

# Fossil mega- and micro-flora from Bernasso (Early Pleistocene, southern France): A multimethod comparative approach for paleoclimatic reconstruction

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Manuscript 419228960b31306bfdba73ad9b2d0252 1 Fossil mega- and micro-flora from Bernasso (early Pleistocene, southern France): a 2 multimethod comparative approach for palaeoclimatic reconstruction 3 Girard, V.<sup>1,2</sup>\*, Fauguette, S.<sup>1</sup>, Adroit, B.<sup>3</sup>, Suc, J.-P.<sup>4</sup>, Leroy, S.A.G.<sup>5</sup>, Ahmed, A.<sup>2</sup>, Paya, A.<sup>2</sup>, Ali, 4 A.A.<sup>1,2</sup>, Paradis, L.<sup>1</sup>, Roiron, P.<sup>1</sup> 5 6 7 <sup>1</sup> ISEM, Université de Montpellier, CNRS, IRD, EPHE, Montpellier, France 8 <sup>2</sup> Département Biologie-Ecologie, Faculté des Sciences, Université de Montpellier, France. 9 <sup>3</sup> State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, 10 Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China 11 <sup>4</sup> Sorbonne Université, CNRS-INSU, Institut des Sciences de la Terre Paris, ISTeP UMR 7193, F-75005 Paris, France 12 <sup>5</sup> Laboratoire méditerranéen de préhistoire Europe Afrique, Ecosystèmes Quaternaires 13 Aix Marseille Univ, CNRS, Minist Culture, LAMPEA, UMR 7269, 5 rue du Château de l'Horloge, BP 647, 13094 Aix-14 en-Provence Cedex 2, France

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## **Abstract**

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Bernasso is an early Pleistocene locality that has a well-dated floral fossil content including both pollen grains and megaremains. Pollen record shows vegetation changes corresponding to two glacial and one interglacial periods. The megafloral fossil assemblage was interpreted as an association of present-day Mediterranean and Caucasian taxa that developed during a late interglacial stage of the beginning of the Pleistocene. In the present study, climatic reconstruction using the Climate Leaf Analysis Multivariate Program (CLAMP) and the Leaf Margin Analysis (LMA) methods based on the megaflora on one hand and using the Climatic Amplitude Method (CAM) based on the pollen flora on the other hand have been used to check the qualitative climatic estimates based on the comparison between palaeovegetation data and similar modern ecosystems. CLAMP and LMA analyses show that the Bernasso climate was colder than the present-day climate of Southern France and of the Hyrcanian and Euxinian regions. On contrary, CAM shows mean annual temperatures higher than the modern Bernasso temperature and equivalent to the temperature of the Hyrcanian and Euxinian regions. Mean annual precipitation and relative humidity reconstructed by CLAMP and CAM are in agreement and indicate that the climate was wetter than today at Bernasso. The differences between the three methods highlight important methodological biases that could be solved by including additional calibration sites in Europe and in the Mediterranean region.

**Key-words**: CLAMP analyses; Leaf Margin Analysis; Climatic Amplitude Method

# 1. Introduction

40	Many methods for palaeoclimatic reconstruction exist such as Climate Leaf Analysis
41	Multivariate Program (CLAMP; Wolfe, 1993), Leaf Margin Analysis (LMA; Wilf, 1997),
42	Coexistence Approach (Mosbrugger and Utescher, 1997) that are generally applied on leaves
43	assemblages, the Modern Analog Technique (MAT; Guiot, 1990) used on the recent Quaternary
44	period for which modern analogues of pollen data may be found, isotopic analysis (Covey and
45	Haagenson, 1984), Climatic Amplitude Method (CAM; Fauquette et al., 1998a and b) especially
46	developed for periods without modern pollen assemblages analogues, "Climate Reconstruction
47	Analysis using Coexistence Likelihood Estimation" (CRACLE; Harbert and Nixon, 2015). Despite
48	this plethora, it appears that they cannot be used in all cases and they all present different biases that
49	affect the reliability of climatic reconstruction (e.g. Uhl et al., 2007a; Blonder et al., 2012; St.
50	Jacques et al., 2015). Climate reconstruction techniques based on leaf physiognomy (such as
51	CLAMP and LMA) tend to underestimate palaeotemperature (Kowalski and Dilcher 2003). Such
52	differences have been interpreted as a consequence of the fact that fossil floras are mostly
53	composed by species from wet environments (Kowalski and Dilcher 2003). Uhl et al. (2007a)
54	compared the results given by different leaf physiognomic techniques (CLAMP, LMA, CA and
55	ELPA - European Leaf Physiognomic Approach) applied on diverse Cenozoic palaeofloras. Uhl et
56	al. (2007a) highlighted that the differences between the different methods mostly depend on the age
57	of the fossil localities: differences are more marked for Neogene floras than for Palaeogene ones.
58	The same authors also showed that, in general for the Neogene, CLAMP provides lower estimation
59	of temperature than CA and ELPA. Blonder et al. (2005) also highlighted a possible bias for leaf
60	physiognomy methods. Before fossilisation, leaves fall on the grounds where death processes
61	happen. In particular, Blonder et al. (2005) studied shrinkage and showed that it can strongly affect
62	leaf area (reduction of 22% of the leaf area in average on the 3401 studied leaves, with a maximum
63	of 82% of shrinkage). Such variation can deeply affect palaeoclimatic reconstructions based on leaf
64	physiognomy only. Concerning pollen-based climate reconstruction, St. Jacques et al. (2015)
65	showed that human activities have more or less altered the modern vegetation and hence the pollen
66	rain at least since the mid-19th century. Calibrations for palaeoclimate reconstructions based on

modern pollen assemblages or pollen distribution are thus somehow biased.

Bernasso (southern France) is a fossil locality of the Early Pleistocene (Ildefonse et al., 1972; Ambert et al., 1990) that yielded well-documented micro- and megaflora (Suc. 1978; Leroy and Roiron, 1996). Bernasso palaeoflora was a unique plant assemblage, mixing both Mediterranean and Caucasian taxa (Suc, 1978; Vernet, 1981; Leroy and Roiron, 1996). Whereas the Bernasso palaeoflora is well-known, its climatic significance can be improved. In particular, we do not know why a mixed vegetation developed at Bernasso at the beginning of the Pleistocene. The coexistence of Caucasian and Mediterranean taxa needs specific climatic conditions: combination of Caucasian climatic conditions and Western Mediterranean climatic conditions. So, in order to understand the development of the atypical palaeoflora of Bernasso, Leaf Margin Analysis (LMA; Wilf, 1997), Climate Leaf Analysis Multivariate Program (CLAMP; Wolfe, 1993, 1995) analysis based on the megaflora and Climatic Amplitude Method (CAM; Fauquette et al., 1998a and b) based on pollen data were applied to mega- and micro-fossil assemblages to better characterise the climatic conditions that controlled the vegetation development in the Bernasso area at the beginning of the Pleistocene. This study has provided an opportunity to compare climatic estimates obtained through three methods based on leaf material and pollen data and to make quantitative instead of qualitative reconstructions.

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## 2. Material and methods

2.1. Site of Bernasso

The fossil locality of Bernasso (43°43'34"N, 3°15'25"E) is located in the northwestern part of the Hérault Department (southern France), at an altitude of 512 m asl (Fig. 1). Today, at Lunas (altitude of 371 m asl), the nearest small town at ~5 km from Bernasso (Fig. 1), the climatic parameters are the following: a mean annual temperature of 12.8°C, a mean temperature of the coldest month of 4.8°C, a mean temperature of the warmest month of 21.3°C, a mean annual precipitation around 720 mm (source: https://fr.climate-data.org).

The site of Bernasso represents lacustrine deposits (diatomites and clays) that formed in the volcanic context of the Escandorgue Massif that was active at the end of the Pliocene and beginning

of the Pleistocene. As a consequence of this volcanic activity, a basalt flow completely blocked a palaeovalley, which resulted in the formation of the lake of Bernasso in which pollen grains and fossil leaves were preserved. For more details about the geological and sedimentological contexts, see following references: Ildefonse, 1970; Ildefonse et al., 1972, 1976; Suc, 1978; Ambert et al., 1990; Leroy, 1990; Leroy and Seret, 1992; Roiron, 1992; Leroy and Roiron, 1996.

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Ambert et al. (1990) and Løvlie et al. (1992) showed that the entire succession belongs to a reverse palaeomagnetic time-interval between the end of the Matuyama period (top of normal Chron C2an.1n at 2.581 Ma; Hilgen et al., 2012) and beginning of the normal Olduvai episode (base at 1.945 Ma; Hilgen et al., 2012), dates confirmed by K-Ar dating. Considering this chronological frame, Leroy and Roiron (1996) placed the Bernasso floral succession within the oxygen isotope stratigraphic interval MIS 81 to 73. Suc and Popescu (2005) refined the correlation with the oxygen isotope stratigraphy with respect to the feature and amplitude of climatic changes suggested by the pollen record: the Bernasso floral succession spanned MIS 82 to MIS 78, i.e. from about 2.2 to 2.1 Ma. On the basis of pollen record (Suc, 1978), three successive pollen zones have been defined illustrating different vegetation types: the oldest (pollen zone I) and the youngest (pollen zone III) are dominated by a steppe assemblage and correspond to dry and/or cold periods, the intermediate zone (pollen zone II) indicates a vegetation that developed under a wetter and warmer climate (Fig. 2). By comparison to regional pollen diagrams and to other glacial-interglacial cycles, pollen zone II has been attributed to the last part of an interglacial when the climate was already cooling down, but with still relatively high precipitation (Leroy, 1990, 2007). Outcrop collapse did not allow sampling the transition from pollen zone I to pollen zone II; hence a hiatus is recognised despite the attempt to fill it in by making a borehole (core BNI). Pollen zones I and III provided only pollen, while in one horizon of pollen zone II an abundant megafloral assemblage including leaves and fruits has been found (Ildefonse et al., 1976) (Fig. 2).

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## 2.2. The fossil megaflora

More than 800 fossil leaves, attributed to 23 different taxa (for details, see Leroy and

Roiron, 1996), were collected at Bernasso. These leaves are now preserved in the Collection of the Institut des Sciences de l'Evolution of Montpellier (ISEM) (contact: vincent.girard@umontpellier.fr) and form part of the palaeontological Collection of the University of Montpellier (https://collections.umontpellier.fr/; contact: suzanne.jiquel@umontpellier.fr). When the present study was conducted, the collection was split into two sub-collections, one housed in the ISEM, one housed in the former Centre de Bioarchéologie et d'Ecologie of Montpellier. The present study was conducted on this second sub-collection that represents only 590 leaves. No particular selection was done to partition the collection and the subset used in this study contains all the species and morphological variants found at Bernasso.

The most abundant megaremains correspond to the species *Carpinus orientalis* Mill., *Parrotia persica* (DC) C.A. Mey., and the genera *Acer* L. and *Carya* Nutt. The other leaves are mostly angiosperms (15 taxa) and only few correspond to ferns (1 taxa) and gymnosperms (only 2 needles). For more details about this fossil assemblage, see Leroy and Roiron (1996) and the Appendix.

## 2.3. The fossil microflora

On the basis of pollen record (Suc, 1978), three successive pollen zones have been defined illustrating different vegetation types: the oldest (pollen zone I) and the youngest (pollen zone III) are dominated by a steppe assemblage and correspond to dry and/or cold periods, the intermediate zone (pollen zone II) indicates a vegetation that developed under a wetter and warmer climate (Fig. 2). Unfortunately, a hiatus has been identified between pollen zones I and II. By comparison to regional pollen diagrams and to other glacial-interglacial cycles, pollen zone II has been attributed to the last part of an interglacial when the climate was already cooling down, but with still relatively high precipitation (Leroy, 1990, 2007). Pollen zones I and III provided only pollen, while the abundant megafloral assemblage including leaves and fruits has been found in pollen zone II (Ildefonse et al., 1976) (Fig. 2).

In the present study, we focus on the three pollen records covering pollen zone II: 1) the megaflora layer itself (Leroy and Roiron, 1996), 2) the outcrop studied by Suc (1978) and 3) the

borehole BN I (Leroy and Roiron, 1996) (Fig. 2). The taxa recorded are given Table S2. In pollen zone II, pollen data point to an environment dominated by a vegetation rich in arboreal taxa such as *Carya, Pterocarya, Celtis, Ulmus-Zelkova, Carpinus orientalis, Acer, Parrotia persica, Alnus*, etc. Gymnosperms like *Tsuga, Abies, Picea* are also present in the pollen data (Suc, 1978). Pollen zone II has been related to a warm and wet climatic phase, but already belonging to the end of an interglacial (Suc, 1978; Leroy, 1990; Leroy and Roiron, 1996; Leroy, 2007).

Based on these pollen data, palaeoclimate has been reconstructed using the Climatic Amplitude Method (CAM) in which the climatic requirements of modern taxa are transposed to fossil data (Fauquette et al., 1998a, b). This approach relies on the relationship between the relative pollen abundance of each individual taxon and climate. It takes into account not only presence/absence criterion as in the Coexistence Approach (Utescher and Mosbrugger, 1997) but also pollen percentages to provide more reliable reconstructions.

The most probable climate for a fossil pollen assemblage is estimated as the climatic interval in which the highest number of taxa can exist and a "Most Likely Value" (MLV) corresponding to a weighted mean according to the size of the climatic intervals of all taxa. As the precision of the information obtained from a taxon's climatic interval is inversely related to the width of this interval, the weights are greater for taxa with smaller intervals (for more details, see Fauquette et al., 1998a).

Pinus pollen grains are excluded from the pollen sum as they are generally over-represented due to a prolific production and over-abundance due to long-distance transport. Moreover, at the genus taxonomic level, the various species of Pinus develop under a large variety of climates and Pinus is thus not really informative. High latitude/altitude taxa are also excluded from the reconstruction process to avoid a cold bias linked to pollen transport from higher elevations (Fauquette et al., 1998a). The excluded taxa are defined on the basis of their occurrence in modern vegetation zones (Fauquette et al., 2018): vegetation types described for the Neogene and lower Pleistocene are found today in the Southeastern China (Wang, 1961; Hou, 1983). There, the vertical distribution of vegetation is characterized from the base to the top of the mountains by evergreen broad-leaved forest, mixed evergreen and deciduous broad-leaved forest, PicealTsuga forest, Abies

forest and high mountain meadows (Wang, 1961; Hou, 1983). In our study, this altitudinal stratification and the absence of high altitude taxa in the megaflora are the base for excluding the modern high altitude taxa from the climatic reconstruction in order to infer the low to middle-low altitude climate (Fauquette et al., 1998a). Comparison with other diatomite palaeofloras justifies also this choice. Indeed at Murat (Roiron, 1991), the high percentages of *Abies* pollen grains in the diatomites are associated with *Abies* megafossils (leaves and reproductive structures), which is not the case at Bernasso.

# 2.4. Methods used for palaeoclimatic quantification

The Leaf Margin Analysis (LMA) is used to provide mean annual temperature estimates. It was applied on the leaves of Bernasso with the different equations derived by Wolfe (1979), Wilf (1997), Gregory-Wodzicki (2000), Greenwood et al. (2004), Traiser et al. (2005) and Miller et al. (2006) for the different regions of the globe. The only one available for Europe (Traiser et al., 2005) is compared to other equations of the Northern Hemisphere, as it is the equation with the weakest correlation between the mean annual temperature and proportion of entire margined leaves (Traiser et al., 2005).

The Climate Leaf Analysis Multivariate Program (CLAMP) was also applied to the fossil leaves of Bernasso. The online CLAMP application was used for this purpose (Wolfe, 1993, 1995; <a href="http://clamp.ibcas.ac.cn/">http://clamp.ibcas.ac.cn/</a>). Since its initial introduction, CLAMP has undergone continuing development (Kovach and Spicer, 1995; Wolfe and Spicer, 1999; Spicer, 2007, 2008; Spicer et al., 2004, 2009) including an online version (Yang et al., 2015) and now encompasses 32 morphological characters of leaves concerning the shape and size of the leaf, its margin (presence or absence of teeth), the shape of the leaf apex, base and surface. For each morphological character, a value between 0 and 1 was attributed according to standard CLAMP protocols. All the data were summarized in a matrix (Table S1). This was then analysed with the CLAMP online canonical correspondence analysis (CCA). We tested the different CLAMP calibrations that concern the Northern and Southern hemispheres to provide ranges of values for different environmental parameters from Bernasso. Two plant species from Bernasso were not taken into account (Aspidium

meyeri, Filicophyta and Ceratophyllum demersum, Ceratophyllaceae, aquatic angiosperm) because they do not correspond to woody dicotyledon angiosperms. CLAMP does not provide directly mean annual precipitation data but precipitation during the three wettest and driest months, which allow estimating the mean annual precipitation. It can be estimated as an interval comprised between a low value of precipitation (LMP) and a high value (HMP). The low value can be calculated as follows:

 $LMP = 3 \times 3DRY + 3WET (1)$ 

- where 3DRY corresponds to the precipitation during the three driest months and 3WET to the precipitation during the three wettest months. The high value can be calculated as follows:
- $\text{HMP} = 3\text{DRY} + 3 \times 3\text{WET}$  (2).
- 217 LMP and HMP provide an interval of precipitation between a very low value (nine "dry" months
  218 and three "wet" months) and a very high value of precipitation (three "dry" months and nine "wet"
  219 months), the real mean annual precipitation being between these two extreme values.

Using pollen data, palaeoclimate is reconstructed with the Climatic Amplitude Method (CAM) in which the climatic requirements of modern taxa are transposed to fossil data (Fauquette et al., 1998a, b). This approach relies on the relationship between the relative pollen abundance of each individual taxon and climate. It takes into account not only presence/absence criterion as in the Coexistence Approach (Mosbrugger and Utescher, 1997) but also pollen percentages to provide more reliable reconstructions.

The most probable climate for a fossil pollen assemblage is estimated as the climatic interval in which the highest number of taxa can exist and a "Most Likely Value" (MLV) corresponding to a weighted mean according to the size of the climatic intervals of all taxa. As the precision of the information obtained from a taxon's climatic interval is inversely related to the width of this interval, the weights are greater for taxa with smaller intervals (for more details, see Fauquette et al., 1998a).

*Pinus* pollen grains are excluded from the pollen sum as they are generally over-represented due to a prolific production and over-abundance due to long-distance transport. Moreover, at the genus taxonomic level, the various species of *Pinus* develop under a large variety of climates and

Pinus is thus not really informative. High latitude/altitude taxa are also excluded from the reconstruction process to avoid a cold bias linked to pollen transport from higher elevations (Fauquette et al., 1998a). The excluded taxa are defined on the basis of their occurrence in modern vegetation zones (Fauquette et al., 2018): vegetation types described for the Neogene and Early Pleistocene are found today in the Southeastern China (Wang, 1961; Hou, 1983). There, the vertical distribution of vegetation is characterized from the base to the top of the mountains by evergreen broad-leaved forest, mixed evergreen and deciduous broad-leaved forest, *PicealTsuga* forest, *Abies* forest and high mountain meadows (Wang, 1961; Hou, 1983). In our study, this altitudinal stratification and the absence of high altitude taxa in the megaflora are the base for excluding the modern high altitude taxa from the climatic reconstruction in order to infer the low to middle-low altitude climate (Fauquette et al., 1998a). Comparison with other diatomite palaeofloras justifies also this choice. Indeed at Murat (Roiron, 1991), the high percentages of *Abies* pollen grains in the diatomites are associated with *Abies* megafossils (leaves and reproductive structures), which is not the case at Bernasso.

## 3. Results

The results obtained with the three methods (LMA, CLAMP, CAM) are summarized in Figures 3 (temperatures) and 4 (precipitation) and are detailed in Tables S3 (LMA results), S4 (CLAMP results) and S5 (CAM results) of the Supplementary material. Figure S1 shows CLAMP CCA plots of physiognomic space obtained with the global CLAMP calibration.

In what concerns CLAMP, we only retain in the discussion the results obtained with the calibrations from the Northern Hemisphere. Indeed, Calib 5 to Calib 7 correspond to calibrations for Asian vegetation that suffer strong monsoonal climate (Calib5 and Calib6) and for 378 sites from all continents (Calib7). Due to their specificity, these last three calibrations were not analyzed in our study, but the complete CLAMP calibrations are however given Supplementary Table S4.

Regarding CAM, the climatic conditions reconstructed from pollen data of the leaf level and of pollen zone II data (borehole BN I and outcrop) are summarized in the Supplementary Table S5.

Concerning Bernasso mean annual temperatures, CLAMP and LMA show similar ranges but are lower than that reconstructed by CAM. In the same way, CLAMP indicates once again largely lower values for mean temperature of the coldest and warmest months than CAM (Fig. 3). However, mean annual precipitation and relative humidity are in agreement between both methods (Fig. 4 and Supplementary Table S4 and S5), even if precipitation is slightly higher with CLAMP than with CAM.

## 4. Discussion

Comparison to modern floras highlighted similarities between the Bernasso palaeoflora and the modern flora of the Hyrcanian (South of the Caspian Sea) and the Euxinian (East of the Black Sea) regions (Ambert et al., 1995; Leroy and Roiron, 1996). The climate under which Bernasso palaeovegetation grew was thus interpreted by these authors, by comparison with modern climatic data from diverse stations of the Caucasian region (Table S6; see also Table 4 in Leroy and Roiron, 1996), as similar to that of both regions, i.e. characterised by a mean annual temperature of 14-17°C, temperature of the coldest month of 5-6.5°C and of the warmest month of 24-26.5°C and high precipitation (more than 800 mm per year). The Bernasso palaeoflora was estimated to have thus developed under a warmer (+ 2 to 5°C) and wetter (at least + 300 to 500 mm per year) climate than today. However, the presence of taxa such as *Carpinus orientalis*, *Acer monspessulanum* L., *Celtis australis* L., *Fraxinus ornus* L. in the megaflora (Leroy and Roiron, 1996) and *Olea*, *Phillyrea*, *Philomis* cf. *fruticosa* and *Quercus ilex*-type in the pollen flora (Suc, 1978), suggests that the Bernasso palaeoflora was exposed to climatic conditions that made the occurrence of typical Mediterranean sclerophyllous elements possible in the underneath vegetation belt (Suc, 1978).

# 4.1. Comparison of the results obtained with the three methods

CLAMP and LMA indicate mean annual temperatures largely lower than the modern temperatures observed in the Caucasian region and Lunas near Bernasso (Fig. 3). The CAM values are furthermore in agreement with the temperatures deduced by Leroy and Roiron (1996) and are

Leroy and Roiron (1996) could have thus misjudged the Bernasso palaeoclimate.

close to the modern Hyrcanian values. Compared to the Hyrcanian region (that Leroy and Roiron (1996) supposed to be a modern analogue to the fossil flora of Bernasso), all the methods provide very low temperature values of the coldest month (Fig. 3 and Table S6). Concerning this parameter, the very low temperature values with CLAMP (-3.79 to -6.33° C) seem to be incompatible with the presence of mesothermic Mediterranean sclerophyllous taxa (Leroy and Roiron, 1996) that do not support such negative temperatures (Quézel and Médail, 2003) (Fig. 3 and Table S6). Concerning the temperature of the warmest month, CLAMP values (17.18 to 19.19°C) are also very low compared to those of the supposed analogue of the Hyrcanian region. On the contrary, CAM values for this parameter of more coherent with those of the supposed analogue of the Hyrcanian region (Fig. 3 and Table S6).

Precipitation results are included in the precipitation range of the Hyrcanian region that has precipitation varying at low altitude from 500-600 mm to the East to 2000-2200 mm to the West (Fig. 4 and Table S6; Molavi-Arabshahi et al., 2016; Iran Meteorological Organization (IRIMO), http://www.irimo.ir/eng/). Leroy and Roiron (1996) suggested that the Bernasso palaeoflora grew under a humid (perhaps very humid) climate and our results tend to support their hypothesis. However, Suc (1978) and Leroy and Roiron (1996), on the basis of pollen data, interpreted the climate of the pollen phase II (during which megaremains were deposited) as warm and wet with only a weak hydric seasonality (weak decrease in summer precipitation). CLAMP results do not completely confirm this last conclusion and show that the hydric seasonality could have been wellmarked, with a ratio between wettest and driest months according to some CLAMP calibrations varying from ca. 1.4:1 to 5.7:1. The question of a possible seasonal drought is still unsolved, especially as the CLAMP global calibration places Bernasso between East Asian (excluding Southeastern), North American and Russian localities (Supplementary Figure S1). It could have been the case as it is today in the Mediterranean region, but no reconstruction, whatever the method used, allows to confirm it and no leaf specimen from Bernasso displays obvious functional adaptation to drought.

In the CAM, high latitude-altitude taxa are excluded from the reconstruction process to

avoid a cold bias linked to pollen transport from higher vegetation belts. The Bernasso valley was a long, narrow and steep-sided valley (Ildefonse et al., 1972), as today, and the palaeoforest was growing from the lake level to the plateau at the top of the canyon. Suc (1978) and Leroy and Roiron (1996) suggested that an altitudinal zonation of the palaeoflora existed. They advocated that the mid-altitudinal mixed forest on the slopes of the Bernasso palaeocanyon was composed of *Carpinus orientalis*, *Parrotia persica* and several species of *Acer. Carya* and *Zelkova* should have grown only in sheltered areas of the palaeocanyon. Gymnosperms like *Tsuga*, *Abies*, *Picea* are present in the pollen flora (Suc, 1978), but they were certainly not growing close to the lake shoreline as no leaf or cone specimens have been found in the megaflora (Leroy and Roiron, 1996). These pollen grains certainly came from a conifer forest growing at higher altitude. Such an altitudinal zonation may be found today in the Southern Caspian Sea region (Rmezani et al., 2013) even if it is incomplete as *Abies*, *Picea* and *Tsuga* are absent there. It may be also found in China, in the subtropical evergreen broad-leaved forest region (Hou, 1983).

However, taking into account the high percentages of *Tsuga* in the pollen data (Suc, 1978; Leroy and Roiron, 1996), although this taxon is considered as a middle to high altitude-latitude taxon and is not present in the megaflora (Leroy and Roiron, 1996), we could hypothesize that *Tsuga* was developing relatively close to the lake, as it was in the case of a nearby maar lake in Nogaret (1.9 Ma; Brugal et al., 1990; Leroy and Seret, 1992). We thus made a climate reconstruction with the CAM including the climatic requirements of this taxon. The obtained temperatures are lower than the temperatures estimated excluding *Tsuga*: mean annual temperatures are between 11 and 15°C (most likely value ~13°C), mean temperature of the coldest month between -2 and 5°C (most likely value ~1.3°C), mean temperature of the warmest month between 23 and 27°C (most likely value ~24.8°C). Remarkably, mean annual precipitation and relative humidity are equivalent to values without *Tsuga*. In any case the temperatures are never as low as the CLAMP and LMA temperatures.

Adroit et al. (2016) supported the fact that the Bernasso flora should have existed under a high mean annual precipitation on the basis of the low diversity and high quantity of galling found on the fossil leaves of Bernasso. However, the analysis of plant insect interactions on modern and

fossil leaves of *Parrotia persica* made a likely correlation between mean annual precipitation and proportions of insect damages on leaves unclear (Adroit et al., 2018). More in-depth analyses are in development to improve our understanding of the links between plant-insect interactions and climatic parameters. These future results will possibly help clarifying Bernasso palaeoclimate.

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## 4.2. Potential and limits of the methods

The three methods used in the present study have the advantage to give quantitative instead of qualitative reconstruction of the climate that allows direct comparisons. However, each quantitative methodology proposing climatic reconstructions based on biological palaeoproxies has its own characteristics influencing the results. For the CAM, we decided to exclude the high altitude/latitude taxa based on their absence in the megaflora and on their modern altitudinal distribution. However, reconstructions based on leaf physiognomy (LMA, CLAMP) methods give generally lower temperature values when applied to European palaeobotanical records (e.g. Utescher et al., 2000; Uhl et al., 2003, 2006, 2007a, b; Peppe et al., 2011; Thiel et al., 2012). In fact the modern datasets used to calibrate the relationships does not originate from modern floras distributed evenly worldwide (Yang et al., 2015). For CLAMP, the available modern data sets do not include data from southern Europe (only five sites in the United Kingdom and some sites in western FSU; Yang et al., 2015), nor from the Middle East (http://clamp.ibcas.ac.cn). This may be problematic as many authors have shown that temperate floras of different continents may have different leaf-climate relationships (e.g. Gregory-Wodzicki, 2000; Greenwood et al., 2004) that led to significant differences in temperature estimates up to 5°C or more (Jordan, 2011). The case of the Bernasso megaflora falls into this gap as it is composed of a mixture of taxa living today in the Mediterranean region and in the SW Asia (including the Hyrcanian region). However Yang et al. (2015) showed that, in general, CLAMP results seem to be more influenced by climate than biogeography, corroborating CLAMP results. Also CLAMP calibrations have been validated against isotopic methods and found to give reliable results, in any case for the Early Eocene and Miocene periods in the Southern Tibet (Xu et al., 2017 and references therein).

Moreover, the modern dataset incorporates many types of sites including dry land sites although fossil megafloras are predominantly deposited in wet land sites, which also leads to discrepancies. Due to this bias, Kowalski and Dilcher (2003) indicated that physiognomic methods lead to an underestimation of temperatures between 2.5 and 10°C. With the results obtained by CLAMP and LMA methods in this study, one can note that the low temperatures estimated for Bernasso are found today in southern Norway, at Kristiansand (58°09'N, at sea level, source: <a href="https://fr.climate-data.org">https://fr.climate-data.org</a>) (Fig. 3; Table S6). Applying the range of underestimation of the mean annual temperature given by Kowalski and Dilcher (2003), we obtain a corrected mean annual temperature for Bernasso comprised between 7°C and 17°C, a range of mean annual temperature more consistent with the results given by the CAM, even if it is still slightly lower.

Peppe et al. (2011) made reconstructions using "digital leaf physiognomy" calibrated on modern data corresponding to 92 sites sampled in biomes where fossil leaves are generally preserved. The correlations between the chosen leaf characters and climate parameters show that these physiognomic variables are linked to climate. When applying this calibration to fossil floras, the authors obtained a warmer and wetter climate, similar to that estimated by other independent palaeo-proxies (Peppe et al., 2011). However, it is noteworthy that improvements can be made, particularly in adding more modern sites to have a larger training set of data in calibrating the model with additional sites that are still absent from this database (for instance from Europe and Africa, Peppe et al., 2011).

All these evidences indicate that the CLAMP method seems not optimal to reconstruct the climate of the early Pleistocene in Europe because of the lack of modern data to calibrate the method on European ecosystems (Uhl et al., 2007a). These results are thus opposite to those of Xia et al. (2009) and Bondarenko et al. (2013) in which CLAMP analyses provided coherent results with other palaeoclimate reconstruction methods. CLAMP results from Bernasso probably reflect the absence of modern analogues from Mediterranean climate in CLAMP. At Bernasso, palaeotemperatures estimated by CLAMP and LMA are lower than those given by CAM. Also, as the quantification by CLAMP and LMA made on Bernasso remains unique, it is difficult to see if the Bernasso results are similar to other regional results or different from them. The values obtained

with CAM are in agreement with the climate reconstructed at Garraf in Northern Spain for the same period (Fauquette et al., 1998a). It thus appears that, at a regional scale, CAM provides coherent results and may be used to reconstruct the climate at the beginning of the Pleistocene, at least in the South European region.

#### **5. Conclusions**

The fossil site of Bernasso is remarkable, recording both leaves and pollen grains that allows applying different climatic reconstruction methods and thus comparing results. Climatic reconstruction using CLAMP and LMA methods based on megaflora on one hand and using the Climatic Amplitude Method (CAM) based on pollen flora on the other hand have been made to check the values given in an earlier study based on the comparison between palaeovegetation data and similar modern ecosystems. In the latter study, the climate at Bernasso was compared to the modern climate of the Hyrcanian and Euxinian regions.

The comparisons of the three methods used in this study highlight their complementarity as LMA and CLAMP are based on leaf physiognomy and do not take into account the taxonomy of the plants, whereas CAM is based on the modern climatic requirements of the taxa present in the pollen flora from the same sediment level. CLAMP provides supplementary data about precipitation pattern (*e.g.* precipitation during the three wettest and driest months) that can be partly compared to the CAM results (*i.e.* mean annual precipitation).

However, despite this possible complementarity, the results of this study highlight important differences between the three methods. CLAMP and LMA analyses show that late-interglacial Bernasso climate was colder than the present-day climate in Southern France and in the Hyrcanian region. Against all expectations, the obtained values are found today in southern Norway (58°09'N at sea level; Fig. 3; Table S6). CAM shows mean annual temperatures higher than the modern Bernasso mean annual temperature and equivalent to the temperature of the Hyrcanian region. For what concerns mean temperature of the coldest and warmest months, CLAMP indicates again lower values than the Climatic Amplitude Method. The only parameters more or less in agreement between CLAMP and CAM are mean annual precipitation and relative humidity; the climate was

430 wetter than today at Bernasso with the existence of a weak precipitation seasonality highlighted in 431 the CLAMP results. 432 The two physiognomic methods lead to an underestimation of temperatures from 2.5 to 10°C may be due to problems of calibration. Absence of calibration sites in Europe and in the 433 434 Mediterranean region are a critical problem in the underestimation by CLAMP. Calibrations are 435 also still needed for the Climatic Amplitude Method in order to have a better precision on the 436 presence of some taxa in the local flora deduced from pollen data and to get more accurate climatic 437 reconstruction. 438 439 440 **Acknowledgments** 441 We thank Frédéric Jacques (Chinese Academy of Sciences) for its assistance in the preparation of 442 CLAMP files. We express our gratitude to Robert Spicer for its constructive comments on an earlier 443 version of the manuscript and his helps in improving our discussion about the different 444 methodological biases. 445 This is publication n° 201x–00x of the Institut des Sciences de l'Evolution de Montpellier 446 (France). 447 448 449 References Adroit, B., Malekhosseini, M., Girard, V., Abedi, M., Rajaei, H., Terral, J.F., Wappler, T., 450 451 2018. Changes on pattern of plant insect interactions on the Persian ironwood (*Parrotia persica*) 452 over the last 3 million years. Review of Palaeobotany and Palynology. 453 https://doi.org/10.1016/j.revpalbo.2018.06.007 454 Adroit, B., Wappler, T., Terral, J.F., Ali, A.A., Girard, V., 2016. Bernasso, a paleoforest from the 455 early Pleistocene: New input from plant-insect interactions (Hérault, France). Palaeogeography, 456 Palaeoclimatology, Palaeoecology 446, 78-84.

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Figure captions

Figure 1 – Location map of Bernasso situated in the Northwestern part of the Hérault Department (Southern France).

Figure 2 – Lithology, synthesized pollen diagrams of the three pollen records and position of the

megaflora layer. Pollen diagrams of the exposed section refer to Suc (1978), those of the Borehole

BNI and Leaf outcrop refer to Leroy (1990) and Leroy and Roiron (1996).

http://www.irimo.ir/eng/), see Table S6 for more details.

Figure 3 – Comparison of the temperatures (in °C) estimated with the three methods, in blue the mean temperature of the coldest month, in black the mean annual temperature and in red the mean temperature of the warmest month. For LMA and CLAMP, the darker bars correspond to the estimated values and the intervals to the standard errors for LMA regression equations Reg 1, Reg 2, Reg 7 and Reg 8 and CLAMP calibrations Calib 1 to Calib 4. See details for LMA and CLAMP calibrations in Tables S3 and S4. For CAM, the intervals correspond to the estimated climate and the darker bars to the Most Likely Values (weighted means), see details in Table S5. The green bands correspond to the modern annual temperature at Kristiansand in Southern Norway, Lunas in Southern France (source: https://fr.climate-data.org) and in the East and West Hyrcanian regions in Iran (Molavi-Arabshahi et al., 2016; source: Iran Meteorological Organization (IRIMO),

Figure 4 - Comparison of the precipitation (in mm) estimated with four different calibrations of CLAMP and with CAM. For CLAMP calibrations, the calibrations Calib1 and Calib2 correspond to Physg3brcAZ calibration (based on 144 modern vegetation sites from the Northern Hemisphere temperate regions; Calib2 was obtained thanks to a meteorological correction applied in Calib1); the calibrations Calib3 and Calib4 correspond to Physg3arcAZ calibration (based on 173 modern vegetation sites from the Northern Hemisphere including samples from areas with pronounced winter cold; Calib4 was obtained thanks to a meteorological corrections applied in Calib3). Calib5 is an Asian calibration. For CAM, the intervals correspond to the estimated climate and the darker bars to the Most Likely Values. The four yellow bands correspond to the modern annual

641 precipitation at Kristiansand in Norway, Lunas in Southern France (source: https://fr.climate-642 data.org) and in the East and West Hyrcanian regions in Iran (Molavi-Arabshahi et al.2016; source: 643 IRIMO, http://www.irimo.ir/eng/), see Table S6 for more details. 644 **Supplementary material** 645 Figure S1 - Canonical correspondence analysis (CCA) plots showing the place of Bernasso within 646 647 the 378 vegetation sites available in CLAMP. A- axes 1-2 space; B- axes 1-3 space; C- axes 2-3 648 space. Climate vectors are positioned for information. MAT- mean annual temperature; CMMT-649 cold month mean temperature; WMMT- warm month mean temperature; LGS- length of the growing season; GSP- growing season precipitation; MMGSP- mean monthly growing 650 651 season precipitation; 3-WET- precipitation during the three wettest months; 3-DRY-652 precipitation during the three driest months; SH- specific humidity; RH- relative humidity; 653 ENTHAL- enthalpy (modified from Yang et al., 2015). 654 655 **Table S1** - Data matrix input to on-line CLAMP analysis tool. 656 **Table S2** – List of the pollen taxa recorded respectively in the outcrop, leaf level and borehole. High latitude/altitude taxa that are excluded of the climatic reconstruction process are indicated in 657 658 bold and taxa used to reconstruct the climate are underlined. The Mediterranean sclerophyllous taxa 659 have been also excluded because they probably inhabited a lower vegetation belt than that of the Bernasso interglacial forest. The others correspond to taxa that do not give precise climatic 660 661 information because of large climatic amplitudes or to taxa for which we do not know the climatic requirements. 662 663 Table S3 – Mean Annual Temperature (MAT) obtained from the different LMA regression 664 equations considering that Bernasso megaflora contains 25.00% untoothed leaf taxa, as shown in Table S1. Reg 1, Reg 2, Reg 7 and Reg 8 are reported on Figure 3. 665 666 **Table S4** – CLAMP results obtained from the Bernasso megaflora. Calib 1 to 4 are reported on 667 Figures 3 and 4. Table S5 – Climatic estimates obtained with the Climatic Amplitude Method using pollen data of 668

669	the leaf level and of the pollen zone II (borehole BN I in Leroy and Roiron (1996) and outcrop in
670	Suc (1978)). Values are reported on figures 3 and 4.
671	
672	Table S6 – Climatic parameters of the three modern analogues used in the discussion: the
673	Hyrcanian region (data obtained from Molavi-Arabshahi et al. (2016) and IRIMO
674	(http://www.irimo.ir/eng/), Kristiansand (Norway) and at Lunas (France) (data obtained from
675	Climate-data - <a href="http://fr.climate-data.org">http://fr.climate-data.org</a> ).

677

# 678 Table S1

Species*	Dissec					character State		
Species	Unlobed	Lobed	No Teeth	Teeth Regular	Teeth Close	Teeth Round	Teeth Acute	Teeth Compound
Acer integerrimum	0	1	1	0	0	0	0	0
Acer opulifolium	0	1	0.5	0.5	0.5	0.25	0.25	0
Acer protojaponicum	0	1	0	1	1	0.5	1	0
Acer pseudomonspessulanum	0	1	1	0	0	0	0	0
Carpinus orientalis	1	0	0	1	1	0	1	1
Carpinus suborientalis	1	0	0	1	1	0.5	1	1
Carya minor	1	0	0	1	1	0.5	1	0
Celtis sp	1	0	0	1	0.5	0.5	1	0
Fraxinus ornus	1	0	0	1	0.5	0.5	1	0
Hedera helix	0.5	0.5	1	0	0	0	0	0
<i>Ilex</i> sp	0.5	0.5	0	0.5	0.5	0.25	1	0
Parrotia persica	1	0	1	0	0	0	0	0
Populus tremula	1	0	1	0	0	0	0	0
Prunus sp	1	0	0	1	1	0.5	1	0
cf. Salix caprea	1	0	0	1	1	0.5	1	0
Sorbus domestica	1	0	0	1	1	0.5	1	0
Tilia sp	1	0	0	0.5	1	0.5	0.5	1
Vitis sp	0.5	0.5	0	0.5	0.5	0.5	0.5	0
Zelkova acuminata	1	0	0	1	1	0.5	1	0
Zelkova crenata	1	0	0	1	1	0.5	1	0
Dicot. Indet. 1	0	1	0	1	1	0.5	0.5	0
Dicot. indet. 2	1	0	0	1	1	0.5	0.5	0
Character state score	15.5	6.5	5.5	15	14.5	7.5	14.25	3
No. character states present	22	22	22	22	22	22	22	22
Percent Score	70.45	29.55	25.00	68.18	65.91	34.09	64.77	13.64

	Size Character States											
Species	Nano- phyll	Leptop- hyll I	Lepto- phyll II	Micro- phyll I	Micro- phyll II	Micro-phyll III	Meso- phyll I	Meso- phyll II	Meso-phyll III			
Acer integerrimum	0	0	0	0	0.5	0.5	0	0	0			
Acer opulifolium	0	0	0	0	0.5	0.5	0	0	0			
Acer protojaponicum	0	0	0	0.5	0.5	0	0	0	0			
Acer pseudomonspessulanum	0	0	0	0.5	0.5	0	0	0	0			

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Dicot. Indet. 1	0	0	0	0.5	0.5	(	0	0	0	0
Dicot. indet. 2	0	0	0	1	0	(	0	0	0	0
Character state score	0	0	0	4.5	10.5	4	4	3	0	0
No. character states present	22	22	22	22	22	2	22	22	22	22
Percent Score	0.00	0.00	0.00	20.45	47.73	18	.18	13.64	0.00	0.00
Species			Apex Chara						haracters St	
Species	Apex E	marginate	Apex Round	Apex Acute	e Apex Atte	nuate	Base C	ordate I	Base Round	Base Acute
Acer integerrimum		0	0	0	1		1	-	0	0
Acer opulifolium		0	0	0	1		1	-	0	0
Acer protojaponicum		0	0	1	0		1	-	0	0
Acer pseudomonspessulanun	ı	0	0.5	0.5	0		0.	5	0.5	0
Carpinus orientalis		0	0	1	0		C	)	1	0
Carpinus suborientalis		0	0	1	0		C	)	1	0
Carya minor		0	0	1	0		C	)	0	1
Celtis sp		0	0	1	0		C	)	0	1
Fraxinus ornus		0	0	1	0		C	)	0	1
Hedera helix		0	0	1	0		0.	5	0	0.5
<i>Ilex</i> sp		1	0	0	0		C	)	1	0
Parrotia persica		0	0	1	0		C	)	0	1
Populus tremula		0	1	0	0		C	)	1	0
Prunus sp		0	0	0	1		C	)	1	0

Carpinus orientalis	0	0	0	0.5	0.5	0	0	0	0
Carpinus suborientalis	0	0	0	0	1	0	0	0	0
Carya minor	0	0	0	0	0	0	1	0	0
Celtis sp	0	0	0	0.5	0.5	0	0	0	0
Fraxinus ornus	0	0	0	0	0.5	0.5	0	0	0
Hedera helix	0	0	0	0	1	0	0	0	0
<i>Ilex</i> sp	0	0	0	0	0	0	1	0	0
Parrotia persica	0	0	0	0	0.5	0.5	0	0	0
Populus tremula	0	0	0	0	0	1	0	0	0
Prunus sp	0	0	0	0	1	0	0	0	0
cf. Salix caprea	0	0	0	0	1	0	0	0	0
Sorbus domestica	0	0	0	1	0	0	0	0	0
<i>Tilia</i> sp	0	0	0	0	0	0.5	0.5	0	0
Vitis sp	0	0	0	0	0	0.5	0.5	0	0
Zelkova acuminata	0	0	0	0	1	0	0	0	0
Zelkova crenata	0	0	0	0	1	0	0	0	0
Dicot. Indet. 1	0	0	0	0.5	0.5	0	0	0	0
Dicot. indet. 2	0	0	0	1	0	0	0	0	0
Character state score	0	0	0	4.5	10.5	4	3	0	0
No. character states present	22	22	22	22	22	22	22	22	22
Percent Score	0.00	0.00	0.00	20.45	47.73	18.18	13.64	0.00	0.00

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Charies		Length to	Width Char	acter States		Shape C	haracter	States
Species	L:W<1:1	L:W 1-2:1	L:W 2-3:1	L:W 3-4:1	L:W>4:1	Obovate	Elliptic	Ovate
Acer integerrimum	1	0	0	0	0	1	0	0
Acer opulifolium	1	0	0	0	0	1	0	0
Acer protojaponicum	1	0	0	0	0	0	0.5	0.5
Acer pseudomonspessulanum	1	0	0	0	0	1	0	0
Carpinus orientalis	0	1	0	0	0	0	1	0
Carpinus suborientalis	0	1	0	0	0	0	1	0
Carya minor	0	0	0	0.5	0.5	0	1	0
Celtis sp	0	0	1	0	0	0	0	1
Fraxinus ornus	0	0	1	0	0	0	1	0
Hedera helix	0.5	0	0.5	0	0	0	0	1
<i>Ilex</i> sp	0	0	1	0	0	0	1	0
Parrotia persica	0	1	0	0	0	0.5	0.5	0
Populus tremula	1	0	0	0	0	0	0	1
Prunus sp	0	0	1	0	0	0	1	0
cf. Salix caprea	0	0	1	0	0	0	1	0
Sorbus domestica	0	0	1	0	0	0	1	0
Tilia sp	1	0	0	0	0	1	0	0
Vitis sp	1	0	0	0	0	0	0	1
Zelkova acuminata	0	0	1	0	0	0	1	0
Zelkova crenata	0	0	1	0	0	0	1	0
Dicot. Indet. 1	0	0	1	0	0	0	0	1
Dicot. indet. 2	0	0	1	0	0	0	0	1
Character state score	7.5	3	10.5	0.5	0.5	4.5	11	6.5
No. character states present	22	22	22	22	22	22	22	22

Percent Score	34.09	13.64	47.73	2.27	2.27	20.45	50.00	29.55
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\* for more details about scoring of the characters: http://clamp.ibcas.ac.cn/Clampset2.html

Scores are the consensus of four independent scorers. CLAMP scores 32 character states; only those characters represented in the Bernasso megaflora are presented here. Descriptions of all character states and the details of the scoring method can be found on the CLAMP web site (<a href="http://clamp.ibcas.ac.cn">http://clamp.ibcas.ac.cn</a>).

# Table S2

	Outcrop	Leaf level	Borehole
Abies	X	X	X
<u>Acer</u>	X	X	X
Alnus	X	X	X
Amaranthaceae	X	X	X
Apiaceae	X		X
Araliaceae			X
<u>Artemisia</u>	X	X	X
Asteraceae Asteroideae	X		X
Asteraceae Cichorioideae	X	X	X
Betula	X	X	X
Brassicaceae	X	X	X
Buxus sempervirens	X	X	X
<u>Carpinus</u>	X	X	X
<u>Carya</u>	X	X	X
Caryophyllaceae	X		
Castanea	X		
Cathaya	X		X
<u>Celtis</u>	X	X	X
Centaurea			X
Cladium mariscus type			X
Corylus			X
Crassulaceae			X
Cupressaceae	X		X
Cyperaceae	X		X
Dipsacaceae			X
Elaeagnus	X		X
<u>Engelhardia</u>			X
Ephedra		X	X
Erica cf. arborea	X	A	A
Ericaceae	X		X
Erodium	A		A
<u>Eucommia</u>	X	X	X
Fagus	X	A	X
Fraxinus	X		X
Galium	X		А
Gentianaceae	A	X	X
Hedera	X	Λ	X
Helianthemum	Α		
			X
Ilex Ilex aquifolium type	X	X	X
	X		•
Juglans	X		X
Lamiaceae	X		
Ligustrum			X
Liliaceae		X	
<u>Liquidambar</u>			X
Lonicera	X	X	
<u>Myrica</u>			X
Myriophyllum			X
Olea	X		
<u>Parrotia cf. persica</u>		X	X
Parthenocissus			X
Phillyrea		X	
Phlomis		X	

Picea	X	X	X
Pinaceae	X	X	X
Pinus	X	X	X
Plantago	X		
Poaceae	X	X	X
Polygonum		X	X
Populus	X		
Potamogeton	X		
<u>Pterocarya</u>	X		
Quercus deciduous type	X		X
Quercus ilex-coccifera type	X		X
Ranunculaceae	X		X
<u>Rhamnus</u>	X		
Rumex	X		
Salix	X		
Scabiosa		X	
<u>Tilia</u>	X		X
Tsuga	X		X
Typha	X		
Typha cf. latifolia		X	
<u>Ulmus</u>		X	
Ulmus-Zelkova type	X	X	X
Urticaceae	X		X
Monoletes spores		X	
Thelypteris cf. palustris			X
Selaginella sibirica			X
Osmunda			X
Sphagnum			X

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# 690 Table S3.

Regression equation	Standard error of	Sources	Region	MAT (°C)
for MAT	estimate (°C)			
Reg1 = 30.6P + 1.14	0.8	Wolfe, 1979	East Asia	8.79
Reg2 = 28.6P + 2.24	2.0	Wilf, 1997	North America, Caribbean	9.39
Reg3 = 27.5P + 1.36	3.3	Gregory-Wodzicki, 2000	North America, Japan,	8.24
			Caribbean, South Pacific	
Reg4 = 24.9P + 3.53	2.2	Gregory-Wodzicki, 2000	North America, Japan,	9.76
			Caribbean, South Pacific	
Reg5 = 22.0P + 1.32	3.0	Greenwood et al., 2004	Eastern Australia	6.82
Reg6 = 27.0P - 2.12	2.2	Greenwood et al., 2004 Eastern Australia		4.63
Reg7 = 31.4P + 0.512	1.7	Traiser et al. 2005	Europe	8.36
Reg8 = 28.99P + 1.32	0.12	Miller et al., 2006	Central and North America	8.57

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# 692 Table S4.

Calibration*	MAT (°C)	CMMT (°C)	WMMT (°C)	3DRY (mm)	3WET (mm)	LMP (mm)	HMP (mm)
Calib1	4.95	-6.33	17.30	142.1	525.6	951.9	1718.9
	± 2.0	± 3.4	± 2.7	± 13.7	± 20.6	± 61.7	± 75.5
Calib2	5.53	-6.01	17.80	316.2	436.6	1385.2	1626.0
	± 2.1	± 3.4	± 2.5	± 5.9	± 22.9	± 40.6	± 74.6
Calib3	7.42	-3.79	19.19	141.3	537.2	961.1	1752.9

	± 2.8	± 4.0	± 3.1	± 13.2	± 19.4	± 59.0	± 71.4
Calib4	7.42	-4.23	19.67	313.7	446.7	1387.8	1653.8
Call04	± 2.8	± 3.8	± 3.0	± 5.9	± 22.1	± 39.8	± 72.2
Calib5	7.46	-3.59	18.56	174.7	609.6	1133.7	2003.5
	± 2.5	± 4.1	± 3.0	± 10.4	± 23.9	± 55.0	± 82.0
Calib6	7.51	-3.23	19.51	184.2	664.3	1216.9	2177.1
	± 2.3	± 3.6	± 2.8	± 9.5	± 35.8	± 64.2	± 116.9
Calib7	2.15	-13.46	17.18	87.1	500.5	761.8	1588.6
	± 4.0	± 6.7	± 3.9	± 13.0	± 32.2	± 71.2	± 109.5

\* The calibrations Calib1 and Calib2 correspond to Physg3brcAZ calibration (based on 144 modern vegetation sites from the Northern Hemisphere temperate regions; Calib2 was obtained thanks to a meteorological correction applied in Calib1). The calibrations Calib3 and Calib4 correspond to Physg3arcAZ calibration (based on 173 modern vegetation sites from the Northern Hemisphere including samples from areas with pronounced winter cold; Calib4 was obtained thanks to a meteorological corrections applied in Calib3). Calib 5-7 respectively correspond to calibrations for Asian vegetations that suffer strong monsoonal climate (Calib5 and Calib6) and for 378 sites from all continents (Calib7). Due to their specificity, these 3 last calibrations were not analysed in this study, but results are presented in this table. For more details, see CLAMP online: http://clamp.ibcas.ac.cn/
MAT – Mean annual temperature; CMMT – Mean temperature of the coldest month; WMMT – Mean temperature of the warmest month; GSP – Precipitation during the growing season; 3DRY – Precipitation during the 3 driest months; 3WET – Precipitation during the 3 wettest months; LPM – Lower estimation of the mean annual precipitation; HPM – Higher estimation of the mean annual precipitation; RH – Relative humidity.

## 706 Table S5.

Parameter*	MAT (°C)	MTC (°C)	MTW (°C)	MAP (mm)	RH (%)
Leaf level	11 – 15 – 20	-2 - 1.6 - 5	24 – 25 – 27	700 – 1100 – 1350	66 – 75 – 80
Borehole & outcrop	11 - 15.5 - 20	-2.2 - 3.2 - 8	24 - 25.7 - 27.7	700 – 1055 – 1320	66 – 75 – 81

\* MAT – mean annual temperature; MTC – mean temperature of the coldest month; MTW – mean temperature of the warmest month; MAP – mean annual precipitation; RH – relative humidity. All parameters are given as an interval and a Most Likely Value which corresponds to a weighted mean.

# 717 Table S6.

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Parameters*	MTC (°C)	MAT (°C)	MTW (°C)	DMP (mm)	MAP (mm)	WMP(mm)
West Hyrcanian region	6.65	15.77	25.85	37.15	1377.6	220.55
East Hyrcanian region	8.0	17.51	27.75	16.2	671.95	112.8
Kristiansand (Norway)	0.1	7.5	15.5	57	1260	160
Lunas (France)	4.8	12.8	21.3	33	723	82

\* MTC - mean temperature of the coldest month; MAT – mean annual temperature; MTW – mean temperature of the

warmest month; DMP – precipitation during the driest month; MAP – mean annual precipitation; WMP – precipitation

during the wettest month.







