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

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Ms for Climate of the Past

Abstract

There has been considerable debate about the degree to which climate has driven societal changes in the eastern Mediterranean region, partly through reliance on a limited number of qualitative records of climate changes and partly reflecting the need to disentangle the joint impact of changes in different aspects of climate. Here, we use tolerance-weighted Weighted Averaging Partial Least Squares to derive reconstructions of mean temperature of the coldest month (MTCO), mean temperature of the warmest month (MTWA), growing degree days above a threshold of 0°C (GDD0) and plant-available moisture, represented by the ratio of modelled actual to equilibrium evapotranspiration ($\alpha$) and corrected for past CO\textsubscript{2} changes for 71 individual pollen records from the Eastern Mediterranean region covering part or all of the interval from 12.3 ka to the present. We use these reconstructions to create regional composites that illustrate the long-term trends in each variable. We compare these composites with transient climate model simulations to explore potential causes of the observed trends. We show that the glacial-Holocene transition and the early part of the Holocene was characterised by conditions colder and drier than present and low plant availability moisture. Rapid increases in temperature and moisture occurred between ca 10.3 and 9.3 ka, considerably after the end of the Younger Dryas. Although the time series are characterised by centennial-to-millennial oscillations, MTCO showed a gradual increase from 9 ka to the present, consistent with the expectation that winter temperatures were forced by orbitally-induced increases in insolation during the Holocene. MTWA also showed an increasing trend from 9 ka and reached a maximum of ca 1.5°C greater than present at ca 4.5 and 5 ka, followed by a gradual decline towards present-day conditions. A delayed response to summer insolation changes is likely a reflection of the persistence of the Laurentide and Fennoscandian ice sheets; subsequent summer cooling is consistent with the expected response to insolation changes. Plant-available moisture increased rapidly after between 11 and 9.3 ka and conditions were slightly wetter than today between 9-810-6 ka, but thereafter $\alpha$ declined gradually. These trends likely reflect changes in atmospheric circulation and moisture advection into the region, and were probably too small to influence summer temperature through
land-surface feedbacks. Differences in the simulated trajectory of α in different models highlight the
difficulties in reproducing circulation-driven moisture advection into the eastern Mediterranean.

1. Introduction

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

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

Much of our current understanding of climate changes in the Eastern Mediterranean region is based on the
qualitative interpretation of individual records (e.g. Roberts et al., 2019). Oxygen-isotope records from
speleothems or lake sediments have been used to infer changes in moisture availability through the Holocene
(e.g. Bar-Matthews et al., 1997; Cheng et al., 2015; Dean et al., 2015; Burstyn et al., 2019) as have pollen-
based reconstructions of changes in vegetation (e.g. Bottema, 1995; Denéfle et al., 2000; Sadori et al., 2011).
Pollen records can also be used to make quantitative reconstructions of seasonal temperatures, and
precipitation or plant-available water (Bartlein et al., 2011; Chevalier et al., 2020). Quantitative
reconstructions of past climates have been made for individual records from the Eastern Mediterranean
region (e.g. Cheddadi and Khater, 2016; Magyari et al., 2019), and syntheses of pollen-based quantitative
climate reconstructions have included sites from this region (Davis et al., 2003; Mauri et al., 2015; Herzschuh
et al., 2022). Davis et al. (2003) provided a composite curve of seasonal temperature changes, but not moisture
changes; both summer and winter temperatures showed very little variation (<1°C) through most of the
Holocene. Mauri et al. (2015) is an updated version of the Davis et al. (2003) reconstructions, with more sites
included but showing similarly muted temperate changes in the Eastern Mediterranean region. Herzschuh et
al. (2022) showed more homogenous changes in both temperature and precipitation across the Eastern
Mediterranean region but it is difficult to compare the two reconstructions directly because they used
different reconstruction techniques. None of the existing reconstructions take account of the impact of
changing CO₂ levels on vegetation which could potentially affect the reconstructions of moisture variables (Prentice et al., 2022). Thus, there is a need for well-founded reconstructions of climate, particularly climate variables that are relevant for human occupation and agriculture, to be able to address questions about the interactions between climate and society in the Eastern Mediterranean region.

Here, we provide new quantitative reconstructions of seasonal temperature and plant-available moisture for 71 sites from the Eastern Mediterranean region (defined by the Eastern Mediterranean-Black Sea-Caspian Corridor, EMBSeCBIO, project as the region between 20°E – 62°E, 29°N – 49°N) (20°E – 62°E, 29°N – 49°N), including a correction for the impact of changing CO₂ levels on plant-available moisture reconstructions. We use these reconstructions to document the regional trends in climate from 12.3 ka to the present. We then explore how far these trends can be explained by changes in external forcing by comparing the reconstructions with transient climate model simulations.

2. Methods

2.1. Modern pollen and climate data

The modern pollen dataset was obtained from version 1 of the SPECIAL Modern Pollen Data Set (SMPDSv1, Harrison, 2019), which provides relative abundance data from 6459 terrestrial sites from Europe, the Middle East and northern Eurasia, assembled from multiple public sources or provided by the original authors. The SMPDS pollen records have been taxonomically standardized, filtered to remove obligate aquatics, insectivorous species, introduced species, or taxa that only occur in cultivation, and to group taxa with only sporadic occurrences into higher taxonomic levels (genus, sub-family or family) and consequently provides relative abundance data for 247 pollen taxa (Supplementary Table 1). We used the 5840 SMPDS sites from the area between 20°W to 62°E and 29°N and 75°N to construct the training data set (Supplementary Figure 1); the sampling outside this box is limited and likely not representative of the diversity of the climate gradients.

At sites with multiple modern samples, we averaged the taxon abundances across all samples, to minimise over-representation of some localities and hence specific climates, in the training dataset. We used the 195 pollen taxa that occurred at more than 10 sites (Supplementary Table 1) to derive climate-abundance relationships.

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

The fossil pollen dataset for eastern Mediterranean region was obtained from the Eastern Mediterranean-Black Sea Caspian Corridor (EMBSeCBIO) database (Harrison et al., 2021), which contains information from 187 records from the region between 20°E and 62°E and between 29°N and 49°N and 20°E and 62°E. (Note this is a more limited region than used for the modern training data set.) We discarded records (a) from marine environments or very large lakes (>500 km²), (b) with no radiocarbon dating, (c) where the age of the youngest pollen sample was unknown, (d) where there is an hiatus after the youngest radiocarbon date, (e) where more than half of the radiocarbon dates were rejected by the original authors, and (f) where more than half of the ages were based on pollen correlation with other radiocarbon-dated records. However, we kept records where there is an hiatus but where there are sufficient radiocarbon dates above the hiatus to create an age model for the post-hiatus part of the record. We constructed new age models for all the remaining sites (121) using the IntCal20 calibration curve (Reimer et al., 2020) and the ‘rbacorn’ R package (Blauw et al., 2021) in the framework of the ‘AgeR’ R package (Villegas-Diaz et al., 2021). Some of these records have no modern samples, where modern was defined as 0-300 yr BP, and thus could not be used to calculate climate anomalies. As a result, 71 pollen records (Figure 1; Supplementary Table 2) were used for the climate reconstructions. These records have a mean length of 6594 years and a mean resolution of 228 years. The records were taxonomically standardized for consistency with the training dataset.

2.3 Climate reconstructions

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

We evaluated the fxTWA-PLS models by comparing the reconstructions against observations using pseudo-removed leave-out cross-validation, where one site was randomly selected as a test site and geographically and climatically similar sites (pseudo sites) were removed from the training set to avoid redundancy in the climate information inflating the cross-validation. We selected the last significant component (p-value ≤ 0.01) and assessed model performance using the root mean square error of prediction (RMSEP). The degree of compression was assessed using linear regression and local compression was assessed by loess regression (locfit). Climate reconstructions were made for every sample in each fossil record using the best models and sample specific errors were estimated via bootstrapping. We applied a correction factor (Prentice et al., 2022) to the reconstructions of α to account for the impact of changes in atmospheric CO₂ levels on water-use efficiency, specifically the increased water use efficiency under high CO₂ levels characteristic of the recent past and the low CO₂ levels that would have reduced water use efficiency during the late glacial and thus could have influenced the reconstructions during the earliest part of the records which could have impacted the reconstructions during the earliest part of the records. The correction was implemented using the package.
The TraCE not model in TRACE forcing results in a much stronger Atlantic Meridional Overturning Circulation during the Holocene in the flux of 21 k. The simulations were run from 6 k to 1950 CE, the MPI simulation from 7.95 ka to 1850 CE, and two versions of the IPSL (Institut Pierre Simon Laplace) Earth System Model version 2 (Sidorenko et al., 2019), and two versions of the IPSL (Institut Pierre Simon Laplace) Earth System Model. The IPSL and AWI simulations were run from 6 ka to 1950 CE, the MPI simulation from 7.95 ka to 1850 CE. We used a longer transient simulation covering the period from 11.5 ka made with the LOVECLIM model (Goosse et al., 2010) which, in addition to orbital and greenhouse gas forcing, accounts for the waning of the Laurentide and Fennoscandian ice sheets (Zhang et al., 2016). Finally, we used two transient simulations from 22 ka to present made using the Community Climate System Model (CCSM3; Collins et al., 2006). Both were forced by changes in orbital configuration, atmospheric greenhouse gas concentrations, continental ice sheets and meltwater fluxes, but differ in the configuration of the meltwater forcing applied after the Bølling warming (14.7 ka). In the first simulation (TRACE-21k-I; Liu et al., 2009), there was a sustained meltwater flux of ~0.1 Sv from the Northern Hemisphere ice sheets to the Arctic and North Atlantic until ca 6 ka, and a continuous inflow of water from the North Pacific into the Arctic after the opening of the Bering Strait. The second simulation (TRACE-21k-II; He and Clark, 2022) had no meltwater flux during the Bølling warming or the Holocene but applied a flux of ~ 0.17 Sv to the North Atlantic during the Younger Dryas (12.9-11.7 ka). The difference in meltwater forcing results in a much stronger Atlantic Meridional Overturning Circulation during the Holocene in the TRACE-21k-II simulation compared to the TRACE-21k-I simulation. Details of the model simulations are given in Supplementary Table 3. The use of multiple simulations allows the identification of robust signals that are not model-dependent (see e.g. Carré et al., 2021) and also the separation of the effects of different forcings. The TraCE-21k-I data were adjusted to reflect the changing length of months during the Holocene, (related to
the eccentricity of Earth’s orbit and the precession-determined time of year of perihelion), whereas the other simulations were not. However, this makes little practical difference for the selection of variables used here (Supplementary Figure 4).

**Outputs from each simulation were extracted for the EMBSeCBIO domain (20°W–55°W, 29°N–49°N)**

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

**3. Results**

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

Model performance

The assessment of the model through cross-validation showed that it reproduces the modern climate variables reasonably well (Table 1, Supplementary Table 4). The best performance is achieved by α (R² = 0.73, RMSEP = 0.15) and MTCO (R² = 0.73, RMSEP 3.7°). The models for GDD0 (R² = 0.69, RMSEP = 880) and MTWA (R² = 0.63, RMSEP = 3.22) were also acceptable. The slopes of the regressions ranged from 0.78 (MTWA) to 0.86 (MTCO), indicating that the degree of compression in the reconstructions in small (Table 1). Thus, the downcore fxTWA-PLS reconstructions of all the climate variables can be considered to be robust and reliable, a small degree of compression in the reconstructions (Table 1).

### 3.2. Holocene climate evolution in the region

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

Winter temperature showed a cooling trend between 12.2 ka and 11 ka, with reconstructed MTCO ca 8°C lower than present at 11 ka (Figure 5). There was a moderate increase in MTCO after 11 ka, followed by a more pronounced increase of ca 5°C between 10.3 and 9.3 ka. Winter temperatures were only ca 2°C lower than present at the end of this rapid warming phase. There are relatively large uncertainties on the MTCO reconstructions prior to 10.3 ka, so the trends in the early part of the record are not well constrained. However, the phase of rapid warming between 10.3 and 9.3 ka (and the subsequent part of the record) is well
**constrained.** MTCO continued to increase gradually through the Holocene, although multi-centennial to millennial oscillations were superimposed on the general trend.

The initial trends in summer temperature were broadly similar to those in MTCO, with a cooling between 12.3 and 11 ka and reconstructed MTWA ca 2°C lower than present at 11 ka (Figure 5). Summer temperature increased thereafter, albeit with pronounced millennial oscillations, up to ca 4.5°C when MTWA was ca 1.5°C higher than present. There was a gradual decrease in summer temperature after ca 4.5 ka. The GDD0 reconstructions showed similar trends to MTWA, reaching maximum values around 4.5°C when the growing season was ca 150 degree days greater than today. The subsequent decline in GDD0 was somewhat flatter, which presumably reflects the influence of still-increasing winter temperatures on the length of the growing season.

The trends in α differ from the trends in temperature. Conditions were similar to present around 11.5 ka (Figure 5). Between 11 and 10 ka, there was a rapid increase in α. Values of α were higher than present (>0.1) between 10 to 6 ka. Subsequently, there was a gradual and continuous decrease in α until the present time. The correction for the physiological impact of CO$_2$ levels was, as expected, largest during intervals when CO$_2$ was lowest (i.e. prior to 11 ka) (Supplementary Figure 4). The reconstructions with and without the correction are not statistically different between 10 and 5 ka, taking account the uncertainties in the reconstructions, but the correction produced marginally wetter reconstructions after 5 ka, with a maximum difference of 0.08. However, the gradually declining trend in moisture availability towards the present is not affected by the CO$_2$ correction. Around 11.5 ka, the driest conditions were prevalent, with α being 0.01 lower than it is today (Figure 5). Between 11 and 10 ka, there was a rapid and nearly linear rise in α. From 10 to 6 ka, α values remained above 0.1, peaking around 8 ka. Subsequently, there was a gradual and continuous decrease in α until the present time. The correction for the physiological impact of CO$_2$ levels was, as expected, largest during intervals when CO$_2$ was lowest (i.e., prior to 11.5 ka) (Supplementary Figure 4). This correction resulted in the driest conditions at 11.5 ka, rather than at the beginning of the record. The reconstructions with and without the correction are not statistically different between 10 and 5 ka, but the correction produced marginally wetter reconstructions after 5 ka. However, the trend of gradual decline in moisture availability towards the present is not affected by the CO$_2$ correction.

### 3.3. Comparison with climate simulations

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

The TRACE-21k-I simulation shows peak summer temperatures between 11-9 ka, when MTWA was ca. 3°C
greater than present (Figure 6). The TRACE-21k-II simulations is initially colder than the TRACE-21k-I
simulation and the peak in summer temperatures occurs at 9 ka, when MTWA was ca 2.5°C greater than
present (Figure 6). The LOVECLIM simulation is warmer than present from 11.5 ka, but peak warming is only
reached at 7.5 ka when MTWA is ca 2°C (Figure 7). All three simulations show a gradual decrease in summer
temperature through the Holocene after this initial peak. This decreasing trend is also seen in the PACMEDY
simulations from 6 ka (or 8 ka in the case of the MPI simulation) onwards (Figure 8) and the magnitude of the
change over this interval (ca 2°C from 6ka onwards) is similar to that shown by the TRACE and the LOVECLIM
simulations. This similarity suggests that the simulated response is a direct reflection of the change in orbital
forcing. However, the reconstructed changes in summer temperature do not show this gradual decline.
Reconstructed MTWA is ca 4°C colder than the model predictions at 9 ka. The reconstructions show a gradual
increase in MTWA from -8 to 4.5 ka. Changes in reconstructed temperatures at 4.5 ka are of a similar
magnitude to simulated temperatures at this time (ca 1°C greater than present) although the late Holocene is
marked by a cooling trend as seen in the simulations. Thus, while the simulated late Holocene trend is
consistent with orbital forcing being the main driver of summer temperatures in the EMBScebIO region, the
early to mid-Holocene trend is not. Previous modelling studies have suggested that the timing of peak warmth
differs in different regions of Europe and is associated with the impact of the Fennoscandian ice sheet on
regional climates (Renssen et al., 2009; Blascheck and Renssen, 2013; Zhang et al., 2016). The differences in
the timing of peak warmth in the EMBScebIO region in the TRACE-21k-II and LOVECLIM simulations would be
consistent with this argument but suggest that the timing and magnitude are model-dependent. It is therefore
plausible that the reconstructed trend in MTWA at least during the early Holocene reflects the influence of
the relict Laurentide and Fennoscandian ice sheets in modulating the impact of increased summer insolation
until the mid-Holocene. Given that GDD0 is a reflection of both changes in season length, as influenced by
winter temperatures, and summer warming, the difference between simulated and reconstructed MTWA are
also seen in GDD0 trends during the early part of the Holocene (Figure 6).

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

The three temperature-related variables, MTCO, MTWA and GDD0, all show relatively warm conditions around the late glacial/Holocene transition (ca. 12 ka) followed by a cooling that was greatest between ca. 11 and 10 ka. This pattern is also shown in regional composites (Figure 9) derived from the reconstructions by Mauri et al. (2015) and Herzschuh et al. (2022). However, the magnitude of the cooling shown in the Mauri et al. (2015) and Herzschuh et al. (2022) reconstructions is small compared to our reconstructions. The cool interval starts somewhat later and persists until 9 ka in the Mauri et al. (2015) reconstructions, but this is partly a reflection of the fact that these reconstructions were only made at 1 ka intervals and thus the transitions are less well constrained than in either our reconstructions or those of Herzschuh et al. (2022). This cool interval and the marked warming seen after 10.3 ka in our reconstructions, does not correspond to the Younger Dryas and the subsequent warming. Although the Younger Dryas is considered to be a globally synchronous event (Cheng et al., 2020) and is generally considered coeval with Greenland Stadial I (Larsson et al., 2022), it does not appear to be strongly registered in the EMBSeCBIO region in any of the quantitative climate reconstructions. This is consistent with earlier suggestions based on vegetation changes that the Younger Dryas was not a clearly marked feature over much of this region (Bottema, 1995).

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

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

Several methodological issues could be responsible for the differences between the three sets of reconstructions, and in particular the anomalous moisture trends shown by Herzschuh et al. (2022).
Specifically, Herzsuh et al. (2022) used (1) a unique calibration data set for each fossil site based on modern samples within a 2000 km radius of that site, rather than relying on a single training data set; (2) a limited set of 70 dominant taxa rather than the whole pollen assemblage; and (3) included marine records from e.g. the Black Sea, which were excluded in the other reconstructions because they sample an extremely large area and thus are unrepresentative of the local climate.

Reconstructed MTWA shows a gradual increase through the early Holocene with maximum values of around 1.5°C greater than present reached at ca 4.5 ka. Previous modelling studies have shown the timing of maximum warmth during the Holocene in Europe varied regionally and was delayed compared to the maximum of insolation forcing and varied regionally as a consequence of reflected the impact of the Fennoscandian ice sheet on surface albedo, atmospheric circulation and heat transport (Renssen et al., 2009; Blascheck and Renssen, 2013; Zhang et al., 2016, Zhang et al., 2023). Two of the simulations examined here show a delay in the timing of peak warmth, which occurred ca 9 ka in the TRACE-21k-II simulation and ca 7.5 ka in the LOVECLIM simulation. Although both sets of simulations include the relict Laurentide and Fennoscandian ice sheets, neither has realistic ice sheet and meltwater forcing. In the case of the LOVECLIM simulation, for example, the Fennoscandian ice sheet was gone by 10 ka whereas in reality it persisted until at least 8.7 ka (Patton et al., 2017). Thus, the impact of the Fennoscandian ice sheet in delaying orbitally-induced warming could have been greater than shown in this simulation.

In addition to differences in the way in which ice sheets and meltwater forcing are implemented in different models, models are also differentially sensitive to the presence of the same prescribed ice sheet (Kapsch et al., 2022). Thus, it would be useful to examine the influence of more realistic prescriptions of the relict ice sheets on the climate of the EMBSeCBIO region using multiple models, and preferably transient simulations at higher resolution or regional climate models. Nevertheless, the way in which ice sheets and meltwater forcing are implemented varies between models; models are also differentially sensitive to the presence of relict ice sheets (Kapsch et al., 2022). It would be useful to examine the influence of the ice sheets on the climate of the EMBSeCBIO region using transient simulations at higher resolution or regional climate models. It has been suggested that meltwater was routed to the Black and Caspian Seas via the Dnieper and Volga Rivers during the early phase of deglaciation (e.g. Yanchilina et al., 2019; Aksu et al. 2022; Vadsaria et al., 2022) and it would also be useful to investigate the impact of this on the regional climate.

The availability of water is a crucial factor in the viability of early agriculture (Richerson et al., 2001; Zeder, 2011). We have shown that α values were similar to today around 11 ka, but there was a rapid increase in moisture availability after ca 10.5 ka such that α values were noticeably higher than present between 10 to 6 ka, followed by a gradual and continuous decrease until the present time. Changes in the late Holocene are small even at centennial scale (Figure 5). The reconstructed trends in α are not captured in the simulations, which show different trends during the late Holocene. Thus, it is unlikely that the gradual increase in aridity during the late Holocene is a straight-forward response to orbital forcing. Changes in α in the EMBSeCBIO region are likely to be primarily driven by precipitation changes, which in turn are driven by changes in atmospheric circulation. Differences in the trend of moisture availability between the models imply that the nature of the changes in circulation varies between models and thus the simulations do not provide a strong basis for explaining the observed patterns of change in moisture availability. Earlier studies, focusing on the western Mediterranean (Liu et al., 2023), Europe (Mauri et al., 2014) and central Eurasia (Bartlein et al., 2017), have shown that models have difficulty in simulating the enhanced moisture transport into the Eurasian continent shown by palaeoenvironmental data during the mid-Holocene and during the late Holocene. Changes in precipitation can also affect land-surface feedbacks. Liu et al. (2023), for example, have argued that enhanced moisture transport into the Iberian peninsula during the mid-Holocene led to more vegetation cover and
increased evapotranspiration and had a significant impact in reducing growing season temperatures. Differences in the reconstructed trends of summer temperature and plant-available moisture through the Holocene suggest that this land-surface feedback was not an important factor influencing summer temperatures in the EMBSeCBIO region. Nevertheless, differences in the strength of land-surface feedbacks between models could also contribute to the divergences seen in the simulations. It would be useful to investigate the role of changes in atmospheric circulation for precipitation patterns during the Holocene in the EMBSeCBIO region using transient simulations at higher resolution or regional climate models. We have shown that conditions were markedly drier than today (anomaly ≈ 0.2) similar to today around 11 ka but that moisture availability increased to levels only very slightly higher than today (anomaly ≈ 0.05–0.075) between 9 and 8 ka, before declining to present-day levels. The initial increase in plant-available water, as indexed by $\alpha$, could have contributed to promoting the viability of agriculture, as suggested by Richerson et al. (2001). However, subsequent changes are small even at centennial scale (Figure 5). The reconstructed trends in $\alpha$ are not captured in the IPSL-CM6 and MPI simulations. Although influenced by summer temperature-driven changes in evaporation, changes in $\alpha$ in the EMBSeCBIO region are likely to be primarily driven by precipitation changes, which in turn are driven by changes in atmospheric circulation. There are indeed large-simulated changes in atmospheric circulation through the Holocene in e.g. the LOVECLIM simulations (Supplementary Figure S1) but, as pointed our earlier, differences in the trend of moisture availability between the models imply that the nature of the changes in circulation varies between models and thus does not provide a strong basis for explaining the observed patterns of change in moisture availability. Furthermore, earlier studies, focusing on the western Mediterranean (Liu et al., 2023), Europe (Mauri et al., 2014) and central Eurasia (Bartlein et al., 2017), have shown that models have difficulty in simulating the enhanced moisture transport into the Eurasian continent shown by palaeoenvironmental data during the mid-Holocene and during the late Holocene. Liu et al. (2023) have argued that enhanced moisture transport into the Iberian Peninsula during the mid-Holocene led to more vegetation cover and increased evapotranspiration and had a significant impact in reducing growing season temperatures. However, the differences in the trends of summer temperature and plant-available moisture through the Holocene suggest that this land-surface feedback was not an important factor influencing summer temperatures in the EMBSeCBIO region.

The timing of the transition to agriculture in the eastern Mediterranean is still debated (Asouti & Fuller, 2012). It has been argued that climatic deterioration and population growth during the Younger Dryas triggered a shift to farming (Weiss & Bradley, 2001; Bar-Yosef et al., 2017). The presence of morphologically altered cereals by the end of the Pleistocene has been put forward as evidence for an early transition to agriculture (Bar-Yosef et al., 2017), but it has also been pointed out that the evidence for cereal domestication before ca 10.5 ka is poorly dated and insufficiently documented (Nesbitt, 2002) and that crops did not replace foraging economies until well into the Holocene (Smith, 2001; Willcox, 2012; Zeder, 2011). The availability of water is a crucial factor in the viability of early agriculture (Richerson et al., 2001; Zeder, 2011). We have shown that moisture availability was higher than today during the first part of the Holocene (10–6 ka) but similar to today until ca 10.5 ka. Wetter conditions during the early Holocene could have been a crucial factor in the transition to agriculture, and our findings support the idea that this transition did not happen until much later than the Younger Dryas or late glacial/Holocene transition. Further exploration of the role of climate in the transition to agriculture would require a more comprehensive assessment of the archaeobotanical evidence. The issue could also be addressed using modelling to explore how the reconstructed changes in regional moisture availability and seasonal temperatures would impact crop viability (see e.g. Contreras et al., 2019).

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

5. Conclusions

We have reconstructed changes in seasonal temperature and in plant-available moisture from 12.3 ka to the present from 71 sites from the EMBSeCBIO domain to examine changes in the regional climate of the eastern Mediterranean region. We show that there are regionally coherent trends in these variables. The large increase in both summer and winter temperatures during the early Holocene considerably post-dates the warming observed elsewhere at the end of the Younger Dryas, supporting the idea that the impact of the Younger Dryas in the EMBSeCBIO region was muted. Subsequent changes in winter temperature are consistent with the expected response to insolation changes. The timing of peak summer warming occurred later than expected as a consequence of insolation changes and likely, at least in part, reflects the influence of the relict Laurentide and Fennoscandian ice sheets on the regional climate. Drier-than-present conditions are reconstructed at ca. 11.5 ka at the beginning of the Holocene, but there is a rapid increase in plant-available moisture between 11 and 9-10 ka, which could have promoted the adoption of agriculture in the regional crops. However, changes in plant-available water during the middle and late Holocene are small even considering centennial-scale variability.

Data availability.

Code for the reconstructions of the climatic variables:
https://github.com/esmeraldacs/EMBSeCBIO_Holocene_climate

Author Contributions

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

Competing Interests

The authors declare there are no competing interests.

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References


Hengl, T.: Potential distribution of biomes (Potential Natural Vegetation) at 250 m spatial resolution [data set], https://doi.org/10.5281/zenodo.3526620, 2019 (last accessed 17 April 2023)


Liu, Z., Otto-Bliesner, B. L., He, F., Brady, E. C., Tomas, R.. Clark, P. U., Carlson, A. E., Lynch-Stiegltiz, J., Curry, W., Brook, E., Erickson, D., Jacob, R., Kutzbach, J., and Cheng, J.: Transient Simulation of Last Deglaciation


Prentice, I.C., Villegas-Diaz, R., and Harrison, S.P.: codos: 0.0.2 (0.0.2). Zenodo.

https://doi.org/10.5281/ZENODO.5083309, 2022 (last accessed 17 April 2023)


Sadori, L., Jahns, S., and Peyron, O.: Mid-Holocene vegetation history of the central Mediterranean,


Figure and Table Captions

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

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

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

Figure 4. Time series of reconstructed anomalies of plant available moisture, expressed as the ratio between potential and actual evapotranspiration (α), at individual sites. A correction to account for the direct physiological impacts of CO₂ on plant growth has been applied to the reconstructed α. Entities are arranged by latitude (N-S). Information about the numbered individual sites can be found in Supplementary Table 1.

Figure 5. Composite changes in reconstructed mean temperature of the coldest month (MTCO), mean temperature of the warmest month (MTWA), growing degree days above a base level of 0°C (GDD₀), and plant available moisture expressed as the ratio between potential and actual evapotranspiration (α). A correction to account for the direct physiological impacts of CO₂ on plant growth has been applied to the reconstructions of α. The green line/dark blue line is a loess smoothed curve through the reconstruction with a window half width of 500 years; the green shading shows the uncertainties based on 1000 bootstrap resampling of the records. The bottom panel shows the number of records used to create the composite through time.

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

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

Figure 8. Simulated regional changes in mean temperature of the coldest month (MTCO), mean temperature of the warmest month (MTWA), and growing degree days above a base level of 0°C (GDD₀) in the EMBSeCBIO domain from the four PACMEDY simulations. The models are: Max Plank Institute Earth System Model (MPI),
Alfred Wagener Institute Earth System Model simulations (AWI), Institute Pierre Simon Laplace Climate Model TR5AS simulation (IPSL-CM5) and Institute Pierre Simon Laplace Climate Model TR6A V simulation (IPSL-CM6).

Loess smoothed curves were drawn using a window half width of 500 years and the envelope was obtained through 1000 bootstrap resampling of the sequences.

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

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