

4.1.4. Pollen Analysis: Not Just a Qualitative Tool

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ABSTRACT: Pollen analysis is seen as a largely qualitative method, but recent developments in analytical techniques, technologically and theoretically, have directed a move towards a greater use of quantitative interpretation. Use of these new methods allows more detailed information to be obtained from pollen data and in turn widens the scope for use of this technique. It is often assumed that pollen analysis only informs on the terrestrial changes in vegetation, but these analytical developments mean pollen data can be used to infer changes in climate, human activity and societal development, all of which are central to obtaining a holistic view of landscape change. This paper outlines the range of contributions pollen data can make to studies along with the considerations required to ensure reliable and informative data is obtained.

KEYWORDS: Fossil; Pollen; quantitative analysis; site selection

Introduction

Palaeoecology is the study of long-term vegetation patterns and encompasses a number of palaeoenvironmental techniques used to investigate past changes in these terrestrial environments, and pollen analysis is one of the most established methods. Being preserved in anoxic environments, pollen grains provide a valuable window into the past as identification to family, genus, and even species, level can be made from distinct morphological characteristics (Figure 1). First championed by von Post (1916) the theoretical and methodological developments that have occurred since this time have pushed the capabilities of the technique, and the current research agendas highlight further the potential that pollen analysis has to inform on key debates.

Sitting in a laboratory, at a microscope and counting pollen grains may not be as appealing as scaling mountains or wading in rivers, but the data obtained can be key to an understanding of human, climatic and wider environmental patterns and impacts in the past. The flora is intimately related to earth system processes and pollen analysis (palynology) can unlock the role of vegetation

in such systems over time. Information about the type, density and spatial patterns of past vegetation has implications for many areas of geographical science and assists in fine-tuning climate models. Importantly, global models are used to predict future changes, and a necessary stage is validation often using palaeoenvironmental, e.g. pollen, data (Anderson et al., 2006, Gaillard et al., 2010).



Figure 1: An image showing modern Picea pollen grains.

Pollen analysis is frequently used to investigate the environmental context of archaeological artefacts to enhance their interpretation, particularly with respect to

settlement, adoption of agriculture and woodland removal (Edwards and MacDonald, 1991; Edwards, 2004).

A further dimension comes from palynological contributions to landscape management via habitat conservation and the mitigation of predicted changes in climate (Birks, 1996, Willis et al., 2007, Willis and Birks, 2006). Current vegetation patterns are the result of complex interactions over many years and pollen analysis supplies longer-term views of change which can aid formulation of suitable action plans for the landscape.

Basics of pollen analysis

In order that pollen data can be used in the ways mentioned above, suitable samples have to be collected. This involves considerations of data collection, taphonomy / preservation and analysis.

Data collection and site selection

The main focus here will be upon lakes and peat bogs, as these often provide the most favourable conditions for preservation which are anoxic conditions preventing desiccation of the pollen grains. Such environments are used in the majority of pollen studies, but research have shown that palynomorphs (pollen and related microfossils) can be obtained from e.g. soils (Dimbleby, 1985),

speleothems (Caseldine et al., 2008), fluvial material (Brown, 1997; Brown, 1999) and marine cores (van Campo et al, 1982; Wilmshurst et al, 1999; McGlone, 2001). The preservation and differential source area of pollen from such contexts can hamper interpretation (Birks and Birks, 1980). In light of this, a number of issues have to be considered to ensure that the information obtained from palynology will be suitable to support any hypotheses being proposed.

A pollen sample combines locally and regionally derived pollen grains; the former is from vegetation immediately surrounding the depositional basin, whereas the latter is a homogenous representation of regional vegetation that is collected, carried and deposited by airflows. Also, in basins with inflows or steep catchments, a fluvial input can introduce a secondary long-distance component. These differing origins influence the recruitment of pollen between environments (Jacobson and Bradshaw, 1981; Sugita, 1994).

For example, an entire lake surface is the catchment for pollen transported by airflows, which is subsequently mixed through the water column to be deposited on the sediment surface at the bottom of the lake. In contrast, once pollen has been deposited on the surface of a peat bog there is little movement and behaves as a static point

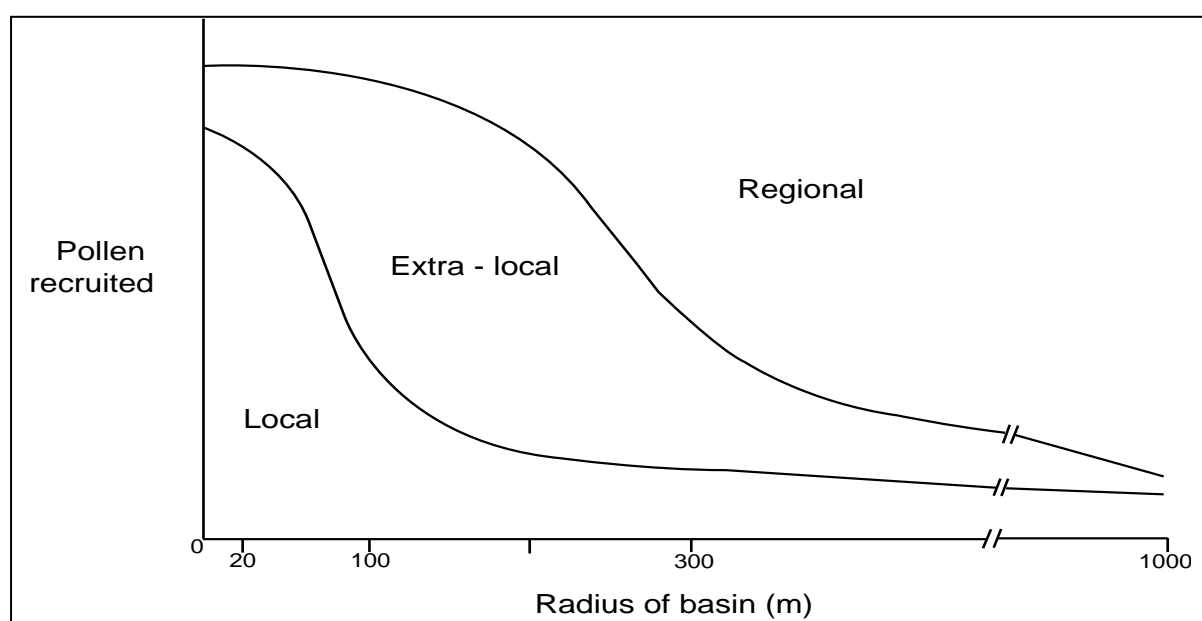


Figure 2: The recruitment of pollen to deposition basins (after Jacobson and Bradshaw, 1981).

source. Due to these differences, a pollen sample contained within a lake represents a much larger area of vegetation than that of a peat bog. Unsurprisingly, peat bogs often have a strong local representation from the mire vegetation (e.g. Cyperaceae [sedges]) as a pollen sample is a point source. In lakes, as the entire water surface collects pollen and is mixed before the pollen is deposited, the size of the lake also acts as a variable. For instance, the larger lake surface area the greater the amount of pollen contributed from the atmosphere, which in turn increases the area of the landscape that is reflected (cf. Figure 2) (Jacobson and Bradshaw, 1981; Sugita, 1994).

Simulations by Sugita (1994) show the effect that different lake radii have upon the signature for vegetation in the pollen assemblages. Figure 3 shows that the representation of the landscape from lakes

with a radius $>750\text{m}$ display more homogenous patterns than smaller lakes which show greater heterogeneity. Taxon-specific factors also have a role in determining the occurrence and quantity of a taxon in a pollen sample. Firstly, plants that are insect-pollinated (entomophilous) tend to be under-represented in the pollen record compared to those that are wind-pollinated (anemophilous) as the former produce less pollen which are not as well equipped for wind dispersal. Secondly, the amount of pollen produced differs between plants and this can influence their representation in the fossil record. For example *Pinus* (Pine) is a high pollen producer, whereas *Juniperus* (Juniper) is comparably lower - therefore the presence of low quantities of *Juniperus* in the pollen record may be highly significant. Some environmental factors influencing pollen productivity include: climate, specifically July temperature of previous

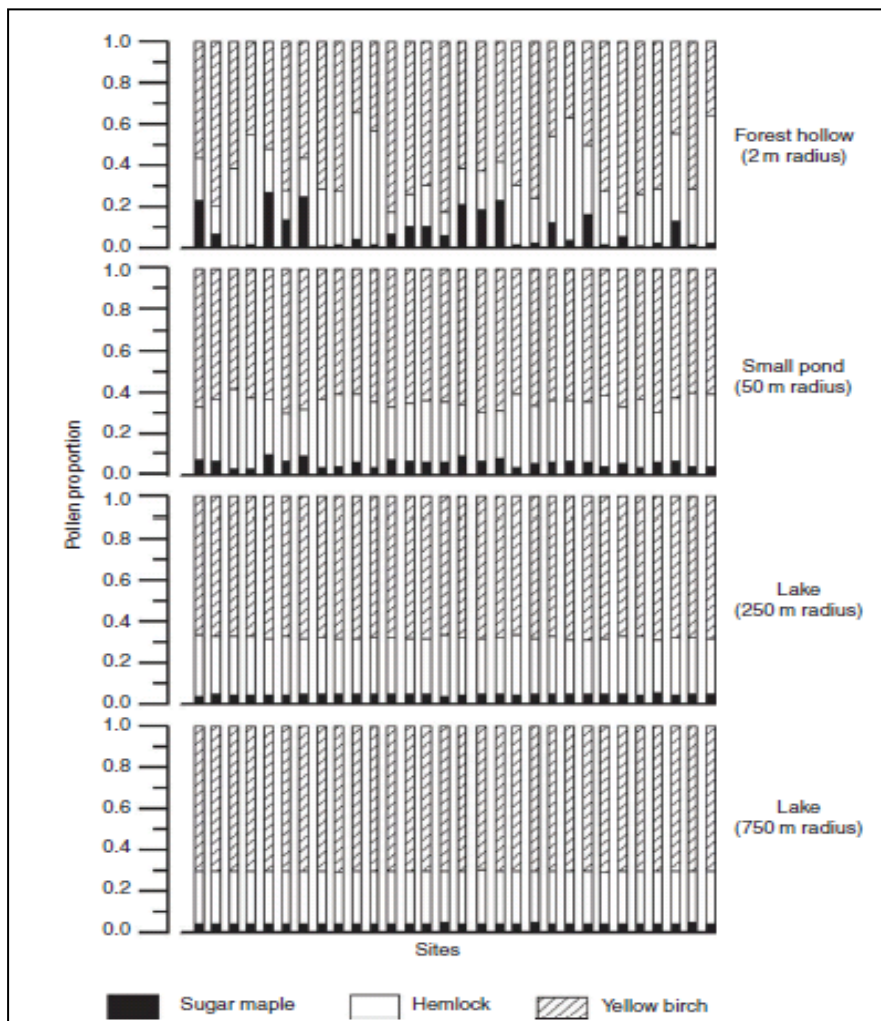


Figure 3: Simulated pollen proportions from different sized lakes within the same region (from Sugita, 1994).

years, which influences the flowering time (Barnekow *et al.*, 2007; Huusko and Hicks, 2009); vegetation patterning and structure which controls light availability; and location in relation to the taxon habitat range, as stressed individuals will apportion less energy to pollen production. Finally, as pollen grains are morphologically distinct, the size, shape and features can aid or hamper dispersal. Thus, *Pinus* pollen has two air bladders increasing its suitability and efficiency for wind dispersal, further influencing its over-representation in pollen samples. Research is underway to understand more fully the range of influences upon pollen productivity and the biases that are present in pollen assemblages (Broström *et al.*, 2008).

Taphonomy and preservation

Complications in deriving and interpreting pollen data arise from the depositional environment and specifically the preservation status of polleniferous material. In some situations, there can be mechanical, chemical and biological agents that breakdown the exine of the pollen grain. The severity of this damage can be recorded and used to further understand environmental conditions (Tweddle and Edwards, 2010), but in some cases the severity is such that it can induce bias into the pollen assemblage. In this case, it is very difficult to quantify the abundance of grains and species that have been affected although Bunting and Tipping (2000) devised a method to assess the degree of post-depositional influences and as such the amount of bias within the pollen assemblage. Studies have investigated the type and degree of degradation that can affect samples, and results suggest that the sporopollenin content of the grain's exine, which is species-specific, is a major control (Cushing, 1967; Havinga, 1984; Twiddle and Bunting, 2010). However, the processes responsible for the damage and the morphology of the grain also have a significant role and, as a result, details of this are uncertain.

A related issue is taphonomy, not only in terms of damage to grains but also their redistribution, and although this is primarily confined to lakes, peat bogs are not excluded (Clymo and Mackay, 1987). Processes such

as sediment focusing, scavenging and within-lake processes (e.g. thermal over-turning of the water body) redistribute grains and have been noted as influencing the relative proportions and concentration of grains (Davis, 1968; 1973; Davis and Brubaker, 1973; Davis *et al.*, 1984). Moreover, this can be species-specific, as for instance in the correlation between pollen release and the period of overturning in a lake (Davis, 1968). The occurrence and degree of influence these processes have is also exacerbated by lake basin morphology. Lehman (1975) showed that this characteristic gives rise to the uneven accumulation of sediment, and in turn the distribution of pollen over the sediment surface influencing the ability to replicate pollen records (Edwards, 1983). Also, within lakes fluvial input can distort the representation of the landscape vegetation, not only from inlets but also overland flow, as effectively shown in studies by Peck (1973), Bonny (1978) and more recently Wilmshurst and McGlone (2005). For this reason, closed basins, those with no inlet or outlet, are preferentially sought in order to minimise the risk of distortion from these sources. In many situations the issues described are difficult to detect and counteract. Sedimentological analyses and dating methods are often required, in addition to assessments of phenomena such as pollen condition, in order to assess adequately the likelihood and extent of such influences.

Data presentation

Qualitative presentation of data is normally made using percentages, but taxa are interrelated. Therefore, as taxon 1 varies taxon 2 mirrors the change regardless of whether these are occurring within the vegetation itself (Birks and Birks, 1980). Concentrations, the total grains deposited per unit volume of sediment, are often used to support interpretations from the percentage profile and to detect changes in the number of grains reaching the basin either as a result of floristic variations or changes in sedimentation (Figure 4). These are the most frequently used methods of data presentation. When a robust chronology is available, Pollen Deposition Rates (PDRs) or Pollen Accumulation Rates (PARs) – often called 'influx' – can be calculated. Defined by

Davis (1969) as 'the net number of grains accumulated per unit area of sediment surface per unit time', presented as $\text{cm}^{-2} \text{yr}^{-1}$; PDRs values give a better approximation of changes in the vegetation coverage or changes in the sedimentation rate and studies have demonstrated that variations within percentage data can be highlighted as artefacts of the method when PDRs are used as a comparison (Davis, 1967; Davis and Deevey, 1964; Hicks, 2001; Hyvärinen, 1975; Seppa and Hicks, 2006). Despite their benefits, limitations have to be considered and addressed on a site-specific basis (Bennett, 1994; Giesecke and Fontana, 2008; Pennington, 1996).

Analytical methods

The analytical methods used in pollen analysis have developed to provide semi-quantitative and quantitative data, a move from the more descriptive stance of some earlier studies. Use of these can require a greater investment, both in time and financially, during primary data collection and processing, but the output presents an alternative view of the raw data and can target specific hypotheses being addressed. Methods are available to directly obtain estimates of vegetation coverage and

landscape patterning or indirectly to derive climate information relationship.

Climate reconstruction

Pollen has been shown to respond to fluctuations in past temperatures and precipitation patterns because of its representation of vegetation patterns. This relationship, and abundant terrestrial sources, has encouraged the development and use of analytical techniques to derive past climatic information from pollen data.

One of the earliest analytical techniques proposed was the indicator species approach (Iversen, 1944) which uses overlapping climate ranges of specific taxa to derive estimates of past temperature regimes. From this the Modern Analogue Technique (Overpeck et al., 1985), the biomisation approach (Prentice et al., 1996) and more recently the transfer function have all developed and have been applied in multiple studies to test the underlying methods and assumptions. Table 1 provides an introduction to the aims of the methods, key references associated with them and some of the limitations.

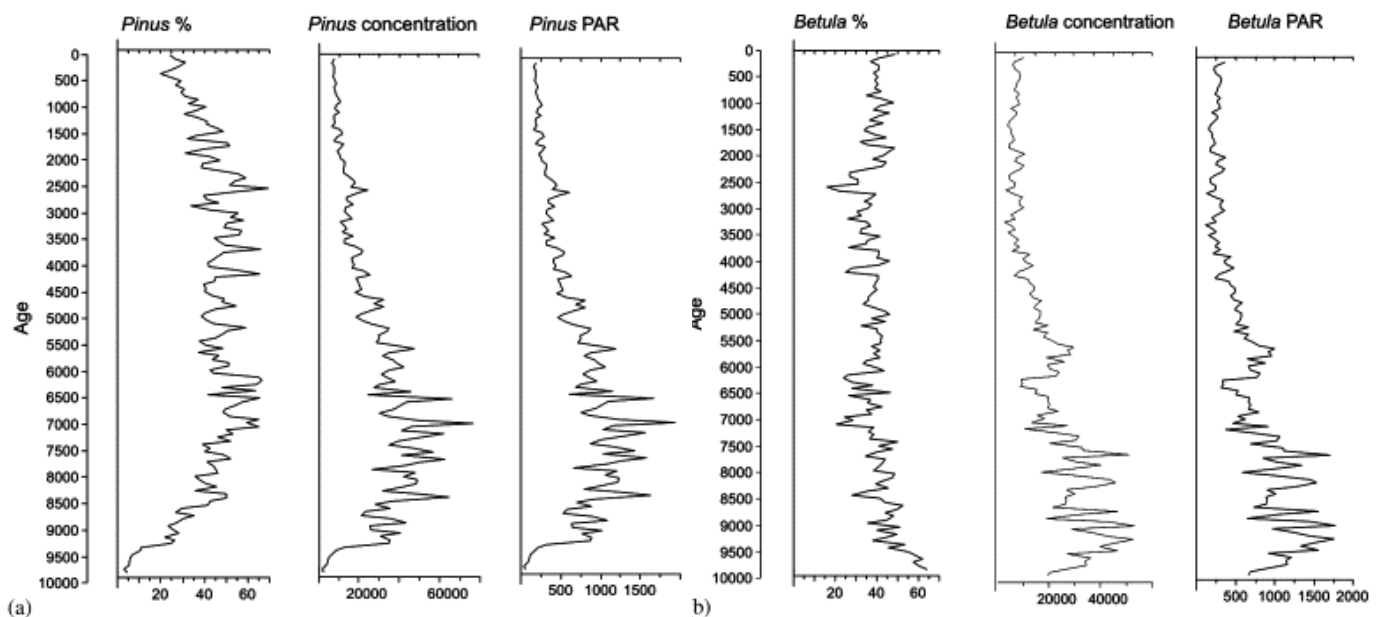


Figure 4: Differences between pollen data is presented using different methods including percentage, concentration and PAR format, (a) Pinus and (b) Betula. The data were collected from sites in northern Fennoscandia (Seppa and Hicks, 2006).

Method	Details	Limitations	Selected references
Indicator species	Based upon the presence/absence of individual taxa. A climatic range can be defined using the overlap of taxa within a single assemblage.	Pollen morphology cannot always distinguish to species level.	Iversen, 1944
Biomisation	Plant Functional Types (PFTs) are constructed using fossil pollen assemblages based upon the habitat preferences and biological function. These attributes along with present distribution of these types are used to infer past climatic variability by combining them to create biomes. Comparison with modern data can be used to infer changes in climate. More recently, process-based vegetation models such as BIOME3 and BIOME4 have been developed.	Defining the affinity cores to identify the PFT for each sample can be problematic. Also, a single sample can be applied to multiple PFTs, especially where the habitat tolerance of a species is wide or at the margins between two biomes.	Prentice et al., 1992; 1996; Edwards, 2007; Kaplan et al., 2003.
Modern Analogue Technique (MAT), Response surfaces	To identify modern environments analogous to those of the past, dissimilarity matrices are used to compare fossil pollen samples and those taken from a range of contemporary environments. The data used for the comparisons are pollen proportions from the samples which can be either the full range of taxa in each sample or a selected group of taxa e.g. representative proportion or main taxa. For those modern samples selected as suitable analogues, supplemental environmental data, e.g. climate, soils, vegetation structure, can be extrapolated to aid interpretation of the relevant fossil horizons.	Non-analogue situations can be encountered and limit the information that can be gained. These are frequently seen in studies that address Late-Glacial environments and those that have been subjected to intensive human interference. Error can be induced into the results if the size of the sampling locations for the fossil and modern sites are not harmonised. The climatic regions from which the modern samples are collected can be too large, such that some variation identified may be statistical artefacts.	Overpeck et al., 1985; Gavin, 2003; Wahl, 2004; Jackson and Williams, 2004; Bartlein et al, 1986; Cheddadi et al, 1998
Transfer function	A modern pollen dataset is used to derive a correlation, e.g. habitat range, of individual taxa for specific climatic variables. Using these known relationships, multivariate analysis is used to extrapolate this information to pollen data in fossil assemblages, e.g. WA, WA-PLS to reconstruct temperature and precipitation regimes.	The analysis is frequently based upon linear correlation between the pollen type and a climatic variable. Mostly, this is not the case and responses are unimodal so the taxa included and suitability of analysis applied can influence the interpretation of the results. Also, removing noise from the overall climate signal can be complex, but by transformation of the pollen data prior to the analysis the influence of this can be minimised. An edge effect can affect the reconstructions; this occurs when a taxon is present at the limit of its range or representation in the modern data.	Seppa and Birks, 2001; Seppa et al 2004; Seppa and Bennett, 2003; Birks and Seppa, 2004

Table 1: A summary of quantitative analytical methods that can be applied to pollen data

General limitations have been raised by numerous authors (MacDonald and Edwards, 1991; Seppa and Bennett, 2003). Firstly, the relationship between pollen and climate is not straightforward and rarely in equilibrium as a linear correlation between pollen and a single climatic factor, while biological influences are not accounted for. Although a number of studies have undertaken climate reconstructions based on pollen (Cheddadi et al., 1998; Peyron et al., 1998), critical evaluation of the reconstructed parameter is required to establish its value. Secondly, pollen morphology and most importantly species distinction, has models assume. Many of the reconstruction methods assume a linear or unimodal response to the climatic factor, being calculated - e.g. precipitation or summer temperature, but it can be difficult to ascertain a role in the performance of all the approaches. Most pollen types can be identified to genus level, but frequently species can occupy different habitats and climatic zones (e.g. species of *Juniperus* and *Betula*). When such taxa are present, the predictive capacity of the analytical method is compromised, especially when dealing with Late-Glacial sites because the climatic envelope of some taxa may not be strictly confined to low temperature regimes e.g. *Betula*. Finally, assessing the validity of the model output is critical to evaluating the reliability of the results obtained. Uncertainty estimators and validation tools can be used to assess the model performance, but assessment of the latter is complex and limits the value that can be placed upon the results obtained (Birks and Seppa, 2004). Investment in Bayesian methods to improve error estimations, spatial and multiproxy representation of climate from pollen data could provide a solution and enhance interpretations (Ohlwein and Wahl, 2012).

Vegetation data

One of the recent developments in pollen analysis is the availability of quantitative modelling software. Arising from the understanding that pollen production and dispersal is not even between species, mechanistic models provide a correction for this bias allowing a more faithful account of changes within the vegetation patterns. Currently, two models are available which are

constructed using very similar algorithms, but different approaches.

The Landscape Reconstruction Algorithm (LRA: Sugita, 2007a, b) uses pollen counts from both large and small lakes to calculate vegetation coverage within defined spatial extent (Figure 5). As a pollen sample from a lake is composed of pollen recruited from a regional (~100km radius) and locally derived areas (~10km) (Figure 2), the LRA uses sites from large lakes to estimate regional vegetation coverage using REVEALS, the first stage of the process. By defining the influence of regional vegetation, it is possible to obtain a purely local signal from smaller sites used in the second stage of the model, LOVE. Restrictions on the spatial extent represented are controlled by the size of the sites used within the model and this provides the freedom to generate data specific to the hypothesis being addressed. By isolating these spatial scales, changes become more visible leading to more informed interpretations. Validation studies have been conducted using this software, showing the potential for improving understanding of past landscape changes (Soepboer et al., 2010; Sugita et al., 2010) along with the necessary cautions and considerations that must be made when using such models (Hellman et al., 2007).

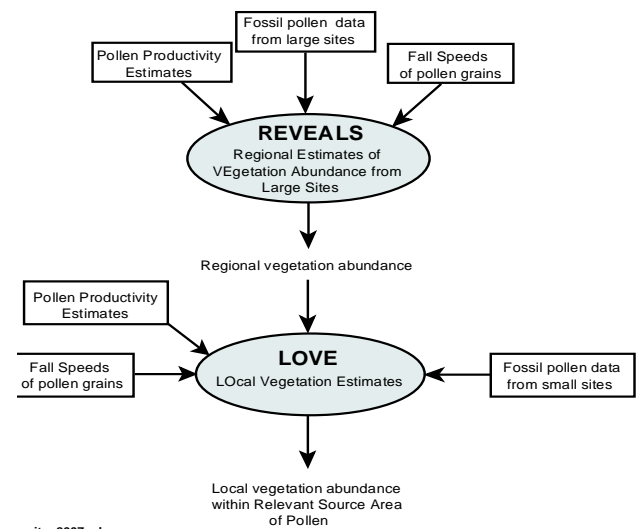


Figure 5: Components of the Landscape Reconstruction Model (Sugita, 2007 a, b).

The Multiple Scenario Approach (Bunting and Middleton, 2009) creates images of past landscapes and is a highly informative tool, especially for archaeological applications (Bunting et al., 2007). Incorporating elements of MAT, numerous grids (hypothetical landscapes) are created from which pollen assemblages at target site(s) can be generated. Using dissimilarity coefficients, the most probable landscapes can be selected when compared to actual pollen data from the target site, and used as scenarios to address the original hypotheses. When using multiple target sites, the model can be used to construct potential spatial patterns of past landscapes (Bunting et al., 2007; Pratt, 2007).

Although the output generated differs between the models, there are *a priori* specifications that have to be considered for both approaches. Firstly, the models require parameter data in the form of fall speeds of pollen grains, atmospheric properties (standard data are often used) and pollen productivity estimates. Studies have shown that changes in these components can be significant to model output, especially with productivity estimates (Bunting et al., 2004; Neilsen and Sugita, 2005). Secondly, a robust chronology is essential to ensure that when multiple sites are used, the equivalent horizons are selected.

Conclusion

Pollen is often considered a qualitative tool that has limits in its interpretative capacity, but this is far from the truth. This paper has tried to show that consideration of specific project aims in light of the strengths and limitations of pollen analysis can yield highly informative quantitative data, far from the descriptive results often sought from pollen analysis. Development of analytical tools and theoretical understanding is encouraging pollen data to be reconsidered as a quantitative technique which can be effectively applied to address key debates. Where this has been done, the results show that pollen analysis is far from a descriptive tool, and further research will help pollen archives reach their full potential.

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