

Large, near-term increases in climate-induced tree growth may help offset impacts of increasing disturbance across Canadian boreal forest

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Abstract

Large projected increases in forest disturbance pose a major threat to future wood fibre supply and carbon sequestration in the cold-limited, Canadian boreal forest ecosystem¹⁻⁴. Given the large sensitivity of tree growth to temperature, warming-induced increases in forest productivity have the potential to reduce these threats, but research efforts to date have yielded contradictory results attributed to limited data availability, methodological biases, and regional variability in forest dynamics⁵⁻⁸. Here we apply a novel machine-learning algorithm to an unprecedented network of over 1 million tree growth records from 18,715 permanent sample plots distributed across both Canada and the US, spanning a 16.5°C climatic gradient, and project the near-term (2050s time period) growth of the six most abundant tree species in the Canadian boreal forest. Our results reveal a large, positive effect of increasing thermal energy on tree growth for most of the target species, leading to 40-52% projected gains in growth with climate change under RCP 4.5 and 8.5. The magnitude of these gains, which peak in the colder and wetter regions of the boreal forest, suggests warming-induced growth increases should no longer be considered marginal, but may in fact significantly offset some of the negative impacts of projected increases in drought and wildfire on wood supply and carbon sequestration and have major implications on ecological forecasts and the global economy.

Main

The Canadian boreal forest—comprising one third of the global boreal forests and over 8% of the world's forests—is one of the few remaining intact natural biomes^{9,10}. Its growth is an important regulator of global atmospheric carbon flux¹¹ and sustains the largest softwood lumber and newsprint industry in the world¹².

Unfortunately, Canada's boreal forest is expected to be disproportionately affected by global warming as temperatures raise faster at higher latitudes^{4,13}. Future warmer, drier conditions are projected to intensify the natural fire regime, with dire consequences on the goods and services the boreal forest provides^{14,15}. Current estimates suggest that growth increases of 50% or more may be necessary to offset future wood fibre and carbon losses from fire in the boreal^{2,16,17}. However, future warming may also have potential to accelerate the productivity of the boreal forest, currently limited by its cold climate^{6,18,19}, which could help offset increases in disturbance²⁰. The potential benefit of enhanced growth trends remains controversial and overlooked, mainly because of limited data availability, methodological biases, and regional variability in forest dynamics⁵⁻⁸. Indeed, large discrepancies reported between empirical tree growth observations and dynamic vegetation models suggest substantive inaccuracies in our ability to predict growth in response to climate²¹⁻²⁴. Yet, our capacity to anticipate the future health of the boreal forest, and its recovery from intensifying disturbances, hinges on our ability to accurately project future boreal growth.

Today, process-based, dynamic vegetation models are the standard approach to project the impacts of climate change on forest growth^{24,25}. However, many are limited by overly simplistic assumptions of tree ecophysiology and population dynamics^{26,27}. Notably, optimal tree growth is typically expected to occur under climates found at the center of a species geographical range, declining towards the edges. Unfortunately, this approach tends to ignore the complex, non-linear nature of tree growth, controlled by interacting climate variables such as temperature and precipitation⁵, that may be further modulated by tree size^{28,29}, age³⁰, crown position³¹, genotype³², competition^{33,34}, and soil moisture conditions³⁵. Consequently, more robust, empirically derived estimates of climate-growth relationships are needed to refine models and improve ecological forecasts to inform adaptive forest management strategies.

Up to now, matching annual tree ring widths with historical climate has been the preferred approach to estimate empirical, species-specific climate-growth relationships in the boreal^{7,36,37}. However, such approaches are subject to several critical biases^{38–40}. The largest being missing information on past changes in forest stand conditions, referred to as the ‘fading record’ problem, which can lead to false attribution of long-term growth changes to climate when, in fact, it may be more related to forest stand dynamics⁴¹. Moreover, tree ring studies unintentionally tend to sample fast-growing trees in young plots and slow-growing trees in old plots, which can mistype or exaggerate growth changes^{40,42}. Only recently have researchers begun to explore an alternative approach: leveraging the broadly distributed, repeatedly measured, forest permanent sample plots (PSPs) networks that cover wide climatic gradients and the geographical ranges of most boreal tree species in North America. This novel use of ‘old’ plot networks—initially established for forest inventory purposes—is not burdened by the same biases as tree ring sampling⁷, but no study has yet merged all major available sample plot networks from both the US and Canada to provide a more definitive evaluation of boreal tree species climate sensitivity across their native range.

In this study, we compiled over 1 million tree growth records from 18,715 permanent sample plots (Fig. 1a), spanning a 16.5°C climatic gradient distributed across both Canada and the US to study the influence of climate on tree growth for the six most abundant boreal tree species in North America, including balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). Specifically, we used a novel machine learning algorithm—boosted regression tree (BRT) analysis—to disentangle non-linear and interacting climatic controls on tree growth, while controlling for tree size, competition with neighboring trees, topography, and soil characteristics. Fitted, species-specific BRT models were then used to predict the future growth of the Canadian boreal forest under different climate forcing scenarios for the near-term 2050s time period. By including growth observations in our training

data that extend beyond the boreal forest into each species' warmer, southern range limits, it permitted us to simulate the growth response of most of Canada's boreal forest to projected climate change without extrapolating beyond the observed climate-growth inference space (Fig. 1b).

Drivers of boreal tree growth

The fitted BRT models had good explanatory power, with pseudo- R^2 ranging between 32.8% (white birch) and 54.8% (jack pine) on the training data (Extended Data Table 1). Model error (NRMSE; see Methods) remained low, ranging from 13.6% (jack pine) to 18.5% (white birch).

For each tree species, at least one of the thermal-related climate variables (i.e. $T_{\text{max}_{\text{summer}}}$, $T_{\text{min}_{\text{winter}}}$ and FFP) ranked among the three strongest predictors of growth (Extended Data Table 1). Of these, $T_{\text{max}_{\text{summer}}}$ and FFP (both indicators of growing season heat availability) were most influential, but their effect on growth varied by species (Fig. 2). White spruce was the only species to display a clear temperature optimum, with large positive warming effects up to a $T_{\text{max}_{\text{summer}}}$ of 22.5 °C, followed by growth declines under warmer summer temperatures (Fig. 2a). Remaining species either maintained a positive growth response to warming across all summer temperature gradients (balsam fir, jack pine, white birch), or their growth alternated between positive and neutral responses to additional heat (aspen, black spruce), but none displayed negative growth responses to warming. Winter temperature had lower RI values than $T_{\text{max}_{\text{summer}}}$ or FFP for all species but jack pine (Extended Data Table 1), whose growth increased under warmer winter temperatures (Extended Data Fig. 1).

Summer precipitation had a general, positive influence on the growth of all species (Fig. 2c), which increased under higher temperatures, revealing a strong interaction between precipitation and temperature (Friedman's H-statistics > 0.1; Fig. 2e). White spruce was the most sensitive to precipitation-related variables, with large growth reductions under low PPT_{summer} gradients (BAI of 10 $\text{cm}^2\cdot\text{year}^{-1}$ when $PPT_{\text{summer}} > 400$ mm to 6 $\text{cm}^2\cdot\text{year}^{-1}$ when $PPT_{\text{summer}} < 210$ mm). Moreover, its large growth decline under high temperatures was only marginally offset by higher precipitation (Fig. 2e). Aspen displayed a continuous, positive response to increasing PPT_{summer} (Fig. 2c) which was strongest under higher temperatures ($T_{\text{max}_{\text{summer}}}$ above 25 °C; Fig. 2e). Jack pine displayed the weakest interaction between temperature and precipitation. Precipitation as snow (PPT_{snow}) displayed higher RI scores than PPT_{summer} for all species but white spruce. However, PPT_{snow} impacts on growth were inconsistent across species (Extended Data Fig. 1). Only jack pine displayed a clear PPT_{snow} optimum, with growth peaking under 270 mm of snow, while other species displayed little change (balsam fir, black spruce, white birch) or complex responses with changing snow levels (e.g., white spruce and aspen).

Tree size (i.e. DBH) was the strongest predictor of growth in all species models and displayed a positive, linear effect on growth for all species (Extended Data Table 1; Extended Fig. 1). Interestingly, its effect varied with temperature, where larger trees displayed stronger warming gains in growth relative to smaller trees (Extended Data Fig. 2; Supplementary Text 1). Competition (BA) was the 3rd most important model predictor across species, and had a consistently, strong suppressing effect on tree growth (Fig. 2d). Competition levels also affected temperature responses, as positive warming effects were overall stronger under conditions of low competition (Fig. 2f; Supplementary Text 1).

For all species but black spruce, site conditions (i.e., slope, aspect, and soil moisture regime) had only minor influence on growth, with overall low RI scores (0.06 to 5.73, ranking between 4th-10th; Extended Data Table 1). Similar to other species, black spruce displayed lower growth on hydric soils (Extended Data Fig. 1), but soil moisture regime had a stronger influence on black spruce growth (RI = 19.44) relative to other species. The high RI of soil moisture regime on black spruce growth is likely due to the greater prevalence of black spruce in wetlands relative to other species. For example, in Ontario, Canada, black spruce made up 96% of study trees found in wetlands (within the hydric soil moisture class).

Projected growth under climate change

When we applied the fitted BRT models to future climate projections, we observed an average increase of 40-52% in the combined growth of all studied species over the next 30 years (for the 2050s) across the boreal forest under RCP 4.5 and 8.5. Due to similarity in projected responses between the two climate forcing scenarios, hereafter we focused only on results from RCP 8.5.

The large overall positive growth responses reported here varied substantially among regions. The eastern Canadian boreal region displayed the highest gains in growth, with a projected 80% increase in growth over the Boreal Shield East ecozone for the 2050s driven by the abundance of black spruce, balsam fir and jack pine (Fig. 3). One exception was the boreal portion of the Atlantic Maritime ecozone, projected to display much lower growth gains of 12%, likely associated with the relatively warmer and wetter baseline climate condition and lower projected warming. In Central Canada, the Boreal Plains and Boreal Shield West displayed moderate gains of 33 to 45%, respectively, driven by growth increases from jack pine (in the Boreal Shield West), black spruce and aspen (Fig. 3). The net gain in growth in the Boreal Plains was reduced by the poor performance of white spruce in the region. Finally, growth in the high-latitude, westernmost Taiga Plains ecozone was projected to increase by more than 56% on average, due to large increases in aspen growth and moderate increases in white spruce growth (Fig. 3).

These growth trends across ecozones are due, in part, to species-specific performances under baseline and future climate conditions (Fig. 3). Across all ecozones, balsam fir ($64\pm 53\%$; median \pm SD and hereafter), jack pine ($50\pm 155\%$) and aspen ($43\pm 29\%$) displayed the highest median gains in growth under RCP 8.5, relative to baseline climate, followed by black spruce ($37\pm 48\%$), white birch ($24\pm 64\%$) and white spruce ($7\pm 103\%$). Still, species responses varied spatially within ecozones (at the ecodistrict level) and across ecozones. In the eastern boreal region (east of 80°W), all species were projected to accelerate their growth by $2\pm 220\%$ (white spruce) to $105\pm 241\%$ (jack pine; Fig. 4). In the same region, growth increases were maximal north of 50°N , with larger gains of $101\pm 52\%$ (black spruce) to $508\pm 233\%$ (jack pine), and more moderate gains of $71\pm 329\%$ for white spruce and $46\pm 58\%$ for aspen (Fig. 4). In Central Canada ($80\text{--}100^\circ\text{W}$), jack pine, balsam fir and aspen were projected to experience large, homogeneous gains in growth ranging between $44\pm 24\%$ (aspen) and $76\pm 30\%$ (balsam fir), while black spruce ($23\pm 50\%$) and white birch ($20\pm 26\%$) displayed latitudinally contrasted growth responses with gains in northern cold ecodistricts and declines in warmer, drier ecodistricts within the Boreal Shield West ecozone and the western portion of the Boreal Shield East ecozone (Fig. 4). On the contrary, no significant change in median white spruce growth was expected ($+6\pm 21\%$) in the central region, despite some localized growth declines up to 60%. Similar trends were observed in western regions (west of 100°W), although several species displayed marginal growth anomalies in ecodistricts bordering the Rocky Mountains within the Taiga Plains and Boreal Plains ecozones (Fig. 4).

Discussion

The results presented in this study confirm the strong role of temperature and water availability as drivers of boreal tree growth. The overall large, positive relationship between thermal energy (warmer but also longer growing season) and growth supports earlier findings from controlled experiments^{43,44}, remote sensing observations^{8,19}, tree-ring analyses¹⁸, and forest inventory approaches^{45,46}. Temperature is critical to many biochemical processes such as photosynthesis, which can benefit from warming in cold ecosystems due to quicker enzymatic functions, leading to higher carbon assimilation⁴³. Additionally, warming-induced lengthening of the growing season expands the growing period and allows earlier leaf-flush in deciduous species, which can stimulate carbon sequestration⁴⁷. Here, in the cold-limited boreal forest, climate warming is likely to promote C assimilation, nutrient uptake, and C sequestration, leading to greater radial growth^{4,8,48,49}. However, our analysis also highlights the strong control of local water availability on the growth trajectory of boreal trees in response to warming, consistent with previous research from in situ experiments³⁵, tree-ring analyses^{5,36,50,51}, forest inventory approaches^{52,53} and remote sensing observation^{19,54}. Warming-induced increases in atmospheric vapor pressure deficit can inhibit photosynthesis and carbon uptake, with higher risks of carbon starvation and hydraulic failure due to decline in stomatal conductance^{55–57}. Similarly, increases in temperature-induced evaporation may cause water stress, reductions in turgor pressure, stomatal closure, and decline in photosynthesis and

carbon uptake^{35,58}. This warming-induced water stress, along with increasing respiration cost, has been reported to dampen tree growth and increase risks of tree mortality in different regions^{59–62}.

The overall large gains in growth projected here for most of the Canadian boreal forest, especially in the eastern, wetter region, do not suggest a strong moisture limitation for most of this ecosystem in the near-term (2050s) under climate change. Our conclusions are in line with recent observations of positive growth trends in boreal and temperate forests^{6,8,19,37,45,46,63,64}, as well as earlier growth projections from empirical⁵ and modeling approaches^{22,24}, but contradict other studies^{65–68}. Such divergences may be due to certain limitations inherent to the approaches used to confront this complex issue. Process-based, dynamic vegetation models rely heavily on leaf-level processes^{26,27}, which tend to produce substantive inaccuracies in predicting tree growth responses to climate²⁴, while growth projections from tree-ring data tend to confound historical forest stand development processes with climate effects on growth^{38–42}. Here, despite their coarser time resolution and higher cost in data acquisition, well-replicated permanent sample plots offer an exhaustive, more accurate portrait of climatic regulation on boreal tree growth.

Within our overall projection of growth enhancement across the boreal forest, large discrepancies were observed among regions which tracked local variations in hydroclimate and species composition^{4,6,8}. The projected trend of greater gains in growth at higher latitudes, in line with previous research, is likely caused by the stronger current thermal limitation on growth in colder boreal regions, combined with higher projected rates of climate warming^{5,54,69}. We also report a longitudinal trend in growth responses, where wetter eastern ecozones displayed the largest growth gains, and drier, central ecozones the least, including marginal declines, suggesting drier parts of the boreal biome will become more vulnerable to growth reductions under warming^{18,19,70,71}. The marginal decline observed in some western and southern ecodistricts is likely associated with a drier moisture balance combined with limited increases in precipitation. The reduced gains in central Canada may also be attributed in part to the higher proportion of white spruce, which is the only species studied here to display a rapid growth decline in the near-term, in agreement with multiple empirical studies^{5,72,73}. White spruce growth decline has been repeatedly associated with high temperatures in excess of the species physiological thresholds^{74,75}. Among the six species studied here, white spruce also displayed the highest sensitivity to low water availability, in line with recent reports of drought-induced growth decline, and even mortality, in central and western Canada for that species^{72,73,76–78}.

Climate driven increases in rates of natural disturbances are expected to have a growing impact on boreal forest wood supply and carbon storage³. Notably, significant reductions in forest cover are projected

following forest regeneration failure from successive disturbances^{79–81}, or combinations of disturbances⁸². However, our growth projections (40–52% on average across Canada's boreal ecozones) are much higher than reported by previous studies⁵ and are in line with the magnitude of future growth required to offset wood fiber and carbon losses from increasing fire in the boreal forest^{2,16,17}, especially in Eastern Canada¹. The acceleration of growth in black spruce, jack pine and aspen reported here is particularly noteworthy given these species have been identified as most vulnerable to future intensification of drought in south-central Canada (aspen) and fire in central and eastern Canada (black spruce and jack pine)¹. Even so, our projections should be interpreted carefully as they do not include future changes in forest properties such as composition, age, disturbance rates, or account for genetic variations within species across their geographic range, which can influence forest level responses to climate change^{1,4,30,32}. We also emphasize that growth is but one of several processes, such as recruitment and mortality, that drive forest-level productivity and demographics, and therefore must be interpreted accordingly. However, some of the plots which we excluded from our analysis due to excessive mortality could have suffered severe climatic anomalies such as the 2001–2002 drought in Central Canada⁸³, leading to potential underestimation of their impact on growth. Such events are important catalysts of forest type transitions but were relatively rare (less than 0.1% of sites were excluded due to excess mortality) and species-specific growth rates remain a critical predictor of post-disturbance recovery⁸⁴. Lastly, it is critical the empirically derived estimates of climate-growth relationships presented here be used to benchmark and parameterize process-based, dynamic vegetation models to help improve ecological forecasts and inform adaptive management strategies⁸⁵. Contrary to previous studies, our results suggest the effects of climate change on boreal forest growth may be highly underestimated in the near term (2050s), which could have major ramifications on future wood fibre supply, carbon storage and global economy.

Methods

Study area

Our study spans a wide environmental gradient, mainly encompassing the boreal and northern temperate forests of eastern and central North America (Fig. 1a), covering a large extent of the geographical range of boreal tree species. Climate ranges from subarctic in the north, with cool, short summers and long, cold winters, to temperate in the south, with hot summers and mild winters, covering a wide gradient in mean annual temperature (-4.9 to 11.6°C), precipitation (350.5 to 1959.4 mm), and frost-free period (56.4 and 178.8 days). The boreal forest is dominated by cold-adapted tree species, such as white spruce, black spruce, balsam fir, trembling aspen and white birch, but our study area also includes the southern range of these boreal species, where they co-occur with warmer-adapted temperate tree species such as red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*) and eastern hemlock (*Tsuga canadensis*). In addition to management, boreal forest dynamics are driven by large-scale disturbances such as wildfires and insect outbreaks, along with pathogens, wind, flooding and ice storms, with varying intensity and frequency across regions and forest types⁴.

Data and sampling design

We obtained forest stand and tree information from repeatedly-measured PSPs distributed across eastern and central North America, including the US Forests Inventory and Analysis (FIA) program (31 eastern states), Canada's National Forest Inventory (NFI) program, as well as the Canadian PSPs programs from the provinces of Nova Scotia, New Brunswick, Quebec, Ontario, Manitoba, Saskatchewan, and Alberta. Note that remeasurements from NFI plots were not yet available during this analysis, but these plots were used to project future growth (described later in Methods). All PSPs follow fixed radius plots designs. Plot design and sampling procedures are consistent among US FIA plots, but vary across Canadian jurisdictions⁸⁶⁻⁹³. Thus, for all plot measurements, the following plot and tree selection procedures were applied to standardize and compile all observations into a single, comprehensive database. We included plots with known location, which had been remeasured consecutively, and which contained at least one of the study species. We excluded suppressed trees and disturbed plots for which growth can be limited by non-climatic factors. To identify suppressed trees, missing canopy position data for some jurisdictions led us to compute for each tree the basal area of larger trees (BAL)⁹⁴, where dominant trees tend to display low BAL values. The distribution of BAL values in plots for which canopy position data was available showed $BAL \leq 17.4 \text{ m}^2 \cdot \text{ha}^{-1}$ in 75% of dominant-codominant trees. Trees with BAL values above that threshold were considered suppressed and excluded. Plots with known severe natural (e.g. insects, disease, fire) or anthropogenic (silviculture) disturbance history were also excluded. In the absence of disturbance records, we excluded plots with unusually high annual mortality rates (i.e., above 4%)⁹⁵. This selection procedure excluded 84.8% of initial plots, where 18,715 repeatedly measured PSPs (Fig. 1a), 388,816 individual trees, and 1,055,413 tree measurements remained for further analysis. The selected PSPs are well distributed among all forested ecozones in Canada's boreal forest east of the Rockies, from the cool and wet Atlantic Maritime ecozone to the cold and semiarid in Taiga Plains ecozone (Fig. 1a).

Response variable

Annual basal area increment (BAI, in $\text{cm}^2 \cdot \text{year}^{-1}$) was considered as our response variable, as it is an important indicator of tree species performance and commonly used to quantify tree growth in boreal forests⁵. The annual BAI of each individual tree was calculated as the difference in basal area between two successive measurements over the time interval between plot measurements in years. Anomalous BAI values of each species were removed using Tukey's approach, where outliers were defined as values more than three times the interquartile range from the quartiles of the species-specific BAI distribution. Following this procedure, less than 3% of records of each species were removed. Alternative outlier detection methods including random sampling, visual examination, as well as exclusion of values outside the 95% percentile across species-specific BAI distributions had no impact on our modelling results.

Explanatory variables

Climate

Historic climate data used to train species-specific BRT models for each specific plot location and measurement interval was obtained from 1-km resolution interpolated climate grids provided by Natural Resources Canada⁹⁶. To assess the control exerted by heat on tree growth, mean maximum summer temperature ($T_{\max_{\text{summer}}}$; May-September; range: 16 to 30 °C), mean minimum winter temperature ($T_{\min_{\text{winter}}}$; January-March; range: -33 to -5 °C) and frost free period (FFP; range: 45 to 179 days) were calculated, since they are well-correlated with tree growth during the growing season²⁵, restrict growth in colder environments^{97,98}, and are commonly used to evaluate the impact of growing season length on growth, respectively. Species geographical distributions along the range of these variables was generally similar (Extended Data Fig. 3).

Mean summer precipitation (PPT_{summer} ; May-September; range: 217-880 mm) and precipitation as snow (PPT_{snow} ; January-March; range: 23-917 mm) were calculated to assess the control of water availability on growth. PPT_{summer} is a hydrologic index well-correlated with growing season water availability that impacts tree growth⁹⁷. PPT_{snow} was used to account for the long-lasting effects of spring snowmelt on growing season water availability, estimated as the total snowfall from January to March. Balsam fir, white birch and black spruce were more abundant at high PPT_{summer} (median values of 500, 486 and 454 mm, respectively) than other species (median values of 395 - 409 mm; Extended Data Table 1). Similar distribution patterns were displayed along January to March snowfall among species (Extended Data Fig. 3). However, balsam fir, white birch and black spruce were more abundant at high snow amounts (median values of 289-338 mm) than other species (median values of 134-182 mm; Extended Data Table 1). At each plot, climatic variables were averaged over the period between successive measurements (e.g. the interval between the i^{th} and $i+1^{\text{th}}$ measurements) to obtain interval-specific climate estimates.

Stand characteristics

Slope inclination and aspect, which influence the amount of solar radiation reaching the forests, were calculated from a 1 arc second (approximately 30 m) resolution digital elevation model (DEM) provided by the US Geological Survey (<https://viewer.nationalmap.gov/basic/>) for Canadian PSPs, but derived from actual plot records for the US FIA plots. All calculations were completed in R⁹⁹ using the raster package¹⁰⁰. The majority of plots were located on relatively flat sloped landscapes (median value of 2% and 95th percentile of 16%; Extended Data Fig. 3). Aspect was determined as a continuous variable, then

transformed as one of three categories: 1) SE-SW (corresponding to the warm aspect); 2) NW-NE and flat (cold aspect); 3) SE-NE and SW-NW (moderate aspect). All tree species were most abundant on moderate versus cold or warm aspects (Extended Data Fig. 3).

Soil moisture regime can have strong effects on nutrient availability, root distribution, photosynthesis rate and thus mediate tree growth^{35,101}. We derived an index of the local soil moisture regime for each PSPs using physiographic class (US PSPs) or from plot field observations of soil moisture and/or drainage, texture, and organic matter composition (Canadian PSPs). Records of soil moisture regime from all PSPs were standardized and transformed into one of three categories: 1) xeric (dry site); 2) mesic; and 3) hydric (wet site). Species were most common on mesic sites, except jack pine, which was more frequent on xeric sites (63% of sampled jack pine trees) and black spruce, which was more common on hydric sites than other species (Extended Data Fig. 3).

Competition

Although our analysis was limited to dominant and codominant trees, we calculated a plot-level competition index (BA) to account for competition for resources from neighboring trees. For each plot and corresponding measurement, BA was computed as the sum of all individual basal areas for trees with a diameter at breast height (1.3 m, DBH) ≥ 9 cm, scaled to a hectare (units of $\text{m}^2 \cdot \text{ha}^{-1}$). Competition levels and their distribution was similar across species, with median BA values ranging between 17.7 (black spruce) and 28.4 $\text{m}^2 \cdot \text{ha}^{-1}$ (white spruce; Extended Data Table 1 and Extended Data Fig. 3).

Tree size

Tree diameter at breast height (DBH, referred to hereafter as tree size), was used to control for tree size effects on growth, as size is highly correlated with tree growth and mediates climate-growth relations²⁹. The distribution of DBH was similar across all sampled species (Extended Data Fig. 3), although white spruce tended to be larger (median values of 23 cm) than other species (median values extending from 13 to 18 cm; Extended Data Table 1).

Model fitting and performance

A description of the response and explanatory variables can be found in Extended Data Table 2. To investigate the effects of climate on tree growth while controlling for endogenous (e.g. tree size) and site-level conditions (e.g. plant competition, soil moisture regime, slope and aspect), we employed boosted

regression tree (BRT) analysis. BRT analysis is a machine learning, ensemble modeling method in which many simple regression trees, generated using recursive binary splits based on the explanatory power of a single variable (or predictor) at each split, are fitted in a step-wise manner¹⁰². BRT analysis accommodates many of the violations of conventional, parametric statistics (e.g., multiple linear regression) that are common to ecological data, including missing data, departures from normality and homogeneity of variance, and strong collinearity among explanatory variables¹⁰². While BRT has been shown to outperform other tree-based machine learning methods in predictive performance tests¹⁰³, we did try other machine learning approaches, including the random forest algorithm, but found minimal differences, and chose to focus on BRT analysis to reduce complexity and ease interpretation of models.

All BRT models were fitted using the R *gbm* package¹⁰⁴. Individual BRT models were fitted for each tree species to uncover species-specific climate controls on growth. To produce unbiased estimates of model performance, the data was split into training (80% of initial data) and test sets (remaining 20%). We used BAI as the response variable assuming a Gaussian distribution. The species-specific BRT models were first “tuned” by searching the optimum combination of model hyperparameters, including learning rate (shrinkage: 0.001, 0.05, 0.1), number of trees (n.trees: 1000-6000), maximum depth of each tree (interaction.depth: 2-5), and minimum number of observations in the terminal nodes of trees (n.minobsinnode: 5, 10). Hyperparameter tuning was carried out using 10-fold cross validation on the training set using “*caret*” package in R¹⁰⁵ (Extended Data Table 3).

The performance of the final species-specific BRT models was assessed using pseudo-R² and normalized root mean square error (NRMSE) metrics, calculated as the square of the correlation coefficient between the observed and predicted values of the response variable, and the ratio of root mean square error to the mean of corresponding observed response variable for each species (Extended Data Table 1). Relationships between the explanatory variables and BAI were evaluated using variable relative importance (RI) scores, smoothed partial dependence plots (PDPs), and interaction plots. Variable RI is estimated from the number of times a variable is selected to split a tree and the improvement of this split, and measures the relative influence of each explanatory variable on the response variable using a 0-100 scale¹⁰⁶. We used smoothed PDPs to visualize the relationships between explanatory and response variables using the ‘*pdp*’ package¹⁰⁷ and loess smoothing function in R. Partial dependence plots represent the effect of an explanatory variable on the response variable while keeping all other explanatory variables constant at their median level¹⁰⁷. In addition, two-way interactions were tested for a subset of variables based on their known interactive effects (e.g. temperature and precipitation, climate and BA, climate and DBH). The strength of interactive effects was computed using Friedman’s H-statistic, ranging between 0 and 1, with larger values indicating greater interaction¹⁰⁸. There is currently no

universally agreed upon value of H-statistic that signifies significant interaction, therefore we chose to investigate any 2-way interactions that resulted in an H-statistic > 0.1.

Simulated growth under future climate

To predict the future growth of Canada's boreal forest under different climate change scenarios for the near-term 2050s time period, 1-km resolution baseline climate normals data and time series climate projection data were obtained from Natural Resources Canada⁹⁶. The baseline climate normals data was obtained by averaging historic climate over the decades 1981 to 2010. Climate projections are model ensembles averaged from five Earth System Models using monthly data downloaded from the World Climate Research Program (WCRP) Climate Model Intercomparison Project Phase 5 (CMIP5) archive for two different radiative forcing scenarios, i.e., Representative Concentration Pathway (RCP)¹⁰⁹ 4.5 and 8.5. The RCP 4.5 represents a stabilization scenario in which radiative forcing stabilizes shortly after 2100, without overshooting the 4.5 W·m⁻² radiative forcing target level. While RCP 8.5 pathway leads to radiative forcing of 8.5 W·m⁻² by 2100 and continues to increase for some time afterward. Climate projections for the 2050s time period were obtained by averaging the time series climate projection data over three decades (2041 to 2070). Climate models project a faster rate of warming at higher latitudes, along with potential increases in precipitation in eastern North America under climate change (Extended Data Fig. 4).

We simulated the growth (BAI, cm²·year⁻¹) of inventory stems within the five ecozones of Canada that encompass most of the boreal forest east of the Rocky Mountains, including the Taiga Plains, Boreal Plains, Western Boreal Shield, Eastern Boreal Shield, and Atlantic Maritime ecozones¹¹⁰. To do so, we combined the tree lists from the most recent PSPs and NFI plots (Fig. 1a). We then simulated individual tree growth using the fitted, species-specific BRT models under baseline (1981-2010 climate normals) and projected climate conditions of both RCP 4.5 and 8.5 for the near-term (2050s time period). For these simulations, only climate variables were permitted to vary according to different climate change scenarios (baseline climate normals, RCP 4.5 and 8.5 at 2050s), while all non-climatic variables (i.e. competition, tree size, soil moisture regime, slope and aspect) were kept constant. Individual tree growth estimates were summed per plot and then scaled per hectare. Relative growth change under each climate change scenario was calculated at the plot-level relative to baseline climate conditions. Growth changes were averaged over ecologically homogeneous spatial units nested within ecozones called ecodistricts, and across ecozones^{110,111}.

Simulating growth responses outside the observed climate range of the training climate data can introduce model bias and uncertainty¹¹². To help counter this problem, our training data included growth

observations across each species' southern geographic range, well beyond the southern boundary of the boreal forest. At least 4 out of the total 5 projected climatic variables under each climate change scenario remained within the range of the historic observed climate data used to train the BRT models for each species, thus minimizing extrapolation (Fig. 1b).

Data availability

The stand and tree information from the Canadian provincial PSPs and NFI PSPs that support the finding of this study were used under license for the current study, while the US FIA PSP dataset is publicly available at <https://www.fia.fs.fed.us/>. However, the datasets generated during and/or analyzed in the current study are available upon reasonable request following the approval by the corresponding authorities.

Code availability

Code is available upon request.

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Figures

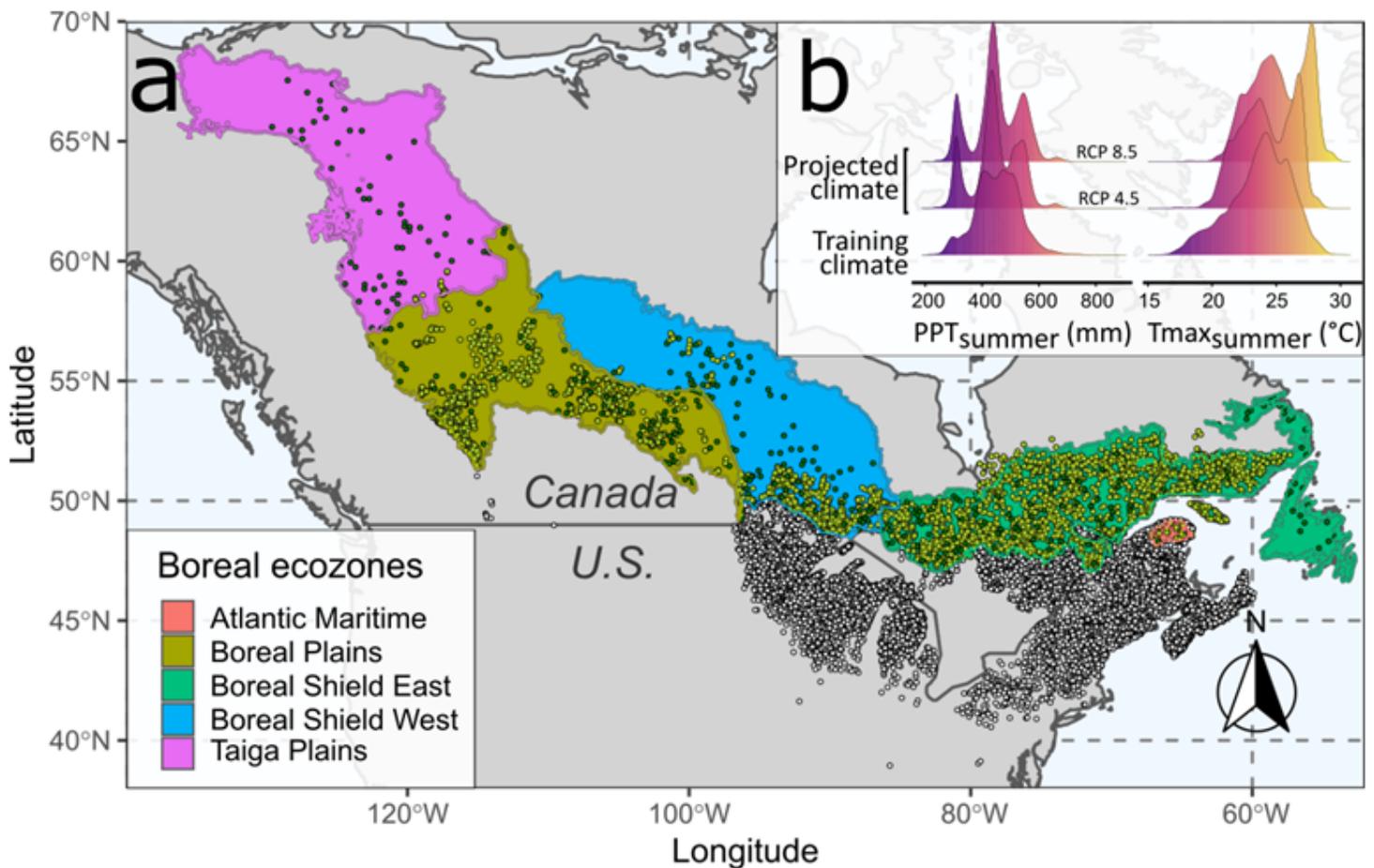


Figure 1

Location of permanent sample plots (PSPs) and distribution of their associated climate spaces. (a) Plots within (light green) and south (white) of the boreal forest region were used to calibrate boosted regression

tree models. National Forest Inventory (NFI) sample plots (dark green) and boreal PSPs (light green) were used to simulate growth under projected climate. Colored regions represent the main boreal ecozones under study. (b) Comparison of climate spaces between the historic training climate data (including plots south of the boreal forest region) and projected climate (limited to the boreal forest region), represented as kernel density estimates of historic and future PPT_{summer} and T_{maxsummer} under two radiative forcing scenarios (RCP 4.5 and 8.5) for the 2050s time period. By including plots south of the boreal forest region in the training data, our projections mostly remained within the observed historic training data climate space, thus limiting extrapolation.

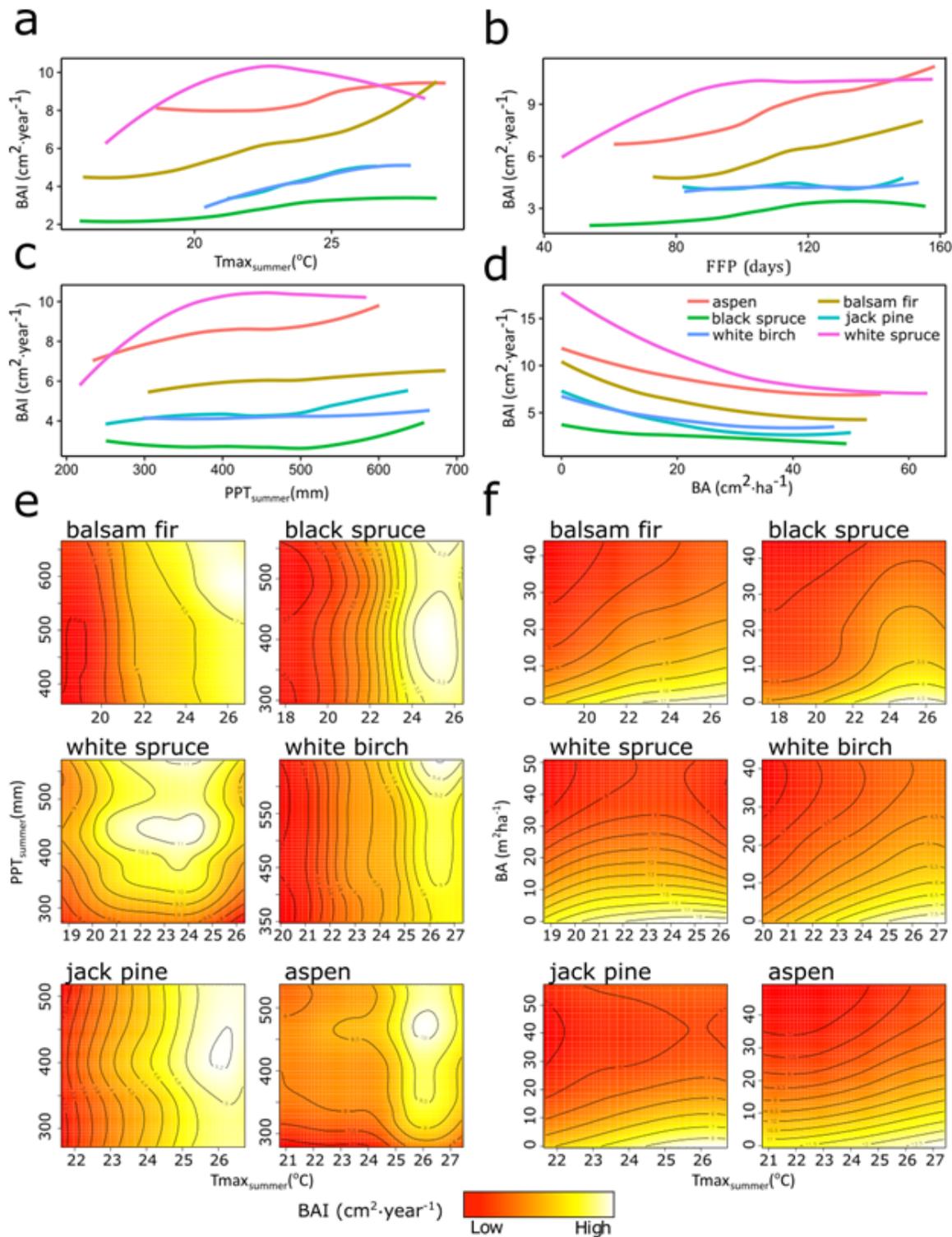


Figure 2

Predicted growth response to climate and competition. (a-d) Growth response to $T_{\text{max,summer}}$, FFP, PPT_{summer} and BA, respectively, across species. Curves represent smoothed partial dependence plots derived from fitted, species-specific boosted regression tree models. (e) Interactive effects of summer temperature and precipitation on the growth of study species, showing stronger temperature forcing on growth under higher precipitation. (f) Interactive effects of summer temperature and competition (BA) on

the growth, showing stronger temperature forcing on growth under low competition. In (e) and (f), only values within the 5-95th quantiles of the corresponding gradients are displayed.

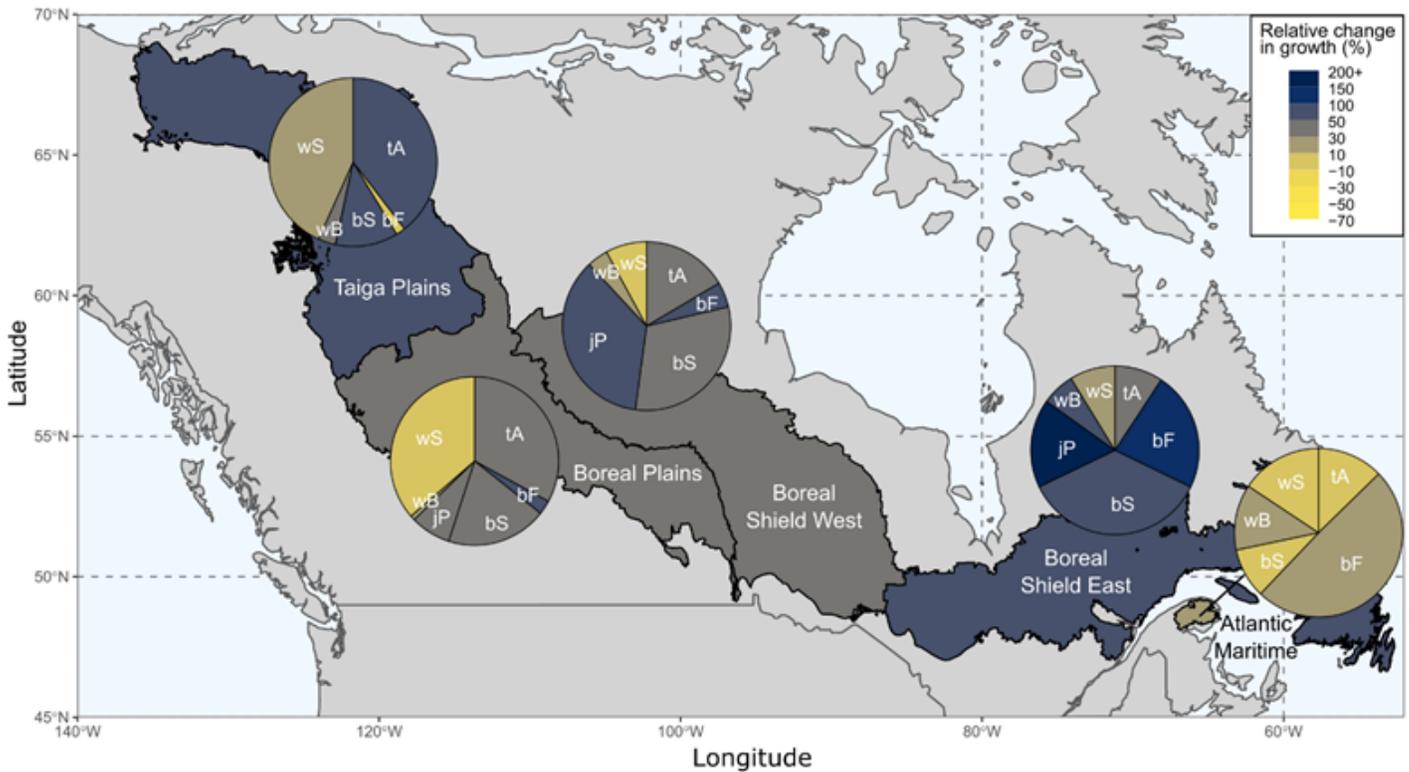


Figure 3

Relative change in growth projected for each Canadian boreal forest ecozone under radiative forcing scenario RCP 8.5 for the 2050s. The pie charts indicate the relative contribution of each species to the overall change per ecozone, based on the relative total basal area per species. bS: black spruce; bF; balsam fir; jP: jack pine; wS: white spruce; wB: white birch; tA: trembling aspen.

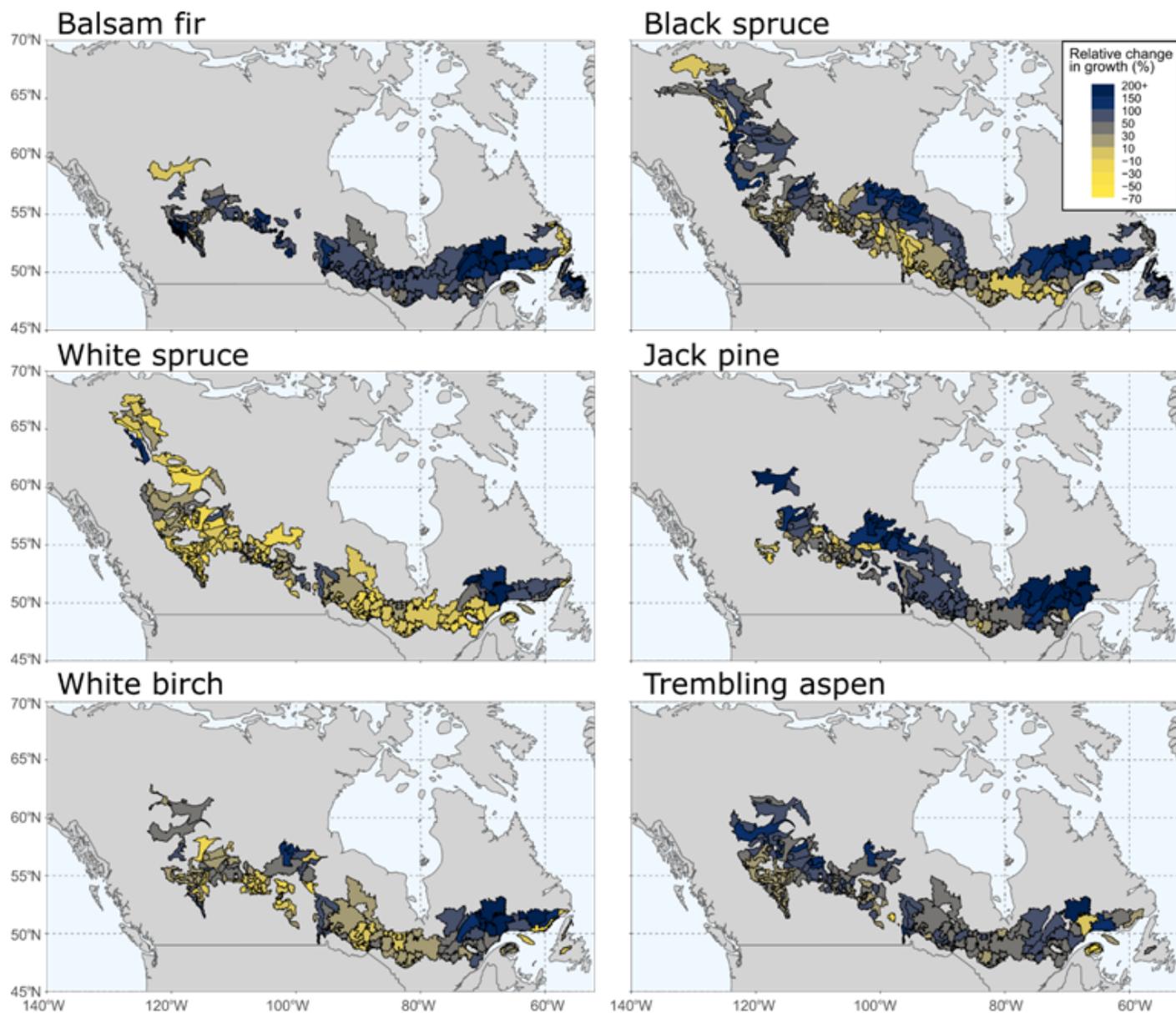


Figure 4

Relative change in tree growth projected for the six study species in each Canadian boreal forest ecodistrict under radiative forcing scenario RCP 8.5 for the 2050s time period.

Supplementary Files

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