# Monitoring climate sensitivity shifts in tree-rings of eastern boreal North America using model-data comparison

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Keywords: boreal forests, North America, bioclimatic models, climate change, climate-growth relationships, black spruce, *Picea mariana*

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C.O., M.P.G. and I.D. designed research; C.O. and M.P.G. performed research; C.O. and M.P.G. contributed new reagents/analytic tools; C.O. and M.P.G. analyzed data; and C.O., M.P.G., I.D., A.H., and Y.B. wrote the paper.

Abstract

The growth of high-latitude temperature-limited boreal forest ecosystems is projected to become more constrained by soil water availability with continuing warming. The purpose of this study was to document ongoing shifts in tree growth sensitivity to the evolving local climate in unmanaged black spruce (*Picea mariana* (Mill) B.S.P.) forests of eastern boreal North America [49°N-52°N, 58°W-82°W] using a comparative study of field and modeled data. We investigated growth relationships to climate (gridded monthly data) from observed (50 site tree-ring width chronologies) and simulated growth data (stand-level bioclimatic model) over 1908-2013. No clear strengthening of water control upon tree growth in recent decades was detected. Despite climate warming, photosynthesis (main driver of bioclimatic models) and xylem production (main driver of radial growth) have remained temperature-limited. Analyses revealed, however, a weakening of the influence of growing season temperature on growth during the mid- to late-20$^{th}$ century in observed data, particularly at high-latitude (> 51.5ºN) mountainous sites. This divergence was absent from simulated data which resulted in a clear model-data desynchronization. Thorough investigations revealed that both phenomena were mostly linked to the quality of climate data, precipitation data being of particular concerns. The scarce network of weather stations over eastern North America affects the accuracy of local climate variability and critically limits our ability to monitor climate change impacts on high-latitude ecosystems while drought severity is projected to rise. Climate estimates from remote sensing could help address some of these issues in the future.

## Introduction

Tree growth rates are well correlated with spatial and temporal climate variability (Gifford and Evans 1981; Rennenberg and others 2006; Wu and others 2012; Vlam and others 2014; Gricar and others 2015). During the last century, increasing anthropogenic activities have altered global climate and local weather dynamics (Mann and others 1998; IPCC 2014), thereby affecting tree growth processes. Tree growth in many boreal regions lost its positive response to rising temperatures during the late-20th century (D'Arrigo and others 2008), a phenomena often in parallel with increased sensitivity of tree growth to precipitation and drought severity (Buermann and others 2014; Galván and others 2015; Latte and others 2015). But causes for changing climate sensitivity in tree-rings vary and may also result from responses to other phenomena associated with changing cloud cover, delayed snowmelt and increasing local pollution (Vaganov and others 1999; D'Arrigo and others 2008). Furthermore, links between temporal variations in tree responses to climate and climate change likely involve cross-scale interactions between abiotic and biotic variables, e.g., tree age/size and site characteristics effects on tree growth (Carrer and Urbinati 2004; Rossi and others 2008; Ibáñez and others 2014; Navarro-Cerrillo and others 2014) and insect herbivory (Krause and others 2012; Fierravanti and others 2015). The evaluation of climate change impacts on tree growth dynamics remains challenging (Girardin and others 2016b).

In the boreal forest of eastern North America, seasonal temperatures have increased by as much as 3ºC since the beginning of the 20$^{th}$ century (Hansen and others 2010; Jaume-Santero and others 2016), while seasonal precipitation have shown variable patterns (Wang and others 2014). Studies have reported a decrease in tree growth sensitivity to growing season temperature at historically 'temperature-limited' high latitude and high altitude forests (Jacoby and D'Arrigo 1995; Briffa and others 1998; Galván and others 2015). In parallel, growth declines have been reported during the late 20$^{th}$ century (Girardin and others 2016a) and occurrence of years with extremely low growth in the boreal forest of eastern North America has increased over the 20$^{th}$ century (Ols and others 2016). Both phenomena have been attributed to increased drought impacts on tree growth. Projections have shown that during the next century, soil water availability, atmospheric water demand and heat stress in the boreal forest of eastern North America will increasingly limit tree growth as a consequence of the

continuing warming (Girardin and others 2016b; Novick and others 2016). The degree to which this forest will adapt to warmer and drier conditions, e.g. by increasing their water use efficiency, is uncertain (Charney and others 2016). It is, therefore, important that these ecosystems are continuously monitored to detect early warning signs of changes in climatic controls of tree growth (Gauthier and others 2015). However, such an observation-based monitoring is complicated by the large spatial extent of the boreal forest of eastern North America and by the multiple species involved.

Forest growth models facilitate the exploration of tree growth processes and their expected relationship to the evolving local climate. Such a bioclimatic model can be built upon sets of mathematical equations accounting for non-linear relationships between specific environmental and physiological variables derived from empirical observations (Landsberg and Waring 1997; Misson 2004). Studying the coherency in climatic signals contained in empirical tree growth data and simulated tree-growth data may help understand whether variations in tree-growth responses to climate emerge from changing climate alone or from changes in tree-growth sensitivity to climate. Modelling may also help studying tree growth and its sensitivity to climate in areas where ground sampling is more difficult due to the remoteness of locations and costs associated with this type of sampling.

In this study, we explore the possibilities of monitoring shifts in tree growth sensitivity to climate in boreal black spruce forests in eastern North America by comparing observed and model-based climate-growth relationships over 1908-2013. Observed data consisted of a newly acquired network of 50 annually resolved and absolutely dated black spruce tree-ring width chronologies covering latitudinal and longitudinal gradients of eastern boreal North America [49°N-52°N, 58°W-82°W, Fig. 1]. As for the model-based data, we used a stand-level bioclimatic model, based on the Physiological Principle Predicting Growth (3PG) model (Landsberg and Waring 1997), to simulate yearly site-specific net primary production (NPP) for the period encompassing observed data (i.e. 1908-2013). Two hypotheses were formulated on the basis of the widely accepted evidence that temperatures have been rising in the study region:

(H1) Yearly variability in tree growth is under the control of climate. The validity of this hypothesis implies a significant correlation between tree-ring width data and climatically driven simulations of NPP;

(H2) The control of water on tree growth has increased over time along with the rise of temperature, particularly at high-latitude and high-altitude forests. This implies an increased positive sensitivity to precipitation both in tree-ring width data and climatically driven simulations of NPP.

## Material and methods

*Study area*

The study area consists of three latitudinal transects (western, central and eastern; Fig. 1a) established in northern boreal Quebec (Ols and others 2016). The topography in this area is characterized by low plains in the west (200-350 m above sea level [a.s.l.]) and by mountains, particularly pronounced in the north, central and eastern regions (up to 1128 m a.s.l. in the Otish Mountains). The two main climatic gradients in the study area are a decreasing temperature gradient from south to north and an increasing summer (June to August) precipitation gradient from west to east (Fig. 1b). The eastern region is regularly prone to spruce budworm outbreaks (Boulanger and Arseneault 2004).

*Tree-ring width measurements*

Tree-growth data (n= 890 trees) were collected at 50 sites located along the three latitudinal transects (Fig. 1a, Table S1) (Ols and others 2016). All sites were unmanaged old-growth pure black spruce (*Picea mariana* (Mill) B.S.P.) forests growing on xeric to meso-xeric soils (Direction des inventaires forestiers 2015). Between 10 and 27 dominant trees (standing living or dead) were sampled per site (one core per tree). Sampled cores were processed using standard procedures and rings were visually cross-dated prior to measuring. Tree-ring width measurements were detrended using a 60-yr spline to eliminate noise caused by site- and biological-related effects (e.g. competition, self-thinning and aging) (Cook and Peters 1997). Detrended ring-width measurements were then processed using autoregressive modeling to remove autocorrelation (pre-whitening) and averaged into site-specific residual tree-ring width (RWI) chronologies using a robust bi-weighted mean.

*Climate data*

Climatological data used as input for the bioclimatic model and in the calculations of climate-growth relationships were monthly means of maximum (Tmax) and minimum (Tmin) temperatures, and monthly total precipitation (Prec), all extracted from the 0.5° x 0.5° CRU TS 3.22 database (Harris and others 2014). The climatic characteristics of each study site were extracted over the 1901-2013 period, using a site-centered 0.5° x 0.5° grid cell. We retrieved data from twenty-one grid cells, with each grid cell containing between 1 and 7 study sites. Consequently, some study sites presented identical climatic characteristics (Table S1). To test the influence of climate data type on model simulations and climate-growth relationships, site-specific climate data (Tmin, Tmax and Prec) were also extracted over the 1901-2013 period (using the same procedures as above) from three alternative databases: (1) the Canadian software BioSIM (Régnière and others 2014), (2) the combined 0.5° x 0.5° CRU TS 3.22 temperature (Harris and others 2014) and GPCC precipitation (Full Data Reanalysis Version 7) (Schneider and others 2015), and (3) Twentieth Century Reanalysis (20CR) (Compo and others 2011) datasets. The 20CR data are derived from oceanic temperature and surface pressure data, and do not incorporate precipitation and station temperature records (Compo and others 2011); 20CR may thus be viewed as independent from all other climate products.

The boreal region of eastern Canada is not covered by a dense network of weather stations (Fig. S1). In many instances, the existing stations have been running intermittently (Girardin and others 2016b). To capture precipitation and temperature input data accuracy through space and time, the number and location of meteorological stations used for climatic interpolations within our study area were extracted. We also extracted the only long-running hydrological record of the study area: the 1960-1993 De Pontois river flow from HYDAT 28.0 (Water Survey of Canada, http://www.ec.gc.ca/rhc-wsc) (Table S3) , and used this record as a surrogate for drought conditions (Haslinger and others 2014).

*Forest attributes*

Biometric information necessary for the model simulation was obtained as follows. First, the above-ground biomass in mega-grams per hectare ($W_{abg}$) was estimated at each study site using country-wide species-specific allometric equations (Paré and others 2013) applied to site-specific basal area (Table S2). Site-specific topography data (slope and aspect values; Table S2) were then extracted from Canada 3D, a digital elevation model produced by the Canadian Forestry Service (Natural Resources Canada 2002) using the ArcGIS® software (ESRI 2011). Finally, historical patterns of defoliation severity by the spruce budworm (1967–2016), compiled from Quebec's provincial annual surveys (Ministère des Forêts, de la Faune et des Parcs du Québec (MFFPQ) 2014), were extracted for each of our sites.

*Net primary productivity data*

Net primary production (NPP) at our 50 sites was simulated using the StandLEAP model (version 0.1 SVN) (Girardin and others 2016b). StandLEAP is a generalized plot-level model based on the 3PG model (Landsberg and Waring 1997) that is applicable to relatively homogeneous forests. It was developed for the estimation of forest productivity over large areas (e.g. Girardin and others 2016b) but with a spatial resolution sufficiently fine for forest management (e.g. Raulier and others 2000; Coulombe and others 2009; Anyomi and others 2014). StandLEAP can be parameterized for individual species and its application to any stand does not require fine-tuning of the model to fit the data. The model has been tested against numerous independent tree-ring datasets in western, central and eastern Canada (Girardin and others 2008, 2011b, 2011a, 2012, 2014, 2016b). In StandLEAP, parameters are set up to fully characterize the impact of many interacting and non-linear modifiers of carbon flux quantities (e.g. growth and respiration). Absorbed photosynthetically active radiation (APAR) is related to growth primary production (GPP) using a radiation use efficiency (RUE) coefficient that differs among locations and through time as a function of environmental constraints. Constraints take the form of species-specific parameters ($f_1 \ldots f_n$) that take on a value of 1 under average conditions; they are closer to zero to represent increasing limitations, or above 1 as conditions improve towards optimum. Constraints represent the impact of soil drought (Bernier and others 2002), frost (Aber and others 1996) (both limited to a maximum of 1.0), mean maximum and minimum daily

air temperature, vapor pressure deficit (VPD), monthly radiation, and leaf area index (where values greater than 1.0 are possible) on GPP. The following equation summarizes these functions:

$$GPP = APAR \times (\overline{RUE} \times f_1 f_2 ... f_n), \quad (1)$$

where $\overline{RUE}$ represents a species-specific mean value of RUE applicable to the entire species' range. Canopy light absorption and photosynthesis parameters were derived from metadata generated using a more detailed multi-layer, hourly time-step model of canopy photosynthesis and transpiration called FineLEAP (Raulier and others 2000; Hall and others 2006). Representation of photosynthesis in FineLEAP is based on the equations of Farquhar and others (1980). Additional details of the procedure and origin of the basic field measurements and procedure for estimation of parameters for radiation interception, radiation- and water-use-efficiency can be found in Hall and others (2006). NPP is computed monthly, after partitioning respiration into maintenance (Rm) and growth (Rg: a fixed proportion of the difference between GPP and Rm) quantities and subtracting these from GPP. Maintenance respiration is computed as a function of temperature using a $Q_{10}$ relationship (Ågren and Axelsson 1980; Ryan 1991; Lavigne and Ryan 1997). Acclimation of respiration to temperature is modelled using the equation of Smith and others (2016). As in 3-PG, part of NPP is first allocated to fine roots (Eq. (13) in Landsberg and Waring 1997) on a yearly basis and then to replacement of carbon biomass lost to leaf and fine woody litter turnover. The remaining NPP is then allocated to increments in stand carbon compartments of foliage, branches, coarse roots and stems. The modifier for soil water availability is based on modeled water balance coupled with transpiration and NPP, as described by Bernier and others (2002). The impact of $CO_2$ fertilization is included through a modifier of the potential water use efficiency, as described by Girardin and others (2016b). The active soil depth was set to 600mm at all sites (Table S2). An active soil depth between 300 and 900mm has generally been accepted as a desirable range for black spruce (Viereck and Johnston 1990; Girardin and others 2016b). Three sites (namely, 39, 45 and 47, Table S2) had their above-ground biomass truncated to a maximum value of 110 Mg/ha, because of estimated field values reaching higher than typical conditions for which the model was calibrated. StandLEAP runs on a monthly time-step. All carbon flux quantities used in this study were made insensitive to changing forest age over time, by

fixing constant forest attributes (e.g. biomass and stem densities) across all simulation years. Carbon flux quantities solely express direct climate influences on plant growth, avoiding the influence of post-fire stand dynamics on fluxes (e.g. Girardin and others 2011a; Pan and others 2011) and allowing a direct comparison with climatically-driven tree-ring width measurements collected from old-growth forest stands. The model does not simulate soil processes other than water balance, since it implicitly assumes constant soil nutrient properties and turnover. Furthermore, computations assume the absence of insect outbreaks.

*Correlation between tree-ring and NPP metrics*

Monthly NPP values obtained from modelling were summed up from July the previous year to June the year of growth, to represent carbon quantities mobilized and allocated to growth from one year to the next (as in Girardin and others 2016b). Carry-over effects from the previous growing season have been reported to affect significantly tree growth the following season, and particularly in a harsh environment (Babst and others 2014; Ols and others 2016). Lower carbohydrate reserves the following growing season, can notably decrease the capacity of trees to respond to favorable growth conditions. The correspondence between annual RWI and NPP metrics were then explored through moving correlations (one-sided test) at site level. Correlations were computed in R (R Core Team 2015) using 21-yr windows incremented by five years from 1908 to 2013. The null hypothesis of no positive correlation between RWI and NPP was rejected when $p < 0.05$. Temporal stability in correlations between RWI and NPP metrics were also investigated at regional level using the same moving-correlation procedure as above. Regional RWI and NPP metrics were computed as a robust bi-weighted mean of all site-specific metrics. The significance of each 21-yr correlation averaged across sites was evaluated using a competitive test, which combines the probabilities of dependent tests using the Fisher's method (Dai and others 2014). Applied to our specific case, it compares, for each 21-yr period, the distribution of $p$ values of all site-specific NPP and RWI correlations to the distribution of randomly selected 100,000 vectors of $p$ values of similar length. Competitive tests were computed in R using the *competitive.test* function available in the *CombinePValue* package (Dai 2014).

*Climate-growth relationships*

Coherency in the climatic signals contained in RWI and NPP metrics were investigated by correlation analyses. First, correlations between tree-growth metrics and monthly climate data were computed using 21-yr windows incremented by five years from 1908 to 2013 using the *treeclim* package (Zang and Biondi 2015). Climate data included monthly maximum and minimum temperatures and monthly total precipitation. Months spanned from May the previous year to August the year of growth. Site-specific moving correlations were then averaged across all sites to characterize monthly climate-growth relationships at the scale of our study area. The following hypotheses, based on the earlier work by Girardin and others (2016b), were postulated and tested using one-sided tests: (1) growth is positively correlated with previous year September through current year May (hereafter September-May) temperatures, (2) growth is negatively correlated with June-August temperatures, and (3) growth is positively correlated with precipitation, regardless of the month. Alternatively, we also tested the inverse versions of hypotheses 1 to 3: growth is (4) negatively correlated with September-May temperatures, (5) positively correlated with June-August temperatures, and (6) negatively correlated with precipitation. Hypotheses 1-6 were considered true both for months of the previous and current growing season year. These procedures were run both for RWI and NPP series. Note that stronger correlations observed with NPP can logically emerge from computation alone, since NPP is itself computed from these climate data. The significance of each 21-yr correlation averaged across sites was evaluated using the competitive test described earlier. We opted for six one-sided hypotheses instead of three two-sided hypotheses because under two-sided testing the meta-analysis is particularly sensitive when both strong positive and negative effects occur across sites (Whitlock 2005). Finally, the distributions of site-specific correlations with monthly climate variables of the two metrics were compared using the Wilcoxon-Mann-Whitney and Kolmogorov-Smirnov tests.

## Results

*Climate sensitivities in tree growth metrics*

RWI was generally positively correlated with current year spring and summer temperatures (Fig. 2a). However, these correlations decreased substantially and became non-significant during the mid- to

late-20th century (Fig. 2a). This decrease in correlation corresponded with the emergence of significant negative correlations with previous summer and previous October temperatures (maximums and minimums) from the 1940s to 1990s, and with current spring precipitation during a brief period covering the 1960-80s (Fig. 2a). In addition, significant positive correlations between RWI and early winter temperatures were observed during the late-20th century (Fig. 2a). The correlation between RWI metrics and De Pontois summer (mean June to August) river flow of the year prior to growth, and over 1960-1993, was significantly positive (median correlation of 0.31), especially at high latitudes (>51.5ºN) (Fig. 3). In summary, annual growth variability in this boreal region of eastern North America has shifted from being positively correlated with growing-season temperature early in the 20th century, to being negatively correlated with summer temperature during the mid-century, and then back to being positively correlated with temperature during the late-20th century. There was no clear evidence of a strengthening of tree growth sensitivity to precipitation throughout the 1908-2013 period, using CRU precipitation data (Fig. 2a).

Relationships between NPP and monthly climate variables were similar to those observed for RWI metrics (Fig. 2b, c). NPP correlated positively with current year temperatures, but this relationship was much weaker from 1958 to 1988 (Fig. 2b). Between 1973 and 1998 there was an emergence of significant negative correlations with previous summer temperature (Fig. 2b). Unlike with RWI, there was a period of sustained significant positive correlations with July or August precipitation during the year contemporaneous to growth from 1933 to 1998 (Fig. 2b). Wilcoxon-Mann-Whitney tests indicated that the distribution of correlations between NPP and monthly temperature (minimum and maximum) was generally more homogeneous than with RWI (Fig. 2c). By contrast, the distributions of correlations to precipitation for both metrics were mostly similar. This was also observed using the Kolmogorov-Smirnov test (Fig. S2). NPP metrics and De Pontois summer river flow were not significantly correlated ($p > 0.05$) (data not shown). However, these variables were significantly correlated after a first-difference transformation in 33 of the 50 study sites, mostly north of 51.5ºN and west of 74.0ºW (median correlation of 0.32; correlation pattern similar to the RWI pattern presented in Fig. 3d but with both variables taken on their non-lagged calendar years; results not shown). In summary, NPP variability shifted from being temperature-driven in the early-20th

century (an indication of temperature limitation on the rate of photosynthesis), to precipitation-driven during the mid- to late-20th century (i.e. the influence of available moisture), and then again temperature-driven during the late-20th century.

*Synchronicity in tree growth metrics*

Correlations between site-specific RWI and NPP metrics at regional level were often positive and significant during the early-20th century and throughout the late-20th to early-21st centuries (Fig. 4). However, a clear desynchronization was observed in the middle of the century at almost all sites, when correlations substantially decreased to become negative and occasionally significantly negative (Fig. 5, left-hand panels). Although its duration and timing differed across sites, this desynchronization was most prominent in mountainous north easternmost sites (Fig. 6d), i.e. in areas ongoing the most rapid warming (Fig. 1a). First-differencing (subtraction of the value at $year_t$ by the value at $year_{t-1}$) of the RWI and NPP data enhanced correlations during the late-20th century but decreased correlations during the early-20th century across the whole area (Fig. 5, right-hand panels). It is noteworthy that the same mid- to late-20th century desynchronization between observed and simulated tree-growth metrics was obtained using alternative climate datasets, albeit there were variations in the onset and duration of this desynchronization depending on the data products (Fig. S3). For instance, correlations between NPP and RWI were improved during the 1933-1963 period when fed by simulations of the NPP driven by the 20CR data, albeit it did not fully compensate for model-data desynchronization (Fig. S3d).

## Discussion

The purpose of this study was to document shifts in tree growth sensitivity to climate in temperature-limited boreal forest ecosystems of eastern boreal North America over 1908-2013 using a comparative study of field and modeled data.

Despite climate warming in the study area (Figs. 1a and S4), there was no clear evidence for a strengthening of radial tree growth (RWI) sensitivity to precipitation during recent decades (Fig. 2). The post-1980 significant positive correlations between (1) growing-season temperature and radial

growth (Fig. 2c), and between (2) radial growth and modeled productivity (NPP) across the entire study region (Fig. 4) indicate that both photosynthesis (the main driver of the model) and xylem formation (the main driver of radial growth) have until recently remained temperature-limited. This contradicts earlier findings reporting the strengthening of soil water availability control on tree growth in the boreal forest of eastern North America over the 20th century (see Introduction). The response of tree radial growth in our studied regions is therefore different from the response frequently reported in the literature for the boreal forest. A likely reason for this lack on increased sensitivity of tree growth to precipitation may be that, despite rising temperature (Fig. 1a), the atmospheric water demand may have decreased over the course of the 20th century in our study area (Fig. S5; also see Fig. S9 in Girardin and others 2016b). A decrease in water demand, coupled with a potential increase in water use efficiency under elevated atmospheric $CO_2$ concentrations, may have contributed to the stabilization of tree dependence on incoming precipitation necessary for soil water recharge.

Our results revealed that while modeled productivity remained somewhat spring temperature sensitive over the entire study period, the positive influence of growing season temperature on radial growth disappeared. This phenomenon occurred in parallel with an increased sensitivity to moisture, as indicated by the negative correlation between radial growth and summer temperature, by the positive correlation between radial growth and the De Pontois summer river flow, and by the positive correlation between modeled productivity and July precipitation. However, during this same period the overall region-wide significant synchrony between modeled productivity and radial growth also dropped to become insignificant, particularly at eastern high-latitude mountainous sites, i.e. those undergoing the strongest warming (Fig. 1a). These sudden model-data desynchronization is noteworthy and deserves attention, as it may impair our capacity to monitor shifts in tree growth sensitivity to climate in these forests. Below we discuss three factors that may be involved in this desynchronization: accuracy of input climate data, the advent of external factors in the ecosystem, and model uncertainties.

Climate data uncertainties have a large influence on model-based estimations of historical and ongoing ecosystem processes: the choice of climate dataset, with those of precipitation being of particular concern, affects the capacity to identify drivers of variability in empirical data products and

model results (e.g. Daly and others 1994; Ito and others 2017; Wu and others 2017). For example, the probability of a false negative result (e.g. a significant RWI-precipitation correlation not detected when a true relationship exists) could theoretically be higher at sites where climate data quality is lowest (Wilson and others 2007). In the current study, the quality of climate data is likely to be a critical factor explaining the drop in model-data correspondence during the mid- to late-20$^{th}$ century. First, the desynchronization in model-data correspondence was most prominent at sites located above 51.5ºN (Fig. 5c), that is, where station density is low (Figs. 5 and S1). There is, therefore, an apparent relationship between station density and climate signal degradation.

Additionally, weak model-data correspondence was clearly linked to altitudinal differences between reference stations (mainly located along the coast) and mountainous sampled sites, with a higher capacity to detect a positive correlation between radial growth and modeled productivity at low altitude sampling locations (Fig. 6d). This bias finds explanation in the fact that CRU temperature interpolations over boreal eastern North America do not depict altitudinal climate gradients (Fig. S6). Our capacity to model forest growth in mountainous regions is hence very likely hindered by inaccuracies of temperature and precipitation estimates at these high-altitude sites. The variations in the onset and duration of the desynchronization between radial growth and modeled productivity across climate data products illustrate the problem of climate data uncertainties. Noteworthy is that the onset of the desynchronization between radial growth and modeled productivity coincides with a period of high weather station density in the region (Figs. 6a and S1b&c) but also of high uncertainty in estimates of precipitation data in the region (Figs. S1c and S7). Indeed, cross-correlations between CRU and the 20th Century Reanalysis (20CR) gridded data show a strong inconsistency during the period 1940-1980 (Fig. S7), a sign of significant error in the estimation of climatic data either in one or the other climatic product.

Last, the formulation of the model used herein may be missing important dynamic processes associated with insect outbreaks, carbohydrate mobilization and storage, snow accumulation and thawing, initiation of leaf-out and growth processes.

Notably, outbreaks of the eastern spruce budworm, regular in the boreal forest of eastern North America, could have contaminate field data by disrupting radial growth responses to local climate and

caused the model-data desynchronization (Girardin and others 2016b), simulations being computed in an outbreaks-free environment. However, we did not observe any obvious abrupt growth decline or release, typical of severe outbreak defoliation on these site chronologies (Figs. 4 and S7). Also, most of the sites showing desynchronization were located in an area that did not show historical evidence of spruce budworm outbreaks during the 1947-1958, 1975-1992 and 2007-2016 periods (Fig. 6b). Furthermore, the sampled stands were free of the main budworm host-species *Abies balsamea*. Although the influence of such disturbance on growth can not entirely be ruled out, its role on the observed model-data desynchronization can be only minor. It may, however, become an important concern if this experimental design is to be applied in regions where this disturbance is recurrent (Girardin and others 2016b).

Our experimental design assumes that radial growth and modeled productivity are directly comparable analogs. This, however, disregards documented evidences that shifts in radial growth sensitivity, to temperature for instance, emerge from changes in allocation of assimilates within a tree (Lapenis and others 2013). Assimilates allocation is strongly sensitive to stand density (e.g. denser stands favoring allocation to terminal buds to increase access to light) and climate (e.g. drier climate favoring allocation to roots to increase access to water). The period of desynchronization was characterized by a decrease in spring precipitation and an increase in spring temperature (Fig. S4). Such climatic conditions may have temporarily favored the allocation of assimilates to the root system against radial growth, disrupting radial growth responses to climate. In a sensitivity analysis in which the total annual productivity data were substituted with the productivity fraction allocated to the stem (as in Girardin and others 2008), we noted an improved model-data correspondence during the first half (1940-1960) of the divergent period (Fig. S9). But the correspondence deteriorated substantially during the second half (1960-1980) (Fig. S9). Moreover, any of the sites showing model-data desynchronization were located in open-canopy stands nearby the limit between the spruce-moss and spruce-lichen domains, located north of 51.5°N (Robitaille and Saucier 1998). Hence there are no reasons to believe that height growth would have been favored against diameter growth during the mid- to late-20th century. Model-data desynchronization during the mid- to late-20$^{th}$ century, therefore, do not appear linked to shifts in field growth allocation patterns.

If we do not question the quality of precipitation data, the sudden negative sensitivity to spring precipitation in radial growth over the mid- to late-20th century, not observed with modeled productivity, may be indicative of a stronger negative impact of spring precipitation on tree growth (Huang and others 2010; Girard and others 2011; Ols and others 2016). Sites presenting a sudden negative sensitivity to spring precipitation were the ones undergoing the strongest warming (Fig. 1a) and were mainly located in high-altitude mountainous areas (Fig. 6d). Snow dynamics (fall and melting) influence tree growth and climate-growth relationships at boreal latitudes (Frechette and others 2011; David 2015), particularly along altitudinal gradients (Trujillo and others 2012). Notably, a thick spring snow cover may delay the start of the growing season through delayed snow melt (Vaganov and others 1999). The current model formulation does not include a dynamic snow model, as in Terrier and others (2013). This may mislead the onset and duration of the drought season and ultimately affect the capacity to uncover drivers associated with the water balance at high-altitude sites.

## Conclusion

Climate change and its impact on high-latitude boreal ecosystems are now recognized. There is no doubt that, in the near future, intensive efforts will need to be taken to monitor these impacts in order to pave the way for adaptation and mitigation solutions (Gauthier and others 2015). This will require tools to adequately link ecosystem dynamics to atmospheric properties. In this view, we showed that bioclimatic models can track fairly well processes leading to forest growth variability of the northernmost boreal forest of eastern North America through space and time when growth remains temperature-limited (Girardin and others 2008, 2016b). Our work nevertheless illustrated some of the challenges that hinder the capacity to keep monitoring high-latitude boreal ecosystems at fine-scale across a diversity of landscapes. Among issues, uncertainties in climate data are of particular concern. Many of the temperature-limited regions of boreal Canada are covered by a scarce network of weather stations, which affects accuracy of local climate variability estimates and make it difficult to relate climate to ecosystems' dynamics. Availability of climate data may, therefore, critically limit our ability to monitor climate change impacts on high-latitude forest ecosystems while drought severity is

projected to rise. Recent estimates of climate data, notably of precipitation and snow cover, through remote sensing could help address some of these issues in the future.

Acknowledgements

We are thankful to Emeline Chaste for GIS analyses and to Xiao Jing Guo for assistance with StandLEAP. This study was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC Strategic and Discovery Grants), by the Nordic Forest Research Cooperation Committee (SNS), by the Canadian Forest Service and by the Research Council of Norway (grant 160022/E50). This work was also supported by a fellowship from the Forest Complexity Modelling program. Authors do not present any conflicts of interests.

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Figure legends

**Figure 1.** (a) Location of the black spruce forests under study, eastern Canada. The sampling sites (*n* = 50) are shown accordingly with the positioning of transects along the west to east gradient (*colored symbols*). Slopes of linear trends (ºC per year) in summer (June to August) mean daily maximum temperatures from 1901 to 2013 are shown in background colors. (b) Distribution of sampling sites within gradients of mean annual temperature (MAT; ºC) and mean annual precipitation total (MAP; mm). The CRU TS 3.22 database (Harris, Jones, Osborn, & Lister, 2014) was used for generating this climate information.

**Figure 2.** Average correlations between monthly climate data and (a) RWI and (b) NPP metrics across all sites over 1908-2013. Analyses were conducted using 21-yr moving windows incremented by 5 years. (c) Comparison of the distributions of correlations obtained in (a) and (b), for each month and period combinations, using a Wilcoxon-Mann-Whitney test. Monthly climate variables included minimum (Tmin) and maximum (Tmax) temperatures, and total precipitation (Prec) extracted at site level from the 0.5° x 0.5°CRU database (Harris and others 2014). Months spanned from May the year previous to growth to August of the current year. Current year months start with a capital letter. The significance of each averaged correlation across sites was evaluated under two sets of climate-growth hypotheses using one-sided competitive tests (see 2.7 Climate-growth relationships). Open circles and black dots on panels (a) and (b) identify significant ($p < 0.05$) correlations under hypotheses 1-3 and 4-6, respectively. Black dots on panel (c) stand for no significant ($p > 0.05$) differences in the distribution of correlations.

**Figure 3.** (a) Mean of site RWI chronologies above 51.5°N. (b) Mean July to September river flow measured at the De Pontois river station (53°N-74°W, Table S3) over 1960-1993. (c) Biplot of the De Pontois river flow of the year previous to growth and RWI of the year contemporaneous to growth over 1961-1994. A linear regression with 95% confidence interval is shown: $R^2$=0.24. (d) Site-specific correlation between De Pontois river flow and RWI. Blue and red circles represent negative and

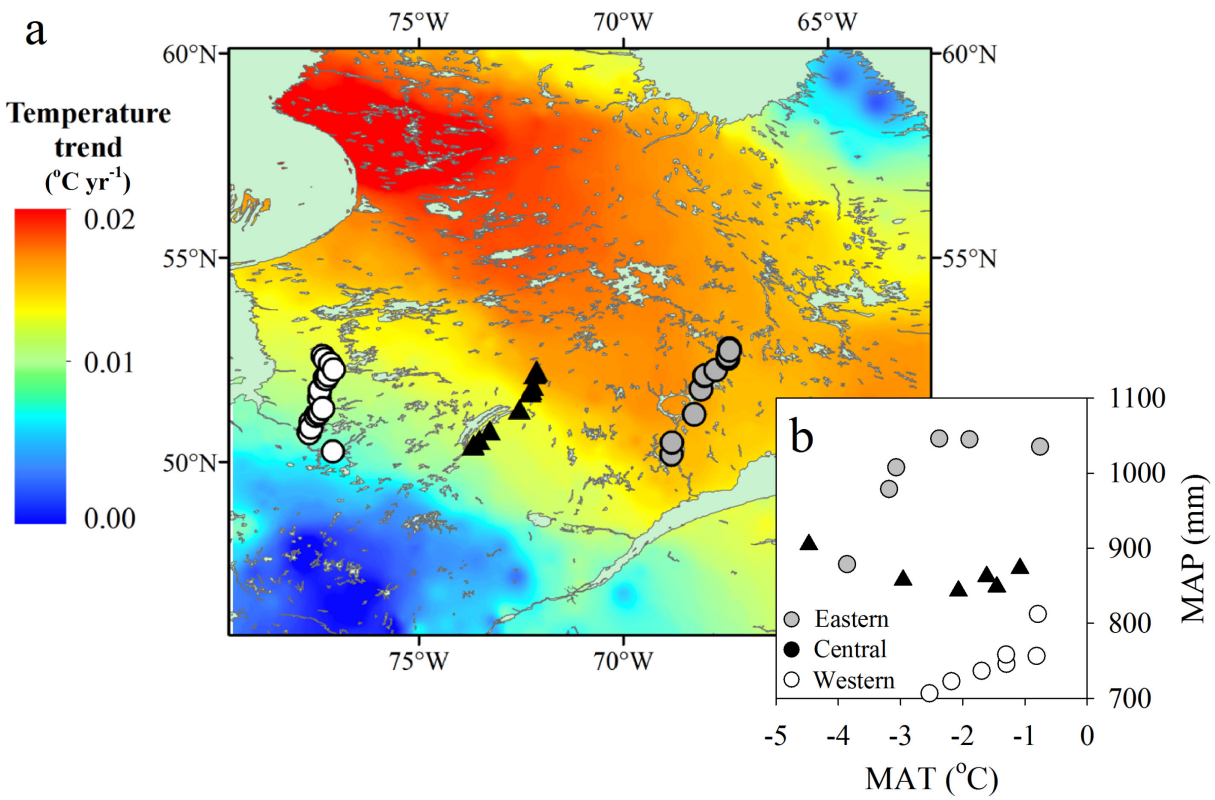
positive correlations, respectively; the larger the circle, the higher the correlation value. Black contours indicate significant correlations ($p < 0.05$).

**Figure 4.** (a) Average tree-ring width indices (black line) and net primary production (red line) chronologies across all sites ($n = 50$) over 1908-2013. (b) Moving correlations between both metrics were computed using 21-yr windows incremented by one year. Correlations are plotted on the central year of each interval. Significant correlations ($p < 0.05$) are indicated with black dots.

**Figure 5.** Pearson correlations between site-specific RWI and NPP metrics during five different 21-yr periods: (a) 1913-1933, (b) 1933-1953, (c) 1953-1973, (d) 1973-1993, and (e) 1993-2013. Correlations were computed using original (left-hand panels) and first-differenced (right-hand panels) metrics. Blue and red circles represent negative and positive correlations, respectively. The larger the circle, the higher the correlation value (|r|). Black contours delineating circles indicate significant correlations ($p < 0.05$). Black crosses indicate the position of meteorological stations available for that period.

**Figure 6.** Potential factors involved in the low RWI-NPP correlation from 1953 to 1993. (a) Changes in the median distances of weather stations closest to the sampling site over the years (blue: precipitation; red: temperature), with 95% confidence intervals computed from exact bootstrap resampling. Lower values denote a densification of the weather station network; higher values denote a scarce weather station network. (b) Vertical bars: percentage of sites located within a defoliated polygon of Quebec's provincial annual surveys covering 1967 to 2006 (source: MFFPQ 2014); the inset map shows the projected defoliated areas from 1974 to 1978 (gray shading) relative to the position of the sampling sites (black dots). Classes denote the percentage of needle loss on the annual shoot: light (1 to 35%), moderate (36 to 70%), and severe (71 to 100%). (c) Site-specific altitude (alt., above sea level) against the standard deviation (SD) of the altitudinal gradients between the four nearest weather stations and each site, as estimated using the software BioSIM over 1953-1993 (Régnière and others 2014). If the four nearest stations didn't all present climate records over the entire period, additional stations were added until the full period was covered. Site-specific 1953-1993

RWI-NPP correlations are plotted using transect-specific symbols: circles for West, squares for Central and triangles for East. Blue and red symbols represent negative and positive correlations, respectively; the larger the symbol, the higher the correlation value. Black contours indicate significant correlations ($p < 0.05$). (d) Altitudinal gradient (map) versus the distribution of the 1953-1993 NPP-RWI correlations (Jarvis and others 2008). The larger the circle, the higher the correlation value. Note that the altitudinal scale was truncated to 800m to enhance contrasts between low and high-altitude sampling sites.




717

718 **Figure 1.**

**Figure 2.**

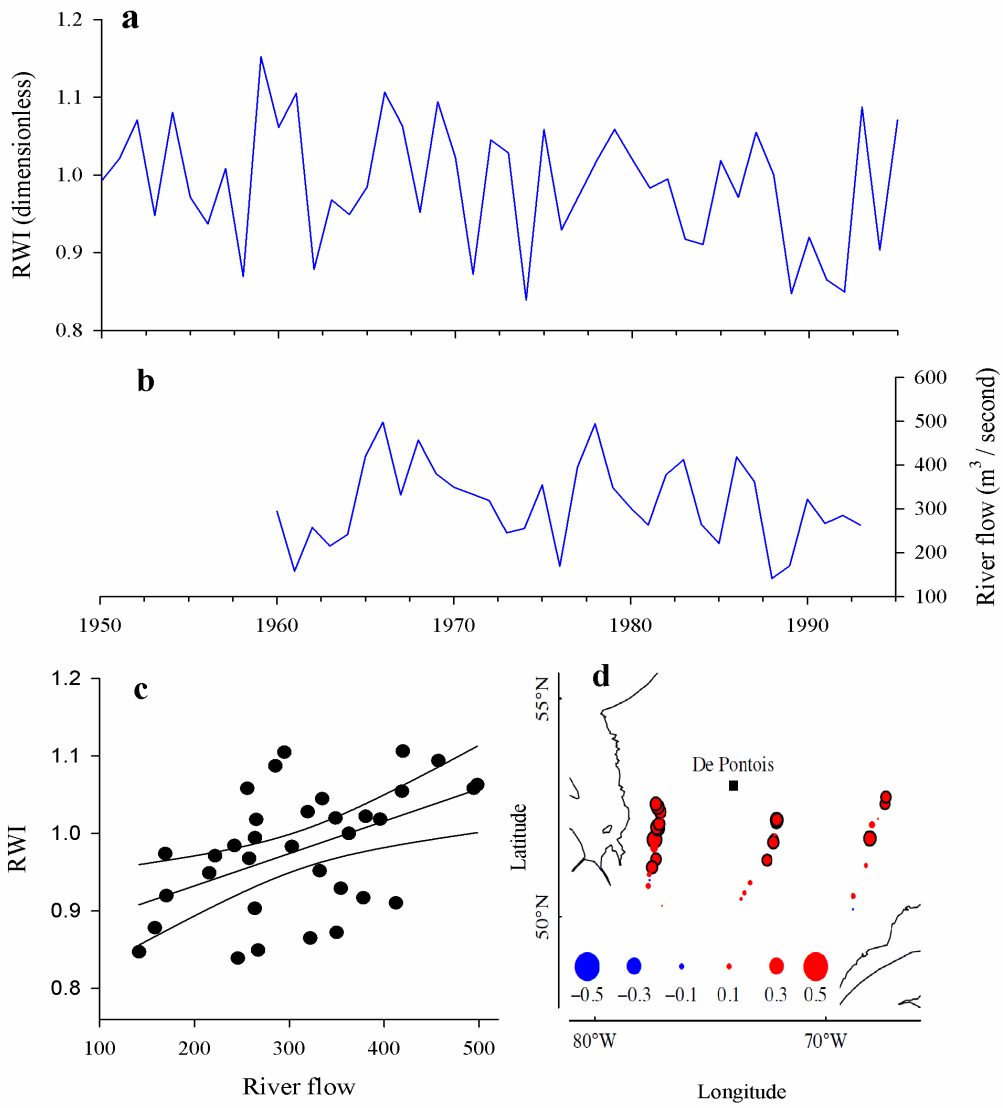

a
RWI (dimensionless)
1.2
1.1
1.0
0.9
0.8
b
River flow (m3 / second)
600
500
400
300
200
100
1950
1960
1970
1980
1990
c
RWI
River flow
d
Latitude
55°N
50°N
De Pontois
−0.5
−0.3
−0.1
0.1
0.3
0.5
80°W
70°W
Longitude

**Figure 3.**

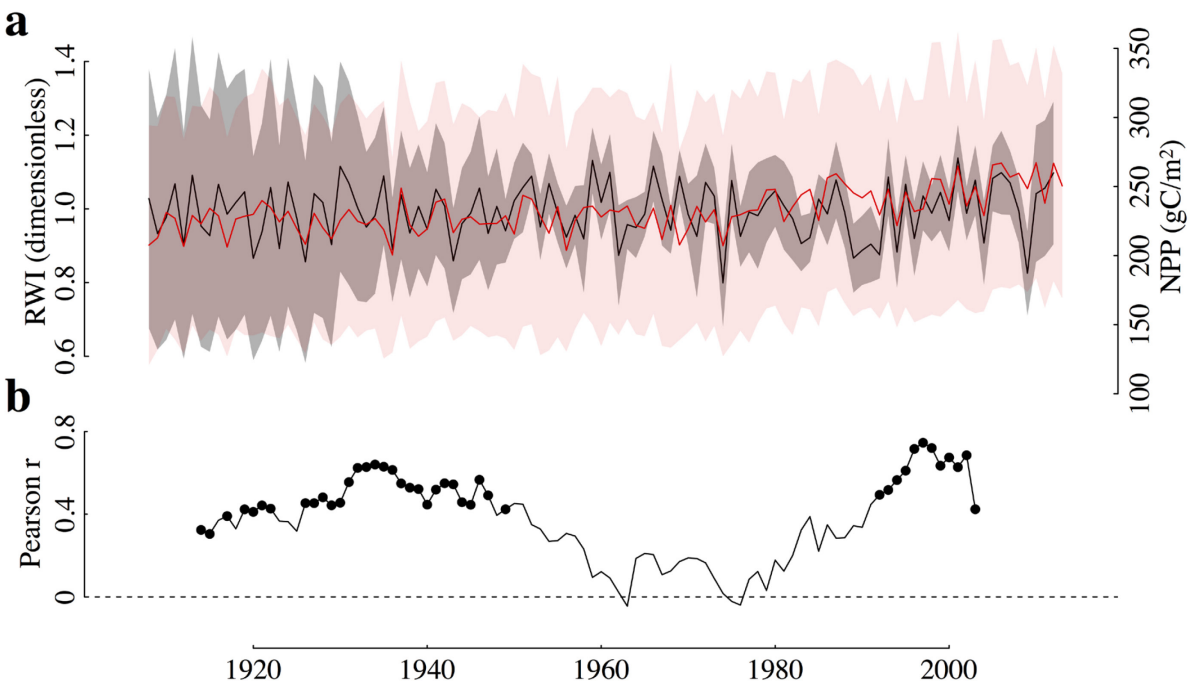

a
RWI (dimensionless)
0.6
0.8
1.0
1.2
1.4
NPP (gC/m²)
100
150
200
250
300
350
b
Pearson r
0
0.4
0.8
1920
1940
1960
1980
2000

**Figure 4.**

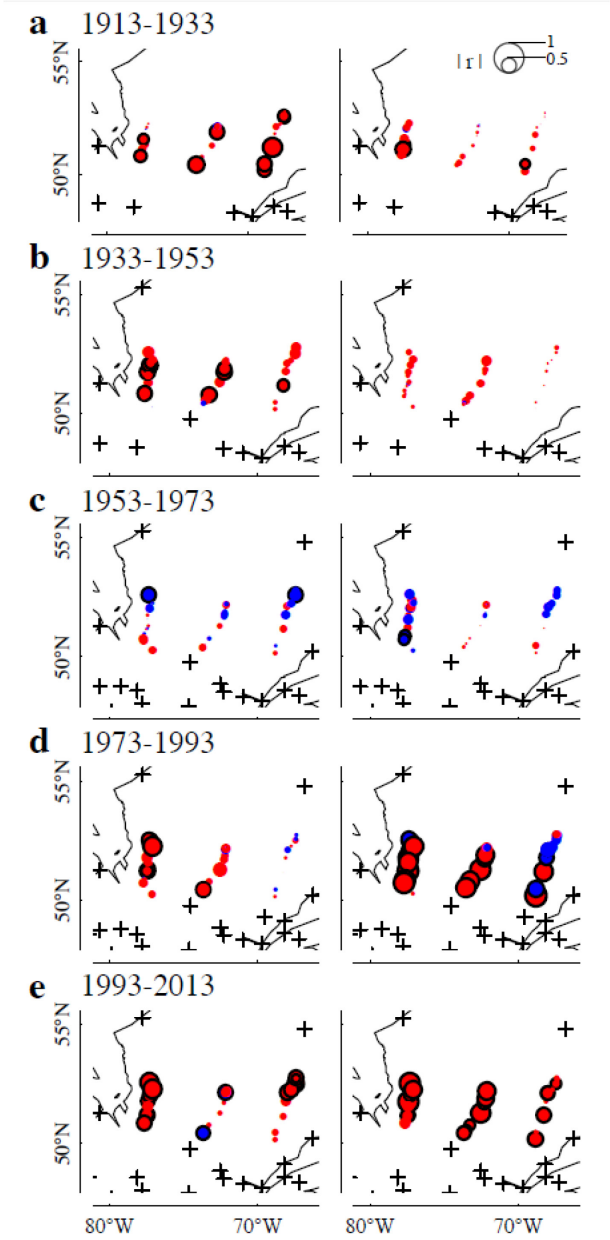

a 1913-1933
b 1933-1953
c 1953-1973
d 1973-1993
e 1993-2013
55°N
50°N
80°W
70°W
| r |
1
0.5

**Figure 5.**

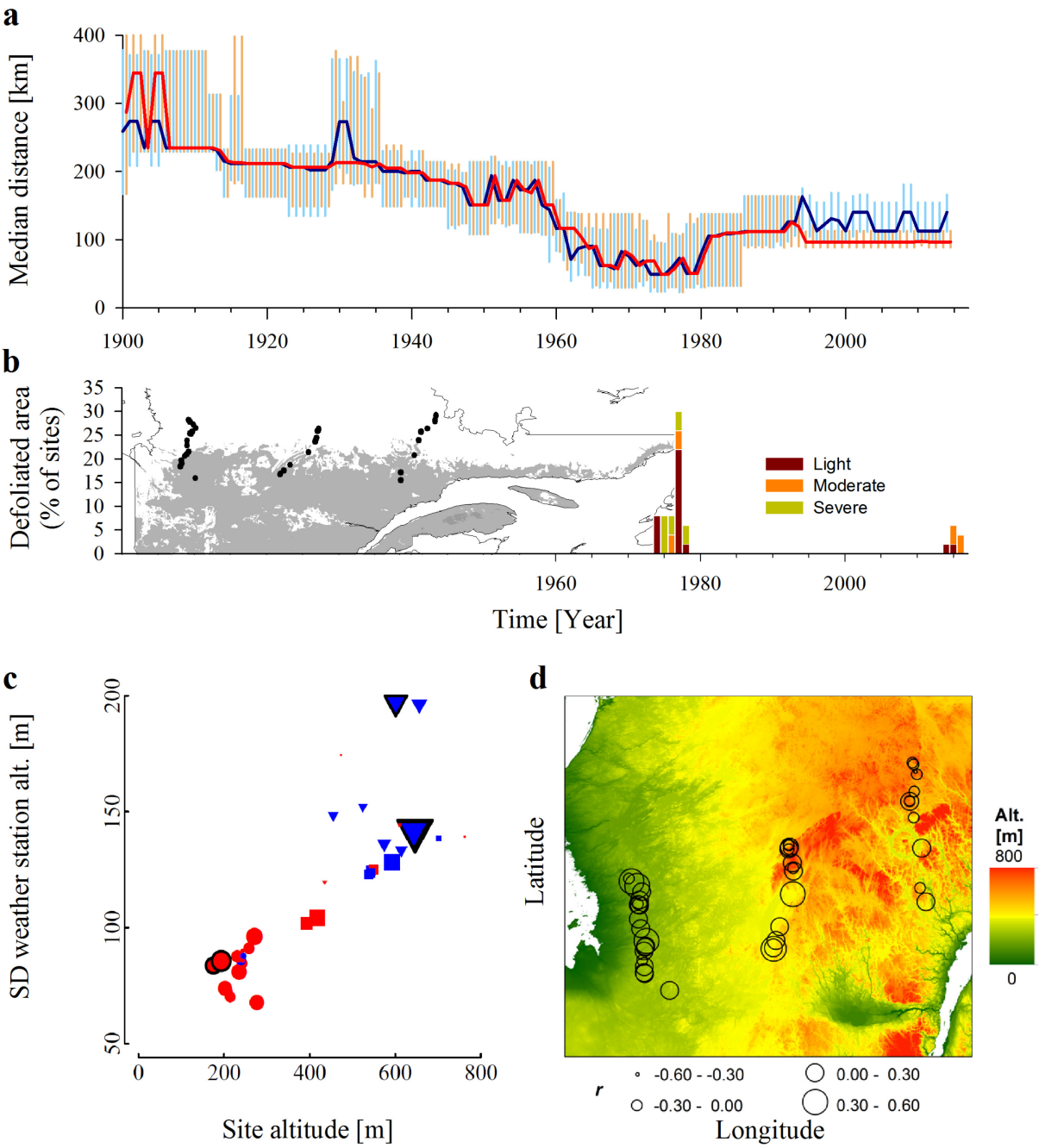

a
Median distance [km]
400
300
200
100
0
1900
1920
1940
1960
1980
2000
b
Defoliated area (% of sites)
35
30
25
20
15
10
5
0
Light
Moderate
Severe
1960
1980
2000
Time [Year]
c
SD weather station alt. [m]
200
150
100
50
0
200
400
600
800
Site altitude [m]
d
Latitude
Longitude
Alt. [m]
800
0
r
-0.60 - -0.30
-0.30 - 0.00
0.00 - 0.30
0.30 - 0.60

**Figure 6.**