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TITLE PAGE

The climate, the fuel and the land use: long-term regional variability of biomass burning in boreal forests

Running head: Drivers of Holocene boreal biomass burning

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ABSTRACT

The influence of different drivers on changes in North American and European boreal forests biomass burning (BB) during the Holocene was investigated based on the following hypotheses: land use was important only in the southernmost regions, while elsewhere climate was the main driver modulated by changes in fuel type. BB was reconstructed by means of 88 sedimentary charcoal records divided into six different site clusters. A statistical approach was used to explore the relative contribution of (1) pollen-based mean July/summer temperature and mean annual precipitation reconstructions, (2) an independent model-based scenario of past land use (LU), and (3) pollen-based reconstructions of plant functional types (PFTs) on BB. Our hypotheses were tested with: (1) a west-east northern boreal sector with changing climatic conditions and a homogeneous vegetation, and (2) a north-south European boreal sector characterized by gradual variation in both climate and vegetation composition.

The processes driving BB in boreal forests varied from one region to another during the Holocene. However, general trends in boreal biomass burning were primarily controlled by changes in climate (mean annual precipitation in Alaska, northern Quebec and northern Fennoscandia, and mean July/summer temperature in central Canada and central Fennoscandia) and, secondarily, by fuel composition (BB positively correlated with the presence of boreal needleleaf evergreen trees in Alaska and in central and southern Fennoscandia). Land use played only a marginal role. A modification towards less flammable tree species (by promoting deciduous stands over fire-prone conifers) could contribute to reduce circumboreal wildfire risk in future warmer periods.

INTRODUCTION

The circumboreal forest is the second largest terrestrial biome in the world, currently containing *ca* 33% of the global forest cover (FAO, 2001), and the main stock of continental carbon (Scharlemann et al., 2014). Fire is the primary process which organizes the physical and biological attributes of the boreal biome over most of its range, including diversity and biogeochemistry (White Paper Science Team, 2015), although the response and pattern vary across continents and regions with important differences between North America and Eurasia (Lehsten et al., 2014; Rogers et al., 2015). The boreal forest composition can be altered by changes in fire frequency, size and severity (Chen et al., 2009; Johnstone et al., 2010), whereas the transformed plant cover can provide a different fuel composition that subsequently feeds new fire regimes (D'Antonio & Vitousek, 1992; Higuera et al., 2009; Girardin et al., 2013). Fire has also the potential to consume significant portions of the soil carbon pool and to release this carbon into the atmosphere, with consequences for greenhouse gas concentrations and thus for the global climate (Bergstrom et al., 2007; Bond-Lamberty et al., 2007; Abbott et al., 2016).

Due to their location at climatically sensitive high northern latitudes, the circumboreal regions have been suggested to be significantly affected by the on-going anthropogenic global warming (IPCC, 2014), with a subsequent increase in the frequency, intensity and areal extent of fires (Soja et al., 2007; Flannigan et al., 2009a). Furthermore, the occurrence of dry hot summers characterized by high pressure followed by thunderstorms without accompanying rains might increase the chance of lightning, the only natural cause of fire ignition in boreal forests (Stocks et al., 2003; Kasischke et al., 2010; Rolstad et al., 2017; Veraverbeke et al., 2017).

Even though these regions are still sparsely populated in comparison to other mid- and low-latitudinal ecosystems, humans have played an important role in the diversification of boreal fire regimes on the timescales of decades to centuries (Sanderson et al., 2002). The human influence has varied regionally and included slash-and-burn cultivation practices, agricultural deforestation, wood production and intentional burning to improve grazing habitat (Niklasson & Granström, 2000; Drobyshev et al., 2004; Flannigan et al., 2009b). While today fire plays a minor role in European boreal forests due to aggressive fire suppression policies (Granström & Niklasson, 2008; Halme et al., 2013), North America has still huge tracts of unmanaged boreal forests that include large burned areas (Gauthier et al., 2015; Parisien et al., 2016).

Scientists and policy makers need a long-term view of biomass burning variability to place modern fire processes and management in a meaningful context (Girardin et al., 2013). Palaeoecological research can help elucidate the main processes of changes in biomass burning (hereafter BB) by providing records of fire occurrence at stand to regional scales and at decadal to millennial scales (Gavin et al., 2007). It can therefore offer an important reference for ecosystem-based strategies aimed at maintaining ecological processes, habitats and species (Willis & Birks, 2006). Even if the future might not resemble any time in the past (Jackson & Williams, 2004), a better understanding of processes causing the variability observed in palaeorecords is fundamental for improving the ability to manage ecosystems during current and future environmental changes (Flessa et al., 2005; Bergeron et al., 2010). Society's perception has begun to change in boreal regions as forest policies have progressed from fire suppression to prescribed burning in order to use fire as a tool for ecosystem management (Ward & Mawdsley, 2000; Granström, 2001).

Within this context, BB in North American and European boreal forests during the last 11,000 years was reconstructed based on sedimentary charcoal records, divided into six different site clusters (Figure 1). The relative role of temperature, precipitation, plant functional types and land use on the historical geography of BB was tested by means of a statistical approach. Asian boreal forests were not taken into account due to the low persistent number of charcoal records available for this area (Hawthorne et al., 2018).

Three hypotheses were proposed (Figure 1): (H1) climate drove Holocene trends in BB in regions with the same fuel type (e.g., needleleaf/tundra dominance); (H2) climate-controlled patterns of Holocene BB were mitigated at a regional scale by trees' flammability; (H3) land use had a limited explanatory power during most of the Holocene, except for the southernmost European boreal regions concerned by farming practices. An alternative hypothesis would be that each region displays its own temporal trend under the complex effect of plant migrations, trajectories of precipitation pattern or interaction between temperature and precipitation, which control the evapotranspiration and thus fuel moisture, and biomass productivity and accumulation.

The use of a west-east northern boreal sector based on four site clusters from Alaska to northern Fennoscandia enabled testing our hypotheses with a different climatic pattern, a rather homogeneous vegetation dominated by tundra shrubs/trees and boreal needleleaf evergreen trees and an evenly low importance of land use, while a north-south European boreal sector of three site clusters from northern to southern Fennoscandia provided the opportunity to explore our hypotheses with a dataset characterized by a gradual variation in climate, a change in vegetation composition from boreal needleleaf evergreen trees in the north to boreal and cool-temperate broadleaf trees in the south, and a progressive increase towards the south of land use importance (Figure 1). This experimental design permitted a large-scale investigation of the most important biome on Earth for the linkage between fire and the carbon budget (Kasischke & Stocks, 2000).

MATERIALS AND METHODS

Records of past biomass burning activity

Charcoal data from 88 sedimentary series located within the boreal biome (a transcontinental circumpolar band situated approximately between 50^{o}N and 70^{o}N latitude; Figure 2 and S1) and covering part or all of the Holocene were selected from the latest version of the Global Charcoal Database (GCD v3, Marlon et al., 2016) compiled by the Global Palaeofire Working Group (GPWG, www.paleofire.org) and from regional syntheses (Molinari et al., 2013; Clear et al., 2014). Where multiple records (i.e., macro and micro-charcoal data) were available from the same site, all were included in the dataset.

The good geographical coverage of charcoal records from North America and Europe provides an excellent basis for reconstructing broad-scale changes in boreal forests BB. In order to examine the spatio-temporal patterns of changes, the study region was divided into six site clusters (Figs. 1 & 2): Alaska, central Canada (east of the Canadian cordillera and west of the Hudson Bay: from Northwest Territories to western Ontario), northern Quebec, northern Fennoscandia, central Fennoscandia and southern Fennoscandia. In Fennoscandia, sites are from Norway, Sweden, Finland and western Russia.

After selection, all charcoal records were first converted to a common time scale in calibrated years before present (hereafter cal yr BP), following the protocol described in Power et al. (2008) by using either the original authors' published chronology or new age-depth models created using the median calibrated radiocarbon age. All charcoal data were then transformed to influx values (CHAR, i.e., the number, area or weight of particles.cm^{-2}.yr^{-1}). In order to allow comparisons within and between charcoal records obtained from heterogeneous depositional environments and quantified with different laboratory techniques, a standardization procedure was required including a min-max rescaling of CHAR values followed by a Box-Cox transformation to homogenize the within-records variance (Power et al., 2008). Finally, a Z-score transformation was carried out using a base period most representative of the entire dataset (i.e,. the interval between 4000 and 200 cal yr BP), excluding the industrial period due to the very different trends in charcoal records (Marlon et al., 2008). Although the base period only extended to 200 cal yr BP, the majority of the charcoal records extended up to the present time (-60 yr BP, where CE 1950 = 0 yr BP). In order to reduce the influence of records with high sample resolution and to avoid data interpolation for records with a lower resolution, transformed charcoal data from each site (hereafter tCHAR) were then bootstrap re-sampled 999 times with a moving window procedure using non-overlapping bins of 50-years. Re-sampled series were then aggregated and smoothed by fitting a locally weighted regression with a 500-year half window width. Regional charcoal composite series mean and 90% confidence intervals were calculated by averaging the smoothed and bootstrapping series (Daniau et al., 2012). A smoother with a 250-year bandwidth was calculated for highlighting higher-frequency trends in the tCHAR series. Composite curves for this study were produced with the method implemented in the *R* (R Core Team, 2016) package *paleofire* (Blarquez et al., 2014).

A pairwise correlation between tCHAR *Z*-scores was performed to test if proximal sites had a high correlation coefficient compared with distant sites, for an estimation of the spatial dependence between Holocene trends in BB. Because each record had a different time-span and resolution, we trimmed the temporal extent for each pair of sites to the overlapping period and interpolated tCHAR Z-scores at 100 years temporal resolution.

Palaeoclimate reconstructions

Regional climate changes in boreal forests through the Holocene were reconstructed based on the literature (see S2 for details). Mean July temperature anomalies and mean annual precipitation anomalies for North America were provided by Viau et al. (2006) and Viau & Gajewski (2009), while Mauri et al. (2015) provided pollen-based quantitative reconstruction of summer (JJA) temperature and precipitation anomalies for the European sites. All authors used the Modern Analogue pollen-climate calibration Technique (MAT, Overpeck et al., 1985; Guiot, 1990) for their reconstructions and included a series of sensitivity tests and quality control checks. Confidence intervals were estimated based on the transfer function uncertainties (for more information see Viau et al., 2006 and Mauri et al., 2015 in SI). For North America, modern pollen data were derived from the Brown University dataset (Avizinis & Webb, 1995) and fossil pollen data were compiled from the North American Pollen database (NAPD). For the European sites, surface samples were obtained from the European Modern Pollen Database (EMPD) and fossil pollen data were compiled from the European Pollen Database (EPD). Chronological control was based on individually fitted age-depth models created for each pollen time series based on a calibrated radiocarbon time-scale. Radiocarbon dates were calibrated using the INTCAL98 (Stuiver et al., 1998) for North American series and the OXCAL3.5 program (Bronk Ramsey, 2001) for the European pollen time series.

For this study, palaeoclimate data were expressed as standardized deviation (Z-scores) from the mean values for the period between 4000 and 200 cal yr BP. Only climate records located less than 200 km away from a selected charcoal record were taken into consideration (Figure 2). Composite time series were then created by averaging across all selected sites in each sector and cluster, with a resolution of 100 years (Figure 3). Chronological uncertainties were within the range of radiocarbon dates' uncertainties used to establish the age-depth models for each individual record. The decreasing site density in older periods resulted in less confident reconstructions during the early Holocene.

Reconstruction of land use

The Kaplan & Krumhardt anthropogenic land cover change scenario (KK10, Kaplan et al., 2011) was used to estimate the importance of land use (hereafter LU) on BB between 8000 cal yr BP and the present time at each selected site (Figure 2). KK10 estimates the spatial and temporal pattern of anthropogenic land cover change on the basis of population and properties of the physical environment, employing an empirically derived non-linear model to quantify the relationship between population density and LU. The environmental variables controlling the spatial pattern of LU (climate, soil type and slope) represent the 20th century conditions and are static in time. LU represents land primarily used for agriculture and animal production (pasture and open rangelands), and occurs only where climate and soil properties support these uses (Kaplan et al., 2009). For this reasons, although we acknowledged that hunter-gatherers/foragers were widely distributed across Northern Hemisphere high-latitudes in the early Holocene and that these people might have used fire as an important part of their hunting and gathering strategy, LU in the boreal biome was assumed to be insignificant before 8000 BP. Furthermore, since the KK10 scenario neither considers rangelands for subarctic animals (e.g., reindeers) nor managed forests among the land uses, LU in the boreal biome is constrained to the warmer parts of the region. For this study, we generated composite LU time series by averaging across all pixels co-located with the selected charcoal records in each sector and cluster, with a temporal resolution of 100 years (Figure 4).

Reconstruction of vegetation composition

For an estimation of major changes in vegetation composition through time, fossil pollen data available from the same site or from a site located not more than 100 km away from a charcoal record (Figure 2) were extracted from the *Neotoma* database (www.neotomadb.org) or from the literature by digitizing the published diagrams using the program DATA MUGGER 1.1 (Jones, 2011; see S3 for more information). Mean pollen percentages at 1000 years intervals were calculated for each selected site. In our analyses, chronological uncertainties were within the range of radiocarbon dates' uncertainties used to establish the age-depth models for each individual record.

Pollen percentages threshold values proposed by Davis & Jacobson (1985), Davis et al. (1991), Pardoe (2001) and Lisitsyna et al. (2011) were used to establish the presence of a particular species within approximately 50 km from the study site on the basis of its pollen proportion in the sediment (S4, Table S1). For each taxon, pollen percentages below the threshold values were not taken into consideration. Corrections factors were then applied in order to achieve a closer approximation to vegetation cover (S4, Table S2). For the calculation of the correction factors we followed Binney et al. (2011). This method is a simplification of the REVEALS model (Sugita, 2007) that takes into account the different production and dispersal of pollen among taxa. As a final step, the percentage cover of different plant functional types (hereafter PFTs, Table 1) was calculated for each single site taken into consideration. Taxa division in different groups of PFTs followed Prentice et al. (1996) and Williams et al. (1998). In order to visualize long-term changes in North American and European boreal forest PFTs, eight time series were then created by averaging across all selected sites in each sector and cluster with a 1000 years temporal resolution.

Statistical analyses of proxy time series

The *R* package *relaimpo* provides several metrics for assessing the relative importance of predictors in linear models (Grömping, 2006). For our analyses, we firstly used the *relaimpo* package to calculate the importance of climate variability (mean July [for North America] or summer [for Fennoscandia] temperature anomalies and mean annual precipitation anomalies) and LU on BB over the Holocene (expressed as tCHAR Z-scores). The choice of using a linear model instead of a more elaborate technique was mainly due to its high interpretability (most users are acquainted with this technique). Furthermore, the (relatively low) amount of data did not allow using a more advanced method (i.e., GAM, which would have required an explicit estimation of distributions). For these analyses, all the data were expressed as standardized deviations (Z-scores) from the mean values over the period between 4000 and 200 cal yr BP. For each sector and cluster, the analyses were performed by comparing the previously constructed composite time series (Figs. 3 & 4) with the charcoal composite curves (Figure 6), with a temporal resolution of 100 years.

In a second step, we used the *relaimpo* package to estimate the relative importance of changes in major vegetation cover expressed as PFTs groups on Holocene BB. In this case, due to the lower temporal resolution (i.e., 1000 years) and the consequent lower data availability, the analyses were not performed on composite time series. Here we compared mean tCHAR Z-scores and mean percentage cover of different PFTs at 1000 years intervals, by grouping together the sites included in the same sector or cluster.

To select the "optimal" model given all possible sets of predictors, we used the Akaike's Information Criterion (AIC) values (Akaike, 1973). AIC incorporates both model fit and model complexity, with more complex models being penalised relative to simpler ones; better models have lower AIC values relative to others in the same candidate set (Anderson, 2008; Zuur et al., 2009). Given the small number of predictors, we generated all possible models and the one with the lowest AIC value was selected. In case of two correlated predictors, this method chose the one which resulted in a better model.

As we performed multiple tests based on the same dataset, we increased the rate of type I error. To control this error rate, we thus adjusted the *p*-values by using the Holm-Bonferroni correction (Holm 1979), a standard procedure which incrementally decreases the α levels to reach significance.

Since our datasets were a set of composite curves or a set of PFTs percentages with the related tCHAR Z-scores per site, some of the co-variates were unavoidably correlated to some extent with each other and this questioned the levels of the *p*-values. This has been further considered in S5. Despite methodological difficulties, the use of the AIC allowed the selection of the model with the highest information content and the removal of variables that were correlated to another covariate but that did not increase the model's performance. However, during the evaluation of our results it has to be kept in mind that – to some degree – it was impossible to avoid violating the assumption of independence between covariates.

RESULTS

Holocene trends in boreal forests biomass burning

The pairwise correlation analysis performed between tCHAR Z-scores (Figure 5) did not show higher correlation coefficients between proximal sites compared to distant sites. It was thus possible to discard a spatial dependence Holocene trends in BB.

The composite charcoal curves (Figure 6) documented the changing spatial and temporal patterns in North American and European boreal forests BB during the Holocene. The reconstruction of BB across each selected sector and cluster showed different trajectories during the recorded time span.

After a minimum *ca* 10,000 cal yr BP (with large uncertainties), the northern boreal sector (Figure 6a) was characterized by a general increase in BB until *ca* 5500 cal yr BP. A plateau was registered between 5000 and 2000 cal yr BP, followed by a decrease *ca* 1500 cal yr BP. Since this period onwards BB rose again, with maximum values during recent times.

The European boreal sector (Figure 6b) showed low but increasing values of BB at the beginning of the Holocene (a time characterized by high uncertainties). After a peak at 10,500 cal yr BP, a minimum was reached *ca* 9700 cal yr BP. Then BB increased until 7500 cal yr BP. The following 5000 years were characterized by values below the long-term mean. Since 1000 cal yr BP, BB increased continuously, reaching a maximum at the present time.

Regarding the clusters, in Alaska (Figure 6c) BB was characterized by low values during the early Holocene, with a minimum *ca* 10,000 cal yr BP. A monotonic increase was recorded throughout the whole Holocene, until a first maximum *ca* 2100 cal yr BP. The last 250 years showed a sharp rise in BB.

Due to the late retreat of the Laurentide Ice Sheet cover in central and eastern Canada (Dyke, 2004), charcoal records from these regions only spanned the last 8300 and 7300 cal yr BP, respectively. BB in central Canada (Figure 6d) was low during the period 8300-7200 cal yr BP. Then it reached a maximum between 6400 and 5400 cal yr BP. The following millennium was marked by a decrease, with a minimum at 4000 yr BP. BB remained low until 1500 cal yr BP, and increased slightly during the last 1000 years.

In northern Quebec (Figure 6e), BB was low at the beginning of the recorded period, while an increase began from 6600 cal yr BP, with a maximum between 6200 and 4800 cal yr BP (with large uncertainties). Then BB decreased to attain a plateau during the period 4500-1500 cal yr BP. Since 1500 cal yr BP, BB decreased again, reaching a minimum *ca* 200 cal yr BP. A rise was recorded in the last *ca* 150 years.

In northern Fennoscandia (Figure 6f), BB was characterized by low values (with large uncertainties) at the beginning of the Holocene. Then BB progressively increased, reaching a peak *ca* 8000 cal yr BP. After that, the composite charcoal curve showed low values between 7500 and 5500 cal yr BP. Despite some oscillations, from this time onwards BB presented a progressive increase and reached maximum values during recent centuries.

In central Fennoscandia (Figure 6g), the composite charcoal curve showed high and low values during the early Holocene. A minimum was reached *ca* 9700 cal yr BP and a maximum *ca* 8700 cal yr BP, both with large uncertainties. After that BB presented a monotonic but slight decrease, remaining below the long term mean until 2500 cal yr BP. Since 1700 cal yr BP, BB was marked by an important increase, with a maximum at the present time.

BB in southern Fennoscandia (Figure 6h) oscillated between 11,000 and 4000 cal yr BP (with large uncertainties), with two maxima *ca* 9000 and *ca* 7500 cal yr BP, and three minima *ca* 8300, *ca* 6500, *ca* 4000 cal yr BP. Since this last minimum onwards, BB started to progressively increase, with a maximum *ca* 300 cal yr BP. A downturn was recorded during the last 250 years.

Biomass burning versus *climate and land use*

For each sector and cluster, the AIC models were tested with various sets of climatic (mean July [for North America] or summer [for Fennoscandia] temperature and mean annual precipitation) and land use (LU) combinations. The model with the smallest AIC score (i.e., the “optimal model”) was selected as the most appropriate in explaining the regional variation in BB during the Holocene.

The results (Figure 7; S6, Table S1) showed that, in the northern boreal sector, BB was mainly related to mean July/summer temperature (positively) and to mean annual precipitation (negatively), while in the European boreal sector BB tended to significantly increase during periods characterized by low annual precipitation, and *vice versa*.

At the cluster level, mean July/summer temperature was correlated with multi-millennial BB variability in Alaska (positively), central Canada (positively) and in central Fennoscandia (negatively). Additionally, the analyses underlined the general negative relationship between mean annual precipitation values and BB in Alaska, northern Quebec and in northern Fennoscandia. A positive relationship between long-term trends of BB and LU was identified only in southern Fennoscandia. Due to the fact that the models for the European boreal sector and for southern Fennoscandia were not significant when corrected for multiple testing, these results have to be cautiously considered.

Holocene trajectories of plants functional types

Reconstructions of changes in major boreal forest composition based on PFTs in North America and Europe showed different trajectories during the Holocene (Figure 8). Despite that, the common pattern was the increase in boreal needleleaf evergreen trees (NE), except for central Canada where the values remained rather steady since 8000 cal yr BP.

The northern boreal sector (Figure 8a) was dominated by needleleaf/broadleaf deciduous trees/shrubs (NBD) during the early and mid-Holocene, while – since 4500 cal yr BP – this PFT was progressively replaced by NE. Low amounts of boreal evergreen shrubs (ES) were present during the whole time period recorded, with a maximum during the last millennia.

The European boreal sector (Figure 8b) was dominated by NBD between 11,000 and 10,000 cal yr BP. After this period onwards, NE was the main functional type. ES and cool temperate broadleaf trees (TB) were present throughout the whole Holocene. ES were characterized by a peak at the beginning Holocene and by a monotonic increase since 4000 cal yr BP, while TB reached a maximum between 7000 and 6000 cal yr BP and then progressively decreased until the present time.

At the cluster level, in Alaska (Figure 8c) the entire Holocene was characterized by the dominance of NBD, in this case mainly shrubs and trees species typical of tundra vegetation. The early Holocene was dominated by *Betula*, *Salix* and *Populus*, with little abundance of NE (*Picea glauca*). During the following millennium, *Alnus* progressively replaced *Populus*, and *Picea mariana* immigrated into the area. From 6000 cal yr BP onwards there was an increase in NE (*Picea mariana* and *P. glauca*) in a landscape always dominated by NBD (mainly *Betula* and *Alnus*). During the last 2000 years the presence of ES (Ericaceae) was also recorded, but with low percentages.

Central Canada (Figure 8d) was dominated by NE during the entire period taken into consideration. While until 5000 cal yr BP the forest cover was mainly composed by *Picea glauca* and *Pinus*, from this time onwards *Picea mariana* progressively substituted *P. glauca*. The presence of NBD (*Alnus* and *Betula*) was relatively low but constant throughout the Holocene, with a small decrease during the last two millennia. Between 5000 and 7000 cal yr BP and during the last 1000 years ES (Ericaceae) increased.

In northern Quebec (Figure 8e) NBD (*Betula* and *Alnus*) dominated the forest cover between 7300 (i.e., the beginning of the recorded period) and 5000 cal yr BP. Since this period onwards the landscape was characterized by the dominance of NE (mainly *Picea mariana*). ES (mainly Ericaceae) were recorded throughout the entire recorded time frame, but with low percentages compared to other PFTs.

In Northern Fennoscandia (Figure 8f) the entire Holocene was dominated by NE (mainly *Pinus* and, during the last 4000 years, *Picea*). Despite some oscillations, a monotonic increase was recorded both in NE and ES (dominated by Ericaceae, with low percentages of *Juniperus*). NE reached a maximum around 1000 cal yr BP, and then slightly decreased. A constant decline in NBD (mainly *Betula*) was observed.

In central Fennoscandia (Figure 8g) the early Holocene was characterized by the dominance of NBD (mainly *Betula* and *Salix*, with small abundance of *Populus*), followed by ES (Ericaceae, with low percentages of *Juniperus*), NE (*Pinus*) and TB (*Corylus* and *Ulmus*). Since 10,000 cal yr BP NE (*Pinus* before 7000 cal yr BP, and *Pinus* and *Picea* afterwards) started to increase, reaching a maximum during the present time (dominated by *Picea*, with less *Pinus*). In comparison, NBD (mainly *Betula* and *Alnus* with little abundance of *Populus*) and ES constantly decreased throughout the Holocene, with just a small increase in ES during the last millennium. TB (mainly *Corylus* and *Tilia*) were characterized by low percentages during the entire Holocene, with a maximum between 6000 and 5000 cal yr BP.

Between 11,000 and 6000 cal yr BP southern Fennoscandia (Figure 8h) was dominated by NE (*Pinus*), followed by NBD (mainly *Betula* with small percentages of *Alnus*), TB (mostly *Corylus* and *Quercus*) and ES (Ericaceae with low amounts of *Juniperus*). The subsequent two millennia were characterized by a decrease in NE (*Pinus* with less abundance of *Picea*), and NBD (*Betula*, *Alnus* and *Populus*) dominated the forest cover. During this period TB decreased, while ES increased. Since 4000 cal yr BP onwards NE rose again, with a maximum at the present time (dominated by *Pinus*, with *Picea*). During the last millennium TB (mainly *Quercus* and *Corylus*) reached their minimum, while a peak was recorded in ES (Ericaceae).

Biomass burning versus *plant functional types*

For each sector and cluster, the AIC models were tested with various sets of PFTs combinations and the model with the smallest AIC score (i.e., the "optimal model") was selected as the most appropriate in explaining the regional variation in BB during the Holocene.

The results (Figure 9; S6, Table S2) showed that in the northern boreal sector Holocene BB was negatively correlated to the presence of needleleaf/broadleaf deciduous trees/shrubs (NBD) and positively correlated to the occurrence of evergreen shrubs (ES). In the European boreal sector BB tended to significantly increase during periods characterized by a higher percentage of needleleaf evergreen trees (NE) and ES.

At the cluster level, NE were positively related with multi-millennial variability of BB in Alaska, and in central and southern Fennoscandia. This relationship also existed for central Canada but – due to the fact that the model was not significant when corrected for multiple testing – this result has to be prudently considered. Furthermore, BB tended to be higher during periods characterized by a higher proportion of ES in northern Fennoscandia, although the model was not significant when corrected for multiple testing. No correlation between long-term trends of BB and changes in vegetation composition was found in northern Quebec.

DISCUSSION

The present study of Holocene boreal forests biomass burning has taken into consideration a broad spatial and temporal scale, and has explored the linkages between fire and climate components, fuel type and anthropogenic land cover change by means of a statistical approach. By considering six different site clusters and two different sectors, our results have underlined the spatial and temporal variability in BB existing within the boreal biome and have allowed a better understanding of the most important processes responsible for main changes in fire activity in these regions. However, additional high-resolution analyses of charcoal series from regions inadequately represented by the present dataset (i.e., most of all, Asia) are needed. It is in fact obvious that, despite the small amounts of data presently included in the GCD v3 from these areas (Hawthorne et al., 2018), fire in Asian boreal forests has major ecosystem and global environmental consequences by contributing to the global carbon budget.

Functional role of climate on biomass burning

Northern boreal sector Warmer summers and/or drier conditions were generally associated with higher BB in this sector during the Holocene. However, not all clusters presented the same relation to climatic components. While in Alaska both high summer temperature and low annual precipitation explained variations in BB, in northern Quebec and in northern Fennoscandia dryness seemed to be a prerequisite for increasing BB. In comparison, in central Canada – that is a dry area – only temperature drove BB, whatever the precipitation trend (generally low). This non-uniform behavior of the relationship between climate components and BB was previously reported in a global investigation of changes in boreal fire activity during the 20th century (Girardin et al., 2009). The functional role of precipitation highlighted by our analysis differs substantially from the conclusions reached by Daniau et al. (2012), indicating a global millennial scale effect of temperatures since the Last Glacial Maximum. In boreal ecosystems (basically characterized by cold climate conditions with a rather short fire season) precipitations strongly affected BB, with the exception of dry regions. Temperature (not necessarily with higher values) acted as a secondary climatic driver if dryness was supported by arctic cold air masses (Carcaillet & Richard, 2000).

European boreal sector BB was chiefly controlled by mean annual precipitation values in northern Fennoscandia (negative relationship) and by mean summer temperatures in central Fennoscandia (negative relationship), while climatic conditions were not significant statistical drivers in the southernmost areas. The low BB during the early Holocene in the northern regions was likely to be the result of the stronger flow of moist and warm Atlantic air masses into this area until *ca* 9000 cal yr BP (Hammarlund et al., 2002). The following increase in BB benefitted from dry summers registered between 8500 and 6500 cal yr BP (Seppä & Birks, 2001; Rosén et al., 2001), while the wetter conditions during the following 4000 years (Calvo et al., 2002; Kultti et al., 2006) were associated with a decrease in BB. The negative correlation between Holocene BB and summer temperatures in central Fennoscandia was probably connected to changes in fuel type that offset the influence of climate, as already suggested by Brown & Giesecke (2014).

Functional role of fuel type on biomass burning

Northern boreal sector Although a strong negative correlation was underlined between boreal needleleaf/broadleaf deciduous trees and shrubs (NBD) and Holocene BB for this sector, at the cluster level the results were rather different.

In particular, long-term BB activity in Alaska was explained by changes in boreal needleleaf evergreen trees (NE), mainly dominated by *Picea mariana* with small amounts of *Picea glauca*. Previously site-specific studies (e.g. Lynch et al., 2003; Higuera et al., 2009; Brubaker et al., 2009) supported this observation, documenting an increase in fire activity in association with the east-west migration of the highly flammable *Picea mariana*, regardless of the specific time of its increase during the Holocene (Hu et al., 2006).

NE also showed a positive correlation with BB in central Canada, but there the strength of the relationship was limited. In this region, the progressive replacement of the tundra vegetation with *Picea glauca*, *P. mariana* and *Pinus banksiana* during the early and mid-Holocene probably caused a rise in BB by providing more flammable fuel, whatever the f composition. Insteaad, the decline in *Picea mariana* and *Pinus banksiana* around 5500 BP and 2000 BP led to a decrease in BB.

In accordance with previous site-specific investigations (Carcaillet et al., 2001; 2010), our PFTs-based study indicated that there was no significant correlation between plant cover and BB in northern Quebec. This observation contrasts with studies reporting higher BB when the landscape was dominated by fire-prone conifers such as *Picea mariana* and *Pinus banksiana,* although this relationship was prevalent in the boreal mixed-wood forest, an area not explored here (Girardin et al., 2013; Blarquez et al., 2015).

Finally, as a resulting effect of burning on the expansion of post-fire shrubs, boreal evergreen shrubs (ES) showed a positive relationship with BB in northern Fennoscandia.

European boreal sector Generally speaking, the main PFT that contributed to the mitigation of the climate effect on BB in this sector during the Holocene was the needleleaf evergreen trees (NE), followed by the evergreen shrubs (ES).

In southern Fennoscandia the linkage between NE (dominated by *Pinus*) and BB (partly confounded by the occurrence of anthropogenic fires) is supported by traditional ecological knowledge, suggesting that *Pinus sylvestris* is a shade-intolerant species normally favored by moderate burning (Zackrisson, 1977). Furthermore, previous observations by Bradshaw et al. (2010) and Greisman & Gaillard (2009) documented an expansion of conifers and the simultaneous increase of fire activity in this region.

For central Fennoscandia this NE-BB correlation was already proposed by Brown & Giesecke (2014). During the early and mid-Holocene, in fact, the forests had a greater deciduous component, switching to needleleaf evergreen composition since *ca* 3000 BP, with a positive effect on burning. It is not clear if increasing fire activity linked to *Pinus* and *Picea* facilitated their dominance by feedbacks, or if the higher abundance of these two species altered the amount of cool temperate broadleaf trees (TB) that started to decrease afterwards. As the fire regime remained stable during this period, PFTs occurrence did not depend solely on fire pattern. However, given that the climate was cooler and moister during the late Holocene (Hammarlund et al. 2003; Bakke et al., 2008; Seppä et al., 2009) albeit burning activity increased gently until now, it seems more plausible that, as the amount of thermophilous vegetation decreased and conifers profited from the lack of competition, this contributed to increase the overall flammability of forests.

In northern Fennoscandia, where NE were dominant since the deglaciation, their variation had no effect. Here, ES alone acted as a major driver of BB. This is consistent with existing ecological understanding, which suggests that the regeneration of Ericaceae is often stimulated by fires (Bradshaw et al., 2010).

Influence of land use on biomass burning

Northern boreal sector In accordance with other studies (e.g., Carcaillet et al., 2007; Marlon et al., 2013; Blarquez et al., 2015), our statistical analyses did not highlight a significant relationship between land use and BB in any of the northern boreal forests clusters. However, we did not rule out the potential influence of first American nations on local fire activity in North America before the European colonization and the impact of the first settlements since the 19th century (Weir et al., 2000; Fastie et al., 2002; Natcher et al., 2007; Blarquez et al., 2018), as well as the anthropogenic use of fire between the 18th and the 20th centuries in northern Fennoscandia (Zackrisson, 1977; Segerström et al., 1994; Granström & Niklasson, 2008; Aakala et al., 2018).

European boreal sector Land use primarily controlled changes in BB in southern Fennoscandia during the Holocene. Previous studies (e.g., Lagerås, 2000; Lindbladh et al., 2003; Olsson et al., 2010) suggested that, since *ca* 3500 BP, people started to promote fires by means of slash-and-burn cultivation and forest pasture burning. Additionally, the decreasing BB from the mid-1700s onwards has been explained by a cessation of the use of fire as a land management tool, increased value of timber resources and by active fire suppression (Wallenius, 2011).

For central Fennoscandia, it is possible that past fire dynamics were partly or locally due to human activities. Evidence for anthropogenic influence on fire regime since Medieval times has been proposed before (Pitkänen et al., 2002; Segerström & Emanuelsson, 2002; Alenius et al., 2008). However, our analysis failed to identify a statistically significant correlation between land use and BB at millennial time scales. This could be due to the difficulty in modeling past population densities, or to a weak importance of human impact on central Fennoscandian fire regime when the entire Holocene was considered.

Finally, our results supported Carcaillet et al. (2007) indicating that humans did not play a significant role in shaping northern Fennoscandian fire regime.

To conclude, although at millennial time scale different drivers of biomass burning can be strongly intercorrelated (i.e., climate and land use affect vegetation changes and their relationships with fire activity and, simultaneously, fuel composition, sometime controlled by human activities, has effects on the interplay between climate and BB), the results presented in this large-scale analysis support our initial hypotheses. Temperature and/or precipitation drove millennial-scale biomass burning in boreal region with a similar fuel type (H1). In particular, in dry areas, an increase in temperature better explained changes in BB, while in wetter regions low precipitation was the main driver. This pattern was mitigated by the relative abundance of evergreen or deciduous trees/shrubs (H2), with the evergreen needleleaf component normally increasing BB activity. In view of a future warmer climate, we thus suggest that a reduction of wildfire could be reached by the use of forest management practices aiming to gradually promote a modification of vegetation composition towards less flammable deciduous species. This would increase the winter albedo (due to the absence of leaf) and the summer evapotranspiration (higher for broadleaf trees than for needleleaf trees), which would cool and counteract regional warming, and would improve the resilience of forests to fire and climatic changes. Finally, land use explained Holocene BB only in southernmost European boreal regions (H3).

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TABLES

TABLE 1. Plant functional types (PFTs) and pollen taxa assigned to them (after Prentice et al., 1996; Williams et al., 1998).

Plant functional type definition	**PFT**	**Plant taxa/pollen types**
Boreal needleleaf evergreen trees	NE	*Abies, Picea, Pinus, Thuja*
Boreal needleleaf/broadleaf deciduous trees/shrubs	NBD	*Alnus, Betula, Larix, Populus, Salix*
Boreal evergreen shrubs	ES	Ericaceae, *Juniperus*
Cool temperate broadleaf trees	TB	*Carpinus, Corylus, Fraxinus, Quercus, Tilia, Ulmus*

FIGURE CAPTIONS

FIGURE 1 Conceptual study design based on boreal forest regions that contain sedimentary charcoal time series. Hypotheses linking biomass burning (BB) and different drivers are displayed in red.

FIGURE 2 Location map of the selected charcoal (full/empty dots), pollen (yellow asterisks), climate (triangles) and land use (squares) records divided into the six site clusters selected for the present study. See S1, S2 & S3 for details.

FIGURE 3 Pollen-based reconstruction of mean July/summer temperature (black line) and mean annual precipitation (grey line) values for the northern boreal sector (**a**), the European boreal sector (**b**), Alaska (**c**), central Canada (**d**), northern Quebec (**e**), northern Fennoscandia (**f**), central Fennoscandia (**g**) and southern Fennoscandia (**h**). Original data for **(a)**, **(c)**, **(d)**, **(e)** by Viau et al. (2006) and Viau & Gajewski (2009); for **(b)**, **(f), (g), (h)** by Mauri et al. (2015).

FIGURE 4 Composite time series of Holocene land use (LU) based on the KK10 scenario (Kaplan et al., 2011).

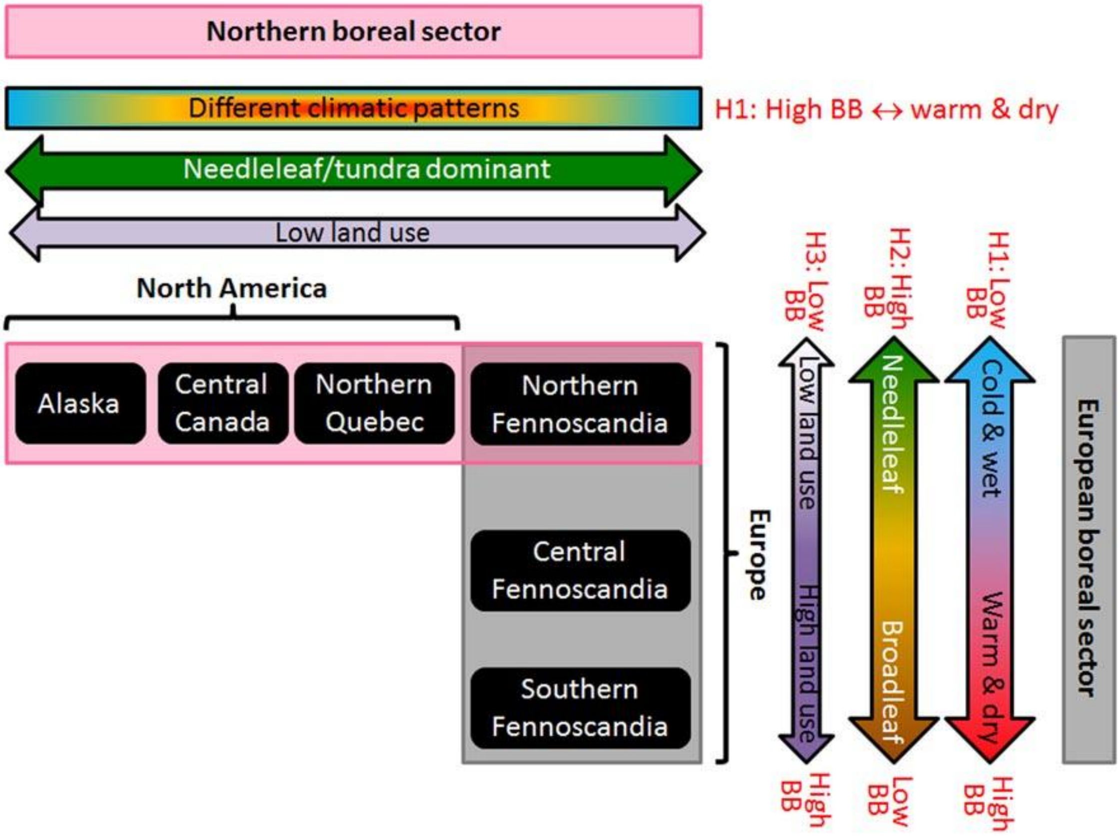
FIGURE 5. Pairwise correlations (*r*-values) of tCHAR Z-scores with respect to distance classes between sites across North American (**a**) and European (**b**) boreal forests.

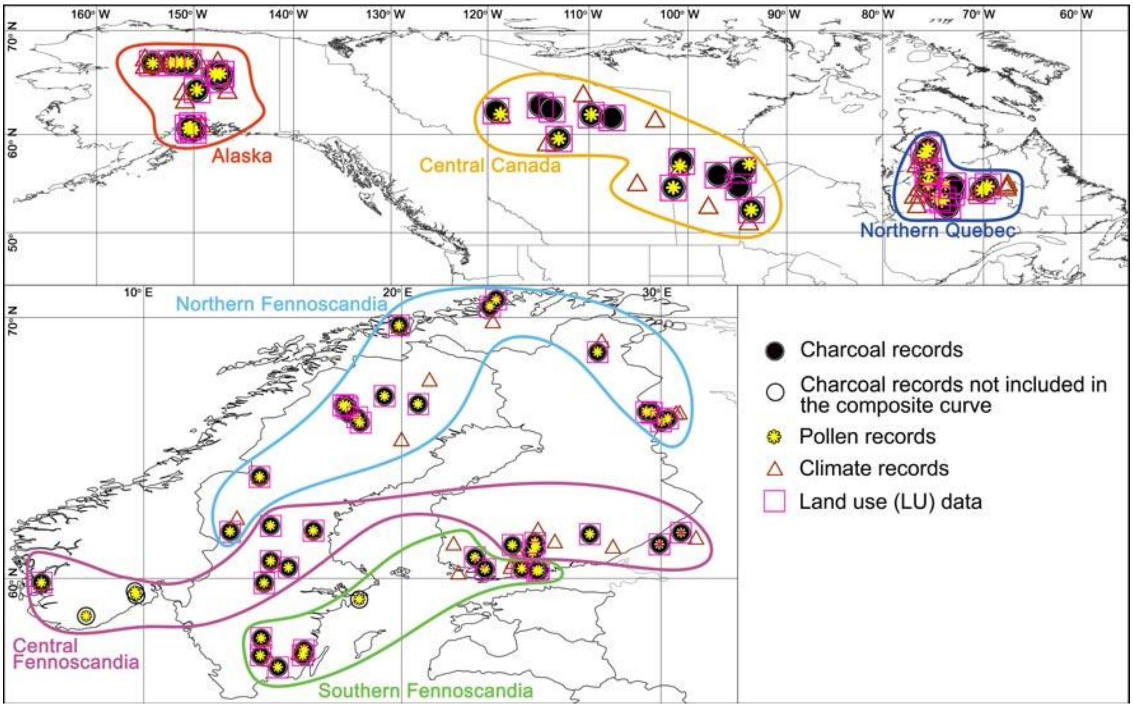
FIGURE 6 Reconstruction of boreal forests biomass burning over the Holocene for the northern boreal sector (**a**), the European boreal sector (**b**), Alaska (**c**), central Canada (**d**), northern Quebec (**e**), northern Fennoscandia (**f**), central Fennoscandia (**g**) and southern Fennoscandia (**h**). The composite curves have been smoothed using a 250- (dashed line) and a 500-year (black line) window half width, respectively. Grey shading represents the 90% bootstrap confidence intervals from the 500-years smoothing window per 1000-years bootstrap analysis.

FIGURE 7 Best-fitted models according to the AIC and results of the relative importance analysis of climate and land use (LU) on biomass burning over the Holocene for the northern boreal sector (**a**), the European boreal sector (**b**), Alaska (**c**), central Canada (**d**), northern Quebec (**e**), northern Fennoscandia (**f**), central Fennoscandia (**g**) and southern Fennoscandia (**h**). The significance values, the direction of the relationship and the proportion of variance explained by each predictor are indicated. Detailed information is given in S6, Table S1.

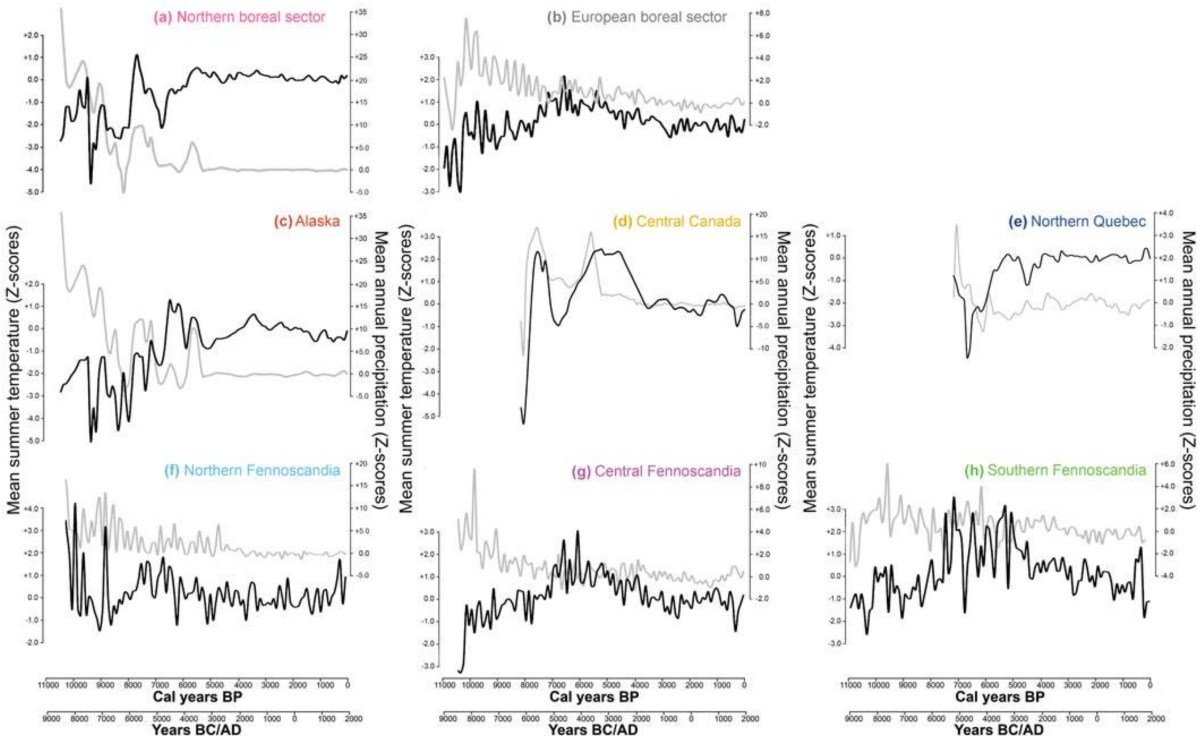
FIGURE 8 Reconstruction of forest composition expressed as main plant functional types (PFTs) percentage coverage for the northern boreal sector (**a**), the European boreal sector (**b**), Alaska (**c**), central Canada (**d**), northern Quebec (**e**), northern Fennoscandia (**f**), central Fennoscandia (**g**) and southern Fennoscandia (**h**) based on pollen data. Time series were created by averaging across all selected sites in each sector and cluster.

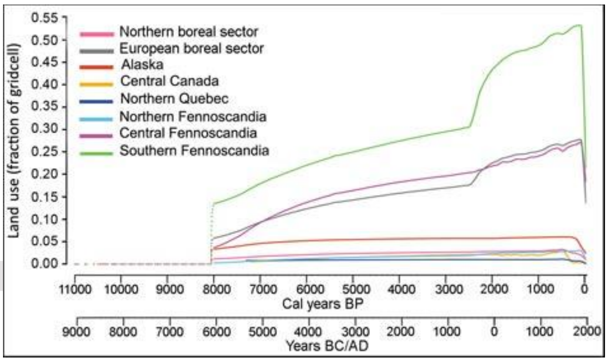
FIGURE 9 Best-fitted model according to the AIC and results of the relative importance of changes in different plant functional types (PFTs) on biomass burning over the Holocene for the northern boreal sector (**a**), the European boreal sector (**b**), Alaska (**c**), central Canada (**d**), northern Quebec (**e**), northern Fennoscandia (**f**), central Fennoscandia (**g**) and southern Fennoscandia (**h**). The significance values, the direction of the relationship and the proportion of variance explained by each predictor are indicated. Detailed information is given in S6, Table S2.

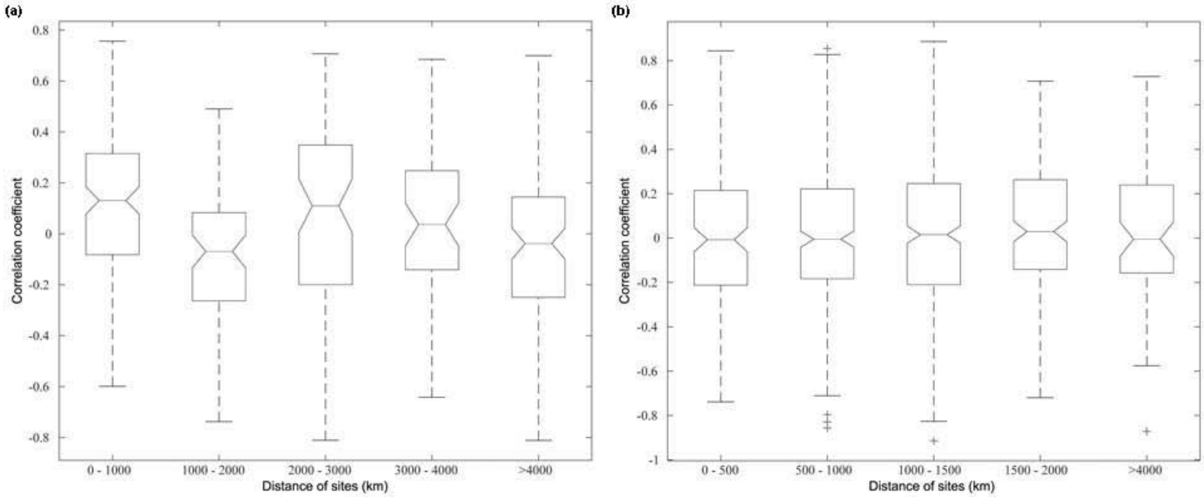


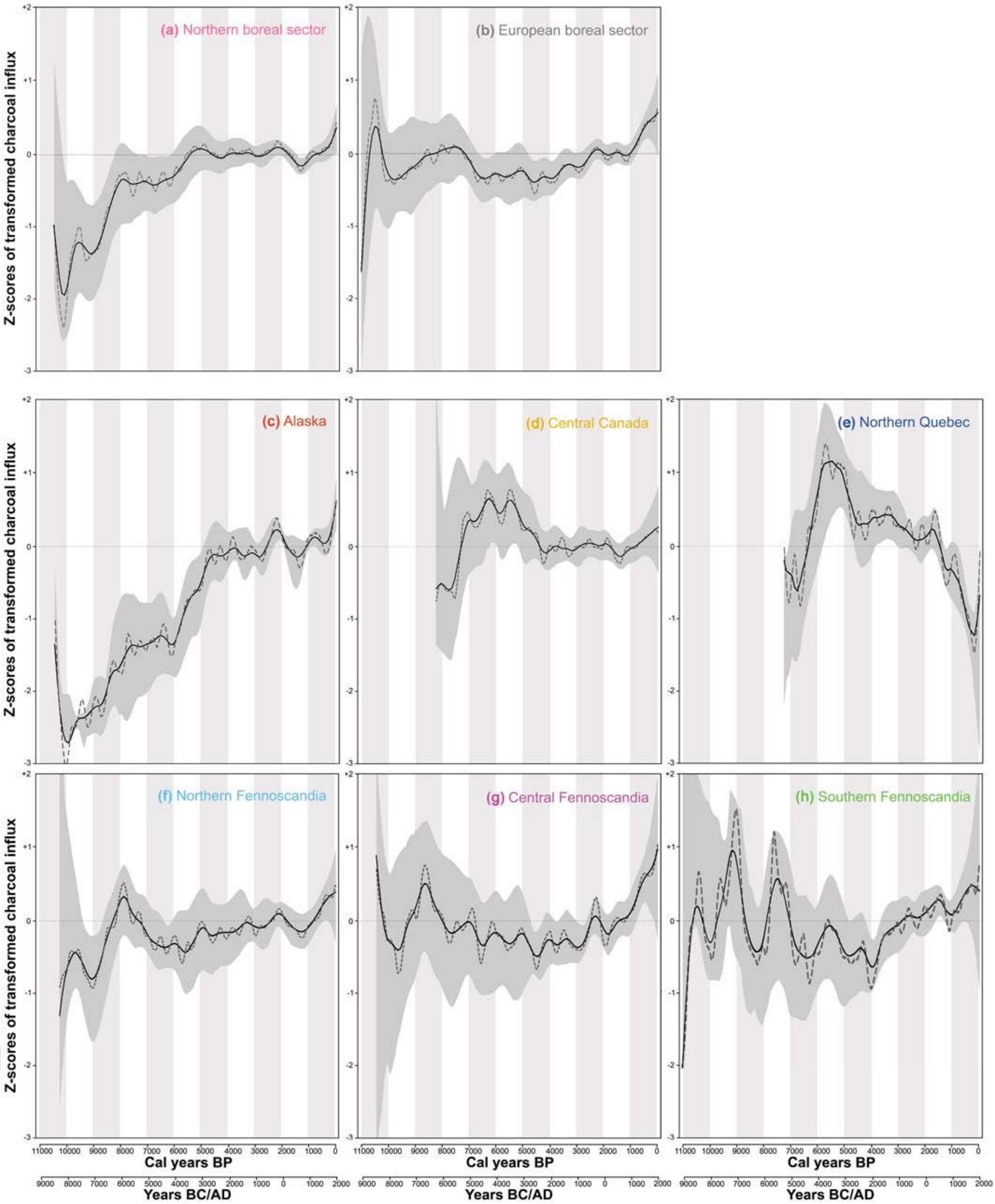


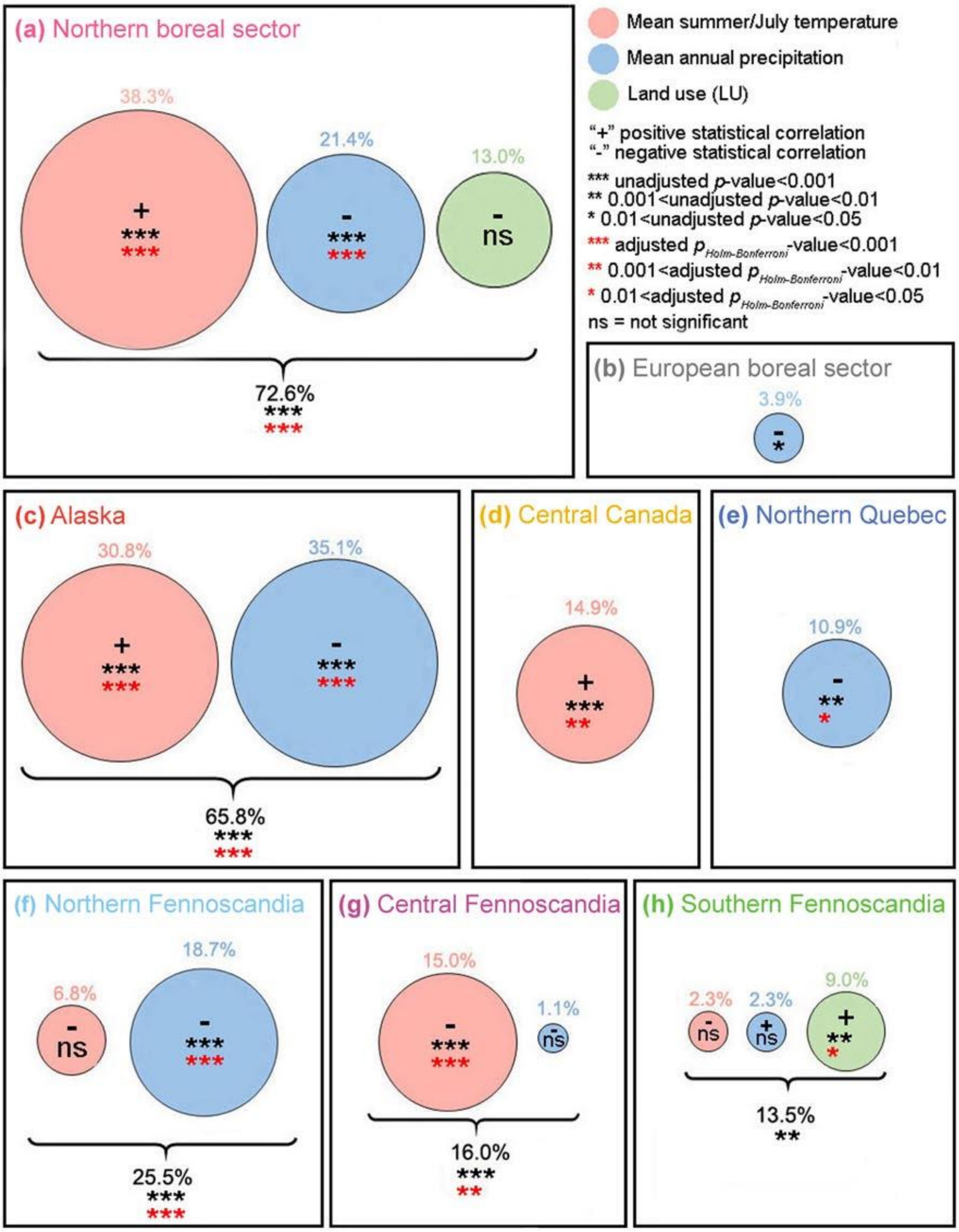
160° W
150° W
140° W
130° W
120° W
110° W
100° W
90° W
80° W
70° W
60° W
70° N
60° N
50° N
Alaska
Central Canada
Northern Quebec
10° E
20° E
30° E
Northern Fennoscandia
Central Fennoscandia
Southern Fennoscandia
Charcoal records
Charcoal records not included in the composite curve
Pollen records
Climate records
Land use (LU) data


(a) Northern boreal sector
(b) European boreal sector
(c) Alaska
(d) Central Canada
(e) Northern Quebec
(f) Northern Fennoscandia
(g) Central Fennoscandia
(h) Southern Fennoscandia
Mean summer temperature (Z-scores)
Mean annual precipitation (Z-scores)
Cal years BP
Years BC/AD

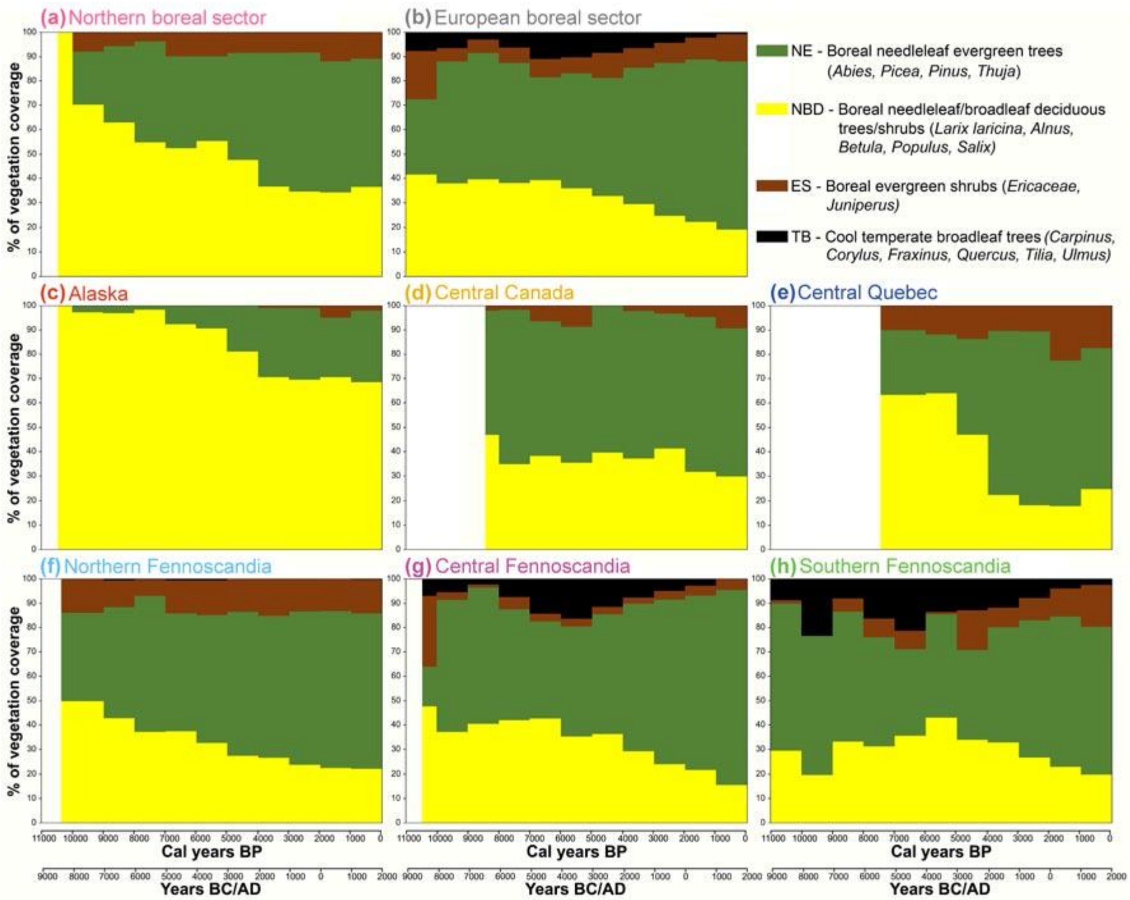

Northern boreal sector
European boreal sector
Alaska
Central Canada
Northern Quebec
Northern Fennoscandia
Central Fennoscandia
Southern Fennoscandia
Land use (fraction of gridcell)
Cal years BP
Years BC/AD

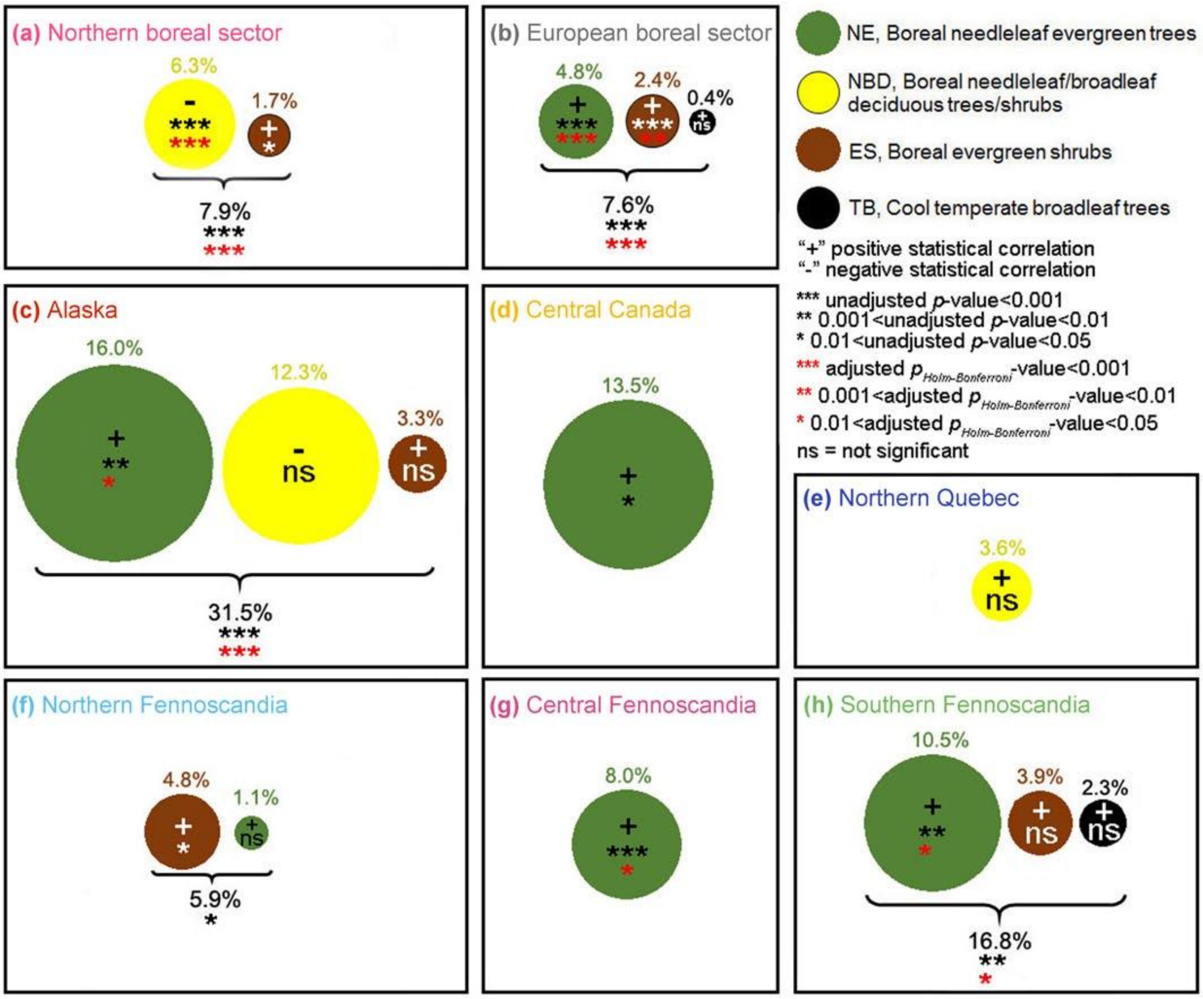

(a)
Correlation coefficient
Distance of sites (km)
0 - 1000
1000 - 2000
2000 - 3000
3000 - 4000
>4000
(b)
Correlation coefficient
Distance of sites (km)
0 - 500
500 - 1000
1000 - 1500
1500 - 2000
>4000


(a) Northern boreal sector
(b) European boreal sector
(c) Alaska
(d) Central Canada
(e) Northern Quebec
(f) Northern Fennoscandia
(g) Central Fennoscandia
(h) Southern Fennoscandia
Z-scores of transformed charcoal influx
Cal years BP
Years BC/AD



(a) Northern boreal sector
38.3%
21.4%
13.0%
+
***
***
-
***
***
-
ns
72.6%
***
***
Mean summer/July temperature
Mean annual precipitation
Land use (LU)
"+" positive statistical correlation
"-" negative statistical correlation
*** unadjusted p-value<0.001
** 0.001<unadjusted p-value<0.01
* 0.01<unadjusted p-value<0.05
*** adjusted p Holm-Bonferroni-value<0.001
** 0.001<adjusted p Holm-Bonferroni-value<0.01
* 0.01<adjusted p Holm-Bonferroni-value<0.05
ns = not significant
(b) European boreal sector
3.9%
-
*
(c) Alaska
30.8%
35.1%
+
***
***
-
***
***
65.8%
***
***
(d) Central Canada
14.9%
+
***
**
(e) Northern Quebec
10.9%
-
**
*
(f) Northern Fennoscandia
6.8%
18.7%
-
ns
-
***
***
25.5%
***
***
(g) Central Fennoscandia
15.0%
1.1%
-
***
***
-
ns
16.0%
***
**
(h) Southern Fennoscandia
2.3%
2.3%
9.0%
-
ns
+
ns
+
**
*
13.5%
**


(a) Northern boreal sector
(b) European boreal sector
NE - Boreal needleleaf evergreen trees (Abies, Picea, Pinus, Thuja)
NBD - Boreal needleleaf/broadleaf deciduous trees/shrubs (Larix laricina, Alnus, Betula, Populus, Salix)
ES - Boreal evergreen shrubs (Ericaceae, Juniperus)
TB - Cool temperate broadleaf trees (Carpinus, Corylus, Fraxinus, Quercus, Tilia, Ulmus)
(c) Alaska
(d) Central Canada
(e) Central Quebec
(f) Northern Fennoscandia
(g) Central Fennoscandia
(h) Southern Fennoscandia
% of vegetation coverage
Cal years BP
Years BC/AD



(a) Northern boreal sector
6.3%
-
***
***
1.7%
+
*
7.9%
***
***
(b) European boreal sector
4.8%
+
***
***
2.4%
+
***
**
0.4%
+
ns
7.6%
***
***
NE, Boreal needleleaf evergreen trees
NBD, Boreal needleleaf/broadleaf deciduous trees/shrubs
ES, Boreal evergreen shrubs
TB, Cool temperate broadleaf trees
"+" positive statistical correlation
"-" negative statistical correlation
*** unadjusted p-value<0.001
** 0.001<unadjusted p-value<0.01
* 0.01<unadjusted p-value<0.05
*** adjusted p Holm-Bonferroni-value<0.001
** 0.001<adjusted p Holm-Bonferroni-value<0.01
* 0.01<adjusted p Holm-Bonferroni-value<0.05
ns = not significant
(c) Alaska
16.0%
+
**
*
12.3%
-
ns
3.3%
+
ns
31.5%
***
***
(d) Central Canada
13.5%
+
*
(e) Northern Quebec
3.6%
+
ns
(f) Northern Fennoscandia
4.8%
+
*
1.1%
+
ns
5.9%
*
(g) Central Fennoscandia
8.0%
+
***
*
(h) Southern Fennoscandia
10.5%
+
**
*
3.9%
+
ns
2.3%
+
ns
16.8%
**
*