Post-1980 shifts in the sensitivity of boreal tree growth to North Atlantic Ocean dynamics and seasonal climate

Tree growth responses to North Atlantic Ocean dynamics

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ABSTRACT

The mid-20th century changes in North Atlantic Ocean dynamics, e.g. slow-down of the Atlantic meridional overturning thermohaline circulation (AMOC), have been considered as early signs of tipping points in the Earth climate system. We hypothesized that these changes have significantly altered boreal forest growth dynamics in northeastern North America (NA) and northern Europe (NE), two areas geographically adjacent to the North Atlantic Ocean. To test our hypothesis, we investigated tree growth responses to seasonal large-scale oceanic and atmospheric indices (the AMOC, North Atlantic Oscillation (NAO), and Arctic Oscillation (AO)) and climate (temperature and precipitation) from 1950 onwards, both at the regional and local levels. We developed a network of 6,876 black spruce (NA) and 14,437 Norway spruce (NE) tree-ring width series, extracted from forest inventory databases. Analyses revealed post-1980 shifts from insignificant to significant tree growth responses to summer oceanic and atmospheric dynamics both in NA (negative responses to NAO and AO indices) and NE (positive response to NAO and AMOC indices). The strength and sign of these responses varied, however, through space with stronger responses in western and central boreal Quebec and in central and northern central Sweden and across scales with stronger responses at the regional level than at the local level. Emerging post-1980 associations with North Atlantic Ocean dynamics synchronized with stronger tree growth responses to local seasonal climate, particularly to winter temperatures. Our results suggest that ongoing and future anomalies in oceanic and atmospheric dynamics may impact forest growth and carbon sequestration to a greater extent than previously thought. Cross-scale differences in responses to North Atlantic Ocean dynamics highlight complex interplays in the effects of local climate and ocean-atmosphere dynamics on tree growth processes and advocate for the use of different spatial scales in climate-growth research to better understand factors controlling tree growth.

Keywords
Climate change, Dendrochronology, Climate-growth interactions, Response functions, Teleconnections, Arctic amplification.

INTRODUCTION

Terrestrial biomes on both sides of the North Atlantic Ocean are strongly influenced by Arctic and Atlantic oceanic and atmospheric dynamics (D'Arrigo *et al.*, 1993; Ottersen *et al.*, 2001; Girardin *et al.*, 2014). Some mid-20th century changes in the dynamics of the North Atlantic Ocean have been considered as early signs of tipping points in the Earth climate system (Lenton *et al.*, 2008; Lenton, 2011). The Atlantic Meridional Overturning Circulation (AMOC) exhibited an exceptional slow-down in the 1970s (Rahmstorf *et al.*, 2015). The cause of this slow-down is still under debate, but possible explanations include the weakening of the vertical structure of surface waters through the discharge of low-salinity fresh water into the North Atlantic Ocean, due to the disintegration of the Greenland ice sheet and the melting of Canadian Arctic glaciers. A further weakening of the AMOC may possibly lead to a wide-spread cooling and decrease in precipitation in the North Atlantic region (Sgubin *et al.*, 2017), subsequently lowering the productivity of land vegetation both over northeastern North America and northern Europe (Zickfeld *et al.*, 2008; Jackson *et al.*, 2015). Despite increasing research efforts in monitoring climate-change impacts on ecosystems, effects of late 20th century changes in North Atlantic Ocean dynamics on mid- to high-latitude terrestrial ecosystems remain poorly understood.

The dynamics of North Atlantic oceanic and atmospheric circulation, as measured through the AMOC, North Atlantic Oscillation (NAO) and Arctic Oscillation (AO) indices, strongly influence climate variability in northeastern North America (NA) and northern Europe (NE) (Hurrell, 1995; Baldwin & Dunkerton, 1999; Wettstein & Mearns, 2002). NAO and AO indices integrate differences in sea-level pressure between the Iceland Low and the

Azores High (Walker, 1924), with high indices representative of increased west-east air circulation over the North Atlantic. Variability in AMOC, NAO and AO indices affects climate dynamics, both in terms of temperatures and precipitation regimes: periods of high winter NAO and AO indices are associated with below-average temperatures and more sea ice in NA and a warmer- and wetter-than-average climate in NE. Periods of low winter NAO and AO indices are, in turn, associated with above-average temperatures and less sea ice in NA and a colder- and dryer-than-average climate in NE (Wallace & Gutzler, 1981; Chen & Hellström, 1999). Low AMOC indices induce a wide-spread cooling and decrease of precipitation across the high latitudes of the North Atlantic region (Jackson *et al.*, 2015).

Boreal forests cover most of mid- and high-latitude terrestrial regions of NA and NE and play an important role in terrestrial carbon sequestration and land-atmosphere energy exchange (Betts, 2000; Bala *et al.*, 2007; de Wit *et al.*, 2014). Boreal forests are sensitive to climate change (Gauthier *et al.*, 2015). Despite general warming and lengthening of the growing season at mid- and high-latitudes (Karlsen *et al.*, 2009; IPCC, 2014), tree growth in many boreal regions lost its positive response to rising temperatures during the late-20th century (Briffa *et al.,* 1998). An increasing dependence on soil moisture in the face of the rapid rise in summer temperatures may counterbalance potential positive effects on boreal forest growth of increased atmospheric CO_2 concentrations (Girardin *et al.*, 2016). During the late 20th century, large-scale growth declines (Girardin *et al.*, 2014) and more frequent low growth anomalies (Ols *et al.*, 2016)- in comparison with the early 20th century- have been reported for pristine boreal spruce forests of NA. In coastal NE, climatic changes over the 20th century have triggered shifts from negative significant to non-significant spruce responses to winter precipitation (Solberg *et al.*, 2002). Annual variability in boreal forest tree growth patterns have shown sensitivity to sea ice conditions (Girardin *et al.*, 2014; Drobyshev *et al.*, 2016) and variability in SSTs (Lindholm *et al.*, 2001). All changes in boreal tree growth patterns and climate-growth interactions listed above may be driven by the dynamics of the North Atlantic Ocean. Understanding current and projected future impacts of North Atlantic Ocean dynamics on boreal forest ecosystems and their carbon sequestration capacity calls for a deeper spatiotemporal analysis of tree growth sensitivity to large-scale oceanic and atmospheric dynamics.

The present study investigates tree growth responses to changes in North Atlantic Ocean dynamics of two widely distributed tree species in the boreal forests of northeastern North America (black spruce) and northern Europe (Norway spruce). We investigated tree-growth sensitivity to seasonal large-scale indices (AMOC, NAO; AO) and seasonal climate (temperature and precipitation) over the second half of the 20th century. We hypothesize that shifts in tree growth sensitivity to large-scale indices and local climate are linked to major changes in North Atlantic Ocean dynamics. This study aims to answer two questions: (i) has boreal tree growth shown sensitivity to North-Atlantic Ocean dynamics? and (ii) does tree growth sensitivity to such dynamics vary through space and time, both within and across NA and NE?

MATERIAL AND METHODS

Study areas

We studied two boreal forest dominated areas under the influence of large-scale atmospheric circulation patterns originating in the North Atlantic: the northern boreal biome of the Canadian province of Quebec (50°N-52°N, 58°W-82°W) in NA and the boreal biome of Sweden (59°N-68°N, 12°E-24°E) in NE (Fig. 1a). The selection of the study areas was based on the availability of accurate annually-resolved tree growth measurements acquired from forest inventories.

In northern boreal Quebec, mean annual temperature increases from north to south (-5 to 0.8°C) and total annual precipitation increases from west to east (550 to 1300 mm), mainly due to moisture advection from the North Atlantic Ocean during the winter (Gerardin & McKenney, 2001). In boreal Sweden, annual mean temperature increases from north to south (-2 to 6°C) and annual total precipitation decreases from west to east (900 to 500 mm), mostly because of winter moisture advection from the North Atlantic Ocean that condenses and precipitates over the Scandinavian mountains in the west (Sveriges meteorologiska och hydrologiska institut (SMHI), 2016).

The topography in northern boreal Quebec reveals a gradient from low plains in the west (200-350 m above sea level [a.s.l.]) to hills in the east (400-800 m a.s.l.). In boreal Sweden, the topography varies from high mountains (1500-2000 m a.s.l.) in the west to low lands (50-200 m a.s.l.) in the east along the Baltic Sea. However, mountainous coniferous forests are only found up to ca. 400m a.s.l. in the north (68°N) and ca. 800m a.s.l. in the south (61°N).

Tree growth data

We studied tree growth patterns of the most common and widely distributed spruce species in each study area: black spruce (*Picea mariana* (Mill.) Britton) in Quebec and Norway spruce (*P. abies* (L.) H. Karst) in Sweden. A total of 6,876 and 14,438 tree-ring width series were retrieved from the Quebec (Ministère des Ressources naturelles du Québec, 2014) and Swedish forest inventory database (Riksskogstaxeringen, 2016), respectively. We adapted data selection procedures to each database to provide as high local coherence in growth patterns as possible.

For Quebec, core series were collected from dominant trees on permanent plots (three trees per plot, four cores per tree) between 2007 and 2014. Permanent plots were situated in unmanaged old-growth black spruce forests north of the northern limit for timber exploitation.

Core series were aggregated into individual tree series using a robust bi-weighted mean (robust average unaffected by outliers, Affymetrix 2002). To enhance growth coherence at the local level, we further selected tree series presenting strong correlation ($r > 0.4$) with their respective local landscape unit master chronology. This master chronology corresponds to the average of all other tree series within the same landscape unit (landscape units are 6341 km^2 on average and delimit a territory characterized by specific bioclimatic and physiographic factors (Robitaille & Saucier, 1998)). This resulted in the selection of 790 tree series that were averaged at the plot level using a robust bi-weighted mean. The obtained 444 plot chronologies had a common period of 1885-2006 (Table 1). Plot chronologies were detrended using standard procedures, i.e., log transformation, 32-year spline de-trending, and pre-whitened using autocorrelation removal (Cook & Peters, 1981). Detrending aims at removing low-frequency age-linked variability in tree-ring series (decreasing tree-ring width with increasing age) while keeping most of the high-frequency variability (mainly linked to climate). Pre-whitening removes all but the high frequency variation in the series by fitting an autoregressive model to the detrended series. The order of the auto-regressive model was selected by Akaike Information Criterion (Akaike 1974).

For Sweden, core series were collected within the boreal zone of the country (59°N-68°N) on temporary plots between 1983 and 2010. Temporary plots were situated in productive forests, i.e. those with an annual timber production of at least 1m^3/ha. These forests encompass protected, semi-natural and managed forests. In each plot, 1 to 3 trees were sampled, with 2 cores per tree. Swedish inventory procedures do not include any visual and statistical cross-dating of core series at the plot level. To filter out misdated series, we, therefore, aggregated core series into plot chronologies using a robust bi-weighted mean, and compared them to Norway spruce reference chronologies from the International Tree-Ring Data Base (International Tree Ring Data Bank (ITRDB), 2016). Theses aggregations resulted in 4067 plot chronologies. In total, seven ITRDB reference chronologies were selected (Fig. 1b), all representative of tree growth at mesic sites in boreal Sweden. Plot and reference chronologies were detrended and pre-whitened, using the same standard procedures as the Quebec data. Each plot chronology was then compared with its geographically nearest reference chronology - determined based on Euclidean distance - using Student's t-test analysis (Student 1908). Plot chronologies with a t-test value lower than 2.5 with their respective nearest reference chronology were removed from further analyses (the t-test value threshold was set up according to the mean length of plot chronologies (Table 1)). A total of 1256 plot chronologies (with a common period of 1936-1995) passed this quality test (Table 1).

Table 1. Characteristics of tree-ring width chronologies*

	Quebec	Sweden
Plot chronologies		
Number	444	1256
Mean length (SD) [yrs.]	191 (59)	80 (3)
Grid cell chronologies		
Number	36	56
Plot chronologies per grid cell (SD)	12 (8)	23 (13)
Mean length (SD) [yrs.]	230 (47)	81 (13)
Common period	1885-2006	1936-1995
Regional chronologies		
Number	3	3
Grid cell chronologies per cluster	7/10/19*	14/19/23**
Length [yrs.]	212/196/263*	81/81/79**
Common period	1812-2008	1929-2008

*data for Q_W, Q_C and Q_E chronologies respectively; ** Data for of S_S, S_C and S_N chronologies respectively;

Spatial aggregation of plot chronologies into regional chronologies in each study area

Quality checked chronologies at the plot level were aggregated into 1° x 1° latitude-longitude grid cell chronologies within each study area (Fig. 1b). Grid cell chronologies were calculated as the robust bi-weighted mean of all plot chronologies within each grid cell. Grid cells containing less than three plot chronologies were removed from further analyses. This resulted in a total of 36 and 56 grid cell chronologies in Quebec and Sweden, respectively (Fig. 1b, Table 1). Grid cells contained, on average, 12 and 23 plot chronologies in Quebec and Sweden, respectively (Table 1).

To investigate the influence of spatial scale in climate-growth sensitivity analyses, we performed an ordination of grid cell chronologies within each study area over their common period (Fig. 1c). The common period between grid cell chronologies was 1885-2006 and 1936-1995 in Quebec and Sweden, respectively. Ordination analyses were performed in R using the Euclidean dissimilarities matrices (*dist* function) and the Ward agglomeration (*hclust* function) methods. Three main clusters were identified in each study area (Fig. 1c). Spatial extents of all clusters were consistent with well-defined bioclimatic regions, providing support to data selection procedures. In Quebec, clusters identified in the West (Q_W) and the East (Q_E) corresponded well to the drier and wetter northern boreal region, respectively (Fig. 1b & c). In Sweden, the cluster identified in the South (S_S) corresponded to a combination of the nemo-boreal and southern boreal zones (Moen, 1999). The Swedish central (S_C) and northern (S_N) clusters corresponded to the mid-boreal and northern boreal zones, respectively (Fig. 1b & c) (Moen, 1999). Regional chronologies were built as the average of all grid cell chronologies within a cluster. In Sweden, inter-cluster correlations were all significant and ranged from 0.77 (S_S vs S_N) to 0.94 (S_C vs S_N). In Quebec, inter-cluster correlations were all significant and ranged from 0.44 (Q_W vs Q_E) to 0.52 (Q_C vs Q_E) (see Appendix S1-S3 in Supporting Information). Henceforward, the terms ‘local level’ and ‘regional level’ refer to analyses focusing on the grid cell chronologies and the six regional chronologies, respectively.

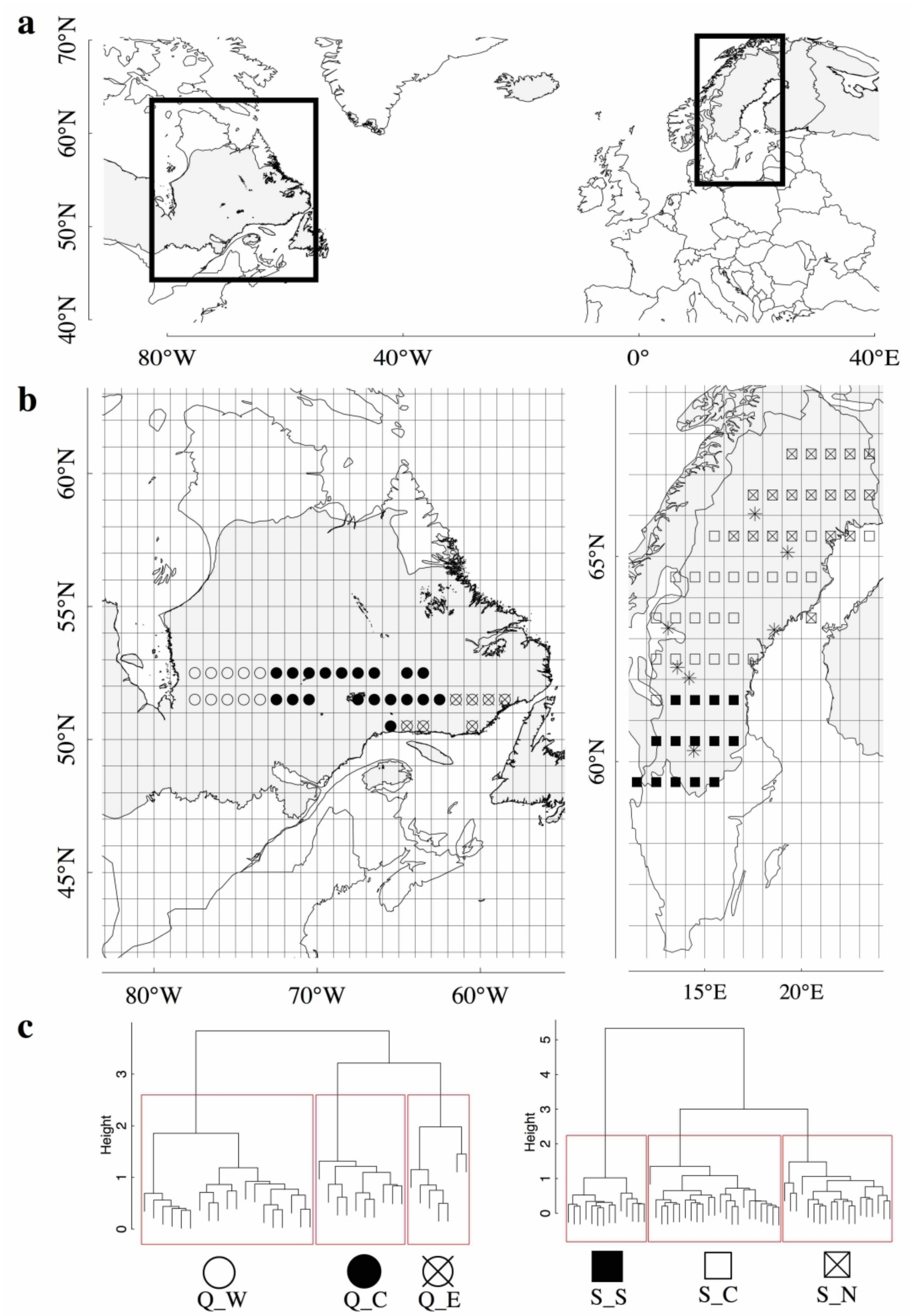

Figure 1 a: Location of the two study areas (black frame); b & c: Clusters identified in each study area by ordination of 1° x 1° latitude-longitude grid cell chronologies. Ordination analyses were performed over the common period between grid cell chronologies in each study area using Euclidean dissimilarities matrices and Ward agglomeration methods. The common period was 1885-2006 for Quebec and 1936-1995 for Sweden. Ordinations included 36 and 56 grid cell chronologies in Quebec and Sweden, respectively. A western (Q_W), central (Q_C) and eastern (Q_E) cluster in Quebec and a southern (S_S), central (S_C) and northern (S_N) cluster were identified in Sweden. Reference chronologies from the ITRDB

used for the cross-dating of plot chronologies in Sweden are indicated with a ⁎ (swed011, swed012, swed013, swed014, swed015, swed017 and swed312). The grey shading indicates the boreal zone delimitation according to Brant *et al.* (2003).

Climate data

We extracted local seasonal mean temperature and total precipitation data (1950-2008) for each grid cell from the CRU TS 3.24 1° x 1°(Harris *et al.*, 2014), with seasons spanning from the previous (pJJA) through the current summer (JJA). Climate data were further aggregated at the regional level as the robust bi-weighted mean of climate data of all grid cells contained in each regional cluster (Fig. 1b & c). Seasonal AMOC indices (1961-2005, first AMOC measurements in 1961) were extracted from the European Center for Medium-Range Weather Forecast (Ocean Reanalysis System ORA-S3). Seasonal AO and NAO indices (1950-2008) were extracted from the Climate Prediction Center database (NOAA, 2016). Seasonal AMOC, NAO, and AO indices included previous summer, winter (DJF), and current summer. All seasonal climate data were downloaded using the KNMI Climate Explorer (Trouet & Van Oldenborgh, 2013) and were detrended using linear regression and thereafter pre-whitened (autocorrelation of order 1 removed from time series).

Links between seasonal climate and growth patterns

Analyses were run over the 1950-2008 period (the longest common period between tree growth and climate data), except with AMOC indices, which were only available for 1961-2005. Tree growth patterns were correlated with seasonal climate variables (previous-to-current summer temperature averages and precipitation sums) and seasonal indices (previous summer, winter, and current summer AMOC, NAO, and AO) at the regional and local levels. To minimize type I errors, each correlation function was tested for 95% confidence intervals using 1000 bootstrap samples. In addition, moving correlation analyses were performed at the regional level, using the same procedures as above. All calculations were performed using the R package *treeclim* (Zang & Biondi, 2015). For more details regarding bootstrapping procedures please see the description of the "*dcc*" function of this package.

RESULTS

Tree growth responses to seasonal climate

Some significant climate-growth associations were observed at the regional level (Fig. 2). Significant associations at the local level displayed strong spatial patterns and revealed heterogeneous within-region growth responses (Figs. 3 and 4). Moving correlations revealed numerous shifts in the significance of climate-growth associations around 1980 (Fig. 5).

Quebec

No significant climate-growth associations were observed at the regional level in western boreal Quebec over the entire study period (Fig. 2). Some significant positive responses to previous winter and current spring temperatures were observed at the local level, but these concerned a minority of cells (Fig. 3). Moving correlations revealed that Q_W significantly correlated with previous summer precipitation (negatively) before the 1970s, with previous winter temperatures (positively) from the 1970s and with current spring temperatures (positively) from 1980 (Fig. 5).

Tree growth in central boreal Quebec was significantly and positively correlated with current summer temperatures at the regional and local levels (Figs. 2 and 3). Numerous negative correlations between tree growth in that region and spring precipitation were observed at the local level (Fig. 3). Moving correlations revealed an emerging correlation between Q_C and previous winter temperatures in the early 1970s (significant during most intervals up to most recent years) (Fig. 5).

No significant climate-growth associations were observed in eastern boreal Quebec at the regional level (Fig. 2). At the local level, some positive significant correlations with current summer temperatures were observed (Fig. 3). Moving correlations revealed that Q_E correlated significantly and positively with current summer temperatures up to the early 1970s (Fig. 5).

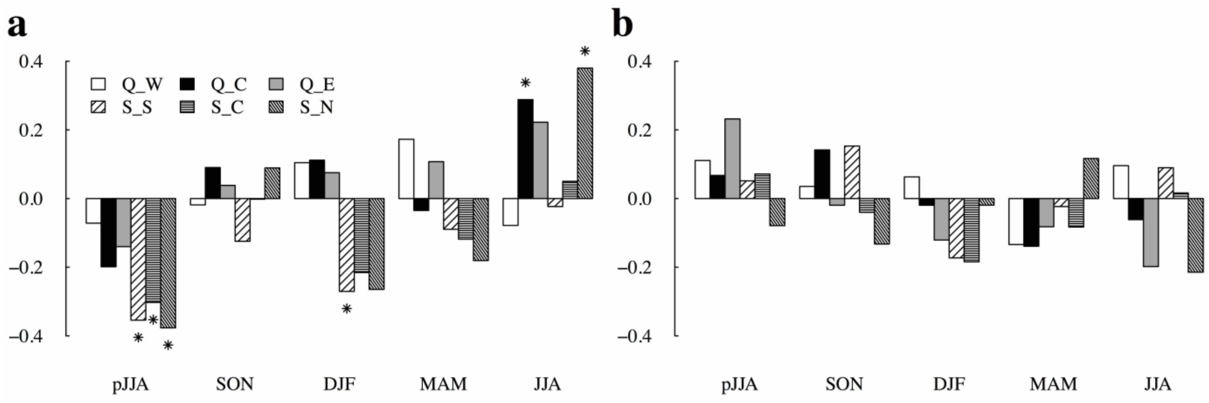

Figure 2. Tree growth responses to seasonal mean temperature (a) and total precipitation (b) at the regional level over the 1950-2008 period, as revealed by correlation analyses. Analyses were computed between the six regional chronologies (Q_W, Q_C, and Q_E in NA; and S_S, S_C and S_N in NE) and seasonal climate data. Climate data were first extracted from the CRU TS 3.24 1° x 1° (Harris *et al.*, 2014) for each grid cell and then aggregated at the regional level by a robust bi-weighted mean. Seasons spanned from previous (pJJA) to current summer (JJA). Significant correlations ($P < 0.05$) are marked with a star.

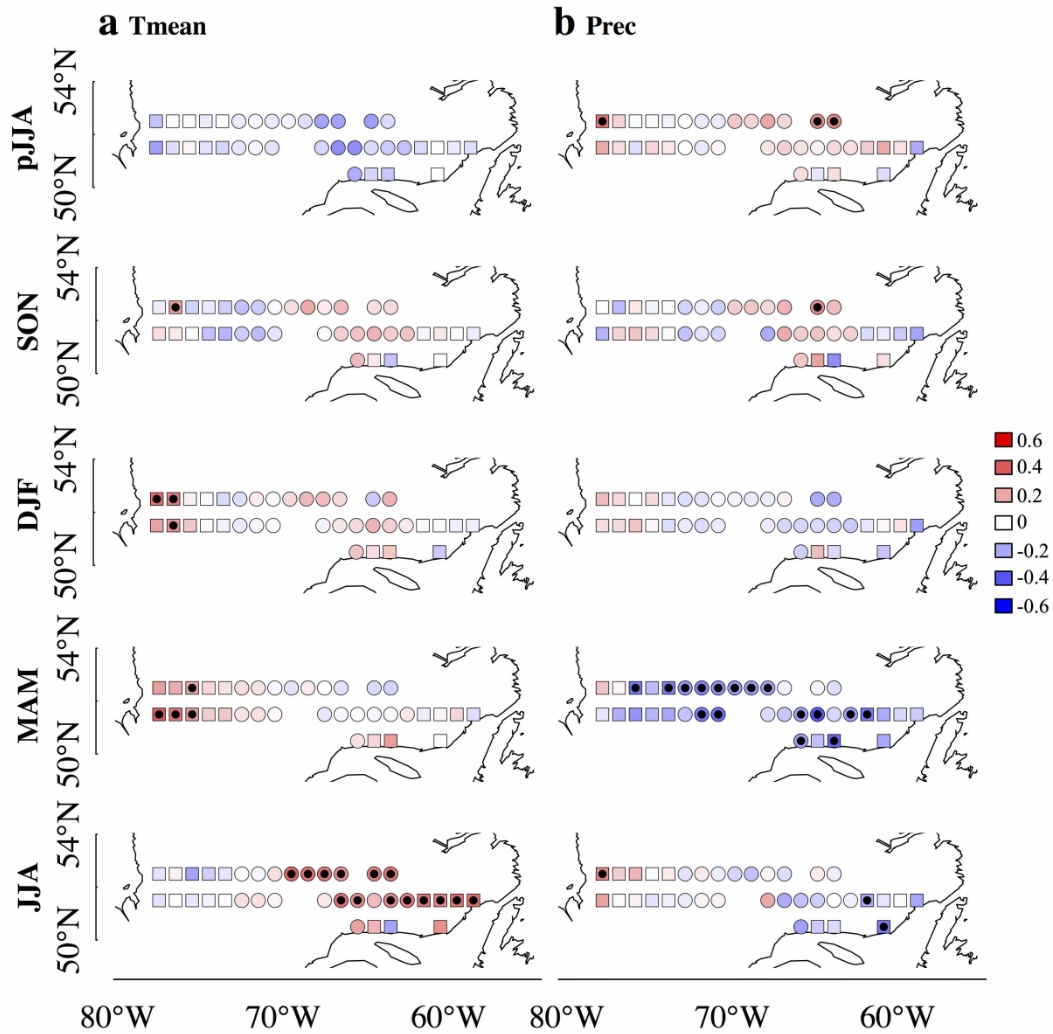

Figure 3. Tree growth responses to seasonal mean temperature (a) and total precipitation (b) at the local level over the 1950-2008 period in Quebec, as revealed by correlation analyses. Analyses were computed between grid cell chronologies and local seasonal climate data extracted for each grid cell from the CRU TS 3.24 1° x 1° (Harris *et al.*, 2014). Seasons spanned from previous (pJJA) to current summer (JJA). To visualize separation between regional clusters (Q_W, Q_C, and Q_E, cf. Fig. 1) correlation values at Q_C grid cells are plotted with circles. Significant correlations ($P < 0.05$) are marked with a black dot.

Sweden

Tree growth in southern boreal Sweden correlated significantly and negatively with previous summer and winter temperatures at the regional and local levels, the correlation with winter temperatures concerning however only a minority of cells (Figs. 2 and 4). Moving correlations indicated that the negative association with previous summer temperatures remained significant up to the early 1990s and that the negative association with winter temperatures emerged after 1980 (Fig. 5).

In central boreal Sweden, tree growth significantly and negatively correlated with previous summer temperatures both at the regional and local levels (Figs. 2 and 4). Some additional significant correlations with winter temperatures (negative) and with current summer temperatures (positive) were observed at the local level (Fig. 4). Moving correlation analyses revealed a significant positive correlation between S_C and current summer temperatures that dropped and became non-significant at the end of the study period (Fig. 5). In addition, the correlation between S_C and previous summer precipitation shifted from significantly negative to significantly positive during the 1980s (Fig. 5). S_C became significantly and negatively correlated with previous summer temperatures after the 1980s and stopped being significantly and negatively correlated with previous autumn precipitation and with winter temperatures at the end of the 1970s (Fig. 5).

Tree growth in northern boreal Sweden correlated significantly with previous summer (negatively) and current summer temperatures (positively) both at the regional and local levels (Figs. 2 and 4). At the local level, tree growth in some cells significantly and negatively correlated with winter temperatures (Fig. 4). Significant and negative responses to current summer precipitation were observed at northernmost cells (Fig. 4). Moving correlations revealed that the positive association with current summer temperatures was only significant at the beginning and at the end of the study period (Fig. 5). After the 1980s, significant positive associations with previous autumn temperatures emerged (Fig. 5) and the significant negative association with winter temperatures disappeared.

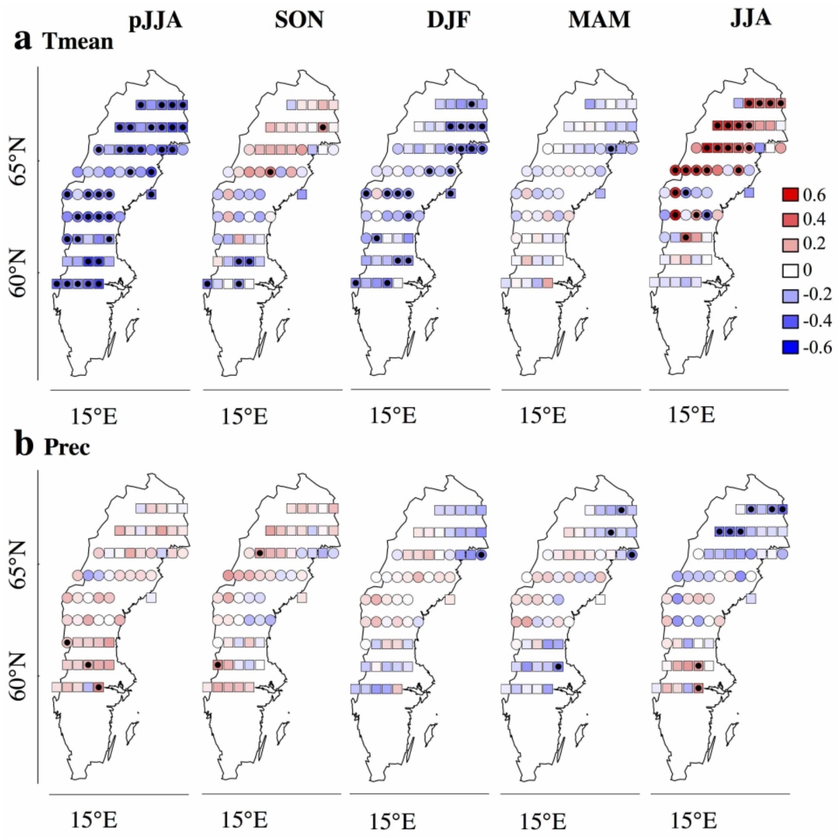

Figure 4. Tree growth responses to seasonal mean temperature (a) and total precipitation (b) at the local level over the 1950-2008 period in Sweden, as revealed by correlation analyses. Analyses were computed between grid cell chronologies and local seasonal climate data extracted for each grid cell from the CRU TS 3.24 1° x 1° (Harris *et al.*, 2014). Seasons spanned from previous (pJJA) to current summer (JJA). To visualize the separation between regional clusters (S_S, S_C, and S_N, cf. Fig. 1) correlation values at S_C grid cells are plotted with circles. Significant correlations ($P < 0.05$) are marked with a black dot.

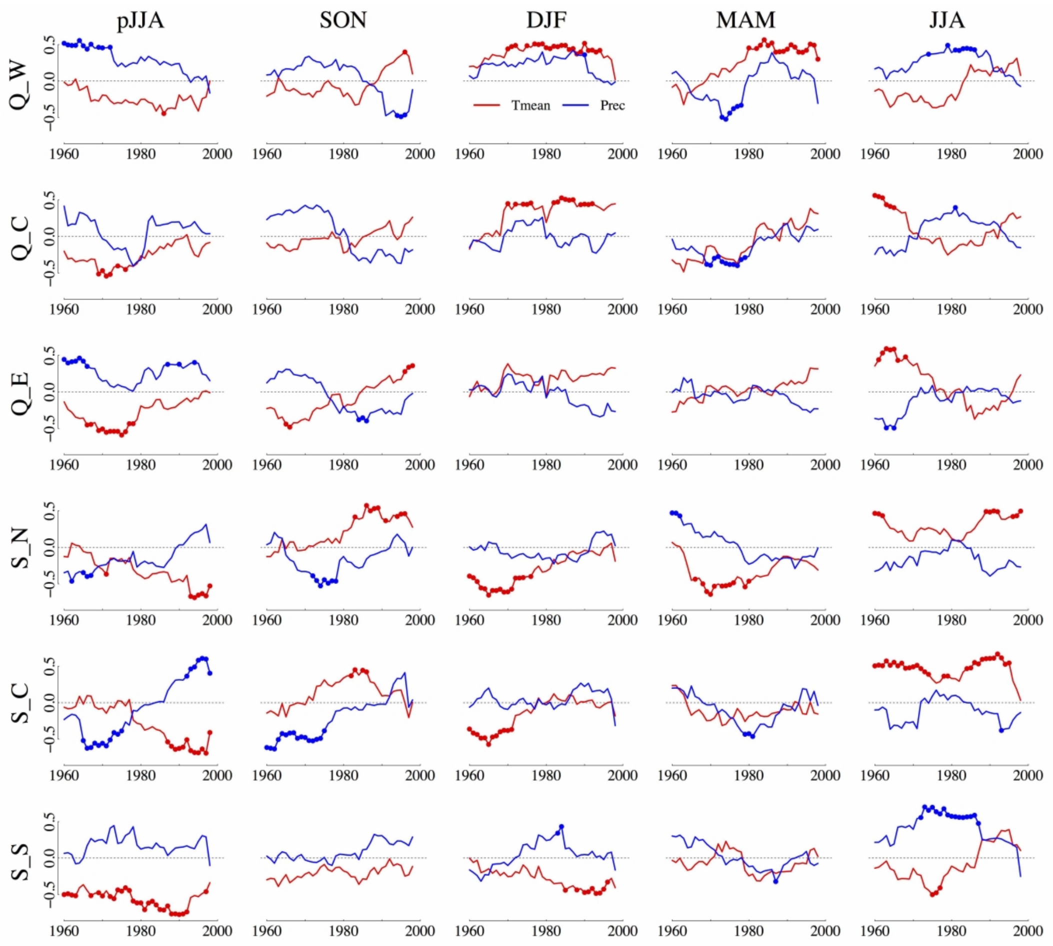

Figure 5. Moving correlations between regional seasonal mean temperature (red lines) and total precipitation (blue lines), and the six regional chronologies (Q_W, Q_C, and Q_E in NA; and S_S, S_C and S_N in NE) over the 1950-2008 period. Climate data were first extracted for each grid cell from the CRU TS 3.24 1° x 1° (Harris *et al.*, 2014) and then aggregated at the regional level by robust bi-weighted mean. Seasons spanned from previous (pJJA) to current summer (JJA). Moving correlations were calculated using 21-yr windows moved one year at a time and are plotted using the central year of each window. Windows of significant correlations ($P < 0.05$) are marked with a dot.

Links between tree growth patterns and large-scale indices

Some significant associations were found between tree growth and large-scale indices (Figs. 6, 7, and 8). Moving correlation analyses revealed some shifts from pre-1980 insignificant to post-1980 significant correlations (Fig. 9). The seasonal indices involved in these shifts varied across regional chronologies.

Quebec

Tree growth in western boreal Quebec was significantly and negatively associated with the winter AMOC and the winter AO indices at the regional level (Fig. 6). At the local level, these associations concerned, however, a minority of cells (Fig. 7). Moving correlations revealed that the regional negative association with winter AMOC was only significant in the recent part of the study period (Fig. 9). Significant negative correlations between Q_W and current summer NAO and AO indices were observed from the 1980s up to the most recent years, at which point they show a steep increase and become non-significant (Fig. 9).

In central boreal Quebec, no significant associations between tree growth and seasonal indices were identified at the regional or local level (Figs. 6 and 7). Moving correlations indicated significant negative correlations between Q_C and previous summer NAO and AO indices of during the 1980s and current summer NAO and AO indices from the 1980s up to the most recent years (Fig. 9).

No significant association was identified between large-scale indices and tree growth in eastern boreal Quebec (Figs. 6, 7, and 9).

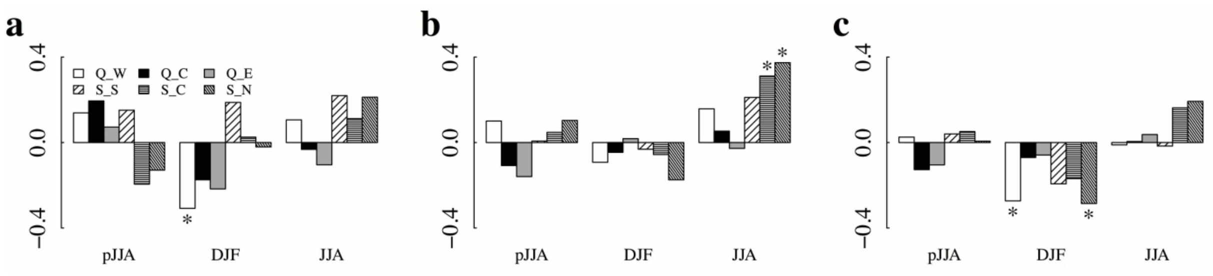

Figure 6. Correlation between seasonal AMOC (a), NAO (b), and AO (c) indices and the six regional chronologies (Q_W, Q_C, and Q_E in NA; and S_S, S_C and S_N in NE). Seasonal indices include previous summer (pJJA), winter (DJF), and current summer (JJA), and were calculated as mean of monthly indices. Correlations were calculated over the 1961-2005 period for AMOC, and over the 1950-2008 period for NAO and AO. Significant correlations ($P < 0.05$) are marked with a star.

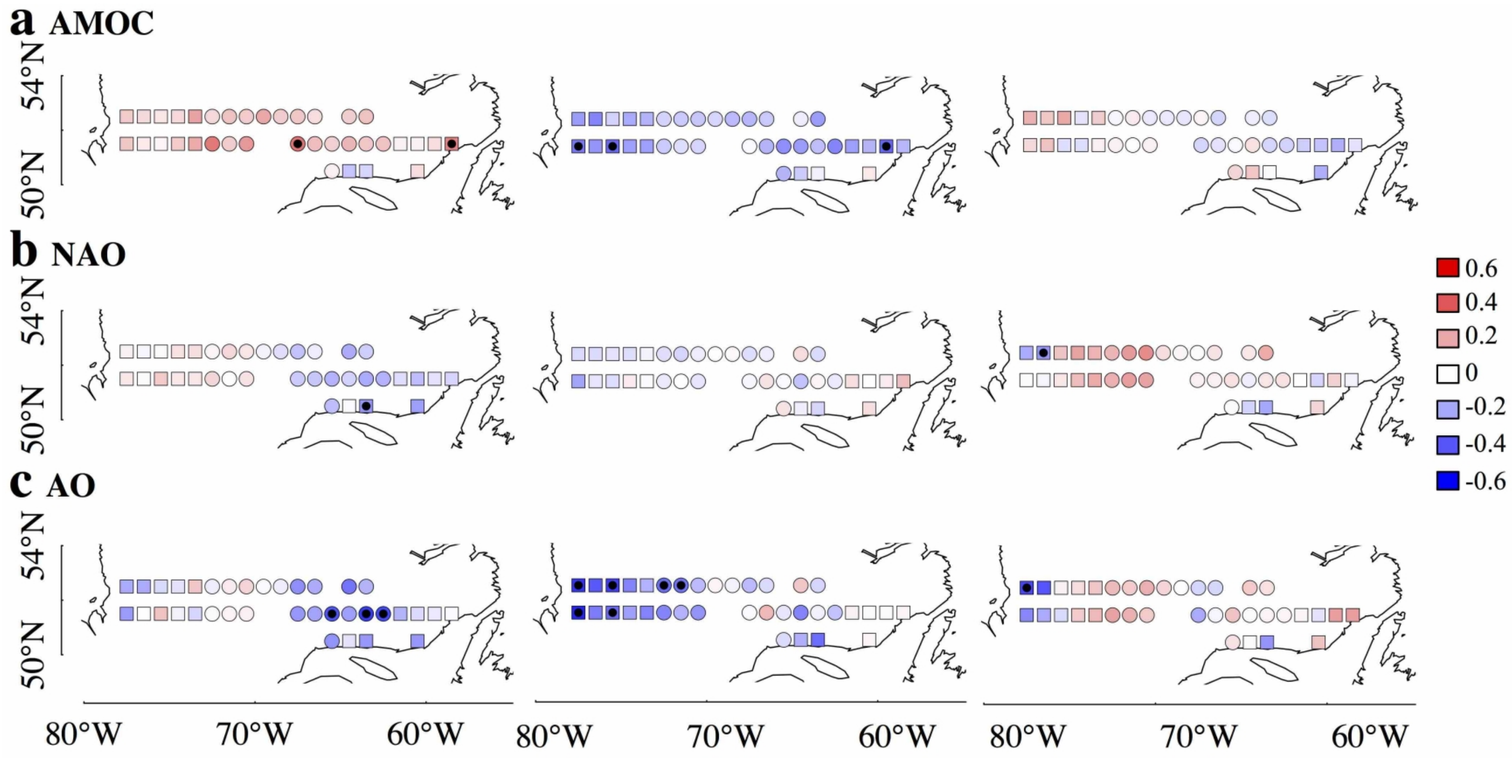

Figure 7. Correlation between seasonal AMOC (a), NAO (b), and AO (c) indices, and growth patterns at the local level in Quebec. Seasonal indices include previous summer (left-hand panels), winter (middle panels), and current summer (right-hand panels), and were calculated as mean of monthly indices. Correlations were calculated over the 1961-2005 period for AMOC, and over the 1950-2008 period for NAO and AO. To visualize the separation between regional clusters, correlation values at Q_C grid cells are plotted with circles. Significant correlations ($P < 0.05$) are marked with a black dot.

Sweden

No significant association between tree growth in southern boreal Sweden and seasonal large-scale indices was identified at the regional or local level (Figs. 6 and 8). Moving correlations revealed, however, significant negative associations between S_S and the winter AMOC index before the 1980s (Fig. 9).

In central boreal Sweden, tree growth significantly and positively correlated with the current summer NAO index at the regional level (Fig. 6). At the local level, this correlation concerned, however, a minority of cells (Fig. 8). Moving correlations revealed that the significant positive association with the current summer NAO index emerged in the early 1980s (Fig. 9) and that S_C significantly correlated with the current summer AMOC index during the 1980s (Fig. 9).

In northern boreal Sweden, tree growth significantly correlated with the current summer NAO index (positively) and with the winter AO index (negatively) at the regional level (Fig. 6). At the local level, the positive association with summer NAO concerned a large majority of cells and the negative association with the winter AO index only concerned very few cells (Fig. 8). Moving correlation analyses indicated that the positive association between S_N and the current summer NAO index was only significant after the 1980s and that S_N significantly correlated with current summer AMOC during most of the 1980s (Fig. 9).

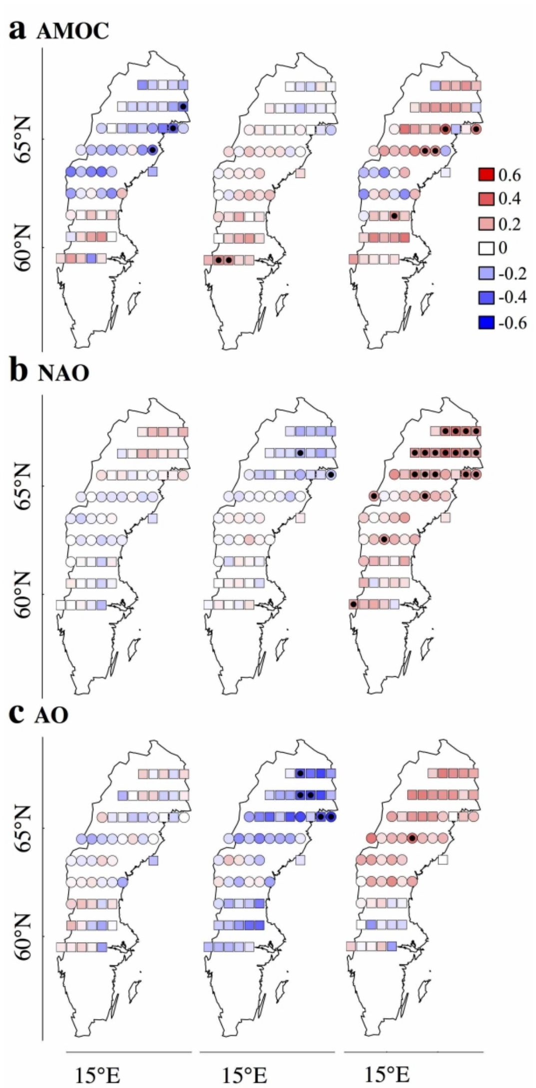

Figure 8. Correlation between seasonal AMOC (a), NAO (b), and AO (c) indices, and growth patterns at the local level in Sweden. Seasonal indices were calculated as mean of monthly indices and include previous summer (left-hand panels), winter (middle panels), and current summer (right-hand panels). Correlations were calculated over the 1961-2005 period for AMOC, and over the 1950-2008 period for NAO and AO. To visualize the separation between regional clusters, correlation values at S_C grid cells are plotted with circles. Significant correlations (*P* < 0.05) are marked with a black dot.

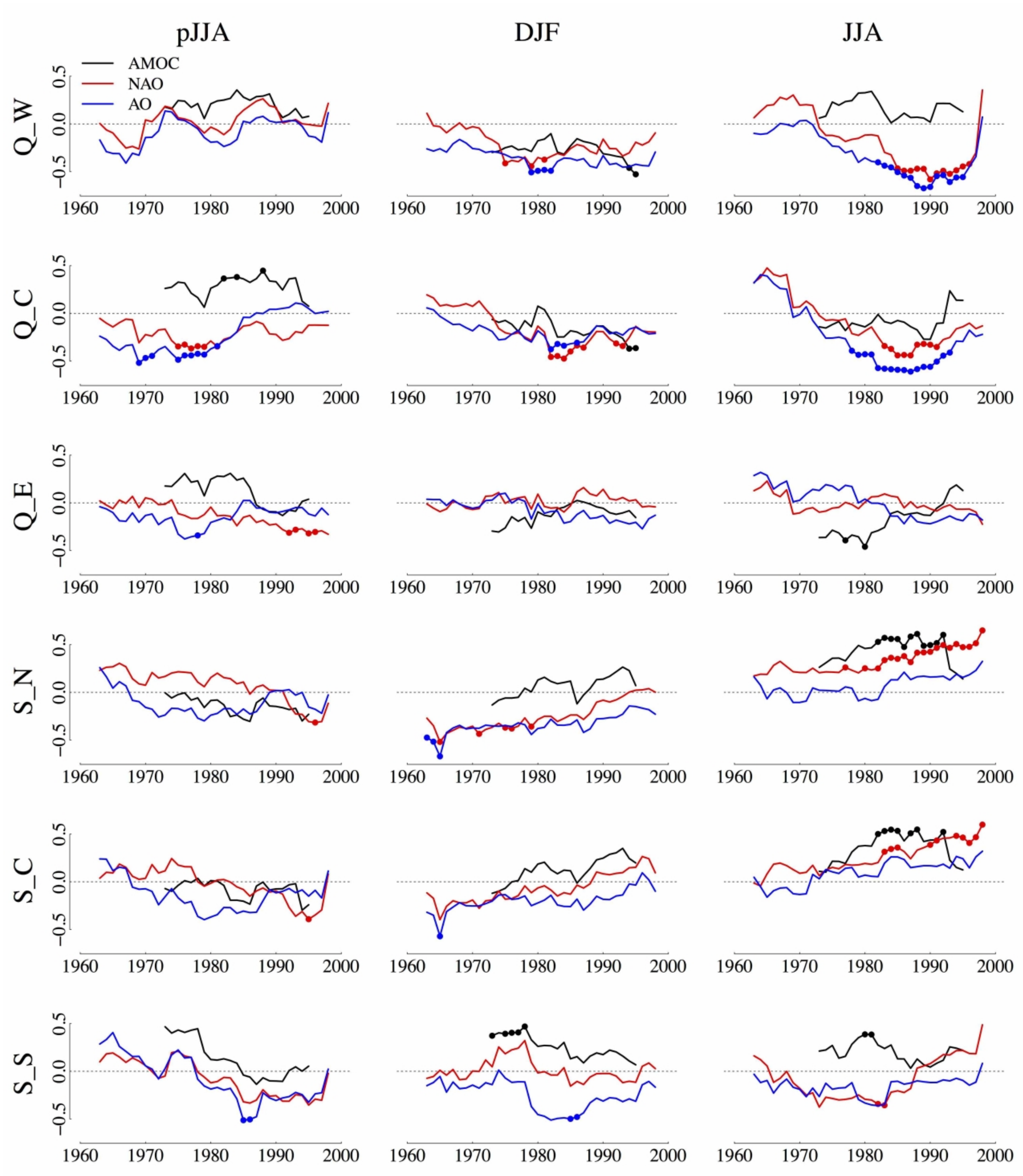

Figure 9. Moving correlations between previous summer (pJJA; left-hand panels), winter (DJF; middle panels) and current summer (JJA; right-hand panels) large-scale indices, and the six regional chronologies (Q_W, Q_C, and Q_E in NA; and S_S, S_C and S_N in NE). Large-scale indices include AMOC (black), NAO (red), and AO (blue). Moving correlations were calculated using 21-yr windows moved one year at a time and are plotted using the central year of each window. Correlations were calculated over the 1961-2005 period for AMOC, and over the 1950-2008 period for NAO and AO. Windows of significant correlations ($P < 0.05$) are marked with a dot.

DISCUSSION

Spatial aggregation of tree growth data

The high correlation between the regional chronologies in NE (Appendix S1), especially between the central and northern chronologies, could have supported the construction of one single boreal Sweden-wide regional chronology. Climate-growth analyses at the regional and local level revealed, nevertheless, clear differences across space in tree growth sensitivity to climate (Fig. 4) and to large-scale indices (Fig. 8), with a higher sensitivity in northernmost forests. The aggregation of tree growth data across space, even if based on objective similarity statistics (Appendix S1), may, therefore, mask important local differences in climate-growth interactions (Macias *et al.* 2004). Our results demonstrate that spatial aggregation should not be performed without accounting for bioclimatic domains especially when studying climate-growth interactions. In practice, one should at least check that a spatial similarity in tree growth patterns is associated with spatial similarity in seasonal climate. The use of both the regional and local scales regarding climate-growth interactions, as in the present study, is, therefore, recommended to exhaustively and more precisely capture cross-scale diverging and emerging tree growth patterns and sensitivity to climate.

Post-1980 shifts towards significant influence of large-scale indices on boreal tree growth

The emergence of a post-1980 significant positive tree growth response to current summer NAO indices in central and northern boreal Sweden (Fig. 9) appears to be linked to spatial variability in the NAO influence on seasonal climate (Fig. 10). Summer NAO has had little to no influence on summer climate variability over the entire period 1950-2008 in boreal Quebec or Sweden (see Appendix S4 in Supporting Information). However, the partitioning of the period into two sub-periods of similar length (1950-1980 and 1981-2008) revealed a northeastward migration of the significant-correspondence field between summer NAO indices and local climate, particularly in NE (Fig. 10). Over the 1981-2008 period, the summer NAO index was significantly and positively associated with temperature and negatively with precipitation in boreal Sweden (Fig. 10). Higher growing-season temperatures, induced by a higher summer NAO, might have promoted the growth of temperature-limited Swedish boreal forest ecosystems, explaining recent positive response of tree growth to this large-scale index observed in the central and northern regions (Fig. 9). The northeastward migration of the NAO-climate spatial field may be an early sign of a northward migration of the North Atlantic Gulf stream (Taylor & Stephens, 1998) or a spatial reorganization of the Icelandic-low and Azores-high pressure NAO's nodes (Portis *et al.*, 2001; Wassenburg *et al.*, 2016). The August Northern Hemisphere Jet over NE reached its northernmost position in 1976 but thereafter moved southward, despite increasing variability in its position (Trouet *et al* 2018). This southward migration of the jet may weaken the strength of the observed post-1980 positive association between boreal tree growth and the summer NAO index in NE in the coming decades.

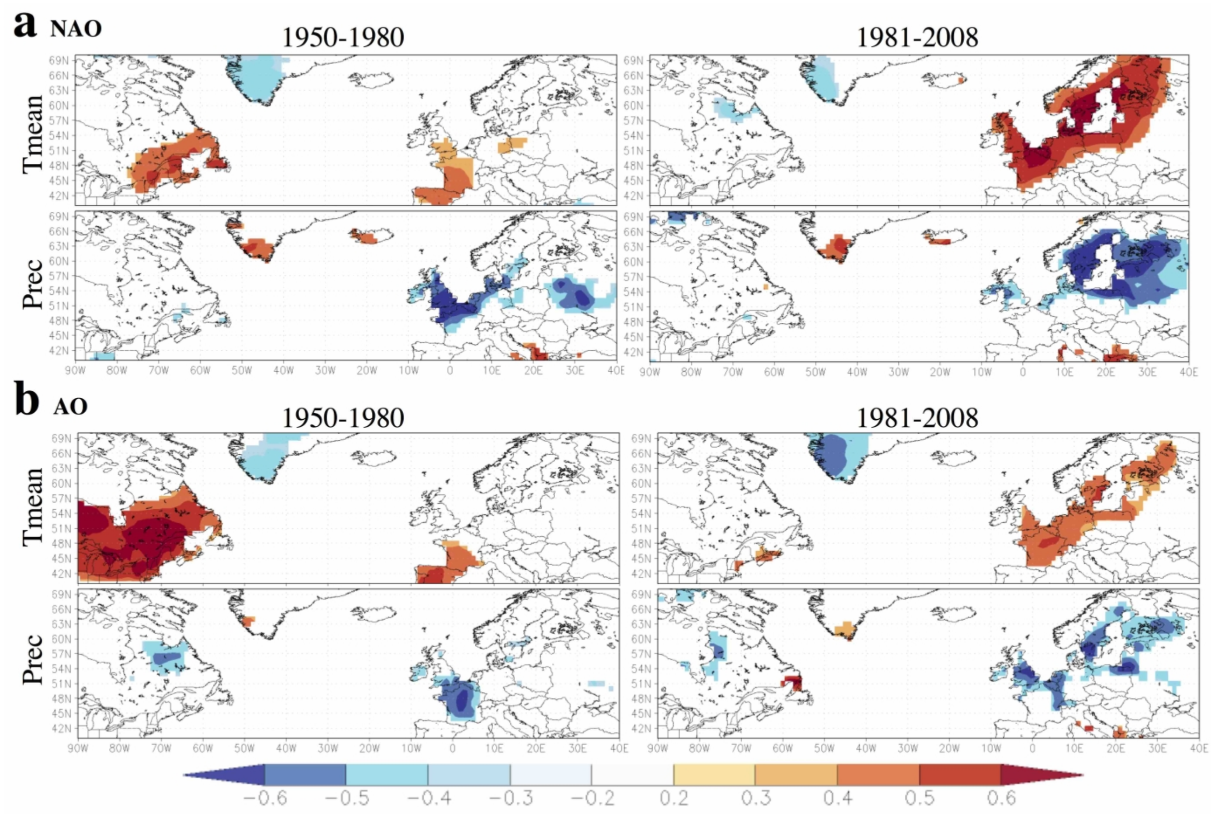

Figure 10. Correspondence between summer NAO indices and local summer climate (mean temperature and total precipitation) between 1950 and 1980 (left-hand panels) and between 1981 and 2008 (right-hand panels). NAO indices over the 1950-2008 period were extracted from NOAA's climate prediction center. Summer mean temperature and total precipitation are those of CRU TS 3.24 1° x 1° (Harris *et al.*, 2014). All correlations were computed in the KNMI Climate Explorer (https://climexp.knmi.nl (Trouet & Van Oldenborgh, 2013)). Indices and climate variables were normalized (linear regression) prior to analyses. Only correlations significant at $P < 0.05$ are plotted.

The post-1980 significant negative associations between tree growth and summer NAO and AO indices in boreal Quebec are more challenging to interpret. There was no evident significant tree growth response to summer temperature in these regions when analyzed over the full 1950-2008 period (Fig. 4). Yet, unstable associations between tree growth and temperatures, shifting from a negative correlation with preceding summer temperature to a positive association with winter temperatures in the 1970s (in central Quebec), and spring temperatures from the 1980s (in western Quebec only) (Fig. 5). These associations indicate that tree growth in boreal Quebec has been limited by winter and spring climate since the 1970s and 1980s, respectively. Below-average summer temperatures induced by high summer NAO and AO may exacerbate the sensitivity of tree growth to low temperatures. Noting that no significant post-1980 association was observed between temperature and summer NAO and AO indices in Quebec (Fig. 10), the emerging negative tree growth response to summer NAO and AO indices may indicate a complex interplay between large-scale indices and air mass dynamics and lagged effects over several seasons (Boucher *et al,* 2017).

In western Quebec, tree growth was negatively influenced by the winter AMOC index at the regional level (Fig. 6). This relationship appears to be linked to a significant positive association between tree growth and spring temperature (Figs. 5 and 9). Positive winter AMOC indices are generally associated with cold temperatures in Quebec, and particularly so in the West (see Appendix S4 in Supporting Information). Positive winter AMOC indices are associated with the dominance dry winter air masses of Arctic origin over Quebec, and may thereby delay the start of the growing season and reduce tree-growth potential.

Forest dynamics in NA have been reported to correlate with Pacific Ocean indices such as the Pacific Decadal Oscillation (PDO) or the El-Nino Southern Oscillation (ENSO), particularly through their control upon fire activities (Macias Fauria & Johnson 2006, Le Goff *et al.,* 2007). These indices have not been investigated in the present study but might present some additional interesting features.

Contrasting climate-growth associations among boreal regions

Post-1980 shifts in tree growth sensitivity to seasonal climate differed among boreal regions. In NA, we observed the emergence of significantly positive growth responses to winter and spring temperature. In NE, observed post-1980 shifts mainly concerned the significance of negative growth responses to previous summer and winter temperatures. Warmer temperatures at boreal latitudes have been reported to trigger contrasting growth responses to climate (Wilmking *et al.*, 2004) and to enhance the control of site factors upon growth (Nicklen *et al.*, 2016). This is particularly true with site factors influencing soil water retention, such as soil type, micro-topography, and vegetation cover (Düthorn *et al,* 2013). Despite a generalized warming at high latitudes (Serreze *et al.,* 2009), no increased sensitivity of boreal tree growth to precipitation was identified, except in central Sweden where tree growth became positively and significantly correlated to previous summer precipitation (Fig. 5). This result underlines that temperature remains the major-growth limiting factor in our study regions.

The observed differences in tree growth response to winter temperature highlight diverging non-growing season temperature constraints on boreal forest growth. While warmer winters appear to promote boreal tree growth in NA, they appear to constrain tree growth in boreal NE. Such opposite responses to winter climate from two boreal tree species of the same genus might be linked to different winter conditions between Quebec and Sweden. In NA, winters conditions are more continental and harsher than in NE (Appendix S5). Warmer winters may therefore stimulate an earlier start of the growing season and increase growth potential (Rossi *et al.,* 2014). However, warmer winters, combined with shallower snow-pack, have been shown to induce a delay in the spring tree growth onset, through lower thermal inertia and a slower transition from winter to spring (Contosta *et al.*, 2017). This phenomenon might explain the negative association between tree growth and winter temperatures observed in NE.

The post-1970s growth-promoting effects of winter and spring temperature in NA (Fig. 5) suggest, as ealier reported by Charney *et al.* (2016) and Girardin *et al.* (2016), that, under sufficient soil water availability and limited heat stress conditions, tree growth at midto high-latitudes can increase in the future. However, warmer winters may also negatively affect growth by triggering an earlier bud break and increasing risks of frost damages to developing buds (Cannell *et al.*, 1986) or by postponing the start of the growing season (see above, Contosta *et al.*, 2017). This might provide an argument against a sustained growth-promoting effect of higher seasonal temperatures (Girardin *et al.,* 2014).

Gradients in the sensitivity of tree growth to North Atlantic Ocean dynamics across boreal Quebec and Sweden

Trees in western and central boreal Quebec, despite being furthest away from the North Atlantic Ocean in comparison to trees in eastern boreal Quebec, were the most sensitive to oceanic and atmospheric dynamics, and particularly to current summer NAO and AO indices after the 1970s. Tree growth responses to large-scale indices were stronger and more spatially homogeneous than tree growth responses to regional climate. This suggests that growth dynamics in western and central boreal Quebec, despite being mainly temperature-limited, can be strongly governed by large-scale oceanic and atmospheric dynamics (Boucher *et al.,* 2017). Western boreal Quebec is the driest and most fire-prone of the Quebec regions studied here. Soil water availability in this region strongly depends on winter precipitation. High winter AMOC indices are associated with the dominance of Arctic air masses over NA and leads to decreased snowfall (see Appendix S4 in Supporting Information). The stronger tree growth sensitivity to winter AMOC indices in that region over the entire study period, can, therefore, directly emerge from the correspondence between AMOC and winter snow fall. Large-scale indices, through their correlation with regional fire activity, can also possibly override the direct effects of climate on boreal forest dynamics (Drobyshev *et al.*, 2014; Zhang *et al.*, 2015). Fire activity in NA strongly correlates with variability in atmospheric circulation, with summer high-pressure anomalies promoting the drying of forest fuels and increasing fire hazard (Skinner *et al.*, 1999, Macias Fauria & Johnson 2006) and low-pressure anomalies bringing precipitation and decreasing fire activity.

In Sweden, the northernmost forests were the most sensitive to North Atlantic Ocean dynamics, particularly to the summer NAO (Fig. 8). These high-latitude forests, considered to be ‘Europe’s last wilderness’ (Kuuluvainen *et al.*, 2017), are experiencing the fastest climate changes (Hansen *et al.*, 2010). Numerous studies have highlighted a correspondence between tree growth and NAO (both winter and summer) across Sweden (D'Arrigo *et al.*, 1993; Cullen *et al.*, 2001; Linderholm *et al.*, 2010), with possible shifts in the sign of this correspondence along north-south (Lindholm *et al.*, 2001) and west-east gradients (Linderholm *et al.*, 2003). Our results identified a post-1980 positive correspondence between tree growth and summer NAO, however spatially restricted to the northernmost regions (Figs. 8 and 9). This emerging correspondence appears linked to the combination of a growth-promoting effect of higher temperature at these latitudes (Fig. 5) and a northeastward migration of the spatial correspondence between NAO and local climate (Fig. 10). Boreal forests of Quebec (western and central) and Sweden (central and northern) emerged as regions sensitive to large-scale climate dynamics. We, therefore, consider them as the most suitable for a long-term survey of impacts of ocean-atmosphere dynamics on boreal forest ecosystems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Cross-correlation between regional chronologies.

Appendix S2 Regional chronologies obtained after ordination and spatial aggregation of tree growth data.

Appendix S3. Characteristics of regional chronologies.

Appendix S4. Correlation maps between seasonal climate indices and local climate.

Appendix S5. Winter temperature averages over 1950-2008 in the study region

SUPPORTING INFORMATION

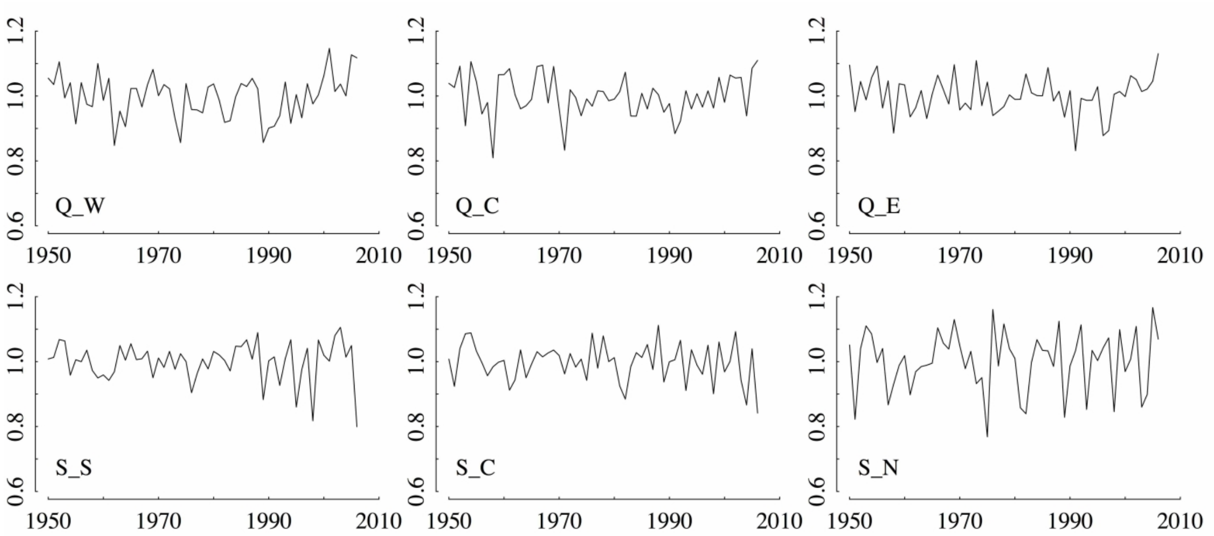
Post-1980 shifts in the sensitivity of boreal tree growth to North Atlantic Ocean dynamics and seasonal climate

Clémentine Ols, Valérie Trouet, Martin P. Girardin, Annika Hofgaard, Yves Bergeron & Igor Drobyshev

Appendix S1. Pearson cross-correlation between the six regional chronologies over the 1928-2008 period. Significance levels are indicating as follow: * - *P* < 0.01; **- *P* < 0.001

	S_N	S_C	S_S	Q_W	Q_C	Q_E
S_N	1					
S_C	0.94**	1				
S_S	0.77**	0.88**	1			
Q_W	-0.03	-0.01	0.01	1		
Q_C	-0.07	-0.07	-0.07	0.49**	1	
Q_E	0.05	0.10	0.10	0.44*	0.52**	1

Appendix S2. Growth patterns of the six regional chronologies obtained after ordination and spatial aggregation of forest inventory tree growth data in each study area (cf. Fig. 1): a western (Q_W), central (Q_C), and eastern (Q_E) chronology in Quebec, and a southern (S_S), central (S_C) and northern (S_N) chronology in Sweden. Curves are plotted over the 1950-2008 period, the common period between all regional chronologies (see Table 1 for chronologies' characteristics).

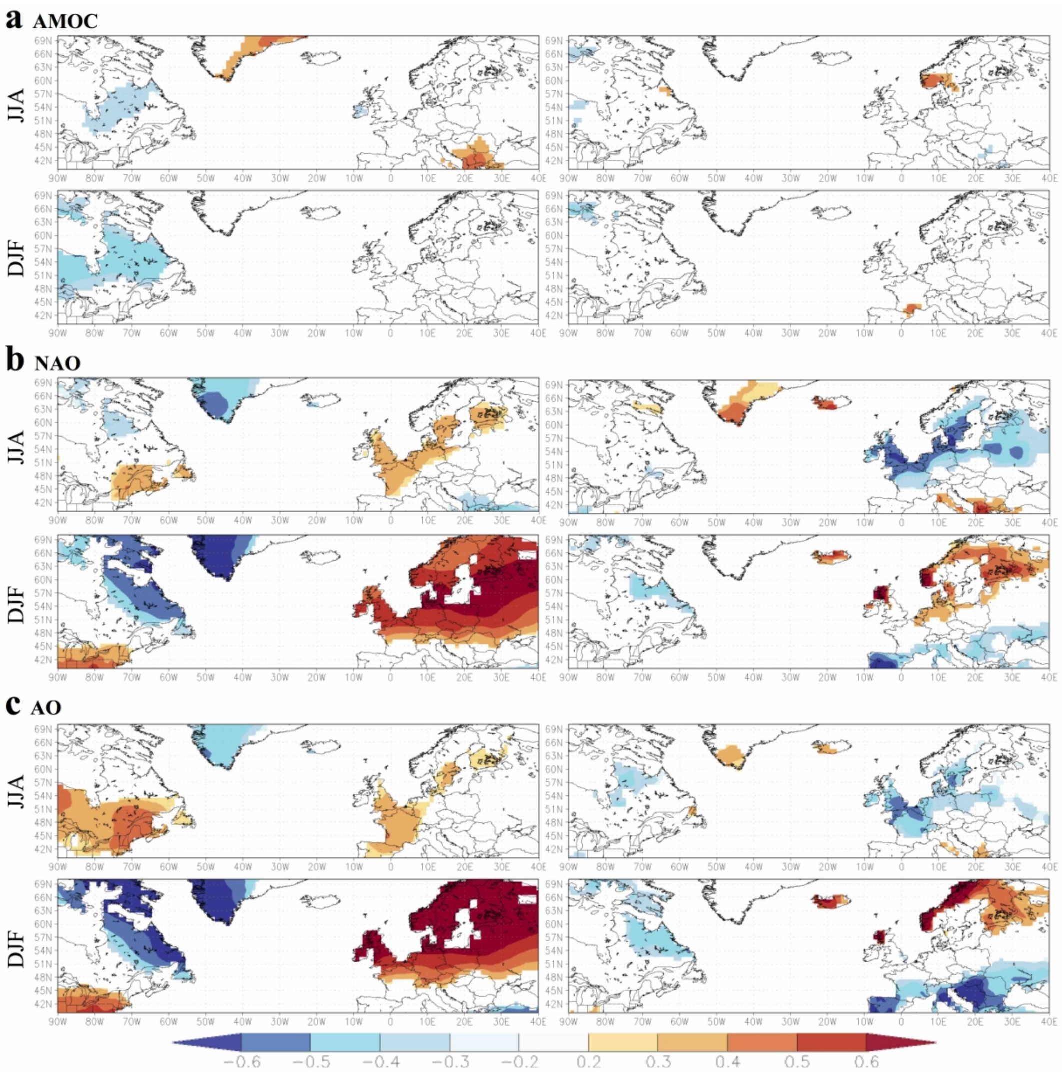


Appendix S3. Characteristics of regional chronologies over 1950-2008. See Appendix S2 for chronologies abbreviations. EPS - Expressed population signal; SNR - Signal to noise ratio, Rbar - mean of all the correlations between different cores;

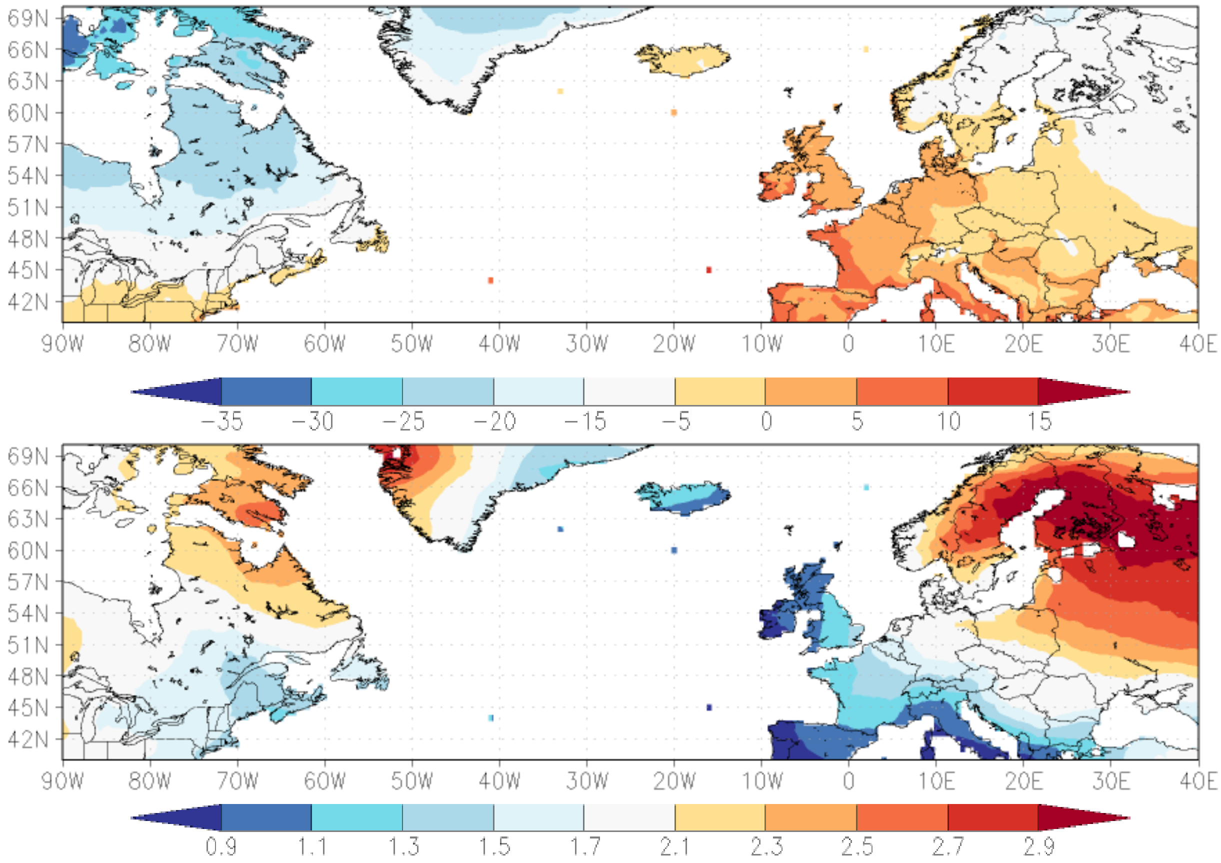
Chronology	EPS	SNR	Rbar
S_S	0.954	20.898	0.603
S_C	0.971	33.241	0.601
S_N	0.975	38.454	0.677
Q_W	0.925	12.246	0.554
Q_C	0.967	29.429	0.609
Q_E	0.824	4.687	0.401

* Eq. 1 in Biondi and Qeadan 2008. Calculated using the *rwl.stats* function in dplR (R environment)

Appendix S4**.** Correlation maps between seasonal climate indices and temperature (left panels) and precipitation (right panels). Indices include the AMOC (a), extracted from ECMWF over the 1961-2005 period, and NAO (b) and AO (c), extracted from NOAA's climate prediction center over the 1950-2008 period. Mean temperature and total precipitation are those of CRU TS 3.24 1° x 1° (Harris *et al.*, 2014). All correlations were computed for summer and winter season in the KNMI Climate Explorer (https://climexp.knmi.nl (Trouet & Van Oldenborgh, 2013)). Indices and climate variables were normalized (linear regression) over the 1950-2008 period (over the 1961-2005 period for AMOC) prior to analyses. Only correlations significant at $P < 0.05$ are plotted.



Appendix S5. Mean (upper panel) and standard deviation (lower panel) of winter (DJF) land temperatures [°C] over 1950-2008. Maps were computed in the KNMI Climate Explorer (https://climexp.knmi.nl) using the CRU TS4.01 0.5°x0.5° monthly dataset (Harris *et al.*, 2014). Only correlations significant at $P < 0.05$ are plotted.



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