



Fire-vegetation interactions during the last 11,000 years in boreal and cold temperate forests of Fennoscandia

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ABSTRACT

The long-term ecological interactions between fire and the composition of dominant trees and shrubs in boreal and cold temperate Fennoscandian forests are still under discussion. We hypothesized that fire-prone taxa should abound during periods and regions characterized by higher fire disturbance, while fire-intolerant taxa should dominate when and where fire activity is low. Biomass burning (BB) is here investigated based on 69 sedimentary charcoal records. For the same sites, the relative contribution of pollen-based reconstructions of dominant vegetation cover divided into three different fire-sensitivity classes is explored by means of a statistical approach. The overall patterns found across Fennoscandia suggest that Ericaceae (mainly *Calluna*), *Pinus*, *Betula* and *Populus* are strongly positively correlated with multi-millennial variability of BB in both boreal and cold temperate forests, confirming their fire-prone character (taxa adapted/favoured by burning). Positive but much weaker (and not always significant) relationships also exist between long-term trends in BB and *Fagus*, *Quercus*, *Corylus*, *Alnus*, *Juniperus*, *Carpinus* and *Salix*, fire-tolerant taxa that survive low/moderate intense fires because of specific functional traits or their rapid, enhanced regeneration after fire. A strong negative significant correlation is instead detected between BB and *Picea*, *Ulmus*, *Tilia*, *Fraxinus*, which are fire-intolerant taxa and can locally disappear for a short time after a fire. This large-scale analysis supports our initial hypothesis that tree and shrub dominance was closely linked to biomass burning since the onset of the Holocene in the study regions. Fire was an important ecosystem disturbance in Fennoscandia influencing long-term vegetation dynamics and composition over the last 11,000 years, although human activities probably altered the strength of fire-vegetation interactions during more recent millennia.

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1. Introduction

It is well established that anthropogenic global warming has recently affected high northern latitudes more than other regions worldwide (IPCC, 2014). Rapidly increasing temperatures, potential shifts towards more flammable vegetation and intensifying lightning and human-induced ignition are expected to lead to a rise in Fennoscandian forest fires (Flannigan et al., 2013), as predicted by ecosystem-fire model studies (Krawchuk et al., 2009; Kloster et al.,

2012; Wu et al., 2015). However, despite their global consequences in terms of biogeochemical cycles and hydrology in Nordic ecosystems (Abbott et al., 2016), the long-term relationships between fire and vegetation dynamics are still under discussion and not completely understood (Archibald et al., 2018).

Concern about an increasing fire risk in Fennoscandia has been raised by the outbreak of large wildfires during summers 2014 and 2018 (ca. 14,000 and 25,000 ha of burned forests in Sweden, respectively; Gustavsson, 2014; San-Miguel-Ayanz et al., 2018), with significant alteration of ecosystem services, notably to agriculture, forestry, water supplies and socioenvironmental functions. Apart from those extreme events, today fire occurrence in Fennoscandia is still generally very low (Drobyshev et al., 2012), with only

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around 0.004% of forest land burning annually (San-Miguel-Ayanz et al., 2018). The development of fire suppression policies started in the 1860s by established public forest services (Niklasson and Granström, 2000; Ruuttula-Vasari, 2004), and the transition from traditional fire-related livelihoods (*i.e.*, slash-and-burn cultivation) to modern agriculture and forestry at the end of the 19th century (Granström and Niklasson, 2008) have been suggested as probable explanations for fires' decline in Fennoscandia. However, prior to the beginning of the 20th century, wildfires have been a major landscape-scale disturbance shaping vegetation composition for millennia (Tryterud, 2003; Carcaillet et al., 2012; Brown and Giesecke, 2014; Aakala et al., 2018), with an annual area burnt more than 250 times higher than today (over 1% per year; Wallenius, 2011).

Understanding how different taxa respond to long-term fire disturbance is useful for predicting the properties and the distribution of many ecosystems. While fire-intolerant species can locally disappear for a short time after a fire, fire-tolerant species generally survive fires of low/moderate intensity because of specific functional traits or their rapid, enhanced regeneration after fire. Fire-prone species develop many traits that enable population persistence under a given fire regime; furthermore, some of these taxa display a remarkable adaptation to fire and may be considered favoured by burning.

The interpretation of paleorecords based on sedimentary pollen and charcoal provides information about vegetation and fire dynamics and their possible drivers at different temporal and spatial scales (Molinari et al., 2018; Feurdean et al., 2020). Additionally, they can be used to infer the ecological impact of changing fire regimes over millennia. Vegetation composition can be altered for long by changes in fire frequency, size, intensity, severity and seasonality (Jasinski and Payette, 2005; Higuera et al., 2008; Genries et al., 2009) and, at the same time, the new vegetation cover can provide a different fuel type that leads to different fire regimes (Clark et al., 2001; Higuera et al., 2009; Falk et al., 2011). However, lack of vegetation alteration despite changes in biomass burning (hereafter BB) can illustrate fire-resilience of ecosystems and reveal fire-tolerance of species (Carcaillet et al., 2019). Exploring the long-term relationship between changes in vegetation composition and

fire regime is critical to predict the occurrence and magnitude of future fires in order to limit their negative impact on ecosystem services (Iglesias et al., 2015).

Within this context, we hypothesized that over the last 11,000 years in boreal and cold temperate forests of Fennoscandia fire-prone species were more abundant during periods characterized by higher fire disturbance, while fire-intolerant species dominated when BB was low. We statistically tested this hypothesis for the whole Holocene, as well as for the late-, middle- and early-Holocene by (i) reconstructing BB based on sedimentary charcoal records from lakes and peat bogs from the study regions (Fig. 1), and (ii) exploring the relative contribution of the dominant vegetation cover based on sedimentary pollen series from the same sites. Fifteen most common tree and shrub taxa in boreal and cold temperate Fennoscandian forests (Table 1) were divided into three different fire-sensitivity classes ("fire-intolerant trees/shrubs, hereafter FI", "fire-tolerant trees/shrubs, hereafter FT" and "fire-prone trees/shrubs, hereafter FP"). By testing our hypothesis based on taxon-specific fire behaviour, we will be able to verify temporal and spatial relationships between vegetation and fire dynamics during postglacial periods, when climate and plant communities were different from today as an ecology rule, a prerequisite for future climate projections. This large-scale, multi-millennial investigation is performed in one of the regions most affected by the ongoing global warming (IPCC, 2014), where frequency, severity and areal extent of fires are likely to increase in the future (Kasischke and Stocks, 2000).

2. Materials and methods

2.1. Records of past fire activity

Variations in Holocene BB across Fennoscandia were analysed based on 69 sedimentary charcoal series (located between 6° and 31°E and 55° and 71°N, Fig. 1) covering part or all of the last 11,000 years. Charcoal data were selected from the latest version of the Global Charcoal Database (GCD v4.0.6) compiled by the Global Palaeofire Working Group (GPWG, <http://gpwg.org>), from the European Pollen Database (EPD, <http://www.epd.eu>).

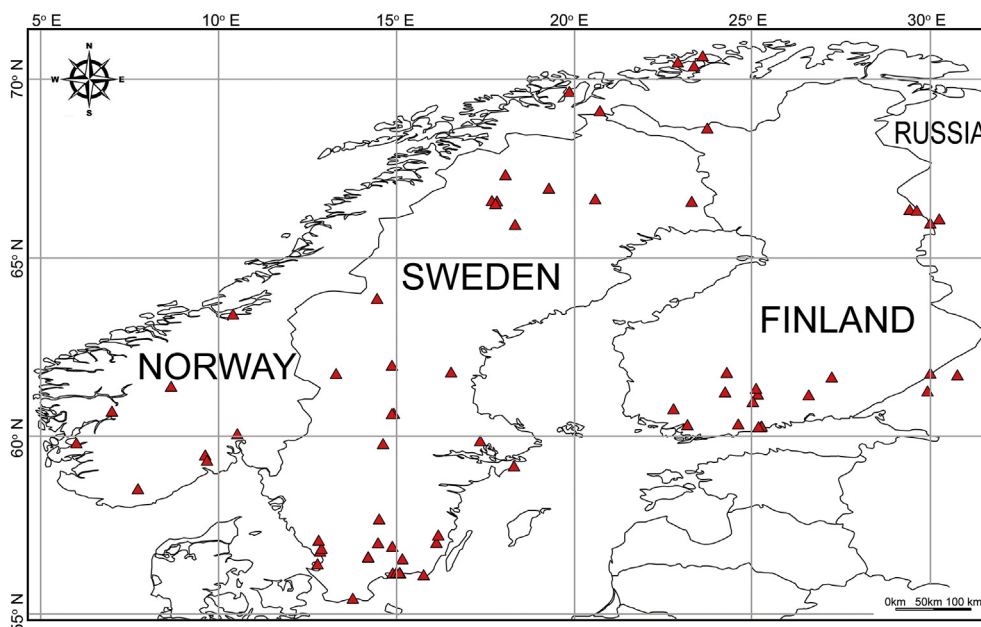


Fig. 1. Location map of the selected charcoal and pollen records.

Table 1

Fire-sensitivity classes of dominant trees and shrubs, and the pollen taxa assigned to them (after Tinner et al., 2000♦; Keller et al., 2002♦; Thomas et al., 2007♦; Conedera, 2009♦; Blarquez and Carcaillet, 2010#; Maringer et al., 2016♦; Fréjaville et al., 2018*). Concerning the collective pollen taxa “Ericaceae”, *Calluna vulgaris* was the most common pollen type in the dataset. Actually, on a total of 38 sites with Ericaceae pollen presence, 13 sites (34%) contained only *Calluna*, and 13 (34%) had *Calluna* (with higher percentages) and “Ericaceae undifferentiated” (with lower percentages). In 9 sites (24%), the Ericaceae were not distinguished at the genus level. Only 3 sites (8%) had *Empetrum* (with percentages always <1%). *Vaccinium* never appears in the pollen diagrams of the studied sites. See Table 1 Supporting Information S2 for detailed information about pollen percentage threshold values and correction factors.

| Fire-sensitivity class | Definition | Plant taxa/pollen types |
|-----------------------------------|--|---|
| Fire-intolerant trees/shrubs (FI) | Taxa subjected to biomass decrease or local extinction after a fire | <i>Fraxinus excelsior</i> ♦, <i>Picea abies</i> ▼, <i>Tilia cordata</i> ♦, <i>Ulmus</i> sp.♦ |
| Fire-tolerant trees/shrubs (FT) | Taxa resistant to low/moderate intense fire because of specific functional traits or their rapid, enhanced regeneration after fire | <i>Alnus</i> sp.▼, <i>Carpinus betulus</i> ♦, <i>Corylus avelana</i> ♦.▼, <i>Fagus sylvatica</i> ♦.♦.▼.#, <i>Juniperus communis</i> *, <i>Quercus</i> sp. (deciduous)♦.▼.*, <i>Salix</i> sp.♦.♦.▼ |
| Fire-prone trees/shrubs (FP) | Taxa normally adapted/favoured by fire | <i>Betula</i> ♦.▼.#, Ericaceae (in our dataset mainly <i>Calluna</i>)♦.▼.#, <i>Pinus sylvestris</i> ♦, <i>Populus tremula</i> ♦ |

europollendatabase.net/index.php), from previous syntheses (Molinari et al., 2013, 2018; Kuosmanen et al., 2018) or were provided by the original authors. The good geographical coverage of charcoal records provides a reasonable basis to determine broad-scale past BB in the selected regions. Metadata including detailed information about each record are presented in Supporting Information Appendix S1.

All charcoal data were first converted to influx values (CHAR, i.e., the number, area or weight of particles · cm⁻² · year⁻¹). To allow comparison within and between charcoal records obtained from various depositional environments and quantified with different laboratory techniques, a standardization procedure was applied (Power et al., 2008). This technique includes: 1) a min-max rescaling of CHAR values, 2) a Box-Cox transformation to homogenize the within-record variance and 3) a Z-score conversion using a base period most representative of the entire dataset, i.e., the interval between 4000 and 0 calibrated years before present (hereafter, cal BP). Transformed charcoal data were then bootstrap re-sampled 999 times with a moving window procedure using non-overlapping bins of 50-years. This reduces the influence of records with high sample resolution, and avoids data interpolation for records with a lower resolution. Re-sampled time series were then aggregated and smoothed with a 500-year loess smoother. Charcoal composite series mean and 95% confidence intervals (hereafter CI) were calculated by averaging the smoothed and bootstrapped data series (Danianu et al., 2012). A composite curve was produced with the method implemented in the R (R Core Team, 2016) package “paleofire” version 1.2.4 (Blarquez et al., 2014).

For the statistical analyses, mean transformed charcoal values (hereafter, tCHAR Z-scores) were calculated for each selected site at 1000-year time intervals. Furthermore, six maps of mean tCHAR Z-scores were produced in order to highlight the most important spatial and temporal trends in BB during the Holocene. Pairwise correlations between the charcoal records were performed to test if proximal sites had a high temporal correlation compared with distant sites, for an estimation of the spatial dependence between Holocene trends in tCHAR Z-scores BB at 1000-year temporal resolution. Additionally, a semivariogram, which is a plot of semi-variance versus range, was generated for each time slice of 1000 years.

2.2. Reconstruction of dominant vegetation cover

For an estimation of major changes in vegetation composition through time, fossil pollen data available from the same site as the charcoal record were provided by the original author or extracted from the literature by digitizing the published diagrams using the program DATA MUGGER 1.1 (Jones, 2011). See Supporting

Information S1 for more detailed information.

Mean pollen percentages at 1000-year intervals were calculated for each selected site. Pollen percentage threshold values (Davis and Jacobson, 1985; Pardoe, 2001; 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 (Table 1 Supporting Information S2). For each taxon, pollen percentages below the threshold values were not taken into consideration. Subsequently, correction factors (Binney et al., 2011) were applied in order to achieve a closer approximation to vegetation cover (Table 1 in Supporting Information S2). This method is a simplification of the REVEALS model (Sugita, 2007a), which considers the different production and dispersal of pollen among taxa.

As a final step, the percentage cover of different taxa grouped according to their fire-sensitivity class (Table 1) was calculated for each single site.

To evaluate long-term trends of different fire sensitivity classes, we applied the same standardization procedure used for sedimentary charcoal data to the three previously selected groups of plant taxa (Table 1). The procedure includes 1) a min-max rescaling of FI, FT and FP, 2) a Box-Cox transformation to homogenize the within-record variance and 3) a conversion to Z-scores using a base period 4000-0 cal BP. Transformed FI, FT and FP data were then re-sampled using a bootstrapping procedure 999 times with a moving window procedure using non-overlapping bins of 50-years. Re-sampled series were aggregated and smoothed by fitting a locally weighted regression with a 500-year half window width. Composite series mean and 95% CI were calculated by averaging the smoothed and bootstrapped data series. For the statistical analyses, for each selected site, mean Z-scores transformed values were calculated for each fire-sensitivity class (tFI Z-scores, tFT Z-scores and tFP Z-scores) at 1000-year time intervals. Furthermore, six maps were produced in order to highlight the most important spatial and temporal trends in fire-sensitivity classes of dominant vegetation cover during the Holocene.

2.3. Statistical analyses of proxy time series

Ordination by principal component analysis (PCA) was performed for evaluating the relationship between trends in BB (tCHAR Z-scores) and fire-sensitivity classes of dominant vegetation cover (tFI Z-scores, tFT Z-scores and tFP Z-scores) for each selected site. We also determined the coefficient of Pearson's correlation (r) and the p -value to measure the strength of the linkage between the two selected variables. 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. It is important to stress that this kind of analysis tests the relationship between the variables taken into consideration but not the direction of the causality.

With the aim of exploring possible differences in the role of vegetation on fire behaviour through time, the analyses were carried out for the whole Holocene (11,000 cal BP–Present), as well as for three different time periods, *i.e.*, the early- (11,000–8000 cal BP), middle- (8000–4000 cal BP) and late-Holocene (4000 cal BP–Present) where “Present” corresponds to the date of our study.

3. Results

3.1. Main trajectories of biomass burning during the Holocene

The composite charcoal record (Fig. 2), the pairwise correlation

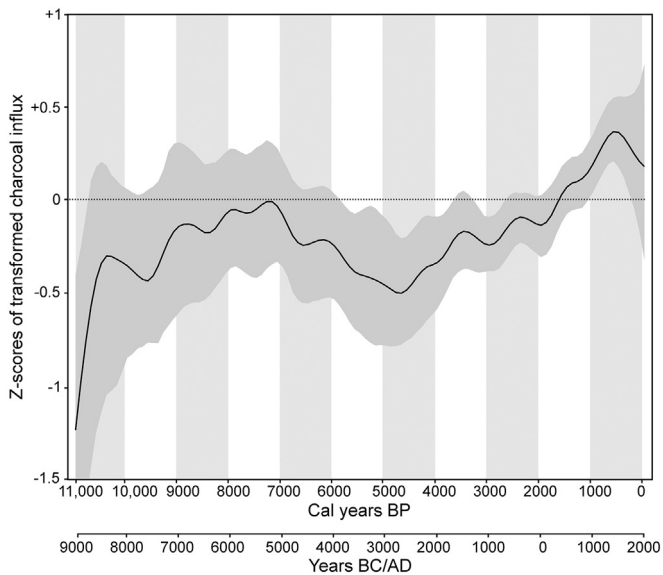


Fig. 2. Trend of biomass burning over the Holocene in Fennoscandia. The composite charcoal curve has been smoothed using a 500-year window half width. Grey shading represents the 95% CI calculated using the bootstrap procedure.

analysis between sites (Fig. 3a), the semivariogram (Fig. 3b) and the tCHAR Z-score maps (Fig. 4 and Table 2 Supporting Information S2) document main changes in spatial and temporal patterns of BB over the last Holocene. After a minimum at 11,000 cal BP (with large uncertainties), the regional synthesis shown by the composite charcoal curve (Fig. 2) indicates low fluctuating but increasing BB until 7300 cal BP (with centennial-scale decreases around 9500 and 8400 cal BP). A low and decreasing trend characterizes the interval between 7300 and 4600 cal BP, with only a weak oscillation around 6100 cal BP. Despite some small oscillations, BB starts to increase monotonously after 4600 cal BP, reaching values above the long-term mean from 1600 cal BP onwards. The Holocene tCHAR attains its maximum around 500 cal BP. A downturn in BB is recorded during the last centuries.

The pairwise correlation analysis performed between the tCHAR Z-scores (Fig. 3a) shows a low but positive spatial correlation between sites. However, there is no pattern of higher spatial correlation coefficients (r -values) between proximal sites compared to distant sites, indicating no or weak spatial correlation effect when analysing the entire charcoal dataset. Furthermore, the semivariogram (Fig. 3b) shows that during the period 4000–1000 cal BP the variance between the data is weak, while it reaches the highest values between 11,000 and 7000 cal BP. Intermediate values characterize the periods 7000–4000 cal BP and 1000–Present cal BP. These results reflect the choice of a base period between 4000 and 0 cal BP for the Z-scores transformation. The slightly lower semivariance observed for the sites located within a distance of 200 km from each other is due to the low number of sites which contribute to this variability (Fig. 3b). From a distance of 500 km onwards, there is no visible trend in the between-site semivariability. These results allow to discard a spatial dependence between Holocene trends in BB and permit the use of linear regression techniques for the statistical analyses (although the applied PCA removes any spatial dependency by default).

The charcoal map for the period 10,000–11,000 cal BP (Fig. 4f) shows an average tCHAR Z-score below the long term mean (Table 2 in Supporting Information S2), with negative values for 64% of the records (three of them, in southern Norway, strongly negative). The few positive values are located in southern Sweden and southern Finland, and one strong positive in Russia. Between 8000 and 9000 cal BP, the average Z-score increases, with values above the long-term mean for 53% of records (Table 2 in Supporting

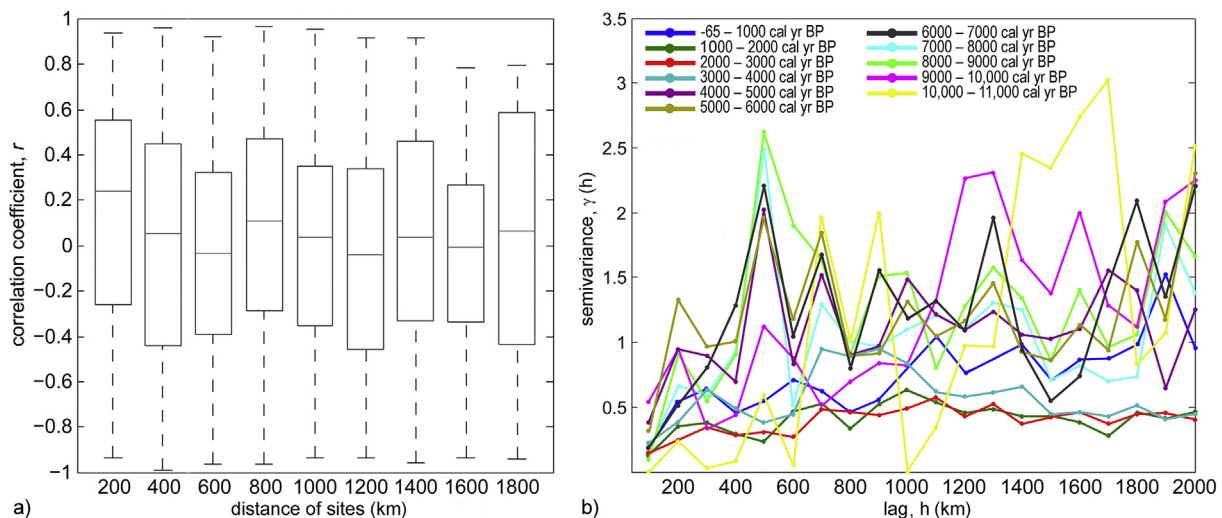


Fig. 3. Biomass burning analyses in space and time. (a) Pairwise correlations (r -values) between tCHAR Z-scores of sites with respect to distance classes between these sites across Fennoscandia. (b) Semivariogram of tCHAR Z-scores at 1000-yr temporal resolution.

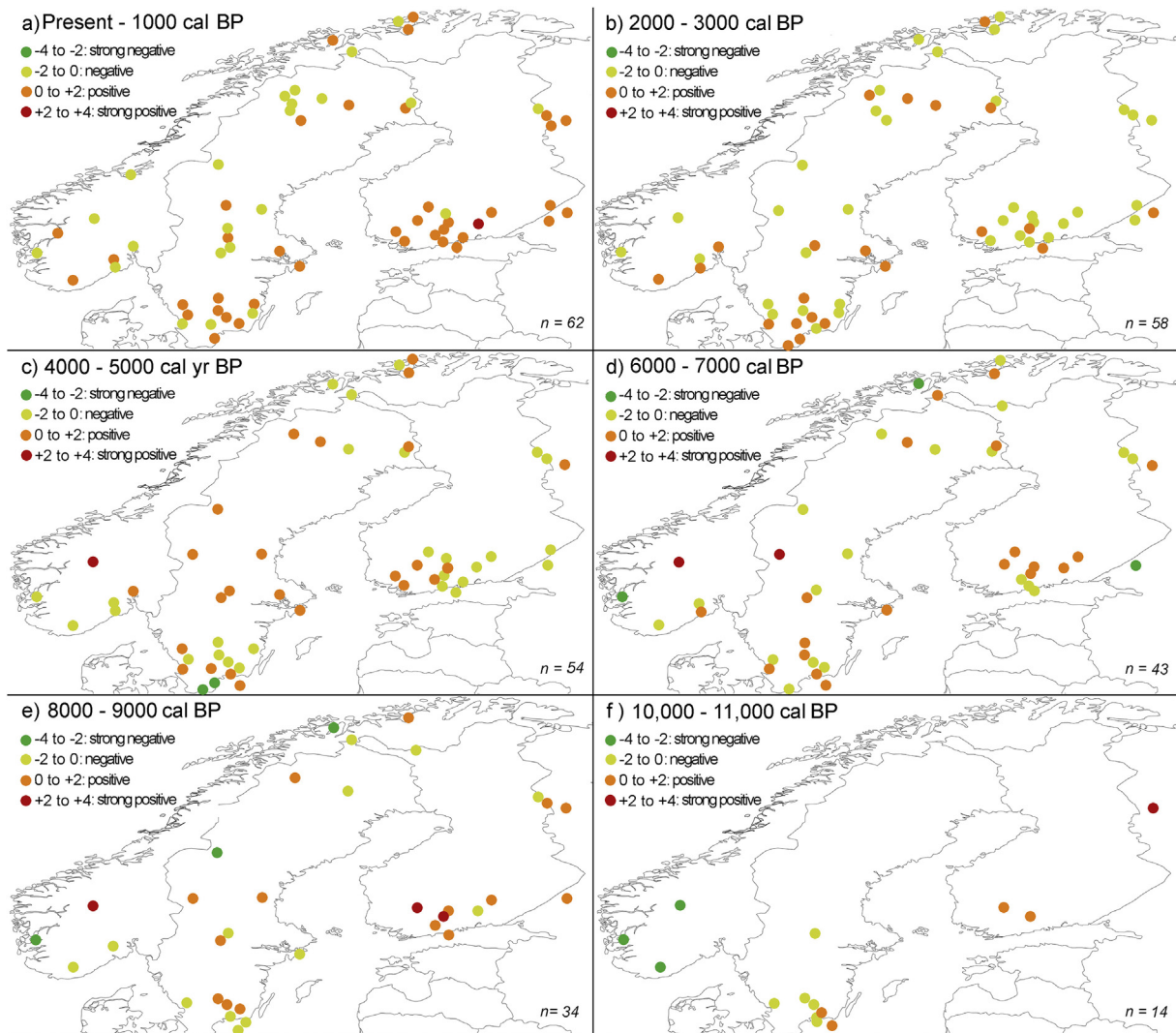


Fig. 4. Maps of mean Z-scores of transformed charcoal influx for (a) Present–1000 cal BP, (b) 2000–3000 cal BP, (c) 4000–5000 cal BP, (d) 6000–7000 cal BP, (e) 8000–9000 cal BP and (f) 10,000–11,000 cal BP. Four equal-frequency Z-score clusters were used to summarize the spatio-temporal trends in Fennoscandia fire activity during the Holocene. See Table 2 in Supporting Information S2 for more detailed information.

Information S2). These positive values are concentrated in southern Finland, where are also located the three sites with strong positive Z-scores (Fig. 4e). During the period 6000–7000 cal BP (Fig. 4d), the overall mean Z-score decreases again, with 51% of records with negative values (Table 2 in Supporting Information S2). Both the few strong negative (three sites) and strong positive (two sites) values are sparsely located. Average tCHAR Z-score continue to decrease between 5000 and 4000 cal BP (Fig. 4c), with 54% of records below the long-term mean. Two records in southern Sweden have strong negative values, while the only one strongly positive is recorded in southern Norway. The period 2000–3000 cal BP (Fig. 4b) is characterized by a slightly increase in the mean Z-score (Table 2 in Supporting Information S2). Despite that, 62% of charcoal records (concentrated in southern Finland) have negative values. The charcoal map for the last millennium (Fig. 4a) shows an average tCHAR above the long-term mean (Table 2 in Supporting Information S2). 65% of records (mainly located in southern Finland and southern Sweden) have positive values, and only one of them, in southern Finland, has a strong positive Z-score.

3.2. Main trajectories of dominant vegetation cover during the Holocene

The reconstruction of the main dynamics of fire-sensitivity classes of dominant trees and shrubs show different trends during the last 11,000 years (Fig. 5abc). Despite high uncertainties between 11,000 and 10,000 cal BP, FI (Fig. 5a) increase continuously over the Holocene. More specifically, FI are characterized by values below the long-term mean during the early- and middle-Holocene, but display positive values from 3000 cal BP onwards. A maximum is then reached during the last millennium. A quite different trajectory is shown by FT (Fig. 5b), which are characterized by low (below the long-term mean, with high uncertainties) but increasing values between 11,000 and 9000 cal BP. Over the period 9000–7000 cal BP, FT reach values above the long-term mean and continue to increase. After a maximum between 8000 and 7000 cal BP, FT start to decline continuously (with negative values from 3000 cal BP onwards). A minimum is attained during the interval 2000–1000 cal BP, while a small increase is recorded during the last millennium. FP display low values below the long-term mean with

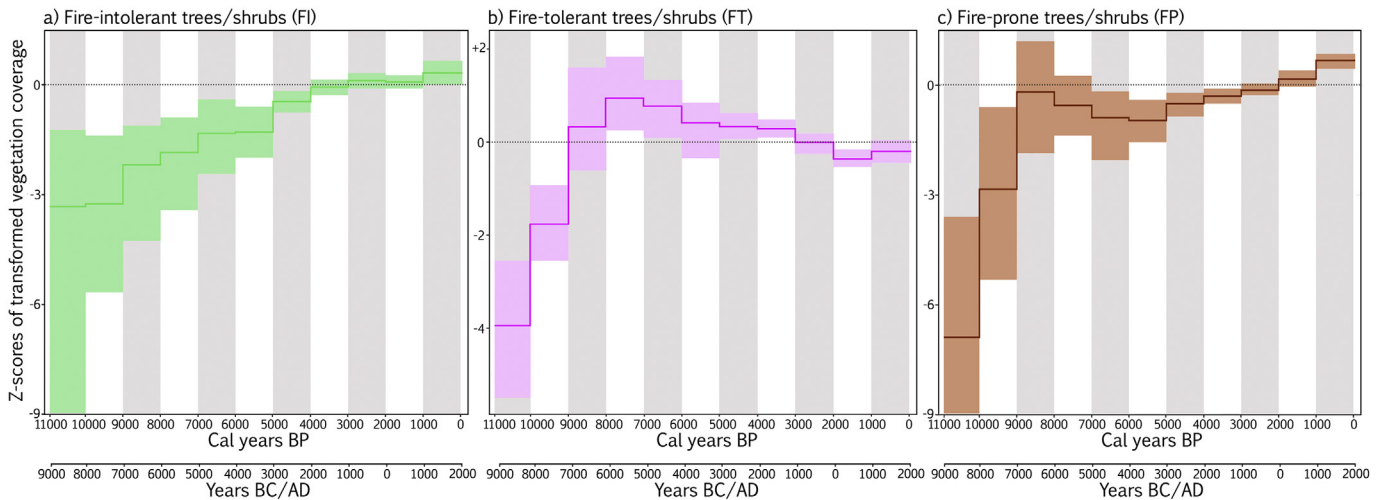


Fig. 5. Reconstruction of changes in fire-sensitivity classes of dominant vegetation cover in Fennoscandia over the Holocene: (a) fire-intolerant (FI), (b) fire-tolerant (FT), and (c) fire-prone (FP) trees/shrubs. The composite curves have been smoothed using a 500-year window half width. Colour shading represents the 95% CI calculated using the bootstrap procedure. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

high uncertainties, but the trend increased between 11,000 and 9000 cal BP (Fig. 5c). Then FP start to decrease, reaching a minimum during the interval 6000–5000 cal BP. Since this period onwards, FP are marked by a rise. Values above the long-term mean characterize the last 2000 years, with a maximum during the last millennium.

Maps of average tFI, tFT and tFP Z-scores (Fig. 6) underline the most important spatial patterns in changes of different fire-sensitivity classes of dominant vegetation cover during the Holocene (Table 2).

Between 10,000–11,000 cal BP (Fig. 6f), all classes present very low mean Z-scores (Table 2). Notably, FI are characterized by negative values for 93% of sites (43% of them strongly negative, mainly located in southern Sweden). The FT record negative Z-scores for 93% of sites (64% of them strongly negative), while FP have negative values for 71% of sites (strongly negative for 57% of them, concentrated in southern Norway and Sweden). During the period 8000–9000 cal BP (Fig. 6e), the overall mean average for the three classes increases. However, FI is still characterized by negative Z-scores for 73% of records (26% strongly negative, mainly in southern Finland). On the contrary, FT and FP are characterized by 50% of sites with positive values. Of them, strong positive FT and FP are detected for 21% (mainly in southern Finland) and 23% of sites (sparsely located), respectively. Between 6000 and 7000 cal BP (Fig. 6d), the average FI value increases but still remains below the long-term mean, with negative Z-scores for 60% of sites (26% of them, strongly negative, are concentrated in southern Finland). FT average Z-score slightly decreases but still remains positive for 77% of sites (23% of them are strongly positive). FP mean value also decreases, with negative Z-scores for 63% of sites (23% of them strongly negative). The period 4000–5000 cal BP (Fig. 6c) shows a constant increase of FI and FP average values, despite negative Z-scores for 59% and 63% of sites, respectively. On the contrary, FT mean value continue to decrease, even if 68% of sites have positive Z-scores. Between 2000 and 3000 cal BP (Fig. 6b), the mean FI Z-score increases, with positive values for 62% of sites. FT mean value slightly decreases, even if 52% of records are characterized by with positive values. On the contrary, FP mean value slightly increases, despite negative values for 55% of the sites. The last millennium (Fig. 6a) shows an increasing FI and FP mean Z-scores (with positive values for the 62% and the 69% of sites, respectively). On the contrary, the FT average value slightly decreases, with 60% of sites having negative Z-scores.

3.3. Correlation between biomass burning and fire-sensitivity classes

The relationship between changes in Holocene BB and different fire-sensitivity classes of dominant vegetation cover was analysed by relating tCHAR Z-scores and Z-scores of FI, FT and FP inferred from pollen data using PCA (Fig. 7). The vectors representing fire-sensitivity classes point in different directions. FI are more correlated to the first component or axis (PC1), except for the late Holocene when they are closer to PC3 (Fig. 7d). Whatever the time period considered, FT are more correlated with PC2, and FP are closer to PC3. BB is always more correlated to PC4 (not shown in the figure), meaning that its contribution to the analysis is low (for the whole Holocene <4% of the explained variance cumulated on the first four axes, Table 3 in Supporting Information S2). On the contrary, the analysis is chiefly controlled by FI and FT (for the whole Holocene >44 and > 33% of the explained variance cumulated on the first four axes, respectively). This means that the division of dominant vegetation composition based on its fire behaviour of the different tree and shrub taxa was consistent. The comparison of PCA' results for the whole Holocene with those of the early- and the middle-Holocene displays the same hierarchy. The eigenvalues of the different PCA axes during the early Holocene is very large (cumulated eigenvalues = 64.9) and very small during the late Holocene (cumulated eigenvalues = 2.3), indicating the greatest and the smallest dispersion of data, respectively. As already shown by the semivariogram (Fig. 3b), the lower variability between the data during the late Holocene is due to the choice of a base period between 4000 cal BP and Present. The middle Holocene reveals the most similar dispersion with the whole Holocene (cumulated eigenvalues = 23.2 and 21.3, respectively), indicating that the correlation between fire and vegetation during these two periods was similar. Furthermore, both for the whole Holocene and for the different time periods, the vector for tCHAR is closest to the vector of tFT and tFP and opposed to the tFI' vector. Over the Holocene, the correlation between BB and FT and between BB and FP is thus higher than the one found between BB and FI.

Generally, the comparison between trends in BB and the three fire-sensitivity classes of dominant vegetation during different time periods (Table 3) shows that FP are strongly positively correlated with multi-millennial variability of BB (r always >+0.40 and p <<0.001). Positive but much weaker relationships also exist

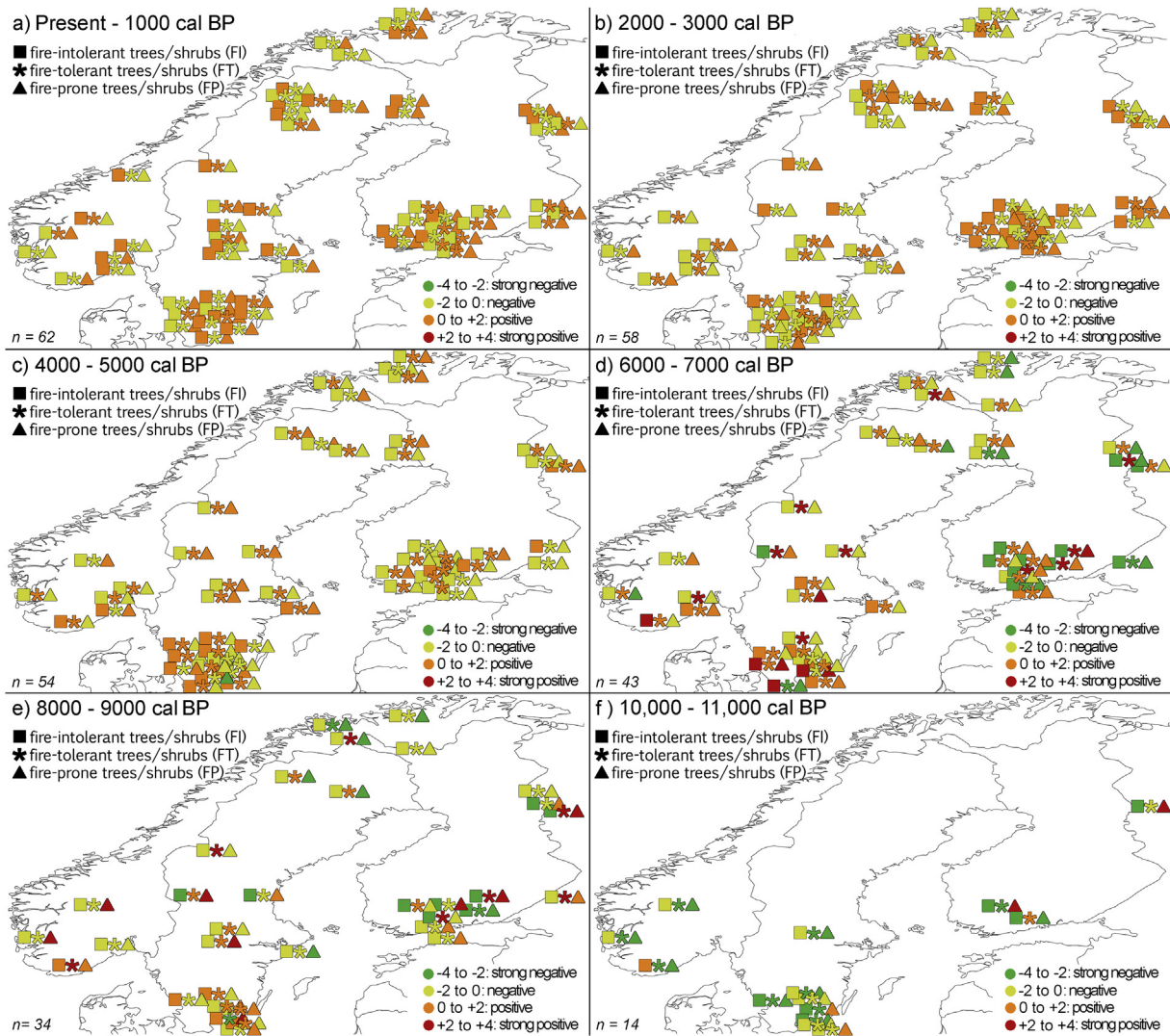


Fig. 6. Maps of mean Z-scores of transformed fire-sensitivity classes of vegetation cover for (a) Present– 1000 cal BP, (b) 2000–3000 cal BP, (c) 4000–5000 cal BP, (d) 6000–7000 cal BP, (e) 8000–9000 cal BP and (f) 10,000–11,000 cal BP. Four equal-frequency Z-score groupings were used to summarize the spatio-temporal trends in Fennoscandia fire-sensitivity classes during the Holocene. See Table 2 for more detailed information.

Table 2

Holocene trends of different fire-sensitivity classes of dominant vegetation cover in Fennoscandia expressed by mean Z-score (standard deviation, sd) and percentage of negative (–) and positive (+) site numbers.

| Cal BP (tot # sites) | Z-score FI | | | Z-score FT | | | Z-score FP | | |
|----------------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| | mean (sd) | + (#strong) | – (#strong) | mean (sd) | + (#strong) | – (#strong) | mean (sd) | + (#strong) | – (#strong) |
| 11,000–10,000 (14) | –3.80 (5.0) | 7% (0) | 93% (6) | –3.24 (2.6) | 7% (0) | 93% (9) | –2.75 (4.8) | 29% (2) | 71% (8) |
| 9000–8000 (34) | –2.64 (4.3) | 27% (0) | 73% (9) | 0.90 (3.5) | 50% (7) | 50% (3) | 0.90 (3.5) | 50% (8) | 50% (7) |
| 7000–6000 (43) | –1.39 (4.2) | 40% (4) | 60% (11) | 0.68 (3.2) | 77% (10) | 23% (4) | –1.34 (3.9) | 37% (4) | 63% (10) |
| 5000–4000 (54) | –0.33 (0.9) | 41% (0) | 59% (0) | 0.40 (0.9) | 68% (0) | 32% (0) | –0.43 (1.1) | 37% (0) | 63% (1) |
| 3000–2000 (58) | 0.11 (0.3) | 62% (0) | 38% (0) | –0.01 (0.8) | 52% (0) | 48% (0) | –0.11 (0.7) | 45% (0) | 55% (0) |
| 1000–Present (62) | 0.17 (1.0) | 62% (0) | 38% (0) | –0.23 (1.0) | 40% (0) | 60% (0) | 0.45 (0.9) | 69% (0) | 31% (0) |

between FT and long-term trends of BB (r always $>+0.10$ with $p < 0.01$ during the whole and the late Holocene, but $p > 0.10$ during the early- and the middle-Holocene). Instead, a quite strong negative correlation is detected between BB and FI, with r always < -0.17 and $p < 0.001$ (except during the middle-Holocene where $p = 0.021$). These trends are confirmed when the entire Holocene is taken into consideration as well as for the different time periods (early-, middle- and late-Holocene). However, while

the correlation is always significant for FP (positively) and FI (negatively), for FT it is weakly (positively) significant or not significant.

In order to shed more light on the relationships between Holocene BB and the different tree and shrub taxa, the same statistical methodology used for the fire-sensitivity classes was applied to each pollen type considered. Due to the limited amount of data available for certain taxa (*Fagus*, *Carpinus*, *Fraxinus*, *Salix* and

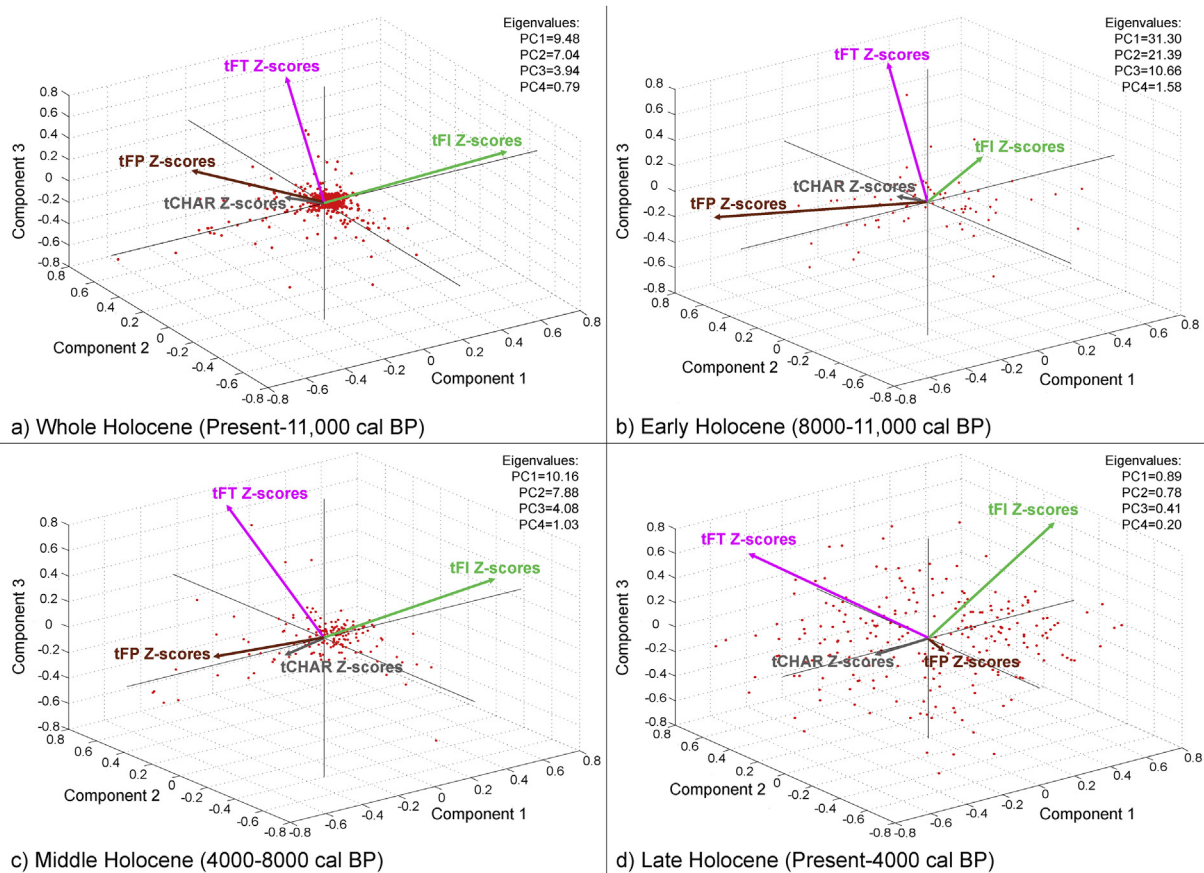


Fig. 7. PCA between biomass burning inferred from tCHAR Z-scores (grey vector) and different fire-sensitivity classes of dominant vegetation cover inferred from Z-scores of fire-intolerant (FI, green vector), fire-tolerant (FT, purple vector) and fire-prone (FP, brown vector) trees/shrubs for (a) the whole Holocene, (b) the early Holocene, (c) the middle Holocene and (d) the late Holocene. The variation retained by each principal component (explained by the eigenvalues) is also given. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3

Results of the Pearson's correlation analysis between Fennoscandia biomass burning activity and different fire-sensitivity classes of dominant vegetation cover on millennial time scales. For the whole Holocene, the correlation was also analysed for each different pollen taxa. Significant correlation coefficients (r), p -values and adjusted $p_{\text{Holm-Bonferroni}}$ -values are in bold.

| Time period | Fire-sensitivity class | r | p -value | $p_{\text{Holm-Bonferroni}}$ -value | Taxon | r | p -value | $p_{\text{Holm-Bonferroni}}$ -value |
|-----------------|------------------------|--------------|--------------|-------------------------------------|------------------|--------------|---------------------------|-------------------------------------|
| Whole Holocene | FI | -0.23 | <<0.001 | <<0.001 | <i>Fraxinus</i> | -0.25 | 0.067 | 0.538 |
| | | | | | <i>Picea</i> | -0.32 | <<0.001 | <<0.001 |
| | | | | | <i>Tilia</i> | -0.20 | 0.003 | 0.025 |
| | | | | | <i>Ulmus</i> | -0.22 | <0.001 | 0.007 |
| | FT | +0.13 | 0.005 | 0.026 | <i>Alnus</i> | +0.05 | 0.308 | 1.54 |
| | | | | | <i>Carpinus</i> | +0.02 | 0.893 | 1.41 |
| | | | | | <i>Corylus</i> | +0.08 | 0.191 | 1.34 |
| | | | | | <i>Fagus</i> | +0.13 | 0.575 | 2.30 |
| | | | | | <i>Juniperus</i> | +0.04 | 0.622 | 2.30 |
| | | | | | <i>Quercus</i> | +0.09 | 0.216 | 1.34 |
| FP | +0.41 | <<0.001 | <<0.001 | <i>Salix</i> | +0.01 | 0.704 | 1.87 | |
| | | | | <i>Betula</i> | +0.32 | <<0.001 | <<0.001 | |
| | | | | Ericaceae | +0.48 | <<0.001 | <<0.001 | |
| | | | | <i>Pinus</i> | +0.40 | <<0.001 | <<0.001 | |
| | <i>Populus</i> | +0.32 | <<0.001 | 0.003 | | | | |
| Early Holocene | FI | -0.42 | <0.001 | 0.001 | | | not enough data available | |
| | FT | +0.16 | 0.164 | 0.328 | | | | |
| | FP | +0.40 | <0.001 | 0.003 | | | | |
| Middle Holocene | FI | -0.17 | 0.021 | 0.062 | | | not enough data available | |
| | FT | +0.10 | 0.173 | 0.328 | | | | |
| | FP | +0.43 | <<0.001 | <<0.001 | | | | |
| Late Holocene | FI | -0.36 | <<0.001 | <<0.001 | | | not enough data available | |
| | FT | +0.17 | 0.007 | 0.030 | | | | |
| | FP | +0.44 | <<0.001 | <<0.001 | | | | |

Populus) during the early Holocene, we only considered the whole Holocene without division into different time periods. The results of the statistical analyses (Table 3) show a significant strong positive correlation between long-term trends of BB and Ericaceae, *Pinus*, *Betula* and *Populus* (r always >0.32 and $p < 0.001$). Non-significant relationships exist between BB and *Fagus*, *Quercus*, *Corylus*, *Alnus*, *Juniperus*, *Carpinus* and *Salix* (r always <0.13 and $p > 0.19$). A strong negative significant correlation is detected between *Picea* and *Ulmus* and multi-millennial variability of BB ($r = -0.32$ and -0.22 , respectively and $p < 0.001$). A negative significant (but much weaker) relationship also exists between BB and *Tilia* ($r = -0.20$, $p < 0.01$), whereas for *Fraxinus* the relationship is not significant ($r = -0.25$; $p > 0.05$).

4. Discussion

By studying the long-term interactions between different fire-sensitivity classes of vegetation cover and biomass burning, our results revealed that the dominance of trees and shrubs was strongly connected with fire regime during the postglacial in Fennoscandia. Specifically, when the entire Holocene is considered, our data support the initial hypothesis that fire-prone and, to a less extent, fire-tolerant taxa are more abundant during periods characterized by higher fire disturbance on vegetation, while fire-intolerant trees and shrubs dominate when biomass burning is low. Despite the limited amount of data available for the early Holocene compared to the middle and late Holocene, these conclusions are confirmed for all the three different time periods considered, although human activities probably altered the strength of fire-vegetation interactions during the last millennia. Fire thus clearly appears as a chief functional driver of tree and shrub abundance in boreal and cold temperate forests of Fennoscandia.

4.1. Fire-vegetation interactions

By selecting dominant taxa according to their fire strategies, our analyses indicate that vegetation composition significantly interplayed with the fire regime throughout the Holocene. Fire resistant taxa dominated when more frequent fires occurred, because of their low fire-induced mortality rates (Rogers et al., 2015). As shown by our results, during periods of higher biomass burning, the sites were dominated by fire-prone species (i.e., *Pinus*, *Betula*, *Populus* and Ericaceae). These taxa typically develop strategies to protect meristems of the whole plant or some plant sections, like roots or underground stems. Furthermore, the morphological traits of *Pinus*, *Betula* and *Populus* allow these species to quickly colonize burned soils (Bradshaw et al., 2010) and, for *Populus*, to resprout (De Chantal et al., 2005). Thick bark protects the cambium and increases the species' chance of survival (Nikolov and Helmsaari, 1992) by reducing the wood susceptibility (Fréjaville et al., 2013). Similarly, high crown-base height helps trees to escape fires (Fréjaville et al., 2018), for instance here in *Pinus sylvestris* or *Populus tremula*. Additionally, most of taxa belonging to the Ericaceae family (chiefly *Calluna vulgaris*) are fire-adapted plants because their meristems are protected in soil if fire is not too intense; thanks to a rapid post-fire seed production, the abundance of *Calluna* increases on recently burned sites and regenerates well by seed from the soil seed-bank (Mallik et al., 1984).

Fire-tolerant taxa include species that show pronounced negative relationships with fire without suffering local extinction (i.e., *Alnus*, *Carpinus*, *Juniperus*), species whose presence is not clearly connected with changes in biomass burning (i.e., *Quercus*), or species slightly favoured by fire due to their re-sprouting trait (i.e.,

Corylus, *Salix*) or their enhanced regeneration after fire (i.e., *Fagus*) (Goldammer and Furyaev, 1996; Niklasson et al., 2002). Reasonably, due to the lack of a common rule on the relationship between fire-tolerant taxa and fire, our results show a general low positive and not significant correlation between the species included in this class and multi-millennial BB variability.

Fire-intolerant taxa typically lack fire-adapted morphological traits (Fréjaville et al., 2013) and are usually found in mesic environments where fires are infrequent (Nikolov and Helmsaari, 1992). Therefore, as highlighted by our findings, it is likely that during periods of lower BB the vegetation was dominated by these species (i.e., *Picea*, *Fraxinus*, *Tilia* and *Ulmus*). *Picea* has thin bark and shallow roots making it susceptible to fire (Zackrisson, 1977; Pennanen, 2002). Among studies supporting our results in the study area, it has been suggested that *Picea* was most often the dominant tree species in northern Swedish areas where fires were rare or absent (Linder et al., 1997). It has also been argued that the expansion of *Picea* during the late Holocene in boreal Scandinavia caused the decline in fire activity by altering microclimate conditions beneath the canopy by increasing the moisture Ohlson et al. (2011). Additionally, Clear et al. (2015) documented a decline in fire activity when *Picea* established as the dominant species in an old-growth forest of southern Finland. The same authors also testify the severe reduction/local extinction of *Fraxinus*, *Tilia* and *Ulmus* after a fire, and the strongly connected occurrence of these taxa with low fire frequencies.

4.2. Risks and uncertainties associated with such large-scale reconstruction

The different spatial resolutions represented by the pollen and charcoal palaeorecords selected for this synthesis is one of the important limitations of our study. During the last fifty years, investigations of pollen-vegetation relationships and attempts to calibrate these relationships through estimates of pollen productivity, dispersal and pollen source area have significantly advanced the ability to reconstruct past plant cover on a quantitative basis (i.e., Parsons and Prentice, 1981; Sugita, 1994). In this study, we applied a simplified version of the REVEALS model (Sugita, 2007a) in order to account for different production and dispersal of pollen among taxa, with the expectation that this should improve the accuracy of our results than by using pollen percentages alone.

Concerning the spatial fidelity of charcoal accumulation, an increasing body of literature on charcoal production, deposition and dispersal after experimental burning (i.e., Clark et al., 1998; Ohlson and Tryterud, 2000; Lynch et al., 2004) has formed general consensus that charcoal source area is on the order of few hundred meters (first and main charcoal load) to few kilometres (secondary load), depending greatly upon fire-intensity, particle size and weather conditions during fires (wind). Thus, finer particles are normally transported longer distances (up to 30 km) through the atmosphere than coarser particles, although considerable variability exists among different estimates due to context variability, e.g. fire-severity and area of experimental and empirical fires (i.e., Clark, 1988; Higuera et al., 2007; Hennebelle et al., in press).

The use of the Landscape Reconstruction Algorithm (LRA, Sugita, 2007a, b) would have provided pollen-based reconstructions of regional and local vegetation in quantitative terms, i.e., plant cover at a known spatial scale (few meters to kilometres from the centre of the lake or peat). Although more time consuming compared to the approach followed in this study, the Sugita's method would have increased the precision of our vegetation cover reconstructions. However, given the need of further investigations about the spatial extent of burning associated with a charcoal

record (Kelly et al., 2013), we believe that the systematic use of the LRA approach would not have significantly improved our results.

Despite these uncertainties, the investigation of the long-term relationship between fire and fuel presented here gives us a clear indication that Fennoscandian vegetation composition strongly interacted with fires during the Holocene. The chicken or egg causality dilemma about the driver of this interaction, however, is not solved by our research. The statistical analyses here performed, in fact, can detect correlation between datasets rather than causation. Only site-specific, high-resolution and spatially-accurate studies based on numerical analyses (e.g., Blarquez and Carcaillet, 2010) can indeed answer the question “Is it fire or fuel that controls the system?”

4.3. Suggestions for reducing fire risk in Fennoscandia

The Environmental Outlook to 2030 of the Organisation for Economic Co-operation and Development (OECD) suggests that northern European forest fires will increase concurrently with longer fire seasons (EEA, 2019). Furthermore, together with a rise in droughts, storms, logging and consumption of wood for fuel, increasing fires are expected to reduce forest ecosystem services. At the same time, as a result of a warmer climate and longer growing seasons, a shift of forest tree species towards higher altitudes and latitudes, an expansion of fire-prone areas and an increase in forest growth are expected. These combined impacts will considerably affect forest structure and the functioning of forest ecosystems. By removing soil organic matter, severe fires might cause erosion and loss of nutrients and biodiversity, which may turn forest soils into carbon sources for transfer toward the atmosphere with consequences on climate warming (Santín and Doerr, 2016).

As tragically seen with extreme heat waves combined with droughts in 2014 and even stronger in summer 2018 and spring 2019, with the ongoing global warming Fennoscandian forests become more susceptible to fires. This rising risk has already been forecasted by model simulations, showing that the warmest month and net forest productivity are the main drivers of increasing fire probabilities (Moritz et al., 2012). Projected changes in meteorological forest fire danger during the period 2071–2100 (in an average year) for a high emissions scenario compared with the period 1981–2010 demonstrate that, even if the average fire danger will not significantly change in Fennoscandia (except at higher northern latitudes), the risk of extreme fire events in these regions can increase substantially (de Rigo et al., 2017). Furthermore, based on the present study, we show that fire-prone trees and shrubs are favoured by fires, and fires are stimulated in forests dominated by these species that produce more ignitable and consumable ecosystems. This positive feedback should naturally sustain fire-prone forests, unless plant cover was modified to reduce the fuel flammability by supporting fire-intolerant species at best, such as *Picea*, *Tilia* or *Fraxinus*. It has been demonstrated that vegetation can offset the effect of climate on fire regime (Girardin et al., 2013; Dash et al., 2016). Therefore, the promotion of broadleaf trees in mixed forests could decrease the intensity and rate of fire spread, improving suppression effectiveness and reducing wildfire impacts (Hirsch et al., 2004). Finally, thanks to their higher albedo and summer evapotranspiration, the increasing dominance of broadleaf taxa could also counteract regional warming (Rogers et al., 2013).

5. Conclusions

Despite the importance of integrating vegetation attributes into models forecasting future fire risk (Iglesias et al., 2015), this is one of the few palaeoecological studies providing information about quantified forest taxa reconstructions to support fire histories.

Model simulations forecast a rise in temperature with increasing atmospheric greenhouse gas concentrations for the end of the 21st century (IPCC, 2014) and a probable intensification of fire hazard (Flannigan et al., 2009; Moritz et al., 2012). As shown in this paper, taxa with different flammability characteristics interact with past fire occurrence in different ways, preserving a general pattern throughout the Holocene. This is an indication that, amongst other drivers such as climate and anthropogenic activities, vegetation is dependent on biomass burning and, *vice versa*, biomass burning is fuel-dependent. As already suggested (Ohlson et al., 2011; Girardin et al., 2013; Héon et al., 2014), changes in fuel availability and type could thus alter long-term fire ignition and spread (Clark et al., 2001). Our palaeoenvironmental study explores this relationship in a long-term perspective and presents useful information for improving the ability to manage ecosystems during current and future environmental changes (Dearing et al., 2012; Conedera et al., 2017; Velez et al., 2018). In a changing world, where higher fire activity constitutes an unknown factor in the global carbon cycle and a potential threat to ecosystem services, fire management based on interdisciplinary knowledge represents a challenge.

Data availability statement

Sedimentary charcoal data used in this analysis are either stored in the Global Charcoal Database (<http://paleofire.org>) and accessible through the paleofire package (Blarquez et al., 2014) for R (R Development Core Team, 2016), or are available from the corresponding author upon request. Fossil pollen data can be obtained from the corresponding author or from the original published papers (detailed information in Supporting Information S1).

Author contributions

C.M. conceived and designed the study, compiled and analysed the data, made the figures and drafted the manuscript. V.L. designed and carried out the statistical analyses. C.C. and R.H.W.B. contributed to the writing and editing of the manuscript. G.E.H. contributed with unpublished charcoal and pollen data. All authors read and approved the final manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2020.106408>.

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