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POLLEN-BASED CLIMATE RECONSTRUCTIONS IN THE EUROPEAN PLEISTOCENE: THE MODIFIED INDICATOR SPECIES APPROACH AS A TOOL FOR QUANTITATIVE ANALYSIS

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ABSTRACT. To obtain quantitative palaeoclimate data from Pleistocene pollen records we analyzed the potential of the indicator species approach introduced by Iversen (1944). The methodology of this approach was modified to increase its climatic resolution: In contrast to the original concept, all members from an assemblage are evaluated. Thus we established a databank describing the climatic requirements of 85 plant taxa from European pollen records. As a second step, a procedure is introduced to assess the 70% probability intervals for the actual temperatures within the original intervals obtained through the approach. For the routine evaluation of the mean January and July temperatures a computer algorithm executing the calculation steps was developed. The modified approach was applied to the Holsteinian pollen sequence of Lac du Bourget (northern French Alps). For this pollen record our modified approach yields a detailed temperature reconstruction for cold and warm episodes. The resolution for the mean January and July temperatures varies between less than 1 and 2.5°C.

KEY WORDS: pollen, megafloras, indicator species approach, quantitative palaeoclimatic reconstruction, Pleistocene, Holsteinian

INTRODUCTION

For quantitative reconstructions of past Quaternary climate conditions, pollen and spores have proven to be the best proxies in terrestrial depositional environments (Birks & Birks 1980). Their parent plants are very sensitive to climatic changes, and they are abundant in a wide range of continental sedimentary settings, thus allowing a high temporal and spatial resolution as well as a relatively continuous record of climate reconstructions (e.g. Tzedakis *et al*. 1997).

Quantitative palaeoclimate analyses using pollen and spores so far are mostly based on the quantitatitive relationship between relative pollen abundances and climate factors. The approaches relying on this principle have yielded palaeoclimatic data reaching back as far as 140,000 years (Guiot *et al*. 1989). Each of these techniques, i.e. transfer functions (e.g. Howe & Webb 1983, Bartlein & Webb 1985, Huntley & Prentice 1988), pollen-climate response surfaces (e.g. Bartlein *et al*. 1986, 1998, Prentice *et al*. 1991), or modern analogues methods (e.g. Guiot 1987, Guiot *et al*. 1989), however, also have important limitations. Most notably, not all plant communities and climate scenarios known from the Pleistocene are represented today. This implies a lack of modern analogues for certain fossil pollen spectra (Guiot 1987, Aaby & Tauber 1995) which may result in inaccurate or even unrealistic climate reconstructions. Moreover these approaches are sensitive to taphonomic processes which may have influenced the assemblages the study material is derived from. Finally they do not allow the quantitative climatic evaluation of megafloral remains (fruits, seeds, leaves, twigs, or wood) which often can be identified to a lower taxonomic level than pollen and spores and thus may yield more specific climate information.

The objective of this paper is to investigate a method for quantitative palaeoclimate reconstructions applicable to sporomorphs and megafloras which evaluates the palaeoclimate merely based on the presence/absence of taxa. We therefore analyze the capacity and further develop the methodology of the so-called "indicator species approach" (Iversen 1944, Grichuk 1969, Grichuk *et al*. 1984). The basic principle of this approach is that for the taxa from an assemblage their specific requirements with respect to at least two selected climate parameters are established and then the palaeoclimate is determined as situated within the mutual intersection of their tolerance ranges. This concept, although neglecting the climate information inherent in relative abundances, has a number of advantages as compared to the methods discussed above: Most notably, it is independent from modern analogues in terms of plant communities since the members from an assemblage are evaluated independently from each other. Second, it is relatively robust to taphonomic bias, i.e. to the distortion of relative abundances within a given pollen spectrum. Furthermore its application is not restricted to pollen spectra, but is also possible with respect to megafloral assemblages.

DATABASE

As a first step we established a databank which so far contains the climatic requirements of 85 plant taxa described from European Quaternary pollen records. So far information regarding six climate parameters (mean temperatures of the coldest and warmest months, mean annual temperature, mean annual precipitation, mean minimum and mean maximum monthly precipitation) is available. The climatic requirements were obtained from the geographical distribution areas of the specific plants as described in the literature (e.g. Frenzel 1968, Jalas & Suominen 1989, Meusel & Jäger 1992). The sizes, shapes and positions of these areas are controlled by a multitude of factors such as competition with other species, nutrient supply, and day length. Climate, however, is considered the most potent factor regulating their confinement (Woodward 1987).

For each of the taxa examined the specific climatic data from within the distribution areas were determined on the basis of the global climatology of New *et al*. (in press) which provides values for each of the considered different climate parameters in a resolution of 0.5° latitude by 0.5° longitude. Depending on the size of the specific distribution areas between 800 and 10,000 geographical points and their corresponding climate data per taxon were measured. So far we have focussed on the the concurrent consideration of the mean temperatures of the coldest and warmest months (MTC and MTW). The relevance of these climate parameters in defining a plant's distribution area has been described by many authors (e.g. Iversen 1944, Walter & Straka 1970, Huntley 1992).

METHOD

A fundamental step in the climate reconstruction is the transformation of the modern geographical distribution areas of each of the taxa from a fossil floral assemblage into climatic distribution areas. This is achieved by plotting the climate values from within the plants geographical distribution areas into a diagram whose axes are climatic parameters such as the MTC and MTW (Fig. 1). The obtained area of overlap of all taxa then represents the climatic space or thermosphere in which all these taxa can coexist and thus expresses the specific climatic requirements of the fossil assemblage. For instance, the assemblage shown in Fig. 1 consists of the plant taxa A, B, and C. The area of overlap formed by their climatic envelopes is characterized by intervals of -4.7 to -0.2°C for the MTC and 13.4 to 15.6°C for the MTW. The most straightforward climatic interpretation of the area of overlap relies simply on the extreme values for each climate parameter. This procedure, however, does not utilize the full climatic resolution of the technique. In two-dimensional diagrams, for instance, the obtained values define a rectangle with respect to the common climatic space which is larger than the actual, irregularly shaped area of overlap. Direct interpretation of the area of overlap thus bears the potential to further constrain the size of the common climatic space as compared to the rectangle evaluation, but handling, evaluating and illustrating this information gain is very complex.

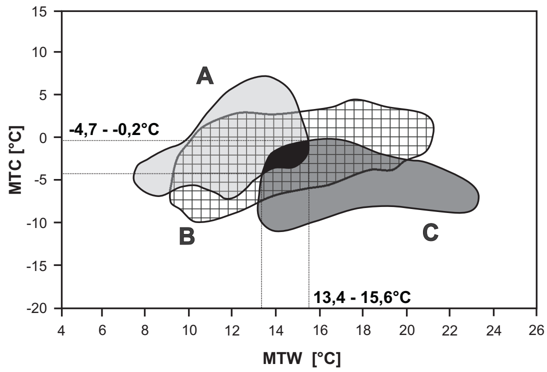

Fig. 1. Principle of the indicator species approach. The common climatic space of the taxa A, B, and C is marked in black. Common climatic intervals range from -4.7 to -0.2°C for the MTC and 13.4 to 15.6°C for the MTW

For a given assemblage it is possible that the climatic distribution area for a taxon does not overlap with the areas of the other members of the assemblage. This can be due to the fact that either the database used does not fully cover the geographical and thus also climatic distribution areas of the taxa from the assemblage, the climatic and/or ecological requirements of the recent representatives of some taxa from the assemblage may have changed with time, or that the taxon does not represent an original member of the assemblage, but is derived from a very different environment or reworked from older strata.

METHODOLOGY OF THE APPROACH

Mathematically the crucial step in the methodology of the approach is to register and describe the modern plants climatic distribution areas and to find an algorithm for the calculation of the thermospheres. In case of two-dimensional reconstructions, the modern plants climatic distribution areas can be described by (n, m) matrices whose sizes depend on the resolution desired and climatic range to be covered. The matrices A_p describing the climatic distribution areas of the recent plants p, $1 \leq p \leq r$ (with r as the maximum number of recent plants)

may be defined as $$A_p = \begin{bmatrix} a^p_{11} & . & . & . & a^p_{1m} \\ . & & & & . \\ . & & & & . \\ . & & & & . \\ a^p_{n1} & . & . & . & a^p_{nm} \end{bmatrix},$$

where a_{pij} describes the occurrence of a given plant p for a MTC c_i and MTW w_j for $1 \leq i \leq n$ and $1 \leq j \leq m$.

The notation is

$$a^p_{ij} := \begin{cases} 1 \text{ if } (c_i, w_j) \text{ is situated within the envelope of plant } p \\ 0 \text{ otherwise} \end{cases}$$

for $1 \leq i \leq n$ and $1 \leq j \leq m$. This means that each matrix Ap either contains entries of 1, if at a specific position a combination of MTC and MTW values is realized, or of 0, if no such combination exists at that point. In this way the climatic distribution areas of all Recent plants are expressed. The common climatic space of an assemblage then is computed by overlaying the single matrices: With I_k being the index set of all plants from the assemblage k to be evaluated, the common climatic space F_k can be expressed as

$$F_k = \begin{bmatrix} \prod_{p \in I_k} a_{11}^p & \cdots & \prod_{p \in I_k} a_{1m}^p \\ \vdots & & \vdots \\ \prod_{p \in I_k} a_{n1}^p & \cdots & \prod_{p \in I_k} a_{nm}^p \end{bmatrix}.$$

In other words, the entry at a given point within F_k is exactly 1, if all single entries within the A_p , $p \in I_k$ are 1. Thus the resulting matrix again only contains values of 1 or 0 and fully describes the common climatic space of the assemblage. From this matrix, the minimum and maximum values for the MTC and MTW as well as the area of the climatic space can be extracted.

POSITIONS OF ACTUAL CLIMATE VALUES WITHIN CALCULATED INTERVALS

There is a priori no restraint where within the calculated climatic space or interval the climate value actually measured for this flora is situated. In practice, however, additional information on the actual positions within the calculated intervals is highly desirable. In order to obtain an indication for these positions, we generated more than 3,000 artificial floras from all European vegetational and geographical units on the basis of our databank. The MTC and MTW intervals calculated for these floras then were compared to the temperature values as given for each of the corresponding geographical positions by New *et al*. (in press). The results show a high statistical correlation between the extreme values of the calculated temperature intervals as well as the interval widths and the 'real' temperatures within these intervals: For very cold floras, which at the same time have the widest intervals of coexistence, the actually prevailing temperatures are found in the lowermost, i.e. coldest parts of the calculated intervals. With increasing minimum temperatures and decreasing interval widths, the positions of the 'real' temperatures gradually shift towards the higher, i.e. warmer parts of the pertinent computed intervals. This correlation allows to gain further information from the common climatic as the probable position of the actually prevailing temperature within the calculated interval can be assessed. For the routine application of this constraining procedure to floral assemblages we chose to determine the 70% probability intervals for the actual temperatures within the originally calculated climatic spaces.

APPLICATION TO A FOSSIL POLLEN RECORD

To practically apply the modified approach to Pleistocene pollen spectra, we selected a pollen record from the section Aéroport Militaire du Bourget-du-Lac from the Holsteinian of the northern French Alps (Fig. 2). This palynoflora is derived from shaly coals reaching 3.5 meters in thickness. The coals are underlain by clastic limnoglacial sediments which were deposited after glacial retreat, and are overlain by fine clastic sediments glacially deformed at least once during the Weichselian Cold Stage. U-Th and ^{14}C dating yielded ages of 78,000 years BP and minimum ages of >46,000 and >50,000 years BP, respectively, for the series (Gremmen & Hannss 1994). Due to its stratigraphic position with respect to the overlying Quaternary sequence the examined section is assigned a Holsteinian age (Hannss unpublished data).

The section, which is palynologically represented in 52 samples, comprises an entire temperate stage including the immigration and extinction of thermophilous deciduous forest elements. It has been subdivided into six pollen zones (Peschke, unpublished data) which are briefly described in the following: Zone A documents the *Pinus*-*Betula* phase of an ending cold stage with abundant NAP. The AP are dominated by *Pinus* and *Betula*, *Alnus* and *Salix* are present in low numbers. In zone B *Pinus* reaches its maximum abundance in the entire section. At the same time *Corylus* appears, and the percentages of *Betula* and NAP decline. Zone C encompasses the immigration of thermophilous deciduous forest elements: *Picea* values increase, whereas *Pinus* and *Betula* abundances decline steadily. NAP abundances are low and lack heliophytes and cold stage indicators. Zone D represents a mixed oak forest phase with high abundances of *Abies* and *Alnus*. *Carpinus* is also present. The optimum of the entire temperate stage can be assumed in the upper part of zone D due to the onset of *Taxus* and an increase of mixed oak forest elements. Core loss, however, renders an interpretation of this period impossible. In zone E mixed oak forest elements, *Carpinus*, and *Corylus* slowly retreat and are replaced by *Picea*. In the upper part of the zone *Pinus* and *Betula* become more abundant. Zone F is dominated by *Picea* and *Pinus* which make up for more than 80% of total pollen. *Carpinus* has disappeared from the pollen spectrum, and neither mixed oak forest elements nor *Corylus* play a role in the forest vegetation. NAP is only present in low numbers and barely contains heliophytes.

The three-dimensional illustration of the climatic spaces reconstructed by the indicator species approach on the basis of all taxa shows the general trend in terms of climatic change (Fig. 3). Large spaces with long distances between MTC maxima and minima indicate cold

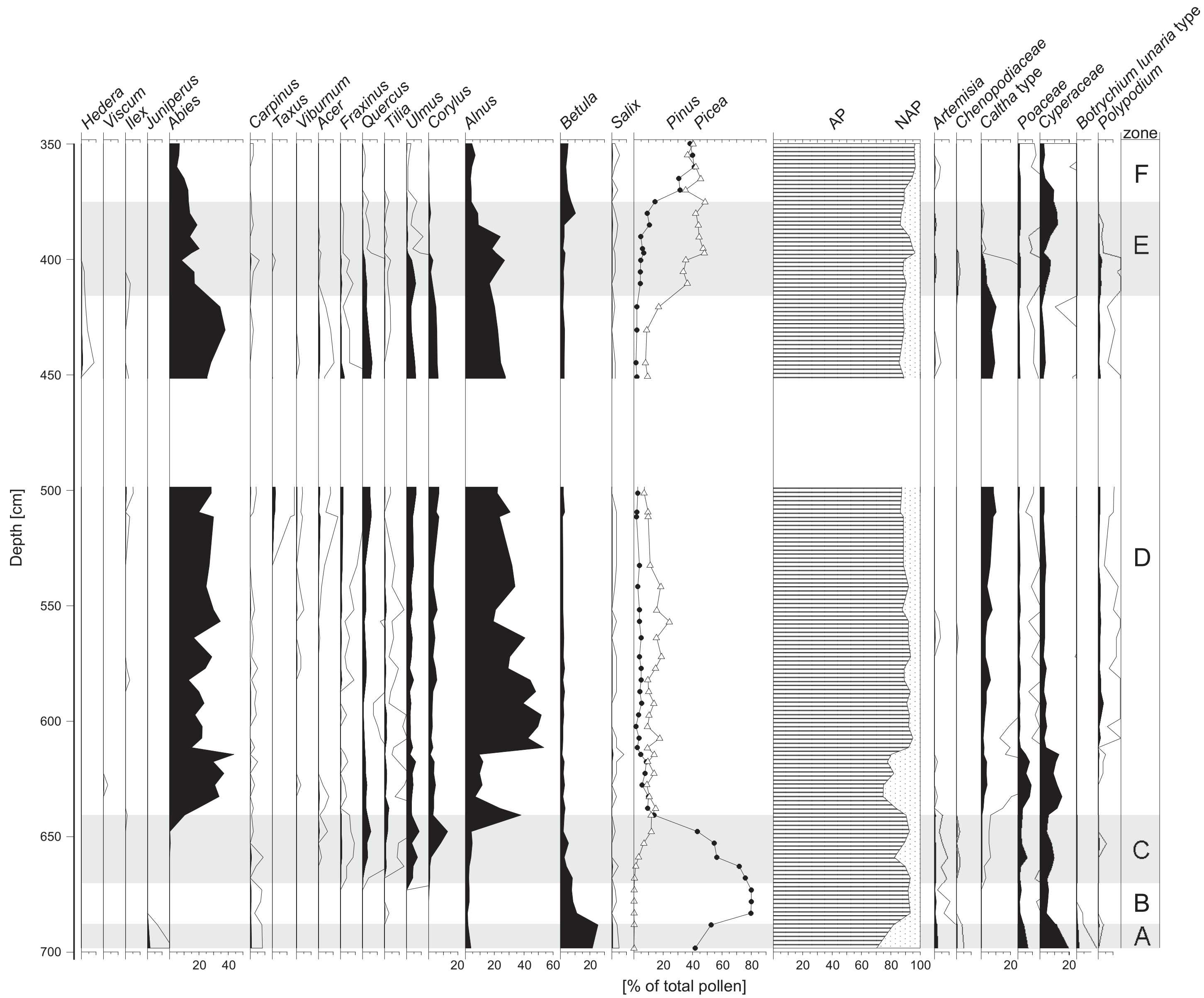

Fig. 2. Pollen diagram of the Aéroport Militaire du Bourget-du-Lac section. A part of the taxa has been omitted for greater clarity. Modified after Peschke (unpubl. data)

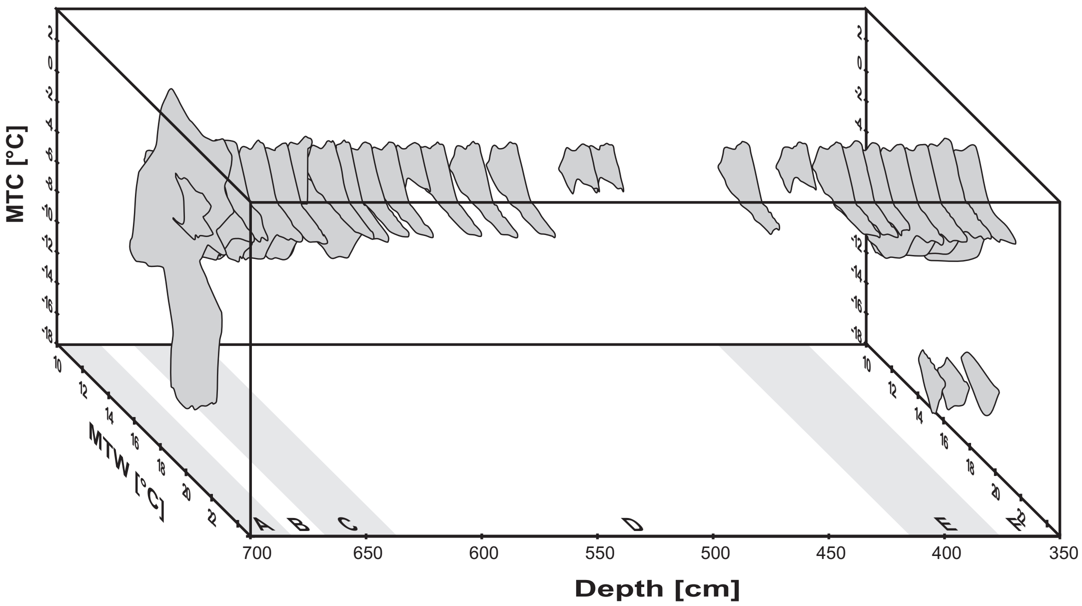

Fig. 3. Three-dimensional illustration of the climatic spaces for the Aéroport Militaire du Bourget-du-Lac section. Large spaces with wide distances between MTC extreme values indicate cold episodes, small spaces with short distances for both climate factors characterize warm periods

floras and therefore cool periods. In the contrary, small spaces with short distances for both climate factors occur during warm periods. The temperature values as resulting from the application of the constraining procedure at the same time corroborate and differentiate the signal obtained from the pure indicator species approach (Fig. 4). The 70% probability intervals confirm the temperature deterioration at the transition of the zones A and B. For zone B they suggest MTC minimum values between -10 and -14°C and corresponding MTW values ranging from 19 to 20.5°C. This testifies to a high continentality for that time. During zone C the probability intervals for the MTC shift towards higher temperatures and remain stable all through zone D and the early part of zone E. They are situated near the upper boundary of the climatic intervals as obtained by the pure indicator species approach and range from 1 to 2°C. This MTC signal is combined with MTW temperature fluctuations between 17 and 21°C. Thus the degree of continentality has obviously decreased for this warm period. If compared to Recent temperatures in the Lac du Bourget region, the MTC and MTW intervals of the upper zone C, zone D and early zone E are in good agreement with the corresponding values as realized today (1.5°C and 20.1°C, respectively). With the end of zone E and the onset of zone F the MTC values covered by the probability intervals drastically drop from between 1 and 2°C to between -12 and -14°C. The corresponding MTW temperatures also decline, but to a lesser extent. This again implies a strong increase in continentality with the end of the warm episode represented by zone D and lower zone E and indicates the beginning of a new cold stage.

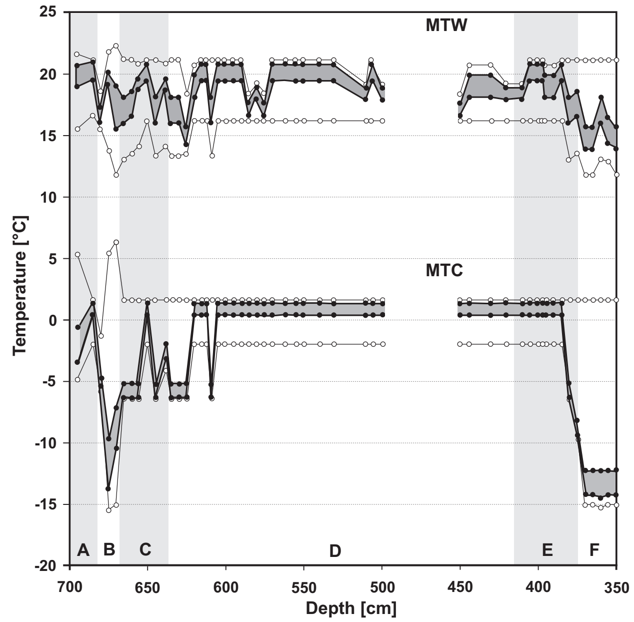

Fig. 4. Application of the 70% probability procedure to the Aéroport Militaire du Bourget-du-Lac section

DISCUSSION AND CONCLUSIONS

The modified indicator species approach can serve as a useful tool for obtaining quantitative palaeoclimatic data from pollen sequences from all periods of the Quaternary. As it relies on the presence/absence of taxa only and does not evaluate taxon percentages, it is fully independent from modern analogues in terms of plant communities. At the same time it exhibits a high degree of robustness to taphonomic alterations of the original associations and thus is applicable to material from a wide range of depositional environments. The application to fossil megafloral assemblages is possible and, since megafloral remains often can be determined to the species level, may provide even more specific climate information than pollen. The resolution with respect to temperature parameters is highest in warm periods and lowest in cold episodes. This can be attributed to two reasons: During cold episodes plant diversities are generally lower than in warmer periods due to the extreme environmental conditions. At the same time, cold stage climates generally exhibit a larger degree in continentality than temperate stages. Under such conditions continental taxa, which are a priori very tolerant to temperature changes, generally prevail. Their climatic spaces are wider than those of more oceanic taxa. Additional information on the position of the actually prevailing temperature value within the calculated intervals can be obtained by an additional procedure. It calculates the 70% probability for these positions and thus drastically increases the resolution for both for colder and warmer episodes. Altogether, the modified indicator species approach can make a valuable contribution to fully exploit the potential of Quaternary pollen and megafossil assemblages for quantitative palaeoclimate analyses. As it is independent of modern analogues in terms of plant communities, it allows to apply pollen-based quantitative climate reconstructions further back to the geologic past.

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