

Historical distribution modelling: an extension of biogeographical methods for use in palaeoecological studies

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Our understanding of the major biological developments and ecological regime shifts that have occurred over the history of our planet are largely informed from palynostratigraphy. From the composition of pollen types found in sediments it has been possible to reconstruct detailed time series of vegetation cover, associated climate, and even metrics of productivity. However, despite the enviable temporal resolution of datasets arising from such studies, the geographic distribution of sampled pollen cores is patchy: some areas present technical challenges for sampling or lack sites with suitable taphonomic properties.

In order to help reconstruct a more complete spatio-temporal picture of vegetation cover, palaeoecologists have begun to import statistical tools from modern biogeography. These ‘species distribution models’ (SDMs) have proven very useful in modern ecology for a variety of uses such as estimating the range of species with few observation records (rare species and/or ones of conservation concern), assessing the risk from invasive species, and determining the climatic limitations to a species range. Unfortunately, classical SDMs exhibit a number of characteristics that have, until recently, limited their applicability in palaeoecology. Firstly, SDMs define a regression relationship between the occurrence of the taxa in question and the climate that is then projected onto the relevant location or time period that the investigators wishes to make a prediction for. This assumes that the relationship between the occurrence frequency and the climate is constant across the study time period. This assumption of niche uniformitarianism may be reasonable in modern ecological studies but quickly breaks down when the study period spans millennia or longer. Secondly, SDMs typically use occurrence data (presence/absence) and/or frequency data in building these climate relationships. The pollen assemblage data that is garnered from most palynostratigraphical studies is instead compositional in nature. This causes problems in standard SDMs as it is difficult to disentangle the potential scenario where a taxa is declining in relative frequency because the climate is changing in a way that is making the local environment less suitable for it, from another scenario where the climate is changing to be more favourable to one of the other taxa in the pollen assemblage.

We present here an extension of a particular class of SDMs, implemented as Multinomial Gaussian Markov Random Fields (Multinomial-GMRFs), to allow for the correct treatment of compositional pollen assemblage data. These models allow for a relaxation of the principle of niche uniformitarianism by allowing for a plastic niche response over time whilst ensuring that correct notions of temporal dependency are observed. We demonstrate how these models can be used to reconstruct pollen inflow distributions over time (related to the spatio-temporal distribution of the relevant taxon) and produce estimates of niche shift. The tools described here are included as part of the **Palaeo-Geographic Analysis** package (PAGAN) for the R statistical platform: a package currently in development as a product of the quantitative palaeoecological working group of the European Pollen Database (EPD).