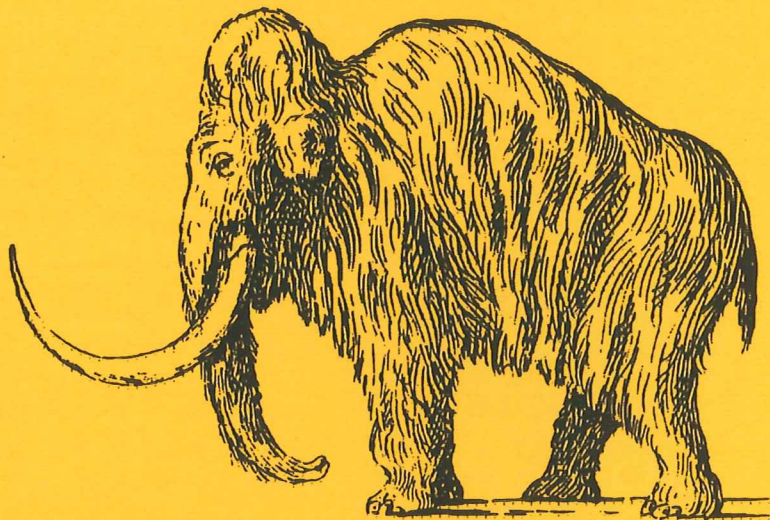


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The openness of the present-day landscape reflected in pollen assemblages from surface sediments in lakes - a first step towards a quantitative approach for the reconstruction of ancient cultural landscapes in south Sweden

Anna Broström

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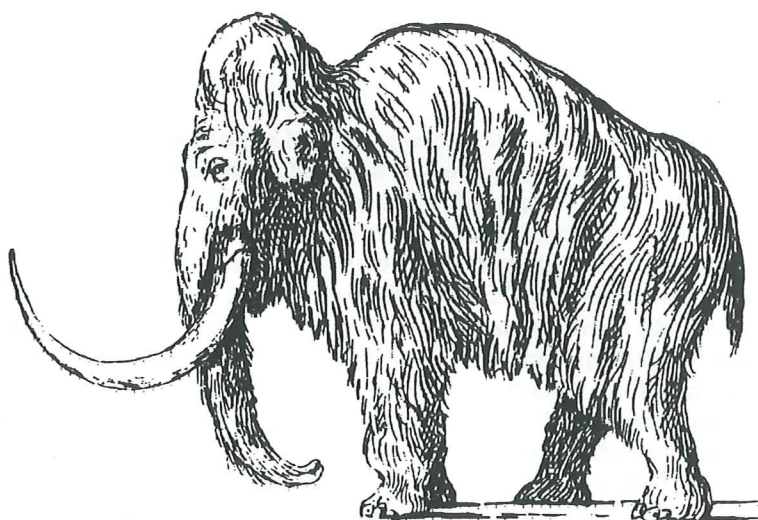
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Kvartärgeologi



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Summary

The aim of this study was to analyse how the composition and in particular the openness of the present-day landscape is reflected in pollen assemblages from surface sediment in lakes. The study is a continuation of an earlier pilot study including thirteen sites and a first step in an attempt to find a method of quantifying ancient cultural landscape in terms of surface areas from fossil pollen records using the modern analogue approach. Surface sediments from twenty two small lakes (0.5-20 ha) located mainly in the forest region of south Sweden were collected and analysed for pollen. The composition of the landscape surrounding the lakes within a 1000 m and 500 m radius was mapped using aerial photos. Despite the large variation in openness of the landscape mapped the variation of the relationship AP/NAP was low. This contrasts with the results of the pilot study in which the sites were selected mainly in the agricultural region of south Sweden and the variation of the relationship AP/NAP was higher. The pollen and landscape data were analysed using numerical ordination techniques, PCA and RDA. Despite the fact that the compositional gradient of the pollen assemblages was small it was possible to detect a pattern of variation and to analyse to what extent landscape data could explain the pollen data. The two dominant pollen taxa *Betula* and *Pinus* are uncorrelated to relevant landscape units such as coniferous forest and deciduous forest. This implies that these taxa are primarily of regional origin and can not be directly related to the local landscape around the lakes. Gramineae, Cerealia, *Filipendula* and *Salix* are positively correlated to cultivated land within both radius. *Quercus* and *Fagus* have a positive correlation with deciduous forest within 1000 m radius but not within 500 m radius. Therefore, it is suggested that the landscape units cultivated land and deciduous forest within 1000 m radius are reasonably well reflected in the pollen assemblages and that this radius is a good approximation of the relevant pollen source area of such sites. An important conclusion of this work is also that the performance of the modern analogue approach is improved if the modern data set is collected in the same vegetation region as the fossil pollen record used for reconstruction of past landscapes.

Introduction

The reliability of pollen analysis as a tool in the reconstruction of past vegetation depends on the precise understanding of how vegetation composition is reflected in pollen assemblages (von Post 1916). One possible approach to evaluate this reliability is to study the relationship between recent vegetation and modern pollen assemblages and to use the so-called modern analogue approach (Overpeck *et al.* 1985) to reconstruct past vegetation and landscape composition. For this purpose, different kinds of pollen deposit can be studied, e.g pollen traps (Ritchie and Lichti Federovich 1967, Andersen 1974, Hicks and Hyvärinen 1986),

moss polsters (Andersen 1970; Hicks 1977; Bradshaw and Webb 1985; Gaillard *et al.* 1992, 1994) and surface sediments in lakes (Davis 1963; Lichti-Federovich and Ritchie 1968; Prentice 1978). Empirical and modelling studies have shown that the pollen assemblage in a deposit depends on the pollen source area. This is in turn related to the kind of deposit e.g trap, moss polster, or lake sediment and the properties of the depositional environment of which basin size is often the most important (Prentice 1985 and Sugita 1994). The composition of the pollen assemblage also depends on the pollen production and dispersal of each individual taxon involved (Andersen 1970, Davis 1967, Prentice 1985). Each pollen taxon has

its own pollen-source area because of individual dispersal properties (Bradshaw and Webb 1985). In his simulation models, Sugita (1994, in press) defined the "relevant pollen source area" of a site as the area within which differences in plant abundance are recorded as variance in pollen assemblages among sites super imposed on a constant pollen background. Beyond this "relevant area", the pollen becomes nearly constant in all sites within the same vegetation region. Sugita (1994, in press) also showed by model simulations that the "relevant pollen source area" is the area of vegetation from which, on average, only 30-45% of the total pollen arriving at a given site is derived. This figure is valid for the site sizes and the taxa considered in the model simulation and is not necessarily valid for other circumstances. For the forest composition considered in Sugita's (1994) simulations, the "relevant pollen source area" is 50- 100 m in radius for a forest hollow, 300- 400 m for a small pond (50 m in radius) and, 600- 800 m radius for a medium size lake (250 m in radius). Therefore, when reconstructing past vegetation it is important to have the correct size of site (hollow, pond or lake) for the particular purpose of the study. In a small lake (1-20 ha) the vegetation of a more restricted pollen-source area is reflected. This also means that the mosaic of vegetation might be reflected in more detail (Gaillard *et al.* in press, Sugita *et al.* in press). Both empirical and modelling studies have considered primarily the composition of forest vegetation in relation to pollen assemblage (Andersen 1970; Davis 1963; Bradshaw and Webb 1985; Jackson 1990,1991; Prentice 1985; Sugita 1994).

The relationship between pollen assemblages and different degrees of landscape openness has not been studied systematically until recently (Hicks 1992, in press; Gaillard *et al.* in press). In a pilot study Gaillard *et al.* (in press) analysed the relationships between pollen assemblages in surface sediments from lakes and various degrees of openness in the landscape. Thirteen small lakes (1-20 ha) in modern analogues of ancient cultural landscapes were studied. The vegetational composition in the pollen-source area ranged from completely forested to completely open. The degree of detail in the landscape mapping was found to be weakly reflected in the pollen composition. However, the pollen data showed significant gradients of variation, in particular arboreal pollen (AP) versus non-arboreal (NAP), and pastoral indicators versus arable indicators. The best relationship were found between AP and NAP with dense forest and open land. The size of this pilote training set is small, and sites where the pollen source area has 30 to 60% tree cover are not represented. Therefore, the aim of this study was to enlarge the data set of Gaillard *et al.* (in press) and to complete the data set with semi-open landscape units, so as to be able

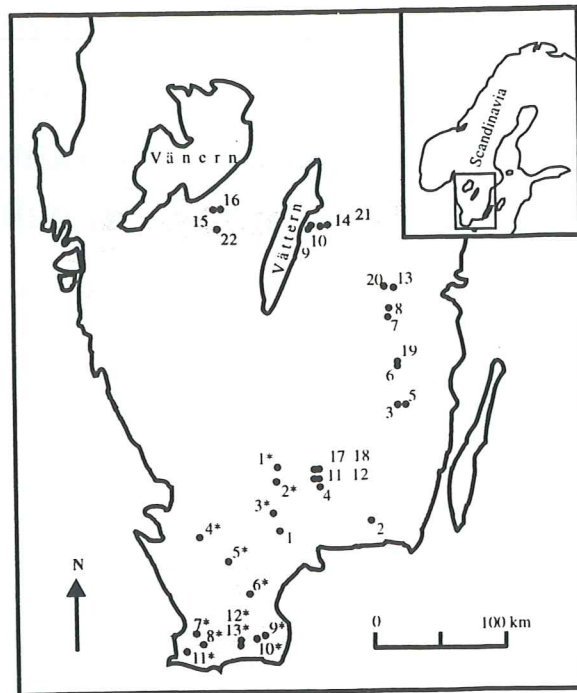


Fig. 1. Location of the 22 lakes (1-22) included in the study and the 13 lakes (1*-13*) included in the pilot study by Gaillard *et al.* (in press). The grey and white areas represent agricultural and forest region, respectively (from Agriculture, The National Atlas of Sweden 1992).

to better identify the correlations between pollen taxa and landscape units. This work can be seen as a first step towards the quantification of landscape units on the basis of pollen composition of lake sediments and hence a contribution towards a better understanding and interpretation of pollen diagrams at this landscape scale.

Site selection and description

The selection of sampling sites followed three major criteria. Firstly, the lake had to be located in a landscape characterised by a relatively old-fashioned traditional type of land-use. It is essential in a study of modern analogues that the present landscape resembles as closely as possible the landscapes that will be reconstructed using the modern analogue approach (Gaillard *et al.*, in press). Secondly, the lake had to be rather small, because the major aim of this study was to explore the quantitative relationships between pollen and open land, and because empirical and modelling studies have shown that local opening of the landscape will be best registered in a small lake, 200 ha and preferably 1-20 ha (Sugita, in press). The first criterion, however, already severely restricts the choice of sites. Therefore when no small lakes were available, small sheltered bays of larger lakes were selected. Thirdly, the landscape surrounding

Tab. 1. Location (longitude and latitude) and characteristics of the 22 lakes included in the present study. The hydrological catchment area were roughly estimated from topographical maps at a scale of 1: 50 000.

Nr	Lake name	Lake surface (ha)	Hydro logical catchment area (ha)	Longitude	Latitude
1	Lommagylet	0.5	5	14° 23' W	56° 20' N
2	Långasjögöl	2.0	20	15° 22' W	56° 20' N
3	Älgasjön	19.2	500	15° 41' W	57° 02' N
4	Pöl i Lönsbygden	1.0	none	14° 42' W	56° 32' N
5	Göljhultsgölen	1.8	none	15° 44' W	57° 02' N
6	Svartgöl	2.2	none	16° 15' W	57° 21' N
7	Lillesjön	7.9	none	15° 52' W	57° 46' N
8	Egegölen	0.1	none	15° 51' W	57° 48' N
9	Sättradammen	6.2	100	14° 49' W	58° 16' N
10	Pöl vid Sanden	1.3	none	14° 49' W	58° 16' N
11	Svartsjön	15.1	bay	14° 41' W	56° 35' N
12	Toftagöl	1.0	none	14° 40' W	56° 35' N
13	Knoken	2.0	200	15° 54' W	57° 54' N
14	Bursjön	2.0	none	14° 54' W	58° 17' N
15	Stjälkholmasjön	1.1	none	13° 34' W	58° 27' N
16	Marielundssjön	1.3	30	13° 35' W	58° 27' N
17	Bjurkärre inre	3.9	bay	14° 40' W	56° 38' N
18	Bjurkärre yttre	2.4	bay	14° 40' W	56° 38' N
19	Malghultsgölen	4.1	100	16° 14' W	57° 24' N
20	Pöl vid Åsunden	0.2	none	15° 51' W	57° 54' N
21	Ljungtorpasjön	1.5	none	14° 55' W	58° 17' N
22	Barnasjön	0.2	none	13° 36' W	58° 20' N

the lakes (within a 1000 m radius) had to vary from site to site, in order to obtain a gradient of open land versus forest in the data set. In order to complement the earlier pilot study of Gaillard *et al.* (in press) most sites were selected in semi-open landscapes.

Twenty two lakes were selected in southern Sweden following the above criteria (Fig. 1). U. Emanuelsson helped in the selection of areas characterised by traditional, old fashioned landscape management. The size of the lakes varies between 0.5 ha and 19.2 ha (Table 1). The area investigated can be subdivided into two landscape regions, a forest landscape and an agricultural landscape (Fig. 1). Fifteen lakes occur in the forest region and seven in the agricultural region. Of the thirteen sites studied by Gaillard *et al.* (in press), five are located in the forest region and eight in the agricultural region.

Methods

Pollen data

The surface sediments used for the pollen analysis were collected in the middle of each lake or small bay (one sample per lake), with a surface sediment sampler (Aaby and Digerfeldt 1986). The uppermost 2 cm of sediment were sampled and were assumed to represent not more than the last ten years of sediment accumulation (Gaillard *et al.* in press). The pollen samples were prepared following conventional methods (Berglund and Ralska-Jasiewiczowa 1986). In each sample, 1000-1500 pollen and spores were counted and identified using the pollen keys of Moore *et al.* (1991) and Punt *et al.* (1976-1995). The pollen taxonomy and nomenclature follow those adopted

by the European Pollen Database (Gaillard *et al.*, unpublished document), i.e the pollen taxonomy is mainly according to the keys mentioned above and the nomenclature follows Flora Europaea (Tutin *et al.* 1964-1980).

Landscape data

Colour InfraRed (CIR) aerial photos were used for mapping of the landscape around each lake. CIR aerial photos have the potential to provide great detail in vegetation mapping, provided the analyst

has a good botanical knowledge and interpretative experience (Ihse 1978; Ihse *et al.* 1993). As emphasized above modelling pollen-source areas in forested regions has shown that pollen records from small sites (50-250 m radius) will record differences of vegetation between sites for an area of 300-800 m radius around the site (Sugita 1994, in press). Because modelling of pollen-source areas in semi-open and open landscapes has not yet been attempted, we are restricted to the choice of arbitrary areas for vegetation mapping, i.e 500 m and 1000 m radius, following the methodology adopted by Gaillard *et al.* (in press). It was hoped

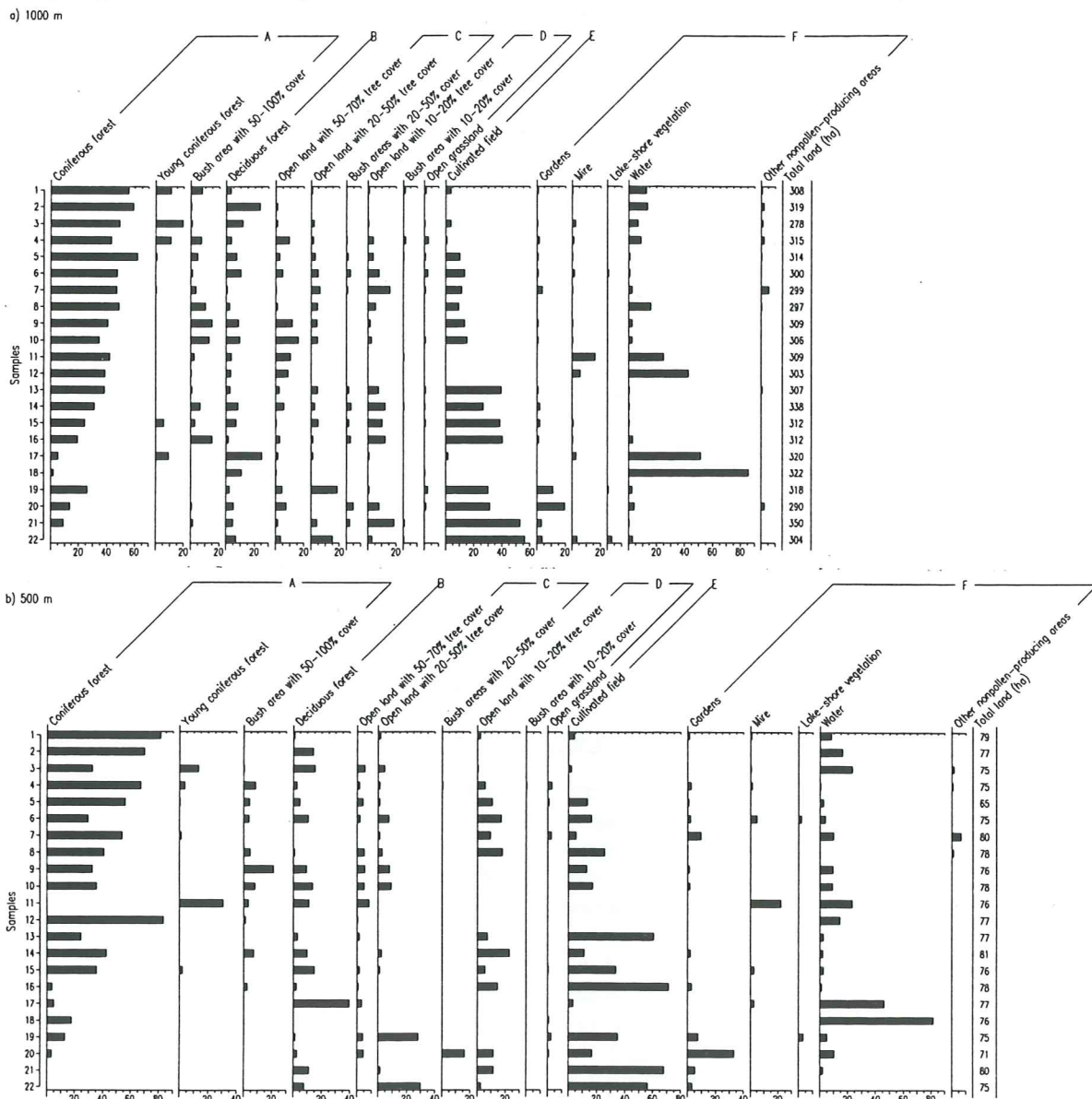


Fig. 2. Landscape data. The 16 landscape units identified and mapped from aerial photos. Units expressed as percentages of total land mapped (to the right) a) 3 100 m² within 1000 m radius and b) 780 m² within 500 m radius. The letter A-F denotes the new broader landscape units used in the numerical analysis (see text for further explanations) A) Coniferous forest 50% tree cover, B) Deciduous forest 70%, C) Semi-open land 20-70% tree cover, D) Open land 0-20% tree cover, E) Cultivated land, and F) Others.

that one of these areas would be close to the size of the relevant pollen-source areas of the lake sites. For mapping, the vegetation within the 1000 m radius area was classified into 16 units (Fig. 2). These units are a simplification of those used in the pilot study of Gaillard *et al.* (in press) and were chosen to explore more specifically the relationships between pollen and landscape units with different degrees of openness.

The CIR aerial photos at a scale of 1:30 000 were interpreted in stereo pairs with an Aviopret Zeiss stereoscope with a zoom magnification of 2-15 times. The stereo pairs provide a three-dimensional picture of the landscape, which helps to identify the different vegetation units. These units were delineated and classified by codes on transparencies. The minimum area interpreted was 0.25 ha. Before measuring the area of each landscape unit with a planimeter (King 1971), the interpretation transparencies were enlarged to a scale of 1:10 000.

Numerical analysis

Because of the complexity of the data set (72 taxa, 16 landscape variables in 22 samples) it is necessary to use numerical techniques to explore the pollen/landscape relationships and to identify correlations between modern pollen spectra and quantitative landscape variables.

Principal Component Analysis- PCA

The variation in the overall pollen data set and correlations between pollen taxa can be explored with ordination techniques. Because the compositional gradient in the pollen data is rather small (2 standard deviation units; SD), the linear ordination technique of PCA was used (Ter Braak 1987a). PCA redefines the original variables, in this case the pollen taxa, as linear combinations of taxa, concentrates the major patterns of variation within the pollen data into the first few principal components, and relegates the less coherent patterns and "noise" in the pollen data to later components (Birks 1995). In PCA, the explanatory variables are theoretical variables estimated from the abundance of taxa in the set of samples collected (Ter Braak 1987a). These variables are defined as eigenvalues (λ) and can also be expressed as the percentage of variance explained in the data set. The PCA analysis is illustrated by a co-ordinate system where the explanatory variables are represented as principal component axes (λ_n). The first axis (λ_I) explains the variation in the pollen data best. The second and later axes also explain the variation in the pollen data but with the constraint that these axes are uncorrelated with the previous PC axes. The first (λ_I) and second (λ_{II}) PC axes explain the main part of the variation found in the

data. The third (λ_{III}) and fourth (λ_{IV}) axes may also be considered, although they never explain as much variation as the two first axes.

In this co-ordinate system, the position of a pollen taxon is illustrated by an arrow starting at the origin and ending at the position (or score) of the particular pollen taxon. The position of one pollen taxon in the ordination is determined by the variation of its abundance in the samples and the importance of that variation for the overall variation in the total pollen data set. From its position in the co-ordinate system, it can be concluded how important this particular pollen taxon is for the variation in the total data set and how the taxon is correlated to other taxa. The pollen taxa best fitted to the same axis, and with arrows pointing in the same direction, are said to be positively correlated. If their arrows are pointing in opposite directions they are negatively correlated. Pollen taxa fitted to two different axes are often uncorrelated (Ter Braak 1987a).

The position of the samples, i.e pollen assemblages, can also be plotted in the co-ordinate system. Knowing the landscape characteristics of each site where the samples were collected, an "environmental dimension" can be added indirectly to the interpretation of the plot. For instance, if the site has a large percentage of open land, and the sample is plotted close to non-arboreal pollen (NAP) taxa, this might indicate that there is a positive relationship between open land and NAP taxa.

Redundancy Analysis RDA

Redundancy analysis is the canonical or constrained form of PCA, which implies that both pollen data and landscape data can be analysed together. The pollen taxa are the response variables. They are constrained by the predictor or explanatory variables, in this case the landscape variables. The importance of both pollen and landscape data for the overall variation in the data set can be explored. Also, correlations either between the constrained pollen taxa or between pollen taxa and landscape units can be analysed. Both pollen and landscape data are illustrated by arrows. The rules used for the interpretation of PCA plots are valid in RDA plots.

Within the RDA analysis, a forward selection procedure was performed (Ter Braak 1990). This is a technique used to select a minimal set of landscape variables that explains the variation in the pollen data almost as well as when all the landscape variables are used. Further, to find out whether each of these variables are statistically significantly unrestrained the Monte Carlo permutation (MCP) tests were used (Ter Braak 1990). MCP test replaces conventional F or Student t-tests in multivariate multiple regression such as RDA. The result of the MCP test is a p-value that

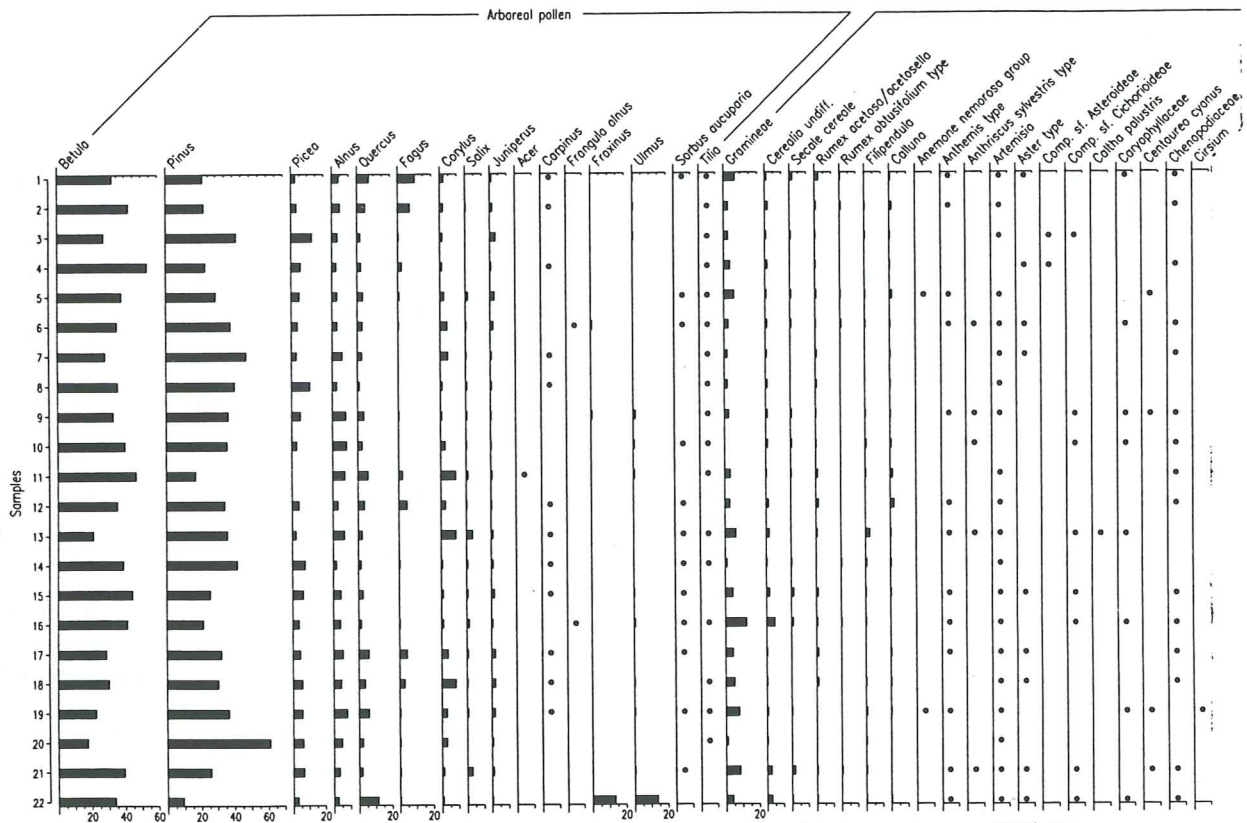


Fig. 3. Pollen diagram of all taxa counted in the 22 samples expressed as percentages of terrestrial sum (to the right). Taxa with low percentages (1%) are represented by a dot, indicating presence. Local taxa; Pteridophytes, Telmatophytes, Limnophytes and Sphagnum were excluded from the terrestrial sum. The samples are ordered according to an approximative landscape gradient from high to low percentage of tree cover within the assumed pollen-source area

should be <0.05 if the selected landscape variable is statistically significant in the overall RDA model. The shortcomings of the MCP tests are the same as in F or Student t-tests. When applied stepwise, the test does not control in any way for the overall size of the test. In practical terms this means that too many variables will be judged significant (Ter Braak 1987a, 1990).

Inverse RDA

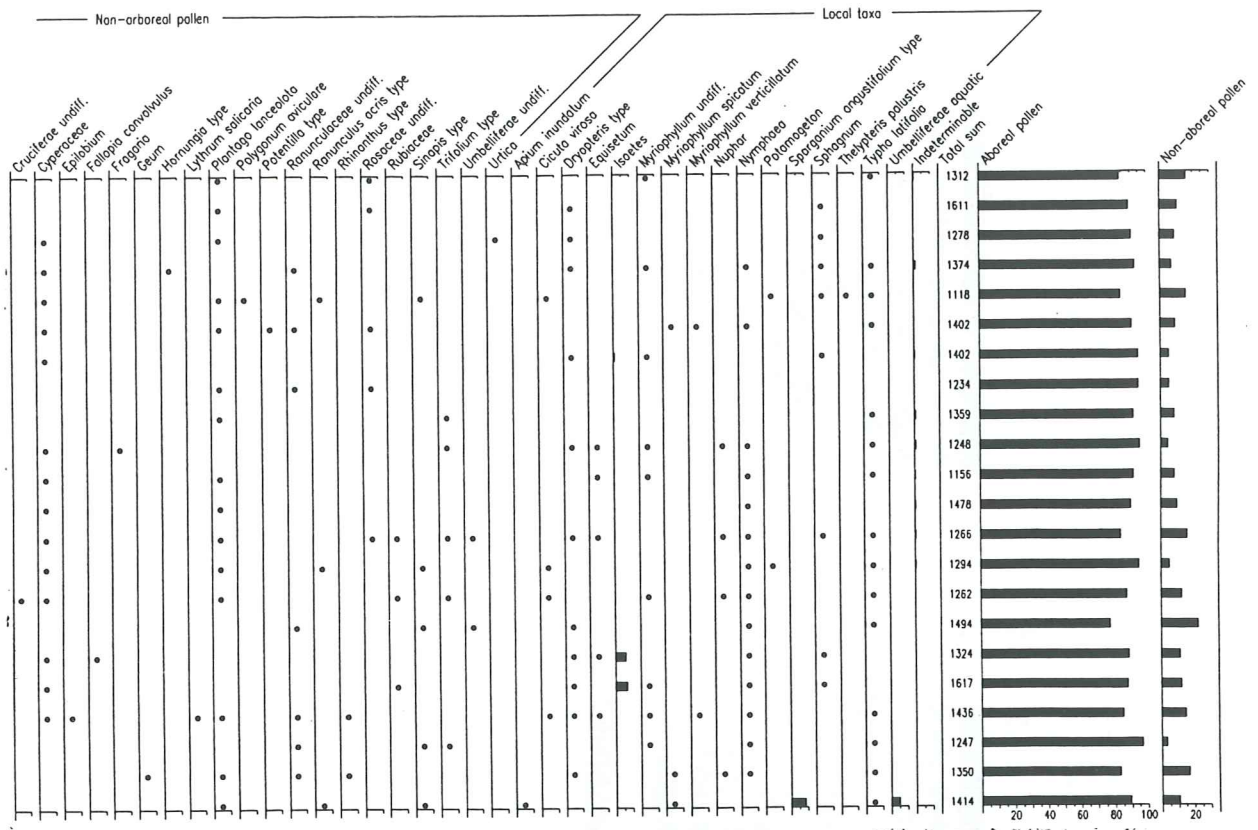
Inverse RDA is an unconventional form of RDA that was used by Odgaard (1992) and Anderson *et al.* (1996). In this analysis, the pollen taxa are defined as the predictor variables and the landscape data serve as the response variables. Forward selection selects a few pollen taxa that explain the variation in the landscape data almost as well as the full set of pollen taxa.

All the ordination analyses were implemented by the CANOCO program version 3.12 (Ter Braak 1987a, 1990). Before each type of analysis, the compositional gradient length of the data set was estimated. This was done by using the unimodal version of PCA and RDA namely detrended correspondence analysis, DCA and detrended canoni-

cal correspondence DCCA, respectively. In all cases the compositional gradient was 2 SD (standard deviations) which means that the data set has a mainly linear structure and that linear-based analyses are appropriate.

In the data set, the occurrences of pollen taxa are expressed as percentages of the total terrestrial pollen types counted in each sample, and the landscape units are expressed in percentages of the total area investigated. To avoid taxa or landscape units with large percentages dominating the analysis, a logarithmic transformation was performed ($\ln(a + c)$, where $a=1$ and $c=1$; Ter Braak 1987a). Moreover, double centering was used, which is appropriate for the analysis of closed percentages data with linear methods (Ter Braak 1987b)

Before performing the numerical analyses, pteridophytes, telmatophytes, limnophytes and bryophytes were excluded from the pollen and spores sum. This is because these taxa are likely to be of very local origin, and are not relevant to the sort of correlation we are investigating in this study, i.e. the relationship between terrestrial pollen and landscape units such as forested and open land.



Results

Pollen data

All 72 pollen and spores taxa counted are presented in Figure 3. The sample sites are classified into the four major groups based on the extent of forest cover, the sites characterised by high forest cover being placed at the top of the diagram, and those with low forest cover at the bottom of the diagram. In spite of the significant gradient of forest cover represented by the sites studied, it is striking that the non-arboreal pollen (NAP)/arboreal pollen (AP) relationship shows little variation from site to site. The NAP values do not exceed 20 %, and they shows little variation between 10% and 20 %. *Betula* and *Pinus* pollen are dominant in all samples. Further more, 14 pollen taxa are relatively common i.e they occur in almost all samples. These are *Alnus*, *Salix*, *Quercus*, *Fagus*, *Picea*, *Corylus*, Gramineae, *Juniperus*, *Calluna*, *Rumex acetosa/acetosella* type, *Anthemis* type, *Filipendula*, *Cerealialia* and *Secale cereale*. The remaining 58 taxa occur in less than 11 samples.

Mapping of the landscape units

The variation in the area of the different landscape units around the lake is relatively large (Figs. 2a,

2b, 4a, and b). The dominant units, within both the 1000 m and 500 m radius are "Coniferous forest" and "Cultivated land", which they are negatively correlated to each other. The pattern of variation between sites seems to be very similar for the 1000 m and 500 m radius areas. It is clear that samples 11,12,17, and 18 differ significantly from the rest because they are characterised by large areas of water surrounding them. They were, therefore, excluded from the data set before numerical analysis (see below).

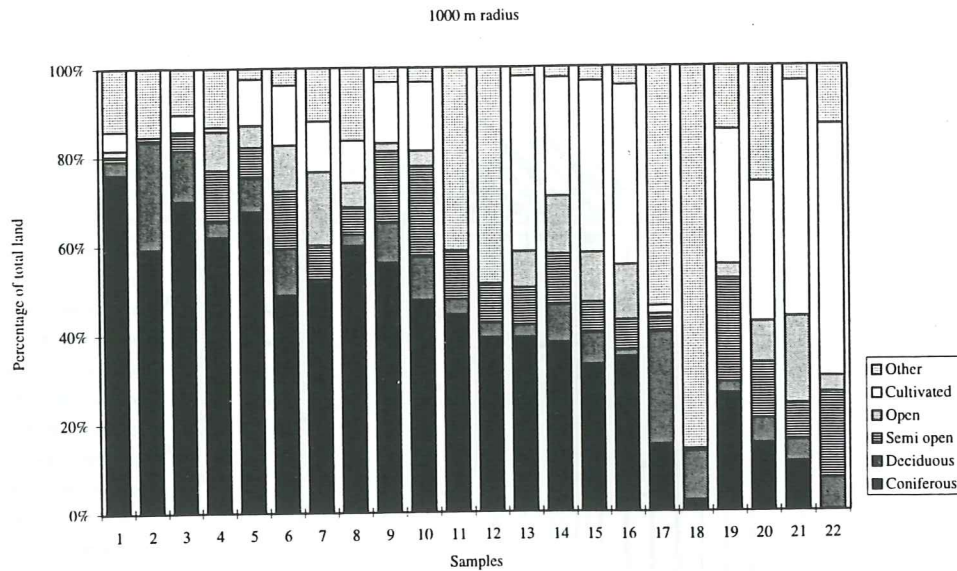
Numerical analysis

Analysis of the pollen data

PCA was performed in order to find out whether the variation in the pollen data and the correlations between taxa were relevant to the purpose of the study, i.e whether there was a relevant variation in the pollen data, and whether this variation was explained by common pollen types. Moreover, it could give a first idea of whether the variation in the pollen data could be explained by variation in the landscape around the lakes.

A first PCA performed on the total pollen data clearly showed that sample 22 was an outlier, as it explained the major variation on PCA axis I. This sampling site is situated in a very open landscape but a dense zone of trees grows around the lake,

a



b

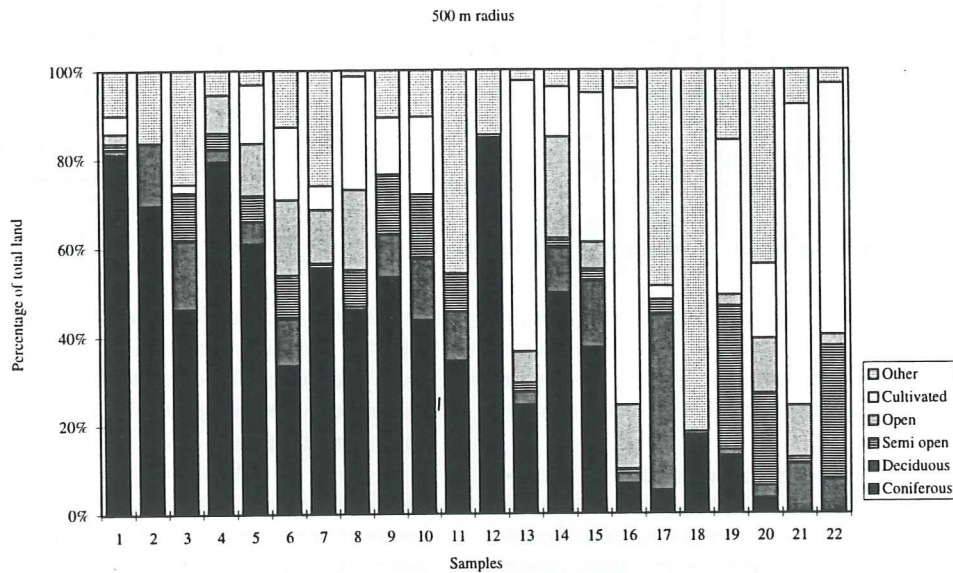


Fig. 4. The distribution of the six broader landscape units used in numerical analysis. Note the dominant units "Coniferous" and "Cultivated" both within a) 1000 m radius and b) 500 m radius.

which is strongly reflected in the pollen spectra. Therefore, this sample was excluded from the data set used in the following analyses.

From the original sum of 55 + 2* pollen taxa (* taxa groups Arboreal pollen, AP, and Non Arboreal pollen, NAP), 20 pollen taxa and the NAP group were excluded. The taxa excluded occurred in less than 4 samples and their maximum percentage of occurrence was less than 0.5%. These arbitrary exclusion criteria were assumed to be reasonable. NAP was excluded simply because it is negatively correlated with AP.

A second PCA (Fig. 5) was performed on a data set including 21 samples, and 35 + 1* pollen taxa (*AP). The first two principal components (axes I and II in the plot) explain 50 % of the variation in the pollen data set, the first axis representing 31%. The third and fourth axes explain 25 % together.

The plot is difficult to interpret in "ecological-landscape" terms. However, two main, superimposed patterns can be recognised. If the pattern of NAP is considered separately, *Rumex acetosa/acetosella* type and *Calluna* are positively correlated and best fitted to axis I. *Cerealia*, *Secale* and *Rumex obtusifolius* type are negatively correlated to *Filipendula* on axis II. Gramineae is best fitted to axis III and Cyperaceae to axis IV. For the AP taxa the pattern is as follows, on axis I *Fagus* and *Quercus* are negatively correlated to *Pinus* and *Picea*. Axis II contrasts samples with high versus low percentages of *Alnus* and *Corylus*. *Salix*, *Betula* and *Juniperus* are best fitted to axes III and IV, respectively.

The analyses show that the variation in the pollen data is small, but may be relevant for the question posed in the study, i.e whether quantita-

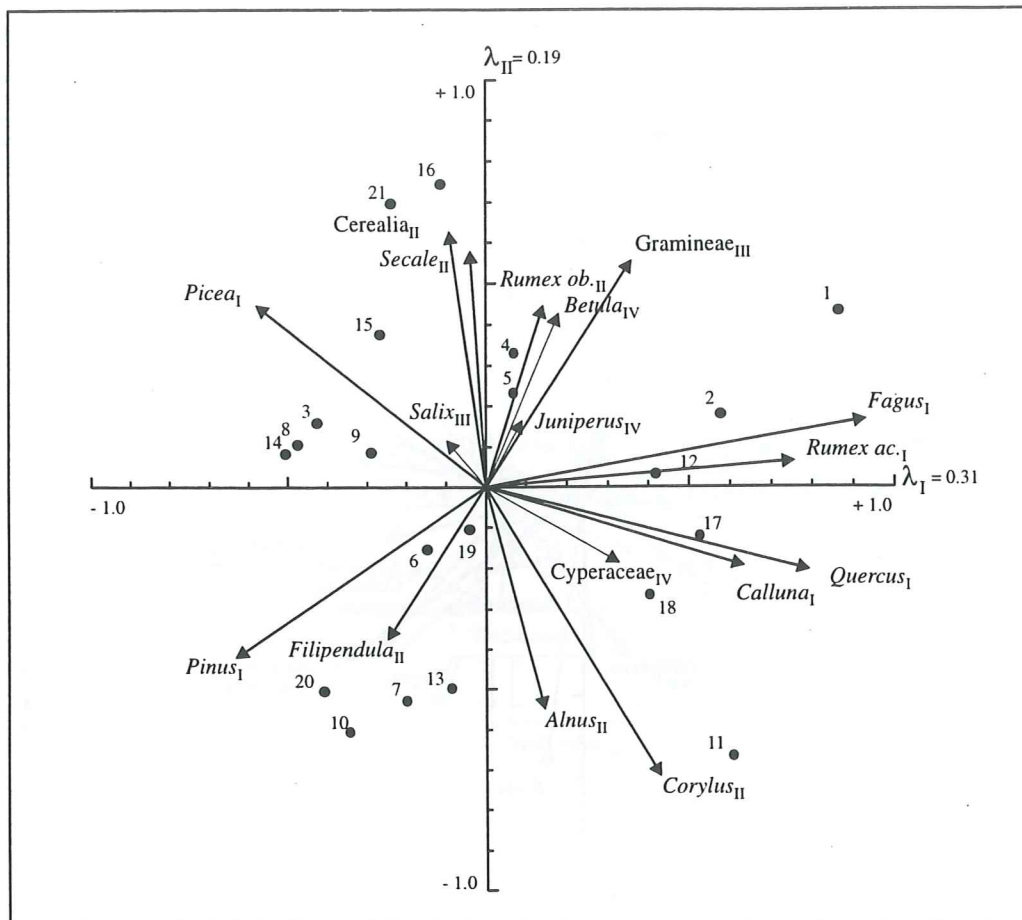


Fig. 5. PCA (axes I and II) of 21 surface pollen samples (dots) and 36 pollen taxa (arrows). To avoid crowding in the plot, the positions of only a few pollen taxa are shown. Pollen taxa that are relatively frequent and that explain a large part of the variation in the data set were selected. I and II are eigenvalues of axes I and II and can also be expressed as the explanatory percentage of variation in the total data set, i.e. 31% and 19% respectively. Each pollen taxon has a subscript that indicates to which axis it is best fitted axes III and IV included. Scores of pollen taxa are weighted mean sample scores.

tive landscape characteristics explain the composition of the pollen assemblages found in lake surface sediments from small lakes. Among the AP *Fagus*, *Quercus*, *Pinus*, *Picea*, *Corylus* and *Alnus* explain the major variation in the pollen data and among NAP these are *Calluna*, *Rumex acetosa/acetosella* type, *Cerealia*, *Secale*, *Rumex obtusifolius* type and *Filipendula*. *Pinus* and *Picea* are negatively correlated to *Quercus*, *Fagus*, *Rumex acetosa/acetosella* type and *Calluna* on axis I, and *Alnus* and *Corylus* are negatively correlated to *Rumex obtusifolius* type, *Cerealia* and *Secale* on axis II. This means that there are gradients in both the NAP and AP that may be associated with the degree of landscape openness and with various forests.

Pollen/ landscape relationships -1000 m radius landscape data

RDA was used to explore directly the relationships between the pollen data and the landscape data.

Four samples (11,12,17 and 18) were excluded before the first RDA analysis was performed. These samples are from sites characterised by large areas of water that are practically non pollen producing. The pollen producing part of the landscape represents a much smaller area than in the other samples. For this reason they are not comparable to the others in terms of the landscape data.

A first RDA analysis was performed on 17 samples with 35 + 1* pollen taxa and the original 16 landscape units, as mapped on the aerial photos (see Methods). The results showed large variance inflation values (VIF) for the landscape variables, which indicates that the landscape variables are strongly correlated (Ter Braak 1987a). Therefore, an interpretation of the RDA plot can be questionable. However, because the intersite correlation values are not affected by the inflation factors, these values could be used to understand to what axes the landscape variables were best fitted. Nothing, however, could be said about the correlation

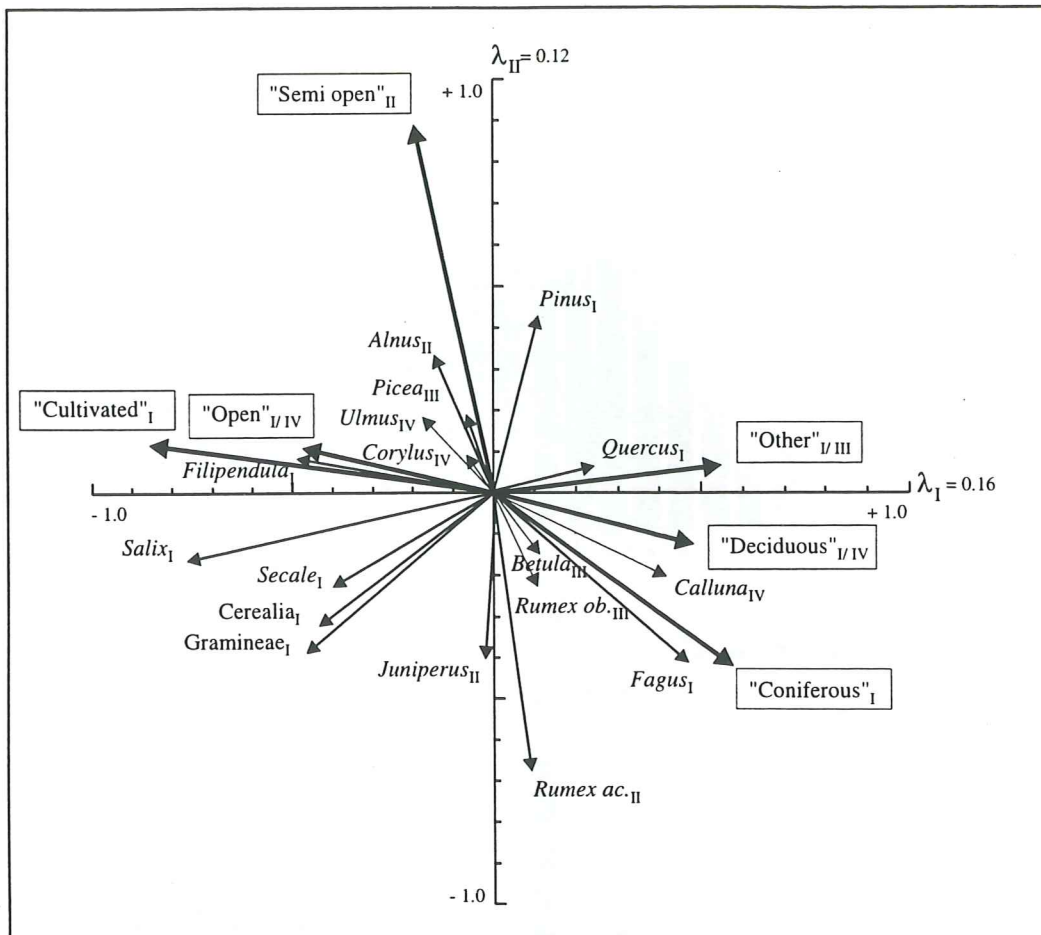


Fig. 6. RDA (axes I and II) of 17 samples and 36 pollen taxa in relation to 6 landscape variables (within squares). To avoid crowding in the plot, the position of only a few selected pollen taxa and the landscape units are shown, represented by arrows. I and II are eigenvalues of axes I and II and can also be expressed as the explanatory percentage of variation in the total data set. Each variable has a subscript that indicate to which axis it has the best fit, axes III and IV included. Scores of pollen taxa and landscape variables are weighted mean sample scores. a) 1000 m radius area and b) 500 m radius area.

of landscape variables with pollen taxa. Therefore, we considered that the analysis was not informative.

In an attempt to reduce the variance inflation values of the landscape units, these were regrouped into six broader units, "Coniferous" (70% tree cover), "Deciduous" (70% tree cover), "Semi open" (20-50% tree cover), "Open" (0-20% tree cover), "Cultivated", and "Other" (Fig. 3a,b and 4a,b). A new RDA showed that these larger units were less correlated with each other (lower variance inflation factor, 8.5). Therefore, an interpretation of the plot was considered more reliable (Fig. 6a).

The two first RDA axes explain 28% of the variance in the constrained pollen data. Axes III and IV together only explain 8% of the variation. *Salix*, *Gramineae*, *Filipendula*, *Cerealia*, *Secale* and the landscape variable "Cultivated" are negatively correlated with *Fagus* and "Coniferous" on axis I.

Pinus and *Alnus* are negatively correlated with *Juniperus* and *Rumex acetosa/acetosella* type on

axis II. The landscape variable "Semi open" also has its best fit on axis II. Surprisingly, it is positively correlated with *Pinus* and *Alnus*. *Picea*, *Corylus*, *Quercus*, *Betula*, *Ulmus*, *Calluna*, *Rumex obtusifolius* type and "Deciduous", "Open" and "Other" are best fitted to axes III and IV. There is no positive correlation between *Pinus*, *Picea* and "Coniferous", but there is some correlation between *Fagus*, *Quercus*, and "Deciduous forest".

A forward selection procedure was performed to find the landscape variables that explain the variation in the data set almost as well as when all landscape variables are included. Moreover, MCP tests were performed to test the statistical significance of these variables.

"Cultivated" and "Semi open" are significant variables, and they explain 25% of the total variation, compared to 36% explained by all landscape units. The third landscape unit selected, "Coniferous", is not statistically significant. An inverse RDA was performed to find the pollen taxa that explain most

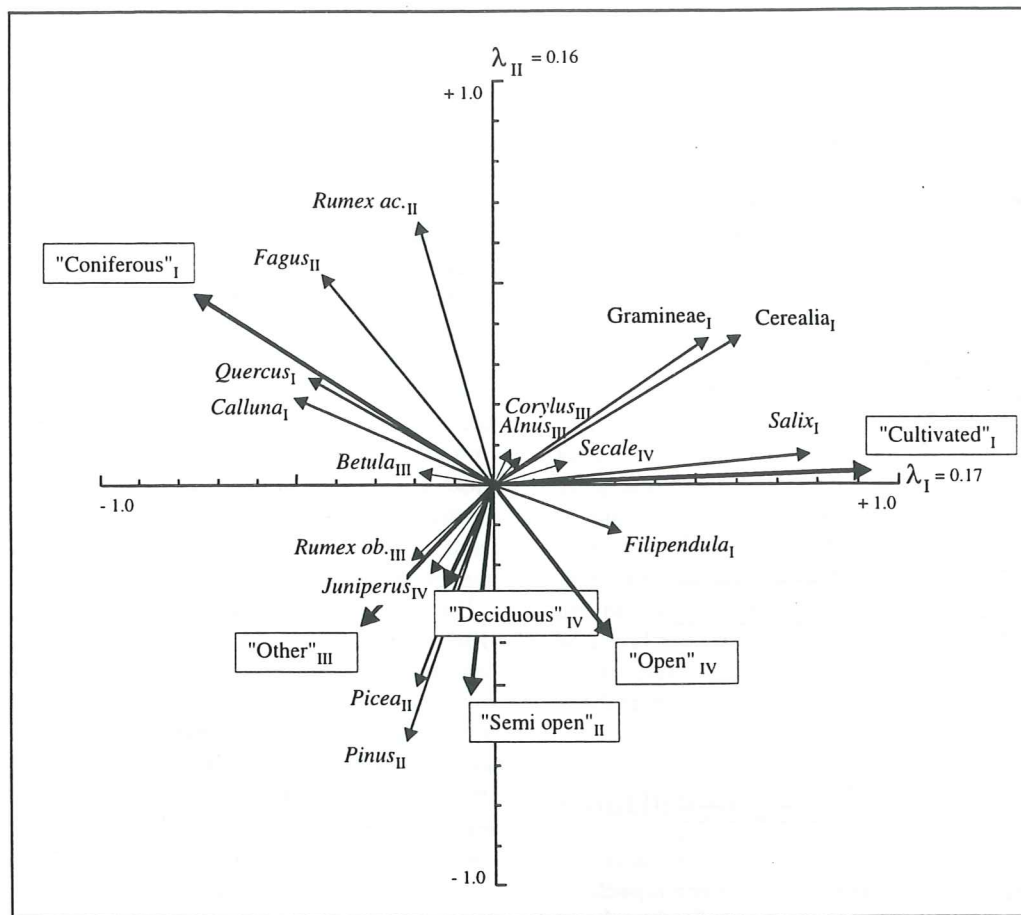


Fig. 6b. RDA, 500 m radius area. For explanation, see Fig. 6a.

of the variation in the data set. *Fagus*, Gramineae, and AP were found by forward selection to be statistically significant (MPC tests).

Pollen/ landscape relationships -500 m radius landscape data

RDA was also performed with the landscape data from within the 500 m radius, to see whether the correlations within this radius were similar to those obtained within the 1000 m radius area. The analysis was performed on the same 17 samples, 35+1 pollen taxa, and the six landscape variables defined above (Fig. 4 b). The first two axes explain together 32% of the total variation, whereas axes III and IV explain only 11%. As for the 1000 m radius landscape data, *Salix*, Gramineae, Cerealia, *Filipendula*, and "Cultivated" are negatively correlated to *Quercus*, *Calluna* and "Coniferous" on axis 1. *Secale* is now correlated with axis IV, with low explanatory power.

Pinus, *Picea*, and "Semi open" are negatively correlated to *Fagus* and *Rumex acetosa/acetosella* type on axis II. There is no landscape variable positively correlated with *Fagus* and *Rumex acetosa/acetosella* type.

Alnus, *Corylus*, *Betula*, *Rumex obtusifolius* type, *Juniperus* and *Secale* are fitted to axes III or IV

together with the landscape variables "Deciduous", "Open", and "Other". They are of little importance for the total variation in the data set.

"Cultivated" and "Coniferous" were selected by forward selection and are found to be statistically significant (MCP test). Together, they explain 29% of the variation, compared to 46% explained by all landscape variables.

In an inverse RDA *Salix* and *Alnus* were selected by forward selection as significant "predictors" in MPC tests.

In conclusion, the use of six landscape units instead of sixteen provides a better and more reliable picture of pollen/landscape relationships. The landscape variables most important to the variation in the pollen data are "Cultivated", "Semi open", and "Coniferous". Within both the 1000 m and 500 m radius areas "Cultivated" is positively correlated to *Salix*, Gramineae, *Filipendula*, and Cerealia. This implies that these taxa may be relevant to predict and reconstruct the area of cultivated land. There is some positive correlation between *Fagus*, *Quercus*, and "Deciduous" within the 1000 m radius area. This may imply that, at this scale, these taxa may be relevant to predict and reconstruct the area of deciduous forest (see however discussion below). Another way to illustrate the correlations seen in the RDA plots (Fig. 6a, b)

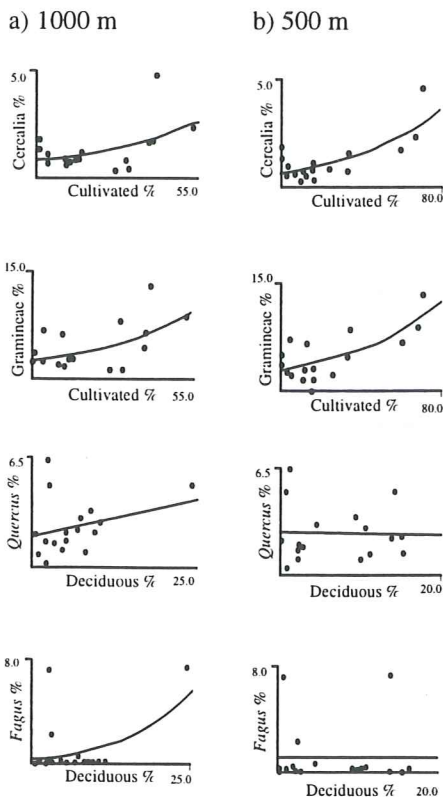


Fig. 7. Linear regressions between selected pollen taxa and landscape units within a) 1000 m radius (left) and b) 500 m (right). This is another way to illustrate some of the correlations in Figure 6a and 6b.

is by simple regressions (Fig. 7). The RDA also shows that "Semi open" and "Coniferous" have no correlations with relevant taxa within either of the pollen-source areas, hence *Pinus* and *Picea* are positively correlated with "Semi open" and not with "Coniferous". This shows that these landscape variables at the chosen scale do not explain the variation in *Pinus* and *Picea* pollen. *Fagus* is correlated to "Coniferous" in our data set, and this correlation also has no "landscape-ecological" relevance for our purpose (see discussion below). The landscape units "Deciduous", "Open", and "Other" are best fitted to axes III and IV, thus not important to the major variation in the pollen data.

In conclusion, the major variation in the pollen data can be explained by at least one landscape unit namely "Cultivated" within both selected pollen-source areas.

Discussion

Despite the large variation in landscape composition between sites, the variation in composition of the pollen assemblages is small. In the pilot study by Gaillard *et al.* (in press) the composition of the

pollen assemblages showed larger variations from lake to lake (Fig. 8). This difference may be explained by the differential input of regional pollen as discussed by Sugita (1994) in the two studied areas. The samples of this study and the samples of the pilot study were collected in two distinct vegetation regions (Fig. 1). Most sites included in the study of Gaillard *et al.* (in press) are located in the agricultural zone of southernmost Sweden, except for five sites, whereas most sites selected for the present study belong to the forest region of south Sweden, except for seven sites east and west of Lake Vättern (Fig. 1). The low variation in composition of the pollen assemblages and particularly the low NAP percentages, is caused by a more substantial input of regional AP pollen due to the dominance of high pollen producing taxa such as *Picea* and *Pinus* in the regional pollen source area.

Even though the variation in the pollen data, as illustrated by the short compositional gradient length (2.0 SD) is low it is shown that it is possible to detect major gradients relevant for the purpose of the study. Well-represented landscape units such as "Cultivated" may explain the major variation in the pollen assemblages, and well-represented pollen taxa are responsible for the major variation in the pollen data. The RDA plots show that there is correlation between NAP such as Gramineae and Cerealia and the areas of open cultivated land, and some correlation between AP such as *Fagus* and *Quercus* and deciduous forest. These correlations are also illustrated by simple regressions (Fig. 7). However, in the latter case, there are not enough

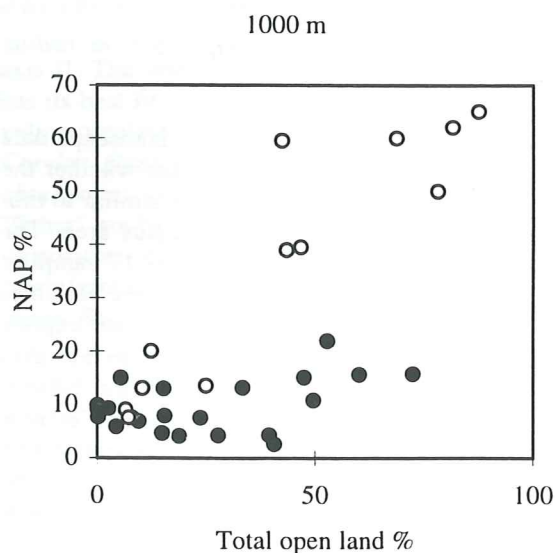


Fig. 8. The relationship between non-arboreal pollen (NAP) and total open land which includes the broader landscape units D) Open land with 0-20% tree cover E) Cultivated land, in the 22 samples of the present study (dots) and the 13 samples of the pilot study (circles).

sites with significantly high pollen values of *Fagus* (2 sites) and *Quercus* (4 sites) to be sure that the correlations are valid (Fig. 7). The four samples excluded in the RDA were relatively rich in *Fagus* pollen. Of the remaining samples, only two (1 and 2) have relatively high percentages of this taxon. These two samples obviously had a very large influence in the analyses, which is seen in the importance of *Fagus* influencing the major variation in the total pollen data in all numerical analyses (Figs. 5 and 6). Therefore, it is obvious that more data should be collected from areas characterised by deciduous forest in order to test these results.

There are some taxa of particular interest worthy of discussion. *Salix* and *Filipendula* are correlated to "Cultivated" together with NAP taxa in the RDA plot. For *Salix* this could be explained by the plantation and cultivation of *Salix* species in recent years in Sweden, but such cultivation was not observed in the field. A more plausible explanation would be that *Salix* as a light demanding shrub/tree may be rather common in the vegetation characteristic for the border zone between forest and field. *Salix* also occur together with *Filipendula* in the ditches between the fields. Therefore, the observed correlation seen between *Salix* and *Filipendula* and cultivated areas in both RDA may well not be accidental.

Betula and *Pinus* are the two dominant taxa in the pollen diagram. The numerical analyses show that *Betula* does not explain the variation in the pollen data very well (best fit to axis IV). In contrast *Pinus* is fitted to the first two axes throughout the analyses and is thus a taxon important to the total variation in the pollen data. Despite this, it has no positive correlation with the area of coniferous forest. This implies that the scale used for the vegetation data is not relevant for these two taxa and that it is presumably too small relative to their individual pollen source areas. Both taxa are characterised by high pollen productivity and long distance transport of their pollen. Therefore, they obviously include a large portion of the regional pollen input.

On the basis of these new data, it is clear that the regression models obtained for the 13 sites in southernmost Sweden (Gaillard *et al.* in press) cannot be applied for the reconstructions of the area of open land in forested regions such as those investigated in the present study. The analysis of the pollen/landscape relationships presented here show, however, that the variation in the data set, and the correlations obtained would allow us to go on with further analysis of the data set. One way of continuing the analysis of our data would be to develop partial least square (PLS) regression models that may have good predictive abilities for landscape units such as open cultivated land and forested land (Gaillard *et al.* in press; Korsman and

Birks 1996; Ter Braak *et al.* 1993). These would, however, be valid only for this type of regional landscape with large areas of coniferous forest and relatively small openings.

If PLS regression models with good predictive abilities can be derived from this data set, these models will be useful for more precise quantitative reconstructions of the degree of landscape openness in areas where coniferous forest have played a significant role in the past. This has been the case for the last 1000 years in the Småland Uplands (Lagerås 1996) and for much longer periods of the Holocene north of Småland.

A more efficient approach for developing this kind of study would be to use digital images and geographical information system (GIS) techniques to obtain rapidly landscapes data for varying of sizes of pollen-source areas and then to correlate them directly with pollen data. GIS technique cannot provide as much detail in the landscape data as aerial photos can, but they would allow to further studies on the relationships between pollen and landscape openness at different spatial scales.

Conclusions

1. Despite the large variation of landscape openness within the assumed pollen-source area (1000 m and 500 m radius) the variation in AP/NAP is low. This was not the case in the pilot study of Gaillard *et al.* (in press) where the variation in both landscape openness and AP/NAP was relatively high. This can be due to the major characteristics of the two regions in which the sites were selected, mainly agricultural in the pilot study and mainly forested in the present investigation.
2. The dominance of the high pollen producers and long-dispersed pollen taxa *Betula* and *Pinus* and the fact that these taxa are not correlated to any relevant landscape unit such as "Deciduous" and "Coniferous", respectively, implies a significant regional input of those pollen types.
3. Gramineae, Cerealia, *Filipendula* and *Salix* are positively correlated to landscape unit "Cultivated" within both assumed pollen-source areas. This implies that these areas are relevant to predict cultivated land from these taxa in particular Gramineae and Cerealia.
4. The weak but positive correlations between *Quercus* and *Fagus* and "Deciduous" within the 1000 m radius suggest that this may be a relevant pollen-source area to predict deciduous forest. However, more sites with a dominance of deciduous forest should be included in the data set to get a better predictive model.

5. The present study implies that when reconstructing and quantifying past vegetation openness it is important that the modern analogues are from the same vegetational region as the fossil pollen sequence and/or that the past vegetation is composed broadly of the same major long-distance transported pollen taxa. Considering the two assumed pollen-source areas used here, it appears that cultivated land could be predicted within both but deciduous forest only within the larger 1000 m radius. Therefore, in a more complete picture of the landscape as a first approximation we suggest that the 1000 m radius may be the most relevant for quantifying landscape composition in terms of cultivated land and deciduous forest (i.e. *Quercus* and *Fagus*)

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