Estimating source area of pollen and pollen productivity in the cultural landscapes of southern Sweden - developing a palynological tool for quantifying past plant cover

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Estimating source area of pollen and pollen productivity in the cultural landscapes of southern Sweden

– developing a palynological tool for quantifying past plant cover

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Avhandling

att med tillstånd från Naturvetenskapliga Fakulteten vid Lunds Universitet för avläggande av filosofie doktorsexamen, offentligen försvaras i Palaestra, Paradisgatan 4, Lund, fredagen den 11 oktober 2002 kl. 10.15.

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Contents

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by
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This thesis is based on four papers and the present synthesis. The four papers are listed below and presented as appendices I–IV.

Appendix I – **Broström, A., Gaillard, M., Ihse, M. and Odgaard, B. (1998).** Pollen-landscape relationships in modern analogues of ancient cultural landscapes in southern Sweden – a first step towards quantification of vegetation openness in the past. *Vegetation History and Archaeobotany* 7, 189–201.

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

Appendix III – **Broström, A., Sugita, S. and Gaillard, M.-J. (2002).** Pollen productivity estimates for the reconstruction of past vegetation cover in the cultural landscape of southern Sweden. *Holocene*, in press.

Appendix IV – **Broström, A., Sugita, S., Gaillard, M.-J. and Pilesjö, P. (2002).** Estimating spatial scale of pollen dispersal in the cultural landscape of southern Sweden. Manuscript.

I am the first author of all papers except paper II. First authorship implies that I am responsible for all data collection and analysis, and for the text and illustrations.

As a third author, I have contributed to paper II with pollen and vegetation data from the semi-open region, suggestions about the landscape designs used for the simulations, and comments on the discussion of the results. I was also in charge of the practical preparation of the final revised version of the manuscript for publication.

Vegetation history and Archaeobotany, Springer Verlag (Appendix I) and The Holocene, Arnold publishing (Appendices II and III) have both given permission for the respective papers to be reprinted.

All primary results are presented in appendices I–IV. They are referred to in the text according to their respective Roman numeral. Moreover, figures and tables are referred to as follows: (II:4) means figure 4 in Appendix II, (III:I) means Table 1 in Appendix III.

Introduction

Pollen analysis is a useful tool for reconstructing past vegetation changes at various temporal and spatial scales, from stand-scale changes over a few hundred years to a few thousand years up to sub-continental changes reflecting variations in climate over 100 000 of years (Jacobson and Bradshaw, 1981; Huntley and Birks, 1983; Bradshaw and Webb, 1985; Huntley and Webb, 1988). Records of fossil pollen also have great potential for the quantitative reconstruction of vegetation characteristics at various temporal and spatial scale (e.g. Gaillard *et al.*, 1994, 1998, 2000). The ability to quantify past land-cover changes from fossil pollen, open versus forested vegetation in particular, would be a very valuable asset within several areas of research. Vegetation history in general becomes more useful if several vegetation parameters can be quantified. A more accurate picture of past plant diversity and the way this has changed through time would be of special interest. Within the field of archaeology, estimates of the magnitude of land-use changes resulting from forest clearing, grazing or cultivation would be desirable. In combination with historical and archaeological data, pollen data could provide a more precise understanding of the human impact on the landscape through time. Within the field of climate research, simulations of past climate using general circulation models (GCM), have shown that the changes in albedo and land-surface roughness resulting from changes in vegetation cover have significant feedback effects on climate (e.g. Noblet *et al.*, 1996; Broström *et al.*, 1998). Therefore, the development of reliable and robust techniques for inferring past quantitative changes in land cover from pollen data would be very useful in the analysis of the possible impact of past natural and human-induced land-cover changes on past climate and bio-geochemical cycles at regional and global scales.

From the time when the technique of pollen analysis was invented (von Post, 1916), the importance has been recognised of a good understanding of the relationship between the pollen assemblages retrieved and the surrounding vegetation (Jackson, 1994). Recent developments in the theory of pollen analysis and in the statistical techniques for interpreting fossil pollen have considerably improved the quantitative reconstruction of vegetation, i.e. (1) modelling to predict the spatial scales of the landscapes represented in different types and sizes of sedimentary archives for pollen i.e. lakes, ponds and forest hollows (Prentice, 1985; Prentice, 1988; Sugita, 1993; Sugita, 1994), and (2) the use of modern and historical analogues to generate predictive models of the quantitative relationship between pollen assemblages and vegetation characteristics such as species representation, floristic diversity, vegetation openness and land-use/management types (Gaillard *et al.*, 1994; Odgaard, 1994; Odgaard and Rasmussen, 1998; Odgaard, 1999; Odgaard and Rasmussen, 2000).

In comparison with other fossil proxy records of vegetation characteristics, such as plant macrofossils or insects, pollen records have a unique potential for quantifying changes in vegetation features, such as openness. Pollen grains are the fossil remains of vegetation which are most abundant and best dispersed. Furthermore, the use of the modern analogue approach, combined with the application of models of pollen dispersal and deposition, is probably the soundest direction to take in applying pollen analysis to the reconstruction of past vegetation/landscape in quantitative terms at a local to regional scale. Even though the quantitative calibration of pollen in terms of vegetation is a very complex matter, it is worth taking the trouble to achieve this goal, because it is theoretically possible and provides an unique opportunity to develop the field of vegetation history.

Rationale and aims of the study

This thesis is a contribution to the development of an interpretation tool that will enable the reconstruction of past landscapes from pollen records as precisely as possible in terms of composition, abundance and distribution of plant species. The interpretation tools currently available, such as pollen percentages or pollen accumulation rates, are insufficient to provide this kind of detailed information. The first step is to understand the pollen-vegetation relationship as correctly as possible, and to estimate the components necessary for a quantitative reconstruction. These components are (1) the pollen productivity and fall speed of pollen for the plant taxa characteristic of the landscape being studied, (2) the source area of pollen for the basin size from which the fossil record is being retrieved, and (3) the background pollen loading to that basin i.e. the part of the total pollen loading that comes from beyond the source area (see section on the theoretical framework of pollen analysis below).

The aims of this thesis are:

1. To explore pollen-vegetation relationships in the ancient, traditional cultural landscape of southern Sweden (Figs 1, 2) in order to provide insights into the potential for reconstructing past cultural landscapes in quantitative terms, i.e. actual areas of cultivated fields, hay meadows, pasturelands, and various forest types (deciduous, coniferous or mixed) (Appendices I and II).
2. To identify and define the spatial scale of the landscape reflected by pollen assemblages in deposition-

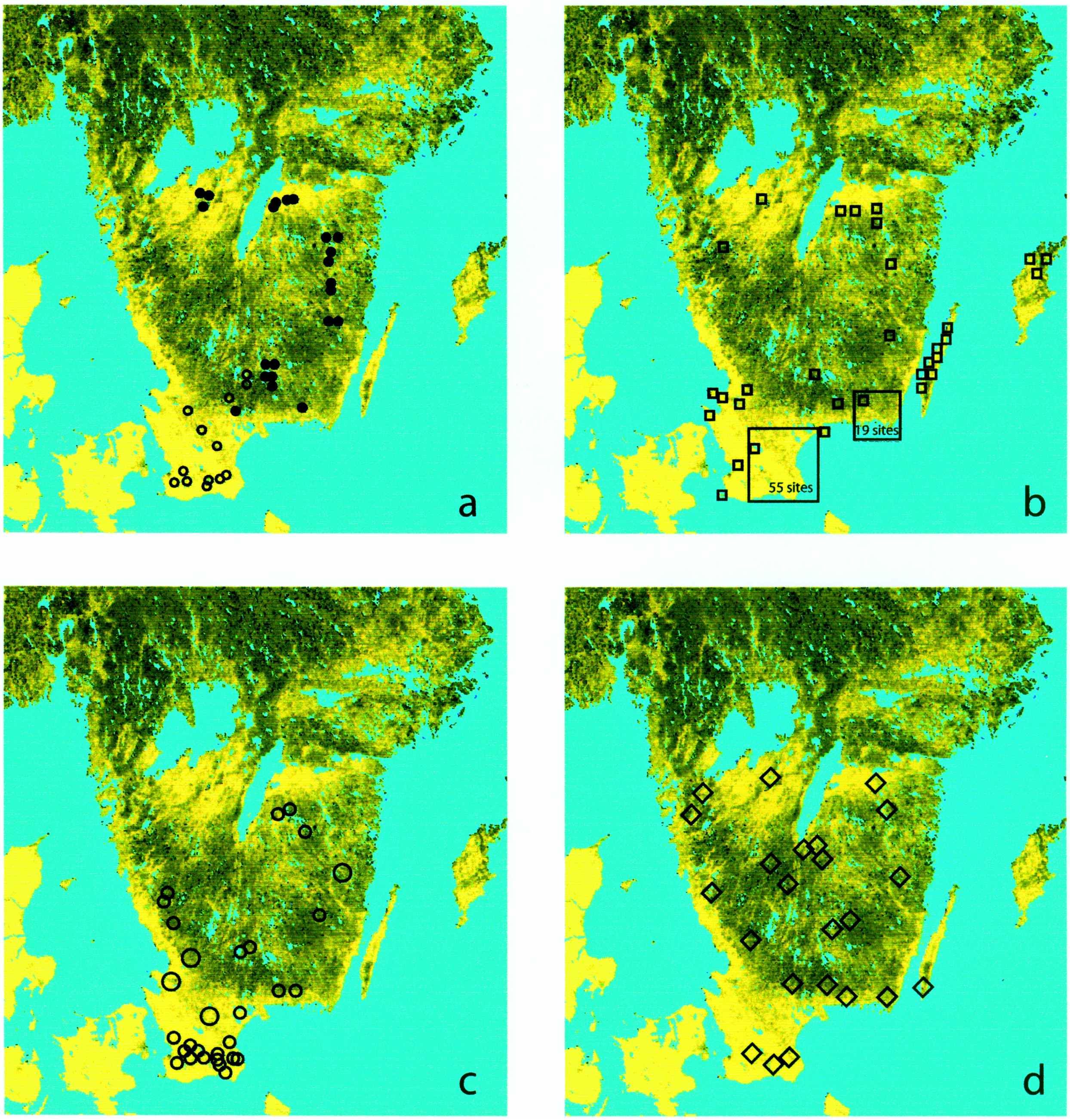

Figure 1. The area of study; the Open and Semi-Open Regions of southern Sweden. a) 35 small lake sites: filled circles (Appendix I), unfilled circles (Gaillard *et al.*, 1998), b) 124 moss polster sites with vegetation surveys within a 100 × 100 m square around the pollen sample (Gaillard *et al.*, 1992; Gaillard *et al.*, 1994) used for the pollen productivity estimates in Appendix II, c) 42 moss polster sites with vegetation surveys within 1500 m radius around the pollen sample used for the pollen productivity estimates in Appendix III, d) 23 small and medium lake sites included in the synthesis of the development of the cultural landscape in southern Sweden by Berglund *et al.* (in press).

al basins of various types and sizes, i.e. small lakes and moss polsters (Appendices II and IV).

3. To produce pollen productivity estimates for the major plant taxa characteristic of past cultural landscapes in southern Sweden. This step implied the development of optimal designs in field sampling and vegetation surveying for the collection of relevant pollen and vegetation data (Appendix III).
4. To identify the potentials and limits of using mechanistic models of pollen dispersal and deposition to reconstruct past landscapes from fossil pollen records (Appendices II and IV).

Figure 2. The cultural landscape in southern Sweden in a) the Open Region (Backåkra, Skåne 1999), b) the Semi-Open Region (Ire, Blekinge 1999), c) grazed meadow (Borrås, Halland 2000), d) heathland (Mästocka, Halland 2000). Photo: Anna Broström.

The theoretical framework of pollen analysis

Since the early 1960's, many studies had the aim to calibrate modern pollen assemblages in terms of current vegetation, and to apply these tools to the reconstruction of past vegetation composition from fossil pollen records (e.g. Andersen, 1970; Gaillard *et al.*, 1994). However, the interpretation of fossil pollen records has been, and still is, largely qualitative or semi-quantitative, relying mainly on indicator species and qualified "guesstimates" (Prentice and Parsons, 1983). This situation arises primarily from the fact that the pollen-vegetation relationship is complex. It involves many factors which affect the final deposition of pollen in a basin (lake, bog or mire) (Fig 3). Because of this complexity, the theoretical framework developed by Prentice in the 1980's, and by Sugita in the 1990's, has not been actively endorsed by most palynologists. Therefore, it is necessary to consider the modern models of pollen dispersal and deposition in the context of their historical perspective in order to fully understand their value and implications. Reviews of the model development described below are found in Prentice and Parsons (1983), Jackson (1994) and Sugita (1998).

The R-value model

Davis (1963) recognised the pollen productivity of individual species and the distance between the plant and the point of pollen deposition as the major factors affecting the representation of pollen taxa in a pollen assemblage. She calculated a correction factor, i.e. the R-value that allows the transformation of pollen percentages into relative abundances of a taxon in the source vegetation within a specified area. The R-value (r_i) is taxon-specific, and it can be derived and applied according to the following function:

$$p_{ik} = r_i \times v_{ik} \qquad (1)$$

where p_{ik} is the abundance of taxon i in the pollen assemblage at site k, and v_{ik} is the abundance of taxon i in the surrounding vegetation of a specified area A_n. The weaknesses of the R-value model and its application by Davis were twofold. Firstly, R-values appeared to vary too much from site to site, and from region to region (Livingstone, 1968; Parsons and Prentice, 1981). Davis (1963) suspected this, but she underestimated its importance. Secondly, the background component, that is pollen coming from outside the area A_n was not recognised as a possible problem when infer-

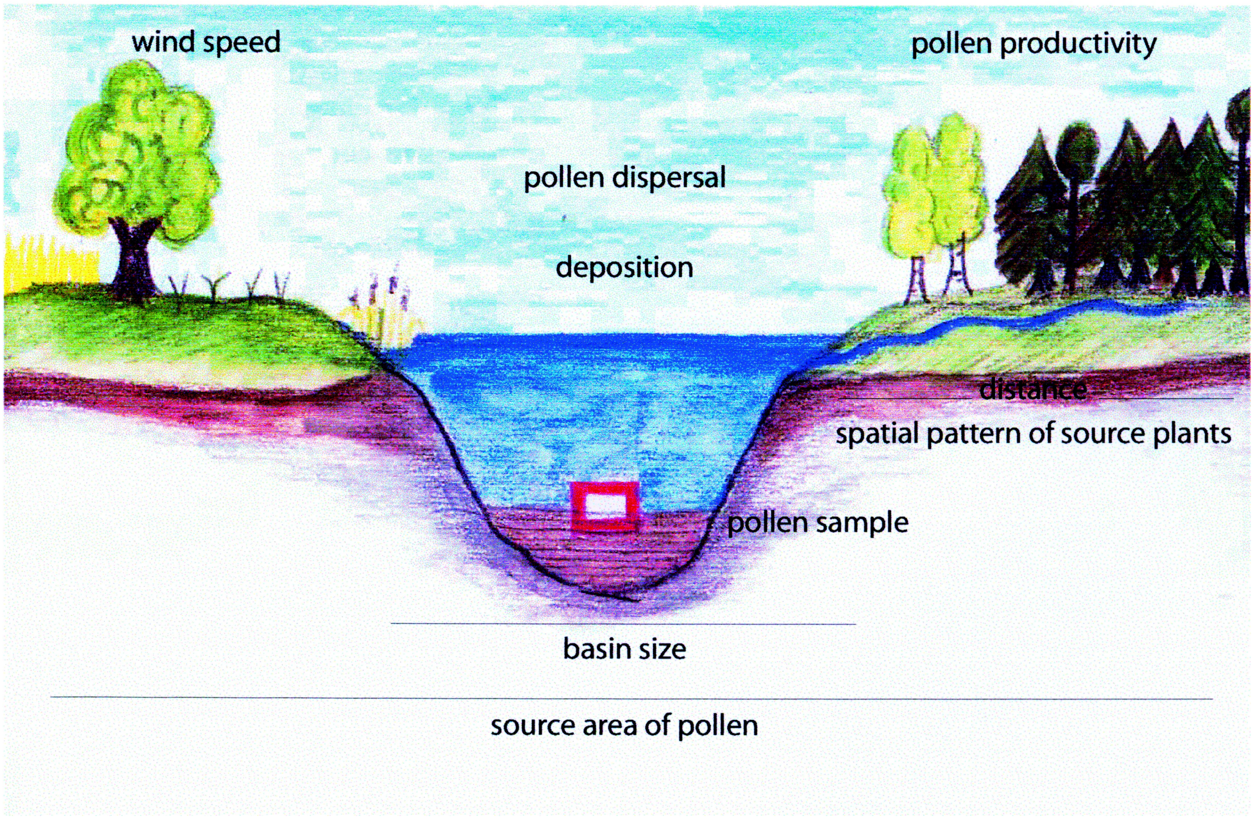

Figure 3. The major factors affecting the pollen-vegetation relationship; Pollen productivity, pollen dispersal and deposition, the spatial pattern of plants i.e. distance from pollen sample point, and the basin size. The size of the source area of pollen is dependant of the basin size.

ring R-values. As a matter of fact, R-values inferred from empirical data collected in different areas may differ considerably (Parsons and Prentice, 1981; Prentice and Parsons, 1983). The difficulties encountered with R-values, both in theory and practice, led many authors in the 1960's and 1970's to take a very critical and pessimistic view of using the model in reconstructing past vegetation from fossil pollen data (Faegri, 1966; Comanor, 1968; Livingstone, 1968; Birks, 1973)

Andersen's model

The most serious drawback of Davis' R-value model was the lack of a clearly defined pollen source area, and the significant effect of the background pollen loading on the R-values (Livingstone, 1968; Parsons and Prentice, 1981). Andersen (1970) suggested that the pollen-vegetation relationship could be expressed by a linear model which included a "background " component (i.e. pollen from outside the surveyed area):

$$p_{ik} = r_i \times v_{ik} + p_{0i} \qquad (2)$$

Expressed in graphical terms (Fig 4), r_i is the slope coefficient of the pollen-vegetation relationship for taxon i and p_{0i} is the y-intercept for taxon i, the background component. The empirical data collected by Andersen (1970) for validation of this model were pollen assemblages from moss polsters, and vegetation surveys in closed forest. The pollen data were expressed in semi-absolute units and the vegetation data in absolute units. Correction factors were then inferred for the major tree species of southern Scandinavia (Andersen, 1970).

The Extended R-Value (ERV)-model

The Extended R-Value (ERV) model was developed by Parsons and Prentice (1981) and Prentice and Parsons (1983) to estimate pollen productivity α_i and background pollen z_i using pollen and vegetation percentages instead of semi-absolute data i.e. pollen accumulation rates as in Andersen's model. However, when using percentage data for the linear model proposed by Andersen (1970), the Fagerlind effect is introduced. This effect occurs when a linear relationship becomes non-linear when absolute measured variables are converted to percentages. In other words, an increase in the pollen percentage of taxon i need not imply an increase in vegetation percentage of the same taxon i, and similarly an increase in vegetation per-

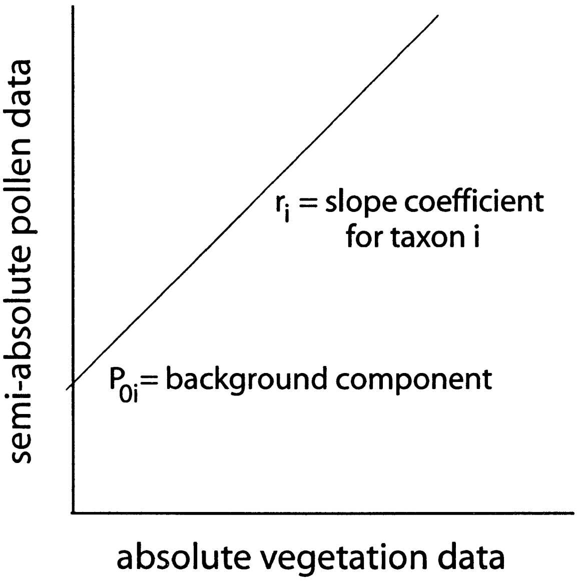

Figure 4. The pollen-vegetation relationship for taxon i in the linear model of Andersen (1970), using semi-absolute pollen data and absolute vegetation data. The slope is the pollen representation factor or slope coefficient (r_i) and the y-intercept is the background pollen component (p_{0i}) for taxon i.

centage need not imply an increase in pollen percentage. The Fagerlind effect can be particularly strong when there is a plant taxon with abundances higher than 30% in the data-set (Fagerlind, 1952; Prentice and Webb, 1986). The ERV-models incorporate a "correction" or approximation that eliminates this effect.

The basic equation of the ERV-models partitions the pollen deposition into two components; a first, variable component ($\alpha_i v_{ik}$) representing pollen from within a certain radius of the point of pollen deposition, and a second, constant background component (z_i), representing the input of pollen from beyond this radius, i.e.

$$p_{ik} = \alpha_i \times v_{ik} \times f_k + z_i \qquad (3)$$

where p_{ik} is the pollen deposition in percentages, and v_{ik} the plant abundance in percentages for taxon i at site k. The relative pollen representation of taxon i is accounted for by the parameters α_i, and z_i (Parsons and Prentice, 1981; Prentice and Parsons, 1983). The pollen productivity (α_i) for taxon i is expressed relative to the other taxa included in the sample, of which one is set at unity. The site specific factor (f_k) varies according to the abundance and parameter values of all the taxa at site k, and it compensates for the Fagerlind effect (Fagerlind, 1952; Prentice and Webb, 1986).

Prentice and Parson (1983) proposed two sub models, ERV-model 1 and 2, using different assumptions for the background component (z_i). Sugita (1994) proposed a third sub-model, ERV-model 3. The three ERV-models differ in terms of pollen and vegetation data input format, and how the background pollen is defined (Sugita, 1994) (Fig 5). ERV-models 1 and 2 use pollen and vegetation proportions. ERV-model 1 assumes a species-specific constant background in pollen proportion, whereas ERV-model 2 assumes a species-specific constant background in the ratio of pollen loading to total plant abundance for all the taxa involved (Prentice and Parsons, 1983). ERV-model 3 uses pollen proportion and absolute plant abundance data, and assumes constant background pollen loading between sites (Sugita, 1994). For all models, the assumption of a constant background pollen input is reasonable as long as the background pollen loading is small relative to total pollen deposition (Jackson and Kearsley, 1998).

For ERV-model 3, equation (3) becomes:

$$p_{ik} \times Y_k = \alpha_i \times \psi_{ik} + \omega_i \qquad (4)$$

where p_{ik} is the pollen proportion of taxon i at site k, α_i is the pollen productivity of taxon i relative to one taxon set to unity, ψ_{ik} is the distance-weighted absolute plant abundance of taxon i within a given radius from the pollen sample at site k, and ω_i is the background pollen loading coming from beyond a given radius of vegetation survey. Y_k is the total relative pollen loading at site k, also called the site factor by Prentice and Parsons (1983).

When absolute plant abundance data are available the interpretation of the background component (z_i) is the most straight-forward, using ERV-model 3 (Sugita, 1994). The relative pollen loading of each taxon can be recalculated as a percentage of the total pollen loading coming from beyond a given distance (Sugita, 1994; Calcote, 1995). ERV-model 1 or 2 should be used when only pollen and vegetation percentage data are available. There is no obvious reason why one model should be chosen in preference to another. Instead both sub-models can be used, and if they provide comparable parameter estimates, i.e. pollen productivity (α_i) and background pollen loading (z_i), they can be considered robust (Prentice and Parsons, 1983).

It is important to capture the pollen samples' "view of the landscape" when modelling the pollen-vegetation relationship (Webb *et al.*, 1981). Therefore, distance weighting of plant abundance should be applied when ERV-model estimates of pollen productivity and background pollen input are calculated. In this way, plants closer to the sampling point contribute more pollen than plants further away. Once the vegetation has been surveyed at increasing distances from the pol-

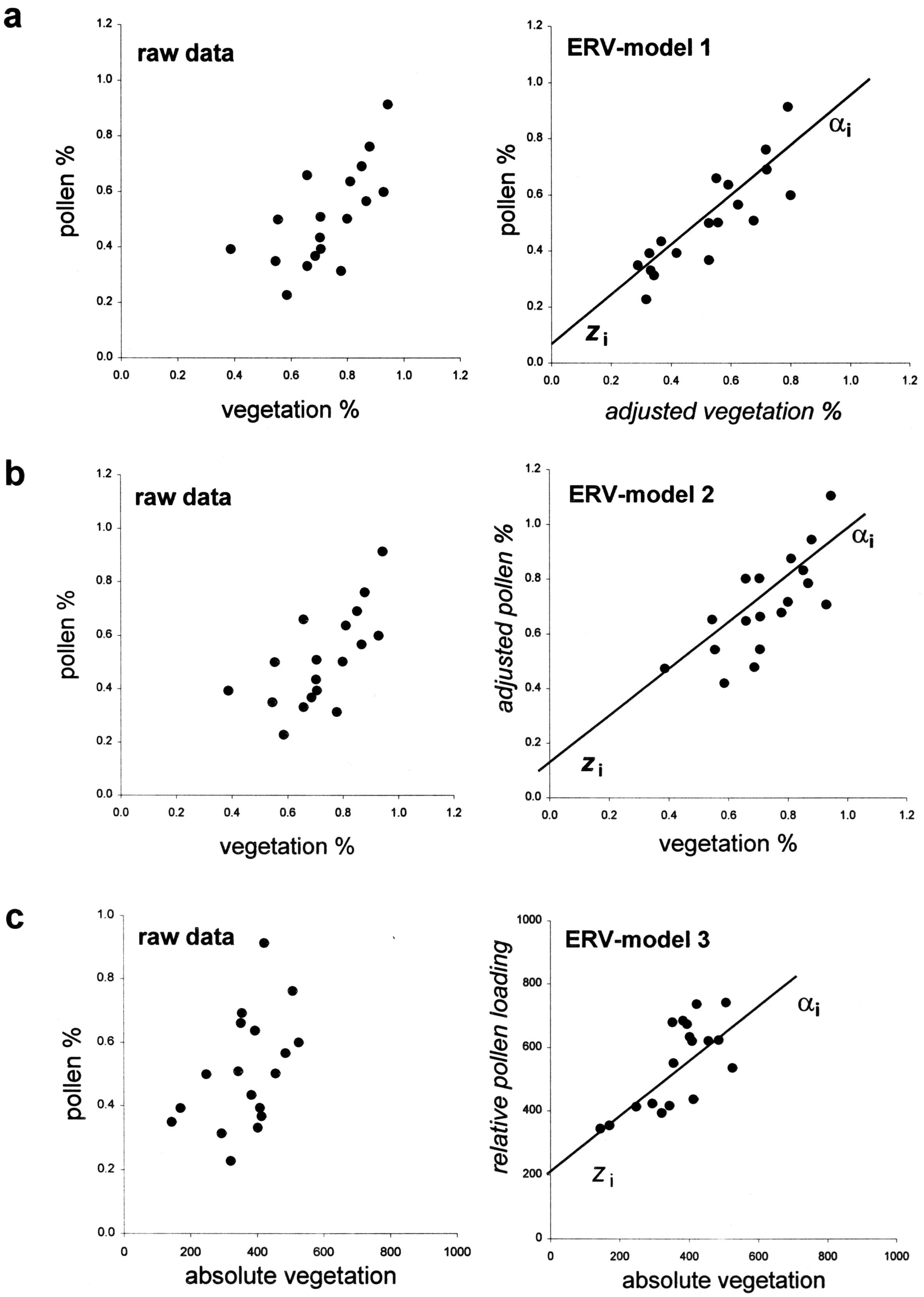

Figure 5. The Extended R-value (ERV)-models estimate the pollen representation factor α_i and background component z_i for taxon i from pollen and vegetation data. The pollen-vegetation relationship for taxon i is shown for raw data in first column. The goodness-of-fit for model-specific adjusted data to the linear model is shown in the second column, a) ERV-model 1, b) ERV-model 2 and c) ERV-model 3. The differences between the three ERV-models in terms of pollen and vegetation data input format, and how the background pollen is defined is explained in the text.

len loading point, there are several possible methods to perform distance-weighting. This question is further discussed in Appendix III. The simplest is to weight the vegetation data by dividing the plant abundance by the distance (1/d), or its square ($1/d^2$) (Calcote, 1995; Jackson and Kearsley, 1998). A more sophisticated method, taxon-specific distance weighting, takes into account the dispersal ability of the pollen grain of each taxon, based on the size, form and density of the grain (Prentice, 1985). Calcote (1995) demonstrated that $1/d^2$ is a good approximation of the taxon-specific distance weighting.

The link between the original ERV-models 1 and 2 and a mechanistic model describing the relationship between pollen loading on a sedimentary basin and the surrounding vegetation is provided by Prentice (1985, 1988).

The Prentice-Sugita model

The Prentice model (1985) has been further developed by Sugita (1993, 1994). The Prentice-Sugita model describes the functional relationship between pollen loading on a sedimentary basin and four factors affecting pollen loading: pollen productivity, pollen dispersal, spatial distribution of source plants and basin size (Prentice, 1985; Prentice, 1988; Sugita, 1994; Sugita, 1998). The Prentice model describes pollen loading at a central point in the depositional basin (Prentice, 1985) and is, therefore, appropriate for predicting pollen deposition on bogs and fens (Sugita, 1994). The Sugita-model describes pollen loading on the entire surface of the sedimentary basin, and was developed to predict pollen deposition in lakes.

The assumptions of the Prentice-Sugita model (Sugita, 1994; Sugita, 1998) are as follows:

1) The sampling basin (bog or lake) is a circular opening in the forest canopy. Basin size is expressed as the radius of a basin.
2) Pollen dispersal is even in all directions.
3) The dominant agent of pollen transport is wind above the canopy.
4) Pollen productivity is constant for each taxon.
5) The spatial distribution of each plant taxon is expressed as a function of distance (metres) from a point at the centre of the basin.
6) Arc-wise pollen deposition is expressed as a function of distance from a point source, derived from a diffusion model of small particles from a ground-level source (Sutton, 1953; Chamberlain, 1975). The shape of the dispersal function is mainly determined by wind speed and the species-specific fall speed of pollen.

The model provides a mathematical description of the pollen assemblage's "perspective of the landscape". The pollen dispersal function defines the contribution of pollen to the assemblage from a plant taxon at a given distance. In other words the further away a plant is from the site the less it contributes to the pollen assemblage. There is no consideration of topography or differences in plant height in the model.

The relevant source area of pollen – RSAP

The goodness of fit of pollen and vegetation data to the ERV-model, and the correlation between pollen and vegetation data for each taxon will increase with an increase in the area of vegetation surveyed, up to a certain distance. The distance will differ for individual taxa, depending on the ability of the respective pollen grains to disperse, as shown for major tree taxa in southern Sweden by Prentice *et al.* (1987). However, a pollen sample contains several taxa reflecting the distribution of the source plants in the landscape. Therefore, it is essential to perform parameter estimations and analyse the goodness-of-fit of the pollen-vegetation relationship of several taxa simultaneously. Sugita (1994) introduced the concept of the "relevant source area of pollen" (RSAP) defined as the distance beyond which the correlation between pollen deposited at a site and the surrounding vegetation does not improve. This also implies that the pollen loading (in terms of amount and composition) coming from beyond this distance is constant between sites. The pollen coming from within this area is the part of the pollen loading that is uniquely reflected at a given site (lake, bog, hollow or moss polster), thus exhibiting the site-to-site variation among multiple sites. How the relevant source area of pollen is obtained using ERV-models is explained in the methodological section.

POLLSCAPE a computer simulation model

POLLSCAPE makes it possible to estimate pollen dispersal and deposition in heterogeneous vegetation both in simulated landscapes (Sugita, 1994; Davis and Sugita, 1996) and in real landscapes (Sugita *et al.*, 1997). POLLSCAPE uses the Prentice-Sugita model to describe the pollen dispersal and deposition in heterogeneous landscapes (Sugita, 1998). The assumptions, such as equal wind directions, no topographic features, and pollen transport above the tree canopy, are the same as in Prentice (1985, 1988) and Sugita (1993). POLLSCAPE consists of three sub-units; landscape design, vegetation data extraction and simulation of pollen dispersal and deposition (Fig 6) (Sugita, 1998). A more detailed description is found in Appendix IV. The simulation experiments have provided useful insights. For example, simulations of pollen representation of forest vegetation in lake basins of

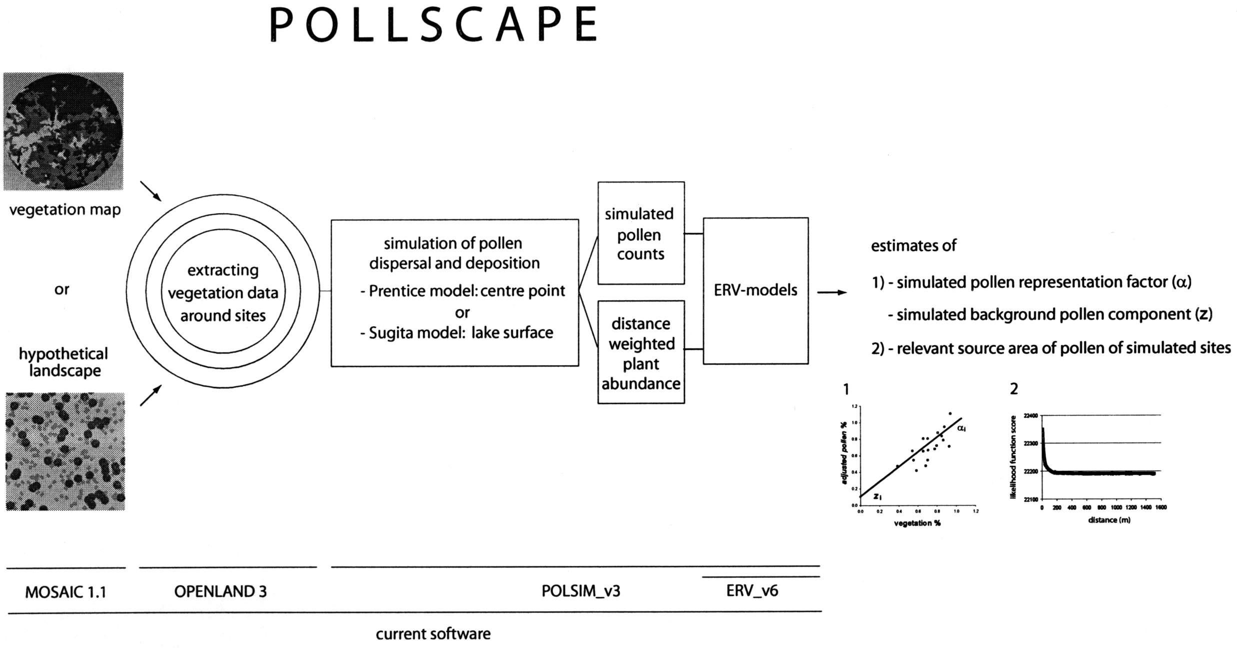

Figure 6. The POLLSCAPE simulation model for heterogeneous vegetation (Sugita, 1994) from input to output. The current version of the program package contains three sub-units MOSAIC v1.1 (Middleton and Bunting, in prep) for landscape design, OPENLAND3 (Eklöf *et al.*, in prep) for vegetation data extraction and POLSIM v3 (Sugita unpublished) for simulation of pollen dispersal and deposition. The simulated pollen assemblage and distance-weighted vegetation data can be used to estimate simulated pollen representation factor, background pollen component and relevant source area of pollen of simulated sites.

various sizes demonstrate larger site-to-site variation in pollen loading in smaller lakes than in larger lakes (Sugita, 1994). This implies that small basins are suitable for detecting vegetation changes at the stand scale, while larger lakes are appropriate for reconstructing vegetation changes at the regional scale. The importance of selecting the optimal basin size suitable for linear calibration methods was also demonstrated by simulations. The lakes should be of equivalent or of smaller size than the grain size of the patches of vegetation in the landscape that is to be reconstructed (Sugita, 1994). Also, insights into the possibility of detecting past disturbances, such as fire, using fossil pollen samples have been gained using simulations (Sugita *et al.*, 1997). If vegetation is replaced by a non-pollen producing area, the latter must be ten times larger and occur close to the lake shore in order to be registered in the pollen record. Even if the disturbances are large (e.g. 2500 ha) and occur 100–500 m away from the lake shore they will not be detectable in the pollen loading. This is in accordance with what is shown in pollen traps near cultivated fields within the boreal forests in northern Finland (Hicks, 1998). Irrespective of whether the trap is 250 m or 2500 m away from the cultivated area, this area does not show up in the herb pollen taxa, which have the same low values at both distances and do not reflect the presence of the cultivated field.

The model predictions using POLLSCAPE have been validated by two empirical studies using small hollows (Calcote, 1995), and a small lake (Sugita *et al.*, 1997) within forested vegetation in North America. In the first study, the RSAP for hollows in two forests with a different vegetation composition was estimated to 100 m and 50 m, which confirmed the values predicted by the model (Calcote, 1995). In the second study, the pollen assemblage in the surface sediment from a small lake was comparable to the predicted pollen assemblage (Sugita *et al.*, 1997).

In the theoretical framework for the pollen/vegetation relationship described above assumptions are simplified in such a way that the effects of changes in major factors (such as pollen dispersal, pollen productivity, spatial distribution of plants, and basin size) on pollen representation of vegetation can be clarified (Sugita, 1998). As G.E.P Box, a renowned statistician put it: "All models are wrong, some models are useful" (Siegel, 1988). POLLSCAPE could be useful in designing research projects and selecting sampling strategies. It would also be able to provide the relevant spatial scale needed to answer specific scientific questions (Sugita, 1998). However, it is important to stress that the models should, as far as possible, be continuously validated with empirical data (Calcote, 1995; Sugita *et al.*, 1997). Comparisons between simulation models and empirical data will be beneficial for model improvement and the spatially precise interpretation of fossil pollen data.

Reconstruction of past cultural landscapes

The traditional pollen-analytical tools used for reconstructing past cultural landscapes in Europe since the 1960's

The vast amount of information presented in a traditional pollen diagram has to be organised in order to make the interpretation procedure easier. The pollen taxa can be grouped into ecological units where the non-arboreal pollen taxa (NAP) are separated into apophytes, i.e. shrubs, herbs and graminids favoured by humans, and anthropochors, i.e. herbs and graminids introduced by humans (Berglund, 1969). These groups can be further divided according to indicator species of various types of land use, e.g. cultivated land, fallow land, wet meadows and pastures, dry pastures, grazed woodlands and ruderal communities (Behre, 1981, 1986, 1988). These groups can be presented as cumulative percentage diagrams. This type of data handling has been widely applied in studies of past human impact in Europe (Ralska-Jasiewiczowa, 1977; Hicks, 1985; Vorren, 1986; Berglund, 1991; Gaillard and Göransson, 1991; Regnéll, 1991).

Total Non-Arboreal Pollen (NAP) percentages have also been used to assess cover of open land in the landscape (e.g. Berglund, 1991; Frenzel *et al.*, 1994). For Europe, maps have been produced using NAP percentages at 195 sites for two time-slices i.e.1800 yr BP (the Roman Iron Age) and 1450 yr BP (the Migration period). These maps are intended to express the extent of treeless vegetation through Europe during those two periods (Frenzel, *et al.*, 1994). Interpretation difficulties due to differences in basin type (lake and bog), and size (1–5000 ha) are pointed out by the authors. The differences in the maps were interpreted in terms of aforestation in central Europe from 1800 to 1450 yrs. BP, little change in Scandinavia, and mixed aforestation and deforestation in the British isles. Note that this tentative synthesis does not include any attempt at a calibration of pollen percentage in terms of vegetation cover. These are simply raw percentage NAP data that imply a series of interpretation problems that are further developed below. For a more thorough overview of the methodologies used in the reconstruction of past European cultural landscapes, consult the review of Gaillard (2000).

Cultural landscape history in southern Sweden – a question of interpretation?

Although southern Sweden is an area with a high frequency of palaeoecological studies, there have been only a few attempts to synthesise these studies (Berglund, 1996; Berglund *et al.*, in press). The latest synthesis is largely based on a compilation of total NAP percentage curves from twentythree fossil pollen records from lakes of comparable size in southern Sweden (Fig 1d, 7). In addition, the first occurrence of Cerealia and *Plantago lanceolata* pollen grains at each site is considered, as well as a series of pollen indicators of various land-use practices.

The two major regions used by the authors, and designated as "coastal/flatlands" and "inland/upland" can be compared to the areas referred to as the Open and Semi-Open Regions in this thesis. The coastal/flatland is characterised by early human impact from early Neolithic time, and the expansion of open land throughout history. This is also the region that is the most open and cultivated today. The inland/upland generally has a lower frequency of pollen indicating open-land, which is interpreted as a consequence of the dominance of forested areas throughout history. Significant human impact appeared later, and the expansion of the open-land is assumed to have been modest.

On the basis of these pollen data, combined with archaeological and historical records, the history of the cultural landscape of southern Sweden is interpreted as being clearly heterogeneous both in time and space. According to the authors there is an overall similarity in the development of the landscape from the time of the first human impact until today (Fig 7). However, the synthesis also reveal caveats in the source material, and difficulties in merging the interpretations of the fossil records involved. From the sites which are included, it was not possible to determine whether the changes in vegetation recorded by the fossil pollen did occurring close to the sites or are reflecting changes on a larger, regional scale. Therefore, the asynchronous patterns of change through time recorded in the pollen records, also become difficult to interpret. Similar problems had to be faced in the synthesis of past vegetation changes reconstructed for a more restricted area: the Ystad region in the southernmost part of Sweden (Berglund, 1991). This illustrates the obvious need for a robust methodology, in particular for quantitative reconstructions of open versus forested land from fossil pollen records.

The twenty-three fossil records used in the analysis differ in quality, especially with respect to their chronologies (Fig 7). However, on the basis of the pollen-analytical information, it was possible to describe the landscape history for the last 6000 years and identify five tentative phases. A summary of each phase by Berglund *et al.* (in press) is presented below, followed by own comments on the difficulties of interpretation. They should be seen as challenges to improve the tool of interpretation in the future, and will be revisited later in the discussion part of this thesis.

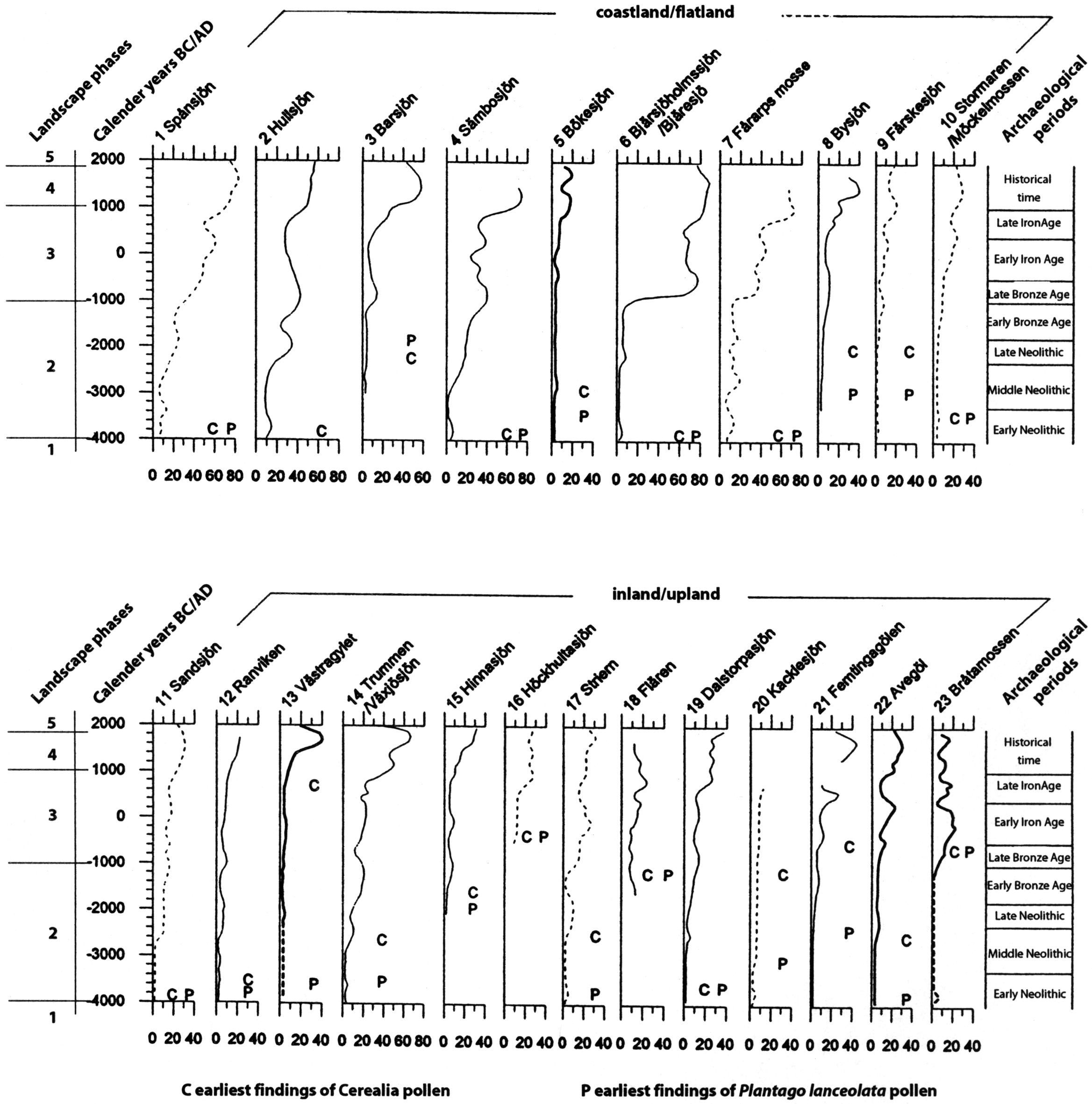

Figure 7. Summary pollen diagrams of herb taxa percentages in 23 lakes in southern Sweden, from the synthesis on the development of the cultural landscape in Southern Sweden over 6000 cal. yrs. by Berglund *et al.* (in press). The diagrams are geographically grouped in coastland/flatland (upper) and inland/upland (lower). The five landscape phases discussed in the text, the chronology in calendar years are indicated to the left and archaeological periods to the right of the diagrams. The curve signature varies depending on the radiocarbon dating quality of the pollen records in three categories. (1) bold line indicates AMS dating on terrestrial macrofossils or conventional dating of *Sphagnum* peat, (2) the fine line indicates a series of conventional or AMS dating on bulk sediment or correlated to a nearby well dated-record and (3) the dashed line indicates few conventional dating on bulk sediment.

1. Forested landscape with a very low representation of herb pollen, before 6000 cal. yrs. BP (Mesolithic). The landscape was dominated by broad-leaved forest. There are indications of human settlement all over southern Sweden. Low frequencies of herb pollen are mostly interpreted as natural openings caused by wind, fires, grazing animals and wetlands. However, the impact of tree cutting around human settlements is considered. There is some weak and often debated evidence for cultivation (Jennbert, 1984; Göransson, 1986; Berglund, 1991).

2. Forested landscape with a low representation of herb pollen, 6000–3000 cal. yrs. BP (Neolithic and Early Bronze Age). The landscape is still characterised by broad-leaved forest. The herb pollen frequencies are rather low for both the inland/upland and coastal/flatland regions, although higher NAP values in the coastal records are interpreted as grazing in the forest by cattle kept by humans. Pollen indicating cultivation is almost exclusively concentrated to the coastal areas, but also occurs sparsely in the inland records. The inland/upland region has a mosaic-landscape

with high topographical and geological variation. Cultivation was most probably restricted to the best and most easily cultivated soils. Archaeological finds of both permanent and non-permanent settlements indicate a mobile population, and the existence of cultivated fields. Within the coastal/flatlands region, there is a further increase in herb pollen percentages between 4500 and 4000 cal. yrs. BP (Middle-late Neolithic).

3. A large increase in the representation of herb pollen, indicating half open grazing land and permanent fields in the coastal/flatland region and ambulating cultivation in the inland/upland region, 3000–1500/1000 cal. yrs. BP (Late Bronze Age and Iron Age). There is a significant increase in pollen taxa indicating both grazing and cultivation over all of southern Sweden. This increase is most pronounced in the flatlands of southernmost Sweden. During the last part of this period (Late Iron Age), settlements become permanent, and cultivation occurs on permanent fields restricted to the fertile soils. Manuring is now common practice. The increase in tree pollen at around 1500 cal. yrs. BP (Migration Period) at some sites is interpreted as aforestation of areas characterised by poor soils, which is also a result of the ongoing concentration of settlements. Moreover, the aforestation at some sites may have been caused by war, the black-death, soil degradation, and/or climate change.

4. The persistent representation of high herb pollen values reflecting the expanding villages with an infield/out-land system all over southern Sweden, 1500/1000 to 100 cal. yrs. BP (Iron Age, Middle Age and Modern Times). The pollen records, together with all other agrarian-historical evidence, show a large expansion of both cultivation and cattle management during the Late Iron Age. Permanent settlements aggregated to villages were consolidated, and there was some settlement expansion into the marginal areas. Consolidation of the villages was accompanied by a more strict division of the landscape into infields (cultivated fields and hay meadows) close to the village and outland (grazing land), outside the village and infield. The outland was often situated on poorer soils, and consisted of open heath land, shrub-land with *Juniperus*, and half-open forested land. Also, the forests on wet ground were often cut down for hay production. There was a large variation in the land-use types during this time, which may be related to the optimal occurrence of a number of pollen taxa during this phase, a possible reflection of particularly high plant diversity.

5. A decrease in herb pollen, representing the modern agricultural landscape with a concentration of cultivated fields, and aforestation of marginal areas: during the last 100 years. Agricultural rationalisation led to big structural changes in the south Swedish landscape. These shifts changed the landscape from a small-scale mosaic into a large-scale monotonic structure of large areas covered by cultivated fields or planted forests (outland in the inland/upland region). From this time on, cattle are often kept in cowsheds, and less grazing land is needed. Aforestation occurs in much of the outland of the inland/upland region. There are still some small-scale, traditional agricultural areas left, scattered throughout the modern landscape.

In conclusion, the development of the cultural landscape is interpreted as a complex process as shown by the compilation of the NAP curves (Fig 7). In the coastal/flatland region, NAP percentage values are commonly high and exhibit a more significant increase around 4500 and 1000 cal. yrs. BP than in the inland/upland. The timing of the so called "expansion" phase is not synchronous between sites, not even within the two regions.

There are a series of interpretation problems and challenges related to the use of NAP percentages in reconstructing past landscapes:

A first, major task is to overcome the problem of herb taxa being underrepresented in comparison with tree taxa. When a regional landscape is dominated by forest vegetation (such as during phases 1 and 2) the area of open vegetation will most probably be underestimated. This question has been a source of frustration for most palynologists. Vera (2000), a nature conservationist, has used this draw-back of pollen analysis to question the interpretation made for the initial phases of deforestation. The fringe between open land and forest contains shrubs, many of which are insect pollinated and therefore, occur very sparsely in the pollen records. They can only be used as indicator taxa for the presence of openings (Vera, 2000). *Corylus* is an exception, and high pollen percentages of this species may reflect a high frequency of fringes in the landscape (Vera, 2000). When relying on the wind pollinated herb taxa for quantitative estimates of open areas, there is an obvious need to correct for the under representation of the herb pollen.

A second, major interpretation challenge is to translate the changes in NAP percentages through time into vegetation/landscape changes and to assess whether these changes are of regional character or changes on a more local scale. Does 20% of herb pollen taxa in the pollen assemblages from the two contrasting regions in southern Sweden represent the same extent of open land around the sites being studied? Does 20% of herb taxa represent local open areas close to the site being studied or the overall extent of open land in the entire region? In order to disentangle the origins of the pollen, a possible strategy is to study a network of local sites and compare the pollen records. However, the next question then arises of the size of the area each individual site actually records and on the proportion of pollen that is common to all the sites in the network, i.e. the background or regional pollen component. It is only with more precise knowledge on the pollen-source area and the background pollen component of each site that it is possible to say something about the quantitative implication of e.g. 20% NAP in a pollen record. In other words, the interpretation of temporal changes in NAP percentages at a single site, or spatial differences in NAP percentages between sites, may be meaningless without the essential information mentioned above. These problems are particularly acute in the interpretation of phases 3 to 5. Only similar temporal patterns of change in the NAP percentages between sites may be interpreted with confidence as regionally synchronous changes in landscape. Asynchronous changes may represent local changes that do not occur everywhere in the landscape at the same time, but may also be due to other parameters influencing the deposition of NAP in the basins under consideration. NAP percentages cannot be translated in a straight forward way into quantitative estimates of openness (i.e. Appendix II).

Another aspect where quantification becomes important is when plant diversity is to be assessed from pollen data. Plant diversity is not only measured by the number of plant taxa but also by the number of individuals for each taxon and their spatial distribution, i.e. evenness. Calibration of the number of pollen taxa in terms of the number of plant species is another complex issue that has been discussed thoroughly by Odgaard (1999, 2001).

In conclusion, the questions that are still unsolved in terms of interpreting the pollen records, and reconstructing past cultural landscapes in southern Sweden are as follows:

Phase 1: Do low NAP percentages reflect actual openings in the landscape? How large and how frequent where those openings in the broad-leaved forest?

Phase 2: Does the increase in NAP percentages around 4500 cal. yrs. BP in most sites of the coastal/flatland region and some sites in the inland/highland region correspond to a regional change in the overall cultural landscape of southern Sweden?

Phase 2 to 5: Are the differences in NAP pollen percentages between regions, i.e. generally higher NAP in sites from the coast/flatland, an expression of a regionally more open, and settled landscape then the inland/highland? Do the differences in NAP pollen percentages between sites reflect a variation in the extent of openings around each site, or are they due to other site factors such as differences in pollen source areas and background pollen loading? Do increases and decreases in NAP percentages always represent deforestation and aforestation, respectively and in that case are they local or regional ?

Phase 4 and 5: Do the optima in NAP percentages during phase 4 represent a period of maximum landscape openness at the regional scale or is the following decrease in NAP due to other landscape vegetation characteristics during the last 500–100 years of history?

Past land-use types: quantitative and qualitative reconstructions

The theoretical models of pollen dispersal and deposition have been exclusively developed for forest vegetation in the northern hemisphere. Thanks to the development of a theoretical framework for pollen analysis, relatively good estimates of pollen productivity for most North American and European tree taxa have been provided (Davis, 1963; Andersen, 1970; Prentice and Parsons, 1983; Prentice, 1985; Sugita, 1993; Sugita, 1994). For the reconstruction of past cultural landscapes such as those which have prevailed in Europe since the Late Bronze Age, estimates of the pollen representation of herbaceous plants and shrubs in relation to those of the trees are needed. In addition, pollen productivity for trees in open land situations should be investigated.

Previous studies of the pollen representation of herbaceous plants in cultural landscapes have used the modern analogue approach (Berglund *et al.*, 1986; Gaillard *et al.*, 1994; Hjelle, 1999). This approach implies that modern pollen assemblages from ancient landscape-vegetation types similar to those that the researcher is attempting to reconstruct (analogues) are used for the reconstruction. This is done either by means of the comparative approach, i.e. by comparing pollen spectra from various types of modern vegetation communities directly with the fossil pollen assemblages (e.g. Wright, 1967; Birks and Birks, 1980; Berglund *et al.*, 1986; Gaillard *et al.*, 1992), or by using empirical data to estimate those parameters needed for a quantitative reconstruction, such as pollen productivity (Hjelle, 1998b). In all these studies, pollen samples have been collected from moss polsters within selected vegetation types and vegetation has been mapped on a very local scale (1 × 1 m, 10 × 10 m and 100 × 100 m). A set of numerical analysis techniques have been used to explore the pollen-vegetation relationship and work out possible calibration models. A major aim in the studies of Berglund (1986), Gaillard *et al.* (1992, 1994) in southern Sweden, and Hjelle (1998 b) in south-western Norway was to find out whether different types of land use such as grazing, mowing, and cultivation could be separated by significantly different pollen assemblages.

In Berglund *et al.* (1986), *Quercus* and *Juniperus* were shown to be overrepresented, and *Plantago lanceolata* underrepresented in pollen samples. For Poaceae, the overall correlation was poor. It was also shown that fossil samples interpreted in terms of prevailing pasturelands had the greatest similarity with the modern analogues of open and semi-open vegetation types. Gaillard *et al.* (1992, 1994) used pollen assemblages from modern analogues of an ancient cultural landscape (Fig 1b) to reconstruct past land-use and soil conditions in south Sweden, 3000–0 BP. These studies showed that grazed pastures and mowed meadows can be separated on the basis of pollen assemblages, but that pollarding cannot be inferred from pollen data. Land-use types (grazing, mowing, cereal cultivation) and land-use intensity (grazing pressure) were successfully reconstructed using the comparative approach and numerical techniques (Canonical Correspondence Analysis and weighted average calibration methods) (Gaillard *et al.*, 1992; Gaillard *et al.*, 1994). Hjelle (1998 b) studied herb pollen-vegetation relationships in grazed and mowed grasslands. She was able to demonstrate an overrepresentation of pollen from anemophilous taxa or entomophilous taxa with numerous exposed anthers (e.g. *Ranunculus acris* t., *Achillea* t. and *Centaurea nigra* t.) and an underrepresentation of pollen from specialised entomophilous taxa or taxa with open blossom but few anthers (e.g. *Ajuga* t., *Galium* t. and *Alchemilla*). She also calculated R-values (relative to Poaceae) for 39 taxa and pollen productivity estimates relative to Poaceae for eleven taxa. The reasons for the observed mismatch in pollen/vegetation relationships were suggested to be: (1) differences in background pollen between the regions studied, and (2) underrepresentation of pollen from entomophilous taxa. Hjelle (1998b) showed that modern pollen assemblages from mown and species-rich grazed vegetation were comparable to distinct zones of similar pollen assemblages in the fossil records. However, for other land-use types, such as outland pastures and grazed forest, indicator taxa were still necessary for the interpretation.

These studies have contributed more precise interpretations in terms of the qualitative and quantitative characteristics of the landscape, such as land-use types, grazing pressure and soil chemistry. Moreover, a better understanding of the pollen representation of herbaceous taxa in cultural landscapes was gained by using R-values and pollen productivity estimates to correct fossil pollen assemblages. The next objective is to obtain quantitative estimates of the areas covered by the various landscape-vegetation units within the cultural landscape, e.g. cultivated fields, grasslands, or stands of deciduous trees.

Reconstructing the spatial cover of various landscape units

As a first step, an empirical study (Gaillard *et al.*, 1998) was carried out in the cultural landscape of southern Sweden. Because the ultimate goal of the research project was the quantitative reconstruction of the cultural landscape at the local scale, small lakes were selected as the pollen deposition basins. Empirical data from the Ystad area, southern Sweden, i.e. modern pollen assemblages from small lakes and related landscape maps served as a guideline for the choice of an arbitrary area that was expected to be best represented by the pollen. The areas within 500 and 1000 m radius around the lakes were assumed to be a reasonable guess. In a pilot study (Gaillard *et al.*, 1998), the surface sediments of 13 lakes were sampled for pollen and the vegetation surrounding them was mapped using aerial photos. The pollen-vegetation data-set was analysed with ordination techniques. On the basis of the pollen assemblages, sites where grazing was the dominant land-use were statistically separated from sites where cultivated fields prevailed. Generalised linear models showed good relationships between NAP and AP percentages, and percentage cover of various landscape units as mapped within 500 m and 1000 m. PLS (Partial Least Square) regression models with good predictive ability were also inferred for the percentage cover of selected broad landscape units (i.e. total open land, total forested land, and dense forest) and were applied to a fossil pollen record. A comparison of the PLS regression model-reconstructions with historical maps showed that the model performed reasonably well, for a quantitative reconstruction of total open-land and dense forest. The conclusion was that calibration, as performed in these studies, is possible, but that the calibration tool obtained might be valid only for the type of landscape studied in this case. Moreover, the dataset was too small to ensure a robust calibration and had therefore to be extended. At this stage of the research Sugita (1994) provided the inspiration for exploring the question of the relevant source area of pollen in the cultural landscapes of southern Sweden.

Reconstructing and quantifying cultural landscape characteristics – a research strategy for the present thesis

The first question to consider when aiming at a quantitative reconstruction of vegetation changes from fossil pollen is the scale of the landscape to be reconstructed (Jacobson and Bradshaw, 1981). In the case of cultural landscapes, the mosaic pattern of vegetation units such as open grassland, cultivated fields, and tree stands needs to be reflected in the pollen assemblages if land-use and landscape openness are to be reconstructed in quantitative terms. From empirical and simulation studies, we know that pollen assemblages from smaller basins such as ponds and forest hollows, reflect vegetation at the local scale, while pollen assemblages from large lakes represent plant distribution at a more regional scale (Webb *et al.*, 1978; Sugita, 1994). Therefore, small lakes (1–20 ha) should be appropriate for retrieving fossil pollen records which detect significant changes in the cultural landscape.

A pollen sample from a particular basin can be considered to contain both a "signal" and a "background" component (Prentice, 1988). The pollen in the signal component comes from the area closest to the basin, while the background component originates from outside that area. Sugita (1994) defined the concept "relevant source area of pollen" as the area for which the pollen-vegetation correlation is optimal, and hence, beyond which the correlation does not improve. Considering several small lakes in a vegetation region, the signal component will be unique for each lake, while the background component will be identical for all the lakes (Fig 8). Therefore, if local changes around the small lakes are to be reconstructed, the background component must be estimated. One possible strategy for assessing the influence of the background component on the pollen representation of vegetation is to use simulation models and validate them with empirical data (Prentice, 1985; Sugita, 1993; Sugita, 1994). Pollen data from large basins tend to sense the surrounding vegetation as homogeneous and, therefore, they represent a good estimate of the regional vegetation (Sugita, 1994). In order to assess the signal and background pollen components for small basins, it is necessary to use pollen-vegetation datasets from basins of different size (Fig 8). In this way it may be possible to reconstruct both local, contrasting changes and regional changes. Crucial factors for reliable estimates of the contribution of background pollen, and for quantitative landscape reconstructions are the pollen productivity and dispersal ability of the taxa characteristic of the landscape being studied. An important feature of the strategy is to use both the empirical and simulation results in a cohesive and interactive fashion, to improve the predictive power by repeating model predictions, and to gather data in the field to test the model results, and, if necessary, improve the models.

Following the reasoning above, Sugita (2000) has proposed the "Landscape Reconstruction Algorithm" as a robust research strategy for reconstructing heterogeneous, mosaic, vegetation. The Landscape Reconstruction Algorithm was originally developed for reconstructing past changes in tree composition in forest vegetation at the stand scale using pollen data from forest hollows as sediment basins. However, it was assumed that a similar strategy could be used for reconstructing open to semi-open landscape-mosaics. The theoretical background of the Landscape Reconstruction Algorithm is based on the experience and insights

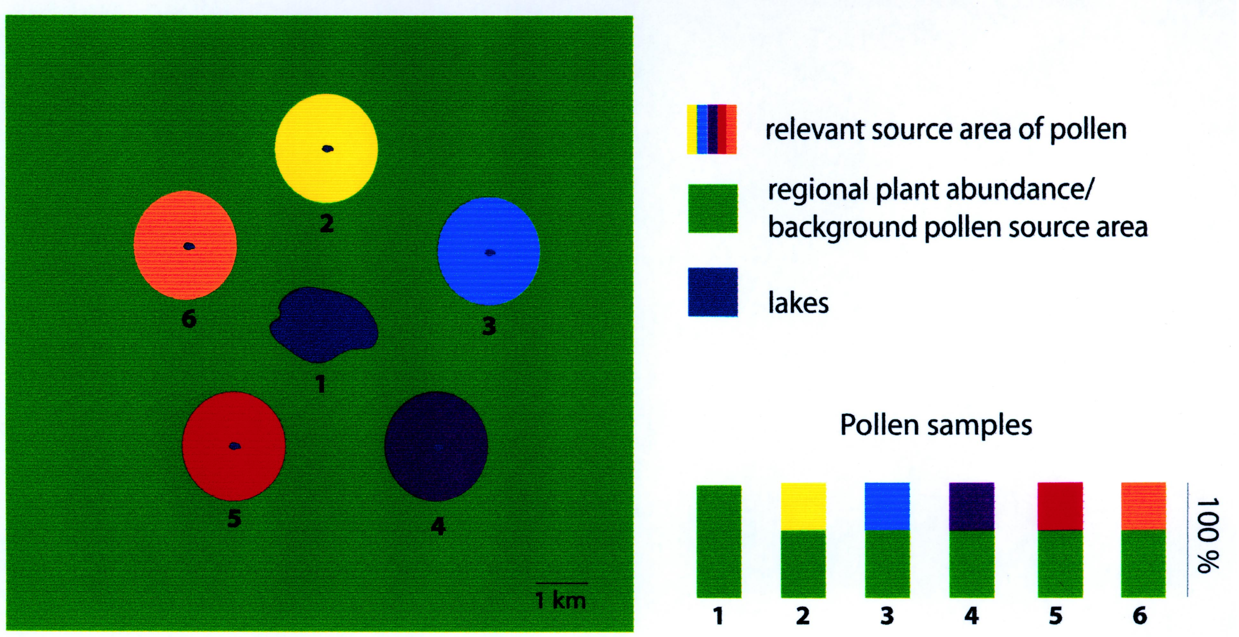

Figure 8. A schematic landscape with one large and five small lakes with their respective relevant source area of pollen (RSAP). The pollen samples from the small lakes consist of pollen coming from within the relevant pollen source area and beyond, i.e. background pollen. The pollen sample in the large lake reflects the regional plant abundance and the background pollen for the small lakes.

obtained from both empirical and simulation studies (Prentice, 1985; Prentice *et al.*, 1987; Sugita, 1994; Calcote, 1995; Sugita , 1998). To apply this strategy in southern Sweden for reconstructing cultural landscapes, the RSAP of the basins where the fossil records are to be retrieved is needed. Pollen productivity estimates of the plant taxa characteristic of the landscape are one of the important parameters required to estimate the RSAP and the background pollen loading.

On the basis of all the aspects considered above, the subsequent and logical steps of the research presented in this thesis, were as follows:

1. Increase the existing pollen dataset and proceed with the exploration of pollen-vegetation relationships in the cultural landscape of southern Sweden (paper I).
2. Estimate the relevant source area of pollen (RSAP) for the cultural landscapes of southern Sweden (papers I, II and IV).
3. The results of the two first steps clearly showed that a mechanistic modelling approach was needed to achieve the ultimate goal of the research effort, i.e., quantitative reconstructions of vegetation cover in the past cultural landscape of southern Sweden. Therefore, pollen productivity estimates for plant taxa characteristic of cultural landscapes, and estimates of pollen source areas and background pollen loading were needed (papers III and IV).

Materials and methods

Area of study

Geology

In this thesis the study area, southern Sweden, is divided into two broad sub regions called "Open Region" and "Semi-Open Region" in the following text. These sub regions are defined primarily on the basis of today's vegetation (see below), but also have distinctive geological contrasts. Southern Skåne (Open Region) is dominated by Cambro-Silurian and Cretaceous sedimentary bedrock overlaid by clayey till. Altitudes are less than 100 m a.s.l., and the topography is flat or smoothly hummocky. North of this area (Semi-Open Region) the bedrock consists of Archean gneiss and granites overlaid by silty-sandy till. Altitudes are between 200 and 500 m a.s.l., and the topography is more broken (Berglund *et al.*, 1996).

Climate and vegetation

Southern Sweden consists of two vegetation zones: the southernmost nemoral zone with a potential vegetation dominated by broad-leaved forest and, further North, the boreo-nemoral zone dominated by a mixture of coniferous and broad-leaved deciduous forest (Sjörs, 1963). The threshold of days per year with temperatures above 5°C, is 200–210 for the nemoral zone, and 190–200 for the boreo-nemoral zone. Southern Sweden is characterised by mean annual temperatures of 5–7°C (Vedin, 1995), and an annual precipitation of 600–1000 mm (Alexandersson and Andersson, 1995). The modern landscape can be subdivided into two distinct regions which largely co-incide with these broad vegetation zones: the southernmost, open agricultural region (Open Region) with less than 50% forest cover, and the semi-open, mixed agricultural and forested region (Semi-Open Region) with 50–90% forest cover (Fig 1).

The Open Region (southern Skåne) is characterised by having cultivated fields and pastures, covering 60–80% of the area. Small patches of woodland consisting of broad-leaved, cool-temperate trees, such as *Fagus sylvatica, Quercus robur, Tilia cordata, Fraxinus excelsior*, *Ulmus glabra* and *Betula pendula* are scattered in the landscape (Berglund *et al.*, 1996). The Semi-Open Region (northern Skåne, Halland, Småland, Blekinge and Östergötland) is covered with forests within which there are scattered open patches of cultivated fields and pasture. Coniferous trees, *Picea abies* and *Pinus sylvestris*, dominate the forest, while cool-temperate deciduous trees occur mainly near farms and in meadows (Berglund *et al.*, 1996) (Fig 1).

Pollen data – sampling and analysis

Moss polsters

Moss polsters were collected in grasslands to obtain pollen productivity estimates for plant taxa characteristic of the ancient traditional cultural landscape of southern Sweden. In earlier studies, moss polsters were found to be effective natural pollen traps for these taxa (Berglund *et al.*, 1986). Several authors have discussed the question of the number of years represented in moss polsters, which was thought to be between one and 10 years according to the type/species of moss collected and the part of the moss used for the analysis (e.g. Boyd, 1986; Cundill, 1986). Moss polsters were collected in a central part of the grassland (Fig 9, III:6), within a circular area of 0.5 m radius where the concentration of bare moss was high. Within this area, ten sub-samples of moss were taken, and only the green part of the moss was used. The sub-samples were then put into a plastic bag and amalgamated into one sample, by tearing the moss into pieces and mixing them well. This procedure evens out any variation in very local pollen deposition, as described by Berglund *et al.* (1986), and Gaillard *et al.* (1992, 1994).

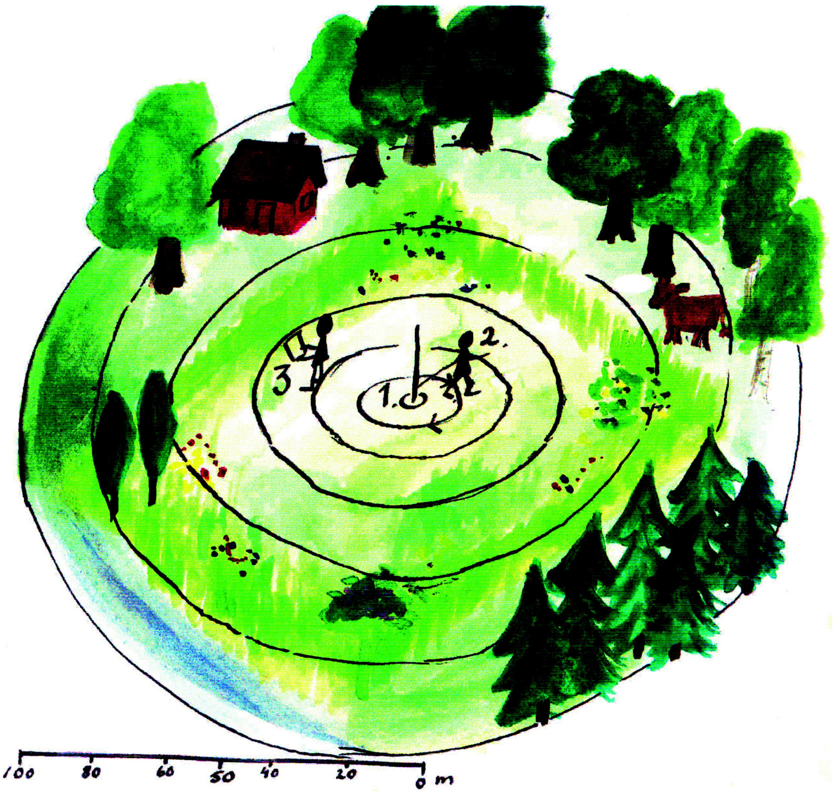

Figure 9. Description of fieldwork for sampling pollen and vegetation data for PPE in non-fertilised grassland of the ancient traditional cultural landscape of Southern Sweden. (1) moss polsters are sampled for pollen, the vegetation (2) is surveyed in great detail within 0–10 m and (3) a map is drawn for the vegetation within 10–100 m radius from the pollen sampling point (see further details in Appendices III and IV).

Lake surface sediments

The top two centimetres of surface sediment were sampled in the central part of the lakes during winter, using a surface sediment sampler (Aaby and Digerfeldt, 1986). Two centimetres of surface sediment normally represent a maximum of ten years of sediment accumulation in the eutrophic to oligotrophic lakes of southern Sweden. By taking a sample of this size the inter-annual variation in pollen deposition is averaged out (Gaillard *et al.*, 1998).

Pollen analysis

Pollen grains were extracted from lake sediments using conventional methods (Berglund and Ralska-Jasiewiczowa, 1986). The amalgamated moss polster samples were boiled in NaOH and washed through a filter (mesh size 255 µm) before extracting pollen using acetolysis. In each sample, 1000–1500 pollen grains were counted and identified with the help of pollen keys (Moore *et al.*, 1991; Punt *et al.*, 1976–1995) and the reference collections at Växjö University and Lund University. Pollen taxonomy and nomenclature follow those adopted by the European Pollen Database (Gaillard *et al.*, 1993), i.e. pollen taxonomy is mainly according to the keys most commonly used by European pollen analysts (see above), and nomenclature follows Flora Europea (Tutin *et al.*, 1964–1980).

Vegetation data – surveys and analysis

The vegetation survey around the lakes (Appendix I) and moss polsters (Appendix III and IV), followed two different strategies, because the purpose and requirements of the studies differed. Lake surface sediments were collected in order to correlate the pollen assemblages obtained from the lakes with broad vegetation classes identified from aerial-photos (Fig 10). In contrast, the moss polsters were sampled in order to obtain pollen productivity estimates for those herb plant taxa characteristic of the traditional cultural landscape. In this latter case, the study required much more detailed data on the distribution of individual plant taxa. Therefore, a thorough field survey of the area closest to the moss sampling point was needed, as well as a more detailed vegetation classification combined with ground-truth control for the interpretation of the aerial-photos. In both cases, colour infrared (CIR) aerial-photos were used, as they provide the best possible interpretation in terms of detailed vegetation characteristics (Ihse *et al.*, 1993)

The vegetation surrounding the lakes was classified within 500 and 1000 m radius. This scale was considered appropriate for the analysis of pollen-vegetation relationships (Gaillard *et al.*, 1998). For the vegetation surrounding the moss polsters, a radius of 1500 m was chosen based on the simulation estimates of the rele-

Figure 10. The mosaic of the cultural landscape of southern Sweden and the major land-use types: cultivated fields, open and semi-open pastureland, deciduous forest and coniferous forest.

vant source area of pollen for forest hollows in the same region (Appendix II). The vegetation survey followed a time-cost effective methodology (III:6). Because of the limited dispersal of most herb pollen, very detailed information about the vegetation composition up to 10 m from the pollen sampling point was needed, whereas vegetation from 10 to 1500 m could be classified into broader vegetation types, with the dominant species determined for each type. Vegetation data were collected in the field out to 100 m radius, and extracted from aerial photos between 100 and 1500 m radius. A field survey was necessary within the 100 m radius, because the resolution of the colour infrared aerial photos does not provide sufficiently detailed information. All vegetation maps were digitised and further processed in Geographical Information System (GIS) software (ArcInfo and IDRISI). The digitised vegetation maps permit calculations of area, allowing plant abundance data to be extracted in the proper format for further analysis. A complete description of the vegetation surveys and analyses is found in Appendix III.

Data analysis

Numerical techniques

Numerical techniques were used to explore the pollen/landscape relationships and to identify correlation between pollen assemblages from surface sediments in small lakes and quantitative landscape variables in the area surrounding them (Appendix I). All the ordination analyses were implemented by the CANOCO program version 3.12 (Ter Braak, 1987; Ter Braak, 1990).

Principal Component Analysis (PCA)

PCA, a linear ordination technique (Ter Braak, 1987; Ter Braak, 1990) was used to analyse the variation in plant composition between sites and to identify correlation between pollen taxa. It was also used to test whether the variation in composition of the pollen assemblages between sites could be explained by variation in the landscape surrounding the lakes.

Redundancy Analysis (RDA) and Monte Carlo permutation test MCP

Redundancy analysis is the canonical or constrained form of PCA, which implies that pollen and landscape data can be analysed together. The importance of both pollen and landscape data for the overall variation in the data-set can be explored. Moreover, correlations between the constrained pollen taxa or between pollen taxa and landscape units can be analysed. Within the RDA analysis, a forward selection procedure was performed (Ter Braak, 1990). This is a technique used to select a minimal set of predictive variables (in this case landscape variables) that explains the variation in the pollen data almost as well as all the landscape variables together. Further, the Monte Carlo permutation (MCP) test (Ter Braak, 1990) was applied to test whether each of these variables was statistically significant.

Inverse RDA

Inverse RDA (an unconventional form of RDA (Odgaard, 1992; Anderson *et al.*, 1996)) was applied to extract the pollen taxa that best explain the variation in the landscape data. In this analysis, the pollen taxa were defined as the predictor variables (instead of response variables as in normal RDA), and the landscape data represented the response variables (instead of the predictor variables as in normal RDA). Forward selection was applied to identify the smallest number of pollen taxa that best explain the variation in the landscape data almost as well as all the pollen taxa together.

Estimation of pollen productivity and background pollen using ERV-models

The ERV-models use the pollen and vegetation data to estimate a linear relationship between them. To visualise the goodness of fit of the data to the model-estimated linear relationship, the vegetation or the pollen data have to be transformed (Fig 5). For ERV-model 1, the

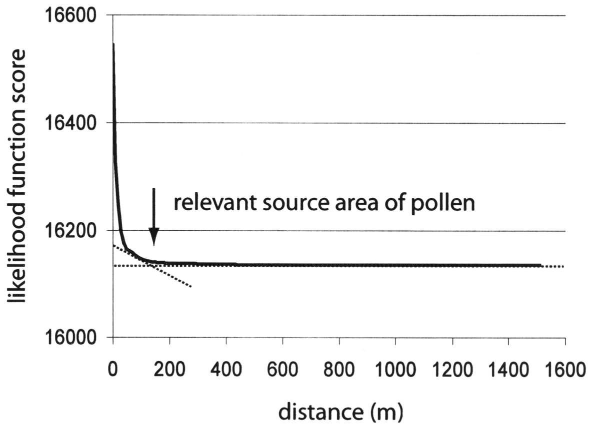

Figure 11. Estimates of relevant source area of pollen (RSAP) is derived from the likelihood function scores over distance of the goodness-of-fit of the pollen and vegetation relationship in an ERV-model. The score declines with increasing distance from the pollen sampling area and reaches an asymptote when the pollen-vegetation correlation does not improve. The distance at which the score reaches an asymptote depicts the RSAP by intercept between a prolongation of the lowest score and the declining curve.

vegetation data are adjusted, while for ERV-models 2 and 3 the pollen proportions are adjusted in model-specific ways. When graphically presented as scatter diagrams the adjusted data show a better linear relationship between pollen and vegetation data than using the uncorrected data, and the slope and intercept represent the pollen representation factor (α_i) and background component (z_i) estimated by the model, respectively (Fig 5). See also the section above on ERV-models.

Estimation of the "relevant source area of pollen" (RSAP) using likelihood function scores

The relevant source area of pollen (RSAP), defined as the area beyond which the correlation of pollen and vegetation data does not improve, can be estimated using the maximum likelihood method of the ERV-models (Sugita, 1994; Calcote, 1995; Sugita, 1998). The ERV-models estimate the pollen representation factor (α_i) and background pollen (z_i) from pollen and plant abundance data, by assessing and maximising the likelihood function score. The likelihood function scores can be calculated over distance and changes in the scores depict the changes in the goodness-of-fit of the data to the linear model between pollen loading and plant abundance (Prentice and Parsons, 1983; Sugita, 1994). The likelihood function score decreases as the area of vegetation survey increases, and approaches an asymptote when the goodness of fit of the pollen-vegetation data to the model-estimated linear relationship does not improve with distance, i.e. the radius of the area of vegetation surveyed (Sugita 1994). The estimate of RSAP is derived from the interception between the prolongation of the line best fitted to the lowest likelihood function score and the end of the score of decrease (Fig 11). A more detailed description of the method is found in Appendix IV.

Computer simulations

POLLSCAPE a computer simulation model

The computer program package POLLSCAPE written by Sugita (1994) simulates pollen dispersal and deposition in a heterogeneous landscapes (Fig 6). The models involved in the program were originally created for forested landscapes and are based on simple assumptions (see section on "The theoretical framework of pollen analysis"). For simulations, either hypothetical landscapes and vegetation data created within POLLSCAPE, or real vegetation maps in digitised format may be used. POLLSCAPE allows the user to design hypothetical landscapes characterised by heterogeneous vegetation comprised of circular patches of different size within a matrix. The matrix and each patch are defined by specific species compositions of one or several taxa. Patch size and the overall occurrence (coverage) of patches in the landscape can be defined and altered. The patches are randomly distributed in a large-scale landscape (e.g. a 50 × 50 km plot). In each simulation, a set of basins can be either systematically positioned or randomly distributed within the central part of the landscape (e.g. 4 × 4 km), the latter in order to avoid an edge effect. The mean plant abundance can then be calculated within concentric rings around the basin. The increment between the rings may be altered. This procedure allows for distance weighting of the plant abundance, which is needed for calculating the mean pollen loading on a bog or lake surface using either Prentice's (1985) or Sugita's (1993) model, respectively. The proportions of the individual taxa in the area are used as the regional plant cover for calculating the background component of the pollen loading (Sugita, 1994). The simulated pollen loading and distance weighted plant abundance may finally be input to ERV-models for estimating the relevant source area of pollen. The current version of the POLLSCAPE program package consists of three sub-units; MOSAIC (Middleton and Bunting, in prep.) for landscape design, OPENLAND3 (Eklöf *et al.*, in prep.) for vegetation extraction, and POLSIM (Sugita, unpublished) for simulation of pollen dispersal and deposition. Further details are found in Appendix IV.

Results – Summaries of papers

Paper I – Pollen-landscape relationships in modern analogues of ancient cultural landscapes in southern Sweden – a first step towards quantification of vegetation openness in the past

The aim of this study was to further explore the pollen-landscape relationships in the Open and Semi-Open Regions using small lakes by enlarging the pilot data-set collected earlier by Gaillard *et al.* (1998). The initial intention was to develop the calibration tool worked out in that first study. The lake sites were chosen in areas characterised by ancient traditional cultural landscapes, implying a specific vegetation structure and composition (see Introduction and Fig 2). Twenty-two lakes were sampled for surface sediment (Fig 1a and I:I). The sites in the new study were selected mainly in the Semi-Open Region, while the existing data-set (Gaillard *et al.*, 1998) included a dominance of sites from the Open Region. The vegetation was surveyed from colour infrared aerial photos, within 500 and 1000 m from the pollen sampling point, and classified into six major units, i.e. coniferous forests, deciduous forests, semi-open grasslands, open grasslands, cultivated fields and others (i.e. non-pollen producing areas) (I:3). Within 1000 m radius around the lakes, the sites varied in landscape-openness along a gradient from mainly open to mainly forested (I:4). Principal Component Analysis (PCA) and Redundancy Analysis (RDA) were used to explore the correlation between pollen taxa, pollen assemblages, and vegetation units (I:6, I:7).

The pollen assemblages were characterised by low site-to-site variation in the percentages of tree and herb taxa, despite large variations in landscape composition within the 1000 m radius area. However, significant correlation was found between pollen taxa and vegetation units within both the 500 and 1000 m radii around the lakes (I:7). The open-land taxa such as Poaceae, Cerealia, *Filipendula* and *Salix* showed good correlation with the vegetation unit “cultivated fields” within both radii. Poaceae and *Filipendula* also showed a correlation, although weak, with the unit “open grasslands” within 1000 m radius. A weak correlation was found between the tree taxa *Quercus* and *Fagus,* and the vegetation unit “deciduous forests” within 1000 m radius. However, no correlation could be demonstrated between the dominant tree taxa in the region, i.e. *Betula* and *Pinus,* and the vegetation units “deciduous forests” and “coniferous forests”, respectively. From these results it was concluded that a 1000 m radius area around small lakes (0.1–19.2 ha) was a suitable spatial scale for quantitative reconstruction of the type of landscape and the broad vegetation units used in the study, such as cultivated fields and open grasslands in particular, and possibly deciduous forests.

A comparison of the results of this study with those of the pilot investigation of Gaillard *et al.* (1998) revealed a major difference between the two contrasting regions, Open and Semi-Open, in terms of the variation in NAP percentages in relation to vegetation openness around the site (I:9). This was tentatively explained by the large differences in the overall regional plant abundance within the two regions, resulting in a different background pollen input. In the Semi-Open Region, the background pollen is dominated by *Betula* and *Pinus* whereas in the Open Region, the background pollen input is dominated by Poaceae and Cerealia. Therefore, the open grassland vegetation is more strongly reflected in pollen assemblages from lakes situated in the southernmost region. This comparison also emphasised that the calibration model used by Gaillard *et al.* (1998) was not suitable as a general calibration model valid in a range of differing landscape types. Therefore, no new calibration equation was proposed in Paper I. Background pollen input was assumed to affect the NAP/open land relationship too severely. This study led to the insight that the methodology proposed by Sugita (1994), would help to test the hypothesis of the influence of the background pollen. Moreover, it would enable rough estimates of relevant source area of pollen in the cultural landscapes of southern Sweden. These aspects are the foci in paper II.

Paper II – Landscape openness and pollen records: a simulation approach

The three major aims of this study were first, to test whether simulation models could predict the NAP/open-land relationships observed in the empirical data of Gaillard *et al.* (1998) and Paper I. Second, to predict relevant source area of pollen for small lakes in the two contrasting cultural landscapes types of southern Sweden. Thirdly, to test the applicability of the POLLSCAPE simulation model originally developed for forest vegetation (Sugita, 1994) in open and semi-open vegetation. Two landscape scenarios with simplified vegetation patterns and composition, mimicking the Open and Semi-Open Regions of southern Sweden were created in POLLSCAPE (II:1, II:2). The landscapes were simplified using sixteen taxa grouped in six vegetation classes. The pollen dispersal and deposition in small lakes (100 m radius) randomly distributed in the landscape was simulated. The relevant source are of pollen was estimated from the simulated pollen and vegetation data using ERV-models. The simulated pollen-vegetation relationship was compared with the empirical data of Gaillard *et al.* (1998) and Appendix I.

The simulations overestimated the percentages of Poaceae, Cerealia and *Quercus,* and underestimated those of Cyperaceae, *Pinus* and *Alnus,* but predictions of the percentages of the remaining ten taxa were comparable (II:3). The relevant source area of pollen for the lakes in both the simulated Open and Semi-Open landscapes was estimated to 800–1000 m radius (II:5), which agreed with the assumptions inferred from the significant correlation between the empirical pollen and vegetation data within 1000 m radius (Appendix I). Moreover, a comparison of simulated and the empirical NAP/open-land relationships within 1000 m radius showed strikingly similar patterns (II:4). In the Open Region a nearly one-to-one NAP/open-land relationship could be seen e.g. 40–50% open-land within 1000 m radius around the lake was reflected by 40% NAP in the sample, and 70–90 % open-land was reflected by 50–65% NAP. Whereas, in the Semi-Open Region there was no such relationship e.g. 50–80% of open-land were reflected by less than 20% NAP in the sample, and less than 50% open-land was reflected by 2–15% NAP. This implies that in the Semi-Open Region the areas of open-land around the sites can be significantly underestimated when inferring landscape-openness from NAP percentages.

The data-model comparison confirms that POLLSCAPE works in open and semi-open vegetation, despite the fact that the model assumptions do not take into account wind direction, topography, and the differences in height of trees and herbs in the cultural landscape. The simulations suggest that the largest area potentially reconstructable by using pollen data from small lakes is 800–1000 m radius, if a landscape mosaic consisting of patches not smaller than 100 m radius, is to be reconstructed (II:5). The results also illustrate that NAP percentages always underestimate the percentage cover of open-land surrounding the site, and that this feature is more pronounced in forested regions. The simulation approach is a useful tool to identify the most significant factors affecting pollen-vegetation relationships. However there is a need to improve the simulations and parameter estimates.

In conclusion, the hypothesis about the effect of background pollen on the NAP/open-land relationship is confirmed by the simulations. Moreover, the simulation model works in both Open and Semi-Open Regions. Therefore, the mechanistic modelling approach is appropiate and may be pursued using the strategy proposed within the Landscape Reconstruction Algorithm (Sugita, 2000). This strategy requires as accurate pollen productivity estimates (PPE) as possible for herb taxa, and these were not available. Thus, PPE for herb taxa characteristic of the traditional cultural landscapes of southern Sweden were needed. This is the focus of paper III.

Paper III – Pollen productivity estimates for the reconstruction of past vegetation cover in the cultural landscape of southern Sweden

The aim of this study was to obtain pollen productivity estimates for herb plant taxa characteristic of open and semi-open cultural landscapes in southern Sweden. For this purpose, moss polsters were sampled for pollen in non fertilised grasslands at forty two sites with twenty one localities in each region (Figs 1c, 2, 9). Particular effort was put into designing an appropriate fieldwork methodology in order to obtain the necessary and adequate pollen and vegetation data for estimating pollen productivity. The vegetation surrounding the sampling points was surveyed in concentric rings out to 1500 m radius (III:6), so that vegetation data could be distance-weighted i.e. plants further away from the pollen sample point get less weight than plants closer to it. Vegetation surveys were made in detail in the field within 100 m and from aerial photos between 100 and 1500 m (see section on material and method and Appendix III for further details).

Extended R-value (ERV) models were used to estimate pollen productivity from the pollen and vegetation data using the maximum likelihood method (described in the section on material and methods above and in further detail in Appendix III). For comparison, the estimates were calculated using all three ERV-sub-models, three different distance weighting procedures, and three data-sets i.e. one data-set including data from the entire region and two data-sets separating the data from the Open and Semi-Open Regions (III:4). The three sub-models provided comparable estimates in order of magnitude, although the values obtained with ERV-model 3 were systematically higher than those from the other two models. However, considering the standard deviation, the values were comparable for all except four taxa. The taxon-specific distance-weighting method provided more reasonable estimates than the approximation using 1/d and 1/d^2 (where d is the distance from the pollen sample point). Finally the PPE based on the data from all forty two sites were more robust than the ones obtained separately from the two sub-data-sets Open and Semi-Open. The reason for this was that several taxa did not have sufficient variation in plant abundance within each sub-data-set. If the sub-data-sets are to be enlarged in the future, effort should be put into sampling sites in such a way that variation in plant species abundance is sufficiently large for all taxa.

In conclusion PPE for twelve plant taxa characteristic of the south Swedish cultural landscape now exist (III:4). A satisfactory methodology for pollen/vegetation data collection and analysis in order to calculate PPE has been developed. A comparison of the pollen productivity of the herb and tree taxa showed that common trees in the region (*Betula, Pinus, Querces* and *Fagus*) produce six to eight times as much pollen as Poaceae (III:5b). A comparison with other studies of herb pollen productivity (Hjelle, 1998a) emphasised the need for similar studies in other landscape types and vegetation regions. It seems that several method and/or region related factors may influence PPE. Further empirical data and simulation exercises are required to ensure a full understanding of the PPE and their robustness (see also general discussion below). Nevertheless, we can now use the PPE obtained so far for model simulations of pollen deposition in landscapes with a mosaic of open and forested vegetation. Moreover, the PPE values can be used in the various steps of the Landscape Reconstruction Algorithm of Sugita (2000). The large data-set of this study also provided appropriate vegetation data for estimation of the relevant source area of pollen (RSAP) for moss polsters. This is the focus of paper IV.

Paper IV – Estimating spatial scale of pollen dispersal in cultural landscape of southern Sweden

The aim of this paper was to estimate the relevant source area of pollen (RSAP) of moss polsters in the ancient, traditional cultural landscapes of southern Sweden. Beyond this area the pollen-vegetation relationship does not improve, which is implied in the definition of RSAP. Therefore, the RSAP estimate can be a useful guideline for how far out the vegetation must be surveyed in order to obtain reliable PPE in future studies (Sugita, 1994). In this study the same pollen-vegetation data-set from the forty two moss-polsters as in Appendix III was used. Twenty taxa (nine tree and eleven herb taxa), representing 80–90% of the surveyed vegetation cover and pollen sample assemblage, were included in the analysis. ERV-model 3 was used to estimate RSAP and background pollen input from beyond RSAP, both in Open and Semi-Open Regions. POLLSCAPE simulations (see Paper II above) using both simplified landscape designs and real world vegetation maps were used to provide a more precise understanding of the results obtained with empirical data.

The estimates of RSAP are obtained by visual inspection of the likelihood function score plotted against distance (further explained in the method section and Fig 11). The likelihood function score for the Open Region showed the “expected” pattern and a RSAP of 400 m can be derived from it (IV:2a). The likelihood function score for the Semi-Open Region showed an “unexpected” pattern and, therefore, RSAP cannot be evaluated from it (IV:2b). Simulations using simple hypothetical landscapes to obtain simulated pollen and vegetation data showed that sample design affects the likelihood function scores. When sites are systematically selected in openings in the Semi-Open Region the simulated likelihood score exhibited the same unexpected pattern as in the empirical data. However, in simulations with systematically selected sites in the Open Region as well as randomly distributed sites in both Open and Semi-Open Regions the likelihood function score showed an expected pattern. Simulations also demonstrated that the patch size of the vegetation types included in the landscape had an effect on the RSAP. For landscapes with large patches simulations generally predicted a larger RSAP than for landscapes with smaller patch size.

Consequently, in order to obtain reliable RSAP, sites should be randomly selected. However, in our study a systematic site selection in grasslands appears to be a good approximation to random selection in the case of the Open Region. This can be explained by the fact that the coverage of grasslands in the overall landscape is large and most sites would be situated in open areas, even though they are randomly selected. Therefore it is possible to derive a RSAP for moss polsters of ca 400 m in the Open region. However, in the Semi-Open Region the systematic selection means that sites within the forest are omitted, which, nevertheless is a large component of the semi-open landscape, and therefore has an effect on the pattern of the likelihood score. Even though the two regions have contrasting species compositions, the patch size is comparable. Simulations based on randomly selected sites in both the Open and the Semi-Open Region predict similar RSAPs, which suggest that the RSAP for moss polsters in the Semi-Open Region might similarly be ca 400 m.

In conclusion, the study strongly emphasised the importance of random site selection for data collection aimed at inferring the RSAP for a particular landscape type. The simulations also predicted that landscapes with similar patch size also have similar RSAPs for a particular basin size, in this case moss polsters. The effect of patch size on RSAP implies that, for future studies, the vegetation structure should be analysed. If it is similar to the patch size in the present study, a spatially-precise vegetation survey within at least ca 400 m would be required and remote-sensing vegetation data out to 1000 m with less spatial resolution would be informative for the RSAP estimates.

Discussion

The comparative approach versus the mechanistic-modelling approach

Within this thesis both a comparative approach (Appendix I) and a mechanistic model approach (Appendix II, IV) are used to analyse the pollen-vegetation relationship. Although the main focus of this work has been on the mechanistic model approach it should be emphasised that both approaches are needed. However, they are useful for different purposes. The comparative approach performs well for the reconstruction of qualitative characteristics of the landscape such as land-use/management types (e.g. Berglund *et al.* 1992, Gaillard *et al.* 1992). The comparative approach may also be useful to reconstruct characteristics such as grazing pressure and soil pH (e.g. Gaillard *et al.* 1997).

However, the comparative approach is not the most appropriate strategy to quantify areas of various vegetation units (Gaillard *et al.* 1998, Appendix II). The mechanistic model is so far the most sound approach in this case. However, it requires several data-sets of pollen assemblages from basins of different size, and related vegetation surveys. It is therefore work-intensive before it can be applied to fossil records. It is certainly wise to combine the two approaches. For example the mechanistic model approach can be used to estimate RSAP for sites in a study which is using the comparative approach.

Because the mechanistic model approach relies on the pollen-vegetation relationship for individual taxa it works for non-analogue situations in the past as well, whereas, the comparative approach relies on a comparison between modern and fossil pollen assemblage. Therefore, a vegetation composition analogous to the one to be reconstructed must be sampled in the modern landscape. It is important to stress that the calibration data-set eventually obtained by either of these two approaches can only be used for reconstructing vegetation with a similar species composition and structure to the one used for the empirical calibration. Today, each calibration data-set is unique to a region. Therefore, effort should be made to compare similar studies from different regions, to synchronise research strategies and to solve mutual methodological problems in order to obtain as robust estimates as possible, particularly of pollen productivity.

Pollen productivity estimates (PPE) of herbs and trees – their reliability and area of use

The studies within this thesis have provided PPE for fourteen tree and eleven herb taxa characteristic of the ancient traditional cultural landscapes of southern Sweden (Fig 12). How reliable are these estimates and are they comparable to previous estimates for tree taxa (Andersen, 1970) and herb taxa (Hjelle, 1998a)?

First of all the sample designs have to be compared between the studies. The PPE for tree and herb taxa in southern Sweden are based on two different data-sets. In both cases moss polsters were used to collect pollen data but the scale and resolution of the vegetation surveys differ. The PPE for tree taxa, except *Picea* and *Pinus* (Prentice *et al.*, 1987) (Appendix II) are based on 124 pollen samples from moss polsters (Gaillard *et al.*, 1992; Gaillard *et al.*, 1994). This data-set was originally collected to obtain a calibration model using the comparative approach. At each site, the vegetation was surveyed within a 10 × 10 m and a 100 × 100 m square around the pollen sample. This sample design did not allow for distance weighting of the vegetation. Moreover, the area surveyed for the vegetation data was too small to achieve the best possible fit of the pollen-vegetation relationship, particularly for tree taxa. The values published in paper II should therefore be used with caution. However, the high PPE for *Quercus*, *Betula* and *Alnus* were comparable to the values obtained from closed forest in Denmark (Andersen, 1970).

The data-set used in this thesis to calculate PPE for herb taxa is based on a sample design that allows distance-weighting and the vegetation is surveyed within a larger area (1500 m radius). Three different methods of distance weightings ($1/d$, $1/d^2$ and taxon-specific distance weighting using dispersal function) have been used and compared. Previous studies have shown that $1/d^2$ is a good approximation for the taxon-specific distance weighting (Calcote, 1995). However, in the present study $1/d^2$ gave unreasonably high PPE for *Juniperus* and Cerealia (III:4). This suggests that the taxon-specific distance weighting should preferably be used when data on fall speed is available.

The original idea was to calculate PPE for both herbs and trees. However, the PPE obtained for the trees in this analysis were low compared to those obtained in previous studies. This might be explained by low frequencies of tree pollen in the data-set except for *Pinus*, *Betula* and *Alnus.* As a consequence the variation in pollen percentages between sites was too small for most tree taxa. This is a direct result of the selection of sites primarily in open grassland. There were often no trees within a 40 m radius around the pollen sample. Therefore, the data-set was more suitable for calculating PPE for herb taxa (Paper III).

However, the two data-sets have three taxa (*Juniperus*, Poaceae and Cyperaceae) in common, which enables a comparison of herb and tree PPE (Fig 12). Although these should still be used with caution they are

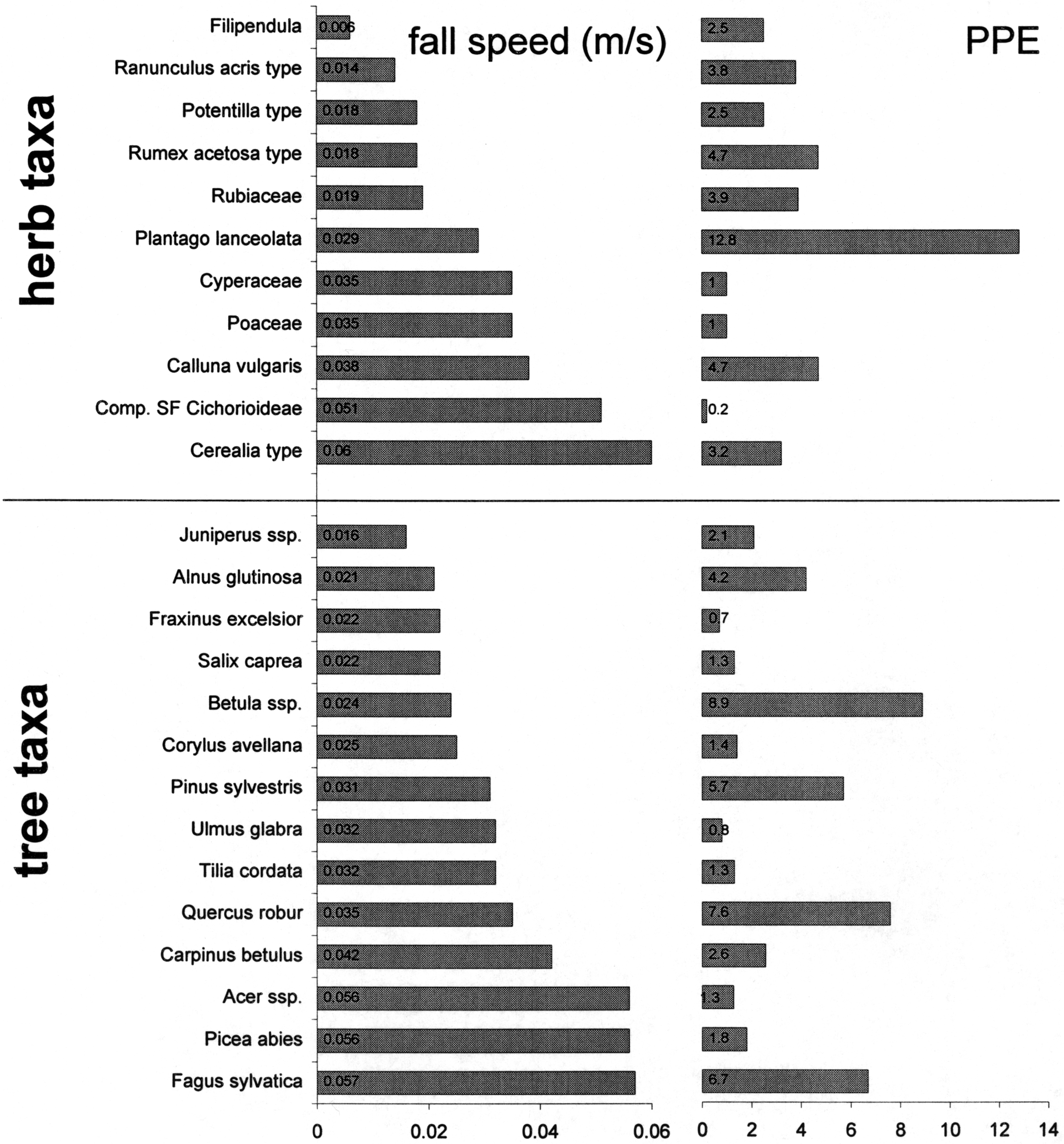

Figure 12. The fall speed (m/s) and pollen productivity for 25 plant taxa characteristic of the cultural landscape of southern Sweden. The pollen productivity estimates are relative to Poaceae set to one (see further details in Appendices II and III).

the best estimates to date for southern Sweden. In order to obtain reasonable estimates for tree taxa that can be directly compared to herb taxa, the data-set should be completed with sites characterised by a higher abundance of tree taxa close to the pollen samples.

A comparison of PPE for ten herb taxa obtained from southern Sweden and south-western Norway (Hjelle, 1998a) shows that in both studies, *Plantago lanceolata*, *Calluna vulgaris*, and Rubiaceae have the first, second, and fourth largest PPE, respectively (III:5). However, the PPE obtained in the present study are higher than those obtained by Hjelle for all taxa. This may be explained by differences in environmental factors or in sample design. Differences in pollen production between southern Sweden and south-western Norway may be explained by climatic conditions, e.g. differences in precipitation. Differences in species included in the pollen types e.g. Poaceae may also play a role. In both the present and Norwegian study, Poaceae has been used as the reference taxon. The reason for this is that it is abundant at all sites, and shows a relatively large gradient of variation in the pollen-vegetation data. However, Poaceae contains a large number of species that may have different pollen productivity and the species composition within the group may vary between sites and regions. When the group is used as a reference taxon, the possible differences in the species represented may affect the rest of the estimates, as they are relative to the reference taxon. Therefore, it would be preferable to use a precise species such as *Plantago lanceolata* or *Calluna vulgaris* as the reference taxon. However, for the stability of the ERV-model analysis a taxon with intermediate PPE should be used (Prentice and Parsons, 1983), which is not the case of *Plantago lanceolata*. The problem with *Calluna vulgaris* is that it is not present, or abundant enough at all sites. In spite of the problems related to Poaceae as a reference taxon and, in spite of differences in sample design between the two studies, the PPE values are broadly comparable, which is encouraging.

The annual variability in pollen productivity can be a problem when inferring robust PPE from pollen assemblages in moss polsters. Hicks (2001) has recorded annual variation in pollen deposition in Tauber traps within the boreal forest zones of northern Fennoscandia over an 18-year period. The yearly pollen deposition reflects climate, primarily the temperature of the growing season of the year before pollen emission, and presumably the inter annual variability in pollen production of the plant taxa in the region. The variation is shown to be large especially for *Pinus* and *Betula*. Because such variation exists, the pollen data used for PPE should represent several years of pollen rain. However, the exact number of deposition years in a moss polster is not known. A recent comparison between pollen collected in Tauber traps and moss polsters showed that pollen assemblages in the green part of the moss polsters represent only one, or possibly two years of deposition (Räsänen, personal communication). If this is generally the case it could be critical for PPE which might differ depending on the year of sampling. Therefore, several years of continuous sampling should be aimed at. In this way the pollen loading could be averaged over several years, and biases in annual variability evened out.

Interestingly, *Plantago lanceolata* has a higher PPE than all the tree taxa, and it has comparatively light pollen that is easily transported. This would partly explain why *Plantago lanceolata* is often one of the first and best represented human-indicator species at the time of the first significant forest clearings of Neolithic age in southern Sweden (Digerfeldt, 1972; Thelaus, 1989; Gaillard and Göransson, 1991; Lagerås, 1996), a phenomenon also described in all Europe by many authors.

The PPE of Cerealia in the present data-set needs to be discussed. In our study this pollen taxon mainly comprises the pollen morphological types *Triticum* and *Hordeum*, but also in a few cases *Avena* and *Secale*. Both *Triticum* and *Hordeum* types may include species of wild grasses. Moreover, the cultivated fields always occurred at a greater distance than 100 m from the pollen samples and, therefore, received a low weighting. These facts may explain why Cerealia pollen was assigned a high representation relative to the cover of cultivated fields in the vegetation data i.e. the slope of the linear pollen-vegetation relationship for this taxon was steep and a higher PPE than expected was obtained. Empirical studies of pollen representation close to cultivated fields show relatively small amounts of Cerealia pollen. This is a combination of low transportability of the large pollen grain and bad release of pollen in the case of *Hordeum* and *Avena* (Vuorela, 1973). In order to get reliable PPE for Cerealia taxa, moss polsters close to ancient traditionally managed fields should be sampled. A few such sites were included in the study by Gaillard *et al.* (1994). The PPE for Cerealia published in paper II should, therefore, be reliable and may be used until better PPE are available for cereals.

The importance of fieldwork design cannot be emphasised enough. In the present study, we have set up a sampling design for pollen and vegetation data which allows distance-weighting of the vegetation. The resolution of the vegetation survey is finer close to the pollen sample point than it is further away. This is reasonable considering that the main focus has been on PPE for herb taxa. Sites should be selected to meet the criteria of sufficient gradient of variation in abundance of the plant taxa for which pollen productivity are to be estimated.

The Relevant Source Area of Pollen (RSAP) in the cultural landscape of southern Sweden – implications

The relevant source area of pollen (RSAP) as defined by Sugita (1994) can be described as the relevant source area of the total pollen assemblage. When aiming at a quantitative reconstruction of landscape characteristics, it is of little use to consider the individual source area of each single pollen taxon. Therefore, estimating RSAP using ERV-models is a useful tool for obtaining insights into the possible scale of reconstruction in the landscape being studied.

In papers I and II, both empirical data and simulations indicate that the RSAP for small lakes in the Open and Semi-Open Regions of southern Sweden is 800–1000 m. However, the empirical and simulated data were analysed using different methods. Therefore, the empirical data of paper I can only be considered to be a very rough validation of the model prediction in paper II. In order to validate the estimates of RSAP predicted by the model more properly vegetation data should be collected so that distance weighting methods can be used. Moreover, the vegetation survey should be performed in such a way that plant abundance for individual taxa may be extracted.

Sugita (1994) showed by simulations that, among the important factors affecting RSAP, the basin size and vegetation structure could be more important than the others (Fig 13, Table 1). Changes in taxa number or composition did not alter the size of the RSAP. The RSAP for small ponds and lakes (50 and 250 m in radius, respectively) in North America were predicted to be 300–400 and 600–800 m, respectively. In southern Sweden, the predicted RSAP for small lakes (100 m in radius) is larger (800–1000 m). This might be due to the occurrence of infrequent patch types in the landscape. It means that, in this landscape type a larger area has to be surveyed for vegetation to achieve optimal pollen/vegetation relationships. The RSAP for moss polsters (0.5 m) was estimated at 400 m in the Open Region, on the basis of empirical pollen vegetation data. Note that the RSAP for moss polsters in the simulated landscapes in paper II was estimated at 400–500 m (Sugita, unpublished data). This implies that the simulated RSAP is validated by empirical data, and thus that the hypothetical landscapes of paper II are mimicking the cultural landscape of southern Sweden correctly. As expected, small depositional basins have a smaller RSAP than larger basins.

The simulations in Appendix IV demonstrate the importance of selecting sites randomly in the landscape to obtain reliable estimates of RSAP. The sites should adequately represent all the vegetation types characteristic of the landscape for which the RSAP is to be estimated. Also, the patchiness of the vegetation was shown to have a significant effect on the RSAP, i.e. the larger the patches are the larger the RSAP is. A similar result was obtained by Bunting *et al.* (submitted). It is explained by the fact that constant background between sites will be obtained closer to the pollen sampling point when the patches are small and evenly distributed in the landscape.

The use of the mechanistic-modelling approach in the reconstruction of past cultural landscapes

POLLSCAPE simulations have been proved to be useful in both open and semi-open vegetation (Appendix II and IV). When using simulation models, it is important to attempt validation of the results predicted

Table 1. Summary of the estimates of relevant source area of pollen (RSAP) of basins of various size in simulation and empirical studies (see also Fig 13).

vegetation type	S simulated/ E empirical	basin type	basin size (m radius)	RSAP (m radius)	location	author
Forest	S	hollows	2	50 –100	N Michigan, USA	Sugita (1994)
Forest	E	hollows	5	50	N Michigan, USA	Calcote (1995)
Forest	E	hollows	5	100	NW Wisconsin, USA	Calcote (1995)
Semi-Open	S	hollows	5	800–1000	S Sweden	Appendix II
Open	S	hollows	5	800–1000	S Sweden	Appendix II
Forest	S	lakes	50	300–400	N Michigan, USA	Sugita (1994)
Forest	S	lakes	250	600–800	N Michigan, USA	Sugita (1994)
Semi-Open	S	lakes	100	800–1000	S Sweden	Appendix II
Open	S	lakes	100	800–1000	S Sweden	Appendix II
Semi-Open	E	moss polsters	0.5	400 (?)	S Sweden	Appendix IV
Open	E	moss polsters	0.5	400	S Sweden	Appendix IV
Semi-Open simplified	S	moss polsters	0.5	200	S Sweden	Appendix IV
Open simplified	S	moss polsters	0.5	200	S Sweden	Appendix IV
Semi-Open real world map	S	moss polsters	0.5	800–1000	S Sweden	Appendix IV
Open real real world map	S	moss polsters	0.5	800–1000	S Sweden	Appendix IV
Semi-Open as in Appendix II	S	moss polsters	0.5	400 –500	S Sweden	Sugita (unpublished)
Open as in Appendix II	S	moss polsters	0.5	400–500	S Sweden	Sugita (unpublished)

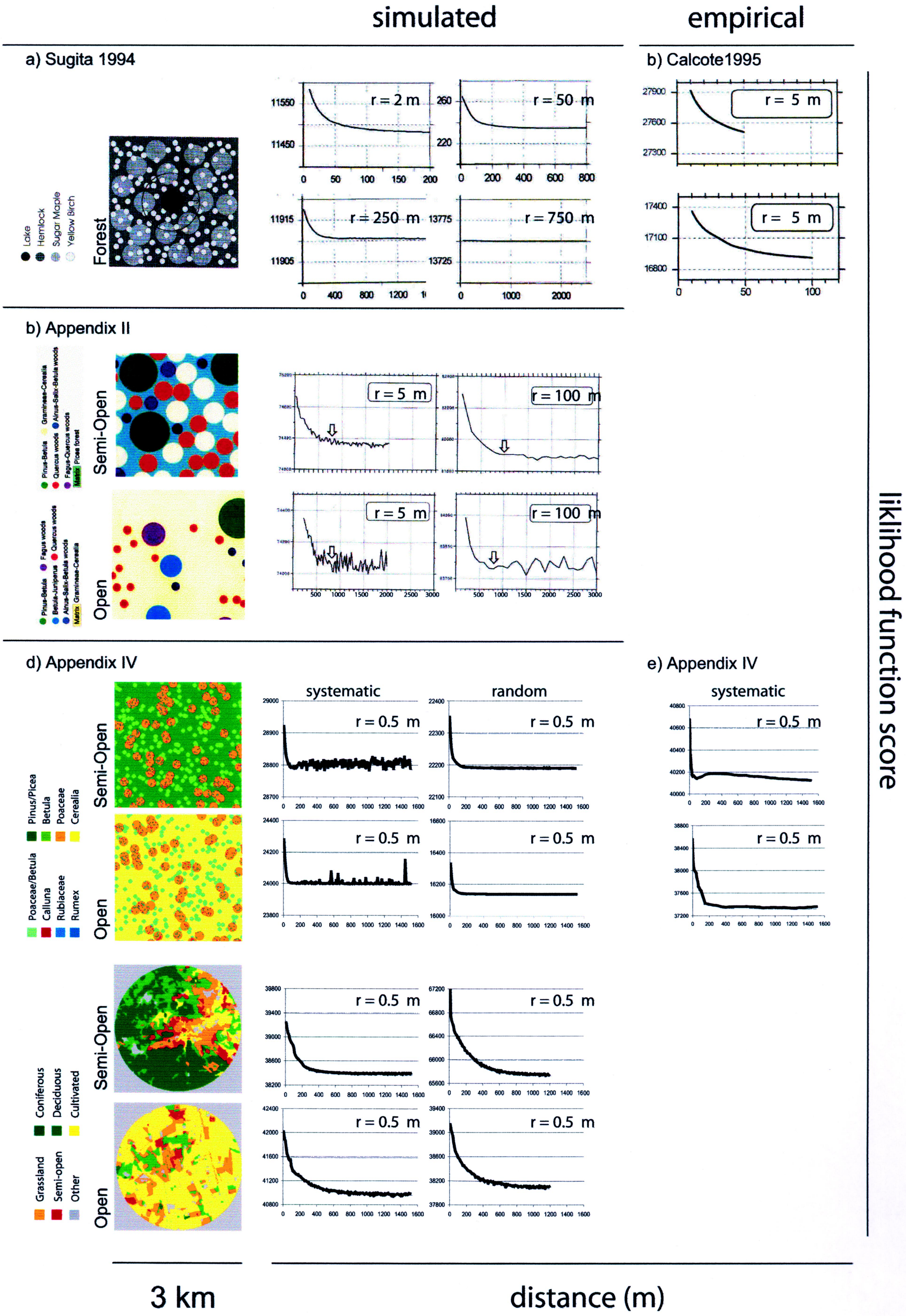

Figure 13. Summary of the simulated and empirical estimates of relevant source area of pollen (RSAP) of basins of various size. In the first column: the vegetation maps of the simulated landscapes, in the second and third the simulated and in the fourth column the empirical estimates of RSAP derived from the likelihood function scores. The radius (r) of the basin is indicated in each figure. a) simulations of four different basin size in forested vegetation in northern Michigan, USA (Sugita, 1994), b) empirical estimates of RSAP for forest hollows northern Michigan, USA (upper) and north west Wisconsin, USA (lower) (Calcote, 1995). c) simulation of hollows and small lakes in Open and Semi-Open Region of southern Sweden (Appendix II), d) simulated and e) empirical estimates of RSAP for moss polsters sites Open and Semi-Open Region of southern Sweden (Appendix IV). Se also Table 1.

by the model. Simulations were used for data-model comparison in Paper II, and to test the effect of sample design in Paper IV. It was possible to simulate pollen assemblages and obtain RSAP (likelihood function scores) in open and semi-open landscapes, and the empirical and simulated results were comparable. This suggests that simulations can be used before fieldwork planning to test various ideas about pollen-vegetation relationships in the landscape to be studied.

The problem of herb taxa being underrepresented in comparison with tree taxa, which implies that areas of open land are likely to be underestimated, has been illustrated by the empirical and simulated NAP/open-land relationship (paper II). The PPE for 25 tree and herb taxa now available make it possible to overcome the problem of the underestimation of open-land by using these PPE in further mechanistic modelling. The next step will be to estimate background pollen loading for the landscapes to be reconstructed and for the basins from which fossil pollen data are collected. Additionally, the PPE can be used in simulations using various hypothetical landscape scenarios. For example a series of scenarios of closed forest within which open-land gradually increases could provide insights into the question of how large and how many openings there need to be in order for them to be reflected in the pollen assemblage. This could be a possible way of testing the hypothesis by Vera (2000) that the forests of the Middle Holocene were more open than has previously been believed.

The challenge of reconstructing the heterogeneity of past cultural landscapes and of assessing whether changes occur at a local or regional scale (Berglund *et al.*, in press) (see introduction section) may be met by a network of sites of different sizes together with the mechanistic modelling proposed in the Landscape Reconstruction Algorithm (Sugita, 2000). By estimating the background pollen loading and subtracting it from the total pollen loading, it may be possible to reconstruct strictly local vegetation changes and distinguish these from regional ones. The local changes around several small basins will reflect the landscape heterogeneity. In this way real patterns of past deforestation and aforestation in the landscape could be followed. This approach is probably the only one at hand today to attempt answering unsolved questions on the history of cultural landscapes in Southern Sweden.

The results in paper II show that the extent of open-land in the Semi-Open Region is strongly underestimated. The generally lower NAP percentages in sites from the inland/upland region certainly indicate a more forested landscape than that of the coastland/flatland region. However, the NAP underestimates the degree of openness of inland/upland mosaic landscape as a whole, and especially of the local openness around each of the sites studied. Differences in NAP percentages between sites are difficult to interpret as long as the estimates of RSAP and background pollen for the respective basins are not available. Increases and decreases in NAP% do not necessarily reflect deforestation and aforestation, respectively. Other local and/or regional changes in the vegetation composition and structure in particular may produce similar changes. In consequence, synchronous changes between sites from a large region are easier to interpret than asynchronous changes between sites. In southern Sweden, increases in NAP around 4500, 3000 and 1000 cal. yrs. BP in most sites of both sub-regions are certainly a reflection of general deforestation in the entire area, however this is more pronounced in the coastal/flatland area around 4500 and 3000 cal. yrs. BP. Similarly, the synchronous decrease in NAP around 1500 cal. yrs. BP in the majority of sites is likely to represent a general aforestation of areas that were previously open.

However, the NAP curve from two sites in the synthesis of Berglund *et al.* (in press) illustrate the need for an interpretation tool that distinguish between local pollen loading and the background pollen loading. In Bökesjön in the coastal/flatland the NAP curve never exceeds 20%, which is much lower than for other sites within the region. Similarly, in Trummen in the inland/upland the NAP% curve exceeds 40% which is higher than other sites in the region. This may indicate that Bökesjön lies in an area of the coastland/flatland that was more forested than the parts of the sub-region were the other sites are situated. Moreover, the very low NAP percentages do not need to imply very small openings locally. As a matter of fact, Bökesjön belongs to a part of Skåne that is slightly higher in altitude, i.e. Romelåsen esker, and probably represented a kind of inland/upland area inside the coastal/flatland sub-region. This is also confirmed by archaeological and historical sources (Berglund *et al.* 1991). Similarly, lake Trummen is relatively large and has accordingly a larger RSAP than the other sites of the sub-region inland/upland. Moreover, it is located outside the town of Växjö and in an area that was exploited intensively relatively to other areas of the sub-region inland/upland. It is therefore dangerous to generalise the interpretation of a few pollen records in terms of regional changes that would be valid for large areas that may in fact been very heterogeneous in terms of landscape structure.

Finally, the first occurrence of *Plantago lanceolata* and Cerealia around 6000 cal. yrs. BP in many of the sites may well indicate larger openings than has previously been believed. The results in paper I and II show that, in a forested landscape, the occurrence of relatively large open areas may be missing from the pollen record. Only regionally, relatively widely distributed openings will be registered. Of course, these openings were characterised by many more herb taxa, but their pollen productivity and/or pollen transportability are too low for a sufficient representation in the pollen rain compared to that of *Plantago lanceolata*. As mentioned above, simulations could be used to test such hypothesis. However, it is also essential to combine pollen analysis with other proxy records of landscape openness, such as insect remains, if we are to answer the questions raised by Vera (2000), and need to reconstruct local vegetation structure in more detail.

Conclusions

A series of conclusions may be drawn from the results in this thesis, and may be grouped into general major conclusions and more specific conclusions on various aspects of landscape reconstruction.

Major conclusions

- Reliable quantitative reconstruction of past vegetation requires: a) robust models of pollen dispersal and deposition, b) good estimates of the important components of the pollen-vegetation relationship such as pollen productivity estimates and background pollen loading and c) a multiple-site approach including basins of various size. The computer simulation model POLLSCAPE developed for forest vegetation (Sugita, 1994) has been shown to be applicable in both open and semi-open vegetation. Validation of the models with empirical pollen-vegetation data is necessary if the mechanistic-modelling approach is to be used as a reliable research strategy (papers I and II).
- A better understanding of the spatial scale of pollen dispersal, and thus the reconstructed landscape is essential. Although a number of physical and biological factors affect the RSAP, the patch size distribution of the landscape mosaic is certainly one of the major factors (paper IV).

Specific conclusions

Pollen productivity estimates – PPE

- PPE for 25 plant taxa (11 herbs and 14 trees) characteristic of the ancient traditional cultural landscapes of southern Sweden are now available. A sampling design has been developed for pollen and vegetation data which enables reliable estimates of PP and RSAP. This requires data collection that allows distance-weighting of the vegetation. The importance of using a taxon-specific distance weighting method has been demonstrated (paper III).

Relevant source area of pollen – RSAP

- The RSAP in the ancient traditional cultural landscape of the Open and Semi-Open Regions in southern Sweden is ca 400 m for moss-polsters and 800–1000 m for small lakes, respectively. The relationship between basin size and RSAP, that smaller basins have a smaller RSAP is thereby confirmed (papers II and IV).
- Selecting site locations randomly and making the spatial resolution of the vegetation survey appropriate for the patch sizes of the vegetation itself are critical for obtaining a reliable RSAP (paper IV).

Traditional interpretation tools versus the mechanistic-modelling approach, what's new?

- The NAP/open-land relationship is significantly different between the Open and Semi-Open Regions, which illustrates that the cover of open-land is likely to be strongly underestimated on the basis of NAP percentages alone, in a forested/open-land mosaic landscape. This is because of the differences in background pollen loading in the small lakes in the two contrasting regions (papers II and IV).
- Provided that the past and present landscapes have a similar patch-size distribution of the landscape mosaic, the RSAP obtained from empirical data and the model simulations suggests that a quantitative reconstruction of the past cultural landscape in southern Sweden would be possible within 1000 m radius around small lakes, and 400 m radius around soil profiles (papers I, II and IV).
- The high values obtained for the PPE for *Plantago lanceolata* might suggest that the first occurrences of this taxon in fossil records may indicate larger openings in the forest than was previously assumed (paper III).
- The availability of PPE and the POLLSCAPE computer simulation model makes it possible to predict pollen assemblages in landscape scenarios and test various interpretation hypotheses (paper II and III).

Prospects

- The estimation of the background pollen loading in small lakes in the Open and Semi-Open Regions will be the next component to add to the Landscape Reconstruction Algorithm for the cultural landscape of southern Sweden. For this purpose, the PPE and pollen samples from two to three large (175 ha) lakes in each region can be used to estimate regional plant abundance. If the estimates are successfully validated with observed data, background pollen can be estimated using the mechanistic modelling approach.

- Simulations of various present and past landscape scenarios using existing PPE and fall speeds can be performed. However the existing PPE are only valid for southern Sweden. Therefore, similar studies are encouraged in other landscape types and vegetation regions for comparison. Such studies have already been initiated through the NorFA POLLANDCAL network (www.ibp.vxu.se/forskn/pollandcal).
- So far we have obtained PPE for eleven herb taxa common in both the present and past cultural landscape. Most of them are common in the fossil pollen records. There are, however, at least two other taxa, *Artemisia* and Chenopodiaceae, missing from the present data-set but often occurring abundantly in the fossil records. When enhancing the present data-sets effort should be made to incorporate more sites with these two taxa.
- Long-term palaeoecological studies are critical for various conservation issues, because the dynamics and history of plant diversity in cultural landscapes are important source of information influencing policy and management decisions (Lindbladh and Bradshaw, 1998; Odgaard, 2001). Disturbances in the vegetation, such as forest cutting and changes in land use, are important factors influencing species richness (e.g. Odgaard, 1999). The concept of plant species diversity contains two major components i.e. species richness and equitability (Kempton, 1979). Species richness is the number of species found in the sample, whereas equitability describes the number and distribution of individuals for each species. Palynological equitability is hard to estimate due to the difficulty of quantifying the number of individuals for each taxon represented in a sample. Quantitative estimates of vegetation are needed to be able to assess equitability and are, therefore, critical to the estimates of plant diversity from palynological richness (Odgaard, 2001). The present dataset will be explored within the field of pollen/floristic diversity relationship in the near future.
- Simulations can be used for different scenarios of vegetation composition and structure in the past landscape to test interpretations inferred from the fossil pollen by comparing simulated and empirical pollen assemblages, such studies are in progress within the NorFA POLLANDCAL network (www.ibp.vxu.se/forskn/pollandcal). Moreover, an improvement has been to merge simulation models with Geographical Information Systems (GIS) using the sub-program OPENLAND 3 (Eklöf *et al.*, in prep) within POLLSCAPE, enabling vegetation data from real world maps to be easily extracted. This improvement gives the possibility of using real world maps to create simulation scenarios of both present and past landscapes. In GIS soil maps can be overlaid with hydrology maps for instance and thereby show spatial patterns of suitable condition for certain vegetation e.g. *Pinus* forests on well drained sandy soils and *Alnus* on wet organic soils. For the past landscape, the hydrological conditions can be altered, and thereby the spatial pattern of vegetation. In addition, the spatial distribution of archaeological finds can be overlaid on the map and provide information about openings in the forest. Pollen dispersal and deposition can then be simulated in those landscapes and the simulated pollen assemblages can be compared to the empirical fossil ones.

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Anna Broström

Svensk sammanfattning

Den här avhandlingen är ett bidrag till utvecklingen av en metodik som gör det möjligt att med hjälp av fossila pollen, d.v.s. pollen som lagrats i mossar och sjöar, rekonstruera historiska och förhistoriska landskap så precist som möjligt vad gäller utbredning av skog, olika typer av öppen mark samt vegetationens sammansättning. Den tolkningsmetodik som för närvarande finns tillgänglig ger inte den möjligheten.

Information om hur landskapet och vegetationen förändrats över tiden är intressant ur flera aspekter. Vegetationshistoria i sig är intressant eftersom den ger ett långtidsperspektiv för ekologiska processer som t.ex. hur successionen av trädarter i en skog har skett. För arkeologer är det intressant att veta hur det sett ut runt utgrävda boplatser, d.v.s. hur stora arealer som var öppen mark och hur stora arealer som varit skogsklädda. Inom klimatforskning är det viktigt att känna till hur landytan har sett ut, t.ex. proportionerna mellan ljus gräsvegetation och mörk skogsvegetation eftersom landytans utseende har visat sig ha avgörande betydelse för värmeutbytet mellan jordytan och atmosfären.

Hittills har fossila pollen som arkiverats i sjösediment använts för att beskriva förändringar i vegetation. Men det har inte gått att säga för hur stort område förändringarna gäller eller hur stora förändringarna har varit, bara att det varit ”öppnare” eller mer ”slutet” i väldigt grova termer. Om man ska rekonstruera det forna kulturlandskapet noggrant med avseende på expansion av jordbruk, betesdrift och skogsnäring är detta är inte tillräckligt eftersom det i det sammanhanget är nödvändigt att veta arealen av de olika markslagen.

Första steget i metodutvecklingen är att förstå sambandet mellan nedfallna pollen och vegetationen runtomkring så korrekt som möjligt. Detta är inte helt okomplicerat, andelen av olika pollentyper i ett prov kan inte direkt översättas i andel avspeglad vegetation. Dels producerar olika växtarter olika mycket pollen i förhållande till varandra, dels transporteras olika pollentyper olika långt p. g. a. storlek, form och tyngd. Dessutom har studier visat att sjöns storlek har betydelse för hur stort upptagningsområdet för deponerade pollen är. Ju större sjö desto större landskapsområde avspeglas. Upptagningsområdets storlek påverkas också av vegetationens struktur, d.v.s. hur de olika växtarterna är fördelade i landskapet. Ett teoretiskt begrepp är det ”relevanta källområdet för pollen” som definieras som det område med en viss radie runt pollenprovet där sambandet mellan nedfallna pollen och vegetation är som bäst. Om man karterar vegetation utanför detta område så kommer inte korrelationen mellan pollenprov och vegetation att förbättras. Det beror på att ett pollenprov dels består av pollen som kommer från det relevanta källområdet och dels av s.k. bakgrundspollen, som kommer utanför detta område.

Målsättningen med denna avhandling har varit att:

1) Undersöka sambandet mellan nedfallna pollen och vegetationens sammansättning i det gamla traditionella kulturlandskapet i södra Sverige för att sedan kunna dra slutsatser om arealfördelningen mellan öppen mark och skog, i termer om odlad mark, slåtterängar, betesmarker, ädellövskog, lövskog och barrskog i förhistoriska och historiska landskap.
2) Identifiera och definiera i hur stort område av landskapet pollenprover från små sjöar och mossprover i gräsmark representerar.
3) Uppskatta relativ pollenproduktivitet för de växtgrupper som är karakteristiska för det gamla traditionella kulturlandskapet i södra Sverige. Detta har krävt utveckling av en optimal design för provtagningsmetodik och vegetationskartering för insamling av relevanta pollen- och vegetationsdata.
4) Undersöka möjligheter och begränsningar i att använda datorsimuleringsmodeller för att rekonstruera det forna landskapet med hjälp av pollen.

Fältstudier har bedrivits i södra Sverige och undersökningsområdet kan med avseende på landskapet delas upp dels i en öppen region (sydvästra Skåne) där landskapet domineras av odlad och betad mark med spridda skogsdungar, (trädtäckningsgrad under ca 50%), dels i en halv-öppen region (Norra Skåne, Blekinge, Halland, Småland och Östergötland) som domineras av skogsvegetation med spridda öppningar av odlad och betad mark (trädtäckningsgraden mellan 50 och 90%).

Hur stort område runt en liten sjö är rekonstruerbart?

För att ta reda på hur stort område som är möjligt att rekonstruera runt en liten sjö (1–20 ha) d.v.s. i hur stor radie runt sjön där korrelationen mellan pollenprovet och omkringliggande vegetation är god provtogs 22 småsjöar mestadels i den halv-öppna regionen. Ett pollenprov togs i ytsedimentet i mitten av sjön, vegetationen karterades med hjälp av flygfoton i en 500 och 1000 m radie runt sjön och delades in i sex klasser, odlad mark, öppen gräsmark, halvöppen gräsmark, lövskog, barrskog och övrig mark (mestadels ej pollenproducerande). Statistiska analyser visade att det fanns en god korrelation mellan pollentyper såsom sädesslags pollen (Cerealia), gräspollen (Poaceae) och älgörtspollen (*Filipendula*) och vegetationsklassen odlad mark både inom 500 och 1000 m radien. Vidare fanns en svag korrelation mellan gräs- och älgörtspollen och vegetationsklassen öppen mark inom 1000 m, samt en svag korrelation mellan bok (*Fagus*) och ek (*Quercus*) pollen och vegetationsklassen lövskog inom 1000 m radien. Dock fanns det ingen korrelation mellan tall (*Pinus*), gran (*Picea*) respektive björk (*Betula*) och al (*Alnus*) pollen och vegetationsklasserna barrskog och lövskog. Detta betyder att 1000 m radie runt sjön är en bra skala när vegetationsklasser typiska för kulturlandskapet såsom odlad mark, öppen mark och ädellövskog ska rekonstrueras. Däremot är den för liten för rekonstruktion av barrskogs- och trivial lövskogsvegetation som innehåller arter som producerar mycket pollen som transporteras långt. Även sjöar med stor andel öppen mark inom 1000 m radien innehöll stor procent av tall- och björkpollen vilket tyder på att de är långtransporterade bakgrundspollen.

Kan dator simuleringar av pollen spridning och deposition även användas i öppen och halvöppen vegetation?

Det datorprogram paket, POLLSCAPE, som finns tillgängligt för simulering av pollenspridning och deponering är utvecklat endast för skogsvegetation. Dessutom är det baserat på förenklande antagande såsom att pollenspriding sker enbart över trädkronorna, att landskapet är platt, samt att det inte finns någon dominerande vindriktning. En målsättning var att se om sådana simuleringar fungerade för södra Sveriges kulturlandskap som karakteriseras av både öppen och beskogad mark, och i såfall om de simulerade resultaten av pollen och vegetationssambandet överensstämde med resultatet från fältstudier.

I POLLSCAPE skapades två mycket förenklade landskap som liknar de i den öppna regionen respektive den halv-öppna regionen och små sjöar (100 m radie) placerades ut. Sedan simulerades pollenspridning och deposition i sjöarna. De simulerade pollenproverna visade sig stämma relativt väl överens med verkliga data. Det relevanta källområdet för pollen för de simulerade sjöarna beräknades till 800–1000 m radie. Simulerade och verkliga pollen och vegetationsdata jämfördes även med avseende på andelen örtpollen och andelen öppen mark inom en 1000 m radie runt sjöar både i den öppna regionen och den halv-öppna regionen. Både simuleringar och verkliga data visade att i den öppna regionen motsvarade andelen örtpollen andelen öppen mark inom 1000 m radien medan andelen örtpollen aldrig översteg 20% i den halv öppna regionen trots att andelen öppen mark inom 1000 m radien översteg 80% runt vissa sjöar. Anledningen är att sammansättningen i bakgrundpollen (d.v.s. pollen som härstammar utanför 1000 m radien runt pollenprovet) skiljer sig mellan de två regionerna. I den öppna regionen består bakgrundspollen till stor del av örtpollen och förstärker därför sambandet mellan örtpollen och öppen mark inom 1000 m radien. Däremot i den halv-öppna regionen domineras bakgrundspollen av trädpollen som gör att det inte finns något samband mellan andelen örtpollen och andelen öppen mark inom 1000 m radien. Det betyder att arealen öppenmark underskattas i ett halv-öppet landskap som i sin helhet domineras av skogsvegetation. Slutsatsen av dessa resultat är att simuleringsprogrammen kan användas även i öppna och halv-öppna landskap och att de tillsammans med insamlade data kan tillföra insikter om sambandet mellan pollenprover och vegetation.

Uppskattning av relativ pollenproduktivitet hos växtarter karakteristiska för kulturlandskapet

De två viktigaste orsakerna till att procentandelen pollen i ett prov inte direkt kan översättas i procentandel av omkringliggande vegetation är skillnad i pollenproduktivitet och spridningsförmåga. För att kunna räkna ut hur stor andel av ett pollenprov som består av bakgrundspollen, d.v.s. pollen som producerats utanför det relevanta källområdet för pollen, krävs att man känner till hur stor pollenproduktiviteten är hos de olika växtarterna relativt varandra. Dessutom är pollenproduktivitet nödvändiga indata till datorsimuleringar.

Uppskattning av pollenproduktivitet har räknats fram för 25 växtarter (14 träd och 11 örter) karakteristiska för kulturlandskapet i södra Sverige. Pollenprover samlades in från mosstussar på marken och korrelerades med omkringliggande vegetation med avseende på arternas täckningsgrad. Mossa fungerar som en naturlig pollenfälla och har fördelen att man kan samla pollenprover i den vegetationstyp man är intresserad av och inte enbart är hänvisad till sjöar eller mossar.

De relativa pollenproduktivitetsvärdena för trädarterna baserades på ett dataset där vegetationen karterats i en 10 × 10 m och en 100 × 100 m fyrkant runt pollenprovet. Det var ingen optimal provtagningsmetod eftersom vegetationen inte kunde distansvägas d.v.s. att träd som står närmare provtagningspunkten får större vikt än träd som står längre ifrån. Trots detta visade sig de erhållna värdena vara jämförbara med tidigare studier gjorda i Danmark.

De relativa pollenproduktivitetsvärdena för örter baserades däremot på ett dataset där datainsamlingen planerades så att distansvägning av de olika växtarterna var möjlig. Pollenprovet togs i mosstussar inom en cirkel med 0,5 m radie och vegetationen karterades i detalj inom koncentriska ringar runt pollenprovet så att distansvägning av växterna kunde utföras. Med några få undantag (halvgräs och korgblommiga växter) producerade örterna mer pollen än gräsarterna

(Poaceae). De växter som producerade mest pollen var i fallande ordning svartkämpar (*Plantago lanceolata*), ängssyra (*Rumex acetosa*) och ljung (*Calluna vulgaris*). Jämfört med gräs (Poaceae) producerar de vanligaste trädarterna björk, ek, tall och bok sex till åtta gånger så mycket pollen per ytenhet.

Det relevanta källområdet för pollen i mosstuss prover

Hur stort område som vegetationskarterades (1500 m radie) runtom mosstuss proverna var godtyckligt bestämt och väl tilltaget. För att inför framtida provtagning veta vad som egentligen är det optimala provtagningsområdet där pollen- och vegetationskorrelationen inte förbättras beräknades det relevanta källområdet för pollen i mosstussar. I den öppna regionen var det relevanta källområdet för pollen i mosstussar ca 400 m radie runt mossprovet. I den halv-öppna regionen var det relevanta källområdet för pollen mer svårbestämt. Detta beror på att det krävs slumpmässig provtagning överallt i landskapet för att beräkningarna ska bli tillförlitliga. I denna undersökning skedde pollenprovtagningen endast i gräsmarker, även i den halv-öppna regionen eftersom huvudsyftet var att samla in data för örters pollenproduktivitet. I den halv-öppna regionen hade provtagningspunkter därför behövt läggas även i skogsvegetation. I den öppna regionen kan provtagningen däremot anses vara slumpmässig, eftersom landskapet här domineras av öppen mark.

Datorsimuleringar med både systematiskt och slumpmässigt utplacerade provtagningspunkter bekräftade detta påstående. Simuleringar med slumpmässiga provtagningspunkter gav samma radie för det relevanta källområde för pollen både i det öppna och halv-öppna landskapet, vilket skulle tyda på att radien för det relevanta källområde för pollen i mosstussar är ca 400 m även i det halv-öppna landskapet.

Slutsatser

- I södra Sverige har det relevanta källområdet för pollen för små sjöar en radie av 800–1000 m. För mosstussprover i både öppna och halv-öppna landskap har det relevanta källområdet för pollen en radie på ca 400 m. För att få fram tillförlitliga beräkningar av relevanta källområdet för pollen krävs slumpmässig provtagning.
- Att sambandet mellan andelen örtpollen och andelen öppen mark skiljer sig mellan den öppna och halv-öppna regionen har visats både i fältstudier och datorsimuleringar. I sjöar i det halv-öppna landskapet är örtpollen underrepresenterade i förhållande till omkringliggande öppen mark. Uppskattningen av öppen mark genom fossila örtpollen har hittills troligtvis underskattas kraftigt speciellt i landskap som består av en mosaik av skog och öppen mark.
- Datorsimuleringar i POLLSCAPE har visat sig vara användbara även för öppen och halv-öppen vegetation, trots att det utvecklats för skogsvegetation och bygger på kraftiga förenklingar. Det ska dock understrykas att modellerna bör jämföras med verkliga pollen- och vegetations data.
- I och med denna undersökning finns nu pollenproduktivitetsvärden för 25 växtarter (14 träd och 11örter) som är karakteristiska för det traditionella kultur landskapet i södra Sverige. De kan användas för att beräkna tillförseln av bakgrundspollen i pollenprover i små sjöar och som indata i datorsimuleringar.

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