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


A R T I C L E   I N F O

Article history:
Received 18 November 2013
Received in revised form 13 May 2014
Accepted 27 May 2014
Available online 2 June 2014

Keywords:
Coexistence approach
Guidelines
Palaeoclimate reconstruction
Palaeobotany
Cenozoic

A B S T R A C T

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. 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.

© 2014 Elsevier B.V. All rights reserved.

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 phytoecoenoses 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, 2014; http://dx.doi.org/10.1016/j.palaeo.2014.05.031 0031-0182/© 2014 Elsevier B.V. All rights reserved.)
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 megaflores 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 pre-selected 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.nclime.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.
model proxy comparisons (e.g., Utescher et al., 1997; Gebka et al., 1999; Micheels et al., 2007; Steppuhn et al., 2007; Micheels et al., 2009, 2011; Tang et al., 2013), CA results have provided valuable information for the understanding of large-scale climate patterns and processes over time and space. Moreover, the application of the CA evidenced the close correlation of marine and continental time series (Mosbrugger et al., 2005; Utescher et al., 2009a; Larsson et al., 2011; Utescher et al., 2012; Rasmussen et al., 2013), and revealed orbital forcing (Utescher et al., 2009b; Ivanov et al., 2011; Kern et al., 2011; Utescher et al., 2012) and short-term climate variability at suborbital scales (Kern et al., 2012).

Methodological comparisons and validations of the CA have been performed by applying the CA on different plant organ groups (leaves, seeds, wood, pollen) of one fossil flora (e.g., Mosbrugger and Utescher, 1997; Pross et al., 1998; Utescher et al., 2000; Pross et al., 2001; Bruch and Kovar-Eder, 2003; Liang et al., 2003; Utescher et al., 2012; Bondarenko et al., 2013), on the application of different methods on the same flora (e.g., Liang et al., 2003; Uhl et al., 2003; Roth-Nebelsick et al., 2004; Poole et al., 2005; Uhl et al., 2006, 2007a,b; Pross et al., 2012; Bondarenko et al., 2013), or on the comparison of CA results with other proxies (e.g., Uhl, 2006; Enron et al., 2011; Harzhauser et al., 2011, 2012; Pross et al., 2012; van Dam and Utescher, submitted for publication). In particular, the methodological differences between physiognomic and NLR approaches have been widely discussed in the literature, where a general agreement of results has been stated by various authors (e.g., Wing and Greenwood, 1993; Herman and Spicer, 1997; Mosbrugger and Utescher, 1997; Wilf, 2000). Especially, applications of the two most common leaf-based physiognomic methods, the LMA (Leaf Margin Analysis) as well as CLAMP (Climate Leaf Analysis Multivariate Program), and CA on an identical flora show consistent data in general (e.g., Liang et al., 2003; Uhl et al., 2003; Roth-Nebelsick et al., 2004; Uhl et al., 2006, 2007a,b; Xing et al., 2012; Bondarenko et al., 2013). Thus, the application of the CA has proven its consistency and reliability in palaeoclimatic reconstructions and its potential to provide important and reproducible results.

The collection of extensive CA-based palaeoclimate data derived from the palaeobotanical record has been made possible due to the international research network NECLIME (Neogene Climate Evolution in Eurasia) which was established in 1999. The main objectives of NECLIME are: (1) the quantitative reconstruction of the Neogene climate evolution in Eurasia and its patterns in time and space based on proxy data and their quantitative climatic interpretation by means of standarised techniques, (2) the reconstruction of Neogene regional and global atmospheric circulation patterns via climate modelling, (3) the analysis of the interaction between palaeogeography, vegetation and climate. More details about the concept, structure and members of NECLIME can be found on the NECLIME website (www.neclime.de).

More than 15 years have passed since the original publication of the Coexistence Approach by Mosbrugger and Utescher (1997); therefore now is an appropriate time to summarise experience, discuss the methodology accompanying its use, and to revisit the method in the light of new technological developments. Finally, we draw conclusions about the future of the Coexistence Approach as a method to reconstruct palaeoclimate.

2. The Coexistence Approach: the basics

The Coexistence Approach (CA) by Mosbrugger and Utescher (1997) is a nearest living relative method, which relies only on the presence/absence of a plant taxon within a fossil assemblage and the climatic requirements of its modern relatives. It avoids any statistical processing or further assumptions, except those given in Mosbrugger and Utescher (1997), which read as follows:

1. For fossil taxa systematically closely related nearest living relatives (NLRs) can be identified.
2. The climatic requirements of a fossil taxon are similar to those of its nearest living relative.
3. The climatic requirements or tolerances of a nearest living relative can be derived from its area of distribution.
4. The modern climatic data used are reliable and of good quality.

Accepting these assumptions, quantitative climatic results for a fossil flora can easily be reconstructed by the CA according to the following steps:

(i) For each fossil taxon, the NLR is determined.
(ii) For each NLR the modern distribution area is compiled.
(iii) From each distribution area the range of single climate parameters is determined separately.
(iv) For each climate parameter analysed, the climatic ranges, in which a maximum number of NLRs of a given fossil flora can coexist (i.e. the coexistence interval), is determined independently and considered the best description of the palaeoclimatic situation in which the given fossil flora once lived (Fig. 2A).

The application of the classical CA is facilitated by the Palaeoflora database (www.palaeoflora.de) which compiles information for steps (i) to (iii) as derived through ongoing analyses and contains climatic information about more than 1600 mostly European and Asian plant taxa. Their climatic requirements are derived from meteorological stations within the respective distribution area (see Section 4.2). Furthermore, the computer program ClimStat (CLIMATE STATistic tool; non-commercial java application by A. Heinemann) provides an easy tool for generating the coexistence intervals in step (iv). The database provides climate data for seven different climatic parameters, including the mean annual temperature (MAT), coldest month mean temperature

![Fig. 2. Case studies in the reconstruction of the coexistence intervals (dashed lines) using hypothetical MAT ranges for NLR taxa A through E. A: all taxa coexist; B: the majority of taxa coexist, taxon E is identified as outlier; C: an ambiguous solution is obtained.](image-url)
(CMT), warmest month mean temperature (WMT), mean annual precipitation (MAP), mean precipitation of the wettest month (MPwet), mean precipitation of the driest month (MPdry) and mean precipitation of the warmest month (MPwarm).

Because the Coexistence Approach relies only on the presence or absences of taxa and not on their abundances it is largely independent of sampling size or sampling intensity and can be applied on all plant fossil organs, and where the assemblage is diverse, the CA is robust to taphonomic filtering. Each taxon (even each specimen) provides its climatic information for the analysis, independent of the occurrence of other taxa or other specimens. In extremis, a single (reliably determined) fossil can provide valuable palaeoclimatic information. However, climatic intervals of a single taxon usually are wide and therefore do not offer useful precision. A higher number of taxa – the consideration of all taxa of a given flora – can usually yield narrower intervals (higher resolution) and more precise results. Although the CA can work with at least two known NLRs with climate data, only the analysis of a high number of taxa has the potential to detect errors, or evolutionary drift within the dataset, or evolutionary drift of a taxon regarding its environmental tolerances, and thus increases the reliability of reconstruction. Generally, a fossil flora should at least have ten climatically significant taxa, i.e. with NLRs with available climate data (Mosbrugger and Utescher, 1997). In single cases, a lower number of taxa contributing with climate data can be admitted, depending on the problem and resolution required.

There is no definite way to identify the accuracy of the method. Accuracy is likely to vary according to various factors such as regional and stratigraphical representativeness of the considered flora, diversity, floristic composition, taxonomic level, and quality of climate data. Accuracy also varies with respect to the parameter examined (see Section 4.2). A high diversity of the analysed record generally enhances the climatic resolution of CA reconstructions and, as a function of the grade of overlapping, accounts for a higher statistical significance of the results (Mosbrugger and Utescher, 1997). The quality of the primary climate data defining the boundaries of resulting coexistence intervals likewise plays an important role for estimating the accuracy of the calculated climate data. Therefore, these data should be verified, especially in the case of non-overlapping and if ambiguous solutions are obtained (see Sections 3.1 and 3.3). Short of inventing a time machine, accuracy of the CA can only be assessed using consilience between multiple palaeoclimate proxies, and this applies to all palaeoclimate proxies.

Even if the CA potentially offered perfect accuracy, each of the analytical steps includes the potential for error. Moreover the basic assumptions needed for the CA, such as the identification of proper NLRs (see Section 3.3), the reliability of the climate data set used (see Section 4), or the applicability of the method in general (see Section 6) needs examining. These issues are discussed in the following sections.

3. Determination of nearest living relatives

Being a taxonomic approach, the CA is closely connected to the quality of determination of the fossils and the reliability of recognising their NLRs. Those are all general tasks and problems in palaeobotany and are therefore not confined to the application of the CA. However, the level of determination of each taxon as well as the assignment of one (or several) NLRs to a fossil taxon considerably impacts the CA results. The identification of palaeobotanical remains and their NLRs depends on organ type and preservation status. Depending on morphological traits displayed by the fossil taxon, and closeness of phylogenetic relations to modern species the taxonomic level of NLR identification varies between species, genera or family levels.

Considering fossil pollen grains, it has been notoriously difficult for a long time, to trace their botanical affinities. Nowadays, however, many problems can be solved due to the combined use of the light and scanning electron microscopy (TLM/SEM) (e.g., Ferguson et al., 2007). In addition, the introduction of a standardised terminology of recent and fossil pollen micromorphology by Punt et al. (2007) and Hesse et al. (2009) has improved the possibility to compare and correctly identify the NLRs. Moreover, several important pollen atlases were published, e.g. the Atlas of Pollen and spores of the Polish Neogene (Stuchlík, 2001, 2002, 2009) for the Cenozoic of Central Europe, which provide not only highly valuable light and scanning electronic microscopic pictures for comparison, but also important remarks towards the pollen taxon’s NLRs. Other examples can be found for lower vascular plants (Grimsson et al., 2011), gymnosperms (Grimsson and Zetter, 2011; Grimsson et al., 2011), and angiosperms (e.g., Quercus, Liu et al., 2007; Lagerstroemia, Liu et al., 2008; Fagaceae, Denk et al., 2012).

With megafossil remains, major progress has been made in the identification of suitable NLRs within the past two decades of palaeobotanical research by using classical techniques such as comparative morphology and leaf anatomy (e.g., Mai and Walther, 2000; Kunzmann and Mai, 2005; Kovar-Eder et al., 2006; Erdei et al., 2007; Teodoridis et al., 2009; Collinson et al., 2012; Kvaček and Walther, 2012). Moreover, the NLR concept of taxonomic units has benefited from recent advances in the study of morphotypes. In particular, the “whole plant approach” and the introduction of complex taxa may prove beneficial for developing sound NLR concepts and is, in addition, essential to unravel true palaeobiodiversity. Examples for recently established complexes are Cruigia bronni Ung. complex (Worobiec et al., 2010), and Reevesia hurnikii Kvaček complex (Worobiec et al., 2012), allowing the attribution of leaves, fruits and pollen to one single fossil species. Moreover, phylogenetic studies became increasingly important over the last decade (e.g., Fagaceae, Manos et al., 2001; Denk et al., 2012; Cupressaceae, Yang et al., 2012; Meliaceae, Müllner et al., 2010). The improved understanding of phylogenetic relations within plant families and genera may facilitate the better identification of modern reference taxa or clades thus rendering NLR concepts more reliable (cf. also reports of the NECLIME working group on taxonomy of the Neogene macrobotanical records at http://www.neclime.de/).

Although these innovations are important, data are constantly being improved and therefore the related data sets needed for the CA have to be checked by the user before each application because a precise taxonomy is the first step in improving CA results and precision. As this represents a crucial step in the CA, NECLIME members have set up working groups organising data input from current taxonomical research. These are separated into a working group on taxonomy of the Neogene macrobotanical record of Eurasia, taxonomy of Neogene palynomorphs, and the ‘working group on fossil wood’. The main focus of the working groups is to continuously update the Palaeoflora database. This work encompasses (1) the taxonomical and climatic (re-)evaluation of (critical) taxa, (2) systematic studies on families and form taxa (e.g., due to new advances in molecular phylogenetics), (3) changes in taxonomy and NLR concepts (e.g., due to new advances in molecular phylogenetics), (4) the search for data on missing taxa, and (5) considerations and re-evaluation of Neogene palynomorph records using TLM/SEM in combination. In this context the role of reference collections is essential. Collection of new materials and exchange between existing collections underpins the sound identification of fossil plant remains and related NLRs. Reports on the results of each of the working group meetings and updates concerning the fossil taxa and their NLR concept can be accessed at the NECLIME website (www.neclime.de ‘groups’).

3.1. The concept and power of outliers

The Coexistence Approach determines the climatic interval in which all fossil taxa could coexist (Fig. 2A). The result of the application is a coexistence interval, analysed separately for each climate parameter. However, in some cases, not all intervals of individual taxa overlap the resulting coexistence interval and this can be caused by various factors. Plant taxa whose climatic requirements do not overlap with those of the majority of taxa in a fossil flora are denoted as outliers (cf. Mosbrugger and Utescher, 1997, p. 66, and Fig. 2B). The concept of
outliers, their presence and proportion constitutes a crucial aspect in CA analyses because it provides an estimate regarding the significance and reliability of the determination of the fossil taxon and hence its palaeoclimatic reconstruction (cf. relative percentage of overlapping taxa, climatic homogeneity of a fossil flora; Mosbrugger and Utescher, 1997). Moreover, it represents a particular strength of the CA due to unravelling various sources of uncertainty.

Uncertainties in CA analysis can be referred to (1) an unclear/wrong NLR concept for the fossil taxon, (2) differing climatic requirements of fossil and NLRs (evolution), (3) lack of climatic representativeness of the present-day plant distribution area (relict, recent evolution of competitor taxa and/or pathogens, unclear natural distribution due to early cultivation or anthropogenic restriction), and (4) incomplete database entries concerning climate data of NLRs (Mosbrugger and Utescher, 1997; cf. Section 4.2). Having excluded errors regarding point (4), problematic palaeobotanical taxa regarding points (1) to (3) become obvious when applying the CA to numerous fossil floras, because these taxa frequently stand out in the analyses. These are denoted as permanent outliers (Mosbrugger and Utescher, 1997).

According to the above, the reasons for the permanent outlier status of a plant taxon are its unclear NLR concept (1), differing climatic requirements of a fossil and its NLRs (2), and problematic climatic representativeness of the extant reference taxon (3) (cf. also ‘relics’ in Section 3.2). While reason (1) might be avoided by new taxonomical/phylogenetic evidence, those of (2) and (3) represent sources of possible error that cannot be overcome.

Our experience using the CA, has led to several new conclusions. Once identified, permanent outliers should be excluded from CA analyses because they do not contribute reliable data. In theory, outliers should not influence the CA results at all (cf. Mosbrugger and Utescher, 1997, p. 73). Nevertheless, practice has shown that while outliers may not affect the whole palaeoclimatic reconstruction, they sometimes form consistent coexistence intervals for one climate parameter only (e.g., permanent outlier regarding temperature variables/overlapping for precipitation). As a consequence the program ClimStat suggests an erroneous climatic interval for the whole fossil flora and so biases the reconstruction. To avoid this, the CA reconstruction of each climatic parameter has to be determined in detail before the outlier is removed from the analysis manually. The characteristics defining a “permanent climatic outlier” are not universal but related to the specific palaeoclimatic situation existing in a given region at a given time; e.g., tropical outlier such as Cedrela in a temperate climate (Mosbrugger et al., 2005) or the dry adapted Tetraclinis in a wet climate (van Dam and Utescher, submitted for publication). More examples of permanent outliers are summarised in Table 1.

Despite the above, every study must consider each possible outlier separately, and even then it cannot be guaranteed that an outlier is successfully identified in a CA application. However, the outlier concept employed in the CA constitutes an interesting alternative to other concepts (cf. relic, false friends; Kvaček, 2007) because of the empirical way in which ‘soft’ data are treated (climate requirements of extant plants in a fossil world). Furthermore, although the identification of outliers related to the evolution of a single taxon appears to be highly problematic, in a few cases such as in the late Cenozoic adaption of Tetraclinis and Sequoia to seasonally dry climates it visualizes the potential of plants to adapt towards changing environmental factors. As regards modern Sequoia, it grows under more humid conditions than it appears from ‘classic’ precipitation values, owing to its adaptation to absorb water directly from clouds (Burgess and Dawson, 2004). Thus, the relevance of ‘unconventional’ environmental parameters in habitat preference of taxa, such as fog occurrence, and their identification may also contribute to the outlier status of a taxon. Likewise, the identification of outliers represents a positive side-effect in the application of the CA to multiple palaeofloras and may help to understand changes in the climatic adaptations of taxa throughout Earth history.

3.2. Relict taxa in CA analyses

One possible cause of low precision in the CA is the lack of regional and/or climatic representativeness of the present day distribution of NLRs. This is often linked to the concept of ‘relic taxa’. From the perspective of chorology of modern plants, the term is used for plants which were abundant in a large area in geological times, but now only occur at one or a few small areas. Relictual plant populations are remnants ‘left behind’ from larger populations of plants, which have managed to survive despite changes in the environment. Usually it is considered that the reduction of the area of distribution of relicts is a climatically driven (e.g., the extinction of plant taxa in the course of the Pleistocene glaciation events). However, other abiotic and biotic factors influence plant distribution, e.g., palaeogeographic changes (mountain uplifting, geographic isolation of populations, appearance/closure of land bridges, edaphic changes, etc.), fast spread of herbivorous animals, viruses and plant disease, competition between plants in an ecosystem, etc. In modern plant geography, many of these so-called relic taxa are also termed

<table>
<thead>
<tr>
<th>Taxon/NLR</th>
<th>Time frame</th>
<th>Type</th>
<th>Temperature</th>
<th>Precipitation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sequoia, diverse morphospecies/S. sempervirens</td>
<td>Palaeogene</td>
<td>Monotypic, relic</td>
<td>MAT ca. 9–15 °C</td>
<td>Too cool</td>
</tr>
<tr>
<td>Comptonia, diverse morphospecies/Comptonia peregrina</td>
<td>Palaeogene</td>
<td>Monotypic</td>
<td>MAT ca. 3–15 °C</td>
<td>Too cool</td>
</tr>
<tr>
<td>Scindapsus, Uropathites, diverse morphospecies/Scindapsus, Uropathita</td>
<td>Neogene</td>
<td>Unclear botanical affinity: NLR</td>
<td>MAT ca. 25–28 °C</td>
<td>22–27 °C</td>
</tr>
<tr>
<td>Cassia, diverse morphospecies/Cassia</td>
<td>Neogene</td>
<td>Unclear botanical affinity</td>
<td>MAT ca. 17–28 °C</td>
<td>Too warm</td>
</tr>
<tr>
<td>Cedrela, diverse morphospecies/Cedrela</td>
<td>Neogene</td>
<td>In many cases uncertain botanical affinity</td>
<td>MAT ca. 20–26 °C</td>
<td>Too warm</td>
</tr>
<tr>
<td>Cathaya, few morphospecies/Cathaya</td>
<td>late Neogene</td>
<td>Relic</td>
<td>MAT ca. 17–22 °C</td>
<td>Too warm</td>
</tr>
<tr>
<td>Glyptostrobus, diverse morphospecies belonging to 2 ecotypes (Kvaček, 2007)/Glyptostrobus lineatus</td>
<td>late Neogene</td>
<td>Relic, natural distribution problematic (cf. Kvaček, 2007)</td>
<td>MAT ca. 17–22 °C</td>
<td>Too warm</td>
</tr>
<tr>
<td>Matudaea, few morphospecies/Matudaea trinervia</td>
<td>Later Palaeogene</td>
<td>Relic</td>
<td>MAT ca. 19–26 °C</td>
<td>Too warm</td>
</tr>
<tr>
<td>Tetraclinis, diverse morphospecies/Tetraclinis articulata</td>
<td>Cenozoic</td>
<td>Relic (cf. also Kvaček, 1986; Mai, 1995)</td>
<td>MAP ca. 250–500 mm</td>
<td>Too dry</td>
</tr>
<tr>
<td>Sciadopitys ternata/Sciadopitys verticillata</td>
<td>Cenozoic, some regions</td>
<td>Relic</td>
<td>MAP ca. 1300–6000 mm</td>
<td>Too wet</td>
</tr>
</tbody>
</table>
Relic taxa considered to bias CA reconstruction (Kvaček, 2007). Climate data estimated from vegetation (Kvaček, 2007) and Palaeoflora data used in CA reconstructions. Highlighted data show no overlapping.

<table>
<thead>
<tr>
<th>Fossil taxon</th>
<th>NLRs</th>
<th>Climate data estimated from vegetation (Kvaček, 2007)</th>
<th>Palaeoflora climate data used in CA application</th>
</tr>
</thead>
<tbody>
<tr>
<td>Craugia (complex taxon)</td>
<td>Craugia</td>
<td>Early Oligocene: Kundratice — MAT 15 °C, CMT 1 °C; Bechlejovice — MAT 15.3–16.6 °C; CMT 10.0–10.2 °C; Early Miocene: Cyprip Shale — MAT 15 °C, CMT &gt;1 °C; Pliocene: Platania — MAT 13–15 °C, CMT 1–10 °C</td>
<td>MAT 15.6–22 °C, CMT 3.8–13.6 °C</td>
</tr>
<tr>
<td>Tetraclinis, diverse morphospecies</td>
<td>Tetraclinis articulata</td>
<td>Late Eocene (see Mai, 1995): Zeitz — MAT 15–20 °C, CMT 6–13 °C; Early Oligocene: Haselbach — MAT 10–15.5 °C, CMT 2–4 °C; Kundratice — MAT 15 °C, CMT &gt;1 °C; Early to Middle Miocene: Wackersdorf — MAT 14–18 °C, CMT 2–8 °C; Kreuzau — MAT 11–16 °C, CMT 3 °C; Pliocene: Willershausen — CMT 0–5 °C; WMT 13–17 °C</td>
<td>MAT 15.6–19.9 °C, CMT 7.1–12.3 °C</td>
</tr>
<tr>
<td>Platanus, diverse morphospecies</td>
<td>Platanus</td>
<td>Late Eocene: Zeitz — MAT 15–20 °C, CMT 6–13 °C; Early Oligocene: Haselbach — MAT 10–15 °C, CMT 2–4 °C; Early Miocene: Ipolytarnóc — MAT 20 °C, CMT 1 °C; Late Miocene: Delureni — MAT 15 °C, CMT 2–4 °C</td>
<td>MAT 6.6–27.4 °C, CMT —10.9–25.6 °C</td>
</tr>
<tr>
<td>Trigonobalanopsis</td>
<td>E.g. Trigonobalanus/Castanopsis (T. rhamnoides)</td>
<td>Late Eocene: Staré Sedlo — MAT 15–20 °C, CMT 6–13 °C; Early Oligocene: Wackersdorf — MAT 14–18 °C, CMT 2–8 °C</td>
<td>MAT 9.3–27.7 °C, CMT 1.5–27.2 °C</td>
</tr>
</tbody>
</table>
Cercidiphyllaceae, Hamamelidaceae, Platanaceae, Betulaceae, Juglandaceae, Tilieaeae, Ulmaceae, Fagaceae, and deciduous conifers such as *Metasequoia* and *Glyptostrobus* (Mai, 1995). A comparable evolutionary change is also evident in the southern hemisphere (e.g., continental drying, fragmentation/dislocation of continental area due to plate tectonics). Taking these facts into account, it is obvious that palaeotropical taxa progressively gain relict status throughout the Cenozoic, leading to 70 palaeotropical relict taxa in the Plio-/Pleistocene in western Eurasia (Mai, 1995). The growing and shrinking of plant distribution areas over time contribute to increasing uncertainties and reduced preciseness of the CA further back in time.

In order to address the above aspects, a specific study about the use of relicts in quantitative palaeoclimatic reconstruction using taxonomical approaches (in this case the CA) was carried out by Kvaček (2007). In that work the author discusses a selection of seven relict taxa (cf. Table 2) which he refers to as ‘false friends’ because they appear to bias the actual palaeoclimatic reconstructions (Table 2). Next to their relict character (e.g., *Glyptostrobus*), these partly have a complex or unclear NLR concept as well (e.g., Trigonobalanoids). Moreover, the author points out problems when attempting the reconstruction of palaeorequirements for these selected taxa by employing climatic tolerances of extant reference phytocoenoses for the fossil communities in which these plants thrived. The considerations presented in Kvaček (2007) are very helpful for identifying fossil plant taxa potentially affecting CA reconstructions although a clear identification is not always possible due to the limitations of the CA analysis.

Another common reason leading to ambiguous results are problems related to the NLR concept or incomplete data about the NLR’s climatic requirements. Before beginning considerations described in the above paragraph, the NLR concept should be evaluated critically (see also Section 3.2). In fossil megafossils, identifications of NLRs at species level may be problematic because the number of diagnostic characters identifiable from the fossil materials usually is limited and only available for a single organ. Also, many NLR concepts at the species level are often debated vigorously. In palynology, the ‘type’ status of identification accommodates these uncertainties. Even with extant taxa, taxonomy may no longer be valid (e.g., Taxodiaceae, Tilieaeae) or/and some of the modern taxa cited as NLRs in palaeobotanical literature have an unclear taxonomical status and may be treated in a different way depending on the flora used (e.g., treated as synonym, subspecies, variety). All these points may introduce uncertainties and bias distribution information from analogue or digital resources. In the application of the CA on modern florae, multiple coexistence intervals should not occur. When ambiguous solutions are obtained in CA analysis, all fossil taxa involved, their NLRs and their associated climate data sets should be carefully checked for errors or incompleteness before interpreting the result in terms of possible taphonomic effects. However, a prerequisite for a successful survey is the availability of sufficient precise information. This leads directly to the problem area that we term “climatic requirements of modern taxa”. This includes retrieval techniques and types of available resources.

4. Determination of climatic requirements of modern plant taxa

One basic assumption (3) of the Coexistence Approach is that ‘The climatic requirements or tolerances of a nearest living relative, and thus of the fossil taxon, can be derived from its area of distribution’ (Mosbrugger and Utescher, 1997). This strongly depends on two sources of information, on plant distribution and on modern climate data. Both issues have their own inherent problems and potential sources of errors related to their methodologies. In order to address this specific problem, a working group on ‘Digital data on plant distribution’ has been initiated in NECLIME discussing new techniques and updates to improve the datasets underlying the CA.

4.1. Distribution information and maps

The first step to obtain data on climate space for NLRs is to define the spatial distribution of each taxon of interest. The distribution of a plant (as well as any organism) is influenced by numerous factors, such as abiotic components (e.g., climate, soil chemistry and geographical barriers), as well as biotic factors (e.g., competition, symbioses, availability of specific pollinators and anthropogenic disturbances, the distribution (environmental tolerance) of pathogens). For some taxa, these may be the limiting requirements, while the actual distribution of others is mainly caused by their climatic preferences. By focusing on the climatic distribution, various sources of uncertainty are evident due to the different quality and resolution of information.

Basically, primary data on the plant distribution mainly derives from herbaria. Several platforms allow inspecting specimens and all accompanying information (e.g., Chinese Virtual Herbarium, Muséum National d’Histoire Naturelle in France), although the precision of the geographic information available in each case is highly inconsistent. These vary from GPS coordinates for single trees to locations given at county level, which fail to incorporate boundary changes that have taken place over time (e.g., for most of the older Chinese specimen records). Because the primary information is based on samples, it corresponds to plots, which then are extrapolated into distribution areas with specific problems of their own, particularly in mountain areas and regions with steep relief.

Considering these issues, information is limited at best to an estimate of the real areal distribution including its uncertainties. Nevertheless, mapping plant distributions is a classical method in botany and the basis for a variety of modern applications, especially in climate-
vegetation modelling (Thompson et al., 1999), as well as species distribution modelling (Peterson et al., 2011). Several sources of distribution maps are available online, e.g., at The Global Biodiversity Information Facility (GBIF) (http://www.gbif.org/), The Atlas of United States Trees (http://esp.cr.usgs.gov/data/atlas/little/), and Flora Europaea (http://www.luomus.fi/english/botany/afe/index.htm). Additionally, various books give printed maps for plant distributions in specific regions like China (Fang et al., 2011), SW Asia (e.g., Browicz and Zielinski, 1982, 1984), and the former Soviet Union (Sokolov et al., 1977, 1980, 1986). NECLIME is compiling such information for relevant taxa at Chorotree (www.chorotree.de). Still more difficult are taxa, whose distribution information is given only as descriptive data only (e.g., Flora of China (http://www.efloras.org), Seed Plants of China (Wu and Ding, 1999), Atlas of Woody Plants in China (Fang et al., 2009, 2011)). These unfortunately provide insufficient data to determine reliably plant spatial distributions and climatic requirements. Understanding this variability in data quality and resolution is crucial for the successful application of the CA.

4.2. Climate data: meteorological station data and gridded data

After the distribution area of a NLR is reliably defined, or defined with known uncertainties, the climatic data within this spatial range can be assessed. In the first publication of the Coexistence Approach (Mosbrugger and Utescher, 1997), the climate observation data were retrieved for six ‘extreme’ meteorological stations situated within the distribution range of each NLR. Actually, the availability of digital station data, e.g. the Global Climate Data Atlas (Müller and Hennings, 2000) facilitates the identification of station providing extremes for the respective variables. The development of geographic information systems (GIS) in recent years allows for alternative methods, such as using gridded global datasets (New et al., 2002; Hijmans et al., 2005). Climatological information for points or areas can thus be easily extracted from such datasets using GIS software.

Issues with modern climate data are not specific to the CA but are common to methods and applications that require calibration based on observations of the modern world. Generally, point data from meteorological stations are similar to those obtained for those locations from gridded datasets, as these are constrained by the actual data. They are, however, rarely identical. Calculating the differences between mean annual temperature values of meteorological data from Müller and Hennings (2000) with WORLDCLIM datasets (Hijmans et al., 2005) at different resolutions shows that these can still differ by as much as 5 °C for the same location with the best results being at 2.5 arcmin resolution (Fig. 3; Table 3). Similar results have been obtained across three different gridded data sets for New Zealand (Kennedy et al., 2014, unpublished data). The different WORLDCLIM data sets also show increased disagreement with increasing altitudes emphasizing the problem of correctly representing climate in mountain regions as discussed by Hijmans et al. (2005) (Fig. 4). Moreover, gridded datasets from different sources can also vary considerably in detail due to different interpolation methods, especially for regions with low coverage with meteorological stations like islands and high latitudes (Hijmans et al., 2005). It is worth mentioning that in topographically complex areas a major problem is that aspect (slope angle and orientation) is not incorporated into gridded data sets if the grid size, or the average distance between the meteorological stations used in the interpolation, are larger than the characteristic length of topographic granularity. This can result in large temperature and humidity differences for the same elevation. Station data, on the other hand, have inherent problems as well. They invariably run for different time intervals, have gaps in the records, and have different instrument calibrations. This means that in general, the uncertainties are difficult to quantify, unlike gridded data which can be filtered for poor data more easily.

The decision as to which climate data source is chosen for the CA depends on various factors, for example the availability of data and the precision of distribution information. Currently new databases are under construction to compile requirements of modern taxa based on gridded climate data for areas with low coverage of meteorological stations (e.g., for Africa: Bruch et al., 2012). However, in some regions it is difficult to obtain station data at all, but in those regions gridded data also offer the lowest accuracy for exactly the same reason.

Experience has shown that the accuracy of gridded climate data extracted for a given plant distribution area can be problematic, especially if chorological data are incomplete or of low resolution. Contrary to the deliberate choice of extreme meteorological stations, avoiding subareas with extreme orographic structuring or highly patchy occurrence of a plant taxon, the extraction of all gridded data within a distribution area with ill-defined boundaries bears high uncertainties. Those can be considered during the analysis by buffering the distribution data

![Fig. 3. Comparison of meteorological data from Müller and Hennings (2000) covering 1961–1990 with gridded WORLDCLIM data (interpolations of observed data, representative of 1950–2000; Hijmans et al., 2005) in different resolution, i.e., 10 arcmin, 2.5 arcmin, and 30 arcsec.](image-url)
Parameters (MAP, MPdry, MPwet, MPwarm) are provided on request.

Based on the application on 357 Cenozoic floras, we recognise that selection, educated or otherwise, of specific station data to define a climatic envelope for a taxon introduces an unwelcome element of subjectivity, but until adequate digital chorological information for the required NLRs is available in a global context, and a standardised algorithmic expression, corrected for altitude and aspect, can be appointed for gridded data, the original approach of Mosbrugger and Utescher (1997) retains considerable merit.

The figures given as coexistence interval boundaries stem directly from the primary climate data sets without further processing. Thus, it is obvious that these boundaries are of the same type and quality as the modern climate data used to identify the requirements of a plant. Based on the application on 357 Cenozoic floras with a mean diversity of 29 taxa having climate data (Fig. 7; see also Appendix 1), the precision of the CA results, i.e. the width of the coexistence interval is determined as 2.1 °C at a mean (std. 1.35 °C) for MAT. Precipitation-related parameters are in general more difficult to assess because of the high local variability in the modern data sets; here, the achievable precision is even more dependent on the quality of the available chorological information and primary climate data. Coexistence intervals <1 °C for MAT and <100 mm for MAP, respectively, represent valid solutions in the sense of the CA algorithm, but are usually considered to be beyond the resolution of the primary data, even if high resolving chorological and climatological sources are employed (see also Section 5).

In general, palaeoclimatic reconstructions using the CA should be based on a single source of data consistently, i.e. a single clearly specified meteorological data set. It also has to be appreciated that the character of data resulting from CA analysis is the same as the character of the input data. If meteorological station data are chosen the results represent a best estimate of the palaeoclimatic conditions as they would have been measured by a ‘paleo-station’. If global gridded data in 10 arcmin resolution are considered, the results represent values of 10 arcmin ‘paleo-grid cells’. Those values cannot be interpreted as being equivalent to recent meteorological station data as they are interpolated and therefore generally smoothed.

5. The database — Palaeoflora

Palaeoflora (Utescher and Mosbrugger, 2013) has been designed to provide essential information about fossil taxa, their related NLRs, and their climatic requirements required for the CA. The database was established in 1990 and has been continually growing, as well as being updated and corrected on a regular basis. Palaeoflora currently includes ca. 5800 macrobotanical and 2500 microbotanical taxa, and for ca. 1630 modern taxonomical units (species, genera, families) for which climate data are available. Palaeoflora is maintained in the context of NECLIME and hence profits immensely from co-operations within the network and the activities of the NECLIME working groups on taxonomy of the macro- and microbotanical record (see Section 3 and materials and reports available on the NECLIME website). Details on data collected, literature resources and main contributors can be accessed at the Palaeoflora website (http://www.palaeoflora.de). The Palaeoflora website provides free access to fossil macro- and microbotanical taxa stored in the database, corresponding NLRs, as well as MAT requirements. Additional climatic parameters with respect to two temperature variables (CMT, WMT), and four precipitation parameters (MAP, MPdry, MPwet, MPwarm) are provided on request.

Palaeoflora climate data are mainly based on meteorological stations, which are carefully chosen in order to represent the climatic space of a modern taxon with respect to the variables. As regards the selection of suitable stations, we follow the procedure described in Mosbrugger and Utescher (1997). Furthermore, climate datasets in Palaeoflora provide additional parameter ranges such as potential evaporation and relative humidity, although these entries are currently incomplete. Data

Table 3
Statistical characteristics of the differences between MAT from different sources. Preciseness is highest and scatter lowest for 30 arcsec (mean of differences).

<table>
<thead>
<tr>
<th>ΔMAT [°C]</th>
<th>n</th>
<th>Correlation coefficient</th>
<th>Arithmetic mean</th>
<th>Standard deviation</th>
<th>Standard error</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Meteo minus 10 arcmin</td>
<td>1088</td>
<td>0.9925</td>
<td>0.1797</td>
<td>1.1564</td>
<td>0.0351</td>
<td>-8.7</td>
<td>7.8</td>
</tr>
<tr>
<td>Meteo minus 2.5 arcmin</td>
<td>1088</td>
<td>0.9962</td>
<td>-0.0108</td>
<td>0.8186</td>
<td>0.0248</td>
<td>-5.9</td>
<td>5.2</td>
</tr>
<tr>
<td>Meteo minus 30 arcsec</td>
<td>1088</td>
<td>0.9966</td>
<td>-0.0288</td>
<td>0.7703</td>
<td>0.0234</td>
<td>-7.9</td>
<td>5.6</td>
</tr>
</tbody>
</table>

Fig. 4. Divergence of meteorological data from Müller and Hennings (2000) (covering 1961–1990) and gridded WORLDCLIM data (interpolations of observed data, representative of 1950–2000; Hijmans et al., 2005) in different resolutions, i.e., 10 arcmin, 2.5 arcmin, and 30 arcsec, related to altitude (resolution 30 arcsec).
not freely accessible are usually provided in exchange for information on fossil evidence and NLR assignments. This is useful to keep the NLR concept of the database up to date and for detecting erroneous entries.

Unlike data retrieval in the early years of the CA, where a total of six stations were used to describe the climatic range of a taxon, today a considerable number of stations can be effectively checked for extremes by using GIS compatible files of the Müller and Hennings (2000) selection of global station data, regional compilations (e.g., for China: State Bureau of Meteorology, 2002), as well as the digital collection of various chorological resources compiled in the Chorotree project (http://www.chorotree.de). The use of station data accommodates the lack of digital data on plant distribution, coarse raster data (e.g., Flora Europaea) and/or incomplete point data (e.g., GBIF). Moreover, station data can be retrieved easily also for analogue plant distribution maps (e.g., Meusel or incomplete point data (e.g., GBIF). Moreover, station data can be re-

Table 4

<table>
<thead>
<tr>
<th>Modern taxon</th>
<th>Distribution area represented by Palaeoflora MAT data; (% of gridded cells)</th>
<th>MATMin (Thompson et al., 1999)</th>
<th>MATMax (Thompson et al., 1999)</th>
<th>MAT range (Thompson et al., 1999)</th>
<th>MATMin (Palaeoflora)</th>
<th>MATMax (Palaeoflora)</th>
<th>MAT range (Palaeoflora)</th>
<th>Climate range represented by Palaeoflora database; (% of gridded cells)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer pennsylvanicum</td>
<td>91.55</td>
<td>−0.1</td>
<td>15.7</td>
<td>18.4</td>
<td>2.8</td>
<td>15.6</td>
<td>12.8</td>
<td>86.49</td>
</tr>
<tr>
<td>Acer rubrum</td>
<td>88.93</td>
<td>−1.1</td>
<td>23.8</td>
<td>24.9</td>
<td>3.4</td>
<td>23.9</td>
<td>20.5</td>
<td>82.33</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>98.15</td>
<td>1.3</td>
<td>20.0</td>
<td>18.7</td>
<td>3.4</td>
<td>20.8</td>
<td>17.4</td>
<td>93.05</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>84.23</td>
<td>−1.1</td>
<td>15.8</td>
<td>16.9</td>
<td>3.4</td>
<td>15.6</td>
<td>12.2</td>
<td>72.19</td>
</tr>
<tr>
<td>Amelanchier glabra</td>
<td>83.77</td>
<td>8.0</td>
<td>20.3</td>
<td>12.3</td>
<td>9.9</td>
<td>17.9</td>
<td>8.0</td>
<td>65.05</td>
</tr>
<tr>
<td>Amelanchier octandra</td>
<td>98.43</td>
<td>8.0</td>
<td>15.5</td>
<td>7.5</td>
<td>9.9</td>
<td>15.6</td>
<td>5.7</td>
<td>76.00</td>
</tr>
<tr>
<td>Alnus rubra</td>
<td>96.80</td>
<td>−3.7</td>
<td>15.1</td>
<td>18.8</td>
<td>−0.3</td>
<td>13.8</td>
<td>14.1</td>
<td>75.00</td>
</tr>
<tr>
<td>Alnus rugosa</td>
<td>98.70</td>
<td>−12.5</td>
<td>12.1</td>
<td>24.6</td>
<td>−8.9</td>
<td>11.8</td>
<td>20.2</td>
<td>84.15</td>
</tr>
<tr>
<td>Alnus serrulata</td>
<td>98.57</td>
<td>3.4</td>
<td>20.9</td>
<td>17.5</td>
<td>5.4</td>
<td>20.8</td>
<td>15.4</td>
<td>88.00</td>
</tr>
<tr>
<td>Betula lenta</td>
<td>98.51</td>
<td>4.4</td>
<td>16.3</td>
<td>11.9</td>
<td>5.7</td>
<td>15.6</td>
<td>9.9</td>
<td>83.19</td>
</tr>
<tr>
<td>Betula nigra</td>
<td>99.94</td>
<td>5.9</td>
<td>20.3</td>
<td>14.4</td>
<td>6.6</td>
<td>21.3</td>
<td>14.7</td>
<td>102.08</td>
</tr>
<tr>
<td>Betula papyrifera</td>
<td>99.99</td>
<td>−12.2</td>
<td>11.4</td>
<td>23.6</td>
<td>−11.9</td>
<td>12.5</td>
<td>24.4</td>
<td>103.39</td>
</tr>
<tr>
<td>Carya caroliniana</td>
<td>94.75</td>
<td>2.5</td>
<td>28.2</td>
<td>25.7</td>
<td>3.4</td>
<td>21.1</td>
<td>17.7</td>
<td>68.87</td>
</tr>
<tr>
<td>Carya aquatica</td>
<td>92.55</td>
<td>13.7</td>
<td>23.0</td>
<td>9.3</td>
<td>13.3</td>
<td>21.1</td>
<td>7.8</td>
<td>83.87</td>
</tr>
<tr>
<td>Carya cordiformis</td>
<td>91.97</td>
<td>3.6</td>
<td>20.1</td>
<td>16.5</td>
<td>5.7</td>
<td>21.3</td>
<td>15.6</td>
<td>96.28</td>
</tr>
<tr>
<td>Carya ovata</td>
<td>93.43</td>
<td>3.6</td>
<td>22.4</td>
<td>18.8</td>
<td>5.7</td>
<td>21.1</td>
<td>15.4</td>
<td>81.91</td>
</tr>
<tr>
<td>Carya tomentosa</td>
<td>98.61</td>
<td>5.1</td>
<td>21.9</td>
<td>16.8</td>
<td>7.9</td>
<td>20.8</td>
<td>12.9</td>
<td>76.79</td>
</tr>
<tr>
<td>Castanea pumila</td>
<td>92.88</td>
<td>8.0</td>
<td>21.5</td>
<td>13.5</td>
<td>11.8</td>
<td>21.3</td>
<td>9.5</td>
<td>70.37</td>
</tr>
<tr>
<td>Celtis occidentalis</td>
<td>99.91</td>
<td>1.8</td>
<td>18.7</td>
<td>16.3</td>
<td>2.5</td>
<td>17.1</td>
<td>14.6</td>
<td>89.57</td>
</tr>
<tr>
<td>Corylus florida</td>
<td>89.64</td>
<td>5.5</td>
<td>22.0</td>
<td>16.5</td>
<td>9.3</td>
<td>20.8</td>
<td>11.5</td>
<td>69.70</td>
</tr>
<tr>
<td>Fraxinus americana</td>
<td>96.28</td>
<td>0.1</td>
<td>21.7</td>
<td>21.6</td>
<td>4.4</td>
<td>21.1</td>
<td>16.7</td>
<td>77.31</td>
</tr>
<tr>
<td>Juglans cinerea</td>
<td>99.83</td>
<td>1.4</td>
<td>17.0</td>
<td>15.6</td>
<td>5.6</td>
<td>16.7</td>
<td>11.1</td>
<td>71.15</td>
</tr>
<tr>
<td>Juglans nigra</td>
<td>99.51</td>
<td>5.9</td>
<td>21.4</td>
<td>15.5</td>
<td>5.6</td>
<td>18.8</td>
<td>12.2</td>
<td>78.71</td>
</tr>
<tr>
<td>Picea glauca</td>
<td>96.40</td>
<td>−12.2</td>
<td>8.6</td>
<td>20.8</td>
<td>−8.9</td>
<td>6.9</td>
<td>15.8</td>
<td>75.96</td>
</tr>
<tr>
<td>Picea mariana</td>
<td>91.78</td>
<td>−12.4</td>
<td>10.7</td>
<td>23.1</td>
<td>−8.9</td>
<td>9.3</td>
<td>18.2</td>
<td>78.79</td>
</tr>
</tbody>
</table>

To demonstrate the nature of Palaeoflora climate data, a comparison between data obtained from overlapping digital plant distribution and a gridded climatology (Thompson et al., 1999) is shown for 25 important arboreal North American plant taxa, frequently encountered in modern surface samples (Whitmore et al., 2005) (Table 4; Fig. 5). As evident from the plot, MAT data cited in the Palaeoflora comply at a mean for only 80% of the entire MAT ranges reported for the selected taxa by Thompson et al. (1999), but reflect mean MAT conditions of 95% of their distribution area according to Thompson et al. (1999) (measured in number of grid cells). From a different perspective, plant occurrences in only 5% of the distribution area grid cells account for the extension of the climatic range of a plant by a mean of 15%. In extreme cases, 0.5% of recorded grid cells cause widening of the MAT range by ca. 28% (Juglans cinerea, cf. Fig. 5). Hence, Palaeoflora data may not include the extremes of climatic ranges where the taxa exist close to their limit. On the one hand, too narrow ranges may lead to non-overlapping in CA analysis and thus to ambiguous solutions (cf. wrong climate data in Section 3.3) making revision of the primary data necessary. On the other hand, the preclusion of the extreme ends minimizes errors introduced by a rare climatic situation, such as specific local microclimatic conditions, unusually high snow depths, stands that are not in equilibrium with climate, or the impact of poor climatic data in high altitudinal areas. For the majority of NLR taxa required for Cenozoic palaeoclimate reconstruction, available chorological information does not precisely resolve the extremes (cf. Section 4.1). Hence, the tendency of the Palaeoflora database to reflect core ranges where taxa potentially are encountered with a high probability seems to us as overall suitable solution for reconstructing regional climate of the past.
does contain erroneous entries in view of the heterogeneity of available floristic information for extant plants alone (see Section 4.1). This fact has been already emphasized in the original description of the CA method and Palaeoflora database (Mosbrugger and Utescher, 1997; p. 65). To make this transparent, users of the online version of the Palaeoflora database are asked to report on data entries ‘needing updating or correction’ (http://www.palaeoflora.de/home). Only with such information from a group effort is it possible to continuously improve the quality of the database. Thus, input from Palaeoflora users and our own revisions allow regular updates of Palaeoflora data entries.

Furthermore, the CA is not confined to the use of Palaeoflora data. Any source for the climatic requirements for extant plants can be used as shown in several studies applying the CA based on other data sets, e.g., restricted to China (Zhao et al., 2004; Kou et al., 2006; Xia et al., 2009) or gridded data (Bruch et al., 2012).

6. The principal applicability of the CA

It is largely accepted that, apart from other factors outlined in Section 3.2, climate intensely affects the distribution of plants. Examples for exceptionally sensitive variables are e.g., the length and temperatures of the growing season, water availability during germination, or the number of days with ground frost or extreme cold. These are commonly denoted as bioclimatic variables (Hijmans et al., 2005), as they directly influence the distribution of many plants and therefore are used to model vegetation distribution (e.g., François et al., 2011). Moreover, climate variables can be tuned to address specific question such as past monsoon intensity (Jacques et al., 2014). Also, plant species may be more sensitive to the variability of climate over time and to climatic extremes than to climatological means (i.e., averages over 30 or 50 years). A change in climate variability is expected to significantly impact vegetation (Reyer et al., 2013). For instance, Dury et al. (2011) demonstrated using a dynamic vegetation model that the increase in climate interannual variability anticipated under global warming will have large impacts on the net primary productivity of European vegetation in the future, especially in the Mediterranean area. To involve this effect in palaeoclimate reconstruction time series instead of climatological means could be used to identify the requirements of taxa. In principle, all these variables can directly be assessed from the distribution area of a modern plant taxon and thus can be used in CA climate reconstructions, provided that the information is available for all NLRs of the fossil flora analysed.

Annual and monthly means of temperature and rainfall, as commonly reconstructed in CA applications, reflect the sensitivity of plants less directly, but are important key variables as they can easily be compared with respective climatic data obtained from other proxies such as stable isotopes or with data obtained from palaeoclimate modelling. It is beyond the scope of this paper to discuss dependence of plants on e.g. MAT in more detail, but the high dependence becomes obvious when plant distribution maps are overlain with MAT isotherms. Fig. 6 might be suggestive for a rough impression of signals that plants can resolve with respect to MAT. This plot shows MAT requirements for ca. 250 North American woody plants (data from Thompson et al., 1999) sorted with respective climatic data obtained from other proxies such as stable isotopes or with data obtained from palaeoclimate modelling. The so-called extinct or fossil climates, de fined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflora data. Annual and monthly means of temperature and rainfall, as commonly defined to the use of Palaeoflor
may have occurred e.g. under differing continent configuration or higher global mean temperature under a raised contents in atmospheric greenhouse gases. In general, such conditions may still be reconstructed with methods calibrated on modern climate (Jacques et al., 2014). This is possible because today’s ‘interglacial’ world has a wider climatic range compared to the equable conditions mainly prevailing during the Cenozoic (Wing and Greenwood, 1993). However the possibility still exists that past climates may include conditions not found in today’s world, which may account for the continued failure of climate models to reproduce palaeoclimates consistent with a range of proxies despite decades of model development (Valdes, 2000; Spicer et al., 2013).

When making CA reconstructions for climate variables close to their extant limit, real values are expected to be close or equal to the upper limit of the suggested coexistence interval. However, the fact that in the CA each climate variable is considered separately allows for the reconstruction of a climatic situation characterised by a parameter combination not existing today. Examples for extinct climates proposed are climates of Northern Germany during several Neogene time spans, using a 6-dimensional climatic space for reconstruction (Utescher et al., 2009a). These obviously are periods with very mild winters and generally low seasonality as compared to today. This supports the assumption of the existence of Cenozoic, non-analogue climates as assumed before by various other authors (e.g., Mosbrugger et al., 2005; Williams and Jackson, 2007; Böhme et al., 2008).

Other than these moderate parameter combinations unfamiliar in the present day the existence of extinct climates substantially differing from modern are as yet a purely theoretical concept and it is difficult to see how they could be detected. Climate modelling would be one approach but models tend to be inherently conservative (Spicer et al., 2008, 2013) and like the real world are constrained by the laws of energy conservation and motion. Any extinct climate would have been similarly constrained. However, being adjusted to optimally reproduce present-day conditions models still fail to simulate characteristic patterns in past climate such as continental interior equability (Wing and Greenwood, 1993; Spicer et al., 2008, 2013), or high latitude warmth (e.g., Uhl et al., 2007a,b; Spicer and Herman, 2010) as suggested by a diversity of proxies, including those based on plants using both NLR and physiognomic approaches.

Other than extinct climates, there is clear evidence for past time periods with substantially raised atmospheric CO₂ (e.g., Pagani et al., 2011). Affecting photosynthesis, the atmospheric level of this greenhouse gas potentially impacts the temperature and humidity demands of plant taxa. It is known from CO₂ enrichment experiments that stomatal conductance decreases with increasing atmospheric CO₂ (e.g., Leuning, 1995, and references therein) resulting in transpiration loss. Hence, water demand of a plant is expected to be reduced at elevated CO₂ (Bader et al., 2013). At the same time it was shown that some plants respond to elevated CO₂ levels with a lower freeze-tolerance (Royer et al., 2002). According to this, the atmospheric CO₂ level may modify the relationship between climate (especially precipitation) and the presence/absence of plant species. These effects are demonstrated by modelling studies at the level of plant functional types (CARAIB dynamic vegetation model) by François et al. (2006), who obtained very different biome reconstructions for the Late Miocene under two different CO₂ forcings using the same climatic conditions, and by model projections of species distribution shifts in dependence of prescribed CO₂ (Cheaib et al., 2012). Hence, it could be argued that the climatic requirements defined for the NLR taxa are only valid under atmospheric CO₂ close to modern. However, the above observations regarding the effects of CO₂ are the result of short-term experiments using Free-Air CO₂ Enrichment (FACE) or carried out on juvenile trees in growth cabinets or glass houses. Because plants have the ability to moderate growth and architecture under different environmental constraints (e.g. stomatal characteristics and leaf size are not only CO₂ dependent but are also a function of water availability, light environment and wind stress) (e.g., Hikosaka et al., 2005; Taub, 2010), cell wall versus lumen size in wood (e.g., Wiemann et al., 1998), and even differentially allocate resources in the face of potential pathogen threat (e.g., Freeman and Beattie, 2008) it is possible that CO₂ responses observed in the short term (<10² years) can only be extrapolated to longer timescales (>10³ years) with great caution. If short term observations regarding CO₂ effects on temperature requirements of plants species do reflect long term responses it is difficult to see why both taxon-based methods like the CA and physiognomic methods such as CLAMP yield palaeotemperature estimates similar to those obtained by isotopic methods and do not show any systematic offset (Mosbrugger et al., 2005). Thus it is assumed that errors in CA reconstructions introduced by CO₂, if any, are fairly minor and presumably impact only the reconstruction of precipitation, essentially in areas where water is the main limiting factor, such as in sub-desertic areas or savannahs, i.e., where the change in stomatal conductance induced by CO₂ increase is expected to have the largest effect on the plant–water relationship.

7. Conclusions and outlook

With more than 15 years of experience of using the Coexistence Approach on Cenozoic micro- and macroflorabotanical records, it is clear that the method provides a robust palaeoclimatic proxy. Results are consistent with respect to global climate and environment, and predominantly consistent with data obtained from a large variety of other proxies for example isotope geochemistry, climate data based on the interpretation of small mammal communities or other independent plant-based palaeoclimatic approaches. New technologies have allowed...
and helpful suggestions. This work is a contribution to NECLIME (Neogene Climate Evolution of Eurasia).

References


