Holocene fire and vegetation dynamics in the northern European forests

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy

by

Jennifer L. Clear

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Abstract

Fire has not always been so elusive in the northern European forest yet forest management and active fire suppression has created an ecosystem almost free of fire. This absence of fire is thought to have contributed to the widespread dominance of *Picea abies* as well as the decline in deciduous species and subsequent loss of floristic diversity. Forest fires in general are driven by a complex interplay between natural (climate, vegetation and topography) and anthropogenic disturbance and through palaeoecology we are able to explore spatio-temporal variability in the drivers of fire and changing fire dynamics. This thesis explores spatial and temporal variability in Holocene vegetation and disturbance dynamics through stand-scale palynology. Pollen and macroscopic charcoal are used to reconstruct past vegetation and fire dynamics with local- and regional-scale pollen-derived quantitative vegetation reconstructions able to identify both large-scale ecosystem response and local-scale disturbance. Spatio-temporal heterogeneity and variability in biomass burning is explored to identify the drivers of fire and palaeo-vegetation reconstruction is compared to process-based, climate-driven dynamic vegetation model output to test the effect of fire frequency as a driver of vegetation composition and dynamics. Early-Holocene fire was driven by natural climate variations and fuel availability. The establishment and spread of *Picea abies* (Norway spruce) appears to be driven by an increase in continentality although local disturbance cannot be ruled out. The expansion of *Picea* led to a step-wise reduction in regional biomass burning and the now widespread dominance of *Picea abies* is responsible for the low fire frequency observed through Fennoscandia. The mid-Holocene decline in deciduous species was primarily driven by localised anthropogenic disturbance and may have been assisted by the shift to cooler, wetter climate conditions. There is an underlying natural fire frequency of approximately 400 years observed in southern Finland and without intensive anthropogenic disturbance floristic diversity may have remained locally, to the present day. Stand-scale palynology is able to record past local disturbance at a high spatial precision however more than one site is required to understand regional disturbance and the variable controls of fire dynamics.

Acknowledgements

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Chapter 1

1 Introduction

1.1 Motivations for research

'Fire is the most important disturbance dynamic in the boreal forest' is a broad statement often used to introduce fire as a disturbance mechanism that drives natural forest succession (Bergeron *et al*., 1998) with stand age, composition and structure often determined by the last fire event (Engelmark *et al*., 1993; Engelmark, 1994). Yet fire is not necessarily a universal feature of the Fennoscandian ecosystem but oscillates through time with climate variability (Willis and Birks 2006), dominant vegetation type (Ohlson *et al.* 2011) and anthropogenic disturbance. Although humans have been using fire since the early- to mid-Pleistocene (Bowman *et al.* 2011) it is only since the mid- to late- Holocene that anthropogenic disturbance has altered the fire regime in Fennoscandia, firstly through 'swidden' slash and burn cultivation (e.g. Sarmela, 1987; Alenius *et al*., 2013; Reitalu *et al*., 2013) and later through widespread fire suppression (Zackrisson, 1977; Wallenius, 2011) and prescribed burning (e.g. Rowe & Scotter, 1973; Halme *et al*., 2013). Although the application of prescribed burning aims to re-introduce fire into the boreal forest, only 2-3% of Finnish forest was burnt between 1920 and 1990 compared with 50-75% of forest burnt between 1700 and 1920 using traditional slash and burn techniques (Parviainen, 1996). Fire disturbance in a forest system is a key element of regeneration and a facilitator of biodiversity so much so that a lack of fire may have a negative effect on biodiversity and ecosystem function (Granström, 2001). The reduction or lack of fire in recent centuries has impacted forest biodiversity by favouring the expansion of *Picea abies* (Bjune *et al*., 2009a) and endangered fire-dependent species of insects (Lindbladh *et al*., 2007; Kouki *et al*., 2012) and higher plants (Risberg & Granström, 2012). To understand the lack of fire in the northern European forests and associated loss in diversity we need to explore the drivers of fire, climate, vegetation and anthropogenic disturbance (Whitlock *et al*., 2010).

The mid- to late-Holocene expansion of *Picea abies* in an east to west trajectory across Fennoscandia (Giesecke & Bennett, 2004; Seppä *et al*., 2009a) diversified the fire regime (Bradshaw *et al*., 2010; Ohlson *et al*., 2011) from a fire prone to a fire free environment (Ohlson & Tryterud, 1999; Tryterud, 2003). Yet the expansion of *Picea* coincided with an intensification of anthropogenic disturbance (e.g. Sarmaja-Korjonen, 1998; Molinari *et al*., 2005; Bjune *et al*., 2009a) that may have facilitated the spread of *Picea* but also makes it difficult to disentangle natural and anthropogenic disturbance and subsequently the effect *Picea* may exert over the fire regime. Further, the associated drivers behind the mid-Holocene decline in broad-leaf deciduous species (e.g. *Quercus*, *Salix*, *Tilia cordata* and *Ulmus glabra*) range from: climate - with a trend to cooler wetter conditions (e.g. Bjune *et al*., 2009b; Seppä *et al*., 2009b); competition - driven by the expansion of both *Picea* (e.g. Bradshaw & Hannon, 1992; Hörnberg *et al*., 2011) and *Fagus* (e.g. Bradshaw & Lindbladh, 2005); as well as anthropogenic disturbance through selective slash and burn cultivation and grazing (e.g. Sarmela, 1987; Nilsson, 1997). Understanding the drivers behind the mid-Holocene decline in deciduous species and associated loss in floristic diversity (e.g. Hannon *et al*., 2000; Berglund *et al*., 2008) is important for conservation and management policies. Using long-term palaeoecological data we can be used to explore spatio-temporal variability in fire, the major drivers of fire and the ecosystem impacts. This knowledge can provide a useful background for modern-day ecology and conservation practice (Willis & Birks, 2006).

1.2 Thesis aims and objectives

The broad scope of this thesis aims to explore spatial and temporal variability in Holocene vegetation and disturbance dynamics throughout Fennoscandia and Denmark with particular focus on fire. This will be achieved initially through stand-scale pollen and macroscopic charcoal analysis to reconstruct past vegetation dynamics and fire disturbance. Local- and regional-scale pollen-derived quantitative vegetation reconstruction will be combined to identify large-scale ecosystem response and local-scale disturbance to explore the drivers of Holocene vegetation dynamics. Spatio-temporal heterogeneity and variability in biomass burning will be explored to identify the main drivers of fire in the northern European forests. Finally palaeo-vegetation reconstruction will be compared to a process-based, climate-driven dynamic vegetation model output to explore the effect of fire frequency on vegetation composition and dynamics.

The following specific questions will be addressed:

- What are the main drivers of Holocene vegetation and fire variability?
- What are the controls behind and the consequences of the mid- to late-Holocene spread of *Picea abies*?
- What caused the mid- to late- Holocene decline in deciduous tree species and decline in floristic diversity?
- How does fire vary spatially and temporally and is there any underlying 'natural' fire frequency?
- What are the drivers and controls of fire variability and how does this feedback to vegetation dynamics?
- How can palaeoecological data contribute to conservation policies?

1.3 Thesis structure and overview

This thesis comprises ten chapters including four manuscripts that have been accepted, submitted or prepared for submission to be published in international peer-reviewed journals (Chapters 5 to 8)

Chapter 1: Introduces the research themes of the thesis and outlines the aims and objectives of the study. A clear overview of the thesis structure is presented and the status of manuscripts is outlined with detailed author contributions.

Chapter 2: Is a brief review of fire in Fennoscandia. It explains the importance of fire research and explores the natural dominant drivers of forest fires; Climate, topography and vegetation in addition to anthropogenic disturbance.

Chapter 3: Is a review of palynological techniques with a focus on stand-scale palynology, pollen analysis, charcoal analysis and radiocarbon dating.

Chapter 4: Outlines the regional settings and introduces the methods and techniques used in the thesis.

Chapter 5: Holocene fire frequency variability in Vesijako, Strict Nature Reserve, Finland, and its application to conservation and management – published in Biological Conservation. This chapter applies palynological environmental reconstruction to ecological conservation and management through a detailed high resolution pollen and charcoal record from a forest hollow. The role of fire as a driver of vegetation dynamics is discussed in relation to conservation and particularly the use of fire as a tool for forest management.

Chapter 6: Quantitative vegetation reconstruction to identify local and regional vegetation dynamics and disturbance history in southern Finland – manuscript to be submitted to a yet undetermined journal. This chapter combines local and regional scale quantitative vegetation analysis to explore the individual drivers (climate, fuel type and anthropogenic disturbance) of Holocene vegetation dynamics.

Chapter 7: Holocene fire in Fennoscandia and Denmark – published in International Journal of Wildland Fire. This chapter combines charcoal and fire scar data for Fennoscandia and Denmark to explore temporal and spatial variability in the fire regime.

Chapter 8: The influence of fire frequency on forest vegetation in northern Europe: past, present and future – manuscript to be submitted to Global Ecology and Biogeography. This chapter is a data model comparison that explores fire frequency as a driver of vegetation dynamics through combining palaeoecological fire data with LPJ-GUESS model simulations.

Chapter 9: Is an extended discussion that addresses the running themes in the four manuscripts (Chapters 5-8).

Chapter 10: Sums up the conclusions and wider implications of the research in the thesis and outlines the limitations and the potential for further work.

1.4 Status of manuscripts

Chapter 5: Clear, J.L., Seppä, H., Kuosmanen, N., Bradshaw, R.H.W. (2013) Holocene fire frequency variability in Vesijako, Strict Nature Reserve, Finland, and its application to conservation and management. *Biological Conservation* 166, 90-97.

Author contribution:

Clear, J.L. – Main author responsible for data collection, data processing, collating, data interpretation, figures and tables (with site map assistance from Suzanne Yee) and manuscript preparation.

Kuosmanen, N. – Manuscript review.

Seppä, H. – In depth discussion and manuscript review.

Bradshaw, R.H.W. – In depth discussion and detailed manuscript review.

Chapter 6: Clear, J.L., Heikki Seppä., Anna Birgitte Nielsen., Tejia Alenius., Bradshaw, R. H. W. Quantitative vegetation reconstruction of local and regional vegetation dynamics and disturbance history in southern Finland. Manuscript

Author contribution:

Clear, J.L. – Main author responsible for data collection and processing, statistical analysis, data modelling, figure presentation and manuscript preparation.

Seppä, H. – Manuscript review.

Nielsen, A.-B. – Discussion, assistance with model runs and manuscript review.

Alenius, T. – Manuscript review.

Bradshaw, R.H.W. – Discussion and manuscript review.

Chapter 7: Clear, J.L., Molinari, C., Bradshaw, R.H.W. Holocene fire review of Fennoscandia: A synthesis of published charcoal and fire scar records. *International Journal of Wildland Fire*, accepted.

Author contribution:

Clear, J.L. – Main author responsible for data collection and processing, statistical analysis, figure presentation and manuscript preparation.

Molinari, C. – In depth discussion and manuscript review.

Bradshaw, R.H.W. – In depth discussion and manuscript review.

Chapter 8: Clear, J.L., Allen, K.A., Lehsten, V., Bradshaw, R.H.W. The influence of fire frequency on forest vegetation in northern Europe: past, present and future. Manuscript

Author contribution:

Clear, J.L. – Main author responsible for palaeo-data collection and processing, figure presentation and manuscript preparation.

Allen, K.A. – In depth discussion, model runs and manuscript review.

Lehsten, V. – Discussion and manuscript review.

Bradshaw, R.H.W. – Discussion and manuscript review.

1.4.1 Authors overall contributions

The author was present and assisted with field work at all four of the Finnish sites: Vesijako (site 1), Sudenpesä (2), Lakka Hollow (3) and Rentukka Hollow (4) during the summers of 2008 and 2009. Unfortunately the author could not be present for fieldwork at the Russian site, Kukka Hollow (5) in 2010 and the work was carried out by Richard Bradshaw (University of Liverpool, UK), Heikki Seppä and Niina Kuosmanen (University of Helsinki, Finland). The author dissected and sub sampled all cores, selected and prepared samples for radiocarbon dating and prepared and analysed all pollen samples. The author prepared and counted all Finnish charcoal samples and Russian samples with assistance from Karen Halsall (University of Liverpool, UK) in preparation, photographic analysis and calculation of charcoal area in Kukka Hollow. All statistical work in R and CANOCO was conducted by the author as well as the maps created using ARC GIS with assistance from Richard Chiverrell and Daniel Schillereff (University of Liverpool, UK). The LRA model was developed by Shinya Sugita (University of Tallinn, Estonia) with the model runs conducted by the author with assistance from Anna Birgitte Nielsen (Lund University, Sweden). LPJ-GUESS model was developed in Lund University, Sweden and the model runs were made by Kath Allen (University of Liverpool, UK). The author was responsible for all figure preparation with some assistance from Suzanne Yee (University of Liverpool, UK) in the preparation and presentation of Vesijako map. Data analysis, interpretation and manuscript preparation was the responsibility of the author with helpful comments from co-authors.

Chapter 2

2 Drivers of fire in Fennoscandia

2.1 Importance of fire research

Forest fires are neither a new phenomenon nor a new concept yet in recent decades research into fire has experienced a surge of interest, in most part, due to an increased awareness of climate change (e.g. Flannigan, 2005; Girardin *et al*., 2010). Forests worldwide and, in particular, the circum-boreal forest is an extensive and dynamic carbon reservoir (Flannigan, 2005) with natural inter-annual variability in terrestrial, biosphere and atmospheric CO_2 fluxes (Prentice *et al.*, 2011). This natural balance of biomass uptake and release of CO_2 is generally in equilibrium however, small imbalances such as variations in fire can have a substantial impact on total terrestrial to atmosphere CO_2 flux (Cox *et al*., 2000). This in turn feeds back into the climate system contributing to a positive climate-carbon cycle with a net transfer of carbon from the terrestrial biosphere to the atmosphere (Cox *et al.*, 2000; Bowman, 2009; Prentice *et al.*, 2011) contributing to an ongoing increase in net atmospheric CO_2 (Jacobson, 2004) and other greenhouse gasses e.g. CH_4 and CO (Prentice *et al.*, 2011).

Knowledge of natural fire regimes has become pressingly more important with potentially unprecedented future climate change and its consequential impact on the fire regime; most notably fire frequency, size and severity (Bergeron, 2002). Not only is there the potential for climate change to increase the frequency and severity of the natural fire regime (e.g. Kasischke *et al*., 1995: Marlon *et al*., 2009) there is also fire-climate feedback consequences where a change in the fire regime may, in turn, affect the future climate through changes in albedo (Bergeron *et al.*, 1998). However, conflicting results suggest an increase in fire may not accelerate climate warming (Randerson *et al.*, 2006) and an increase in future precipitation may reduce fire frequency and result in less frequent, more intense fires due to fuel accumulation (Flannigan *et al.*, 1998). Although it remains uncertain how climate change will affect future fire regimes there is an element of increased risk especially in a world of expanding population and increased land use pressures (Bowman *et al*., 2009). Fire becomes more hazardous with environmental competition for space and risk mitigation is a priority to prevent or reduce potential economic and livelihood loss associated with fire (Bowman *et al.*, 2011).

Fire research is fundamental for forest management with knowledge of fire regimes important for modern day conservation, restoration and management practices (Birks, 1996b). Fire is beneficial in the natural setting and forest fires are considered the principal natural process for the renewal of boreal forest (Bradshaw, 1993) promoting gap dynamics, regeneration of forest, and biodiversity (Lindbladh *et al*., 2003). Fire is episodic by nature (Marlon *et al.*, 2013) and the last fire event (or other significant disturbance event e.g. wind disturbance or insect outbreak) often determines a forest stand structure; age and composition of species (Bradshaw & Hannon, 1992). If fire became less frequent, a potential scenario in the boreal forest (Flannigan *et al*., 1998), then ecosystems would lose the benefits associated with fire disturbance. To begin to understand how the fire regime may change in the future we first need to understand past fire regimes and the past and present controls on forest fire dynamics.

2.2 Holocene drivers of forest fires

Large-scale climatic variability controlled fire during the glacial and inter-glacial cycles of the Quaternary (Marlon *et al.*, 2009). Pre-Quaternary, fire was controlled or limited by oxygen, climate or heat and vegetation or fuel limitation (Figure 2.1) with evidence of fire present since the appearance of terrestrial plants in the Silurian approximately 420 Ma (Scott, 2000; Scott *et al*., 2006).

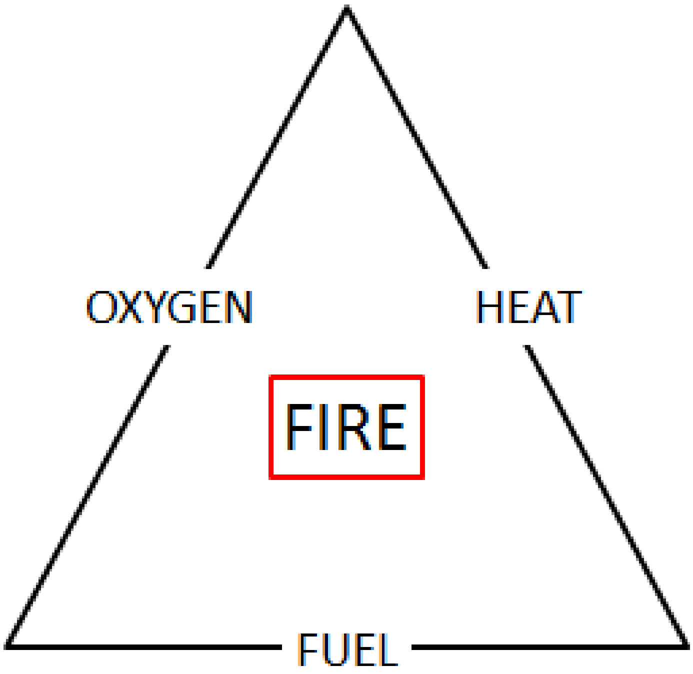


Figure 2.1: Fire triangle of the three basic requirements for successful fire ignition; oxygen, heat and fuel.

More recently during the Holocene, approximately the last 11700 (yrs before 2000) (Walker *et al*., 2009) natural controls on fire are driven by complex interactions between climate, vegetation and topography (Pyne *et al.,* 1996). The controls of fire are often portrayed as a set of superimposed triangles, with processes ranging from oxygen to weather to climate, combustion to fuel to vegetation, and local to landscape to regional drivers over broadening spatial and lengthening temporal scale (Whitlock *et al*., 2010) (Figure 2.2).

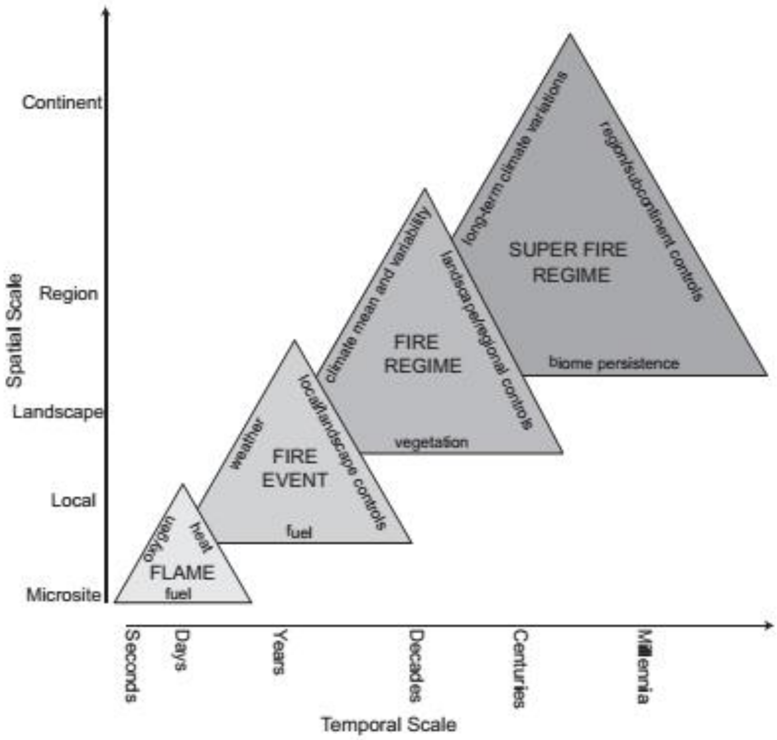


Figure 2.2 Controls of fire at multiple temporal and spatial scales conceptualised as fire triangles after (Whitlock *et al.*, 2010)

Each triangle is complex and focuses on fire on a different spatio-temporal scale and while fire knowledge is usually focused on the local to landscape scale it is important to look at the bigger ‘triangle’ to understand the drivers of fire and to appreciate long-term and large-scale risks. Figure 2.2 highlights the complexity of the fire system with each natural control; climate, vegetation and topography not mutually exclusive and with extensive feedbacks associated between them. In addition anthropogenic disturbance has the ability to alter each natural control of fire, as well as fire directly, so it becomes difficult to disentangle the intertwined nature of climate, vegetation and human disturbance as drivers of fire (Marlon et al 2013). Figure 2.3 is an adaption to the fire triangle that incorporates anthropogenic disturbance as well as feedbacks highlighting the complexity of the Holocene fire regime.

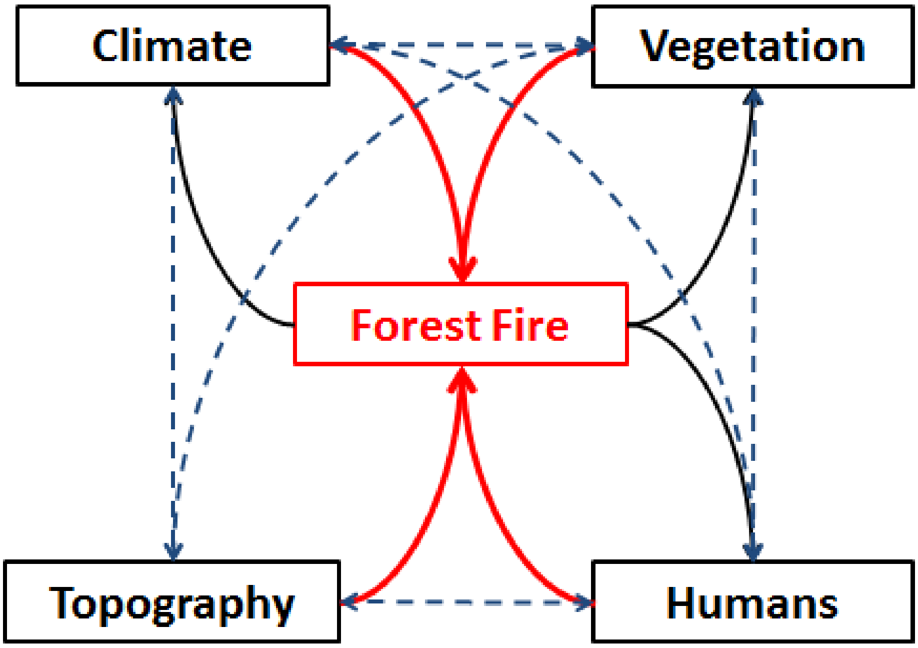


Figure 2.3: Schematic diagram of the Holocene drivers of fire and feedbacks

→ denotes the direct drivers of forest fire

--→ indicates the complex feedbacks between the individual fire drivers

→ is the feedbacks between the fire regime and the drivers of fire

2.2.1 Climate

The magnitude of climate change during the Holocene is relatively slight compared to previous Quaternary climate fluctuations associated with glacial and interglacial cycles (Figure 2.4). Yet Holocene climate oscillations remain sufficient to drive significant variability in forest fire activity (e.g. Marlon *et al*., 2013).

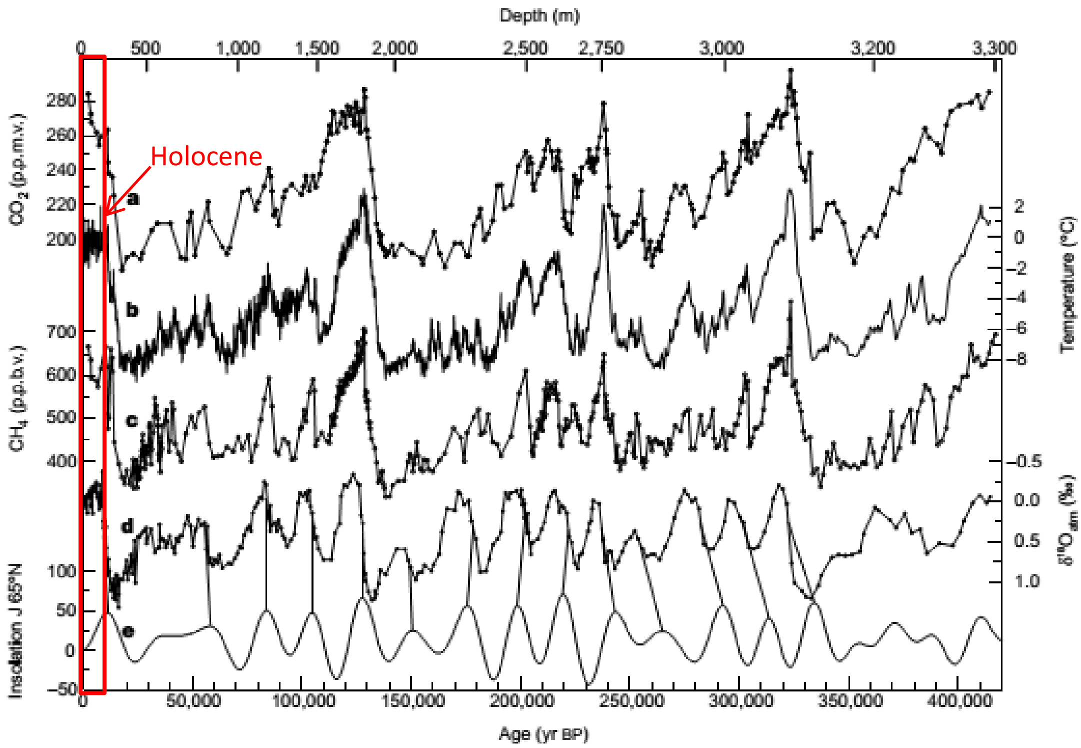


Figure 2.4: Vostok Ice core time series reconstruction of CO_2, Temperature, CH_4 and $\delta^{18}O$ to highlight Holocene variability in comparison to previous Quaternary fluctuations after (Petit *et al.*, 1999)

Climate dynamics control fire ignition, fuel moisture and fire spread (Whitlock *et al*., 2010). Individually these controls vary long-term due to decadal and millennia variations in solar radiation (Millspaugh *et al*., 2000) however, short-term daily to monthly weather variability has a direct impact on the probability of fire ignition and subsequent fire behaviour. The most important variables to determine fire ignition potential, fuel moisture content and prospective fire spread are temperature, relative humidity, precipitation and wind speed (van Wagner, 1979; 1982). Natural fire ignition is caused by lightning (Gromtsev, 2002) with the annual fire season varying in peak ignitions and length, usually on a gradient scale over distance. For example, in Finland fire ignition probability peaks in late May and early June in southern Finland but not until the end of June in northern Finland with a three-fold increase in the average annual ignition probability between north-eastern (3%) and south-western (9%) Finland (Larjavaara *et al*., 2004). There is also a steep gradient in ignition density recorded in Sweden with the highest rate of ignition recorded in south-eastern regions declining in a north and west trajectory. Both north and south Sweden have an ignition density peak in early July but the fire season is between 4 to 6 weeks longer in the south (Granström, 1993). Variability in weather is also the main driver of fuel moisture processes with small magnitude weather changes having an immediate impact on fuel moisture content (van Wagner, 1987; Pyne *et al*., 1996). Long term drought has the ability to reduce fuel moisture over time increasing the ignition potential (Linderholm & Molin, 2005). Once fire ignition is successful, wind speed and wind direction determine the spread of fire and an increase in wind speed or sudden directional change has the ability to facilitate large fires (Pyne *et al.,* 1996).

In Fennoscandia climate, seasonality and weather changeability is controlled by the North Atlantic Oscillation (NAO) which exhibits considerable variability on a range of time scales between weekly to decadal and millennial (Marshall *et al.*, 2001; Visbeck *et al.*, 2001). Holocene climate variability in Fennoscandia has been reconstructed from a range of proxies; pollen (Antonsson & Seppä, 2007), dendrochronology (Helama *et al.*, 2009), chronomids (Korhola *et al.*, 2002) and diatoms (Larsen *et al.*, 2006) and when combined in a multi-proxy approach can give an insight into past climatic changes. Climate reconstruction inferred from these proxies suggests that during the early-Holocene both temperature (Antonsson *et al.*, 2006) and precipitation were low (Larsen *et al.*, 2006) followed by a gradual increase in temperature until approximately 9000 cal. yrs. BP (Heikkilä & Seppä, 2003). Episodes of high fire activity were relatively common in the early-Holocene despite the low temperatures (Marlon *et al.*, 2013) suggesting dry conditions may have aided early-Holocene fire variability. After this early phase of warming there is a period of cooling recorded throughout Fennoscandia between approximately 8800 to 7800 cal. yrs. BP. Glacial expansion was recorded in Norway (Nesje *et al.*, 2001; Nesje *et al.*, 2006) together with increased winter snow estimates from varved lake sediment in Sweden (Zillén & Snowball, 2009) and cooling recorded in pollen, diatoms and chironomid records (Rosén *et al.*, 2001; Korhola *et al.*, 2002; Larsen *et al.*, 2006). Records in fire activity during this cold event often referred to as the ‘8.2 ka event’ commonly show low fire activity (Greisman & Gaillard, 2009; Carcaillet *et al.*, 2012; Molinari *et al.*, 2013). After 8000 cal. yrs. BP temperature began to increase and climate became warm and stable (e.g. Davis *et al.*, 2003; Larsen *et al.*, 2006) during a period known as the Holocene Thermal Maximum (HTM) with temperatures ranging from between 1.5˚C to 3˚C warmer than today (Seppä & Birks, 2001; Heikkilä & Seppä, 2003; Bjune *et al*., 2004; Antonsson & Seppä, 2007; Bjune & Birks, 2008). High fire activity was recorded during warm, dry conditions (Greisman & Gaillard, 2009) with modest changes in fire during the mid-Holocene most likely reflecting climate rather than increases in population size or cultivation area (Marlon *et al.,* 2013). A trend to cooler wetter conditions followed the Holocene Thermal Maximum (HTM) declining from around 4000 cal. yrs. BP (Heikkilä & Seppä, 2003; Larsen *et al.*, 2006; Antonsson & Seppä, 2007; Brown *et al*., 2012) up until the present day. However, this declining trend in temperature was punctuated by the Medieval Warm Period (MWP) between approximately 1100 and 800 cal. yrs. BP (Helama *et al.*, 2009; Luoto *et al.*, 2009; Helama *et al.*, 2010). During the MWP it becomes increasingly difficult to distinguish between the natural and anthropogenic influence on fire as it is during this period that permanent settlement and agriculture became widespread in Fennoscandia (e.g. Sarmela, 1987; Alenius *et al.* 2008; Berglund *et al*., 2008a). A further diversion away from the general climatic cooling trend of the late-Holocene is the Little Ice Age (LIA) recorded between approximately 700 and 200 cal. yrs. BP (Helama *et al.*, 2009; Luoto *et al.*, 2009; Seppä *et al.*, 2009; Helama *et al.*, 2010) with glacial expansion recorded in Norway (Nesje *et al.*, 2001). Although it remains difficult to disentangle the climate – anthropogenic fire signal, fire frequency has generally been lower in the past few centuries potentially due to climate controls (e.g. Bradshaw & Zackrisson, 1990; Bergeron & Archambault, 1993; Flannigan *et al.*, 1998; Carcaillet *et al.*, 2007).

2.2.2 Topography

Local geographical conditions such as elevation, slope and aspect create local spatial variability in weather conditions (Pyne *et al.,* 1996) highlighted by the increase in lightning strikes and increased occurrence of fire recorded on islands compared to the mainland in the boreal zone in both Sweden (Wardle *et al.*, 2003; Niklasson *et al.*, 2010) and Canada (Bergeron, 1991). Also topography is highly important for driving fire behaviour as natural barriers such as rocks, lakes and streams can act as fire breaks (Parviainen, 1996; Pyne *et al*., 1996). A study by Hellberg *et al.,* (2004) concluded that fire intervals were nearly two times longer in mire rich landscapes compared to mire-free areas.

2.2.3 Vegetation

Fire ignition potential and fire behaviour is also controlled by fuel type, species dominance and age structure (Pyne *et al.,* 1996) as well as the fuel conditions such as fuel moisture content which is predominantly driven by climate (Whitlock *et al*., 2010). However vegetation has the ability to affect fire in its own capacity. There are three fuel types available within a forest environment: underground fuel such as roots and buried litter; surface fuel or ground litter; and crown or canopy fuel. Combined these three fuel types make up the total fuel load consisting of both living and dead plant biomass material (Pyne *et al*., 1996). The majority of fire ignitions take place in the surface fuel and subsequently develop into low intensity ground fires or surface fires (Granström, 1996). However, in most cases canopy fires also ignite in the surface fuel and are able to develop from a combination of heat intensity and fuel arrangement that allows for continuity between fuel layers, often due to an understory of vegetation in uneven aged forest stands acting as a fuel ladder (Tanskanen *et al*., 2006). These crown fires are often supported by surface fires (Pyne *et al.,* 1996). Fuel type can control both the type of fire as well as the potential for fire ignition (e.g. Tanskanen *et al*., 2005; Ohlson *et al.*, 2011). In the northern boreal forests of Fennoscandia there are two dominant conifer species; *Pinus sylvestris* (Scots pine) and *Picea abies* (Norway spruce). During an experimental burn *Pinus* dominated stands were three times more likely to ignite than *Picea* stands (Tanskanen *et al*., 2005) with *Pinus* stands more likely to experience high frequency, low intensity surface fires (Zackrisson, 1977; Engelmark, 1984) and *Picea* dominated stands more likely to experience low frequency, high intensity crown fires (Tanskanen, 2007). *Picea abies* dominated stands can also create a natural fire break as demonstrated in an experimental burn (Figure 2.4) when *Pinus* forest burnt at a low intensity and *Picea* forest act as a fire boundary.

Figure 2.5: Experimental burn near Jyväskylä, Finland showing burnt *Pinus* stand in-front of a dense un-burnt *Picea* stand.

Early-Holocene warming and deglaciation led to the gradual vegetation development in Fennoscandia (Lundqvist, 1986). Initially an expansion of high diversity tundra-steppe (Berglund *et al*., 2008b) was replaced by relatively low diversity boreal *Pinus-Betula* woodland (Björck & Möller, 1987; Berglund *et al*., 2008b). This increase in vegetation no doubt contributed to the episodes of high fire activity during the early-Holocene (Marlon *et al.*, 2013). The mid-Holocene Thermal Maximum (HTM) was characterised by a high diversity of nemoral broadleaf woodland (Berglund *et al*., 2008b). Modern day temperate forests in southern Fennoscandia burn less than their boreal forest counterparts (Pitkänen *et al.*, 1999) suggesting any increase in mid-Holocene fire was controlled by other factors. The mid- to late-Holocene spread of *Picea abies* expanded in a wave like distribution across Fennoscandia from east to west (Tallantire 1972; Giesecke & Bennett, 2004) with fire activity linked with facilitation of the local establishment of *Picea* (Hörnberg *et al*., 2011) as well as the local establishment of *Fagus* in southern Sweden (Björkman, 1997; Björkman & Bradshaw, 2006). However, Bradshaw & Lindbaldh (2005) suggest that the patchy establishment of *Fagus* was driven by disturbance whereas *Picea* expansion tracked regional climate variability and elsewhere in southern Sweden high fire frequency may have initially prevented *Picea abies* establishment (Bradshaw, 2003). The late-Holocene vegetation dynamics are a combination of the spread of *Picea* across Fennoscandia (Giesecke & Bennett, 2004; Seppä *et al*., 2009a) which may have altered the boreal fire regime (Ohlson *et al*., 2011) and late-Holocene human influence that facilitated the spread of *Fagus* through intensive modification of fire disturbance. (e.g. Björkman 1997; Bradshaw & Lindbladh, 2005; Björkman & Bradshaw, 2006).

2.2.4 Anthropogenic disturbance

The natural spatial and temporal disturbance regimes have been profoundly affected by anthropogenic disturbance. This artificial disturbance not only drives forest disturbance dynamics but has also had clear consequences for the current tree species and age composition (Uotila *et al.,* 2002) with the relative abundance of individual forest taxa significantly influenced by human impact (Reitalu *et al.* 2013). This idea that disturbance controls vegetation dynamics is not a new concept with Cajander (1926) suggesting ”where there has been disturbance, through fire grazing or other agencies, the vegetation will differ from that of the normal type because even in the earlier stages after the disturbance, the vegetation becomes characteristic of the quality of the locality.” Yet it remains difficult to identify anthropogenic land use in palaeoecological and archaeological records (Sarmaja-Korjonen 2003b). Although humans have been using fire since the early-mid Pleistocene (Bowman *et al.*, 2011), it is only since the mid- to late-Holocene that anthropogenic intervention has modified boreal Fennoscandian fire regimes from their ‘natural’ state.

Fishing and hunting culture had already evolved in southern Finland by 9000 cal. yrs. BP (Sarmela, 1987) but it was not until between 7500 and 5700 cal. yrs. BP that the region experienced major population growth associated with high summer temperatures and subsequent high productivity of terrestrial, lacustrine and marine ecosystems (Tallavaara & Seppä, 2011). Alenius *et al*., (2013) recorded the oldest evidence of cultivation in northern Europe with evidence of buckwheat cultivation dating to approximalty 7200 cal. yrs. BP recorded in southern Finland. These findings question the route and source of the spread of cultivation into Finland suggesting buckwheat cultivation emerged as a product of trade with Asia rather than the existing theory of cultivation methods emerging in Finland from the fertile lands of the Balkans and central Europe (Alenius *et al*., 2013). Equivalent, old Mesolithic, hunter-gatherer settlements have been found in northern Sweden dating to approximalty 8600 cal. yrs. BP (Hörnberg *et al*., 2007).

Further evidence of early anthropogenic impact in southern Finland, also recorded by Alenius *et al*., (2013) is dated to approximately 6200 cal. yrs. BP where an increase in charcoal abundance and finds of *Hordeum* in the pollen record is linked to late-Mesolithic and Neolithic Stone Age clearance of deciduous species and is associated with decline in *Pinus* and *Betula* pollen. An increase in non-arboreal pollen is recorded from approximately 6200 cal. yrs. BP in Norway (Overland &

Hjelle, 2009) and there is evidence of grazing recorded in southern Sweden at approximately 6000 cal. yrs. BP (Lagerås, 1996).

A decline in human population is recorded between 5500 and 4000 cal. yrs. BP and correlates with the onset of late-Holocene cooling and major forest ecosystem change (Tallavaara & Seppä, 2011). The cause of the forest ecoystem change is the late expansion of *Picea abies* accountable for a changing forest ecosystem from that of a mixed, diverse, species rich environment to the current species poor, coniferous dominated forest. Between 6000 and 4300 cal. yrs BP Alenius *et al*., (2013) records little evidence of anthropogenic activity. The first signs of cultivation in the Lammi district of southern Finland are recorded between 4500 and 4000 cal. yrs. BP (Tolonen, 1980) and weak signs of early slash and burn and barley cultivation are recorded elsewhere in southern Finland approximately 4300 cal. yrs. BP (Alenius *et al.,* 2009; 2013). An increase in *Juniperus* pollen is potentially indicative of forest opening caused by fire disturbance and this is reviewed as evidence for possible grazing around 4100 cal. yrs. BP (Alenius *et al.* 2013). Between 4000 and 2000 cal. yrs. BP, during the time when permanent agriculture became established and expanded, human impact was estimated as the strongest driver of forest compositional change (Reitalu *et al.,* 2013). Clear changes in the forest pollen assemblage indicates grazing (Alenius *et al.,* 2009) and cereal cultivation (Alenius *et al.* 2013) approximatly 4000 cal. yrs. BP. It is not until approximatly 3500 cal. yrs. BP that the link between environmental proxies and population breaks down due to the intensification of agriculture (Tallavaara & Seppä, 2011) with substantial forest clearance recorded in Norway (Overland & Hjelle, 2009).

By 3000 cal. yrs. BP swidden (slash and burn) cultivation, animal husbandry, fishing and hunting made up the swidden culture that thrived in southern Finland (Sarmela, 1987). Between 3000 and 2000 cal. yrs. BP in southern Finland, Sarmaja-Korjonen, (1998) records an increase in charcoal in lake deposits associated with an increase in forest clearance driven by local anthropogenic disturbance and Tolonen, M. (1980) recorded forest clearance through burn-beat cultivation during this period. There are two types of 'swidden' or slash and burn cultivation recorded in Finland: early 'Lehtipuukaski' or burn clearance of broadleaf trees that occurred near to villages; and later 'Huuhtakaski' or burn clearance of mature coniferous forest stands that were cut down for cultivation and grazing that are most prolific between 1500 and 450 cal. yrs. BP (Sarmela, 1987; Parviainen, 1996).

In eastern Finland, the earliest signs in the pollen data of possible anthropogenic origin are recorded from 3600 cal. yrs. BP with further evidence of increased human impact without cultivated pollen types present around 2500 cal. yrs. BP and the onset of cultivation recorded from 1400 cal. yrs. BP (Alenius *et al*., 2008). Grönlund, (1991) also records evidence of slash and burn cultivation in eastern Finland between 1300 and 1200 cal. yrs. BP.

Further evidence of cultivation is recorded in southern Sweden from approximately 2300 cal. yrs. BP (Lagerås, 1996) and in northern Norway approximately 2250 cal. yrs. BP where an increase in coprostanol linked to human and animal faeces are recorded in lake sediments (D'Anjou, *et al*., 2013).

The *Alnus* decline in southern Finland between 2000 and 800 cal. yrs. BP appears to be associated with slash and burn cultivation, agriculture and finally permanent field cultivation (Sarmaja-Korjonen, 2003a). It is approximately 1200 cal. yrs. BP when evidence of settlements (Sarmela, 1987) and permanent field cultivation becomes apparent in the pollen diagrams in southern Finland (Alenius *et al.* 2008), with an increase in allochthonous material and increased erosion recorded in lake sediments. This intensive period of slash and burn is associated with the invention of the plough and the ability to 'plough' nutrient rich, heavy clay soils and the onset of 'Huuhtakaski' or coniferous slash and burn (Alenius *et al.* 2013). This cultivation type quickly began to spread inland after previously being confined to the southern Finnish heartland. This expansion of permanent cultivation correlates with the Medieval warm period (MWP) estimated between 1000 and 800 cal. yrs. BP, when permanent village communities were established (Tavitsainen *et al*., 1998). This type of settlement is also associated with population growth and colonization of new areas in the eastern interior Lake District of Finland (Alenius *et al.* 2009). Permanent arable fields and continued slash and burn are recorded in southern Sweden between approximately 700 and 100 cal. yrs. BP (Lagerås, 1996). Between

600 and -15 cal. yrs. BP is the most intensive land-use phase in eastern Finland with primitive swidden cultivation and arable cultivation practised simultaneously with permanent field cultivation, animal husbandry and hunting (Alenius *et al.,* 2008). Rapid population growth from 500 cal. yrs. BP (Kononen & Kirkinen, 1969) led to intensive phases of slash and burn and further settlement between 450 and 350 cal. yrs. BP (Sarmela, 1987) and further between 350 and 50 cal. yrs. BP (Grönlund, 1991).

Fire scars are excellent proxies to record anthropogenic fire history and in studies by Lehtonen (1996) as well as Lehtonen and Huttunen (1997), fire increased in eastern Finland between 400 – 100 cal. yrs. BP linked to active slash and burn cultivation. Slash and burn was used in Finland up until 1960 until it was replaced by less expensive and risky mechanical site preparation techniques (Parviainen, 1996). With active slash and burn banned, and active fire suppression laws in place the area burned throughout Fennoscandia was reduced (Zackrisson, 1977; Niklasson & Granström, 2000). The 20th century reduction in fires was so significant that fire based ecological processes are considered endangered (Rassi, 2003). Present-day fire management in the boreal zone has been in the form of fire suppression (Wallenius, 2011) with the intention of protecting the forest, economy, property and life. However, if a fire ignited by lightning does not immediately threaten human population or infrastructure, they are sometimes allowed to burn freely (Bowman *et al.*, 2011). Biodiversity and stand regeneration demand more fire in the form of controlled burns. However there are problems associated with a lack of knowledge of traditional fire use, high operation costs and fears of fire escaping or not achieving the burnt target (Bowman *et al.*, 2009). Furthermore, fire services continue with natural fire suppression due to lack of fire surveillance and not being able to make realistic assessments of fire danger in different situations (Bowman *et al.*, 2011).

Chapter 3

3 Methods Review

3.1 Natural archives

Sediment accumulation in a range of anoxic depositional environments i.e. lakes, bogs and forest hollows form natural archives that record an analogue of past environmental change (Jacobson & Bradshaw, 1981). Continuous, high resolution analysis of physical, chemical and biological proxies from these archives can be used to reconstruct past temporal and spatial environmental change with varying precision (Bradshaw, 2007). These biogeophysical proxies e.g. pollen, charcoal and macrofossils can give insight into gradual long-term development as well as rapid onset of environmental change and can be useful to help understand past vegetation dynamics (e.g. Giesecke, 2005), climate change (e.g. Davis *et al.*, 2003) as well as natural and anthropogenic disturbance (e.g. Hannon *et al.*, 2000). The key to answering these ecological and environmental questions is by using present-day observations (Birks, 1996a) such as observations of present day community assemblage (e.g. Seppä *et al.*, 2009b) and species distribution (e.g. Giesecke *et al.*, 2008) as a key to interpret past environmental change.

Choosing the right environment for the chosen research question is critical as differing depositional environments record information from varying spatial scales. For example, large lakes record regional changes in vegetation dynamics and disturbance history and are most useful in reconstructing regional environmental change and climate reconstruction (e.g. Bjune *et al.,* 2009b). Bjune *et al.*, (2009b) used quantitative reconstruction of July mean temperature based on a pollen-climate transfer function. Smaller enclosed sites (e.g. small lakes and forest hollows) are more suited to reconstruction of local-scale vegetation change and disturbance dynamics (Bjune *et al.,* 2009a).

3.2 Stand-scale Palynology

Small forest hollows are topographic depressions in the forest floor in which sediment accumulates (Overballe-Petersen & Bradshaw, 2011). The spatial distribution of these natural archive sites are geographically limited and although forest peats are found in the tropics and subtropics, almost all of the published stand-scale sites are from former glaciated regions within boreal and temperate forest areas (Bradshaw, 2007). Stand-scale studies began in Draved Skov, Denmark (Iversen, 1964) and have since expanded in Scandinavia (e.g. Bradshaw & Hannon, 1992; Bjune *et al.,* 2009; Overballe-Petersen *et al.,* 2013); central Europe (e.g. Mitchell & Cole, 1998; Bradley *et al*., 2013); British Isles (e.g. Bradshaw, 1981; Edwards, 1986) and North America (e.g. Davies *et al*., 1998; Bradshaw & Webb, 1985). Temporal extents of records vary between a few hundred years (Edwards, 1986) to over ten thousand years (Davies *et al.,* 1998; Overballe-Petersen *et al*., 2013) with the potential to record the entire Holocene depending on the time of deglaciation since the last glacial maximum (LGM) at the chosen site. Individual site resolution is reliant on the depth of sediment accumulation which can range between <1m to >10 meters depending on the sedimentation rate. Most commonly around 1m of sediment is retrieved (Overballe-Petersen & Bradshaw, 2001). This suggests that a sediment profile of c.1 m has the potential to record 10000 years of environmental change at an interpolated temporal resolution of approximately 100 years cm^{-1}. This is not as high a resolution that could be obtained from more rapidly accumulating lake sediments and especially annually varved sediments common in Fennoscandia (e.g. Pitkänen, 2000; Ojala & Alenius, 2005), yet analysis of proxies from forest hollows are excellent recorders of local-scale environmental change and disturbance (Jacobson & Bradshaw, 1981; Overballe-Petersen & Bradshaw, 2011).

3.3 Pollen analysis

The method of analysing pollen from sediment to determine past vegetation response to environmental change has been in use for over a century and was initially used to explore changes in climate (von Post, 1946). However, pollen analysis from stand-scale environments record past pollen assemblages and render it possible to reconstruct vegetation composition dynamics from previous environments. Peat deposits in general differ from lake sediments in that the pollen producers grow on the peat directly at the site itself (Jacobson & Bradshaw, 1981) and are therefore able to reconstruct past environmental change at a high special precision. Sedimentation accumulation in the hollow requires surface waterlogging (anoxic conditions) for continuous preservation of sediment (Jacobson & Bradshaw, 1981) as dry conditions may cause poor preservation of sediment and the site may become prone to hiatuses or breaks in continuous sedimentation (e.g. Overballe-Petersen *et al.*, 2013). Good pollen preservation further requires simple stratigraphical sequencing without mixed or disturbed sediment and limited movement of material after deposition (Jacobson & Bradshaw, 1981). Even assuming continuous, undisturbed sedimentation there are further issues to consider with pollen production, pollen deposition and pollen preservation at the site. These issues cumulate into the need to identify the pollen source area and to quantify pollen records to enable a more quantitative approach to vegetation reconstruction.

3.3.1 Pollen productivity

Individual pollen production varies between species with early empirical pollen productivity estimates (PPE), calculated by comparing pollen with forest composition using transects (Andersen, 1966), concluding that *Pinus* and *Betula* species produce up to eight times more pollen than *Tilia* and *Fraxinus* and that corrections should be made to allow for this inconsistency. Theoretical studies on pollen productivity use extended R value (ERV) models and take into consideration species specific distance weighted dispersal to estimate pollen productivity

(Parsons & Prentice, 1981; Prentice & Parsons, 1983; Prentice, 1985; Sugita, 1993). A more recent extensive collaboration, as a result of the POLLANDCAL network (Gaillard *et al.*, 2008) has calculated PPE throughout Europe: in Finland (Räsänen *et al.*, 2007; Sugita *et al.*, 2010); Sweden (Sugita *et al.*, 1999; Broström *et al.*, 2004; von Stedingk *et al.*, 2008); Norway (Hjelle, 1998); Denmark (Nielsen & Sugita, 2005) and the Czech Republic (Abraham & Kozáková, 2012) to name just a few examples. A review of the on-going efforts was conducted by Broström *et al*., (2008) and through observations at nine study plots identified consistent high pollen producers e.g. *Alnus*, *Betula* and *Pinus* and low pollen producers e.g. *Salix*, *Tilia* and *Ulmus.* Inconsistencies in PPEs related to both methodology and environmental factors. In general vegetation is controlled by biotic (e.g. competition) and abiotic (e.g. climate, disturbance) factors and these environmental factors, particularly climate, influence PPE (Broström *et al*., 2004) and especially near to species ecological limits (Autio & Hicks, 2004).

3.3.2 Pollen dispersal

Pollen dispersal is highly dependent on both the mode of pollination (Tauber, 1967) and the transportation mechanism (Tauber, 1965, 1977). In the northern European forest, pollen grains are predominantly wind-dispersed (anemophilous) which means the size and weight variation between pollen grains is critical in determining the distance of transportation. Wind dispersed pollen can be transported within or above the forest canopy with small grains travelling further (Tauber, 1965). However, certain pollen types are readily dispersed by other methods; insects (e.g. *Rubus* and *Sambucus*), vertebrates (e.g. *Galium*) and water (e.g. *Potamogeton*) being the most common. These methods of dispersal can be considered less reliable causing particular species to be underrepresented in the pollen assemblage.

The timing of pollen production is critical in determining pollen preservation with early season pollen producers e.g. *Corylus* releasing pollen in late winter or early spring when ground frost is still likely. The can lead to poor preservation and potential discrepancies recorded between pollen and macrofossil records in the sediment (Erdtman, 1943). Macrofossils, a fossil large enough to be seen and manipulated by hand e.g. seeds, buds and leaf fractions pre-date pollen analysis and were once the only proxy available to explore past vegetation dynamics (Birks, 2001). Macrofossils are less readily dispersed than most types of wind-dispersed pollen (Birks & Birks, 1980) and thus provide a more localised representation of past vegetation change. Although macrofossils are well preserved in favourable conditions they are relatively rare compared to pollen and require larger volumes of sediment for analysis. However through combining pollen and macrofossil studies in a multi-proxy approach it is possible to reconstruct a more complete picture of past forest development and vegetation change (Hannon *et al*., 2000).

3.3.3 Pollen preservation

Preservation and degradation of pollen spores is a further important consideration. The exine walls of pollen grains are composed of a mixture of cellulose and sporopollenin, a resilient material that is resistant to most chemical and physical degradation, except oxidation (Bennett & Willis, 2001). It is sporopollenin that gives pollen grain their unique identification features that is well preserved in anoxic waterlogged material e.g. lakes, peat and low pH soils. Cushing, (1967) examined the state of fossil pollen preservation in a variety of sedimentation environments and devised six preservation classes: (1) corroded, (2) degraded, (3) crumpled and exine thinned, (4) crumpled but exine normal, (5) broken, and (6) well preserved (Cushing, 1967). It was determined that accurate pollen identification is highly dependable on the environmental setting with pollen best preserved in waterlogged organic environments. Even uniform pollen degradation generates bias towards more unique, distinguishable grains for example, features such as identifiable *pori* and *colpi* can aid identification such that a *Tilia cordata* (Figure 3.1a) pollen grain could be recognisable under all but the most severe degradation, whereas species for example, in the Rosaceae family such as *Rubus* (Figure 3.1b) or *Sorbus* would be extremely difficult to identify.

(a) (b)

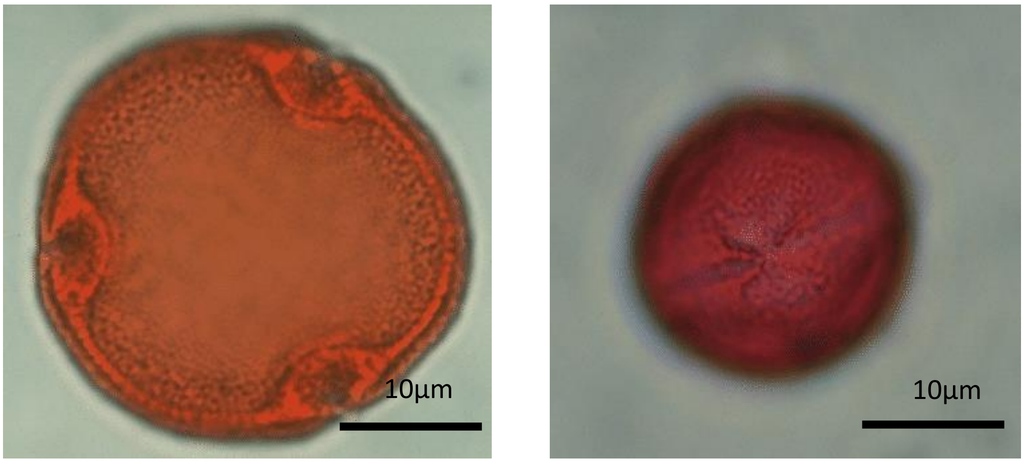


Figure 3.1: (a) *Tilia cordata* pollen grain (b) *Rubus* undiff. pollen grain
Images after (Bennett 1995-2007 Pollen catalogue of the British Isles)

3.3.4 Pollen source area

Pollen source area is dependent on size and type of site as well as pollen types under consideration (Jacobson & Bradshaw, 1981). Oldfield, (1970) acknowledged the problems associated with identifying the pollen source area when using pollen for vegetation reconstruction. A landmark study by Andersen, (1970) compared stand-scale pollen deposition with the surrounding forest vegetation to evaluate source vegetation and stand-scale pollen deposition. It was estimated that the stand-scale pollen source area was 20-30m within a closed-canopy forest (Andersen, 1970). These results were supported by studies by Bradshaw (1981). Further studies by Sugita, (1994) and Calcote, (1995) estimated that between 30-50% of pollen is derived from a source area of between 50-100m with half of the pollen derived from the regional source area (Sugita, 1994; Calcote, 1995). Even though the source area varies between models, the source area of closed-canopy sites remain smaller than larger regional sites (Bradshaw, 2007) and remains sufficient to record stand-scale vegetation heterogeneity (Calcote, 1995) with a high spatial precision.

The Landscape Reconstruction Algorithm (LRA) was developed by Shinya Sugita (Sugita 2007a,b) to quantify vegetation reconstruction from pollen analysis. The method is a multistep framework that incorporates two models: Regional Estimates of Vegetation Abundance from Large Sites, REVEALS (Sugita, 2007a) and LOcal Vegetation Estimates, LOVE (Sugita, 2007b). Regional vegetation cover is estimated using REVEALS by combining local pollen productivity estimates with the source area model described in Prentice, (1985). The regional vegetation (REVEALS) output is then integrated into LOVE to estimate local vegetation cover using the source area model outlined in Sugita, (1994). Through this multistep framework approach it is possible to estimate changes in spatial structure of past vegetation caused by natural and anthropogenic disturbance (e.g. Nielsen & Odgaard, 2005; Gaillard *et al.*, 2008; Hellman *et al.*, 2009).

3.4 Charcoal analysis

Fire is an important driver of ecosystem dynamics in the boreal forest and during each fire event carbonaceous particles are formed. Up to 90% of these particles are <2µm in diameter and are elevated into the air and transported long distances (Chandler *et al*., 1983). However a fraction, 1-3%, of the burning biomass is converted to black pyrogenic carbon including charred particles and charcoal (Preston & Schmidt, 2006). It is these charcoal fragments that are transported, deposited and preserved in the sedimentary record and have long been used in studies of past ecosystem disturbance and fire frequency (Whitlock & Bartlein, 2004) dating back to Iversen, (1941). Support for the use of palaeoecological records based on microscopic and macroscopic charcoal has been rapidly growing in the last decade (Marlon *et al*., 2013) yet there remains no standardised method to analyse charcoal particles in sediment.

3.4.1 Charcoal source area

Predominantly charcoal analysis is focused on lake sediments (Marlon *et al.*, 2013) that receive charcoal through primary (during fire years) and secondary (during non-fire years) deposition associated with slope erosion and littoral re-working (Whitlock & Larson, 2001). Whitlock & Millspaugh, (1996) observed that lakes in both burned and unburned watersheds in Yellowstone National Park, USA received charcoal during the 1988 fires. As in pollen analysis, stand-scale palynology of peat differs from lake deposits in that fire events occur on the terrestrial landscape, potentially directly or near to the site. In a study by Ohlson & Tryterud, (2000) charcoal traps were positioned inside and outside the burn area of a forest recorded macroscopic charcoal (>200µm) and 94% of the charcoal was found in traps within the burnt area. In traps >1m away from the fire edge, microscopic charcoal (<200µm) comprised 55% of all charcoal. These results indicated that macroscopic charcoal can record fire with high spatial precision however, patchy spatial representation of macroscopic charcoal was recorded in traps within the burn area. A further study by Ohlson *et al*., (2006) recorded spatially *in situ* macroscopic charcoal production and deposition within the burnt area.

3.4.2 Microscopic and macroscopic charcoal

Microscopic charcoal (50-80µm) based on pollen slide analysis (Faegri & Iversen, 1975) is a widely used ‘quick and easy’ method (e.g. Swain, 1973, 1978; Clark, 1982; Sarmaja-Korjonen, 1998; Giesecke, 2005) as microscopic charcoal can be identified on slides prepared for pollen analysis. Data are often presented as accumulation rates of area or number of particles or charcoal pollen ratios. Limitations associated with this method are: non-contiguous sampling resulting in breaks in the charcoal record; fragmentation of charcoal during pollen preparation that results in a high abundance of charcoal particles and; determining the charcoal source area (Whitlock & Larson, 2001). Microscopic charcoal source area can be considered to represent the sub-continental to global scale (Clark, 1988a) however remains important for knowledge of fire on a broad spatial scale.

Macroscopic charcoal (ca. >100µm) analysis, yet there is no common consensus on size, was first introduced by Clark (1988b) and has since been widely used (e.g. Millspaugh & Whitlock, 1995; Long *et al.,* 1998; Tinner *et al.,* 1998). Macroscopic charcoal is more representative of local fire events (Carcaillet *et al.*, 2001) however, in a lake environment the charcoal source area remains speculative as lakes integrate charcoal transported from the terrestrial fire source area (Clark, 1988a; Ohlson *et al.*, 2013). Ohlson et al., (2013) concluded that lake sediments contain between 20-80 times more charcoal (630-2930 gm^{-2}) than the average forest soil (34-1646 gm^{-2}) indicating rapid degradation of charcoal in boreal forest soil. Theoretically lakes can obtain their charcoal from the entire terrestrial catchment so maybe charcoal is overrepresented in the lake sediment.

3.4.3 Charcoal methodology

There is no standardised method for the analysis of macroscopic charcoal. Petrographic thin sections (Clark, 1988b) are precise and desirable for varved-sediments to permit annual fire history reconstruction however more commonly, macroscopic charcoal is analysed through sieving methods based on concentration, area, volume and mass (Whitlock & Larson, 2001). Charcoal concentrations do have some relationship with fire (Pitkänen *et al.*, 1999) however, to avoid overrepresentation due to fragmentation it is best to express charcoal results as charcoal area per unit volume of sediment (Mooney & Radford, 2001) after Long *et al.*, (1998) measured volumetric sediment using a nest of sieves to establish class size fractionations of charcoal. Calculating charcoal volumes can be time consuming and the method has been improved by image analysis techniques (Mooney & Black, 2003; Thevenon & Anselmetti, 2007; Halsall, unpublished) used recently by (Overballe-Petersen *et al.*, 2013; Bradley *et al.*, 2013). Yet this method has disadvantages, most notably the requirement to identify charcoal particles over mineral matter. Charcoal is distinguishable by its black crystalline form (Clark, 1984) however it remains difficult to distinguish between charcoal and mineral matter e.g. mica. One identification technique is to apply pressure to the subject, charcoal particles fracture under pressure, however if the particle fractures it becomes more difficult to count. Weng, (2005) proposes volume estimates calculated based on area, which reduced the error induced by fragmentation yet the volume estimate remains a product of the calculated area. Leys *et al*., (2013) recorded a lack of correlation between charcoal concentrations, area and volumetric estimations due to problems associated with fragmentation, however Ali *et al*., (2009) records that the three proxies (charcoal concentration, area and volume) are comparable when using locally defined thresholds to identify fire events.

3.4.4 Interpretation of charcoal records

There is no doubt that charcoal is influenced by multiple sources of variability (Kelly *et al.,* 2011) and charcoal representation in the sediment profile is highly variable within a site (Power *et al.,* 2008), yet when contiguous samples are analysed they have been used to calculate past fire frequency (Whitlock & Larson, 2001). Charcoal records in lake sediments, unless varved (e.g. Pitkänen, 2000), require statistical analysis to identify peak charcoal events against the background noise. The statistical decomposition approach to charcoal accumulation detrends background (noise) signal to identify peak charcoal or fire events with the method gaining both theoretical (Clark, 1988; Higuera *et al*., 2007) and empirical support (Millspaugh & Whitlock, 1995; Gavin *et al.,* 2003; Higuera *et al.,* 2011). Higuera, (2010) introduced the signal to noise index (SNI) as a means to quantitatively assess whether charcoal records are appropriate for peak analysis. Kelly *et al*., (2010) tested the method and indicated that some sediments yield more ambiguous charcoal series than others and SNI is valuable in detecting over-interpretation of weak charcoal signals and has the potential to interpret temporal patterns in the noise itself.

Forest hollows differ in that their source area of macroscopic charcoal records higher spatial precision (Ohlson & Tryterud, 2000) resulting in less background charcoal deposition than would be recorded in lakes. Records without continuous background signal can record unique fire events. However, charcoal deposition from a single event is often distributed over several decades due to secondary deposition (Higuera *et al*., 2005). This becomes problematic if the fire frequency is more frequent than the temporal sedimentation rate.

3.4.5 Charcoal records and fire scars

Combining spatial and temporal resolution of fire history on the regional scale (e.g. Pitkänen *et al*., 1999; Higuera *et al.,* 2011; Kasin *et al*., 2013) through the comparison of charcoal records and dendrochronological fire scars can give an insight into the ability of charcoal to record discrete fire events. With the knowledge that fire scars record fires *in situ*, Higuera *et al.,* (2005) compared macroscopic charcoal records from small forest hollows to fire scars. Analysis of > 500 µm charcoal yielded nearly identical temporal patterns and detection rates to fire scars however, four false positives were identified in the charcoal record and some low and moderate fires did not leave charcoal peaks. These results suggest fire detection depends on severity and spatial scale of fire. Charcoal from stand-scale environments would be most useful in large, severe, infrequent fire events. Further, in a study by Kasin *et al*., (2013) there was no relationship between the age of a given peatland and its content of charcoal when comparing the results to fire scars, assuming fire scars have a high spatial and temporal accuracy.

Dendrochronology is an excellent palaeoecological tool used to reconstruct fire histories *in situ* through fire scars preserved in dead and living trees. These fire scars can be precisely dated using annual tree rings and can give a clear insight into aspects of the fire regime particularly; fire frequency, seasonality and spatial scale. However, records of fire scars are limited both spatially and temporally. Spatially, trees have to survive a fire and remain *in situ* to provide a true record with fire scars and fire scars are also limited to particular tree species e.g. *Pinus sylvestris*. Temporally, with the exception of a few studies (e.g. Niklasson & Granström, 2000; Hellberg *et al.*, 2004; Groven & Niklasson, 2005), typical fire scar chronology rarely reach beyond 600 years (e.g. Zackrisson, 1977; Engelmark, 1984; Lehtonen, 1996; Lehtonen & Huttunen, 1997; Lehtonen & Kolström, 2000; Niklasson & Drakenberg, 2001; Wallenius, 2002a; Wallenius *et al.*, 2004; Wallenius *et al.*, 2007) and are considered somewhat more reliable when reconstructing the fire history for the past 400 to 500 years (e.g. Lehtonen & Huttunen, 1997; Niklasson *et al.*, 2002; Niklasson *et al.*, 2010). Charcoal in the sedimentary record is much more widely available and extensive records of charcoal have been recorded since the appearance of terrestrial plants in the Silurian, approximately 420 mya (Scott & Jones, 1994; Scott, 2000; Scott *et al*., 2006).

3.4.6 Global charcoal records

Combining charcoal records for spatial and temporal resolution analysis on the continental to worldwide scale (e.g. Power *et al.*, 2008; Vannière *et al.*, 2011; Marlon *et al.*, 2013; Molinari *et al.*, 2013) gives a broad insight into past fire history and the drivers of fire activity; climate controls, vegetation type and fuel load and anthropogenic disturbance. These studies indicate that there was less fire activity during the early Holocene compared with recent millenia (Molinari *et al*., 2013) however, episodic fire activity was consistent with climate changes despite low global temperatures and low levels of biomass burning (Marlon *et al*., 2013). There was a nearly-global increase in fire activity beginning around 3000 cal. yrs. BP that can be explained with either climate or human activity and burning has generally decreased during the last centuary during the Industrial Era (Marlon *et al*., 2013; Molinari *et al*., 2013). These, insightful studies highlight the benefits of collaborative research such as the Global Charcoal Database (GCD) and the need for further high resolution charcoal analysis, yet there is still the requirement of establishing a common methodology.

3.5 Chronology

3.5.1 Radiocarbon dating

Establishing an accurate and precise chronology is a pre-requisite for any temporal palynological study (Blaauw & Heegaard, 2012). Radiocarbon ^{14}C dating is a widely used chronological method. There are three naturally occurring carbon isotopes;

^{12}C and ^{13}C are relatively abundant stable isotopes and ^{14}C is scarce and unstable or radioactive (Hua, 2009). These isotopes are produced in the atmosphere, oxidised and transferred to other carbon reservoirs e.g. the biosphere where ^{14}C undergoes radioactive decay. ^{14}C has a half-life of 5730 years (Godwin, 1962) and is detected in the sediment typicaly up to 11 half-lives or approximately 60000 years, the current limit for radiocarbon dating (Blaauw & Heegaard, 2012).

Two methods are available for ^{14}C analysis: Conventional radiocarbon dating, through counting ^{14}C atoms, requires approximately 100g of carbon; and Accelerator Mass Spectrometry (AMS) radiocarbon dating, by counting ^{14}C atoms relative to ^{12}C and ^{13}C which only requires 0.1-10mg of carbon (Hua, 2009; Blaauw & Heegaard, 2012). Further advances allow for as little as 10-20µm of carbon (Hua *et al*., 2004) which allows for the dating of pollen extracted from peat (Brown *et al*., 1989), terrestrial macrofossils (Wohlfarth *et al*., 1998) and charcoal deposits (Gavin, 2001). Ideally peat, such as the sediment found in forest hollows, preserves abundant macrofossils which can be used for AMS ^{14}C dating, but in other cases AMS ^{14}C dating of bulk sediment is required (Yeloff *et al*., 2006). The method of analysing a series of ^{14}C dates from a sequence has been successfully applied to produce precise dating of recent peat profiles (Hua 2009). Bulk peat samples and terrestrial macrofossils were AMS radiocarbon dated in northern Europe. The accumulation rates at each site derived using the two methods were generally similar (Yeloff *et al*., 2006).

Radiocarbon calibration involves using relationships developed by dating materials of known age, notably tree rings dated with annual precision through dendrochronology (Blaauw & Heegaard, 2012) to correct ^{14}C measurements to a calendar timeline. The current ^{14}C calibration curve, IntCal09 (Reimer *et al*., 2009) incorporates large numbers of tree ring measurements for ages under 26000 cal. yrs. BP, where older sections up to 50000 cal. yrs. BP are based on fewer dates derived from marine archives ^{14}C measurements calibrated by comparing with other dating techniques (Blaauw & Heegard, 2012). Large fluctuations in atmospheric $\Delta^{14}C$ concentrations in the last few hundred years driven by climate change (e.g. Little Ice Age and solar activity) and human activity (e.g. nuclear weapon testing) has obscured the natural ^{14}C signal, but the patters in $\Delta^{14}C$ can be used to compare or wiggle match a series of ^{14}C measurements for a specific site or location (Hua, 2009).

3.5.2 Age-depth Models

Age-depth models estimate the calendar age of depths in a core, based on limited numbers of dated depths and on an assumption as to how the deposit has accumulated between those dated depths (Blaauw, 2010). The number of dates needed to construct an age-depth model for a sediment sequence will depend on the required precision and the complexity of sedimentation rate (Telford *et al*., 2004a). Commonly used models are linear interpolation, splines (curved) and linear regression models with different approaches giving very different answers (Bennett, 1994). Common and basic classical approaches use linear interpolation or regression between dated levels with the gradient between the dated intervals used to estimate rates of accumulation, with ages calculated for the intermediate depths (Blaauw & Heegaard, 2012). Interpolation allows for dates to be assigned to non-analysed depths (Blaauw & Heegaard, 2012) and although the dates rely on an unrealistic assumption that changes in sedimentation occur at the dated sample depths (Blaauw, 2010) and do not consider the range of ages as the curve is only drawn through the mean age value (Telford *et al.,* 2004b), linear interpolation often produces what looks like plausible age-depth models (Bennett, 1994). Bayesian age-depth modelling applies bootstrap or Monte Carlo simulations and makes use of more sophisticated iterative sampling methods (Blaauw, 2010). Although Bayesian methods can produce reliable age-depth models, far more forest hollow studies continue to use more basic ‘classical’ age depth models (Blaauw, 2010).

3.6 The application of stand-scale environmental reconstruction

Stand-scale archives provide a useful link between palaeoecologists and contemporary ecologists (Bradshaw 2007) with fossil records replete with examples of long-term biotic responses to climate change (Willis *et al.*, 2010). Specific conservation and management policies can be addressed when observing past long-term dynamics of native species, species invasion and species extinction (Roopnarine & Angielczyk, 2011). Vegetation development, stand-scale structure and response to disturbance can be observed during long-term development and give a clear insight into forest dynamics (e.g. Tolonen, M. 1980; Hannon *et al.*, 2000; Giesecke, 2005b). Species immigration can be explored, such as the expansion of late arriving species to the boreal forest e.g. *Picea abies* (Tallintire, 1972; Giesecke & Bennett, 2004; Seppä *et al*., 2009a) and *Fagus sylvatica* (e.g. Bradshaw *et al.*, 2010b) and their competitive overlap in the southern boreal forest (Bradshaw & Lindbladh, 2005). Further, an insight into the impact these invasive species have on the local forest composition is attainable through stand-scale palynology (e.g. Molinari et al., 2005). Specific ecological questions can be addressed concerning stand-scale palynological richness and compositional turnover (e.g. Bjune *et al*., 2009a) and the associated decline in deciduous species as well as the individual contributions of competition (e.g. Seppä *et al*., 2009c), climate (e.g. Greisman & Gaillard, 2009) and anthropogenic disturbance (e.g. Sarmaja-Korjonen, 1998). Theories and hypotheses such as the Vera hypothesis (Vera, 2000) on forest openness (Mitchell, 2005) and the Ruddiman hypothesis (Ruddiman, 2003) based on early anthropogenic drivers of increased atmospheric CO_2 and CH_4 (Marlon *et al*., 2013). Through palynological observations both Mitchell, (2005) and Marlon *et al*., (2013) query the associated hypothesis. Finally, palynological data can be used to validate dynamic vegetation models (e.g. Cowling *et al*., 2001) which in turn can be used to model future environmental response to potential climate change.

Chapter 4

4 Materials and Methods

4.1 Regional setting

The northern European forests of Fennoscandia (comprising the Scandinavian Peninsula, Finland and Russian Karelia) and Denmark are the focus area for this research. With an extensive latitudinal range between 56˚N to 69˚N (Esseen *et al*., 1997), the forest type ranges from the southern temperate forest to the northern boreal forest (Figure 4.1). The vast extent of Fennoscandia falls within the boreal zone (Esseen *et al*., 1997) with Ahti *et al.,* (1968) subdividing the boreal forest into four biotic zones; hemi, southern, middle and northern boreal, each characterised by their individual forest community composition (Figure 4.1).

Figure 4.1: Northern European vegetation zones after Ahti *et al.,* (1968)

The boreal zonation boundaries are controlled by a number of factors. In Scandinavia (Norway and Sweden) both continentality and altitudinal variation control the extent of each boreal zone. The less extreme seasonal variability, driven by the oceanic climate (Figure 4.2) accounts for the high latitudinal ranges of the hemi-, southern and middle boreal forest zones, while the Scandes mountain range controls the southern extent of the northern boreal zone (Figure 4.1). East of the Scandes mountain range, altitude has less of a control on climate variability with the distinct boreal vegetation zones following the northward decrease in annual mean temperature and subsequently growing season length and sum of growing degree days (Heikkilä, 2010).

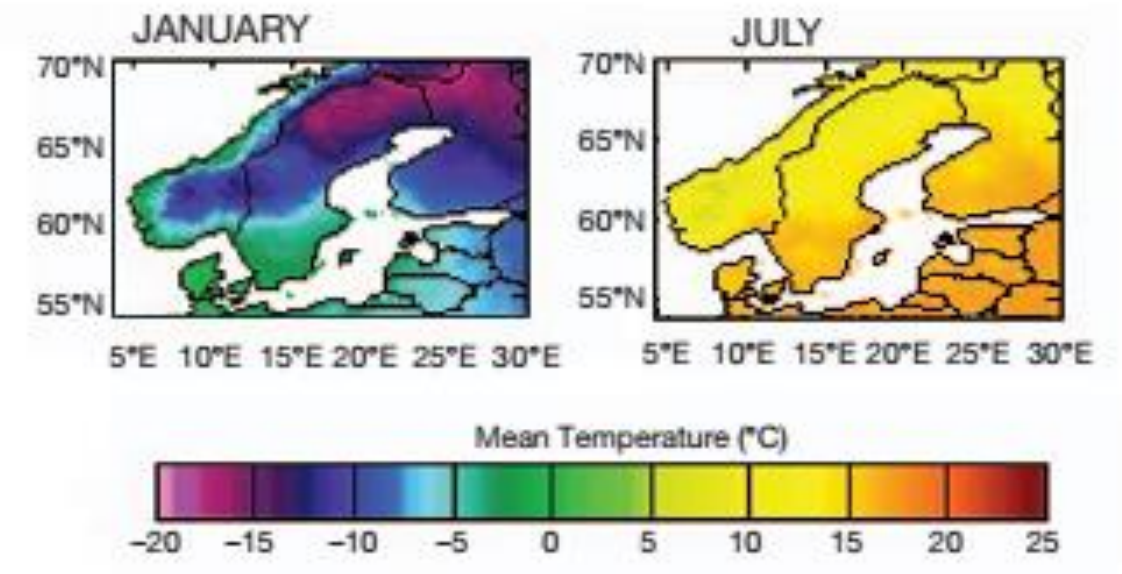


Figure 4.2: Northern Europe mean monthly temperature after New *et al*., (2002)

Northern European climate and seasonality is controlled by atmospheric circulation that drives the prevailing westerlies (e.g. Marshall *et al*., 2001; Chen, 2000; Hurrell, 1995). The dominant westerlies bring warm Atlantic oceanic-air from areas of high pressure in the southwest towards the poles creating maritime climate conditions in western Scandinavia with a low annual temperature range and increasing continentality eastwards (Giesecke *et al*., 2008). The position and strength of the westerlies are determined by high (+ve) and low (-ve) North Atlantic Oscillation

(NAO) phases which are most commonly strongly positive in winter (Chen, 2000; Chen & Hellström, 1999). Under positive NAO conditions both a strong subtropical high pressure (Azores high) and subpolar low pressure (Icelandic low) create a large pressure gradient that develops a persistent northern storm track bringing warmer temperatures and precipitation. Under negative NOA conditions, weak subtropical high pressure and subpolar low pressure create a low pressure gradient with fewer and weaker storms allowing blocking Siberian high pressure systems to divert the westerlies creating hot and dry summer conditions and extreme cold and dry winter conditions (Figure 4.3). It is these fluctuations in the NOA that are responsible for variability in winter temperature and rainfall (Hurrell *et al.*, 1995; Marshall *et al.*, 2001).

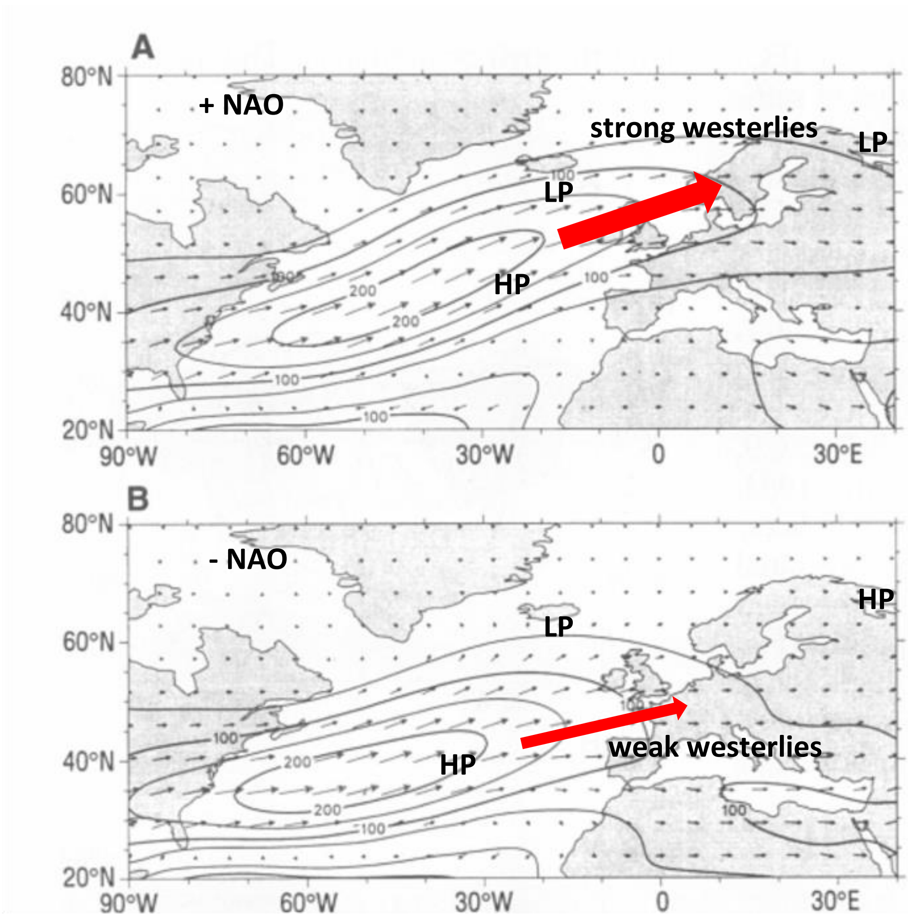


Figure 4.3: North Atlantic Oscillation (NAO) with (A) positive NAO and (B) negative NAO after Hurrell, (1995).

The structure of the northern European forest is relatively simple, dominated by two coniferous species *Picea abies* (Norway spruce) and *Pinus sylvestris* (Scots pine) with scattered deciduous species abundance, most commonly *Betula pubescens* and *B. pendula* (Silver birch and Downy birch), *Alnus glutinosa* and *A. incana* (Black alder and Grey alder) and *Populus tremula* (Common aspen). In addition the temperate, hemi- and southern boreal forests are characterised by thermophilous broad-leaf deciduous species that reach their latitudinal range between 60˚N - 65˚N; *Corylus avellana* (European hazel), *Ulmus glabra* (Wych elm) *Tilia cordata* (small-leaved lime), *Quercus robur* (Pedunculate oak) and *Fraxinus excelsior* (European ash) (Esseen *et al*., 1997; Giesecke *et al*., 2008).

4.2 Methods

Three individual approaches were used to explore fire disturbance and vegetation dynamics in Fennoscandia and Denmark:

4.2.1 **Stand-scale palynology** of sediment cores, obtained from two forest hollow sites located in southern Finland, were studied to gain insight into local vegetation dynamics and fire history using pollen and macroscopic charcoal analysis (Chapter 5 & 6)

4.2.2 A **fire synthesis** of published charcoal data and fire scar records was collated and digitised for Fennoscandia and Denmark to explore spatial and temporal variations in biomass burning and to identify the underlying controls of fire dynamics (Chapter 7)

4.2.3 **Fire frequency model simulations** were tested to explore the effect of fire frequency as a driver of vegetation composition and structure (Chapter 8)

4.2.1 Stand-scale palynology

Closed-canopy small forest hollow sites provide the most useful environment for reconstructing local vegetation (Jacobson & Bradshaw, 1981) and disturbance dynamics (Bradshaw, 2007). Sites were selected from former glaciated regions, where slow-melting glacial margins enabled the formation of lakes and kettle-holes, using topographic maps and subsequent field evaluation. All of the chosen sites demonstrated typical forest hollow characteristics: size <20 m diameter; circular shape encouraging even sediment deposition; topography surrounded by enclosed vegetation with no inflow or outflow channels and located away from the edge of the forest to limit any potential external disturbance in pollen source area from for example, a lake or road (Overballe-Petersen & Bradshaw, 2011). The forest hollows selected are located within southern Finland (Figure 4.4). This region was identified for analysis as there are relatively few stand-scale sites in Finland (e.g. Tolonen, M. 1985) in comparison to a higher density of sites in southern Sweden, Denmark and Norway (e.g. Molinari *et al*., 2005; Hannon *et al*., 2010; Overballe-Petersen *et al*., 2013) contributing to a transect of stand-scale palynological sites that exist across Fennoscandia. In Finland, forested land covers 86% of the country (Finnish Forest Research Institute, 2000) with 90% of all forest cover comprised of *Pinus* or *Picea* dominated stands. Cajander (1926) sub-classified all Finnish forest into three types: mesic-moist moss forest, dry herb forest, and dry moss and lichen forest (Moore, 1927). The forest hollows selected for analysis within this thesis are all representative of mesic moist *Picea abies* dominated forest stands.

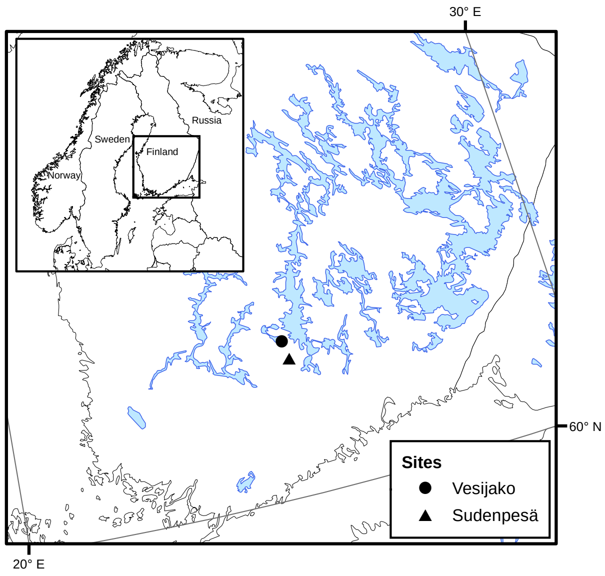


Figure 4.4: Location map of Sudenpesä and Vesijako forest hollows in southern Finland

Cores were extracted from the centre of the forest hollows using a Russian corer (Jowsey, 1966) and were frozen before being subsampled in the laboratory for palaeoecological analysis. Site specific information is available in table 4.1.

	Vesijako	Sudenpesä
Latitude	61˚23' N	61˚11'32.2 N
Longitude	25˚02' E	25˚09'9.5 E
Vegetation zone	southern boreal	
Field work	May 2008	
Length of core (cm)	126	145
Radiocarbon dates	8	9
Pollen analysis		
No of samples	126	184
Sample interval (cm)	1	0.5 – 1
Charcoal analysis		
No of samples	126	184
Sample interval (cm)	1	0.5 – 1

Table 4.1: Site specific information for two small forest hollow environments

Pollen preparation followed standard procedures (Moore, 1991). Five *Lycopodium* tablets (Stockmarr, 1971) were added to a known volume of sediment determined through volumetric displacement and the samples were treated with HCl (Hydrochloric acid), NaOH (Sodium hydroxide) before being sieved at 195µm to enable maximum detection of stomata and larger pollen grains e.g. *Picea abies*. The finer sample residue was further treated with Sodium pyrophosphate and subjected to acetolysis treatment to removed soluble cellulose. Samples were stained with saffron and mounted in glycerol on microscope slides. A minimum of 500 pollen grains were counted per sample at a magnification of x400 and x600 for specific identification with pollen grains identified using Moore *et al.*, (1991) and Bennett (1995-2007) to species level where possible. In Scandinavia species diversity is low allowing for pollen to often be identified to the species level. Macroscopic charcoal analysis involved samples being soaked in NaOH to encourage disaggregation before being wet sieved (>300µm) with the larger sample residue added to 80ml of water. 20ml of sample was added to a petri dish with black brittle crystalline particles identified as charcoal (Swain, 1978). Bulk sediment AMS Radiocarbon dating was used on all samples due to the low presence of terrestrial macrofossils. Radiocarbon ages were calibrated using Clam (Blaauw, 2010). Pollen data are often presented in percentage data, influx or pollen accumulation rates (PARs). Small forest hollows are sensitive to deposition and rapid variability in pollen fluxes. For this reason pollen was presented as percentage data with pollen percentage diagrams drawn up using TILIA and TILIA.GRAPH 2011 version 1.5.12 (Grimm, 2011) and stratigraphically constrained cluster analysis CONISS applied in TILIA including only selected abundant terrestrial pollen taxa (Grimm, 1987).

Charcoal results were presented as total counts of particles >300µm and charcoal influx (particles cm^{-2} yr^{-1}). Fire frequency was calculated by assuming each break in charcoal deposition recorded individual fire events. Deposition of charcoal in small forest hollows lags fire events with charcoal deposition often distributed over several decades due to secondary charcoal deposition (Whitlock & Millspaugh, 1996; Higuera *et al.*, 2005). By assuming deposition characteristics remain constant through time, the second sample to record a consecutive charcoal deposition was used to calculate the fire frequency interval. This became problematic when fire frequency was frequent enough that charcoal from perceived different fire events merged into a continuous charcoal profile. Under these circumstances, where there was a clear second peak in charcoal deposition, two or more fire events were noted to calculate fire frequency.

Correlation between fire disturbance and vegetation dynamics was implemented using cross correlation coefficients of macroscopic charcoal and selected pollen taxa (Green, 1981, 1983; Colombaroli *et al.*, 2008) using the statistical package R (R Development Core Team, 2010). Non-transformed pollen percentage data and raw charcoal counts were used to avoid influx trends caused by the changing sedimentation rate. Continuous sedimentation has to be assumed with the core interpolated to the average sedimentation rate of 42.74 yr cm^{-1} (Chapter 5). Palynological richness (Birks & Line, 1992) was estimated using rarefaction analysis in R (R Development Core Team, 2010). Estimates of the number of expected taxa [$E(T_n)$] was calculated using the lowest total pollen count as the baseline for comparison of palynological richness amongst samples (Chapter 5 & 6). Compositional turnover (Birks, 2007; Bjune *et al.*, 2009a) was estimated using detrended canonical correspondence analysis (DCCA) in CANOCO 4.5 (ter Braak and Šmilauer, 2002). Pollen species were square-root transformed to stabilise variance with age (cal. yrs. BP) applied as the sole constraining variable (Chapter 6).

Local vegetation dynamics were quantified for both Vesijako and Sudenpesä using the Landscape Reconstruction Algorithm (LRA), a multistep framework that incorporates both the REVEALS and LOVE models (Sugita, 2007a, b). REVEALS (REgional Estimates of Vegetation Abundance from Large Sites) model (Sugita, 2007a) estimates regional vegetation composition using pollen assemblages from large sites as well as species-specific pollen productivity and dispersal. The LOVE (Local Vegetation Estimates) model (Sugita, 2007b) estimates local vegetation from small sites by incorporating pollen productivity and dispersal from the regional vegetation estimates derived from the REVEALS output. The LOVE model estimates the distance-weighted vegetation proportion of each pollen taxon within the source area of the site. Pollen dispersal and deposition were calculated using the lake model (Sugita, 1993) to estimate regional vegetation using the programme REVEALS v. 4.2.2 (Sugita, unpublished data). Pollen dispersal and deposition in the small sites followed the model of pollen dispersal (Prentice, 1985) using LOVE v. 3.3 (Sugita, unpublished data). The relevant source area of pollen was set to 50m (Sugita, 1994; Calcote, 1995) and increased in 10m-steps until the estimates of all taxa were ≥0 with a 1 SD threshold with the estimates of regional pollen source area derived from REVEALS model. (Chapter 6)

4.2.2 Fire synthesis

Forest hollow environments are useful in reconstructing local scale disturbance dynamics (Jacobson & Bradshaw, 1981) with lake environments able to reconstruct regional scale dynamics (e.g. Bjune, 2005; Giesecke, 2005; Alenius *et al*., 2008). Through combining both local and regional-scale palyonological and dendrochronological records, fire dynamics can be reconstructed both temporally and spatially on the continental scale. 185 charcoal (both microscopic and macroscopic) and dendrochronological fire scar records spanning 35 years of research were collated from readily available published data. Only charcoal records with trusted dating sources (^{14}C, ^{210}Pb varve counting and pollen cross correlation to dated sites) were included with the aim to be as inclusive as possible. A standard linear age-depth model was applied to all records, where depth data were available, using Clam (Blaauw, 2010) and when published data were plotted against age, the authors' age-depth calculations were accepted.

The data set was spatially divided into four geographical regions based on their current continentality and climate, and six temporal series determined using CONISS analysis (Grimm, 1987) extending back to 13240 cal. yrs. BP. Charcoal data were standardised using a basic (n/max) standardisation and the mean charcoal value was calculated for each time period and compared to the previous time period using the Mann-Whitney U test. Data were plotted using ArcMap10 (ESRI, 2011) on five time series maps with significant ($P < 0.01$ and $P < 0.05$) increases and decreases in charcoal abundance recorded and analysed using box plot transformations in R (R Development Core Team, 2010) for the four pre-determined geographical regions over the six time periods. Fire scar records and charcoal abundance data were combined to estimate the timing of fire suppression throughout Fennoscandia and Denmark. Further details are available in Chapter 7.

4.2.3 Fire frequency model simulations

The effect of fire frequency on vegetation dynamics was tested using the dynamic vegetation model LPJ-GUESS (Smith *et al.*, 2001). LPJ-GUESS is a vegetation model that uses forest gap simulations (Shugart, 1984; Prentice *et al.*, 1993) to simulate vegetation dynamics using pre-determined biophysical and physiological processes (Sitch *et al.*, 2003), plant functional units (Hickler *et al.*, 2004) and bioclimatic limitations (Prentice *et al.*, 1992; Sykes *et al.*, 1996). The fire module (Thonicke *et al.*, 2010) with modifications to adapt the cohort mode to LPJ-GUESS (Lehsten *et al.*, 2009) is simulated based on fuel load. The model was run on 50 replicate patches of 0.1 ha and spun up over a 1000 year period and ran for (a) modern climate scenarios and (b) +2˚C for fire frequencies of between 10 – 1000 years. The model output, leaf area index (LAI), (Chen & Black, 1992) was compared with the pollen data (Chapter 5) that was pre-adjusted to Rpoll values (Miller *et al.*, 2008) to take into consideration individual species production and dispersal. Further details are available in Chapter 8.

Chapter 5

5 Holocene fire frequency variability in Vesijako, Strict Nature Reserve, Finland, and its application to conservation and management

5.1 Abstract

Fire disturbance is considered paramount for regeneration and biodiversity in the boreal forest with prescribed burning widely advocated in present day forest management. Palaeoecological knowledge is beneficial in understanding the role of fire as a driver of past vegetation dynamics. We use a sedimentary pollen and charcoal record to reconstruct 5000 years of fire and vegetation history from a small forest hollow (approximate area 12m^2) in the Vesijako Strict Nature Reserve, currently one of the few remaining old-growth forest stands in southern Finland. Results indicate three distinct periods in the environmental history (1) 5000 – 2000 cal. yrs. BP; semi-natural low frequency (430 year return period), low intensity fires in a diverse mixed stand with little evidence of anthropogenic disturbance and an expanding *Picea abies* (Norway spruce) population (2) 2000 – 750 cal. yrs. BP; anthropogenic-driven high frequency (180 year return period), high intensity stand-replacing fires in a low diversity stand with evidence of slash and burn cultivation and a decline of *Picea* population, (3) 750 cal. yrs. BP to present day; fire absence through a reduction in human-induced fire or active fire suppression and the expansion of the currently dominant *Picea* forest. The changing fire frequency has had a major influence on the forest composition during the last 5000 years. The loss of floristic diversity is associated with an increase in the human use of fire and without this human interference the previously high biodiversity in the stand may have remained up until the present day. If fire remains absent in Vesijako then it is

likely that the *Picea* population will continue to dominate in the stand supporting a negative feedback mechanism that will result in lower frequency, higher intensity fires in the future.

5.2 Introduction

Fire is a significant disturbance agency in the circumboreal forest and there is evidence of varying fire frequencies from charcoal sediment records extending back to the last glacial maximum (Power *et al.*, 2008). Although humans have been using fire since the early-mid Pleistocene (Bowman *et al.*, 2011), it is only since the mid-late Holocene that anthropogenic intervention has modified boreal Fennoscandian fire regimes from their 'natural' state through slash and burn cultivation (Molinari *et al.*, 2005). Almost two centuries of widespread fire suppression in Fennoscandia (Wallenius, 2011), has impacted forest biodiversity by favouring the expansion of *Picea abies* (Bjune *et al.*, 2009a) and endangering fire-dependent species including fungi, insects (Kouki *et al.*, 2012) and higher plants (Risberg & Granström, 2012). Recent attempts have been made to reintroduce burning in designated areas to restore important natural values (Vanha-Majamaa *et al*., 2007; Hyvärinen *et al.*, 2009). However, fire restoration is faced by many challenges, most notably to determine and subsequently attempt to mimic the 'natural' fire regime.

Ecological history is rarely considered in current forest management and conservation practices. However, long-term palaeoecological data can help explore temporal and spatial anthropogenic ecosystem modification, enabling the support of restoration activity designed to foster biodiversity and vital ecosystem functions (Willis & Birks, 2006; Jackson & Hobbs, 2009).

Study of previous fire regimes, notably fire frequency, size and severity prior to any significant human disturbance can provide information and guidelines for present-day and long term management strategies (Bergeron *et al*., 2002). Previous fire history studies and estimates of fire frequencies in Fennoscandia have been based on fire scars (Wallenius *et al.*, 2007; Niklasson *et al.*, 2010), charcoal layers (Pitkänen *et al.*, 2002; Ohlson *et al.*, 2006), charcoal particles analysed from lake sediment (Tolonen, 1983a; Pitkänen & Huttunen, 1999; Carcaillet *et al.*, 2007) and mires (Tolonen, 1985), however charcoal records with high spatial resolution from forest hollows have not yet been used to estimate past fire frequencies in Fennoscandia (Higuera *et al.*, 2005; Bradshaw *et al.*, 2010). Dendrochronology gives useful insight into the fire but records of fire scars are limited both spatially and temporally. Spatially, trees have to survive a fire and remain *in situ* to provide a true record. Temporally, fire scar chronology rarely exceeds 600 years (Wallenius *et al.*, 2007) and are considered somewhat more reliable when reconstructing the fire history for the past 400-500 years (Niklasson *et al.*, 2010). Charcoal in the sedimentary record is much more widely available, but previous work calculating fire frequencies from charcoal records has required sophisticated statistical manipulation to help identify charcoal peaks relating to specific fire events (Carcaillet *et al.*, 2007). This is because charcoal records in sediment usually consist of continuous background levels of charcoal.

5.3 Aims

Here we use a high resolution pollen and charcoal record from a small forest hollow in Vesijako Strict Nature Reserve, Finland, to determine fire frequencies through the last 5000 years and how they are influenced by both natural and anthropogenic factors. We also explore the effects of changing fire frequency on the forest composition and structure and vegetation diversity in the Vesijako reserve and discuss the importance of our results for forest management and biodiversity conservation.

5.4 Materials and methods

5.4.1 Study area and site

Vesijako (61^{o}N; 25^{o}E) is 1700 ha of relatively uninhabited forest situated in the Padasjoki municipality, southern Finland (Figure 5.1). Currently administered by Metsähallitus, Vesijako is a state owned research forest with a long tradition of management for timber production and related ecological research (Heikinheimo, 1915). More recently research in Vesijako has focused on restoration of forest biodiversity through active management, for example selective logging, creating dead wood and prescribed burning (Vanha-Majamaa *et al.*, 2007; Lilja-Rothsten *et al.*, 2008; Shorohova *et al.*, 2008). The forest is located in the southern boreal vegetation zone (Ahti *et al.*, 1968) with an altitude ranging between 100 and 170m a.s.l. The mean annual temperature is 4.2^{o}C, with a July mean of 16.6^{o}C and a February mean temperature of -7.1^{o}C (Pirinen *et al.*, 2012). The mean annual precipitation is 645 mm yr^{-1} and the duration of thermal growing period is 160 days.

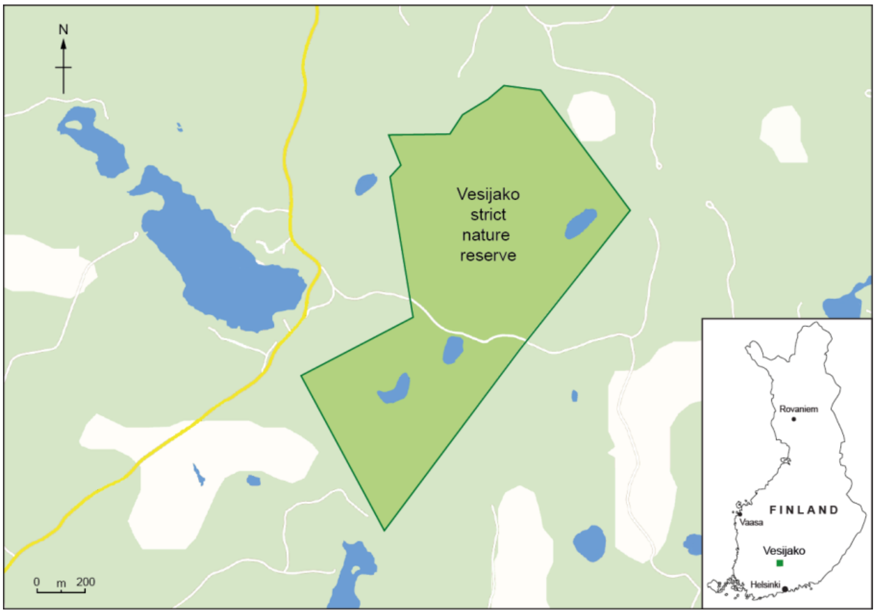


Figure 5.1: Location map of Vesijako Strict Nature Reserve, Finland.

Vesijako Strict Nature Reserve (61^{o}21'N; 25^{o}06'E) is 115 ha located within Vesijako forest and was established by Metsähallitus in 1956. In Finland, a Strict Nature Reserve is a national state-owned conservation reserve protected by law in its natural state and undisturbed condition due to its exceptionally high scientific value (Similä & Junninen, 2012). The primary purpose of Vesijako Strict Nature Reserve is to conserve an intact representative of southern Finnish Lakeland forest and to use it for scientific research (Figure 5.1).The area is considered to be in a near natural state and represents a small but important woodland key habitat of the boreal zone in Finland (Timonen *et al.*, 2011; Rajala *et al.*, 2012). The sampling site, selected for its small forest hollow characteristics (Overballe-Petersen & Bradshaw, 2011) is a wet hollow of approximately 12 m^2 situated within a dense forest stand dominated by *Picea abies* with scattered *Pinus sylvestris, Betula* and *Populus tremula* individuals present at the site (Figure 5.2).

Figure 5.2: Vesijako small forest hollow, Finland. (Photo by J. Clear 2008)

5.4.2 Field, laboratory and statistical methods

A sediment core comprising of three sections, 126 cm in total length, was extracted from the centre of the small forest hollow in Vesijako in May 2008 using a 50 cm long, 5 cm diameter Russian corer (Jowsey, 1966). Sediment was extracted from the surface down, alternating between two separate core holes, to enable a minimum of 10 cm overlap between each section of the core. The core was stored below 5^{o}C at the University of Liverpool. For analysis, the sections were scraped to avoid contamination and 126 sub-samples were taken from the core at 1 cm intervals for pollen analysis, macroscopic charcoal analysis and radiocarbon dating. The use of a single core is normal in palaeoecological research, with the long time series of sub-samples providing a form of replication through the identification of coherent trends and patterns in the analysed data.

5.4.3 Pollen analysis

Pollen preparation followed standard procedures (Moore *et al*., 1991). Samples were stained with saffron and mounted in glycerol on microscope slides for continuous counting at a magnification of x400. A minimum total of 500 terrestrial pollen grains were counted per sample and pollen grains were identified following Moore *et al*., (1991) and Bennett (1995-2007) to species level where possible. The pollen diagrams were drawn up using TILIA and TILIA.GRAPH 2011 version 1.5.12 (Grimm, 2011). Stratigraphically constrained cluster analysis CONISS was conducted in TILIA and included only selected abundant terrestrial pollen taxa (Grimm, 1987).

5.4.4 Macroscopic charcoal analysis

A known volume of sediment was soaked and heated in NaOH, then sieved through 300 µm mesh with material retained in the sieve added to 80 ml double distilled water. 20 ml of sample was added to a Petri dish after stirring and counted using a grid base. Black brittle crystalline particles with angular broken ends were classified as charcoal (Swain, 1973; 1978). Charcoal results were presented as total count of particles >300 µm cm^{-3} and charcoal influx (particles cm^{-2} yr^{-1}) were calculated. Fire frequency was calculated by assuming that each break in the charcoal deposition record separates individual fire events. Deposition of charcoal in small forest hollows lags fire events and charcoal deposition is often distributed over several decades due to secondary charcoal deposition (Whitlock & Millspaugh, 1996; Higuera *et al.*, 2005). Assuming deposition characteristics remain consistent, the second samples to record consecutive charcoal deposition were used to calculate the fire frequency.

5.4.5 Radiocarbon dating

A total of 8 peat samples of were selected from the core for AMS Radiocarbon dating (Table 5.1). The exterior sediment was scraped away to remove possible contaminants and the remaining fraction, between 0.5 and 2 g of sediment, dated. Dates were obtained from Beta Analytic Radiocarbon Dating Laboratory, Florida, California, USA, University of Helsinki, Finland, and Lund University, Sweden. Dates were calibrated and the age-depth calibration curve was calculated using Clam (Blaauw, 2010).

Depth (cm)	Laboratory number	^{14}C Age	Age (cal. yrs. BP)
18	LuS 9887	155 ± 50	148
31	Poz-39981	1190 ± 35	1119
47	Poz-39979	1475 ± 30	1359
66	Poz-39980	2190 ± 30	2228
78	LuS 9886	2780 ± 50	2918
96	Poz-39978	3295 ± 35	3520
108	LuS 9885	3510 ± 50	3783
122	Beta-245766	4360 ± 40	5053

Table 5.1: Radiocarbon dating results of AMS bulk sediment dates for Vesijako, Finland.

5.4.6 Statistical analysis

Cross correlation coefficients of macroscopic charcoal and selected pollen taxa were calculated using the statistical package R (R Development Core Team, 2010) to identify links between fire disturbance and vegetation dynamics (Green, 1981; 1983; Colombaroli *et al.*, 2008). Non-transformed pollen percentage data and charcoal counts were used to avoid influx trends caused by the changing sedimentation rate. To enable calculation of cross correlation, continuous sedimentation has to be assumed and the core was interpolated to the average sedimentation rate of 42.74 yr cm^{-1}. Rarefaction analysis was also conducted in R (R Development Core Team, 2010) to establish variability in palynological richness among samples. The sampling effort or total pollen count varies among samples. Rarefaction analysis uses the sample with the lowest total pollen count as the basis for comparison of palynological richness among all samples (Birks & Line, 1992).

5.5 Results

5.5.1 Pollen and charcoal

Pollen percentage and charcoal accumulation for the last 5000 years (Figure 5.3) have been subdivided visually into three zones corresponding to periods of specific fire history, which are in the region of the stratigraphic zones calculated by CONISS

(Grimm, 1987), in which analysis only the most abundant terrestrial pollen types were included.

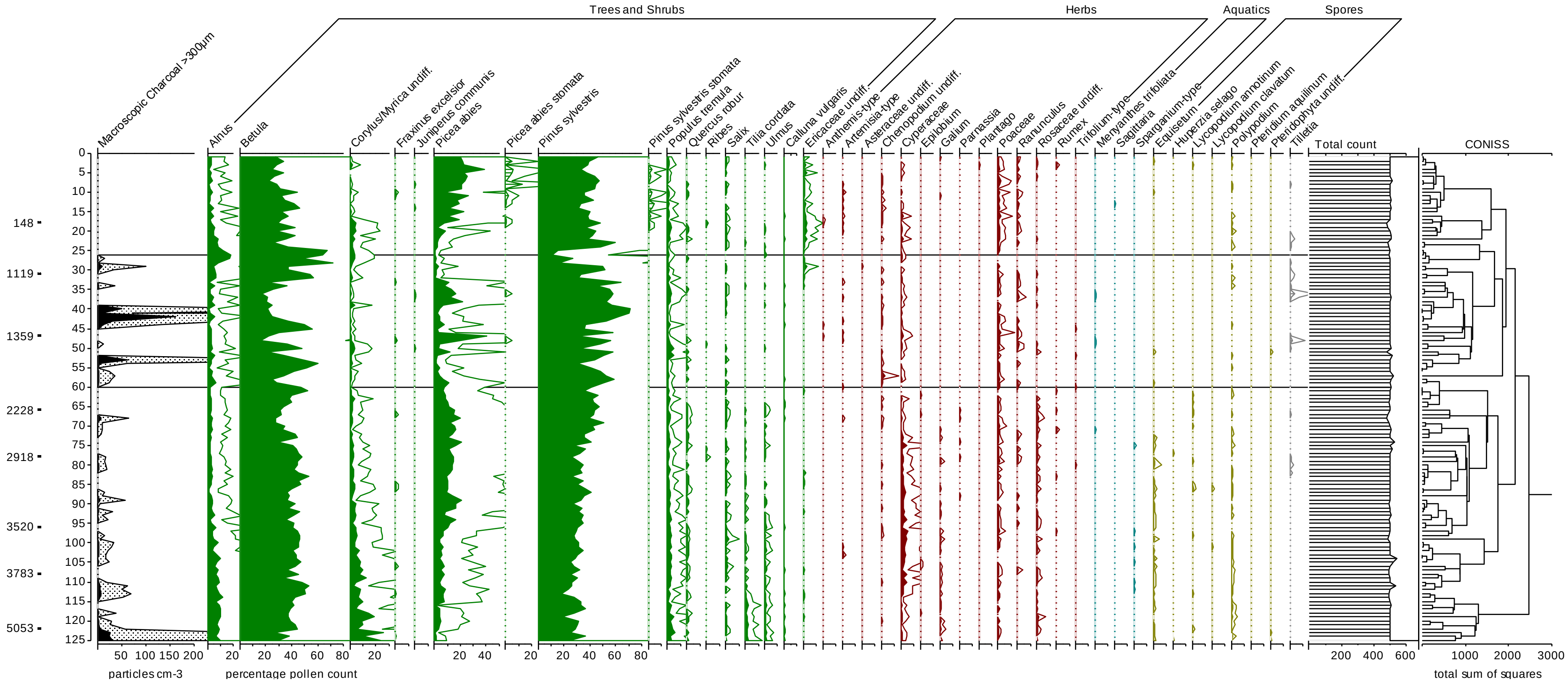
5.5.1.1 Vegetation succession and fire frequency: >5000 – 2000 cal. yrs. BP

The earliest forest composition recorded at Vesijako is that of a co-dominant *Pinus-Betula* stand that was rich in deciduous taxa; *Alnus*, *Corylus avellana*, *Quercus, Salix, Tilia cordata*, and *Ulmus glabra. Polypodium*, a common epiphyte on deciduous trees was most common during this time (Figure 5.3). This 3000 year period was the time of most diverse, species-rich forest composition recorded in Vesijako as shown by the rarefaction analysis (Figure 5.4). As well as the presence of the deciduous trees, other taxa including *Galium*, *Parnassia*, Rosaceae and Cyperaceae were most abundant during this period.

There was a prominent decline in palynological richness between 2200 – 2000 cal. yrs. BP coinciding with the abrupt decline in the presence of most deciduous tree species. There was also a steady overall decline in both *Alnus* and *Corylus*. At approximately 2200 cal. yrs. BP. the fairly consistent presence of *Quercus*, *Tilia* and *Ulmus* abruptly ends (Figure 5.3). A simultaneous decline in *Salix*, *Parnassia*, *Equisetum* and *Sparganium* suggests an environmental shift from a wetter to drier forest stand.

The expansion of *Picea* appears to precede the onset of sedimentation of the Vesijako core. *Picea* values steadily increase reaching 10% of the total pollen sum by 3500 cal. yrs. BP (Figure 5.3). The first anthropogenic pollen indicators appear with *Artemisia*, *Chenopodium*, *Ranunculus* and *Rumex* present just prior to 3500 cal. yrs. BP.

Consistent low level cyclical peaks of charcoal are recorded, with the peaks spread over a maximum of 8 cm of sediment with intervening charcoal-free periods (Figure 5.5). From the charcoal results we can estimate a fire frequency for 3000 years of minimally disturbed forest. This fire frequency was characterised by a continuous steady period of low frequency, probably low intensity fires with an average fire return interval of 430 years. This relatively low level of fire disturbance had minimal effect on the forest structure with limited stand structure dynamics and post fire succession.



Analysis: Jennifer Clear 2008/2009

Figure 5.3: Pollen and charcoal diagram for Vesijako, Finland with pollen expressed as percentage of total pollen count and macroscopic charcoal fragments (>300µm) expressed as charcoal particles cm

5.5.1.2 Significant change in vegetation and fire frequency: 2000 – 750 cal. yrs. BP

The decline in deciduous species; *Quercus*, *Tilia* and *Ulmus* prior to 2000 cal. yrs. BP resulted in a shift in species composition and, in particular, loss of diversity (Figure 5.6) from that of a diverse mixed deciduous and coniferous forest stand with a wide-ranging abundance of herbaceous flora to a forest stand dominated by *Betula* and *Pinus*.

The relative pollen abundance of these dominant species, as well as the less prevalent presence of *Alnus*, *Corylus*, *Picea*, *Populus*, Cyperaceae and Poaceae, show a wide dynamic variance throughout this time period with *Picea* pollen values varying most significantly, and falling under 1% between 800 and 600 cal. yrs. BP (Figure 5.3).

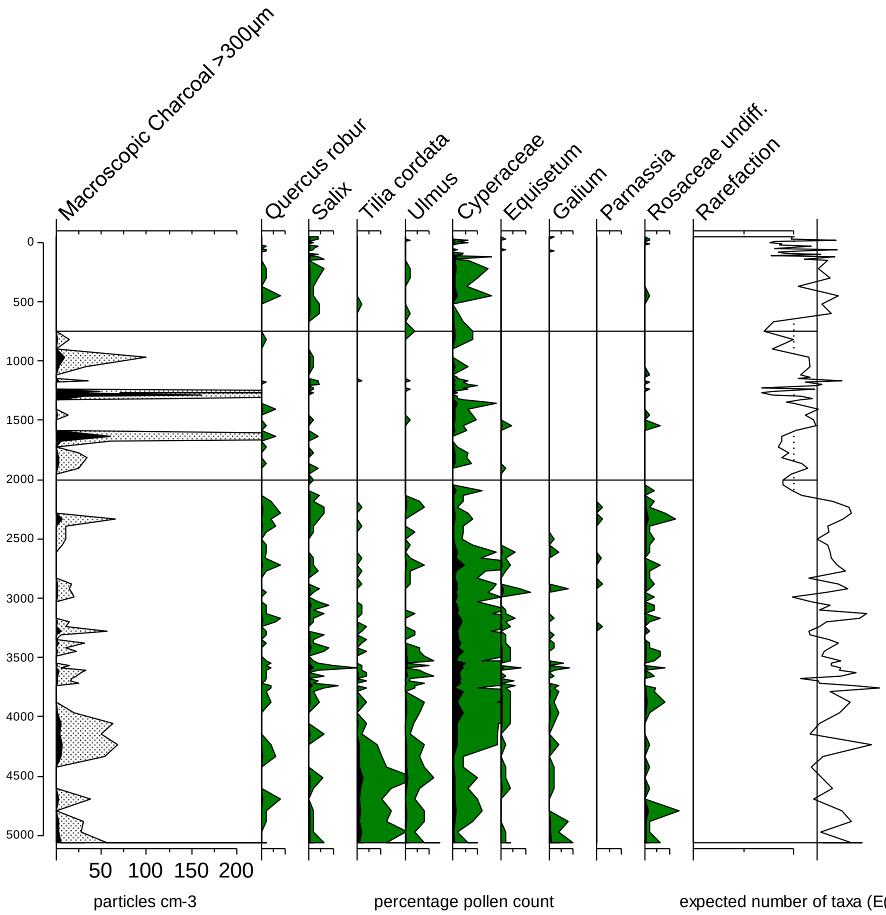


Figure 5.4: Rarefaction analysis curve with rarefaction expressed as expected number of taxa (E(Tn)), macroscopic charcoal (>300µm) expressed as particles cm^{-3}, and selective pollen taxa expressed as a percentage of the overall pollen count.

The charcoal record is characterised by intermittent moderate to high charcoal counts recorded at a higher frequency than prior to 2000 cal. yrs. BP (Figure 5.5). The fire frequency, with an average fire return interval of 180 years, was dominated by larger charcoal peaks than previously recorded. *Alnus*, *Corylus* and *Populus* are early successional species in the boreal forest, which is evident at Vesijako due to their increase following each charcoal peak in the pollen diagram (Figure 5.3). This is particularly evident for *Alnus* and *Corylus* after the last prominent charcoal peak around 800 cal. yrs. BP. Cross correlation analysis (Figure 5.6) shows that these three early successional species enter a positive correlation phase post fire event (at lag 0). *Pinus'* resilience to fire is clear. It managed to retain a stronghold in the stand during periods of abundant charcoal and subsequently decline during periods of post fire regeneration where *Pinus* was temporarily outcompeted (Figure 5.3).

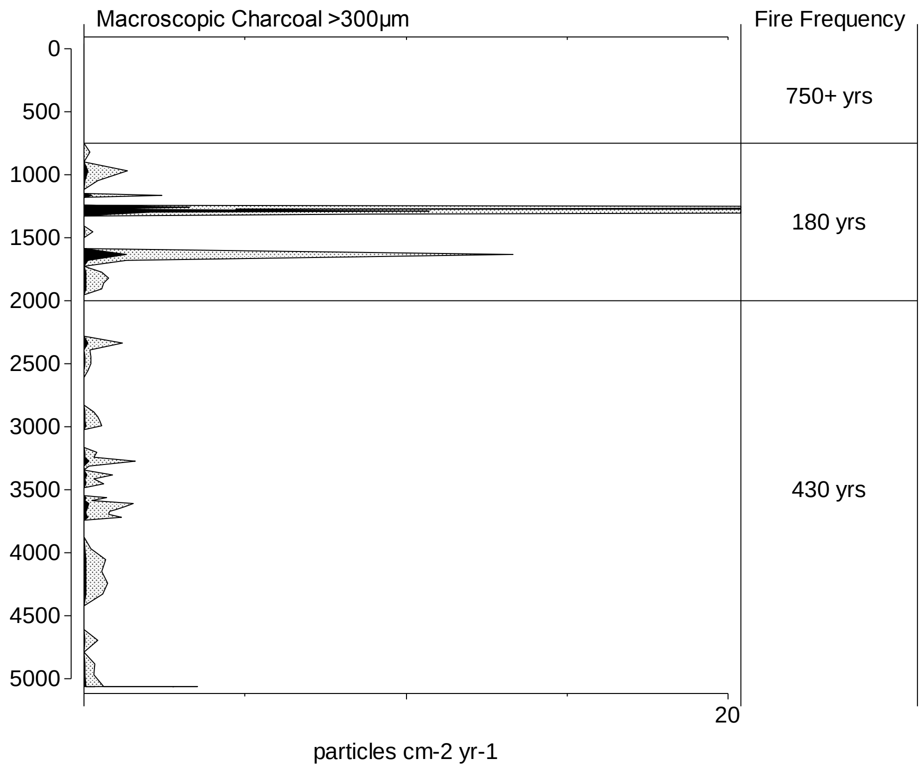
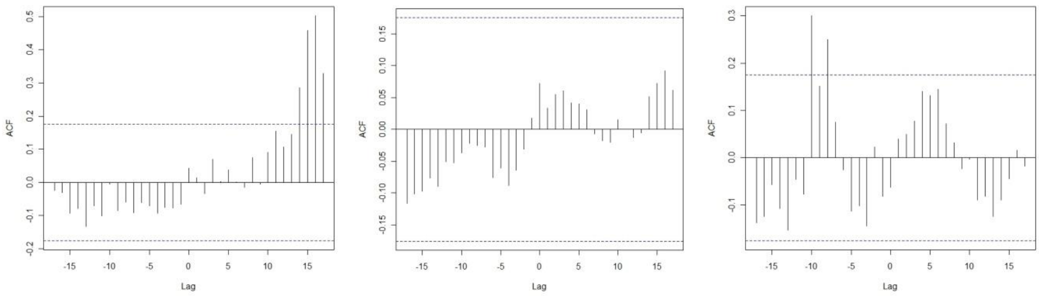


Figure 5.5: Charcoal influx and fire frequency with macroscopic charcoal fragments (>300µm) expressed as influx (particles cm^{-2} $year^{-1}$).

Cross correlation analysis (Figure 5.6) indicates a strong positive correlation with pre- and initially post fire event turning negative after significant time since the last fire. *Picea* appears highly sensitive to these larger fires recorded between 2000 and 750 cal. yrs. BP. However, relative pollen abundance of *Picea* recovers after fire events. There are two prominent spikes in *Tilletia* spores recorded after the two prevalent peaks in charcoal.

Macroscopic charcoal (>300µm) versus

Alnus *Corylus* *Populus*



Pinus *Picea* Ericaceae

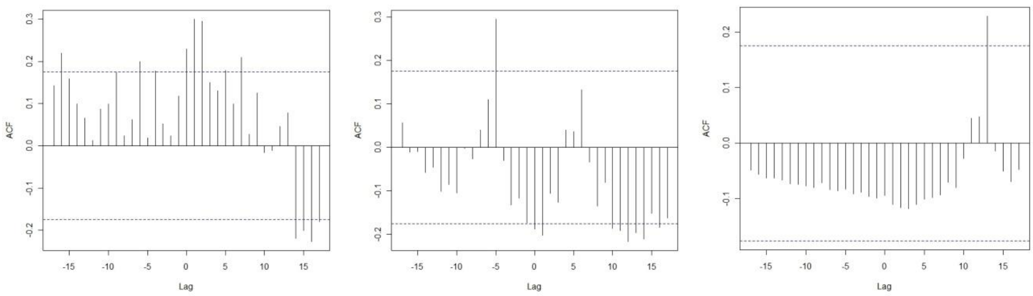


Figure 5.6: Cross correlation analysis of macroscopic charcoal (>300µm) compared with selective pollen taxa. The horizontal axis shows the lag time and the vertical axis is an estimate of the cross correlation coefficient.

5.5.1.3 Fire suppression and the rise of Picea abies: *750 cal. yrs. BP – present day*

Pollen recorded for the past 750 years indicate a somewhat more stable forest composition with *Betula* and *Pinus* occurring with high values in the pollen record stand. The most important vegetation change was that of a slow and gradual increase of *Picea* after 600 cal. yrs. BP and the declining trend of any remaining deciduous taxa, particularly *Alnus* and *Corylus* (Figure 5.3). There is a substantial rise and sustained occurrence of Ericaceae pollen following the last intensive fire over 1000 years ago, which is also recorded in the cross correlation analysis (Figure 5.6). The absence of charcoal through this time period suggests no local burning since approximately 750 cal. yrs. BP (Figure 5.5). The species diversity in the stand increases following the previous period of intensive, high frequency fire (Figure 5.4).

5.6 Discussion

5.6.1 Vesijako fire frequency: the cause and consequences

The local fire frequency in Vesijako remained fairly constant for over 3000 years from approximately 5000 to 2000 cal. yrs. BP. *Picea*, generally known as a fire-sensitive species, expanded into the region approximately 5500 cal. yrs. BP (Giesecke & Bennett, 2004; Seppä *et al.*, 2004) and continued to increase in abundance during this time, suggesting that these fires were most probably low intensity, non stand-replacing fires.

The mid-Holocene mixed forest recorded in Vesijako is well documented in pollen diagrams recorded throughout Fennoscandia (e.g. Donner, 1963; Bradshaw & Hannon, 1992; Molinari *et al.*, 2005; Seppä *et al.*, 2009). The subsequent decline in deciduous species, in particular *Quercus*, *Tilia* and *Ulmus* at approximately 2200 cal. yrs. BP, has been attributed both to *Picea* immigration (e.g. Bradshaw & Hannon, 1992; Giesecke & Bennett, 2004; Hörnberg *et al.*, 2011) and to intensified anthropogenic disturbance (e.g. Lindbladh & Bradshaw, 1998; Hannon *et al.*, 2000; Sarmaja-Korjonen *et al.*, 2003a). In Vesijako, this decline and loss of diversity also coincides with a shift from wetter to drier conditions indicated by declines in taxa such as *Salix*, *Parnassia*, *Sparganium* and *Equisetum*. This shift is most likely due to local terrestrialisation at the site through the slow, consistent peat growth as climate reconstructions during this time suggest a trend to cooler and wetter conditions (Seppä & Birks, 2001). The decrease in late Holocene summer temperature could account for the decline in deciduous species and subsequent expansion of the present day boreal dominance.

Early anthropogenic indications (*Artemisia* and *Chenopodium*) appear in the pollen sequence at approximately 3500 cal. yrs. BP. This early indication of cultural activity, between 4000 and 3000 cal. yrs. BP, has been recorded locally in Finland (Tolonen, 1978, 1980) and throughout Fennoscandia (Tolonen, 1978; Lindbladh, 1999; Molinari *et al.*, 2005). Tilletia spores were frequently recorded after fire since 2000 cal. yrs. BP. These are spores derived from a pathogenic fungus that is normally hosted by cereal crops causing Smut disease in wheat, but can occur in other grasses (Yeloff *et al.*, 2007). However no cereal pollen were recorded in Vesijako. Indications of increased human impact without the presence of cultivated pollen types are evident in Finland from 2500 cal. yrs. BP (Alenius *et al.*, 2008) with slash and burn cultivation in southern Finland from approximately 2400 – 2000 cal. yrs. BP (Tanskanen, 2007). A low level presence of *Juniperus* and high relative pollen abundance of *Picea* after slash and burn events could indicate local grazing animals (Haeggstrom, 1990).

Assuming high intensity fires produce more charcoal (Pitkänen *et al.*, 1999) the shift in fire regime in Vesijako to high frequency, high intensity fires varies from the usual anthropogenic signal of high frequency, low intensity fires (Granström & Niklasson, 2008). The increase in fire frequency is likely the result of intensified anthropogenic impact however the fire intensity appears to be driven by fuel type. Modern day temperate forests in southern Fennoscandia are known to burn less intensely than their boreal forest counterparts with ground vegetation burnt at lower temperatures with less fuel and less charcoal residue than when boreal canopy trees are burnt (Pitkänen *et al.*, 1999). Prior to the deciduous decline, 2200 cal. yrs. BP, the vegetation consisted of a mixed coniferous-deciduous forest and although *Picea* expansion is ongoing prior to the decline in deciduous species, the underlying presence of *Quercus*, *Salix*, *Tilia* and *Ulmus* maintains a mixed forest cohort that may be the key to the low intensity fires observed. However since the decline in deciduous taxa, a shift in forest composition from a mixed coniferous-deciduous stand to a predominantly coniferous forest could be responsible for change in fire intensity: from low intensity ground fires to high intensity stand replacing crown fires.

From 750 cal. yrs. BP onwards, Vesijako enters the present day phase of fire absence however this date is verified by a single radiocarbon date at 31 cm and if this date is removed and the age depth curve recalculated then the timing of fire suppression changes to 480 cal. yrs. BP. Either way the absence of fire in Vesijako occurs long before fire suppression in southern Finland (Wallenius, 2011) where slash and burn remained important until the 20th century (Taavitsainen *et al.*, 1998). An explanation for an early decline in fire could be the ‘human influence hypothesis’ (Wallenius, 2011) suggesting that the majority of past fires were caused by humans therefore any reduction in fires would be a direct result of a decrease in human caused fires. The present day absence of fire means fuel availability is continually increasing. With the combination of the *Picea* dominated forest and availability of fuel, the present day and future fire regime at Vesijako may consist of very low frequency and very high intensity fires given the right climatic conditions.

5.6.2 Fire frequency effects on floristic biodiversity

Fire appears to favour florisitic diversity in Vesijako and the range of species is most diverse when the charcoal record indicates a fire regime of low frequency, low intensity fires prior to 2000 cal. yrs. BP (Figure 5.4). However there appears to be an optimal threshold relating to fire frequency and intensity that, once crossed leads to a reduction in floristic diversity. This coincides with intensified anthropogenic use of fire with an increase in fire frequency about 2000 years ago. This significant loss of species diversity through human modification of the fire regime has been recorded elsewhere in Scandinavia (Lindbladh *et al.*, 2003) as fire disturbance is a key element of regeneration within a forest system (Granström, 2001). Without this intensified anthropogenic interference with the fire frequency the earlier enhanced floristic diversity at Vesijako potentially could have remained to the present day. A significant feature in the forest composition is the strong impact of fire history on *Picea*. The *Picea* population fluctuated strongly during the period of high fire frequency and the species appears to have been almost locally absent at 800 – 600 cal. yrs. BP, followed by its rise to the current dominance after the decline of fire frequency after 750 cal. yrs. BP. It is well established that the regeneration *Picea* is favoured by fire absence (Bradshaw, 1993) and it may suffer lethal damage even with low intensity fires due to its superficial root system, thin bark and low branches (Heikinheimo, 1915; Cajander, 1941; Wallenius, 2004). Charcoal and pollen data also show that the expansion of *Picea* has the potential to further reduce wildfire activity by increasing shadiness, moss cover, and soil moisture (Ohlson *et al.*, 2011). Hence is it possible that the continual fire absence in Vesijako could potentially lead to further loss of forest diversity in the future.

5.6.3 Using palaeoecology as a tool for forest management

Fire frequency in Vesijako is predominantly linked to anthropogenic use of fire and has previously been a significant feature of the ecosystem. Prior to the most significant anthropogenic forest disturbance in Vesijako (pre-2000 cal. yrs. BP) fires were much less frequent with an average fire return period of 430 years. This is a far lower fire frequency than has been previously been recorded in existing fire scar data (Zackrisson, 1977; Engelmark, 1984; Granström & Niklasson, 2008) in the boreal forests of Fennoscandia, highlighting the need to look further back in time, beyond the temporal period of most significant human disturbance, to gain insight into the natural and semi-natural fire regime. Anthropogenic use of fire (post-2000 cal. yrs. BP) significantly increases the fire frequency to an average fire return period of 180 years. Then, with a decrease in the use of fire and ultimately fire suppression by humans, fire becomes absent from the record post-750 cal. yrs. BP. From the fire frequency records in Vesijako, if we could only view the past 2000 years or less as in the case of fire scar histories, we would have an artificially high perception of the fire frequency prior to human suppression in Fennoscandia. Neglecting palaeoecology and using only short term ecological data is short-sighted when the seemingly unprecedented recent events can be placed in a longer term perspective (Whitlock, 2004). There is a baseline fire return interval present at Vesijako and this information may be valuable for management decisions associated with conservation and restoration issues in a time of uncertain climatic change. This past information can be used to address modern day conservation issues by setting a natural variability of fire frequency and severity (Willis & Birks, 2006) to enhance ecosystem resilience to climate change (Holling & Meffe, 1996). Palaeoecology is an excellent tool for understanding our changing environment and the further we can look back into the past, the more we can see and use as a guide to help us deal with the uncertainties in the future.

Chapter 6

6 Quantitative vegetation reconstruction to identify local and regional vegetation dynamics and disturbance history in southern Finland

6.1 Abstract

Vegetation dynamics are controlled by both biotic (e.g. species competition) and abiotic (e.g. climate and both natural and anthropogenic disturbance) drivers and disentangling these complex interactions to identify the role both climate and disturbance play within the boreal forest is challenging. Both biotic and abiotic drivers of vegetation dynamics are explored at the local and regional scale using two local (<18 km apart) stand-scale forest hollows in southern Finland to identify unique and mutual disturbances. Quantitative vegetation reconstruction of the local stand-scale hollows and regional vegetation dynamics are reconstructed for the Holocene using the Landscape Reconstruction Algorithm (LRA) (Sugita 2007a, 2007b). Early-Holocene forest development and vegetation dynamics are primarily driven by climatic variations. In both the regional and local vegetation reconstruction, vegetation development is affected by the '8.2ka cooling event'. *Picea abies* (Norway spruce) is present in southern Finland at approximatly 9500 cal. yrs. BP and between 8500 and 8000 cal. yrs. BP before declining and re-establishing after 7600 cal. yrs. BP. The regional expansion of *Picea* does not coincide with local disturbance or decline in deciduous species but is most likely linked to increased continentality, with both *Picea* abundance and continentality peaking approximately 2000 cal. yrs. BP. The decline in deciduous species corresponds to increased fire frequency at both local sites but occurs more than 1500 years apart. This suggests increased anthropogenic disturbance is the primary

reason for the loss of floristic diversity in southern Finland. The 'natural' fire frequency in the southern Finnish boreal forest is approximately 400 year intervals and this occurs both pre- and post-*Picea abies* establishment.

6.2 Introduction

Boreal forest vegetation dynamics are driven by a complex interplay of biotic and abiotic drivers that are responsible for forest development, composition and structure. Understanding the drivers of past vegetation change is important not only for short-term conservation and silvicultural management (Birks, 1996b) but also for assessing, modelling and forecasting future long-term natural variability and forest structure (e.g. Stocks *et al*., 1998; Cowling *et al*., 2001). Regional climate and local ecosystem processes are the primary controls on vegetation dynamics however disturbance, both natural (e.g. fire, storms and pests) and anthropogenic (e.g. fire, selective cutting and forest management) have ambiguous yet significant roles in driving local vegetation dynamics, with the forest often in a state of disturbance or recovery (Bradshaw, 2003). Disentangling these controls at both the regional and local scale is challenging especially using modern day real-time observations due to the impact and extent of modern-day forest management throughout Fennoscandia (Östlund *et al*., 1997) that destroys any natural climate and disturbance signal.

Observing Holocene vegetation dynamics using proxies such as pollen and charcoal allows for the reconstruction of past vegetation dynamics and fire history (e.g. Bradshaw & Hannon, 1992; Giesecke 2005; Alenius *et al*., 2008; Ohlson *et al*., 2011). Using these proxies we can explore Holocene forest succession and development as well as the potential causes and drivers behind the observed vegetational change and to begin to understand future uncertainties in vegetation dynamics associated with climate and disturbance. However, the relationship between sedimentary pollen records and vegetation cover is not linear (Gaillard *et al*., 2008) and although fossil pollen data give good intuitive analogues of past vegetational change they do not give a spatially explicit description of vegetation and land-cover (Gaillard *et al*., 2010). Choosing the right depositional environment is important to answering specific research questions with palaeoecology (Bradshaw, 2007) and through combining local stand-scale sites with regional (lake) records we can begin to explore spatial heterogeneity and variability in past disturbance and vegetation change through the observation of small scale spatial variability in relation to regional landscape characteristics (e.g. Wier *et al.,* 2000; Wallenius *et al.,* 2004).

Quantitative vegetation reconstruction using the Landscape Reconstruction Algorithm (LRA) embedded in the REVEALS and LOVE models (Sugita 2007a,b) allows more realistic estimation of vegetation cover and land-cover composition than vegetation reconstruction using pollen percentage calculations (Soepboer *et al.* 2010). REVEALS reconstructs regional vegetation and land-scape cover enabling studies into vegetation-climate interactions (Gaillard *et al*., 2010) whereas LOVE, local vegetation estimates can give insights into local scale disturbance dynamics.

6.3 Aims

The aims of this paper are to use pollen-derived quantitative vegetation reconstruction using the Landscape Reconstruction Algorithm at the local (LOVE) and regional (REVEALS) scale to estimate past vegetation cover to gain an insight into Holocene vegetation dynamics in southern Finland. By using two nearby (<18km apart) stand-scales sites and three published regional lake sites, we aim to identify similarities in vegetation dynamics driven by large-scale regional changes e.g. climate as well as variability in exclusively local-scale disturbance to identify the main drivers of vegetation change in southern Finland.

6.4 Materials and methods

6.4.1 Study area and sites

Sudenpesä (61^{o}11'N; 25^{o}09'E) and Vesijako (61^{o}21'N; 25^{o}06'E), two stand-scale sites selected for their forest hollow characteristics (Jacobson & Bradshaw, 1981; Overballe-Petersen & Bradshaw, 2011), are located approximately 18km apart in the southern boreal vegetation zone (Ahti, 1968) southern Finland (Figure 6.1). The mean annual temperature is 4.2°C, with a July mean of 16.6°C and a February mean temperature of -7.1°C (Pentti, 2012) and the mean annual precipitation is 645 mm yr^{-1}. The regional bedrock consists of orogenic granitoides covered with till (Palviainen *et al*., 2009) with Sudenpesä and Vesijako both situated on nutrient-rich drained peatland (Kaila *et al.,* 2012). Sudenpesä forest hollow is located within the old-growth forest of Sudenpesänkangas within the Evo Research forest and measures approximately 15 m^2, Vesijako is situated within the Vesijako strict nature reserve and is approximately $12m^2$ in area. The regional vegetation type is dominated by boreal *Picea* and *Pinus* taiga mixed woodland with *Betula,* however both Sudenpesä and Vesijako forest stands are currently dominated by *Picea abies*.

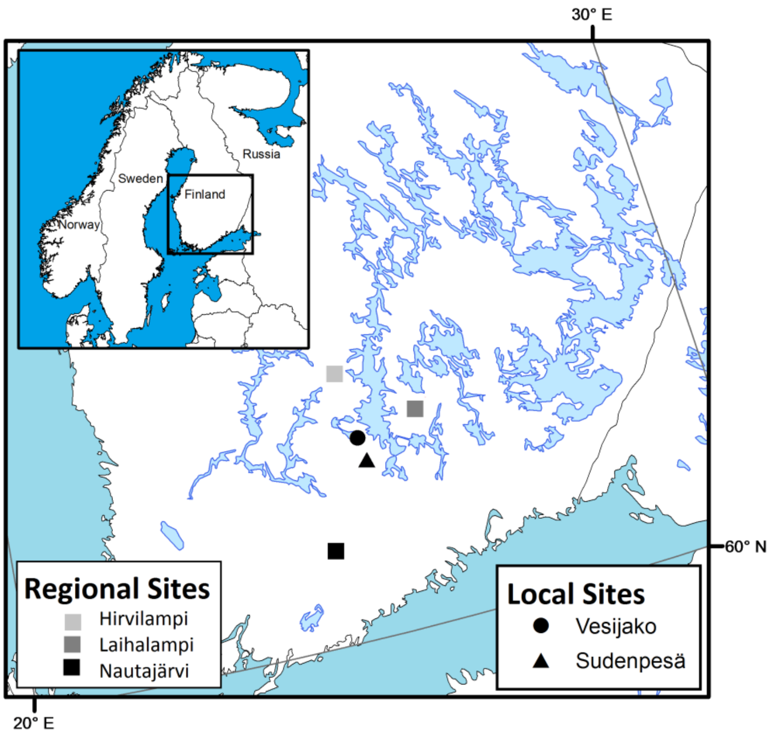


Figure 6.1: Location map of Sudenpesä and Vesijako forest hollows in southern Finland

6.4.2 Field and laboratory methods

Sediment cores were extracted from the centre of both Sudenpesä and Vesijako forest hollows in May 2008 using a 50cm long, 5cm diameter Russian corer (Jowsey, 1966). Sediment extraction at each site comprised three core sections taken from adjacent core holes from the surface down with core drives alternated between two core holes to enable a 10cm overlap. A total of 145 cm of sediment was extracted from Sudenpesä and 126 cm of sediment from Vesijako. Cores were secured in drain piping and cling film before being transported to the University of Liverpool and stored below 5^{o}C prior to sub-sampling. Sudenpesä sediment was sub-sampled at 0.5 cm intervals between 145 cm and 60cm and at 1 cm intervals between 60 cm and 35 cm. Above 35 cm the sediment was poorly compacted, consisting of loose *Sphagnum* and attempts made to retain sediment for analysis failed. Vesijako was sub-sampled at 1 cm intervals for the entire length of the core. Pollen and macroscopic charcoal were analysed from continuous sub-samples with 9 samples selected for AMS radiocarbon dating in Sudenpesä and 8 samples selected for AMS radiocarbon dating in Vesijako.

6.4.3 Pollen analysis

Pollen preparation followed standard procedures (Moore, 1991) with a minimum of 500 terrestrial pollen grains counted per sample and identified to species level where possible following Moore *et al*., (1991) and Bennett, (1995-2007). The pollen diagrams were created using TILIA and TILIA.GRAPH 2011 version 1.5.12 (Grimm, 2011) and a stratigraphically constrained cluster analysis was applied in CONISS on square root transformed data for selected abundant (maximum frequency >1%) terrestrial pollen taxa (Grimm, 1987).

6.4.4 Macroscopic charcoal analysis

Macroscopic charcoal preparation involved a known volume of sediment treated with NaOH to assist with sediment disaggregation before being sieved at 300 µm. Sediment residue retained was added to 80 ml of double distilled water with 20 ml of sampled added to a petri dish for analysis. Black brittle crystalline particles with angular broken ends were classified as charcoal (Swain, 1973, 1978). Charcoal influx (particles cm^{-2} yr^{-1}) was calculated at both sites and fire frequency estimates were derived from the charcoal record by assuming that absence of charcoal over a period separated individual fire events. As deposition of charcoal is often distributed over several decades (Higuera *et al.,* 2005), assuming consistent depositional characteristics, the second sample to record consecutive charcoal was taken as the fire year to calculate fire frequency as described in Clear *et al*., (2013) (Chapter 5). However in Sudenpesä it is possible that fire events may have merged into contiguous charcoal samples, which under the current method for detection of fire years would result in an under estimation of the frequency of fire. When charcoal was recorded continuously over a number of cm, if there was a clear second peak in charcoal abundance then this was calculated as a separate fire event.

6.4.5 Radiocarbon dating

A total of 17 peat samples were selected from Sudenpesä and Vesijako for AMS Radiocarbon dating (Table 6.1). Sediment exterior was scraped to remove possible contaminants and the remaining fraction of sediment between 0.5 – 2 g was dated. Age-depth models were produce for each site (Figures 6.1 and 6.2) from age estimates and surface age (AD 2008) using the Bayesian software Bacon (Blaauw and Christen, 2011). The software divided the cores into 1cm thick sections and estimated the accumulation rate for each section, constrained by prior information on the accumulation rate (a gamma distribution with a mean 10 year cm-1 and shape 1.8) and its variability (memory, a beta distribution with mean 0.25 and shape 2). Dates were calibrated using the IntCal13 curve (Reimer *et al*., 2013). For the radiocarbon ages, a Student-t distribution was used, which better takes into account scatter in the dates (Christen and Perez, 2009).

Depth (cm)	Laboratory number	14C age	Age (cal. yrs. BP)
Sudenpesä			
35 – 36	Hela-1811	Modern	-55
55 – 56	LuS 9884	190 ± 45	162
72 – 73	Hela-1812	1665 ± 30	1574
97 – 97.5	LuS 9883	3515 ± 50	3790
110 – 111	Hela-1813	1575 ± 30	1466
121 – 121.5	LuS 9882	4580 ± 50	5256
129.5 – 130	LuS 9881	6550 ± 50	7220
141 – 141.5	LuS 9880	8045 ± 55	8907
143 – 144	Hela-1814	8735 ± 50	9725
Vesijako			
18 – 19	LuS 9887	155 ± 50	148
31 – 32	Poz-39981	1190 ± 35	1119
47 – 48	Poz-39979	1475 ± 30	1359
66 – 67	Poz-39980	2190 ± 30	2228
78 – 79	LuS 9886	2780 ± 50	2918
96 – 97	Poz-39978	3295 ± 35	3520
108 – 109	LuS 9885	3510 ± 50	3783
122 – 123	Beta-245766	4360 ± 40	5053

Table 6.1: Radiocarbon dating results of AMS bulk sediment dates for Sundenpesä and Vesijako forest hollows, southern Finland

6.4.6 Statistical analysis

Compositional turnover (Birks, 2007; Bjune *et al.,* 2009a) was estimated using detrended canonical correspondence analysis (DCCA) in CANOCO 4.5 (ter Braak & Šmilauer, 2002). Pollen data (species) were square-root transformed to stabilise variance and age (cal. yrs. BP) was applied as the sole constraining variable.

Palynological richness (Birks & Line, 1992) was estimated using rarefaction analysis in R (R Development Core Team, 2010). As the total pollen count varies between samples, estimates of the number of expected taxa [$E(T_n)$] are calculated using the lowest total pollen count as the baseline for comparison of palynological richness amongst samples.

6.4.7 *Quantitative vegetation reconstruction*

Vegetation composition in southern Finland was reconstructed for 10500 cal. yrs. BP using the landscape reconstruction algorithm (Sugita, 2007a, 2007b). This is a two-step model: first the REVEALS model (Sugita, 2007a) estimates regional vegetation composition using pollen assemblages from large sites as well as species-specific pollen productivity and dispersal; secondly the LOVE model (Sugita, 2007b) estimates local vegetation from small sites by incorporating both pollen productivity and dispersal with the regional vegetation estimates derived from the REVEALS output. The LOVE model estimates the distance-weighted vegetation proportion of each pollen taxa within the source area of the site.

Pollen records from three large sites between 100 and 500 ha (Sugita, 2007a) situated in southern Finland: Hirvilampi, 60°37'N; 24°15'E (Rankama & Vuorela, 1988); Laihalampi, 61°29'N; 26°05'E (Heikkilä & Seppä, 2003); and Nautajärvi, 61°48'N; 24°41'E (Ojala & Tiljander, 2003) were combined to estimate regional vegetation using the programme REVEALS v. 4.2.2 (Sugita, unpublished data). Pollen productivity estimates are from the mean values presented in Mazier *et al*., (2010) and pollen fall speed was obtained from Sugita *et al*., (1999). Pollen dispersal and deposition were calculated using the lake model (Sugita, 1993) and an average wind speed of $3 m.s^{-1}$ with neutral atmospheric conditions (Broström *et al*., 2008).

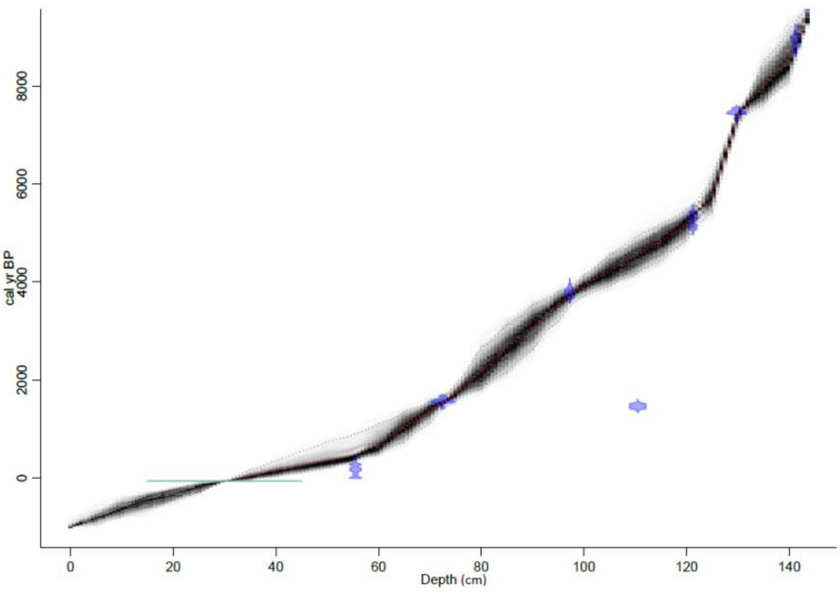
Pollen results from the two small forest hollow sites; Sudenpesä and Vesijako were run for 10000 cal. yrs. BP and 5000 cal. yrs. BP respectively using LOVE v. 3.3 (Sugita, unpublished data). Pollen dispersal and deposition in the small sites followed the model of pollen dispersal (Prentice, 1985). The relevant source area of pollen was set to 50m (Sugita, 1994; Calcote, 1995) and increased in 10m-steps until the estimates of all taxa were ≥0 with a 1 SD threshold with the estimates of regional pollen source area derived from REVEALS model.

6.5 Results

6.5.1 Chronology

The age-depth curve derived from the radiocarbon dates for both Sudenpesä and Vesijako indicate that sediment accumulation is initially slow at both sites before entering a phase of relatively constant sedimentation (Figure 6.2). At Sudenpesä this steady accumulation continues up until the present day with radiocarbon analysis returning a modern age at 35 – 36 cm. The top 35 cm of Sudenpesä consisted of unconsolidated, wet sphagnum with very little sediment available and yielded a very poor record of pollen with no evidence of charcoal. Steady sediment accumulation continues in Vesijako to approximately 1350 cal. yrs. BP. There is uncertainty associated with the radiocarbon date recorded at 31 – 32 cm with a radiocarbon age of 1190 ± 50 years too old to fit linearly with the age-depth curve. This could be caused by a local disturbance such as erosion and in-wash of older sediment (Fowler *et al.* 1986) which is typically recorded during both natural and human disturbance events (Moore, 1986). Through linear age depth interpolation it is estimated that Vesijako extends back to over 5000 cal. yrs. BP and Sudenpesä to nearly 10000 cal. yrs. BP.

(a) Sudenpesä



(b) Vesijako

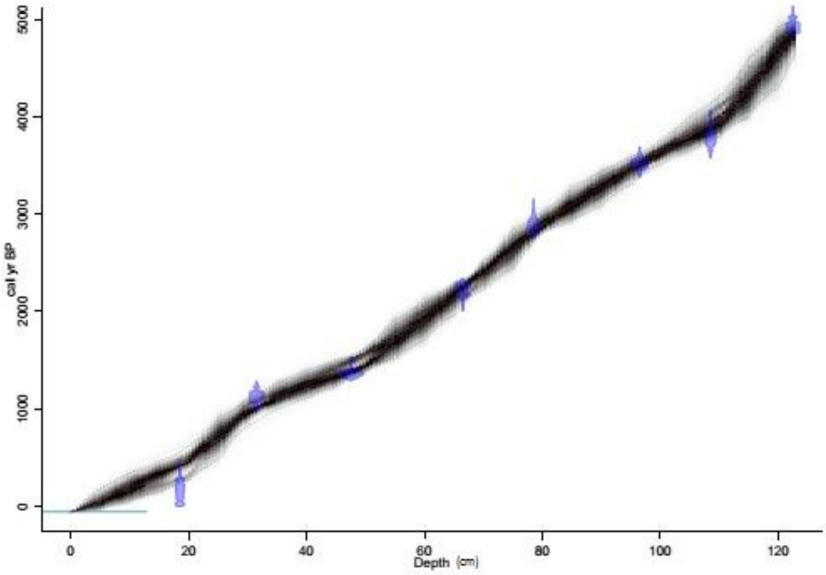


Figure 6.2: Age-depth models for (a) Sudenpesä and (b) Vesijako

6.5.2 Vegetation and disturbance history

Pollen percentage and charcoal accumulation for nearly 10000 cal. yrs. BP in Sudenpesä (Figure 6.3) and over 5000 cal. yrs. BP in Vesijako (see Figure 5.3 Chapter 5) indicates that Sudenpesä extends back almost twice as long compared to the temporal extent of Vesijako.

Sudenpesä (Figure 6.3 and Figure 6.4a) records post-glacial vegetation development with a co-dominant *Betula* and *Populus* stand and high presence of *Corylus* and Ericaceae prior to the rise of *Pinus sylvestris*. Compositional turnover (Figure 6.5a) is initially high during vegetation establishment and declines once *Pinus* is established. There is no charcoal recorded at Sudenpesä for approximately 1500 years suggesting that there was no local fire during this period. The first record of charcoal in Sudenpesä is not until 8800 cal. yrs. BP. Between 8800 – 7800 cal. yrs. BP regular charcoal presence indicates a regular fire occurrence with an average fire return interval of approximately 200 years (Figure 6.4a).

This regular fire occurrence is associated with an increase in *Betula* and decline in *Pinus* pollen. From 7800 to 7100 cal. yrs. BP there is another absence of charcoal suggesting a period of no fire. The absence of charcoal recorded until approximately 7100 cal. yrs. BP coincides with the beginning of an almost continuous underlying presence of *Picea abies*.

Between 7000 – 5100 cal. yrs. BP, regular charcoal indicates a fire return interval of approximately 375 years coinciding with a mixed coniferous-deciduous forest co-dominated by *Betula*, *Pinus* and *Alnus* with an underlying presence of *Corylus*, *Juniperus*, *Picea*, *Populus*, *Quercus*, *Salix*, *Tilia*, *Ulmus*, Cyperaceae and Poaceae.

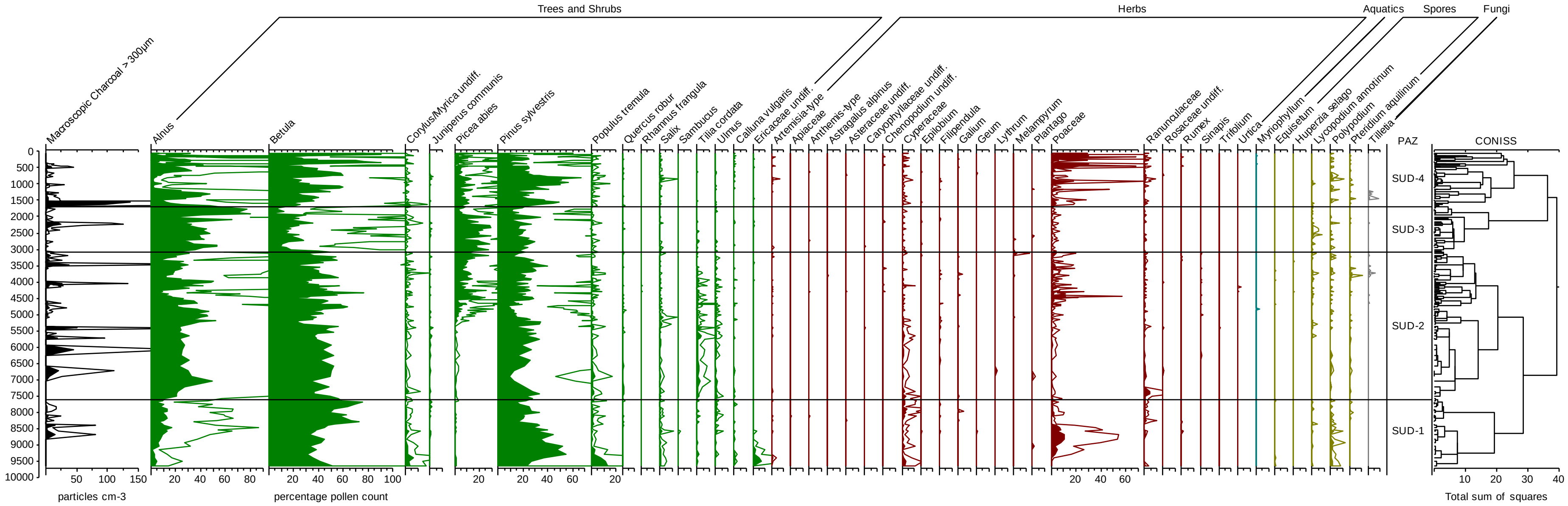


Figure 6.3: Pollen and charcoal diagram for Sudenpesä, Finland with pollen expressed as percentage of total pollen count and macroscopic charcoal fragments (>300µm) expressed as charcoal particles cm^{-3}

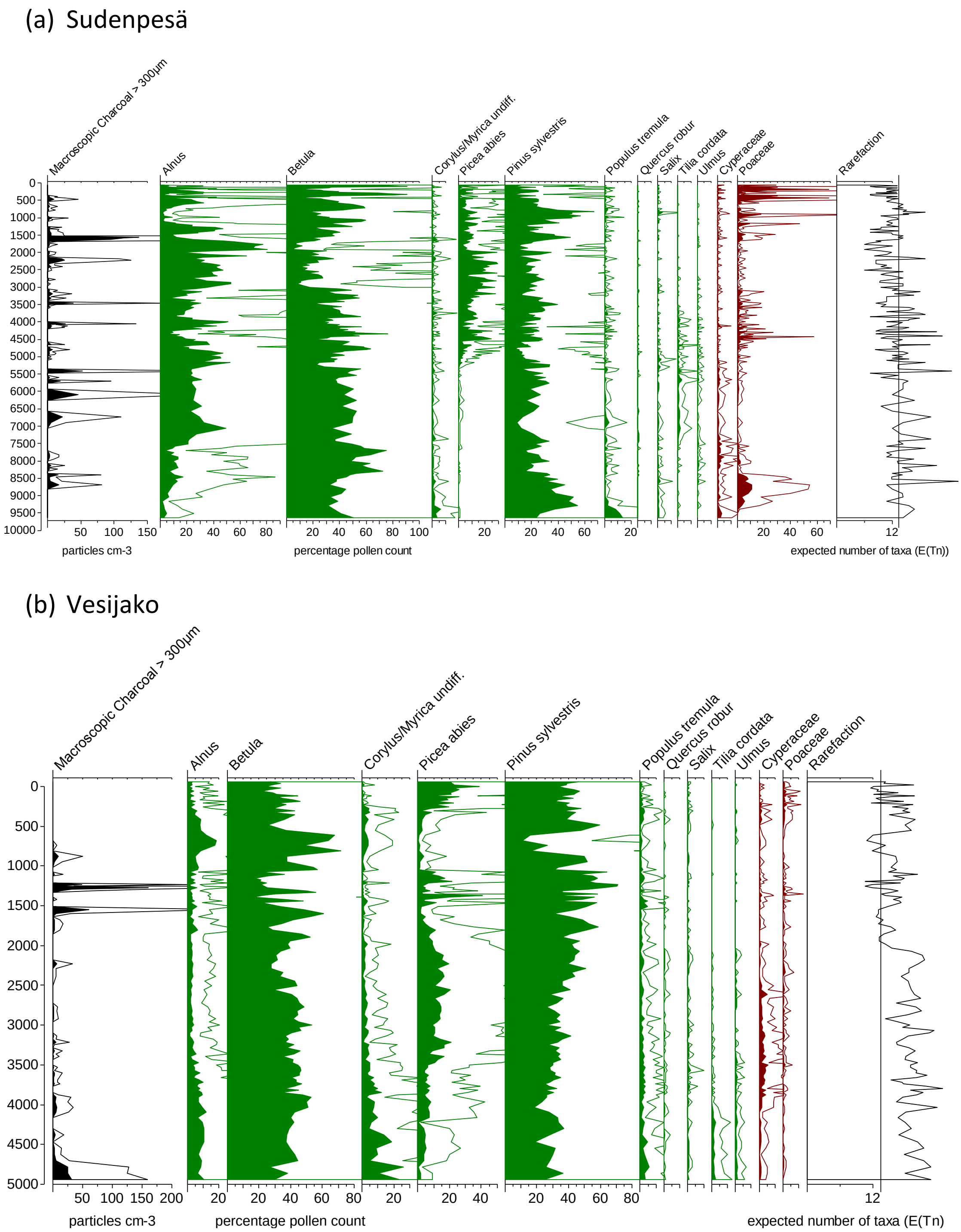


Figure 6.4: Selected pollen, macroscopic charcoal > 300µm and rarefaction analysis for (a) Sudenpesa and (b) Vesijako

The expansion of the continuous curve of *Picea abies* begins at approximately 5200 cal. yrs. BP in Sudenpesä. This rise in *Picea* corresponds to a period of frequent charcoal occurrence with a fire frequency calculation of approximately 100 year intervals between 5100 and 4600 cal. yrs. BP. This suggests increased fire activity associated with the local expansion of *Picea abies*. The charcoal record then records a fire frequency of approximately 400 year intervals between 4600 – 3600 cal. yrs. BP. In Vesijako (Figure 6.4b) the establishment and onset of the continuous curve of *Picea abies* pre-dates the extent of the core (pre-5000 cal. yrs. BP). The fire frequency calculated from charcoal occurrence during this time indicates a fire frequency interval of approximately 430 years. This is not too dissimilar to the 400 year fire frequency recorded at Sudenpesä during the same time period. Rarefaction results record high levels of palynological diversity in both sites, particularly in Vesijako during this time period and also high levels of compositional turnover are recorded at both sites (Figure 6.5a and 6.5b), particularly in Sudenpesä where pollen values are highly variable.

The high palynological richness (Figure 6.4a and 6.4b) and variable compositional turnover (Figure 6.5a and 6.5b) persist in both sites until a decline in deciduous species recorded at both Sudenpesä (from approximately 3500 cal. yrs. BP) and at Vesijako (approximately. 2200 cal. yrs. BP). This decline in deciduous species occurs at the same time as an increase in fire frequency at both sites. In Sudenpesä an increased charcoal frequency is recorded between 3600 – 1600 cal. yrs. BP when the fire frequency interval is approximately 200 years before again returning close to the background level fire frequency of approximately 370 years between 1400 – 400 cal. yrs. BP. In Vesijako charcoal records indicate a fire frequency of 180 years between 2000 – 750 cal. yrs. BP until an abrupt decline in charcoal and absence in fire in Vesijako from 750 cal. yrs. BP to the present day. This recent absence of fire is also recorded in Sudenpesä, however not until approximately 400 cal. yrs. BP up to the present day.

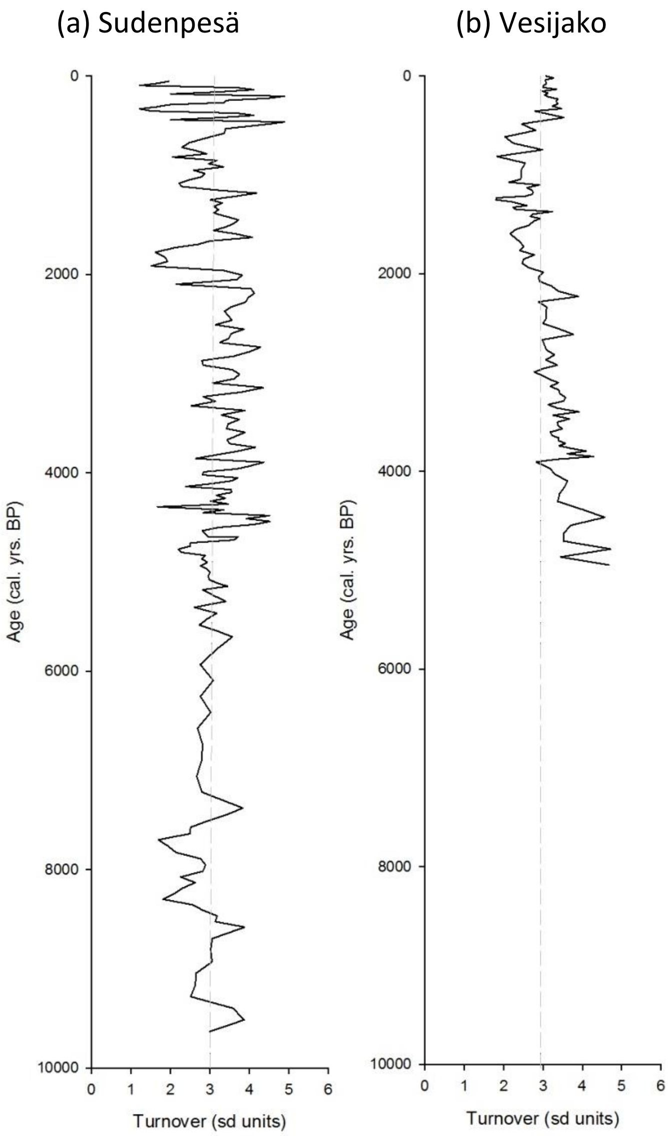


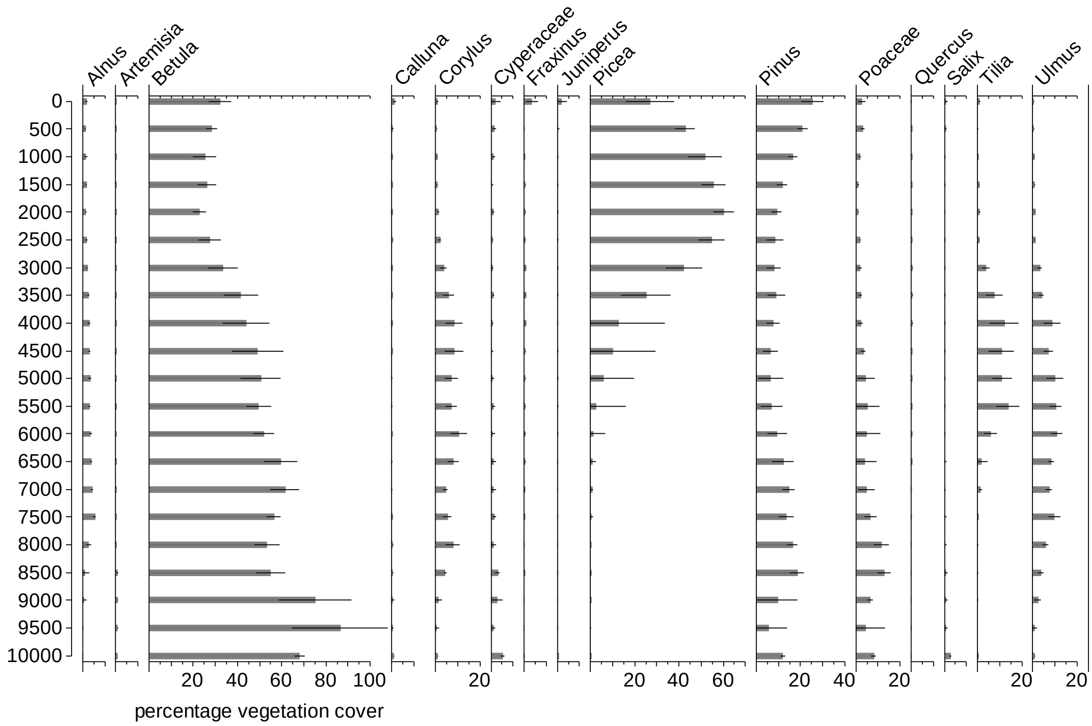
Figure 6.5: Compositional turnover (standard deviation units) for

(a) Sudenpesä and (b) Vesijako

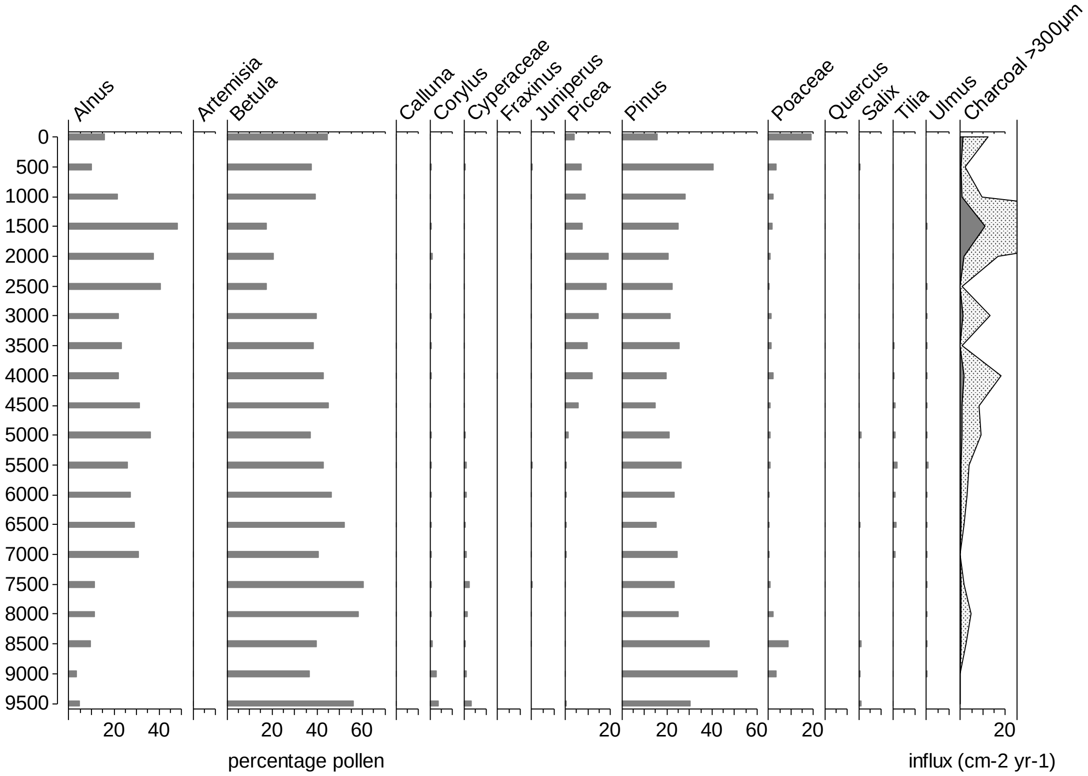
6.5.3 Pollen-based quantitative vegetation reconstruction

Regional pollen-based quantitative vegetation reconstruction derived from three large sites (lakes) in southern Finland is estimated at 500 year time intervals spanning 10000 cal. yrs. BP (Figure 6.6a). Early Holocene pollen-based vegetation reconstruction is dominated by *Betula* and *Pinus* with an underlying presence of *Cyperaceae*, *Poaceae* and *Salix*. During the early Holocene, *Betula* is estimated to between 60-80% of total vegetation land cover. During the early to mid-Holocene although *Betula* remains dominant with an estimated 50-60% of vegetation cover there is an estimated decline in *Pinus* abundance associated with an increase in mixed deciduous taxa; *Corylus*, *Tilia* and *Ulmus*. REVEALS model estimates a low continuous presence of *Picea* from approximately 9000 cal. yrs. BP which begins to increase in abundance regionally at approximately 6000 cal. yrs. BP. Interestingly it is estimated that both *Picea* and *Tilia* vegetation abundance increases at the same time approx. 6000 cal. yrs. BP. There is a decline in deciduous species vegetation abundance, most notably in *Tilia* and *Ulmus* but also a decline in *Corylus* around 3000 cal. yrs. BP. With the decline in mixed deciduous species, *Picea* rises to dominance with between 50-60% of total vegetation cover. This dominance in *Picea* abundance peaks approximately 2,000 cal. yrs. BP before a gradual decline in abundance at which time there is a slight gradual increase in both *Betula* and *Pinus* vegetation cover. The current *Picea-Pinus-Betula* forest that is observed in southern Finland today has been in existence regionally since approximately 2000 cal. yrs. BP.

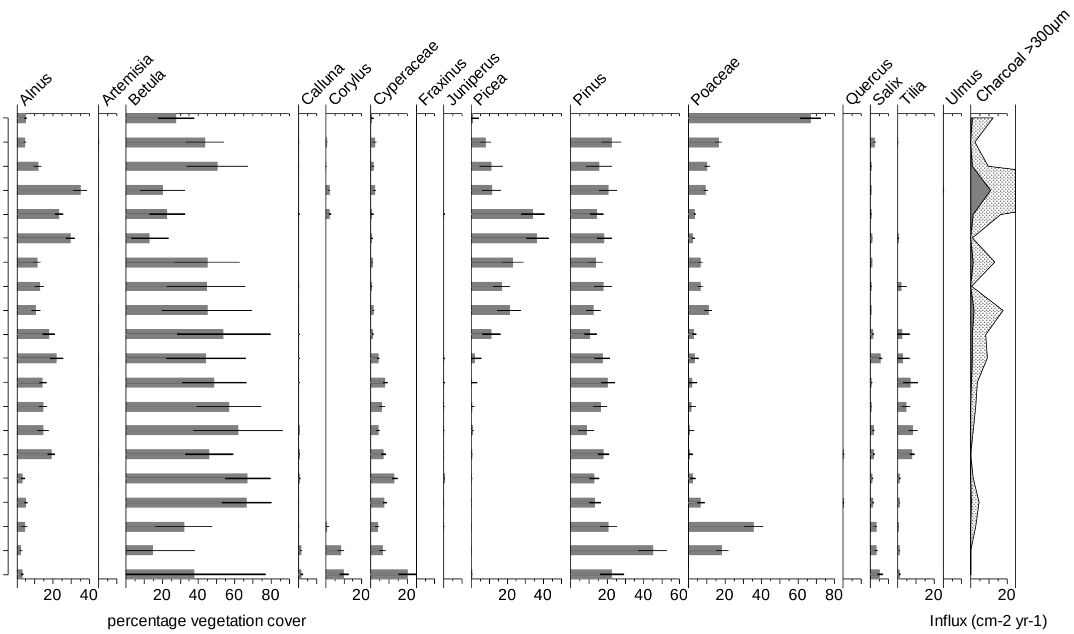
(a) REVEALS model output



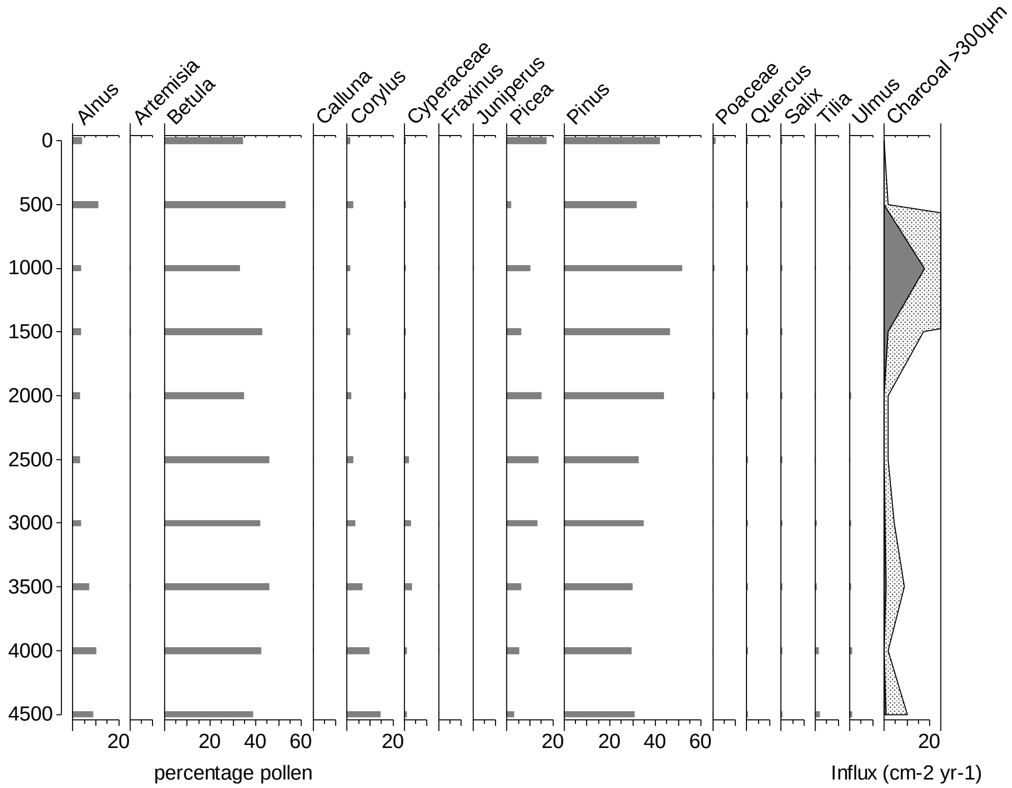
(b) Sudenpesä pollen



(c) Sudenpesä LOVE model output



(d) Vesijako pollen



(e) Vesijako LOVE model output

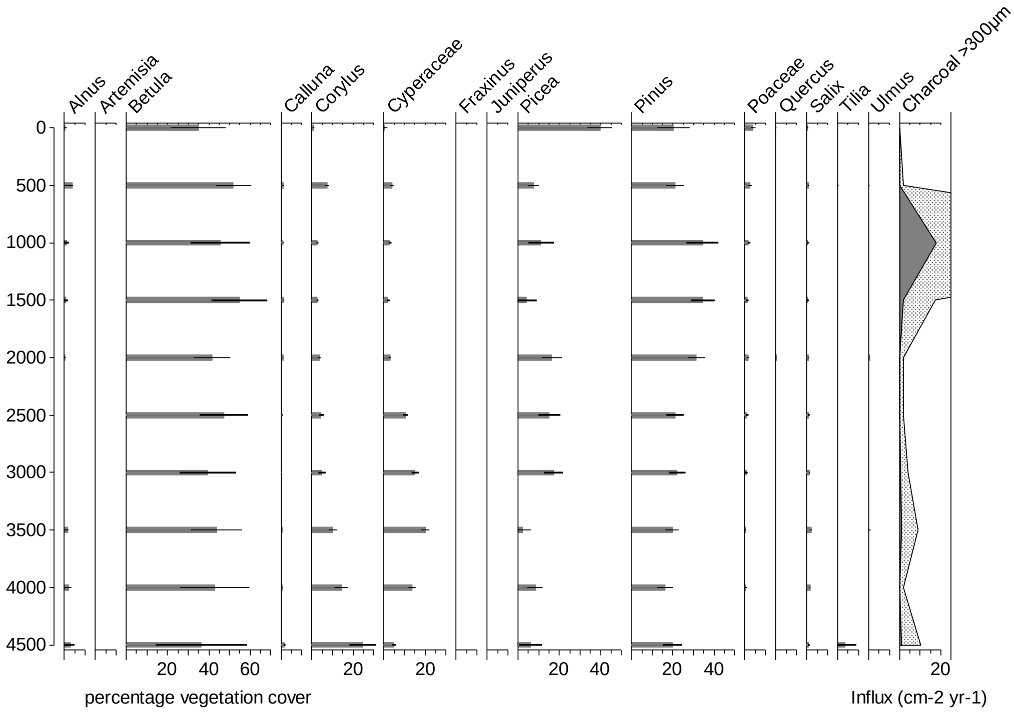


Figure 6.6: Landscape Reconstruction Alogrithm (LRA) output for (a) REVEALS model (b) Sudenpesä 500 year pollen percentage calculations (c) Sudenpesa LOVE model output (d) Vesijako 500 year pollen percentage calculations (e) Vesijako LOVE model output.

The application of the LOVE model incorporates pollen productivity and dispersal mechanisms in local vegetation reconstruction to estimate the local and regionally derived pollen (Figure 6.6c and 6.6e). This results in many of the species estimates being either under or over-represented in the local pollen diagram (Figure 6.6b and 6.6d). *Betula* and *Pinus* are the only species that remain fairly consistent between both the observed pollen data and the model output. Under-representation of species is most common, with Cyperaceae, *Juniper*, *Picea*, *Poaceae*, *Salix* and *Tilia* all estimated to be under-represented in the pollen diagrams. *Artemisia, Quercus and Ulmus* are estimated to be over-represented locally in both Sudenpesä and Vesijako pollen diagrams and their absence in the model output suggests that their presence in the local pollen diagram is derived from the regional pollen source area. *Alnus* is also estimated to be over-represented in both local sites. Unusually *Calluna* and C*orylus* vary between being over or under-represented at the local scale with *Calluna* under-represented in Sudenpesä and over-represented in Vesijako and *Corylus* over-represented in Sudenpesä and under-represented in Vesijako. *Fraxinus* although regionally present, is absent from both local sites.

In Sudenpesä (Figure 6.6c) modelled vegetation cover indicates early Holocene vegetation was dominated by *Pinus*, *Betula*, *Corylus,* Cyperaceae and *Salix*. During the mid-Holocene *Betula* dominates with 50-60% of total vegetation cover and a consistent presence of *Alnus* of between 10-20% total vegetation cover. Estimated *Pinus* vegetation cover declines from nearly 60% in the early-Holocene to approximately 20% during the mid-Holocene. Cyperaceae, *Tilia* and *Salix* decline at approximately 5000 cal. yrs. BP and during the same time *Picea* vegetation abundance begins to increase. *Picea* peaks of 30-40% of total vegetation cover between 2500 – 2000 cal. yrs. BP before declining to between 10-20% at the present day. During the decline in *Picea* both *Betula* and *Pinus* record a slight increase in vegetation cover. The model estimates *Poaceae* to comprise approximately 60% of the modern day vegetation cover.

In Vesijako (Figure 6.6e) the modelled vegetation output indicates a forest cover co-dominated by *Betula* (30-50% abundance) and *Pinus* (20-40%) for the extent of the record (4500 cal. yrs. BP). The mid-late Holocene mixed diverse stand with the continuous presence of *Alnus*, *Calluna*, *Corylus*, *Cyperaceae, Salix* and low presence of *Tilia* persists until approximately 2500 cal. yrs. BP. There is a mid-Holocene increase in *Picea* between 3000 – 2000 cal. yrs. BP before *Picea* declines during the mid-late Holocene and is estimated to peak in abundance, estimated to represent 40% of the total vegetation cover today. Poaceae also peaks in abundance during the modern day however at values much lower than recorded at Sudenpesä.

6.6 Discussion

6.6.1 Climate driven natural forest succession

During the early-Holocene, the retreating ice margin of the Weichselian ice sheet reached southern Finland approximately 13000 cal. yrs. BP (Lunkka *et al*., 2004). This enabled a succession of post-glacial vegetation development, initially with scattered *Betula* stands before the development of the *Pinus-Betula* forest (Björck & Möller, 1987). The absence of fire observed in Sudenpesä prior to 8800 cal. yrs. BP is also evident in the fire maps of Fennoscandia (Clear *et al*. submitted – Chapter 7). Natural fire requires both the availability of fuel (biomass) and favourable climate conditions and although rapid climate warming during the early-Holocene led to the deglaciation of the Weichselian ice sheet (Lundqvist 1986), climate reconstructions indicate low July mean temperatures of c.11^{o}c and high precipitation levels c.600 – 800mm yr^{-1} (Seppä & Birks, 2001). It is only once the forest becomes established that it is able to burn. Between 8800 and 7800 cal. yrs. BP there is increased fire activity with a relatively high fire frequency of approximately 200 year intervals most probably associated with increase in fuel load and cool, dry climate conditions (Seppä *et al.,* 2009b; Zillén & Snowball, 2009).

Further between 8800 and 7800 cal. yrs. BP there is a regional increase in *Betula* and decline in *Pinus* that is observed at the local scale in Sudenpesä and also observed in other palaeoecological records at the local (Bjune *et al.,* 2009a) and regional scale (Giesecke, 2005; Alenius *et al.,* 2013). The climate in northern Europe is strongly dependent on the North Atlantic Oscillation (NAO) intensity and this vegetational change could be linked to the North Atlantic '8.2 ka event' cooling widely recorded (Tinner & Lotter, 2001; Seppä *et al*., 2007) and suggests climate as the controlling driver of the observed changes in vegetation dynamics (Huntley, 1990).

6.6.2 The local establishment of Picea abies

Between 7800 to 7100 cal. yrs. BP the absence of charcoal in Sudenpesä suggests a period without fire, this time is also the onset of the almost continuous curve of *Picea abies.* In Sudenpesä frequent fire is recorded just prior to the low-presence establishment of *Picea*. The stand-scale establishment of *Picea* has frequently been linked to local disturbance, most commonly in western Scandinavia where the increase in *Picea* often coincides with an increase in anthropogenic disturbance (e.g. Molinari *et al.,* 2005; Bjune *et al.,* 2009a). The absence of fire, once *Picea* becomes established, is also evident elsewhere throughout Fennoscandia where *Picea* has the ability to alter the fire regime (e.g. Tallantire, 1972; Ohlson *et al.,* 2011). However, distinguishing between whether or not the absence of fire is a driver or consequence of an increased abundance of *Picea* remains difficult. In Sudenpesä during the establishment of *Picea*, the abundance of *Picea* is negligible, so much so that it could not have been the single cause for the altered local fire regime. This suggests that the observed reduction in fire may be a causal factor of *Picea* establishment rather than the result of the increased abundance of *Picea*. Climate is the most likely cause for the reduction in the local fire frequency.

The early continuous curve or tail associated with *Picea* establishment is not uncommon and is recorded throughout Fennoscandia (Giesecke & Bennett, 2004) as well as modelled in both the local Sudenpesä LOVE output and in the regional REVEALS model. But why does *Picea* not thrive immediately after becoming locally established? *Picea* is a shade intolerant species and as previously mentioned, is commonly associated with disturbance during establishment. Potentially the lack of fire at Sudenpesä between 7800 and 7100 cal. yrs. BP could have reduced the potential for *Picea* to thrive during the early Holocene. However when fire does return to Sudenpesä, approximately 7000 cal. yrs. BP, *Picea* does not thrive thus suggesting that factors other than local scale disturbance act as a control over the rise to dominance of *Picea* in the boreal forest of Fennoscandia. *Picea* is a continental tree with high summer temperature requirements and maximum mean coldest month temperature requirements of -1.5˚C. Precipitation has a strong effect on distribution at low latitudes and temperature is important at higher latitudes and altitudes (Giesecke, 2004). The increase in *Picea* abundance in southern Finland approximately 5500 to 5000 cal. yrs. BP is observed in both the local records of Vesijako and Sudenpesä as well as in the regional modelled data before spreading in a wave like distribution across Fennoscandia (Giesecke & Bennett, 2004). According to Giesecke *et al*., (2008), Gorcynski's index of continentally calculated for Lake Laihalampi (Heikkilä & Seppä, 2003) suggests continentality in southern Finland was at a minimum approximately 7000 cal. yrs. BP and gradually increased between 7000 and 2000 cal. yrs. BP before declining (Giesecke *et al.,* 2008). Interestingly *Picea abies* concentrations also peak in both the regional modelled data as well as the observed local data at approximately 2000 cal. yrs. BP. This suggests climate was the limiting factor for *Picea* establishment in the early-mid Holocene. This is further justified by the low abundance presence of *Picea* recorded 10000 – 9000 cal. yrs. BP and decline before 8000 cal. yrs. BP, modelled in both the local and regional LRA and within pollen records recorded at other sites around southern and northern Finland (e.g. Vasari, 1962, Tolonen, 1967; Tolonen, 1980; Tolonen, 1983b). The theory that continentality controls *Picea* abundance also fits with the *Picea* macrofossils found in the Swedish Scandes mountains (Kullman, 2000, 2001) where outposts of *Picea* population were present during the early post-glacial period approximately 10000 cal. yrs. BP. What is yet to be determined is whether or not these populations emerged from sites of 'cryptic ice age refugia' and survived during the last glacial maximum (LGM) (Huntley & Birks, 1983; Öberg & Kullman, 2001; Anderson *et al*., 2006; Parducci *et al*., 2012) or whether a low-abundance pioneering *Picea* population spread from east to west during the early Holocene (Giesecke & Bennett, 2004). Whatever the reason for these outlying *Picea* populations, their ability to thrive locally in the Scandes mountains between 6000 and 5000 cal. yrs.

BP was controlled by a changing climate, most notably the increased continentality (Giesecke and Bennett 2004). It is during this period approximately 6000 to 5000 cal. yrs. BP that climate became optimal to drive the spread of *Picea* at a maximum spreading rate of 250 m yr^{-1} (Bialozyt *et al*., 2012) in an east-west trajectory across Fennoscandia (Tallintire, 1972; Giesecke & Bennett 2004; Seppä *et al*., 2009a). *Picea* may still be spreading in southern Sweden and Norway (Bradshaw, 2007) but now at its ecological limits, the spread of *Picea* in southern Sweden is partly anthropogenic driven, where it is planted beyond its current climatic range limits (Bradshaw *et al*., 2000).

In Sudenpesä the local establishment of *Picea abies* is associated with increased fire activity with a fire frequency <100 years between 5100 and 4600 cal. yrs. BP. This association between an increased fire frequency just prior to the rise in *Picea* is often interpreted as fire disturbance facilitating the local establishment of *Picea* (e.g. Molinari *et al*., 2005). In Sudenpesä the increased fire occurs after the initial increase in *Picea* abundance with fire frequency declining once *Picea* becomes established. In Sudenpesä this is interpreted as an increase in fire associated with change in fuel type i.e. spruce saplings high ability to burn (Tanskanen *et al*., 2006). It is interesting to note that once *Picea* becomes established in Sudenpesä the fire interval returns to that of the fire frequency recorded prior to *Picea* establishment, approximately 400 year fire intervals. This approximately 400 year fire frequency is also observed in Vesijako during the mid-Holocene. It is well documented that *Picea* has the ability to alter the local microclimate reducing fire ignition potential (Tahskanen *et al*., 2005) thus diversifying the natural fire regime (Ohlson *et al.* 2011) yet this decline in fire frequency is not observed in Sudenpesä and cannot be determined in Vesijako. However the fire frequency in Sudenpesä was already naturally low prior to the establishment of *Picea*. According to Clear *et al.,* unpublished (Chapter 8) to appreciate a decline in fire frequency associated with vegetation dynamics the initial fire frequency would have to have been of a frequency less than 100 year intervals. This may be observed in western Scandinavia where the spread of *Picea* coincided with heightened anthropogenic activity c.2000 cal. yrs. BP (Bradshaw & Hannon, 1992; Lindbladh *et al* 2000) but in southern Finland the fire frequency prior to *Picea* establishment was already naturally low further suggesting that fire frequency was not a factor in the local establishment of *Picea* in southern Finland.

A further point to note is the low representation of *Picea abies* in both the pollen record and within the LRA model output given the present-day dominance of *Picea* at both Sudenpesä and Vesijako. *Picea* is a low pollen producer that produces large pollen grains with a limited dispersal potential (Broström *et al*., 2008) and for this reason the poor representation of *Picea* grains in the pollen diagram is expected. However given the present day dominance of *Picea* at both local stand-scale sites it would be expected to be reflected in the model output. If the LRA underestimates present day abundance of *Picea* with an analogue population for comparison then it is likely that the LRA is also underestimating the past *Picea* abundances during the Holocene.

6.6.3 Floristic diversity and disturbance

Regular fire intervals of approximately 375 years recorded in Sudenpesä between 700 – 3600 cal. yrs. BP is similar to the 430 year fire frequency observed in Vesijako between 5200 – 2000 cal. yrs. BP. This re-occurring fire frequency of approximately 400 years appears to be the most naturally driven fire frequency of the southern boreal forest of Finland and corresponds to the time of greatest floristic diversity at the local scale in Sudenpesä and in Vesijako (Clear *et al*., 2013 – Chapter 5). This also spans the mid-Holocene Thermal Maximum (HTM) and is associated with warmer temperatures and high species diversity throughout Fennoscandia (e.g. Greisman & Gaillard, 2009; Clear *et al*., 2013 – Chapter 5). It is believed that the decline in deciduous abundance is mainly a product of mid-Holocene climate deterioration and that modern pollen-climate calibration data sets can be combined with fossil pollen data sets to produce pollen-climate transfer functions (e.g. Seppä *et al*., 2009b; Bjune *et al*., 2010). Deciduous tree species, especially *Tilia cordata* were outcompeted by the expansion of *Picea* (Seppä *et al.,* 2009a), but in the present study in Sudenpesä, both *Picea* and *Tilia* vegetation abundance increase simultaneously. However in southern Finland an increase in charcoal frequency recorded in both Sudenpesä (3600 and 1600 cal. yrs. BP) and in Vesijako (2000 and 750 cal. yrs. BP) increases the fire frequency interval to 185 and 180 years respectively. This increase in fire frequency corresponds to the abrupt decline in deciduous species abundance at both sites, but 1600 years apart. This is unexpected as the sites are located only 18 km apart. Regionally the LRA output indicates a decline in floristic diversity approximately 3000 cal. yrs. BP. This does not correspond to the increase in abundance of *Picea abies* suggesting species composition was a minor factor in the decline in deciduous species. Likewise the significant difference in timing between the declines in deciduous species locally suggests that a factor other than climate was the main driver behind the decline in deciduous species in southern Finland. By 3000 cal. yrs. BP swidden 'slash and burn' culture thrived in southern Finland (Sarmela, 1987) and focused on the clearance of broadleaf trees (Parviainen, 1996). The establishment of permanent agriculture led to population expansion and anthropogenic disturbance became the strongest driver of forest compositional change (Reitalu *et al*., 2013).

6.6.4 Fire suppression

The period of anthropogenically induced, increased fire frequency abruptly ending in Vesijako approximately 750 cal. yrs. BP before moving into a period of complete fire absence or fire suppression. In Sudenpesä the period of increased fire frequency declines from 1200 cal. yrs. BP but the forest continues to burn at a frequency of approximately 370 year intervals until 108 cal. yrs. BP. This is within the natural fire cycle range and thus cannot be interpreted as active fire suppression. It is approximately 1200 cal. yrs. BP when evidence of permanent settlements appear in southern Finland (Sarmela, 1987) and due to the invention of the plough and the ability to cultivate nutrient rich, heavy soils, broad-leaf slash and burn is replaced by more intensive coniferous slash and burn (Alenius *et al*., 2013). It is possible that both sites Sudenpesä and Vesijako, became less favourable locations during the switch from primitive swidden cultivation to arable cultivation (Alenius *et al*., 2008).

Chapter 7

7 Holocene fire in Fennoscandia and Denmark

7.1 Abstract

Natural disturbance dynamics, such as fire, have a fundamental control on forest composition and structure. Knowledge of fire history and the dominant drivers of fire are becoming increasingly important for conservation and management practice. Temporal and spatial variability in biomass burning is examined using 170 charcoal and 15 fire scar records collated throughout Fennoscandia and Denmark. The changing fire regime is discussed in relation to local biogeographical controls, regional climatic change, anthropogenic land use and fire suppression. The region has experienced episodic variability in the dominant drivers of biomass burning throughout the Holocene creating a frequently changing fire regime. Early-Holocene biomass burning appears to be driven by fuel availability. Increased continentality during the mid-Holocene Thermal Maximum coincides with an increase in fire. The mid-late Holocene front-like spread of *Picea abies* (Norway spruce) and cooler, wetter climatic conditions reduce local biomass burning prior to the onset of intensified anthropogenic land-use while the late-Holocene increase in anthropogenic activity created artificially high records of biomass burning that overshadowed the natural fire signal. An economic shift from extensive subsistence land-use to agriculture and forestry as well as active fire suppression has reduced regional biomass burning. However, it is proposed that without anthropogenic fire suppression, the underlying natural fire signal would remain low due to the now widespread dominance of *Picea abies*.

7.2 Summary

Dominant drivers of biomass burning have varied throughout the Holocene with early-mid Holocene fire controlled by fuel availability, climate and vegetation type. Anthropogenic controls on fire dominate mid-late Holocene biomass burning initially through an increase in ignitions and subsequently through a reduction in human induced ignitions and active fire suppression.

7.3 Introduction

Heavily managed forests and active fire suppression have created an ecosystem almost free of fire throughout Fennoscandia and Denmark (Zackrisson 1977; Wallenius 2011). The absence of fire from the landscape impacts not only natural forest regeneration (Ruokolainen and Salo 2006) but also reduces floral and faunal biodiversity and threatens the survival of red-listed species such as saproxylic beetles, that are reliant on the regular occurrence of forest fire (Lindbladh *et al.* 2003). This absence of fire from the Fennoscandian Boreal ecosystem is thought to have contributed to the widespread dominance of *Picea abies* and subsequent decline in deciduous species (Bjune *et al.* 2009) with *Picea* becoming the most abundant tree species in northern European forests and emerging as a new boreal forest keystone species (Seppä *et al.* 2009). Fire has not always been so rare throughout Fennoscandia and Denmark with fire scars recording a significantly more intensive fire regime in the recent past (e.g. Niklasson and Granström 2000; Power *et al*. 2013; Storaunet *et al*. 2013). Fire scars are valuable for understanding past human fire activity. However, fire scar records rarely exceed 600 years in Fennoscandia (Wallenius *et al.* 2007) and do not exceed beyond the time of significant anthropogenic impact.

The anthropogenic fire signal recorded in fire scars gives an artificially high perception of the historical fire regime that dilutes the natural fire signal in Fennoscandia and Denmark. By contrast, charcoal series record fire history on a palaeoecological perspective, far beyond the temporal capability of fire scars and prior to significant anthropogenic disturbance (Clear *et al*., 2013 – Chapter 5), with macroscopic charcoal recording local fires at a high spatial precision (Ohlson & Tryterud, 2000; Higuera *et al.*, 2007). It is only through palaeoecological data of biomass burning that we can understand the impact of natural drivers of fire and even with minimal anthropogenic disturbance it remains difficult to disentangle the complex interactions of natural drivers of biomass burning: climate variability, vegetation type and fuel availability (Molinari *et al*., 2013).

7.4 Aims

The aim of this paper is to combine available charcoal and fire scar records from Fennoscandia and Denmark to explore spatial and temporal heterogeneity and variability in biomass burning. We aim to identify the changing dominant drivers and controls of fire throughout the early, mid and late-Holocene.

7.5 Materials and methods

7.5.1 Data collection

Charcoal and fire scar data were collated for 143 sites located in Fennoscandia and Denmark between latitude 55˚12’19”– 70˚42’0”N and longitude 5˚19’4”– 32˚44’39”E (Figure 7.1). If available, both macroscopic and microscopic charcoal records from an individual site were included in the analysis as well as duplicated sites by subsequent authors.

A total of 170 charcoal data sets and 15 fire scar records were included in the analysis. Data sources included: 1) raw charcoal data and charcoal influx calculations provided directly by original authors, 2) charcoal records available from the European Pollen Database (EPD) (http://www.europeanpollendatabase.net, Fyfe, 2009), and 3) digitised data from published articles in peer reviewed journals. Published data were digitised using Data Mugger version 1.1 (Welsh *et al*., unpublished). A standard linear interpolation age depth model was applied using

Clam (Blaauw, 2010) to sites with available depth data. Where depth data were not available, charcoal values were digitised directly against age and thus relied on the published, pre-calculated age depth calculations. Raw data supplied directly from authors also consisted of pre-calculated age depth curves. Dating controls on sedimentary charcoal records vary including AMS C^{14} dates, Pb^{210} dating, varve counts and cross-correlation of vegetation with nearby dated sites. Fire scar chronologies were pre-determined by original authors using dendrochronological techniques. All ages were converted to calibrated years before present (hereafter cal. yrs. BP, where 0 cal. yrs. BP = AD 1950), with all-time series constrained between -60 and 13240 cal. yrs. BP (2010 AD – 11940 BC). To include as much data as possible, the charcoal dataset was gathered from sites spanning a wide range of depositional environments including lakes, bogs, mires and forest hollows. Sites have unique depositional features relating to individual site location and biogeography (e.g., site type, elevation, topography and surrounding vegetation type). Site specific information is available in the supplementary information (appendix I).

7.5.2 Spatial and temporal division

All of the sites were spatially sub-divided into four geographical regions based on their present day climate and continentality: Zone 1 consisting of the western coast of Norway and Scandes Mountains; Zone 2 consisting of southern Scandinavian regions including Denmark, southwest Norway and Sweden around the Skagerak and Kattegat Straits; Zone 3 central continental sites comprising of sites in central Sweden; and Zone 4 sites in eastern Fennoscandia including Finland and Russian Karelia (Figure 7.1). To compare time periods with distinctive charcoal records, 100 year charcoal averages were calculated, and a stratigraphically constrained cluster analysis (CONISS) was implemented in TILIA (Grimm, 1987) and identified six time periods: 1) >10000 cal. yrs. BP; 2) 10000 – 7800 cal. yrs. BP; 3) 7800 – 5500 cal. yrs. BP; 4) 5500 – 3000 cal. yrs. BP; 5) 3000 – 700 cal. yrs. BP; and 6) 700 to -60 cal. yrs. BP.

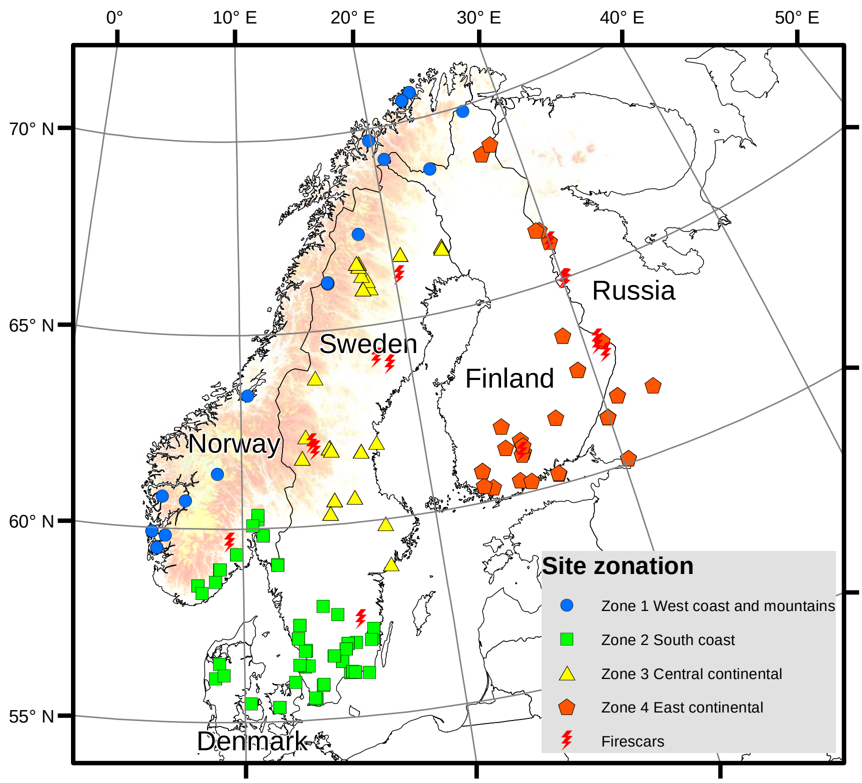


Figure 7.1: Charcoal and fire scar data for 143 individual sites (185 data series) located throughout Fennoscandia and Denmark. The charcoal data are divided into four geographical regions: Zone 1 (West coast and mountains) consisting of the western coast of Norway and Scandes Mountains; Zone 2 (South coast) consisting of southern Scandinavian region including Denmark, southwest Norway and Sweden around the Skagerak and Kattegat Strait; Zone 3 (Central continental) comprising of sites in central Sweden; Zone 4 (East continental) consisting of sites in eastern Fennoscandia including Finland and Russian Karelia. Fire scar records are denoted separately.

7.5.3 Data standardisation and analysis

All charcoal data were standardised using the basic standardisation method (n/max), where n is each charcoal abundance value and max is the maximum charcoal abundance recorded within each site. This method of standardisation causes some loss in the magnitude of data variance however, it is essential for data comparison between sites. For each individual site the standardised mean value (μ) was calculated for each time period (t) and compared to the mean value of the previous time period (μt^{prev}). Any increase (+ve) or decrease (-ve) in the charcoal abundance was calculated ($\mu t - \mu t^{prev}$) to determine the temporal rate of change within any given site. The significance of any rate of change was calculated using a Mann-Whitney U test given the non-normalised distribution of the data with the significance value to accept the null hypothesis (H_0) set at both 5% ($P <0.05$) and 1% ($P <0.01$). The Mann-Whitney U test results comparing the mean charcoal value of each time period (μt) with the mean charcoal value of the previous time period (μt^{prev}) were plotted using ArcMap10 (ESRI 2011) on five time series maps (excluding >10,000 cal. yrs. BP) of Fennoscandia and Denmark (Figure 7.2). Graduated triangles were plotted for two significance levels: $P <0.01$ and $P <0.05$ for both an increase (^) and decrease (v) in mean charcoal abundance relative to the mean of the previous time period. Sites that recorded an increase or decrease in charcoal abundance without significance were denoted with circles. To be represented on a map, a site required available data in both the present and previous time period. Percentage calculations for the number of sites that record significant ($P < 0.01$ and $P < 0.05$) and non-significant ($P \geq 0.05$) increase (+ve) or decrease (-ve) in charcoal abundance were calculated for ($\mu t - \mu t^{prev}$) and are included in table 7.1.

The spatial and temporal distribution of charcoal abundance was analysed using box plot transformations in R (R Development Core Team, 2010) for the four pre-determined geographical regions over the six time periods (Figure 7.3). The 100 year average values calculated for the time series maps were used to estimate charcoal abundance variation within each geographical region previously identified for the last a) 1000 cal. yrs. BP and b) 10000 cal. yrs. BP (Figure 7.4).

Fire scar records and charcoal abundance data were combined to estimate the timing of any decline in fire or fire suppression throughout Fennoscandia and Denmark (Figure 7.5). The date at which the last fire was recorded was used to determine the timing of a decline in fire and assigned to one of the following categories: 1) no fire suppression; 2) fire suppression since 150 cal. yrs. BP (post 1800 AD); or 3) fire suppression before 150 cal. yrs. BP (pre 1800 AD).

7.6 Results

Fire activity over the past 10,000 years was investigated based on 185 records, including 170 macroscopic and microscopic sedimentary charcoal series and 15 fire scars datasets. These records represent 143 different site locations across Fennoscandia and Denmark. The data from the 170 macroscopic and microscopic charcoal records are presented in five time series maps (Figure 7.2) and include the position of the spreading front of *Picea abies* in Fennoscandia (after Giesecke & Bennett, 2004). Temporal resolution of sites range from between a few hundred years to thousands of years with relatively few records available between 10000 and 7800 cal. yrs. BP and with an increase in site abundance for each time period as we approach the present day. The spatial distribution of sites is irregular throughout the study area with data concentrated in areas along the southern coast of Fennoscandia and Denmark. There are relatively few study sites in northern Finland and Russia and along the Norwegian coast. For this reason the data should be interpreted with caution. However, these maps provide a valuable insight into the temporal and spatial variability in palaeofire records throughout Fennoscandia and Denmark.

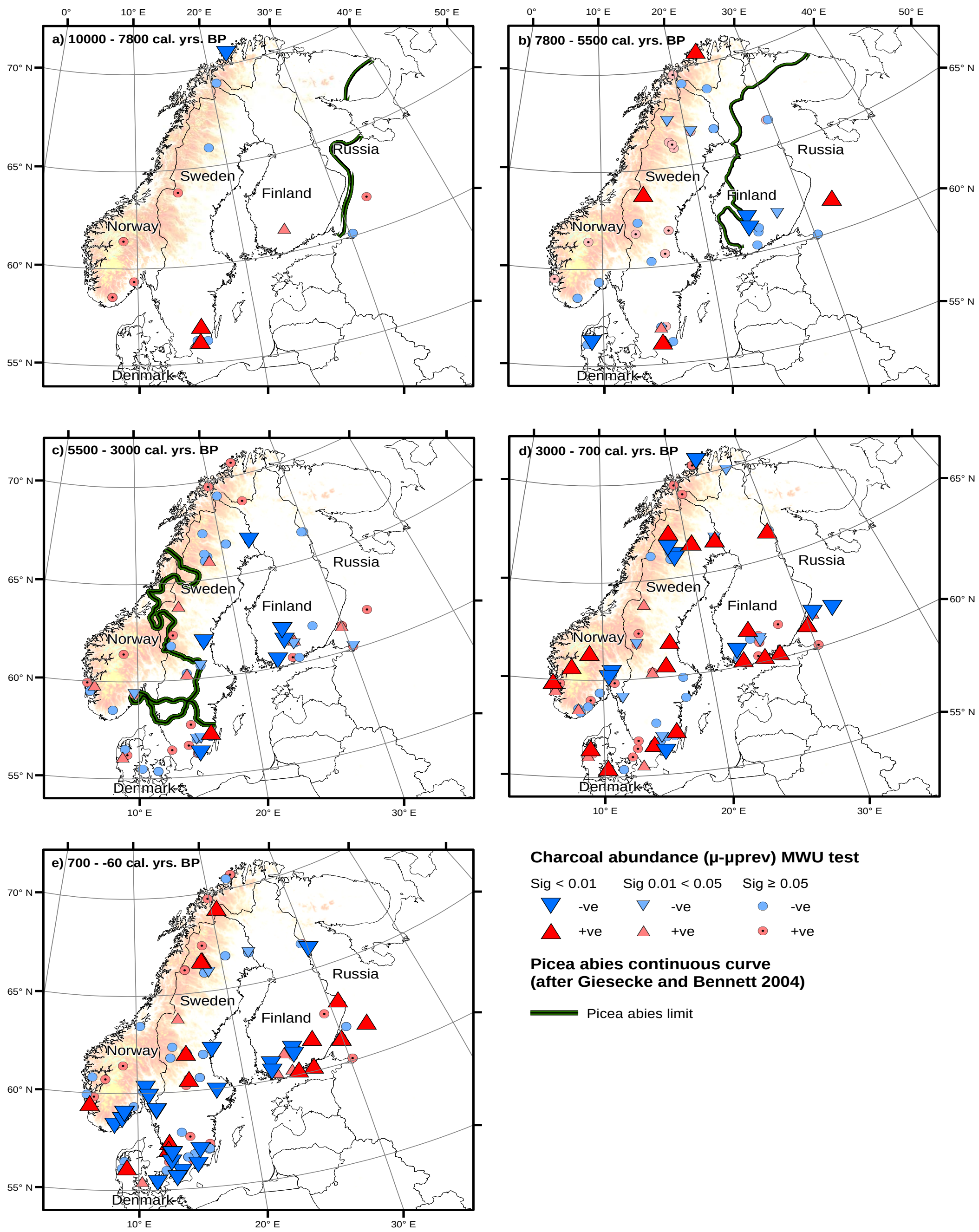


Figure 7.2: Five time series maps: a) 10,000 – 7,800 cal. yrs. BP; b) 7,800 – 5,500 cal. yrs. BP; c) 5,500 – 3,000 cal. yrs. BP; d) 3,000 – 700 cal. yrs. BP; and e) 700 – -60 cal. yrs. BP show the rate of change in sedimentary charcoal abundance compared to the previous time period ($\mu t - \mu t^{prev}$). Any increase or decrease in charcoal abundance is recorded at three significance levels: 1) $P < 0.01$; 2) $P < 0.05$; and 3) $P \geq 0.05$ calculated by the Mann-Whitney U Test. The extent of the continuous curve of *Picea abies* is displayed after Giesecke & Bennett, (2004).

7.6.1 10000 – 7800 cal. yrs. BP

There are relatively few sites (n=16) with sedimentary charcoal records extending back beyond 10000 cal. yrs. BP. These sites are concentrated in western and southern areas of Fennoscandia with no data available for Denmark (Figure 7.2a). 56% of sites record an increase in charcoal abundance compared to the pre-10000 cal. yrs. BP. 25% of all sites record a significant variance (P<0.05) in charcoal abundance with 75% of these sites recording a significant increase in charcoal abundance (Table 7.1).

$\mu t - \mu t^{prev}$		Charcoal abundance (+ve)						Charcoal abundance (-ve)					
cal. yrs. BP	Total number of sites	Mann-Whitney-U Test			% of Sites			Mann-Whitney-U Test			% of Sites		
		P <0.01	P 0.01 <0.05	P ≥0.05	**% (all)**	**% (sig)**	**% sig sites +ve**	P <0.01	P <0.05	P ≥0.05	**% (all)**	**% (sig)**	**% sig sites -ve**
10,000 – 7,800	16	2	1	6	**56**	**19**	**75**	1	0	**6**	**44**	**6**	**25**
7,800 – 5,500	49	3	4	20	**55**	**14**	**58**	3	2	17	**45**	**10**	**42**
5,500 – 3,000	81	1	8	26	**43**	**11**	**41**	6	7	33	**57**	**16**	**59**
3,000 – 700	115	21	14	34	**60**	**30**	**63**	9	12	25	**40**	**18**	**37**
700 – -60	145	19	5	36	**41**	**16**	**44**	25	5	55	**59**	**21**	**56**

Table 7.1: Results of Mann-Whitney U Test and percentage calculations of number of sites that record a relative increase or decrease in charcoal abundance compared to the previous time period.

This indicates an overall increase in burning compared to pre-10000 cal. yrs. BP in southern Norway, southern and central Sweden and southern Finland. Sites that record a decrease in charcoal abundance compared to pre-10000 cal. yrs. BP are located in Russia, northern Norway and in central and southern Sweden. Median charcoal abundance values are generally low for both pre-10000 cal. yrs. BP and 10000 – 7800 cal. yrs. BP with the exception of zone 4 which records the highest overall median charcoal values compared to any other region for any time periods (Figure 7.3). All zones record an increase in median charcoal abundance between pre-10000 cal. yrs. BP and 10000 – 7800 cal. yrs. BP. The mean charcoal curve

(Figure 7.4) is highly variable during 10000 – 7800 cal. yrs. BP probably due to the insufficient number of sites available and therefore these data are interpreted with caution. Peaks in mean charcoal abundance are recorded at 9800 and 9300 cal. yrs. BP driven by an increase in charcoal abundance in regions 3 and 4, at 8400 cal. yrs. BP driven by an increase in average charcoal abundance in zones 1 and 2 and at 7800 cal. yrs. BP due to an increase in average charcoal abundance in zones 2 and 4.

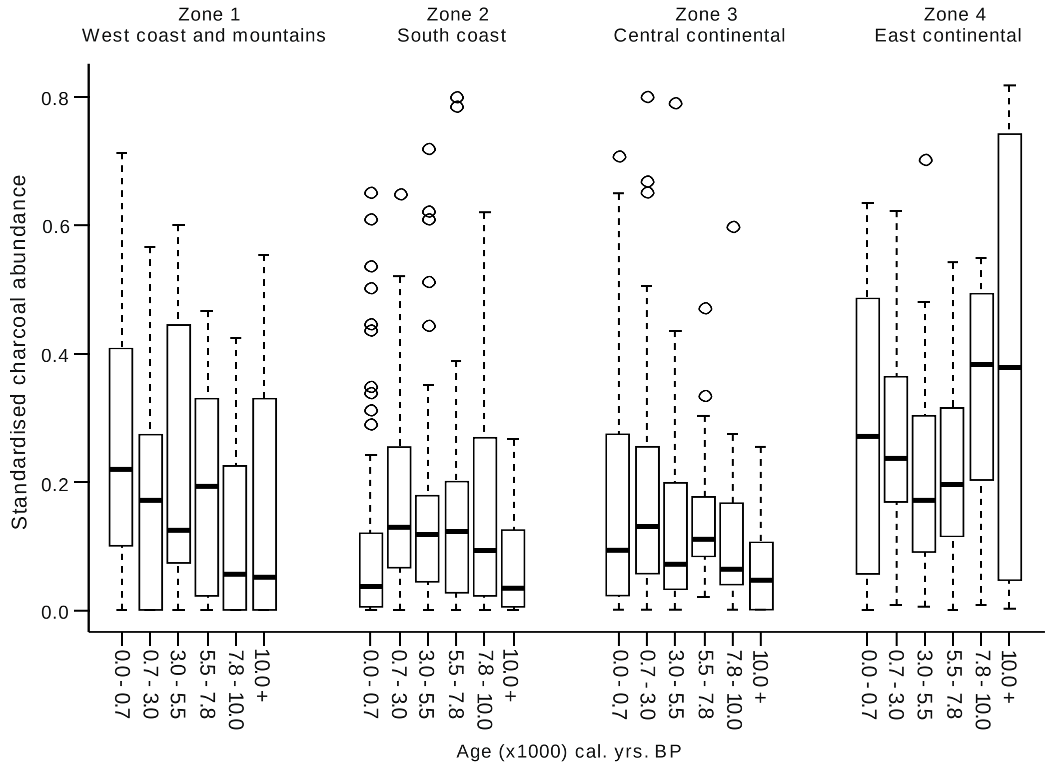


Figure 7.3: Box plots of standardised charcoal abundance for each site divided into four geographical regions over six time periods. The box plots display median charcoal values, minimum and maximum values, 25th and 75th percentiles and outliers.

7.6.2 7800 – 5500 cal. yrs. BP

Sedimentary charcoal data sets (n=49) are more abundant and widespread (Figure 7.2b) compared to the previous time period, with 55% of sites recording an increase in charcoal abundance. 24% of all sites record significant variance (P < 0.01) with 58% of significant sites recording an increase in charcoal abundance (Table 7.1).

a)

b)

c)

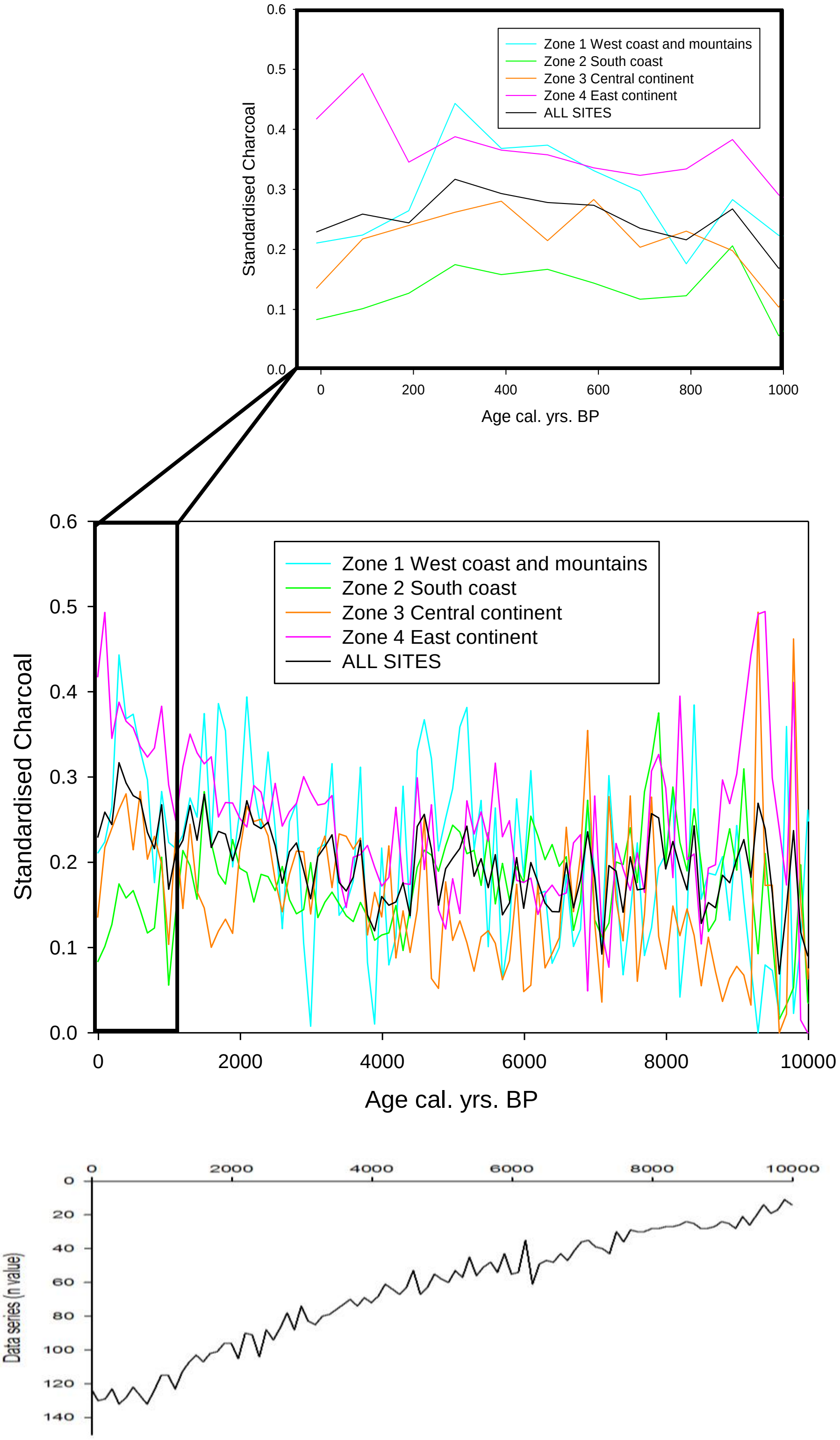


Figure 7.4: Standardised average charcoal abundance for time periods: a) 1,000 cal. yrs. BP; and b) 10,000 cal. yrs. BP at 100 years intervals for four geographical regions as well as the overall average charcoal abundance for all sites in

Fennoscandia and Denmark. The number of sites included in the analysis is displayed in c).

Sites characterised by a significant increase in charcoal abundance are generally located in a band spanning from southern Sweden to north-eastern Norway, with the exception of one site in Russia. On the contrary, there is a general distribution of sites with a decrease in charcoal abundance in Denmark and Finland. Zones 1, 2 and 3 record an increase in median charcoal abundance compared to the previous time period (Figure 7.3), while during this period a sharp decline in charcoal abundance is registered in zone 4. The mean charcoal curve records one peak in abundance values at approximately 6900 cal. yrs. BP driven by consecutive peaks in zones 1,2 and 3 (Figure 7.4).

7.6.3 5500 – 3000 cal. yrs. BP

It is during this time period that the first overall decline in charcoal abundance is recorded with 57% of sites (n=81) observing a reduction in charcoal values. 27% of sites record a significant variance and of these sites 59% record a decline in charcoal abundance (Table 7.1). The sites characterised by the most significant decline ($P < 0.01$) are located in eastern Sweden and western Finland (Figure 7.2c). All zones record a decline in median charcoal abundance (Figure 7.3). There are four peaks in mean charcoal abundance recorded during this time period (Figure 7.4): 5200 cal. yrs. BP driven by a peak in charcoal in zones 1 and 4; 4,500 – 4,400 cal. yrs. BP with peaks in zones 1, 3 and 4; 3700 cal. yrs. BP driven by zone 1 and 3300 cal. yrs. BP driven by zones 1 and 4.

7.6.4 3000 – 700 cal. yrs. BP

60% of sites (n=115) record an increase in charcoal abundance compared to the previous time period (Table 7.1). There are 56 sites (48% of sites) with a significant variance and of these 63% record an increase in charcoal abundance. This is the time period of most significant increase recorded throughout Fennoscandia and Denmark, with all 4 zones experiencing an increase in median charcoal abundance (Figure 7.3). The sites that record a significant decrease in charcoal abundance are generally clustered around the southern coastal areas of Fennoscandia and Denmark, with some isolated sites in northern areas of Norway and Sweden (Figure 7.2d). The mean curve (Figure 7.4) records peaks in charcoal abundance at 2100 and 1500 cal. yrs. BP driven by an increase in charcoal abundance in zones 1,3 and 4; and at 1,300 cal. yrs. BP with peaks in zones 1 and 4.

7.6.5 700 – -60 cal. yrs. BP

Since 700 cal. yrs. BP the largest number of data sets (n=145) record an overall decline in the charcoal abundance, with 59% of sites showing a reduction in charcoal compared to the previous time period (Table 7.1). 37% of sites record significant variance of which 56% of sites record a significant decrease in charcoal abundance. This widespread decline is most notable in a band along the southern coast of Norway, Sweden and Finland that extends north along eastern Sweden (Figure 7.2e). However, this reduction is not uniform throughout the research area: a significant increase in charcoal abundance is recorded in eastern Fennoscandia, central and western Sweden as well as some isolated sites in Norway and Denmark. Box plot observations are divided during this time period with zones 2 and 3 recording a decline in median charcoal abundance whilst zones 1 and 4 record an increase (Figure 7.3). The mean charcoal abundance curve (Figure 7.4) peaks at levels higher than any previous time period between 400 - 300 cal. yrs. BP driven by all four zones. There is a uniform decline in average charcoal abundance with zone 2 recording a decrease in charcoal abundance from approximately 400 cal. yrs. BP followed by a decline in charcoal abundance in zones 2 and 3 around 300 cal. yrs. BP. A decline in mean charcoal abundance in zone 4 is recorded not until 100 cal. yrs. BP (Figure 7.4). This overall decline in charcoal abundance is evident when observing fire absence pre- and post-150 cal. yrs. BP (Figure 7.5). A clear cessation of fire is recorded in 52 charcoal sites and 15 fire scar sites throughout Fennoscandia and Denmark. All fire scar sites record a decline in fire post-1800 AD, whereas over half of the charcoal series record fire suppression pre-1800 AD. Sites indicating an earlier (pre-1800 AD) fire absence are generally located in the southern regions of Fennoscandia with the exception of a few sites in central and northern Sweden, while sites recording a later (post-1800 AD) absence in fire are concentrated in central and northern regions of Sweden, Finland and Russia.

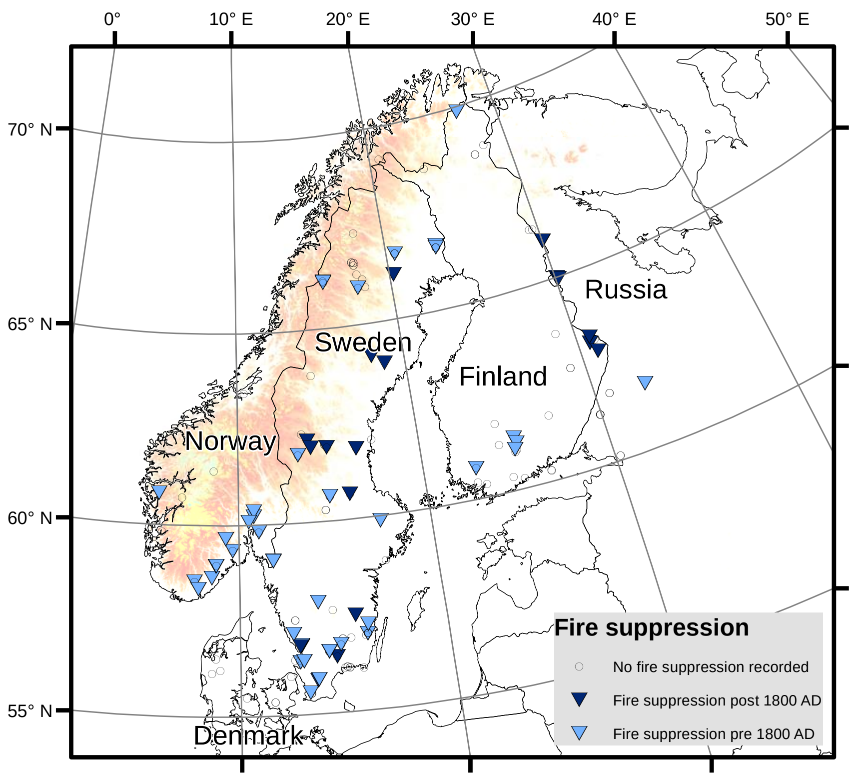


Figure 7.5: Fires suppression denoted by the last recorded date of fire at three time intervals: 1) No fire suppression recorded; 2) Fire suppression recorded post 1800 AD; and 3) Fire suppression recorded pre 1800 AD.

7.7 Discussion

Charcoal (macroscopic and microscopic) and fire scars data give insight into Holocene temporal and spatial variability in biomass burning. The time series, determined through CONISS analysis, correspond to changes in the broad-scale distribution of charcoal in Fennoscandia that may be attributable to changes in the dominant drivers of biomass burning (see Marlon *et al.*, 2013; Molinari *et al.*, 2013). The fire history of Fennoscandia and Denmark can be roughly divided into two periods: the early-mid Holocene natural fire signal, where fuel availability, climate variability and vegetation type are the likely dominant drivers of biomass burning; and the mid-late Holocene anthropogenic fire regime, with human induced ignition and subsequently fire suppression.

7.7.1 Climate, vegetation and fuel availability

Early Holocene warming lead to the retreat of the Weichselian ice margin and a gradual northward and centralised deglaciation of Scandinavia (Lundqvist, 1986). This deglaciation enabled expansion of plant distributions with the development of tundra vegetation dominated by herbs (e.g. *Artemisia* and *Chenopodiaceae*), grasses and sedges with scattered birch stands and intermittent phases of pine-birch forest development (Björck & Möller, 1987). This post-glacial vegetation expansion and increase in fuel availability appears to drive the early Holocene increase in biomass burning (Figure 7.2a). The retreating ice margin reached the Norwegian coast approximately 15000 – 13000 cal. yrs. BP (Andersen, 1979), southern Sweden approx. 13500 cal. yrs. BP (Berglund, 1979) and southern Finland around 13000 cal. yrs. BP (Lunkka *et al*., 2004), enabling earlier vegetation development and potentially an earlier increase in biomass burning compared to the central Fennoscandian sites. This early forest succession and subsequent earlier peak in charcoal abundance would account for the few sites that record a decline in biomass burning since 10000 cal. yrs. BP. The coastal and mountain distribution of sites, in particular sites that record a decline inbiomass burning, are supporting evidence of a multi-domed late glacial ice sheet suggesting mountain areas of Norway and Sweden were ice free by the late Weichselian (Paus *et al* 2006). The last remnants of the ice sheet most likely melted by 8500 cal. yrs. BP in central Scandinavia (Andersen, 1980; Lundqvist, 1986) explaining the absence of early

Holocene sites in this region. Although the early Holocene experienced rapid climatic warming pollen inferred temperature reconstruction indicates mean July temperatures were still low c.11.0˚C, and annual precipitation was high, c.600 – 800 mm (Seppä & Birks, 2001). This coupled with minimal anthropogenic disturbance can explain the general trend of less than average biomass burning during the early Holocene.

The mid-Holocene thermal maximum (HTM) is well documented throughout Scandinavia (Rosén *et al.*, 2001; Seppä & Birks, 2001; Davis *et al.*, 2003) and is characterised by warm, dry climatic conditions. The timing of the HTM varies usually between 6000 – 7000 cal. yrs. BP (Davis *et al.*, 2003) and coincides with an increase in continentality recorded in areas east of the Scandes Mountains (Giesecke *et al.*, 2008). These continental climate conditions could account for the general increase in biomass burning throughout central Fennoscandia and in Russia (Figure 7.2b). Interestingly, Swedish and Finnish sites experience a striking difference in regional biomass burning during this time period with 90% of Finnish sites recording a decline in charcoal abundance, suggesting a factor other than climate and continentality as a possible driver of regional biomass burning.

The reason for the absence of *Picea abies* in the early-Holocene, post glacial Fennoscandian forest development are poorly understood (Bradshaw *et al*., 2000) with vegetation models failing to identify the reason behind the late expansion of *Picea* in Scandinavia (Miller *et al.,* 2008). The mid-late Holocene expansion of *Picea* spread on a broad front moving from east to west into Finland, northern Scandinavia and then south and west towards its present-day limits (Giesecke & Bennett, 2004), with some early Holocene population outliers developing as far west as the Scandes Mountains (Kullman, 2001; Giesecke & Bennett, 2004). The expanding front of *Picea* has been traced onto the time series maps (Figure 7.2) after (Giesecke & Bennett, 2004). The map shows the east-to-west spread of the beginning of the continuous curve of *Picea* in the pollen records. Fire appears to decrease in sites as *Picea* becomes regionally established in Finland (7800 – 5500 cal. yrs. BP) and in Sweden (5500 – 3000 cal. yrs. BP). This negative correlation between *Picea* and fire has been well documented for Fennoscandia, with both the spread of *Picea* being held responsible for a reduction in fire (Ohlson *et al.*, 2011) as well as a decrease in fire being accountable for the subsequent spread of *Picea* (Bjune *et al.*, 2009a). Here our compilation indicates that the change in fire regime occurs once *Picea* is regionally established. Clear *et al.*, (2013) (see Chapter 5) record a similar change in the fire regime linked to fuel type: local fire frequency declines with a shift from a mixed deciduous forest to a predominantly coniferous forest. It should also be considered that approximately 5500 cal. yrs. BP climatic conditions shifted to become predominantly cooler and wetter than the HTM period (Seppä & Birks, 2001). These conditions would also favour a reduction in charcoal abundance and can not be excluded as possible drivers of mid-Holocene biomass burning. After 3000 cal. yrs. BP intensified anthropogenic disturbance of the fire regime makes the *Picea* – climate – fire signal even more difficult to decipher.

7.7.2 Anthropogenic ignition and suppression

A mid-late Holocene increase in biomass burning (Figure 7.2d) with poor regional coherency suggests an increase in the local-scale control of fire by humans. Prior to 3500 cal. yrs. BP human population was largely controlled by environmental factors (Tallavaara & Seppä, 2011). The establishment and expansion of agriculture enabled population growth and human impact is estimated as the strongest driver of forest compositional change (Reitalu *et al*, 2013). The anthropogenic use of fire intensified in conjunction with slash-and-burn activity driven by swiden cultivation and animal husbandry (e.g. Lagerås, 1996; Alenius *et al.,* 2008; D'Anjou *et al*., 2013). The intensification of slash-and-burn activity approximately 1,000 cal. yrs. BP corresponds to the expansion of permanent cultivation and the establishment of permanent village communities (Lagerås, 1996; Tavitsainen et al., 1998, Alenius *et al.,* 2013). The sustained increase in biomass burning during the mid-late Holocene is most likely the result of intensive anthropogenic land use that controlled biomass burning until it peaked at approximately 300 cal. yrs. BP. The subsequent pre-industrial decline in fire recorded throughout Scandinavia (excluding Finland and

Russia) coincides with an economic and cultural transition from traditional livelihoods (such as slash-and-burn) to modern agriculture and forestry (Wallenius, 2011). Intensive commercial forestry operations beginning in the late 1800s is also associated with a reduction in anthropogenic use of fire (Granström & Niklasson, 2008). The delay in fire suppression in the east continental region suggests a later economic and cultural transition. It is not until the 20th century Industrial era (approximately 100 cal. yrs. BP) that there is an overall decline in fire through Fennoscandia and Denmark.

7.7.3 The cause of the late-Holocene decline in biomass burning

The mid-Holocene decline in biomass burning preceded the onset of increased anthropogenic activity and can potentially be linked to the spread of *Picea abies* in Fennoscandia. The subsequent anthropogenic induced increase in biomass burning created an artificially high record of fire that overshadowed the natural signal. The late-Holocene decline in anthropogenic use of fire as well as active fire suppression reduced biomass burning. However, it is likely that without active fire suppression, the natural fire frequency would have remained low due to the widespread dominance of *Picea abies*.

This paper highlights the importance of palaeoecological knowledge and how seemingly unprecedented events can be placed within a long-term perspective (Whitlock, 2004). Using only short-term ecological data provides a modern yet 'short-sighted' view of past environmental change. We should not only look back at the recent past (i.e. when the fire signal was artificially high due to anthropogenic land use), but further back in time to the natural fire signal prior to significant anthropogenic activity (Clear *et al.*, 2013 – Chapter 5). It is likely that without an increase in anthropogenic biomass burning, natural biomass burning would have continued to decline with the increase in dominance of *Picea abies*.

Chapter 8

8 The influence of fire frequency on forest vegetation in northern Europe: past, present and future

8.1 Abstract

Tree species abundance and distribution is primarily controlled by climate yet disturbance dynamics can drive local variability in forest composition and structure. This paper aims to test the role of fire frequency in controlling tree species abundance and distribution in the transition zone between the temperate and boreal forest. The dynamic global vegetation model LPJ-GUESS is used to simulate variable fire frequency scenarios under (a) modern climate conditions and (b) +2^{o}C annual climate forcing. Modelled vegetation data are compared with high resolution palaeoecological data to test the influence of fire frequency on vegetation dynamics and species distribution. Data-model comparisons in the southern boreal forest show that fire frequency exerts control over dominant vegetation type and the distribution of deciduous species. Three fire frequency states are identified (1) high fire frequencies (< 50 year) producing a *Pinus sylvestris* dominated forest, (2) mid-range fire frequencies (50 < 100 years) that generate a co-dominated *Pinus sylvestris – Picea abies* forest and (3) low fire frequencies (>100 years) producing a *Picea abies* dominated forest. Applying a temperature increase of 2^{o}C allows for a greater abundance of deciduous species but only during low fire frequency scenarios of > 100 year intervals. Both model and data suggest that fire frequency, independent of climate, controls community scale variability in vegetation dynamics, with fire frequency states able to explain the dominant vegetation types observed throughout Fennoscandia, both now and in the past. Deciduous tree spatial distribution is primarily controlled by climate but, under a warmer climate scenario, fire frequency exerts the dominant control on the abundance of deciduous trees. Given the low fire frequency currently observed

throughout the southern boreal forest it is likely that any potential future increase in temperature would facilitate a northward expansion of deciduous species. If this was the case, the future fire regime would be dominated by low frequency, low intensity fires. However, under the current scenario, the continued dominance of *Picea abies* would further encourage a fire regime dominated by low frequency, high intensity fires, with a consequent increase in abundance of *Picea abies*.

8.2 Introduction

Global vegetation distribution is predominantly controlled by regional climate variations generating niche environmental conditions that make each biome compositionally unique (Holdridge, 1967). The natural distributions of these biomes are often defined by biophysical limits derived from physiological research e.g. (Prentice *et al.*, 1996; Prentice & Webb, 1998) and each biome has varied with climate fluctuations throughout the Holocene and also undergone varying extents of anthropogenic modification (Woodward *et al.*, 2004). However, variations in regional climate and anthropogenic disturbance alone cannot account for local, small-scale and sub-regional scale differences in vegetation compositional diversity and dominant vegetation type. In the boreal zone local variance in both biogeochemical properties and natural disturbance dynamics play a key role in determining biomass establishment and composition. For example, soil type, soil moisture and aspect can control local variation in vegetation composition (Bonan & Shugart, 1989) while large scale disturbances such as fire, windstorms and insect herbivores often damage specific species and favour others through gap dynamics (Bradshaw, 1993).

Fire is an important natural disturbance in the boreal forest and often stand-scale structure, age and composition is linked to the last major fire disturbance event (Bradshaw, 1993). Fire regime; frequency, size and severity (Bergeron *et al*., 2002) varies spatially throughout the circum-boreal forest yet fire has become much less frequent in the boreal forests of Canada, Fennoscandia and Russia in the recent past (Wallenius, 2011). This lack of modern day natural fire has been attributed both to climate variability (Carcaillet *et al.*, 2007) and more commonly, to anthropogenic fire suppression e.g. (Zackrisson, 1977; Niklasson & Drakenberg, 2001). However, Wallenius (2011) suggests that the observed reduction in fire frequency is a combination of a decline in human induced ignitions and active fire suppression. This is most likely as the perceived decline in fire frequency is usually calculated by comparing modern, observed fire frequency to historical fire frequency derived from dendrochronological fire scar records. These fire scar records are temporally limited in that they only record the recent past of up to 600 years (Wallenius *et al.*, 2007) yet more commonly only a few hundred years, a time when anthropogenically induced fires were at their peak (Wallenius, 2011). Although humans have been present in the boreal zone for the entire Holocene (Bergman *et al.*, 2004) their use of fire has not always been so prevalent (Marlon *et al.*, 2013). By looking a little further back in time, at the semi-natural fire frequency prior to significant human disturbance, it becomes clear that fire was not always so frequent in the boreal forest (Clear *et al.*, 2013). It is these natural and anthropogenic induced variations in fire frequency that may cause local-scale variations in vegetation composition.

The current vegetation of Fennoscandia, although somewhat modified by the forestry industry in the last ca.100 years, is primarily a product of post-glacial vegetation development. Fennoscandian forest composition and structure has experienced some distributional variation in treeline limits and deciduous tree limits driven by climate fluctuations throughout the Holocene (Huntley, 1990). However, *Picea abies*, a now co-dominant species throughout Fennoscandia with *Pinus sylvestris,* was a late addition to the northern European boreal forest. *Picea* spread in a wave like distribution from east-west across Fennoscandia arriving in Finland 5,500 cal. yrs. BP; spreading south through Sweden and Norway thousands of years after all other boreal species had established (Giesecke & Bennett, 2004) and may still be spreading (Bradshaw *et al*., 2000). The limiting factors or controls on the changing distribution and abundance of *Picea abies* in Fennoscandia during the Holocene are still not completely understood and previously modelled bioclimate limitations it appears do not explain Holocene variations in *Picea* distribution, suggesting other restrictions (Miller *et al.*, 2008).

Picea establishment has often been linked to local-scale disturbance e.g. (Molinari *et al.*, 2005; Bjune *et al.*, 2009a) and commonly fire disturbance that creates favourable conditions for *Picea* to establish. However, once established *Picea* creates a forest micro-climate characterised by dark, damp environmental conditions that inhibits natural fire ignition (Tanskanen *et al.*, 2005) with *Pinus* dominated forest known to burn more frequently. Yet, if successful fire ignition occurs, *Picea* is a fire sensitive species (Bradshaw *et al.*, 2010) with thin bark, low branches and saplings that have the potential to create fire ladders and encourage intense canopy fires (Tanskanen *et al.*, 2006). An increase in the dominance of *Picea* can alter the local fire regime (Ohlson *et al.*, 2011) to one characterised by low frequency, high intensity fires (Clear *et al.*, 2013), so the dominant vegetation type may exert a control over fire frequency somewhat independent of climate and anthropogenic disturbance. By combining quantitative palaeo-vegetation reconstruction with a process-based dynamic vegetation model (Miller *et al.*, 2008) we aim to gain insight into the interactions between fire frequency and dominant vegetation type in Fennoscandia.

8.3 Aims

In this paper we simulate varying fire frequencies using the dynamic vegetation model LPJ-GUESS (Smith *et al.*, 2001) and compare the results with palaeoecological observations of Holocene vegetation dynamics from small forest hollows to explore potential fire frequency states and controls over vegetation composition variation within the boreal zone.

8.4 Methods

8.4.1 Site

A stand-scale pollen stratigraphy (Clear *et al.*, 2013) with variable Holocene fire frequency from Vesijako Strict Nature Reserve, southern Finland (61^{o}N; 25^{o}E) in the southern boreal vegetation zone (Ahti *et al.*, 1968) was used in this data-model comparison. The mean annual temperature is 4.2^{o}C with a July mean of 16.6^{o}C and February mean of -7.1^{o}C (Pirinen *et al.*, 2012). The mean annual precipitation is 645 mm yr^{-1}. The site; a closed canopy, wet forest depression of approximately 12m^{2} was selected for its small forest hollow characteristics (Overballe-Petersen & Bradshaw, 2011) and analyzed for pollen to record local-scale (up to 3 ha) variations in vegetation dynamics (Jacobson & Bradshaw, 1981; Sugita, 1994). At present the site is currently dominated by *Picea abies* with scattered individuals of Pinus sylvestris, *Betula* and *Populus tremula*. Macroscopic charcoal records (>300µm) were used as indicators of local fire history (Ohlson & Tryterud, 2000) with fire frequency calculations derived from charcoal influx (particles cm^{-2} yr^{-1}). Field, laboratory and statistical methods are described in detail in Clear *et al*. (2013). Eight AMS radiocarbon dates obtained from the sediment are conformable and show a near linear age depth relationship calculated using the non-Bayesian Clam model (Blaauw, 2010).

8.4.2 LPJ-GUESS model

LPJ-GUESS (Smith *et al.*, 2001) is a dynamic global vegetation model that uses a forest gap model (Shugart, 1984; Prentice *et al.*, 1993; Bugmann, 2001) to simulate vegetation dynamics. Biophysical and physiological processes (Sitch *et al.*, 2003) formulated for the Lund-Potsdam-Jena dynamic global vegetation model (LPJ-DGVM) are applied. The LPJ-DGVM model uses an area-averaged representation of vegetation structure whereas LPJ-GUESS simulates vegetation as age cohorts of species that compete for light and water on 0.1 ha replicated patches. Plant functional units (Hickler *et al.*, 2004) for a number of species are simulated and bioclimatic limits (Prentice *et al.*, 1992; Sykes *et al.*, 1996) define the climate space for which vegetation may occur. Following Farquar *et al.* (1980), the model is driven by light, temperature, precipitation and modern CO_2 air content. Soil conditions modify the water uptake of the plant and CO_2 content influences the assimilation rate.

The fire module is described in Thonicke *et al.* (2010) with the modifications to adapt to the cohort mode of LPJ-GUESS given in Lehsten *et al*. (2009). Fire intensity is simulated based on the fuel load and water content. The plant damage is separated into crown fire damage and cambial damage. While the first is calculated by relating the flame height to the crown height of the individual tree age cohort, the second takes into account the species specific bark thickness in combination with the diameter of the trunk.

The model runs were based on 50 replicate patches of 0.1 ha with each experimental run spun up over 1000 years. The following species were explicitly modelled in this study: *Picea*, *Pinus*, *Betula*, *Populus*, *Tilia*, *Corylus* and *Quercus.*

8.4.3 Model forcing and fire frequency simulations

The dynamic vegetation model LPJ-GUESS was forced with (a) modern climatic conditions using the CRU climate data(http://www.cru.uea.ac.uk/cru/data/hrg.htm) for latitude 61°N and longitude 25°E and (b) the same climate data +2°C to simulate a warmer mid-Holocene climate and potential future warming scenarios. Both climate scenarios were run initially with no fire and then with varying fire frequency intervals: 10 year intervals between 10 – 100 years; 100 year intervals up to 500 years; and at a fire return interval of 1000 years. Fire occurs on day 150 of the specified year.

8.4.4 Comparing observed and simulated vegetation

LPJ-GUESS outputs leaf area index (LAI); one half of the total green leaf area per unit ground surface area (Chen & Black, 1992), which are compared with the pollen data. However, pollen productivity and dispersal vary between species and to enable comparison between the modelled LAI output and pollen data the pollen percentages were adjusted using Rpoll values, pollen values adjusted for species production and dispersal, as described in (Miller *et al.*, 2008). The low floristic diversity in Fennoscandia enables the direct association of pollen types with plant species with the exception of *Betula* that includes both *Betula pendula* and *Betula pubescence*. Both *Betula spp*. are modelled and the LAI output values aggregated for direct comparison to the adjusted Rpoll data.

8.5 Results

8.5.1 Palaeoecological data

Analysis of macroscopic charcoal (>300µm) and pollen data from Vesijako indicate Holocene variability in both fire frequency and vegetation dynamics. There are three clear fire return intervals recorded in the charcoal results: mid-low fire frequency with an average fire return interval of 180 years; low frequency fire with an average fire return interval of 430 years; and an extremely low fire frequency with a fire return interval that, at present, stands at 750 years since the last recorded fire event (Figure 8.1).

Vegetation composition and relative abundance of tree species vary with changes in fire frequency. Low frequency fire with a regularly occurring return period of approximately 430 years is associated with high tree species diversity, including significant presence of deciduous species such as *Corylus avellana*, *Tilia cordata* and *Quercus robur*. The high frequency fire regime, with an average fire return period of approximately 180 years, appears to be too frequent to sustain this abundant mixed deciduous species assemblage, with *Corylus*, *Tilia* and *Quercus* all declining during this period of most frequent fire. It is also during this frequent fire return interval of 180 years that *Picea* values fluctuate in conjunction with fire events. It appears that *Picea* is sensitive to fire as it declines in abundance during fire events but recovers after each significant fire. During the extreme low frequency fire period, with a fire return interval that is currently 750 years since the time of last fire, *Picea* values can be seen to steadily rise until *Picea* becomes the dominant species; as observed at the site at the present day. During this time of extremely low frequency fire, *Populus* and *Corylus* values increase and persist together with low values of *Quercus* and *Tilia*. However, as the time since fire increases and *Picea* dominates the site, the mixed deciduous species decline in abundance with reductions in both present day *Corylus* and *Populus*.

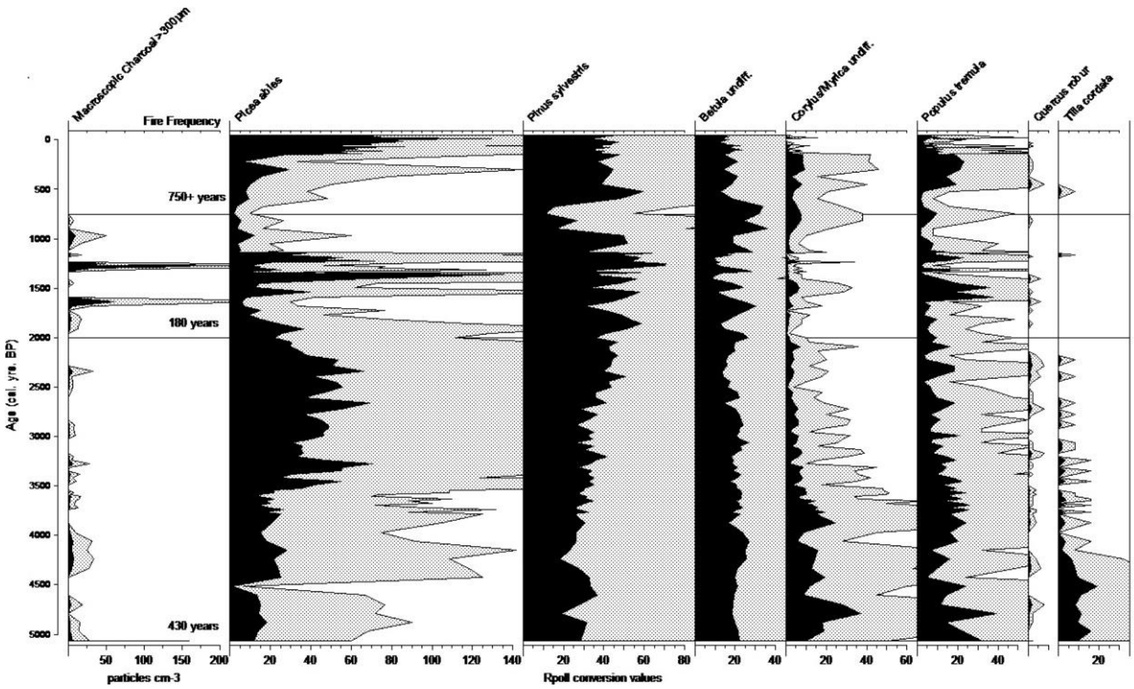


Figure 8.1: Palaeoecological reconstruction of fire and vegetation history for selected species at Vesijako Strict Nature Reserve, Finland. Charcoal is expressed as particles cm^{-3} and pollen percentages converted to R^{poll} values after (Miller *et al.*, 2008).

8.5.2 LPJ-GUESS simulated model data

8.5.2.1 Modern climate scenario

Pinus and *Picea* dominate the simulated outputs with a small presence of mixed deciduous species; *Betula*, *Corylus*, *Quercus*, *Tilia* and *Populus*. The deciduous species' LAI values were combined and plotted as the total sum of deciduous species (Figure 8.2). The highest fire frequency scenarios of 10 and 20 year fire return intervals return a *Pinus* dominated vegetation type with both *Picea* and deciduous species initially establishing before disappearing once fire begins. Fire is too frequent for anything to thrive other than *Pinus*. The modelled fire frequency of 30 years allows some *Picea* establishment and presence for 300 years before *Picea* is outcompeted by *Pinus* due to the recurrent high fire frequency. A fire frequency of 40 years results in a vegetation composition that allows *Picea* to become a co-dominant species with *Pinus* for approximately 100 years before *Pinus* becomes dominant with a subordinate role for *Picea*. With a simulated fire frequency of 50 years, *Picea* becomes a competitive co-dominant species with *Pinus*. The modelled fire frequencies of between 60 – 90 years initially generate an unstable vegetation composition for approximately 300 years with *Picea* and *Pinus* competing for dominance. It is only after this initial period that *Picea* becomes the dominant tree species. Modelled fire frequencies of between 100 and 1000 years return a vegetation composition with *Picea* dominance throughout. *Pinus* initially establishes during these low fire frequency events, but as the time since fire elapses and *Picea* remains dominant, *Pinus* values decline.

The change in relative abundance between *Pinus* and *Picea* (Figure 8.3) clearly indicate the association of *Picea* with longer fire frequency scenarios. Throughout the modern day climate simulations the deciduous species manage to establish prior to the first fire event (Figure 8.2) however they decline irrespective of the fire frequency as *Pinus* and *Picea* outcompete the deciduous species and become the dominant species under high fire frequency and low fire frequency regimes respectively.

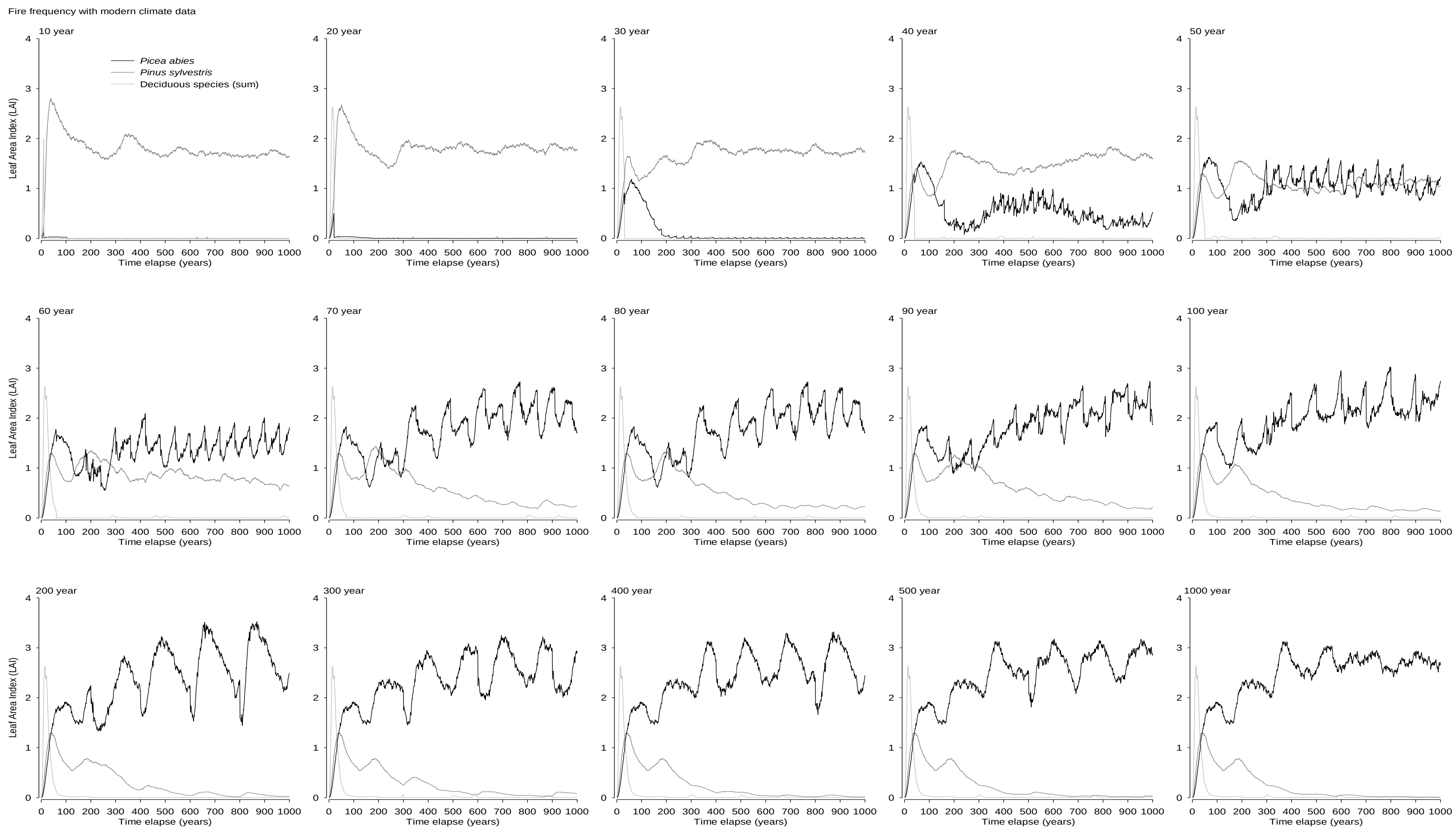
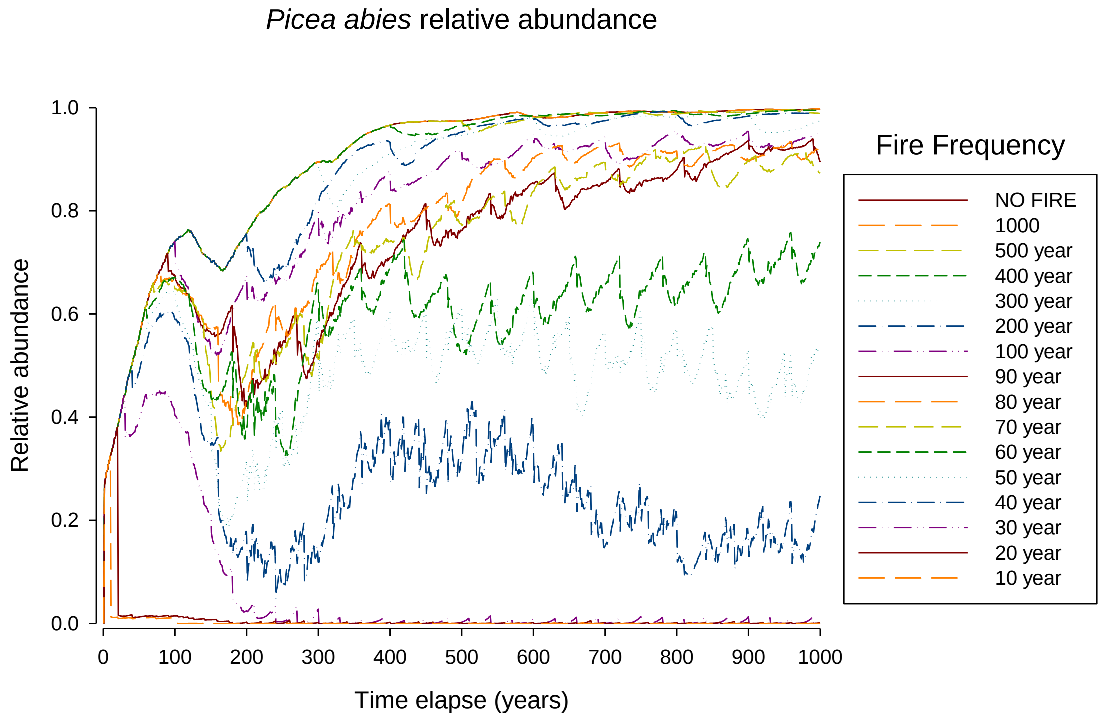


Figure 8.2: Modelled fire frequency vegetation curves for *Picea abies, Pinus sylvestris* and total sum of deciduous species for 15 fire frequency scenarios with modern climate simulated. Vegetation is expressed as Leaf Area Index (LAI)

a)



b)

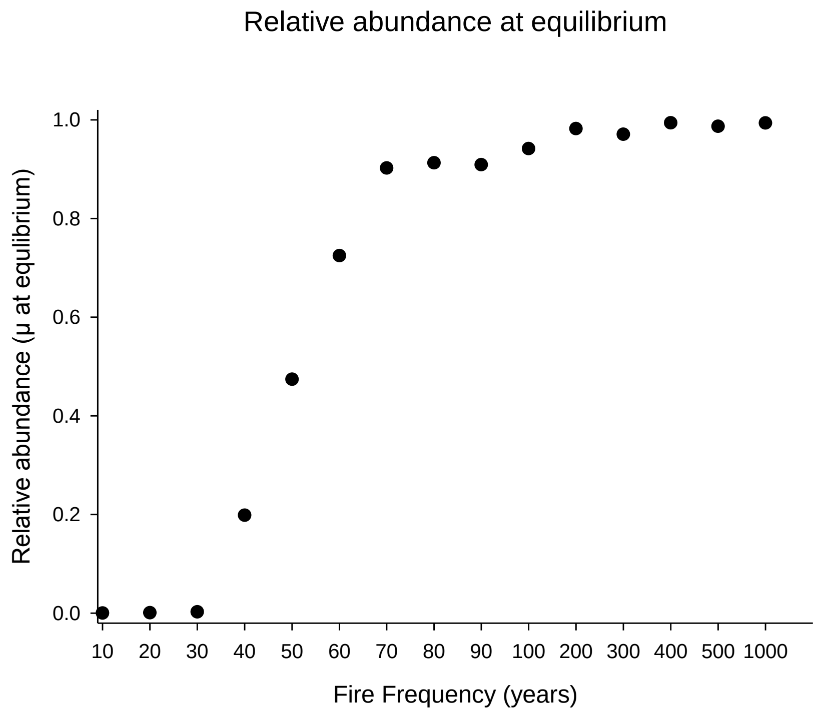


Figure 8.3: Relative abundance of *Picea abies* to *Pinus sylvestris* (a) for all fire frequency scenarios under modern climate conditions and (b) at equilibrium

8.5.2.2 Climate forcing of +2^{o}C

The vegetation composition output for the +2^{o}C climate forcing is comparable to the vegetation output for the present day climate runs for both *Pinus* and *Picea* establishment and dominance. *Pinus* remains the dominant species during high frequency fire events of up to 40 year intervals, with *Picea* first becoming co-dominant before becoming the dominant species once the fire frequency is set at 50 year intervals or longer (Figure 8.4).

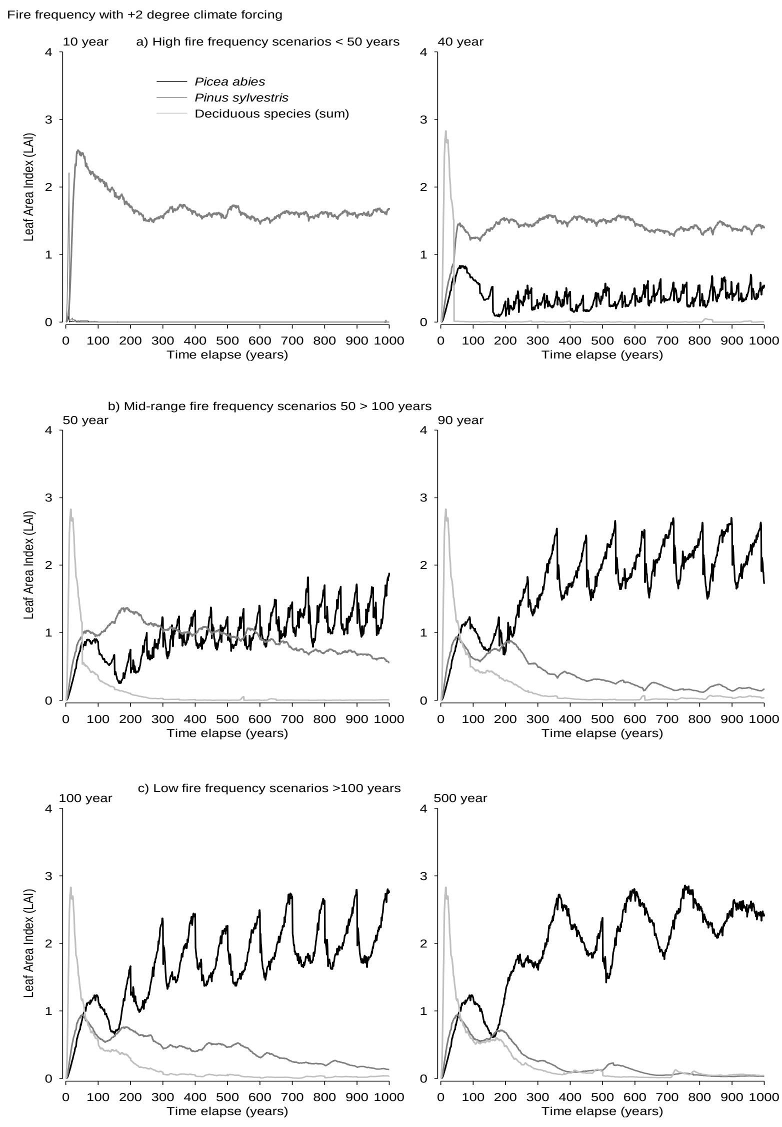


Figure 8.4: Modelled fire frequency vegetation curves for *Picea abies, Pinus sylvestris* and total sum of deciduous species for six fire frequency scenarios under +2^{o}C climate forcing conditions. Fire frequency is categorised into (a) high fire frequency, (b) mid-range fire frequency and (c) low fire frequency with vegetation expressed as Leaf Area Index (LAI)

However, the deciduous vegetation composition is more substantial and is increased under +2^{o}C climate scenario compared to modern day climate. There is still a distinct fire frequency control over the abundance of deciduous species (Figure 8.5). For high fire frequency scenarios of between 10 – 40 years the fire intervals are too frequent for the established deciduous population to survive in abundance. Fire frequencies of between 50 – 90 years permit establishment of deciduous populations and survival for longer periods however, it is only during fire frequencies of 100 year intervals or longer that deciduous tree species are able to remain established and able to thrive. This is particularly the case for modelled fire frequencies of 500 years of more where between 20 – 70% of overall deciduous abundance are estimated for fire frequency intervals of longer than 500 years (Figure 8.5).

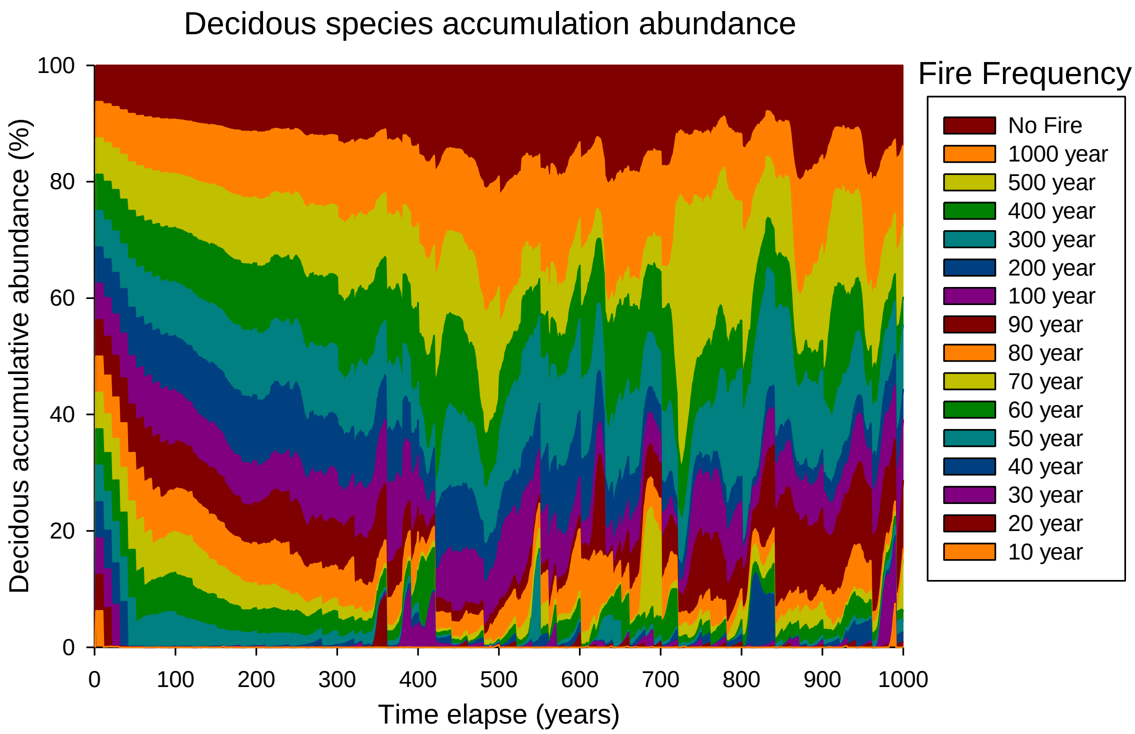


Figure 8.5: Modelled deciduous species accumulation abundance with climate forcing of +2^{o}C for all fire frequency scenarios

8.6 Discussion

8.6.1 Fire frequency as a driver of dominant vegetation type

The southern boreal forest of Fennoscandia is structurally a relatively simple mixed forest (Seppä *et al.*, 2009a) with two dominating conifer species, *Picea abies and Pinus sylvestris* and this is reflected by the modelled vegetation output. Under both model climate scenarios; (a) modern climate and (b) modern climate +2^{o}C, the relative abundances of *Pinus* and *Picea* are controlled by variations in the fire frequency. *Pinus sylvestris* dominates the modelled vegetation output when fire frequencies are simulated at 40 year intervals or less. *Pinus* is moderately fire resistant and able to survive low intensity fires (Granstrom, 2001) this is demonstrated by *P. sylvsetris* thriving during these high fire frequency scenarios. *Picea abies* is initially able to establish but fails to survive once the higher fire frequencies are implemented in the model. *Picea* is a fire sensitive species (Bradshaw *et al.*, 2010) with saplings particularly highly susceptible to fire (Tanskanen *et al.*, 2006). Fire intervals of 30 year or less are simply too frequent to enable *Picea* to continually re-establish and survive. It is only once the fire frequency is modelled at 40 year intervals or longer that *Picea* is able to reach maturity and maintain an underlying presence while *Pinus* remains the dominant species type. These high fire frequency scenarios and the absence or persistently low presence of *Picea* are not observed in the palaeo-data, with the highest fire frequency recorded being approximately 180 years.

In the model output *Picea* is able to compete with *Pinus* once the fire frequency interval is 50 years or longer. Initially the species co-dominate before a shift is observed to *Picea* dominance with an underlying presence of *Pinus*. These mid-range fire frequencies favour *Picea* by enabling saplings to reach maturity and allowing *Picea* to regenerate prior to the next fire event (Liu & Hytteborn, 1991). These highly variable *Picea* fluctuations associated with the intermittent fire frequency are observed in the palaeo-data during the 180 year fire frequency intervals and confirm *Picea* sensitivity to fire and its ability to successfully regenerate under mid-frequency disturbance regimes.

During low fire frequency scenarios of 100 year intervals or longer *Picea abies* becomes the dominant tree species. This creates a closed canopy that inhibits the development and success of other, particularly light-dependant, species including *Pinus* (Liu & Hytteborn, 1991). As the time since the last fire elapses, *Picea* is able to maintain dominance; this is evident in both the model data output and the palaeo-data. The dominance of *Picea* under low fire frequency conditions has the ability to create a positive feedback that maintains a reduced fire frequency and further encourages the dominance of *Picea* (Clear *et al*., 2013).

8.6.2 Fire frequency impact on deciduous species distribution and abundance

The distribution and abundance of deciduous species within the mixed hemiboreal forest (Ahti *et al*., 1968; Esseen *et al.*, 1997), located at the transitional zone between the species rich temperate forest and conifer dominated boreal forest, has been predominantly attributed to climate change (Miller *et al.*, 2008). The climatic influence over deciduous species distribution is also here observed in output from a generalized dynamic vegetation model and palaeoecological data, but it appears to be moderated by fire frequency.

The palaeoecological site, located within the southern boreal vegetation zone (Esseen *et al.*, 1997), is situated just outside the present day abundant deciduous species distribution within the hemiboreal and temperate forest. Under the modern climate scenario, the model output does not identify any variability in deciduous species abundance regardless of the simulated fire frequency. This lack of deciduous abundance is also observed in the vegetation composition of the palaeo-data during the modern day and recent past.

When the model is applied with climate forcing of +2^{o}C the deciduous species abundance increases. However, this increase is not uniform throughout the range of implemented fire frequencies. High fire frequencies of between 10 – 90 year intervals inhibit the success of deciduous species. It is only when the fire frequency interval is set at 100 years or longer that the deciduous trees are able to survive beyond initial establishment. The deciduous species are further able to thrive once the fire frequency interval is 500 years or longer. Fire is not a common natural disturbance event in deciduous forests (Fischer *et al.*, 2013) and in general deciduous trees are not as flammable as conifers and they are not capable of supporting crown fires (Parviainen, 1996). Their susceptibility to fire varies seasonally depending on leaf moisture (Päätalo, 1998). Any increase in deciduous species can create a positive feedback that would further reduce the natural fire frequency (Girardin *et al.*, 2013) not dissimilar to the positive feedbacks linked to *Picea abies* dominance.

In the observed palaeo-data the most abundant presence of deciduous species is associated with a low fire frequency of approximately 430 years, with the deciduous presence declining once the fire frequency increased to approximately 180 years. This is reflected in the +2^{o}C model output where the deciduous species abundance is low during high fire frequency scenarios and becomes more abundant during lower fire frequency intervals, indicating that fire frequency has a significant control over abundance of deciduous species, operating independent of climate. This combined influence of climate and fire frequency as a control over deciduous species abundance aids interpretation of the palaeo-data. Once the high fire frequency of approximately 180 years switches to an extremely low fire frequency with fire return intervals of 750 years onwards, the deciduous vegetation abundance remains low, even though the +2^{o}C climate forced model output indicates that this fire frequency would be within the optimal range to promote deciduous abundance. During the mid-Holocene, when the fire frequency was low and deciduous trees were more abundant, the climate was warmer than the present day (Seppä & Birks, 2001). Even though the fire frequency is now optimal to promote deciduous abundance, the modern day cooler climate inhibits the expansion of deciduous species as observed between the two varying temperature model runs. The temperature increase of 2^{o}C is required to model the palaeo-observed deciduous species abundance during the mid-Holocene.

8.6.3 Modelling fire frequency to understand vegetation dynamics

Comparison of model data output with quantitative palaeoecological data indicates that climate factors alone are unlikely to account for observed vegetation dynamics in the southern boreal forest of Fennoscandia. Variations in fire frequency can control vegetation dynamics independent of climate yet there are mechanistic climatic feedbacks to consider that exert a control over fire frequency. Natural fire ignition, through lightning, relies on an optimal set of climate conditions associated with temperature and precipitation to enable a successful ignition (Larjavaara *et al.*, 2005) and furthermore factors associated with current weather, such as precipitation and wind direction, help determine the fires ability to successfully burn (Pyne *et al*. 1996). However fire is not exclusively controlled by climate with other biogeochemical processes such as slope, aspect, vegetation type as well as anthropogenic structures e.g. roads or natural firebreaks (Parviainen, 1996) influencing fire. Both the model output and palaeo-data also suggest fire frequency has some independence from climate in terms of control over vegetation.

There appear to be fire frequency states independent of climate that determine the dominant vegetation type in northern European forest. A fire frequency state of ≤40 years is required to maintain a *Pinus sylvestris* dominated forest stand with a fire frequency of up to 100 years able to maintain a mixed co-dominant *Pinus* – *Picea* stand. Once the fire frequency is in excess of 100 years, *Picea abies* becomes progressively more dominant during these longer fire frequency intervals. This suggests that under the current low frequency fire regimes observed in Fennoscandia, *Picea* dominance is favoured and if the current fire regime persists then *Picea* may gradually become even more dominant in the landscape. There are also feedbacks to consider that if *Picea* remains dominant under the current low fire frequency scenario then the forest microclimate conditions created by *Picea* make natural fire ignition difficult (Tanskanen *et al.*, 2006), which in turn promotes more extreme low fire frequencies thus further encouraging *Picea* dominance. Likewise, if local temperature were to increase by say 2^{o}C, allowing for an increase in abundance of deciduous species, a positive feedback would further encourage a low fire frequency to persist, even in the event of future warming scenarios.

Climate alone cannot account for the absence or low abundance of *Picea abies* in Fennoscandia during the early to mid-Holocene (Miller *et al.*, 2008) suggesting another, more local control on the distribution. It has been demonstrated in both the model output and palaeo-data that a reduction in fire frequency favours *Picea* establishment and survival. However the wave like spread of *Picea* across Fennoscandia (Giesecke & Bennett, 2004) suggests that it was *Picea* establishment that controlled the fire frequency rather than the fire frequency controlling *Picea* abundance (Clear *et al*., submitted; Ohlson *et al.*, 2011). In the way we used the model we excluded any possible feedback mechanism of *Picea* to control fire frequency since we prescribed the fires. Fire scar records from dendrochronological data frequently record high fire frequencies of between 20 – 50 year intervals (Niklasson & Drakenberg, 2001; Hellberg *et al.*, 2004; Groven & Niklasson, 2005; Wallenius *et al.*, 2007) and rarely record fire frequencies of 100 years or beyond (Zackrisson, 1977; Wallenius, 2002). These high fire frequencies do not always correlate with charcoal records with the assumption that charcoal is less accurate in recording fire by not recording every, particularly low intensity, fire event (Higuera *et al.*, 2005). This is true, as it is impossible to identify fire events at intervals less than the palaeoecological resolution and requires higher chronological precision. However, *Pinus sylvestris* is most commonly used to obtain fire scar records and with the new understanding that *Pinus* abundance is encouraged by high fire frequencies, we can potentially explain why fire scars commonly record high frequency fire regimes but more importantly often fail to recognise low frequency fire regimes. Results suggest fire scars frequently record fire frequency history from *Pinus* dominated stands or, less commonly, from mixed stands yet fail to incorporate fire regimes from *Picea* dominated stands, which introduces bias to views of the fire frequency history in Fennoscandia.

Chapter 9

9 Discussion

9.1 Natural and anthropogenic drivers of Holocene vegetation dynamics

9.1.1 Post-glacial forest development

Early-Holocene warming and the melting of the Weichselian ice sheet (Lundqvist, 1986) led to the progressive development of vegetation in Fennoscandia (Huntley, 1990). Initial tundra vegetation formed, dominated by herbs, grasses and sedges before *Betula* stand development with intermittent phases of *Pinus-Betula* forest (Björck & Möller, 1987). This early-Holocene forest development and vegetation dynamics was driven by gradual climate warming (Huntley, 1990) and is evident in both the Sudenpesä stand-scale pollen record as well as the regional landscape (LRA) quantitative vegetation reconstructions (Chapter 6). Between approximately 8800 and 7800 cal. yrs. BP the rise in *Betula* and decline in *Pinus* and *Alnus* correlates to the early-Holocene climate anomaly or '8200 cal. yrs. BP event' (Tinner & Lotter, 2001; Seppä *et al*., 2007). Variations in the North Atlantic Oscillation (NAO) driven by changes in the oceanic circulations (THC) caused temporary cooling and potential ice sheet re-advance in Europe (e.g. Nesje *et al*., 2001; Kerschner *et al*., 2006). After this intermittent cold period, the climate experienced abrupt high-magnitude warming of about 2˚C in less than 50 years (Veski *et al*., 2004) and natural forest dynamics drove vegetation composition. The early successional development of pioneering species such as *Alnus* and *Corylus* is observed in the cross correlation analysis (Chapter 5). Minimal anthropogenic disturbance consisting of a basic 'hunter and gatherer' lifestyle comprising of fishing and hunting (Sarmela, 1987) and low population levels suggest early-Holocene forest development was driven by natural forest dynamics and climate variability.

9.1.2 Picea abies: the rise of the boreal ecosystem

The absence of *Picea abies* in the early-Holocene post glacial forest development is poorly understood (Bradshaw, 2000). However *Picea* is present at low-levels in southern Finnish pollen records (e.g. Vasari, 1962; Tolonen, K. 1967, 1983b; Tolonen, M. 1980) as well as in Sudenpesä (Chapter 6) prior to 9000 cal. yrs. BP and *Picea* macrofossils, dating to approximately 10000 cal. yrs. BP have been found in the Scandes mountain range, Sweden (Kullman 2000; 2001). After this initial establishment, *Picea* then disappears during the early-Holocene cooling climate anomaly (e.g. Seppä *et al*., 2007) before re-establishing after 8000 cal. yrs. BP. The early semi-continuous curve or tail of low-abundance presence of *Picea* is apparent in Sudenpesä pollen record as well as in the regional LRA vegetation reconstruction (Chapter 6) and is commonly recorded throughout Fennoscandia (Giesecke & Bennett, 2004 and references within). Yet this long tail of low-level presence indicates a factor or process that restricts the ability of *Picea* to fully establish and thrive.

The local establishment of *Picea* is often associated with disturbance dynamics, most commonly natural or anthropogenic fire disturbance (e.g. Molinari *et al*., 2005; Bjune et al., 2009a). Yet the absence of fire during the establishment of *Picea* in Sudenpesä (Chapter 6) and the failure of *Picea* to thrive once fire returns to the site suggests a controlling factor other than a lack of local disturbance.

A rise in the continuous curve in *Picea* abundance is recorded throughout southern Finland approximately 6000 – 5000 cal. yrs. BP. This timing is seen in Vesijako (Chapter 5) and observed in Sudenpesä (Chapter 6) as well as in the regional LRA reconstruction (Chapter 6) and within local and regional pollen diagrams (e.g. Tolonen, M. 1980; Sarmaja-Korjonen, 1998; Jauhiainen *et al*., 2004). *Picea* spread in a wave-like distribution across Fennoscandia (Giesecke & Bennett, 2004; Seppä *et al*., 2009a) beginning in south-eastern Finland approximately 6000 cal. yrs. BP. *Picea* is a continental tree with high summer temperature requirements and maximum mean coldest month temperature requirement of -1.5˚C (Giesecke, 2004). At high latitudes and altitudes temperature is a limiting factor and at low latitudes precipitation has a strong effect on distribution (Giesecke, 2004). The continentality index calculated in Giesecke *et al*., (2008) estimates an increase in continentality recorded between 7000 and 2000 cal. yrs. BP, peaking at 2000 cal. yrs. BP and coinciding with peaks in *Picea* in Vesijako (Chapter 5) Sudenpesä (Chapter 6) and in the regional LRA vegetation reconstruction (Chapter 6). This suggests that the initial rise in abundance and expansion of *Picea abies* in southern Finland abundance may be controlled by climate variability and more specifically continentality. The early low presence of *Picea* during the early-Holocene warming period and subsequent decline during the 8200 cal. yrs. BP cooling anomaly and subsequent re-establishment during warming supports climate as a controlling factor behind the late establishment of *Picea abies*. Further validation of climate as a controller of *Picea* is the macrofossils founds in the Scandes mountains that date to approximately 10000 cal. yrs. BP (Kullman 2000; 2001). A further controlling factor on the distribution of *Picea abies* are the ecological processes associated with seed production, dispersal and germination. Although seeds are readily dispersed over large distances (Giesecke, 2004), seed production varies from year to year (Luomajoki, 1993) and seed germination is correlated to annual precipitation with seed survival dependent on the substrate of the seedbed (Ohlson & Zackrisson, 1992). *Picea* spread at a maximum rate of 250 m yr^{-1} (Bialozyt *et al*., 2012) east to west across Fennoscandia (Tallintire, 1972; Giesecke & Bennett, 2004; Seppä *et al*., 2009a) and south towards its present day limits where it may still be spreading in southern Sweden (Bradshaw, 2007). However *Picea* is at or near to its southern ecological limit and this distributional limit is now mostly anthropogenic driven and it is planted beyond its current climatic range (Bradshaw *et al*., 2000). In a model study by Miller *et al*., (2008) restrictions other than bio-climatic limitations are thought to drive the Holocene distribution of *Picea abies*. The local establishment of *Picea* is often linked to anthropogenic disturbance in southern Scandinavia (e.g. Hannon *et al*., 2010; Lindbladh *et al*., 2003) and humans cannot be ruled out as a facilitating factor in the spread of *Picea* even in southern Finland. Major population growth during the period of high summer temperature and high productivity of terrestrial, lacustrine and marine ecosystems occurred during 7500-5700 cal. yrs. BP

(Tallavaara & Seppä, 2011) however there is little evidence for swidden slash and burn cultivation during this time. Further, the first anthropogenic indicators: *Artemisia*, *Chenopodium*, *Ranunculus* and *Rumex* are recorded in Vesijako (Chapter 5) just prior to 3500 cal. yrs. BP, and correspond to the 10% curve of *Picea*. There is no evidence of human disturbance prior to this time. It remains that the initial rise *Picea abies* and the expansion of the present day boreal ecosystem, at least in southern Finland is predominantly climatically driven.

9.1.3 The decline in deciduous species

During the mid-Holocene approximately 8000 – 4800 cal. yrs. BP, climate was warm and stable (Korhola *et al*., 2002; Seppä *et al*., 2009b) and based on pollen-vegetation reconstructions throughout Fennoscandia (e.g. Jauhiainen *et al*., 2004; Giesecke, 2005) the hemi- and southern boreal forests comprised mixed diverse deciduous-coniferous forest with a high presence of deciduous species e.g. *Alnus*, *Corylus*, *Quercus*, *Salix*, *Tilia* and *Ulmus* (Chapter 5 & 6). The subsequent trend to a cooler wetter environment and decrease in summer temperatures (Seppä & Birks, 2001; Seppä *et al*., 2009b) may account for the mid to late-Holocene decline in deciduous species (e.g. Greisman & Gaillard, 2009) and rise of the present day boreal ecosystem. However the decline in deciduous species throughout Fennoscandia has been attributed to species competition, most notably the late-Holocene immigration of *Picea abies* (e.g. Bradshaw & Hannon, 1992; Hörnberg *et al*., 2011; Seppä *et al*., 2009a) as well as to intensified anthropogenic disturbance (Lindbladh & Bradshaw, 1998; Hannon *et al*., 2000; Sarmaja-Korjonen *et al*., 2003) and particularly the human use of fire (Lindbladh *et al*., 2003).

In southern Finland the local decline in deciduous species corresponds to an increase in fire frequency that occurred in Vesijako approximately 2200 cal. yrs. BP (Chapter 5) and in Sudenpesä approximately 3600 cal. yrs. BP (Chapter 6). These sites are located <18km apart yet there is 1600 years difference in the timing of the deciduous decline suggesting factors other than climate as a control over the decline in deciduous species. Between 4000 and 2000 cal. yrs. BP, permanent agriculture became established and human impact most likely became the main driver of forest compositional change (Reitalu *et al*., 2013). This permanent agriculture coupled with selected swidden cultivation of deciduous species (Parviainen, 1996) suggests human impact as the main driver behind the decline in deciduous species in southern Finland.

When modelling fire frequency effect on deciduous species (Chapter 8) it is clear that climate does exert a control over deciduous distribution abundance with both the modern palaeo-data and model output lacking substantial deciduous species presence. However, when a forced temperature increase of 2˚C is applied, the deciduous species abundance increases, thus supporting as expected a climatic control over deciduous abundance. However, the observed increase in deciduous abundance is not uniform during the different fire frequency scenarios with deciduous species most abundant when fire frequency is greater than 500 year intervals and becoming less abundant as fire becomes more frequent, as observed in the palaeo-data at Sudenpesä and Vesijako (Chapter 5 & 6).

The importance in understanding the controls behind the mid-Holocene decline in deciduous species is that human impact may have caused or contributed to the decline in floristic diversity in the southern boreal forest. The decrease in palynological richness in Vesijako recorded between 2200 – 2000 cal. yrs. BP (Chapter 5) coincides with the local decline in deciduous species and shift in forest composition from a diverse mixed deciduous and coniferous forest stand to a forest stand dominated by *Betula* and *Pinus*. Without this intensified human interference, the previously high biodiversity in the stand may have remained until the present day. Furthermore the decline in deciduous species corresponding to an increase in fire frequency occurring simultaneously in both Vesijako and Sudenpesä (Chapter 5 & 6) suggests increased anthropogenic disturbance is the primary reason for the decline in deciduous species and loss of floristic diversity in southern Finland. If this is correct, then the modern pollen-climate calibration sets combined with fossil pollen data to produce a pollen-climate transfer function (e.g. Seppä *et al*., 2009b; Bjune *et al*., 2010) have to be interpreted with caution. It can be assumed that the presences of deciduous species imply a warmer climate however the absence of such species cannot be used to quantify a trend to a cooler, wetter environment post- Holocene Thermal Maximum (HTM). Further, under future climate warming scenarios and present low fire frequencies, deciduous species can be expected to expand in southern Fennoscandia.

9.2 Spatial and temporal fire variability in Fennoscandia

It is clear that fire regime; notably fire frequency, fire size and fire severity varies spatially throughout the circum-boreal forest with the Canadian and Russia Boreal forest burning more frequently and more severely than their Fennoscandian counterparts (Bergeron *et al*., 2002). Yet fire also varies temporally, and with efforts from the Global Charcoal Database (Power *et al*., 2008; 2009; Marlon *et al*., 2013) and regional fire synthesis papers (e.g. Vannière *et al*., 2011; Molinari *et al*., 2013) also (chapter 7) we can begin to quantify spatial and temporal variability in biomass burning.

9.2.1 Natural early-Holocene fire frequency

Fire requires fuel, heat and a source of ignition with sedimentary charcoal records recorded from as early as the Silurian approximately 420 Ma (Scott & Jones, 1994; Scott, 2000; Scott *et al*., 2006). The lack of early-Holocene fire in Sudenpesä (Chapter 6) and observed in the fire maps (Chapter 7) suggests fuel availability as the main driver of early-Holocene fire variability.

The 'natural' fire frequency observed in the southern boreal forest in Finland is approximately 400 year intervals and is recorded in both Sudenpesä during the early-mid Holocene (Chapter 6) and in Vesijako during the mid-Holocene (Chapter 5). These fires are considered to be low frequency, low intensity non-stand replacing fires as inferred from the corresponding pollen records. This reduction in charcoal frequency and abundance when compared to more modern (mid-late Holocene) records could be perceived as a result of charcoal degradation over time

(Kasin *et al*., 2013), however in Sudenpesä, between 1200 and 108 cal. yrs. BP the charcoal signal returns to the 'natural' fire frequency recording 370 year intervals after intensified anthropogenic disturbance.

9.2.2 Mid-Holocene fire regimes: climate, fuel and anthropogenic disturbance

The mid-Holocene Thermal Maximum (HTM) between approximately 8000 and 4800 cal. yrs. BP (e.g. Rosén *et al*., 2001; Seppä & Birks, 2001; Korhola *et al*., 2002; Davis *et al*., 2003) is well documented throughout Fennoscandia and characterised by warm, dry climatic conditions. This corresponds to an increase in biomass burning in central Fennoscandia (Chapter 7) but applies only to sites in Sweden and not sites in Finland further suggesting increased continentality as a driver of mid-Holocene fire in Sweden (Giesecke *et al*., 2008). A corresponding decline in fire in Finland between 7800 and 5500 cal. yrs. BP (Chapter 7) could also have climatic explanation with a shift to cooler, wetter conditions between 6000 and 5500 cal. yrs. BP (Seppä & Birks, 2001). However this decline in fire corresponds to the timing of the rise and spread of northwards trajectory of *Picea abies* from southern to northern Finland between approximately 6000 and 5000 cal. yrs. BP (Giesecke & Bennett, 2004; Ohlson *et al*., 2011). The link between fire and the spread of *Picea* becomes further evident between 5500 and 3000 cal. yrs. BP where the continuous curve of *Picea* pollen corresponds to a decline in fire in Swedish sites (Chapter 7). Again this could also be linked to climate, yet the step-wise decline in fire suggests a driving mechanism other than a regional decline in climate variability and is most likely the spread of *Picea abies*.

Between 3000 and 700 cal. yrs. BP there is mid-late Holocene increase in biomass burning that is evident in the fire maps (Chapter 7) with a widespread non-coherent increase in charcoal indicative of local-scale fire control, most likely human disturbance. This corresponds to the increased fire frequency in Vesijako with a fire interval of 180 years between 2000 and 750 cal. yrs. BP (Chapter 5) and in Sudenpesä with a fire frequency of 185 years between 3600 and 1600 cal. yrs. BP (Chapter 6). During this time, permanent agriculture was established and human impact is estimated as the strongest driver of forest compositional change (Reitalu *et al.*, 2013). According to the results in Chapter 7, human impact is also the strongest driver of fire frequency during this time. Furthermore, this intensified anthropogenic disturbance masks the influence of climate and *Picea* making the mid-Holocene drivers of fire difficult to disentangle.

9.2.3 Late-Holocene decline in fire

A late-Holocene decline in fire in Fennoscandia is most commonly attributed to human induced fire suppression (e.g. Zackrisson, 1977; Niklasson & Drakenberg, 2001) based on the knowledge that fire has not always been so rare with fire scars recording significantly more intensive fire regimes in the recent past (e.g. Niklasson & Granström, 2000). Yet the timing of fire suppression across Fennoscandia varies. In Vesijako (Chapter 5) the time since last fire is approximately 750 years, substantially longer than regional fire suppression and most possibly a result of intensified land use and the expansion of permanent arable cultivation during the medieval warm period (MWP) between approximately 1000 and 800 cal. yrs. BP (Tavitsainen *et al.*, 1998). In Sudenpesä a reduction in the fire frequency occurs at approximately 1600 cal. yrs. BP however the forest continues to burn with the last recorded fire approximately 108 years ago. This corresponds with the general timing of fire suppression in southern Finland however the fire frequency (between 1600 and 108 cal. yrs. BP) was approximately 370 year intervals and the time since last fire is well within the current fire frequency period. The decline in fire frequency observed around 1600 cal. yrs. BP is possibly the result of a shift in slash and burn cultivation from 'Lehtipuukaski' or deciduous clearance to 'Huuhtakaski' coniferous clearance that was most prolific from 1500 cal. yrs. BP (Sarmela, 1987; Parviainen, 1996). The sustained increase in biomass burning as a result of intensified anthropogenic disturbance, recorded from approximately 3000 cal. yrs. BP (Chapter 7) peaked at approximately 300 cal. yrs. BP with a clear divide in the timing of fire suppression.

A pre-industrial decline in fire in Sweden, Denmark and Norway is associated with an economic and cultural transition from traditional livelihoods to modern agriculture and commercial forestry (Granström & Niklasson, 2008; Wallenius, 2011) with a later decline in fire in Finland and Russia suggesting a later economic shift approximately 100 cal. yrs. BP where traditional livelihoods were important until 20th century industrialisation (Taavitsainen, *et al*., 1998). It is proposed, not that fire suppression occurred earlier in the southern and western regions of Fennoscandia, but that there was a lifestyle change that resulted in a reduction in the number of human induced ignitions (Wallenius, 2011). The 'human influence hypothesis' (Wallenius, 2011) suggests that the majority of previous fires were caused by human ignitions and therefore any observed reduction in fire would be a direct result of a decrease in human induced fires.

The anthropogenically induced increase in biomass burning during the mid-Holocene created an artificially high record of fire that surpassed the natural signal and created a false perception of naturally high fire frequency that is commonly observed in fire scar records. Yet there are two issues: (1) fire scars are temporally limited to the past 600 years (Wallenius, 2011) and while they are excellent at documenting human fire activity they only view the time of most significant anthropogenic impact; and (2) fire scars are most commonly recorded in *Pinus* trees, yet the dominance of *Pinus* within a forest stand is promoted by frequent fire activity (Chapter 8). Fire scars often record past fire frequencies of 20-50 year intervals (e.g. Niklasson & Drakenberg, 2001; Hellberg *et al*., 2004; Groven & Niklasson, 2005; Wallenius *et al*., 2007) and rarely record fire frequencies of 100 years or beyond (Zackrisson, 1977; Wallenius, 2002). But through looking a little further back in time at the semi-natural fire frequency prior to significant human disturbance, it becomes clear that fire was not always so frequent in the boreal forest of Fennoscandia (Chapter 5, 6 and 7). However, it should also be considered that the charcoal record may underestimate the 'true' fire record as in a study comparing charcoal to known fire scar records, charcoal was most accurate in recording high intensity fires and failed to record low and mid-intensity fires (Higuera *et al*., 2008).The perceived late-Holocene decline in fire is likely due to a reduction in the number of human induced ignitions (Wallenius, 2011) and also the widespread dominance a *Picea abies* (Chapter 7) yet it is considered that the current fire frequency of Fennoscandia is at present within its natural range of variability.

9.3 Fire frequency controls on vegetation dynamics

Fire is an important natural disturbance dynamic in the boreal forest and often stand-scale structure, age and composition are linked to the last major fire event (Bradshaw, 1993). When modelling fire frequency effects on vegetation (Chapter 8), fire exerts a control over vegetation dynamics independent of climate with variations in the fire frequency able to explain the dominant vegetation types observed throughout Fennoscandia. Modelled high fire frequency scenarios of less than 40 year intervals return a forest stand dominated by *Pinus sylvestris*. *Pinus* is a moderately fire resistant species and is able to survive low intensity fires (Granström, 2001). *Pinus* resilience to fire is clear in Vesijako (Chapter 5) and thrives pre- and post-fire disturbance which is evident in the cross correlation analysis. Modelled fire frequencies of between 50 and 100 years, return a co-dominant *Pinus-Picea* forest stand. During these mid-range fire frequencies *Picea* is able to compete with *Pinus* as *Picea* saplings are able to reach maturity prior to the next fire event (Liu & Hytteborn, 1991). Modelled fire frequency scenarios of more than 100 year intervals return a stand dominated by *Picea abies*. *Picea* is favoured by fire absence (Bradshaw, 1993) as it suffers lethal damage even during low fire intensity due to a superficial root system, thin bark and low branches (Heikinheimo, 1915; Cajander 1941; Wallenius, 2004). The present absence of fire is throught to have contributed to the widespread dominance of *Picea* throughout Fennoscandia (Bjune *et al*., 2009a). If fire remains absent in Vesijako (Chapter 5) then it is likely that the *Picea* population will continue to dominate in the stand. Further, *Picea* establishment has been linked to local scale fire disturbance (e.g. Molinari *et al*., 2005; Bjune *et al*., 2009a). However, if fire frequency disturbance was required for the establishment of *Picea abies* then the spread and distribution of *Picea* throughout Fennoscandia would have been on a more patchy scale, therefore it is more likely that climate and ecological limits were the driver behind the mid to late-Holocene expansion of *Picea abies* even though local disturbance may have helped facilitate this spread.

When modelling fire frequency under warmer climate scenarios (Chapter 8), there is an apparent increase in deciduous species, but only during low fire frequencies. There is an optimal threshold relating to fire frequency and fire intensity that leads to a reduction in floristic diversity (Chapter 5). As the fire frequency is currently so low in Fennoscandia, an increase in temperature may result in a northward expansion of deciduous species.

9.3.1 Vegetation-fire feedbacks

Variations in fire frequency can control vegetation dynamics independent of climate yet there are vegetation-fire feedbacks to consider that in turn exert a control over the fire frequency. *Pinus* dominated forests burn frequently (e.g. Wallenius *et al*., 2002; Tanskanen *et al*., 2005) promoting high frequency, low intensity ground fires. These low intensity fire regimes enable the preservation of fire scars (e.g. Zackrisson 1977; Niklasson & Granström, 2000) due to the low mortality rates of *Pinus* and indicate that fire scars are biased towards high frequency, low intensity fires (Wallenius, 2002) also (Chapter 8). *Picea* stands are dominated by low frequency, high intensity stand-replacing canopy fires as observed in Vesijako (Chapter 5). *Picea* has the ability to alter the local microclimate reducing fire ignition potential (Tanskanen *et al*., 2005) by increasing shadiness, moss cover and soil moisture (Ohlson *et al*., 2011) and can work as a fire break during low intensity ground fires (Tanskanen, 2007). The step-wise decline in fire during *Picea* establishment is evident throughout Fennoscandia with a decline in fire in Finland between 7800 and 5500 cal. yrs. BP and in Sweden between 5500 and 3000 cal. yrs. BP (Chapter 7). This suggests *Picea* has the ability to alter not only the local but regional fire regime from a fire-prone to a fire-free environment (Tallantire, 1972; Ohlson & Tryterud, 1999; Ohlson *et al*., 2011). However, if fire ignition occurs, *Picea* is a fire sensitive species (Bradshaw *et al*., 2010) with thin bark and low branches and saplings that create ideal fire ladders and encourage intense canopy fires (Tanskanen *et al*., 2006). In Vesijako (Chapter 5) fire frequency and intensity appear to be somewhat driven by fuel type with a shift from low intensity ground fires to high intensity stand-replacing fires. This corresponds to a change from mixed deciduous-coniferous forest to coniferous dominated forest. Modern day temperate forests burn less than their boreal forest counterparts with ground vegetation burnt at lower temperatures with less charcoal residue than when boreal canopy trees burn (Pitkanen *et al*., 1999). The underlying temperate forest species presence in Vesijako until 2000 cal. yrs. BP (Chapter 5) many have resulted in the forest burning less intensively. The present day absence or low frequency of fire at the stand-scale and throughout Fennoscandia is a result of the wide spread dominance of *Picea abies*. This decline in fire frequency was observed prior to the onset of intensified anthropogenic disturbance that created a perception of a previously natural high fire frequency (Chapter 7). Without active fire suppression in Fennoscandia the fire frequency would remain low due to the dominance of *Picea abies* (Chapter 7). The low fire frequency created by *Picea* dominance allows for the fuel to build up creating the potential for future high intensity fires at a continued low frequency. Further, during these long fire frequency intervals and under optimal climate conditions *Picea* may become progressively more dominant in the future and create a vegetation-fire regime feedback that further promotes low frequency, high intensity future fires (Chapter 5, 7 & 8). However under a warmer climate scenario (Chapter 8) if fire remains low throughout Fennoscandia then it is likely that deciduous species will expand creating a positive feedback that would further reduce the natural fire frequency (Girardin *et al*., 2013) yet promote low frequency, low intensity fires.

9.4 Implications for conservation and management policy

Heavily managed forests and active fire suppression in Fennoscandia have created an ecosystem almost free from fire (Zackrisson, 1977; Ohlson *et al*., 2001; Wallenius, 2011). The absence of fire from the landscape impacts both natural forest regeneration (Ruokolainen & Salo, 2006) and flora and fauna biodiversity (Lindbladh *et al*., 2003). In Vesijako (Chapter 5) fire has been absent from the landscape for approximately 750 years with prescribed burning advocated in the surrounding forest (Shorohova *et al*., 2008) and throughout Fennoscandia. If fire history was reconstructed in Vesiajko approximately 1000 years ago then it would be perceived that the fire frequency had changed from frequent re-occurring fire at 180 year intervals to fire absence spanning the last 750 years (Chapter 5). Anthropogenic fire signal gives an artificially high perception of the historical fire regime by diluting the natural fire signal. If we only look back at the recent past, when the fire signal was artificially high we get a biased view of the fire history. Palaeoecology is rarely considered in current forest management and conservation practice, yet long-term ecological data can help explore past fire variability to enable the support of restoration activity designed to foster biodiversity and vital ecosystem function (Willis & Birks, 2006; Jackson & Hobbs, 2009). Macroscopic charcoal views fire history on a palaeoecological perspective beyond the temporal capability of fire scars at a high spatial precision (Ohlson & Tryterud. 2000; Higuera *et al*., 2007). Only through palaeoecological knowledge of biomass burning can we understand the impacts of natural drivers of vegetation and fire dynamics (Chapter 5, 6 and 7). In Vesijako (Chapter 5) fire was much less frequent in the past with a fire return period of 430 cal. yrs. BP and less frequent that previously recorded from fire scar data (Zackrisson, 1977; Engelmark, 1984; Granström & Niklasson, 2008). There is a baseline fire return interval of approximately 400 years in Vesijako and in Sudenpesä (Chapter 5 & 6) that may be valuable for management decisions associated with conservation and restoration management. The past can be used to address modern day conservation issues by setting a natural variability of fire frequency and severity (Willis & Birks, 2006) to enhance ecosystem resilience to climate change (Holling & Meffe, 1996).

Chapter 10

10 Conclusions

10.1 Conclusions and wider implications

The work conducted for this thesis explores spatial and temporal variability in vegetation and disturbance dynamics in Fennoscandia and Denmark during the Holocene. It highlights the requirement of a multi-method approach to explore past environmental change through combining palaeoecology with quantitative analysis and modelling. What is perceived from palaeoecology can be explored and either clarified or rejected using modelling and quantitative analysis. It is only through combining these techniques that can we begin to understand drivers of vegetation and disturbance dynamics in the northern European forest and elsewhere. Through exploring multiple sites of local-scale vegetation and disturbance history we can begin to understand local disturbance dynamics. But only through combining this local information with regional data can we gain the insight required to disentangle the drivers of Holocene vegetation and disturbance dynamics. This highlights the benefits of collaborative working groups such as the EPD and GCD and the requirement for cooperation to collate existing palaeoecological data. Further, the standardisation of methods is essential if we are to further understand environmental change on a spatial scale. Ultimately, the further back in time we can explore past vegetation and disturbance dynamics, the better we can understand past and future environmental change. Although the baseline conditions may have changed, insight into past reference boundaries is essential for modelling and forecasting. If we can accurately model the past to reflect the observed palaeoecological record then we can begin to model and forecast future scenarios. Whilst the past analogue may be inappropriate for real-time conservation and management, there is still an archive of knowledge available to assist with present day and future management decisions.

The main results and implications of this work can be summarised as follows:

- Early-Holocene fire and vegetation dynamics were primarily driven by climate variability and vegetation-fire feedbacks. Although humans were present, their basic hunter and gatherer lifestyle initiated low-level anthropogenic disturbance. In order to observe natural or semi-natural forest dynamic response to climate change and to explore the main drivers behind vegetation and fire dynamics we have to view the time of minimal anthropogenic impact. Using palaeoecological records enables us to do this and while quantifying temporal and spatial accuracy remains challenging, palaeoecology gives an insight into past natural vegetation dynamics and disturbance history.
- *Picea abies* was present in low-level populations in southern Finland prior to 9,000 cal. yrs. BP then declined and re-established after 8,000 cal. yrs. BP. These early-Holocene population fluctuations and the mid- to late-Holocene spread of *Picea* across Fennoscandia can be attributed to changing climate and more specifically increased continentality. *Picea* and continentality peak simultaneously at approximately 2000 cal. yrs. BP. Ecological factors control the spread of *Picea abies* and the local effect of natural and anthropogenic disturbance cannot be ruled out in assisting the spread of *Picea,* especially in western Fennoscandia where *Picea* is planted beyond its ecological limits. Even in Finland 6000 cal. yrs. BP, population increase linked with a more favourable climate (HTM) and ecosystem productivity may have helped facilitate the spread of *Picea abies*. However, the primary control on the early-Holocene low presence and mid- to late-Holocene spread of *Picea abies* is climate.
- The mid-late Holocene decline in deciduous species was primarily driven by localised anthropogenic disturbance assisted by a trend to cooler, wetter climate conditions post-HTM. This suggests intensive anthropogenic disturbance was responsible for the loss of floristic diversity which might

otherwise have remained up until the present day. Deciduous species are generally controlled by climatic parameters yet within these boundaries, deciduous abundance is driven by other factors. It is proposed that anthropogenic disturbance played a significant role in the mid-Holocene decline in deciduous species through selective swidden cultivation and increased fire disturbance. This has implications for pollen-climate transfer models with the presence of deciduous species able to identify particular climatic boundaries but a decline of deciduous species abundance cannot be used to infer a change in climatic conditions.

- The spread of *Picea abies* across Fennoscandia reduced the regional biomass burning prior to the mid-Holocene increase in anthropogenic disturbance. This indicates that there is a range of natural variability in fire and fire frequency does not remain stable during the Holocene.
- This anthropogenic increase in fire, when observed in the palaeo-record, indicates that fires were much more frequent in the recent past. However, prior to intensified anthropogenic disturbance the fire frequency was much lower than can be observed in the fire scar records. This suggests that the current perception that fires have always been more frequent in Fennoscandia in the past needs to be re-evaluated.
- The now widespread dominance of *Picea abies* suggests that the low fire frequency observed throughout Fennoscandia is semi-natural and without intensive anthropogenic disturbance, fires were and would have always remained low frequency, even prior to the rise in *Picea abies*.
- There has no doubt been a decline in fire in the recent past but this cannot be attributed to fire suppression alone. The 'human influence hypothesis' or reduction in the number of human caused ignitions is the main reason for the observed decline in fire frequency with the timing of the decline in fire earlier in southwestern Fennoscandia and later in north and eastern Fennoscandia where traditional livelihoods remained up until the 20th Century.

- Dominant vegetation type exerts a control over the fire regime somewhat independently of climate. If vegetation drives fire frequency then fire scars recorded from *Pinus sylvestris* trees are biased towards recording high fire frequencies and fail to identify other fire regimes i.e. from *Picea abies* dominated stands. This suggests natural fire frequency in Fennoscandia is overestimated regardless of past anthropogenic disturbance.
- There are important vegetation-fire feedbacks that control vegetation and disturbance dynamics. The current dominance of *Picea abies* inhibits natural fire ignitions favouring *Picea* dominance. These positive feedbacks cannot be underestimated when understanding vegetation and disturbance dynamics in the northern boreal forest.
- Although the fire regime varies spatially and temporally throughout the Holocene, there is an underlying 'natural' fire frequency of approximately 400 years observed in southern Finland that is evident during the early, middle and late-Holocene.
- Small forest hollow environments are able to record discrete fire events to high spatial precision and therefore are excellent archives of local disturbance. Through combining more than one stand-scale site and regional site data we can begin to explore regional disturbance dynamics. This insight into local and regional disturbance events enables us to begin to disentangle the Holocene drivers of vegetation dynamics and their associated feedbacks.

10.2 Limitations and further work

Palaeoecology provides an insight into past environmental change that is invaluable for understanding drivers of vegetation and disturbance dynamics. However, there are limitations associated with palaeoecology that are challenging to overcome. Combining information on past climate, anthropogenic impact and vegetation development as drivers of fire history is problematic when; (1) each driver is individually difficult to quantify, (2) the drivers are not mutually exclusive and (3) there are feedbacks associated with the fire disturbance. While fossil pollen data has its limitations it remains an excellent proxy to record past vegetation dynamics. Counting 1000 pollen grains rather than 500 would have been beneficial to better understand species population dynamics, particularly during the early-Holocene low-population presence of *Picea abies*. If macrofossil analysis was conducted alongside pollen analysis the presence of macrofossils would confirm the local presence of particular species. Further, dating macrofossil remains is considered more accurate than dating bulk sediment. The potential for studying macrofossils during this thesis was limited by sediment availability. The use of a 5 cm diameter Russia corer while good in penetrating the ground retrieves relatively little sediment compared to the larger 10 cm diameter corer. Analysis of pollen and charcoal at 1 cm intervals or in some cases 0.5 cm intervals leaves little if any sediment remaining. A preliminary search for macrofossils yielded insufficient quantities for radiocarbon dating and subsequently the sediment used for dating could not be analysed. More sediment would have enabled complementary analysis of further sedimentary properties such as loss on ignition (pre-TGA!), geochemical analysis (pre-core scanner!) and magnetic susceptibility. These methods may have identified external impacts on the observed results for example; a peak in inorganic sediment coupled with a peak in charcoal could be indicative of an in-wash event. Sedimentary charcoal is the only method available for studying past fire history beyond the temporal extent of fire scars, yet it remains difficult to extract high fire frequencies from charcoal records due to the low temporal resolution of sedimentation. Even at 1cm or 0.5cm analysis each sample is representative of 10s of years. The deposition of charcoal often lags fire events and is distributed over a number of samples with high fire frequencies often merging into seemingly one event. This highlights the need for statistical analysis in determining peak charcoal events. Further, the practical application of a fire frequency of 400 years to conservation and management policies is unsuitable when more immediate solutions are required.

Additional analysis of pollen and charcoal records, particularly from stand-scale forest hollow environments in regions with few or no local stand-scale records would further contribute to our understanding of vegetation and disturbance dynamics. This particularly applies to eastern Finland and Russia and would contribute to the existing transect of forest hollows across Fennoscanida. In addition to the work carried out in this thesis the author has begun to explore vegetation and disturbance dynamics in three more sites (Figure 10.1)

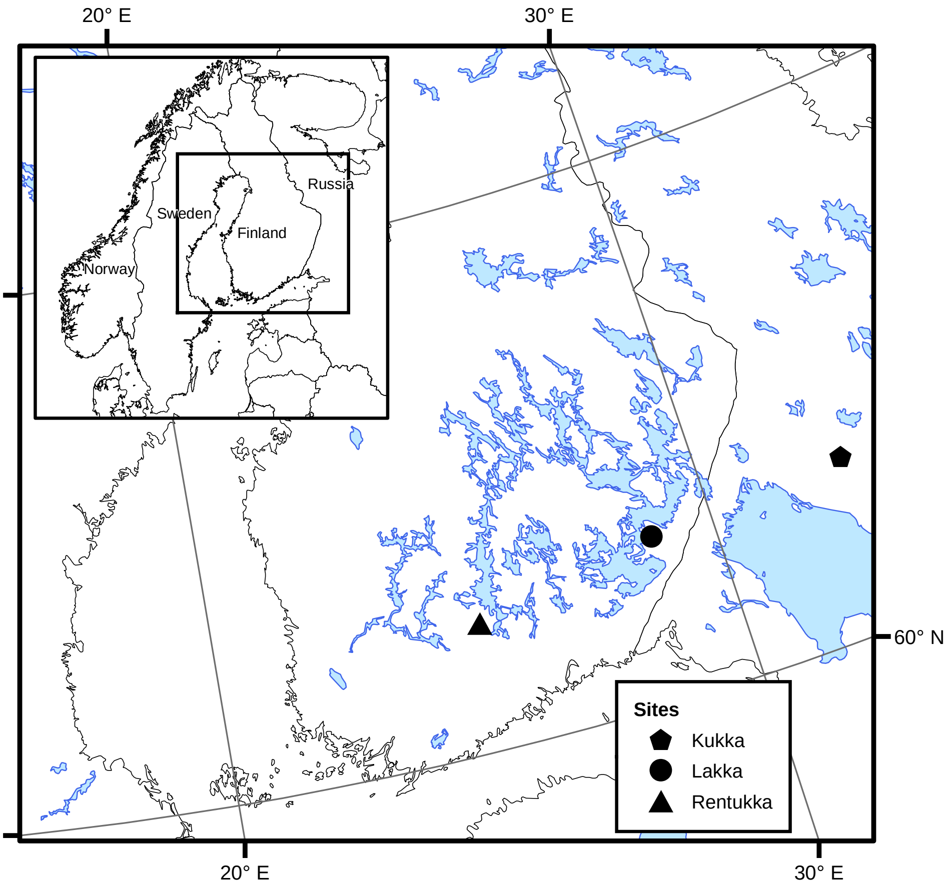


Figure 10.1: Location map of Kukka, Rentukka and Lakka Hollow

Kukka Hollow (61˚39’ N: 32˚44’ E) is located in Russia and was sampled in May 2010 along with another stand-scale site *Larix* Hollow, currently being analysed by Nina Kuosmanen in Helsinki University. Lakka Hollow (61˚32’ N: 28˚47’ E) and Rentukka Hollow (61˚11’32.3 N: 25˚09’9.5 E) are both located in Finland and were sampled in June 2009. Lakka Hollow is located in eastern Finland and Rentukka hollow is situated in southern Finland near to Vesijako and Sudenpesä. Fieldwork, laboratory analysis and palaeoecological work followed standard procedures as outlined in chapter 4. Preliminary analysis of the cores is outlined in table 10.1.

	Kukka Hollow Russia	Lakka Hollow Finland	Rentukka Hollow Finland
Latitude	61˚39' N	61˚32' N	61˚11'32.3 N
Longitude	32˚44' E	28˚47' E	25˚09'9.5 E
Vegetation zone	Southern boreal vegetation zone (all sites)		
Field work	May 2010	June 2009	June 2009
Length of core (cm)	609	169	124
Radiocarbon dates	1	0	0
Pollen analysis			
No of samples	61	16	13
Sample interval (cm)	10	10	10
Charcoal analysis			
No of samples	609	169	124
Sample interval (cm)	1	1	1

Table 10.1: Site specific information for three small forest hollow environments

Preliminary results are as follows…

Kukka Hollow, Russia (Figure 10.2) has discrete charcoal events that extend up to the surface of the core suggesting a fire regime maintained until the present. Fire appears less frequent prior to 450 cm and most frequent at approximately 200 cm and near to the surface of the core. The estimated temporal extent of the core is approximately 10000 cal. yrs. BP or older based on the basal pollen composition with abundance of *Betula* and *Populus* and low values of *Pinus*. Around 550 cm the sharp rise in *Pinus* pollen abundance, decline in *Betula* and increase in *Picea* suggest a change in climatic conditions that would be interesting to date due to the potentially early presence of *Picea abies*. The rise in *Picea* abundance occurs after 400 cm and does not correspond to a decline in deciduous species.

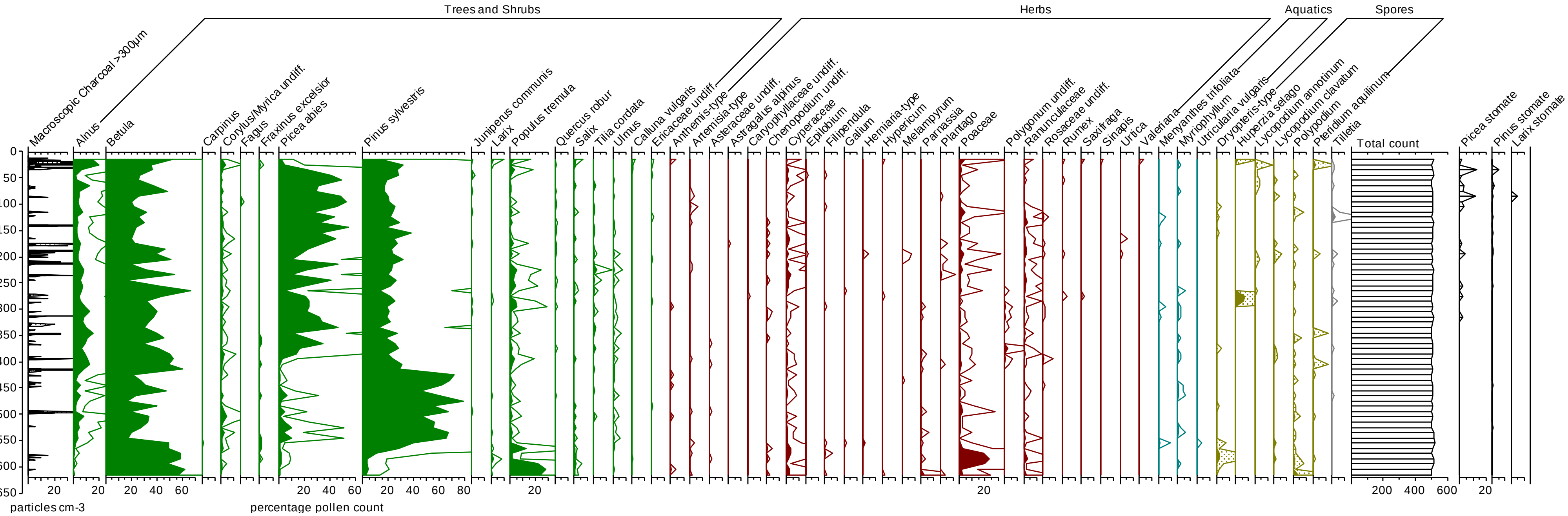


Figure 10.2: Pollen and charcoal diagram for Kukka Hollow, Russia with pollen expressed as percentage of total pollen count and macroscopic charcoal fragments (>300µm) expressed as charcoal particles cm^{-3}.

There is a prominent decline in deciduous species at approximately 200 cm with a simultaneous decline in *Tilia* and *Ulmus* and potential increase in charcoal abundance. This again will be interesting to date to help determine the driver of the mid-Holocene decline in deciduous species. *Picea abies* is most abundant between 150 and 50 cm and declines towards the most recent past, during the period of most abundant charcoal.

Lakka Hollow, Finland (Figure 10.3) records less discrete charcoal events with an abundance of charcoal between 150 and 105 cm and relatively little charcoal as we approach the surface of the core. There is an absence of charcoal between approximately 85 and 65 cm and again between 40 and 30 cm and during the last 20 cm of the core suggesting a period of fire absence in the most recent past. The extent of the core is somewhat less clear than in Kukka Hollow. The low presence of *Picea abies* suggests the core extends back beyond 6000 cal. yrs. BP however the frequent charcoal abundance could be responsible for keeping the *Picea* values low. Further pollen analysis on this section of the core prior to dating the basal layer could be advisable. There is no clear decline in deciduous species recorded yet again stressing the need for further pollen analysis. However the presence of *Tilia* and *Ulmus* between 100 and 40 cm suggests this section of the core could at least partly correspond to the mid-Holocene Thermal Maximum.

Rentukka Hollow, Finland (Figure 10.4) is situated in the region of Sudenpesä and Vesijako hollows. The palynological record records more charcoal abundance in the bottom half of the core between approximately 125 and 80 cm. After 80 cm charcoal abundance becomes less frequent with periods of no charcoal including the last 25 cm of the core suggesting periods of fire absence. The 10% values of *Picea abies* near to the base of the core suggest this core may be less than 6000 years old with the peak in charcoal at approximately 60 cm potentially corresponding to the peak in continentality and could be dated to approximately 2000 cal. yrs. BP. There is a decline in *Salix* and *Ulmus* that also occur at approximately 60 cm.

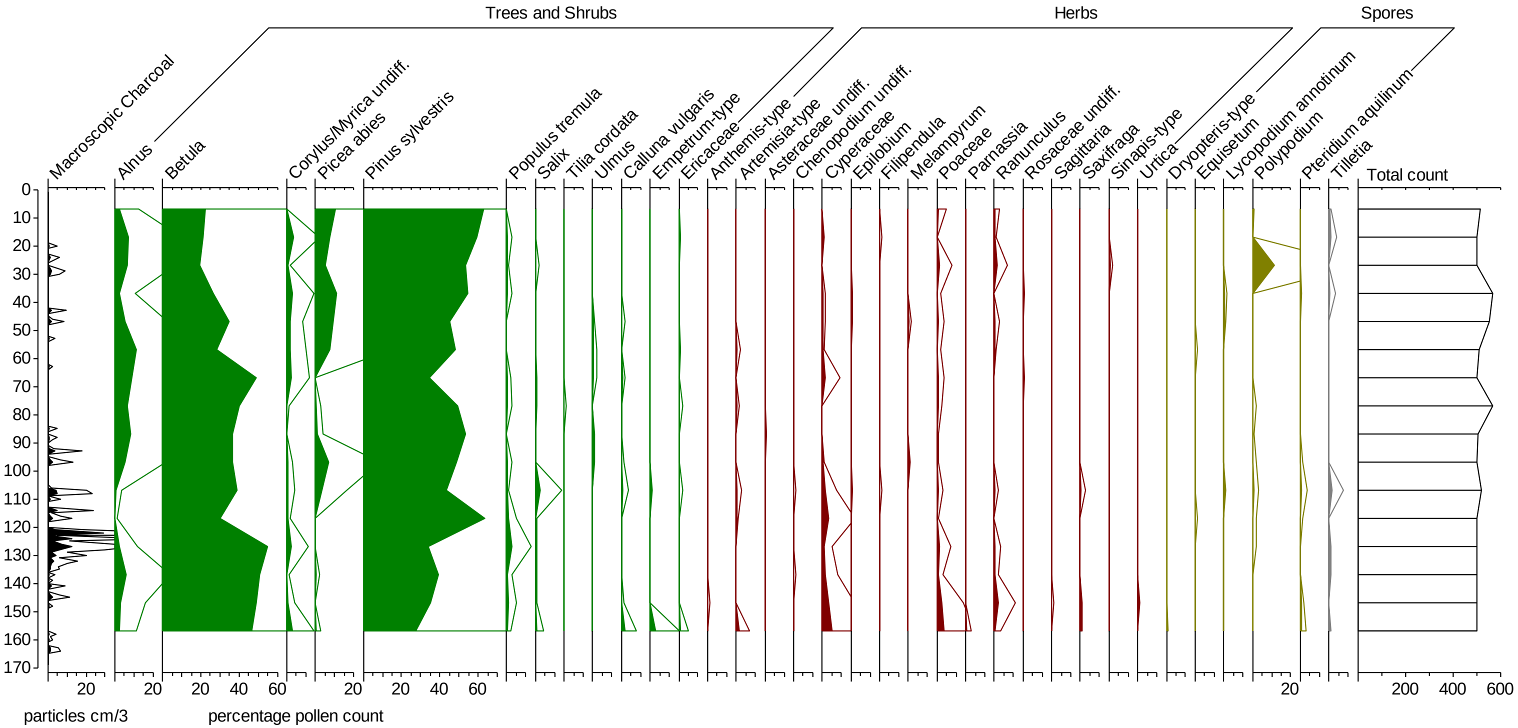


Figure 10.3: Pollen and charcoal diagram for Lakka Hollow, Finland with pollen expressed as percentage of total pollen count and macroscopic charcoal fragments (>300µm) expressed as charcoal particles cm^{-3}.

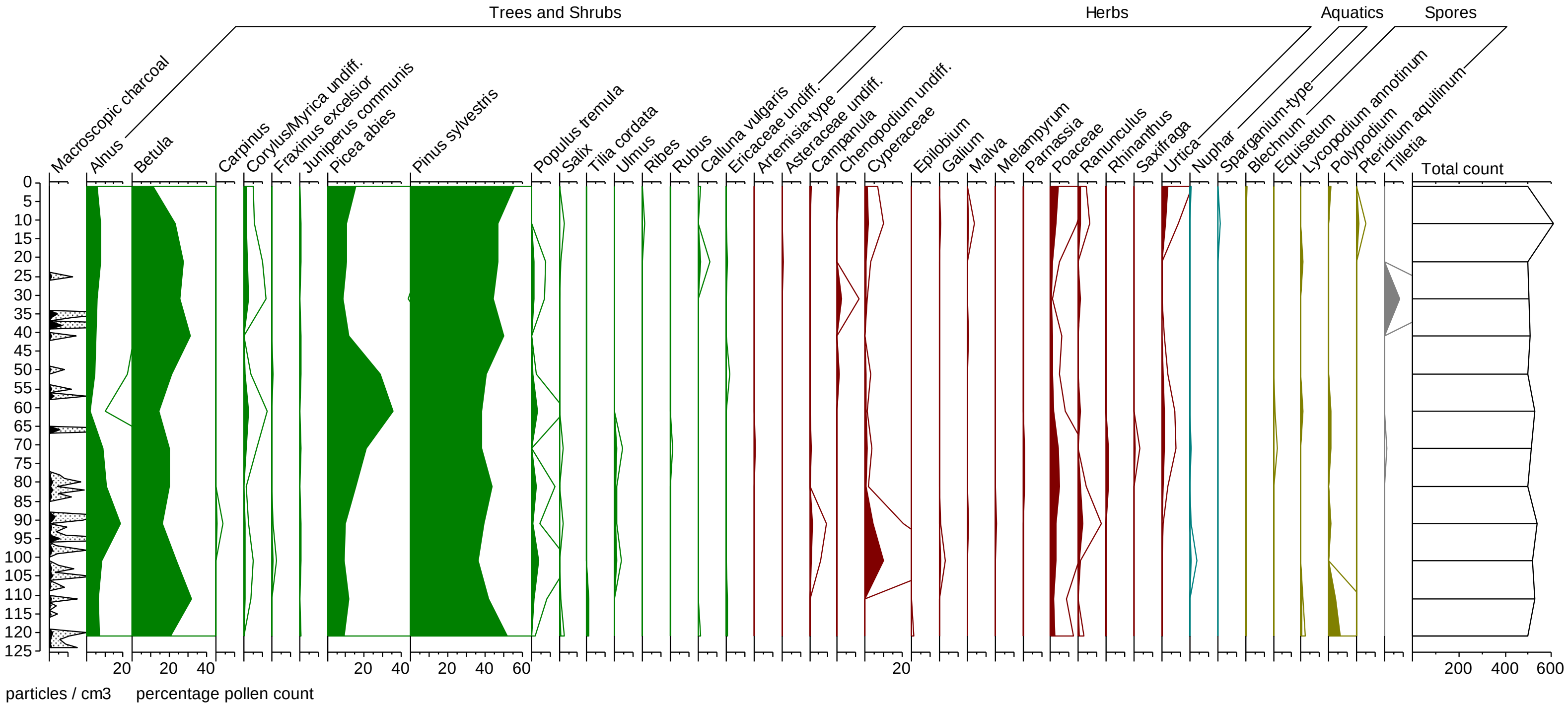


Figure 10.4: Pollen and charcoal diagram for Rentukka Hollow, Finland with pollen expressed as percentage of total pollen count and macroscopic charcoal fragments (>300µm) expressed as charcoal particles cm^{-3}.

These cores will be dated in the coming months and further analysed at 1cm intervals and will eventually assist in the understanding of vegetation and disturbance dynamics in the northern European forest. A further project that may assist with the understanding behind the decline in deciduous species is the analysis of the timing of deciduous species decline in existing palaeo-data cores following the method outlined in Chapter 6. A Fennoscandian analysis of the decline in deciduous species could be compared to model climate data, rise in *Picea abies* as well as intensified anthropogenic impact. If the spatial scale of the temporal decline is varied and patchy then there are drivers other than the trend to cooler, wetter conditions after the mid-Holocene Thermal Maximum that controls the widespread decline in deciduous species.

References

Abraham, V., Kozáková, R. (2012) Relative pollen productivity estimates in the modern agricultural landscape of Central Bohemia (Czech Republic). *Review of Palaeobotany and Palynology* 179, 1-12.

Ahti, T., Hämet-Ahti, L., Jalas, J. (1968) Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5, 169-211.

Alenius, T., Mikkola, E., Ojala, A. (2008) History of agriculture in Mikkeli Orijärvi, eastern Finland as reflected by palynological and archaeological data. *Vegetation History and Archaeobotany* 17, 171-183.

Alenius, T., Lavento, M., Saarnisto, M. (2009) Pollen-analytical results from Lake Katajajarvi - Aspects of the history of settlement in the Finnish inland regions. *Acta Borealia* 26, 136-155.

Alenius, T., Mökkönen, T., Lahelma, A. (2013) Early farming in he northern Boreal zone: Reassessing the history of landuse in southeastern Finland through high-resolution pollen analysis. *Geoarchaeology*: *An International Jouranal* 28, 1-24

Andersen, B.G. (1979) The deglaciation of Norway 15,000–10,000 B.P. *Boreas* 8, 79-87.

Andersen, B.G. (1980) The deglaciation of Norway after 10,000 B.P. *Boreas* 9, 211-216.

Andersen, S.T. (1966) Tree-pollen rain in a mixed decidous forest in south Jutland (Denmark). *Review of Palaeobotany and Palynology* 3 267-275.

Andersen, S.T. (1970) The relative pollen productivity and pollen representation of north European trees, and correction factors for tree pollen spectra. *Danmarks Geologiske Undersøgelse II* 96, 1-99.

Anderson, L.L., Hu, F.S., Nelson, D., Petit, R.J., Paige, K.N. (2006) Ice-age endurance: DNA evidence of a white spruce refugia in Alaska, *PNAS* 103, 12447-12450.

Antonsson, K., Brooks, S.J., Seppä, H., Telford, R.J., Birks, H.J.B. (2006) Quantitative palaeotemperature records inferred from fossil pollen and chironomid assemblages from Lake Gilltjärnen, northern central Sweden. *Journal of Quaternary Science* 21, 831-841.

Antonsson, K., Seppa, H. (2007) Holocene temperatures in Bohuslan, southwest Sweden: a quantitative reconstruction from fossil pollen data. *Boreas* 36, 400-410.

Autio, J., Hicks, S. (2004) Annual variations in pollen deposition and meteorological conditions on the fell Aakenustunturi in northern Finland: potential for using fossil pollen as a climate proxy. *Grana* 43, 31-47.

Bennett, K.D. (1995-2007) Pollen catalogue of the British Isles. Available online at: <http://chrono.qub.ac.uk/pollen/pc-intro.html> (Accessed 2008-2012).

Bennett, K.D. (1994) Confidence intervals for age estimates and deposition times in late-Quaternary sediment sequences. *The Holocene* 4, 337–348.

Bennett, K.D., Willis, K. (2001) Pollen. In Smol, J.P., Birks, H.J.B., Last, W.M. (eds.). Tracking environmental change using lake sediments. Volume 3: Terrsetrial, algae and siliceous indicators, Kluwer Academic Publishers, Dordrecht, The Netherlands. 5-31

Bergeron, Y. (1991) The influence of island and mainland lakeshore landscapes on Boreal forest fire regimes. *Ecology* 72, 1980-1992

Bergeron, Y., Archambault, S. (1993) Decreasing frequency of forest fires in the southern boreal zone of Québec and its relation to global warming since the end of the ‘Little Ice Age’. *The Holocene* 3, 255-259

Bergeron, Y., Engelmark. O., Harvey, B., Morin, H., Sirois, L. (1998a) Key issues in the disturbance dynamics in Boreal forests. *Journal of Vegetation Science* 9, 463-468.

Bergeron, Y., Richard, P.J.H., Carcaillet, C., Gauthier, S., Flannigan, M., Prairie, Y.T. (1998b) Variability in fire frequency and forest composition in Canada's southeastern Boreal forest: A Challenge for Sustainable Forest Management. *Conservation Ecology* 2, 6.

Bergeron, Y., Luduc, A., Harvey, Brian, D., Gauthier, S. (2002) Natural fire regime: A guide for sustainable management of the Canadian Boreal forest. *Siliva Fennica* 36, 81-95.

Berglund, B.E. (1979) The deglaciation of southern Sweden 13,500-10,000 B.P. *Boreas* 8, 89-117.

Berglund, B.E., Gaillard, M.-J., Björkman, L., Persson, T. (2008a) Long-term changes in floristic diversity in southern Sweden: palynological richness, vegetation dyanmics and land-use. *Vegetation History and Archaeobotony* 17, 573-583.

Berglund, B.E., Persson, T., Björkman, L. (2008b) Late Quaternary landscape and vegetation diversity in a North European perspective. *Quaternary International* 184, 187-194.

Bergman, I., Olofsson, A., Hörnberg, G., Zackrisson, O., Hellberg, E. (2004) Deglaciation and colonization: Pioneer settlements in northern Fennoscandia. *Journal of World Prehistory* 18, 155-177.

Bialozyt, R., Bradley, L.R., Bradshaw, R.H.W. (2012) Modelling the spread of *Fagus sylvatica* and *Picea abies* in southern Scandinavia during the late Holocene. *Journal of Biogeography* 39, 665-675.

Birks, H.H. (2001) Plant Macrofossils. In Smol, J.P., Birks, H.J.B., Last, W.M. (eds.). Tracking environmental change using lake sediments. Volume 3: Terrsetrial, algae and siliceous indicators, Kluwer Academic Publishers, Dordrecht, The Netherlands. 49-73

Birks H.J.B. (1996a) Statistical approaches to interpreting divresity patterns in the Norwegian mountain flora. *Ecogeography* 19, 332-340.

Birks H.J.B. (1996b) Contributions of Quaternary palaeoecology to nature conservation. *Journal of Vegetation Science* 7, 89-98.

Birks, H.J.B. (2007) Estimating the amount of compositional change in late-Quaternary pollen-stratigraphical data. *Vegetation History and Archaeobotany* 16, 197-202.

Birks. H.J.B., Birks H.H. (1980) Chapter 5 in Quaternary Palaeoecology, Edward Arnold, London. 66-84

Birks, H.J.B., Line, J.M. (1992) The use of Rarefaction analysis for estimating Palynological Richness from Quaternary pollen-analytical data. *The Holocene* 2, 1-10.

Björkman, L. (1997) The history of *Fagus* forest in southwestern Sweden during the last 1500 years. *The Holocene* 7, 419-432.

Bjorkman, L., Bradshaw, R. (2006) The immigration of *Fagus sylvatica* L. and *Picea abies* (L.) Karst. into a natural forest stand in souther Sweden during the last 2000 years. *Journal of Biogeography* 23, 235-244.

Bjune, A. E., Birks, H.J.B., Seppä, H. (2004) Holocene vegetation and climate history on a continental–oceanic transect in northern Fennoscandia based on pollen and plant macrofossils. *Boreas* 33, 211-223.

Bjune, A.E. (2005) Holocene vegetation history and tree-line changes on a north-south transect crossing major climate gradients in southern Norway – Evidence from pollen and plant macrofossils in lake sediments. *Review of Palaeobotany and Palynology* 133, 249-275.

Bjune, A.E., Birks, H.J.B. (2008) Holocene vegetation dynamics and inferred climate changes at Svanåvatnet, Mo i Rana, northern Norway. *Boreas* 37, 146-156.

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

Bjune, A., Seppä, H., Birks, H. (2009b) Quantitative summer-temperature reconstructions for the last 2000 years based on pollen-stratigraphical data from northern Fennoscandia. *Journal of Paleolimnology* 41, 43-56.

Björck, S., Möller, P. (1987) Late Weichselian environmental history in southeastern Sweden during the deglaciation of the Scandinavian ice sheet. *Quaternary Research* 28, 1-37.

Blaauw, M. (2010) Methods and code for 'classical' age-modelling of radiocarbon sequences. *Quaternary Geochronology* 5, 512-518.

Blaauw, M., Christen, J.A. (2011) Flexible palaeoclimate age-depth models using an autoregressive gamma process. *Bayesian Analysis* 6, 457-474.

Blaauw, M., Heegaard, E. (2012) Estimation of age-depth relationships. In Birks H.J.B., Lotter A.F., Juggins, S., Smol, J.P. (Eds.) Tracking environmental change using lake sediments. Springer, Netherlands, 397-413.

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., D'Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F., Keeley, J.E., Krawchuk, M.A., Kull, M.A., Marston, J.B., Moritz, M.A., Prentice, I.C., Roos, C.I., Scott, A.C., Swetnam, T.W., van der Werf, G.R., Pyne, S.J. (2009) Fire in the Earth system. *Science* 324, 481-484.

Bowman,. D.M.J.S., Balch, J., Artaxo, P., Bond, W.J., Cochrane, M.A., D'Antonio, C.M., DeFries, R., Johnston, F.H., Keeley, J.E., Krawchuk, M.A., Kull, C.A., Mack, M., Moritz, M.A., Pyne, S., Roos, C.I., Scott, A.C., Sodhi, N.S., Swetnam, T.W. (2011) The human dimension of fire regimes on Earth. *Journal of Biogeography* 38, 2223-2236.

Bradley, L.R., Giesecke, T., Halsall, K., Bradshaw, R.H.W. (2013) Exploring the requirement for anthropogenic disturbance to assist the stand-scale expansion of *Fagus sylvatica* L. outside southern Scandinavia. *The Holocene* 23, 579-586.

Bradshaw, R.H.W. (1993) Tree species dynamics and disturbance in three Swedish boreal forest stands during the last two thousand years. *Journal of Vegetation Science* 4, 759-764.

Bradshaw, R.H.W. (2007) Stand-scale Palynology. In Elias, S.A. (ed). Encyclopaedia of Quaternary science. Elsevier, Amsterdam.

Bradshaw, R.H.W. (1981) Quantitative reconstruction of local woodland vegetation using pollen analysis from a small basin in Norfolk, England. *Journal of Ecology* 69, 941-955.

Bradshaw, R.H.W., Webb, T. (1985) Relationships between contemporary pollen and vegetation data from Wisconsin and Michigan, USA. *Ecology* 66, 721-737.

Bradshaw, R.H.W., Zackrisson, O. (1990) A two thousand year history of a northern Swedish Boreal forest stand. *Journal of Vegetation Science* 1, 519-528.

Bradshaw, R.H.W., Hannon, G.E. (1992) Climatic change, human influence and disturbance regime in the control of vegetation dynamics within Fiby forest, Sweden. *Journal of Ecology* 80, 625-632.

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.

Bradshaw, R.H.W., Holmqvist, B.H., Cowling, S.A., Sykes, M.T. (2000) The effects of climate change on the distribution and management of *Picea abies* in southern Scandinavia *Canadian Journal of Forest Research* 30, 1992-1998.

Bradshaw, R.H.W., Lindbladh, M., Hannon, G.E. (2010a) The role of fire in southern Scandinavian forests during the late Holocene. *International Journal of Wildland Fire* 19, 1040-1049.

Bradshaw, R.H.W., Kito, N., Giesecke, T. (2010b) Factors influencing the Holocene history of *Fagus*. *Forest Ecology and Management* 259, 2204-2212.

Broström, A., Sugita, S., Gaillard, M.-J. (2004) Pollen productivity estimates for the reconstruction of past vegetation cover in the cultural landscape of southern Sweden. *The Holocene* 14, 368-381.

Broström, A., Nielsen, A., Gaillard, M.-J., Hjelle, K., Mazier, F., Binney, H., Bunting, J., Fyfe, R., Meltsov, V., Poska, A., Räsänen, S., Soepboer, W., von Stedingk, H., Suutari, H., Sugita, S. (2008) Pollen productivity estimates of key European plant taxa for quantitative reconstruction of past vegetation: A review. *Vegetation History and Archaeobotany* 17, 461-478.

Brown, K.J., Seppä, H., Schoups, G., Fausto, R.S., Rasmussen, P., Birks, H.J.B. (2012) A spatio-temporal reconstruction of Holocene temperature change in southern Scandinavia. *The Holocene* 22 165-177.

Brown, T.A., Nelson. D.E., Mathewes, R.W., Vogel, J.S., Southon, J.R. (1989) Radiocarbon dating of pollen by Accelerator Mass Spectrometry. *Quaternary Research* 32, 205-212.

Bugmann, H. (2001) A review of forest gap models. *Climatic Change* 51, 259-305.

Calcote, R. (1995) Pollen source area and pollen productivity: Evidence from forest hollows. *Journal of Ecology* 83, 591-602.

Carjander, A.K. (1949) Forest types and their significance. *Acta For*estalia *Fennica* 56, 1-71.

Carcaillet, C., Bouvier, M., Fréchette, B., Larouche, A.C., Richard, P.J.H. (2001) Comparison of pollen-slide and sieving methods in lacustrine charcoal analyses for local and regional fire history. *The Holocene* 11, 467-476.

Carcaillet, C., Bergman, I., Delorme, S., Hornberg, G., Zackrisson, O. (2007) Long-Term Fire Frequency not liked to Prehistoric occupation in Northern Swedish Boreal Forest. *Ecology* 88, 465-477.

Carcaillet, C., Hörnberg, G., Zackrisson, O. (2012) Woody vegetation, fuel and fire track the melting of the Scandinavian ice-sheet before 9500 cal yr BP. *Quaternary Research* 78, 540-548.

Chandler, C., Cheney, P., Thomas, P., Trabaud, L., Willians, D. (1983) Fire in forestry volume 1. Fire behavior and effects. Wiley, New York. 450pp

Chen, D. (2000) A monthly circulation climatology for Sweden and it's application to a winter temperature case study. *International Journal of Climatology* 20, 1067-1076.

Chen, D., Hellström, C. (1999) The infleuce of the North Atlantic Oscillation on the regional temperature variability in Sweden: Spatial and temporal variations. *Tellus* 51, 505-516.

Chen, J.M., Black, T.A. (1992) Defining leaf area index for non-flat leaves. *Plant, Cell & Environment* 15, 421-429.

Christen, J.A., Perez, S. (2009) A new robust statistical model for radiocarbon data. *Radiocarbon* 51, 1047-1059.

Clark, R.L. (1982) Point count estimation of charcoal in pollen preparations and thin sections of sediments. *Pollen et Spores* 24, 523-35.

Clark, J. S. (1988a) Particle motion and the theory of charcoal analysis: source area, transport, deposition and sampling. *Quaternary Research* 30, 67-80.

Clark, J. S. (1988b) Stratigraphic charcoal analysis on petrographic thin sections: application to fire history in northwestern Minnesota. *Quaternary Research* 30, 81-91.

Clear, J.L., Seppä, H., Kuosmanen, N., Bradshaw, R.H.W., (2013) Holocene fire frequency variability in Vesijako, Strict Nature Reserve, Finland, and its application to conservation and management. *Biological Conservation* 166, 90-97.

Clear, J.L., Molinari, C., Bradshaw, R.H.W. Holocene fire in Fennoscandia and Denmark. *International Journal of Wildland Fire*, submitted.

Colombaroli, D., Vannière, B., Emmanuel, C., Magny, M., Tinner, W. (2008) Fire—vegetation interactions during the Mesolithic—Neolithic transition at Lago dell'Accesa, Tuscany, Italy. *The Holocene* 18, 679-692.

Cowling, S.A., Sykes, M.T., Bradshaw, R.H.W. (2001) Palaeovegetation-model comparisons, climate change and tree succession in Scandinavia over the past 1500 years. *Journal of Eclogy* 89, 227-236.

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J. (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408, 184-187.

Cushing, E.J. (1967) Evidence for differential pollen preservation in late quaternary sediments in Minnesota. *Review of Palaeobotany and Palynology* 4, 87-101.

D'Anjou, R.M., Bradley, R.S., Balascio, N.L., Finkelstein, D.B. (2013) Climate impacts on human settlement and agricultural activities in northern Norway revealed through sediment biogeochemistry. *PNAS* 109, 20332-20337.

Davies, M.B., Calcote, R.R., Sugita, S., Takahara, H. (1998) Patchy invasion and the origin of a henlock-hardwoods forest mosaic. *Ecology* 79, 2641-2659.

Davis, B.A.S., Brewer, S., Stevenson, A.C., Guiot, J. (2003) The temperature of Europe during the Holocene reconstructed from pollen data. *Quaternary Science Reviews* 22, 1701-1716.

Donner, J.J. (1963) The zoning of the post-glacial pollen diagrams in Finland and the main changes in the forest composition. *Acta Botanica Fennica* 65.

Edwards, M.E. (1986) Disturbance histories of four Snowdonian woodlands and their relation to Atlantic bryophyte distrinutions. *Biological Conservation* 37, 301-320.

Engelmark, O. (1984) Forest fires in the Muddus National Park (northern Sweden) during the past 600 years. *Canadian Journal of Botany* 62, 893-898.

Engelmark, O., Bradshaw, R.H.W., Bergeron, Y. (1993) Disturbance dyanmics in Boreal forest. *Journal of Vegetation Science* 3, 729-732.

Engelmark, O., Kullman, L., Bergeron, Y. (1994) Fire and age structure of Scots pine and Norway spruce in northern Sweden during the past 700 years. *New Phytologist* 126, 163-168.

Erdtman, G. (1943) An introduction to pollen analysis. Waltham, Mass, Chronica Botanica, 239 pages

ESRI (2011) ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

Esseen, P.-A., Ehnström, B., Ericson, L., Sjöberg, K. (1997) Boreal Forests. *Ecological Bulletins* 46, 16-47.

Farquhar, G.D., von Caemmerer, S., Berry, J.A. (1980) A biochemical model of photosynthetic CO_2 assimilation in leaves of C3 species. *Planta* 149, 78-90.

Fischer, A., Marshall, P., Camp, A. (2013) Disturbances in Deciduous Temperate forest ecosystems of the northern hemisphere: Their effects on both recent and future forest development. *Biodiversity and Conservation* 22, 1863-1893.

Finnish Forest Research Institute, (2000) Finnish Statistical Yearbook of Forestry. Gummerus Kirjapaino Oy, Jyväskylä, Finland ISBN 951-40-1752-8

Flannigan, M.D., Amiro, B.D., Logan, K.A., Stocks, B.J., Wotton, B.M. (2005) Forest fires and climate change in the 21st Century. *Mitigation and Adaptation Strategies for Global Change* 11, 847-859.

Flannigan, M.D., Bergeron, Y., Engelmark, O., Wotton, B.M. (1998) Future wildfire in Circumboreal forests in relation to global warming. *Journal of Vegetation Science* 9, 469-476.

Fowler, A.J., Gillespie, R., Hedges, R.E.M (1986) Radiocarbon dating of sediments. *Radiocarbon* 28, 441-450.

Fyfe, R.M., de Beaulieu, J.-L., Binney, H., Bradshaw, R.H.W., Brewer, S., Le Flao, A., Finsinger, W., Gaillard, M.-J., Giesecke, T., Gilromera, G., Grimm, E.C., Huntley, B., Kunes, P., Kühl, N., Leydet, M., Lotter, A.F., Tarasov, P.E., Tonkov, S. (2009) The European Pollen Database: Past efforts and current activities. *Vegetation History and Archaeobotany* 18, 417-424.

Gaillard, M.-J., Sugita, S., Bunting, J., Dearing, J., Bittmann, F. (2008) Human impact on terrestrial ecosystems, pollen calibration and quantitative reconstruction of past land-cover. *Vegetation History and Archaeobotany* 17, 415-418.

Gaillard, M.-J., Sugita, S., Bunting, M., Middleton, R., Broström, A., Caseldine, C., Giesecke, T., Hellman, S., Hicks, S., Hjelle, K., Langdon, C., Nielsen, A.-B., Poska, A., von Stedingk, H., Veski, S. (2008) The use of modelling and simulation approach in reconstructing past landscapes from fossil pollen data: a review and results from the POLLANDCAL network. *Vegetation History and Archaeobotany* 17, 419-443.

Gaillard, M.J., Sugita, S., Mazier, F., Trondman, A.K., Broström, A., Hickler, T., Kaplan, J.O., Kjellström, E., Kokfelt, U., Kuneš, P., Lemmen, C., Miller, P., Olofsson, J., Poska, A., Rundgren, M., Smith, B., Strandberg, G., Fyfe, R., Nielsen, A.B., Alenius, T., Balakauskas, L., Barnekow, L., Birks, H.J.B., Bjune, A., Björkman, L., Giesecke, T., Hjelle, K., Kalnina, L., Kangur, M., van der Knaap, W.O., Koff, T., Lagerås, P., Latałowa, M., Leydet, M., Lechterbeck, J., Lindbladh, M., Odgaard, B., Peglar, S., Segerström, U., von Stedingk, H., Seppä, H. (2010) Holocene land-cover reconstructions for studies on land cover-climate feedbacks. *Climate of the Past* 6, 483-499.

Gavin, D.G. (2001) Estimates of inbuilt age in radiocarbon age of soil charcoal for fire history studies. *Radiocarbon* 43, 27-44.

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. (2004) The Holocene spread of spruce in Scandinavia. Comprehensive summaries of Uppsala Dissertations from the Faculty of Science and Technology. Uppsala, Sweden.

Giesecke, T. (2005a) Holocene forest development in the central Scandes Mountains, Sweden. *Vegetation History and* Archaeiobotany 14, 133-147.

Giesecke, T. (2005b) Holocene dynamics of the southern boreal forest in Sweden. *The 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.

Giesecke, T., Bjune, A.E., Chiverrell, R.C., Seppä, H., Ojala, A.E.K., Birks, H.J.B. (2008) Exploring Holocene continentality changes in Fennoscandia using present and past tree distributions. *Quaternary Science Reviews* 27, 1296-1308.

Girardin, M.P., Ali, A.A., Hély, C. (2010) Wildfires in Boreal ecosystems: Past, present and some emerging trends. *International Journal of Wildland Fire* 19, 991-995.

Girardin, M.P., Ali, A.A., Carcaillet, C., Blarquez, O., Hély, C., Terrier, A., Genries, A., Bergeron, Y. (2013) Vegetation limits the impact of a warm climate on boreal wildfires. *New Phytologist* 199, 1001-1011.

Godwin, H. (1962) Half-life of radiocarbon. *Nature* 195, 984

Granström, A. (2001) Fire management for biodiversity in the European Boreal forest. *Scandinavian Journal of Forest Research* 16, 62-69.

Granström, A. (1993) Spatial and temporal variation in lightning ignitions in Sweden. *Journal of Vegetation Science* 4, 737-744.

Granström, A. (2006) Fire ecology in Sweden and future use of fire for maintaining biodiversity. In Goldammer, J.G., Furyaev, V.V. (eds) Fire in Ecosystems of Boreal Eurasia 48. Springer, Netherlands 445-452.

Granström, A., Niklasson, M. (2008) Potentials and limitations for human control over historic fire regimes in the boreal forest. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363, 2351-2356.

Green, D.G. (1981) Time series and postglacial forest ecology. *Quaternary Research* 15, 265-277.

Green, D.G. (1983) The ecological interpretatoin of fine resolution pollen records. *New Phytologist* 94, 459-477.

Greisman, A., Gaillard, M.-J. (2009) The role of climate variability and fire in early and mid Holcoene forest dynamics of southern Sweden. *Journal of Quaternary Science* 24, 593-611.

Grimm, E. (1987) CONISS: A FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences* 13, 13-35.

Grimm, E.C. (2011) TILIA and TILIA.GRAPH. Illinois State Museum, Springfield.

Grönlund, E. (1991) Sediment characteristics in relation to cultivation history in two varved lake sediments from East Finland. *Hydrobiologia* 214, 137-142.

Gromtsev, A. (2002) Natural disturbance dynamics in the boreal forests of European Russia: a review. *Silva Fennica* 36, 41–55.

Groven, R., Niklasson, M. (2005) Anthropogenic impact on past and present fire regimes in a boreal forest landscape of southeastern Norway. *Canadian Journal of Forest Research* 35, 2719-2726.

Haeggstrom, C.A. (1990) The infleuce of sheep and cattle grazing on wooded meadows in Aland, SW Finland. *Acta Botanica Fennica* 141, 1-28.

Hannon, G.E., Bradshaw, R.H.W., Emborg, J. (2000) 6000 Years of Forest Dynamics in Suserup Skov, a Seminatural Danish woodland. *Global Ecology and Biogeography* 9, 101-114.

Hannon, G.E., Niklasson, M., Brunet, J., Eliasson, P., Lindbladh, M. (2010) How long has the 'hotspot' been 'hot'? Past stand-scale structures at Siggaboda nature reserve in southern Sweden. *Biodiversity Conservation* 19, 2167-2187.

Harrison, S.P., Sanchez Goni, M.F. (2010) Global patterns of vegetation response to millennial-scale variability and rapid climate change during the last glacial period. *Quaternary Science Reviews* 29, 2957-2980.

Heikinheimo, O. (1915) Kaskivikjelyn vaikutus Suonen metsiin. *Metsähallituksen julkaisuja* 2, 1-264.

Heikkilä, M., Seppä, H. (2003) A 11,000 yr palaeotemperature reconstruction from the southern boreal zone in Finland. *Quaternary Science Reviews* 22, 541-554.

Helama, S., Seppä, H., Birks, H.J.B., Bjune, A.E. (2010) Reconciling pollen-stratigraphical and tree-ring evidence for high- and low-frequency temperature variability in the past millennium. *Quaternary Science Reviews* 29, 3905-3918.

Helama, S., Timonen, M., Holopainen, J., Ogurtsov, M.G., Mielikäinen, K., Eronen, M., Lindholm, M., Meriläinen, J. (2009) Summer temperature variations in Lapland during the Medieval Warm Period and the Little Ice Age relative to natural instability of thermohaline circulation on multi-decadal and multi-centennial scales. *Journal of Quaternary Science* 24, 450-456.

Hellberg, E., Niklasson, M., Granstrom, A. (2004) Influence of landscape structure on patterns of forest fires in boreal forest landscapes in Sweden. *Canadian Journal of Forest Research* 34, 332-338.

Hellman, S., Bunting, M.J., Gaillard, M.J. (2009) Relevant source area of pollen in patchy cultural landscapes and signals of anthropogenic landscape disturbance in the pollen record: A simulation approach. *Review of Palaeobotany and Palynology* 153, 245-258.

Hickler, T., Smith, B., Sykes, M.T., Davis, M.B., Sugita, S., Walker, K. (2004) Using a generalized vegetation model to simulate vegetation dynamics in northeastern USA. *Ecology* 85, 519-530.

Higuera, P.E., Sprugel, D.G., Brubaker, L.B. (2005) Reconstructing fire regimes with charcoal from small-hollow sediments: a calibration with tree-ring records of fire. *The Holocene* 15, 238-251.

Higuera, P.E., Peters, M.E., Brubaker, L.B., Gavin, D.G. (2007) Understanding the origin and analysis of sediment-charcoal records with a simulation model. *Quaternary Science Reviews* 26, 1790-1809.

Higuera, P.E., Gavin, D.G., Bartlein, P.J., Hallett, D.J. (2010) Peak detection in sediment-charcoal records: impacts of alternative data analysis methods on fire-history interpretations. *International Journal of Wildland Fire* 19, 996-1014.

Higuera, P. E., Whitlock, C., Gage, J. (2011) Linking tree-ring and sediment–charcoal records to reconstruct fire occurrence and area burned in subalpine forests of Yellowstone National Park, U.S.A. *The Holocene* 21, 327-292.

Hjelle, K.L. (1998) Herb pollen representation in surface moss samples from mown meadows and pastures in western Norway. *Vegetation History and Archaeobotany* 7, 79-96.

Holdridge, L.R. (1967) Life Zone Ecology. Tropical Science Centre, San Jose, Costa Rica 149 pages

Holling, C.S., Meffe, G.K. (1996) Command and control and the pathology of natural resource management. *Conservation Biology* 10, 328-337.

Hörnberg, G., Bohlin, E., Hellberg, E., Bergman, I., Zackrisson, O., Olofsson, A., Wallin. J.-E., Påsse, T. (2007) Effects of Mesolithic hunter-gatherers on local vegetation in a non-uniform glacio-isostatic land uplift area, northern Sweden. *Vegetation History and Archaeobotany* 15, 13-26.

Hörnberg, G., Staland, H., Nordström, E.-M., Korsman, T., Segerström, U. (2011) Fire as an important factor for the genesis of Boreal *Picea abies* swamp forests in Fennoscandia. *The Holocene* 22, 203-214.

Hua, Q. (2009) Radiocarbon: A chronological tool for the recent past. *Quaternary Geochronology* 4, 378-390.

Hua, Q., Zoppi, U., Wiliams, A.A., Smith, A.M. (2004) Small-mass AMS radiocarbon analysis at ANTARES. *Nuclear Instruments and Methods in Physics Research B* 223-224, 284-292.

Huntley, B. (1990) European post-glacial forests: compositional changes in response to climatic change. *Journal of Vegetation Science* 1, 507-518.

Huntley, B., Birks, H.J.B. (1983) An atlas of past and present pollen maps for Europe: 0-13000 years ago. Cambridge University Press. Cambridge.

Hurrell, J.W. (1995) Deadal trends in the North Atlantic Oscillation: Regional Temperatures and precipitation. *Science* 269, 676-679.

Hyvärinen, E., Kouki, J., Martikainen, P. (2009) Prescribed fires and retention trees help to conserve beetle diversity in managed Boreal forests despite their transient negative effects on some beetle groups. *Insect Conservation and Diversity* 2, 93-105.

Iversen, J. (1941) Land occupation in Denmarks Stone Age. *Danmarks Geologiske Undersogelse* 66, 1-68.

Iversen, J. (1964) Retrogressive vegetational succession in the Postglacial. *Journal of Ecology* 52, 59-70.

Jackson, S.T., Hobbs, R.J. (2009) Ecological restoration in the light of ecological history. *Science* 325, 567-569.

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

Jacobson, M.Z. (2004) The short-term cooling but long-term global warming due to biomass burning. *Journal of Climate* 17, 2909-2926.

Jauhiainen, S., Pitkainen, A., Vasanderl, H. (2004) Chemostratigraphy and vegetation in two Boreal mires during the Holocene. *The Holocene* 14, 769-779.

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

Kaila, A., Asam, Z.-u.-Z., Sarkkola, S., Xiao, L., Laurén, A., Vasander, H., Nieminen, M. (2012) Decomposition of harvest residue needles on peatlands drained for forestry – Implications for nutrient and heavy metal dynamics. *Forest Ecology and Management* 277, 141-149.

Kasin, I., Blank, Y-.I., Storaunet, K.O., Rolstad, J., Ohlson, M. (2013) The charcoal record in peat and mineral soil across a Boreal landscape and possible linkages to climate change and recent fire history. *The Holocene* 23, 1052-1065.

Kasischke, E.S., Christensen, N.L., Stocks, B.J (1995) Fire, global warming and the carbon balance of boreal forests. *Ecological Applications* 5, 437-451.

Kerschner, H., Hertl, A., Gross, G., Ivy-Ochs, S., Kubik, P.W. (2006) Surface exposure dating of moraines in the Kromer valley (Silvretta Mountains, Austria) – Evidence for glacial response to the 8.2 ka event in the Eastern Alps? *The Holocene* 16, 7-15.

Könönen, A.V.A., Kirkinen, H (1969) Pohjois-Karjalan historia I. Karjalaisen Kulttuurin Edistämissäätiö. Joensuu pp. 183.

Korhola, A., Vasko, K., Toivonen. T.T., Olander, H. (2002) Holocene temperature changes in northern Fennoscandia reconstructed from chironomids using Bayesian modelling. *Quaternary Science Reviews* 21, 1841-1860.

Kouki, J., Hyvärinen, E., Lappalainen, H., Martikainen, P., Similä, M. (2012) Landscape context affects the success of habitat restoration: large-scale colonization patterns of saproxylic and fire-associated species in Boreal forests. *Diversity and Distributions* 18, 348-355.

Kullman, L. (2000) The geographical history of *Picea abies* in northern Sweden and adjacent parts of Norway. A contrarian hypothesis of postglacial tree-immigration patterns. *Geo*-Öko 21, 141–172.

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.

Lagrås, P. (1996) Farming and forest dynamices in an agriculturally marginal area of southern Sweden, 5000 BC to present: a palynological study of Lake Avegöl in the Småland Uplands. *The Holocene* 6, 301-314.

Larjavaara, M., Kuuluvainen, T., Tanskanen, H., Venäläinen, A. (2004) Variation in forest fire ignition probability in Finland. *Silva Fennica* 38, 253–266.

Larjavaara, M., Pennanen, J., Tuomi, T.J. (2005) Lightning that ignites forest fires in Finland. *Agricultural and Forest Meteorology* 132, 171-180.

Larsen, J., Bjune, A.E., de la Riva Caballero, A. (2006) Holocene environmental and climate history of Trettetjørn, a low-Alpine lake in western Norway, based on subfossil pollen, diatoms, oribatid mites, and plant macrofossils. *Arctic, Antarctic, and Alpine Research* 38, 571-583.

Lehsten, V., Tansey, K., Balzter, H., Thonicke, K., Spessa, A., Weber, U., Smith, B., Arneth, A. (2009) Estimating carbon emissions from African wildfire. *Biogeosciences* 6, 349-360.

Lehtonen, H., Huttunen, P., Zetterberg, P. (1996) Influence of man on forest fire frequency in North Karelia, FInland, as evidenced by fire scars on Scots pines. *Annales Botanici Fennici* 33, 257-263.

Lehtonen, H., Hutunen, P. (1997) History of forest fires in eastern Finland from the fifteenth century AD – The possible effects of slash-and-burn cultivation. *The Holocene* 7, 223-228.

Leys, B., Carcaillet, C., Dezileau, L., Ali, A,A., Bradshaw, R.H.W. (2013) A comparison of charcoal measurements for reconstruction of Mediterranean palaeo-fire frequency in the mountains of Corsica. *Quaternary Research* 79, 337-349.

Lilja-Rothsten, S., de Chantal, M., Peterson, C., Kuuluvainen, T., Vanha-Majamaa, I., Puttonen, P. (2008) Microsites before and after restoration in managed

Picea abies stands in southern Finland: Effects of fire and partial cutting with dead wood creation. *Siliva Fennica* 42, 165-175.

Lindbladh, M. (1999) The influence of former land-use on vegetation and biodiversity in the Boreo-Nemoral zone of Sweden. *Ecography* 22, 485-498.

Lindbladh, M., Bradshaw, R.H.W. (1998) The origin of present forest composition and pattern in southern Sweden. *Journal of Biogeography* 25, 463-477.

Lindbladh, M., Bradshaw, R.H.W., Holmqvist, B.H. (2000) Pattern and process in South Swedish forest during the last 3000 years, sensed at stand and regional scale. *Journal of Ecology* 88, 113-128.

Lindbladh, M., Niklasson, M., Nilsson, S.G. (2003) Long-time record of fire and open canopy in a high biodiversity forest in southeast Sweden. *Biological Conservation* 114, 231-243.

Linderholm, H.W., Molin, T. (2005) Early nineteenth century drought in east central Sweden infeered from dendrochronological and historical archives. *Climate Research* 29, 63-72.

Liu, Q., Hytteborn, H. (1991) Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. *Journal of Vegetation Science* 2, 391-402.

Lundqvist, J. (1986) Late Weichselian glaciation and deglaciation in Scandinavia. *Quaternary Science Reviews* 5, 269-292.

Lunkka, J.P., Johansson, P., Saarnisto, M., Sallasmaa, O. (2004) Glaciation of Finland. In: Quaternary glaciations: extent and chronology. Developments in Quaternary Science 2. Elsevier, Amsterdam, 93–100.

Luomajoki, A. (1993) Climate adaption of Norway spruce (*Picea abies* (L.) Karsten) in Finland based on male flowering phenology. *Acta Forestalia Fennica* 242, 1-26.

Luoto, T.P., Sarmaja-Korjonen, K., Nevalainen, L., Kauppila, T. (2009) A 700 year record of temperature and nutrient changes in a small eutrophied lake in southern Finland. *The Holocene* 19, 1063-1072.

Maizer, F., Kuneš, P., Sugita, S., Trondman, A.-K., Bronström, A., Gaillard, M.-J. (2010) Pollen-inferred quantitative reconstructions of Holocene land-cover in NW Europe for the evaluation of past climate-vegetation feedbacks –

evaluation of the REVEALS-based reconstruction using the Czech Republic database. *Geophysical Research Abstracts* Vol. 12: EGU2010-4248.

Marlon, J.R., Bartlein, P.J., Walsh, M.K., Harrison, S.P., Brown, K.J., Edwards, M.E., Higuera, P.E., Power, M.J., Anderson, R.S., Briles, C., Brunelle, A., Carcaillet, C., Daniels, M., Hu, F.S., Lavoie, M., Long, C., Minckley, T., Richard, P.J.H., Scott, A.C., Shafer, D.S., Tinner, W., Umbanhowar, C.E., Whitlock, C. (2009) Wildfire responses to abrupt climate change in North America. *Proceedings of the National Academy of Sciences* 106, 2519-2524.

Marlon, J.R., Bartlein, P.J., Daniau, A.-L., Harrison, S.P., Maezumi, S.Y., Power, M.J., Tinner, W., Vanniére, B. (2013) Global biomass burning: a synthesis and review of Holocene paleofire records and their controls. *Quaternary Science Reviews* 65, 5-25.

Marshall, J., Kushnir, Y., Battisti, D., Chang, P., Czaja, A., Dickson, R., Hurrell, J., McCatney, M., Saravana, R., Visbeck, M. (2001) North Atlantic climate variability: phenomena, impacts and mechanisms. *International Journal of Climatology* 21, 1863-1898.

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 on Holocene vegetation change in Fennoscandia. *Journal of Ecology* 96, 247-259.

Millspaugh, S.H., Whitlock, C. (1995) A 750-year fire history based on lake sediment records in central Yellowstone National Park, USA. *The Holocene* 5, 283–292.

Mitchell, F.J.G. (2005) How open were European primeval forests? Hypothesis testing using palaeoecological data. *Journal of Ecology* 93, 168-177.

Mitchell, F.J.G., Cole, E. (1998) Reconstruction of long-term successional dynamics of temperate woodland in Białowieża Forest, Poland. *Journal of Ecology* 86, 1042-1059.

Molinari, C., Bradshaw, R.H.W., Risbøl, O., Lie, M., Ohlson, M. (2005) Long-term vegetational history of a *Picea abies* stand in south-eastern Norway: Implications for the conservation of biological values. *Biological Conservation* 126, 155-165.

Molinari, C., Lehsten, V., Bradshaw, R.H.W., Power, M.J., Harmand, P., Arneth, A., Kaplan, J.O., Vannière, B., Sykes, M.T. (2013) Exploring potential drivers of European biomass burning over the Holocene: a data-model analysis. *Global Ecology and Biogeography* DOI: 10.1111/geb.12090.

Mooney, S., Radford, K. (2001) A simple and fast method for the quantification of macroscopic charcoal in sediments. *Quaternary Australasia* 19, 43-46.

Mooney, S., Black, M. (2003) A simple and fast method for calculating the area of macroscopic charcoal isolated from sediments. *Quaternary Australasia* 21, 18-21.

Moore, B. (1927) Cajander's theory of forest types. *Ecology* 8, 135-137.

Moore, P.D., Webb, J.A., Collinson, M.E. (1991) Pollen Analysis. Blackwell Scientific Publications, Oxford.

Nesje, A., Matthews, J.A., Dahl. S.O., Berrisford, M.S., Andersson, C. (2001) Holocene glacier fluctuations of Flatebreen and winter-precipitation changes in the Jostedalsbreen region, western Norvay, based on glaciolacustrine sediment records. *The Holocene* 11, 267-280.

Nesje, A., Bjune, A.E., Bakke, J., Dahl, S.O., Lie, Ø., Birks, H.J.B. (2006) Holocene palaeoclimate reconstructions at Vanndalsvatnet, western Norway, with particular reference to the 8200 cal. yr BP event. *Holocene* 16, 717-729.

Nielsen, A.B., Odgaard, B.V. (2005) Reconstructing land cover from pollen assemblages from small lakes in Denmark. *Review of Palaeobotany and Palynology* 133, 1-21.

Nielsen, A.B., Sugita, S. (2005) Estimating relevant source area of pollen for small Danish lakes around AD 1800. *The Holocene* 15, 1006-1020.

Niklasson, M., Granström, A. (2000) Numbers and sizes of fires: Long-term spatially explicit fire history in a Swedish Boreal landscape. *Ecology* 81, 1484-1499.

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., Drobyshev, I., Zielonka, T. (2010) A 400-year history of fires on lake islands in South-East Sweden. *International Journal of Wildland Fire* 19, 1050-1058.

Nilsson, S.G. (1997) Forests in the Temperate-Boreal transition: Natural and man-made features. *Ecological Bulletins* 46, 61-71.

Öberg, L., Kullman, L. (2011) Antcient subalpine clonal spruces (*Picea abies*): Sources of pogtglacial vegetation history in the Swedish Scandes, *Arctic* 64, 183-196.

Ohlson, M., Zackrisson, O. (1992) Tree estabishment and microhabitat relationships in North Swedish peatland. *Canadian Journal of Forest Resarch* 22, 1869-1877.

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. *The Holocene* 10, 519-525.

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

Ohlson, M., Brown, K.J., Birks, H.J.B., Grytnes, J.-A., Hörnberg, G., Niklasson, M., Seppä, H., Bradshaw, R.H.W. (2011) Invasion of Norway spruce diversifies the fire regime in boreal European forests. *Journal of Ecology* 99, 395-403.

Ohlson, M., Kasin, I., Wist, A.N., Bjune, A.E. (2013) Size and spatial structure of the soil and lacustrine charcoal pool across a Boreal forest watershed. *Quaternary Research,* doi.org/10.1016/j.yqres.2013.08.009.

Ojala, A.E.K., Tiljander, M. (2003) Testing the fidelity of sediment chronology: Comparison of varve and paleomagnetic results from Holocene lake sediments from central Finland. *Quaternary Science Reviews*, 22, 1787-1803.

Ojala, A.E.K., Alenius, T. (2005) 10 000 years of interannual sedimentation recorded in the Lake Nautajärvi (Finland) clastic-organic varves. *Palaeogeography, Palaeoclimatology, Palaeoecology* 219, 285-302.

Oldfield, F. (1970) Some aspects of scale and complexity in pollen-analytically based palaeoecoogy. *Pollen et Spores* 12, 163-172.

Östlund, L., Zackrisson, O., Axelsson, A.-L. (1997) The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research* 27, 1198-1206.

Overballe-Petersen, M.V.A.B., Bradshaw, R.H.W. (2011) The selection of small forest hollows for pollen analysis in boreal and temperate forest regions. *Palynology* 35, 146-153.

Overballe-Petersen, M.V., Nielsen, A.-B., Bradshaw, R.H.W. (2012) Quantitative vegetation reconstruction from pollen analysis and historical inventory data around a Danish small forest hollow. *Journal of Vegetation Science* 24, 755-771.

Overballe-Petersen, M.V., Nielsen, A.B., Hannon, G.E., Halsall, K., Bradshaw, R.H.W. (2013) Long-term forest dynamics at Gribskov, eastern Denmark with early-Holocene evidence for thermophilous broadleaved tree species. *The Holocene* 23, 243-254.

Overland, A., Hjelle, K. (2009) From forest to open pastures and fields: cultural landscape development in western Norway inferred from two pollen records representing different spatial scales of vegetation. *Vegetation History and Archaeobotany* 18, 459-476.

Palviainen, M., Finér, L., Laiho, R., Shorohova, E., Kapitsa, E., Vanha-Majamaa, I. (2009) Carbon and nitrogen release from tree stumps in boreal clear-cut forests. International Symposium 'Rout Research and Applications' RootRAP 2-4 September Boku, Vienna, Austria.

Parducci, L., Jørgensen, T., Tollefsrud, M.M., Elverland, E., Alm, T., Fontana, S.L., Bennett, K.D., Haile, J., Matetovici, I., Suyama, Y., Edwards, M.E., Andersen, K., Rasmussen, M., Boessenkool, S., Coissac, E., Brochmann, C., Taberlet, P., Houmark-Nielsen, M., Larsen, N.K., Orlando, L., Gilbert, M.T.P., Kjær, K.H., Alsos, I.G., Willerslev, E. (2012) Glacial Survival of Boreal Trees in Northern Scandinavia. *Science* 335, 1083-1086.

Parsons, R.W., Prentice, I.C. (1981) Statistical approaches to R-values and pollen vegetation relatioship. *Review of Palaeobotany and Palynology* 32, 127-152.

Paus, A., Velle, G., Larsen, J., Nesje, A., Lie, Ø. (2006) Lateglacial nunataks in central Scandinavia: Biostratigraphical evidence for ice thickness from Lake Flåfattjønn, Tynset, Norway. *Quaternary Science Reviews* 25, 1228-1246.

Parviainen, J. (1996) Impact of fire on Finnish forests in the past and today. *Siliva Fennica* 30, 353-359.

Patterson, T.R., Fishbein, E. (1989) Re-examination of the statistical methods used to determine the number of point counts needed for micropalaeontological quantitative research. *Journal of Paleontology* 63, 245-248.

Petit, J.R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J.M., Basile, I., Bender, M., Chappellaz, J., Davis, M., Delaygue, G., Delmotte, M., Kotlyakov, V.M., Legrand, M., Lipenkov, V.Y., Lorius, C., Pepin, L., Ritz, C., Saltzman, E., Stievenard, M. (1999) Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica, *Nature* 399, 429-436.

Pirinen, P., Henriikka, S., Aalto, J., Kaukoranto J-P., Karlsson, P., Ruuhela, R. (2012) Climatological statistics of Finland 1981-2010. Finnish Meteorological Institute, Climate Change.

Pitkänen, A. (2000) Fire frequency and forest structure at a dry site between AD 440 and 1110 based on charcoal and pollen records from a laminated lake sediment in eastern Finland. *The Holocene* 10, 221-228.

Pitkänen, A., Huttunen, P. (1999) A 1300-year forest-fire history at a site in eastern Finland based on charcoal and pollen records in laminated lake sediment. *The Holocene* 9, 311-320.

Pitkänen, A., Lehtonen, H., Huttunen, P. (1999) Comparison of sedimentary microscopic charcoal particle records in a small lake with dendrochronological data: Evidence for the local origin of microscopic charcoal produced by forest fires of low intensity in eastern Finland. *The Holocene* 9, 559-567.

Pitkänen, A., Huttunen, P., Jungner, H., Tolonen, K. (2002) A 10,000 year local forest fire history in a dry heath forest site in eastern Finland, reconstructed from charcoal layer records of a small mire. *Canadian Journal of Forest Research* 32, 1875-1880.

Power, M., Marlon, J., Ortiz, N., Bartlein, P., Harrison, S., Mayle, F., Ballouche, A., Bradshaw, R., Carcaillet, C., Cordova, C., Mooney, S., Moreno, P., Prentice, I., Thonicke, K., Tinner, W., Whitlock, C., Zhang, Y., Zhao, Y., Ali, A., Anderson, R., Beer, R., Behling, H., Briles, C., Brown, K., Brunelle, A., Bush, M., Camill, P., Chu, G., Clark, J., Colombaroli, D., Connor, S., Daniau, A.L., Daniels, M., Dodson, J., Doughty, E., Edwards, M., Finsinger, W., Foster, D., Frechette, J., Gaillard, M.J., Gavin, D., Gobet, E., Haberle, S., Hallett, D., Higuera, P., Hope, G., Horn, S., Inoue, J., Kaltenrieder, P., Kennedy, L., Kong, Z., Larsen, C., Long, C., Lynch, J., Lynch, E., McGlone, M., Meeks, S., Mensing, S., Meyer, G., Minckley, T., Mohr, J., Nelson, D., New, J., Newnham, R., Noti, R., Oswald, W., Pierce, J., Richard, P., Rowe, C., Sanchez Goñi, M., Shuman, B., Takahara, H., Toney, J., Turney, C., Urrego-Sanchez, D., Umbanhowar, C., Vandergoes, M., Vanniere, B., Vescovi, E., Walsh, M., Wang, X., Williams, N., Wilmshurst, J., Zhang, J. (2008) Changes in fire regimes since the Last Glacial Maximum: An assessment based on a global synthesis and analysis of charcoal data. *Climate Dynamics* 30, 887-907.

Power, M.J., Marlon, J.R., Bartlein, P.J., Harrison, S.P. (2009) Fire history and the Global Charcoal Database: A new tool for hypothesis testing and data exploration. *Palaeogeography, Palaeoclimatology, Palaeoecology* 291, 52-59.

Prentice, I.C. (1985) Pollen representation, source area, and basin size: Toward a unified theory of pollen analysis. *Quaternary Research* 23, 76-86.

Prentice, I.C., Parsons, R.W. (1983) Maximum likelihood linear calibration of pollen spectra in terms of forset composition. *Biomectrics* 39, 1051-1057.

Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A., Solomon, A.M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography* 19, 117-134.

Prentice, C.I., Sykes, M.T., Cramer, W. (1993) A simulation model for the transient effects of climate change on forest landscapes. *Ecological Modelling* 65, 51-70.

Prentice, I.C., Guiot, J., Huntley, B., Jolly, D., Cheddadi, R. (1996) Reconstructing biomes from palaeoecological data: A general method and its application to European pollen data at 0 and 6 ka. *Climate Dynamics* 12, 185-194.

Prentice, I.C., Webb, T. (1998) BIOME 6000: Reconstructing global mid-Holocene vegetation patterns from palaeoecological records. *Journal of Biogeography* 25, 997-1005.

Prentice, I.C., Kelley, D.I., Foster, P.N., Friedlingstein, P., Harrison, S.P., Bartlein, P.J. (2011) Modeling fire and the terrestrial carbon balance. *Global Biogeochemical Cycles* 25, 1-16 GB3005.

Pyne, S., Andrews, P.L., Laven, R.D. (1996) Introduction to wildland fire. John Wiley & Sons, New York-Chichester-Brisbane-Toronto-Singapore.

Päätalo, M-.L. (1998) Factors influencing occurrence and impacts of fires in northern European forests. *Silva Fennica* 32(2), 185-202

R Deveopment Core Team. (2010) R: A languate and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rajala, T., Peltoniemi, M., Pennanen, T., Mäkipää, R. (2012) Fungal community dynamics in relation to substrate quality of decaying Norway spruce (*Picea abies* [L.] Karst.) logs in Boreal forests. *FEMS Microbiology Ecology* 81, 494-505.

Randerson, J.T., Liu, H., Flanner, M.G., Chambers, S.D., Jin, Y., Hess, P.G., Pfister, G., Mack, M.C., Treseder, K.K., Welp, L.R., Chapin, F.S., Harden, J.W., Goulden, M.L., Lyons, E., Neff, J.C., Schuur, E.A.G., Zender, C.S. (2006) The impact of Boreal forest fire on climate warming. *Science* 314, 1130-1132.

Rankama, T., Vuorela, I. (1988) Between inland and coast in Metal Age Finland of Southern Ha'me during the Iron Age. *Memoranda Societatis Pro Fauna et Flora Fennica* 64, 25-34.

Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Burr, G.S., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., McCormac, F.G., Manning, S.W., Reimer, R.W., Richards, D.A., Southon, J.R., Talamo, S., Turney, C.S.M., van der Plicht, J., Weyhenmeyer, C.E. (2009) IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP. *Radiocarbon* 51, 1111–1150.

Reitalu, T., Seppä, H., Sugita, S., Kangur, M., Koff, T., Avel, E., Kihno, K., Vassiljev, J., Renssen, H., Hammarlund, D., Heikkilä, M., Saarse, L., Poska, A., Veski, S. (2013) Long-term drivers of forest composition in a boreonemoral region: the relative importance of climate and human impact. *Journal of Biogeography* 40, 1524-1534.

Risberg, L., Granström, A. (2012) Seed dynamics of two fire-dependent Geranium species in the Boreal forest of southeastern Sweden. *Botany* 90, 794-805.

Roopnarine, P.D., Angielczyk, K.D. (2011) The evolutionary palaeoecology of species and the tragedy of the commons. *Biology Letters* 23, 147-150.

Rosén, P., Segerström, U., Eriksson, L., Renberg, I., Birks, H.J.B. (2001) Holocene climatic change reconstructed from diatoms, chironomids, pollen and near-infrared spectroscopy at an Alpine lake (Sjuodjijaure) in northern Sweden. *The Holocene* 11, 551-562.

Rowe, J.S., Scotter, G.W. (1973) Fire in the Boreal forest. *Quaternary Research* 3, 444-464.

Ruddiman, W.F. (2003) The anthropogenic greenhouse era began thousands of years ago, *Climate Change* 61, 261 – 293.

Ruokolainen, L., Salo, K. (2006) The succession of boreal forest vegetation during ten years after slash-burning in Koli National Park, eastern Finland. *Annales Botanici Fennici* 43, 363-378.

Räsänen, S., Suutari, H., Nielsen, A.B. (2007) A step further towards quantitative reconstruction of past vegetation in Fennoscandian Boreal forests: Pollen productivity estimates for six dominant taxa. *Review of Palaeobotany and Palynology* 146, 208-220.

Sarmaja-Korjonen, K. (1998) Latitudinal differences in the influx of microscopic charred particles to lake sediments in Finland. *The Holocene* 8, 589-597.

Sarmaja-Korjonen, K. (2003a) Contemporaneous *Alnus* decline and the beginning of Iron Age cultivation in pollen stratigraphies from southern Finland. *Vegetation History and Archaeobotany* 12, 49-59.

Sarmaja-Korjonen, K., Kultti, S., Solovieva, N., Väliranta, M. (2003b) Mid-Holocene palaeoclimatic and palaeohydrological conditions in northeastern European Russia: A multi-proxy study of Lake Vankavad. *Journal of Paleolimnology* 30, 415-426.

Sarmela, M. (1987) Swidden cultivation in Finland as a cultural system. *Suomen antropologi* 4

Scott, A.C. (2000) The pre-Quaternary history of fire. *Palaeogeography, Palaeoclimatology, Palaeoecology* 164, 281-329.

Scott, A.C., Jones, T.P. (1994) The natural and influence of fire in Carboniferous ecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology* 106, 91-112.

Scott, A.C., Glasspool, I.J. (2006) The diversification of Paleozoic fire systems and fluctuations in atmospheric oxygen concentration. *Proceedings of the National Academy of Sciences*, *U.S.A*. 103, 10861-10865.

Seppä, H., Birks, H.J.B. (2001) July mean temperature and annual precipitation trends during the Holocene in the Fennoscandian tree-line area: Pollen-based climate reconstructions. *The Holocene* 11, 527-539.

Seppä, H., Hannon., G.E., Bradshaw, R.H.W. (2004) Holocene history of Alpine vegetation and forestline on Pyhäkero mountain, northern Finland. *Arctic, Antarctic, and Alpine Research* 36, 607-614.

Seppä, H., Birks, H.J.B., Giesecke, T., Hammarlund, D., Alenius, T., Antonsson, K., Bjune, A.E., Heikkila, M., Macdonald, M.G., Ojala, A.E.K., Telford, R.J., Veski, S. (2007) Spatial structure of the 8200 cal. yrs. BP event in Northern Europe. *Climate of the Past* 3, 165-195.

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.

Shorohova, E., Kapitsa, E., Vanha-Majamaa, I. (2008) Decompostion of stumps in a chronosequence after clear-felling vs. clear-felling with prescribed burning in a southern Boreal forest in Finland. *Forest Ecology and Management* 255, 3606-3612.

Shugart, H.H. (1984) *A Theory of forest dynamics. The Ecological Implications of Forest Succession Models*. Springer, New York.

Similä, M., Junninen, K. (2012). Ecological restoration and management in Boreal forests - best practices from Finland. Metsähallitus, Natural Heritage Services, Vantaa.

Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K., Venevsky, S. (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology* 9, 161-185.

Smith, B., Prentice, I.C., Sykes, M.T. (2001) Representation of vegetation dynamics in the modelling of terrestrial ecosystems: Comparing two contrasting approaches within European climate space. *Global Ecology and Biogeography* 10, 621-637.

Soepboer, W., Sugita, S., Lotter, A.F. (2010) Regional vegetation-cover changes on the Swiss Plateau during the past two millennia: A pollen-based reconstruction using the REVEALS model. *Quaternary Science Reviews* 29, 472-483.

Stockmarr, J. (1971) Calcium tablets with spores used in absolute pollen analysis. *Pollen et Spores* 13, 615-621.

Stocks, B.J., Fosberg, M.A., Lynham, T.J., Merns, L., Wotton, B.M., Yang, Q., Jin, J.-Z., Lawrence, K., Hartley, G.R., Mason, J.A., McKenney, D.W. (1998) Climate change and forest fire potenitial in Russian and Canadian boreal forest. *Climate Change* 38, 1-13.

Storaunet, K.O., Rolstad, J., Toeneiet, M., Blanck, Y.-L. (2013) Strong anthropogenic signals in historic forest fir regime: a detailed spatiotemporal case study from south-central Norway. *Canadian Journal of Forest Research* 43, 836-845.

Sugita, S. (1993) A model of pollen source area for an entire lake surface. *Quaternary Research* 39, 239-244.

Sugita, S. (1994) Pollen representation of vegetation in Quaternary sediments: Theory and method in patchy vegetation. *Journal of Ecology* 82, 881-897.

Sugita, S., Gaillard, M.-J., Broström, A. (1999) Landscape openness and pollen records: A simulation approach. *The Holocene* 9, 409-421.

Sugita, S. (2007a) Theory of quantitative reconstruction of vegetation I: Pollen from large sites REVEALS regional vegetation composition. *The Holocene* 17, 229-241.

Sugita, S. (2007b) Theory of quantitative reconstruction of vegetation II: All you need is LOVE. *The Holocene* 17, 243-257.

Sugita, S., Hicks, S., Sormunen, H. (2010) Absolute pollen productivity and pollen–vegetation relationships in northern Finland. *Journal of Quaternary Science* 25, 724-736.

Swain, A.M. (1973) A history of fire and vegetation in northeastern Minnesota as recorded in lake sediments. *Quaternary Research* 3, 383-396.

Swain, A.M. (1978) Environmental changes during the past 2000 years in North-central Wisconsin: Analysis of pollen, charcoal, and seeds from varved lake sediments. *Quaternary Research* 10, 55-68.

Sykes, M.T., Prentice, I.C., Cramer, W. (1996) A bioclimatic model for the potential distributions of north European tree species under present and future climates. *Journal of Biogeography* 23, 203-233.

Taavitsainen, J.-P., Simola, H., Grönlund, E. (1998) Cultivation history beyond the periphery: Early agriculture in the North European Boreal forest. *Journal of World Prehistory* 12, 199-253.

Tallantire, PA (1972) Spread of Spruce (*Picea abies* (L.) Karst) in Fennoscandia and possible climatic implications. *Nature* 236, 64-65.

Tallavaara, M., Seppä, H (2011) Did the mid-Holocene environmental changes cause the boom and bust of hunter-gatherer population size in eastern Fennoscandia? *The Holocene* 22, 215-225.

Tanskanen, H. (2007) Fuel conditions and fire behavior characteristic of managed *Picea abies* and *Pinus sylvestris* forests in Finland. Dissertationes Forestales 40, University of Helsinki, Finland.

Tanskanen, H., Venalainen, A., Puttonen, P., Granstrom, A. (2005) Impact of stand structure on surface fire ignition potential in *Picea abies* and *Pinus sylvestris* forests in southern Finland. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 35, 410-420.

Tanskanen, H., Granström, A., Venäläinen, A., Puttonen, P. (2006) Moisture dynamics of moss-dominated surface fuel in relation to the structure of *Picea abies* and *Pinus sylvestris* stands. *Forest Ecology and Management* 226, 189-198.

Tauber, H. (1965) Differential pollen deposition and the interpretation of pollen diagrams, *Dansmarks Geologiske Undersoglse II* 89, 1-69.

Tauber, H. (1967) Investigations of the mode of pollen transfer in forested areas, *Pollen et Spores* 13, 615-621.

Tauber, H. (1977) Investigations of aerial pollen transport in a forested area, *Dansk botanisk Arkiv* 32, 1-121.

Telford, R.J., Heegaard, E., Birks, H.J.B. (2004a) All age-depth models are wrong: but how badly? *Quaternary Science Reviews* 23, 1-5.

Telford, R.J., Heegaard, E., Birks, H.J.B. (2004b) The intercept is a poor estimate of a calibrated radiocarbon age, *The Holocene* 14, 296-298.

ter Braak, C.J.F., Šmilauer, P. (2002) CANOCO reference manual and CanoDraw for Windows user's guide: Software for canonical community ordination (version 4.5). Microcomputer Power.

Thevenon, F., Anselmetti, F.S. (2007) Charcoal and fly-ash particles from Lake Lucerne sediments (central Switzerland) characterized by image analysis: Anthropogenic, stratigraphic and environmental implicaitons. *Quaternary Science Revews* 26, 2631-2643.

Thonicke, K., Spessa, A., Prentice, I.C., Harrison, S.P., Dong, L., Carmona-Moreno, C. (2010) The influence of vegetation, fire spread and fire behaviour on biomass burning and trace gas emissions: Results from a process-based model. *Biogeoscience* 7, 1991-2011

Timonen, J., Gustafsson, L., Kotiaho, J.S., Mönkkönen, M. (2011) Hotsopts in cold climate: Conservation value of woodland key habitats in Boreal forests, *Biological Conservation* 144, 2061-2067.

Tinner, W., Lotter, A.F. (2001) Central European vegetation response to abrupt climate change at 8.2ka. *Geological Society of America* 29, 551-554.

Tolonen, K. (1967) Uber die Entwicklung der Moore im finnischen Nordkarelien. *Annales Botanici Fennici* 4, 219–416.

Tolonen, K. (1983a) The post-glacial fire record. In: Wein, R.W., MacLean, D.A. (Eds.) The Role of Fire in Northern Circumpolar Ecosystems. John Wiley, New York, 21-44.

Tolonen, K. (1983b) The history of Norway spruce, *Picea abies*, in Finland. *Sorbifolia* 14, 53–59.

Tolonen, M. (1978) Palaeoecology of annually laminated sediments in Lake Ahvenainen, S.Finland 1. Pollen and charcoal analysis and their relation to human impact. *Annales Botanici Fennici* 15, 177-208.

Tolonen, M. (1980) Post-glacial pollen stratigraphy of Lake Lamminharvi, S.Finland. *Annales Botanici Fennici* 17, 15-25.

Tolonen, M. (1985) Palaeoecological reocrd of local fire hisory from a peat deposit in SW Finland. *Annales Botanici Fennici* 22, 15-29.

Tryterud, E. (2003) Forest fire history in Norway: From fire-disturbed pine forests to fire-free spruce forests. *Ecography* 26, 161-170.

Uotila, A., Kouki, J., Kontkanen, H., Pulkkinen, P. (2002) Assessing the naturalness of Boreal forests in eastern Fennoscandia. *Forest Ecology and Management* 161, 257-277.

Vanha-Majamaa, I., Lilja, S., Ryömä, E., Kotiaho, J.S., Laaka-Lindberg, S., Lindberg, H., Puttonen, P., Tamminen, P., Toivanen, T., Kuuluvainen, T. (2007) Rehabilitating Boreal forest sturcture and species composition in Finland through logging, dead wood creation and fire: The EVO experiment. *Forest Ecology and Management* 250, 77-88.

van Wagner, C.E. (1979) A laboratory study of weather effects on the drying rate of Jack Pine *(Pinus Banksiana)* Litter. *Canadian Journal of Forest Research* 9, 267-275.

van Wagner, C.E. (1982) Initial moisture content and the exponential drying process. *Canadian Journal of Forest Research* 12, 90-92.

Vannière, B., Power, M.J., Roberts, N., Tinner, W., Carrión, J., Magny, M., Bartlein, P., Colombaroli, D., Daniau, A.L., Finsinger, W., Gil-Romera, G., Kaltenrieder, P., Pini, R., Sadori, L., Turner, R., Valsecchi, V., Vescovi, E. (2011) Circum-Mediterranean fire activity and climate changes during the mid-Holocene environmental transition (8500-2500 cal. BP). *The Holocene* 21, 53-73.

Vasari, Y. (1962) A study of the vegetational history of the Kuusamo district (North east Finland) during the late Quaternary period. *Annales Botanici Societatis Zoologicae Botanicae Fennicae Vanamo* 33, 1–138

Vera, F.W.M. (2000) Grazing Ecology and Forest History. CAB International, Wallingford, 506 pages

Veski, S., Seppä, H., and Ojala, A. E. K. (2004) Cold event at 8200 yr B.P. recorded in annually laminated lake sediments in eastern Europe, *Geology* 32, 681–684.

Visbeck, M.H., Hurrell, J.W., Polvani, L., Cullen, H.M. (2001) The North Atlantic Oscillation: Past, present, and future. *Proceedings of the National Academy of Sciences* 98, 12876-12877.

von Post, L. (1916) Forest tree pollen in south Sweden peatbog strata sequences. *Pollen et Spores* 9, 375-401.

von Stedingk, H., Fyfe, R.M., Allard, A. (2008) Pollen productivity estimates from the forest—tundra ecotone in West-central Sweden: Implications for vegetation reconstruction at the limits of the boreal forest. *The Holocene* 18, 323-332.

Walker, M., Johnsen, S., Rasmussen, S. O., Popp, T., Steffensen, J.-P., Gibbard, P., Hoek, W., Lowe, J., Andrews, J., Björck, S., Cwynar, L. C., Hughen, K., Kershaw, P., Kromer, B., Litt, T., Lowe, D. J., Nakagawa, T., Newnham, R., Schwander, J. (2009) Formal definition and dating of the GSSP (Global Stratotype Section and Point) for the base of the Holocene using the Greenland NGRIP ice core, and selected auxiliary records. *Journal of Quaternary Science* 24, 3–17.

Wallenius, T.H. (2002) Forest age distribution and traces of past fires in a natural Boreal landscape dominated by *Picea abies*. *Siliva Fennica* 36, 201-211.

Wallenius, T. (2011) Major decline in fires in confierous forests - Reconstructing the phenomenon and seeking for the cause. *Silva Fennica* 45, 139-155.

Wallenius, T.H., Kuuluvainen, T., Vanha-Majamma, I. (2004) Fire history in relation to site type and vegetation in Vienansalo windlerness in eastern Fennoscandia, Russia. *Canadian Journal Forestry Restoration* 34, 1400-1409.

Wallenius, T.H., Pitkänen, A., Kuuluvainen, T., Pennanen, J., Karttunen, H. (2005) Fire history and forest age distribution of an unmanaged *Picea abies* dominated landscape. *Canadian Journal of Forest Research* 35, 1540-1552.

Wallenius, T.H., Lilja, S., Kuuluvainen, T. (2007) Fire history and tree species composition in managed *Picea abies* stands in southern Finland: Implications for restoration. *Forest Ecology and Management* 250, 89-95.

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.

Whitlock, C. (2004) Land management - Forests, fires and climate. *Nature* 432, 28-29.

Whitlock, C., Millspaugh, S.H. (1996) Testing the assumptions of fire-history studies: An examination of modern charcoal accumulation in Yellowstone National Park, USA. *The Holocene* 6, 7-15.

Whitlock, C., Larson, C. (2001) Charcoal as a fire proxy. In Smol, J.P., Birks, H.J.B., Last, W.M. (eds.). Tracking environmental change using lake sediments. Volume 3: Terrsetrial, algae and siliceous indicators, Kluwer Academic Publishers, Dordrecht, The Netherlands. 1-23.

Whitlock, C., Bartlein, P.J. (2004) Holocene fire activity as a record of past environmental change. In Gillespie, A., Porter, S.D. (eds.) Developments in Quaternary Science Volume 1. Elsevier, 479-489.

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.

Willis, K.J., Bailey, R.M., Bhagwat, S.A., Birks, H.J.B. (2010) Biodiversity baselines, thresholds and resilience: Testing predictions and assumptions using palaeoecological data. *Trends in Ecology & Evolution* 25, 583-591.

Wohlfarth, B., Skog, G., Possnert, G., Holmquist, B. (1998) Pitfalls in the AMS radiocarbon-dating of terestrial macrofossils. *Journal of Quaternary Science* 13, 137-145.

Woodward, F.I., Lomas, M.R., Kelly, C.K. (2004) Global climate and the distribution of plant biomes. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 359, 1465-1476.

Yeloff, D., Bennett, K.D., Blaauw, M., Mauquoy, D., Sillasoo, Ü., van der Plicht, J., van Geel, B. (2006) High precision ^{14}C dating of Holocene peat deposits: A comparison of Bayesian calibration and wiggle-matching approaches. *Quaternary Geochronology* 1, 222–235.

Yeloff, D., Charman, D., van Geel, B., Mauquoy, D. (2007) Reconstruction of hydrology, vegetation and past climate change in bogs using fungal microfossils. *Review of Palaeobotany and Palynology* 146, 102-145.

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

Zillén, L., Snowball, I. (2009) Complexity of the 8 ka climate event in Sweden recorded by varved lake sediments. *Boreas* 38, 493-503.

Appendix 1

Charcoal

Denmark

Site_No	Name	Reference	Easting	Northing	Depositional Environment	Elevation (m)	Radiocarbon Dates	Char_Method	Char_size	Temp_start	Temp_end	Temp_extent	Digitisation method
1a	Suserup Skov	Hannon *et al.*2000	11.565361	55.362682	Forest Hollow	22	6	SIEV	>200µm	3	6109	6106	Digitised againts Age
1b	Suserup Skov	Hannon *et al.*2000	11.565361	55.362682	Forest Hollow	22	6	SIEV	<200µm	-24	6029	6053	Digitised againts Age
2	Solsø	Odgaard 1992	8.633333	56.133333	Lake	NOTK	27	POLS	NOTK	0	8319	8319	Age/Depth Calculated
3	Skånsø	Odgaard 1992	8.828889	56.509722	Lake	NOTK	23	POLS	NOTK	0	6423	6423	Age/Depth Calculated
4	Dallund Sø	Bradshaw *et al.* 2005	10.266593	55.482924	Lake	12	20	SIEV	>500µm	-12	6836	6848	Digitised againts Age
5	Kragsø	Odgaard 1994	9.022755	56.212673	Lake	NOTK	13	POLS	NOTK	13	9361	9348	Digitised againts Age
6	Gribskov	Overballe-Petersen *et al.* 2013	12.333333	56.000000	Forest Hollow	NOTK	10	SIEV	>125µm	-56	7109	7165	Digitised againts Age

Norway

Site_No	Name	Reference	Easting	Northing	Depositional_Environment	Elevation (m)	Radiocarbon_Dates	Char_Method	Char_size	Temp_start	Temp_end	Temp_extent	Digitisation method
7a	Grostjørna	Eide *et al*. 2006	7.733333	58.533333	Lake	180	7	SIEV	Macro	0	11492	11492	Age/Depth Calculated
7b	Grostjørna	Eide *et al.* 2006	7.733333	58.533333	Lake	180	7	POLS	Micro	0	11737	11737	Age/Depth Calculated
8	Kilden	Jensen 2004	23.600000	70.700000	Mire	15	5	POLS	>20µm	0	9927	9927	Age/Depth Calculated
9	Nor-Mon	Jensen 2004	23.600000	70.700000	Mire	13	3	POLS	>20µm	1212	4168	2956	Age/Depth Calculated
10	Sundm	Jensen 2004	23.600000	70.700000	Peat	19	4	POLS	>20µm	-40	6577	6617	Age/Depth Calculated
11a	Kapteinstjørn	Molinari *et al.* 2005	9.669575	59.332593	Forest Hollow	590	9	SIEV	>250µm	-55	9867	9922	Age/Depth Calculated
11b	Kapteinstjørn	Molinari *et al.* 2005	9.669575	59.332593	Forest Hollow	590	9	SIEV	>63µm	-55	10517	10572	Age/Depth Calculated
12	Pau1	Tryterud 2003	7.950000	58.333333	Bog	260	1	SIEV	>500µm	0	3140	3140	Age/Depth Calculated
13	Jom1	Tryterud 2003	8.616667	58.633333	Swamp	370	14	SIEV	>500µm	0	3385	3385	Age/Depth Calculated

Norway (continued)

Site_No	Name	Reference	Easting	Northing	Depositional_Environment	Elevation (m)	Radiocarbon_Dates	Char_Method	Char_size	Temp_start	Temp_end	Temp_extent	Digitisation method
14	Sol1	Tryterud 2003	8.816667	58.950000	Swamp	400	2	SIEV	>500µm	0	1045	1045	Age/Depth Calculated
15	Sol2	Tryterud 2003	8.833333	58.950000	Bog	380	2	SIEV	>500µm	0	3990	3990	Age/Depth Calculated
16	Sol3	Tryterud 2003	8.833333	58.950000	Swamp	390	2	SIEV	>500µm	0	1220	1220	Age/Depth Calculated
17	Lun1	Tryterud 2003	11.716667	59.066667	Swamp	230	1	SIEV	>500µm	0	2363	2363	Age/Depth Calculated
18	Lun2	Tryterud 2003	11.716667	59.040000	Swamp	220	3	SIEV	>500µm	0	5345	5345	Age/Depth Calculated
19	Øst1	Tryterud 2003	11.033333	59.816667	Swamp	240	1	SIEV	>500µm	0	3005	3005	Age/Depth Calculated
20	Øst2	Tryterud 2003	11.033333	59.816667	Swamp	270	2	SIEV	>500µm	0	3595	3595	Age/Depth Calculated
21	Sko1	Tryterud 2003	10.783333	60.233333	Swamp	610	2	SIEV	>500µm	0	3595	3595	Age/Depth Calculated
22	Gul2	Tryterud 2003	10.800000	60.350000	Bog	740	2	SIEV	>500µm	0	3122	3122	Age/Depth Calculated
23	Ott1	Tryterud 2003	5.766667	60.816667	Bog	280	1	SIEV	>500µm	0	1544	1544	Age/Depth Calculated
24a	Årum	Bjune *et al.* 2009	5.616667	59.483333	Forest Hollow	445	4	POLS	>60µm	37	9519	9482	Digitised againts Age
24b	Årum	Bjune *et al.* 2009	5.616667	59.483333	Forest Hollow	445	4	POLS	<60µm	0	9673	9673	Digitised againts Age
25	Barheivatn	Bjune *et al.* 2004	19.850000	69.700000	Lake	317	Cross-correlation	POLS	NOTK	250	9603	9353	Age/Depth Calculated
26	Dalmutladdo	Bjune *et al.* 2004	20.716667	69.166667	Lake	355	11	POLS	NOTK	0	10644	10644	Age/Depth Calculated
27	Brurskardtjorni	Bjune 2005	8.666667	61.416667	Lake	1309	6	POLS	NOTK	0	12125	12125	Age/Depth Calculated
28	Trettetjorn	Bjune 2005	7.000000	60.716667	Lake	810	9	POLS	NOTK	0	13240	13240	Age/Depth Calculated
29	Vestre Oykjamyrtorn	Bjune 2005	6.000000	59.816667	Lake	570	11	POLS	NOTK	0	13101	13101	Age/Depth Calculated
30	Tømmerholt	Hafsten 1992	10.400000	63.440000	Bog	200	3	POLS	NOTK	0	1400	1400	Age/Depth Calculated
31	Oppkuven	Ohlson and Tryterud 1999	10.516667	60.083333	Peat	600	2	SIEV	>500µm	28	4676	4648	Age/Depth Calculated
32	Fitjar (basin)	Overland and Hjelle 2009	5.319167	59.918889	Lake	NOTK	7	POLS	Micro	0	7047	7047	Age/Depth Calculated
33	Fitjar (infield)	Overland and Hjelle 2009	5.317778	59.918889	Medow	NOTK	2	POLS	Micro	785	3356	2571	Age/Depth Calculated
34	Vatnan 5	Vorren *et al.* 2005	22.900000	70.533333	Mire	31	3	POLS	NOTK	225	5387	5162	Age/Depth Calculated
35	Gåshopen	Vorren *et al.* 2005	22.900000	70.533333	Mire	12	1	POLS	NOTK	1360	5893	4533	Age/Depth Calculated
36	Husfjord	Vorren *et al.* 2005	22.900000	70.533333	Mire	30	1	POLS	NOTK	7741	10506	2765	Age/Depth Calculated

Sweden

Site_No	Name	Reference	Easting	Northing	Depositional_Environment	Elevation (m)	Radiocarbon_Dates	Char_Method	Char_size	Temp_start	Temp_end	Temp_extent	Digitisation method
37a	Kuusivaara	Hornberg *et al.* 2011	23.300000	66.666667	Swamp Forest	230	6	SIEV	>1000µm	-55	6640	6695	Age/Depth Calculated
37b	Kuusivaara	Hornberg *et al.* 2011	23.300000	66.666667	Swamp Forest	230	6	SIEV	500>1000µm	-55	6640	6695	Age/Depth Calculated
37c	Kuusivaara	Hornberg *et al.* 2011	23.300000	66.666667	Swamp Forest	230	6	SIEV	250>500µm	-55	6640	6695	Age/Depth Calculated
38a	Kuusivaara	Segerström *et al.* 2008	23.296055	66.614145	Swamp Forest	240	7	SIEV	>1000µm	-55	7893	7948	Age/Depth Calculated
38b	Kuusivaara	Segerström *et al.* 2008	23.296055	66.614145	Swamp Forest	240	7	SIEV	500>1000µm	-55	7893	7948	Age/Depth Calculated
38c	Kuusivaara	Segerström *et al.* 2008	23.296055	66.614145	Swamp Forest	240	7	SIEV	100>500µm	-55	7893	7948	Age/Depth Calculated
38d	Kuusivaara	Segerström *et al.* 2008	23.296055	66.614145	Swamp Forest	240	7	SIEV	10>50µm	-55	7893	7948	Age/Depth Calculated
39a	Makkassjön	Korsman and Segerström 1998	20.578338	66.675901	Lake	415	SCP, Pb, Pollen	POLS	>250µm	-55	10198	10253	Age/Depth Calculated
39b	Makkassjön	Korsman and Segerström 1998	20.578338	66.675901	Lake	415	SCP, Pb, Pollen	POLS	100>250µm	-18	10198	10216	Age/Depth Calculated
40	Lattok	Carcaillet *et al.* 2007	18.344972	65.956938	Lake	480	8	SIEV	>160µm	0	10134	10134	Digitised againts Age
41	Raigejegge	Carcaillet *et al.* 2007	18.213335	66.156943	Lake	480	8	SIEV	>160µm	67	9101	9034	Digitised againts Age
42	Lövnäs	Carcaillet *et al.* 2007	17.900836	66.310834	Lake	515	5	SIEV	>160µm	10	9436	9426	Digitised againts Age
43	Abborrtjärnen	Giesecke 2005	14.376959	63.809822	Lake	387	6	POLS	NOTK	0	10230	10230	Digitised againts Age
44	Styggtjärnen	Giesecke 2005	13.565717	62.316410	Lake	715	6	POLS	NOTK	10	9970	9960	Digitised againts Age
45	Trälhultet	Lindbladh *et al.* 2008	12.900000	56.800000	Forest Hollow	100	4	SIEV	>250µm	59	2575	2516	Digitised againts Age
46	Holkåsen	Lindbladh *et al.* 2008	12.900000	56.800000	Forest Hollow	100	6	SIEV	>250µm	15	3671	3656	Raw data
47	Kalvaberget	Lindbladh *et al.* 2008	12.906262	56.817065	Forest Hollow	100	7	SIEV	>280µm	-21	2511	2532	Digitised againts Age
48	Nynäs	Cousins *et al.* 2002	17.380813	58.840554	Fen	NOTK	3	POLS	NOTK	385	4048	3663	Age/Depth Calculated
49	Hunnemara	Yu *et al.* 2005	14.893692	56.168568	Lake	3	10	SIEV	NOTK	3101	12148	9047	Age/Depth Calculated
50	Smygen Bay	Yu *et al.* 2005	15.117140	56.152276	Lake	-1	12	SIEV	NOTK	1561	10908	9347	Age/Depth Calculated
51	Sjuodjijaure	Rosén *et al.* 2001	18.066667	67.366667	Lake	826	11	POLS	NOTK	131	9660	9529	Age/Depth Calculated
52a	Skärsgölarna	Lindbladh *et al.* 2003	16.103234	56.997101	Wetland	NOTK	7	SIEV	>200µm	-23	7466	7489	Age/Depth Calculated

Sweden (continued)

Site_No	Name	Reference	Easting	Northing	Depositional_Environment	Elevation (m)	Radiocarbon_Dates	Char_Method	Char_size	Temp_start	Temp_end	Temp_extent	Digitisation method
52b	Skärsgölarna	Lindbladh *et al.* 2003	16.103234	56.997101	Wetland	NOTK	7	SIEV	100>200µm	-23	7466	7489	Age/Depth Calculated
52c	Skärsgölarna	Lindbladh *et al.* 2003	16.103234	56.997101	Wetland	NOTK	7	SIEV	50>100µm	-23	7466	7489	Age/Depth Calculated
52d	Skärsgölarna	Lindbladh *et al.* 2003	16.103234	56.997101	Wetland	NOTK	7	SIEV	25>50µm	-23	7466	7489	Age/Depth Calculated
52e	Skärsgölarna	Lindbladh *et al.* 2003	16.103234	56.997101	Wetland	NOTK	7	SIEV	>50µm	-23	7466	7489	Age/Depth Calculated
53a	Makkassjön	Rosén and Hammarlund 2007	20.578338	66.675901	Lake	415	SCP, Pb, Pollen	SIEV	>250µm	-17	8916	8933	Digitised againts Age
53b	Makkassjön	Rosén and Hammarlund 2007	20.578338	66.675901	Lake	415	SCP, Pb, Pollen	SIEV	100>250µm	-17	8916	8933	Digitised againts Age
54	TrygåsenS	Segerström *et al.* 1996	13.300000	61.770000	Forest hollow	565	3	SIEV	>500µm	-55	9462	9517	Age/Depth Calculated
55	TrygåsenO	Segerström *et al.* 1996	13.300000	61.770000	Mire	565	6	SIEV	>500µm	-21	3423	3444	Age/Depth Calculated
56	Bråtamossen	Lagerås *et al.* 1995	14.525097	57.675307	Bog	300	9	POLS	25>250µm	-50	6922	6972	Age/Depth Calculated
57a	Bökeberg	Regnell *et al.* 1995	13.250317	55.544369	Lake	50	12	SIEV	Macro	5485	7623	2138	Age/Depth Calculated
57b	Bökeberg	Regnell *et al.* 1995	13.250317	55.544369	Lake	50	12	SIEV	10>25µm	5485	7623	2138	Age/Depth Calculated
57c	Bökeberg	Regnell *et al.* 1995	13.250317	55.544369	Lake	50	12	SIEV	>25µm	5485	7623	2138	Age/Depth Calculated
58a	Siggaboda	Bjorkman and Bradshaw 1996	14.570851	56.468442	Forest hollow	NOTK	5	SIEV	>250µm	27	2767	2740	Digitised againts Age
58b	Siggaboda	Bjorkman and Bradshaw 1996	14.570851	56.468442	Forest hollow	NOTK	5	SIEV	>25µm	23	2863	2840	Digitised againts Age
59	Fiby Forest	Bradshaw and Hannon 1992	17.364341	59.879486	Peat	NOTK	3	SIEV	NOTK	31	3992	3961	Digitised againts Age
60	Råshult (in field)	Lindbladh and Bradshaw 1998	14.200000	56.616667	Wetland	NOTK	7	SIEV	NOTK	32	4452	4420	Digitised againts Age
61	Råshult (out field)	Lindbladh and Bradshaw 1998	14.200000	56.616667	Wetland	NOTK	2	SIEV	NOTK	22	5548	5526	Digitised againts Age
62	Djäknabygd	Lindbladh and Bradshaw 1998	14.200000	56.616667	Wetland	NOTK	5	SIEV	NOTK	86	5930	5844	Raw data
63	Penningholm	Bradshaw and Zackrisson 1990	17.430913	61.989376	Peat	425	5	SIEV	NOTK	11	2561	2550	Digitised againts Age
64	Skallskog large	Segerström and Emanuelsson 2002	14.867622	60.640172	Mire	300	5	POLS	>40µm	-51	1449	1500	Age/Depth Calculated
65a	Skallskog small	Segerström and Emanuelsson 2002	14.867622	60.640172	Mire	370	2	POLS	50>200µm	17	1045	1028	Age/Depth Calculated
65b	Skallskog small	Segerström and Emanuelsson 2002	14.867622	60.640172	Mire	370	2	POLS	>200µm	17	1045	1028	Age/Depth Calculated
66a	Eriksberg	Hannon *et al.* 2000	15.000000	56.183333	Forest hollow	NOTK	4	SIEV	<200µm	119	7414	7295	Raw data
66b	Eriksberg	Hannon *et al.* 2000	15.000000	56.183333	Forest hollow	NOTK	4	SIEV	<200µm	43	6246	6203	Digitised againts Age

Sweden (continued)

Site_No	Name	Reference	Easting	Northing	Depositional_Environment	Elevation (m)	Radiocarbon_Dates	Char_Method	Char_size	Temp_start	Temp_end	Temp_extent	Digitisation method
67	Sörevik	Berglund *et al.* 2005	15.763067	56.117600	Medow	NOTK	12	SIEV	NOTK	7374	10771	3397	Age/Depth Calculated
68	Kalvöviken	Berglund *et al.* 2005	15.109873	56.166183	Medow	NOTK	8	SIEV	NOTK	3251	10739	7488	Age/Depth Calculated
69	Storasjö	Olsson *et al.* 2010	15.292108	56.928264	Bog	255	9	POLS	Micro	50	10862	10812	Digitised againts Age
70a	Kalven	Bindler *et al.* 2011	12.670000	57.470000	Lake	150	Varve counts	POLS	>100µm	-41	1019	1060	Digitised againts Age
70b	Kalven	Bindler *et al.* 2011	12.670000	57.470000	Lake	150	Varve counts	POLS	50>100µm	-41	1019	1060	Digitised againts Age
71a	Stavsåkra	Greisman and Gaillard 2009	14.900000	56.916667	Bog	187	9	POLS	>25µm	1204	8352	7148	Digitised againts Age
71b	Stavsåkra	Greisman and Gaillard 2009	14.900000	56.916667	Bog	187	9	POLS	10>25µm	1204	8352	7148	Digitised againts Age
72a	Low Impact Area	Josefsson *et al.* 2009	17.816667	66.616667	Mire	510	3	POLS	>150µm	-36	2172	2208	Age/Depth Calculated
72b	Low Impact Area	Josefsson *et al.* 2009	17.816667	66.616667	Mire	510	3	POLS	50>150µm	-36	2172	2208	Age/Depth Calculated
73a	Munka	Josefsson *et al.* 2009	17.783333	66.550000	Mire	460	3	POLS	>150µm	-36	4126	4162	Age/Depth Calculated
73b	Munka	Josefsson *et al.* 2009	17.783333	66.550000	Mire	460	3	POLS	50>150µm	-36	4126	4162	Age/Depth Calculated
74a	Akkapakte	Josefsson *et al.* 2009	17.683333	66.633333	Mire	480	9	POLS	>150µm	-18	2667	2685	Age/Depth Calculated
74b	Akkapakte	Josefsson *et al.* 2009	17.683333	66.633333	Mire	480	9	POLS	50>150µm	-18	2667	2685	Age/Depth Calculated
75	Ängersjötjärn	Karlsson *et al.* 2010	14.866667	61.999722	Mire	400	4	POLS	50>150µm	160	1516	1356	Age/Depth Calculated
76a	Gammelvallen Frosktjärnsberget	Karlsson *et al.* 2010	14.816667	61.983333	Mire	490	4	POLS	>150µm	-7	2666	2673	Age/Depth Calculated
76b	Gammelvallen Frosktjärnsberget	Karlsson *et al.* 2010	14.816667	61.983333	Mire	490	4	POLS	50>150µm	-7	2666	2673	Age/Depth Calculated
77a	Öjingsvallen	Karlsson *et al.* 2010	14.933333	61.916667	Mire	430	4	POLS	>150µm	-50	3151	3201	Age/Depth Calculated
77b	Öjingsvallen	Karlsson *et al.* 2010	14.933333	61.916667	Mire	430	4	POLS	50>150µm	-50	3151	3201	Age/Depth Calculated
78a	Gieddeålge	Staland *et al.* 2011	15.687056	66.224861	Mire	710	3	POLS	>50µm	-50	1216	1266	Age/Depth Calculated
78b	Gieddeålge	Staland *et al.* 2011	15.687056	66.224861	Mire	710	3	POLS	25>50µm	-50	1216	1266	Age/Depth Calculated
79a	Varenodjukke	Staland *et al.* 2011	15.668806	66.202622	Mire	680	4	POLS	>50µm	-50	2415	2465	Age/Depth Calculated
79b	Varenodjukke	Staland *et al.* 2011	15.668806	66.202622	Mire	680	4	POLS	25>50µm	-50	2415	2465	Age/Depth Calculated
80	Reference area	Staland *et al.* 2011	15.668806	66.223389	Mire	670	4	POLS	>50µm	-50	4903	4953	Age/Depth Calculated
81	Holtjarnen	Giesecke 2005	15.930134	60.650005	Lake	232	7	SIEV	NOTK	-53	10406	10459	Digitised againts Age

Sweden (continued)

Site_No	Name	Reference	Easting	Northing	Depositional_Environment	Elevation (m)	Radiocarbon_Dates	Char_Method	Char_size	Temp_start	Temp_end	Temp_extent	Digitisation method
82	Koltjarnen	Giesecke 2005	16.529959	61.819888	Lake	715	6	POLS	NOTK	68	9205	9137	Digitised againts Age
83	Bocksten A	Bjorkman 1997	12.566667	57.116667	Mire	NOTK	6	SIEV	25>250µm	-29	2564	2593	Age/Depth Calculated
84	Bocksten B	Bjorkman 1997	12.566667	57.116667	Mire	NOTK	3	SIEV	25>250µm	-27	4536	4563	Age/Depth Calculated
85	Killeröd	Hannon and Gustafsson 2004	12.816667	56.383333	Medow	NOTK	5	SIEV	>280µm	25	2207	2182	Raw data
86	Kåremosse	Hannon *et al.* 2008	12.783333	56.416667	Fen	130	5	SIEV	NOTK	650	9017	8367	Raw data
87	Osaby (in field)	Lindbladh 1999	14.783333	56.766667	Peat	165	8	SIEV	NOTK	4	4102	4098	Digitised againts Age
88	Osaby (out field)	Lindbladh 1999	14.783333	56.766667	Wetland	165	6	SIEV	NOTK	21	3869	3848	Digitised againts Age
89	Stor-Flen I	Segerström 1997	14.583333	60.300000	Swap forest	270	4	POLS	NOTK	1195	6853	5658	Age/Depth Calculated
90	Stor-Flen II	Segerström 1997	14.583333	60.300000	Swap forest	270	4	POLS	NOTK	160	9481	9321	Age/Depth Calculated
91	Torup	Hultberg *et al.* 2010	13.205533	55.563111	Wetland	50	6	SIEV	NOTK	8	5887	5879	Raw data
92	Island A	Hornberg *et al.* 2004	17.853300	65.958100	Lake	4	3	SIEV	NOTK	23	6874	6851	Age/Depth Calculated
93	Island B	Hornberg *et al.* 2004	17.853300	65.958100	Lake	6	5	SIEV	NOTK	30	7682	7652	Age/Depth Calculated
94	Nissatorp	Lindbladh and Bradshaw 1998	14.200000	56.616667	Wetland	NOTK	2	NOTK	NOTK	72	2088	2016	Raw data
95	Bohult	Bradshaw *et al.* 1997	16.166667	57.233330	Mire	NOTK	NOTK	SIEV	NOTK	99	7167	7068	Raw data
96	Dömestorp	Hannon 2002	12.985833	56.400000	Wetland	NOTK	4	SIEV	NOTK	17	2508	2491	Raw data
97	Häggenäs	G. E. Hannon (unpubl. data)	13.600000	55.883333	?	NOTK	NOTK	NOTK	NOTK	6	1711	1705	Raw data
98	Kalvaberget	Hannon 2002	12.850000	56.783333	?	NOTK	NOTK	NOTK	NOTK	9	2633	2624	Raw data
99	Vasahus	G. E. Hannon (unpubl. data)	13.633333	55.900000	?	NOTK	NOTK	NOTK	NOTK	58	3318	3260	Raw data
100	Hälledam	G. E. Hannon (unpubl. data)	12.566667	56.433333	?	NOTK	NOTK	NOTK	NOTK	16	2962	2946	Raw data
101	Ekenäs	G. E. Hannon (unpubl. data)	16.016667	56.950000	?	NOTK	NOTK	NOTK	NOTK	8	3554	3546	Raw data
102	Ryfors	G. E. Hannon (unpubl. data)	13.833333	57.916667	?	NOTK	NOTK	NOTK	NOTK	61	1689	1628	Raw data
103	Kölksjänen	K. Brown (unpubl. data)	16.533333	61.816667	Lake	715	NOTK	NOTK	NOTK	-60	9431	9491	Raw data
104	Holtjarnen	K. Brown (unpubl. data)	15.933333	60.650000	Lake	232	NOTK	NOTK	NOTK	15	10019	10004	Raw data

Finland

Site_No	Name	Reference	Easting	Northing	Depositional_Environment	Elevation (m)	Radiocarbon_Dates	Char_Method	Char_size	Temp_start	Temp_end	Temp_extent	Digitisation method
105	Laukunlampi	Tolonen 1983	29.166667	62.666667	Lake	NOTK	Varve counts	NOTK	NOTK	339	949	610	Digitised againts Age
106	Ahvenainen	Tolonen 1978	25.116667	61.033333	Lake	122	Varve counts	POLS	NOTK	-26	6131	6157	Digitised againts Age
107	Salo Pukkila	Tolonen 1983	23.166667	60.333333	Mire	29	4	POLS	NOTK	190	5300	5110	Age/Depth Calculated
108	Palomäki	Tolonen 1985	22.716667	60.416667	Mire	NOTK	Cross-correlation	POLS	NOTK	-33	3899	3932	Age/Depth Calculated
109	Pönttölampi	Pitkänen and Huttunen 1999	30.966670	63.166667	Lake	173	Varve counts	POLS	NOTK	4	1247	1243	Digitised againts Age
110	Laukunlampi	Pitkänen 2000	29.167744	62.667117	Lake	84	Varve counts	POLS	NOTK	851	1515	664	Digitised againts Age
111	Ristijärvi	Pitkänen and Grönlund 2001	28.950000	63.616667	Lake	106	Varve counts	POLS	NOTK	1450	2045	595	Digitised againts Age
112	Iso Lehmälampi	Sarmaja-Korjonen 1998	24.600000	60.350000	Lake	NOTK	4	POLS	NOTK	0	9143	9143	Age/Depth Calculated
113	Etu-Mustajärvi	Sarmaja-Korjonen 1998	25.005384	60.984835	Lake	NOTK	3	POLS	NOTK	0	9400	9400	Age/Depth Calculated
114	Ylimmäinen Kuivajärvi	Sarmaja-Korjonen 1998	29.619048	66.362787	Lake	NOTK	Cross-correlation	POLS	NOTK	0	9158	9158	Age/Depth Calculated
115	Putaanlampi	Sarmaja-Korjonen 1998	29.415423	66.381107	Lake	NOTK	Cross-correlation	POLS	NOTK	0	9667	9667	Age/Depth Calculated
116	Jierstivaara	Sarmaja-Korjonen 1998	23.733300	68.666700	Lake	NOTK	3	POLS	NOTK	4333	8056	3723	Age/Depth Calculated
117	Storträsk	Sarmaja-Korjonen 2003	25.166667	60.266667	Lake	NOTK	3	POLS	NOTK	0	6281	6281	Age/Depth Calculated
118	Hältingträsk	Sarmaja-Korjonen 2003	25.233333	60.266667	Lake	NOTK	NOTK	POLS	NOTK	0	4900	4900	Age/Depth Calculated
119	Hämpträsk	Sarmaja-Korjonen 2003	25.261179	60.285049	Lake	NOTK	5	POLS	NOTK	0	5334	5334	Age/Depth Calculated
120	Vesijako	J.L. Clear (unpubl. Data)	25.100000	61.350000	Forest hollow	NOTK	8	SIEV	>250µm	-55	5438	5493	Age/Depth Calculated
121	Lake Orijärvi	Alenius *et al.* 2008	27.234285	61.666743	Lake	89.7	5	SIEV	NOTK	44	9624	9580	Age/Depth Calculated
122a	Kontolanrahka	Väliranta *et al.* 2007	22.775927	60.798551	Bog	NOTK	40	SIEV	>100µm	11	5015	5004	Digitised againts Age
122b	Kontolanrahka	Väliranta *et al.* 2007	22.775927	60.798551	Bog	NOTK	40	POLS	<100µm	11	5015	5004	Digitised againts Age
123a	Einehiemmet	Hicks 1993	27.533333	68.666667	Mire	NOTK	2	POLS	<40µm	-39	530	569	Age/Depth Calculated
123b	Einehiemmet	Hicks 1993	27.533333	68.666667	Mire	NOTK	2	POLS	>40µm	-39	530	569	Age/Depth Calculated
124	Sudenpesä	J.L. Clear (unpubl. Data)	25.152639	61.192306	Forest hollow	NOTK	8	SIEV	>250µm	165	9861	9696	Age/Depth Calculated
125	Konilampi	Jauhiainen *et al.* 2004	24.283300	61.800000	Fen	155	5	POLS	NOTK	859	9410	8551	Digitised againts Age

Finland (contnued)

Site_No	Name	Reference	Easting	Northing	Depositional_Environment	Elevation (m)	Radiocarbon_Dates	Char_Method	Char_size	Temp_start	Temp_end	Temp_extent	Digitisation method
126	Viheriaisenneva	Jauhiainen *et al.* 2004	24.233300	61.250000	Bog	160	9	POLS	NOTK	98	10305	10207	Age/Depth Calculated
127	Maajärvi	Kuoppamaa *et al.* 2009	28.329639	68.844472	Mire	NOTK	8	POLS	NOTK	-52	71	123	Digitised againts Age
128	Njargajavri	Väliranta *et al.* 2005	27.166667	69.866667	Lake	355	8	SIEV	>125µm	-50	5145	5195	Age/Depth Calculated

Russia

Site_No	Name	Reference	Easting	Northing	Depositional_Environment	Elevation (m)	Radiocarbon_Dates	Char_Method	Char_size	Temp_start	Temp_end	Temp_extent	Digitisation method
129a	Kirjavalampi	Alenius et al 2004	30.761000	61.730000	Lake	17	3	POLS	10>50µm	-39	3287	3326	Age/Depth Calculated
129b	Kirjavalampi	Alenius et al 2004	30.761000	61.730000	Lake	17	3	POLS	>50µm	-39	3287	3326	Age/Depth Calculated
130a	Ilponlampi	Huttunen et al 1994	30.249167	60.123333	Lake	285	4	POLS	<25µm	0	12082	12082	Age/Depth Calculated
130b	Ilponlampi	Huttunen et al 1994	30.249167	60.123333	Lake	285	4	POLS	>25µm	0	12082	12082	Age/Depth Calculated
131	Paanajarvi Picea	Wallenius et al 2005	30.000000	66.000000	Mire	NOTK	1	SIEV	>200µm	-4	1106	1110	Age/Depth Calculated
132	Kukka Hollow	J. L. Clear (unpubl. Data)	32.744167	61.650000	Forest hollow	NOTK	1	SIEV	>250µm	93	11067	10974	Age/Depth Calculated
133a	Pieni-Kuuppalanlampi	Miettinen *et al.* 2002	29.916667	61.283333	Lake	27	6	POLS	10>25µm	-16	6572	6588	Age/Depth Calculated
133b	Pieni-Kuuppalanlampi	Miettinen *et al.* 2002	29.916667	61.283333	Lake	27	6	POLS	26>50µm	-16	6572	6588	Age/Depth Calculated
133c	Pieni-Kuuppalanlampi	Miettinen *et al.* 2002	29.916667	61.283333	Lake	27	6	POLS	51>100µm	-16	6572	6588	Age/Depth Calculated
133d	Pieni-Kuuppalanlampi	Miettinen *et al.* 2002	29.916667	61.283333	Lake	27	6	POLS	>100µm	-16	6572	6588	Age/Depth Calculated
133e	Pieni-Kuuppalanlampi	Miettinen *et al.* 2002	29.916667	61.283333	Lake	27	6	POLS	NOTK	-16	6572	6588	Age/Depth Calculated

Fire Scars

Norway

Site_No	Name	Reference	Easting	Northing	Temp_start	Temp_end	Temp_extent
134	Eldferdalen	Groven and Niklasson 2005	9.316667	59.650000	-50	1200	1250

Sweden

Site_No	Name	Reference	Easting	Northing	Temp_start	Temp_end	Temp_extent
135	Muddus	Engelmark 1984	20.250000	66.150000	-33	537	570
136	Norra Kvills	Niklasson and Drakenberg 2001	15.600000	57.500000	-50	550	600
137	Linsell	Hellberg *et al.* 2004	13.866667	62.133333	-50	800	850
138	Grimsjön	Hellberg *et al.*2004	14.033333	61.950000	-50	700	750
139	Vindelälven	Zackrisson 1977	18.100000	64.150000	-25	399	424
140	Lödge	Niklasson and Granstrom 2000	18.800000	63.933333	-50	850	900

Finland

Site_No	Name	Reference	Easting	Northing	Temp_start	Temp_end	Temp_extent
141	Lammi & Padasjoki	Wallenius *et al.* 2007	25.016667	61.050000	-50	511	561
142	Autiovaara, Patvinsuo	Lehtonen *et al.* 1996	30.666667	63.116667	-44	538	582
143	Kitsi	Lehtonen and Huttunen 1997	30.750000	63.266667	-44	547	591
144	Ahvenjarvi	Lehtonen and Huttunen 1997	30.950000	62.850000	-44	591	635
145	Pippokangas	Matthews *et al.* 2005	24.000000	68.000000	514	7800	7286

Russia

Site_No	Name	Reference	Easting	Northing	Temp_start	Temp_end	Temp_extent
146	Paanajarvi Picea	Wallenius *et al.* 2005	30.000000	66.000000	-51	565	616
147	Viena	Lehtonen and Kolstrom 2000	30.083333	65.000000	-48	550	598
148	Vienansalo	Wallenius *et al.* 2004	30.183333	64.966667	-50	600	650