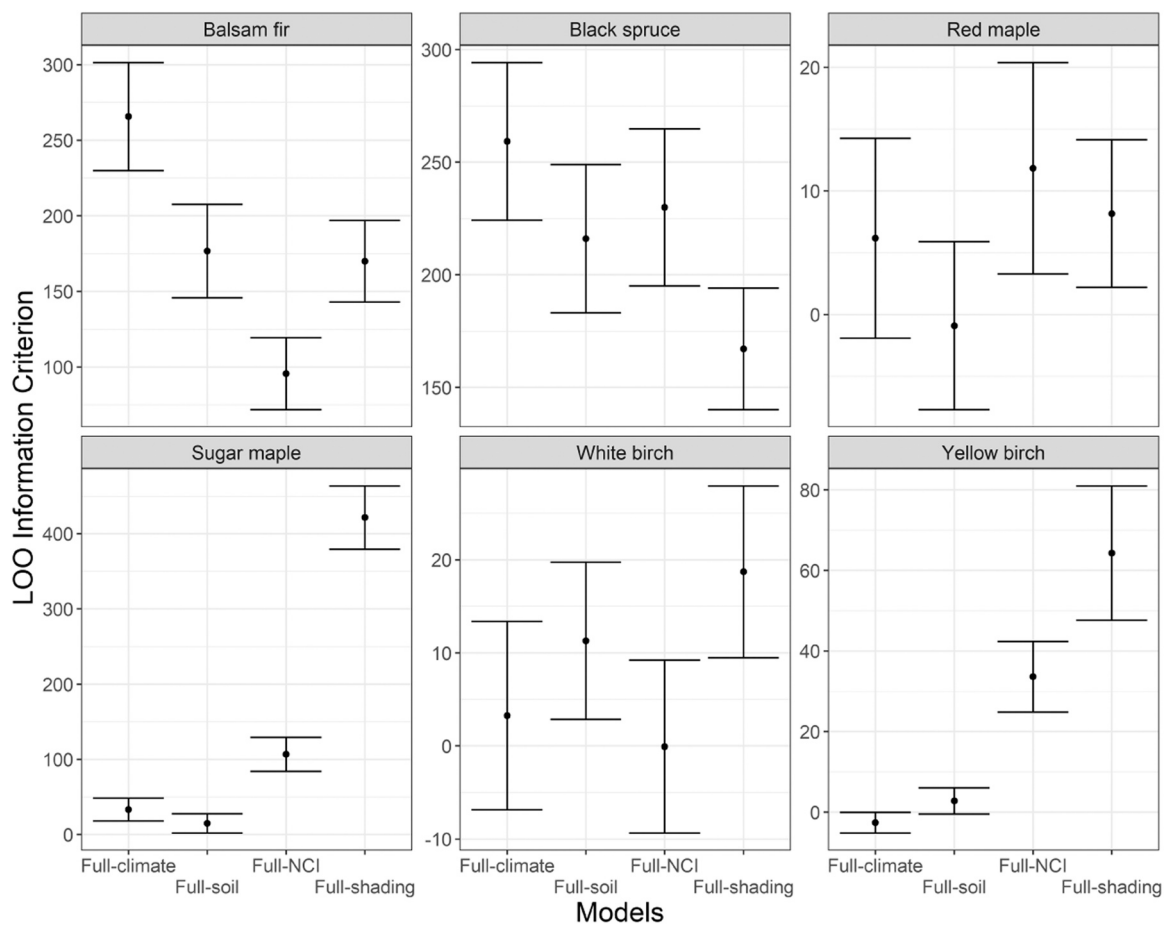Tree growth responses to soil variables were found to be influenced

Fig. 2. Importance of specific groups of variables in the models explaining the growth of each study tree species (log(mm.year^{-1})). The importance is based on the comparison between LOO Information Criterions between the full model and the model without one group. Higher values indicate greater importance of the group in the final model. Conversely, values below zero suggest that the removal of the group improves the model. NCI stands for Neighbourhood Competition Index.
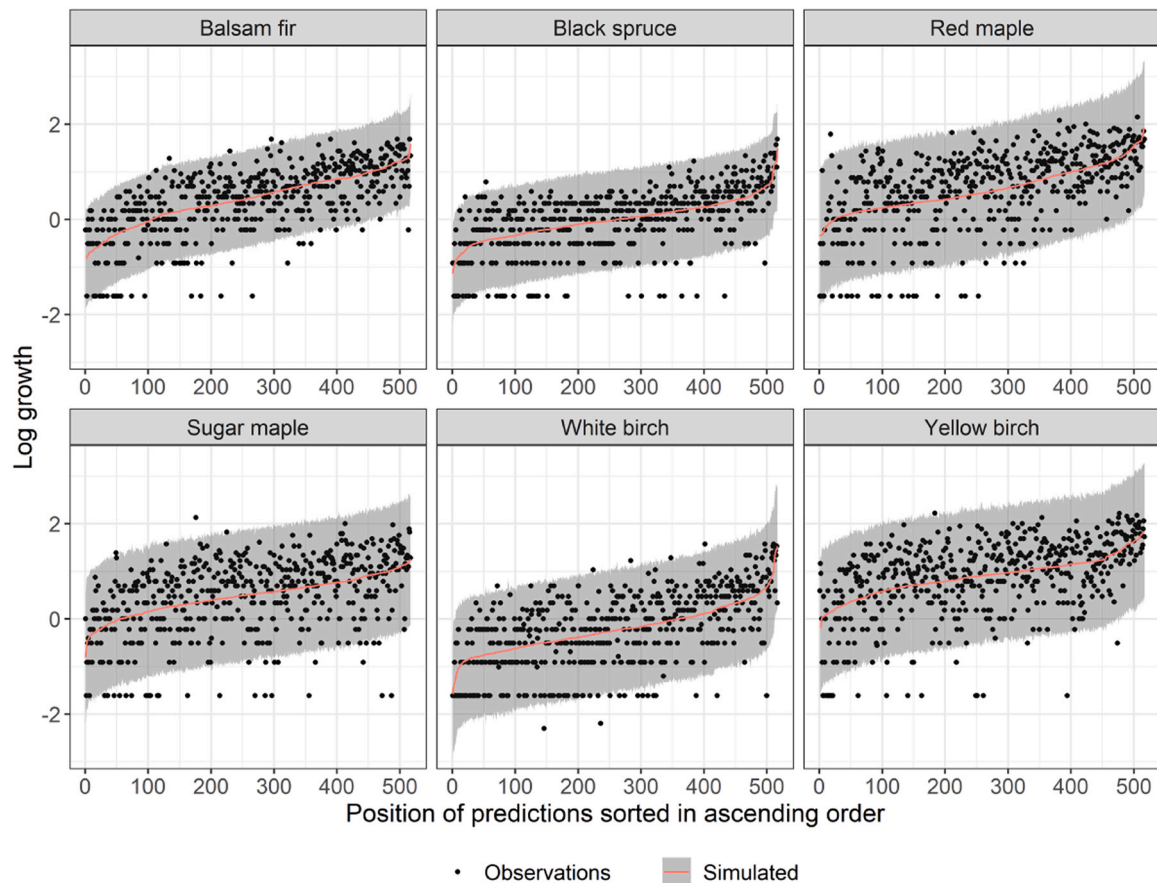
Fig. 3. Predicted and observed growth sorted by their prediction positions. Simulated growth is represented by the mean line and 95% confidence intervals. The actual growth observations are shown as points. To address the issue of overplotting due to a high number of observations, we randomly selected 517 predictions for each species, which corresponds to the lowest number of observations among the species, namely red maple.

by climate conditions and competition of neighbouring trees (Fig. 6). Tree growth increases with CEC, except for yellow birch with null intraspecific competition and for black spruce only with low temperature. White birch and red maple showed a stronger positive response to higher CEC, modulated by temperature and precipitation levels. Both sugar maple and balsam fir exhibited increased growth with higher CEC, with a low interaction effect of competition. Black spruce growth was inversely related to CEC and soil acidity, especially in presence of coniferous competitors. Sugar maple growth was negatively affected by the proportion of clay, and the negative impact was further amplified under lower intraspecific competition.

4. Discussion

4.1. How tree species growth responses to climate and soil properties are modulated by competition?

In this study, we investigated the interplay of tree species growth responses with climate, soil properties, competition, and the amount of light received by the trees in mixed forest stands of Quebec. A large dataset was used including temperate and boreal forest stands where the position of each tree is monitored at each inventory date. We find that tree growth was regulated by each of these factors individually and by the interactions among them. Our findings highlight the critical role of competition in shaping tree growth responses within climate and soil gradients but were highly species-specific, i.e., the direction and strength of these effect varied with tree species as suggested by other studies (Ford et al., 2017). It is worth noting that the shading effect emerged as a key factor influencing the growth of all examined tree

species.

The contrasting results of competition interactions with climate and soil properties for different tree species is shown by the negative effects (i.e. higher intra-specific competition corresponds to increased sensitivity of tree growth to climate or soil variables with growth reductions becoming more plausible) observed for balsam fir, sugar maple, and black spruce and the positive effects for red maple and yellow birch. These results feed the ongoing debates between the Stress Gradient Hypothesis and the CSR (competitive, stress-tolerant, ruderal) Strategy Theory (Coates et al., 2013). According to the Stress Gradient Hypothesis, in stressful environmental conditions like drought or low nutrients availability, competition among species may decrease (Lortie and Callaway, 2006; Maestre et al., 2009). This could explain why some tree species that compete for resources in less stressful environments are less sensitive to competition during drought periods (Aussenac et al., 2019). For example, red maple and yellow birch may be better suited to exploit available resources in a competitive environment when conditions are stressful. On the other hand, the CSR Strategy Theory focuses on species life strategies (Tilman, 1985). According to this theory, competition for resources is a key factor explaining tree communities especially in challenging environmental conditions such as drought or low nutrient availability where tree competitions should be exacerbated (Tilman, 1985). During prolonged drought periods, water availability decreases, intensifying competition among species (Ford et al., 2017; Castagneri et al., 2022; Kulha et al., 2023). With increasingly hotter summers and reduced precipitation, soil water availability is expected to become a problematic factor for tree growth, and intra-specific competition could further deteriorate growth (Magalhães et al., 2021). Thus, species like balsam fir, sugar maple, and black spruce, might be disadvantaged in
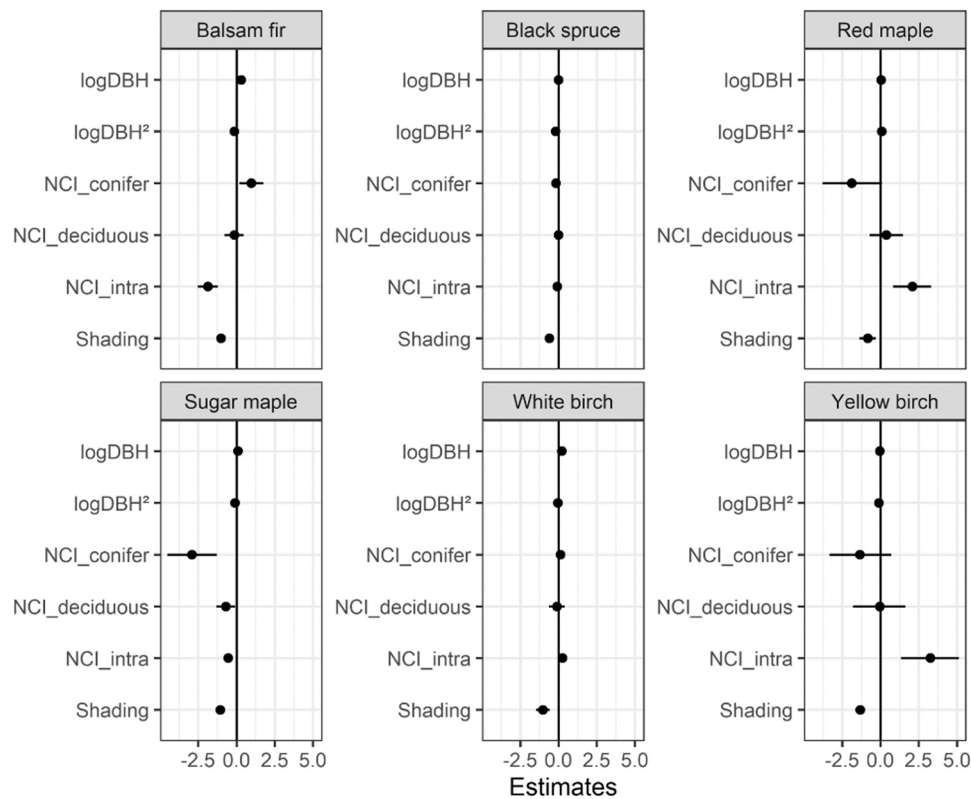
Fig. 4. Model estimates of DBH, competition and shading effects for each species after model selection. The points represent the median of the estimates, and the error bars indicate the 2.5th - 97.5th quantile range of the posterior distributions. The model was highly constrained for tree DBH, leading to small error bars. DBH stands for Diameter at Breast Height and NCI stands for Neighbourhood Competition Index.

competitive environments such as dryer conditions.

Other studies have demonstrated that the interactions between competition and environmental variables can shape tree growth responses. Coates et al. (2013) also illustrated that the growth of dominant tree species in the sub-boreal spruce region of the Canadian boreal forest was influenced by interactions between tree competition and soil fertility, and this interaction was specific to each species and environmental context. Oboite and Comeau (2020) suggested that an increase in intraspecific competition would likely lead to reduced tree growth among dominant species in western Canada and Alaska as the climate warms. They also observed that the effects of interactions between interspecific competition and a warmer climate was species-specific. Chavardès et al. (2022) demonstrated that the growth responses of black spruce and jack pine (*Pinus banksiana Lamb.*) in the mixedwood boreal forests of western Quebec generally exhibited a negative correlation with temperature, particularly when intraspecific competition was higher. Our results precise these competition-environment interactions for the dominant tree species in Quebec by taking advantage of a large and detailed forest inventory dataset that includes the precise coordinates of each tree.

4.2. Importance of climate-soil interactions on tree growth rate

Among the considered variables, only CEC has been consistently selected in all models for all tree species. This variable is a robust proxy for soil fertility (Weil. and Brady, 2016). In addition to the positive effect of CEC on tree growth (except for black spruce), we observed that the interaction between CEC and climate is important, especially in the case of red maple, black spruce, and white birch. For example, the growth of red maple was positively influenced by higher temperatures, and decreased when soil fertility was low and the proportion of clay in the soil was high.

Our findings suggest that optimal sugar maple growth is associated with specific soil conditions such as nutrient-rich soils with low clay content (Schaberg et al., 2006). Since the 1970 s, sugar maple has been experiencing a decline in growth and regeneration due to multiple factors (Bishop et al., 2015; Boakye et al., 2023). The primary factor contributing to this decline is likely the soil acidification resulting from atmospheric pollution and associated to a decrease of nutrient availability (Duchesne et al., 2002; Sullivan et al., 2013; Collin et al., 2016). Although soil acidity was not selected in our model for sugar maple, it includes CEC showing the importance of nutrient concentration in soils. Another factor that may have contributed to the sugar maple's growth decline is the invasive behaviour of American beech (*Fagus grandifolium* Ehrh.), which can establish rapidly and compete with sugar maple (Duchesne et al., 2005; Gravel et al., 2011). Our model was built with data from mature stands, and competition between sugar maple and other deciduous was less intense than with conifers. However, the species was highly sensitive to the amount of light intercepted by other trees confirming the results of other studies focussing on the beech-maple interactions (Beaudet et al., 1999; Nolet et al., 2015). This increased competition can exert significant pressure on sugar maple growth, mitigating the beneficial effects of nutrient-rich soils (Collin et al., 2017). We determined that the growth of sugar maple decreased as temperatures rise, so the temperature increase due to climate change should not necessarily improve the growth conditions of sugar maple (Boakye et al., 2023).

4.3. Implications for forest management

By the year 2100, it is anticipated that certain tree species will face climates that are currently outside their current distribution range (McKenney et al., 2011). For instance, the black spruce southern distribution range is located in southern Quebec. Under the most favorable
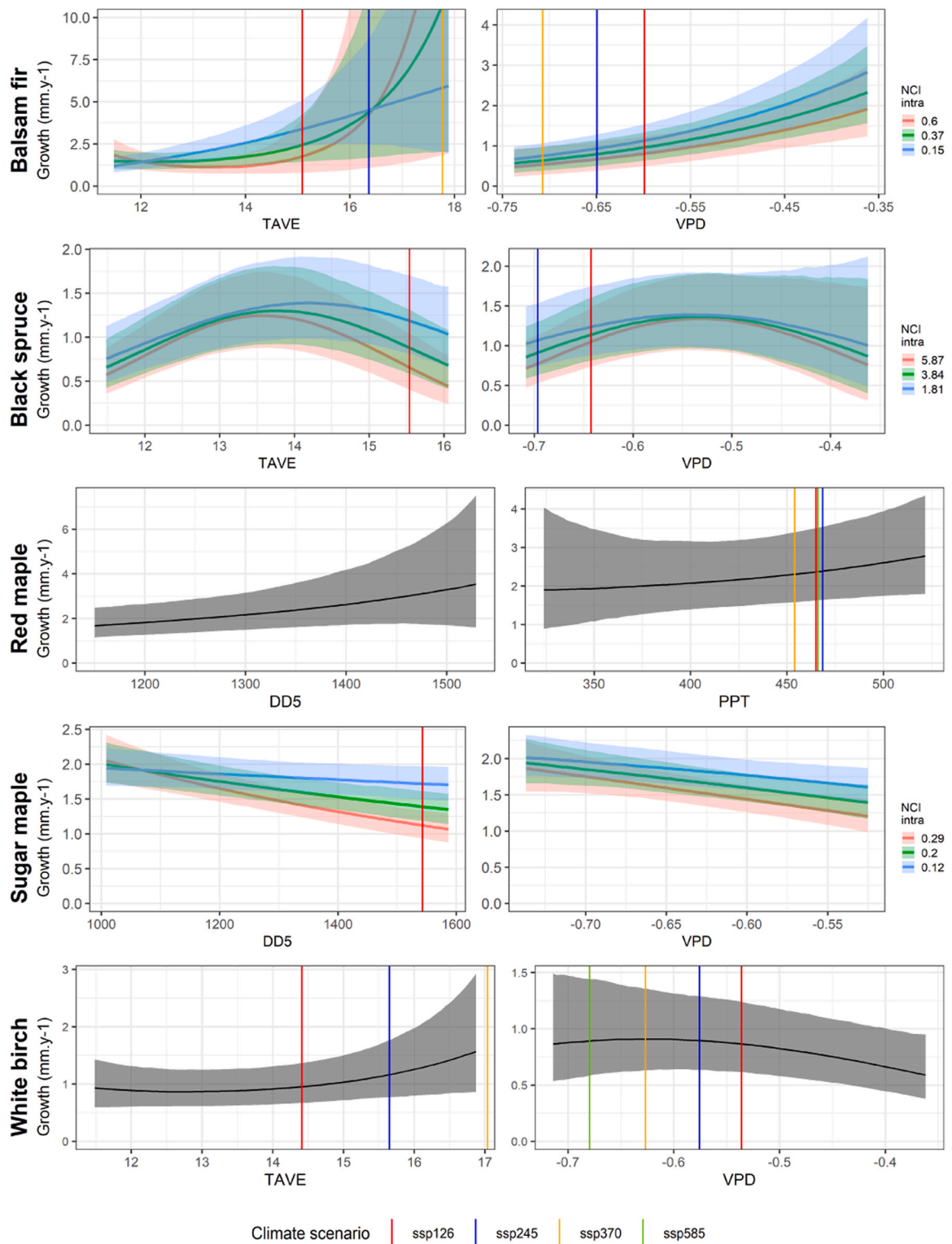
Fig. 5. Radial growth of tree species in relation to climate variables and interactions with intra-specific competition. The green line corresponds to the mean of the interaction variable, and the red and blue lines correspond to the mean plus and minus one standard deviation, respectively. Error areas correspond to the 5th and the 95th quantile Bayesian confidence intervals. All linear, quadratic and interaction effects can be found in the supporting information. Colored vertical lines represent mean future climate variable values (2100 horizon; four considered climate scenarios) at the RESEF sites where the species are present. Only future climate values inside our prediction range are shown. TAVE stands for average temperature during growing season, VPD stands for Vapour Deficit Pressure, PPT stands for precipitation and NCI stands for Neighboring Competition Index.
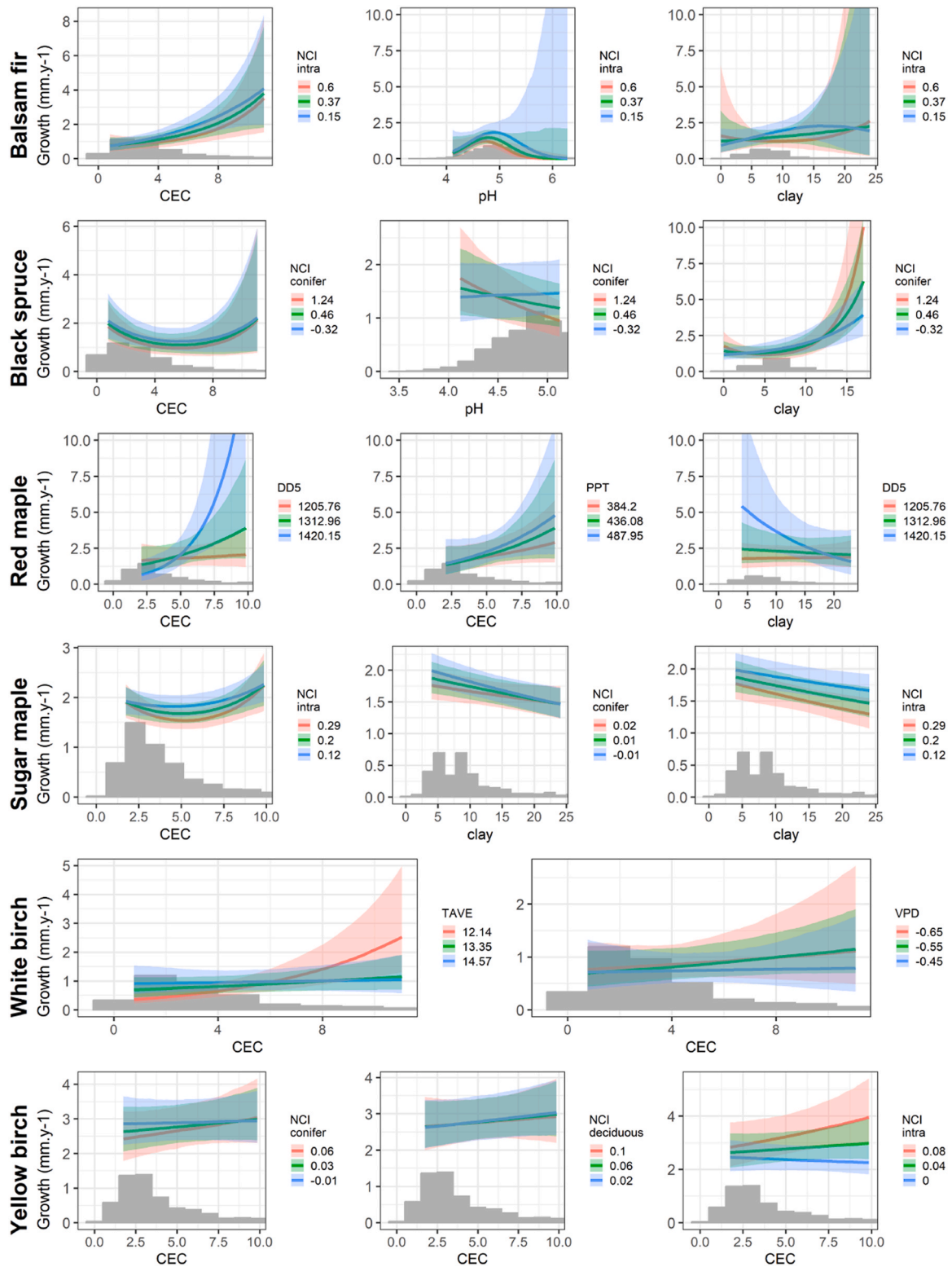
Fig. 6. Growth of the selected tree species in relation to soil properties and interactions with competition and climate variables. The green line corresponds to the mean of the interaction variable, and the red and blue lines correspond to the mean plus and minus one standard deviation, respectively. Error areas correspond to the 5th and the 95th quantile Bayesian confidence intervals. All linear, quadratic and interaction effects can be found in supporting information D. We also displayed histograms depicting the frequency distribution of soil properties in the permanent plot of Quebec where the species is present. CEC stands for Cation Exchange Capacity, TAVE stands for average temperature during growing season, VPD stands for Vapour Deficit Pressure, DD5 stands for growing degree day, PPT stands for precipitation and NCI stands for Neighboring Competition Index.

climate scenario, we found that black spruce will be already approaching the upper threshold of its current temperature niche in our study region. Girardin et al. (2016) found that the growth and productivity of black spruce may be compromised in the future, potentially leading to a decline in growth rates due to a lack of soil water availability especially in the southern part of its distribution range. On the other hand, the climate may increase the growth of this species farther north, with the release of climate constraints such as an extended growing season and higher summer temperatures (D'Orangeville et al., 2016; Pedlar and McKenney, 2017; Gennaretti et al., 2017; Moreau, Chagnon et al., 2020). These results may have profonde implications for the forest sector in Quebec which currently depend on black spruce logging. It is imperative that alternative and sustainable management options are thoroughly explored and implemented to ensure the resilience and long-term viability of the forestry industry in Quebec (Noualhaguet et al., 2023).

Our study highlights the crucial importance of considering interactions between soil, climate, and competition when modeling tree growth, especially in the context of assessing the impacts of climate change. We observed that, with the anticipated climate warming trend, the growth of black spruce and sugar maple is expected to decrease. This decline should be exacerbated by high levels of competition, particularly intraspecific competition. Therefore, to achieve high productivity in stands containing these species, it is essential to mitigate intraspecific competition by diversifying tree species composition. Indeed, greater species diversity in forest stands may imply complementary niches and interactions, and may result in improved resistance to drought (Aussenac et al., 2019) and insect infestations (Chavardès et al., 2022). Tree diversity is often advocated to enhance the resistance and resilience of forest ecosystems to various environmental constrains (Cappuccino et al., 1998; Paquette and Messier, 2011; Charnley et al., 2017).

Conversely, other species such as red maple and yellow birch may better tolerate intra-specific competition, especially in favorable microsite conditions with nutrient-rich soils, low clay content and higher air temperatures (Collin et al., 2016). Considering the high performance of red maple in a warmer climate and the decline of sugar maple since the 1970 s in Quebec (Boakye et al., 2023), it is advisable for the forest industry to increase the exploitation of red maple even in the boreal zone where it is currently present only in marginal populations. This will be particularly possible if the wood quality of red maple at the northern limit of its distributional range will be high enough under future climate conditions (Havreljuk et al., 2013).

CRediT authorship contribution statement

Gennaretti Fabio: Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Marchand Philippe:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Conceptualization. **Soubeyrand Maxence:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Bergeron Yves:** Writing – review & editing, Funding acquisition. **Duchesne Louis:** Writing – review & editing, Investigation, Data curation.

Declaration of Competing Interest

We have no conflict of interest to declare.

Data Availability

Datasets and codes used in this study have been archived on a GitHub repository and can be found at https://zenodo.org/doi/10.5281/zenodo.10211375.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121731.

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