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The Coexistence Approach—Theoretical background and practical considerations of using plant fossils for climate quantification

T. Utescher[a,j,*], A.A. Bruch[b], B. Erdei[c], L. François[d], D. Ivanov[e], F.M.B. Jacques[f], A.K. Kern[g], Y.-S.(C.) Liu[h], V. Mosbrugger[a], R.A. Spicer[i]

[a] Senckenberg Research Institute/BiK F (Loewe), Senckenberganlage 25, 60325 Frankfurt am Main, Germany
[b] Heidelberg Academy of Sciences and Humanities, Research Center 'The Role of Culture in Early Expansions of Humans' at Senckenberg Research Institute, Senckenberganlage 25, 60325 Frankfurt am Main, Germany
[c] Hungarian Natural History Museum, Botanical Department, Könyves K. krt. 40, Budapest 1087, Hungary
[d] Unité de Modélisation du Climat et des Cycles Biogéochimiques (UMCCB), Université de Liège, Bât. B5c, Allée du Six Août 17, B-4000 Liège, Belgium
[e] Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Acad. G. Bonchev Str., bl. 23, BG-1113 Sofia, Bulgaria
[f] Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, PR China
[g] State Museum of Natural History Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany
[h] Department of Biological Sciences, East Tennessee State University, Johnson City, TN 37614, USA
[i] Environment, Earth and Ecosystems, Centre for Earth, Planetary, Space and Astronomical Research, The Open University, MK7 6AA, UK
[j] Steinmann Institute, University of Bonn, Nussallee 8, 53115 Bonn, Germany

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ABSTRACT

The Coexistence Approach was established by Mosbrugger and Utescher (1997) as a plant-based method to reconstruct palaeoclimate by considering recent climatic distribution ranges of the nearest living relatives of each fossil taxon. During its existence for over more than 15 years, its basics have been tested and reviewed in comparison with other terrestrial and marine climate reconstruction techniques and climate modelling data. However, some controversies remain about its underlying data or its applicability in general.

In view of these controversies this paper discusses the power and limitations of the Coexistence Approach by summarising past results and new developments. We give insights into the details and problems of each step of the application from the assignment of the fossil plant to the most suitable nearest living relative, the crucial consideration of the usefulness of specific taxa towards their climatic values and the correct interpretation of the software-based suggested palaeoclimatic intervals. Furthermore, we reflect on the fundamental data integrated in the Coexistence Approach by explaining different concepts and usages of plant distribution information and the advantages and disadvantages of modern climatic maps. Additionally, we elaborate on the importance of continually updating the information incorporated in the database due to new findings in e.g., (palaeo-)botany, meteorology and computer technology.

Finally, for a transparent and appropriate use, we give certain guidelines for future applications and emphasize to users how to carefully consider and discuss their results. We show the Coexistence Approach to be an adaptive method capable of yielding palaeoclimatic and palaeoenvironmental information through time and space.

1. Introduction

Plant-based palaeoenvironmental reconstruction is a widely accepted method used for studying palaeoclimate. This potential was already recognised by Shen Kuo in the 11th century in China (Needham, 1986), as well as later in the 19th century of Europe by Heer (1855, 1856, 1859), who quantitatively estimated Neogene palaeoclimate based on plant fossils for the first time. Subsequently, biological palaeoclimate proxies have mostly relied on the principle of physiological actualism, which assigns identical dependencies of modern morphological or taxonomical units on environmental constraints to their comparative fossil equivalents. Without this principle, there would not be any correlation between the dependencies of modern and fossil phytocoenoses on changing environments (e.g., Mai, 1995; Tiffney, 2008). Therefore, several methods were developed in an attempt to reconstruct and quantify palaeoenvironmental and palaeoclimatic parameters.

Among various more specific approaches such as the analysis of stomatal data, plant–insect interaction, or biomarkers, there are two classical complementary procedures to trace past climate from plant fossils (Chaloner and Creber, 1990). One is based on physiognomy, which takes advantage of empirical correlations between climate parameters and specific plant traits like leaf anatomy (e.g., Bailey and Sinnott,

* Corresponding author at. Steinmann Institute, Nussallee 8, 53115 Bonn, Germany.
E-mail addresses: abruch@senckenberg.de (A.A. Bruch), andrea.kern@smns-bw.de (A.K. Kern).

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1915, 1916; MacGinitie, 1969; Parkhurst and Loucks, 1972; Wolfe, 1979; Wing and Greenwood, 1993; Wolfe, 1993, 1995; Wilf, 1997; Wiemann et al., 1998; Spicer et al., 2009; Teodoridis et al., 2011) or wood anatomy (e.g., Wheeler and Baas, 1993; Wiemann et al., 1998, 1999; Terral and Mengüal, 1999). As a consequence, to a large extent these are independent of taxonomic determinations. These methods are still being actively developed through more comprehensive calibration sets (e.g. Jacques et al., 2011a) and improved analytical techniques (e.g. Teodoridis et al., 2011) to overcome discrepancies between estimated and observed modern data (Wiemann et al., 2001). Thus, precision and universal applicability in time and space are continuously improved.

The second method to reconstruct palaeoclimate is based on the nearest living relative (NLR) approach. This method relies on the close relationship between modern and fossil plants and assumes that the fossil taxon had the same climatic requirements as its modern representatives. Hence, it is applied mainly in the Quaternary and Neogene, where evolutionary change of environmental requirements of each plant is regarded as minimal (e.g., MacGinitie, 1941; Hickey, 1977; Chaloner and Creber, 1990; Mosbrugger, 1999). Based on this assumption, the environmental tolerance of a modern plant with a known climatic distribution can be used to estimate the past climate. Likewise, by using the taxa of a plant fossil assemblage, the climatic information of each modern representative can be compared. If no evolutionary changes in environmental tolerance have taken place, overlapping climatic ranges between modern representatives should be the result and represent the palaeoclimate. Initial approaches in this direction were made using selected key taxa (Iversen, 1944; Hintikka, 1963; Grichuk, 1969; Zagwijn, 1996). Later, due to increasing computational facilities, all available information could be analysed and climatic ranges incorporating all relevant taxa were included in analyses. Various techniques were developed (Kershaw and Nix, 1988; Kershaw, 1997; Mosbrugger and Utescher, 1997; Fauquette et al., 1998; Klotz, 1999; Kühl et al., 2002; Greenwood et al., 2003, 2005; Klotz et al., 2006; Kou et al., 2006; Utescher et al., 2009a) differing in the method of compilation of climatic requirements, specialisation regarding organ type of fossils including the use of abundance, continental or global adaptability, as well as the application of calibration procedures, and statistical treatment of data and outliers, each having its specific strengths. The Bioclimatic Analysis approach (Kershaw, 1997; Greenwood et al., 2003, 2005) uses climatic envelopes of NLRs obtained from bioclimatic modelling of distributions of modern plant taxa (BIOCLIM). It includes a statistical treatment of outliers, and is mainly applied to micro- and megafloras of North America, Oceania, Arctic, and Antarctica. The Climate Amplitude Method (CAM) introduced by Fauquette et al. (1998) employs, secondary to the coexistence aspect, modern European pollen profiles for calibration, and therefore has its focus of application in younger Neogene European microfloras, while the Probability Coexistence Spheres (PCS) developed by Klotz (1999) is based on European plant distribution and the specific structure of the modern climate space of Europe serving for a statistical calibration procedure. Therefore, both latter methods are well best suited for the analysis of later Neogene and Holocene European palynomorph records. In the Probability Density Functions (pdf) method introduced by Kühl et al. (2002), pdfs estimated for monthly mean January and July temperatures of preselected taxa are used in order to define the most likely climate conditions. The Calibrated Coexistence Approach (Utescher et al., 2009a) employs global modern climate space in order to calibrate fossil climate conditions and at the same time specifies present-day regions that correspond to the fossil climate.

Among those technique based on the NLR concept the Coexistence Approach (CA) by Mosbrugger and Utescher (1997) was one of the first to propose a standardised procedure. The straightforward use of the climatic requirements of modern plants in a global context with respect to single parameters, and the absence of further calibration using modern pollen profiles or chorological aspect brings about robustness and universal applicability. Therefore, it has become a widely used tool to reconstruct palaeoenvironment based on a fossil plant assemblage and has yielded results in various applications from late Cretaceous to Pleistocene, well interpretable in the context of data obtained from other proxies (more than 150 publications, see 'publications' at www.neclime.de and published CA data from Eurasia on Fig. 1; Appendix 2). For comparative studies on regional and continental scale (e.g., Bruch et al., 2004; Mosbrugger et al., 2005; Bruch et al., 2006; Akgün et al., 2007; Bruch et al., 2007; Utescher et al., 2007; Akkiraz et al., 2011; Bruch et al., 2011; Ivanov et al., 2011; Liu et al., 2011; Quan et al., 2011, Utescher et al., 2011; Erdei et al., 2012; Miao et al., 2012; Popova et al., 2012; Quan et al., 2012; Yao et al., 2012) or

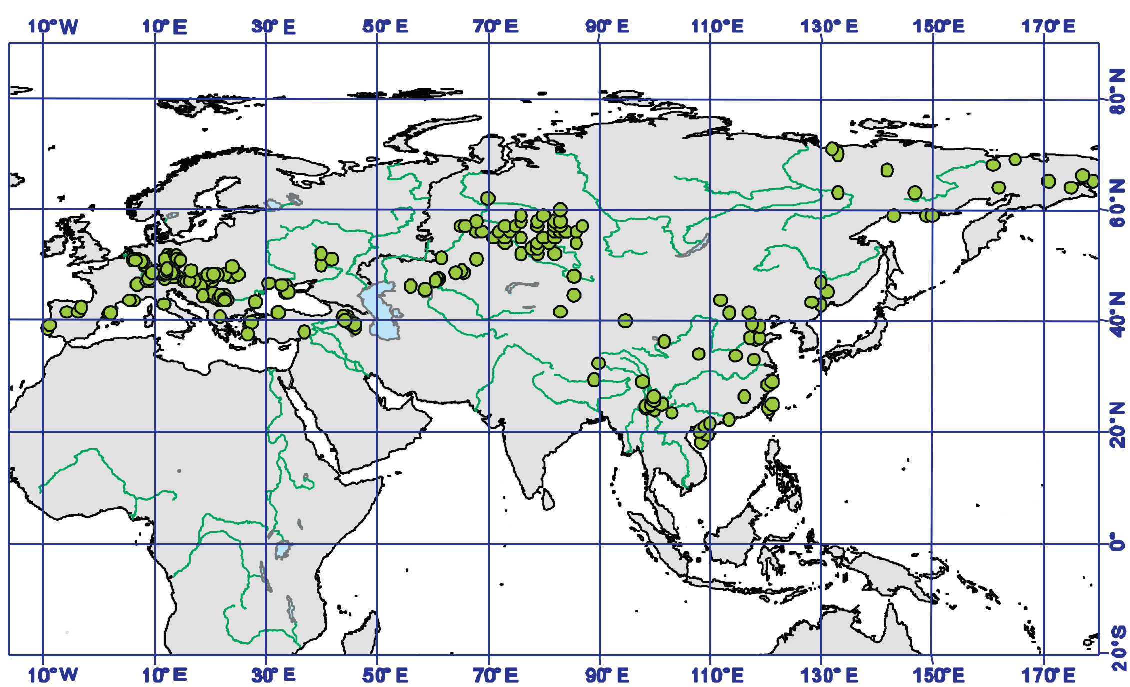

Fig. 1. Cenozoic sites of Eurasia with CA climate data sets published in Pangaea (www.pangaea.de). For coordinates and corresponding doi codes cf. Appendix 2.