

# Greater tree species diversity and lower intraspecific competition attenuate impacts from temperature increases and insect epidemics in boreal forests of western Quebec, Canada

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## Abstract

We investigated how the surrounding environment influences the growth of dominant trees and their responses to temperature and insect epidemics in boreal forests of eastern Canada. We focused on 82 black spruce and jack pine focal trees in stands spanning a double gradient of species diversity and soil texture within a 36 km<sup>2</sup> area of western Quebec. For these trees, we compared their diameter at breast height, growth rates, temperature–growth relations, and growth during insect defoliator epidemics. We used linear models to study how surrounding tree attributes and soil properties affected the growth of focal trees. Models showed that tree growth responses and responses to temperature and insect epidemics were generally negative with higher intraspecific competition and positive with greater tree species diversity. Growth of both species benefitted from lower soil sand content. Our research offers novel insights on the potential role of the surrounding environment, notably tree competition and species diversity, in mitigating the vulnerability of eastern Canada's boreal trees to anthropogenic climate change and insect epidemics.

**Key words:** basal area increments, forest tent caterpillar, growing season length, eastern spruce budworm, summer heat stress

## Résumé

Nous avons étudié comment le milieu environnant influence la croissance d'arbres dominants et leurs réponses à la température et aux épidémies d'insectes dans les forêts boréales de l'est du Canada. Nous nous sommes concentrés sur 82 épinettes noires et pins gris dans des peuplements couvrant un double gradient de diversité d'espèces et de texture du sol dans une zone de 36 km<sup>2</sup> de l'ouest du Québec. Pour ces arbres, nous avons comparé leur diamètre à hauteur de poitrine, leur taux de croissance, les relations température–croissance et la croissance pendant les épidémies d'insectes défoliateurs. Nous avons utilisé des modèles linéaires pour étudier comment les attributs des arbres environnants et les propriétés du sol affectaient la croissance des arbres focaux. Les modèles ont montré que les réponses de la croissance des arbres et les réponses à la température et aux épidémies d'insectes étaient généralement négatives avec une compétition intraspécifique accrue entre arbres et positives avec une plus grande diversité d'espèces d'arbres. La croissance des deux espèces a bénéficié d'une teneur en sable plus faible dans le sol. Notre recherche offre de nouvelles perspectives sur le rôle potentiel du milieu environnant, notamment de la compétition et de la diversité des espèces d'arbres, dans l'atténuation de la vulnérabilité des arbres boréaux de l'est du Canada au changement climatique anthropogénique et aux épidémies d'insectes.

**Mots-clés :** accroissement de la surface terrière, livrée des forêts, longueur de la saison de croissance, tordeuse des bourgeons de l'épinette, stress thermique estival

# 1. Introduction

Anthropogenic climate change is expected to impact the growth of trees in boreal forests of Northeastern America directly through increasing temperatures (D'Orangeville et al. 2016; Pau et al. 2022) and indirectly through more frequent disturbances such as insect epidemics (Navarro et al. 2018). For these forests, simulations reveal that high temperature increases in the range of 4–6 °C are expected by 2071–2100 (Price et al. 2013), which may lead to irreversible changes in forest composition and loss of forest cover (Boulanger et al. 2022). At the species level, growth of trees can vary based on life-history strategies and sensitivity to climate and insect epidemics (Brecka et al. 2020). Apart from these strategies and sensitivities, growth of trees can also depend on the surrounding environment, including soil properties (Marchand et al. 2019), and within stand competition and species diversity (Aussenac et al. 2019). Concerns about vulnerabilities of boreal forests to increasing temperatures and insect epidemics (Gauthier et al. 2014) and the paucity of knowledge on how site-specific factors could affect their impacts mean that additional information about the growth of boreal tree species in different surrounding environments is warranted.

Testing relations between monthly to seasonal temperature and tree growth (i.e., temperature–growth relations) and estimating the impact of insect epidemics on tree growth are approaches that can be used independently or in combination (Drobyshev et al. 2013; Chavardès et al. 2021). Such approaches offer information on how temperature benefits or limits growth of different tree species, and whether these species have positive or negative growth responses associated with insect epidemics. With this information, alongside future climate and insect epidemic scenarios, researchers can better anticipate the growth of boreal trees.

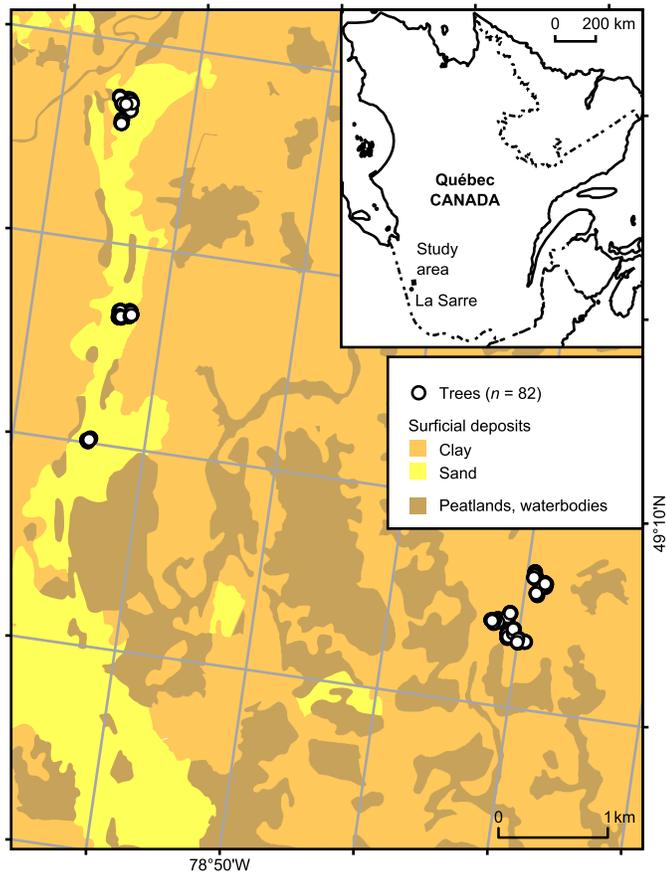
The enhancement of tree species diversity within stands is often invoked in boreal regions as an approach to mitigate direct and indirect impacts of increasing temperatures on forests (Felton et al. 2016; Hisano et al. 2019). Diversity within stands can benefit growth of trees in several ways, for example through niche partitioning over space, including via rooting systems (Houle et al. 2014; Mekontchou et al. 2020) and canopy layers (Jucker et al. 2020), or over time such as via distinct start and end dates for vegetative growth across tree species (Huang et al. 2010). Diverse tree species in forest stands can also exhibit differing growth responses to disturbances such as insect epidemics (Chavardès et al. 2021), thereby stabilizing tree biomass (Aussenac et al. 2016). Conversely, dominance by tree species with given traits can affect ecosystem processes (i.e., selection effects), and functional identity of some species rather than species richness per se can be the most important promoting factor of ecosystem multifunctionality (i.e., species identify effect) (Mouillot et al. 2011; Jochum et al. 2020).

The benefits of tree species diversity could be outweighed by other factors in the surrounding environment, particularly under the pressure of increasing temperatures and more frequent insect epidemics. For example, stand tree structure affects the diffusion potential of insects via crown contact among nearby trees (Régnière and Fletcher 1983). Stand tree structure also affects competition among neighboring trees

(Luo and Chen 2011), with larger and nearer trees increasing interspecific and intraspecific competition and reducing growing space for other trees (Looney et al. 2016); consequently, dense stands tend to have fewer large trees than more open stands (Casper et al. 2011). Apart from stand tree structure, the type and depth of the soil surficial deposit accessible to roots may determine the availability of key nutrients and water conditions influencing the growth of boreal tree species (Belleau et al. 2011). Compared to soil surficial deposits with finer clay, coarser textured deposits composed of sand and gravel tend to have more rapid drainage (Bartlett et al. 2002) and are often less productive for tree growth (Béland and Bergeron 1996). When overlaid by a deep organic layer, shallow-rooted tree species are less productive (Laamrani et al. 2014), in part because of difficulty reaching key nutrients from deeper surficial deposits (Dimitrov et al. 2014). To date, the relative importance of environmental factors for the growth of boreal trees, temperature–growth relations, and impacts from insect epidemics remains insufficiently understood. A comprehensive approach including multiple environmental factors can help identify how tree growth in this biome could be enhanced or limited in the future. Furthermore, a comprehensive approach may be used to determine whether a specific factor is significant even after accounting for confounding factors.

In our study, the main objective was to investigate how temperature and insect epidemics impact the growth of boreal tree species across a double gradient composed of tree species diversity and soil texture. The objective can help ascertain whether diversity effects are persistent under climate change and whether tree responses depend on the species (e.g., via selection and species identify effects), biotic composition (e.g., via stand structure, biodiversity, and complementarity effects), or the physical environment (e.g., via the soil) (Loreau and Hector 2001; Loreau et al. 2001). We focused on two regionally dominant tree species, black spruce (*Picea mariana* (Mill.) BSP), and jack pine (*Pinus banksiana* Lamb.) in stands with a range of tree species diversity and growing on clay to sandy surficial deposits within the black spruce–feather moss bioclimatic domain of western Quebec, Canada. We applied an individual-based sampling and measured a suite of characteristics on focal trees and variables from their surrounding environment to analyze their impact on the individual tree responses. Namely, we aimed to determine which tree attributes (i.e., composition and structure) and soil properties (i.e., organic layer depth, soil texture, and chemical properties) mostly influenced the growth of the two tree species and their responses to temperature and insect epidemics of eastern spruce budworm (*Choristoneura fumiferana* Clem.) and forest tent caterpillar (*Malacosoma disstria* Hübn.). Our main working hypotheses were that greater tree species diversity, lower competition, and richer clay soils decrease boreal tree vulnerability to increasing temperatures and insect epidemics, and that sandy soils with faster drainage increase moisture limitations and exacerbate impacts of summer heat stress.

**Fig. 1.** Map of the study area with the 82 trees located on clay or sand surficial deposits in boreal forests of western Quebec, Canada (Ministère des Forêts, de la Faune et des Parcs 2020a). The inset map shows the study area relative to the La Sarre weather station.



## 2. Materials and methods

### 2.1. Study area

The study area extends from 49°09' to 49°12'N and 78°48' to 78°53'W within the clay belt of the black spruce-feather moss bioclimatic domain of western Quebec (Saucier et al. 2011) (Fig. 1). Forest stands in the study area are at a comparable successional stage, having established after a fire that had occurred in 1916 (Légaré et al. 2005). These stands are mostly dominated by black spruce and to a lesser extent by trembling aspen (*Populus tremuloides* Michx.) on clay surficial deposits and dominated by jack pine and black spruce on sand surficial deposits (Ministère des Forêts, de la Faune et des Parcs 2020a). The climate normals from 1991 to 2020 generated for the nearest weather station at La Sarre (48°47'N, 79°13'W, 244 m.a.s.l.) using ClimateNA show mean annual air temperature is 1.8 °C, with mean monthly temperatures of 17.6 and –16.8 °C for July and January, respectively (Wang et al. 2016). Total annual precipitation averages 836 mm, with 555 mm (66%) occurring as rain from April to November (Wang et al. 2016).

### 2.2. Double gradient of species diversity and soil texture

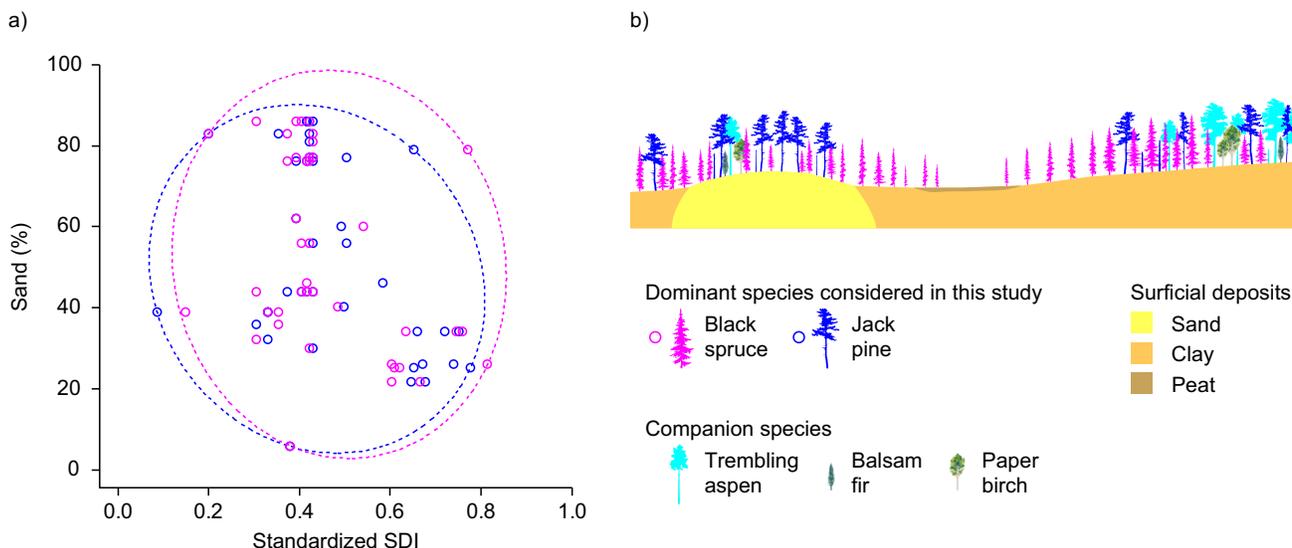
In a restricted study area (6 km × 6 km), we selected trees in nine forest stands providing a local gradient of different environments from low to high neighboring species diversity and from clay to sandy soil surficial deposits. Within this study area, we selected dominant or co-dominant trees ≥10 cm diameter at breast height (DBH) of two different species (black spruce and jack pine) in environments spanning a range of composition types (from pure to mixed-species stands according to basal area proportion) and over surficial deposits with a range of particle sizes (from clay to sand). Of the 128 selected trees, only 82 were sampled because they satisfied the following criteria: there were no signs of later disturbances in the encompassing environment relative to the 1916 large fire that originated in the stands and organic layer depth was <30 cm. As a result of our individual based sampling, we obtained the double gradient of species diversity and soil texture (Fig. 2).

### 2.3. Growth characteristics measured on focal trees

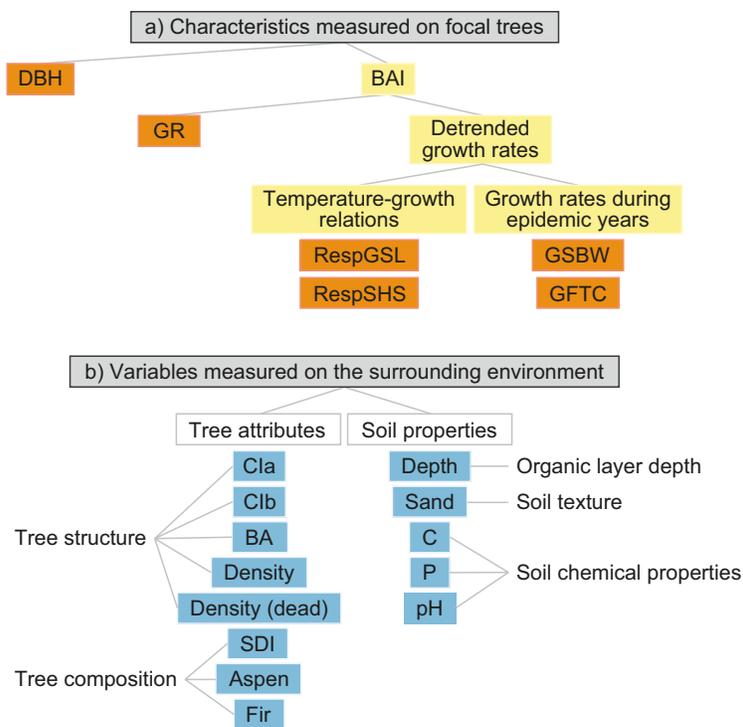
For each sampled tree (hereinafter “focal tree”;  $n = 82$ ), we measured a suite of characteristics (Fig. 3). For each focal tree, we recorded the species ( $n = 41$  black spruce and  $n = 41$  jack pine) and measured the DBH. To assess radial growth of each focal tree, we extracted increment cores taken ~20 cm from the ground. All cores were mounted on wooden supports and sanded and then scanned at 1200 dots per inch resolution to measure ring-widths series using the program *CooRecorder* 9.6 (Larsson 2020). We visually cross-dated and statistically verified ring dates using the programs *COFECHA* (Holmes 1983) and *Cdendro* 9.6 (Larsson 2020). For each ring-width series, we estimated the distance to pith to calculate basal area increments (BAIs) using the R package “*dplr*” (Bunn 2008). We estimated the cambial age for each series to identify the start of maximum sample depth ( $n = 82$ ) and omit juvenile growth in our analyses. This resulted in the period 1955–2018 with stable tree sample depth without juvenile growth. Using the chronologies of BAIs for black spruce and jack pine, we calculated average growth rates ( $\text{cm}^2 \cdot \text{year}^{-1}$ ) over 1955–2018 (hereinafter, “GR”).

To quantify associations between focal tree growth responses and interannual climate variability or growth responses and insect epidemics, we detrended individual BAI chronologies. Following a sensitivity analysis using splines of different lengths, we selected a 30-year spline to attenuate variation due to stand-level dynamics. Using the detrended BAI chronologies, we tested temperature–growth relations and compared the impacts of recorded insect epidemics on growth. Specifically, we focused temperature–growth relations on two surrogates of the growing season length and summer heat stress. These surrogates are two important temperature variables for tree growth in the study area (Chavardès et al. 2021) and were obtained by calculating the mean of average temperatures for April and September and June–August, respectively, between 1955 and 2018 at the La Sarre weather station with climate data generated us-

**Fig. 2.** (a) Double gradient of species diversity and soil texture visualized by the Standardized Shannon diversity index (standardized SDI or Shannon Equitability Index =  $SDI/\log(S)$ , measured on the nearest 30 trees) versus percentage sand content in the soil for the 82 trees, including black spruce ( $n = 41$ ) and jack pine ( $n = 41$ ). Dotted lines represent minimum spanning ellipses, including all data of one species. (b) Toposequence showing the two dominant and three companion species along with surficial deposits. [Colour online.]



**Fig. 3.** Summary of the sampling design for each (a) focal tree ( $n = 82$ ) and its (b) surrounding environment. We measured growth characteristics of focal trees (orange boxes) and environmental variables (blue boxes; only variables that were not excluded due to high multicollinearity according to Pearson’s correlation coefficients are shown). Growth characteristics were represented by diameter at breast height (DBH), average growth rates over 1955–2018 (GR), tree response to growing season length (RespGSL) or summer heat stress (RespSHS), and growth response during spruce budworm epidemics (GSBW) or forest tent caterpillar epidemics (GFTC). The selected environmental variables were organic layer depth (Depth), percentage sand content (Sand), total carbon (C), phosphorous (P), pH, competition indices a and b (Cia; Cib) and corresponding interspecific and intraspecific competition indices ( $Cia_{inter}$ ,  $Cib_{inter}$ ,  $Cia_{intra}$ , and  $Cib_{intra}$ ), total basal area (BA), total density (Density), total density of dead trees (Density (dead)), Shannon diversity index (SDI), total density of trembling aspen (Aspen), and total density of balsam fir (Fir). Yellow boxes represent procedures used to calculate growth characteristics. [Colour online.]



ing ClimateNA (Wang et al. 2016). The correlations between detrended individual BAI chronologies and growing season length or summer heat stress were used as an index of tree response to temperature (hereinafter, “RespGSL” and “RespSHS,” respectively). We calculated Pearson’s product-moment correlations functions using the R package “treeclim” (Zang and Biondi 2015).

To describe the impacts on radial growth by recorded spruce budworm and forest tent caterpillar epidemics in the study area, we first defined the intensity of epidemic years over the study area. We defined budworm epidemic intensity with a 9-year triangular impact (0.2, 0.4, 0.6, 0.8, 1.0, 0.8, 0.6, 0.4, and 0.2) (after Rossi et al. 2018) centered on 1974 (value = 1.0), the most widespread epidemic year during the 1970s in our study area. Forest tent caterpillar epidemic intensity was assigned to 1.0 for the years 1980 and 2001 and to 0.5 for the year 2000, according to recorded intensity of epidemics (Bergeron et al. 2002; Ministère des Forêts, de la Faune et des Parcs 2020b). To obtain an index of epidemic impact on the growth of specific trees, we calculated mean detrended BAI values weighted by intensity during budworm or caterpillar epidemic years for each tree (hereinafter, “GSBW” and “GFTC”, respectively).

## 2.4. Variables measured on the surrounding environment

We characterized the surrounding environment of each focal tree by establishing a cell including 30 neighboring trees using a modified n-tree design (Jonsson et al. 1992; Lessard et al. 2002). In each cell, we measured a suite of variables to characterize the environment (Fig. 3). We assessed the surrounding tree structure and composition based on the focal tree and its nearest 30 trees as follows. We measured the DBH of each tree or snag (DBH  $\geq$  5 cm) and distances from the focal tree to distal trees. For each distal tree, we recorded species (black spruce, jack pine, trembling aspen, balsam fir (*Abies balsamea* (L.) Mill.), or paper birch (*Betula papyrifera* Marsh.)) and status (live or dead). With these measurements, we calculated two competition indices (CI<sub>a</sub> and CI<sub>b</sub>) developed by Rouvinen and Kuuvulainen (1997) and a distance-independent competition index (CI<sub>c</sub>) as follows:

$$(1) \quad CI_{a_i} = \sum_{j=1}^{30} \frac{\left(\frac{d_j}{d_i}\right)}{L_{ij}^2}$$

$$(2) \quad CI_{b_i} = \sum_{j=1}^{30} \frac{\left(\frac{d_j}{d_i}\right)^2}{L_{ij}}$$

$$(3) \quad CI_{c_i} = \frac{\sum_{j=1}^{30} d_j}{30 d_i}$$

where CI<sub>a<sub>i</sub></sub>, CI<sub>b<sub>i</sub></sub>, and CI<sub>c<sub>i</sub></sub> are competition indices CI<sub>a</sub>, CI<sub>b</sub>, and CI<sub>c</sub>, respectively, for focal tree *i*; *d<sub>j</sub>* is the DBH of distal tree *j*; *d<sub>i</sub>* is the DBH of the focal tree *i*; and *L<sub>ij</sub>* is the distance between the focal tree and distal tree. To assess interspecific and intraspecific competition separately based on CI<sub>a</sub> and CI<sub>b</sub>, we calculated CI<sub>a<sub>inter</sub></sub>, CI<sub>b<sub>inter</sub></sub>, CI<sub>a<sub>intra</sub></sub>, and CI<sub>b<sub>intra</sub></sub>, respectively. For the 30 nearest trees from each focal tree, we calculated to-

tal basal area (m<sup>2</sup>·ha<sup>-1</sup>) and density (stems·ha<sup>-1</sup>) of living and dead trees and of dead trees only. With the recorded species information, we calculated the Shannon diversity index (SDI) (Shannon 1948) as follows:

$$(4) \quad SDI = - \sum_{h=1}^S p_h \ln p_h$$

where *p<sub>h</sub>* is the proportion of species *h* relative to the total number of individuals, and *S* is the total number of species. We calculated the total basal area and total density of trembling aspen trees around focal trees to assess whether presence of trembling aspen, the preferred diet of forest tent caterpillar (Nicol et al. 1997), could impact during caterpillar epidemics the growth of companion species like black spruce or jack pine. We also calculated the total basal area and total density of balsam fir trees around focal trees to assess whether presence of balsam fir, the preferred diet of spruce budworm, could impact the growth of black spruce, another host species of budworm (Hennigar et al. 2008). To assess soil properties in each cell, we determined the organic layer depth and collected a sample of the underlying soil surficial deposit (from 21 to 44 cm in depth depending on the organic layer depth) to measure percentage clay and sand content, an indication of soil texture, and to measure the following chemical properties: total C, total N, C/N, K, P, CEC, and pH.

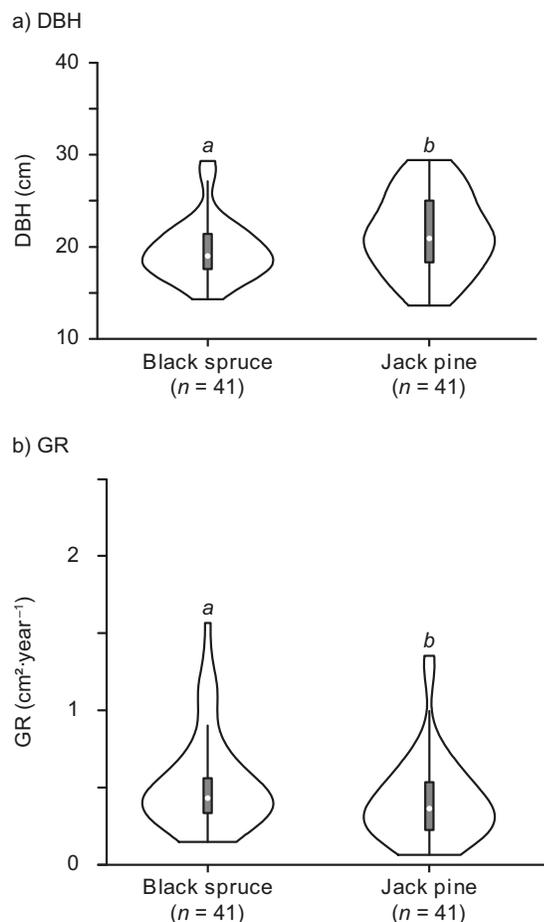
## 2.5. Statistical analyses

We assessed significant differences in individual tree growth responses between species by using viola plots and by conducting six Mann–Whitney rank sum tests due to some significant departures from normality. Specifically, we assessed for differences in median values between species for each of the six characteristics: DBH, GR, RespGSL, RespSHS, GSBW, and GFTC.

To describe associations among the variables measured on the surrounding environment (hereinafter, “environmental variables”), we calculated Pearson’s correlation coefficients among environmental variables for all 82 trees and for all trees by species. To address multicollinearity among environmental variables, we excluded those with high Pearson’s correlation coefficients ( $\geq$  0.80; Berry and Feldman 1985) from subsequent analyses (namely, percentage clay content, total N, C/N, K, CEC, CI<sub>c</sub>, total basal area of dead trees, total basal area of aspen, and total basal area of fir).

We fitted linear regression models including the species effect and interaction terms to assess associations between the six growth characteristics measured on the focal tree (DBH, GR, RespGSL, RespSHS, GSBW, and GFTC) and the remaining 17 environmental variables (organic layer depth, percentage sand content, total carbon, phosphorous, pH, CI<sub>a</sub>, CI<sub>b</sub>, CI<sub>a<sub>inter</sub></sub>, CI<sub>b<sub>inter</sub></sub>, CI<sub>a<sub>intra</sub></sub>, CI<sub>b<sub>intra</sub></sub>, total basal area, total density, total density of dead trees, SDI, total density of aspen, and total density of fir). We initially explored models with forward and backward stepwise selections with the MASS package in R (Venables and Ripley 2002). To obtain parsimonious models, we also removed iteratively non-significant variables (*p* values  $\geq$  0.05) from the final models if present. For all models,

**Fig. 4.** (a) Viola plots showing diameter at breast height (DBH) and (b) average growth rates over 1955–2018 (GR) of black spruce and jack pine. Significant differences between species were assessed by conducting Mann–Whitney rank sum tests. Different lowercase letters denote significant differences between median values ( $\alpha = 0.05$ ).



we assessed multicollinearity among variables by computing variance inflation factors with the VIF function of the CAR package in R (Fox and Weisberg 2019) and verified that model assumptions were met with regards to normality and homoscedasticity using Shapiro–Wilk and Breusch–Pagan tests, respectively, in addition to quantile–quantile and residual plots. We applied a VIF threshold of 5.0 (Zuur et al. 2010; Dorman et al. 2013) and threshold of  $p \geq 0.05$  for Shapiro–Wilk and Breusch–Pagan tests. Given heteroscedasticity in models using DBH, GR, and SBW, we applied transformations and used instead the inverse of DBH, the natural logarithm of GR, and the inverse of SBW.

### 3. Results

#### 3.1. Individual tree growth responses

Compared to jack pine, black spruce had significantly smaller DBH ( $p$  value = 0.038) (Fig. 4a) but higher GR ( $p$  value = 0.049 and  $p$  value < 0.001, respectively) (Fig. 4b). RespGSL was generally positive for both species but was sig-

nificantly higher for black spruce relative to jack pine ( $p$  value < 0.001) (Fig. 5a). RespSHS was mostly negative for spruce and positive for pine, leading to significantly different median values between species ( $p$  value < 0.001). GSBW was below average and significantly lower for black spruce relative to jack pine ( $p$  value < 0.001), whereas GFTC was not significantly different between species ( $p$  value = 0.441), with both species mostly displaying positive growth responses (Fig. 5b).

#### 3.2. Predictions of tree growth responses from environmental variables

Environmental variables describing surrounding tree attributes (i.e., composition and structure) and soil properties (i.e., organic layer depth, soil texture, and chemical properties) explained tree growth responses across linear regression models (Table 1). We present below the results for strongly significant models with  $p$  values < 0.001. For the five presented models, the proportion of variance explained (adjusted  $R^2$ ) ranged from 0.36 to 0.62.

Black spruce and jack pine DBH decreased significantly with greater intraspecific and interspecific tree competition (CIb;  $p$  values < 0.001) and higher soil sand content ( $p$  values  $\leq 0.020$ ) but increased significantly with greater surrounding trembling aspen density ( $p$  values  $\leq 0.004$ ) (model adjusted  $R^2 = 0.62$ ). For both species, GR decreased significantly with greater intraspecific competition (CIb<sub>intra</sub>;  $p$  values  $\leq 0.001$ ) but increased significantly with greater surrounding tree species diversity (SDI;  $p$  values < 0.001) (model adjusted  $R^2 = 0.36$ ). With black spruce, RespGSL increased significantly with greater diversity ( $p$  value < 0.001) (model adjusted  $R^2 = 0.37$ ) and RespSHS increased significantly with higher surrounding balsam fir density ( $p$  value = 0.001) (model adjusted  $R^2 = 0.42$ ). GSBW decreased significantly with greater intraspecific competition for black spruce ( $p$  value < 0.001) and decreased significantly with higher aspen density for jack pine ( $p$  < 0.001) (model adjusted  $R^2 = 0.46$ ).

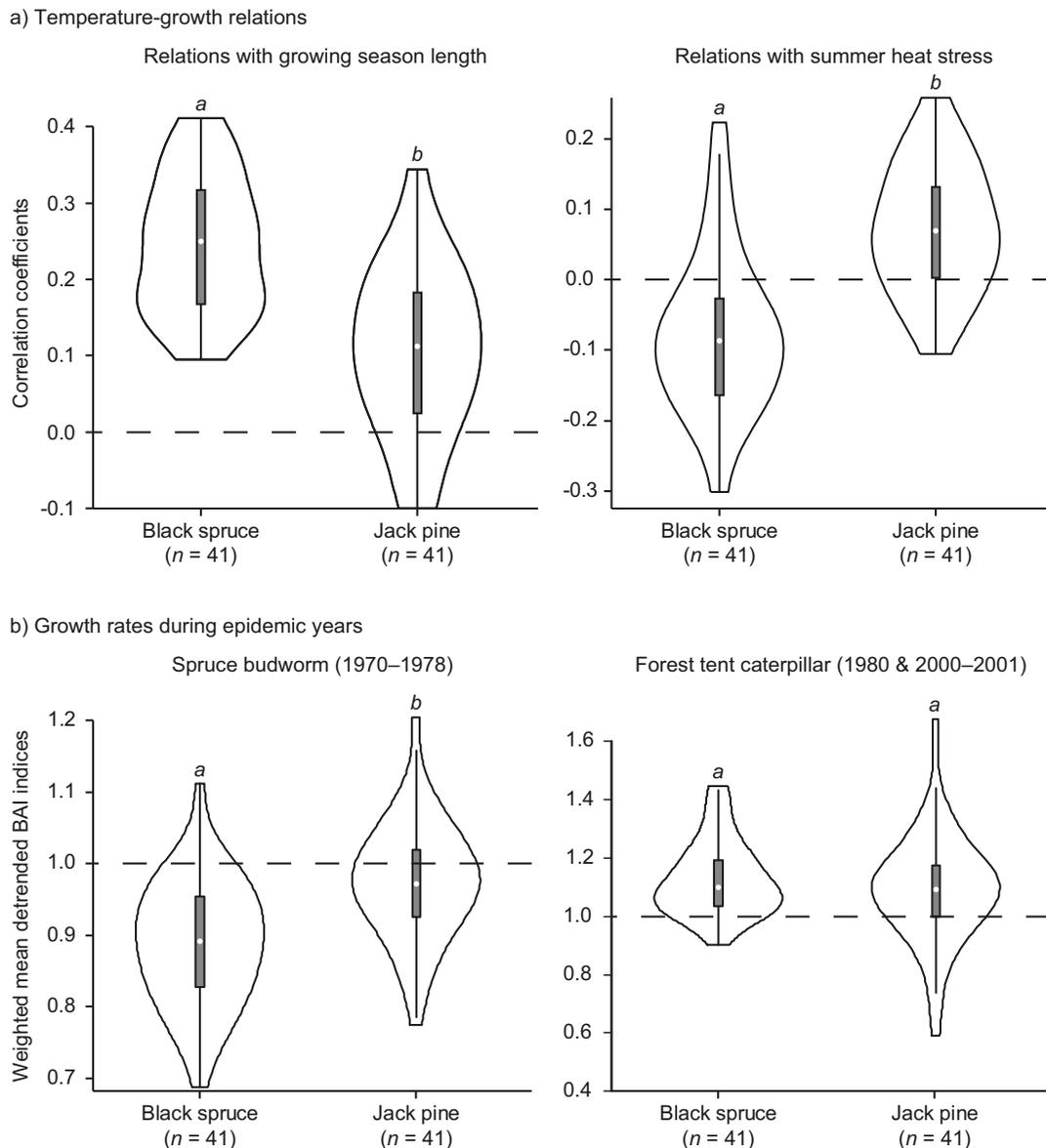
## 4. Discussion

Our approach based on a double gradient provided insights on boreal tree growth responses explained by life-history attributes, temperature, and insect disturbances and the importance of surrounding tree attributes and soil properties in predicting focal tree growth. We first discuss individual tree growth responses for each of the dominant boreal tree species, followed by our model interpretations that decipher the relative strength of surrounding environmental variables in explaining boreal tree growth.

#### 4.1. Explaining individual tree growth responses by species according to life-history attributes, temperature–growth relations, and insect epidemics

Individual tree growth responses for black spruce and jack pine were influenced by life-history attributes, temperature, and insect epidemics. In our study area, we found that jack pine generally had larger DBH than black spruce, likely due to

**Fig. 5.** Viola plots showing (a) temperature–growth relations for the detrended basal area increment chronologies of black spruce and jack pine with growing season length (mean average temperature values for April and September during the year of ring formation) and with summer heat stress (mean average temperature values from June to August during the year of ring formation) from 1955 to 2018 and (b) weighted mean detrended basal area increment (BAI) indices of black spruce and jack pine during epidemic years of spruce budworm or forest tent caterpillar. Significant differences between species were assessed by conducting Mann–Whitney rank sum tests. Different lowercase letters denote significant differences between median correlation values ( $\alpha = 0.05$ ).



differences in shade tolerance and initial growth rates following the 1916 fire. Compared to shade-tolerant black spruce, jack pine is shade intolerant (Burns and Honkala 1990). Following a disturbance like a high-severity stand-replacing fire, black spruce can establish, persist in the subcanopy, and grow slowly, whereas jack pine requires high initial growth rates following establishment to maintain its crown in the rising canopy with access to sunlight (Burns and Honkala 1990). From 1955 to 2018, jack pine growth rates decreased and were lower relative to black spruce, likely due to greater tree competition over time and age-related BAI decline.

We found that longer growing seasons benefitted black spruce more than jack pine, corroborating results by Hofgaard et al. (1999) who documented increased radial growth with warmer conditions during spring especially for black spruce. Warmer springs imply an earlier onset of the growing season, resulting in increased radial growth for both species (Boakye et al. 2021). Moreover, Chavardès et al. (2021) found that black spruce in the study area benefits from warmer temperatures during fall when the species is in mixed stands with trembling aspen. As aspen loses foliage during fall, neighboring black spruce receive more sun-

**Table 1.** Variable statistics for the linear regression models predicting growth characteristics of focal black spruce ( $n = 41$ ) and jack pine ( $n = 41$ ) by environmental variables.

Characteristic of the focal tree	Variable	Estimate	SE	<i>t</i> value	<i>p</i> value	Adjusted $R^2$
Inverse(DBH)	Intercept	0.021	0.004	4.81	<0.001	0.62
	Species:Spruce	0.015	0.006	2.76	0.007	
	Cib:Spruce	0.002	4e-4	5.28	<0.001	
	Cib:Pine	0.005	0.001	8.16	<0.001	
	Aspen:Spruce	-2e-5	5e-6	-3.29	0.002	
	Aspen:Pine	-1e-5	4e-6	-2.93	0.004	
	Sand:Spruce	1e-4	4e-5	2.38	0.020	
	Sand:Pine	1e-4	4e-5	2.76	0.007	
Ln(GR)	Intercept	5.526	0.182	30.39	<0.001	0.36
	SDI:Spruce	1.299	0.292	4.46	<0.001	
	SDI:Pine	1.076	0.242	4.45	<0.001	
	Cib <sub>intra</sub> :Spruce	-0.108	0.032	-3.34	0.001	
	Cib <sub>intra</sub> :Pine	-0.168	0.042	-4.03	<0.001	
RespGSL	Intercept	0.104	0.034	3.03	0.003	0.37
	SDI:Spruce	0.189	0.046	4.08	<0.001	
	SDI:Pine	0.006	0.045	0.13	0.900	
RespSHS	Intercept	0.071	0.016	4.28	<0.001	0.42
	Species:Spruce	-0.170	0.023	-7.31	<0.001	
	Fir:Spruce	0.001	3e-4	3.38	0.001	
	Fir:Pine	5e-5	3e-4	0.20	0.840	
Inverse(GSBW)	Intercept	1.049	0.017	60.61	<0.001	0.46
	Cib <sub>intra</sub> :Spruce	0.021	0.005	3.86	<0.001	
	Cib <sub>intra</sub> :Pine	-0.012	0.006	-1.98	0.051	
	Aspen:Spruce	1e-4	5e-5	1.50	0.138	
	Aspen:Pine	2e-4	7e-5	3.47	<0.001	

**Note:** Growth characteristics were represented by DBH, average GR over 1955–2018, RespGSL, RespSHS, and GSBW. Given heteroscedasticity in models using DBH, GR, and GSBW, we applied transformations and used instead Inverse(DBH), Ln(GR), and Inverse(GSBW). The retained environmental variables in the models were Species, Sand, Cib, Cib<sub>intra</sub>, SDI, Aspen, and Fir. All explanatory variables were tested considering interactions with species identity. Statistics include the variable coefficient estimate, standard error, *t* value, and *p* value, and the model adjusted  $R^2$ . DBH, diameter at breast height; GR, growth rates; RespGSL, tree response to growing season length; RespSHS, tree response to summer heat stress; GSBW, growth response during spruce budworm epidemics; Inverse(DBH), inverse of DBH; Ln(GR), natural logarithm of GR; Inverse(GSBW), inverse of GSBW; Species, species identity; Sand, percentage sand content; Cib, competition index b; Cib<sub>intra</sub>, intraspecific competition index b; SDI, Shannon diversity index; Aspen, total density of trembling aspen; Fir, total density of balsam fir.

light (Constabel and Lieffers 1996), and, when this coincides with seasonally warmer than average conditions, spruce radial growth may be prolonged due to the combined effect of light and temperature (Way 2011). Between species, black spruce showed a marked decrease in growth with warmer summers, an indication of summer heat stress, whereas jack pine did not. This finding likely reflects shallow black spruce rooting systems (Mekontchou et al. 2020) and low adaptability to dry atmospheric conditions (Marchand et al. 2021), indicating that spruce is more susceptible to summer heat stress and associated lower moisture availability in the soil and air, respectively. Conversely, jack pine growth could respond positively under moderate temperature-increase scenarios (Pau et al. 2022).

Black spruce was significantly impacted by the 1970s spruce budworm epidemic and presented generally above average growth alongside jack pine during the 1980 and 2000–

2001 forest tent caterpillar epidemics. Black spruce is not the preferred diet of spruce budworm (Hennigar et al. 2008), but its presence across stands in the study area is common relative to balsam fir, thus making spruce a ubiquitous target tree for budworm. Moreover, the 1970s generally coincided with warmer than average temperatures during the growing season in the region (Environment Canada 2022). These warmer temperatures may have induced an earlier budburst for black spruce during this decade, making them more susceptible to budworm attack (Bellemin-Noël et al. 2021). During the two forest tent caterpillar epidemics, non-host black spruce and jack pine may have benefited from severe reductions of growth in surrounding host trembling aspen in the study area (Chavardès et al. 2021). This latter finding suggests tree species diversity could attenuate some negative impacts from future forest tent caterpillar epidemics.

## 4.2. Importance of surrounding tree attributes and soil properties in explaining species-level growth responses

### 4.2.1. Impact of the surrounding environment on species-level DBH and growth rates

By analyzing DBH, alongside average growth rates during the last circa 60 years, we found that size and radial growth of black spruce and jack pine benefitted from surrounding species diversity but were limited by greater competition, notably of intraspecific nature. Black spruce, with its shade tolerance and shallow root system, is complementary with other species like shade intolerant and deeper-rooted jack pine or trembling aspen (Burns and Honkala 1990). For example, potential hydraulic lift from deeper-rooted species like trembling aspen (Way et al. 2013) can provide additional soil moisture to shallower-rooted species like black spruce. In addition, niche partitioning for the recovery of nitrogen (N) is documented by Houle et al. (2014), whereby black spruce recovers N from the organic layer, and jack pine recovers it from deeper mineral soils. Interestingly, jack pine DBH increased with higher density of surrounding trembling aspen. Aspen in the study area was commonly found on clay surface deposits but rarely found on sandy deposits, likely due to its susceptibility towards root damage from fire on sandy deposits with faster drainage and thus lower moisture content (Zasada et al. 1992). Live trembling aspen on rich clay surface deposits grows well in the study area, implying that surviving shade-intolerant jack pine also needs to grow well to compete for sunlight access (Longpré et al. 1994). On less rich and more xeric sandy deposits, jack pine and black spruce growth was limited and reflected in smaller DBH.

### 4.2.2. Impact of surrounding tree diversity on black spruce growth responses to temperature

We found positive black spruce responses to longer growing seasons with greater surrounding tree species diversity. We also found that spruce growth benefits from surrounding balsam fir when summers were warmer. Our findings corroborate other research showing that diversity can mitigate impacts from increasing temperatures on forest growth (Hisano et al. 2018, 2019; Fichtner et al. 2020; Searle and Chen 2020). In the same study area, growth rates of black spruce are higher during longer growing seasons in mixed stands with trembling aspen (Chavardès et al. 2021). Moreover, diverse stands including balsam fir could benefit spruce growth during unfavorable periods such as warm summers because of how fir recycles nutrients efficiently, thereby enhancing soil productivity and tree growth (Nagati et al. 2019). The presence of fir and its mycorrhizal associates in the study area (Nagati et al. 2019) could also retain ground moisture more efficiently (Augé et al. 2001), thereby supporting black spruce during periods of higher heat stress. These interpretations promote the benefits of greater tree species diversity within stands and forests in the context of increasing temperatures,

at least for black spruce. Indeed, diversity could better sustain ecosystem functioning and enhance resilience to rising summer temperatures (Hisano et al. 2018).

### 4.2.3. Surrounding tree structure explains species-level growth responses to spruce budworm

During the 1970s spruce budworm epidemic, black spruce growth was limited in cells with greater intraspecific competition, an indication that increased presence of surrounding host spruce with crowns more likely to be in contact facilitated budworm diffusion (Régnière and Fletcher 1983). The effects of such contact could amplify the severity of budworm epidemics should spruce budburst and budworm emergence synchronize (Bellemin-Noël et al. 2021). During the budworm epidemic, higher jack pine growth was predicted by lower surrounding trembling aspen density. Our finding suggested that non-host jack pine responded positively with fewer surrounding non-host trees competing for resources. These interpretations underscored that tree responses to epidemics were spatially heterogeneous and influenced by surrounding tree structure and composition.

## 5. Conclusion

Our findings highlighted how stand composition and structure could play key roles in influencing the vulnerability of boreal forests to anticipated changes in climate. Notably, promoting tree species diversity and limiting intraspecific tree competition were emphasized in our models as enhancing growth of focal trees regardless of the focal species. Our findings complemented those of Jucker et al. (2020) who review the benefits of boreal tree diversity towards growth because of niche complementarity and those of Wu et al. (2012) who advocate for lower stand densities to mitigate impacts on growth and tree mortality from anticipated droughts. We also found that sandy soils with faster drainage limited growth of black spruce and jack pine, an indication that increased moisture stress could affect growth of these tree species in the future, although the impact would likely vary under different climate change scenarios (Pau et al. 2022). Our research revealed complex interactions across the double gradient of tree species diversity and soil texture but generally support management practices that maintain or enhance tree species diversity and mitigate intraspecific competition to decrease forest vulnerability to anthropogenic climate change and its indirect influence on insect disturbances.

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### Data availability

The data that support this study are archived at the International Research Laboratory on Cold Forests and will be shared upon reasonable request to the corresponding author.

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RDC, LB, PG, HM, YB, and FG conceptualized the project. RDC wrote the original draft. RDC collected data. RDC and FG conducted formal analyses. RDC, LB, PG, HM, YB, and FG acquired funding. YB and FG provided supervision. VP provided resources and visualization. All authors reviewed manuscript drafts and gave final approval for publication.

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### Competing interests

The authors declare there are no competing interests.

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