

# Pollen-based reconstructions of Holocene climate trends in the eastern Mediterranean region

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*Ms for Climate of the Past*

## 1 Abstract

2 There has been considerable debate about the degree to which climate has driven societal changes in the  
3 eastern Mediterranean region, partly through reliance on a limited number of qualitative records of climate  
4 changes and partly reflecting the need to disentangle the joint impact of changes in different aspects of  
5 climate. Here, we use tolerance-weighted Weighted Averaging Partial Least Squares to derive reconstructions  
6 of mean temperature of the coldest month (MTCO), mean temperature of the warmest month (MTWA),  
7 growing degree days above a threshold of 0°C (GDD0) and plant-available moisture, represented by the ratio  
8 of modelled actual to equilibrium evapotranspiration ( $\alpha$ ) and corrected for past CO<sub>2</sub> changes for 71 individual  
9 pollen records from the Eastern Mediterranean region covering part or all of the interval from 12.3 ka to the  
10 present. We use these reconstructions to create regional composites that illustrate the long-term trends in  
11 each variable. We compare these composites with transient climate model simulations to explore potential  
12 causes of the observed trends. We show that the glacial-Holocene transition and the early part of the Holocene  
13 was characterised by conditions colder than present. Rapid increases in temperature occurred between ca  
14 10.3 and 9.3 ka, considerably after the end of the Younger Dryas. Although the time series are characterised  
15 by centennial-to-millennial oscillations, MTCO showed a gradual increase from 9 ka to the present, consistent  
16 with the expectation that winter temperatures were forced by orbitally-induced increases in insolation during  
17 the Holocene. MTWA also showed an increasing trend from 9 ka and reached a maximum of ca 1.5°C greater  
18 than present at ca 4.5 and 5 ka, followed by a gradual decline towards present-day conditions. A delayed  
19 response to summer insolation changes is likely a reflection of the persistence of the Laurentide and  
20 Fennoscandian ice sheets; subsequent summer cooling is consistent with the expected response to insolation  
21 changes. Plant-available moisture increased rapidly after 11 ka and conditions were wetter than today  
22 between 10-6 ka, but thereafter  $\alpha$  declined gradually. These trends likely reflect changes in atmospheric  
23 circulation and moisture advection into the region, and were probably too small to influence summer  
24 temperature through land-surface feedbacks. Differences in the simulated trajectory of  $\alpha$  in different models  
25 highlight the difficulties in reproducing circulation-driven moisture advection into the eastern Mediterranean.

## 1. Introduction

27 The Eastern Mediterranean region is a critical region for examining the long-term interactions between climate  
28 and past societies because of the early adoption of agriculture in the region, which has been widely associated  
29 with the rapid warming at the end of the Younger Dryas (Belfer-Cohen and Goring-Morris, 2011). Societal  
30 collapse and large-scale migrations have been associated with climates less favourable to agriculture during  
31 the 8.2 ka event (Weninger et al., 2006) or to major changes in agricultural practices (Roffet-Salque et al.,  
32 2018). Subsequent periods of less favourable climate, particularly prolonged droughts, have been associated  
33 with the fall of the Akkadian empire ca. 4.2 ka (Cookson et al., 2019), and the end of the Late Bronze Age and  
34 the beginning of the Greek Dark Ages ca 3.2 ka (Kaniewski et al., 2013; Drake, 2012). However, the attribution  
35 of changes in human society to climate changes is not universally accepted. Flohr et al. (2016), for example,  
36 analysed radiocarbon-dated archaeological sites for evidence of societal changes in response to climate  
37 changes in the early Holocene, particularly the 8.2 ka event, and found no evidence of large-scale site  
38 abandonment or migration although there were indications of local adaptations. However, since Flohr et al.  
39 (2016) did not compare the archaeological records to region-specific climate reconstructions, it is difficult to  
40 assess how far local responses might reflect differences in climate between the sites. Even the societal  
41 response to the early Holocene warming appears to have differed across the region (Roberts et al., 2018).

42 The need to understand the interactions between climate and past societies in the Eastern Mediterranean is  
43 given further impetus because human modification of the landscape has the potential to affect climate directly  
44 through changes in land-surface properties. The degree to which human modifications of the landscape had a  
45 significant impact on global climate before the pre-industrial period is debated (Ruddiman, 2003; Joos et al.,  
46 2004; Kaplan et al., 2011; Singarayer et al., 2011; Mitchell et al., 2013; Stocker et al., 2017), but these impacts  
47 were likely to be more important in regions with a long history of settlement and agricultural activities  
48 (Harrison et al., 2020).

49 Much of our current understanding of climate changes in the Eastern Mediterranean region is based on the  
50 qualitative interpretation of individual records (e.g. Roberts et al., 2019). Oxygen-isotope records from  
51 speleothems or lake sediments have been used to infer changes in moisture availability through the Holocene  
52 (e.g. Bar-Matthews et al., 1997; Cheng et al., 2015; Dean et al., 2015; Burstyn et al., 2019) as have pollen-  
53 based reconstructions of changes in vegetation (e.g. Bottema, 1995; Denèfle et al., 2000; Sadori et al., 2011).  
54 Pollen records can also be used to make quantitative reconstructions of seasonal temperatures, and  
55 precipitation or plant-available water (Bartlein et al., 2011; Chevalier et al., 2020). Quantitative  
56 reconstructions of past climates have been made for individual records from the Eastern Mediterranean  
57 region (e.g. Cheddadi and Khater, 2016; Magyari et al., 2019), and syntheses of pollen-based quantitative  
58 climate reconstructions have included sites from this region (Davis et al., 2003; Mauri et al., 2015; Herzschuh  
59 et al., 2022). Davis et al. (2003) provided a composite curve of seasonal temperature changes, but not moisture  
60 changes; both summer and winter temperatures showed very little variation ( $<1^{\circ}\text{C}$ ) through most of the  
61 Holocene. Mauri et al. (2015) is an updated version of the Davis et al. (2003) reconstructions, with more sites  
62 included but showing similarly muted temperate changes in the Eastern Mediterranean region. Herzschuh et  
63 al. (2022) showed more homogenous changes in both temperature and precipitation across the Eastern  
64 Mediterranean region but it is difficult to compare the two reconstructions directly because they used  
65 different reconstruction techniques. None of the existing reconstructions take account of the impact of  
66 changing  $\text{CO}_2$  levels on vegetation which could potentially affect the reconstructions of moisture variables  
67 (Prentice et al., 2022). Thus, there is a need for well-founded reconstructions of climate, particularly climate

68 variables that are relevant for human occupation and agriculture, to be able to address questions about the  
69 interactions between climate and society in the Eastern Mediterranean region.

70 Here, we provide new quantitative reconstructions of seasonal temperature and plant-available moisture for  
71 71 sites from the Eastern Mediterranean region (defined by the Eastern Mediterranean-Black Sea-Caspian  
72 Corridor, EMBSecBIO, project as the region between 20°E – 62°E, 29°N – 49°N), including a correction for the  
73 impact of changing CO<sub>2</sub> levels on plant-available moisture reconstructions. We use these reconstructions to  
74 document the regional trends in climate from 12.3 ka to the present. We then explore how far these trends  
75 can be explained by changes in external forcing by comparing the reconstructions with transient climate model  
76 simulations.

77

## 78 **2. Methods**

### 79 **2.1. Modern pollen and climate data**

80 The modern pollen dataset was obtained from version 1 of the SPECIAL Modern Pollen Data Set (SMPDSv1,  
81 Harrison, 2019), which provides relative abundance data from 6459 terrestrial sites from Europe, the Middle  
82 East and northern Eurasia, assembled from multiple public sources or provided by the original authors. The  
83 SMPDS pollen records have been taxonomically standardized, filtered to remove obligate aquatics,  
84 insectivorous species, introduced species, or taxa that only occur in cultivation. The removal of cultivars is  
85 designed to minimise the influence of anthropogenic signals on the reconstructions. We then grouped taxa  
86 with only sporadic occurrences into higher taxonomic levels (genus, sub-family or family). Consequently, the  
87 data set provides relative abundance data for 247 pollen taxa (Supplementary Table 1). We used the 5840  
88 SMPDS sites from the area between 20°W to 62°E and 29°N and 75°N to construct the training data set  
89 (Supplementary Figure 1); the sampling outside this box is limited and likely not representative of the diversity  
90 of the climate gradients. At sites with multiple modern samples, we averaged the taxon abundances across all  
91 samples, to minimise over-representation of some localities and hence specific climates, in the training  
92 dataset. We used the 195 pollen taxa that occurred at more than 10 sites (Supplementary Table 1) to derive  
93 climate-abundance relationships.

94 We focus on reconstructing bioclimatic variables that fundamentally control plant distribution, specifically  
95 related to winter temperature limits, accumulated summer warmth and plant-available moisture (Harrison et  
96 al., 2010). The bioclimatic data for each modern site was obtained from Harrison et al. (2019), a dataset that  
97 provides estimates of mean temperature of the coldest month (MTCO), growing degree days above a base  
98 level of 0°C (GDD0), and a moisture index (MI) defined as the ratio of annual precipitation to annual potential  
99 evapotranspiration at each modern pollen site, derived using a geographically-weighted regression of version  
100 2.0 of the Climate Research Unit (CRU) long-term gridded climatology at 10 arc minute resolution (CRU CL  
101 v2.0; New et al., 2002). MTCO and GDD0 were taken directly from the data set. Since Harrison et al. (2019) do  
102 not provide mean temperature of the warmest month (MTWA), we calculated this based on the relationship  
103 between MTCO and GDD0 given in Wei et al. (2021). We derived an alternative moisture index,  $\alpha$ , which is the  
104 ratio between modelled actual and equilibrium evapotranspiration, from MI following Liu et al. (2020). MI and  
105  $\alpha$  both provide good indices of plant-available moisture, but since  $\alpha$  has a natural limit in wetter conditions it  
106 is more suitable for discriminating differences in drier climates.

## 107 2.2. Fossil pollen data

108 The fossil pollen dataset for eastern Mediterranean region was obtained from the Eastern Mediterranean-  
109 Black Sea Caspian Corridor (EMBSecBIO) database (Harrison et al., 2021), which contains information from  
110 187 records from the region between 20°E and 62°E and between 29°N and 49°N. (Note this is a more limited  
111 region than used for the modern training data set.) We discarded records (a) from marine environments or  
112 very large lakes (>500 km<sup>2</sup>), (b) with no radiocarbon dating, (c) where the age of the youngest pollen sample  
113 was unknown, (d) where there is an hiatus after the youngest radiocarbon date, (e) where more than half of  
114 the radiocarbon dates were rejected by the original authors, and (f) where more than half of the ages were  
115 based on pollen correlation with other radiocarbon-dated records. However, we kept records where there is  
116 an hiatus but where there are sufficient radiocarbon dates above the hiatus to create an age model for the  
117 post-hiatus part of the record. We constructed new age models for all the remaining sites (121) using the  
118 IntCal20 calibration curve (Reimer et al., 2020) and the 'rbacon' R package (Blaauw et al., 2021) in the  
119 framework of the 'AgeR' R package (Villegas-Diaz et al., 2021). Some of these records have no modern samples,  
120 where modern was defined as 0-300 yr BP, and thus could not be used to calculate climate anomalies. As a  
121 result, 71 pollen records (Figure 1; Supplementary Table 2) were used for the climate reconstructions. These  
122 records have a mean length of 6594 years and a mean resolution of 228 years. The records were taxonomically  
123 standardized for consistency with the training dataset.

## 124 2.3 Climate reconstructions

125 We used tolerance-weighted Weighted Averaging Partial Least Squares (*fxTWA-PLS*, Liu et al., 2020) regression  
126 to model the relationships between taxon abundances and individual climate variables in the modern training  
127 dataset and then applied these relationships to reconstruct past climate using the fossil assemblages. *fxTWA-*  
128 *PLS* reduces the known tendency of regression methods to compress climate reconstructions towards the  
129 middle of the sampled range by applying a sampling frequency correction to reduce the influence of uneven  
130 sampling of climate space, and by weighting the contribution of individual taxa according to their climate  
131 tolerance (Liu et al., 2020). Version 2 of *fxTWA-PLS* (*fxTWA-PLS2*, Liu et al., 2023), applied here, uses P-spline  
132 smoothing to derive the frequency correction and also applies the correction both in estimating climate  
133 optima and in the regression itself, producing a further improvement in model performance relative to version  
134 1 as published by Liu et al. (2020).

135 We evaluated the *fxTWA-PLS* models by comparing the reconstructions against observations using pseudo-  
136 removed leave-out cross-validation, where one site was randomly selected as a test site and geographically  
137 and climatically similar sites (pseudo sites) were removed from the training set to avoid redundancy in the  
138 climate information inflating the cross-validation. We selected the last significant component ( $p$ -value  $\leq 0.01$ )  
139 and assessed model performance using the root mean square error of prediction (RMSEP). The degree of  
140 compression was assessed using linear regression and local compression was assessed by loess regression  
141 (*locfit*). Climate reconstructions were made for every sample in each fossil record using the best models and  
142 sample specific errors were estimated via bootstrapping. We applied a correction factor (Prentice et al., 2022)  
143 to the reconstructions of  $\alpha$  to account for the impact of changes in atmospheric CO<sub>2</sub> levels on water-use  
144 efficiency, specifically the increased water use efficiency under high CO<sub>2</sub> levels characteristic of the recent past  
145 and the low CO<sub>2</sub> levels that would have reduced water use efficiency during the late glacial and thus could  
146 have influenced the reconstructions during the earliest part of the records. The correction was implemented  
147 through the package *codos*: 0.0.2 (Prentice et al., 2022) with past CO<sub>2</sub> concentration values derived from the  
148 EPICA Dome C record (Bereiter et al., 2015).

#### 149 **2.4. Construction of climate time series**

150 To obtain climate time series representative of the regional trends in climate, we first screened the  
151 reconstructions to remove individual samples with (a) low effective diversity ( $< 2$ ) as measured using Hill's  $N_2$   
152 diversity measure (Hill, 1973), which could indicate low pollen counts or local contamination, and (b) sample-  
153 specific errors above the 0.95 quantile to remove obvious outliers. This screening resulted in the exclusion of  
154 only a small number of individual samples (see Supplementary Figure 2). We then averaged the reconstructed  
155 values in 300-year bins (slightly larger than the average resolution of the records, 228 years) with 50% overlap.  
156 The first bin centred on 150 yr BP, and subsequent bins were centred at 150 yr increments throughout the  
157 record. We excluded any bins with only one sample. The binned values of individual sites were averaged to  
158 produce a regional composite of the anomalies for each climate variable, where the modern baseline was  
159 taken as the first 300-yr bin centred on 150 yr BP. These time series were smoothed using locally weighted  
160 regression (Cleveland & Devlin, 1988) with a window width of 1000 years (half-window width 500 years) and  
161 fixed target points in time to highlight the long-term trends. Confidence intervals (5<sup>th</sup> and 95<sup>th</sup> percentiles) for  
162 each composite were generated by bootstrap resampling by site over 1000 iterations. We examined the  
163 impact of the CO<sub>2</sub> correction on reconstructed  $\alpha$  (Supplementary Figure 3); this had no major effect on the  
164 reconstructed trends except during the earliest part of the record.

#### 165 **2.5. Climate model simulations**

166 We compared the reconstructed climate changes with transient climate model simulations of the response to  
167 external forcing, to determine the extent that the reconstructed climate changes reflect changes in known  
168 forcing. We used transient simulations of the response to orbital and greenhouse gas forcing in the later  
169 Holocene from four models participating in the PAleao-Constraints on Monsoon Evolution and Dynamics  
170 (PACMEDY) project (Carré et al., 2021): the MPI (Max Planck Institute) Earth System Model version 1.2  
171 (Dallmeyer et al., 2020), the AWI (Alfred Wegener Institute) Earth System Model version 2 (Sidorenko et al.,  
172 2019), and two versions of the IPSL (Institut Pierre Simon Laplace) Earth System Model. The IPSL and AWI  
173 simulations were run from 6 ka to 1950 CE, the MPI simulation from 7.95 ka to 1850 CE. We used a longer  
174 transient simulation covering the period from 11.5 ka made with the LOVECLIM model (Goosse et al., 2010)  
175 which, in addition to orbital and greenhouse gas forcing, accounts for the waning of the Laurentide and  
176 Fennoscandian ice sheets (Zhang et al., 2016). Finally, we used two transient simulations from 22 ka to present  
177 made using the Community Climate System Model (CCSM3; Collins et al., 2006). Both were forced by changes  
178 in orbital configuration, atmospheric greenhouse gas concentrations, continental ice sheets and meltwater  
179 fluxes, but differ in the configuration of the meltwater forcing applied after the Bølling warming (14.7 ka). In  
180 the first simulation (TRACE-21k-I: Liu et al., 2009), there was a sustained meltwater flux of  $\sim 0.1$  Sv from the  
181 Northern Hemisphere ice sheets to the Arctic and North Atlantic until ca 6 ka, and a continuous inflow of water  
182 from the North Pacific into the Arctic after the opening of the Bering Strait. The second simulation (TRACE-  
183 21k-II; He and Clark, 2022) had no meltwater flux during the Bølling warming or the Holocene but applied a  
184 flux of  $\sim 0.17$  Sv to the North Atlantic during the Younger Dryas (12.9-11.7 ka). The difference in meltwater  
185 forcing results in a much stronger Atlantic Meridional Overturning Circulation during the Holocene in the  
186 TRACE-21k-II simulation compared to the TRACE-21k-I simulation. Details of the model simulations are given  
187 in Supplementary Table 3. The use of multiple simulations allows the identification of robust signals that are  
188 not model-dependent (see e.g. Carré et al., 2021) and also the separation of the effects of different forcings.  
189 The TraCE-21k-I data were adjusted to reflect the changing length of months during the Holocene, (related to  
190 the eccentricity of Earth's orbit and the precession-determined time of year of perihelion), whereas the other

191 simulations were not. However, this makes little practical difference for the selection of variables used here  
192 (Supplementary Figure 4).

193 Outputs from each simulation were extracted for land grid cells in the EMBSecBIO domain (20° E – 55° E, 29° N  
194 – 49° N; this region extends slightly less far eastwards than the EMBSecBIO region as originally defined but  
195 there are no pollen sites beyond 55° E). MTCO and MTWA were extracted directly; GDD0 was obtained by  
196 deriving daily temperature values from monthly data using a mean-preserving autoregressive interpolation  
197 function (Rymes & Myers, 2001). Daily values of cloud cover fraction and precipitation were obtained from  
198 monthly data in the same way, and used to estimate MI, i.e. the ratio of annual precipitation to annual  
199 potential evapotranspiration, through the R package *smpds* (Villegas-Diaz & Harrison, 2022) before converting  
200 this to  $\alpha$  following Liu et al. (2020). For consistency with the reconstructed time series, climate anomalies for  
201 30-yr bins for each land grid cell within the EMBSecBIO domain were calculated using the interval after 300 yr  
202 BP as the modern baseline. Since the spatial resolution of the models varies (Supplementary Table 3), and in  
203 any case is coarser than the sampling resolution of the individual pollen records precluding direct comparisons  
204 except at a regional scale, we used all of the land grid cells within the EMBSecBIO domain and did not attempt  
205 to select grid cells coincident with the location of pollen data. A composite was produced by averaging the  
206 grid cell time series, which was then smoothed using locally weighted regression (Cleveland & Devlin, 1988)  
207 with a window width of 1000 years (i.e. a half-window width of 500 years) and fixed target points in time.  
208 Confidence intervals (5th and 95th percentiles) for each composite were generated by bootstrap resampling  
209 by grid cell over 1000 iterations.

## 210 **3. Results**

### 211 **3.1. Performance of the fxTWA-PLS statistical model**

212 The assessment of the model through cross-validation showed that it reproduces the modern climate variables  
213 reasonably well (Table 1, Supplementary Table 4). The best performance is achieved by  $\alpha$  ( $R^2 = 0.73$ , RMSEP =  
214 0.15) and MTCO ( $R^2 = 0.73$ , RMSEP 3.7°). The models for GDD0 ( $R^2 = 0.69$ , RMSEP = 880) and MTWA ( $R^2 = 0.63$ ,  
215 RMSEP = 3.22) were also acceptable. The slopes of the regressions ranged from 0.78 (MTWA) to 0.86 (MTCO),  
216 indicating that the degree of compression in the reconstructions is small (Table 1). Thus, the downcore fxTWA-  
217 PLS reconstructions of all the climate variables can be considered to be robust and reliable.

### 218 **3.2. Holocene climate evolution in the region**

219 Down-core reconstructions showed broadly coherent signals, although there was variation in both the timing  
220 and magnitude of climate changes across the sites, reflecting differences in latitude and elevation (Figures 2,  
221 3, 4). Nevertheless, the records indicated coherent regional trends over the past 12 ky.

222 Winter temperature showed a cooling trend between 12 and 11 ka, with reconstructed MTCO ca 8°C lower  
223 than present at 11 ka (Figure 5). There was a moderate increase in MTCO after 11 ka, followed by a more  
224 pronounced increase of ca 5°C between 10.3 and 9.3 ka. Winter temperatures were only ca 2°C lower than  
225 present at the end of this rapid warming phase. There are relatively large uncertainties on the MTCO  
226 reconstructions prior to 10.3 ka, so the trends in the early part of the record are not well constrained. However,  
227 the phase of rapid warming between 10.3 and 9.3 ka (and the subsequent part of the record) is well  
228 constrained. MTCO continued to increase gradually through the Holocene, although multi-centennial to  
229 millennial oscillations were superimposed on the general trend.

230 The initial trends in summer temperature were broadly similar to those in MTCO, with a cooling between 12.3  
231 and 11ka and reconstructed MTWA ca 2°C lower than present at 11 ka (Figure 5). Summer temperature

232 increased thereafter, albeit with pronounced millennial oscillations, up to ca 4.5 ka when MTWA was ca 1.5°C  
233 higher than present. There was a gradual decrease in summer temperature after ca 4.5 ka. The GDDO  
234 reconstructions showed similar trends to MTWA, reaching maximum values around 4.5 ka when the growing  
235 season was ca 150 degree days greater than today. The subsequent decline in GDDO was somewhat flatter,  
236 which presumably reflects the influence of still-increasing winter temperatures on the length of the growing  
237 season.

238 The trends in  $\alpha$  differ from the trends in temperature. Conditions were similar to present around 11.5 ka  
239 (Figure 5). Between 11 and 10 ka, there was a rapid increase in  $\alpha$ . Values of  $\alpha$  were higher than present ( $>0.1$ )  
240 between 10 to 6 ka. Subsequently, there was a gradual and continuous decrease in  $\alpha$  until the present time.  
241 The correction for the physiological impact of CO<sub>2</sub> levels was, as expected, largest during intervals when CO<sub>2</sub>  
242 was lowest (i.e. prior to 11 ka) (Supplementary Figure 4). The reconstructions with and without the correction  
243 are not statistically different between 10 and 5 ka, taking account the uncertainties in the reconstructions, but  
244 the correction produced marginally wetter reconstructions after 5 ka, with a maximum difference of 0.08.  
245 However, the gradually declining trend in moisture availability towards the present is not affected by the CO<sub>2</sub>  
246 correction.

### 247 **3.3. Comparison with climate simulations**

248 The TRACE-21k-I simulation (Figure 6) shows an initial winter warming between 12-11 ka but MTCO is still ca  
249 3°C lower than present at 11 ka. There is a gradual increase in MTCO from 11 ka onwards, although with  
250 centennial-scale variability and a more pronounced oscillation corresponding to the 8.2 ka event. The TRACE-  
251 21k-II simulation is initially slightly colder and displays a two-step warming with a peak at 8.5 ka, when MTCO  
252 is ca 1.5°C lower than present. The later Holocene trend is similar to that shown in TRACE-21k-I. The LOVECLIM  
253 simulation produced generally warmer conditions than either of the TRACE simulations: MTCO is ca 2.5°C  
254 lower than present at 11 ka but the two-step warming is more pronounced and peak warming occurs  
255 somewhat later at ca 7.5 ka when MTCO was only ca 0.25°C lower than present (Figure 7). While all three  
256 models show a rapid warming comparable to the reconstructed warming between 10.3 and 9.3 ka, it is clear  
257 that differences in the ice sheet and meltwater forcings affect both the magnitude and the timing of this trend.  
258 The overall magnitude of the warming after 9 ka in the TRACE-21k-I simulation is consistent with the  
259 reconstructions of MTCO (anomalies of 2.4°C and 2.6°C for model and data respectively). The mid-to late  
260 Holocene trend is similar in the PACMEDY simulations (Figure 8) to both TRACE-21k simulations, both in sign  
261 and in magnitude (ca 1°C between 6 ka and present) and both are consistent with the reconstructions ( $-0.9 \pm$   
262  $0.7^\circ\text{C}$ ). The continuous increase of MTCO is consistent with the change in winter insolation. Given the  
263 similarities between the PACMEDY simulations (which only include orbital and greenhouse gas forcing) and  
264 the LOVECLIM and TRACE simulations, which also include forcing associated with the relict Laurentide and  
265 Fennoscandian ice sheets, it seems likely that orbital forcing was the main driver of winter temperatures in  
266 the EMBSecBIO region during the later Holocene.

267 The TRACE-21k-I simulation shows peak summer temperatures between 11-9 ka, when MTWA was ca. 3°C  
268 greater than present (Figure 6). The TRACE-21K-II simulations is initially colder than the TRACE-21k-I  
269 simulation and the peak in summer temperatures occurs at 9 ka, when MTWA was ca 2.5°C greater than  
270 present (Figure 6). The LOVECLIM simulation is warmer than present from 11.5 ka, but peak warming is only  
271 reached at 7.5 ka when MTWA is ca 2°C (Figure 7). All three simulations show a gradual decrease in summer  
272 temperature through the Holocene after this initial peak. This decreasing trend is also seen in the PACMEDY  
273 simulations from 6 ka (or 8 ka in the case of the MPI simulation) onwards (Figure 8) and the magnitude of the  
274 change over this interval (ca 2°C from 6ka onwards) is similar to that shown by the TRACE and the LOVECLIM

275 simulations. This similarity suggests that the simulated response is a direct reflection of the change in orbital  
276 forcing. However, the reconstructed changes in summer temperature do not show this gradual decline.  
277 Reconstructed MTWA is ca 4°C colder than the model predictions at 9 ka. The reconstructions show a gradual  
278 increase in MTWA from 9 to 4.5 ka. Changes in reconstructed temperatures at 4.5 ka are of a similar magnitude  
279 to simulated temperatures at this time (ca 1°C greater than present) although the late Holocene is marked by  
280 a cooling trend as seen in the simulations. Thus, while the simulated late Holocene trend is consistent with  
281 orbital forcing being the main driver of summer temperatures in the EMBSecBIO region, the early to mid-  
282 Holocene trend is not. Previous modelling studies have suggested that the timing of peak warmth differs in  
283 different regions of Europe and is associated with the impact of the Fennoscandian ice sheet on regional  
284 climates (Renssen et al., 2009; Blascheck and Renssen, 2013; Zhang et al., 2016). The differences in the timing  
285 of peak warmth in the EMBSecBIO region in the TRACE-21k-II and LOVECLIM simulations would be consistent  
286 with this argument but suggest that the timing and magnitude are model-dependent. It is therefore plausible  
287 that the reconstructed trend in MTWA at least during the early Holocene reflects the influence of the relict  
288 Laurentide and Fennoscandian ice sheets in modulating the impact of increased summer insolation until the  
289 mid-Holocene. Given that GDD0 is a reflection of both changes in season length, as influenced by winter  
290 temperatures, and summer warming, the difference between simulated and reconstructed MTWA are also  
291 seen in GDD0 trends during the early part of the Holocene (Figure 6).

292 The simulations do not show consistent patterns for the trend in  $\alpha$ . The TRACE-21k-I simulation (Figure 6)  
293 shows a gradual increase, with minor multi-centennial oscillations from 12 ka to present. (Available model  
294 output variables are not sufficient to calculate  $\alpha$  for the TRACE-21k-II or LOVECLIM simulations). One of the  
295 PACMEDY simulations (IPSL-CM5) shows an increase from the mid-Holocene (Figure 8) although the simulated  
296 change is an order of magnitude smaller than over the comparable period in the TRACE-21k-I simulation. The  
297 AWI model shows no trend in  $\alpha$  over this period; the remaining two models show increasing aridity from the  
298 mid-Holocene to present (Figure 8). These three models are all broadly consistent with the reconstructions  
299 since the reconstructed decrease in  $\alpha$  is small. However, the differences in the sign of the trend between the  
300 different models indicates that changes in moisture are not a straightforward consequence of the forcing, but  
301 must reflect model-dependent changes in moisture supply via changes in atmospheric circulation.  
302 Reconstructions of Holocene climates in Iberia have suggested that land-surface feedbacks associated with  
303 changes in moisture availability have a strong influence on summer temperature (Liu et al., 2023). There does  
304 not seem to be strong evidence for this in the EMBSecBIO region, given the difference in the trends of  $\alpha$  and  
305 MTWA and the muted nature of the trend in  $\alpha$ .

306

#### 307 **4. Discussion**

308 The three temperature-related variables, MTCO, MTWA and GDD0 all show relatively warm conditions around  
309 the late glacial/Holocene transition (ca 12 ka) followed by a cooling that was greatest between ca 11 and 10  
310 ka. This pattern is also shown in regional composites (Figure 9) derived from the reconstructions by Mauri et al.  
311 al. (2015) and Herzschuh et al. (2022). However, the magnitude of the cooling shown in the Mauri et al. (2015)  
312 and Herzschuh et al. (2022) reconstructions is small compared to our reconstructions. The cool interval starts  
313 somewhat later and persists until 9 ka in the Mauri et al. (2015) reconstructions, but this is partly a reflection  
314 of the fact that these reconstructions were only made at 1 ka intervals and thus the transitions are less well  
315 constrained than in either our reconstructions or those of Herzschuh et al. (2022). This cool interval and the  
316 marked warming seen after 10.3 ka in our reconstructions, does not correspond to the Younger Dryas and the



317 subsequent warming. Although the Younger Dryas is considered to be a globally synchronous event (Cheng et  
318 al., 2020) and is generally considered coeval with Greenland Stadial I (Larsson et al., 2022), it does not appear  
319 to be strongly registered in the EMBSeCBIO region in any of the quantitative climate reconstructions. This is  
320 consistent with earlier suggestions based on vegetation changes that the Younger Dryas was not a clearly  
321 marked feature over much of this region (Bottema, 1995).

322 We have shown that winter temperatures increased sharply between 10.3 and 9.3 ka, but then continued to  
323 increase at a more gradual rate through the Holocene. The increase of ca 7.5°C is of the same order of  
324 magnitude to the increase shown in the TRACE-21K-II simulation (ca. 5°C) and in the LOVECLIM simulation (ca.  
325 3°C). This increasing trend is also seen in the Mauri et al. (2015) reconstructions of MTCO (Figure 9), although  
326 the change from the early Holocene to the present is much smaller (ca 0.5–1°C) in these reconstructions than  
327 in our reconstructions and Mauri et al. (2015) do not show marked cooling around 11 ka. Nevertheless, the  
328 consistency between the two reconstructions and between our reconstruction and the simulated changes in  
329 MTCO supports the idea that these trends are a response to orbital forcing during the Holocene. Our  
330 reconstructions show a gradual increase in summer temperature, as measured by both MTWA and GDD0,  
331 from ca 10 to 5 ka when MTWA was ca 1°C warmer than present, followed by a gradual decrease towards the  
332 present. This is not consistent with previous reconstructions. Mauri et al. (2015) show an overall increasing  
333 trend from 9 ka to present. The Herzschuh et al. (2022) shows a completely different pattern, with the  
334 maximum in July temperature at ca. 9 ka and an oscillating but declining trend thereafter (Figure 9).

335 These differences between the three sets of reconstructions are too large to be caused by differences in the  
336 age models applied. They are also unlikely to reflect differences in sampling, since the number of sites used is  
337 roughly similar across all three reconstructions (71 sites versus 67 sites from Herzschuh et al., 2022 and 409  
338 grid points, based on 57 sites, from Mauri et al., 2015); most sites are common to all three analyses. The  
339 differences must therefore be related to the reconstruction method. Herzschuh et al. (2022) used the  
340 regression-based approach, Weighted Average Partial Least Squares (WA-PLS), that is the basis for our  
341 reconstruction technique, fxTWA-PLSv2. Mauri et al. (2015) used the modern analogue technique. However,  
342 after taking account of differences caused by the temporal resolution, there is greater similarity between our  
343 reconstructions and those of Mauri et al. (2015) than between either of these reconstructions and the  
344 Herzschuh et al. (2022) reconstructions.

345 Several methodological issues could be responsible for the differences between the three sets of  
346 reconstructions, and in particular the anomalous moisture trends shown by Herzschuh et al. (2022).  
347 Specifically, Herzschuh et al. (2022) used (1) a unique calibration data set for each fossil site based on modern  
348 samples within a 2000 km radius of that site, rather than relying on a single training data set; (2) a limited set  
349 of 70 dominant taxa rather than the whole pollen assemblage; and (3) included marine records from e.g. the  
350 Black Sea, which were excluded in the other reconstructions because they sample an extremely large area and  
351 thus are unrepresentative of the local climate. However, inclusion of records from the Black Sea in our  
352 reconstructions does not have a substantial impact on either the magnitude or the trends in climate. Thus, it  
353 seems likely that the differences between these two reconstructions reflects the use of a unique calibration  
354 data set for each fossil site and the limited set of taxa included.

355 Reconstructed MTWA shows a gradual increase through the early Holocene with maximum values of around  
356 1.5°C greater than present reached at ca 4.5 ka. Previous modelling studies have shown the timing of  
357 maximum warmth during the Holocene in Europe was delayed compared to the maximum of insolation forcing  
358 and varied regionally as a consequence of the impact of the Fennoscandian ice sheet on surface albedo,  
359 atmospheric circulation and heat transport (Renssen et al., 2009; Blascheck and Renssen, 2013; Zhang et al.,

360 2016; Zhang et al., 2023). Two of the simulations examined here show a delay in the timing of peak warmth,  
361 which occurred ca 9 ka in the TRACE-21k-II simulation and ca 7.5 ka in the LOVECLIM simulation. Although  
362 both sets of simulations include the relict Laurentide and Fennoscandian ice sheets, neither has realistic ice  
363 sheet and meltwater forcing. In the LOVECLIM simulation, for example, the Fennoscandian ice sheet was gone  
364 by 10 ka whereas in reality it persisted until at least 8.7 ka (Patton et al., 2017). Thus, the impact of the  
365 Fennoscandian ice sheet in delaying orbitally induced warming would likely have been greater than shown in  
366 this simulation. In addition to differences in the way in which ice sheets and meltwater forcing are  
367 implemented in different models, models are also differentially sensitive to the presence of the same  
368 prescribed ice sheet (Kapsch et al., 2022). Thus, it would be useful to examine the influence of more realistic  
369 prescriptions of the relict ice sheets on the climate of the EMBSecBIO region using multiple models, and  
370 preferably transient simulations at higher resolution or regional climate models. It has been suggested that  
371 meltwater was routed to the Black and Caspian Seas via the Dnieper and Volga Rivers during the early phase  
372 of deglaciation (e.g. Yanchilina et al., 2019; Aksu et al. 2022; Vadsaria et al., 2022) and it would also be useful  
373 to investigate the impact of this on the regional climate.

374 We have shown that  $\alpha$  was similar to today around 11 ka, but there was a rapid increase in moisture availability  
375 after ca 10.5 ka such that  $\alpha$  values were noticeably higher than present between 10 to 6 ka, followed by a  
376 gradual and continuous decrease until the present time. Changes in the late Holocene are small even at  
377 centennial scale (Figure 5). The reconstructed trends in  $\alpha$  are not captured in the simulations, which show  
378 different trends during the late Holocene. Thus, it is unlikely that the gradual increase in aridity during the late  
379 Holocene is a straight-forward response to orbital forcing. Changes in  $\alpha$  in the EMBSecBIO region are likely to  
380 be primarily driven by precipitation changes, which in turn are driven by changes in atmospheric circulation.  
381 Differences in the trend of moisture availability between the models imply that the nature of the changes in  
382 circulation varies between models and thus the simulations do not provide a strong basis for explaining the  
383 observed patterns of change in moisture availability. Earlier studies, focusing on the western Mediterranean  
384 (Liu et al., 2023), Europe (Mauri et al., 2014) and central Eurasia (Bartlein et al., 2017), have shown that models  
385 have difficulty in simulating the enhanced moisture transport into the Eurasian continent shown by  
386 palaeoenvironmental data during the mid-Holocene and during the late Holocene. Changes in precipitation  
387 can also affect land-surface feedbacks. Liu et al. (2023), for example, have argued that enhanced moisture  
388 transport into the Iberian peninsula during the mid-Holocene led to more vegetation cover and increased  
389 evapotranspiration and had a significant impact in reducing growing season temperatures. Differences in the  
390 reconstructed trends of summer temperature and plant-available moisture through the Holocene suggests  
391 that this land-surface feedback was not an important factor influencing summer temperatures in the  
392 EMBSecBIO region. Nevertheless, differences in the strength of land-surface feedbacks between models could  
393 also contribute to the divergences seen in the simulations. It would be useful to investigate the role of changes  
394 in atmospheric circulation for precipitation patterns during the Holocene in the EMBSecBIO region using  
395 transient simulations at higher resolution or regional climate models.

396 The timing of the transition to agriculture in the eastern Mediterranean is still debated (Asouti & Fuller, 2012).  
397 It has been argued that climatic deterioration and population growth during the Younger Dryas triggered a  
398 shift to farming (Weiss & Bradley, 2001; Bar-Yosef et al., 2017). The presence of morphologically altered  
399 cereals by the end of the Pleistocene has been put forward as evidence for an early transition to agriculture  
400 (Bar-Yosef et al., 2017), but it has also been pointed out that the evidence for cereal domestication before ca  
401 10.5ka is poorly dated and insufficiently documented (Nesbitt, 2002) and that crops did not replace foraging  
402 economies until well into the Holocene (Smith, 2001; Willcox, 2012; Zeder, 2011). The availability of water is  
403 a crucial factor in the viability of early agriculture (Richerson et al., 2001; Zeder, 2011). We have shown that

404 moisture availability was higher than today during the first part of the Holocene (10-6 ka) but similar to today  
405 until ca 10.5 ka. Wetter conditions during the early Holocene could have been a crucial factor in the transition  
406 to agriculture, and our findings support the idea that this transition did not happen until much later than the  
407 Younger Dryas or late glacial/Holocene transition. Further exploration of the role of climate in the transition  
408 to agriculture would require a more comprehensive assessment of the archaeobotanical evidence. The issue  
409 could also be addressed using modelling to explore how the reconstructed changes in regional moisture  
410 availability and seasonal temperatures would impact crop viability (see e.g. Contreras et al., 2019).

411 We have focused on the composite picture of regional changes across the EMBSecBIO region, in order to  
412 investigate whether these changes could be explained as a consequence of known changes in forcing. The  
413 data set also provides information on the trends in climate at individual sites. These data could be used to  
414 address the question of whether population density or cultural changes reflect shifts in climate (e.g. Weninger  
415 et al., 2006; Drake, 2012; Kaniewski et al., 2013; Cookson et al., 2019; Weiberg et al., 2019; Palmisano et al.,  
416 2021). In addition, it would also be possible to use these data to explore the impact of climate changes on the  
417 environment, including the natural resources available for people (Harrison et al., 2023).

418

## 419 **5. Conclusions**

420 We have reconstructed changes in seasonal temperature and in plant-available moisture from 12.3 ka to the  
421 present from 71 sites from the EMBSecBIO domain to examine changes in the regional climate of the eastern  
422 Mediterranean region. We show that there are regionally coherent trends in these variables. The large  
423 increase in both summer and winter temperatures during the early Holocene considerably post-dates the  
424 warming observed elsewhere at the end of the Younger Dryas, supporting the idea that the impact of the  
425 Younger Dryas in the EMBSecBIO region was muted. Subsequent changes in winter temperature are  
426 consistent with the expected response to insolation changes. The timing of peak summer warming occurred  
427 later than expected as a consequence of insolation changes and likely, at least in part, reflects the influence  
428 of the relict Laurentide and Fennoscandian ice sheets on the regional climate. There is a rapid increase in  
429 plant-available moisture between 11 and 10 ka, which could have promoted the adoption of agriculture in the  
430 region.

431

### 432 **Data availability.**

433 Code for the reconstructions of the climatic variables:

434 [https://github.com/esmeraldacs/EMBSecBIO\\_Holocene\\_climate](https://github.com/esmeraldacs/EMBSecBIO_Holocene_climate)

### 435 **Author Contributions**

436 ECS, SPH, ICP designed the study; EM, SPH and ECS revised EMBSecBIO database including the construction  
437 of new age models; PJB, HR and YZ provided climate model output; ECS performed the analyses; SPH and ECS  
438 wrote the first draft of the paper; all authors contributed to the final version.

### 439 **Competing Interests**

440 The authors declare there are no competing interests.

### 441 **Acknowledgements.**

442 We thank members of the SPECIAL team in Reading and from the Leverhulme Centre for Wildfires,  
443 Environment and Society for useful discussions about these analyses.

444 **Financial support.**

445 ECS and SPH acknowledge funding support from the ERC-funded project GC2.0 (Global Change 2.0: Unlocking  
446 the past for a clearer future, grant number 694481) and from the Leverhulme Centre for Wildfires,  
447 Environment and Society through the Leverhulme Trust, grant number RC-2018-023.

448

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## 732 **Figure and Table Captions**

733 Figure 1. Distribution of pollen records used in the climate reconstructions. The colour coding shows the length  
734 of the record.

735 Figure 2. Time series of reconstructed anomalies of mean temperature of the coldest month (MTCO) for  
736 individual records. Entities are arranged by latitude (N-S). Information about the numbered individual sites  
737 can be found in Supplementary Table 1.

738 Figure 3. Time series of reconstructed anomalies of mean temperature of the warmest month (MTWA) for  
739 individual records. Entities are arranged by latitude (N-S). Information about the numbered individual sites  
740 can be found in Supplementary Table 1.

741 Figure 4. Time series of reconstructed anomalies of plant available moisture, expressed as the ratio between  
742 potential and actual evapotranspiration ( $\alpha$ ), at individual sites. A correction to account for the direct  
743 physiological impacts of CO<sub>2</sub> on plant growth has been applied to the reconstructed  $\alpha$ . Entities are arranged  
744 by latitude (N-S). Information about the numbered individual sites can be found in Supplementary Table 1.

745 Figure 5. Composite changes in reconstructed mean temperature of the coldest month (MTCO), mean  
746 temperature of the warmest month (MTWA), growing degree days above a base level of 0°C (GDD0), and plant  
747 available moisture expressed as the ratio between potential and actual evapotranspiration ( $\alpha$ ). A correction  
748 to account for the direct physiological impacts of CO<sub>2</sub> on plant growth has been applied to the reconstructions  
749 of  $\alpha$ . The dark blue line is a loess smoothed curve through the reconstruction with a window half width of 500  
750 years; the green shading shows the uncertainties based on 1000 bootstrap resampling of the records. The  
751 bottom panel shows the number of records used to create the composite through time.

752 Figure 6. Simulated regional changes in mean temperature of the coldest month (MTCO), mean temperature  
753 of the warmest month (MTWA), growing degree days above a base level of 0°C (GDD0), and plant available  
754 moisture expressed as the ratio between potential and actual evapotranspiration ( $\alpha$ ) in the EMBSecBIO  
755 domain from the TRACE-21K-I (green) and TRACE-21K-II (red) transient simulations. It is not possible to  
756 calculate changes in  $\alpha$  for the TRACE-21K-II simulation from the available data. Loess smoothed curves were  
757 drawn using a window half width of 500 years, and the envelope was obtained through 1000 bootstrap  
758 resampling of the sequences. The top panel shows the changes in summer and winter insolation ( $Wm^{-2}$ ) at 40°  
759 N.

760 Figure 7. Simulated regional changes in mean temperature of the coldest month (MTCO), mean temperature  
761 of the warmest month (MTWA), and growing degree days above a base level of 0°C (GDD0) in the EMBSecBIO  
762 domain from the LOVECLIM transient simulation. It is not possible to calculate changes in  $\alpha$  for the LOVECLIM  
763 simulation from the available data. Loess smoothed curves were drawn using a window half width of 500  
764 years, and the envelope was obtained through 1000 bootstrap resampling of the sequences.

765 Figure 8. Simulated regional changes in mean temperature of the coldest month (MTCO), mean temperature  
766 of the warmest month (MTWA), and growing degree days above a base level of 0°C (GDD0) in the EMBSecBIO  
767 domain from the four PACMEDY simulations. The models are: Max Plank Institute Earth System Model (MPI),  
768 Alfred Wagener Institute Earth System Model simulations (AWI), Institute Pierre Simon Laplace Climate Model

769 TR5AS simulation (IPSL-CM5) and Institute Pierre Simon Laplace Climate Model TR6A V simulation (IPSL-CM6).  
770 Loess smoothed curves were drawn using a window half width of 500 years and the envelope was obtained  
771 through 1000 bootstrap resampling of the sequences.

772 Figure 9. Comparison of regional composites of reconstructed seasonal temperatures from this study with  
773 those derived from Mauri et al. (2015) and Herzschuh et al. (2022). Mauri et al. (2015 provide mean  
774 temperature of the coldest month (MTCO) and mean temperature of the warmest month (MTWA)  
775 reconstructions, which can be directly compared with our reconstructions. Herzschuh et al. (2022) only  
776 provide reconstructions of July temperature. Our reconstructions are shown in blue, reconstructions based on  
777 the Mauri et al. (2015) data set are shown in green, and reconstructions based on the Herzschuh et al.  
778 reconstruction are shown in orange. The solid line is a loess smoothed curve through the reconstruction with  
779 a window half width of 500 years; the shading shows the uncertainties based on 1000 bootstrap resampling  
780 of the records.

781 Table 1. Leave-out cross-validation fitness of fxTWA-PLSv2 for mean temperature of the coldest month  
782 (MTCO), mean temperature of the warmest month (MTWA), growing degree days above base level 0°C (GDD0)  
783 and plant-available moisture ( $\alpha$ ) with p-spline smoothed fx estimation, using bins of 0.02, 0.02 and 0.002,  
784 showing results for the selected component for each variable. RMSEP is the root-mean-square error of  
785 prediction. p assesses whether using the current number of components is significantly different from using  
786 one component less. The degree of overall compression is assessed by linear regression of the cross-validated  
787 reconstructions onto the climate variable, where b1 and b1.se are the slope and the standard error of the  
788 slope, respectively. The overall compression is reduced as the slope approaches 1. Full details for all the  
789 components are given in Supplementary Table 4.

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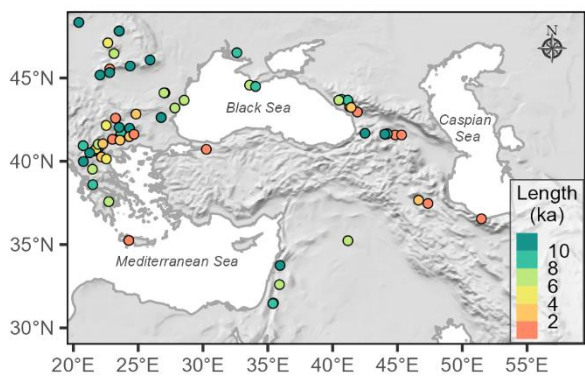
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795 Figure 1. Distribution of pollen records used in the climate reconstructions. The colour coding shows the  
796 length of the record.



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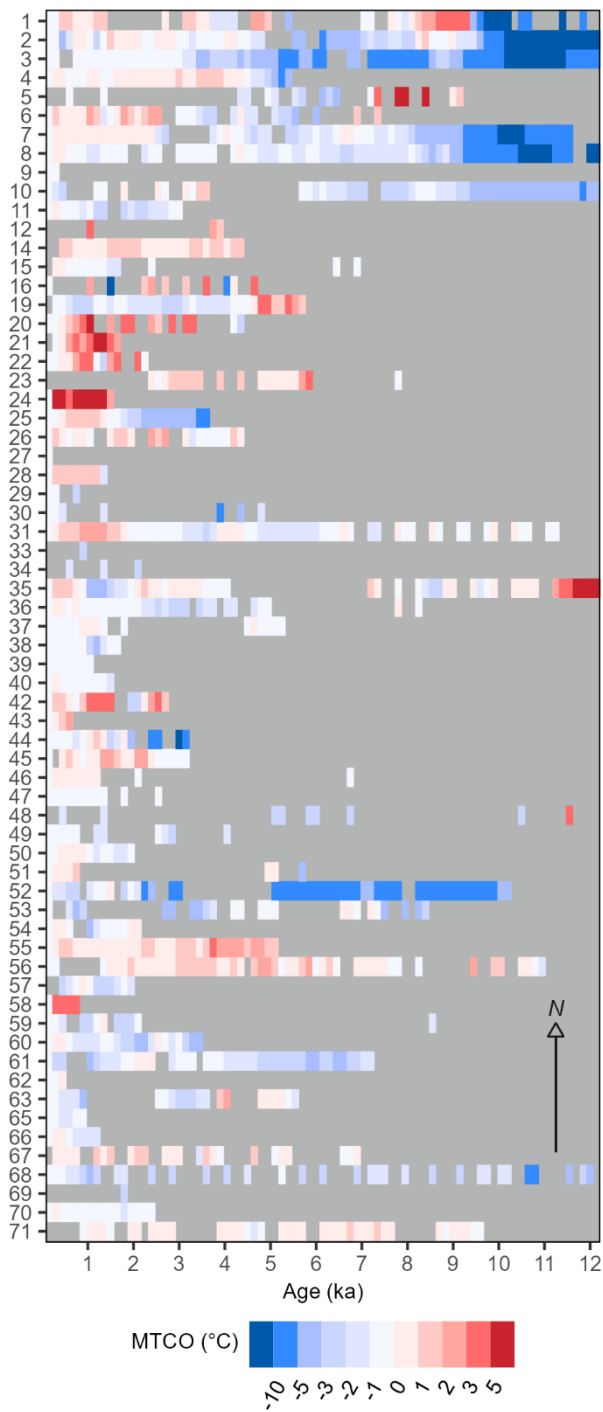
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805 Figure 2. Time series of reconstructed anomalies of mean temperature of the coldest month (MTCO) for  
806 individual records. Entities are arranged by latitude (N-S). Information about the numbered individual sites  
807 can be found in Supplementary Table 1.



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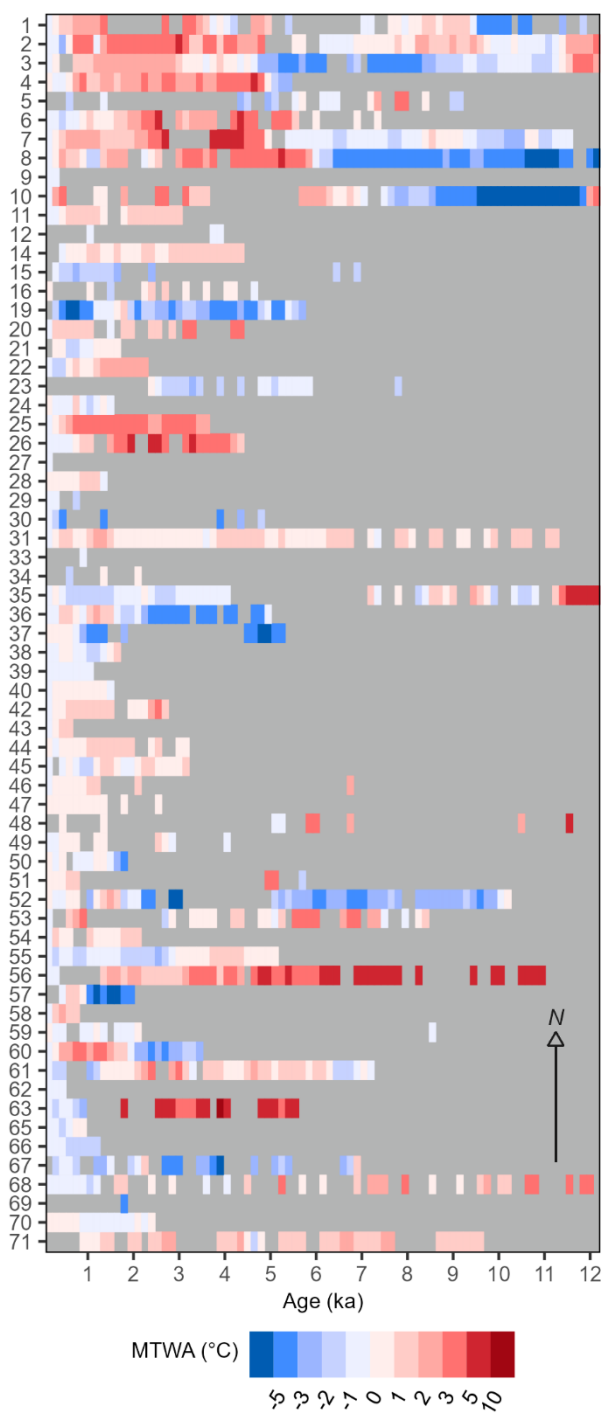
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813 Figure 3. Time series of reconstructed anomalies of mean temperature of the warmest month (MTWA) for  
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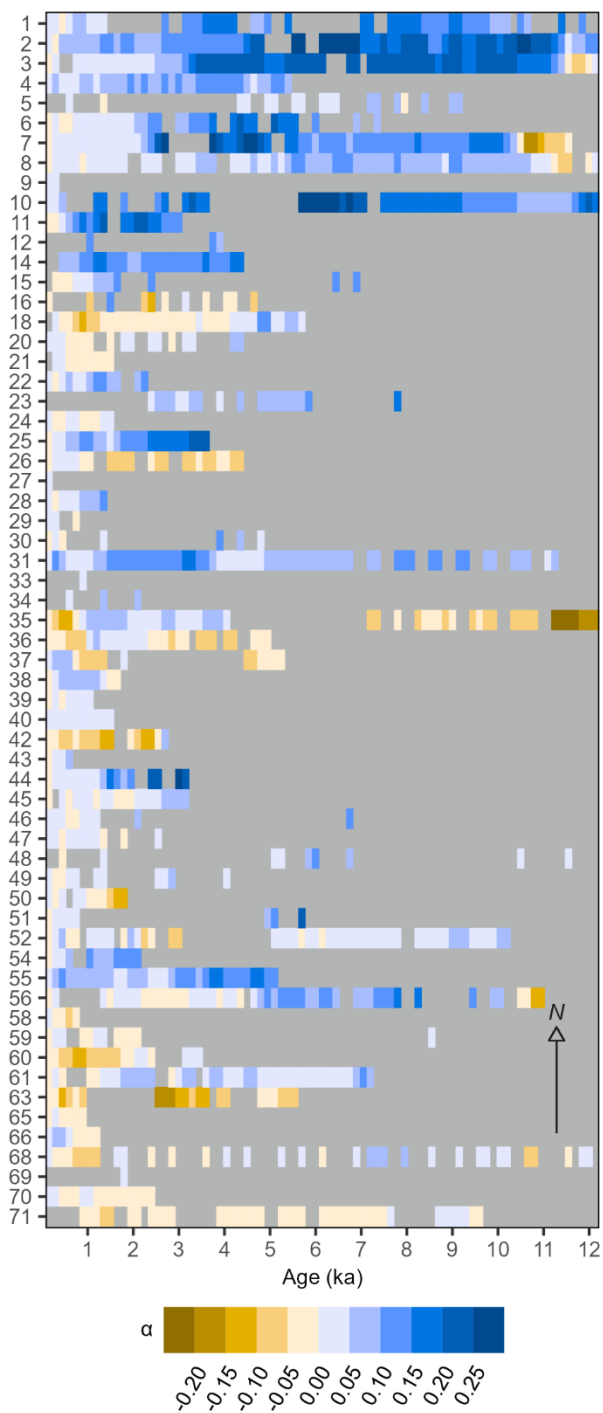
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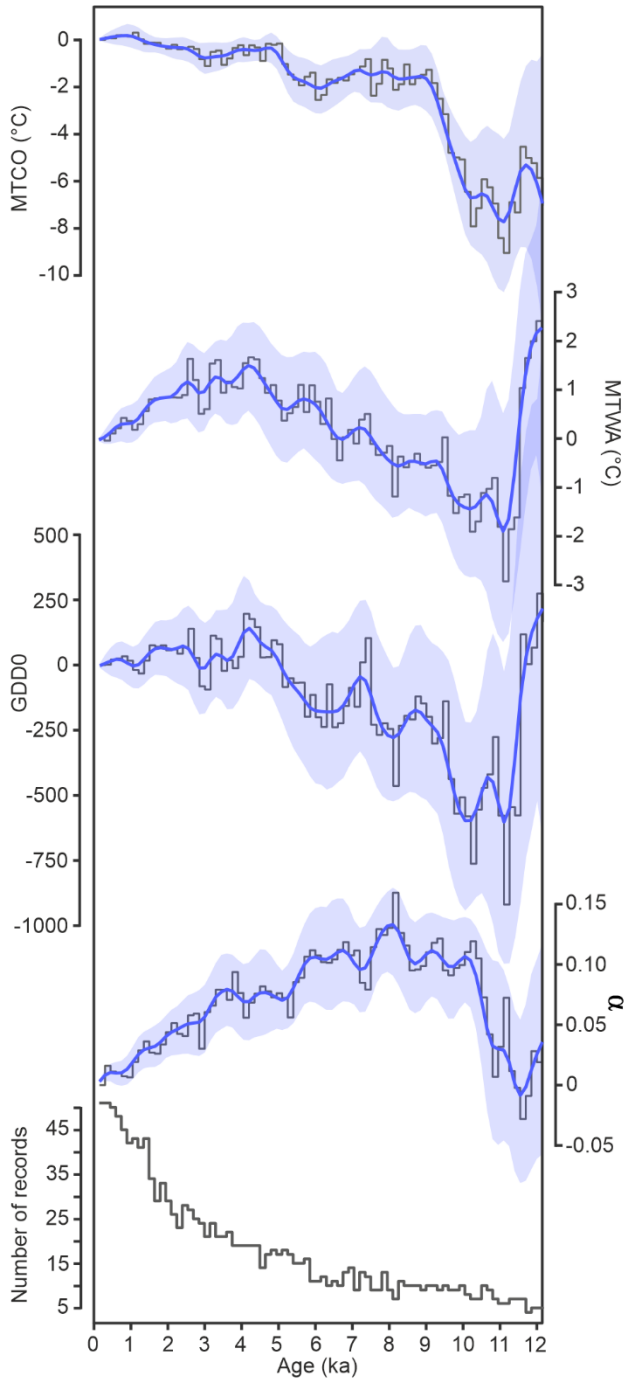


820 Figure 4. Time series of reconstructed anomalies of plant available moisture, expressed as the ratio between  
821 potential and actual evapotranspiration ( $\alpha$ ), at individual sites. A correction to account for the direct  
822 physiological impacts of CO<sub>2</sub> on plant growth has been applied to the reconstructed  $\alpha$ . Entities are arranged  
823 by latitude (N-S). Information about the numbered individual sites can be found in Supplementary Table 1.



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827 Figure 5. Composite changes in reconstructed mean temperature of the coldest month (MTCO), mean  
 828 temperature of the warmest month (MTWA), growing degree days above a base level of 0°C (GDD0), and  
 829 plant available moisture expressed as the ratio between potential and actual evapotranspiration ( $\alpha$ ). A  
 830 correction to account for the direct physiological impacts of CO<sub>2</sub> on plant growth has been applied to the  
 831 reconstructions of  $\alpha$ . The dark blue line is a loess smoothed curve through the reconstruction with a window  
 832 half width of 500 years; the blue shading shows the uncertainties based on 1000 bootstrap resampling of the  
 833 records. The bottom panel shows the number of records used to create the composite through time.

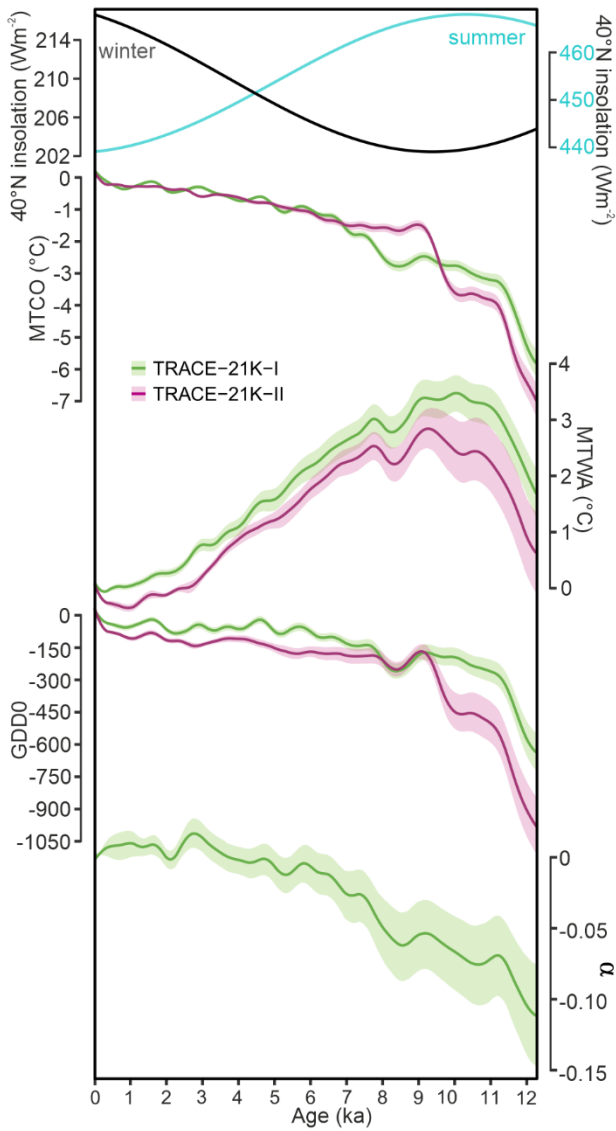


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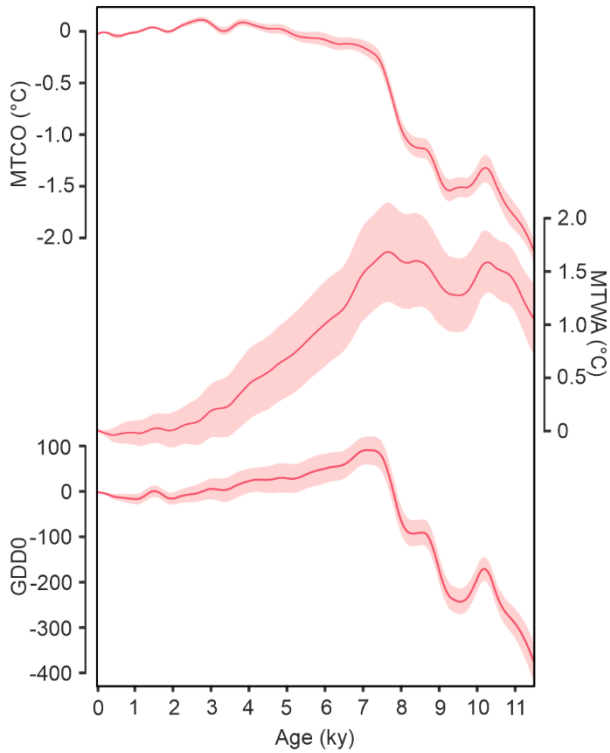
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837 Figure 6. Simulated regional changes in mean temperature of the coldest month (MTCO), mean temperature  
 838 of the warmest month (MTWA), growing degree days above a base level of 0°C (GDD0), and plant available  
 839 moisture expressed as the ratio between potential and actual evapotranspiration ( $\alpha$ ) in the EMBSecBIO  
 840 domain from the TRACE-21K-I (green) and TRACE-21K-II (red) transient simulations. It is not possible to  
 841 calculate changes in  $\alpha$  for the TRACE-21K-II simulation from the available data. Loess smoothed curves were  
 842 drawn using a window half width of 500 years, and the envelope was obtained through 1000 bootstrap  
 843 resampling of the sequences. The top panel shows the changes in summer and winter insolation ( $\text{Wm}^{-2}$ ) at 40°  
 844 N.



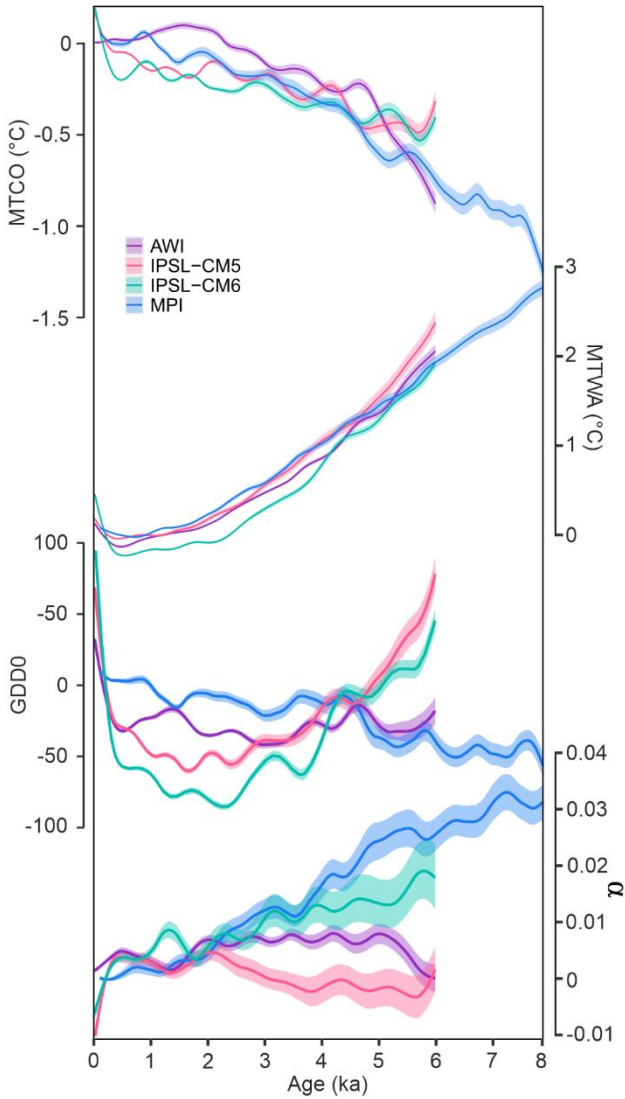
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852 Figure 7. Simulated regional changes in mean temperature of the coldest month (MTCO), mean temperature  
853 of the warmest month (MTWA), and growing degree days above a base level of 0°C (GDD0) in the EMBSeCBIO  
854 domain from the LOVECLIM transient simulation. It is not possible to calculate changes in  $\alpha$  for the LOVECLIM  
855 simulation from the available data. Loess smoothed curves were drawn using a window half width of 500  
856 years, and the envelope was obtained through 1000 bootstrap resamplings of the sequences.



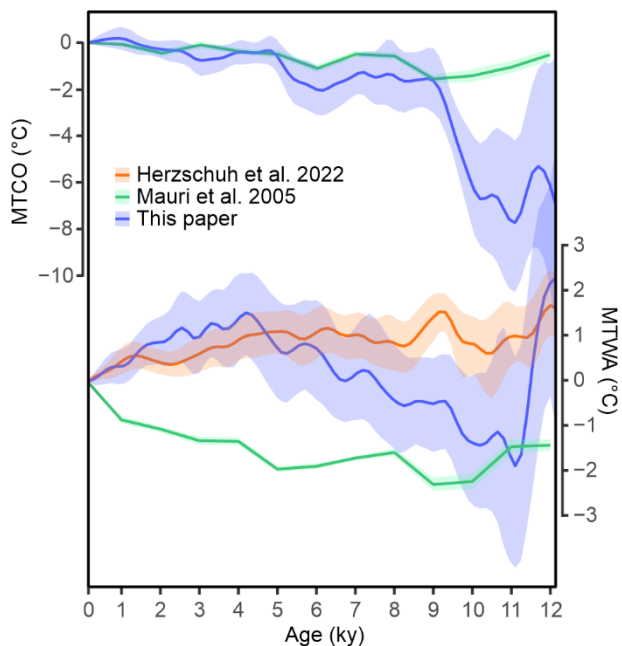
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871 Figure 8. Simulated regional changes in mean temperature of the coldest month (MTCO), mean temperature  
 872 of the warmest month (MTWA), and growing degree days above a base level of 0°C (GDD0) in the  
 873 EMBSeCBIO domain from the four PACMEDY simulations. The models are: Max Plank Institute Earth System  
 874 Model (MPI), Alfred Wagener Institute Earth System Model simulations (AWI), Institute Pierre Simon Laplace  
 875 Climate Model TR5AS simulation (IPSL-CM5) and Institute Pierre Simon Laplace Climate Model TR6A V  
 876 simulation (IPSL-CM6). Loess smoothed curves were drawn using a window half width of 500 years and the  
 877 envelope was obtained through 1000 bootstrap resampling of the sequences.



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886 Figure 9. Comparison of regional composites of reconstructed seasonal temperatures from this study with  
887 those derived from Mauri et al. (2015) and Herzschuh et al. (2022). Mauri et al. (2015 provide mean  
888 temperature of the coldest month (MTCO) and mean temperature of the warmest month (MTWA)  
889 reconstructions, which can be directly compared with our reconstructions. Herzschuh et al. (2022)  
890 only provide reconstructions of July temperature. Our reconstructions are shown in blue, reconstructions based on  
891 the Mauri et al. (2015) data set are shown in green, and reconstructions based on the Herzschuh et al.  
892 reconstruction are shown in orange. The solid line is a loess smoothed curve through the reconstruction with  
893 a window half width of 500 years; the shading shows the uncertainties based on 1000 bootstrap resampling  
894 of the records.



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898 **Table 1.** Leave-out cross-validation fitness of fxTWA-PLSv2 for mean temperature of the coldest month  
 899 (MTCO), mean temperature of the warmest month (MTWA), growing degree days above base level 0°C (GDD0)  
 900 and plant-available moisture ( $\alpha$ ) with p-spline smoothed fx estimation, using bins of 0.02, 0.02 and 0.002,  
 901 showing results for the selected component for each variable. RMSEP is the root-mean-square error of  
 902 prediction. p assesses whether using the current number of components is significantly different from using  
 903 one component less. The degree of overall compression is assessed by linear regression of the cross-validated  
 904 reconstructions onto the climate variable, where b1 and b1.se are the slope and the standard error of the  
 905 slope, respectively. The overall compression is reduced as the slope approaches 1. Full details for all the  
 906 components are given in Supplementary Table 4.

Variable	Selected component	R2	Average bias	RMSEP	p	b1	b1.se
<b>MTCO</b>	<b>4</b>	<b>0.73</b>	<b>-0.22</b>	<b>3.67</b>	<b>0.001</b>	<b>0.86</b>	<b>0.01</b>
<b>MTWA</b>	<b>2</b>	<b>0.63</b>	<b>-0.10</b>	<b>3.22</b>	<b>0.001</b>	<b>0.78</b>	<b>0.01</b>
<b>GDD0</b>	<b>2</b>	<b>0.69</b>	<b>56.46</b>	<b>880.33</b>	<b>0.001</b>	<b>0.79</b>	<b>0.01</b>
<b><math>\alpha</math></b>	<b>2</b>	<b>0.73</b>	<b>-0.01</b>	<b>0.15</b>	<b>0.001</b>	<b>0.80</b>	<b>0.01</b>

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