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Invasion of Norway spruce diversifies the fire regime in boreal European forests

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Summary

1. Global wildfire activity and biomass burning have varied substantially during the Holocene in both time and space. At the regional to continental scale, macroclimate is considered to be the predominant control regulating wildfire activity. By contrast, the role of forest tree composition is often considered as a subsidiary factor in studies addressing temporal variation in regional wildfire activity.

2. Here, we assemble a spatially comprehensive data set of 75 macroscopic charcoal records that reflect local burning and forest landscapes that are spread over a substantial part of the European boreal forest, spanning both oceanic and continental climates.

3. We show that the late-Holocene invasion of Norway spruce *Picea abies*, a new forest dominant in northern Europe, significantly reduced wildfire activity, thus altering forest disturbance dynamics at a subcontinental scale.

4. *Synthesis*. Our findings show that a biotic change in the local forest ecosystem altered the fire regime largely independent of regional climate change, illustrating that forest composition is an important parameter that must be considered when modelling future fire risk and carbon dynamics in boreal forests.

Key-words: charcoal, climate change, forest history, Holocene, palaeoecology and land-use history, *Picea abies*, species invasion, spruce forest, wildfire activity

Introduction

Changes in the abundance of a single species can trigger profound alterations in the properties of an ecosystem (Chapin *et al*. 2004). Indeed, the invasion of Norway spruce *Picea abies* in northern Europe during the late Holocene (Tallantire 1972; Giesecke & Bennett 2004) transformed forests over a subcontinental area, culminating in the emergence of a new boreal forest keystone species (Seppä *et al*. 2009a). Both forest structure and biodiversity were significantly altered as Norway spruce replaced the previous dominants, mainly pine and birch, to become the most abundant tree species in North European forests (Seppä *et al*. 2009a). Given that Norway spruce invaded northern Europe from the east (Tallantire 1972; Giesecke & Bennett 2004), forest transformation reached northern Sweden about 4000 years ago (Fig. 1). Thereafter, spruce advanced in a south-westerly direction as an apparent wave of expanding populations, propelled by a combination of driving forces that are not yet fully understood (Giesecke & Bennett 2004). Climatic change is postulated as a possible causal forcing mechanism (Tallantire 1972; Bradshaw & Lindbladh 2005), although other possible drivers include rate of local adaptation (Kullman 2001), competitive suppression (Miller *et al*. 2008; Seppä *et al*. 2009a) and human land use (Bjune *et al*. 2009). Today the natural limit of spruce distribution in northern Europe occurs in western Norway (Fig. 1).

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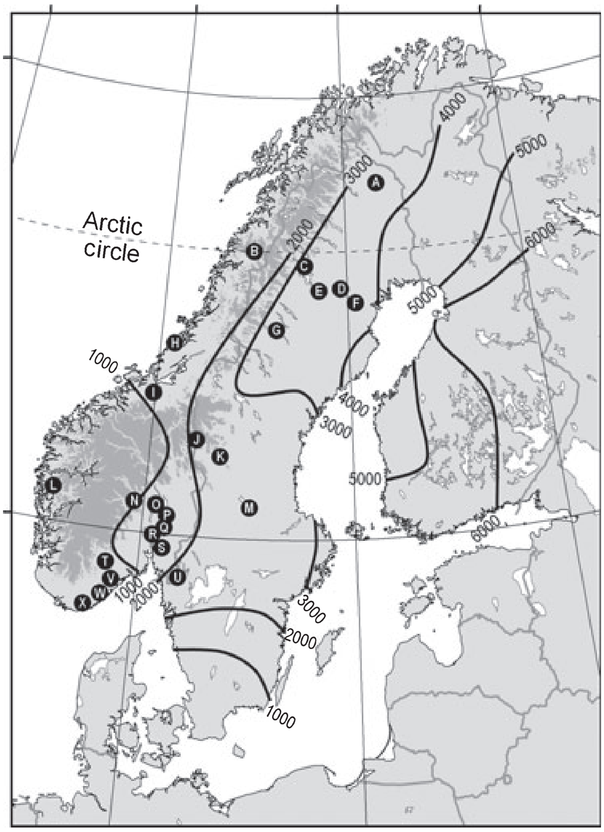

Fig. 1. Location of the study sites and the Holocene invasion of the Norway spruce forest in northern Europe. The study sites are located in the Scandinavian countries of Norway and Sweden and each dot represents a landscape location in which one or more peat or humus profiles were sampled for charcoal content. Dark grey areas are mountains. The invasion of spruce is generalized from Giesecke & Bennett (2004). The contours are for calibrated years BP (see Table S1 for further information about the study sites).

One important ecosystem process to be affected by this late-Holocene ecosystem transformation was fire regime (Tryterud 2003), which describes the pattern of fire at any given location through time including the frequency, intensity, seasonality, extent and type of burning. Variations in fire regime are controlled by a complex interplay of climatic variability, vegetation and fuel characteristics, sources of ignition and human activities (Lynch, Hollis & Hu 2004; Colombaroli, Marchetto & Tinner 2007; Odion, Moritz & DellaSala 2010). During the Holocene, global wildfire activity and biomass burning are known to have varied substantially in both time and space (Carcaillet *et al.* 2002; Power *et al.* 2008), often in response to changes in the climate system (Carcaillet *et al.* 2001; Brown *et al.* 2005; Marlon *et al.* 2009) or human activity (Willis & Birks 2006). At the regional to continental scales, climatic factors are frequently proposed as the predominant controls regulating fire regime (Carcaillet *et al.* 2001; Whitlock, Shafer & Marlon 2003; Westerling *et al.* 2006). For example, recent climate warming coupled with high fuel loads are proposed as the dominant factors contributing to the current increase in wildfire activity in the western USA, Europe and Australia (Pausas 2004; Westerling *et al.* 2006; Pitman, Narisma & McAneney 2007). Moreover, there is also general agreement that recent climate warming has lengthened the fire season and increased the burned area across boreal forests world-wide (Soja *et al.* 2007). Commensurate with these changes, it is now predicted that rising summer temperatures will increase the risk of fire in the circumboreal area by 50%, significantly increasing the area burned by the end of this century (Flannigan *et al.* 2009). In contrast to climate, forest tree composition is often considered as a subsidiary factor in studies addressing temporal variation in wildfire activity at the regional to continental scales (Marlon, Bartlein & Whitlock 2006; Gavin *et al.* 2007). It has, however, recently been shown that interactions between forest tree species composition and fire have the potential to overshadow direct effects of climate change on fire regimes in boreal forests of Alaska (Brubaker *et al.* 2009; Higuera *et al.* 2009), revealing that vegetation composition can be an important driver of wildfire activity. Consequently, vegetation composition requires much more consideration than hitherto when considering climate change, fire risk and carbon transfer between the boreal forest and the atmosphere.

Here, we assemble an extensive network of peat, humus and tree-ring records from forest landscapes spanning the longitudinal axis of Scandinavia to analyse late-Holocene stand-scale forest composition and fire disturbance in the boreal forest of northern Europe (Fig. 1). Forest peat and humus records are the main target for our study because they contain stratigraphic sequences of pollen and macroscopic charred particles (≥ 0.25 mm) that reveal the history of local forest composition and stand-scale burning at a high spatial resolution over a millennial Holocene time-scale (Jacobson & Bradshaw 1981; Ohlson & Tryterud 2000). The samples were collected using a nested sampling strategy with a broad coverage of the European boreal zone, combined with a denser sampling strategy at eight localities where up to 15 spruce forest sites were investigated within a given forest landscape. Given that spruce invaded time-transgressively throughout the study region in a north-east–south-west direction during the last 4000 years (Fig. 1), this sampling strategy was used to facilitate a comparison of fire history before and after local spruce invasion at both local and regional spatial scales. Thus, through comparison of charcoal and spruce pollen records it is possible to assess the influence of both climate and vegetation composition on the fire regime. For example, if regionally synchronous changes in charcoal content are detected independent of the presence or absence of spruce, then macroscale climatic factors must be considered as the likely driving mechanism in the absence of human activity. Alternatively, if there was a significant change in the fire regime following the local invasion of spruce, then forest tree species and vegetation composition should be considered as an important regulator of boreal wildfire. Here, we show that the local invasion of spruce was a key contributor to the alteration of wildfire activity, suggesting that vegetation change combined with climate change can produce ecological changes of much greater magnitude than would be expected from climate change alone.

Materials and methods

STUDY SITES

We have sampled a total of 75 spruce forest sites located in 24 forest landscapes in boreal Europe (Fig. 1). All sites are closed-canopy sites and were selected to record the Holocene history of local spruce invasion and wildfire disturbance (Jacobson & Bradshaw 1981; Ohlson & Tryterud 2000). The latitudinal and longitudinal extents of the sites are 1080 and 880 km, respectively, and their altitude ranges from 210 to 830 m above sea level. Thus, the sites are spread over a substantial part of the European boreal forest, spanning both oceanic and continental climates. Consequently, our study sites are considered to be a representative sample of the boreal spruce forests in north-western Europe.

Scots pine *Pinus sylvestris* L. and Norway spruce *Picea abies* (L.) Karst. are the two dominant trees in the study area. Pine is most common on dry sites and nutrient-poor peatlands, whereas spruce typically dominates on mesic and moist sites with a more favourable nutrient status. Among the broad-leaved trees, birches (*Betula pubescens* Ehrh. and *Betula pendula* Roth.) are most common. The field-layer vegetation on the spruce sites is dominated by dwarf shrubs, of which bilberry *Vaccinium myrtillus* L. is the most abundant, whereas the forest-floor vegetation is typically composed of feather mosses, peat mosses and haircap mosses. (See Table S1 in Supporting Information for information about the study sites.)

CHARCOAL AND POLLEN ANALYSIS

Peat and raw humus cores were collected in the spruce forest sites using a 5-cm-diameter Russian corer (Jowsey 1966). Each core contained the entire organic-soil profile and extended into the underlying mineral soil. The length of the soil cores ranged from 26 to 646 cm (Table S2). Volumetric samples (10 cm^3) were removed contiguously in 1-cm intervals from each core, yielding a total of 8672 samples. Each sample was prepared for macroscopic charcoal analysis by soaking in water and sieving through a 250-μm mesh (Whitlock & Larsen 2001). The number of charcoal particles in each sample was counted on a gridded Petri dish. Only particles that were black, brittle and crystalline with broken angular ends were classified as macroscopic charcoal.

Samples for pollen analysis were taken at regular levels and a minimum of 300 tree pollen grains were counted at each level. The level at which *Picea* pollen exceed 2% of the tree pollen sum was identified and used to define local spruce invasion (Tallantire 1972; Giesecke & Bennett 2004) and hence the pre- and post-spruce sections of the cores.

Pre- and post-spruce charcoal deposition rates were calculated for a subset of 30 sites from which radiocarbon dates were obtained for the basal part of the soil cores (Table S2). Given that the timing of the local spruce forest invasion is known by radiocarbon dates from these sites, or can be estimated from the literature (Table S2), average pre- and post-spruce charcoal deposition rates were estimated. The subset of soil cores with dated basal parts were also used to estimate pre- and post-spruce peat accumulation rates. These averaged 0.34 ± 0.04 and 0.31 ± 0.03 L peat m^{-2} $year^{-1}$, respectively ($n = 30$; mean ± 1 SE) and did not differ significantly. Site-specific age-depth modelling by simple linear interpolation confirmed a generally constant rate of peat accumulation at the individual site (Fig. S1). However, peat accumulation rates varied among sites (Table S2), which is typical for boreal peatlands within Norway spruce forests (Ohlson & Tryterud 1999; Pitkänen, Tolonen & Jungner 2001; Pitkänen *et al.* 2003; Ohlson, Korbøl & Økland 2006). Much of this variation is determined by local peat-basin characteristics such as hydrology and vegetation composition. Occurrence of fire can add further to this variation as peatland fires may combust surface soil and slow down peat accumulation (Pitkänen, Turunen & Tolonen 1999). Comparison of data from boreal peatlands that were repeatedly affected by fire and similar peatlands that were less affected by fire actually indicates that increased frequencies of local peat surface fires result in a decrease in the rates of peat accumulation rates (Kuhry 1994). Gavin (2003) illustrates the problems of establishing detailed chronologies for forest soil profiles due to fire-losses of surface soil and mixing of charcoal into deeper soil layers.

We established approximate chronologies for sites that were not radiocarbon dated by assuming constant rates of humus or forest-peat accumulation between the basal parts of the organic-soil profile, the level at which spruce forest develops as shown palynologically (which is of known age, see Table S2) and the soil surface. This assumption is reasonable given the age-depth modelling and that the average pre- and post-spruce peat accumulation rates were similar in the subset of cores that were dated, although the possibility of irregular accumulation rates and of gaps in the undated profiles cannot be ignored. The resulting chronologies in this study should thus be regarded as approximate and liable to considerable uncertainties.

The difference between pre- and post-spruce charcoal concentrations was tested statistically using a randomization procedure (Manly 1997). Restricted randomizations were performed to account for the effect of site by randomizing the samples site-specifically. The randomizations were done 999 times and a Monte Carlo *P*-value was estimated by counting the number of permutations that had a larger difference between the mean values (two-sided test) than the observed difference. To assess the spatial change in fire concomitant with spruce invasion, mean pre- and post-spruce charcoal concentrations were estimated for each sampling site. The averaged concentration data were entered into ArcGIS 8.2®, a GIS developed by ESRI (Environmental Systems Research Institute, Inc., Redlands, California, USA) and interpolated via inverse distance weighting using a minimum of five neighbours and a power of two regarding the influence of surrounding points. Similar rates of peat accumulation in the pre- and post-spruce sections of the cores justify the use of charcoal concentration values in the randomization test and in the GIS.

TREE-RING ANALYSIS

Scots pine forests on shallow and dry soils border the spruce forests at locations F and U (Fig. 1). We searched for wood that could have recorded past fires in those pine forests to check for differences between the spruce and pine forests with regard to recent fire regimes (i.e. occurrence of fire during the last few centuries). Living trees, snags, fallen logs and stumps of different age were sampled with a chain saw. Partial cross-sections of wood were cut out and fire scars were recorded and dated by counting tree rings as described by Niklasson & Granström (2000).

DATA PRESENTATION

The major emphasis of this article is on differences in charcoal values between the pre- and post-spruce sections defined palynologically in the 75 soil profiles examined and not on detailed temporal patterns between profiles. For ease of data display, charcoal concentrations in our profiles are plotted in Fig. 2 according to the proportion of the profile that is post-spruce as determined from our palynological data. Profiles with the highest post-spruce proportion (i.e. A2, V2) are

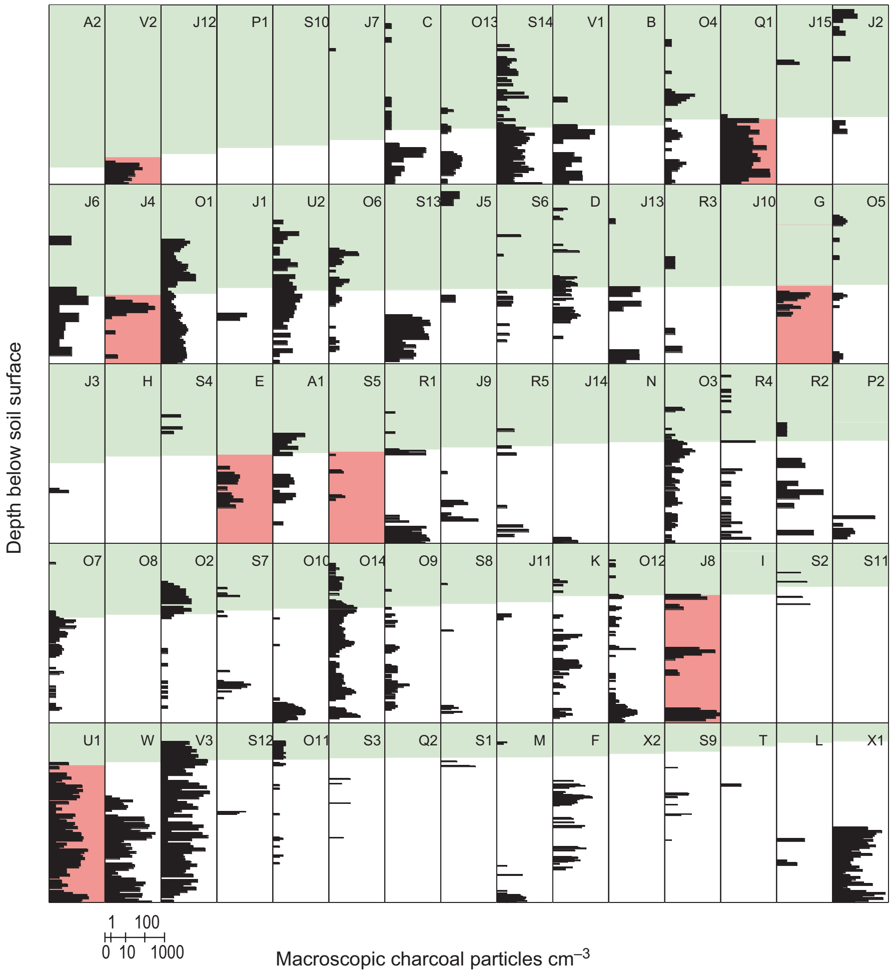

Fig. 2. Schematic illustration of the amount of charcoal in peat and raw humus cores from 75 Scandinavian forest sites. Each core represents the complete organic-soil profile from the top-soil down to the underlying mineral soil, with core depth ranging from 26 to 646 cm. The sites are arranged according to the proportion of the spruce section of the core that is marked in green. Red-labelled sites indicate tight correspondence between local spruce invasion and permanent termination of charcoal deposition. Each core is designated by an alpha-numeric code, with the letters referring to the locality shown in Fig. 1 and the numbers indicating a given core at the sites with dense sampling. Note the log scale for the number of charcoal particles and that the depth scale is relative (see Table S2 for absolute core-depth data).

plotted from left to right and from top to bottom. To illustrate the fine-scale charcoal patterns within a seemingly uniform spruce forest landscape in central Norway (site J; Fig. 1), charcoal concentrations in the 15 profiles sampled are plotted stratigraphically in relation to the local establishment of spruce and their geographical position within the 3000 × 500 m study area (Fig. 4).

Results

TRENDS IN CHARCOAL RECORDS

Most of the soil cores record a change in charcoal concentration from high basal values to low upper values. There is, however, considerable variation in charcoal concentration and frequency between sites, indicating much variation in the fire regime (Fig. 2). For example, 13 of 75 sites yielded no macroscopic charcoal through time, regardless of the presence or absence of spruce. Some of these sites are located in the moist suboceanic coastal region of Norway (i.e. sites B, H, I and X2; see Figs 1 and 2). By contrast, sites located further inland in a drier and more continental setting are typically characterized by stratigraphic sequences containing markedly more charcoal (Figs 1 and 2). However, deviations from this pattern are also evident, with some moist suboceanic sites containing substantial amounts of charcoal through time (e.g. sites W and X1) and some drier and more continental sites containing little or no charcoal (sites J10, N and O8; see Figs 1 and 2).

When considering the general pattern of charcoal deposition across the various sites, there is a significant decrease in both the concentration and deposition rate of charcoal following the local invasion of spruce at almost every site excluding the coastal region where little or no charcoal accumulated through time (Figs 2 and 3). The correspondence between local spruce invasion and local cessation of wildfire is strikingly tight at eight sites as indicated by the immediate and permanent termination of a historically substantial charcoal deposition following the establishment of spruce forest (Fig. 2; red-labelled sites). Statistically, the late-Holocene

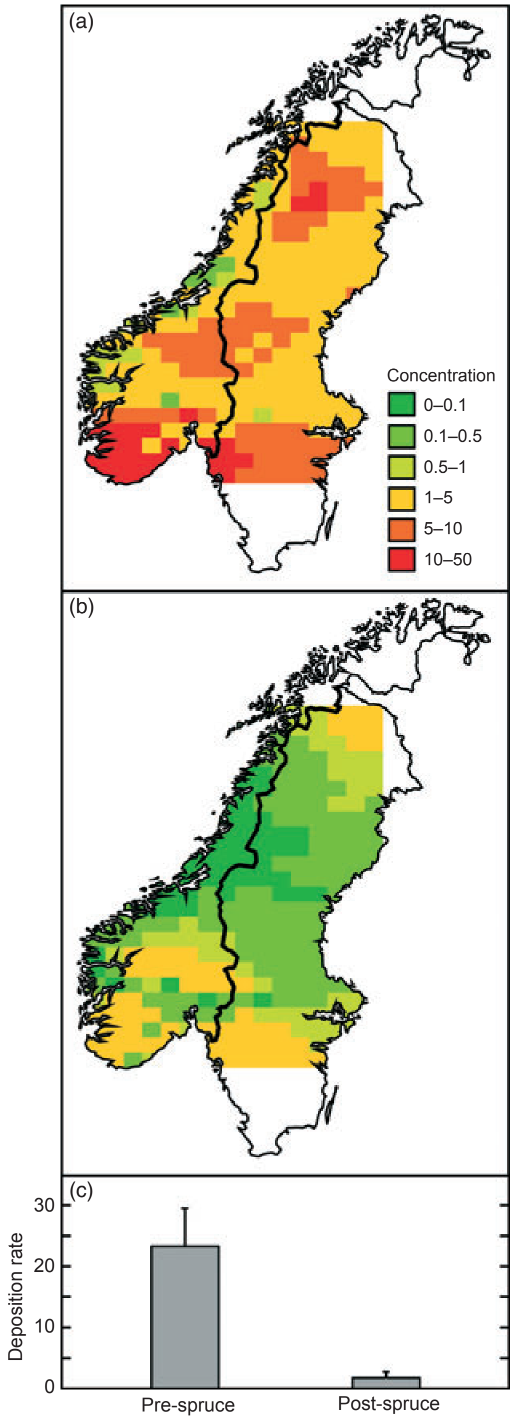

Fig. 3. Spatially interpolated maps of charcoal concentration and deposition rate. (a) Pre-spruce and (b) post-spruce charcoal concentration map (particles cm^{-3}). (c) Annual deposition of macroscopic charcoal particles dm^{-2} before and after local establishment of spruce. Values are mean ± 1 SE. Note that the figure is representative for Norway spruce forests on organic soils only. For simplicity, the Scandinavian mountain range and larger lakes are omitted. For geographic details, see Fig. 1.

decrease in charcoal deposition following the invasion of spruce is unambiguous. For example, charcoal occurred only in the pre-spruce section of cores from 25 sites, while the opposite was the case at three sites (i.e. J7, J15 and S4). Furthermore, the mean number of charcoal fragments per cm^3 soil sample prior to local spruce establishment (4.1 ± 0.3, $n = 5546$; mean ± 1 SE) was significantly higher than after establishment (0.6 ± 0.1, $n = 3108$; $P < 0.001$; Monte Carlo *P*-value from restricted randomization test). Moreover, a greater proportion (18.8%) of pre-spruce samples than post-spruce samples (8.5%) contained charcoal and the subsample of pre-spruce samples actually containing charcoal had, on average, three times as much charcoal particles per cm^3 soil (21.7 ± 1.5, $n = 1045$) than the post-spruce samples containing charcoal (7.1 ± 2.6, $n = 264$).

MULTIPLE SITES WITHIN LANDSCAPES OF UNIFORM REGIONAL CLIMATE

The multiple site observations within a given forest landscape reveal considerable variation in fire regime at a fine spatial scale. This is clearly illustrated by the charcoal records from 15 sites sampled within a rectangular 3000 × 500 m area located in a seemingly homogenous spruce forest landscape at site J in eastern Norway. Here, we found soil cores that contained charcoal throughout the entire soil profiles, others that yielded no charcoal at all, and some that contained charcoal exclusively in either the pre- or post-spruce section of the cores (Fig. 4). Likewise, the charcoal records from the multiple site observations in the forest landscapes at localities O and S (14 sites sampled in each landscape) also show a similar pattern of large variability at fine spatial scales (Fig. 2).

FIRES DATED BY TREE-RING ANALYSIS

Wildfires have occurred frequently in recent time in the Scots pine forests bordering the spruce forests at localities F and U. In particular this was the case at locality U1, where four fire events were recorded in the pine forest during the 19th century (i.e. in 1852, 1838, 1821 and 1816 CE). For locality F, fire-scarred wood recorded seven fire events in the pine forest (i.e. in 1771, 1744, 1649, 1641, 1558, 1449 and 1420 CE). In comparison, wood recording past fires was not found in the spruce forests and their charcoal records indicate a total lack of fire activity at sites F and U1 following the local invasion of spruce (Fig. 2), which occurred about 3600 and 1500 years ago, respectively. Importantly, the charcoal records from these sites are indicative of historical and recurring fires prior to the spruce invasion, thus revealing an apparent shift in the fire regime commensurate with the local establishment and rise of the spruce forest ecosystem.

Discussion

We draw four main conclusions from the results of our study. First, fire disturbance is a less ubiquitous phenomenon in boreal European forests than previously thought. Secondly, regional macroscale climate exerts a broad influence on the fire regime. Thirdly, spruce invasion and the change in dominant tree species had a critical influence on the fire regime, exceeding the influence of late-Holocene climate shifts.

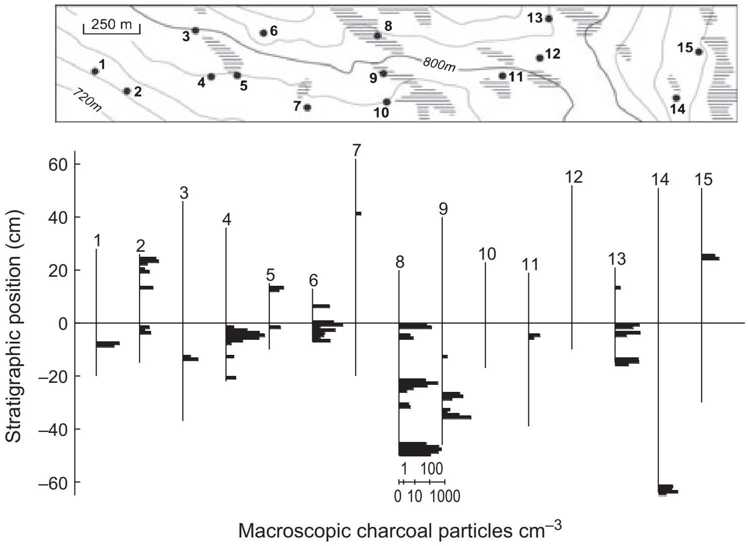

Fig. 4. Multiple site observations of charcoal particles in forest peat and humus profiles in a single forest landscape. Each vertical line represents a charcoal profile from the cores collected at locality J (in Gutulia National Park, just north of Gutulisetrene). The local establishment of the spruce forest about 2200 years ago gives an approximate chronological control and is marked by the horizontal line at the stratigraphic 0 position so that the spruce section of the core is above this line. Note the log scale for the number of charcoal particles. Shaded areas on the map show the location of mires and swamp forests.

Fourthly, the fire regime was diversified by the spruce invasion, which gave rise to a more variable spatial occurrence of fire at the landscape scale.

FIRE DISTURBANCE IS NOT UBIQUITOUS

The view of fire as a significant disturbance agent in boreal forests gradually gained acceptance during the 20th century to create the emerging consensus that boreal forest structure and function are directly attributable to the recurrence and ubiquity of fires (Bonan & Shugart 1989; Johnson 1992; Goldammer & Furyaev 1996). Boreal forest fire return intervals are typically estimated to be between 50 and 200 years (Zackrisson 1977; Bonan & Shugart 1989), bracketed by both longer and shorter estimates (Ohlson & Tryterud 1999; Niklasson & Granström 2000; Czimczik, Schmidt & Schulze 2005). The general importance of fire in the boreal forest ecosystem is emphasized by the premise that fire-free sites are supposed to be very rare (Hörnberg, Ohlson & Zackrisson 1995; Zackrisson *et al.* 1995; Segerström, von Stedingk & Hörnberg 2008). However, of the 75 forest sites analysed in our study, 13 sites yielded no macroscopic charcoal at all, with an additional seven sites producing records characterized by a sporadic single peak occurrence of charcoal particles (i.e. sites J1, J3, J7, J11, J14, J15, S12 and T in Fig. 2). Although charcoal particle data must be interpreted with caution (Ohlson, Korbøl & Økland 2006; Segerström, von Stedingk & Hörnberg 2008) and an absence of charcoal particles cannot unambiguously be considered as firm proof of genuine fire-free conditions (Ohlson & Tryterud 2000), we propose that local and direct fire disturbance has played a subordinate role in about one-third of the study sites during the Holocene. Such a large proportion of sites containing little or no charcoal challenges the common view that wildfire is a ubiquitous, generally important and frequent disturbance agent in the boreal European forest. The idea that fire is less important in boreal European forests than previously thought is corroborated by a recent study (Ohlson *et al.* 2009) that examined the proportion of historically burnt forest ground in a variety of Scandinavian forest landscapes. According to that study, the proportion of forest ground that has burnt is highly variable among landscapes, but reaches an average of *c.* 50% at the broad geographical scale.

The marked variation in the charcoal records (Fig. 2) indicates a profound variability in the fire regime across forest sites. However, a common feature for many sites is the rather sparse occurrence and frequent lack of macroscopic charcoal particles, which are indicative of low-intensity and low-frequency fires that run along the forest ground and do not destroy the majority of the full-sized trees. The prevalence of such low-intensity fires contrasts the fire regimes in boreal Europe with those in boreal North America, which are often high-intensity crown fires that destroy most trees (Preston 2009).

CLIMATE AND SPRUCE INVASION AS DRIVERS OF WILDFIRE ACTIVITY

It is well-established that macroscale climate exerts a broad influence on fire regime (Carcaillet *et al.* 2001; Brown *et al.* 2005; Westerling *et al.* 2006; Kitzberger *et al.* 2007). Consequently, we posit that the prevailing moist conditions in the suboceanic coastal region of Norway inhibit fire, whereas the continental climatic conditions inland are more conducive to burning. Our results indicate that there is a difference in regional charcoal concentrations, with a paucity of charcoal in coastal localities and an abundant occurrence in inland localities (Fig. 2). A similar spatial pattern in charcoal accumulation has been recorded in southern Sweden during the late Holocene (Lindbladh, Bradshaw & Holmqvist 2000).

Many soil cores record a marked change in charcoal concentration from high basal values to low upper values, suggesting a reduction in wildfire activity through time (Fig. 2). This broad-scale pattern is probably driven by the late-Holocene climate trend of cooling and increased general humidity that started about 4500 years ago in boreal Europe (Bjune *et al.* 2005; Wanner *et al.* 2008; Seppä *et al.* 2009b). However, if the regional boreal European climate cooling trend had had a direct and major impact on the fire regime, then a broadly synchronous change in wildfire activity across all sites would be expected, independent of local spruce establishment. Although our site chronologies are approximate, there are no hints of any synchronous change at the regional scale (Fig. 2 and Table S2), implying that factors other than macroclimate were important drivers of the fire regime in northern Europe during this time interval. Instead, our results show a close correspondence between the invasion of spruce and the decline in charcoal concentration, suggesting that a change in the dominant tree species had a critical effect on the fire regime that exceeded the influence of late-Holocene climate change.

In this context, however, it is important to disentangle the effects of climate change from the effects of tree species composition, which is a difficult task. For example, the Norway spruce invasion in boreal Europe is widely attributed to late-Holocene climate cooling (Tallantire 1972; Giesecke & Bennett 2004; Seppä *et al.* 2009a), which reduced wildfire activity, thus facilitating the spread and establishment of Norway spruce that is a fire-sensitive tree species (Niklasson & Drakenberg 2001; Niklasson *et al.* 2010). A late-Holocene climate shift towards cooler and more humid conditions may thus have triggered both a decrease of wildfire activity and the invasion of spruce. Given the fire sensitivity of Norway spruce, it could also be argued that the spruce invasion was a consequence of the decreasing fire activity alone. Whether spruce arrival preceded and caused the change in fire regime at individual sites or whether the climate-induced decrease in fire activity allowed spruce to expand is thus a kind of cause-and-effect dilemma. Nevertheless, our results demonstrate that the invasion of spruce has the potential to be a key determinant of local wildfire activity because of the strikingly tight correspondence between local spruce invasion and local cessation of wildfire (Fig. 2). An important observation in this context is that in the sites that exhibit tight correlation between spruce invasion and fire cessation, the timing of the spruce forest invasion differs by about 2000 years between sites (e.g. sites G and V2, see Fig. 1 and Table S2). If regional climate change during the late Holocene was responsible for the cessation of fire, then it would have happened both synchronously among sites and independently of the local spruce invasion, which clearly is not the case. Consequently, our data suggest that the reduction in fire activity took place site-specifically during or immediately after the spruce invasion. Thus, spruce invasion and the local rise of the spruce forest ecosystem must be viewed as a direct reason for the reduction in fire, possibly because it made the forest denser, darker and cooler in summer and thus locally more humid with moister soil conditions, which all contribute to reduce ignition probability, flammability and fire activity.

The multiple site observations in forest landscapes of uniform regional climate (localities J, O and S) help to distinguish further between climatic and forest compositional influences on the fire regime. The dense sampling strategy provides detailed insights into the nature of the past fire regime. Even at such a fine spatial scale, considerable variation in fire regime is evident, indicating that local topography, vegetation and microclimatic conditions can exert a greater influence on fire variability than regional climate (see Fig. 4). These data emphasize the patchy nature of landscape burning in northern Europe and show that boreal European fires are often ground fires that cover small areas relative to other regions in the boreal zone (Preston 2009). Thus, cautious use must be made of regional mean fire return times in boreal European forests.

INVASION OF SPRUCE AND FIRE-REGIME DIVERSIFICATION

The local forest stand-scale records analysed in this study show that the spread of spruce led to a significant reduction in local fire frequency and severity. However, several independent lake-sediment charcoal records collected from continental settings in the study region record an opposite trend of increased fire activity during the late Holocene (Korsman & Segerström 1998; Giesecke 2005). These diverging patterns probably arise from the inherently different scales of charcoal records in lake sediments and forest soil profiles. Charcoal records derived from lake sediment represent an integrated record of a catchment area that may contain a mosaic of forest types and anthropogenic land-use activities at the landscape scale, whereas forest soil profiles record only local stand-scale burning with high spatial resolution (Jacobson & Bradshaw 1981; Ohlson & Tryterud 2000).

In the European boreal setting, forest types can vary from fire-prone dry pine forest to moist spruce forest, both of which are characterized by unique fire regimes (Zackrisson 1977; Hörnberg, Ohlson & Zackrisson 1995; Goldammer & Furyaev 1996; Niklasson & Granström 2000). For example, while a pine–birch forest was invaded and transformed to a spruce forest at site U1 *c.* 1500 years ago (Fig. 2), pine forests persisted on dry mountain ridges close to the spruce forest site. The forest peat profile at site U1 records the corresponding cessation in fire associated with the local expansion of spruce while the pine forest still burned frequently after the local spruce invasion, as shown by pine tree-ring morphology. A similar pattern with cessation of fire in mesic forest types after spruce invasion and continuation of fires in dry pine forests types is observed at locality F. Thus, local spruce invasion has created a diversification of the fire regime at the landscape scale by reducing wildfire activity significantly in mesic to moist forest types typically occurring in concave landscape forms. The reduction of wildfire activity has profound biological implications as the spruce invasion gave rise to new types of forest ecosystems that are characterized by long-term continuity and that harbour a large proportion of the forest species that are 'red-listed' in boreal

Europe today (Ohlson & Tryterud 1999). Interestingly, in the Alaskan boreal forest, black spruce stands occupy moist and cold soils on north-facing slopes (Johnstone *et al.* 2009). Those stands are still highly flammable, causing short fire rotations to occur on cold and wet sites (Drury & Grissom 2008), which is in contrast with the low flammability of the moist Norway spruce stands in boreal Europe. This contrast is important as it shows that links between wildfire and boreal forest composition are far from universal.

Considering that fire is a key process in the net transfer of carbon from terrestrial ecosystems to the atmosphere (Carcaillet *et al.* 2002; Bowman *et al.* 2009), the reduction in burning associated with the late-Holocene spread of spruce in northern Europe must have significantly reduced this transfer. This reduction probably resulted in increased sequestration of carbon in forest ecosystems (Wardle *et al.* 2003) and possible alteration of average albedo (Randerson *et al.* 2006). Thus, the late-Holocene spread of spruce and the consequent reduction in burning initiated a major biological feedback to the climate system acting through the global carbon cycle.

Conclusions

This study reveals that macroscale climate exerts a broad regional influence on the incidence of fire in north-western Europe, with moist coastal areas less prone to burning compared to drier inland regions. It also reveals that the late-Holocene invasion of Norway spruce markedly affected the fire regime, particularly wildfire occurrence and distribution. A general correspondence between the invasion of spruce and the reduction in charcoal concentrations illustrates that tree species composition is an important factor capable of regulating the fire regime. The spruce invasion also gave rise to a diversification of the fire regime, with emergent spruce-dominated forests less prone to burning compared to the forests that were replaced by spruce forests. The overall reduction in wildfire activity, coupled with the establishment of a disturbance mosaic, facilitated the development of forest ecosystems characterized by long-term stand continuity, which are now the habitat for many rare and threatened species. Thus, we suggest that for the boreal forest ecosystems in northern Europe, there is a need to replace the concept of fire disturbance as a major determinant of boreal forest structure and function in favour of the importance of maintaining biological continuity.

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References

Bjune, A.E., Bakke, J., Nesje, A. & Birks, H.J.B. (2005) Holocene mean July temperature and winter precipitation in western Norway inferred from palynological and glaciological lake-sediment proxies. *Holocene*, **15**, 177–189.

Bjune, A.E., Ohlson, M., Birks, H.J.B. & Bradshaw, R.H.W. (2009) The development and local stand-scale dynamics of a *Picea abies* forest in south-eastern Norway. *Holocene*, **19**, 1073–1082.

Bonan, G.B. & Shugart, H.H. (1989) Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics*, **20**, 1–28.

Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A. *et al.* (2009) Fire in the Earth system. *Science*, **324**, 481–484.

Bradshaw, R.H.W. & Lindbladh, M. (2005) Regional spread and stand-scale establishment of *Fagus sylvatica* and *Picea abies* in Scandinavia. *Ecology*, **86**, 1679–1686.

Brown, K.J., Clark, J.S., Grimm, E.C., Donovan, J.J., Mueller, P.G., Hansen, B.C.S. & Stefanova, I. (2005) Fire cycles in North American interior grasslands and their relation to prairie drought. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 8865–8870.

Brubaker, L.B., Higuera, P.E., Rupp, T.S., Olson, M.A., Anderson, P.M. & Hu, F.S. (2009) Linking sediment-charcoal records and ecological modelling to understand causes of fire-regime change in boreal forests. *Ecology*, **90**, 1788–1801.

Carcaillet, C., Bergeron, Y., Richard, P.J.H., Frechette, B., Gauthier, S. & Praire, Y.T. (2001) Change of fire frequency in the eastern Canadian boreal forests during the Holocene: does vegetation composition or climate trigger the fire regime? *Journal of Ecology*, **89**, 930–946.

Carcaillet, C., Almquist, H., Asnong, H., Bradshaw, R.H.W., Carrion, J.S., Gaillard, M.J. *et al.* (2002) Holocene biomass burning and global dynamics of the carbon cycle. *Chemosphere*, **49**, 845–863.

Chapin, F.S., III, Callaghan, T.V., Bergeron, Y., Fukuda, M., Johnstone, J.F., Juday, G. & Zimov, S.A. (2004) Global change and the boreal Forest: thresholds, shifting states or gradual change? *Ambio*, **33**, 361–365.

Colombaroli, D., Marchetto, A. & Tinner, W. (2007) Long-term interactions between Mediterranean climate, vegetation and fire regime at Lago di Massaciuccoli (Tuscany, Italy). *Journal of Ecology*, **95**, 755–770.

Czimczik, C.I., Schmidt, M.W.I. & Schulze, E.D. (2005) Effects of increasing fire frequency on black carbon and organic matter in Podzols of Siberian Scots pine forests. *European Journal of Soil Science*, **56**, 417–428.

Drury, S.A. & Grissom, P.J. (2008) Fire history and fire management implications in the Yukon Flats National Wildlife Refuge, interior Alaska. *Forest Ecology and Management*, **256**, 304–312.

Flannigan, M., Stocks, B., Turetsky, M. & Wotton, M. (2009) Impacts of climate change on fire activity and fire management in the circumboreal forest. *Global Change Biology*, **15**, 549–560.

Gavin, D.G. (2003) Forest soil disturbance intervals inferred from soil charcoal radiocarbon dates. *Canadian Journal of Forest Research*, **33**, 2514–2518.

Gavin, D.G., Hallett, D.J., Hu, F.S., Lertzman, K.P., Prichard, S.J., Brown, K.J., Lynch, J.A., Bartlein, P. & Peterson, D.L. (2007) Forest fire and climate change in western North America: insights from sediment charcoal records. *Frontiers in Ecology and the Environment*, **5**, 499–506.

Giesecke, T. (2005) Holocene dynamics of the southern boreal forest in Sweden. *Holocene*, **15**, 858–872.

Giesecke, T. & Bennett, K.D. (2004) The Holocene spread of *Picea abies* (L.) Karst. in Fennoscandia and adjacent areas. *Journal of Biogeography*, **31**, 1523–1548.

Goldammer, J.G. & Furyaev, V.V. (1996) *Fire in Ecosystems of Boreal Eurasia. Ecological Impact and Links to the Global System*. Kluwer Academic Publishers, Dordrecht.

Higuera, P.E., Brubaker, L., Anderson, P.M., Hu, F.S. & Brown, T.A. (2009) Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs*, **79**, 201–219.

Hörnberg, G., Ohlson, M. & Zackrisson, O. (1995) Stand dynamics, regeneration patterns and long-term continuity in boreal old-growth *Picea abies* swamp-forests. *Journal of Vegetation Science*, **6**, 291–298.

Jacobson, G.L. & Bradshaw, R.H.W. (1981) The selection of sites for paleovegetational studies. *Quaternary Research*, **16**, 80–96.

Johnson, E.A. (1992) *Fire and Vegetation Dynamics. Studies from the North American Boreal Forest*. Cambridge University Press, New York.

Johnstone, J., Boby, L., Tissier, E., Mack, M., Verbyla, D. & Walker, X. (2009) Postfire seed rain of black spruce, a semiserotinous conifer, in forests of interior Alaska. *Canadian Journal of Forest Research*, **39**, 1575–1588.

Jowsey, P.C. (1966) An improved peat sampler. *New Phytologist*, **65**, 245–248.

Kitzberger, T., Brown, P.M., Heyerdahl, E.K., Swetnam, T.W. & Veblen, T. (2007) Contigent Pacific–Atlantic Ocean influence on multicentury wildfire synchrony over western North America. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 543–548.

Korsman, T. & Segerström, U. (1998) Forest fire and lake-water acidity in a northern Swedish boreal area: Holocene changes in lake-water quality at Makkassjön. *Journal of Ecology*, **86**, 113–124.

Kuhry, P. (1994) The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada. *Journal of Ecology*, **82**, 899–910.

Kullman, L. (2001) Immigration of Picea abies into North-Central Sweden. New evidence of regional expansion and tree-limit evolution. *Nordic Journal of Botany*, **21**, 39–54.

Lindbladh, M., Bradshaw, R.H.W. & Holmqvist, B.H. (2000) Pattern and process in south Swedish forests during the last 3000 years, sensed at stand and regional scales. *Journal of Ecology*, **88**, 113–128.

Lynch, J.A., Hollis, J.L. & Hu, F.S. (2004) Climatic and landscape controls of the boreal forest fire regime: Holocene records from Alaska. *Journal of Ecology*, **92**, 477–489.

Manly, B.F.J. (1997) *Randomisation, Bootstrap, and Monte Carlo Methods in Biology*. Chapman and Hall, London.

Marlon, J., Bartlein, P.J. & Whitlock, C. (2006) Fire-fuel-climate linkages in the northwestern USA during the Holocene. *Holocene*, **16**, 1059–1071.

Marlon, J.R., Bartlein, P.J., Walsh, M.K., Harrison, S.P., Brown, K.J., Edwards, M.E. *et al.* (2009) Wildfire responses to abrupt climate change in North America. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 2519–2524.

Miller, P.A., Giesecke, T., Hickler, T., Bradshaw, R.H.W., Smith, B., Seppä, H., Valdes, P.J. & Sykes, M.T. (2008) Exploring climatic and biotic controls of Holocene vegetation change in Fennoscandia. *Journal of Ecology*, **96**, 247–259.

Niklasson, M. & Drakenberg, B. (2001) A 600-year tree-ring fire history from Norra Kvills National Park, southern Sweden: implications for conservation strategies in the hemiboreal zone. *Biological Conservation*, **101**, 63–71.

Niklasson, M. & Granström, A. (2000) Number and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology*, **81**, 1484–1499.

Niklasson, M., Zin, E., Zielonka, T., Feijen, M., Korczyk, A.F., Churski, M., Samojlik, T., Jedrzejewska, B., Gutowski, J.M. & Brzeziecki, B. (2010) A 350-year tree-ring fire record from Biaowieza Primeval Forest, Poland: implications for Central European lowland fire history. *Journal of Ecology*, **98**, 1319–1329.

Odion, D.C., Moritz, M.A. & DellaSala, D.A. (2010) Alternative community states maintained by fire in the Klamath Mountains, USA. *Journal of Ecology*, **98**, 96–105.

Ohlson, M., Korbøl, A. & Økland, R.H. (2006) The macroscopic charcoal record in boreal forested peatlands in South-east Norway. *Holocene*, **16**, 731–741.

Ohlson, M. & Tryterud, E. (1999) Long-term spruce forest continuity – a challenge for a sustainable Scandinavian forestry. *Forest Ecology and Management*, **124**, 27–34.

Ohlson, M. & Tryterud, E. (2000) Interpretation of the charcoal record in forest soils: forest fires and their production and deposition of macroscopic charcoal. *Holocene*, **10**, 519–525.

Ohlson, M., Dahlberg, B., Økland, T., Brown, K.J. & Halvorsen, R. (2009) The charcoal carbon pool in boreal forest soils. *Nature Geoscience*, **2**, 692–695.

Pausas, J.G. (2004) Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). *Climatic Change*, **63**, 337–350.

Pitkänen, A., Tolonen, K. & Jungner, H. (2001) A basin-based approach to the long-term history of forest fires as determined from peat strata. *Holocene*, **11**, 599–605.

Pitkänen, A., Turunen, J. & Tolonen, K. (1999) The role of fire in the carbon dynamics of a mire, eastern Finland. *Holocene*, **9**, 453–462.

Pitkänen, A., Huttunen, P., Tolonen, K. & Jungner, H. (2003) Long-term fire frequency in the spruce-dominated forests of the Ulvinsalo strict nature reserve, Finland. *Forest Ecology and Management*, **176**, 305–319.

Pitman, A.J., Narisma, G.T. & McAneney, J. (2007) The impact of climate change on the risk of forest and grassland fires in Australia. *Climatic Change*, **84**, 383–401.

Power, M.J., Marlon, J., Ortiz, N. *et al.* (2008) Changes in fire regimes since the Last Glacial Maximum: an assessment based on global synthesis and analysis of charcoal data. *Climate Dynamics*, **30**, 887–907.

Preston, C.M. (2009) Fire's black legacy. *Nature Geoscience*, **2**, 674–675.

Randerson, J.T., Liu, H., Flanner, M.G., Chambers, S.D., Jin, Y., Hess, P.G. *et al.* (2006) The impact of boreal forest fire on climate warming. *Science*, **314**, 1130–1132.

Segerström, U., von Stedingk, H. & Hörnberg, G. (2008) Long-term sustainability of a northern boreal deciduous swamp forest in northern Sweden: succession in the absence of fire. *Holocene*, **18**, 1113–1122.

Seppä, H., Alenius, T., Bradshaw, R.H.W., Giesecke, T., Heikkilä, M. & Muukkonen, P. (2009a) Invasion of Norway spruce (*Picea abies*) and the rise of the boreal ecosystem in Fennoscandia. *Journal of Ecology*, **97**, 629–640.

Seppä, H., Bjune, A.E., Telford, R.J., Birks, H.J.B. & Veski, S. (2009b) Last nine-thousand years of temperature variability in Northern Europe. *Climate of the Past*, **5**, 523–535.

Soja, A.J., Tchebakova, N.M., French, N.H.F., Flannigan, M.D., Shugart, H.H., Stocks, B.J., Sukhinin, A.I., Parfenova, E.I., Chapin, F.S., III & Stackhouse, P.W., Jr (2007) Climate-induced boreal forest change. Predictions versus current observations. *Global and Planetary Change*, **56**, 274–296.

Tallantire, P.A. (1972) Spread of spruce (*Picea abies* (L.) Karst) in Fennoscandia and possible climatic implications. *Nature*, **236**, 64–65.

Tryterud, E. (2003) Forest fire history in Norway: from fire-disturbed pine forests to fire-free spruce forests. *Ecography*, **26**, 161–171.

Wanner, H., Beer, J., Buetikofer, J., Crowley, T., Cubasch, U., Flueckiger, J. *et al.* (2008) Mid- to Late Holocene climate change: an overview. *Quaternary Science Reviews*, **27**, 1791–1828.

Wardle, D.A., Hörnberg, G., Zackrisson, O., Kalela-Brundin, M. & Coomes, D.A. (2003) Long-term effects of wildfire on ecosystem properties across an island area gradient. *Science*, **300**, 972–975.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R. & Swetnam, T.W. (2006) Warming and earlier spring increase western US forest wildfire activity. *Science*, **313**, 940–943.

Whitlock, C. & Larsen, C. (2001) Charcoal as a fire proxy. *Tracking Environmental Change Using Lake Sediments, Vol. 3: Terrestrial, Algal, and Siliceous Indicators* (eds J.P. Smol, H.J.B. Birks & W.M. Last), pp. 75–97. Kluwer Academic, Dordrecht, The Netherlands.

Whitlock, C., Shafer, S.L. & Marlon, J. (2003) The role of climate and vegetation change in shaping past and future fire regimes in the northwestern US and the implications for ecosystem management. *Forest Ecology and Management*, **178**, 5–21.

Willis, K.J. & Birks, H.J.B. (2006) What is natural? The need for a long-term perspective in biodiversity conservation. *Science*, **314**, 1261–1265.

Zackrisson, O. (1977) Influence of forest fires on the North Swedish boreal forest. *Oikos*, **29**, 22–32.

Zackrisson, O., Nilsson, M.-C., Steijlen, I. & Hörnberg, G. (1995) Regeneration pulses and climate-vegetation interactions in nonpyrogenic boreal Scots pine stands. *Journal of Ecology*, **83**, 469–483.

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Supporting Information

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

Table S1. Study site information with references.

Table S2. The soil cores and their content of macroscopic charcoal particles.

Figure S1. Interpolated age-depth relationships for the subset of 30 sites with radiocarbon-dated soil cores.

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