Received: 9 August 2019 | Accepted: 7 October 2019

DOI: 10.1111/1365-2745.13308

RESEARCH ARTICLE

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

Climate teleconnections synchronize *Picea glauca* masting and fire disturbance: Evidence for a fire-related form of environmental prediction

Davide Ascoli[1] | Andrew Hacket-Pain[2] | Jalene M. LaMontagne[3] | Adrián Cardil[4] | Marco Conedera[5] | Janet Maringer[5] | Renzo Motta[1] | Ian S. Pearse[6] | Giorgio Vacchiano[7]

[1]Department of Agricultural, Forestry and Food Sciences, University of Torino, Grugliasco, Italy; [2]Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool, UK; [3]Department of Biological Sciences, DePaul University, Chicago, IL, USA; [4]Department of Crops and Forest Sciences, University of Lleida, Lleida, Spain; [5]Insubric Ecosystems, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Cadenazzo, Switzerland; [6]Fort Collins Science Center, U.S. Geological Survey, Fort Collins, CO, USA and [7]Department of Agricultural and Environmental Sciences, University of Milan, Milan, Italy

Correspondence
Davide Ascoli
Email: d.ascoli@unito.it

Funding information
Natural Environment Research Council, Grant/Award Number: NE/S007857/1; NSF, Grant/Award Number: DEB-1745496

Handling Editor: Peter Bellingham

Abstract

1. Synchronous pulses of seed masting and natural disturbance have positive feedbacks on the reproduction of masting species in disturbance-prone ecosystems. We test the hypotheses that disturbances and proximate causes of masting are correlated, and that their large-scale synchrony is driven by similar climate teleconnection patterns at both inter-annual and decadal time scales.
2. Hypotheses were tested on white spruce (*Picea glauca*), a masting species which surprisingly persists in fire-prone boreal forests while lacking clear fire adaptations. We built masting, drought and fire indices at regional (Alaska, Yukon, Alberta, Quebec) and sub-continental scales (western North America) spanning the second half of the 20th century. Superposed Epoch Analysis tested the temporal associations between masting events, drought and burnt area at the regional scale. At the sub-continental scale, Superposed Epoch Analysis tested whether El Niño-Southern Oscillation (ENSO) and its coupled effects with the Atlantic Multidecadal Oscillation (AMO) in the positive phase (AMO+/ENSO+) synchronize drought, burnt area and masting. We additionally tested the consistency of our synchronization hypotheses on a decadal temporal scale to verify whether long-term oscillations in AMO+/ENSO+ are coherent to decadal variation in drought, burnt area and masting.
3. Analyses demonstrated synchronicity between drought, fire and masting. In all regions the year before a mast event was drier and more fire-prone than usual. During AMO+/ENSO+ events sub-continental indices of drought and burnt area experienced significant departures from mean values. The same was observed for large-scale masting in the subsequent year, confirming 1-year lag between fire and masting. Sub-continental indices of burnt area and masting showed in-phase

© 2019 The Authors. Journal of Ecology
© 2019 British Ecological Society

decadal fluctuations led by the AMO+/ENSO+. Results support the 'Environmental prediction hypothesis' for mast seeding.

4. *Synthesis*. We provide evidence of large-scale synchronicity between seed masting in *Picea glauca* and fire regimes in boreal forests of western North America at both inter-annual and decadal time scales. We conclude that seed production in white spruce predicts changes in disturbance regimes by sharing the same large-scale climate drivers with drought and fire. This gives new insides in a mechanism providing a fire-sensitive species with higher than expected adaptability to changes in climate.

KEYWORDS

AMO, climate change, ENSO, environmental prediction hypothesis, fire ecology, fire regime, mast seeding, reproduction ecology

1 | INTRODUCTION

Climate teleconnections are recurring large-scale patterns of air pressure and circulation anomalies that span large geographical areas (Nigam & Baxter, 2015). In ecology, teleconnections are a relevant phenomenon since they synchronize environmental features such as precipitation, temperature, wind patterns and related geophysical and ecological phenomena through space and time (Mysterud, Stenseth, Yoccoz, Ottersen, & Langvatn, 2003). Showing both yearly variability and long-term oscillatory trends that arise from the non-linear dynamics of the coupled system, teleconnections have cascading effects on ecosystems and organisms at both inter-annual and decadal time scales (Beck, Fletcher, Gadd, Heijnis, & Jacobsen, 2017; Stenseth et al., 2002).

As these climate patterns affect all phenomena simultaneously and force them to fluctuate in synchrony (Liebhold, Koenig, & Bjørnstad, 2004), direct and indirect interactions between organisms and their physical environment emerge (Forchhammer & Post, 2004). So for instance, teleconnections affect both natural disturbance regimes (Mariani et al., 2018; Shabbar & Skinner, 2004) and yearly to decadal fluctuations in large-scale reproduction pulses in seed-masting species (Ascoli, Vacchiano, et al., 2017; Chechina & Hamann, 2019; Strong, Zuckerberg, Betancourt, & Koenig, 2015; Williamson & Ickes, 2002). In-phase fluctuations of seed pulses and disturbance have important consequences for the regeneration dynamics of masting species. Disturbances often promote environmental conditions that favour seed germination, seedling emergence and establishment, including exposed soil, increased light at the forest floor, and low competition by concurring vegetation (Pickett & White, 1985). However, within a few years post-disturbance, these favourable conditions might get lost. Therefore, the timing of reproduction relative to disturbance is key for successful regeneration (Greene et al., 2007; Maringer et al., 2020; Peters, Macdonald, & Dale, 2005; Purdy, Macdonald, & Dale, 2002; van Mantgem, Stephenson, & Keeley, 2006).

Several disturbance-adapted species have evolved strategies to reproduce soon after severe disturbance to obtain a competitive advantage – for example, resprouting or serotiny in fire-prone ecosystems subject to crown-fire regimes (He, Belcher, Lamont, & Lim, 2016; Veraverbeke et al., 2014). Consequently, when disturbance-adapted species co-occur with masting-obligate seeders, the latter will be competitive only when masting occurs shortly after the disturbance (Ascoli, Vacchiano, Maringer, Bovio, & Conedera, 2015; Frey, Ashton, McKenna, Ellum, & Finkral, 2007; Marod, Kutintara, Tanaka, & Nakashizuka, 2002; O'Dowd & Gill, 1984; Wright, Zuur, & Chan, 2014).

Given that both masting and natural disturbances are influenced by large-scale climate patterns (Koenig & Knops, 1998; Seidl et al., 2017), this suggests that the two processes may be related, so as climate patterns conducive to severe large-scale natural disturbances also act as proximate causes of masting synchronizing seed crops over wide areas (Bogdziewicz et al., 2019; Pearse, Koenig, & Kelly, 2016). In such synchronous fluctuation of the two phenomena through space and time, masting species would gain a competitive advantage in disturbance-prone ecosystems (Ascoli, Vacchiano, et al., 2017; Williamson & Ickes, 2002).

Here we test the hypotheses that natural disturbances and proximate causes of masting are correlated, and that the large-scale synchrony of these phenomena is driven by similar large-scale climate drivers (teleconnections) at both inter-annual and decadal time scales. We selected the boreal forest of North America, a biome where disturbances are well-recorded and mainly driven by natural agents. In these areas, the fire regime follows relatively natural cycles of drought and lightening-induced ignitions (Fauria & Johnson, 2006; Hess, Scott, Hufford, & Fleming, 2001; Veraverbeke et al., 2014), driven by large-scale climate patterns at both inter-annual and decadal time scales (Kitzberger, Brown, Heyerdahl, Swetnam, & Veblen, 2007; Shabbar & Skinner, 2004). As study species we chose the obligate-seeder white spruce (*Picea glauca* (Moench) Voss) that persists in a fire-prone environment subjected to a crown-fire regime despite its masting strategy (Michaletz, Johnson, Mell, & Greene, 2013; Pounden, Greene, & Michaletz, 2014). Proximate causes of masting in white spruce are well known (Krebs, LaMontagne,

Kenney, & Boutin, 2012; Roland, Schmidt, & Johnstone, 2014) and a relatively large amount of seed production data is available for this species since the second half of the 20th century across the North American boreal region (Pearse, LaMontagne, & Koenig, 2017).

2 | MATERIALS AND METHODS

2.1 | The study case

White spruce is a masting species that naturally grows over large areas of boreal Canada and Alaska. The frequency of good cone crops is not stationary in time, varying from 2 to 12 years depending on the time period considered and site characteristics (Juday, Barber, & Zasada, 2003; Lamontagne & Boutin, 2007; Roland et al., 2014). Interestingly, white spruce persists under a crown-fire regime (Michaletz et al., 2013; Pounden et al., 2014) despite lacking of fire-related adaptations such as sprouting, heat- or smoke-stimulated flowering or seed germination, or serotiny as it is the case for its associated trees such as the serotinous *Picea mariana* (Mill.) B.S.P. The apparent lack of fire-related adaptations in white spruce makes 'its widespread distribution in fire-prone boreal forests perplexing' (Abrahamson, 2005). However, it is well documented that when white spruce masting follows a fire disturbance, the regeneration pulse is remarkable (Peters et al., 2005; Purdy et al., 2002). Through fire, the reduction of coarse or refractory organic material from the forest floor significantly improves white spruce seed germination, seedling growth and establishment (Greene et al., 2007; Zasada, Sharik, & Markku, 1992). Although white spruce may display a transient aerial seed bank in closed cones that protect seeds from heating during crown fire (Michaletz et al., 2013; Pounden et al., 2014), the regeneration success in burned zones highly depends on the quantity of seeds available in surviving seed trees, particularly in fire skips and surrounding unburned areas (Galipeau, Kneeshaw, & Bergeron, 1997; Greene et al., 1999; Pounden et al., 2014). Likewise, recruitment success decreases with increasing time since fire (Peters et al., 2005; Purdy et al., 2002), highlighting the importance of the timing of masting in relation to fire disturbance.

The proximate causes of masting in white spruce are well described (Juday et al., 2003; Krebs et al., 2012; Roland et al., 2014). Drought stress and warm temperature anomalies induce the differentiation of bud primordia into reproductive staminate and ovulate buds, and several studies found a positive relationship between warm-dry weather and seed crop the following year (Krebs et al., 2016; Roland et al., 2014; Zasada et al., 1992). Large-scale fire disturbances over North American boreal forests are also triggered by warm-dry weather (Kitzberger et al., 2007). Several studies found a significant negative correlation between the Palmer Drought Severity Index (hereafter Drought index) in summer and the annual burnt area (Shabbar, Skinner, & Flannigan, 2010; Xiao & Zhuang, 2007). Widespread drought over large portions of North American boreal forests is linked to climate modes of sea surface temperatures such as El Niño-Southern Oscillation (ENSO) and Atlantic Multidecadal Oscillation (AMO), with significant correlations at both inter-annual and decadal time scales (Shabbar & Skinner, 2004). These teleconnections might synchronize fire disturbance in this region (Beverly, Flannigan, Stocks, & Bothwell, 2011; Hess et al., 2001; Shabbar et al., 2010). Indeed, when ENSO and AMO are both in a positive phase (Enfield, Mestas-nunez, & Trimble, 2001; Mo, Schemm, & Yoo, 2009), their coupled effect seems responsible for synchronous drought (Shabbar & Skinner, 2004) and fire activity over western North America (Kitzberger et al., 2007).

2.2 | Workflow and hypotheses tested

We tested the hypothesis that the same climate drivers synchronize both masting and fire disturbance (hereafter the 'synchronization hypothesis') in the North American boreal forest at both inter-annual and decadal time scales. At an inter-annual timescale, the synchronization hypothesis states that a mast year (*T*) has a high probability of occurrence after large fire disturbance in the year before ($T-1$). Particularly, we tested the following potential correlations (Figure 1): (a) The Drought index at $T-1$ inversely correlates with burnt area in year $T-1$ and masting in year *T*, (b) masting at *T* correlates positively with area burnt the year before ($T-1$), (c) the coupling of positive phases of both ENSO and AMO (AMO+/ENSO+) positively correlates with the Drought index, burnt area at year $T-1$ and masting at *T*.

We additionally tested the consistency of the synchronization hypothesis on a decadal temporal scale verifying if long-term oscillations in AMO+/ENSO+ teleconnections are coherent to decadal variation in the Drought index, burnt area and masting.

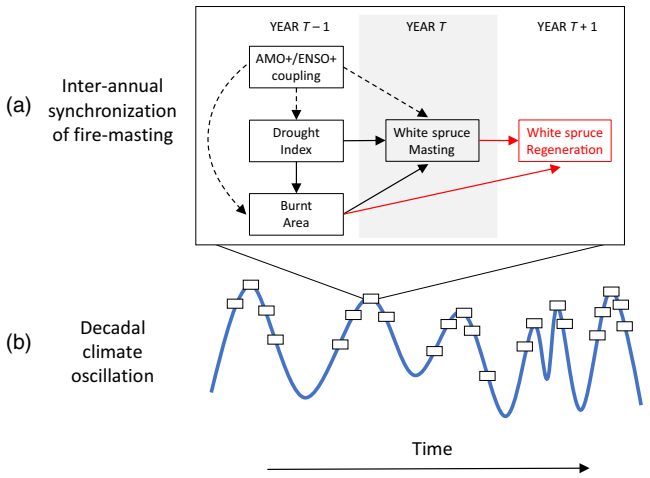

FIGURE 1 Scheme of inter-annual (a) and decadal (b) correlations tested in the present study. (a) The rectangle represents the inter-annual synchronization among climate teleconnections, drought, fire and masting. (b) The blue line represents decadal variation in climate oscillations and white rectangles the occurrence of an inter-annual synchronization between fire and masting (scheme A). Solid arrows in the rectangle indicate correlations tested at regional level, whereas dashed arrows refer to correlations tested at sub-continental level. Relationships indicated in red are not tested in the present study but have been demonstrated in previous studies (Peters et al., 2005; Purdy et al., 2002) [Colour figure can be viewed at wileyonlinelibrary.com]

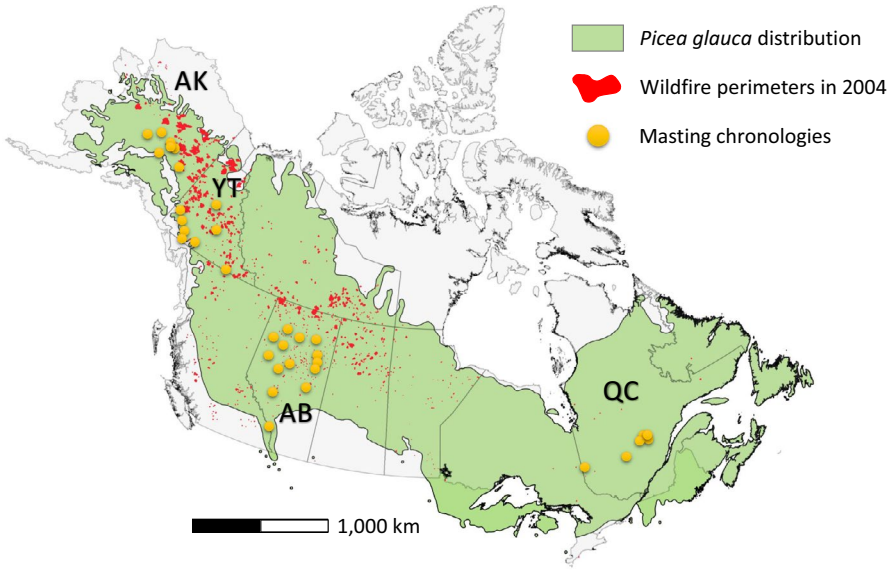

FIGURE 2 Map showing the study area. Acronyms indicate the investigated provinces and states: Alaska (AK), Yukon Territory (YT), Alberta (AB) and Quebec (QC). The green area represents the white spruce distribution across western North America gathered from the US tree Atlas (Little, 1971). Red polygons show synchronous wildfires across western North America in year 2004 in coincidence of a positive phase of both El Niño Southern Oscillation and the Atlantic Multidecadal Oscillation teleconnections (see Table 1). Yellow dots indicate the location of masting site chronologies used in the study (see Table S1). Fire perimeters were provided by the Canadian National Fire Database (Canadian Forest Service, 2017). The white spruce distribution range within the study area was retrieved in a digital format from the US tree Atlas (Little, 1971) [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Data collection

Time series of cone and seed data are available for white spruce for selected sites across the North American boreal region starting from the second half of the 20th century (Pearse et al., 2017). These data were supplemented by an additional exhaustive review of the scientific literature, and some unpublished records. In total, the assembled database included 1,062 yearly observations spanning four regions of North America (Alaska, USA; and Yukon, Alberta, and Quebec in Canada; Figure 2) and the time period 1950 to 2017. Because several sources used the same raw data (Juday et al., 2003; Krebs et al., 2016; Lamontagne & Boutin, 2007; Roland et al., 2014), duplicated data were filtered out. Also, continuous seed production series shorter than eight consecutive years were excluded from further analysis, to avoid bias introduced by short time series. We ended up with a total of 771 distinct yearly observations (data are available on FigShare, see the 'Data availability statement' section).

Data of yearly burnt area for the Canadian part of the study region were retrieved from the Canadian National Fire Database (Canadian Forest Service, 2017). We used data spanning from 1950 to 2017 for Yukon and Alberta, and from 1973 to 2017 for Quebec. Yearly burnt area for Alaska was obtained from the Large Fire Database of the Alaska Fire Service, which dates back to 1950 (Kasischke & Turetsky, 2006).

Gridded values of monthly Palmer Drought Severity Index based on Penman-Monteith potential evapotranspiration with a spatial resolution of 2.5° for the period 1850–2014 were downloaded from public sources (Dai, 2011).

For the ENSO teleconnection, we used the Oceanic Niño Index for the years 1950–2017 obtained by the Climate Prediction Centre of the National Oceanic and Atmospheric Administration (NOAA) of USA. This index corresponds to 3-month running mean of sea surface temperature anomalies in the Niño 3.4 region (5°N–5°S, 120°–170°W) based on centred 30-year base periods updated every 5 years using the Extended Reconstructed Sea Surface Temperature, version 5 (ERSST.v5). The unsmoothed monthly AMO index (Enfield et al., 2001) for the years 1950–2017 was obtained by the Earth System Research Laboratory of NOAA.

The white spruce distribution range within the study area was retrieved in a digital format from the US tree Atlas (Little, 1971).

2.4 | Data processing

The masting database for white spruce included both ordinal and continuous seed series in different classes and units, respectively. Consequently, we harmonized all series to maximize the amount of data available for analyses. Raw ordinal data were harmonized using a five class system (1: no masting; 5: mast year) as in Ascoli, Maringer, et al. (2017); raw continuous series were square-root transformed and re-classified to the five class ordinal scale by dividing the data range into five equal intervals. Drought index and fire data did not require harmonization. To carry out the analyses presented in Section 2.5, harmonized masting series (ORDmast column in the database available on FigShare), Drought index and fire data were aggregated at different spatial scales (regional and sub-continental) as defined below.

2.4.1 | Data aggregation at regional scale

To analyse data series (fire, drought and masting) at the same spatial unit, we aggregated data at the regional scale (i.e. the province/state level: Alaska, Yukon, Alberta and Quebec), since fire data were provided at this scale. In addition, this data aggregation allowed us to obtain long masting chronologies and minimize gaps in our regional time series (Vacchiano et al., 2017).

Regional Drought index series for each region were computed by averaging values for July (i.e. month of bud differentiation) over the white spruce distribution range within Alaska, Yukon, Alberta and Quebec.

We ran a Mantel test to determine the appropriate spatial scale for aggregation of cone production data. We calculated ranked (Spearman) correlations between dissimilarities of masting time series and geographical distance between sites. The existence of spatial aggregation in white spruce masting was confirmed by significantly positive ($p < .01$) Mantel correlation coefficients ($M = 0.73$) and decreasing similarity between cone production time series with increasing distance between them (Figure S1). Some sites were represented by multiple series (e.g. different survey plots at the Bonanza Creek site). As a marked correlation was observed at a fine scale (i.e. similarity >0.6 at 10–20 km distance), we first aggregated such series into site chronologies (SCs) using the most frequently observed masting class for each year at a given site (e.g. Bonanza Creek). This was necessary to avoid assigning a higher weight to sites with many series (e.g. different stands surveyed at the Bonanza Creek site) relative to less intensively sampled sites. SCs were then aggregated into regional chronologies (RCs) using the most frequently observed masting class for each year in a region (i.e. Alaska, Yukon, Alberta, Quebec). In the case of two or more masting classes displaying the same frequency in a given year, we selected the highest masting class or the intermediate, respectively. The final ordinal RCs were 49 years for Alaska (1957–2016), 28 years for Yukon (1987–2016), 61 years for Alberta (1951–2016) and 23 years for Quebec (1989–2014; Table S1).

2.4.2 | Data aggregation at sub-continental scale

To test for correlations with AMO and ENSO, we computed the Drought index, fire and masting indices at a sub-continental scale which is the adequate spatial approach to analyse how teleconnections influence both geophysical and ecological phenomena (Beverly et al., 2011; Forchhammer & Post, 2004; Mysterud et al., 2003). However, since the influence of AMO and ENSO is primarily exerted on western North America (Figure S2) with minor influence on eastern regions (Shabbar & Skinner, 2004), and we observed no positive correlations between cone production in eastern and western Canada (Figure S1), the province of Quebec was excluded from the sub-continental scale that finally included the western regions Alaska, Yukon and Alberta only. The sub-continental fire index was computed by averaging standardized yearly regional series of burnt area and the sub-continental Drought index was computed by averaging values of the Drought index for July over the white spruce distribution range within the western regions considered.

A continuous masting index at the sub-continental scale, as required for statistical analyses at this scale (see Section 2.5), was computed as follows: we computed for each year the difference between the proportions of ordinal site chronologies (SCs) displaying a full mast (class 5, SC-5) and a poor masting (classes 1 and 2, SC-12) after Ascoli, Vacchiano, et al. (2017). This difference generates a continuous index that varies from −1, when all SCs are in classes 1 and 2 (broad masting failure), to +1 when all SCs are in the masting class 5 synchronously throughout Alaska, Yukon and Alberta. Intermediate (zero) values indicate a prevalence of classes 3 and 4, or a balanced distribution of SC-5 and SC-12 (Table S1). The resulting continuous masting index at the sub-continental scale (M_index) covered 59 years from 1957 to 2016 (Table S1).

Since ENSO warm phases (El Niño phase) from winter to summer strongly influence sea surface temperature and air pressure, temperature and moisture in the western North America, particularly during positive phases of AMO (Figure S2), we used the December to August values of both the Oceanic Niño Index and AMO indices. A coupled AMO+/ENSO+ index was computed by running a principal component analysis of the two indices. The yearly scores of the component correlated positively to both ENSO and AMO were used as AMO+/ENSO+ index.

2.5 | Statistical analyses

To examine the temporal association between masting, fire and drought at the inter-annual temporal scale, we used Superposed Epoch Analysis (Baisan & Swetnam, 1990). This test compares the mean values of given environmental variables before, during or after an event with the mean of the same variables across non-event years. The comparison is based on Monte Carlo simulations that randomly pick years, calculate expected means and provide 95% bootstrap confidence intervals. The technique has often been applied to analyse relationships between climate and ecosystem response, for example, climate and fire events (Grissino-Meyer, Romme, Floyd, & Hanna, 2004), or drought and tree mortality (Gea-Izquierdo, Viguera, Cabrera, & Cañellas, 2014). Here, we used Superposed Epoch Analysis for each region separately to assess if the burned area and the Drought index in years before a masting event were significantly different from those recorded in other years. Burned area and Drought index were calculated for a 7-year window centred on the mast year. The number of randomly selected non-masting years used in the comparison was equal to the number of actual masting years. We identified mast events by selecting years displaying a masting class 5 (Table S1). To test for the relationship between fire disturbance and drought, we also ran separate superposed epoch analyses for each region, using burnt area as the dependent variable and years in which the Drought index was less than its 20th percentile as drought events.

To investigate the coupled effect of AMO and ENSO at the sub-continental scale, we defined AMO+/ENSO+ events, that is, when El Niño years (warm phase of ENSO) coincided with a positive phase

of AMO according to the classification provided in Table 1. Then, we ran separate superposed epoch analyses to assess if M_index, the Drought index and fire indices at the sub-continental scale were significantly different than those 1–3 years before and after an AMO+/ENSO+ event (3-year lag). All superposed epoch analyses were performed using the package 'dplr' (Bunn, 2008) within the R statistical framework (R Core Team, 2019). Bootstrap resampling was used to randomly select sets of lag + 1 years from the dataset and to estimate significances for the departures from the mean.

To test whether decadal oscillations in teleconnections are correlated to long-term trends in masting patterns, drought and fire disturbance at the sub-continental scale, we carried out wavelet coherence analysis (Cazelles et al., 2008). Coherence is a measure of the intensity of the covariance of two series in the time–frequency space. The test measures the cross-correlation between two series as a function of time and frequency, allowing the identification of time-localized common oscillatory behaviour. Wavelet coherence is well suited to detect localized correlations of non-stationary signals (Grinsted, Moore, & Jevrejeva, 2004) such as teleconnection indices, drought, fire or masting, that is, series that display a variable frequency through time (Ascoli, Vacchiano, et al., 2017). For these reasons, wavelet coherence has often been used to test for relationships between climatic teleconnections and geophysical and ecological processes (Grinsted et al., 2004).

The use of wavelet coherence required computation of the continuous M_index at the sub-continental scale (see Section 2.4.1). To avoid bias due to non-normality, burnt area and M_index were arcsine-transformed before the wavelet analysis. The analysis was limited to the period 1957–2016 (i.e. the temporal domain of the M_index). Each wavelet coherence analysis was computed with the *wtc* function in the R package 'biwavelet' (Gouhier, Grinstead, & Simko, 2016) using a Morlet continuous wavelet transform and considering the lag-1 autocorrelation of each series. The data were padded with zeros at each end to reduce wraparound effects (Grinsted et al., 2004). Significance of coherence at all frequencies lower than 3 years was tested using a time-average test with 2000 Monte Carlo randomizations.

3 | RESULTS

Superposed Epoch Analyses showed that in each region (Alaska, Yukon, Alberta, Quebec) burnt area was significantly higher during drought events (i.e. July-Drought index < 20th percentile) (Figure 3, first row), and was on average 322% higher than in non-drought years. Consistent with our hypotheses, the July-Drought index was significantly lower than average for the year $T - 1$, that is, the year before a mast event (Figure 3, second row). Consistent with these results, in each considered region (Alaska, Yukon, Alberta, Quebec), the year before a mast event ($T - 1$) showed a significant positive departure from mean burnt area (Figure 3, third row).

During AMO+/ENSO+ events (see Table 1, years indicated in bold), both sub-continental indices of Drought index and burnt area across boreal regions of western North America experienced significant departures from mean values (Figure 4). The same was observed for the M_index in the subsequent year.

Wavelet coherence between teleconnections indexes (both ENSO and AMO+/ENSO+) and M_index, burnt area and the Drought index at the sub-continental scale from 1957 to 2016 showed a significant coherence (Figure 5), which shifted from a frequency domain of 8–11 before 1990 to a frequency of 3–6 years in more recent decades (red regions with black contours in the graph). In most periods, wavelet coherence showed an in-phase fluctuation between teleconnections and sub-continental indices led by ENSO or AMO+/ENSO+ (arrows pointing up and right). In comparison to ENSO, the AMO+/ENSO+ index had a stronger coherence with M_index and burnt area, but a weaker relationship with the Drought index. Notably, a wavelet coherence analysis between the Drought index and burnt area (Figure S3a), and between burnt area and M_index (Figure S3b), displayed a similar non-stationary pattern, with lower frequencies before 1990 (around 11 years) and higher frequencies from 1990 to 2000.

4 | DISCUSSION

4.1 | Inter-annual time scale at regional level

Masting events in white spruce tended to occur in the year after summer drought in the studied regions across North America. This is consistent with previous observations of the temperature and precipitation regulation of reproduction in the genus *Picea* (Ascoli, Vacchiano, et al., 2017; Juday et al., 2003; Krebs et al., 2016; Roland et al., 2014; Selås, Piovesan, Adams, & Bernabei, 2002), confirming that high summer temperatures and aridity at year $T - 1$ (i.e. low values of the Palmer Drought Severity Index) act as climatic cues of reproductive bud initiation, which results in mast seeding in year T.

In accordance with previous studies (Shabbar et al., 2010; Xiao & Zhuang, 2007), we also report a strong association between warm-dry conditions in summer (low values of the Palmer Drought Severity Index) and regional burnt area in all studied North American boreal regions. Interestingly, drought intensity triggering both masting and fire was comparable: the Superposed Epoch Analysis showed that drought intensity in years preceding masting events (mean July-Drought index = −1.43) is similar to the intensity in years with a significantly higher burnt area (mean July-Drought index = −1.48).

Notably, the initial hypothesis of a positive correlation between regional masting at year T and regional burnt area the year before at $T - 1$ (Figure 1) was confirmed. Previous studies investigating the persistence of white spruce in boreal crown-fire regimes stressed the importance of a coincidence between fire and cone production in the same year (Michaletz et al., 2013; Pounden et al., 2014), rather than the year before ($T - 1$) as found in the current study. Under the hypothesis that closed cones protect the transient aerial seed bank during a crown fire, the authors calculated that the probability for white spruce to bear closed cones during a mast event in coincidence with crown-fire disturbance ranged from 5% (Michaletz et al., 2013)

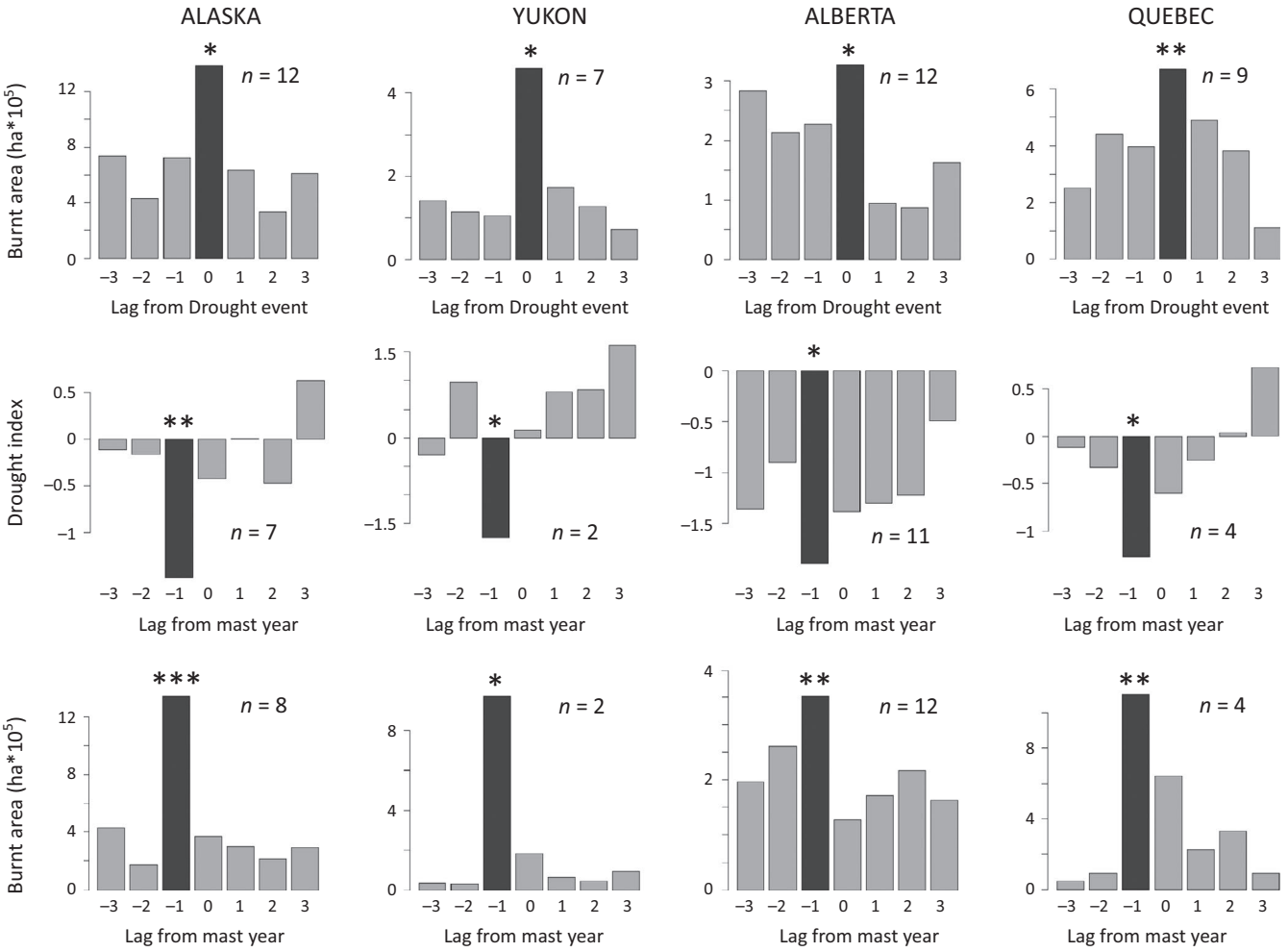

FIGURE 3 Results of the Superposed Epoch Analyses at regional scale. First column: Alaska (period: 1955–2014); second column: Yukon (period: 1984–2014); third column: Alberta (period: 1948–2014); forth column: Quebec (period: 1987–2014). First row: burnt area versus July-Drought index events (<20th percentile of regional series). Second row: July-Drought index versus mast events (class 5). Third row: burnt area versus mast events (class 5). The number of events is reported on each bar graph (*n*=). Black bars indicate significant departure from the mean. Significance levels are: ***$p < .001$; **$p < .01$; *$p < .05$

TABLE 1 Years identified as cool and warm episodes for Atlantic Multidecadal Oscillation (AMO) and El Niño Southern Oscillation (ENSO; 1950–2016)

	AMO	ENSO	AMO+/ENSO+ events
Cool episodes Negative phase (AMO-; La Niña)	1964–1968, 1970–1986, 1989–1994	1950, 1954, 1955, 1964, 1967, 1970, 1971, 1973, 1974, 1975, 1984, 1988, 1995, 1999, 2000, 2005, 2007, 2008, 2010, 2011	
Warm episodes Positive phase (AMO+; El Niño)	1950–1963, 1969, 1987–1988, 1995–2016	1953, 1957, 1958, 1966, 1969, 1982, 1983, 1987, 1991, 1992, 1997, 1998, 2002, 2004, 2015, 2016	1951, 1953, **1957, 1958, 1969, 1987, 1997,1998, 2002, 2004, 2015, 2016**
Neutral phase		1951, 1952, 1956, 1959, 1960, 1961, 1962, 1963, 1965, 1968, 1972, 1976, 1977, 1978, 1979, 1980, 1981, 1985, 1986, 1989, 1990, 1993, 1994, 1996, 2001, 2003, 2006, 2009, 2012, 2013, 2014	

Note: El Niño events (i.e. positive phase of ENSO) are defined as five consecutive overlapping 3-month periods at or above the +0.3° anomaly of the Oceanic Niño Index along the winter to summer seasons. AMO+ years corresponds to positive values of the AMO index. Numbers in bold correspond to AMO+/ENSO+ event years used for superposed epoch analyses in Figure 4.

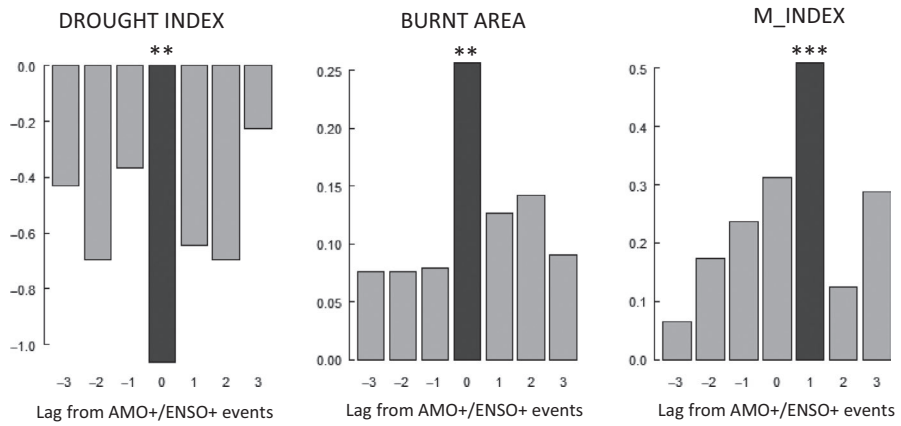

FIGURE 4 Results of the Superposed Epoch Analyses at sub-continental scale using the coupled El Niño Southern Oscillation and Atlantic Multidecadal Oscillation index (AMO+/ENSO+). Left: July-Drought index versus AMO+/ENSO+ events (warm AMO coupling with warm ENSO, 1957–2016). Centre: burnt area versus AMO+/ENSO+ events. Right: M_index versus AMO+/ENSO+ events. The number of AMO+/ENSO+ events used was 10 (see Table 1, years indicated in bold). Black bars indicate significant departure from the mean. Significance levels are: ***$p < .001$; **$p < .01$

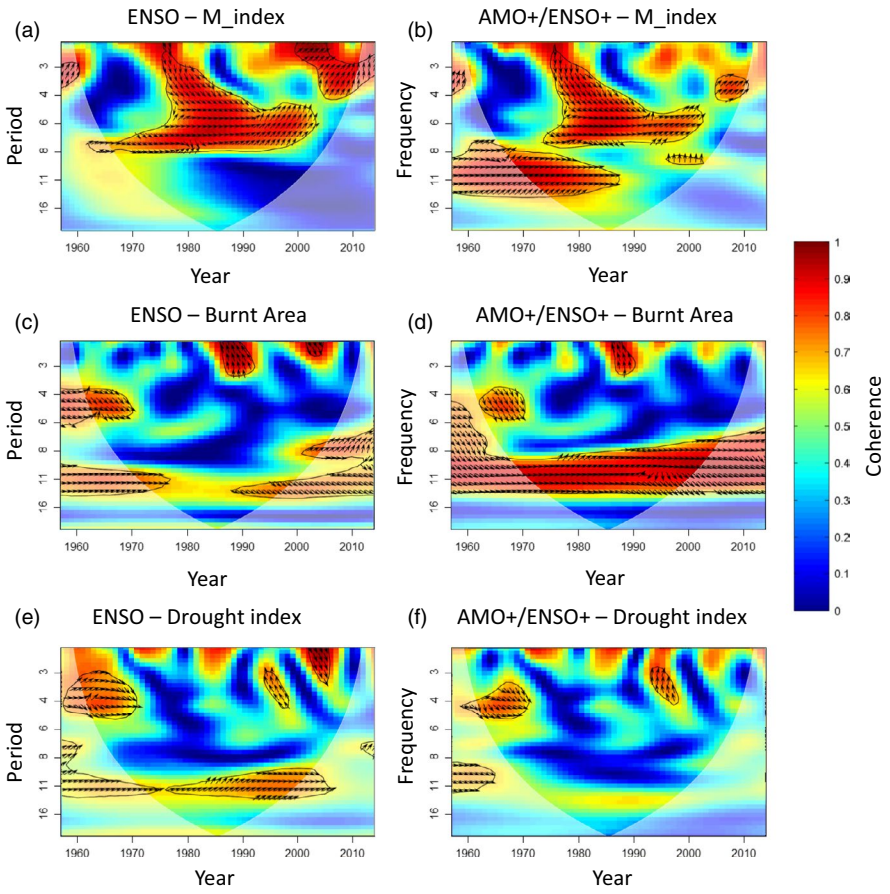

FIGURE 5 Wavelet coherence between the masting index (M_index), Burnt area and Drought indices at the sub-continental scale with the winter El Niño Southern Oscillation index (ENSO) and with the coupled El Niño and Atlantic Multidecadal Oscillation index in the positive phase (AMO+/ENSO+): (a) ENSO versus M_index. (b) AMO+/ENSO+ versus M_index. (c) ENSO versus Burnt Area. (d) AMO+/ENSO+ versus Burnt Area. (e) ENSO versus Drought index. F) AMO+/ENSO+ versus Drought index. Areas of strong coherence in time and frequency scales between series are shown in red. Black contours designate frequencies of significant coherence ($p < .1$, two-sided test) against red noise. Lighter shading shows the cone of influence where edge effects are important. Arrows pointing up and right show in-phase behaviour and teleconnections leading masting, burnt area and the Drought index (please note that the Palmer Drought Severity Index has been changed in sign to aid interpretation) [Colour figure can be viewed at wileyonlinelibrary.com]

to 10% (Pounden et al., 2014). The capacity of white spruce to occasionally behave as an aerial seed bank species is complementary to our hypothesis, but our results show that fire precedes masting more frequently than when they occur in the same year (Figure 3). Indeed, as a consequence of the same drought trigger, the year before a mast event was more likely to experience a significantly positive departure from mean burnt area in all studied regions.

To our knowledge, no prior study has shown a correlation between reproduction in a masting tree species and previous year fire extent. A few studies in fire-prone regions of Australia found that seed production in grass and shrub species displaying heat stimulated seed germination (*Triodia* spp. and *Acacia aptaneura*, respectively) was strongly related to increased fire likelihood in the 24 months after the reproduction event (Wright & Fensham, 2017; Wright et al., 2014). Similarly

to our results for white spruce, in these studies the same climate cue (precipitation in previous months) was responsible for both the induction of flowering and the increase of burnt area, due to fuel build-up and improved fuel connectivity after moist years. A significant increase in burnt area has also been observed after widespread reproduction of bamboo in South-East Asia (Fava & Colombo, 2017), although in this case fire is not driven by weather, but rather by the increase in fuel that followed post-reproduction mortality of bamboo over large areas.

4.2 | Sub-continental scale

AMO is the dominant mode of long-term sea surface temperature variability in the Atlantic Ocean that strongly influences Walker circulation in the tropical Pacific Ocean and modifies ENSO stability over both annual and decadal time spans (Enfield et al., 2001; Levine, McPhaden, & Frierson, 2017). Our results suggest that synchronous drought and fire activity across the studied regions occur when warm phases of AMO and ENSO coincide. This is consistent with previous studies on the coupled effect of warm phases of these two teleconnections (AMO+/ENSO+) on soil moisture content (Shabbar & Skinner, 2004) and synchronous wildfire activity (Kitzberger et al., 2007) across boreal regions of western North America.

Consistent with our initial hypotheses (Figure 1), the sub-continental scale masting index is significantly higher 1 year after AMO+/ENSO+ events, that is, 1 year after synchronous drought and fire activity. Several teleconnection indices were found to correlate with masting and its proximate causes in many tree species and geographical regions, such as the North Atlantic Oscillation for beech (*Fagus sylvatica* L.) and spruce (*Picea abies* (L.) H.Karst.) in Europe (Ascoli, Vacchiano, et al., 2017) or ENSO for Dipterocarpaceae in East Asia and Oceania (Chechina & Hamann, 2019). However, due to the limited availability of seed production data, the effect of the low-frequency component of such teleconnections has been rarely tested.

Additionally, we showed that decadal changes in AMO+/ENSO+ displayed common oscillatory trends with fire and white spruce masting series in the last 60 years. The frequency with which these processes co-varied was not periodic but displayed a non-stationary signal with frequencies shifting from 8 to 11 years towards shorter periods near the mid-1990s. This result highlights the potential role of AMO and ENSO coupling in modulating common shifts in the frequency of both fire disturbance and *Picea glauca* reproduction, not only at inter-annual intervals but also at a decadal time scale. The synchronization between periods of increased fire activity and periods of more frequent large-scale masting would provide white spruce with a strong competitive advantage for its reproduction and long-term persistence in a crown-fire-prone environment and a higher adaptability to changes in fire regimes driven by climate changes.

4.3 | Ecological and evolutionary implications

Juday et al. (2003) speculated that white spruce maximizes the odds that seeds will be released into a recently burnt landscape based on the existence of a common trigger for floral induction and fire disturbance (i.e. summer drought). Indeed, a positive interaction exists between the timing of masting in white spruce and short-term crown-fire effects (Greene et al., 2007; Peters et al., 2005; Purdy et al., 2002). Trees along fire edges or in fire skips, as well as few large surviving individuals in burnt areas, function as seed trees in a post-fire environment (Pounden et al., 2014) and may behave as super-producers accounting for a large portion of overall seed production (Hacket-Pain et al., 2019; Minor & Kobe, 2017). Seeds dispersed shortly after fire germinate more easily due to partial litter consumption, and seedlings can establish more successfully due to canopy openings and lower competition relative to unburnt stands (Peters et al., 2005; Purdy et al., 2002). Such positive feedback has been observed in many other masting tree species whose reproduction is facilitated by forest canopy gaps and soil disturbance (Maringer et al., 2020; O'Dowd & Gill, 1984; van Mantgem et al., 2006). It has also been noted that for some species the proximate causes triggering masting are also associated with an increased probability of natural fire disturbance, for example, stand aging and dead fuel accumulation in bamboo (Keeley & Bond, 1999), dry and hot spells in Norway spruce (Selås et al., 2002), European beech (Ascoli et al., 2015) and Dipterocarpaceae (Williamson & Ickes, 2002), or heavy rains followed by warm periods in *Triodia* spp. (Wright et al., 2014) and *Acacia aptaneura* (Wright & Fensham, 2017). Most of these authors have suggested that this positive feedback supports the 'Environmental prediction hypothesis' for mast seeding (Piovesan & Adams, 2005), which postulates the existence of traits that benefit plants in timing their seed crops using environmental cues to 'predict' which years will be favourable for seedling establishment. As a consequence, these traits may represent the result of a positive selection during evolution. Our findings that seed production follows fire-prone years in *Picea glauca* suggest the possibility that a fire-related form of environmental prediction hypothesis exists in this tree species. However, for such a masting phenology to have evolved, drought and fire must have been correlated with each other in boreal forests for an evolutionarily significant time. This seems highly likely, as increased flammability following drought is an intrinsic feature of circumboreal forest ecosystems (Aakala et al., 2018; Eichler et al., 2011; Kitzberger et al., 2007) that may have existed ever since boreal conditions emerged during the Cretaceous period, following the breakup of Pangaea starting 200 million years ago (Mauseth, 2014). The origin of *Picea* in North America dates back to the early Tertiary or late Cretaceous (100.5–66 million years before present; Ran, Wei, & Wang, 2006), a period of marked global fire activity, including boreal regions (Bond & Scott, 2010). *Picea* persisted in these regions during the last glacial maximum (Zazula, Telka, Harington, Schweger, & Mathewes, 2006) and sedimentological records indicate that in the Lateglacial the appearance of *P. glauca* coincided with increased charcoal indicators of fire (Anderson et al., 2006) with decreased fire return intervals ranging from 200 to 380 years (Tinner et al., 2006). It is likely that white spruce faced recurrent drought-driven fires throughout its evolutionary history. On top of the drought and fire correlation, trees that produced large seed crops in coincidence with suitable post-fire conditions for an increased seed viability,

germination and establishment would be favoured evolutionarily. Indeed, when the drought cue synchronizes mast crops soon after large fire years, it creates an economy of scale (Koenig & Knops, 1998), that is, successful offspring, that might reinforce the feedback loop between the climate pattern and masting (Brunner, Deere, Egas, Eizaguirre, & Raeymaekers, 2019; Moreira, Abdala-Roberts, Linhart, & Mooney, 2015) through directional selection on masting traits in white spruce.

5 | CONCLUSIONS

In this study, we used long-term data of white spruce masting, drought and burnt area in the North-American boreal forests to test the extent to which these processes are synchronized by common large-scale climate patterns (i.e. teleconnections) at both inter-annual and decadal time scales. We report the existence of a common driver (i.e. summer drought) shared by fire and masting. We furthermore showed significant correlations between the coupled effect of positive phases of the Atlantic Multidecadal Oscillation and of the El-Niño Southern Oscillation drought and fire disturbance on one side, and between white spruce masting and previous-year burnt area on the other.

Climate changes will modify large-scale climate patterns such as the Atlantic Multidecadal Oscillation and the El-Niño Southern Oscillation, and related biophysical processes such as fire disturbance (Mariani et al., 2018; Seidl et al., 2017) and plant reproduction (Ascoli, Vacchiano, et al., 2017; Koenig & Knops, 1998). Future changes in fire regimes might be an important driver of boreal ecosystems processes (Kasischke & Turetsky, 2006) affecting species that lack fire adaptive traits such as *Picea glauca*. However, white spruce might show some adaptability to changes in climate teleconnections via the synchronization of its seed crops with changes in disturbance regimes, which provide this fire-sensitive species with higher than expected plasticity and climate adaptation capacity.

ACKNOWLEDGEMENTS

This work was partly supported by the Natural Environment Research Council (NERC) grant no. NE/S007857/1. J.M.L. was supported by NSF grant DEB-1745496. The authors wish to thank Walt Koenig for revising a draft of the manuscript. Thanks also to all provincial and territorial agencies, Parks Canada and the many Canadian Forest Service employees who contributed to the compilation of the Canadian National Fire Database. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the US Government.

AUTHORS' CONTRIBUTION

D.A., A.H.-P., J.M.L., G.V. and M.C. conceived the ideas and designed methodology; J.M.L., I.S.P., A.H.-P. and D.A. collected the data; D.A. and G.V. analysed the data; and D.A. led the writing of the manuscript with contribution from all co-authors. D.A., A.H.-P., J.M.L., A.C., M.C. J.M. R.M. I.S.P. and G.V. contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are published on FigShare with the following https://doi.org/10.6084/m9.figshare.8870288 (Ascoli, 2015) and can be accessed at: https://figshare.com/articles/Picea_glauca_masting_data_across_North_America/8870288. The Oceanic Niño Index for the years 1950–2016 obtained by the Climate Prediction Centre of the National Oceanic and Atmospheric Administration (NOAA) of USA. https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php (last access: 03/08/2019). The unsmoothed monthly AMO index (Enfield et al., 2001) for the years 1950–2016 was obtained by the Earth System Research Laboratory of NOAA. https://www.esrl.noaa.gov/psd/data/correlation/amon.us.data (last access: 03/08/2019).

ORCID

Davide Ascoli https://orcid.org/0000-0002-2671-5122

Jalene M. LaMontagne https://orcid.org/0000-0001-7713-8591

REFERENCES

Aakala, T., Pasanen, L., Helama, S., Vakkari, V., Drobyshev, I., Seppä, H., … Holmström, L. (2018). Multiscale variation in drought controlled historical forest fire activity in the boreal forests of eastern Fennoscandia. *Ecological Monographs*, *88*(1), 74–91. https://doi.org/10.1002/ecm.1276

Abrahamson, I. (2005). *Picea glauca*, white spruce. In Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory.

Anderson, R., Hallett, D., Berg, E., Jass, R., Toney, J., De Fontaine, C., & DeVolder, A. (2006). Holocene development of boreal forests and fire regimes on the Kenai Lowlands of Alaska. *The Holocene*, *16*(6), 791–803. https://doi.org/10.1191/0959683606hol966rp

Ascoli D. (2015). *Picea glauca masting data across North America (Version 1)*. Figshare. https://doi.org/10.6084/m9.figshare.8870288.v1

Ascoli, D., Maringer, J., Hacket-Pain, A., Conedera, M., Drobyshev, I., Motta, R., … Vacchiano, G. (2017). Two centuries of masting data for European beech and Norway spruce across the European continent. *Ecology*, *98*(5), 1473. https://doi.org/10.1002/ecy.1785

Ascoli, D., Vacchiano, G., Maringer, J., Bovio, G., & Conedera, M. (2015). The synchronicity of masting and intermediate severity fire effects favors beech recruitment. *Forest Ecology and Management*, *353*, 126–135. https://doi.org/10.1016/J.FORECO.2015.05.031

Ascoli, D., Vacchiano, G., Turco, M., Conedera, M., Drobyshev, I., Maringer, J., … Hacket-Pain, A. (2017). Inter-annual and decadal changes in teleconnections drive continental-scale synchronization of tree reproduction. *Nature Communications*, *8*(1), 2205. https://doi.org/10.1038/s41467-017-02348-9

Baisan, C. H., & Swetnam, T. W. (1990). Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, U.S.A. *Canadian Journal of Forest Research*, *20*, 1559–1569. https://doi.org/10.1139/x90-208

Beck, K. K., Fletcher, M.-S., Gadd, P. S., Heijnis, H., & Jacobsen, G. E. (2017). An early onset of ENSO influence in the extra-tropics of the southwest Pacific inferred from a 14, 600 year high resolution multi-proxy record from Paddy's Lake, northwest Tasmania. *Quaternary Science Reviews*, *157*, 164–175. https://doi.org/10.1016/j.quascirev.2016.12.001

Beverly, J. L., Flannigan, M. D., Stocks, B. J., & Bothwell, P. (2011). The association between Northern Hemisphere climate patterns and interannual variability in Canadian wildfire activity. *Canadian Journal of Forest Research*, *41*, 2193–2201. https://doi.org/10.1139/x11-131

Bogdziewicz, M., Żywiec, M., Espelta, J. M., Fernández-Martinez, M., Calama, R., Ledwoń, M., … Crone, E. E. (2019). Environmental veto synchronizes mast seeding in four contrasting tree species. *The American Naturalist*, *194*(2), 246–259. https://doi.org/10.1086/704111

Bond, W. J., & Scott, A. C. (2010). Fire and the spread of flowering plants in the Cretaceous. *New Phytologist*, *188*(4), 1137–1150. https://doi.org/10.1111/j.1469-8137.2010.03418.x

Brunner, F. S., Deere, J. A., Egas, M., Eizaguirre, C., & Raeymaekers, J. A. M. (2019). The diversity of eco-evolutionary dynamics: Comparing the feedbacks between ecology and evolution across scales. *Functional Ecology*, *33*(1), 7–12. https://doi.org/10.1111/1365-2435.13268

Bunn, A. G. (2008). A dendrochronology program library in R (dplR). *Dendrochronologia*, *26*(2), 115–124. https://doi.org/10.1016/j.dendro.2008.01.002.

Canadian Forest Service. (2017). *Canadian national fire database – Agency fire data*. Edmonton, Canada: Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre.

Cazelles, B., Chavez, M., Berteaux, D., Ménard, F., Vik, J. O., Jenouvrier, S., & Stenseth, N. C. (2008). Wavelet analysis of ecological time series. *Oecologia*, *156*(2), 287–304. https://doi.org/10.1007/s00442-008-0993-2

Chechina, M., & Hamann, A. (2019). Climatic drivers of dipterocarp mass-flowering in South-East Asia. *Journal of Tropical Ecology*, *35*(3), 108–117. https://doi.org/10.1017/S0266467419000087

Dai, A. (2011). Characteristics and trends in various forms of the Palmer Drought Severity Index during 1900–2008. *Journal of Geophysical Research: Atmospheres*, *116*(D12), 1900–2008. https://doi.org/10.1029/2010JD015541

Eichler, A., Tinner, W., Brütsch, S., Olivier, S., Papina, T., & Schwikowski, M. (2011). An ice-core based history of Siberian forest fires since AD 1250. *Quaternary Science Reviews*, *30*(9–10), 1027–1034. https://doi.org/10.1016/J.QUASCIREV.2011.02.007

Enfield, D. B., Mestas-Nunez, A. M., & Trimble, P. J. (2001). The Atlantic Multidecadal Oscillation and its relation to rainfall and river flows in the continental U. S. The Atlantic multidecadal oscillation and its relation to rainfall and river flows in the continental U. S. *Geophysical Research Letters*, *28*(10), 2077–2080. https://doi.org/10.1029/2000GL012745

Fauria, M. M., & Johnson, E. A. (2006). Large-scale climatic patterns control large lightning fire occurrence in Canada and Alaska forest regions. *Journal of Geophysical Research*, *111*, G04008. https://doi.org/10.1029/2006JG000181

Fava, F., & Colombo, R. (2017). Remote sensing-based assessment of the 2005–2011 bamboo reproductive event in the arakan mountain range and its relation with wildfires. *Remote Sensing*, *9*(1), 85. https://doi.org/10.3390/rs9010085

Forchhammer, M. C., & Post, E. (2004). Using large-scale climate indices in climate change ecology studies. *Population Ecology*, *46*(1), 1–12. https://doi.org/10.1007/s10144-004-0176-x

Frey, B. R., Ashton, M. S., McKenna, J. J., Ellum, D., & Finkral, A. (2007). Topographic and temporal patterns in tree seedling establishment, growth, and survival among masting species of southern New England mixed-deciduous forests. *Forest Ecology and Management*, *245*(1–3), 54–63. https://doi.org/10.1016/J.FORECO.2007.03.069

Galipeau, C., Kneeshaw, D. D., & Bergeron, Y. (1997). White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. *Canadian Journal of Forest Research*, *27*(2), 139–147. https://doi.org/10.1139/x96-148

Gea-Izquierdo, G., Viguera, B., Cabrera, M., & Cañellas, I. (2014). Drought induced decline could portend widespread pine mortality at the xeric ecotone in managed mediterranean pine-oak woodlands. *Forest Ecology and Management*, *320*, 70–82. https://doi.org/10.1016/j.foreco.2014.02.025

Gouhier, T., Grinstead, A., & Simko, V. (2016). *Conduct univariate and bivariate wavelet analyses*. Retrieved from https://github.com/tgouhier/biwavelet

Greene, D. F., Macdonald, S. E., Haeussler, S., Domenicano, S., Noël, J., Jayen, K., … Swift, L. (2007). The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. *Canadian Journal of Forest Research*, *37*(6), 1012–1023. https://doi.org/10.1139/X06-245

Greene, D., Wiorin, H., Charron, I., Zasada, J., Sirois, L., Kneeshaw, D., … Simard, M. (1999). A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research*, *29*(6), 824–839. https://doi.org/10.1139/cjfr-29-6-824

Grinsted, A., Moore, J., & Jevrejeva, S. (2004). Application of the cross wavelet transform and wavelet coherence to geophysical time series. *Nonlinear Processes in Geophysics*, *11*, 561–566. https://doi.org/10.5194/npg-11-561-2004

Grissino-Mayer, H. D., Romme, W. H., Floyd, M. L., & Hanna, D. D. (2004). Climatic and human influences on fire regimes of the southern San Juan Mountains, Colorado, USA. *Ecology*, *85*(6), 1708–1724. https://doi.org/10.1890/02-0425

Hacket-Pain, A., Ascoli, D., Berretti, R., Mencuccini, M., Motta, R., Nola, P., … Vacchiano, G. (2019). Temperature and masting control Norway spruce growth, but with high individual tree variability. *Forest Ecology and Management*, *438*, 142–150. https://doi.org/10.1016/J.FORECO.2019.02.014

He, T., Belcher, C. M., Lamont, B. B., & Lim, S. L. (2016). A 350-million-year legacy of fire adaptation among conifers. *Journal of Ecology*, *104*(2), 352–363. https://doi.org/10.1111/1365-2745.12513

Hess, J., Scott, C., Hufford, G., & Fleming, M. (2001). El Niño and its impact on fire weather conditions in Alaska. *International Journal of Wildland Fire*, *10*(1), 1–13. https://doi.org/10.1071/WF01007

Juday, G., Barber, V., & Zasada, J. (2003). A 200-year perspective of climate variability and the response of white spruce in Interior Alaska. In D. Greenland, D. Goodin, & R. Smith (Eds.), *Climate variability and ecosystem response at long term ecological research (LTER) sites* (pp. 226–250). Oxford University Press.

Kasischke, E. S., & Turetsky, M. R. (2006). Recent changes in the fire regime across the North American boreal region—Spatial and temporal patterns of burning across Canada and Alaska. *Geophysical Research Letters*, *33*(9), L09703. https://doi.org/10.1029/2006GL025677

Keeley, J., & Bond, W. (1999). Mast flowering and semelparity in bamboos: The bamboo fire cycle hypothesis. *The American Naturalist*, *154*(3), 383–391. https://doi.org/10.1086/303243

Kitzberger, T., Brown, P. M., Heyerdahl, E. K., Swetnam, T. W., & Veblen, T. T. (2007). Contingent pacific – Atlantic Ocean influence on multicentury wildfire synchrony over western North America. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(2), 543–548. https://doi.org/10.1073/pnas.0606078104

Koenig, W., & Knops, J. (1998). Scale of mast-seeding and tree-ring growth. *Nature*, *396*(6708), 225–226. https://doi.org/10.1038/24293

Krebs, C. J., LaMontagne, J. M., Kenney, A. J., & Boutin, S. (2012). Climatic determinants of white spruce cone crops in the boreal forest of southwestern Yukon. *Botany-Botanique*, *90*(2), 113–119. https://doi.org/10.1139/b11-088

Krebs, C. J., O'Donoghue, M., Taylor, S., Kenney, A. J., Hofer, E. J., & Boutin, S. (2016). Predicting white spruce cone crops in the boreal

forests of southern and central Yukon. *Canadian Journal of Forest Research*, *47*(1), 47–52. https://doi.org/10.1139/cjfr-2016-0180

Lamontagne, J. M., & Boutin, S. (2007). Local-scale synchrony and variability in mast seed production patterns of *Picea glauca*. *Journal of Ecology*, *95*(5), 991–1000. https://doi.org/10.1111/j.1365-2745.2007.01266.x

Levine, A. F. Z., McPhaden, M. J., & Frierson, D. M. W. (2017). The impact of the AMO on multidecadal ENSO variability. *Geophysical Research Letters*, *44*(8), 3877–3886. https://doi.org/10.1002/2017GL072524

Liebhold, A., Koenig, W. D., & Bjørnstad, O. N. (2004). Spatial synchrony in population dynamics. *Annual Review of Ecology, Evolution, and Systematics*, *35*(1), 467–490. https://doi.org/10.1146/annurev.ecolsys.34.011802.132516

Little, E. (1971). *Atlas of United States trees, volume 1, conifers and important hardwoods*. U.S. Department of Agriculture Miscellaneous Publication 1146, 9 pp, 200 maps.

Mariani, M., Holz, A., Veblen, T. T., Williamson, G., Fletcher, M.-S., & Bowman, D. M. J. S. (2018). Climate change amplifications of climate-fire teleconnections in the southern hemisphere. *Geophysical Research Letters*, *45*, 5071–5081. https://doi.org/10.1029/2018GL078294

Maringer, J., Wohlgemuth, T., Hacket-Pain, A., Ascoli, D., Berretti, R., & Conedera, M. (2020). Drivers of persistent post-fire recruitment in European beech forests. *Science of the Total Environment*, *699*, 134006. https://doi.org/10.1016/j.scitotenv.2019.134006

Marod, D., Kutintara, U., Tanaka, H., & Nakashizuka, T. (2002). The effects of drought and fire on seed and seedling dynamics in a tropical seasonal forest in Thailand. *Plant Ecology*, *161*(1), 41–57. https://doi.org/10.1023/A:1020372401313

Mauseth, J. (2014). *Botany: An introduction to plant biology*. Burlington, MA: Jones & Bartlett Publishers.

Michaletz, S. T., Johnson, E. A., Mell, W. E., & Greene, D. F. (2013). Timing of fire relative to seed development may enable non-serotinous species to recolonize from the aerial seed banks of fire-killed trees. *Biogeosciences*, *10*(7), 5061–5078. https://doi.org/10.5194/bg-10-5061-2013

Minor, D. M., & Kobe, R. K. (2017). Masting synchrony in northern hardwood forests: Super-producers govern population fruit production. *Journal of Ecology*, *105*(4), 987–998. https://doi.org/10.1111/1365-2745.12729

Mo, K. C., Schemm, J.-K.-E., & Yoo, S.-H. (2009). Influence of ENSO and the Atlantic multidecadal oscillation on drought over the United States. *Journal of Climate*, *22*(22), 5962–5982. https://doi.org/10.1175/2009JCLI2966.1. Retrieved from http://www.jstor.org/stable/26258412

Moreira, X., Abdala-Roberts, L., Linhart, Y. B., & Mooney, K. A. (2015). Effects of climate on reproductive investment in a masting species: Assessment of climatic predictors and underlying mechanisms. *Journal of Ecology*, *103*(5), 1317–1324. https://doi.org/10.1111/1365-2745.12434

Mysterud, A., Stenseth, N., Yoccoz, N., Ottersen, G., & Langvatn, R. (2003). The response of terrestrial ecosystems to climate variability associated with the North Atlantic Oscillation. In J. Hurrell, Y. Kushnir, G. Ottersen, & M. Visbeck (Eds.), *Geophysical monograph-American geophysical union* (pp. 235–262). Washington, DC: American Geophysical Union.

Nigam, S., & Baxter, S. (2015). Teleconnections. In G. N. North, J. Pyle, & F. Zhang (Eds.) *Encyclopedia of atmospheric sciences* (2nd edn., Vol. *3*, pp. 90–109). Cambridge, MA: Academic Press, Elsevier.

O'Dowd, D. J., & Gill, A. M. (1984). Predator satiation and site alteration following fire: Mass reproduction of alpine ash (*Eucalyptus delegatensis*) in Southeastern Australia. *Ecology*, *65*(4), 1052–1066. https://doi.org/10.2307/1938313

Pearse, I. S., Koenig, W. D., & Kelly, D. (2016). Mechanisms of mast seeding: Resources, weather, cues, and selection. *New Phytologist*, *212*(3), 546–562. https://doi.org/10.1111/nph.14114

Pearse, I., LaMontagne, J., & Koenig, W. (2017). Inter-annual variation in seed production has increased over time (1900–2014). *Proceedings of the Royal Society B: Biological Sciences*, *284*(1868), 20171666. https://doi.org/10.1098/rspb.2017.1666

Peters, V. S., Macdonald, S. E., & Dale, M. R. T. (2005). The interaction between masting and fire is key for white spruce regeneration. *Ecology*, *86*(7), 1744–1750. https://doi.org/10.1890/03-0656

Pickett, S., & White, P. (1985). *The ecology of natural disturbance and patch dynamics*. New York, NY: Academic Press.

Piovesan, G., & Adams, J. M. (2005). The evolutionary ecology of masting: Does the environmental prediction hypothesis also have a role in mesic temperate forests? *Ecological Research*, *20*(6), 739–743. https://doi.org/10.1007/s11284-005-0096-z

Pounden, E., Greene, D. F., & Michaletz, S. T. (2014). Non-serotinous woody plants behave as aerial seed bank species when a late-summer wildfire coincides with a mast year. *Ecology and Evolution*, *4*(19), 3830–3840. https://doi.org/10.1002/ece3.1247

Purdy, B., Macdonald, S., & Dale, M. (2002). The regeneration niche of white spruce following fire in the mixedwood boreal forest. *Silva Fennica*, *36*(1), 289–306. https://doi.org/10.14214/sf.564

R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org

Ran, J.-H., Wei, X.-X., & Wang, X.-Q. (2006). Molecular phylogeny and biogeography of *Picea* (Pinaceae): Implications for phylogeographical studies using cytoplasmic haplotypes. *Molecular Phylogenetics and Evolution*, *41*(2), 405–419. https://doi.org/10.1016/j.ympev.2006.05.039

Roland, C., Schmidt, J., & Johnstone, J. (2014). Climate sensitivity of reproduction in a mast-seeding boreal conifer across its distributional range from lowland to treeline forests. *Oecologia*, *174*(3), 665–677. https://doi.org/10.1007/s00442-013-2821-6

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., … Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, *7*, 395–402. https://doi.org/10.1038/nclimate3303

Selås, V., Piovesan, G., Adams, J. M., & Bernabei, M. (2002). Climatic factors controlling reproduction and growth of Norway spruce in southern Norway. *Canadian Journal of Forest Research*, *32*(2), 217–225. https://doi.org/10.1139/x01-192

Shabbar, A., & Skinner, W. (2004). Summer drought patterns in Canada and the relationship to global sea surface temperatures. *Journal of Climate*, *17*, 2866–2880. https://doi.org/10.1175/1520-0442(2004)017<2866:SDPICA>2.0.CO;2

Shabbar, A., Skinner, W., & Flannigan, M. D. (2010). Prediction of Seasonal Forest Fire Severity in Canada from Large-Scale Climate Patterns. *Journal of Applied Meteorology and Climatology*, *50*(4), 785–799. https://doi.org/10.1175/2010JAMC2547.1

Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S., & Lima, M. (2002). Ecological effects of climate fluctuations. *Science*, *297*(5585), 1292–1296. https://doi.org/10.1126/science.1071281

Strong, C., Zuckerberg, B., Betancourt, J. L., & Koenig, W. D. (2015). Climatic dipoles drive two principal modes of North American boreal bird irruption. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(21), E2795–E2802. https://doi.org/10.1073/pnas.1418414112

Tinner, W., Hu, F., Beer, R., Kaltenrieder, P., Scheurer, B., & Krähenbühl, U. (2006). Postglacial vegetational and fire history: Pollen, plant macrofossil and charcoal records from two Alaskan lakes. *Vegetation History and Archaeobotany*, *15*(4), 279–293. https://doi.org/10.1007/s00334-006-0052-z

Vacchiano, G., Hacket-Pain, A., Turco, M., Motta, R., Maringer, J., Conedera, M., … Ascoli, D. (2017). Spatial patterns and broad-scale weather cues of beech mast seeding in Europe. *New Phytologist*, *215*(2), 595–608. https://doi.org/10.1111/nph.14600

van Mantgem, P. J., Stephenson, N. L., & Keeley, J. E. (2006). Forest reproduction along a climatic gradient in the Sierra Nevada. *California. Forest Ecology and Management*, *225*(1–3), 391–399. https://doi.org/10.1016/j.foreco.2006.01.015

Veraverbeke, S., Rogers, B. M., Goulden, M. L., Jandt, R. R., Miller, C. E., Wiggins, E. B., … Keeley, J. E. (2014). Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist*, *204*(1), 55–65. https://doi.org/10.1111/nph.12921

Williamson, G. B., & Ickes, K. (2002). Mast fruiting and ENSO cycles – Does the cue betray a cause? *Oikos*, *97*(3), 459–461. https://doi.org/10.1034/j.1600-0706.2002.970317.x

Wright, B., & Fensham, R. (2017). Fire after a mast year triggers mass recruitment of slender mulga (*Acacia aptaneura*), a desert shrub with heat-stimulated germination. *American Journal of Botany*, *104*(10), 1474–1483. https://doi.org/10.3732/ajb.1700008

Wright, B., Zuur, A., & Chan, G. (2014). Proximate causes and possible adaptive functions of mast seeding and barren flower shows in spinifex grasses (*Triodia* spp.) in arid regions of Australia. *The Rangeland Journal*, *36*(3), 297–308. https://doi.org/10.1071/RJ13104

Xiao, J., & Zhuang, Q. (2007). Drought effects on large fire activity in Canadian and Alaskan forests. *Environmental Research Letters*, *2*, 044003. https://doi.org/10.1088/1748-9326/2/4/044003

Zasada, J., Sharik, T., & Markku, N. (1992). The reproductive process in boreal forest trees. In H. H. Shugart (Ed.), *A systems analysis of the global boreal forest* (pp. 85–125). New York, NY: Cambridge Univ. Press. https://doi.org/10.1017/CBO9780511565489.004

Zazula, G. D., Telka, A. M., Harington, C. R., Schweger, C. E., & Mathewes, R. W. (2006). New spruce (Picea spp.) macrofossils from Yukon territory: Implications for late Pleistocene refugia in eastern Beringia. *Arctic*, *59*(4), 391–400. https://doi.org/10.14430/arctic288

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Ascoli D, Hacket-Pain A, LaMontagne JM, et al. Climate teleconnections synchronize *Picea glauca* masting and fire disturbance: Evidence for a fire-related form of environmental prediction. *J Ecol*. 2020;108:1186–1198. https://doi.org/10.1111/1365-2745.13308