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Model-Based Reconstruction of Vegetation and Landscape Using Fossil Pollen

Abstract: We present the theoretical basis and applications of the Landscape Reconstruction Algorithm (LRA), a novel two-step framework of quantitative reconstruction of vegetation and landscape based on an up-to-dated theory of pollen analysis. The LRA uses the REVEALS model to estimate the regional vegetation composition using pollen from multiple sites $\geq 1\text{--}5 \times 10^2$ ha; the LOVE model calculates background pollen and incorporates it into reconstruction of relative vegetation abundance within the relevant source area of pollen for smaller sites $< 10^2$ ha. Extensive simulations and modern validation studies in Skåne and Småland, southern Sweden, show that the LRA can provide accurate estimates of vegetation abundance by correcting for both the non-linear nature of the relationship between pollen percentages and the surrounding vegetation, and the differences in background pollen. Preliminary results suggest that human impacts on land cover were much more profound in southern Sweden than the pollen percentages alone would suggest.

Introduction

Quaternary palaeoecology has become highly relevant to the discussion of global environmental changes, especially the long-term impacts of human activities on the natural world. Conservation biologists and policy makers are now aware of palaeorecords as the baseline data for management and planning of nature reserves and parks. Archaeobotanists and archaeologists argue about cultural, agricultural, and economic characteristics and changes through time using palaeorecords of vegetation and landscapes surrounding settlements and monuments (IVERSEN 1941; BEHRE 1981; GAILLARD 2006). Quantitative reconstruction of climate and landscape is thus crucial for discussing objectively the human impact on changes in climate and other physical, biological, and anthropogenic environments.

Climate reconstruction from various proxies such as fossils and geochemical elements has been quantitative and robust. In contrast, quantitative reconstruction of vegetation and landscape using fossil pollen is surprisingly limited, largely because we lack theoretically-sound concepts and methods. While pollen-based reconstruction of biomes and vegetation types has been informative (e.g. PRENTICE ET AL. 1998), these estimates are qualitative and typological. Palaeoecologists have often used non-arboreal pollen (NAP) percentages to estimate

landscape openness caused by human or natural processes (e.g. BERGLUND 1991). However, this method does not work well in practice or theory (BROSTRÖM ET AL. 1998; SUGITA ET AL. 1999; GAILLARD ET AL. 2000; GAILLARD 2006), and quantitative estimates of past vegetation composition inferred from fossil pollen are still elusive.

SUGITA (2007a; 2007b) proposed a new framework for the quantitative reconstruction of vegetation and landscape, the Landscape Reconstruction Algorithm (LRA), to solve this old but critical problem in palynology and palaeoecology. This is a model-based approach to vegetation reconstruction. Building on the theoretical understanding of the important factors and mechanisms that affect pollen representation of vegetation (PRENTICE 1985; 1988; SUGITA 1993; 1994), the LRA enables us to estimate both regional and local abundance of plants using fossil pollen assemblages. In this paper, we review the conceptual development for the theory of pollen analysis, summarize the significance of the LRA approach, provide some of our preliminary LRA results from southern Sweden, and describe implications of the LRA for future research directions.

Conceptual Development for Quantitative Reconstruction of Vegetation and Landscape

Spatial Scale of Vegetation Represented by Fossil Pollen

Fossil pollen collected from lakes and mires has been the primary data source for vegetation reconstruction. The pollen grains can potentially be carried by the wind for many metres or kilometres, it is difficult to define the spatial scale of the source area for pollen in sediment. Ecological phenomena are scale-dependent, however. Landscape openness caused by humans also cannot be objectively estimated without the knowledge of the source area of pollen. Unless the spatial scale is clearly defined, pollen-based reconstruction and interpretation of vegetation and landscape dynamics would not make sense (SUGITA 1994; 1998; DAVIS 2000).

Assuming vegetation is homogeneous, the spatial scale of pollen source can be calculated as the “characteristic radius” for each taxon (PRENTICE 1988; SUGITA 1993). A certain fraction of pollen, e.g. 50% or 70%, comes from within this radius. However, vegetation is generally heterogeneous. In order to take account of spatial heterogeneity, SUGITA (1994; 1998) proposed the concept of “relevant source area of pollen”, which is defined as the area beyond which correlations between pollen loading in a sedimentary basin and vegetation abundance for all taxa do not continue to improve, even with continued vegetation sampling to greater distances. Pollen loading coming from beyond the relevant source area of pollen (i.e. background pollen) is consistent among similarly-sized sites in a region, even when vegetation and landscape are highly heterogeneous and patchy. This means that differences in pollen loading among similarly-sized sites represent differences in plant abundance within the relevant source area of pollen at individual sites, superimposed on a constant background pollen (SUGITA 1994; 1998; 2006; 2007b).

The important factors affecting the spatial scale of the relevant source area of pollen are the spatial patterns of vegetation and landscape, and the species composition of different stand types (SUGITA 1994; BUNTING ET AL. 2004; HELLMAN ET AL. unpublished). Differences in pollen dispersal characteristics among taxa, wind speed, and atmospheric conditions do not influence the relevant source area of pollen sig-

nificantly (NIELSEN / SUGITA 2005; SUGITA 2007b). The relevant source area of pollen has been quantified empirically in the upper Great Lakes region of the USA (CALCOTE 1995), southern Sweden (BROSTRÖM ET AL. 2005), central Sweden (VON STEDINGK 2006), Denmark (NIELSEN / SUGITA 2005), Switzerland (SOEPBOER ET AL. 2007), and England (BUNTING ET AL. 2005).

Quantitative Reconstruction of Regional Vegetation and Landscape

Background pollen loading coming from beyond the relevant source area of pollen can be quantified if the mean vegetation composition of the region within 100–400 km radius is known (SUGITA 1994; 2007a; 2007b). The first step of the Landscape Reconstruction Algorithm (LRA) is to reconstruct the regional vegetation composition using fossil pollen from sites ≥ 100 –500 ha (Fig. 1). Simulations show that pollen assemblages from these large sites are expected to have small variations among sites and represent regional vegetation well (SUGITA 1994). Therefore, pollen data from a few large sites can be sufficient to estimate the regional vegetation abundance (SUGITA 2007a).

SUGITA (2007a) proposed the REVEALS (Region-

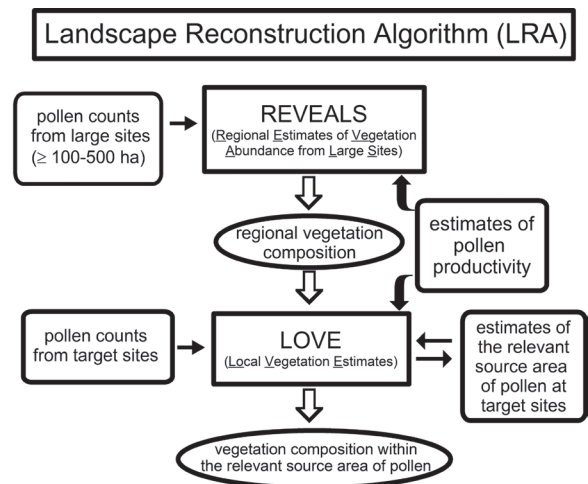


Fig. 1. Framework of the Landscape Reconstruction Algorithm (modified from SUGITA 2007b).

al Estimates of Vegetation Abundance from Large Sites) model to estimate the regional vegetation composition (Fig. 1). This step is important. Background pollen is expected to change through time, because changes in anthropogenic factors and natural environmental forcing including climate, should affect patterns and processes of regional vegetation. The changes in background pollen are easily con-

founded with the non-linear nature of the relationship between pollen percentages and vegetation abundance, making quantitative reconstruction of the past vegetation and landscape difficult (BROSTRÖM ET AL. 1998; SUGITA ET AL. 1999). For this reason, SUGITA (2007a) developed the REVEALS model to estimate changes in the regional vegetation.

The REVEALS model has been tested and validated in two contrasting regions of southern Sweden; the Skåne region characterized by open and agricultural landscapes, and the Småland region by semi-open landscapes. HELLMAN ET AL. (2007) showed that the variations of pollen assemblages within and among lakes ≥ 100 ha are small, and that the regional vegetation composition in percentage cover predicted by REVEALS matches well to that compiled and calculated from vegetation inventory data, satellite and aerial photos, and crop statistics in these two regions.

Quantitative Reconstruction of Vegetation and Landscape within the Relevant Source Area of Pollen

Once the regional vegetation abundance is estimated, the LOVE (Local Vegetation Estimates) model calculates background pollen and incorporates it into reconstruction of relative vegetation abundance within the relevant source area of pollen (Fig. 1). This is the second step of the LRA. Extensive simulation runs show that the LOVE model can correct for the non-linear nature of the relationships between pollen percentages and relative vegetation abundance and estimate relative vegetation abundance accurately (SUGITA 2007b). Empirical testing and validation of the LOVE model is currently underway in southern Sweden, Denmark, Switzerland, and the upper Great Lakes region of the USA. Preliminary results (SUGITA ET AL. unpublished) have shown that the LOVE model works well to predict the local vegetation composition within the relevant source area of pollen, using the pollen data from moss polsters and small lakes in southern Sweden (BROSTRÖM ET AL. 1998; 2004; GAILLARD ET AL. 1998), and from small forest hollows in northern Michigan and northwestern Wisconsin (CALCOTE 1995; PARSHALL / CALCOTE 2001).

Among the assumptions and parameters used in the LRA approach, pollen productivity is one of the important parameters (SUGITA 2007a; 2007b) (Fig. 1). The REVEALS and LOVE models assume

that pollen productivity is constant through time. Some may argue that the LRA approach is flawed because of this assumption. On the contrary, one of the advantages of using a model-based approach to vegetation reconstruction is that assumptions are clearly stated and laid out. Palynologists have rarely spelled out all the assumptions explicitly made for interpretation, thus the interpretation could be difficult to evaluate.

When necessary, effects of a variation of pollen

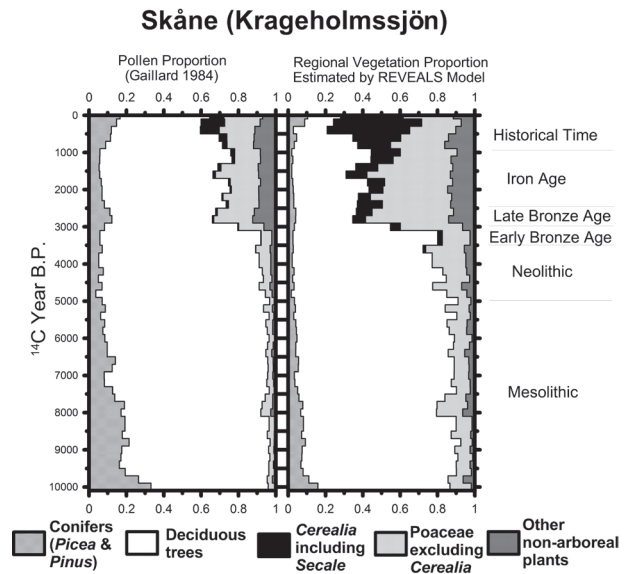


Fig. 2. Summary pollen-percentage diagram (left) and summary diagram of reconstructed abundance of regional (i.e. 10^4 km²) vegetation in Skåne, the southernmost region of Sweden. Skåne is characterized today by open, agricultural landscapes. Chronology in uncalibrated ¹⁴C years BP.

productivity estimates on the uncertainties of the reconstruction can be evaluated in the LRA, and the potential and limits of quantitative reconstruction of vegetation can be objectively assessed. REVEALS and LOVE include several parameters (e.g. pollen productivity and fall speed of pollen) and pollen counts from study sites, thus errors could add up to a large size. Standard errors for the estimates of regional and local vegetation abundance can be calculated using a hybrid of the delta method (STUART / ORD 1994) and Monte Carlo simulations (SUGITA 2007a; 2007b).

Implications and Future Directions

The REVEALS model has already produced important results on the regional changes in vegetation abundance and land use in southern Sweden. Fig. 2

and Fig. 3 suggest that human impact on land cover over the last 3000 years was much more profound than the changes in the pollen percentage alone would suggest. REVEALS was applied to the fossil pollen records from Krageholmssjön (186 ha) in Skåne (GAILLARD 1984) and from Lake Trummen (76 ha) in Småland (DIGERFELDT 1972). The vegetation and landscape reconstruction by REVEALS demonstrates that 60–80% of the region has been unforested since 3000 years ago in Skåne (Fig. 2), and 20–40% of the region over the last 3500 years in Småland (Fig. 3). Pollen proportions underestimate landscape openness in both regions.

These results are the first quantitative estimates of

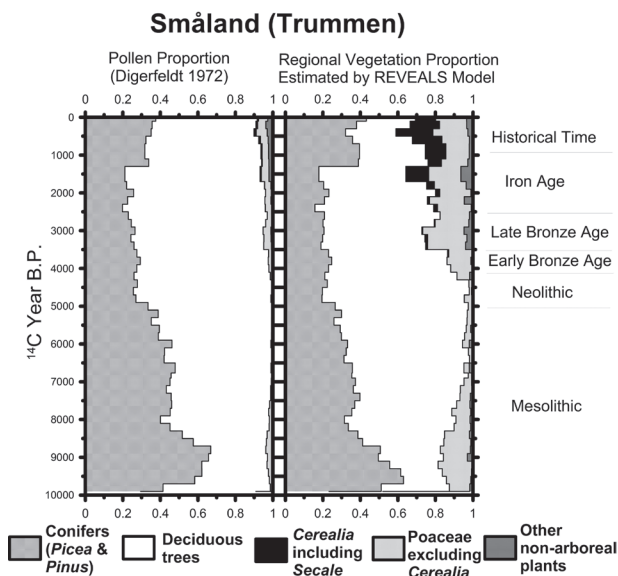


Fig. 3. Summary pollen-percentage diagram (left) and summary diagram of reconstructed abundance of regional (i.e. 10^4 km²) vegetation in Småland, southern Sweden. The Småland region is located to the north of Skåne and is characterized today by semi-open landscapes. Chronology in uncalibrated ¹⁴C years BP.

the changes in regional vegetation using REVEALS. Major changes in human impact during the Late Bronze Age, the Late Iron Age and the Middle Ages, as well as the maximum landscape openness during the 19th century in both Skåne and Småland is in close agreement with archaeological and historical records. The landscape of the two regions over the last 3500 years has been more open than previously suggested, and thus may have had a much larger impact on climate and other environmental factors over the last 3000–3500 years.

The landscape of relatively open woodland reconstructed for Småland in the early Holocene (Fig. 3) is

of particular interest, in view of recent controversy regarding forest cover and the presence of grazing animals (VERA 2000). Recent studies of the fire history in the region clearly show that fires played an important role in forest dynamics and structure (e.g. openness) during early and late Holocene (GAILLARD ET AL. 2007). Similarly, although the large impact of human activities since Late Bronze Age is well known and documented in southern Sweden by archaeological and palaeobotanical data (e.g. BERGLUND 1991; BERGLUND ET AL. 2002), the landscape openness reconstructed by REVEALS is much larger at the regional spatial scale than previously interpreted from non-arboreal pollen (NAP) percentages, in particular for Småland. This new insight is significant for the analysis of archaeological data and for testing the open-woodland hypothesis (VERA 2000) in the region.

Changes in the cultural landscape and its spatial dynamics are one of the active research areas in archaeobotany and archaeology (e.g. BERGLUND 1991; BERGLUND ET AL. 2002; JACOMET ET AL. 2004). Archaeobotanists often use onsite and offsite pollen records to evaluate the types of land use, such as slash-and-burn, pollarding, grazing, and cultivation, and their spatial patterns around the settlement and monument (GAILLARD 2006 and references therein). Pollen percentages are still frequently used (e.g. BERGLUND 1991; BERGLUND ET AL. 2002; NIINEMETS / SAARSE 2006; DRESCHER-SCHNEIDER ET AL. 2007) to estimate when and how much the cultural landscape changed without critical evaluation of the meaning of the percentage values and spatial resolution of the source area of pollen (e.g. landscape openness vs. NAP percentages). An increasing number of modelling studies (e.g. SUGITA ET AL. 1999; CASELDINE / FYFE 2006; SUGITA 2007a; 2007b) has shown that, unless a network of sites and estimates of the relevant source area of pollen for these sites are available, the spatial extent of the cultural landscape and its changes are hard to estimate from pollen percentage data. Our results from southern Sweden (Figs. 2 and 3) are an important step forward for a better understanding of the cultural landscape dynamics in the region using the LRA approach.

Southern Sweden is characterized by many differently-sized lakes and mires. Many other regions do not have an abundance of study sites of different sizes, however. Without large sites or many differently-sized sites, it would be difficult to estimate

regional vegetation abundance through time (SUGITA 2007a); thus the LRA approach would not be applicable. SUGITA ET AL. (2006) proposed another model-based approach, the QAD (Qualitative Assessment of Difference) method that can objectively compare differences between sites in plant abundance within the relevant source areas of pollen using pollen percentages. This method requires pollen counts from sites of similar size in the same region and estimates of pollen productivity, thus is practical in many regions. Although it does not quantify vegetation abundance, we can avoid problems in vegetation reconstruction that are caused by the “closed universe” of pollen percentage data and changes in background pollen.

Over the last several years, the number of arboreal and non-arboreal plant taxa for which reliable estimates of pollen productivity are available has dramatically increased in many parts of northern Europe (HJELLE 1998; SUGITA ET AL. 1999; HICKS 2001; BROSTRÖM ET AL. 2004; NIELSEN 2004; BUNTING ET AL. 2005; SOEPBOER ET AL. 2007; and others). We are now ready to apply the LRA approach for reconstructing both regional and local vegetation and will soon be able to assess the impact of human land use in northern Europe throughout the entire Holocene (ANDERSON ET AL. 2006; GAILLARD 2006).

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