Quaternary Science Reviews 31 (2012) 1-16

Contents lists available at SciVerse ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Invited review

Reconstructing palaeoclimates from biological proxies: Some often overlooked sources of uncertainty

Brian Huntley

School of Biological and Biomedical Sciences, Durham University, South Road, Durham DH1 3LE, United Kingdom

ARTICLE INFO

Article history: Received 21 February 2011 Received in revised form 7 November 2011 Accepted 8 November 2011 Available online 29 November 2011

Keywords: Bioclimatic variables Thermal sum Moisture index Microclimate Mesoclimate Macroclimate Multi-proxy Concurrent reconstruction Ouaternary

ABSTRACT

Palaeoclimatic reconstructions from biological proxies, remains of organisms, suffer from sources of uncertainty that frequently are unacknowledged or even unrecognised. Primary amongst these is the need to identify, using available biological knowledge and understanding, the variables to which the organism(s) providing the proxy are sensitive, and hence that it is appropriate to reconstruct. These variables generally are not those conventionally recorded at meteorological stations, although they may be derived from these simply or using appropriate models. In the case of smaller organisms living close to the ground, in soil, or in aquatic environments, appropriate variables will relate to the microclimate. Reconstructing inappropriate variables introduces uncertainties and, especially under changed climatic conditions, is likely to give inaccurate results.

A second important source of uncertainty arises when variables are reconstructed in isolation. In reality, most organisms respond concurrently to many variables, although two or three of these will usually predominate; these predominant variables also often have interacting effects. Isolating individual variables for reconstruction frequently will result in inaccurate reconstructions, the response to a second variable being aliased as an apparent change in the reconstructed variable. This can be overcome by concurrent reconstruction of the small number of variables that principally determine the distribution and abundance of the organism(s) from which the proxy is derived.

Multi-proxy studies may give greater insight, but only when appropriate variables are reconstructed from each proxy. Further reductions in uncertainty, and new insights, are likely in future to be achieved by making concurrent reconstructions from two or more proxies, rather than, as at present, making separate reconstructions that may give incompatible results. The practice of making one-at-a-time reconstructions from individual samples along a core or profile often generates unrealistic sample-to-sample variability. Recent advances in the application of Bayesian modelling frameworks, however, offer concurrent reconstructions of two or more variables made concurrently for all samples in a sediment sequence. Recent improvements in the tools available to derive age-depth models open the possibility that in the near future it will be possible to make concurrent reconstructions from all samples from each of a series of sediment sequences. Knowledge of the physics of the climate system can then provide constraints on the spatial and temporal patterns in reconstructed values, further reducing their uncertainties.

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1. Introduction

Biological proxies, the remains of various organisms preserved in sediments and other archives, have long been used as a basis for quantitative inferences about past climatic conditions during the Quaternary. One of the best known early examples was the use by Iversen (1944) of pollen of three taxa, *Hedera* (Ivy), *Viscum* (Mistletoe) and *Ilex* (Holly). In northern Europe each of these pollen taxa represents a single plant species; furthermore, all three are entomophilous (insect pollinated), meaning that when their pollen is found in sediments the species can be assumed to have been growing nearby. In addition, the three species have distinct northern and eastern geographical range limits in Europe associated with their differing tolerances with respect to winter cold and their differing requirements with respect to summer warmth (Fig. 1). Thus, depending upon which of the three are represented in a pollen spectrum from a given place and time, Iversen (1944) proposed that both July and January temperatures can be constrained to the range corresponding to the conditions suited





E-mail address: brian.huntley@durham.ac.uk.

^{0277-3791/\$ —} see front matter \odot 2011 Elsevier Ltd. All rights reserved. doi:10.1016/j.quascirev.2011.11.006

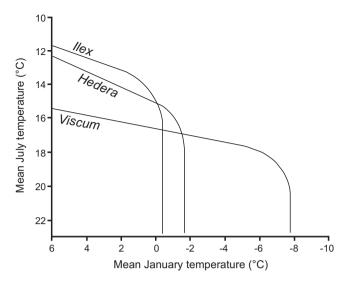


Fig. 1. Winter and summer temperature limits of *Hedera*, *Viscum* and *Ilex* in northern Europe. The three species occur only below and to the left of the lines that indicate their winter and summer temperature limits. That the two variables considered interact to determine the species' range limits is indicated by the upper lines not being parallel to the horizontal axis. Note the reversed scales (Re-drawn from Huntley and Birks, 1983; after Iversen, 1944).

for those taxa represented. Much later, as increasing computing power made possible the use of multivariate data analytical and statistical methods in the development of numerical approaches to the reconstruction of palaeoenvironments, Imbrie and Kipp (1971) pioneered the development of what are often referred to as 'transfer functions'. Their method was based upon a factor analytic approach to multivariate microfossil data from marine sediments and provided reconstructions of ocean temperatures. Since these pioneering studies, a wide range of reconstruction methods has been developed and applied to many different biological proxies. Quantitative reconstructions of climatic variables, of ocean environmental conditions (e.g. seasonal sea surface temperature, sea-ice cover, salinity) or of freshwater conditions (e.g. pH, available phosphorus), derived from biological proxies, are now a routine component of most studies of Quaternary palaeoenvironments.

The purpose of the present paper is not to provide a review of the strengths or limitations of alternative statistical and other methods (e.g. the use of indicator species) that have been applied to make these quantitative reconstructions, nor is it to review the relative advantages or disadvantages of different biological proxies as sources of information about past climates. It is also not my intention to attempt an exhaustive review of the numerous sources of uncertainty in the reconstructed values. Instead, the focus of this paper primarily is upon a key source of uncertainty that frequently is overlooked, as well as upon a second area of uncertainty that rarely is adequately quantified or taken into account. The first of these are the uncertainties that arise as a consequence of decisions made about which, and how many, climatic variables to reconstruct from a given biological proxy, and the second is that which arises when we wish to compare or combine results from the same or different proxies/ reconstruction methods used at different locations, namely the chronological uncertainty in age-depth models for the individual sedimentary records that we wish to compare or combine. The first of these sources of uncertainty will receive the greater amount of attention, principally because it is so often not even perceived as a source of uncertainty by those making quantitative reconstructions.

2. Selecting the appropriate climatic variable(s) to reconstruct

For reasons associated with the temperature-sensitivity of enzyme-catalysed reactions, and hence of metabolic processes generally, the organisms represented by biological proxies will have some sensitivity to "temperature". In the case of terrestrial organisms, because most biological processes occur in an aqueous medium, they also will have some degree of sensitivity to "moisture". Of course, some of the organisms whose remains might be used as proxies for past climatic conditions may also be sensitive to other aspects of climate. For example, many species representing a range of major taxonomic groups exhibit sensitivity to winter snow depth and/or duration, including birds (e.g., amongst species recorded relatively frequently in the Pleistocene fossil record (Tyrberg, 1998), Pyrrhocorax pyrrhocorax – Chough – is a sedentary ground feeder and is absent from areas with regular winter snow cover (Cramp and Perrins, 1994)), mammals (e.g. Alces alces – Elk – cannot tolerate snow depths exceeding ca 70 cm (Wilson and Mittermeier, 2011)) and many plants (Körner, 2003). Nonetheless, as the numerous studies that have fitted species' distribution models or niche models for a wide range of terrestrial organisms have shown (e.g. Huntley et al., 2004, 2007; Araújo et al., 2006; Thuiller et al., 2006, 2005; Settele et al., 2008), "temperature" and "moisture" are guite generally of primary importance, other variables to which individual species or groups of organisms may be sensitive being of secondary importance.

Having recognised the primary importance of "temperature" and "moisture", it is obviously simplest to develop models relating biological proxies to conventionally measured and widely reported climatic variables, for example, mean annual temperature and/or mean annual precipitation. Indeed, a majority of published studies reporting quantitative reconstructions from biological proxies that can be assumed to reflect the regional macroclimate (e.g. pollen) has considered such variables (see e.g. Guiot et al., 1989; Seppä and Birks, 2001; Bigler et al., 2002; Bjune et al., 2004; Xu et al., 2010). In reality, however, the species whose remains provide the biological proxies that we use very rarely respond to such simple climatic variables. In addition, they also rarely respond to individual climatic variables in isolation. Using an inappropriate variable, and/or failing to take into account other interacting variables, will often manifest itself as a systematic shift between geographical regions in the threshold value for the variable used. The study by Conolly and Dahl (1970) of climatic constraints upon the distribution of Arctic-montane plant species in the British Isles provides a clear illustration of this phenomenon, with the limits of various species corresponding to different values of the same climatic variable in Wales versus Scotland.

Rather than selecting from the readily available and widely reported climatic variables, the first step when developing a model relating a biological proxy to climate thus should always be to seek to understand the climatic sensitivities that are likely to determine the range and abundance of the organism(s) whose remains provide the proxy. In doing this it is essential to recognise that whilst some aspects of the climate may operate directly upon the organism, others may operate through indirect mechanisms that nonetheless are just as important. The need to identify sensitivities, and hence to select the appropriate variables, is readily comprehended by considering the sensitivity of a majority of terrestrial species to low temperatures. Whilst the absolute minimum temperature that different species can tolerate varies across major taxonomic and/or functional groups (see e.g. Woodward, 1987; Larcher, 2003), only a minority of species do not exhibit some threshold temperature below which they are unable to survive. In addition, however, a large number of terrestrial species from Download English Version:

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