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Palynological perspectives on vegetation survey: a critical step for model-based reconstruction of Quaternary land cover

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ABSTRACT

1. Quantitative reconstruction of past vegetation distribution and abundance from sedimentary pollen records provides an important baseline for understanding long term ecosystem dynamics and for the calibration of earth system process models such as regional-scale climate models, widely used to predict future environmental change. Most current approaches assume that the amount of pollen produced by each vegetation type, usually expressed as a relative pollen productivity term, is constant in space and time.

2. Estimates of relative pollen productivity can be extracted from extended R-value analysis (Parsons and Prentice, 1981) using comparisons between pollen assemblages deposited into sedimentary contexts, such as moss polsters, and measurements of the present day vegetation cover around the sampled location. Vegetation survey method has been shown to have a profound effect on estimates of model parameters (Bunting and Hjelle, 2010), therefore a standard method is an essential pre-requisite for testing some of the key assumptions of pollen-based reconstruction of past vegetation; such as the assumption that relative pollen productivity is effectively constant in space and time within a region or biome.

3. This paper systematically reviews the assumptions and methodology underlying current models of pollen dispersal and deposition, and thereby identifies the key characteristics of an effective vegetation survey method for estimating relative pollen productivity in a range of landscape contexts.

4. It then presents the methodology used in a current research project, developed during a practitioner workshop. The method selected is pragmatic, designed to be replicable by different research groups, usable in a wide range of habitats, and requiring minimum effort to collect adequate data for model calibration rather than representing some ideal or required approach. Using this common methodology will allow project members to collect multiple measurements of relative pollen productivity for major plant taxa from several northern European locations in order to test the assumption of uniformity of these values within the climatic range of the main taxa recorded in pollen records from the region.

1. Introduction

Pollen analysis is one of the most common methods used to investigate past environments. Pollen and spores (palynomorphs) are widely dispersed as part of the plant reproductive cycle. Plant genetic material is encased within a tough cell wall with complex architecture and a high proportion of sporopollenin. This protective coat preserves well in a wide range of environments, enabling grains which are not successfully dispersed to a female flower or germination point to survive in the sedimentary archive. Palynomorphs are particularly well preserved in waterlogged environments such as lakes and bogs, and the progressive accumulation

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of sediment over time in these systems allows extraction of a series of pollen assemblages, from a core of sediment, which reflect changes in the vegetation cover of the wider landscape over time. However, translating these assemblages into quantitative estimates of vegetation is not a simple exercise; palynomorphs vary in size, shape and dispersibility, and differences in plant reproductive strategy and resource allocation lead to differences in the amount of pollen per unit plant produced by different taxa.

Three broad classes of approach to reconstructing past vegetation from pollen records can be identified: comparison with samples taken from analogous environments with known vegetation (e.g. Overpeck et al., 1985; Nielsen and Odgaard, 2004; Kuneš et al., 2008), biomisation (where pollen types are related to plant functional types, and proportions of functional types used to identify the most likely biome; e.g. Prentice et al., 1996; Prentice et al., 2000; Ni et al., 2010) and application of process-based models (e.g. Sugita, 2007a,b; Bunting and Middleton, 2009). Process-based model approaches take algebraic models of the relationship between pollen assemblages and producing vegetation (i.e. models of the taphonomic process linking them) and use them to translate pollen data into quantitative measures of vegetation cover. Two approaches using the same underlying models of pollen dispersal and deposition are currently being actively applied; the Landscape Reconstruction Algorithm (LRA; Sugita, 2007a,b) and the Multiple Scenario Approach (MSA; Bunting and Middleton, 2009). These are compared in outline in Fig. 1. Quantitative reconstructions of vegetation are important for investigation of a range of important research questions, particularly because they greatly facilitate the use of palaeoecological data to address issues raised within other academic disciplines such as ecology, climatology and archaeology. Gillson and Duffin (2007) used a process-based model to translate tree pollen percentages into past woody plant cover in savannah in southern Africa to inform identification of thresholds of concern for conservation monitoring in the region. The LANDCLIM project is using the LRA approach to reconstruct vegetation cover in northwest Europe on a 100 km grid basis as an input to regional climate models (e.g. Gaillard et al., 2010). In archaeological contexts, the approach allows different archaeologically derived hypotheses about landscape structure to be tested against extant pollen records (e.g. Caseldine et al., 2007; Tipping et al., 2009).

In this paper, we focus on the linear process-based model generally referred to as the Prentice–Sugita model, which underlies the LRA and is the primary model currently being used in the MSA. Linear models have a long history of use in the field (e.g. Davis, 1963, 2000; Andersen, 1970, 1973; Prentice, 1985, 1988; Sugita, 1993, 1994; Jackson, 1994). The model includes a taxon-specific measure of pollen production, which is usually estimated from empirical data. Pollen productivity (α_i) is a simple measure of the amount of pollen released for transport per unit area of pollen-producing vegetation (grains m^{-2} yr^{-1}). However, this is not simple to measure, and pollen productivity is usually estimated and expressed as a dimensionless ratio relative to a reference taxon (e.g. Davis, 1963; Andersen, 1970; Broström et al., 2008), termed the Relative Pollen Productivity (hereafter RPP). The reference taxon provides a benchmark for comparison between taxa and between datasets. Davis (1963) termed the ratio between the amount of pollen of one type present in a sample and the amount of plants producing that pollen type in the surrounding vegetation the R-value, and noted that whilst the absolute R-values calculated varied between sites, the ratio between the R-values of two taxa should be the same. By choosing a single taxon (the 'reference taxon') to always be the denominator in the calculation of this ratio, Andersen (1970) was able to present 'correction factors' for translating pollen percentages into estimates of vegetation abundance; for example, in natural-type forests in Denmark *Quercus* (oak) produced four times as much pollen per unit vegetation area than *Fagus* (beech) whilst *Tilia* (lime) produced only a quarter as much. The reference taxon chosen had to be present in both vegetation and pollen data at every site of interest, since a zero value for the denominator prevents calculation of the ratio.

Estimates of RPP are now derived using a computer-based iterative process of comparing the goodness of fit of a set of linear pollen-vegetation models against empirical datasets consisting of paired vegetation and pollen data for multiple taxa collected at tens of sites (discussed further in Section 2.1 below), rather than by simple ratio-taking, but a reference taxon still needs to be identified as a starting point for the iteration (for this taxon the RPP is set to a value of 1). In theory any taxon can serve as the reference taxon, but given the relatively small size of most empirical datasets reference taxon choice can affect the robustness of the iterative process and therefore of RPP estimates obtained. A good reference taxon is present in both pollen and vegetation data from as many of the sites sampled as possible, has a wide range of values of both parameters across the whole dataset, and is expected to have an intermediate absolute pollen production value. In most studies to date, the pollen taxon Poaceae has been used as the reference taxon (e.g. Hjelle, 1998; Broström et al., 2004; Nielsen and Odgaard, 2004; Räsänen et al., 2007; Soepboer et al., 2007; Mazier et al., 2008; von Stedingk et al., 2008; Poska et al., 2011; Abraham and Kozáková, 2012), although since this pollen taxon can

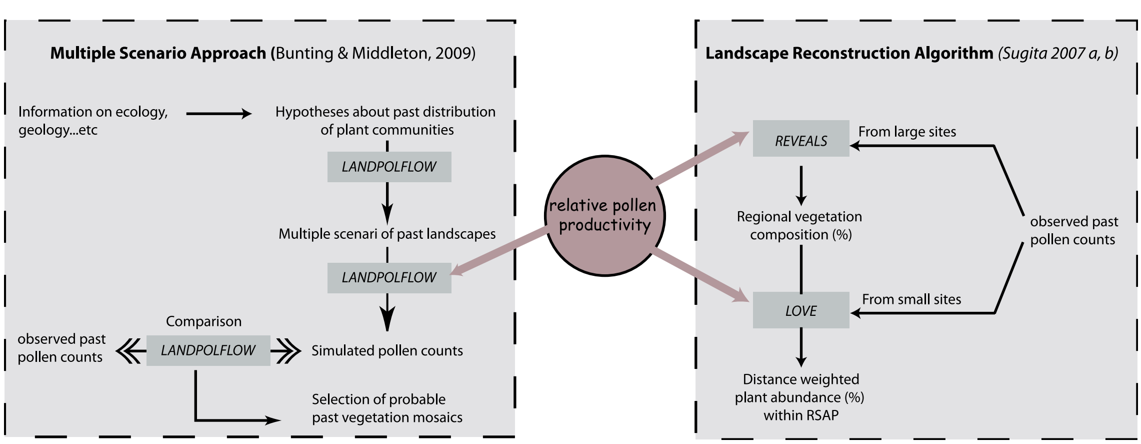

Fig. 1. Schematic summary comparing the strategies for quantitative reconstruction of vegetation cover from pollen records used by the Landscape Reconstruction Algorithm (Sugita, 2007a,b) and the Multiple Scenario Approach (Bunting and Middleton, 2009).