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Characteristics of the temporal, spatial and taxonomic resolution of palynological data from the northern boreal forest of Finnish Lapland

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Academic dissertation to be presented with the assent of the Faculty of Science of the University of Oulu, for public defence in Auditorium GO101, Linnanmaa, on November 27th 2009 at 12 o'clock noon

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Kylvi maita kyyhätteli, kylvi maita, kylvi soita,
kylvi auhtoja ahoja, panettavi paasikoita.

Mäet kylvi männiköiksi, kummut kylvi kuusikoiksi,
kankahat kanervikoiksi, notkot nuoriksi vesoiksi.

Noromaille koivut kylvi, lepät maille leyhke'ille,
tuomet kylvi tuorehille, raiat maille raikkahille,
pihlajat pyhille maille, pajut maille paisuville,
katajat karuille maille, tammet virran vieremille.

-Kalevala-

Characteristics of the temporal, spatial and taxonomic resolution of palynological data from the northern boreal forest of Finnish Lapland

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Abstract

This thesis comprises four original papers which, together, focus on climate and land-use changes in northeastern Finnish Lapland. These changes are investigated at both local and regional scales and at a high temporal resolution by combining the use of pollen accumulation rate (PAR) data with a modelling approach. The central aim of the thesis is to assess what kind of effects climate and land-use changes have on the pollen representation of the vegetation at varying temporal, spatial and taxonomic scales.

The palynological data for this thesis was collected in three different datasets; 1) a peat profile to produce a continuous, near-annual fossil pollen data time series for the last 100 years; 2) a time series of annual pollen deposition in a modified Tauber trap for the last 20 years; and 3) a set of surface sediment samples from five large lakes to supply data from the regional pollen component.

PARs are a good technique for quantifying the surrounding vegetation, as they measure the pollen loading of each species on a surface over a period of time independently of all other species. The modelling approach is based on models of pollen dispersal and deposition and helps in quantifying the spatial pollen-vegetation relationship in a heterogeneous landscape. The pollen loading to a point can be simulated in different vegetational environments using a software package HUMPOL and it is this which has been applied here. For the regional vegetation reconstructions a REVEALS model was used with data from the large sites.

This work reveals that PARs are useful in the north, providing more information than percentages when the vegetation composition is species poor and dominated by only one taxon, such as *Pinus sylvestris*. The modelling approach helps when the aim is to investigate the main characteristics of the vegetation at either local or regional scales, but when trying to detect local forest management or land-use in more detail, PARs tend to work better. This is because, in this particular area locally occurring events are usually at

an extremely limited scale and the vegetation is the same both inside and outside the relevant source area of pollen. Under such conditions in the percentage record, local events become practically invisible.
High temporal resolution PAR data seems to have some potential for reconstructions of summer temperature fluctuations. It has been shown that the pollen productivity of different tree species varies according to summer temperatures and when the pollen data are collected as a continuous time series at an annual resolution, the variation in PAR values reflects the high temporal resolution changes in climate. Separating pollen types to the lowest possible taxonomic level is also worthwhile when there is a good ecological reason to do so i.e. the subspecies have different edaphic constraints or they react differently to some climatic factors, as was concluded with *Betula pubescens* ssp *pubescens* and *B. pubescens* ssp *czerapnovii* in this thesis.

Keywords: Pollen accumulation rates, REVEALS model, simulation approach, July temperature, temporal resolution, spatial resolution, taxonomic resolution, northern boreal forest, Lapland, Finland

CONTENTS

ABBREVIATIONS AND ACRONYMS

AMS	Accelerator mass spectrometry
CLC	CORINE land cover data
ERV	Extended R-value model
GIS	Geographical information system
GLC	Global land cover data
LOVE	Local vegetation estimate
LRA	Landscape reconstruction algorithm
NAP	Non-arboreal pollen types
PAR	Pollen accumulation rate (grains cm^{-2} a^{-1})
PCA	Principal components analysis
REVEALS	Regional estimates of vegetation abundance from large sites
RSAP	Relevant source area of pollen
SCP	Spheroidal carbonaceous particles

LIST OF ORIGINAL PAPERS

This thesis is based on the following four papers, referred to as Papers I, II, III and IV.

I. Kuoppamaa M, Goslar T, Hicks S. (2009) Pollen accumulation rates as a tool for detecting land-use changes in a sparsely settled boreal forest. Vegetation History and Archaeobotany 18:205-217

II. Kuoppamaa M. Simulating pollen loading in a Northern Boreal Forest: the effect of changing forest densities and distribution. (submitted to The Holocene)

III. Kuoppamaa M, Huusko A, Hicks S. (2009) Pinus and Betula pollen accumulation rates from the northern boreal forest as a record of interannual variation in July temperature. Journal of Quaternary Science 24:513-521

IV. Kuoppamaa M. How applicable is the REVEALS model in reconstructing regional vegetation in a monospecific Pinus sylvestris dominated forest of northern Finnish Lapland? (submitted to Journal of Quaternary Science)

CONTRIBUTIONS

The following table indicates the major contributions of the authors of the original articles.

	I	II	III	IV
Planning	MK, SH	MK	AH, MK, SH	MK
Data collection	MK, TG, SH	MK	MK, SH, AH	MK
Data analysis	MK, TG	MK	AH, MK	MK
Interpretation of results	MK	MK	MK, AH, SH	MK
Manuscript preparation	MK, SH, TG	MK	MK, AH, SH	MK

Contributions: MK = Mari Kuoppamaa, SH = Sheila Hicks, AH = Antti Huusko, TG = Tomasz Goslar

All the material in this study was collected by the authors. In Paper I SH was responsible for choosing the site from which the peat monolith was collected and for digging it out, TG was responsible for the AMS ^{14}C datings and construction of the age-depth model, TG also prepared the dating part of the manuscript. The manuscript was prepared by MK and SH with comments from TG. In Paper II MK had the main responsibility, but received comments from SH in planning, interpretation of the results and manuscript preparation. In Paper III SH had the original idea to use the pollen trap data and made the data available, AH did the majority of the planning and data analysis together with MK for calibrating the PAR and temperature data. Interpretation of the results and manuscript preparation were done by MK and AH with comments from SH. Paper IV was written by MK with comments from SH and AH in planning, interpretation of the results and manuscript preparation.

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My gratitude goes also to the staff of the Department of Geosciences at the University of Oulu. I am especially grateful to the whole Palaeoecology group. Both its present and past members: Olga Lisitsyna, Catherina Sokol, Satu Räsänen, Heidi Hyyppä and Henna Sormunen are thanked for interesting conversations, (mostly off topic), during the numerous coffee breaks over the years. Satu Räsänen is especially thanked for all her help with writing and assistance when coring the Nellim profile a little bit deeper; I hope I have a chance to actually investigate that core some day! Antti Pasanen is sincerely thanked for sharing all information and good tips when finishing a PhD thesis.

I would also like to thank the many colleagues and new friends I have met and discussed with during the meetings and workshops held in connection with the NordForsk networks POLLANDCAL and LANDCLIM 10000, the EU 5FP project PINE, the EU 6FP project Millennium and the Pollen Monitoring Programme, for making science so much fun!

I received extremely valuable help in the field from my father Timo Hagberg and Eine Alt during the collection of the lake sediment samples. I am sorry that I could not provide better weather – the horizontally falling snow was certainly not on the list! Hannele and Veijo Mikkola are thanked for providing accommodation during the field trip.

I would like to thank my family and friends for taking my mind off the thesis every now and then, and for pushing me forward when I was losing faith. Most importantly, I would like to thank my two men at home, Kimmo, and Veikka, for all the support, encouragement and joy they have given me during this work.

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INTRODUCTION

The evidence of land-use and climatic change in the pollen record

Pollen analysis as a tool for investigating both land-use and vegetation changes, and climatic change, has a long tradition in Fennoscandia, which is linked to the fact that the founder of the technique was Swedish (Von Post 1916). Numerous studies carried out during the 20th century have concentrated on the relationship between vegetation history and climate or on the impact of agriculture on natural vegetation (e.g. Vuorela 1970; Berglund 1985; Vorren 1986; Gaillard and Berglund 1988; Odgaard 1989; Segerström 1990; Vorren et al. 1990; Grönlund et al. 1992). In the southern part of Fennoscandia this importance of including land-use is natural, as agriculture has been practiced for thousands of years in the area. In the north, however, most of the anthropogenic impact is of non-agricultural origin. The key feature of human impact in this area was for a very long time felling of timber for dwellings or firewood. Over the last half century human impact on the vegetation of northern Fennoscandia has increased in the form of heavy logging for industrial purposes and the building of holiday resorts. Relatively little has been written about this type of impact on the vegetation of the northern boreal forest and how that impact appears in the pollen record. A handful of studies reveal that the anthropogenic influence can be seen as an increase in the quantity of Poaceae pollen or, to a certain extent, in some herb pollen taxa, but only within a very short distance from the site of the actual disturbance (Suominen 1975; Hicks 1993). Investigations by Räsänen et al. (2007), have suggested that in practice the anthropogenic impact cannot necessarily be seen in the pollen record to the degree that might be expected even when the disturbance is heavy and very close to the sampling site. An additional complicating feature when trying to detect human impact from the pollen record this far north, is the limited number of species (in practice the only tree species found in the area are *Betula* spp., *Pinus sylvestris* and *Picea abies*), which include both very high and very low pollen producers, plus a general low diversity of species of which most appear in all vegetation types, at least to some degree.

More studies have been published on the effects of changing climate on the vegetation over the Holocene (e.g. Birks 1990; Cheddadi et al. 1997; Tinner and Lotter 2001; Bjune et al. 2004). This is a rather classical approach to studying changes in vegetation and the arrival or retreat of different tree species when the Holocene climate became first warmer and then a bit cooler again. A fresh angle to the topic was introduced by Hicks (2006) and

Seppä and Hicks (2006) who discussed the possibility of trees existing in the landscape but that they ceased producing pollen due to cooler temperatures. This observation of changing pollen productivity due to changes in temperature is not entirely new, but nevertheless it has been somewhat neglected up until now (Autio and Hicks 2004; Hicks 2006). The fact that the amount of pollen that is released from a tree each year is changing according to the previous year's summer temperatures, and this phenomenon is strongest in the north where trees are growing at their limits, gives an opportunity to use continuous high resolution palynological data to investigate high resolution changes in temperature (e.g. Barnekow et al. 2007; Huusko and Hicks 2009; Kamenik et al. 2009; Paper III).
This thesis will mainly pay attention to the varying temporal, spatial and taxonomic resolution of the pollen-based environmental reconstructions in the north and how these affect the visibility of land-use and climatic changes in the pollen record (Figure 1).

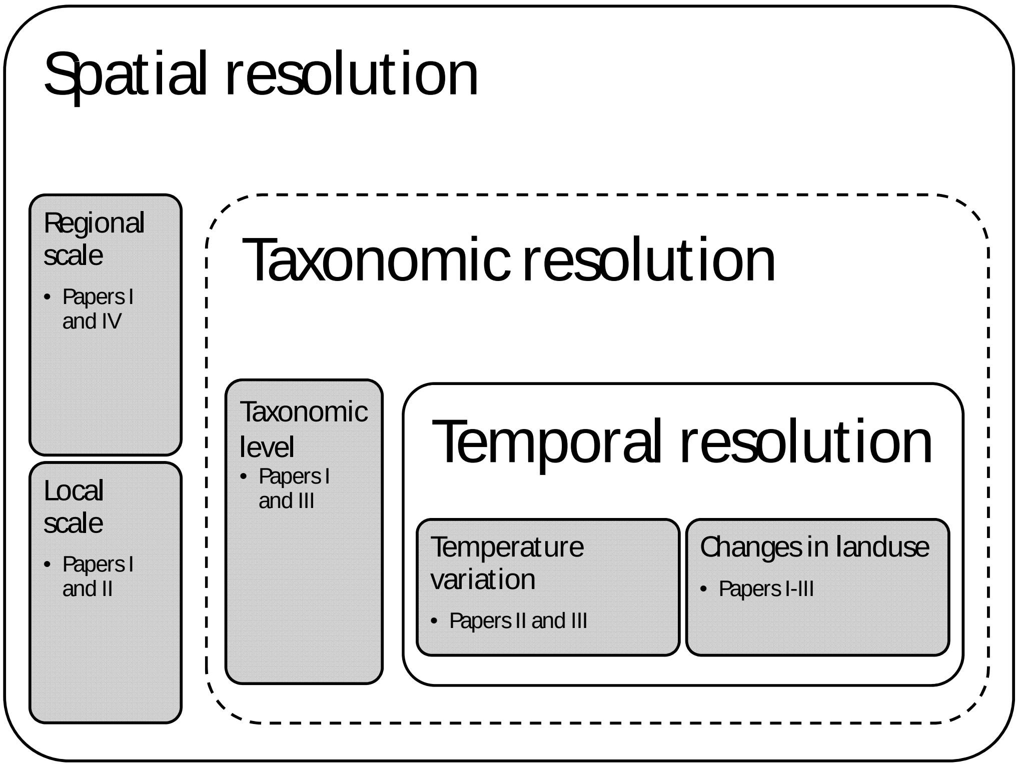

Figure 1 The three key features of the pollen record that are investigated in this thesis.

The resolution of the record

Temporal resolution

A high temporal resolution is important in palynological studies if the aim is to detect short term changes in the environment, and to tell how quickly these changes happened. A continuous time series without gaps in the sampling improves the temporal resolution even more and enables the pinpointing of when exactly certain events started and ended and, in this way, quantifies the length of the events. The temporal resolution of the pollen record is generally affected by the thickness of the sediment sample that will be studied for pollen, the rate of sediment accumulation in the basin, and the accuracy of the age-depth model that was used to produce the chronology. If the aim is to detect short term changes in land-use or climate by pollen studies, as is the case here, a high temporal resolution is imperative, as is also a contiguous way of sampling if the whole series of events is to be recorded without gaps. In the northern boreal forest zone it is usually more appropriate to use peat rather than lake sediment since the former accumulates much more rapidly than the latter and so offers a higher temporal resolution (Hicks and Hyvärinen 1999). Annually laminated lake sediments would give an even better time control but, this far north, the lake sediments usually accumulate so slowly that obtaining a series with a high temporal resolution would be extremely difficult or even impossible (Hicks and Hyvärinen 1999) and, to date, no annually laminated sediments have been found (pers.com.). This research concentrates only on the most recent part of the time series, and aims at the highest possible temporal resolution in order to study the boundaries of pollen analysis as a method for detecting short term variations in land-use and climate.

Spatial resolution

The spatial aspect of the pollen data is to show where things occurred. The spatial scale quantifies at what distance from the sampling site these things happened and how much of the area they covered. In the far north changes in the vegetation usually happen either very locally or, if they are regional, they occur within the same vegetation type. The problem of distinguishing the local pollen signal from the regional one has attracted the interest of many researchers who have addressed it in various ways (Jacobson and Bradshaw 1981; Prentice 1988; Sugita 1994; 1998; Sugita et al. 1999; Calcote 1995; Davis 2000; Bunting et al. 2004; Nielsen and Sugita 2005). The spatial extent of the area that is reflected in pollen data depends mainly on the size of the depositional basin and the idea of 'Relevant Source Area of Pollen' (RSAP, sensu Sugita 1994) is a convenient way of describing quantitatively the spatial scale of the pollen sample's view of heterogenous and patchy vegetation. Pollen loading coming from beyond the relevant source area is considered as the background pollen loading or regional pollen component, which does not vary between similarly sized sites in the landscape. It has been shown that as much as 60% of the total pollen loading at a site can come from outside the radius of the RSAP and can be considered as a regional component (Sugita 1994; Von Stedingk et al. 2008). A quantitative reconstruction of local vegetation cannot be achieved unless this regional component is also taken into consideration (Maher 1963; Andersen 1970; Prentice and Parsons 1983; Parshall and Calcote 2001). Pollen accumulation rates, PARs, (grains cm^{-2} a^{-1}) on the other hand, are influenced by the spatial resolution of the pollen record, but cannot, in themselves, quantify it.

Taxonomic resolution

The taxonomic resolution of pollen data can be used to relate the pollen assemblages to specific climatic, edaphic, or topographic conditions or to investigate the features of fire-regime or anthropogenic activities in the study area. This affects the ecological interpretation of the results, especially if the taxonomy is relevant for a major component of the vegetation, such as trees, where different species of the same genus have very different ecological requirements. When pollen identification is carried out to the lowest possible taxonomic level (e.g. differentiation between different types of *Betula* or Cerealia pollen) and also other types of microfossils such as coprophilous fungal spores or testate amoebae are identified, this adds extra value to the data obtained and the higher taxonomic resolution can prove to be worth the effort when making interpretations. The distribution of different tree species living at their ecological limits in the northern boreal forest opens up the possibility to use the detailed pollen record as a means for investigating changes in the climate over centuries and millennia. It has been shown that pollen production of tree species varies according to summer temperatures so, that the mean summer temperature of the previous year affects the number of pollen grains an individual tree will produce in any given year and this way it is possible to use high temporal resolution pollen data to reconstruct past summer temperature fluctuations (Autio and Hicks 2004; Barnekow et al. 2007; Huusko and Hicks 2009; Kamenik et al. 2009; Paper III). Each tree species, or sub-species in case of *Betula*, has its own requirements in this respect.

The need for quantification

The question of a quantified interpretation of palynological data arose as early as 1916 when Hesselman asked Von Post how it would be possible to distinguish between pollen from a few local trees and pollen produced by distant forests (Hesselman 1916). Hesselman's question remains unanswered when only a single mire or lake is used for vegetation reconstructions but when multiple sites are studied the differences in local vegetation shows up as variation between sites (Sugita 1994; 1998; Davis 2000). This, and understanding the meaning of the heterogeneities in the vegetation and what this means in terms of pollen assemblages, has led to the development of simulation models which help in the effort of quantifying the pollen-vegetation relationship (Sugita 1994; 1998; Sugita et al. 1999).

Pollen accumulation rates (PAR) form an ideal technique for quantifying the surrounding vegetation, as they measure directly the pollen loading of a certain species on a surface in a period of time independently from other species. However, the use of pollen accumulation rates requires a significantly larger amount of work to obtain the data and the need for a robust age-depth chronology is crucial. These, and some other complicating features such as uneven sediment accumulation in lakes, have held back the use of this technique so far (Davis and Deevey 1964; Lehman 1975; Davis and Ford 1982; Davis et al. 1984).

Models of pollen dispersal and deposition

Modelling pollen dispersal and deposition helps in the effort of quantifying the pollen-vegetation relationship in a heterogeneous landscape. The theory relevant for a quantitative reconstruction of a past landscape has developed dramatically over the last decades (Davis 1963; 2000; Parsons and Prentice 1981; Prentice and Parsons 1983; Prentice 1985; Sugita 1994; 1998; 2007a,b). The development of the pollen dispersal and deposition models started with the R-value model by Margaret Davis (1963). The R-value model relates the pollen percentages to vegetation percentages making an effort to reconstruct the past vegetation on the basis of pollen percentages (Davis 1963). The R-value model assumes that pollen loading of a certain species is linearly related to the product of pollen productivity of that species and its abundance in the vegetation around the site. The R-value of that species is defined by dividing the pollen loading – vegetation relationship of that species by the pollen loading – vegetation relationship of a reference species. When the R-value for each individual taxon is known, the vegetation percentages of these taxa can be calculated from an equation. In theory, this should correct for the nonlinear nature of the pollen percentages' representation of the vegetation, the Fagerlind effect (Fagerlind 1952), and improve the goodness-of-fit between the pollen and vegetation data but, unfortunately, it did not work because the vegetation data was recorded only to 500 m and the basin size varied.

The R-value model was then further developed to the Extended R-value (ERV) model by Parsons and Prentice (1981, ERV sub-model 1), Prentice and Parsons (1983, ERV sub-model 2) and Sugita (1994, ERV sub-model 3). The Extended R-value model aims to linearize the non-linear dataset with percentage data by using an iterative approach. ERV sub-models 1 and 2 were designed for datasets constituted from percentage data in both pollen and vegetation (Parsons and Prentice 1981; Prentice and Parsons 1983). ERV sub-model 3 assumes that at the same time as pollen data are available in percentages, the vegetation data is available in absolute units as vegetation abundance.

Another important step towards the quantitative reconstruction of vegetation was taken by Sugita when he introduced the Landscape Reconstruction Algorithm (LRA) (Sugita et al. 1999; Sugita 2007a,b). LRA consists of two models, 'Regional Estimates of VEgetation Abundance from Large Sites' (REVEALS) and 'LOcal Vegetation Estimates' (LOVE) that quantify the vegetation composition at different spatial scales (Sugita 2007a,b). In other words, the LRA framework operates in two steps where the regional vegetation composition is estimated at first by using pollen records from large lakes or bogs and then the vegetation composition of the smaller sites can be reconstructed within their RSAP by incorporating the estimated regional vegetation composition into the picture (Sugita 2007a,b).

Pollen accumulation rates

A quantitative and high temporal and spatial resolution reconstruction of land-use and climate history in these northern boreal forests is a real challenge. One step towards the quantitative reconstruction of tree presence and forest density from fossil pollen data has been made by Hicks (2001) who has determined pollen accumulation rate (PAR) threshold values for the local presence/absence of the three dominant tree taxa of the north, *Pinus sylvestris* L., *Picea abies* (L.) H. Karst, and tree *Betula* (including the mountain birch *Betula pubescens* ssp. *czerepanovii*), based on a long record of annual pollen deposition monitored by modified Tauber traps. These threshold values are with respect to a known basin size. PARs provide a better record of vegetation changes since the representation of each taxon is unaffected by the changes in the abundance of other taxa and the abundance of different species in the vegetation can, in theory, be inferred linearly from the pollen record (Davis and Deevey, 1964). This approach was chosen, because the percentage representation of pollen types is a closed universe and the so called Fagerlind effect (Fagerlind 1952; Prentice and Webb 1986), can cause complications. In particular, in areas where a high pollen producing species, such as Scots pine, is abundant, the use of PARs ensures that the changes occurring in the abundance of low pollen producing species can also be detected.

OBJECTIVES

The central aim of this thesis is to assess the effects that land-use and climate have on the pollen representation of the vegetation at varying temporal, spatial and taxonomic scales in northeastern Finnish Lapland. Particular attention was paid to testing the suitability of different methods to detect and reconstruct the land-use changes or climatic fluctuations and to considering what are the benefits and limitations of these methods (Figure 2).

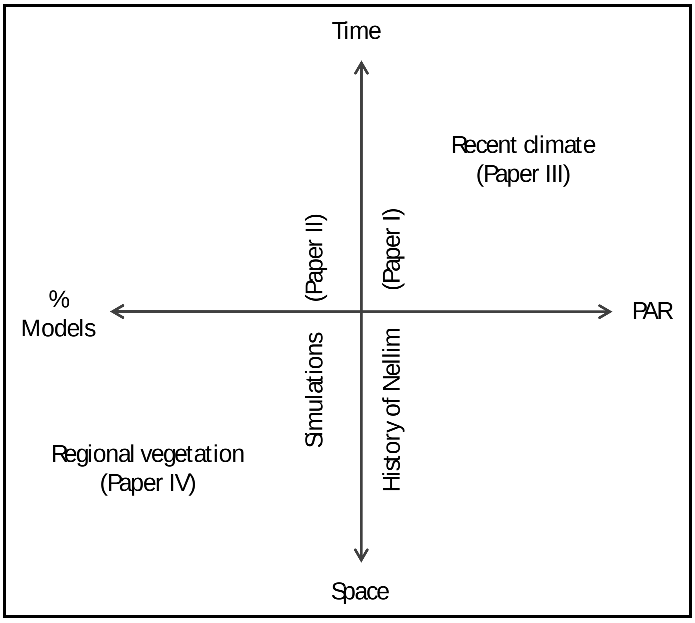

Figure 2 Matrix that illustrates the location of each article in this thesis in relation to temporal - spatial and relative – absolute attributes of the pollen data.

The following questions were addressed:

1. What changes in the land-use at local and regional scales are identifiable in the high temporal resolution fossil pollen accumulation rates data? (Paper I)
2. How the variation in the local land-use over time is reflected in the pollen accumulation rate (PAR) and pollen percentage data, and to what degree it is possible to simulate these changes accurately? (Papers I & II)
3. How applicable is the modelling approach in reconstructing the vegetation of the monospecific *Pinus* dominated forest of northern Finnish Lapland at both local and regional scales and what is the general resolution that these methods can achieve? (Papers I, II & IV)
4. Is it possible to calibrate high temporal resolution fossil pollen data with instrumental temperature records and use the results to reconstruct temperature fluctuations over centuries and millennia? (Paper III)
5. To what degree does a high taxonomic resolution in the pollen record (lowest possible taxonomic level of identification) improve the interpretation of the results? (Papers I and III)

MATERIALS AND METHODS

Study area

The main study site is situated in the small village of Nellim (ca. 200 inhabitants in 2006) in northeastern Finnish Lapland (Figure 3). Nellim was chosen, because it is situated in the northern boreal pine forest where trees are growing close to their extreme limit and are therefore sensitive to any disturbance. Its location north of the *Picea abies* forest line makes the overall picture simple and allows any temporal and spatial changes in the high resolution pollen data to be tracked fairly accurately. A record of annual monitoring of pollen deposition in a modified Tauber trap is available from outside the village which allows a comparison and calibration between the monitored pollen deposition data and the high resolution fossil pollen data. Nellim was also one of the focal sites of the EU-funded project PINE (Predicting Impacts on Natural Ecotones EVK2-CT-2002-00136) and has been the location for detailed socio-economic studies (Riipinen 2005; 2008). The beginning of settlement in the area and the later history of the village and forest management in the area are well documented (Valtanen 1994; Enbuske 2003; Lehtola 2003; Nahkiaisoja and Lehtola 2003; Nahkiaisoja 2006). The surroundings of the village are dominated by coniferous forests with *Pinus* (Figure 4; Figure 5) as the most abundant tree species accompanied by *Betula pubescens* ssp. *pubescens* in the southern part of the area with *Betula pubescens* ssp. *czerepanovii* (Figure 6) becoming more abundant in the north. The region comprises a mosaic of small mires and forests, with a number of different sized lakes, of which the largest one is Lake Inari (Figure 3).

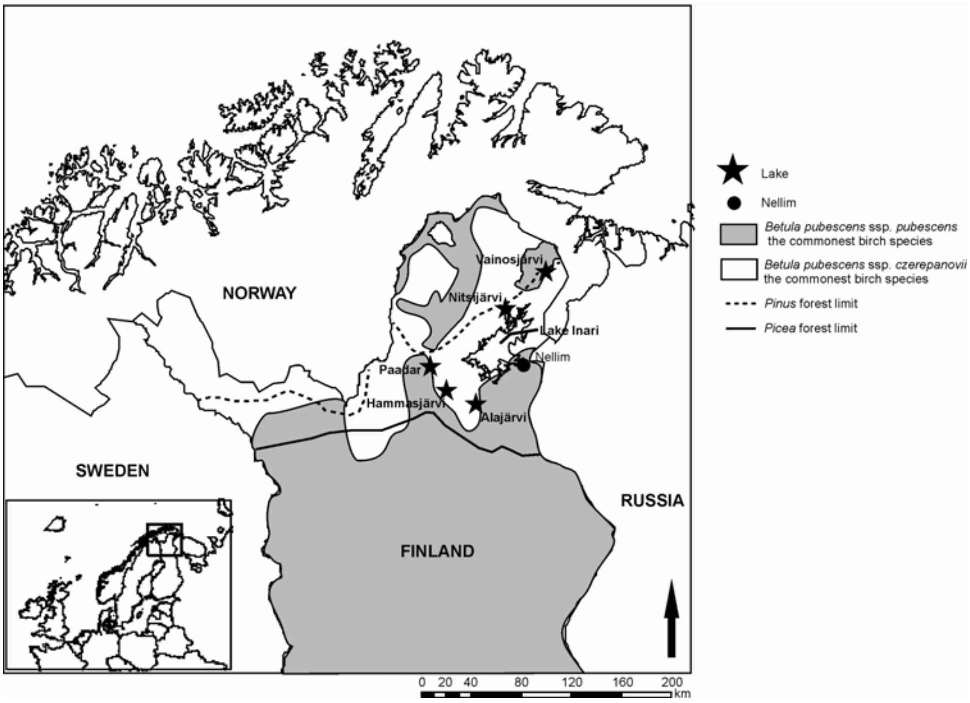

Figure 3 Map showing the location of each pollen dataset and the position of the forest limits of the main tree species in the area.

Figure 4 General view of the Nellim village; it is forested with some small hay fields. The white arrow in the lower right hand picture points to the location where the peat sample fossil pollen dataset was collected (the distance between in and the school pier in the bottom of the frame is about 200 m).

Figure 5 General features of *Pinus sylvestris* forests in northern Finland. Most of the forests are dominated almost entirely by pine and the age distribution of the trees within the forest patches is very homogenous. The trees are usually not very tall and frequently widely spaced.

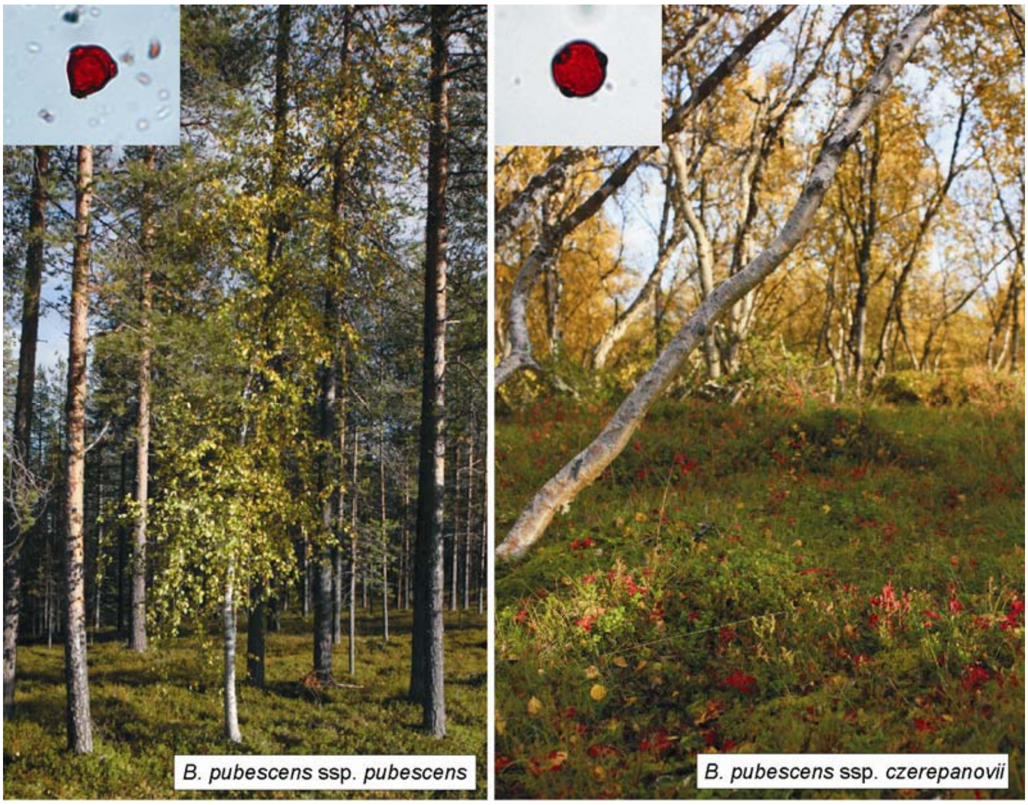

Figure 6 Although, the hybridization causes some complication in separating the downy birch (*Betula pubescens* ssp. *pubescens*) and the mountain birch (*Betula pubescens* ssp. *czerepanovii*) pollen, the higher taxonomic resolution of the pollen data may turn out to be useful when the aim is to reconstruct climatic or edaphic conditions. The pollen of *B. pubescens* ssp. *pubescens* is triangular in polar view with a thick exine and a deep vestibule to the pore while that of *B. pubescens* ssp. *czerepanovii* is generally larger in size, circular in polar view, has a thin exine and shallow pore.

Figure 7 The mires of northern Finnish Lapland usually have some pines growing on them with *Vaccinium spp*. and *Betula nana* growing along the drier strings and Cyperaceae in the wetter flarks.

Pollen datasets

Palynological data for this thesis was collected in three different datasets (Figure 3); 1) a peat profile to produce a continuous fossil pollen data time series for the last 100 years; 2) a time series of annual pollen deposition in a modified Tauber trap for the last 20 years; and 3) a set of surface sediment samples from five large lakes to supply data from the regional pollen component.

Peat data

For the fossil pollen analysis a 36-cm long peat monolith was collected from a *Sphagnum* hummock near the centre of the village on the shore of a small lake Maajärvi (68° 50' 40.1" N, 28° 19' 46.7" E, Figures 3 and 4) in the autumn of 2003. The peat monolith was first sampled for AMS (Accelerator Mass Spectrometry) dating and age-depth model, which was later used to construct a robust chronology to enable sampling at as close to one-year intervals as possible. A 36 cm long sample block of 4 × 4 cm in surface area was sawn from the frozen peat monolith. Sub-samples for pollen preparation were cut contiguously from the frozen block such that the thickness of each sample was as close to one year as possible. Sample thickness was, however, restricted to 2 mm, since thinner samples would not have been accurate enough with this relatively large surface area. Pollen preparation followed a procedure of heating for 10 minutes in 10% KOH to remove the humic material, sieving through 177 μm screen, followed by acetolysis in a water bath for 2 minutes to dissolve the cellulose. The samples were then stained with safranin and mounted in silicone oil to avoid the swelling of pollen grains and enable the differentiation between different types of *Betula* pollen (Terasmäe 1951; Berglund and Ralska-Jasiewiczowa 1986; Hicks 2001). Microscope slides were analyzed and pollen grains counted at 400× magnification and at 1000× magnification for problematic grains. A minimum number of 500 arboreal pollen grains was counted for each sample which gave an adequate precision for the PARs. Spheroidal carbonaceous particles (SCP), charcoal, fungal spores and testate amoebae were counted in parallel with the pollen. The microfossil counts were processed with the Tilia 2.0.b.5 and TGView 2.0.2 programs (Grimm 1990) to produce the diagrams and the results are presented as PARs (grains cm^{-2} a^{-1}). The peat profile and pollen preparations are described in more detail in Paper I.

Pollen trap data

The modern, high temporal resolution reference record of monitored pollen data is available from a network of modified Tauber traps in northern Fennoscandia (Hicks 2001; Huusko and Hicks 2009). The traps are placed in the centres of small mires, and cover the different vegetation zones in the area. Data are collected annually in the autumn so that the whole flowering season's pollen deposition is recorded (for details, see Hicks 2001). In this thesis, the *Pinus* and *Betula* PAR data from trap N7 (covering years 1983–2002, and located at a distance of 2.5 km from the fossil peat profile), was used as a means of calculating the degree to which the fossil data are smoothed.

Lake sediment data

In order to make regional vegetation reconstructions by the REVEALS model, five large lakes (≥100- 500 ha) were selected for collecting the surface sediment samples from the same *Pinus* dominated boreal forest, north of the *Picea abies* treeline, from which the peat monolith was collected. The five large lakes, Alajärvi, Hammasjärvi, Paadar, Nitsijärvi and Vainosjärvi, are scattered evenly over the study area. Surface sediment samples were collected in April 2005 from the frozen surface of the lakes. A LIMNOS type gravity corer (Kansanen et al. 1991) was used to sample the loose surface of the lake sediment. From each of the five lakes five sediment cores were collected so that one core was taken at the center of the lake and four others at 100 m distance from the center in the four main compass directions. Three samples per lake were prepared for pollen analysis and they were selected so that all the lakes have the center sample prepared. Two other samples from each lake were selected so, that they were taken from the diameter of the narrowest part of the elongated lake basin. This arrangement was chosen in order to compare the pollen percentages to see if there would be any significant difference to the results if the distance to the closest lake shore varies. The pollen preparation of the surface sediment samples had a different procedure from the peat samples. It started with sieving through 177 μm sieving cloth, which was followed by the removal of clay by deflocculating the clay minerals with sodium pyrophosphate in a manner described by Bates et al. (1978). The remaining mineral matter was dissolved in cold HF and the sample was washed in hot HCl. After this the preparation followed the standard procedure with acetolysis in a water bath for 2 min to remove the cellulose and heating in 10 % potassium hydroxide (KOH) for 10 min to remove the humic material. In the end the pollen was stained with safranin and mounted in silicone oil (Berglund and Ralska-Jasiewiczowa 1986). Pollen identification was done in the same manner as with the fossil profile. However, this time a minimum number of 1000 arboreal pollen grains were counted for each sample in order to insure smaller standard error in the model runs. Although a complete palynological investigation was made, only eight taxa were used to run the REVEALS model.

Land-use data

Three different sets of land-use data were used in this thesis. Firstly, a literature survey about the land-use history in the area was performed and collated into a table (Table I; Paper I). Secondly, a vegetation map about 11 km x 11 km in size with different age classes of the present day forest was digitized and re-classified to run the simulations in Paper II. The vegetation mosaic was classified according to the age structure of the forest, which allows variation in the otherwise monotonous landscape, because an older, denser forest can be expected to produce more pollen than a young, sparser one. This local grid was nested within a larger one that was compiled from CORINE land cover data (CLC 2000) with the areas inside the adjacent areas of Norway and Russia classified as ‘Mixed forest’. These same basic grids were used to run the simulations in four time windows, but the vegetation composition and density of the different forest patches were changed to correspond to the intensity of forest management in northern Finland during each time period (Finnish Statistical Yearbook of Forestry 2005).

Event	Year	Reference
School closed	2001	Minute from the administrative meeting of Inari board of education
The emission of SCPs drops	1980	Rose (1995)
Extensive logging in northern Finland	1950's → 1990's	Valtanen (1994), Luhta (1999) & Lehtola (2003)
Nellim school opened	1948	Lehtola (2003)
Skolt Sámi evacuees settled in the area, village grows	1944 → 1950's	Lehtola (2003)
Regulating dam at Niskakoski destroyed	1944	Lehtola (2003)
Damming of River Paatsjoki at Jäniskoski	1942	Autere & Liede (1989)
ATIF logging in Inari area	1925 – 1939	Nahkiaisoja and Lehtola (2003)
Main road from Kyrö (Ivalo) to Petsamo extends to Nellim	1922	Suomen virallinen tilasto (1935)
Cleared alignment for the road	1918	Itkonen (1991)
Nellim farm	1876	Nahkiaisoja (2006)

Table I The major events in the land-use history of Nellim.

Thirdly, in Paper IV the REVEALS model's predictions of the regional vegetation were compared to the vegetation data from an area of 250 km X 250 km, which was regarded as large enough an area to represent the regional vegetation for all the lakes. To produce the vegetation data file in this case, European CORINE landcover data (CLC2000) for northern Finland and Global Landcover 2000 (GLC2000) for areas in Norway and Russia were combined. CLC and GLC data were chosen because they are freely available and widely used and it is important to verify their usability in this kind of research. CLC data classes were combined and reduced to 22 classes that are relevant to this area (Table II) and GLC classes were reclassified into corresponding CLC classes (Table III). The differences in vegetation composition between the "Basic CORINE classification) and the "Cropped CORINE classification" (Paper IV) and the frequencies of the different land-cover classes are presented in tabular format in Appendix 1.

CLC CODE	CLC CLASS
0	Non pollen producing areas
1	Water
2	Fields
3	Pastures
4	Coniferous forest on mineral soil
5	Coniferous forest on peatland
6	Deciduous forest on mineral soil, closed
7	Deciduous forest on mineral soil, open
8	Deciduous forest on peatland
9	Mixed forest on mineral soil
10	Mixed forest on peatland
11	Meadows
12	Transitional woodland/shrub, cc<10%
13	Transitional woodland/shrub, cc 10-30%, on mineral soil
14	Transitional woodland/shrub, cc 10-30%, on peatland
15	Mosaic crops/ Tree cover/ Other natural vegetation
16	Transitional woodland/ Shrub above coniferous timberline
17	Transitional woodland/ Shrub under electric cable
18	Moors and heathland
19	Natural grassland
20	Sparsely vegetated areas
21	Open peatlands
22	Wetlands

Table II The 22 CORINE Land Cover classes that were used to compare the regional vegetation to the REVEALS reconstructed vegetation

GLC CLASS		CORRESPONDING CLC CLASS
No data	→	N/A
Tree cover broadleaved, evergreen	→	N/A
Tree cover, broadleaved, deciduous, closed	→	6 Deciduous forest on mineral soil, closed
Tree cover, broadleaved, deciduous, open	→	7 Deciduous forest on mineral soil, open
Tree cover, needle-leaved, evergreen	→	4 Coniferous forest on mineral soil
Tree cover, needle-leaved, deciduous	→	N/A
Tree cover, mixed leaf type	→	9 Mixed forest on mineral soil
Tree cover, regularly flooded, fresh water	→	22 Wetlands
Tree cover, regularly flooded, saline water	→	N/A
Mosaic: Tree cover / Other natural veg.	→	16 Transitional woodland/shrub above conif. timberline
Tree cover, burnt	→	N/A
Shrub cover, closed-open, evergreen	→	18 Moors and heathland
Shrub cover, closed-open, deciduous	→	20 Sparsely vegetated areas
Herbaceous cover, closed-open	→	22 Wetlands
Sparse herbaceous or sparse shrub cover	→	21 Open peatlands
Regularly flooded shrub and/or herbaceous cover	→	21 Open peatlands
Cultivated and managed areas	→	2 Fields
Mosaic: Cropland / Tree cover / Other natural veg.	→	15 Mosaic crops/ Tree cover/ other natural veg.
Mosaic: Cropland / Shrub and/or Grass cover	→	19 Natural grassland
Bare areas	→	0 Non pollen producing areas
Water bodies	→	1 Water
Snow and ice	→	0 Non pollen producing areas
Artificial surfaces and associated areas	→	0 Non pollen producing areas
Cropland, temporarily flooded	→	N/A

Table III Reclassification of the Global Land Cover data to the corresponding CORINE Land Cover classes

Temperature data

For the calibration of pollen deposition with meteorological data a set of instrumental temperature measurements from Nellim (1959–2002; 68° 50’ N, 28° 18’ E) and a longer record from Sodankylä (1908–1994; 67°22’ N, 26°37’ E) were used. The two meteorological stations are some 180 km apart but the measurements do not differ significantly between them and the overall year-to-year variations in monthly mean temperatures are the same. In order to cover the full period of the fossil pollen data, the Sodankylä temperature record was extended further back in time to AD 1881, estimating the monthly mean temperatures using the Ojansuu–Henttonen model (Ojansuu and Henttonen 1983).

Quantification techniques

Models

Simulation approach

Several papers where the pollen deposition has been modelled in different land-use scenarios at different time-windows in the past, have been recently published (Nielsen 2004; Caseldine and Fyfe 2006; Fyfe 2006; Bunting et al. 2007; 2008; Caseldine et al. 2007; Gaillard et al. 2008; Hellman et al. 2009; Soepboer and Lotter 2009; von Stedingk and Fyfe 2009). One increasingly used approach for interpreting the pollen record is the application of simulations, where the pollen loading to a point is simulated in different vegetational environments using a software package such as HUMPOL (Bunting and Middleton 2005) or POLLSCAPE (Sugita 1994; 1998; Sugita et al. 1999). This approach is based on the Prentice-Sugita model of pollen dispersal and deposition (Prentice 1985; 1988; Sugita 1993; 1994).

The basic assumptions of the Prentice-Sugita model are:

1. The sampling basin forms a circular opening in the forest canopy;
2. Pollen is dispersed evenly in all directions;
3. Pollen is mainly transported by wind above the canopy and by gravity beneath the canopy and there are no other significant methods of transport;
4. The pollen productivity of each taxon is constant;

5. The spatial distribution of each taxon in the landscape is expressed as a function of distance from the centre of the depositional basin;
6. Pollen deposition is approximated by a function of distance from the source plant (i.e. point source) derived from Sutton's (1953) diffusion model of small particles from a source at ground level. This means that all plants are assumed to be of the same height, trees and grasses alike, and that the canopy is at ground level.

Modelling pollen deposition at a high spatial resolution in different land-use scenarios is a little problematic in the northern boreal forest, as *Pinus sylvestris*, a relatively high pollen producer, is the dominating species over the entire area.

REVEALS model

The REVEALS model is based on an assumption that pollen counts that come from large sites (≥100-500 ha) do not differ significantly among each other and are therefore representative of the regional vegetation (Sugita 2007a). Other basic assumptions behind the REVEALS model are to some extent similar to the assumptions behind the Prentice-Sugita model:

1. The pollen grains are transported by wind above the canopy, and no other method of transport is taken into account;
2. The sedimentary basin for pollen deposition is a circular opening in the canopy;
3. Dispersal of pollen grains is assumed to be even in all directions;
4. Most of the pollen (i.e. 90%) comes from within Z_{max}, and the amount of pollen coming from outside Z_{max} is insignificant;
5. Pollen productivity estimates with standard errors are available for all taxa that are used for reconstructing regional vegetation.

Pollen Accumulation Rates

Pollen accumulation rates are linearly related to the abundance of different species in the surrounding vegetation and therefore they form a practical method for a quantified interpretation of vegetation from pollen data (Davis and Deevey 1964). In order to calculate PARs with a high degree of precision it is necessary to (1) take known volumes of sediment, (2) have minimal error bars on the pollen concentration calculations and (3) have a robust age-depth chronology for the profile.

Sediment volume and pollen concentration

PARs are calculated by taking the pollen concentration of the sediment and dividing it by the number of years that it has taken for that section of sediment to accumulate. The sediment volume must, therefore, be known together with the exact depth range that it occupies in the profile. The pollen concentration itself is calculated with respect to an added marker grain but the confidence limits on this calculation depend on the ratio between the number of pollen grains counted and the number of marker grains counted in any each sample (Maher 1981). An alternative for this added marker grain method is to take a sub sample of known volume using a micropipette, but with this method every single pollen grain in the sample has to be counted which is time consuming.

Chronology

The number of years of accumulation represented in each sample is an essential part of the PAR calculation. This is why a robust chronology is crucial and, except when dealing with a varved lake sequence, this can only be produced through dating carefully selected short-lived plant material at closely spaced intervals down the profile (e.g. Goslar et al. 2005). The age-depth model for the Nellim profile was calculated as a curve which was as smooth as possible while still passing reasonably close to the probability maxima of calibrated dates, using the algorithm described by Goslar et al. (2009) and taking peat stratigraphy into account. The reliability of the chronology can be assessed for the recent period by looking at additional historically dated events that are recorded in the profile, such as Spheroidal carbonaceous particles (SCPs) which are preserved alongside pollen and can provide an excellent chronological control. Their record can be used as an unambiguous indicator of atmospheric deposition from power plants and other industrial sources because they are not produced by any natural processes (Rose and Appleby 2005). The historically dated rise in industrial activity and the reduction in SCPs towards the end of the 1980s following the clean air act have the same pattern all over Europe and can therefore be used to evaluate the youngest section of the chronology.

Numerical methods

Various statistical approaches were used for testing the results from modelling the land-use changes in the study area and for extracting the climate signal from fossil PAR data.

Land-use changes

The Chi-squared test was used to define whether the pollen loading results from the simulations of the various local land-use scenarios were similar to the observed pollen assemblages (Paper II). The results of these tests are presented in Paper II. However, Chi-squared calculations are considered to be reliable only when less than 20 % of the expected frequencies are smaller than 5 (Saunders and Brown 2007). This pre-requirement is violated with this dataset and thus the p-values are not very reliable.

To assess the within-lake and between-lake differences in pollen datasets that were used for running the REVEALS model, an ordination method Principal Components Analysis (PCA) was used (Paper IV). The PCA was run by CANOCO 4.5, and CanoDraw (Jongman et al.1995; ter Braak 2002). The pollen data used in these analyses were normalized and expressed as percentages of those taxa that were included in the REVEALS model runs (8 taxa). The results and the PCA plot are presented and discussed in Paper IV.

Climate changes

Firstly, in order to test the smoothing inherent in the fossil pollen data, the record of monitored PAR data (years 1983–2002) of *Pinus* and *Betula* from the same area, was smoothed by different intervals from 2- to 7-year moving averages (Paper III). The fossil PAR data from the corresponding time period were smoothed in two blocks by varying intervals of moving averages so that between years AD 2002 and AD 1996 where the temporal resolution of fossil PARs is 1 year, the smoothing intervals used are 2–7 years and before AD 1996 until AD 1980, where the temporal resolution of the record is 2 years, the applied smoothing intervals are from 2 years up to 6, to obtain a continuous record with constant intervals. The smoothed PARs from both fossil and monitored records of *Pinus* and *Betula* were compared on a scatterplot (Paper III).

Later, to test whether the fossil pollen record retains the temperature signal, the July temperature record from northern Finland was smoothed using a weighted mean of 3, 5 and 7 years, as determined by the PAR correlations from comparisons of monitored and fossil pollen PARs (Paper III). *Pinus* and *Betula* PAR values were corrected so that each sample represented the nearest full year. During the last two decades of the 20th century, the rise in biomass has been dramatic in the forests of northern Finland, as the amount of biomass removed from the forests through felling was less than 70% of the biomass increase due to escalating growth (Finnish Statistical Yearbook of Forestry 2005). For the calibration of the temperature record and the fossil PARs this section of the most dramatic rise in PARs (1990–2002) had to be omitted to obtain a normally distributed dataset. PAR values of both taxa and smoothed July mean temperatures were plotted on a scatterplot and equations obtained from the linear regression were used to reconstruct the July temperature from the PARs of both tree species. The accuracy of these reconstructions was assessed by calculating the root mean square deviation (RMSD), which is a measure of the differences between the predicted and observed values and should be close to 0. The results from the linear regression were also tested by resampling the data using both bootstrapping and jackknifing techniques.

Assessing error bars in pollen concentration

The 95% confidence intervals on the *Pinus* and *Betula* pollen concentration values (Papers I (*Pinus* only) and III (*Pinus* and *Betula*)) were calculated using Mosimann's (1965) equation. This method recognizes that the negative binomial distribution approximates to a lognormal distribution when the number of counted marker grains is fairly large. However, it does not recognize the standard deviation in the number of the *Lycopodium* marker grains contained in the tablets or the variation in the sample volume. The sampling procedure for the fossil dataset used in this study, by which slices of varying thickness are cut from a frozen block of peat does not allow any estimation of the mean and standard deviation of the sample volume. It was also not possible to incorporate the standard deviation of the rate of peat accumulation used to convert the pollen concentration values to PARs since this information was not available.

OUTLINE AND SUMMARY OF THE ORIGINAL CONTRIBUTIONS

Paper I - Pollen accumulation rates as a tool for detecting land-use changes in a sparsely settled boreal forest

In the first paper a peat profile from the village of Nellim in northern Finnish Lapland was analyzed at a near-annual resolution in order to test to what degree of accuracy the land-use history of the village could be reconstructed on the basis of organic microfossils. The profile was first AMS ^{14}C dated and a robust age-depth chronology constructed to enable a high temporal resolution in sampling for pollen and microfossil analyses. A set of 47 contiguous samples were treated and counted to produce a PAR diagram. PARs were chosen for use in this study, because they enable a better distinction of the fine spatial and temporal scale human induced changes in the pollen assemblages than the classical percentage representation through the fact that actual changes in the occurrence of each pollen taxon could be followed individually. Changes in the accumulation rate of pine pollen were discovered to reflect changes in forest-use. Both local events affecting the pollen deposition in the immediate surroundings of the village area and regional logging activity in the larger context of the whole of north-eastern Finnish Lapland could be distinguished, thus making pine pollen the most representative proxy in the northern boreal forest. Situations when PARs may not give very reliable results are usually connected to the physiology of the plants (i.e. failing to flower due to cold summers) or to changes in taphonomy between different pollen types. The very local, within-mire changes were deduced from the peat stratigraphy and the testate amoebae but the processes of peat formation may also cause some bias in the representation of the development of the mire surface. When these limitations are recognized in drawing the conclusions, PARs are an important tool for this type of study. Other proxies such as SCPs, testate amoebae and peat stratigraphy, when combined with the pollen analysis, clearly strengthen the interpretation of the results.

Paper II – Simulating pollen loading in a Northern Boreal Forest: the effect of changing forest densities and distribution

In order to see, what is the significance of using small scale forest density changes when simulating pollen deposition in the northern boreal forest situations where the vegetation mosaic is comprised mainly of different forest densities rather than forest types with different species, an observed pollen record from a peat profile collected in the village of Nellim, was compared to a series of simulated pollen assemblages from four time windows, each representing different stages of forest management. Simulations were carried out using the HUMPOL software package which uses the Prentice-Sugita pollen dispersal-deposition model to produce pollen loading data from an actual vegetation scenario or a hypothetical one. The four time windows used were: 1) AD 1880, a time of 'minimal human interference' when the first farm in the area was established; 2) AD 1940, a time of 'moderate human interference' with some selective loggings in northernmost Finland; 3) AD 1970, a time of 'heavy human interference' after the extensive logging in northern Finland; and 4) AD 2000 a 'modern situation with increasing growth of the biomass of the forest'. A second objective of this paper was to investigate the significance of using small scale forest density changes based on the real vegetation maps, where the different aged forests were in their authentic locale vs. randomly created maps with the same vegetation composition, but the vegetation communities placed completely randomly and how this affects the pollen loading. The third point was to calculate the relevant source area of pollen in the Nellim area. The results indicate that simulations replicate the arboreal pollen percentages, which comprise most of the pollen deposited, very well, while the pollen percentages of the non-arboreal taxa differ considerably from the observed data. Although the model is mainly designed for a mosaic of different forest and vegetation types it also seems to work reasonably well when the vegetation mosaic is composed of a series of different densities of the same forest type. The completely random landscape scenarios produce similar results to the ones which use the actual vegetation composition. In both cases the cultural events, such as a growing settlement, cannot necessarily be detected by the simulations in this kind of environment. The relevant source area in the study area is 1000 m which is analogous with the previously published one.

Paper III - Pinus and Betula pollen accumulation rates from the northern boreal forest as a record of interannual variation in July temperature

In this third study, an attempt was made to use fossil *Pinus* and *Betula* PARs data from a peat profile in Nellim, to determine the boundaries of the temporal resolution in the fossil pollen record by comparing the data with a 20-year annually resolved record of monitored pollen deposition data of both taxa from 2.5 km away. The smoothing inherent in the fossil PAR data was found to be about 5 years compared with the annually monitored PARs but, while year-to-year variation in PARs is lost, the overall trend is still preserved. *Betula* pollen accumulation rates were found to be much lower in the fossil record compared to the monitored ones, but nevertheless the retained trend was still found in this dataset, too. Then the information on the annual resolution of the pollen record was used to test the interconnectedness of fossil *Pinus* and *Betula* pollen accumulation rates to the weighted mean of July temperature measurements by calibrating the fossil PARs with the appropriately smoothed temperature record for northern Finland and the possible methods for calibrating *Pinus* and *Betula* PARs so as to reconstruct long-term temperature records from these data was discussed. The correlation between fossil *Betula* PARs and July mean temperatures appears to be much higher than the correlation between fossil *Pinus* PARs and temperature, probably because the subspecies *Betula pubescens* ssp. *pubescens* is at its northern limit in this particular area and the majority of *Betula* pollen in the profile was of the *Betula pubescens* ssp. *pubescens* type. The temperature signal in this dataset was found to be disturbed during the period when the forests in northern Finland were heavily cut and when regenerating trees were reaching maturity. However, the results indicate that for a pollen record covering hundreds of years and without heavy human intervention at the scale of the post- Second World War felling, *Pinus* or *Betula* PARs have the ability to give a low-frequency temperature signal.

Paper IV- How applicable is the REVEALS model in reconstructing regional vegetation in a monospecific Pinus sylvestris dominated forest of northern Finnish Lapland?

In this fourth study the REVEALS model and its ability to reconstruct the regional vegetation was tested in the boreal forest zone of northern Finnish Lapland, where *Pinus sylvestris* is the dominating tree species. This area is especially interesting for testing the model, because the vegetation is vastly monotonous and there is an extreme dominance of a single species with relatively high pollen productivity. To obtain the necessary pollen data for the model runs, five large lakes were sampled for their surface sediment and three sub-samples from each lake were prepared for pollen analysis. European CORINE landcover data (CLC2000) for northern Finland and Global Landcover 2000 (GLC2000) for areas in Norway and Russia were combined to produce a vegetation data file, which was used to compare the model estimates of the regional vegetation with the actual vegetation composition. The classification of the landcover types in the vegetation data had two approaches. First, all taxa used in the model runs were taken into account in each landcover class and both the coverage of standing timber and coverage of the field layer species were taken into account. This was called the 'Basic CORINE classification'. The second method for classifying the data included only the two or three most important taxa in each landcover class, thus only trees in the forest classes and mainly non-arboreal taxa in the more open areas. This was called the 'Cropped CORINE classification'. These two different systems for classifying the vegetation data were rationalized by the model assumption that all pollen grains are released at the same height and this is a way of investigating whether that assumption leads to overestimation of the non-arboreal taxa. Eight main taxa (*Pinus, Betula, Salix, Empetrum, Vaccinium, Calluna,* Cyperaceae, Poaceae) from the vegetation communities in the area were selected to run the model. The REVEALS reconstructions of the regional vegetation were compared with the two types of classification of the actual vegetation data. A comparison of the REVEALS reconstructed vegetation with both the basic and cropped CORINE classification of the actual vegetation shows that the REVEALS model estimates the total proportion of the trees and the non-arboreal taxa well, especially when the cropped CORINE classification of the landcover types is used, as the relationship between the model estimates of the regional vegetation proportions and the actual vegetation are within the error bars. The model, however, does not perform so well when results are compared with the basic CORINE classification, largely because the model assumes that all taxa (trees and forest floor plants) have the same height and perhaps also because of a feature of the non-linear nature of the pollen-vegetation relationship when just one taxon is highly dominant.

DISCUSSION

Land-use and climate in the pollen record

Temporal resolution of the results

Collecting pollen records in a continuous time series and at the highest possible temporal resolution is justified when the research questions to be answered require a detailed knowledge about short term cultural or agricultural history of a specific place, or when there is a need to reconstruct climatic fluctuations at a yearly or decadal scale. In this type of research pollen accumulation rates are superior to the traditional percentage approach in their precision (Papers I and III). A continuous, annual or near-annual resolution also opens up the possibility to combine pollen records with other annual proxies, such as dendrochronological records, and to use these combined datasets to answer research questions more robustly. A clear disadvantage of this type of study is its high cost in both resources and labour, because obtaining a continuous pollen record at the highest possible temporal resolution requires a strong chronological control in the form of several ^{14}C dates throughout the profile, precise sub-sampling of the profile and careful counting of the consecutive samples. Moreover, the sampling for pollen preparations cannot begin until the age-depth model is established which further delays the data collection. High temporal resolution PAR data seems to have some potential for the reconstruction of summer temperatures in the northern boreal forest zone and also in the Alps (Barnekow et al. 2007; Huusko and Hicks 2009; Kamenik et al. 2009; Paper III). However, this approach has a few limitations which need to be considered before continuing with the method. Firstly, the pollen data needs to be collected close to the forest line, to ensure that trees will react strongly enough to the differences in summer temperatures. Secondly, the pollen record should have an annual or near-annual resolution, which in practice means that the sediment used should be peat instead of lake sediments, because the sediment accumulation rate of the former is much faster than the latter this far north, where the annual deposition of lake sediments is less than 1 mm/a opposed to the ca. 5 mm/a of *Sphagnum* peat (Hicks and Hyvärinen 1999). Use of peat, on the other hand, leads to other complications such as the problem of losing the temporal resolution with increasing depth. Also, a robust age-depth chronology is vital for this purpose because the samples should be cut as close to an annual resolution as possible and this would be impossible without a strong chronological control. Lastly, the regional vegetation should be free of any intense forest management or other human interference because that will mask most of the temperature related changes in pollen accumulation rates and result in a disturbed signal.

Spatial resolution of the results

Pollen accumulation rates and pollen percentage data clearly have differing abilities to bring out the changes that happen in land-use at varying spatial scales (Paper I). The main advantage of PARs is in their capacity to provide a straightforward means for quantitatively reconstructing the surrounding vegetation (Davis and Deevey 1964; Hicks 2001). PARs also usually show the anthropogenic impact on the local vegetation better, since the pollen of the herbaceous plants have very low dispersal. They would be overshadowed by tree pollen in the particular area of this research if the traditional percentage manner of presenting the results would be used (Suominen 1975; Hicks 1993; Räsänen et al. 2007; Paper I). This research also implies that PARs have the potential to reveal the regional changes in vegetation, whether these are naturally occurring or human induced, especially when the scale of the changes is as huge as was the felling after the Second World War in northern Finland. This strongly affected the background component of the pollen loading (Paper I). The relatively high cost of producing reliable PARs, however, is a clear disadvantage of the method, since the research takes more time and resources with dense ^{14}C sampling and dating which has to be done before sampling for pollen preparations begins. Also the careful sample preparation and counting are time consuming.

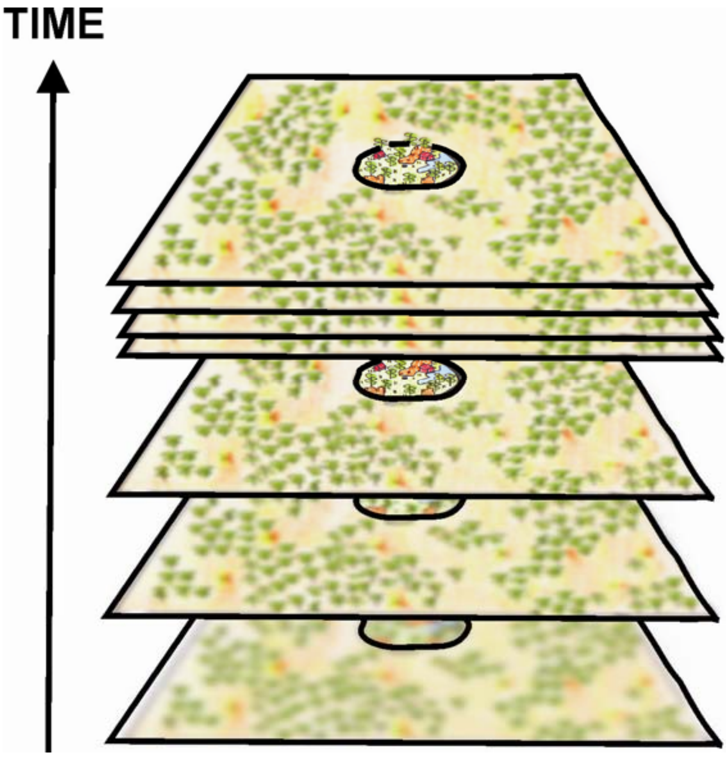

Figure 8 A schematic figure to illustrate the loss of spatial resolution of the pollen data through time. The circle represents the RSAP and the square the 250km X 250km vegetation analysis used in Paper IV.

Figure 9 A comparison between the ground vegetation in a pine forest; dominant taxa are *Empetrum*, *Vaccinium myrtillus* and *V.vitis-idaea* (left) and on a mire; dominant taxa are *Empetrum, V. uliginosum* and *Betula nana* (right).

The modelling approach for quantitative reconstructions of both local and regional vegetation history has its own advantages and disadvantages. This research illustrates, that simulations made on the basis of actual vegetation data at a local scale provide some useful insights into local vegetation history, but they do not give an unambiguous answer as to how the area actually looked and how close to the sampling place a specific disturbance occurred (Figure 8; Paper II). Since the simulations replicate the arboreal pollen percentages, which comprise most of the pollen deposited, very well, this approach seems to be useful in reconstructing the local forest history. This is even true in an environment with different densities of the same forest type. On the other hand, the pollen percentages of the non-arboreal taxa differ considerably from the observed data, and their percentage does not seem to be a good measure of cultural history in the form of human impact or landscape openness, even within the RSAP. The sampling design in Paper II covered the area of the village and even then the results did not produce reliable pollen values. This leads to a question whether a good spatial resolution is achievable, or even necessary, when the vegetation in the whole region is similar (Figure 8). Earlier simulations and observations from empirical studies have also reported similar results; that non-arboreal pollen percentages are not a good measure of landscape openness since the NAP underestimates the vegetation openness and the structure of the landscape within the RSAP in terms of patch size and the position of these patches in the landscape also affect the results (Hicks 1998; Sugita et al. 1999; Hellmann et al. 2009). The next step in a quantitative assessment of the vegetation at a local scale would be the application of the LOVE model (Sugita 2007b). The LOVE estimates of the local vegetation combined with knowledge of the topography and edaphic conditions should help in placing the vegetation units in the landscape, although the problem of equifinity may still remain.

The regional vegetation reconstructions are usually coarse and, in the northern boreal forest, this is even more likely to be the case because the vegetation composition is very simple and species diversity is low. The REVEALS model seems to be able to predict arboreal/non-arboreal pollen proportions from a simplified (i.e. cropped CORINE classification in Paper IV) landscape, but when the field layer flora is also taken into account, the picture becomes more obscure and the more abundant dwarf shrubs become overrepresented, probably because the model assumes all taxa to be of the same height. Moreover *Vaccinium* especially is abundant in most of the vegetation classes (Figure 9). This feature of the model to distinguish between forested and non-forested areas may be valuable and have applications when attempts are made to reconstruct historical changes in regional vegetation. Especially the Late Glacial (LG) – Early Holocene (EH) development when the landscape was more open and *Pinus* was only just migrating into the area could be an ideal scenario to reconstruct with the help of this approach as the forest type in northern Finland today closely resembles the EH situation further south. However, one must keep in mind that the REVEALS model assumes constant pollen productivity through time, which may not be the case in LG – EH situations in the south when climatic conditions or photoperiod were different from the current situation in the north.

Taxonomic resolution of the results

Aiming at a high taxonomic resolution and identifying pollen to the lowest possible taxonomic level helps when a detailed description of anthropogenic impact on the history of an area is to be made. This is particularly true when the aim is to record the history of agriculture and distinguish which plants were cultivated during certain periods. The anthropogenic and agricultural aspect of taxonomic resolution is obviously not so significant in the northern boreal forest, but if PAR data is collected at the highest possible taxonomic resolution e.g. time and effort is put in to identifying separately the different types of tree birch (*Betula pubescens* ssp. *pubescens* and *Betula pubescens* ssp. *czerepanovii*) pollen, this type of information can profitably be used in various applications for reconstructing local forest history or climate (Figure 6). Downy birch and mountain birch are found on different types of substrate in terms of edaphic factors such as soil solution conductivity and soil volumetric water content (Sutinen et al. 2007). Although the hybridization makes it difficult to separate different types of tree birch on the basis of their pollen there are still good ecological reasons to try to do so and the results so far look encouraging. The lower taxonomic level in pollen identification may also help to come around certain “oddities” in results if the two are counted together. Paper III demonstrates that the higher taxonomic resolution that goes down to the lowest taxonomic level (separating downy birch from the mountain birch) is an advantage when using high temporal resolution PAR data for reconstructing summer temperature fluctuations from the pollen record, particularly in areas where the species is growing at its ecological limits. This research illustrates that downy birch (*B. pubescens* ssp. *pubescens*) and mountain birch (*B. pubecens* ssp. *czerepanovii*) behave differently and *B. pubescens* ssp. *pubescens* gives a better correlation with the previous year’s summer temperatures because the species is growing at its ecological limit in the Nellim area.

For modelling purposes the concept of taxonomic resolution has a unique feature in the form of spatial distribution of different taxa between different vegetation zones especially in an area such as northern Finnish Lapland, where the transect across different vegetation zones will have an effect on the ratio between predicted and observed vegetation, not to mention the potentially different pollen productivities of the two birch species (Paper IV). When the modelling approach is restricted to an area, where coniferous forest consists mainly of Scots pine, this feature does not appear to be too significant in terms of complicating the overall picture, but as soon as areas within the spruce forest are included, the problem of distinguishing between different types of coniferous tree species becomes imminent. Obtaining spatial ecological data at a high resolution, where the coniferous species have been categorized and their mass or volume data per hectare is available, is expensive but crucial if the aim is to produce quantitative estimates of absolute vegetation quantities.

CONCLUSIONS

The first of the key aims of this thesis was to assess what kind of effects land-use has on the pollen representation of the vegetation and what methods are suitable for detecting these changes at varying temporal, spatial and taxonomic scales. The northern boreal forest offers its own challenges to the interpretation of pollen data with poor species diversity, but the near-natural state of the landscape also provides possibilities if the aim is to use the data as a modern analogue for earlier stages of the Holocene. This work reveals that PARs work better in the north providing more information than percentages when the vegetation composition is species poor and dominated by only one taxon. The modelling approach helps when the aim is to investigate the main characteristics of the vegetation at either local or regional scales, but when trying to detect local forest management or land-use in more detail, PARs tend to work better. This is because, in this particular area locally occurring events are usually at an extremely limited scale and the vegetation is the same both inside and outside the RSAP. Under such conditions in the percentage record, local events become practically invisible (Table IV).

	Cultural history	Local vegetation history (forest)	Regional vegetation history (forest)	Climate
Temporal resolution	Needs to be high	Can be coarse	Can be coarse	Needs to be annual
Spatial resolution	Needs to be high	Needs to be high	Coarse	Coarse
Taxonomic resolution	Important to distinguish events	B. pub v. B. tort could be significant	Can be coarse	B. pub v. B. tort could be significant
PAR	Important	Important	Not so important	Essential
Simulations (%)	Not very revealing	Partially revealing	-	-
REVEALS (%)	-	-	Partially revealing	-

Table IV A summary of the requirements for temporal, spatial and taxonomic resolution of pollen data when different kinds of research questions are posed together with an assessment of the significance of using PARs, simulations or the modelling approach to answer the same questions.

The second key aim of this research was to study what are the climate-driven effects on the pollen representation of the vegetation and what is the significance of varying the temporal, spatial and taxonomic resolution on that. The evidence suggests that a high (annual) temporal resolution and a continuous time series provides a climate signal, when PARs are used. In this case, PARs have the potential of reflecting the temperature fluctuations and allowing temperature reconstructions if the data has been collected close to the ecological limit of a species, the time series has a robust age-depth chronology and the area has not been under intense forest management or other major human interference. At a lower temporal resolution PARs provide a means for investigating long term changes in climate and regional tree lines, when the values show longer lasting (not annual, because trees cannot live and die so quickly) changes in abundance.

The following answers can be given to the questions listed in the objectives:

1. Identifying local and regional land-use changes from fossil pollen accumulation data require a continuous time series without gaps if the events happening are short in duration, so that the whole event from the very beginning to the end is recorded. Local land-use in the form of a settlement inside a regional northern boreal forest can be seen as an increase in the PARs of non-arboreal taxa if the sample for this type of study has been collected close enough to the actual disturbance. Larger scale changes i.e. heavy cutting of all the trees in extensive areas are more clearly visible as lower temporal resolution changes, since the regeneration of vast forest areas (and the growth of trees to pollen producing age) takes more time.
2. In a species poor area with only one or two dominant taxa, PARs usually provide a better record of the local changes that are related to human activities than percentages, but it must be kept in mind that in the north the local events tend to be very local and a sampling point too far away from the disturbance can result in a dataset that does not show any significant development. Pollen percentage data in itself does not provide very good information about the local vegetation of the northern boreal forest, because of the extreme dominance of Scots pine in the area. The simulation approach was tested for this area by using different densities of the same forest to represent felling and regrowth and the results show that it is possible to simulate the changes in the proportions of the main tree taxa (*Pinus* and *Betula*) fairly accurately, but the local land-use in terms of village development remains invisible.
3. Models help in investigating the main characteristics of the vegetation and they can be useful in this particular area but, because they use percentage pollen data, the extra evidence obtained from the PARs is usually needed to support the interpretation. At the local scale the simulations are able to imitate the arboreal pollen percentages well and it seems that simulations work when reconstructing the local forest history in northern Finnish Lapland. However, the simulated pollen percentages of the non-arboreal taxa differ considerably from the observed ones, and this suggests that the simulations do not necessarily work very well in reconstructing human impact or landscape openness at the local scale when this impact is slight. The regional vegetation reconstructions are coarse in scale and especially so in the northern boreal forest where the vegetation composition is very

simple and species diversity is low. The REVEALS model appears to be able to calculate arboreal/non-arboreal pollen proportions from a simplified landscape, but when the field layer flora, which is more or less the same throughout all the vegetation classes, is also taken into account, the picture becomes more ambiguous and the non-arboreal taxa become overrepresented. The observation that the pollen productivity of at least tree species varies according to summer temperatures, puts one of the basic assumptions of the Prentice-Sugita model in a new light as it assumes constant pollen productivity through time, while in reality PP changes from one year to the next. However, these models are usually used for much coarser temporal scale and the year-to-year variation in PP should not have any effect on the results. This may not be the case, though, for long periods of either hotter or colder weather e.g. the Little Ice Age or the Medieval Warm Period.

4. High temporal resolution PAR data seems to have some potential for reconstructions of summer temperatures as the evidence from both the north and the Alps suggests. It has been shown that the pollen productivity of at least different tree species varies according to summer temperatures and when the pollen data are collected as a continuous time series at an annual resolution, the variation in PAR values reflects the high temporal resolution changes in climate. Using PARs for temperature reconstructions has a few limitations which need to be considered first. The pollen data should be collected close to the ecological limit of the target species, to ensure that trees will react strongly enough to the differences in summer temperatures. The pollen record should also have a robust age-depth chronology and an annual or near-annual resolution of a continuous time-series without any gaps. In the north peat is preferable to lake sediments but this leads to other complications such as the problem of losing the temporal resolution due to increased humification with increasing depth. The regional vegetation should have remained more or less the same throughout the time-series because heavy human impact would hide most of the temperature related changes in pollen accumulation rates and cause a disturbed signal.
5. Separating pollen types to the lowest possible taxonomic level is worthwhile when there is a good ecological reason to do so i.e. the subspecies have different edaphic constraints or they react differently to some climatic factors. The meaning of taxonomic resolution in pollen identification becomes obvious when the aim is to

record the history of agriculture and distinguish which plants were cultivated during certain periods. In the northern boreal forest, achieving PAR data at the highest possible taxonomic resolution means identifying separately the different types of tree birch (*Betula pubescens* ssp. *pubescens* and *Betula pubescens* ssp. *czerepanovii*) pollen. Separating different subspecies may also help with some difficulties that affect the interpretation if the identification is left to a higher taxonomic level. When modelling the regional vegetation the significance of high taxonomic resolution emerges in the form of spatial distribution of different taxa. This is especially true in an area such as northern Finnish Lapland, where a transect across the different vegetation zones has an effect on the ratio between predicted and observed vegetation. If the model runs are restricted to an area, where the vegetation does not have any major zonation, this feature does not appear to be too significant in terms of complicating the overall picture, but as soon as areas from both sides of a taxonomic transect are included the results may become more difficult to interpret if both species are treated as one.

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APPENDIX

CLC code	CLC class	Class frequency	Pin	Bet	Sal	Emp	Vac	Cal	Cyp	Gra
0	Non pollen producing areas	1.79%	0%	0%	0%	0%	0%	0%	0%	0%
1	Water	10.65%	0%	0%	0%	0%	0%	0%	0%	0%
2	Fields	0.17%	0%	0%	5%	0%	0%	0%	0%	70%
3	Pastures	0.00%	0%	5%	5%	0%	0%	0%	0%	70%
4	Coniferous forest on mineral soil	17.38%	100%	0%	0%	20%	30%	0%	0%	0%
5	Coniferous forest on peatland	0.01%	100%	0%	5%	20%	20%	10%	30%	10%
6	Deciduous forest on mineral soil, closed	0.26%	0%	90%	10%	20%	30%	0%	0%	10%
7	Deciduous forest on mineral soil, open	8.37%	0%	60%	20%	20%	30%	0%	0%	10%
8	Deciduous forest on peatland	0.07%	0%	70%	20%	30%	20%	0%	0%	10%
9	Mixed forest on mineral soil	13.23%	60%	40%	0%	20%	50%	10%	0%	5%
10	Mixed forest on peatland	0.14%	70%	30%	5%	20%	20%	0%	30%	0%
11	Meadows	0.00%	0%	0%	15%	10%	10%	0%	10%	70%
12	Transitional woodland/shrub, cc<10%	1.51%	5%	5%	15%	20%	30%	20%	0%	20%
13	Transitional woodland/shrub, cc 10-30%, on mineral soil	0.22%	20%	10%	15%	30%	20%	20%	0%	5%
14	Transitional woodland/shrub, cc 10-30%, on peatland	0.00%	20%	10%	15%	20%	30%	10%	30%	0%
15	Mosaic crops/ Tree cover/ other natural vegetation	0.11%	10%	15%	0%	20%	30%	20%	0%	40%
16	Transitional woodland/shrub above coniferous timberline	8.76%	0%	50%	10%	30%	30%	10%	0%	10%
17	Transitional woodland/shrub under electric cable	0.00%	0%	0%	10%	10%	30%	10%	0%	40%
18	Moors and heathland	3.72%	0%	5%	10%	20%	20%	30%	0%	40%
19	Natural grassland	0.05%	0%	0%	5%	0%	0%	0%	0%	70%
20	Sparsely vegetated areas	11.74%	0%	0%	5%	10%	10%	10%	0%	10%
21	Open peatlands	17.25%	0%	0%	10%	5%	15%	0%	40%	10%
22	Wetlands	4.57%	0%	0%	10%	0%	0%	0%	20%	0%

Appendix 1 A "Basic CORINE classification" with all possible taxa included in each class

CLC code	CLC class	Class frequency	Pin	Bet	Sal	Emp	Vac	Cal	Cyp	Gra
0	Non pollen producing areas	1.79%	0%	0%	0%	0%	0%	0%	0%	0%
1	Water	10.65%	0%	0%	0%	0%	0%	0%	0%	0%
2	Fields	0.17%	0%	0%	5%	0%	0%	0%	0%	70%
3	Pastures	0.00%	0%	5%	5%	0%	0%	0%	0%	70%
4	Coniferous forest on mineral soil	17.38%	100%	0%	0%	0%	0%	0%	0%	0%
5	Coniferous forest on peatland	0.01%	100%	0%	0%	0%	0%	0%	0%	0%
6	Deciduous forest on mineral soil, closed	0.26%	0%	90%	10%	0%	0%	0%	0%	0%
7	Deciduous forest on mineral soil, open	8.37%	0%	60%	20%	0%	0%	0%	0%	0%
8	Deciduous forest on peatland	0.07%	0%	70%	20%	0%	0%	0%	0%	0%
9	Mixed forest on mineral soil	13.23%	60%	40%	0%	0%	0%	0%	0%	0%
10	Mixed forest on peatland	0.14%	70%	30%	0%	0%	0%	0%	0%	0%
11	Meadows	0.00%	0%	0%	0%	0%	0%	0%	0%	60%
12	Transitional woodland/shrub, cc<10%	1.51%	0%	0%	40%	30%	0%	20%	0%	0%
13	Transitional woodland/shrub, cc 10-30%, on mineral soil	0.22%	20%	10%	0%	0%	30%	0%	0%	0%
14	Transitional woodland/shrub, cc 10-30%, on peatland	0.00%	20%	10%	0%	0%	20%	0%	0%	0%
15	Mosaic crops/ Tree cover/ other natural vegetation	0.11%	10%	0%	0%	0%	30%	0%	0%	40%
16	Transitional woodland/shrub above coniferous timberline	8.76%	0%	50%	0%	30%	0%	10%	0%	0%
17	Transitional woodland/shrub under electric cable	0.00%	0%	0%	10%	0%	0%	0%	0%	40%
18	Moors and heathland	3.72%	0%	0%	20%	0%	0%	30%	0%	40%
19	Natural grassland	0.05%	0%	0%	0%	0%	0%	0%	0%	70%
20	Sparsely vegetated areas	11.74%	0%	0%	20%	20%	0%	0%	0%	10%
21	Open peatlands	17.25%	0%	0%	0%	0%	10%	0%	40%	10%
22	Wetlands	4.57%	0%	0%	10%	0%	0%	0%	20%	0%

Appendix 1 B "Cropped CORINE classification" with only the most important taxa included in each class.

ORIGINAL PAPERS

This thesis is based on the following four papers, referred to as Papers I, II, III and IV.

I. Kuoppamaa M, Goslar T, Hicks S. (2009) Pollen accumulation rates as a tool for detecting land-use changes in a sparsely settled boreal forest. Vegetation History and Archaeobotany 18:205-217

II. Kuoppamaa M. Simulating pollen loading in a Northern Boreal Forest: the effect of changing forest densities and distribution. (submitted to The Holocene)

III. Kuoppamaa M, Huusko A, Hicks S. (2009) Pinus and Betula pollen accumulation rates from the northern boreal forest as a record of interannual variation in July temperature. Journal of Quaternary Science 24:513-521

IV. Kuoppamaa M. How applicable is the REVEALS model in reconstructing regional vegetation in a monospecific Pinus sylvestris dominated forest of northern Finnish Lapland? (submitted to Journal of Quaternary Science)