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Regional variability in peatland burning at mid-to high-latitudes during the Holocene

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ABSTRACT

Northern peatlands store globally-important amounts of carbon in the form of partly decomposed plant detritus. Drying associated with climate and land-use change may lead to increased fire frequency and severity in peatlands and the rapid loss of carbon to the atmosphere. However, our understanding of the patterns and drivers of peatland burning on an appropriate decadal to millennial timescale relies heavily on individual site-based reconstructions. For the first time, we synthesise peatland macrocharcoal records from across North America, Europe, and Patagonia to reveal regional variation in peatland burning during the Holocene. We used an existing database of proximal sedimentary charcoal to represent regional burning trends in the wider landscape for each region. Long-term trends in peatland burning appear to be largely climate driven, with human activities likely having an increasing influence in the late Holocene. Warmer conditions during the Holocene Thermal Maximum (~9–6 cal. ka BP) were associated with greater peatland burning in North America's Atlantic coast, southern Scandinavia and the Baltics, and Patagonia. Since the Little Ice Age, peatland burning has declined across North America and in some areas of Europe. This decline is mirrored by a decrease in wider landscape burning in some, but not all sub-regions, linked to fire-suppression policies, and landscape fragmentation caused by agricultural expansion. Peatlands demonstrate lower susceptibility to burning than the wider landscape in several instances, probably because of autogenic processes that maintain high levels of near-surface wetness

Carbon balance
Drought

even during drought. Nonetheless, widespread drying and degradation of peatlands, particularly in Europe, has likely increased their vulnerability to burning in recent centuries. Consequently, peatland restoration efforts are important to mitigate the risk of peatland fire under a changing climate. Finally, we make recommendations for future research to improve our understanding of the controls on peatland fires.

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1. Introduction

Peatlands cover only ~3% of global land area (Xu et al., 2018), but the carbon they store is equivalent to around twice that of global forests (Pan et al., 2011). Peatlands have accumulated ~600 Gt of carbon during the Holocene, primarily at mid-to high-latitudes in the Northern Hemisphere (Yu et al., 2010). Increasingly deeper peatland water tables associated with climate change and human activities (e.g. agriculture, forestry, peat harvesting or road construction) will likely increase the frequency and extent of fires (Flannigan et al., 2009; Turetsky et al., 2015). Furthermore, greater incidence of lightning with warming will increase the frequency of naturally ignited wildfire, particularly in high-latitude ecosystems (He et al., 2022; McCarty et al., 2021). The burning of deep peat releases carbon into the atmosphere that has been stored for centuries or millennia, and may therefore contribute to positive feedbacks influencing climate warming (Davies et al., 2013; Lin et al., 2021). Similarly, burning influences peatland vegetation dynamics, surface moisture and plant productivity – all of which influence the carbon balance (Nelson et al., 2021).

Peatlands are subject to both smouldering and flaming combustion. Smouldering combustion has the potential to cause greater direct carbon losses (Rein, 2013). Smouldering peatland fires can last for months, even burning throughout the winter under the snow layer (Rein and Huang, 2021). Burning of surface vegetation may lead to indirect carbon losses via modification of the peatland thermal regime (Brown et al., 2015) or hydrology (Wilkinson et al., 2020). Peatlands store large amounts of potential fuel in the form of partially decomposed organic matter, but typically have high surface moisture content, which limits the chance of ignition and fire propagation (Frandsen, 1997). Furthermore, wildfire can drive permafrost thaw in boreal peatlands, leading to surface wetting (Gibson et al., 2018). Drying caused by the aggradation of permafrost during the Holocene has been shown to have increased the susceptibility of peatlands to fire in North America (Zoltai et al., 1998). Contemporary climatic warming and human disturbance are thought to be increasing peatland vulnerability to wildfire (Nelson et al., 2021). The composition of vegetation cover is an important influence on peatland fire dynamics. Forested peatlands generally burn more frequently than open peatlands (Kuhry, 1994; Magnan et al., 2012), as these ecosystems have increased above-ground fuel availability (Thompson et al., 2019).

Patterns in peatland burning vary among biomes and can differ from the fire regime at a landscape scale. For example, boreal peatlands in Canada exhibit mean fire return intervals of ~600–2950 years compared to ~200–1150 years in upland forests (Camill et al., 2009). In Europe, a mean fire interval of ~475 years has been estimated from peatland areas in boreal Norway (Ohlson et al., 2006), while a temperate peatland area in continental Europe showed a frequency of 0–2 fires per 1000 years (Marcisz et al., 2019). The complex ecohydrological dynamics of peatlands interact with changes in local and extra-local vegetation composition, climate and human activities to affect the frequency and severity of peatland fires (Feurdean et al., 2022; Morris et al., 2015; Słowiński et al., 2022).

The long timescales involved in peatland development, climatic change, vegetation dynamics and fire regimes mean that contemporary monitoring studies may not provide a full picture of peatland fire dynamics. Several continental and global syntheses have used sedimentary charcoal records to reconstruct biomass burning on millennial timescales (Daniau et al., 2012; Marlon et al., 2008, 2016), but no such studies currently exist specifically for peatlands. Consequently, uncertainties remain regarding the long-term ecology of peatland fires on a continental scale. Here, we use a palaeoenvironmental approach to explore regional variability in peatland burning trends at mid-to high-latitudes in North America, Europe and Patagonia on a timescale that provides a baseline for peatland fire dynamics and to better understand the past and present controls on peatland fire.

2. Materials and methods

2.1. Study regions

We compiled and quality checked macrocharcoal records (we defined macrocharcoal as particles with a diameter >100 µm (Mooney and Tinner, 2011)) spanning 10,000 cal Yr BP to the present day from mid-to high-latitude peatlands in North America (sites = 68, records = 108), Europe (sites = 95, records = 103), and Patagonia (sites = 9, records = 10). The Patagonian region also includes a record from the Falkland Islands (Malvinas). Chronological quality control criteria are outlined in Section 2.3. These data provide good spatial coverage of peatland areas in North America and Europe (Fig. 1; Table S1). We divided North America and Europe into sub-regions to account for spatial differences in modern climate, human occupation and key peatland areas. Only basic analyses were possible for Patagonia due to the low number of sites. We characterised the average modern climatic space of peatland sites and sub-regions using monthly climate data from the CRU TS 4.04 dataset for the 1981–2010 CE period (Harris et al., 2020). These data have been interpolated from climate stations to a 0.5° latitude by 0.5° longitude spatial resolution.

2.2. Charcoal data

Theoretical models suggest that the dispersal distance of charcoal decreases with particle size (Clark, 1988; Clark et al., 1998; Clark and Patterson, 1997; Higuera et al., 2007; Peters and Higuera, 2007). There is evidence that suggests macrocharcoal records (>100–200 µm) represent local scale fires within a few hundred meters (Carcaillet et al., 2001; Clark and Royall, 1995, 1996) or within several kilometres of a coring location (Feurdean et al., 2022, 2020a; Tinner et al., 2006). Source areas of macrocharcoal across Europe may be up to 40 km, but these findings are in relatively open landscapes and specifically for lacustrine settings (Adolf et al., 2018). Peatlands are thought to provide a more localised record of past fire occurrences than lakes because they experience limited secondary deposition by fluvial transport (Florescu et al., 2018; Remy et al., 2018). Furthermore, the peatland records may provide higher resolution information because they are not subjected to the

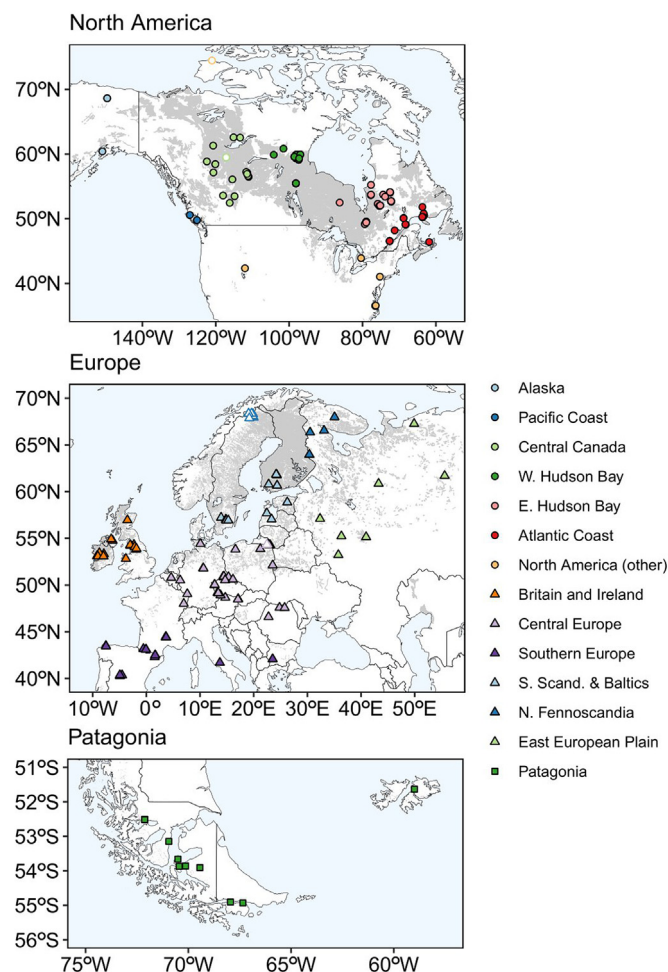


Fig. 1. Site map of peatland record locations and their sub-region. Symbols with a white fill indicate that no charcoal was present throughout a record. Grey shading denotes peatland areas sourced from PEATMAP (Xu et al., 2018).

same sediment reworking as in lakes (Clark and Patterson, 1997; Conedera et al., 2009; Oswald et al., 2005).

For these reasons, we assume that our peatland macrocharcoal records (>100 μm) are primarily a proxy for burning of peatland aboveground vegetation or burning of the peat itself. However, we cannot rule out the influence of some charcoal input from vegetation in immediate vicinity of the peatland and in some instances from a regional source – especially from intense crown fires or those occurring during high winds (Gardner and Whitlock, 2001; Peters and Higuera, 2007). There is evidence of fine-scale variation in the quantity of charcoal within a peatland relating to topography, fuel type and land-use history (Cui et al., 2020; Kasin et al., 2013) that we cannot account for in this study. Similarly, particularly severe in-situ smouldering fires can consume much of the charcoal they produce and cause some loss of the peatland archive (Zaccone et al., 2014).

To enable a comparison of localised peatland burning to that in the wider regional landscape, we selected records that were proximal to our peatland sites (see Fig. S1) from the Global Charcoal Database (GCD) v.4.0.7 using the Paleofire package v.1.2.4 (Blarquez et al., 2014) in R v.4.0.5 (R Core Team, 2021). These records from the GCD include microcharcoal and macrocharcoal and are from a variety of sedimentary archives, excluding those listed as a bog, fen or mire. These records are assumed to provide a record of regional biomass burning (Marlon et al., 2016). We ensured that the wider

landscape sites that pertained to each sub-region were within a convex hull defined by the loci of the peatland sites in that sub-region, or no more than 200 km outside it (150 km in central Europe to avoid duplication of sites). Further details of the wider landscape records selected from the GCD can be found in Fig. S1 and Table S2. Where peatland macrocharcoal records from the GCD met our quality control criteria, we included them in our peatland burning dataset (see Table S1).

2.3. Age-depth modelling

In order to standardise the methodology used for age-depth modelling, we produced new Bayesian age-depth models (Figs. S2–S38) for each peatland record from chronological information such as ^{14}C , ^{210}Pb , tephra layers and spheroidal carbonaceous particles (SCPs), using the rbacon package v.2.5.7 (Blaauw et al., 2021) in R (R Core Team, 2021). We established quality control criteria that required cores to comprise at least ten sample depths, to have a chronology spanning at least 500 years, and to have a date (e.g. ^{210}Pb , ^{14}C or tephra) at least every 2500 years on average. Prior information on accumulation rate and its memory or variability can be found for each age-depth model in Figs. S2–S38.

2.4. Resampling and transformation

The peatland macrocharcoal records that we used have been compiled using a variety of methods (e.g. particle counts, area measurements and relative abundances) and a range of particle size fractions (e.g. >125 μm , >150 μm and >0.5 mm). This variability in measurement approach can result in values that differ by orders of magnitude and therefore data standardisation is required to compare relative changes between records over time (Power et al., 2010). Furthermore, owing to varying accumulation rates within and among cores, standardisation of temporal resolution via binning or smoothing is required to avoid an inflated influence of high-resolution samples on any subsequent analyses. Macrocharcoal occurs in 47.8% (12,321 out of 25,758) of pre-binned peat samples. We used proportional relative scaling (PRS) - developed specifically for systems where fire is rare (McMichael et al., 2021) - and presence/absence analyses to standardise our peatland records (see below).

2.4.1. Proportional relative scaling and presence/absence

For the PRS and presence/absence analyses, we developed a new method to resample the temporal resolution of raw charcoal data proportionally into equal 50-year time bins using depth intervals calculated from age-depth models (Fig. S39). This approach minimises potential distortion from non-contiguous sampling, particularly for records with infrequent sampling (Fig. S40). The proportion of samples containing charcoal is important for calculating both PRS and presence/absence; therefore, we applied the depth binning approach to resample the data prior to calculation of PRS and presence/absence. We calculated presence/absence for each resampled record, and the percentage of sites containing charcoal for each 50-year period in North America, Europe, Patagonia and sub-regions of interest. To calculate PRS for each record, we divided individual resampled charcoal values (C_i) by the maximum resampled charcoal value from that record (C_{max}) and multiplied by 100. We then scaled this value by the proportion of resampled values containing charcoal. The PRS formula applied to our resampled charcoal data is as follows:

$$\text{char}_{\text{pscaled}} = \left(\frac{c_i}{c_{\text{max}}} \times 100 \right) \frac{f}{N}$$

Where $\text{char}_{\text{pscaled}}$ is proportionally relatively scaled charcoal values, c_i is a singular resampled charcoal value within a record, c_{max} is the maximum resampled charcoal value within that same record, f is the number of resampled values containing charcoal (value > 0) within that same record and N is the total number of resampled values within that same record. We subsequently applied a cubic root transformation to PRS values to aid data visualization and reduce positive skew.

PRS adjusts the magnitude of charcoal records by the frequency of charcoal occurrence, down-weighting records with infrequent charcoal. This scaling is based on observations from tropical lake records collected using the same method, where a low frequency of samples containing charcoal was related to a lower maximum abundance of charcoal (McMichael et al., 2021). We assessed the effect of PRS on our data by comparing records from the three most common particle sizes (>150 μm , >0.5 mm and >1 mm) that expressed charcoal quantity as a concentration (particles cm^{-3}). This comparison tested whether, for peatland records analysed in a similar fashion, a greater maximum charcoal value was associated with a higher proportion of samples containing charcoal. We found that the maximum charcoal value (c_{max}) of a record increased across the three particle sizes when a greater proportion of resampled values contained charcoal (Fig. S41). This relationship suggests the down-weighting in PRS of sites exhibiting a low proportion of total samples containing charcoal is an appropriate approach for inter-site comparisons of peatland macrocharcoal data.

2.4.2. Comparison of peatland burning to the wider landscape

The wider landscape charcoal records represent the regional fire signal proximal to our peatland records, while excluding data specifically from peatlands (see Section 2.2 for further details). Sufficient chronological information was not available from the GCD to apply our depth binning approach to sites representing biomass burning in the wider landscape. Therefore, we used an established method from major composite analyses of sedimentary charcoal records from the GCD that involves a Box-Cox, a min-max and a z-score transformation (Daniau et al., 2012; Marlon et al., 2016, 2008). We applied the Box-Cox, min-max and z-score transformations to our peatland dataset (Table S1) and the wider landscape dataset from the GCD (Table S2) using the Paleofire package (Blarquez et al., 2014) in R. The Paleofire package cannot analyse records with a complete absence of charcoal, so these were excluded from this part of the analysis. We pre-binned the data in 50-year non-overlapping bins and used a 500-year smoothing window to produce charcoal composite curves for North America, Europe and sub-regions of interest. There were too few sites in the GCD to produce a robust z-score reconstruction for Patagonia. Similarly, there were too few peatland records to produce sub-region composite curves for Alaska, the Pacific Coast, the East European Plain and Northern Fennoscandia – although these data are included in the continental scale composite curves.

3. Results and discussion

3.1. Overview of findings

North America, Europe and Patagonia exhibited distinct spatiotemporal patterns of peatland burning from 10 ka (with ka meaning calibrated thousands of years before 1950 CE) to the present (Fig. 2). In North America, there was a general increase in

peatland burning from 10 to ~0.5 ka (Fig. 2A and B), but there is a high degree of regional variability (Fig. 3). These burning trends largely correspond with changing climatic conditions and/or vegetation dynamics in the wider landscape, but where these trends diverge peatland autogenic processes may be important. From ~0.5 ka to the present we see a widespread decrease in peatland burning that may have been initiated by the Little Ice Age (LIA) cooling. The tendency of peatlands to retain high surface moisture content even during drought (Kettridge and Waddington, 2014; Morris and Waddington, 2011), and a general policy of fire suppression since the early-twentieth century, may be in part responsible for this recent downturn in burning. We must also consider the possibility that researchers may have avoided disturbed peatland areas affected by recent fires when collecting cores, but this is unlikely to be the sole factor at play here. Our European composite record shows more peatland burning in the early Holocene from 10 to 8 ka, a period during which our database is composed primarily of records from central Europe and southern Scandinavia and the Baltics (Fig. 2). Relatively constant levels of peatland burning are observed after 8 ka, but with marked increases at ~5 ka and from 1.5 to 0.5 ka (Fig. 2). Burning in the wider landscape of Europe increases conspicuously from 6.5 to 5.5 ka and, unlike the peat record, shows an overall increase in the last four centuries.

3.2. Regional analyses

3.2.1. North America

From 10 to 8 ka our records from North America show a slight increase in burning in both peatlands and the wider landscape (Fig. 2) that is coincident with rising summer temperatures at a continental scale (Viau et al., 2006). However, we have a dearth of records in the early Holocene from 10 to 8 ka in North America and therefore cannot make detailed inferences about burning trends for that time. During the early Holocene, growing seasons became gradually longer and warmer in driving widespread peatland initiation in western and eastern North America from ~14.5 ka, with initiation in central Canada and the Hudson Bay lowlands from ~8.5 ka onwards following increasing temperatures and ice sheet retreat (Gorham et al., 2007; Morris et al., 2018; Ruppel et al., 2013).

Warmer and drier conditions during the Holocene Thermal Maximum (HTM) were likely responsible for greater peatland burning from 8 to 7 ka in central Canada (Edwards et al., 1996; Kuhry, 1994). Similarly, increased burning in the wider landscape from 8 to 7 ka (Fig. 3C) coincides with the northward expansion of conifer forests (Williams, 2003) and this may also be a factor in increased peatland burning. Expansion of peatland area in central Canada from ~6 ka onwards suggests reduced aridity (Ruppel et al., 2013; Zoltai and Vitt, 1990), loosely corresponding to lower peatland burning ~7 to ~3 ka although burning in the wider landscape remains elevated until ~5 ka (Fig. 3A–C). Nevertheless, our findings from central Canada prior to ~3 ka for peatlands should be treated with a degree of caution because only a small number of records span this time. Between 3 and 0 ka summer cooling and higher annual precipitation (Viau and Gajewski, 2009) correspond with decreased burning in the wider landscape, while peatland burning begins to decrease at ~1 ka with this trend continuing until present (Fig. 3A–C). Around one fifth of our peatland records from central Canada (22.2%) show local evidence of permafrost aggradation linked to late-Holocene cooling, particularly during the LIA (see Magnan et al., 2018; Pelletier et al., 2017). Drier peatland conditions caused by surface uplift during permafrost aggradation may have contributed to sustained levels of peatland burning until 0.5 ka. Similarly, permafrost thaw driven by twentieth century warming (Pelletier et al., 2017) offers a plausible explanation for a recent

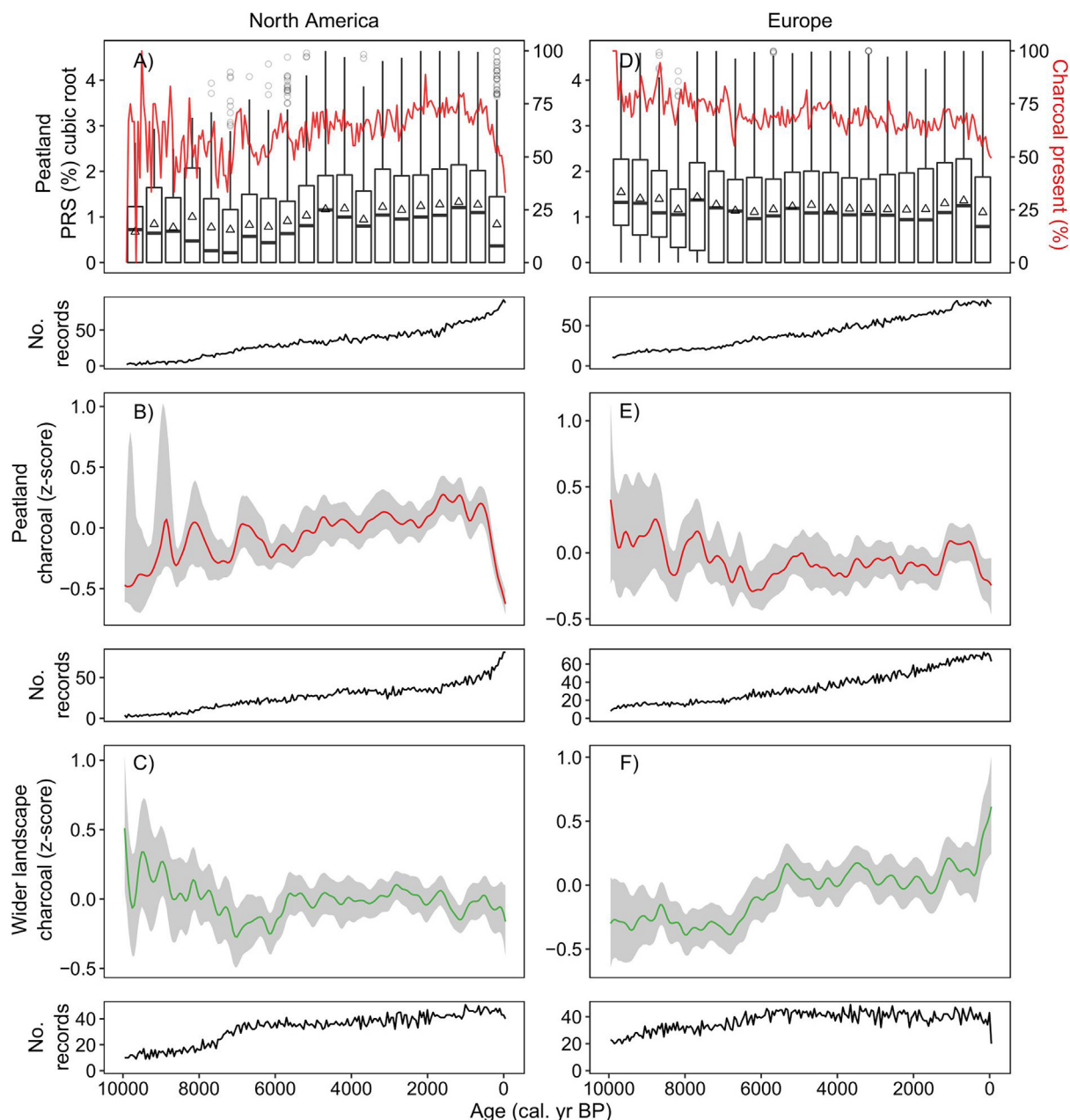


Fig. 2. Peatland and wider landscape burning trends by region. The distribution of proportionally relatively scaled (PRS) charcoal values (cubic root transformed) in 500-year bins for A) North America and D) Europe; box heights represent the upper and lower quartiles, centrelines indicate medians, hollow triangles represent means, whiskers extend to 1.5 times the interquartile range beyond the upper and lower quartiles, and hollow circles represent any values outside the range of these whiskers. Trends in the proportion of records (%) with charcoal present within 50-year bins indicated by the red line. Biomass burning trends for peatlands in B) North America and E) Europe and wider landscape biomass burning for C) North America and F) Europe — all with a 500-year smoothing window and showing 95% bootstrap confidence intervals (1000 cycles). The x-axis units (cal. yr BP) represent years before 1950 CE. For each panel the number of sites corresponds to 50-year time steps.

decrease in peatland burning, although wetting from permafrost thaw can be short-lived (Magnan et al., 2018).

During the mid-Holocene, warm and moist climatic conditions existed across the Hudson Bay region, prior to cooler and generally moist conditions during the Neoglacial from around 2.5 ka onwards (Camill et al., 2012; Hargan et al., 2020; Hobbs et al., 2017). These warmer conditions in the mid-Holocene were associated with less frequent intrusions of cool, dry Pacific or Arctic air masses, resulting in fewer periods of late-spring or summer drought that are conducive to fire activity (Carcaillat and Richard, 2000; Edwards et al., 1996). We observe increasing levels of peatland burning

from 8 to 4.5 ka in the western Hudson Bay, along with increased burning in peatlands and the wider landscape in the eastern Hudson Bay from 7 to 4.5 ka (Fig. 3). However, it should be noted that there are spatial gaps in our dataset with few records from Hudson Bay Lowlands and to the west of James Bay (Fig. 1). During the mid-Holocene many peatlands in the Hudson Bay region were transitioning from wet fens to drier bogs and this reduction in surface wetness and increased potential for the build-up of woody biomass likely made peatlands more susceptible to fire, especially if the sites became forested (Camill et al., 2009; Davies et al., 2023, 2021; Hokanson et al., 2016; Magnan et al., 2020, 2012; van Bellen

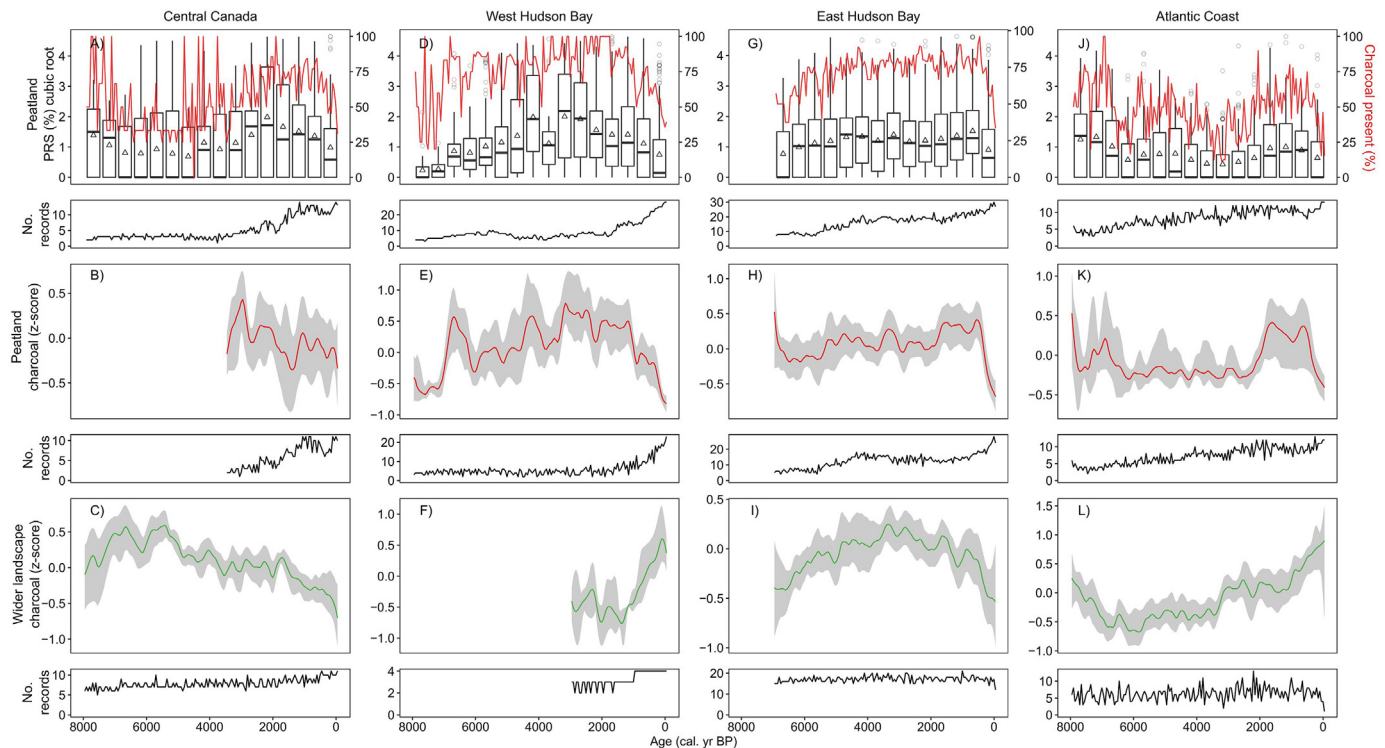


Fig. 3. Peatland and wider landscape burning trends by North American sub-region. The distribution of proportionally relatively scaled (PRS) charcoal values (cubic root transformed) in 500-year bins for A) Central Canada, D) West Hudson Bay, G) East Hudson Bay and J) Atlantic coast; box heights represent the upper and lower quartiles, centrelines indicate medians, hollow triangles represent means, whiskers extend to 1.5 times the interquartile range beyond the upper and lower quartiles, and hollow circles represent any values outside the range of these whiskers. Trends in the proportion of records (%) with charcoal present within 50-year bins indicated by the red line. Biomass burning trends for peatlands in B) Central Canada, E) West Hudson Bay, H) East Hudson Bay and K) Atlantic coast and wider landscape biomass burning for C) Central Canada, F) West Hudson Bay, I) East Hudson Bay and L) Atlantic coast – all with a 500-year smoothing window and showing 95% bootstrap confidence intervals (1000 cycles). The x-axis units (cal. yr BP) represent years before 1950 CE. For each panel the number of sites corresponds to 50-year time steps.

et al., 2012). The timing of fen to bog transitions in the Hudson Bay region exhibits a spatial gradient that mirrors the patterns of isostatic uplift (Glaser et al., 2004). However, the records in this study are generally beyond the margin of marine limit at 8 ka (Fig. 1), so links between fire and isostatic changes remain largely untested for this region. Peatland productivity may have decreased during the Neoglacial, leading to increased surface wetness, and in some instances bog to fen transitions (van Bellen et al., 2013). A clear decline in peatland burning occurred from 0.5 ka to present across the Hudson Bay region, probably initiated by LIA cooling.

On the Atlantic coast of Canada and the northeastern United States, high levels of burning in the wider landscape and peatlands from 8 to 7 ka (Fig. 3J–L) is associated with dry summers during a period of low annual precipitation (Carcaillet and Richard, 2000; Viau and Gajewski, 2009). Increases in peatland and wider landscape burning from around 2 to 0.5 ka are at odds with cooling summer temperatures and increasing annual precipitation in northern Quebec (Viau and Gajewski, 2009). From ~4 ka (and especially from 2 ka) a reduction in broadleaf tree species and a shift to more flammable conifers have been linked to summer cooling (Blarquez et al., 2015), which appears to have driven increased landscape burning (Fig. 3L). Similarly in southern Quebec, a shift to less regular and more intense biomass burning from ~1.5 ka has been linked to indigenous burning practices (Blarquez et al., 2018), but the extent of these practices is widely contested (Barrett et al., 2005). Nonetheless, despite increased burning in the wider landscape from ~4 ka onwards, fire in peatlands only increased modestly from 2 to 0.5 ka (Fig. 3J and K). This greater peatland burning 2 to 0.5 ka is largely driven by increases at two forested

peatland sites (Innu and Gaillard 1; see Supplementary Table 1 and Supplementary data) and an open peatland (Baltic Bog) experiencing a coincident increase in ligneous vegetation (Peros et al., 2016). The typically more open and *Sphagnum*-dominated maritime bogs of the Atlantic coast rarely experience fire (Lavoie et al., 2009; Magnan et al., 2014) and fire frequencies in open peatlands are lower than those with greater tree density (Camill et al., 2009; Kuhry, 1994). The fire regime in southern Quebec shifted to less frequent but more severe fires in the last 1000 years following the spread of native agriculture and particularly following European colonisation (Blarquez et al., 2018; Shiller et al., 2014). These human impacts likely explain the increase in wider landscape burning from 0.5 ka to present. Distance to forest and the presence of conifer trees have been linked to fire susceptibility and intensity in ombrotrophic peatlands (Magnan et al., 2012). Therefore, the contrasting decrease in peatland burning from 0.5 ka to present may be related to the reduced susceptibility of open peatlands to fire as they increased in spatial extent (Payette et al., 2013).

Records from Great Dismal Swamp located on the mid-Atlantic Coastal Plain in the United States, differ in the timing of peak burning from boreal peatlands farther north. Minimal burning occurred prior to ~6.5 ka, but frequent mid-Holocene fires from 6.5 to ~3.7 ka coincided with warm and dry conditions in the region and marsh hydroperiods shortened due in part to slowing rates of sea-level rise (Willard et al., in review). Low levels of fire characterize the late Holocene, when mid-Atlantic winters were cooler and wetter (Watts, 1979; Webb et al., 1987) and most of the Great Dismal Swamp landscape had transitioned from a marsh to a forested wetland at ~3.7 ka (Willard et al., in review). Since

European colonisation, drainage of the peatland and logging activities resulted in periodic severe fires (Spieran and Wurster, 2020).

3.2.2. Europe

Peatlands in Britain and Ireland broadly initiated in the early Holocene, from 10 to 8 ka (Morris et al., 2018), but we were only able to reconstruct peatland burning from 4 ka to present owing to a lack of data prior to this. Peatland sites showed consistently low PRS and presence/absence values throughout, despite changes in wider landscape burning (Fig. 4A–C). The comparatively humid climate of Britain and Ireland (Fig. 7) likely mitigated peatland fire. From the mid-Holocene, burning in the wider landscape appears to be primarily influenced by human activity rather than generally cooling summer temperatures from ~6 ka onwards (Davis et al., 2003; Mauri et al., 2015). Increased burning in the wider landscape ~5 ka (Fig. 4C) may be linked to the human use of fire to clear woodland (Ryan and Blackford, 2010). Similarly, Neolithic population growth from ~5.5 ka is clear in the archaeological record and is associated with a trend of reduced forest cover that has continued to the present (Woodbridge et al., 2014). Decreased burning in the wider landscape from ~2 ka to 0.5 ka may be linked to the conversion of forest to agricultural land, resulting in landscape fragmentation and a loss of fuel for wildfires (Fyfe et al., 2003; Marlon et al., 2013). PRS charcoal values decrease from 0.5 ka to present, whereas z-score and presence/absence values drop initially (0.5–0.2 ka), before increasing slightly from ~0.2 ka (1750 CE) to present (Fig. 4A and B). Cooler, wetter conditions in Britain and Ireland during the LIA (Swindles et al., 2013; Webb et al., 2022)

likely contributed to reduced burning in peatlands and the wider landscape ~0.5 ka. Shifting land management practices, including peatland drainage and prescribed burning of moorlands from ~1850 CE (Holden et al., 2007), are coincident with widespread peatland drying across Britain and Ireland since ~1800 CE (Swindles et al., 2019). These recent human impacts may explain the uptick in the proportion of sites burning in the last two centuries (Fig. 4A).

Central European sites in our database are characterised by greater peatland burning at ~9 ka, before relatively constant levels of burning until the late Holocene, with decreased burning at ~2 ka and an increase from 1 ka to present (Fig. 4D and E). Burning in the wider landscape during the Holocene generally showed a slow increase before 1.5 ka, followed by a steeper increase to present (Fig. 4F). Summer temperatures increased until ~8 ka, before stabilising and showing a general decrease from ~6 ka for the majority of the Holocene (Davis et al., 2003; Mauri et al., 2015). The abundance of flammable conifer species in continental Europe decreases from ~10 ka to ~8 ka and remained relatively constant until ~1.5 ka before decreasing further to the present (Feurdean et al., 2020b). These cooler conditions and a stable or decreasing abundance of flammable coniferous trees from the mid-Holocene onwards, suggest that increased burning in the wider landscape may be because of changing human activity. Wildfires are naturally ignited by lightning, but there is some evidence of hunter-gatherer initiated forest fires from as early as 8.5 ka, with human-related fires intensifying during the Bronze Age (~4–3 ka) and again from 1 ka to present (Bobek et al., 2018; Dietze et al., 2018). Decreased peatland burning at 1.7 ka coincides with a brief period of more humid conditions across central Europe (Fohlmeister et al., 2012). Wetter

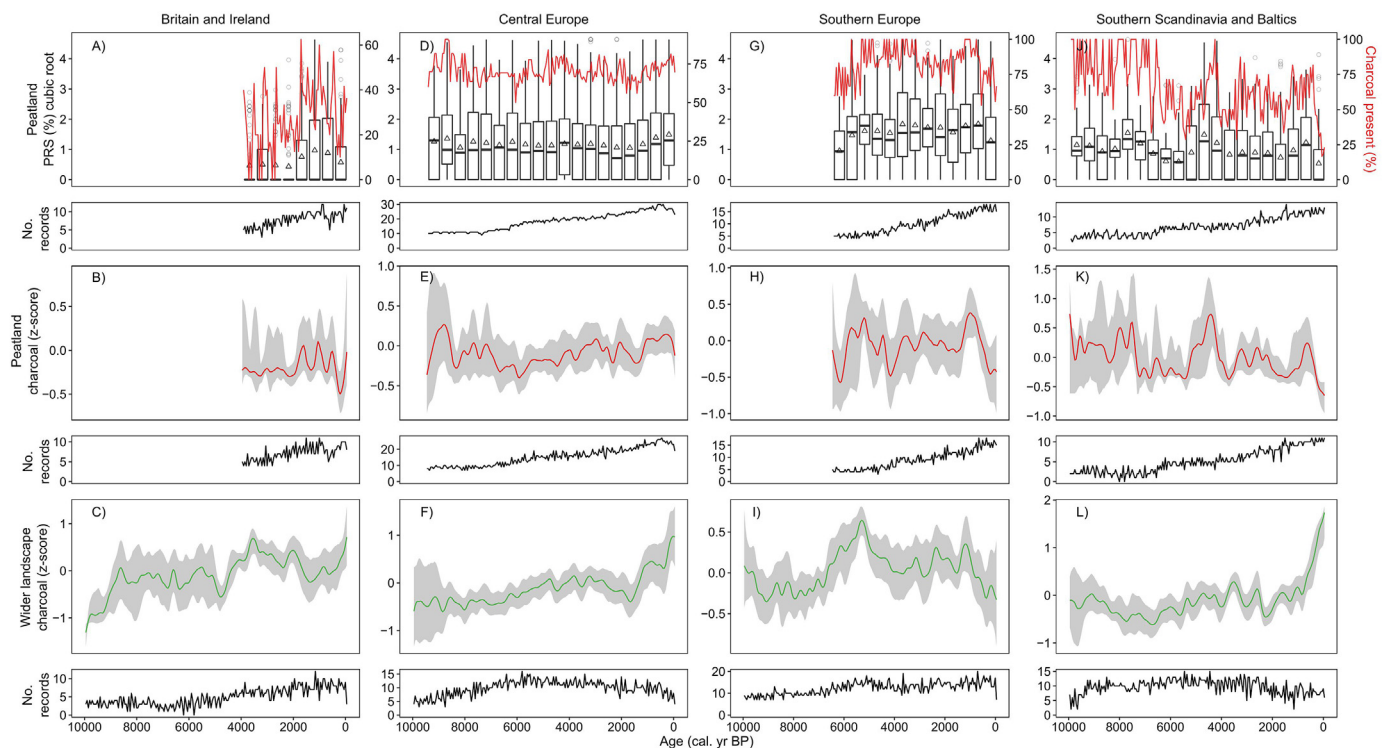


Fig. 4. Peatland and wider landscape burning trends by European sub-region. The distribution of proportionally relatively scaled (PRS) charcoal values (cubic root transformed) in 500-year bins for A) Britain and Ireland, D) Central Europe, G) Southern Europe and J) Southern Scandinavia and Baltics; box heights represent the upper and lower quartiles, centrelines indicate medians, hollow triangles represent means, whiskers extend to 1.5 times the interquartile range beyond the upper and lower quartiles, and hollow circles represent any values outside the range of these whiskers. Trends in the proportion of records (%) with charcoal present within 50-year bins indicated by the red line. Biomass burning trends for peatlands in B) Britain and Ireland, E) Central Europe, H) Southern Europe and K) Southern Scandinavia and Baltics and wider landscape biomass burning for C) Britain and Ireland, F) Central Europe, I) Southern Europe and L) Southern Scandinavia and Baltics – all with a 500-year smoothing window and showing 95% bootstrap confidence intervals (1000 cycles). The x-axis units (cal. yr BP) represent years before 1950 CE. For each panel the number of sites corresponds to 50-year time steps.

climatic conditions may have both increased surface wetness in peatlands (Pleskot et al., 2022) and reduced susceptibility to burning in the wider landscape linked to human activity. However, peatland burning from ~1 ka onwards follows an upward trend in wider landscape burning at ~1.5 ka (Fig. 4E and F), suggesting that human use of fire has exceeded the ability of peatlands to resist burning. Equally, this trend could be an instance where the peatland charcoal record has been dominated by charcoal input from intense extra-local or regional forest burning. Even so, during the LIA from ~1400 CE to 1700 CE, a cool humid maritime climate in western Europe helped maintain wetter peatlands, but many continental peatlands in central Europe experienced drying (Marcisz et al., 2020), likely increasing peatland vulnerability to fire. Similarly, peatland water table reconstructions suggest many peatlands in central Europe have become significantly drier in the last 400 years due to human and climatic factors (Swindles et al., 2019).

Summer temperatures in southern Europe have generally increased since ~8 ka until present (Davis and Brewer, 2009). In addition, summer precipitation decreased throughout the Holocene (Peyron et al., 2011). The pattern of burning is more complex and cannot be explained by climate change alone. Burning increased in peatlands and the wider landscape from ~7 ka to a peak at ~5.5 ka (Fig. 4G–I), which coincided with the onset of the Neolithic and may have been driven by increased slash and burn activities to clear forest for agriculture (Gilck and Poschod, 2021; Rius et al., 2011, 2012). A peak in peatland and wider landscape burning at ~1 ka may have been partially linked to increased farming and settlement following Christian conquest of the Pyrenees (Ejarque et al., 2009), or an increased build-up of woody biomass with a return to previous fire practices following the Roman period (Vanni re et al., 2016). A marked decrease in peatland and wider landscape burning from ~1 ka until present is likely linked to landscape fragmentation and reduced fuel for wildfires with the expansion of agriculture (Marlon et al., 2013), and the onset of cooler conditions ~1400 CE to 1700 CE during the LIA (Mann et al., 2009). Fire suppression policies have been widespread across southern Europe in recent decades (Brotons et al., 2013; Moreira et al., 2011). However, peatland burning remains relatively high in comparison to other regions, which may be attributed to comparatively warm and dry summer conditions (Figs. 6 and 7). Similarly, burning in southern European peatlands shows good correspondence with burning in the wider landscape from 8 ka until present. This correspondence in burning trends suggests that these typically smaller peatlands (Payne, 2018) are either more vulnerable to burning or that they are influenced to a greater extent by non-peatland charcoal originating from the wider landscape.

Southern Scandinavia and the Baltics exhibit more peatland burning from 10 ka to ~7.5 ka in terms of PRS, presences/absence and z-score values (Fig. 4J and K). This early Holocene trend is more subtle in burning of the wider landscape, with slightly elevated burning 10 to ~8.5 ka (Fig. 4L). These higher levels of burning are likely linked to climate and perhaps changes in vegetation. Pollen reconstructions suggest this region was warming during this period, with the HTM between ~8 and 6 ka (Davis et al., 2003; Mauri et al., 2015). However, aquatic plant macrofossil evidence suggests that early Holocene (11.7–7.5 ka) summer temperatures in Fennoscandia were ~2 °C higher than is suggested by pollen reconstructions (V liranta et al., 2015). In terms of vegetation, an increased abundance of flammable coniferous taxa at ~9 ka – as evidenced at Iso Lehmalmampi and Etu-Mustajarvi in southern Finland (Supplementary Table 2; see Sarmaja-Korjonen, 1998) – may have contributed to greater burning at that time. Similarly, a regional transition to broadleaf dominance from ~8 to 6 ka may have mitigated burning during warm conditions (Brown and Giesecke, 2014; Feurdean et al., 2020b). An increase in peatland

burning from 5 to 4 ka may have been influenced by a brief warm, dry phase prior to a general cooling trend from 4 to 2.6 ka in the Baltic region (Hammarlund et al., 2003; Heikkil  and Sepp , 2010), but there is no corresponding increase in burning of the wider landscape. Therefore, the peak in peatland burning around 4.5 ka may have been driven by increasing abundance of woody plants (e.g. *Calluna vulgaris*) under drier conditions, as at Kontolanrahka and M nnikj rve bogs – both included in this analysis (Sillasoo et al., 2011). Increased burning from 1 to 0.5 ka in peatlands and the wider landscape may be linked to warmer conditions during the Medieval Climate Anomaly (MCA) (Mann et al., 2009), alongside increasing intensity of agricultural grazing and burning practices (Olsson et al., 2010). However, from 0.5 ka to present peatland burning decreased, perhaps initiated by LIA cooling initially and in some instances peatland wetting, e.g. at Kontolanrahka bog in southern Finland (V liranta et al., 2007). However, peatland surface moisture trends in recent centuries are inconsistent across southern Scandinavia and the Baltics (Swindles et al., 2019). In contrast to reduced peatland burning, wider landscape burning continued to increase (Fig. 4J–L). This divergent burning trend may be explained by slash-and-burn agricultural practices that were widespread in southern Scandinavia and the Baltics from ~1650 CE to 1850 CE (J  ts et al., 2010; Lehtonen and Huttunen, 1997). These burning practices were typically low intensity and small scale (Parviainen, 2015) and may have kept fuel loads low in the wider landscape and allowed peatlands to be less susceptible to ignition.

3.2.3. Patagonia

In Patagonia, biomass burning in lowland peatland sites appears to be strongly linked to climate. From 10.5 to 7.5 ka, southern Patagonia experienced a warm and dry period during a time of weaker South Westerly Winds (SWWs) (Moreno et al., 2018). This warm, dry period corresponds to greater burning of lowland peatlands from 10 to 6 ka (Fig. 5). From ~6 ka onwards there was a general wetting and cooling of climate due to the equatorial migration of the SWWs and a reduction in summer drought (Markgraf and Huber, 2010; McCulloch et al., 2020). These cooler, wetter conditions in the mid to late Holocene may explain the extremely low levels of burning in southern Patagonian peatlands

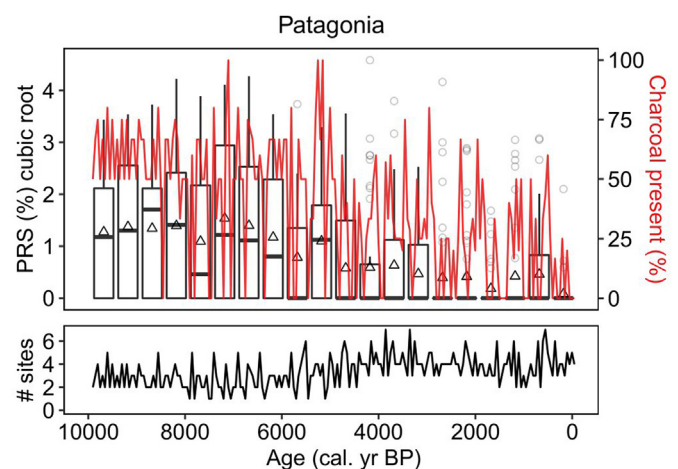


Fig. 5. Peatland burning trends in Patagonia. The distribution of proportionally scaled (PRS) charcoal values (cubic root transformed) in 500-year bins. Box heights represent the upper and lower quartiles, centrelines indicate medians, hollow triangles represent the mean, whiskers extend to 1.5 times the interquartile range and hollow circles represent any values outside the range of these whiskers. Trends in the proportion of samples (%) with charcoal present within 50-year bins indicated by the red line. The x-axis units (cal. yr BP) represent years before 1950 CE. The number of sites corresponds to 50-year time steps.

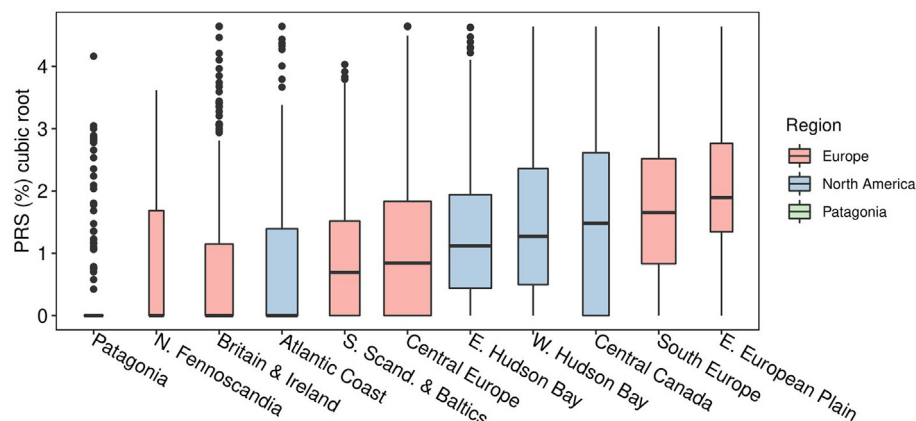


Fig. 6. Distribution of proportional relatively scaled (PRS) charcoal values (cubic root transformed) for 3 to 1 ka, presented by region and sub-region. PRS values are cubic root transformed owing to the skewed distribution of the data. Box heights represent the upper and lower quartiles, centrelines indicate medians, whiskers extend to 1.5 times the interquartile range and black circles show the remaining observations. Box width is proportional to the square root of the number of samples per sub-region.

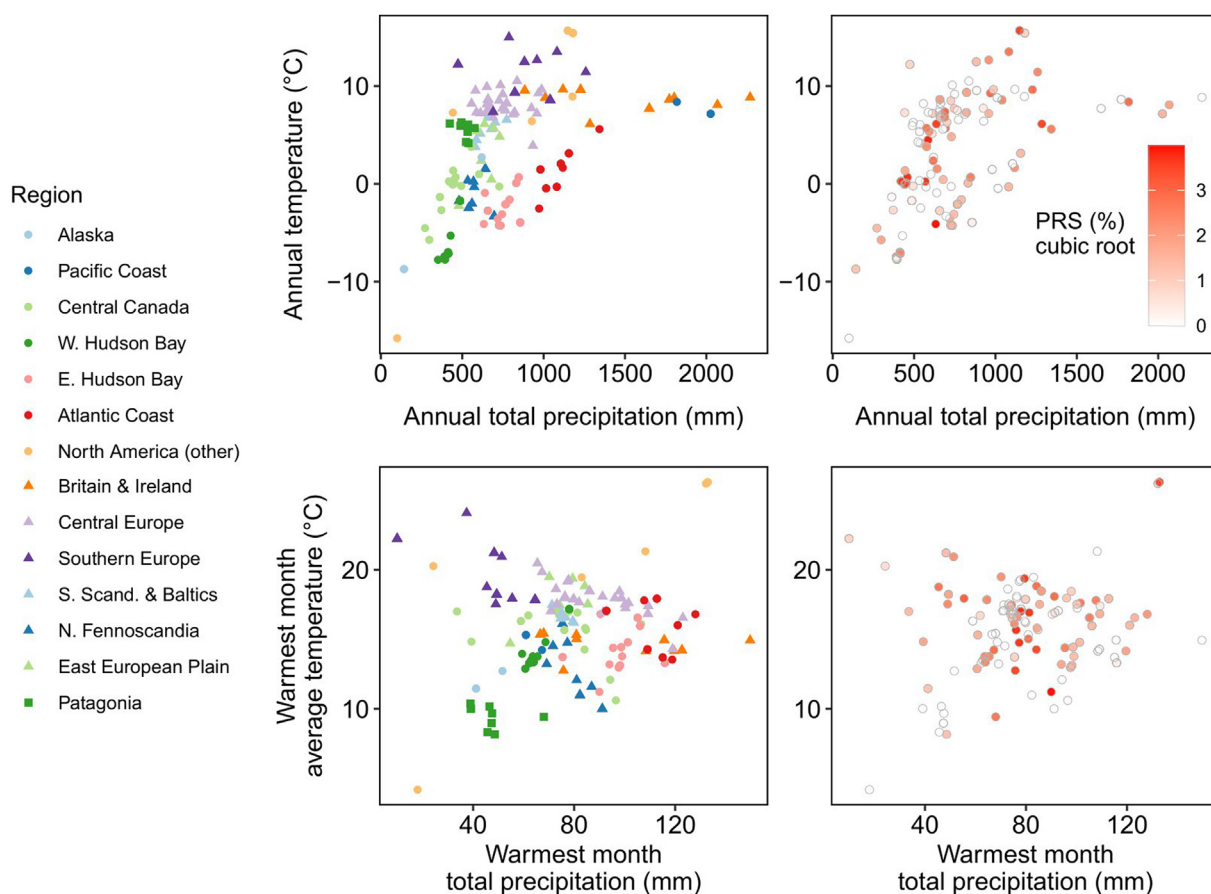


Fig. 7. Climatic space by sub-region and charcoal values. Modern climatic space for peatland records averaged for 1981–2010 CE (Harris et al., 2020) by sub-region for average temperature (°C) and total precipitation (mm) A) annually and B) for the warmest month. Median proportionally relatively scaled (PRS) charcoal values (cubic root transformed) for each record (3–1 ka) in modern climatic space for average temperature (°C) and total precipitation (mm) C) annually and D) for the warmest month.

from 6 ka to present (Fig. 5). Similarly, there is evidence of persistent *Sphagnum* communities in lowland peatlands from ~5.5 ka coincident with reduced summer drought and fire activity (Markgraf and Huber, 2010). The absence of high severity peatland fires was probably favourable to *Sphagnum* mosses in this region (Nelson et al., 2021). Huber and Markgraf (2003) suggest that increased fire activity in a southern Patagonian peatland from

~1600 CE onwards may be linked to changing indigenous hunting practices, following the introduction of horses upon European contact. However, any such increases in recent centuries are not well represented in our regional analysis, suggesting that climate remains the main control on lowland peatland burning in southern Patagonia.

3.3. Peatland burning and climatic space

Our sub-regions show some clear differences in the magnitude of burning (Fig. 6), which may be explained in part by regional differences in climate (Fig. 7). Gridded modern climate data provide good context for the relative differences between sub-regions. We focused on the last 3 ka to 1 ka because this period avoids the time of greatest human impact (1 ka to present) and is long enough to capture meaningful temporal patterns of burning, while maintaining good spatial coverage.

Patagonia, Northern Fennoscandia, and Britain and Ireland demonstrated a median PRS value of zero from 3 to 1 ka, while southern Europe and the East European Plain exhibited the highest burning values (Fig. 6). Northern Fennoscandia contains a higher proportion of records where no charcoal was found (Supplementary Table 1), which likely contributes to these low PRS values. The warmest months in our Patagonian and Northern Fennoscandian sites have relatively low precipitation but are relatively cool compared to the other sub-regions (Fig. 7). However, an annual precipitation of ~1000–1500 mm has been recorded at a number of our Patagonia sites, e.g. at Skyring 1 and Skyring 2 (Broder et al., 2012; Schneider et al., 2003), suggesting our gridded climate data may not be capturing some local variation in rainfall. Nevertheless, low summer temperatures may be allowing peatlands – especially those dominated by *Sphagnum* – to retain surface moisture and to avoid the desiccated conditions that promote fire propagation (Turetsky et al., 2011; Waddington et al., 2015). The high levels of precipitation during the warmest month in Britain and Ireland may prevent conditions favourable to fire. In contrast, southern Europe is characterised by sites with high temperatures and low precipitation for the warmest month, which likely contribute to greater burning (Fig. 7). The East European Plain does not have the hottest or driest summers, on average, yet experiences greater burning than other sub-regions. In this instance, the summary variables presented in Fig. 7 may be less important than short-term climatic and weather variability that may foster peatland fire in the East European Plain. Additionally, the relatively few peatland sites from the East European Plain in comparison to other sub-regions appear to have undergone changes in vegetation structure related to recent slash-and-burn agriculture (Barhoumi et al., 2019) and shifts from minerotrophic to ombrotrophic conditions (Mazei et al., 2020). There are some clear links between burning and climatic extremes, but our findings suggest that peatland fire regimes are influenced by a combination of factors. Our dataset contained 11 peatland records with a complete lack of charcoal, but these are not representative across all sub-regions. To explore the differences in the magnitude of burning more fully, records with a complete absence of charcoal need to be considered across all regions and sub-regions.

3.4. Controls on peatland burning and wider implications

Our composite analysis of peatland macrocharcoal records from mid- to high-latitude peatlands in North America, Europe and Patagonia highlights regional variability in peatland burning during the Holocene. Warmer and drier climatic conditions during the HTM were associated with greater peatland burning in Europe – especially in southern Scandinavia and the Baltics, North America's Atlantic coast, and Patagonia (Figs. 2–5). Cooler or wetter climatic conditions during the Neoglacial coincided with reduced peatland burning in central Canada and the western Hudson Bay (Fig. 3). Similarly, there were widespread decreases in burning linked to the LIA across Europe and North America (Figs. 3 and 4). Therefore, climate appears to be an important control on peatland fire until the late Holocene in Europe and perhaps until the present day in

North America and Patagonia. This echoes findings by Marlon et al. (2013), who suggested that climate is the main influence on global biomass burning for most of the Holocene. However, frequent divergence of peatland burning trends from those of the wider landscape at a regional and sub-regional scale is probably due to local autogenic or human factors – as discussed further below.

Human impacts upon the landscape appears to become more prevalent from the Neolithic onwards in Europe, and increased burning was generally associated with clearance of land for agriculture (Dietze et al., 2018; Gilck and Poschold, 2021; Olsson et al., 2010; Rösch et al., 2017; Ryan and Blackford, 2010). In particular, human-induced fire may have led to increased peatland burning from 7 to 5.5 ka in southern Europe, and from 1 to 0.5 ka in southern Scandinavia and the Baltics (Fig. 4). Paradoxically, there have been widespread reductions in global biomass burning from the late nineteenth century onwards, associated with fire suppression policies and the expansion of agriculture, despite increasing temperatures and rising global population (Marlon et al., 2008). The conversion of land to agricultural uses has reduced fuel for wildfires and decreased landscape connectivity (Arora and Melton, 2018). These processes are probably responsible for recent decreases in burning in the wider landscape in central Canada, eastern Hudson Bay and southern Europe (Figs. 3 and 4). A key uncertainty is whether land-use and fire-suppression policies in the 21st century will be able to offset the influence of warming. A modelling study by Kloster et al. (2012) suggests that management could largely mitigate future carbon emissions from fire, although important uncertainties remain, partly because they did not account for peatland ecosystems.

Differences in burning trends between peatlands and the wider landscape may be a result of autogenic processes that are specific to peatlands, including retention of near-surface moisture even during drought (Waddington et al., 2015), peatland vegetation composition (Magnan et al., 2014) and ecosystem state shifts such as fen-bog transitions (Välimäki et al., 2017). Incidence of peatland fire has been linked to past hydrological disturbances and surface drying in site-specific studies (Feurdean et al., 2022; Gaika et al., 2022). Nonetheless, there are a number of occasions when peatland burning has remained stable or even decreased, while burning in the wider landscape has increased. This trend is in line with the finding that hydrologically connected, unaltered peatlands are resistant to wildland fires owing to a thick layer of surface mosses that keeps moisture retention high (Nelson et al., 2021). The most prominent examples of lower peatland burning than that in the wider landscape, are from ~0.5 ka to present in the Atlantic coast area of North America, and in southern Scandinavia and the Baltics (Figs. 3 and 4). In both instances, increased burning in the wider landscape was likely driven by human activities (Blarquez et al., 2018; Parviainen, 2015). These clear differences suggest a minimal influence of regional charcoal on these peatland macrocharcoal records. However, there are some cores (e.g. Baie and Morts; see Figs. S2 and S4) with an apparent decrease in recent peat accumulation rate (0.5 ka to present) where intense smouldering fires may have consumed peat but left little charcoal (Zaccone et al., 2014). Nevertheless, higher resolution dating is required to corroborate these apparent recent decreases in accumulation rate and the majority of records show no such trend (Figs. S2–S38). The lower susceptibility of peatlands to burning may be linked to cooler conditions during the LIA ~1400 CE to 1700 CE (Mann et al., 2009) in combination with internal mechanisms. More specifically, the mostly extensive, open and *Sphagnum*-dominated peatlands of the Atlantic coast region of North America are generally resistant to fire (Lavoie et al., 2009; Magnan et al., 2014). Here, a lower peatland edge-to-area ratio reduces rates of subsurface losses of water to adjacent forests and lowers the risk of deep burning of peat (Hokanson et al., 2016;

Nelson et al., 2021). Similarly, larger peatland complexes in northern Poland have been shown to be more resistant to disturbances (Marcisz et al., 2019). In contrast, fire records from the smaller and more fragmented peatlands of southern Europe (Payne, 2018) correlated closely with burning in the wider landscape (Fig. 4). This suggests either a greater vulnerability of these ecosystems to burning or that macrocharcoal produced from burning of the wider landscape may be more abundant in smaller peatlands.

Both future climate change and human activities may increase the susceptibility of peatlands to burning. Increased evapotranspiration associated with warmer temperatures and drainage from human activities are both expected to increase peatland drying, leading to greater peatland burning and carbon emissions (Flannigan et al., 2009; Turetsky et al., 2015). However, our results predominantly show recent decreases in peatland burning from ~0.5 ka to present, especially in North America (Figs. 2–4). It is possible that the apparent recent downturn in peatland burning is influenced by a sampling bias. Researchers may have avoided disturbed areas/sites when sampling cores, with only 3.8% of records (with data for surface peat type, $n = 183$) having a clearly decomposed surface (Supplementary Table 1). Yet, peatland vegetation will typically have recovered within decades of a burn (Lukenbach et al., 2016), meaning that this potential sampling bias does not fully explain a downturn in peatland burning during the last ~500 years. Consequently, several other factors may be contributing to this trend. Extensive peatland drying has already been observed in recent centuries across temperate Europe (Swindles et al., 2019), while higher latitudes have experienced wetting and drying linked to local permafrost dynamics (Sim et al., 2021; Zhang et al., 2022). Large areas of peatlands in North America remain relatively intact – just 1.5% of peatlands there are estimated to be degraded, in comparison to 18% in Europe (Urák et al., 2017). Therefore, less modified peatlands in North America may be more resilient to burning (Nelson et al., 2021). Peatland fires commonly initiate elsewhere in the landscape before spreading onto peatlands (Hokanson et al., 2016). Therefore, a reduction in wider landscape burning from ~0.5 ka in some regions likely reduced the potential for peatland vegetation to ignite. Furthermore, the resolution of our analyses (50 years per sample) is unlikely to detect any increased burning in recent decades. The centennial to millennial timescales of peatland fires means that even if the risk of peatland fire has increased with recent climate change and human activities, the impact on peatland fire may not yet be manifest in palaeoenvironmental records. Similarly, peatland ecosystems are generally resilient to disturbance and often exhibit a delayed response to external forcing (Page and Baird, 2016).

We find ample evidence for increased peatland burning during previous warm periods, and in warmer and drier regions (e.g. southern Europe). The vulnerability of peatlands to fire is likely to have been increased by recent climatic warming and anthropogenic management, particularly in Europe where ecosystems have been more heavily modified. For these reasons, policies are needed to enhance peatland resistance and resilience to fire. Rewetting of degraded peatlands has been shown to reduce the risk of deep burns (Granath et al., 2016). Consequently, peatland restoration will be an important strategy to mitigate the impact of climate change and human activities (Baird et al., 2019).

3.5. Recommendations for future research

This study represents a clear step forward in our understanding of the patterns of peatland fire on a continental scale and has allowed us to consider the drivers and controls. Nevertheless, to better quantify the controls on peatland fire, comparison of in-situ peatland charcoal records to datasets of past climate, human

population/density and peatland vegetation and moisture conditions is needed. This comparison needs to be made at suitable spatial and temporal scales. For example, a study linking local ecohydrological proxy data (e.g. testate amoebae and plant macrofossils) with accompanying macrocharcoal data for multiple sites (regionally or globally) would be particularly useful for furthering our understanding of peatland resilience and long-term fire dynamics. Furthermore, widespread implementation of methods exploring the relationship between smouldering peatland fires and hiatuses in peat accumulation (e.g. Zaccone et al., 2014) or linking charcoal morphotypes with fuel types and fire intensity (Feurdean et al., 2020a) could offer insights into the conditions conducive to rapid carbon loss from peatlands. The majority of work quantifying the relationship between source area and charcoal particle size has been conducted specifically for lacustrine settings (e.g. Adolf et al., 2018; Higuera et al., 2007; Peters and Higuera, 2007); however, the taphonomic processes and spatial scales involved in peatland fire are fundamentally different to those in lakes (Remy et al., 2018). Therefore, peatland specific lab and field-based studies would be useful to quantitatively inform peatland fire related research questions. To better compare the magnitude of burning spatially, peatlands with a complete lack of charcoal need to be included for all sub-regions. In terms of data available for inclusion in composite analysis, spatial gaps remain in key peatland areas including: Alaska, the central Hudson Bay Lowlands, the East European Plain and the Western Siberian lowlands. However, there is an opportunity to explore trends and drivers of fire in tropical and sub-tropical peatlands on a continental scale using a similar approach to this study.

4. Conclusions

Our composite analysis of peatland macrocharcoal records from North America, Europe and Patagonia quantifies regional variability in peatland burning at mid-to high-latitudes during the Holocene. Climate appears to be an important control on peatland fire until the mid-Holocene in Europe, and perhaps until the present day in North America and Patagonia. Our analysis suggests that peatland burning is generally higher during warm or dry periods of the Holocene and the magnitude of burning is greater in warmer and drier regions, i.e. southern Europe. There is some correspondence between peatland and wider landscape burning, although peatlands are generally less susceptible to fire, which could plausibly be explained by the persistence of high surface moisture levels and a lower density of woody biomass. Further work quantifying the source area of macrocharcoal specifically in peatlands will help better define these trends. The most prominent example of divergent trends in peatland and wider landscape burning is a reduction in peatland burning since the Little Ice Age across North America and Europe, apart from central Europe. Nonetheless, in the face of climatic and land-use change peatland restoration will be an important tool in reducing the susceptibility of peatlands to fire. Based on our findings we set out a number of recommendations for future research to better understand the controls on peatland fire.

Author contributions

Thomas G. Sim: Conceptualization, Methodology, Formal analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Review & Editing, Visualization, Graeme T. Swindles: Conceptualization, Investigation, Data Curation, Writing – Review & Editing, Supervision, Paul J. Morris: Conceptualization, Writing – Review & Editing, Supervision, Andy J. Baird: Conceptualization, Writing – Review & Editing, Supervision, Angela V. Gallego-Sala: Conceptualization, Writing – Review & Editing, Yuwan Wang:

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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.

Data availability

The data used for this research are available in the supplementary materials.

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Appendix A. Supplementary data

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