

LETTER • OPEN ACCESS

Positive effects of projected climate change on post-disturbance forest regrowth rates in northeastern North American boreal forests

To cite this article: Victor Danneyrolles *et al* 2023 *Environ. Res. Lett.* **18** 024041

View the [article online](#) for updates and enhancements.

You may also like

- [Land cover dynamics following a deforestation ban in northern Costa Rica](#)
M E Fagan, R S DeFries, S E Sesnie *et al.*
- [Carbon cycling in mature and regrowth forests globally](#)
Kristina J Anderson-Teixeira, Valentine Herrmann, Rebecca Banbury Morgan *et al.*
- [Terrestrial carbon losses from mountaintop coal mining offset regional forest carbon sequestration in the 21st century](#)
J Elliott Campbell, James F Fox and Peter M Acton

ENVIRONMENTAL RESEARCH
LETTERS

LETTER

OPEN ACCESS


RECEIVED
13 December 2022REVISED
16 January 2023ACCEPTED FOR PUBLICATION
30 January 2023PUBLISHED
7 February 2023

Original content from
this work may be used
under the terms of the
[Creative Commons
Attribution 4.0 licence](#).

Any further distribution
of this work must
maintain attribution to
the author(s) and the title
of the work, journal
citation and DOI.



Positive effects of projected climate change on post-disturbance forest regrowth rates in northeastern North American boreal forests

Victor Danneyrolles^{1,2,*} , Yan Boucher^{2,3}, Richard Fournier^{1,2} and Osvaldo Valeria^{2,4,5}¹ Département de Géomatique Appliquée, Centre d'Application et de Recherche en Télédétection (CARTEL), Université de Sherbrooke, 2500 Boulevard de l'Université, Sherbrooke QC J1K 2R1, Canada² Centre d'étude de la forêt (CEF), Montréal QC H2X 1Y4, Canada³ Département des Sciences Fondamentales, Laboratoire sur les écosystèmes terrestres boréaux (EcoTer), Université du Québec à Chicoutimi, 555 boulevard de l'Université, Chicoutimi QC G7H 2B1, Canada⁴ Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda J9X 5E4 (QC), Canada⁵ Hemera Centro de Observación de la Tierra, Escuela de Ingeniería Forestal, Facultad de Ciencias, Universidad Mayor, Camino La Pirámide 5750, Huechuraba, Santiago 8580745, Chile

* Author to whom any correspondence should be addressed.

E-mail: victor.danneyyrolles@usherbrooke.ca**Keywords:** climate change, forest regrowth, forest recovery, growth model, forest dynamics, disturbance ecology, site indexSupplementary material for this article is available [online](#)**Abstract**

Forest anthropogenic and natural stand-replacing disturbances are increasing worldwide due to global change. Many uncertainties regarding the regeneration and growth of these young forests remain within the context of changing climate. In this study, we investigate the effects of climate, tree species composition, and other landscape-scale environmental variables upon boreal forest regrowth following clearcut logging in eastern Canada. Our main objective was to predict the effects of future climate changes upon post-logging forest height regrowth at a subcontinental scale using high spatial resolution remote sensing data. We modeled forest canopy height (estimated from airborne laser scanning [LiDAR] data over 20 m resolution virtual plots) as a function of time elapsed since the last clearcut along with climate (i.e. temperature and moisture), tree species composition, and other environmental variables (e.g. topography and soil hydrology). Once trained and validated with ~240 000 plots, the model that was developed in this study was used to predict potential post-logging canopy height regrowth at 20 m resolution across a 240 000 km² area following scenarios depicting a range of projected changes in temperature and moisture across the region for 2041–2070. Our results predict an overall beneficial, but limited effect of projected climate changes upon forest regrowth rates in our study area. Stimulatory effects of projected climate change were more pronounced for conifer forests, with growth rates increasing between +5% and +50% over the study area, while mixed and broadleaved forests recorded changes that mostly ranged from –5% to +35%. Predicted increased regrowth rates were mainly associated with increased temperature, while changes in climate moisture had a minor effect. We conclude that such growth gains could partially compensate for the inevitable increase in natural disturbances but should not allow any increase in harvested volumes.

1. Introduction

Forest natural disturbances are increasing worldwide due to climate change (e.g. fire, drought; Seidl *et al* 2017), while land-use-related disturbances such as logging are also intensifying in many parts of the

world (Hurtt *et al* 2020). Regeneration of severely disturbed forests is undoubtedly among the most powerful drivers of current and future forest dynamics (Danneyrolles *et al* 2019, McDowell *et al* 2020, Seidl and Turner 2022). These young regenerating forests thus play an increasing role in ameliorating

various problems, such as reaching a balance in global carbon dynamics (Pugh *et al* 2019, Cook-Patton *et al* 2020) and maintaining other forest ecosystem services under a warmer and drier climate (Seidl *et al* 2016). Yet, to which extent the projected changes in temperature and moisture will positively or negatively affect the ability of these young forests to regenerate and regrowth remains highly uncertain (Anderson-Teixeira *et al* 2013, McDowell *et al* 2020, Seidl and Turner 2022). These uncertainties are exacerbated in boreal forests, which exhibit more frequent and intense disturbances and slower growth rates than other forest biomes (Gauthier *et al* 2015a, Seidl *et al* 2017, Cook-Patton *et al* 2020). Moreover, these northern latitude forests face higher rates of increasing temperature than any other forest on Earth (IPCC 2021). In this context, insights that are based upon new growth data and more reliable models could improve our understanding and predictability of boreal forest regrowth after stand-replacing disturbance.

After a stand-replacing disturbance, several forest ecosystem characteristics and external environmental drivers may control forest regrowth. First, height growth rates are generally maximal in the early stages following a stand-replacing disturbance and tend to decline progressively with stand age as the trees attain their maximum height (e.g. Ryan *et al* 2004). Second, tree species composition can strongly influence regrowth rates due to inter-specific variability in growth rates and maximum tree height. For example, in North American boreal forests, conifer species generally grow more slowly and reach a shorter maximum height than broadleaved species (e.g. Chen and Popadiouk 2002, Messaoud and Chen 2011). Third, regional climate gradients exert considerable control on tree height growth rates. In boreal forests, temperature is the major limitation to growth rates and to maximum height that is reached by the trees (Boisvenue and Running 2006, Huang *et al* 2010, Messaoud and Chen 2011, D'Orangeville *et al* 2016, 2018). As such, projected increases in temperature for the next few decades should mainly result in net gains in potential boreal forest regrowth (D'Orangeville *et al* 2018, Pau *et al* 2021, Wang *et al* 2023). Fourth, many studies have found that precipitation and climate moisture also significantly influence boreal forest growth, the effects of which can be either positive or negative depending upon interactions between the timing of precipitation, temperature and tree species composition (e.g. D'Orangeville *et al* 2016, 2018, Hellmann *et al* 2016, Oboite and Comeau 2019). Assumptions regarding the effects of projected changes in precipitation on boreal forest growth thus remain highly uncertain. Last, landscape and site characteristics interact with tree species composition and the regional climate gradient

to induce substantial differences in growth rates at the landscape scale. For example, topography results in a high diversity of local temperatures (Nicklen *et al* 2016). Topography, surface deposits, and drainage also strongly control site moisture conditions and soil organic content, with mesic slopes generally leading to better growth rates when compared to poorly drained soils with high organic accumulations at lower slope positions (McKenney and Pedlar 2003, Lavoie *et al* 2007, Laamrani *et al* 2014, Bour *et al* 2021).

In this study, we investigated the effects of climate, tree species composition, and other landscape-scale environmental variables upon boreal forest height regrowth following clearcut logging within a large landscape of eastern Canada. Several previous studies have predicted the effects of projected climate changes upon boreal forest growth using tree rings or height data, usually from mature to over-mature trees, without considering their disturbance history or forest age (Huang *et al* 2010, D'Orangeville *et al* 2016, 2018, Pau *et al* 2021). Yet, climate sensitivity of mature to over-mature trees to changing climate may strongly contrast with the sensitivity of more vigorous young regenerating trees (Duchesne *et al* 2019). Ignoring the central role of stand-replacing disturbances in boreal forest dynamics may introduce substantial bias in growth models and predictions. To our knowledge, no studies have specifically addressed the effects of projected climate changes upon boreal forest height regrowth after stand-replacing disturbance over such large region. Moreover, these previous studies focused upon coarse spatial resolutions that could not consider fine-grain variation in growth rates linked to local site conditions. In this study, we developed a model to predict the effects of future climate changes upon post-logging forest regrowth at a subcontinental scale at high spatial resolution. We used a promising robust and recently developed modeling method that was based upon time-since-last clearcut, together with airborne laser scanning data (i.e. LiDAR; Bour *et al* 2021). Briefly, forest canopy height that was estimated from LiDAR data over 20 m resolution virtual plots was modeled as a function of time that elapsed since the last clearcut logging and recorded climatic conditions, along with tree species composition and other environmental variables (e.g. topography and soil hydrology). The central assumption is that relationships between current regrowth rates and regional climate gradients provide an excellent means of projecting potential changes in growth to increasing temperature and changes in precipitation. Once trained and validated with ~240 000 plots, we used this model to test two main hypotheses: (a) projected climate change should have beneficial effects on boreal forest growth. (b) Such effects would differ with forest

composition (i.e. coniferous vs. broadleaved forests) and local site conditions (i.e. topography and soil hydrology). For that purpose, we predicted potential post-logging forest height regrowth at 20 m resolution across 237 000 km² following different scenarios that depicted a range of projected changes in temperature and moisture across the study area for the period 2041–2070.

2. Materials and methods

2.1. Study area

The study area comprises a 237 000 km² territory of boreal forests in the Province of Quebec, eastern Canada (*sensu* Rowe 1972, Robitaille and Saucier 1998, see figure 1). Mean annual temperatures range from -2°C to 4°C from north to south and climate moisture varies along an east–west gradient, with a rather continental climate to the west (800–1000 mm of annual total precipitation) and a moister oceanic climate to the east (1000–1200 mm of annual total precipitation; figure S1). The east–west gradients also include differences in topography and surface deposits, with smooth slopes and abundant lacustrine clay and organic accumulation to the west, and more rugged relief to the east, with a higher proportion of glacial till and rocky deposits (figure S2). Black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) coniferous species tend to dominate across the whole boreal zone, with occasional presence of paper birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*), together with coniferous white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*; figure S3). Further to the south of the study area, within the temperate zone, warm-adapted broadleaved species such as sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) dominate the landscapes, which contain scattered patches of boreal forest (i.e. dominated by either black or white spruce, balsam fir, jack pine, trembling aspen or paper birch).

Stand replacing disturbances, mostly fire and logging, are widespread within the study area (Boucher et al 2017). According to the Quebec government's forestry maps (MFFP 2018), between 1980 and 2015, ~21% of the forest cover of the study area was clearcut logged, and ~5% burned (i.e. 0.58% and 0.15% per year, respectively). About a quarter of the forests logged since 1980 were replanted, while the rest regenerated naturally. In this study, we concentrated our analyses on clearcut disturbance rather than fire since the annual area affected by logging is more homogeneously distributed in space and time. It is thus much more adapted for developing a space-for-time modeling approach, in which the different sites are used as substitutes for different stages of development depending on their time since the last disturbance.

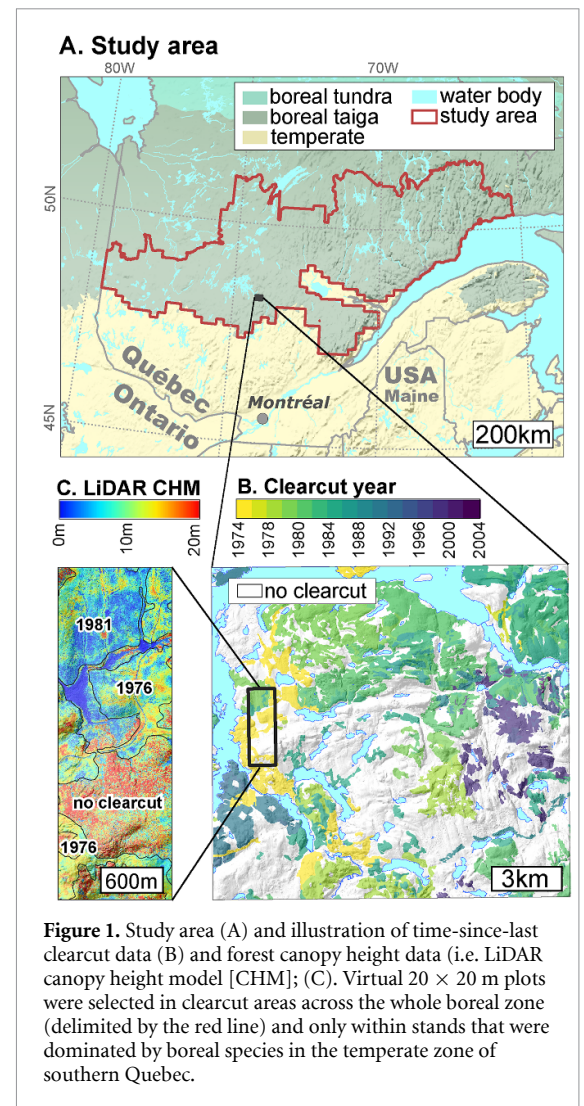


Figure 1. Study area (A) and illustration of time-since-last clearcut data (B) and forest canopy height data (i.e. LiDAR canopy height model [CHM]; (C). Virtual 20×20 m plots were selected in clearcut areas across the whole boreal zone (delimited by the red line) and only within stands that were dominated by boreal species in the temperate zone of southern Quebec.

2.2. Time-since-last clearcut logging data

We extracted time-since-last clearcut data from the Quebec government's latest available forestry maps (MFFP 2018). The polygons that were drawn at the 1:20 000 scale (with a minimum 4 ha area) are based upon the interpretation of high-resolution aerial photographs and annual harvesting reports (figure 1). Each polygon informs on the type and year of the last known stand-replacing disturbance since the 1950s (figure 1), along with the dominant species of the stands. We randomly sampled hundreds of thousands of virtual LiDAR $20 \text{ m} \times 20 \text{ m}$ plots within disturbed sectors of our study area. We also sampled plots in disturbed sectors in the temperate zone southern to the study area (figure 1), but only within stands of forests that were dominated by boreal species (i.e. either black or white spruce, balsam fir, jack pine, trembling aspen, or paper birch). We retained these southern parcels for incorporation into our model because these boreal forests are currently growing under warmer climate conditions, which likely correspond to the projected climate conditions in the boreal zones of the future (figure S1). To the north,

the delimitations of the study area were defined by the availability of LiDAR data (most forests to the north of our study area are not exploited and thus not surveyed in Quebec's government provincial forest inventory program).

According to the forestry maps, all plots that were retained belonged to two clearcut logging categories: clearcut with natural regeneration; and clearcut with tree planting. The plots that were selected were at least 50 m from the clearcut polygon boundaries to avoid edge effects and stand margin delineation errors (see Bour *et al* 2021, for details). The age of each 20 m × 20 m plots within the clearcuts (i.e. time-elapsed-since last disturbance) was then calculated as the difference between LiDAR acquisition year (see details below) and logging or planting year. We only retained plots that were aged >10 years-old, given that trees <10 years-old can be confused with ericaceous shrubs or alder (*Alnus* spp.) (Matasci *et al* 2018). The oldest recorded plots were 70 years-old, given that no reliable logging history data were available prior to 1950. Precommercial thinning is a widespread silvicultural treatment in the boreal forests that reduces stand density and competing vegetation (Ashton & Kelty 2017), which is occasionally applied a few years following post-logging natural regeneration or planting in our study area. In our dataset, 15% of naturally regenerated stands and 3% of plantations were treated using precommercial thinning. Consequently, we considered four distinct types of silvicultural treatment for the following growth analyses: clearcutting with natural regeneration alone (72% of the 238 519 plots in the final dataset); clearcutting with natural regeneration + precommercial thinning (15%); clearcutting with planting (10%); and clearcutting with planting + precommercial thinning (3%).

2.3. Canopy height data

Forest canopy height was determined using airborne LiDAR data that the Quebec government acquired as part of its provincial forest inventory program. For the data that were used in this study, aerial surveys were realized between 2012 and 2019, with point densities ranging from 1.5 to 8 pulses m⁻² (median = 3 pulses m⁻²). Raw point clouds were transformed by analysts from the Quebec government into digital elevation and canopy height models (DEM and CHM, respectively, both at 1 m resolution; figure 1(C)). To do so, raw point clouds were first classified into ground and non-ground returns and a DEM was fitted to the ground returns to produce a 1 m resolution raster. The DEM was subtracted from elevations of all non-ground returns to produce a normalized point cloud. Finally, the height of each 1 m pixel of CHM was defined as the highest return of the normalized point cloud.

The 1 m resolution CHMs were aggregated into the 20 m × 20 m plots simply by assimilating the height of each plot as the 95th percentile (P95) of its CHM pixel heights and after removing pixels <1 m in height. The 95th percentile is frequently used to produce CHM from raw point clouds (White *et al* 2013), and exclusion of the lowest returns (<1 m) is usually applied to remove returns attributable to the herbaceous-shrubby ground vegetation (Nyström *et al* 2012). We also compared this LiDAR-based metric (P95) with field-based measurements of forest canopy height using 249 forest inventory plots that were surveyed in the field during the same year as the LiDAR survey (figure S4). This comparison showed that P95 is very closely related to the mean height of dominant and co-dominant trees that are measured on the field (Pearson $r = 0.89$). To avoid spatial autocorrelation in this forest height measure, we only retained sample plots in clearcuts or planted areas that were separated by a minimum distance of 250 m, a threshold that was validated with a semi-variogram (figure S5).

The 1:20 000 polygons that identified disturbed areas have a minimum area of 4 ha. These polygons can include small patches of remnant forest that have not been harvested (e.g. plots of 20 m × 20 m = 0.04 ha). If such remnant forest patches exist, their occurrence can incur bias in the analysis. To remove this potential bias, we excluded plots in which we identified aberrant heights for a given age from the LiDAR data. The threshold values for identifying aberrant heights were defined using a database of nearly a million trees, from which age and height have been measured within our study area through the provincial forest inventory programs since 1981 (i.e. individual tree field-based height measurements and tree-ring age estimates). Threshold values were estimated separately for the six main species of our study area. To do so, we first calculated the maximum height threshold for a given age as defined by the 99th percentile of field-measured tree height (figure S6). The maximum height threshold per age class and per bioclimatic domain (i.e. part of the Quebec's government ecological classification system; Robitaille and Saucier 1998) was then defined as the mean of individual species threshold weighted by their relative abundance in each bioclimatic domain (figure S6). This final selection excluded ~10 000 plots (~4% of the dataset before filtering), and the final dataset was comprised of 238 519 plots.

2.4. Topographical, climate and forest composition data

We extracted seven explanatory variables that could influence canopy height growth (table 1). First, we extracted the proportion of broadleaved trees at the center of the 20 m × 20 m plots from a 30 m

Table 1. Description of variable sources, type (cont.: continuous), and range in the training and validation datasets. The first number is the mean value in the range column of continuous variables, while numbers within parentheses are minimum and maximum. Climate, topographical and percent of broadleaved trees maps are shown in figures S1, S2 and S7 respectively.

Variables	Source	Type (unit)	Range
Canopy height (P95)	LiDAR	Cont. (m)	9.36 (1.46, 22.320)
Time since last clearcut	Forestry maps	Cont. (year)	30 (10, 70)
Silvicultural treatment	Forestry maps	Categorical	Clearcut, clearcut + thinning, Planting, planting + thinning
Percentage of broadleaved trees	Landsat + field plot model	Cont. (%)	40 (1, 99)
Mean annual temperature (T_{MEAN})	Meteorological	Cont. ($^{\circ}\text{C}$)	1.5 (0.54, 6.15)
Summer climate moisture (CMI_{SM})	Meteorological	Cont. (mm)	-117 (-250, 31)
Elevation	LiDAR	Cont. (m a.s.l.)	432 (3, 1074)
Slope	LiDAR	Cont. (%)	12.6 (0.4–125.7)
TWI	LiDAR	Cont. (no unit)	5.61 (0.3–23.9)
Surface deposit	Forestry maps	Categorical	Glacial tills, Fluvio-glacial tills, Glaciolacustrine clays, Rocky, Organic

raster product that was made available by the Canadian Forest Service (figure S7). The proportion of broadleaved trees has been modeled with Landsat images and is based upon information from more than 10 000 inventory plots (for a more detailed explanation of the methodology, see Guindon *et al* 2020). Second, we extracted several variables from climate gridded datasets (McKenney *et al* 2011) at a 300 arcsecond resolution ($\sim 55 \text{ km}^2$) that contain monthly climate observations since 1950 (figure S1). For each individual $20 \text{ m} \times 20 \text{ m}$ plot, climate normals were calculated as the average of observed variables starting from the year of clearcutting and stopping at the year of LiDAR acquisition. We retained the yearly mean daily temperature (T_{MEAN} , $^{\circ}\text{C}$) and maximum daily temperature (T_{MAX} , $^{\circ}\text{C}$). We also used the mean annual climate moisture index (CMI), which is defined, for a given period, by the sum of total precipitation minus the sum of potential evapotranspiration (the latter was calculated following Baier and Robertson 1965). CMI was calculated for the growing season (May to September; CMI_{GS}) and for the summer period (June to August; CMI_{SM}). Finally, we extracted three variables from LiDAR DEM (1 m resolution) that characterized the topography and soil hydrology of the $20 \text{ m} \times 20 \text{ m}$ plots: mean elevation, slope (%), and topographic wetness index (TWI; Sørensen *et al* 2006). One other variable that was taken from forestry maps characterized five geological surface deposits (figure S2): glacial tills (74% of the entire dataset), lacustrine clays (13%), fluvio-glacial (8%), rocky outcrops (3%) and organic soils (2%).

2.5. Canopy height growth modeling

We used random forest regression (Breiman 2001) to model canopy height growth since such machine learning approaches are non-parametric and very efficient in modeling non-linear ecological data with

complex interactions (Christin *et al* 2019). We used the *ranger* function that is included in the *ranger* package (Wright and Ziegler 2017) to train a random forest regression model with 500 trees and three variables to guide the split at each node. We trained the model with a random sampling of 80% of the original dataset (i.e. 190 815 observations), while we held back the remaining 20% (i.e. 47 704 observations) for measuring model predictive performance. The training and validation datasets exhibited identical distributions for all continuous and explanatory variables that were integrated into the model. In the model, canopy height depends upon the following nine explanatory variables: time-since-last clearcut; silvicultural treatment; temperature; climate moisture (CMI); proportion of broadleaved trees; elevation; slope; TWI; and surface deposits. To retain only two climatic variables accounting for spatio-temporal variability in temperature and moisture, we compared the model output combining temperature (T_{MEAN} , T_{MAX}) and climate moisture (CMI_{GS} , CMI_{SM}) variables. Output with different combinations of temperature and moisture were almost identical (figure S8). Consequently, we retained yearly mean daily temperature (T_{MEAN}) and CMI from June to August (CMI_{SM}) because these two variables exhibited the lowest correlation (Pearson $r = -0.33$), which could help to separate the effects of temperature and moisture on canopy height growth. Overall, all continuous explanatory variables that were included in the model showed low to moderate correlations with one another (figure S9).

2.6. Canopy height growth rate projections across the boreal zone

Once trained, the model was used to produce maps of predicted post-logging forest canopy height growth

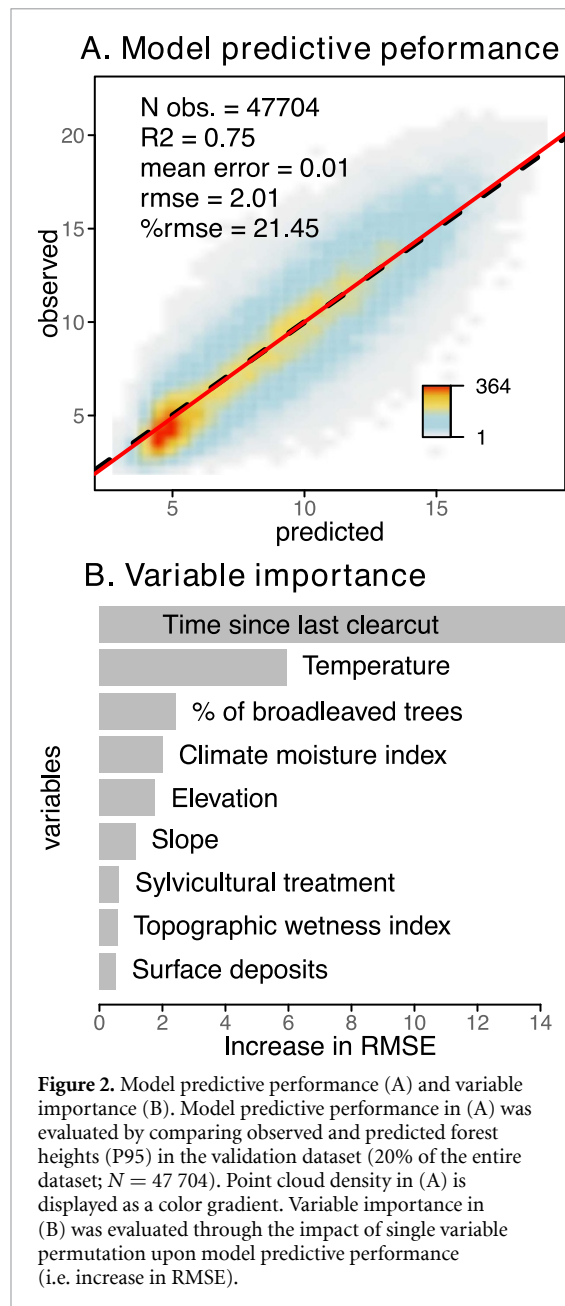
at 20-m resolution across the boreal zone (figure 1) according to 27 scenarios. The 27 scenarios represent all possible combinations of three conditions for T_{MEAN} (baseline, Representative Concentration Pathways (RCP) 4.5, and RCP 8.5), three for CMI_{SM} (baseline, RCP 4.5, and RCP 8.5), and three for cover composition types (coniferous, mixed, broadleaved). T_{MEAN} and CMI_{SM} baseline values were defined from the 40 year normals that were recorded during the 1980–2020 period. Projected T_{MEAN} and CMI_{SM} for the RCP 4.5 and 8.5 emission scenarios correspond to the 2041–2070 normals that were obtained as median values across 11 global circulation models (figure S1; all climate simulations with different models and scenarios were taken from the non-profit OURANOS organization on climate change science, see www.ouranos.ca). In brief, RCP 8.5 represents a high-end climate scenario with continuous high greenhouse gas emissions, while RCP 4.5 is a middle-of-the-road scenario (IPCC 2021). These correspond to an increase in T_{MEAN} of about 2 °C and 3 °C for the RCP 4.5 and 8.5 scenarios, respectively, where increases are relatively uniform across the study area. Projected changes in CMI_{SM} were more spatially contrasted, with a major portion of the study area experiencing more humid climate, while other portions (toward the west) experienced slightly drier climate under both RCP 4.5 and 8.5 scenarios (figure S1). Almost calibration range; see figure S1). To understand how climate change may modify the growth rates of different forest cover composition types, we also set three distinct possibilities with forest cover compositions being fixed to coniferous, mixed, or broadleaved types across the study area (i.e. 5%, 50% and 95% broadleaved trees, respectively). In all scenarios, permanent topographical variables (elevation, slope, surface deposits and TWI) remained unchanged across the study area. Since silvicultural treatments had a marginal effect on modeled height growth (figure S10), we assigned all scenarios with the most common silvicultural treatment (i.e. clearcut alone; 72% of the dataset). For each 20 m × 20 m pixel of the study area and according to these 27 scenarios, we computed potential growth as the predicted height at 50 years, averaged at an annual rate to obtain a map of canopy growth in cm year^{-1} . We chose potential height at 50 years, given that this metric is widely used in forestry (commonly referred as ‘site index,’ e.g. Messaoud and Chen 2011, Pau *et al* 2021), given that most boreal forests of our study region reach a height growth plateau at this age (see section 3). We also computed predicted uncertainty using the quantile random forest regression approach (Meinshausen and Ridgeway 2006) in which the variance of predicted values is quantified between trees within the random forest model and used as a metric of prediction uncertainty. Note that this corresponds to

the uncertainty linked to the random forest modeling approach but not to the uncertainty related to climate projections.

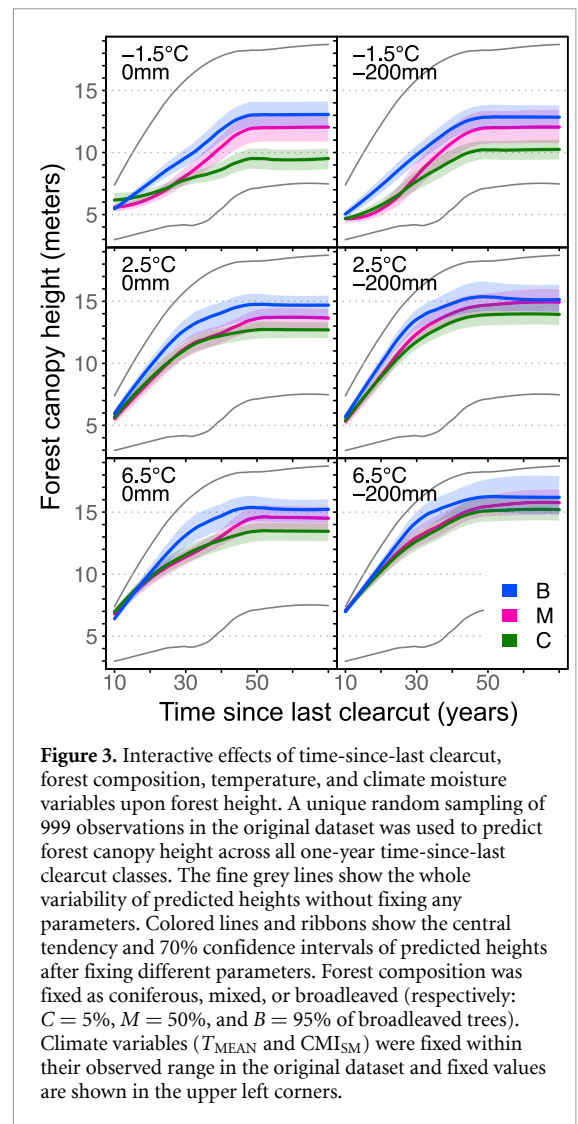
3. Results

The comparison between predicted and observed forest canopy height in more than 47 000 observations from our validation dataset highlighted the strong predictive power of the model (figure 2). The model explained 75% of variation in the validation dataset height (i.e. LiDAR P95) with a linear relationship very close to 1:1, together with a relative RMSE = 21% and a mean error = 0.01 m. The importance of the explanatory variables was measured by permutation tests that were performed on random forest out-of-bag samples (i.e. % increase in MSE; figure 2). Our results show that time-since-last clearcut has the most decisive factor influencing canopy height. Under all environmental conditions, canopy heights tended to assume a logarithmic function of time-since-last clearcut, with the highest growth rates being observed during the first few decades, after which a plateau was reached at about 50 years following clearcutting (figures 3 and S10). The second most influential variable was T_{MEAN} (temperature). Although the weightings of these first two variables dominate, in decreasing order of importance, the other prominent variables were the percentage of broadleaved trees and CMI_{SM} (figure 2). These four variables showed notable interaction effects with one another. Temperature had a significant positive effect on growth rates under all moisture conditions and forest cover composition types (figure 3). Conifer-dominated forests tended to display lower growth rates than mixed and broadleaved forests under all temperature and moisture conditions. These differences were particularly marked in cold and moist sites and disappeared in more hot and dry sites (figure 3). Climate moisture (CMI_{SM}) negatively affected forest growth, particularly in conifer stands. In mixed and broadleaved forests, such effects were attenuated (figure 3). Topographical variables had a secondary influence on canopy height (figure 2). Globally, the best growth rates were found in lower elevation and moderate slopes that were associated with low-moisture glacial, fluvio-glacial or clay deposits (figure S10). In comparison, lower growth rates were found in high altitude sites, high moisture flat sites that were associated with organic deposits, or on rocky deposits (figure S10). Finally, silvicultural treatments had a very limited effect on forest growth compared to other variables that were included in the model (e.g. climate, topography; figures 2 and S10).

During the first 50 years post-logging, projected potential canopy height regrowth rates across the



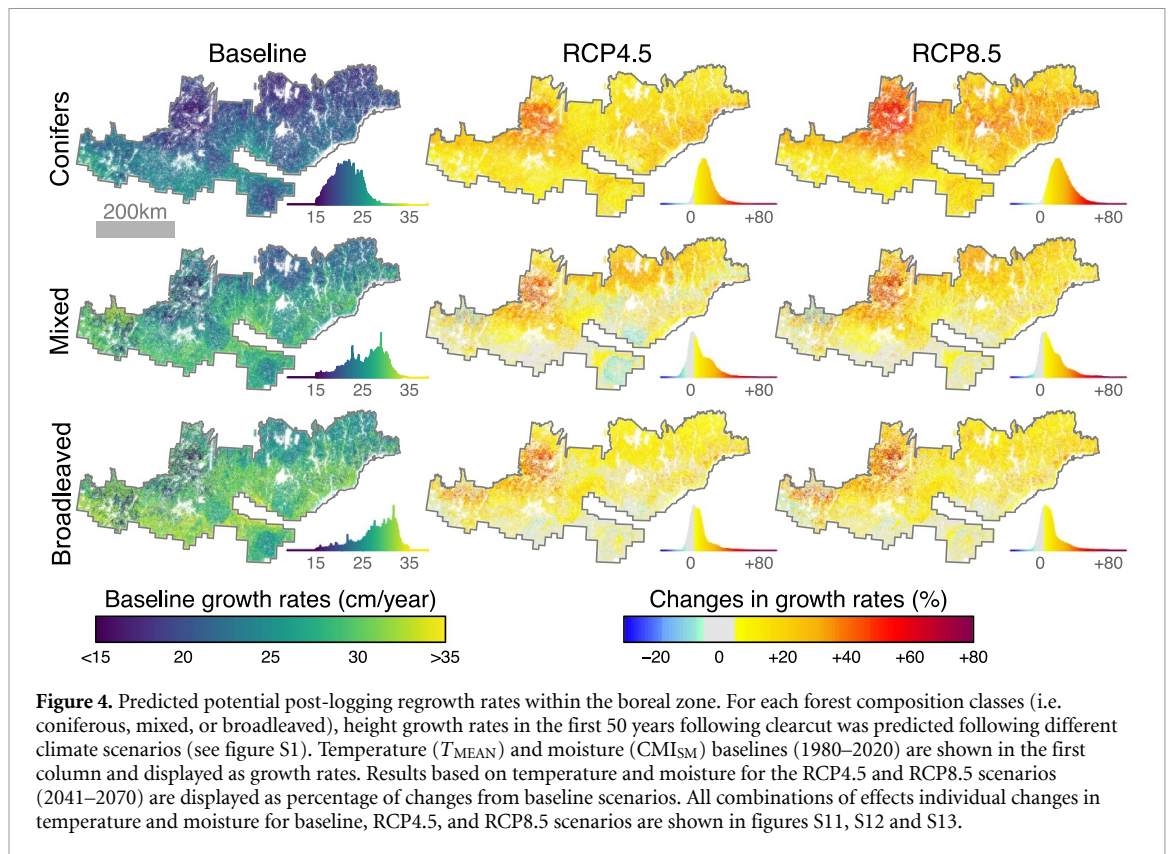
study area following the 27 baseline scenarios (i.e. 1980–2020 climate) ranged from 15 to 35 cm yr⁻¹ (i.e. heights between 7.5 and 17.5 m at 50 years, respectively; figure 4). Conifer-dominated forests showed growth rates ranging from 15 to 25 cm yr⁻¹ in >75% of the study area (i.e. between 7.5 and 12.5 m at 50 years, respectively; figure 4), while median growth rates of mixed and broadleaved forest were ~27 cm yr⁻¹ (i.e. ~13.5 m at 50 years; figure 4). Simulated changes in regrowth rates with different climate change scenarios (i.e. projected climate for the 2041–2070 period) mainly benefited all forest cover composition types (figure 4). Increased regrowth rates were mainly associated with increased temperature, while projected changes in climate moisture had a minimal or even insignificant effect on forest regrowth (figure S11). The stimulatory effects of projected climate change were more pronounced for



conifer forests, with growth rates increasing between 5% and 50% over almost the entire study area in the RCP 8.5 scenario compared to the baseline (figure 4). In comparison, most mixed and broadleaved forests recorded net changes ranging between -5% and 35% under the RCP 8.5 scenario (figures 4 and S12). This larger effect of increased temperature upon conifer forests reduced the initial differences in growth rates between conifers and mixed or broadleaved forests (figure S13). The sites with lowest baseline growth rates (i.e. 15–20 cm yr⁻¹) also recorded the largest proportional increases in growth rates with increased temperatures (figure 4).

4. Discussion

Our modeling approach that was based on airborne LiDAR and time-since-last clearcut data had great power to predict forest regrowth rates after logging in a large landscape of northeastern North American boreal forest. This research represents a significant milestone since it predicts the effects of climate



upon boreal forest regrowth, specifically after stand-replacing disturbance. Previous studies were limited to predicting forest growth without considering disturbance history or forest age (e.g. Huang *et al* 2010, D'Orangeville *et al* 2016, 2018, Pau *et al* 2021). Ignoring such central aspects of boreal forest dynamics may introduce significant bias in model predictions (Duchesne *et al* 2019). Second, compared to models alimented with field-based data, our model is based upon remotely sensed data that are less monetarily costly and time-consuming to acquire, while it can accurately predict forest regrowth rates at the sub-continental scale with much finer spatial grain. In any event, the predicted height growth rates of our model are very consistent with those found in previous studies of the boreal forests (i.e. mostly comprised between 10 and 40 cm yr^{-1} ; Pedlar and McKenney 2017, Oboite and Comeau 2019, Pau *et al* 2021).

The regional gradient of temperature normals had a major positive effect on forest height regrowth rates, with height at 50 years varying from ~ 10 to 12 m in the coldest conditions to ~ 14 –18 m in warmer conditions. This is not surprising given well-known major temperature constraints on forest growth at these northern latitudes (Boisvenue and Running 2006). The main underlying mechanism behind the positive temperature-growth relationship is that increased mean annual temperatures imply longer growing seasons (e.g. Huang *et al* 2010, D'Orangeville *et al* 2016, 2018), thereby allowing trees

to grow faster and taller (e.g. Messaoud and Chen 2011, Pau *et al* 2021). An additional ecological explanation is that southern and warmer boreal forest stands generally grow more densely than those in colder conditions (Beaudoin *et al* 2014). Higher stand density implies higher competition for light, a context in which trees tend to allocate more resources to their growth in height at the expense of radial growth (e.g. McCarthy and Enquist 2007, Schneider *et al* 2018). In our methodological context, higher stand density increases the probability of LiDAR detecting high points of the canopy in the $20 \text{ m} \times 20 \text{ m}$ plots, which may represent a slight bias in our data.

Compared with temperature, the regional gradient of climate moisture normals had a less marked, but nevertheless negative effect on forest regrowth. The effect of climate moisture also substantially interacted with forest composition, since it was more significant for conifer-dominated forests. Such negative effects of climate moisture on boreal tree species growth have already been reported in North American and Eurasian boreal or cold mountain forests (D'Orangeville *et al* 2016, 2018, Hellmann *et al* 2016, Buechling *et al* 2017, Pau *et al* 2021). This counter-intuitive negative effect of climate moisture may be linked to several non-exclusive explanations. First, our study area represents one the wettest boreal regions in the world (annual total precipitation ranging from 800 to 1200 mm versus 250–700 mm for most western North American or Eurasian boreal

forests; D'Orangeville *et al* 2016). The high snowpack meltwater in these rather wet forests may ensure sufficient soil water levels for most of the growing season. The snowmelt can even be delayed at the beginning of the growing season, making growing season climate moisture a non-limiting factor for forest growth (D'Orangeville *et al* 2018). Second, in such context, high growing season precipitation could also incur indirect reduction in forest growth through a decrease in solar radiation and soil temperature (Bergeron *et al* 2007). Yet, previous studies have found that the effect of climate moisture on forest growth became positive after crossing a threshold of warm temperatures, which contrasts with our results (D'Orangeville *et al* 2018, Pau *et al* 2021). This divergence could be explained because our model specifically examines young regenerating stands, which may require less moisture to support their growth than would older stands with larger living biomass and high related water demand (Duchesne *et al* 2019). For example, young northern temperate pine (*Pinus strobus*) plantations have been found to use water more efficiently than older ones that exhibited higher evapotranspiration levels during drought events (Skubel *et al* 2015).

Two principal limits to our approach could also constrain our ability to properly model the effects of climate variables upon forest height growth. First, our model accurately predicted well-known differences among forest composition cover types with slower growth rates for coniferous (i.e. black spruce, balsam fir, and jack pine) compared to broadleaved forests composed of fast-growing, shade-intolerant trembling aspen and paper birch (e.g. Chen and Popadiouk 2002). However, our data only measure forest composition at a functional level (i.e. conifer-broadleaved ratio), but cannot separate forest compositions at the species level. Obviously, the climate gradient in our study area is linked to tree species composition (see figure S3): black spruce dominates the coldest northern sites, while balsam fir and white spruce can represent a major proportion of stands in warmer southern sites. The driest portions of our study area also show the greatest proportions of trembling aspen and jack pine. Since different species within the conifer or broadleaved functional groups broadly diverge in terms of growth rates and climate-growth relationships (D'Orangeville *et al* 2018, Marchand *et al* 2019), some variation in height growth due to species composition is implicitly accounted for in the modeled effects of climate gradients. On an even finer phylogenetic scale, our model does not account for local genetic adaptation within the same species, which may significantly influence tree sensitivity to climate variables (e.g. Depardieu *et al* 2020, Girardin *et al* 2021). The second limit of our approach lies in the use of climate normals that cannot model the effect of single-year climate extremes on forest growth. However,

monthly or yearly events such as extreme summer heat, drought events, or spring frost can have significant and long-lasting effects on forest growth (Marquis *et al* 2020, Marchand *et al* 2021). It is important to note that such limitations of our modeling method could seriously undermine our ability to accurately predict the effects of future climate change upon post-disturbance boreal forest growth.

Regardless of these limits, our simulations with projected changes in climate normals for the 2041–2070 period resulted in an overall increase in potential post-logging forest regrowth. These results are consistent with previous research in our study area (i.e. mostly between -5% and $+50\%$; D'Orangeville *et al* 2018, Pau *et al* 2021), although another recent study found higher near-term increases (i.e. $+40\%$ to $+52\%$ on average across Canada's boreal ecozone for the 2050s time period; Wang *et al* 2023). In our results, beneficial effects are pervasive across the study area, but are more pronounced for conifer forests and for cold northern, slow-growing forests, which agrees with these studies to some extent. Our predicted increases in potential post-logging growth rates are strictly due to increased temperatures since projected changes in climate moisture have virtually no effect (figure S11). This response contrasts with a previous study, which showed that the beneficial effects of increased temperature on boreal forest growth could reverse after crossing a threshold of warmer temperature (about $+3\text{ }^{\circ}\text{C}$ – $4\text{ }^{\circ}\text{C}$), beyond which a negative impact may occur with an associated decrease in climate moisture (D'Orangeville *et al* 2018). This is likely linked to the specific nature of our study that models the growth rates of young, vigorous regenerating trees, rather than the growth of mature to over-mature trees that may be much more sensitive to climate moisture effects (Duchesne *et al* 2019).

5. Conclusions

Our results show an overall beneficial effect of the projected increase in temperature on forest height regrowth in the 50 years following a disturbance in northeastern North American boreal forests. These results provide new knowledge and insights into the effects of future climate change on these forests, which are necessary for sustainable forest management and global change assessments. A marked increase in fire activity and other natural disturbances is expected due to climate change in these boreal forests (e.g. Boucher *et al* 2018, Coogan *et al* 2019, Seidl *et al* 2020). Previous studies modeling the effects of climate change upon forest growth have argued whether their projected changes would be either insufficient (D'Orangeville *et al* 2018, Pau *et al* 2021) or sufficient (Wang *et al* 2023) to compensate for effects of future natural disturbances. Gauthier *et al* (2015b)

have determined that it would take an increase in growth rates of at least 50% on average to offset the loss of biomass due to projected future burned areas alone. In our study area, the provincial government plans near-term increases in harvested volumes (3%, or $\sim 850\,000\text{ m}^3\text{ yr}^{-1}$ over the 2023–2028 period; BFEC 2023), while more long terms changes in harvest rates are much more difficult to predict (ex., horizon 2070). Despite growth gains for this long-term horizon (2040–2070) being a pervasive outcome of our results, they remain limited (i.e. net changes range primarily between -5% and $+50\%$). This suggests that such growth gains could partially compensate for the inevitable future impacts of natural disturbances but should not allow any increase in harvested volumes. In any event, how climate change combines with disturbance regimes to affect boreal forest growth, functioning and management remain a central topic for future research.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: <https://doi.org/10.6084/m9.figshare.20418792.v1>. All raw forest data used in this study are freely available at www.donneesquebec.ca (i.e. LiDAR canopy height models, time-since last clearcut data and other environmental variables). Raw climate data are freely available at www.ouranos.ca. Predicted potential post-logging regrowth rates maps shown in figure 4 are freely available at <https://gis.uqat.ca/portal/>.

Acknowledgments

We thank Batistin Bour, Luc Guindon, Jason Laflamme, Jean-François Bourdon, Martin Riopel, Steve Bedard and Michel Campagna for their support and advice concerning forest-related data. We also thank Pascal Bourgault and Travis Logan for their help in accessing climate data and William F J Parsons for carefully editing the manuscript. We finally thank two anonymous reviewers for their constructive feedback on a previous version of the manuscript. Funding was provided by the *Contrat de service de recherche forestière* number 42332166-1 obtained by R. Fournier of the Université de Sherbrooke from the Ministère des Forêts, de la Faune et des Parcs (Quebec, Canada). This project also benefited from research Grant No. 566938-21 from the Alliance program of the Natural Sciences and Engineering Research Council of Canada (NSERC).

Conflict of interest

The authors have no competing interests to declare.

ORCID iD

Victor Danneyrolles  <https://orcid.org/0000-0002-4839-8164>

References

- Anderson-Teixeira K J, Miller A D, Mohan J E, Hudiburg T W, Duval B D and DeLucia E H 2013 Altered dynamics of forest recovery under a changing climate *Glob. Change Biol.* **19** 2001–21
- Ashton M S and Kely M J 2017 *The Practice of Silviculture: Applied Forest Ecology* (Hoboken, NJ: Wiley)
- Baier W and Robertson G W 1965 Estimation of latent evaporation from simple weather observations *Can. J. Plant Sci.* **45** 276–84
- Beaudoin A, Bernier P Y, Guindon L, Villemaire P, Guo X J, Stinson G, Bergeron T, Magnussen S and Hall R J 2014 Mapping attributes of Canada's forests at moderate resolution through k NN and MODIS imagery *Can. J. For. Res.* **44** 521–32
- Bergeron O, Margolis H A, Black T A, Coursolle C, Dunn A L, Barr A G and Wofsy S C 2007 Comparison of carbon dioxide fluxes over three boreal black spruce forests in Canada *Glob. Change Biol.* **13** 89–107
- BFEC 2023 *Possibilités forestières 2023–2028: Synthèse provinciale des résultats* (Bureau du Forestier en Chef: Gouvernement du Québec)
- Boisvenue C and Running S W 2006 Impacts of climate change on natural forest productivity—evidence since the middle of the 20th century *Glob. Change Biol.* **12** 862–82
- Boucher D, Boulanger Y, Aubin I, Bernier P Y, Beaudoin A, Guindon L and Gauthier S 2018 Current and projected cumulative impacts of fire, drought, and insects on timber volumes across Canada *Ecol. Appl.* **28** 1245–59
- Boucher Y, Perrault-Hébert M, Fournier R, Drapeau P and Auger I 2017 Cumulative patterns of logging and fire (1940–2009): consequences on the structure of the eastern Canadian boreal forest *Landsc. Ecol.* **32** 361–75
- Bour B, Danneyrolles V, Boucher Y, Fournier R A and Guindon L 2021 Modeling post-logging height growth of black spruce-dominated boreal forests by combining airborne LiDAR and time since harvest maps *For. Ecol. Manage.* **502** 119697
- Breiman L 2001 Random forests *Mach. Learn.* **45** 5–32
- Buechling A, Martin P H and Canham C D 2017 Climate and competition effects on tree growth in Rocky Mountain forests Ed F Piper *J. Ecol.* **105** 1636–47
- Chen H Y and Popadiouk R V 2002 Dynamics of North American boreal mixedwoods *Environ. Rev.* **10** 137–66
- Christin S, Hervet É and Lecomte N 2019 Applications for deep learning in ecology Ed H Ye *Methods Ecol. Evol.* **10** 1632–44
- Coogan S C P, Robinne F-N, Jain P and Flannigan M D 2019 Scientists' warning on wildfire—a Canadian perspective *Can. J. For. Res.* **49** 1015–23
- Cook-Patton S C et al 2020 Mapping carbon accumulation potential from global natural forest regrowth *Nature* **585** 545–50
- D'Orangeville L, Duchesne L, Houle D, Kneeshaw D, Cote B and Pederson N 2016 Northeastern North America as a potential refugium for boreal forests in a warming climate *Science* **352** 1452–5
- D'Orangeville L, Houle D, Duchesne L, Phillips R P, Bergeron Y and Kneeshaw D 2018 Beneficial effects of climate warming on boreal tree growth may be transitory *Nat. Commun.* **9** 3213
- Danneyrolles V et al 2019 Stronger influence of anthropogenic disturbance than climate change on century-scale compositional changes in northern forests *Nat. Commun.* **10** 1265

- Depardieu C, Girardin M P, Nadeau S, Lenz P, Bousquet J and Isabel N 2020 Adaptive genetic variation to drought in a widely distributed conifer suggests a potential for increasing forest resilience in a drying climate *New Phytol.* **227** 427–39
- Duchesne L, Houle D, Ouimet R, Caldwell L, Gloor M and Brienen R 2019 Large apparent growth increases in boreal forests inferred from tree-rings are an artefact of sampling biases *Sci. Rep.* **9** 6832
- Gauthier S, Bernier P Y, Boulanger Y, Guo J, Guindon L, Beaudoin A and Boucher D 2015b Vulnerability of timber supply to projected changes in fire regime in Canada's managed forests *Can. J. For. Res.* **45** 1439–47
- Gauthier S, Bernier P, Kuuluvainen T, Shvidenko A Z and Schepaschenko D G 2015a Boreal forest health and global change *Science* **349** 819–22
- Girardin M P, Isabel N, Guo X J, Lamothe M, Duchesne I and Lenz P 2021 Annual aboveground carbon uptake enhancements from assisted gene flow in boreal black spruce forests are not long-lasting *Nat. Commun.* **12** 1169
- Guindon L, Gauthier S, Manka F, Parisien M-A, Whitman E, Bernier P, Beaudoin A, Villemaire P and Skakun R 2020 Trends in wildfire burn severity across Canada, 1985–2015 *Can. J. For. Res.* **51** 1230–44
- Hellmann L *et al* 2016 Diverse growth trends and climate responses across Eurasia's boreal forest *Environ. Res. Lett.* **11** 074021
- Huang J, Tardif J C, Bergeron Y, Denneler B, Berninger F and Girardin M P 2010 Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest *Glob. Change Biol.* **16** 711–31
- Hurt G C *et al* 2020 Harmonization of global land use change and management for the period 850–2100 (LUH2) for CMIP6 *Geosci. Model Dev.* **13** 5425–64
- IPCC 2021 *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge: Cambridge University Press) (<https://doi.org/10.1017/9781009157896>)
- Laamrani A, Valeria O, Bergeron Y, Fenton N, Cheng L Z and Anyomi K 2014 Effects of topography and thickness of organic layer on productivity of black spruce boreal forests of the Canadian Clay Belt region *For. Ecol. Manage.* **330** 144–57
- Lavoie M, Harper K, Paré D and Bergeron Y 2007 Spatial pattern in the organic layer and tree growth: a case study from regenerating *Picea mariana* stands prone to paludification *J. Veg. Sci.* **18** 213–22
- Marchand W, Girardin M P, Hartmann H, Gauthier S and Bergeron Y 2019 Taxonomy, together with ontogeny and growing conditions, drives needleleaf species' sensitivity to climate in boreal North America *Glob. Change Biol.* **25** 2793–809
- Marchand W, Girardin M P, Hartmann H, Lévesque M, Gauthier S and Bergeron Y 2021 Contrasting life-history traits of black spruce and jack pine influence their physiological response to drought and growth recovery in northeastern boreal Canada *Sci. Total Environ.* **794** 148514
- Marquis B, Bergeron Y, Simard M and Tremblay F 2020 Growing-season frost is a better predictor of tree growth than mean annual temperature in boreal mixedwood forest plantations *Glob. Change Biol.* **26** 6537–54
- Matasci G, Hermosilla T, Wulder M A, White J C, Coops N C, Hobart G W, Bolton D K, Tompalski P and Bator C W 2018 Three decades of forest structural dynamics over Canada's forested ecosystems using Landsat time-series and Lidar plots *Remote Sens. Environ.* **216** 697–714
- Mccarthy M C and Enquist B J 2007 Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation *Funct. Ecol.* **21** 713–20
- McDowell N G *et al* 2020 Pervasive shifts in forest dynamics in a changing world *Science* **368** eaaz9463
- McKenney D W, Hutchinson M F, Papadopol P, Lawrence K, Pedlar J, Campbell K, Milewska E, Hopkinson R F, Price D and Owen T 2011 Customized spatial climate models for North America *Bull. Am. Meteorol. Soc.* **92** 1611–22
- McKenney D W and Pedlar J H 2003 Spatial models of site index based on climate and soil properties for two boreal tree species in Ontario, Canada *For. Ecol. Manage.* **175** 497–507
- Meinshausen N and Ridgeway G 2006 Quantile regression forests *J. Mach. Learn. Res.* **7** 983–99
- Messaoud Y and Chen H Y H 2011 The influence of recent climate change on tree height growth differs with species and spatial environment *PLoS One* **6** e14691
- MFFPO 2018 *Cartographie du 5e inventaire écoforestier du Québec méridional: méthodes et données associées* (Ministère des Forêts, de la Faune et des Parcs, Secteur des forêts)
- Nicklen E F, Roland C A, Ruess R W, Schmidt J H and Lloyd A H 2016 Local site conditions drive climate–growth responses of *Picea mariana* and *Picea glauca* in interior Alaska *Ecosphere* **7** e01507
- Nyström M, Holmgren J and Olsson H 2012 Prediction of tree biomass in the forest–tundra ecotone using airborne laser scanning *Remote Sens. Environ.* **123** 271–9
- Oboite F O and Comeau P G 2019 Competition and climate influence growth of black spruce in western boreal forests *For. Ecol. Manage.* **443** 84–94
- Pau M, Gauthier S, Chavardès R D, Girardin M P, Marchand W and Bergeron Y 2021 Site index as a predictor of the effect of climate warming on boreal tree growth *Glob. Change Biol.* **28** 1903–18
- Pedlar J H and McKenney D W 2017 Assessing the anticipated growth response of northern conifer populations to a warming climate *Sci. Rep.* **7** 43881
- Pugh T A M, Lindeskog M, Smith B, Poulter B, Arneeth A, Haverd V and Calle L 2019 Role of forest regrowth in global carbon sink dynamics *Proc. Natl Acad. Sci.* **116** 4382–7
- Robitaille A and Saucier J-P 1998 *Paysages régionaux du Québec méridional* (Gouvernement du Québec, Ministère des ressources naturelles, Québec (Canada))
- Rowe J S 1972 *Forest regions of Canada* (Ottawa: Fisheries and Environment Canada, Canadian Forest Service)
- Ryan M G, Binkley D, Fownes J H, Giardina C P and Senock R S 2004 An experimental test of the causes of forest growth decline with stand age *Ecol. Monogr.* **74** 393–414
- Schneider R, Franceschini T, Fortin M and Saucier J-P 2018 Climate-induced changes in the stem form of 5 North American tree species *For. Ecol. Manage.* **427** 446–55
- Seidl R *et al* 2017 Forest disturbances under climate change *Nat. Clim. Change* **7** 395–402
- Seidl R *et al* 2020 Globally consistent climate sensitivity of natural disturbances across boreal and temperate forest ecosystems *Ecography* **43** 967–78
- Seidl R, Spies T A, Peterson D L, Stephens S L and Hicke J A 2016 Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services *J. Appl. Ecol.* **53** 120–9
- Seidl R and Turner M G 2022 Post-disturbance reorganization of forest ecosystems in a changing world *Proc. Natl Acad. Sci.* **119** e2202190119
- Skubel R, Arain M A, Peichl M, Brodeur J J, Khomik M, Thorne R, Trant J and Kula M 2015 Age effects on the water-use efficiency and water-use dynamics of temperate pine plantation forests: age effects on the water-use efficiency in plantation forests *Hydrol. Process.* **29** 4100–13
- Sørensen R, Zinko U and Seibert J 2006 On the calculation of the topographic wetness index: evaluation of different methods based on field observations *Hydrol. Earth Syst. Sci.* **10** 101–12

- Wang J, Taylor A R and D'Orangeville L 2023 Warming-induced tree growth may help offset increasing disturbance across the Canadian boreal forest *Proc. Natl Acad. Sci.* **120** e2212780120
- White J C, Wulder M A, Varhola A, Vastaranta M, Coops N C, Cook B D, Pitt D and Woods M 2013 A best practices guide for generating forest inventory attributes from airborne laser scanning data using an area-based approach *For. Chron.* **89** 722–3
- Wright M N and Ziegler A 2017 Ranger: a fast implementation of random forests for high dimensional data in C++ and R *J. Stat. Softw.* **77** 1–17