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High temperatures in the terrestrial mid-latitudes during the early Palaeogene

B. D. A. Naafs[1]*, M. Rohrssen[1,2], G. N. Inglis[1], O. Lähteenoja[3], S. J. Feakins[4], M. E. Collinson[5], E. M. Kennedy[6], P. K. Singh[7], M. P. Singh[7], D. J. Lunt[8] and R. D. Pancost[1]

The early Paleogene (56–48 Myr) provides valuable information about the Earth's climate system in an equilibrium high p_{CO_2} world. High ocean temperatures have been reconstructed for this greenhouse period, but land temperature estimates have been cooler than expected. This mismatch between marine and terrestrial temperatures has been difficult to reconcile. Here we present terrestrial temperature estimates from a newly calibrated branched glycerol dialkyl glycerol tetraether-based palaeothermometer in ancient lignites (fossilized peat). Our results suggest early Palaeogene mid-latitude mean annual air temperatures of 23–29 °C (with an uncertainty of ± 4.7 °C), 5–10 °C higher than most previous estimates. The identification of archaeal biomarkers in these same lignites, previously observed only in thermophiles and hyperthermophilic settings, support these high temperature estimates. These mid-latitude terrestrial temperature estimates are consistent with reconstructed ocean temperatures and indicate that the terrestrial realm was much warmer during the early Palaeogene than previously thought.

The early Palaeogene is characterized by an extended period of high atmospheric carbon dioxide (p_{CO_2}) levels[1,2]. Quantification of the temperatures during greenhouse climates is needed because (1) they can be used to evaluate climate model simulations at elevated p_{CO_2} (ref. [3]), (2) temperature governs diverse components of climate dynamics (for example, circulation patterns)[4] and feedback mechanisms within the Earth system (for example, weathering)[5] and (3) they influence biogeochemical processes (for example, the flux of methane from wetlands into the atmosphere)[6]. Although potentially not continuously as hot as the relatively short-lived extreme greenhouse events such as the Palaeocene Eocene Thermal Maximum (PETM), the extended greenhouse climate state of the early Palaeogene is the focus here.

Over the past decade, considerable effort has been made to reconstruct the early Palaeogene greenhouse climate with a variety of calcite-based, leaf physiognomic and organic geochemical proxies. For example, sea surface temperatures (SSTs) have been reconstructed with the organic tetraether index of 86 carbon atoms (TEX_{86}) proxy[7], based on the distribution of isoprenoidal glycerol dialkyl glycerol tetraethers (isoGDGTs), lipids synthesized by Archaea, in marine sediments. These records indicate SSTs significantly higher than modern ones, with SSTs from the southwestern Pacific at 60° S palaeolatitude above 30 °C (ref. [8]). Similarly, calcite-based SST proxies, such as the Mg/Ca ratio or clumped isotopic composition of foraminiferal calcite, indicate significantly elevated SSTs at all latitudes during the early Palaeogene[9]. Together, the SST records indicate ocean temperatures significantly higher than modern ones with most estimates from between 60° S and 50° N above 22 °C (Fig. 1).

Some climate models, such as CCSM3 (Community Climate System Model version 3), can (partly) reproduce these elevated temperatures using 16 times (16×) the modern-day p_{CO_2} levels[10], but such p_{CO_2} values are higher than proxy estimates for the early Palaeogene[1,2]. Other models, such as HadCM3L (Hadley Centre Coupled Model version 3) and ECHAM (European Centre Hamburg Model), generally cannot reproduce the warming at p_{CO_2} levels consistent with the marine proxy estimates[3]. The apparent high SST reconstructions have therefore been attributed to proxy complications, such as a subsurface origin of the lipids used in the TEX_{86} proxy[11], variations in early Palaeogene seawater chemistry compared to modern that especially influences the calcite-based palaeothermometers[12] and/or a seasonal (summer) bias in the marine proxies[13,14]. However, recent model simulations have identified potential biases against polar warming in general circulation models that are tuned to modern conditions[15,16] associated with the representation of cloud properties, which may partly explain the model–data discrepancy at mid/high latitudes.

The available terrestrial temperature proxies, based mainly on leaf physiognomic temperature estimates and the MBT(′)/CBT organic mineral soil temperature proxy, based in turn on the degree of methylation of branched tetraether (MBT) and cyclization of branched tetraethers (CBT) indices of bacterial branched glycerol dialkyl glycerol tetraethers (brGDGTs), suggest that early Palaeogene terrestrial temperatures in general were also higher than modern[10,17,18], but to a lesser degree than indicated by SST reconstructions. There are very few terrestrial temperature data from the (sub)tropics, but almost all estimates indicate mean air temperatures below 22 °C during the early Palaeogene at all latitudes (Fig. 1a). These terrestrial temperature estimates are more consistent with climate model simulations[10], but considerably lower than SST estimates, which presents a conundrum. To understand this greenhouse climate state, independent early Palaeogene temperature estimates are needed to test whether temperatures on land were as high as suggested by marine proxies or as low as indicated by most climate

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[1]Organic Geochemistry Unit, School of Chemistry, School of Earth Sciences, and Cabot Institute, University of Bristol, Bristol, UK. [2]Department of Earth and Atmospheric Sciences, Central Michigan University, Mount Pleasant, MI, USA. [3]School of Life Sciences, Arizona State University, Tempe, AZ, USA. [4]Department of Earth Sciences, University of Southern California, Los Angeles, CA, USA. [5]Department of Earth Sciences, Royal Holloway University of London, Egham, UK. [6]Department of Paleontology, GNS Science, Lower Hutt, New Zealand. [7]Coal and Organic Petrology Lab, Department of Geology, Banaras Hindu University, Varanasi, Uttar Pradesh, India. [8]School of Geographical Sciences and Cabot Institute, University of Bristol, Bristol, UK.
*e-mail: david.naafs@bristol.ac.uk

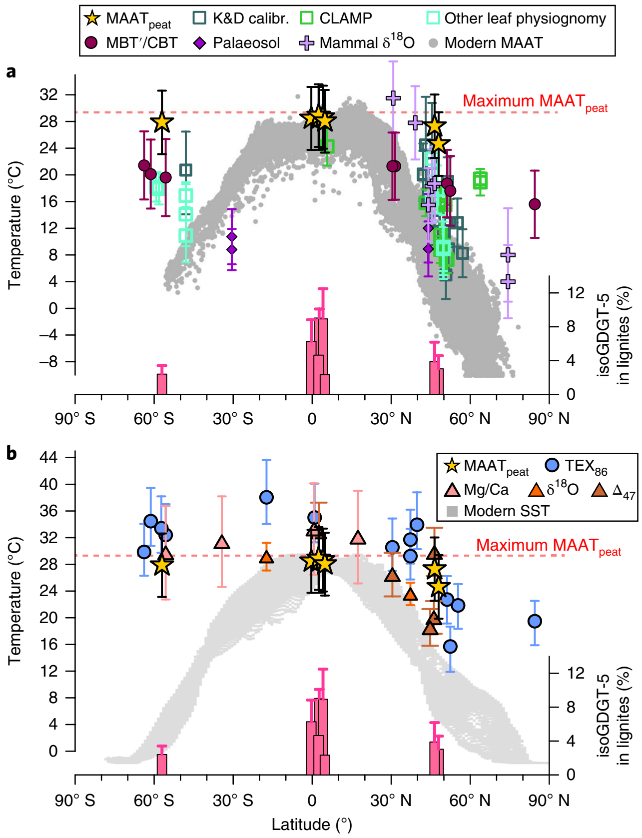

Fig. 1 | Early Palaeogene temperature. a, MAAT$_{peat}$ and abundance of isoGDGT-5 (bar chart) in early Palaeogene lignites together with published temperatures using leaf physiognomy (squares), MBT′/CBT proxy, palaeosol proxies and mammalian δ^{18}O. **b**, MAAT$_{peat}$ and abundance of isoGDGT-5 with published TEX$_{86}$/BAYSPAR-based (blue circles) and calcite-based SSTs (triangles) for the early Palaeogene. Error bars on the temperature data reflect the combined spread in data (1σ) and calibration uncertainty (Supplementary Information), and those for isoGDGT-5 reflect 1σ from the average. Supplementary Information gives all data and references. K&D calibr., Kowalski and Dilcher calibration.

model simulations and many existing terrestrial proxies. For this purpose, here we use the distribution of archaeal and bacterial lipids obtained from lignites (ancient peat) to reconstruct temperatures in early Palaeogene mid-latitude peatlands.

GDGTs in modern peat

A decade of research has demonstrated that in mineral soils the degree of methylation of bacterial brGDGTs, calculated using the degree of methylation of (5-methyl)-branched tetraether (MBT′$_{(5me)}$) index, is correlated with the mean annual air temperature (MAAT)[19,20]. Although temperature is highly correlated with the degree of methylation, the influence of other factors (for example, nutrient content, among others) is currently poorly constrained due to the lack of culture studies. The MBT(′)/CBT mineral soil temperature proxy has been applied to marine sediments to reconstruct early Palaeogene terrestrial temperatures[21]. However, the application of the mineral soil calibration to other climatic archives (for example, peat and by extension lignite) can be problematic as these represent different environmental conditions to those that predominantly comprise the modern mineral soil calibration data set. To address this, a global peat-specific brGDGT temperature calibration that is based on MBT′$_{5me}$ in a diverse range ($n = 470$) of modern peats (MAAT$_{peat}$) was recently developed[22]. This proxy has a calibration error of ±4.7 °C and reaches saturation at 29.1 °C. It is important that in peat settings, MAAT$_{peat}$ is unlikely to record seasonal temperatures, because in peats the brGDGT pool is dominated by bacterial production at a depth below the water table where seasonal temperature fluctuations are muted and converge to MAATs[22]. As with all palaeothermometers, we assume that the strong correlation between the degree of methylation of brGDGTs and temperature observed in the modern calibration data set[22] was the same during the early Palaeogene.

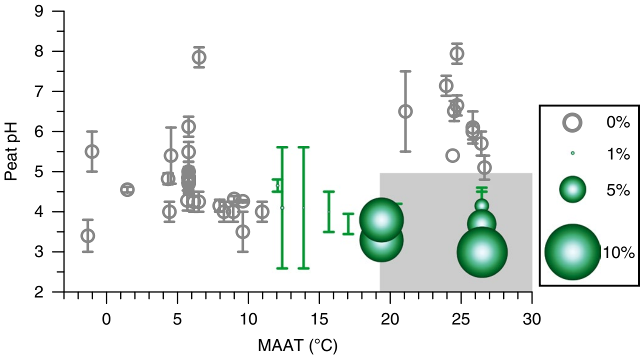

Fig. 2 | isoGDGT in modern peats. Maximum relative abundance of isoGDGT-5 in modern peats plotted against in situ peat pH[22] and MAAT[22]. Vertical bars reflect the range in pH reported for each peat. The shaded area indicates tropical ombrotrophic peats characterized by an isoGDGT-5 abundance >1%.

In addition to Bacteria (that can produce brGDGTs), Archaea also live in peat and their membrane lipids (isoGDGTs) are similarly preserved in ancient peat and lignite. Here we examined the isoGDGT distribution in our previously compiled global database of modern peat[22]. We report isoGDGT-5 (as well as isoGDGT-6 and 7) in modern mesophilic peats. So far, isoGDGTs with more than four cyclopentane rings have only been found in hot springs and cultures of (acido) hyperthermophiles[23]. It has been suggested that the ability to synthesize isoGDGT-5 to 8 is a unique adaptation of extremophiles and does not occur in mesophilic settings[23]. However, our work demonstrates that this biomarker is also present in ombrotrophic (acidic) tropical peats from 20° S–20° N latitudes today. isoGDGT-5 is only present in significant amounts (>1% of total isoGDGT distribution with 1–5 cyclopentane rings) in tropical and ombrotrophic peats with a pH < 5.1 and MAAT > 19.5 °C (Fig. 2). It is absent in all peatlands with a pH > 5.1 or MAAT < 12 °C and present only in trace proportions (<1% of isoGDGTs) in acidic peatlands with MAAT between 12 °C and 19.5 °C. The highest proportion of isoGDGT-5 in the modern database is 9% in an ombrotrophic Indonesian peat (modern MAAT, 26.5 °C, pH 3). The distribution of these compounds in modern peats provides strong evidence that their occurrence (when greater than 1% of the total isoGDGTs with 1-5 cyclopentane rings) is diagnostic for peatlands with high temperatures (>19.5 °C) and low pH (<5.1). We suggest that the proportional abundance of isoGDGT-5 (as well as isoGDGT-6) probably increases with temperature when pH is held constant, although we have insufficient data to convert that into an empirical calibration.

Terrestrial temperatures from early Palaeogene lignites

Here we use the relative abundance of the archaeal lipid isoGDGT-5 and degree of methylation of bacterial brGDGTs (MBT′$_{5me}$) obtained from lignites and newly calibrated proxies using modern peats to reconstruct the temperature in early Palaeogene peatlands (Supplementary Information gives details of the age models).

Ancient peats can be preserved in the form of immature lignites, also known as brown coals, after compaction under low burial pressure and temperatures (<100 °C). We use lignites from Germany (Schöningen), the UK (Cobham), New Zealand (Otaio) and several basins in western India (Barsingsar seam, Bikaner Basin; Kasnau Matasukh seam, Nagaur Basin; Matanomadh and Panandhro seams, Kachchh Basin, and Khadsaliya Clays, Saurashtra Basin). These lignites derive from peatlands influenced by marine incursions and hence reflect the local temperature very near sea level.

As far as is possible, given the difficulties of precise dating in purely continental strata, samples deposited within hyperthermals were avoided (Supplementary Information), such that these samples are expected to represent minimum temperature estimates of the early Palaeogene warmth. However, dating terrestrial sections is difficult and the precise age of all the samples, but especially the Indian lignites, remains difficult to confirm, and it remains possible that more extreme climate states are included.

All the latitudes reported here are best estimates for palaeolatitudes. Early Palaeogene lignites reveal that $\text{MAAT}_{\text{peat}}$ in Schöningen (~46° N) varied between 22.5 and 28 ± 4.7 °C ($n = 39$, $0.87 < \text{MBT}'_{5\text{me}} < 0.98$) and in Cobham (~48° N) between 23.5 and 26 ± 4.7 °C ($n = 7$, $0.90 < \text{MBT}'_{5\text{me}} < 0.94$) during the latest Palaeocene/earliest Eocene (Fig. 1a). At Otaio (~57° S), $\text{MAAT}_{\text{peat}}$ in the earliest Eocene lignites (that is, directly after the PETM) varied between 27 and 29 °C ± 4.7 °C ($n = 7$, $0.91 < \text{MBT}'_{5\text{me}} < 1$), close to the upper limit of $\text{MAAT}_{\text{peat}}$. These mid-latitude temperature reconstructions for the early Palaeogene (22–29 °C), are markedly warmer than present (2–15 °C), even when taking the calibration error of 4.7 °C into account (Fig. 1a). The Indian lignites (~0–5° N) consist of a variety of lignites of early Palaeogene age and are not dated as well. $\text{MAAT}_{\text{peat}}$ in these lignite samples varied between 28 and 29 4.7 °C ($n = 9$, $0.98 < \text{MBT}'_{5\text{me}} < 1$) and were close to the maximum value of the calibration, such that they might be minimum estimates.

All the lignites are also associated with the occurrence of archaeal isoGDGTs with more than four cyclopentane moieties (Fig. 1), predominantly isoGDGT-5 but also isoGDGT-6 in some samples (Supplementary Information). It is unlikely that the presence of these unusual biomarkers is evidence for hyperthermophilic (for example, hot springs) conditions in all of these ancient peatlands. A deep biosphere production of GDGTs during burial at depth is unlikely to be a significant influence on our temperature records as lignite deposits are characterized by low amounts of intact polar lipid GDGTs[24], which argues against an active GDGT-producing microbial community in such settings.

In the early Palaeogene lignites, the abundance of isoGDGT-5 is the highest, on average, in India in the palaeotropics; lower values occur in the mid-latitudes (Fig. 1). The high proportions of isoGDGT-5 in early Palaeogene lignites suggests that acidic peatlands with temperatures higher than 19.5 °C existed at palaeolatitudes of 46–48° N (Cobham and Schöningen) as well as 57° S (Otaio). Moreover, the proportion of isoGDGT-5 in the Indian lignites is higher than that found in any modern peat. We suggest that the higher proportions in the Indian lignites compared to the other Palaeogene sites is not the result of a much lower pH, as there is independent evidence that at least some of the latter were formed in ombrotrophic *Sphagnum* peats[25]. Instead, it is likely that higher proportions of isoGDGT-5 in the Indian lignites indicates MAATs higher than presently found in the low latitudes.

Comparison with existing temperature reconstructions

Collectively, the entire GDGT biomarker distribution yields two independent temperature estimates that originate from two different domains of life, which suggests that mid-latitude terrestrial peatland temperatures were significantly higher than modern during the early Palaeogene period of elevated p_{CO_2}, with values similar to those found only in tropical peatland at present . Although the bacterial-based $\text{MAAT}_{\text{peat}}$ calibration is near its limit in the Indian lignites, high abundances of isoGDGT-5 provide evidence that tropical temperatures were also elevated relative to those of today, consistent with SST reconstructions[9].

The majority of existing multiproxy terrestrial temperature data (for example, foliar physiognomy, MBT′/CBT and so on) suggests that continental temperatures in the mid-latitude Northern Hemisphere (40–60° N) were below 22 °C during the early Palaeogene (Fig. 1a). Some leaf physiognomic estimates from the northwest America, based mainly on the Kowalski and Dilcher calibration[26] and especially the CLAMP (Climate Leaf Analysis Multivariant Program) data, suggest temperatures, within error, to those found at present at these latitudes[10,17]. Similarly, all palaeosol-based temperature estimates obtained using a range of geochemical methods are close to or below modern-day temperatures at similar latitudes[27]. This is difficult to reconcile given the multiproxy evidence for significantly elevated p_{CO_2} levels during the early Palaeogene[1,2]. Such low temperatures in the mid-latitude Northern Hemisphere are also difficult to reconcile with terrestrial temperatures from the high-latitude Northern Hemisphere (>60° N) that range between 14 and 20 °C (refs [28,29]) and widespread evidence of subtropical flora[29,30] and fauna[31,32] in the (high) Arctic.

The $\text{MAAT}_{\text{peat}}$ estimates from the United Kingdom and Germany with average values ~25 and 27 ± 4.7 °C, respectively, indicate that mid-latitude terrestrial temperatures are at the high end of (or higher than) leaf physiognomic proxy estimates for comparable latitudes (Fig. 1a). However, these new data are consistent with summer temperature estimates in excess of 40 °C based on clumped isotopes of palaeosol carbonates from the Bighorn Basin (~45° N palaeolatitude)[33] and δ^{18}O-based terrestrial temperatures from mammalian tooth enamel and fish (gar) scales from the southern United States (~30–40° N) with estimates between 28 and 32 ± 5.5 °C (ref. [34]). Similarly, the data from Schöningen are consistent with early Eocene temperatures of 22.5 ± 2.5 °C based on leaf margin analysis from the nearby Messel oil shale[35]. These new terrestrial temperature estimates are also consistent with TEX_{86}-, Mg/Ca- and clumped isotope-based SST estimates between 19 and 32 °C from the mid-latitude Northern Hemisphere[9,36] (Fig. 1b).

The published early Palaeogene terrestrial temperature estimates from 45–65° S indicate values between ~10 and 20 °C, in general higher than modern values at these latitudes (Fig. 1a). $\text{MAAT}_{\text{peat}}$ estimates from New Zealand are ~5–10 °C higher than existing terrestrial temperature estimates for the region, with an average value of 28 ± 4.7 °C. However, some of the existing terrestrial temperature estimates were obtained from marine sediment cores in the Southern Ocean at ~60° S, but record conditions further south at Wilkes Land (Antarctica) at ~70° S. These indicate the presence of near-tropical forests on Antarctica[37] and, together with plant microfossil evidence from the Tawanui section in New Zealand that indicates the presence of thermophilic taxa directly before and after the PETM[38], they are consistent with high $\text{MAAT}_{\text{peat}}$ values and the presence of isoGDGT-5 in the Otaio lignite. Furthermore, $\text{MAAT}_{\text{peat}}$ is consistent with multiproxy SST estimates from the mid/high-latitude Southern Hemisphere that indicate values between 28 and 35 °C (refs [8,9]) (Fig. 1b).

It is likely that the $\text{MAAT}_{\text{peat}}$ estimates from India of $28\text{–}29 \pm 4.7$ °C represent minimum values, as also indicated by the higher-than-modern abundance of isoGDGT-5. This prevents a direct comparison with published low-latitude SST estimates. Even so, our estimates are slightly higher than the terrestrial temperatures currently suggested for the early Palaeogene of the Indian subcontinent[39], but within error of clumped isotope-based SSTs from the coast of India with values of $30\text{–}35 \pm 2.5$ °C (ref. [9]).

The offset between some of the existing and $\text{MAAT}_{\text{peat}}$ terrestrial temperatures could partly be explained by a potential cold bias

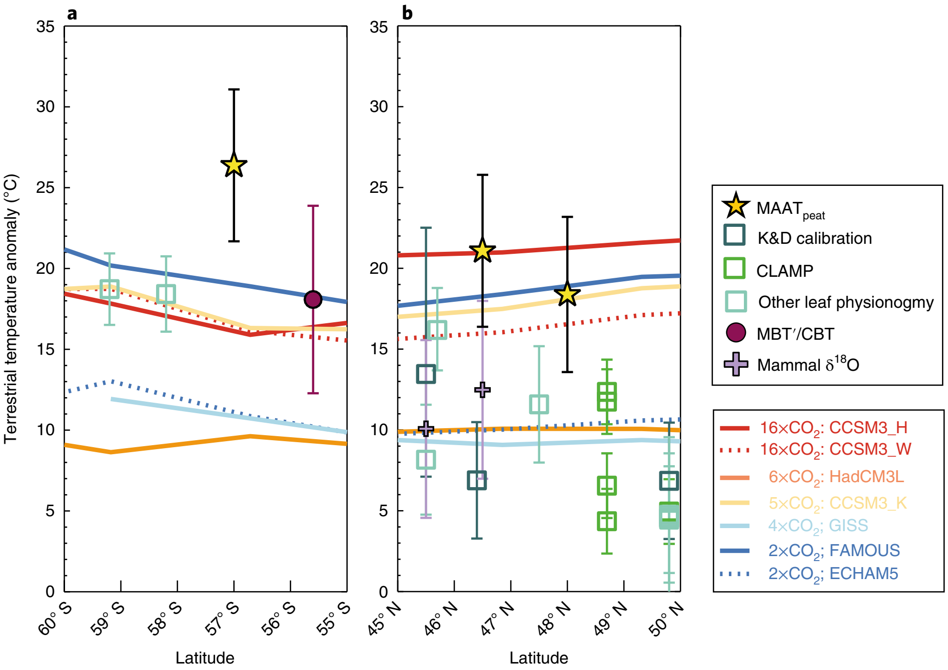

Fig. 3 | Comparison with model data for the early Palaeogene. a,b, The temperature anomaly between the early Palaeogene and present at the palaeolatitude of each location for all the terrestrial temperature data from 55–60° S (**a**) and from 45–50° N (**b**). Error bars reflect the combined spread in data (1σ) and calibration uncertainty (Supplementary Information gives details). Also shown is the zonal mean anomaly (early Palaeogene minus preindustrial) simulated by a range of climate models: 2×CO$_2$ ECHAM5[43], 2×CO$_2$ FAMOUS[16], 4×CO$_2$ GISS[44], 5×CO$_2$ CCSM3_K[15], 6×CO$_2$ HadCM3L[42], 16×CO$_2$ CCSM3_W[41] and 16×CO$_2$ CCSM3_H[10] (Supplementary Information).

in temperatures based on leaf physiognomic and palaeosol proxies[10,27], as well as uncertainty in the palaeo-elevation of several of the archives, especially those from North America. We also note that the MAAT$_{peat}$ estimates are higher than most previously published soil MBT′/CBT-based terrestrial temperature estimates from (proximal) marine sediments (Fig. 1a). Although also based on the distribution of brGDGTs, MBT′/CBT-based temperatures from marine sediments could be biased by their production in the water column or sediments[40]. Marine sediments also represent an integrated temperature across a large catchment area, which potentially includes a contribution from high altitudes. In addition, recent analytical advances urge for caution in interpreting MBT′/CBT data as the original measurements could be biased by co-eluting compounds[19]. As such, some of the original MBT′/CBT data might not reflect the terrestrial temperatures at sea level, which explains the offset with our data.

These lignite-based data therefore reinvigorate the debate about early Palaeogene temperatures: we find new evidence for high temperatures on land that are consistent with SST reconstructions, which resolves the prior conundrum, but retains the discrepancies between data and climate model simulations.

Comparison with climate model simulations

A number of climate models have been used to simulate the early Palaeogene climate, and include CCSM3[10,15,41], HadCM3L[42], ECHAM5[43], FAMOUS (Fast Met Office/UK Universities Simulator)[16] and GISS (Goddard Institute for Space Studies)[44]. Although these climate models originally struggled to simulate warm climates like that of the early Palaeogene, especially when using p_{CO_2} estimates consistent with proxy estimates[3], more recently there has been progress. The latest set of climate model simulations for the early Palaeogene (using CCSM3[15] and FAMOUS[16]) provides a better fit with proxy estimates of SSTs using p_{CO_2} estimates that are consistent with proxy data after changing specific model parameters, such as cloud properties, although they still struggle to reach the extent of warming indicated by SST proxies in the southwestern Pacific. Crucially, for the mid-latitude Northern Hemisphere (45–50 °N) the latest set of climate models fit the MAAT$_{peat}$ temperature data, but are 5–10 °C warmer than most of the published mid-latitude temperature data (Fig. 3b).

However, for the mid-latitude Southern Hemisphere (55–60° S), the magnitude of warming simulated by all climate models is still less than indicated by MAAT$_{peat}$ (Fig. 3a) and published SST estimates[8,45]. This could suggest that climate models are still missing crucial processes. However, it is important to highlight that virtually all mid/high-latitude Southern Hemisphere SST and terrestrial data (including the new MAAT$_{peat}$ data from Otaio) come from the southwestern Pacific and Pacific sector of the Southern Ocean. As such, the high temperatures so far found in the mid/high-latitude Southern Hemisphere might reflect local conditions and not be fully representative of zonal averages[46]. Future terrestrial temperature estimates using early Palaeogene lignites from for example S. America might be able to shed new light on whether these high temperatures were present throughout the mid/high-latitude Southern Hemisphere.

These novel terrestrial temperature estimates have important climatic and biogeochemical implications. For example, studies across microbial to ecosystem scales have demonstrated that methanogenesis rates in peatlands and the emission of methane to the atmosphere increase significantly with increasing temperature[6,47]. Combined with the evidence that indicates that a high p_{CO_2} would have stimulated primary productivity[48], our temperature estimates further suggest that the methane flux for a given areal extent of mid-latitude peatland could have been much greater during the early Palaeogene than at present. As methane is a potent greenhouse gas, our results support previous modelling work[48,49] that indicates the presence of an additional positive feedback mechanism associated with extensive warm mid-latitude peats in a high-CO_2 world that could amplify warming to a greater degree than that estimated with existing or GCM-derived temperature estimates.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available at https://doi.org/10.1038/s41561-018-0199-0.

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Author contributions

B.D.A.N., M.E.C. and R.D.P. designed the project. B.D.A.N. analysed all the samples in the modern peat database for isoGDGTs and wrote the manuscript with contributions from all the authors. M.R. analysed the Indian and Otaio lignite samples for GDGTs and G.N.I. analysed the Cobham and Schöningen lignite samples for GDGTs. B.D.A.N., M.E.C. and E.M.K. developed the database of early Palaeogene terrestrial palaeoclimate proxies. M.E.C. (Cobham and Schöningen samples), E.M.K. (Otaio samples) and P.K.S. (Indian samples) provided age models and the stratigraphic context of the lignites. O.L. provided the modern tropical peat samples from Peru.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to B.D.A.N.

Methods

The biomarkers from the lignites from Schöningen were extracted previously[18]. For this purpose, approximately 0.5–10 g of sediment were extracted via a Soxhlet apparatus for 24 h with dichloromethane:methanol (DCM:MeOH, 2:1 v/v) to yield a total lipid extract (TLE). The TLE was initially separated over silica into neutral and fatty acid fractions using chloroform-saturated ammonia and chloroform:acetic acid (100:1 v/v), respectively. The neutral fraction was subsequently fractionated over alumina into apolar and polar (which contained the GDGTs) fractions using hexane:DCM (9:1 v/v) and DCM:MeOH (1:2 v/v), respectively. The biomarkers from the Cobham lignite were extracted previously[50]. For this purpose, samples were extracted by sonication with a sequence of increasingly polar solvents (four times with DCM, four times with DCM:MeOH (1:1 v/v) and three times with MeOH). The TLEs were separated into three fractions using a column packed with (activated) alumina by elution with hexane (apolar fraction), hexane/DCM (9:1 v/v, 3 ml) and DCM:MeOH (1:2 v/v, 3 ml, polar fraction). Lignites from New Zealand were extracted for 24 h in Soxhlet using DCM:MeOH, (2:1 v/v) and separated over alumina into apolar (hexane:DCM, 9:1 v/v) and polar (DCM:MeOH, 1:2 v/v) fractions. TLEs from the Indian lignites were obtained via microwave extraction (Milestone Inc.) using DCM:MeOH (9:1 v/v) for 10 min at 70 °C. Aliquots of TLE were separated into hydrocarbon (hexane), aromatic (hexane:DCM, 1:1 v/v) and polar fractions (DCM:MeOH, 3:1 v/v) over silica.

For all samples the polar fraction was dissolved in hexane/isopropanol (99:1, v/v) and passed through 0.45 µm polytetrafluoroethylene filters. Fractions were analysed by high-performance liquid chromatography/atmospheric pressure chemical ionisation–mass spectrometry. Instrument methods followed published procedures[51]. Analyses were performed in the selective ion monitoring mode to increase the sensitivity and reproducibility, and $M+H^+$ (protonated molecular ion) GDGT peaks were integrated.

MAATs for the lignites were obtained using the degree of methylation of brGDGTs as reflected in the $\mathrm{MBT'}_{5me}$ index[19] and MAAT_{peat} calibration[22] (Supplementary Information gives additional details):

$$\mathrm{MBT'}_{5Me} = \frac{(\text{brGDGT–Ia} + \text{brGDGT–Ib} + \text{brGDGT–Ic})}{(\text{brGDGT–Ia} + \text{brGDGT–Ib} + \text{brGDGT–Ic} + \text{brGDGT–IIa} + \text{brGDGT–IIb} + \text{brGDGT–IIc} + \text{brGDGT–IIIa})}$$

$$\mathrm{MAAT}_{peat}(^{\circ}\mathrm{C}) = 52.18 \times \mathrm{MBT'}_{5me} - 23.05$$

where brGDGT–Ia, –Ib, and so on represent the abundances of specific brGDGT biomarkers according to the nomenclature of De Jonge et al.[19].

isoGDGT-5 was identified based on relative retention times, as well as co-injection with an acid hydrolysed >95% pure culture of the thermoacidophile *Thermoplasma acidophilum* (Matreya) (Supplementary Information). The relative abundance of isoGDGT-5 was calculated using the respective peak areas of isoGDGTs with one, two, three and five cyclopentane rings:

$$\text{isoGDGT} - 5\ (\%) = 100 \times \frac{(\text{isoGDGT} - 5)}{(\text{isoGDGT} - 1) + (\text{isoGDGT} - 2) + (\text{isoGDGT} - 3) + (\text{isoGDGT} - 5)}$$

where isoGDGT–1, –2, and so on represent the abundances of specific isoGDGT biomarkers according to the nomenclature of Schouten et al.[23]. isoGDGT-4 was excluded from this ratio due to the co-elution with the $[M+H]^+ + 2$ ion of crenarchaeol that also gives *m/z* 1,294 (ref. [52]).

Data availability. The authors declare that all the data supporting the findings of this study are available within the article and its Supplementary Information and, in addition, all modern peat GDGT data are available on the Pangaea database https://doi.org/10.1594/PANGAEA.883765. The compilation of all the previously published terrestrial and marine temperature data from the early Palaeogene together with the original references is also available in the Supplementary Information.

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SUPPLEMENTARY INFORMATION

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High temperatures in the terrestrial mid-latitudes during the early Palaeogene

B. D. A. Naafs[1*], M. Rohrssen[1,2], G. N. Inglis[1], O. Lähteenoja[3], S. J. Feakins[4], M. E. Collinson[5], E. M. Kennedy[6], P. K. Singh[7], M. P. Singh[7], D. J. Lunt[8] and R. D. Pancost[1]

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[1]Organic Geochemistry Unit, School of Chemistry, School of Earth Sciences, and Cabot Institute, University of Bristol, Bristol, UK. [2]Department of Earth and Atmospheric Sciences, Central Michigan University, Mount Pleasant, MI, USA. [3]School of Life Sciences, Arizona State University, Tempe, AZ, USA. [4]Department of Earth Sciences, University of Southern California, Los Angeles, CA, USA. [5]Department of Earth Sciences, Royal Holloway University of London, Egham, UK. [6]Department of Paleontology, GNS Science, Lower Hutt, New Zealand. [7]Coal and Organic Petrology Lab, Department of Geology, Banaras Hindu University, Varanasi, Uttar Pradesh, India. [8]School of Geographical Sciences and Cabot Institute, University of Bristol, Bristol, UK.
*e-mail: david.naafs@bristol.ac.uk

Supplementary information to *High temperatures in the terrestrial mid-latitudes during the early Paleogene* by Naafs et al.

1. Description of lignites and age models

1.1 Schöningen lignite (Germany)

36 samples were collected from Seam 1 in the Schöningen Südfeld mine, northern Germany (51.13°N, 11.00°E) (Fig. S1). Samples no. 33 to 1 were obtained from the high-resolution sampling series of 2008 and 2012[S1,2]. Samples XXIII 4a to XXXIII7b were obtained from subsequent low-resolution sampling[S2]. The lignites in this mine were deposited as peat in a low lying coastal setting[S3] with a paleolatitude of around 46 °N. The seam from which the samples are derived is ~2.7 m thick and is overlain and underlain by brackish to shallow marine, clastic sedimentary deposits[S3,4].

The dinocyst zone D 5nb was recognized above the Main Seam in the nearby Emmerstedt area by Ahrendt et al.[S5]. If the Main seam is coeval at both sites this would indicate that Seam 1 at Schöningen is earliest Eocene. However, within marine Interbed 2, directly above Seam 1, there is a dramatic increase in the abundance of the dinocyst *Apectodinium*[S3] which may represent the onset of the Paleocene-Eocene Thermal Maximum (PETM) as it does at other sites[S6,7]. However, none of the studied samples yielded a negative $\delta^{13}C$ excursion that would suggest it was deposited during the main body of the PETM[S4]. Therefore, Seam 1 is considered to be either very latest Paleocene or very earliest Eocene in age. During the subsequent early Eocene (Seam 3 upwards), there is a long-term temperature maximum recorded from both the lignites and nearshore marine interbeds, consistent with changes in the palynological assemblage[S2,3]. As this interval may include the Early Eocene Climatic Optimum (EECO)[S1], this suggests that Seam 1 was deposisted prior to the EECO. Further details of sample positions and the lignite sequence at Schöningen can be found in the supplementary material to Robson et al.[S1] and Inglis et al.[S2].

1.2 Cobham lignite (UK)

A total of 7 samples were used from the Cobham Lignite Bed at Cobham, UK (51.40°N, 0.40°E). Samples were obtained from previous sampling events[S8]. This lignite was deposited in a low-lying freshwater setting at the southwest shore (very near sea-level) of the North Sea (~48 °N palaeolatitude)[S9,10]. The Cobham Lignite Bed at Cobham comprises a thin clay layer (<3 cm) at the base, overlain by a laminated lignite (~55 cm thick). This is succeeded by another thin clay layer (<10 cm) and overlain by a blocky lignite (~130 cm).

The Cobham Lignite Bed at Cobham is underlain by the Upnor Formation, which, at a nearby site, is dated as latest Palaeocene by means of the occurrence of calcareous nannoplankton zone NP9 and magnetochron C25n in its lower part[S10]. The shallow-marine Woolwich Formation, which overlies the Cobham Lignite Bed at Cobham, contains the *Apectodinum* acme indicating that it is within the PETM[S9,10]. In addition, at Cobham a negative carbon isotope excursion (CIE) of ~ 1 ‰ is present near the top of the laminated lignite (54.4-55.3 cm) slightly below the middle clay layer, interpreted as being the negative CIE characteristic of the PETM[S8-10]. Here we used 7 samples from the lower laminated lignite below the inferred PETM CIE and thus of very latest Paleocene age.

1.3 Indian lignites

Lignites were collected from mines in several sites in the Rajasthan and Gujarat regions of western India (0-5 °N palaeolatitude). Paleogene-age subbituminous coals from the Meghalaya, Assam, and Nagaland regions of northeastern India were also analysed, but these lignites lacked GDGTs due to higher thermal maturity. All of these sections are associated with over- and/or underlying marine sediments, a characteristic consistent with deposition along the coastal margins of India[S11-15]. The elemental composition (relative concentration of C, H, O, N, and S) and TOC (total organic carbon) of the organic matter of Rajasthan and Gujarat lignites, in general, are suggestive of forest vegetation as the main source and peatification under topogenous conditions. This is further supported by the study of paleomires using petrography based information, using macerals as tools, which indicate deposition under tropical humid climatic conditions at a coastal setting with intermittent fluvial incursions[S16-18].

Several lignites from the Kachchh Basin were analysed: one sample from the Matanomadh seam (present-day lat./long.: 23°30’05”N, 68°58’E) and two samples from the Panandhro seam (present lat./long.: 23°41’34”N, 68°46’24”E). The Naredi Formation, including these lignite seams, is largely constrained to the early to early middle Eocene on the basis of the age diagnostic foraminifera and pollen[S11,19,20]. Abundant dinoflagellate cysts in associated shales and mudstones and pollen dominated by mangrove (*Nypa*) imply an occasional marine influence in a near-shore environment[S20].

In addition, 3 lignite samples from the Khadsaliya Clays of the Saurashtra Basin (present lat./long. 21°39’32”N, 72°12’08”E) were analysed. These lignites are considered early Eocene on the basis of pollen and fungal remains[S21,22]. The Khadsaliya Clays comprise gray to greenish-gray clays, carbonaceous clay, and lignite deposited in a woody swamp[S23].

Lastly, 3 lignite samples from the Palana Formation lignites were analyzed; one from the Barsingsar seam, Bikaner basin (present lat./long. 27.84°01N, 73.20°04E); and two from Kasnau Matasukh seam, Nagaur Basin (present lat./long.: 27°06’25”N, 74°04’30”E). The age of the Palana Formation is not well constrained. The Palana Formation was initially assigned to the Eocene on the basis of correlation with lignites in Pakistan[S24] and broad age constraints derived from pollen[S25,26]. However, planktonic foraminifera in the overlying Marh Formation have been suggested to be of late Paleocene-early Eocene age[S27,28]. In addition, the more recently described osteoglossid and lepisosteid fish are consistent with a Paleocene age for the Palana Formation[S29]. As such the Palana Formation is considered of late Paleocene age.

1.4 Otaio River section lignites (New Zealand)

The Paleocene to Eocene Broken River Formation overlain by the early Eocene Kauru Formation is exposed in the Otaio River section, near Otaio Gorge, eastern South Island, New Zealand. The Broken River Formation exposures include two lignite seams >1 m thick and several thinner lignite seams[S30]. Palynological analyses[S31] and unpublished data indicate that the lower portion of the Otaio River section spans the PETM and the rest of the Broken River Formation exposed in the Otaio River section belongs to the New Zealand stages Waipawan to Mangaorapan (56.0 Ma to 48.9 Ma)[S32]. In order to avoid possible overlap with the PETM, we used samples from only the upper lignites, i.e. early Eocene. The 6 samples analysed were taken from thin lignites separated by dark brown sandstones as well as from the c. 2m thick seam at the top of the Broken River Formation exposure in Otaio River. Palynological analyses indicate that the samples fall into the NZ MH1 pollen zone, except for the lowermost sample analysed here (OGp30) which is placed in the PM3b pollen zone.

2. Detection of *iso*GDGT-5 and -6 in peats and lignites

*Iso*GDGT-5 and -6 were identified based on 1) comparison of relative retention times (Fig. S2 and S3) with published data[S33], 2) comparison of LC-MS chromatograms with those of a sample from Champagne pool, a thermal hot spring with a temperature of 75 °C and pH of 5.5 that contains *iso*GDGT-0 to -8[S34], and an acid-hydrolysed extract of the extremophile *Thermoplasma acidophilum* (Matreya, catalog # 1303) (Fig. S4), which is known to produce *iso*GDGT-0 to -6, but not crenarchaeol[S35], and 3) co-injection of a peat sample from Peru and the acid-hydrolysed extract of the extremophile *T. acidophilum* (Fig. S5).

3. Environmental controls on the *iso*GDGT distribution in modern peat

Decades of research, based on both culture experiments and natural archives such as marine sediments and thermal hot springs, have demonstrated that Archaea can alter the distribution of their *iso*GDGT membrane-spanning lipids in response to changes in environmental parameters such as temperature and pH[S36-42]. However, so far it is unknown whether the *iso*GDGT distribution in terrestrial settings such as peats varies according to environmental parameters. Below, we discuss the *iso*GDGT distribution in a wide range of modern peats to assess whether key-environmental parameters such as peat pH and mean air annual temperature have an impact on the *iso*GDGT pool in peats. The peat samples were obtained from a database as described in detail in Naafs et al.[S43,44]. In short, we analyzed >470 samples from 96 different peatlands from around the world for their GDGT distribution. The database consists of peats from a wide range of environments with a total span in mean annual air temperature (MAAT) from -8 to 27 °C and pH range from 3 to 8. pH data does not exist for all peats and *iso*GDGTs were below detection limit in a number of peat samples (predominantly in samples from the very top of peat).

3.1 pH dependence

In thermal hot springs, where *iso*GDGTs are produced by extremophiles, the *iso*GDGT distribution is influenced by environmental factors such as pH, with increasing cyclisation at lower pH and higher temperatures[S34,41,45]. It is largely unknown whether the *iso*GDGT distribution in mesophilic (terrestrial) settings is influenced by pH, although Xie et al.[S46] recently demonstrated that the *iso*GDGT distributions of a number of Chinese and American mineral soils as well as enrichments of terrestrial *Thaumarchaeota* grown over a narrow pH range (6.5 to 8) were correlated with pH.

We found no significant correlation ($R^2<0.2$) between the relative abundance of individual *iso*GDGTs with cyclopentane rings (both if crenarchaeol was included and when not) and pH (Fig. S6). The only *iso*GDGT that had a clear correlation ($R^2=0.56$) with pH was *iso*GDGT-5.

We collected a range of samples from peatlands in the Peruvian Amazon. These tropical peats (MAAT ~26 °C) are located less than 200 km apart, but span a pH range from 6.1 to 3.8. The peats with pH < 5.1 contain *iso*GDGT-5, whereas those with a pH > 5.1 do not (Fig. 2 of main manuscript). To explore this further, we compared the relative abundance of *iso*GDGT-5 relative to the other *iso*GDGTs with cyclopentane rings (5/(1+2+3+5)) to the calcium concentration of individual samples. *Iso*GDGT-4 was excluded from this ratio due to the co-elution with the $[M+H]^+ + 2$ ion of crenarchaeol that also gives *m/z* 1294[S47].

Calcium concentrations in peats are a good indicator of nutrient content and alkalinity (pH) in these peats[S48]. Calcium concentrations are low, typically less than 500 mg/kg dry peat, in nutrient-poor ombrotrophic bogs. River-influenced nutrient-rich minerotrophic peats with pH > 5 are characterized by much higher calcium concentrations, up to 17,000 mg/kg dry peat[S48,49]. When we plot the 5/(1+2+3+5) ratio against calcium concentration for individual peat samples (Fig. S7), it is clear that *iso*GDGT-5 is only present in samples with a low calcium content (< 2000 mg/kg, mostly < 500 mg/kg dry peat) and hence low pH. The CBTpeat'-based pH calibration for peats has a relatively large error of ±0.8 pH units and caution should be taken with applying CBTpeat' to reconstruct absolute pH-values[S43]. Even so, the CBT_{peat}' based pH values for these samples support the inferences derived from Ca ratios. *iso*GDGT-5 is only present in samples with CBT_{peat}'-based pH < 5 and predominantly in samples with CBT'peat-based pH < 4, as seen in the global dataset (Fig. 2 of the main manuscript).

In addition, a 750 cm long peat core from the Aucayacu peatland is characterized by a shift in peat forming environment. Sediments spanning 9 to 5 ka (below 400 cm) formed under minerotrophic conditions with high calcium concentrations (high pH), transitioning to low calcium concentrations (low pH) in the upper 400 cm spanning the late Holocene (last 5 kyr)[S48,50]. This transition occurred as the peat deposit grew higher, out of river influence and into ombrotropic conditions. *iso*GDGT-5 is only present in the ombrotrophic (low pH), upper 400 cm of the core and absent in the underlying minerotrophic (high pH) peat (Fig. S8). Together, the modern surface samples and downcore results indicate a clear pH dependence controlling the abundance of *iso*GDGT-5.

TEX$_{86}$[S38] and the ring index (RI)[S36], established indices that reflect the degree of cyclisation of *iso*GDGTs, did not correlate with pH (Fig. S9).

$$\mathrm{TEX}_{86} = \frac{(iso\mathrm{GDGT\_2} + iso\mathrm{GDGT\_3} + \mathrm{cren.\,isomer.})}{(iso\mathrm{GDGT\_1} + iso\mathrm{GDGT\_2} + iso\mathrm{GDGT\_3} + \mathrm{cren.\,isomer.})}$$

Ring index

$$= \frac{\left(iso\mathrm{GDGT\_1} + 2\ \times\ iso\mathrm{GDGT\_2} + 3\ \times\ iso\mathrm{GDGT\_3} + 4\ \times\ (\mathrm{cren.} + \mathrm{cren.\,isomer})\right)}{(iso\mathrm{GDGT\_0} + iso\mathrm{GDGT\_1} + iso\mathrm{GDGT\_2} + iso\mathrm{GDGT\_3} + \mathrm{cren.} + \mathrm{cren.\,isomer})}$$

3.2 Temperature dependence

Although the relationship differs between settings, both in culture experiments of hyperthermophiles and incubation experiments of mesophiles[S36,40] as well as natural archives such as marine[S38] and lake sediments[S51] and hot springs[S34,41] the degree of cyclization of *iso*GDGTs, reflected in RI and/or TEX$_{86}$, is positively correlated with growth temperature. So far it is largely unknown whether the cyclization of *iso*GDGTs in terrestrial settings is correlated to growth temperature, although there is some recent evidence that suggests that *iso*GDGTs in mineral soil altitude transects from Tanzania and China differ according to temperature[S52,53].

Our results demonstrate that individual *iso*GDGTs with 0-3 cyclopentane rings have either no or weak ($0.1 < R^2 < 0.2$) correlations with MAAT (Fig. S10). Also RI (with or without crenarchaeol) and TEX$_{86}$ have no clear correlation with MAAT (Fig. S11). The lack of correlation between the distribution of *iso*GDGTs and MAAT is likely because the *iso*GDGT pool is derived from a mixture of GDGT-producing archaeal communities that thrive in peats. In regular marine sediments, the majority of GDGTs are derived from (planktonic) marine Thaumarchaeota that modify their membrane lipids depending on temperature, reflected in the TEX$_{86}$ proxy. However the dominance of *iso*GDGT-0 and low abundance of crenarchaeol in almost all peat samples, and resulting consistently low ring index, suggests a dominance of methanogenic Euryarchaeota. Consistent with this, if ring indices are calculated, excluding crenarchaeol, they remain poorly correlated to temperature and pH.

For *iso*GDGT-5 there is currently not enough data to construct a temperature calibration, especially due to the additional influence of pH on the relative abundance of *iso*GDGT-5 (see section 3.1). However, *iso*GDGT-5 is absent in ombrotrophic peats from the mid and high latitudes with MAAT < 12 °C. The highest relative abundance of *iso*GDGT-5 occurs in tropical peats accumulating under highest MAAT, indicating a temperature influence on the relative abundance of *iso*GDGT-5 (Fig. S10).

A combined pH/temperature control on the distribution of *iso*GDGT-5 is supported by four decades of research that reveal a pH and growth temperature dependence on *iso*GDGTs in cultures of acidohyperthermophilic Archaea[S36] and mesocosm experiments of marine Thaumarchaeota[S40], as well as the observed correlation between the degree of cyclization and temperature and/or pH in natural environments such as hot springs[S34] and the open ocean[S38]. Amongst cultured organisms, Euryarchaeota belonging to the order Thermoplasmatales as well as Crenarchaeota of the orders Thermoproteales and Sulfolobales are the only known source organisms of *iso*GDGT-5 to -8[S42]; therefore, it is possible that (uncultured mesophilic) relatives of these specific orders are responsible for the presence of *iso*GDGT-5 to -7 in our modern ombrotrophic tropical peats and early Paleogene lignites.

4. Environmental controls on the *br*GDGT distribution in modern peat

*br*GDGTs are membrane-spanning lipids produced by bacteria, likely acidobacteria[S54-56]. A decade of research has demonstrated that in mineral soils and lakes the degree of methylation of bacterial *br*GDGTs depends on temperature[S57-60]. We recently expanded this by developing a global peat-specific *br*GDGT temperature calibration that is based on the degree of methylation of *br*GDGTs, reflected in the $\mathrm{MBT'_{5me}}$ index[S57], in 470 samples from 96 different of modern peats: $\mathrm{MAAT_{peat}}$[S43]. Importantly, the *br*GDGT data for this peat calibration dataset was generated using the latest HPLC-MS methods[S61] that separate the recently discovered 5- and 6-methyl *br*GDGTs[S62].

$$\mathrm{MBT'_{5me}} = \frac{(\mathrm{Ia} + \mathrm{Ib} + \mathrm{Ic})}{(\mathrm{Ia} + \mathrm{Ib} + \mathrm{Ic} + \mathrm{IIa} + \mathrm{IIb} + \mathrm{IIc} + \mathrm{IIIa})}$$

$$\mathrm{MAAT_{peat}}\ (^\circ\mathrm{C}) = 52.18 \times \mathrm{MBT'_{5me}} - 23.05\ (n = 96, \quad R^2 = 0.76, \quad \mathrm{RMSE} = 4.7\ ^\circ\mathrm{C})$$

In addition, the degree of cyclization of *br*GDGTs in mineral soils can be used to reconstruct pH[S57,58]. We recently demonstrated that also in peat the degree of cyclization of *br*GDGTs, expressed in the $\mathrm{CBT_{peat}}$ index, is correlated with pH[S43], although the correlation is weaker compared to that seen in mineral soils.

$$\mathrm{CBT_{peat}} = \log\frac{(\mathrm{Ib} + \mathrm{IIa}' + \mathrm{IIb} + \mathrm{IIb}' + \mathrm{IIIa}')}{(\mathrm{Ia} + \mathrm{IIa} + \mathrm{IIIa})}$$

$$\mathrm{pH} = 2.49 \times \mathrm{CBT_{peat}} + 8.07 \ (\mathrm{n} = 51, \quad \mathrm{R}^2 = 0.58, \quad \mathrm{RMSE} = 0.8)$$

As lignites are formed from compaction of peat under low burial pressure and temperatures, we apply this peat-specific calibration to reconstruct terrestrial temperatures during the early Paleogene. Inherent to this approach is the assumption that the relationship between $\mathrm{MBT'_{5me}}$ and temperature was the same during the early Paleogene as at present.

GDGTs can be influenced by thermal maturation. Schouten et al.[S42,63] showed that *iso*- and *br*GDGTs are similarly influenced by thermal degradation as GDGTs disappear at hydrous pyrolysis temperatures > 260 °C. Consistent with these experiments, GDGTs appear to be absent in thermally mature coal[S64]. In addition, thermal maturation of GDGTs between ~220 and 260 °C was shown to influence their distribution, with a decrease in the degree of methylation and cyclization[S42,63]. Thus, thermal maturation can not explain the high temperatures we reconstruct for the early Paleogene using lignites as 1) lignites are formed a low burial temperatures (<100 °C) where GDGTs are not influenced, and 2) if thermal degradation would have influenced the *br*GDGTs in our lignites, this would have lowered $\mathrm{MBT'_{5me}}$ and hence resulted in low $\mathrm{MAAT_{peat}}$.

5. GDGT distribution early Paleogene lignites

As explained in the previous section, we assume that the relationship observed in modern peat between $\mathrm{MBT'_{5me}}$ and temperature[S43] was the same during the early Paleogene. This assumption is supported by the observation that the broader GDGT distribution in our lignites, of which the majority formed between 45 and 60 degrees latitude during the early Paleogene, is very similar to modern-day distribution of GDGTs in tropical peats. The lignite and tropical modern-day peat are characterized by a high abundance of *iso*GDGTs with cyclopentane rings (including *iso*GDGT-5), H-*iso*GDGTs[S44] (characterized by a covalent bond between the two alkyl chains[S65]), and dominance of *br*GDGT-Ia over the other *br*GDGTs. On the other hand, the

GDGT distribution in our lignites looks different compared to a modern-day mid-latitude peat (Fig. S12). Modern-day mid-latitude peats lack significant amounts of *iso*GDGTs with cyclopentane rings, do not contain *iso*GDGT-5 or H-*iso*GDGTs, and penta- and hexamethylated *br*GDGT are abundant.

Sinninghe Damsté[S66] recently used a ternary plot of the *br*GDGT distribution in marine sediments and argued that samples that plot off the *br*GDGT distribution seen in the modern mineral soil database contain a contribution of *in situ* *br*GDGT production and do not exclusively contain mineral soil-derived terrestrial *br*GDGTs. Following this approach, if the GDGT distribution of our early Paleogene lignites was not produced in peats, the lignite data should plot outside of distribution of *br*GDGTs in the modern peat database. However, when we compare the *br*GDGT distribution in our early Paleogene lignites to that of modern peats[S43] using ternary plots (Fig. S13), it is clear that the *br*GDGT distribution of early Paleogene lignites looks very similar to that in modern peatlands. We then extended this approach by comparing the *iso*GDGT distribution in our early Paleogene lignites with that seen in modern peats and marine core-top sediments (Fig. S14). The *iso*GDGT distribution in our early Paleogene lignites looks very similar to that seen in modern-day peats with a very low proportion of crenarchaeol and looks very different from the *iso*GDGT distribution of for example marine sediments[S67]. These results highlight that not only MBT'$_{5me}$ (and hence MAAT$_{peat}$) and the abundance of *iso*GDGT-5 in our early Paleogene lignites are similar to modern (tropical) peats, but that the broader GDGT distribution of our early Paleogene lignites is comparable to a modern-day (tropical) peat.

The only difference is the abundance of *iso*GDGT-5 encountered in the Indian lignites, which is higher than found in any modern peat, even in modern tropical peats (MAAT ~ 26.5 °C) with pH ~ 3. As pH of 3 is the most acidic peat environment known, the higher abundance of *iso*GDGT-5 found in the Indian lignites is at least party related to temperatures higher than MAAT > 26.5 °C, inline with our MAAT$_{peat}$ temperature estimates. In addition, it is unlikely that the high abundance of *iso*GDGT-5 in the Indian lignites (compared to the mid-latitude lignites) is the result of a much lower pH. For example there is independent evidence that at least some of the mid-latitude lignites were formed in ombrotrophic (low pH) *Sphagnum* peats[S4] and CBT$_{peat}$' is similar for all lignites.

6. Calculation of paleolatitudes

To be consistent the Ypresian paleolatitudes for all published terrestrial (and marine) sites as well as the lignites were (re)calculated using the models explained in[S68]. These paleolatitudes might differ sligthtly form those reported in the original publications. The uncertainty in the paleolatitude calculations for each site is not known, but can be up to several degrees paleolatitude.

7. Compilation of published early Paleogene terrestrial temperatures

We compiled terrestrial temperature data based on a range of proxy methods as plotted in figure 1. The majority of data is obtained using leaf physiognomy from the early Paleogene (late Paleocene and early Eocene) and derived mainly from the Huber and Caballero[S69] and Yang et al.[S70] compilations (see data file). There are different leaf physiognomy methods and we grouped them into three groups 1) data obtained using the Kowalski and Ditcher (K&D) leaf margin analysis calibration[S71] , 2) data obtained using Climate Leaf Analysis Multivariate Program (CLAMP), and 3) other leaf physiognomy data (e.g. using alternative leaf margin analysis calibrations[S72]). Estimates based on nearest living relatives data from plants (e.g. coexistence approach, bioclimatic analysis, etc) were omitted from figure 1 and 3 because of their reliance on correct identification of the nearest living relative. For comparison, figures S15 and S16 include this nearest living relative tempeature data. In addition, we omitted a number of data points from the various compilations either because the data was confirmed to be middle Eocene in age (Axel Heidelberg, Geiseltal, Puryear-Buchanan, Kisinger Lakes, Chermurnaut Bay, Fossil Hill Flora - King George Island, and James Ross Basin), represented the PETM (Dragon Glacier - King George Island, Hubble Bubble – Bighorn Basin), the age of the data was poorly constrained (Mahenge and Raichikha), or because the altitude correction applied was uncertain (China Gulch, Camanche Bridge, Pentz, Cherokee Site 1, Fiona Hill, Council Hill, Iowa Hill, You Bet 2, Chalk Bluffs – E., Scotts Flat, Gold Bug, Hidden Gold Camp, Woolsey Flat, Mountain Boy, and Pine Grove 1). From Yang et al.[S70] we used the gridded data adjusted.

Where available we show MAAT obtained using different calibrations to show the full uncertainty regarding leaf physiognomy based MAATs. For Climate Leaf Analysis Multivariate Program (CLAMP) data[S70] we use an uncertainty of ± 2 °C (http://clamp.ibcas.ac.cn/CLAMP_Uncertainties.html). We want to highlight that use of the Kowalski and Ditcher (K&D) calibration used in Huber and Caballero[S69] often does lead to higher MAAT estimates compared to other calibrations (e.g. CLAMP), but it is based on a very limited dataset.

All the previously published MBT/CBT-based mineral soil-derived MAAT[S31,73-77], based on the distribution of *br*GDGTs in (proximal) marine sediments, were revised using the updated MBT'/CBT calibration[S78]. The errors shown in figure 1 for the MBT'/CBT based data were obtained by adding the 5 °C calibration error of the MBT'/CBT calibration[S78] to the one standard deviation of the MBT'/CBT data for each site. For $\mathrm{MAAT_{peat}}$ the error bars were calculated the same way, but using a calibration error of 4.7 °C[S43]. Only data spanning the late Paleocene and early Eocene (57-48 Myr) was used (see data file). Where the PETM was recognized; data from the PETM was excluded.

We also included temperature data from early Paleogene paleosols from Argentina[S79] and the USA[S80] as well as early Paleogene δ^{18}O-based terrestrial temperatures from mammalian tooth enamel and fish (gar) scales, all from the Northern Hemisphere[S81,82].

8. Compilation of published early Paleogene sea surface temperatures

To compare our early Paleogene terrestrial temperature data with sea surface temperature (SST) data, we compiled all available published data based on the organic geochemical $\mathrm{TEX_{86}}$ palaeothermometer as well as calcite-based SSTs using Mg/Ca and δ^{18}O of pristine planktonic foraminifera and clumped isotopes (see data file). $\mathrm{TEX_{86}}$-based SSTs were calculated using the BAYSPAR deep time analog approach[S67,83]. Error bars on $\mathrm{TEX_{86}}$-based SST in figure 1 represent the 1σ confidence interval. For the calcite-based proxies the errors were calculated by combining the calibration error and the one standard deviation of the data for each site under different assumptions of early Paleogene seawater composition; $-0.64 < \delta^{18}O_{sw}$ (VSMOW) < -0.21[S84] and $1.5 < (Mg/Ca)_{sw} < 5$[S85]. Only data spanning the late Paleocene and early Eocene (57-48 Myr) was used (see data file). Where the PETM was recognized SST data from the PETM was excluded.

9. Data model comparison

The model-data comparison shown in Figure 3 is carried out using identical methods to those outlined in Lunt et al.[S84]. In brief, the early Paleogene zonal mean near-surface (~2m) continental air temperature is calculated for each of 7 models using different pCO$_2$ concentrations; 2xCO$_2$ ECHAM5[S86], 2xCO$_2$ FAMOUS[S87], 4xCO$_2$ GISS[S88], 5xCO$_2$ CCSM3_K[S89], 6xCO$_2$ HadCM3L[S90], 16xCO$_2$ CCSM3_W[S91] and 16xCO$_2$ CCSM3_H[S69]. The prescribed Eocene paleogeography also varies across the simulations as shown in the relevant references cited above.

An equivalent temperature (but global rather than continental) from an equivalent preindustrial simulation from each model is also calculated, and the difference, early Paleogene minus pre-industrial, is shown as coloured lines in Figure 3. In the nomenclature of Lunt et al.[S84], this is $\left[\overline{LAT_{ep}} - \overline{GAT_{p}}\right]$. On top of these modelled zonal mean anomalies, our compilation of proxy early Paleogene terrestrial temperatures is plotted, including our new MAAT$_{\text{peat}}$ estimates, and including published estimates of uncertainties. These proxy temperatures are plotted as anomalies relative to the zonal mean of observed modern global (not exclusively terrestrial) near-surface air temperatures, (NCEP[S92]), for the period 1981–2010. As such, the proxy data represent temperature anomalies at a single site, whereas the modelled results are zonal means.

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Supplementary figure captions

Figure S1; Present-day location of the lignites used in this study. Map generated using ODV[S93].

Figure S2; HPLC-APCI-MS base peak chromatogram (top) and mass chromatograms of a tropical peat sample from Peru (the Aucayacu peatland, 330 cm depth). Numbers indicate number of cyclopentane moieties in the *iso*GDGTs, while roman numbers highlight the different *br*GDGTs. Cren = crenarchaeol and reg.iso= crenarchaeol regioisomer. In H-*iso*GDGTs the two biphytane chains are covalently bound by a carbon-carbon bond[S65].

Figure S3; HPLC-APCI-MS base peak chromatogram (top) and mass chromatograms of an early Paleogene lignite sample from Cobham (CL70, 11.95 cm). Numbers indicate number of cyclopentane moieties in the *iso*GDGTs, while roman numbers highlight the different *br*GDGTs. Cren = crenarchaeol and reg.iso= crenarchaeol regioisomer. In H-GDGTs the two biphytane chains are covalently bound by a carbon-carbon bond.

Figure S4; HPLC-APCI-MS base peak chromatograms of A) a tropical peat sample from Peru (the Aucayacu peatland, 330 cm depth), B) sample from the Champagne pool hot spring, and C) acid-hydrolized extract of the extremophile *Thermoplasma acidophilum*.

Figure S5; HPLC-APCI-MS base peak chromatograms of A) a tropical peat sample from Peru (the Aucayacu peatland, 330 cm depth) and B) co-injection of the tropical peat sample with the acid-hydrolized extract of the extremophile *Thermoplasma acidophilum* that contains *iso*GDGT-5 but not crenarchaeol.

Figure S6; Fractional abundance of the individual *iso*GDGTs versus peat pH. Horizontal bars reflect range of peat pH[S43], while vertical bars represent 1σ from the average fractional abundance and are based on the analysis of multiple samples from the same peatland. Fractional abundances < 0.001 are not shown.

Figure S7; Relative abundance of *iso*GDGT-5 (%) versus A) calcium content (a measure of pH) for individual samples in a range of tropical peatlands from Peru that all experience the same climate. (Ca content from[S48,49]) and B) CBT_{peat}-based pH. Note that Ca data is not available for every sample.

Figure S8; Downcore relative abundance of *iso*GDGT-5 (%, orange) and calcium content (mg/kg, blue) in the 750 cm long peat core from the Aucayacu peatland in Peru that spans the last 9 kyr. Pie charts reflect the relative distribution of *iso*GDGTs in the top and bottom of the peat. (Radiocarbon ages from[S50])

Figure S9; A) Ring index and B) TEX_{86} versus peat pH. Horizontal bars reflect range of peat pH[S43], while vertical error bars represent 1σ from the average and are based on the analysis of multiple samples from the same peatland.

Figure S10; Fractional abundance of the individual *iso*GDGTs versus overlying mean annual air temperature. Vertical error bars represent 1σ from the average fractional abundance and are based on the analysis of multiple samples from the same peatland. Samples with a fractional abundance < 0.001 are not shown.

Figure S11; A) Ring index and B) TEX_{86} versus mean annual air temperature. Vertical error bars represent 1σ from the average and are based on the analysis of multiple samples from the same peatland.

Figure S12; HPLC-APCI-MS base peak chromatograms highlight the *iso*- and *br*GDGT distribution in A) early Paleogene lignite from UK (Cobham CL70, 11.95 cm), B) modern mid-latitude peat samples from Germany (Bissendorfer Moor, 18 cm depth), and C) modern tropical peat sample from Peru (the Aucayacu peatland, 330 cm depth). Modern MAAT Bissendorfer Moor and Aucayacu are 8.9 C and 26 °C, while pH for these peats is 4 and 3.7, respectively.

Figure S13; Ternary plot of the *br*GDGT-distribution in the modern peat database[S43] and all early Paleogene lignites used in this study. Plot shows the relative abundance of the tetra- (*br*GDGT-Ia, -Ib, and Ic), penta- (*br*GDGT-IIa, -IIa', -IIb, -IIb', -IIc, and -IIc'), and hexamethylated *br*GDGTs (*br*GDGT-IIIa, -IIIa', -IIIb, -IIIb', -IIIc, and -IIIc').

Figure S14; Ternary plot of the *iso*GDGT-distribution in the modern peat database, marine core-top sediments[S67], and all early Paleogene lignites used in this study. Plot shows the relative abundance of the *iso*GDGT with no rings (*iso*GDGT-0), *iso*GDGTs with 1 to 3 cyclopentane rings (*iso*GDGT-1, -2, and -3), and *iso*GDGT with a cyclohexane ring (crenarchaeol).

Figure S15; Same as figure 1 of the main manuscript, but including estimates based on nearest living relatives data (e.g. coexistence approach, bioclimatic analysis, etc.). Leaf physiognomy methods: K&D - Kowalski and Ditcher leaf margin analysis calibration[S71]; CLAMP - Climate Leaf Analysis Multivariate Program[S70]; other leaf physiognomic - for example using alternative leaf margin analysis calibrations[S72] . MAAT – mean annual air temperature.

Figure S16; Same as figure 3 of the main manuscript, but including estimates based on nearest living relatives data (e.g. coexistence approach, bioclimatic analysis, etc.). For abbreviations see Figure S15.

Figure S17; Global temperature anomaly between the early Paleogene and present for all available terrestrial temperature data at the paleolatitude of each location together with the zonal mean anomaly simulated by a range of climate models; 2xCO_2 ECHAM5[S86], 2xCO_2 FAMOUS[S87], 4xCO_2 GISS[S88], 5xCO_2 CCSM3_K[S89], 6xCO_2 HadCM3L[S90], 16xCO_2 CCSM3_W[S91] and 16xCO_2 CCSM3_H[S69].

Figure S1

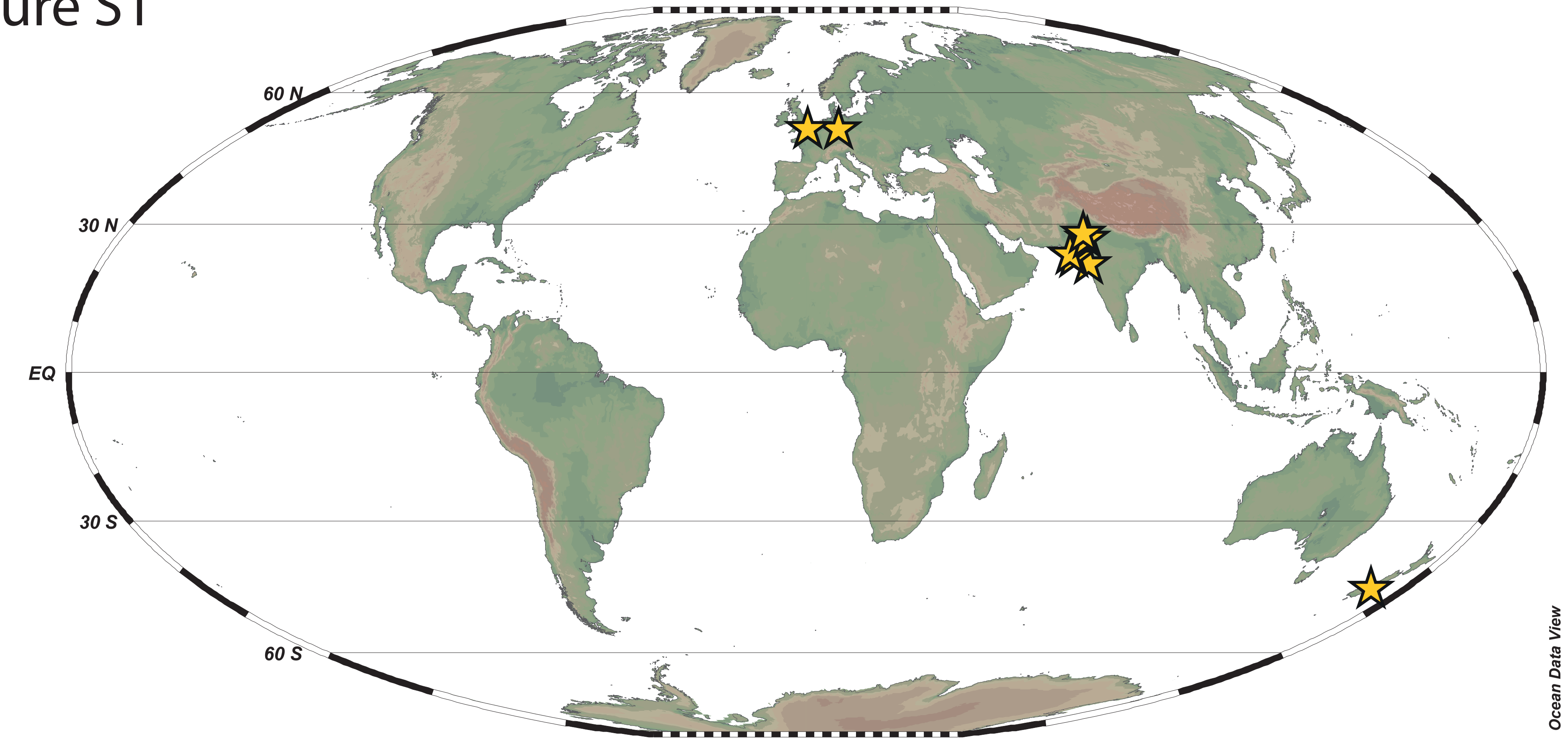


Figure S2

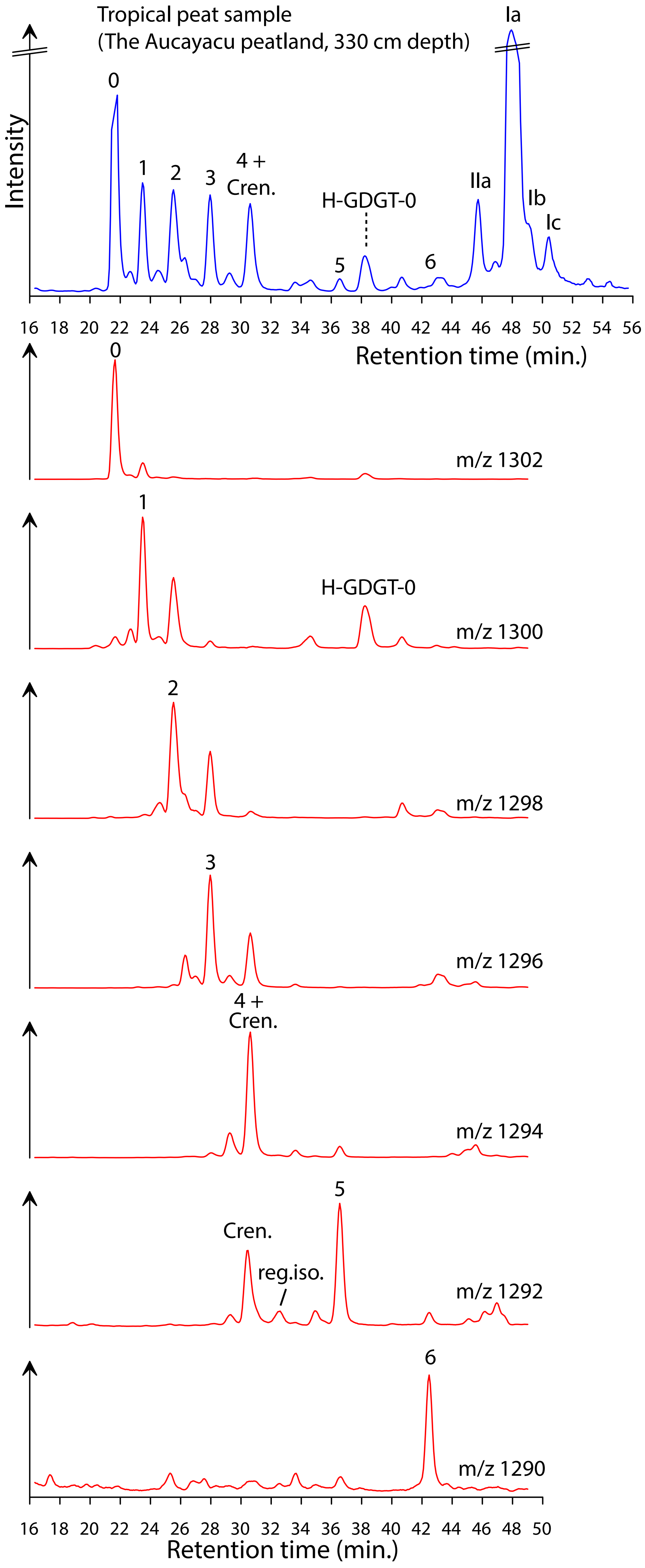

Tropical peat sample
(The Aucayacu peatland, 330 cm depth)
Intensity
0
1
2
3
4 +
Cren.
H-GDGT-0
5
6
IIa
Ia
Ib
Ic
16 18 20 22 24 26 28 30 32 34 36 38 40 42 44 46 48 50 52 54 56
Retention time (min.)
0
m/z 1302
1
H-GDGT-0
m/z 1300
2
m/z 1298
3
m/z 1296
4 +
Cren.
m/z 1294
5
Cren.
reg.iso.
m/z 1292
6
m/z 1290
16 18 20 22 24 26 28 30 32 34 36 38 40 42 44 46 48 50
Retention time (min.)

Figure S3

early Paleogene sample Cobham lignite (CL70, 11.95 cm)

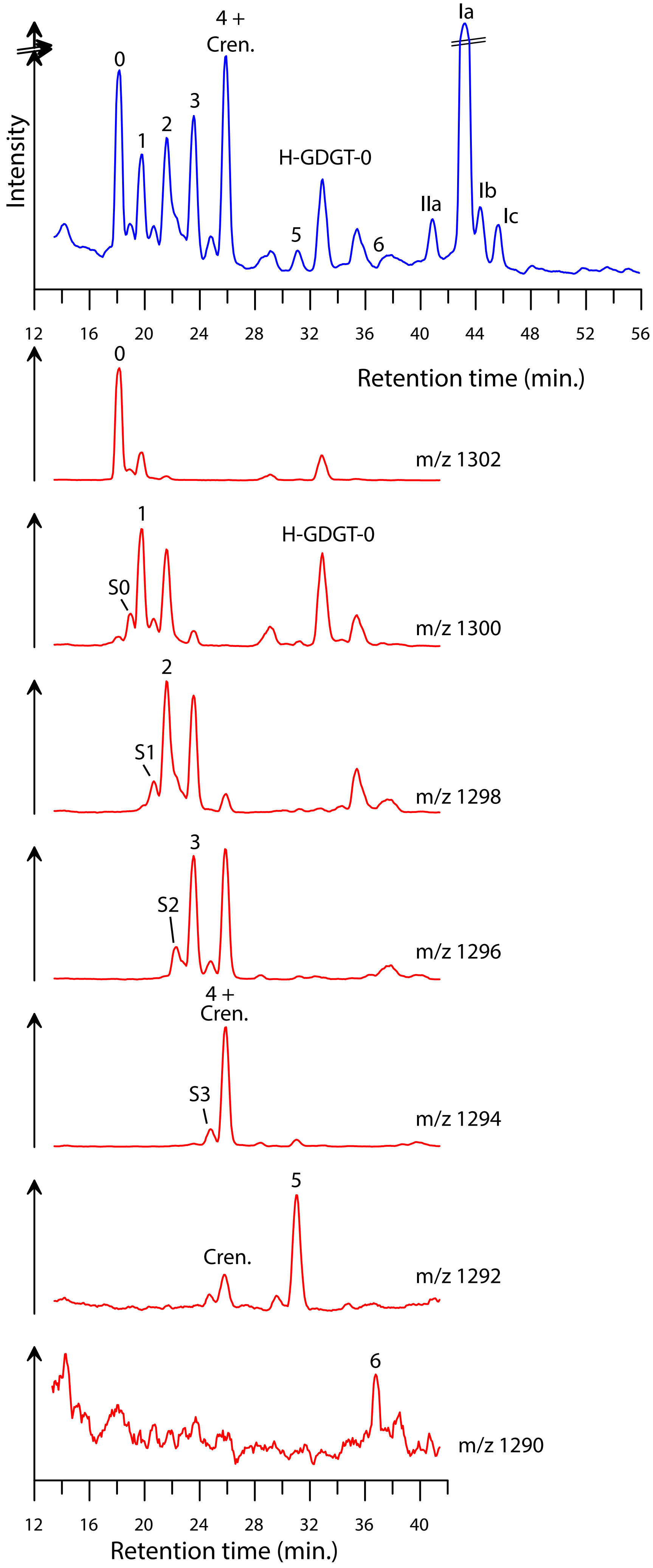


Figure S4

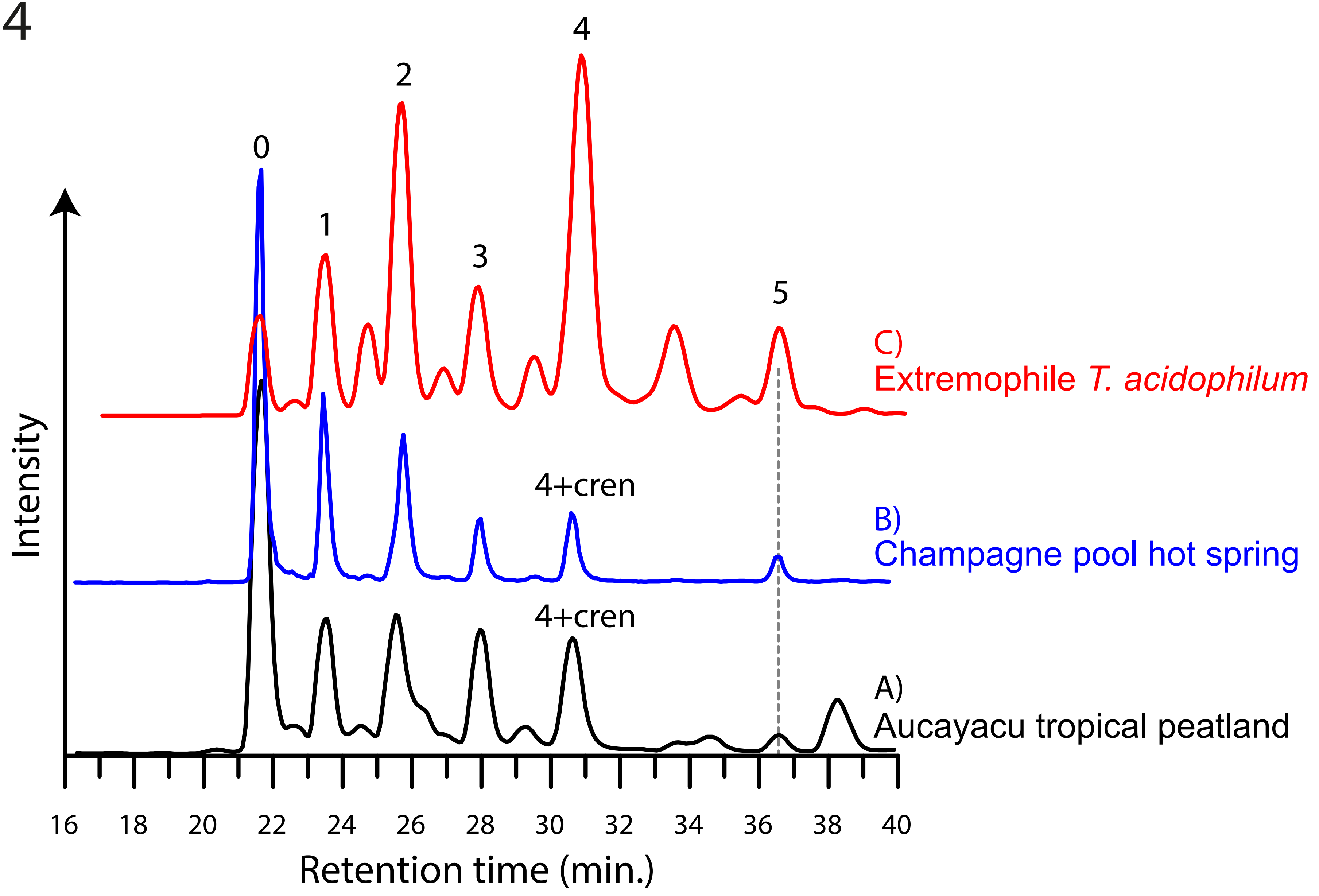

0
1
2
3
4
5
4+cren
4+cren
C)
Extremophile *T. acidophilum*
B)
Champagne pool hot spring
A)
Aucayacu tropical peatland
Intensity
16
18
20
22
24
26
28
30
32
34
36
38
40
Retention time (min.)

Figure S5

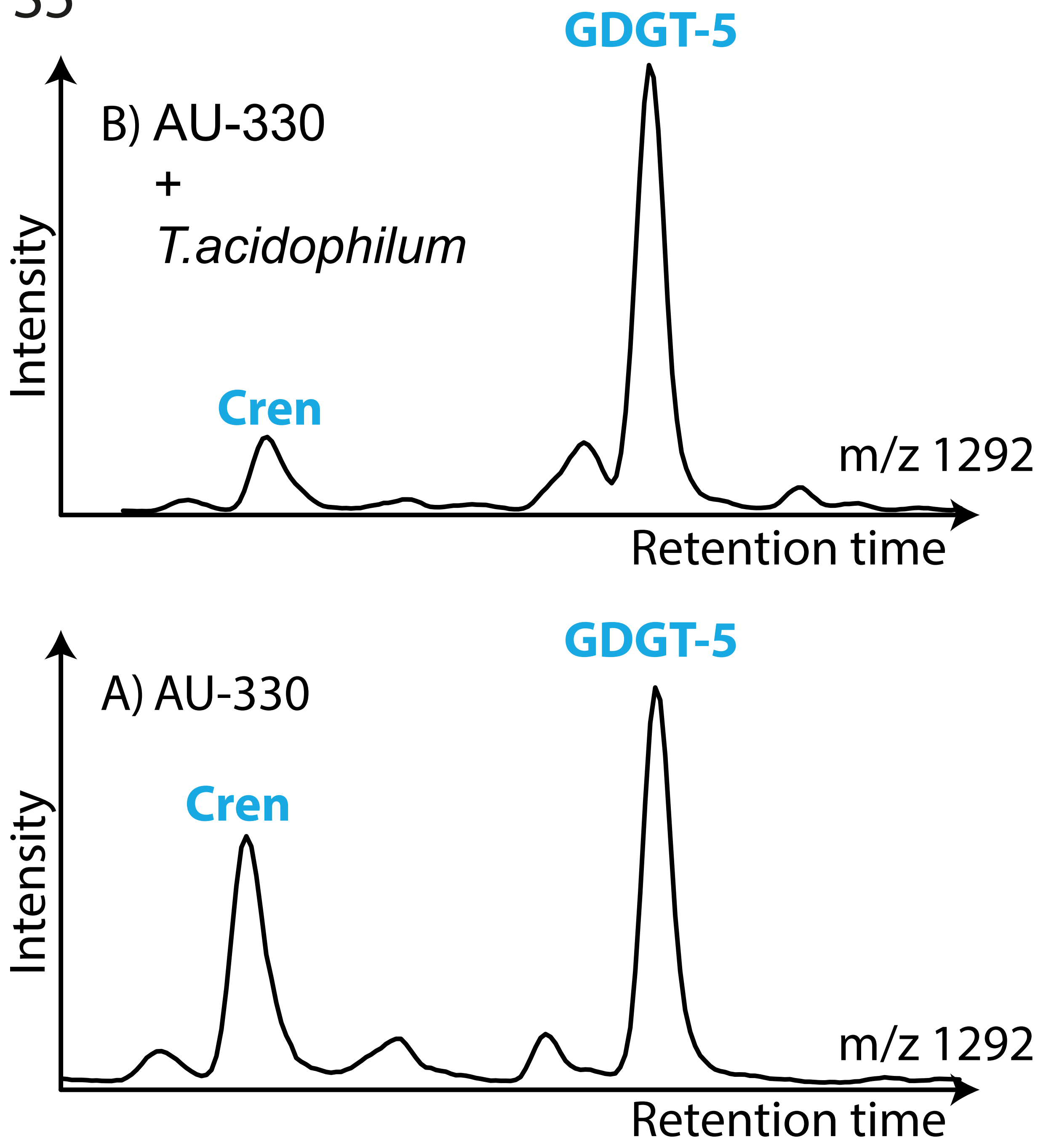

GDGT-5
B) AU-330
+
T.acidophilum
Intensity
Cren
m/z 1292
Retention time
GDGT-5
A) AU-330
Intensity
Cren
m/z 1292
Retention time

Figure S6

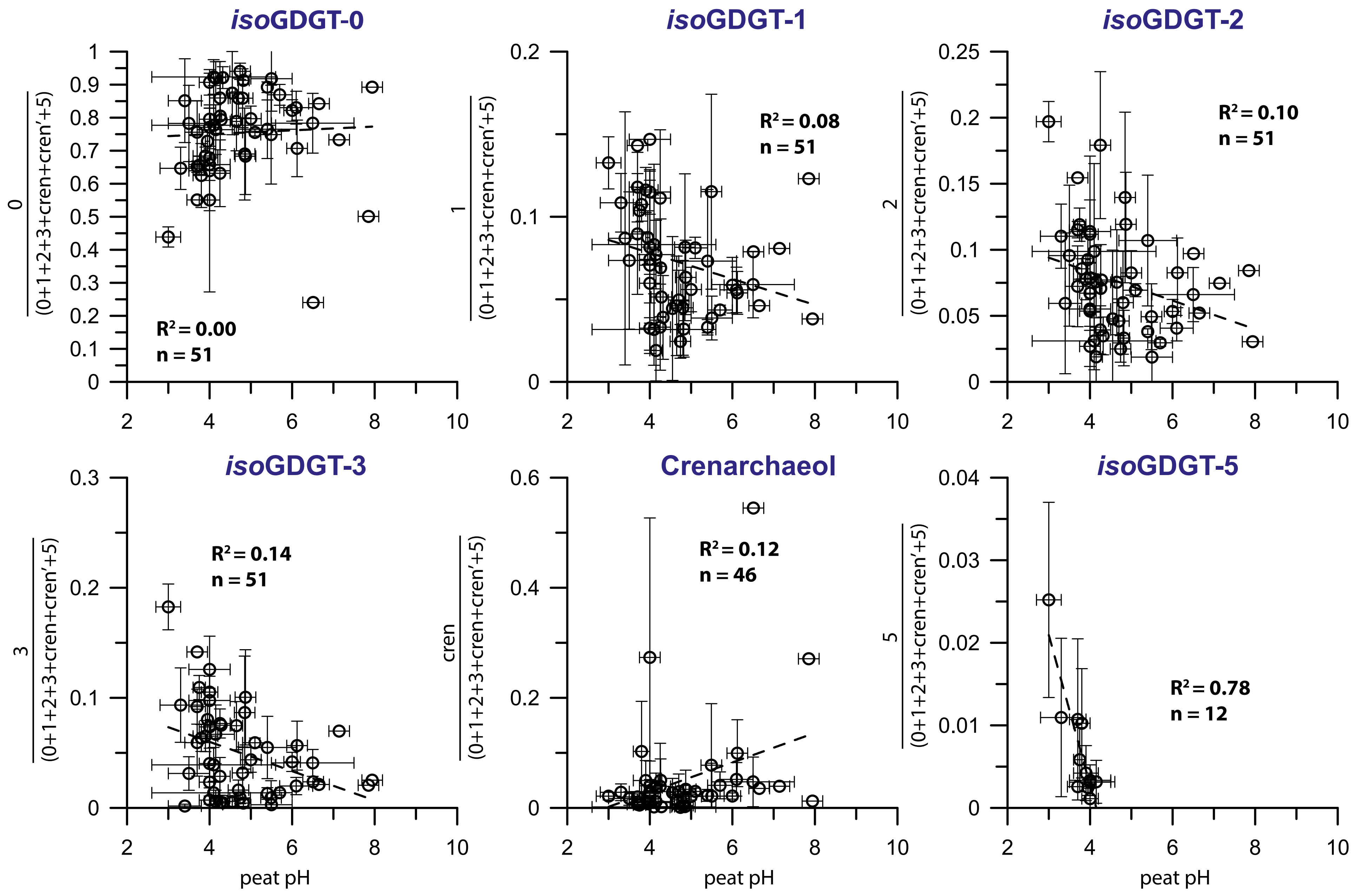

*iso*GDGT-0
0 / (0+1+2+3+cren+cren′+5)
R² = 0.00
n = 51
*iso*GDGT-1
1 / (0+1+2+3+cren+cren′+5)
R² = 0.08
n = 51
*iso*GDGT-2
2 / (0+1+2+3+cren+cren′+5)
R² = 0.10
n = 51
*iso*GDGT-3
3 / (0+1+2+3+cren+cren′+5)
R² = 0.14
n = 51
Crenarchaeol
cren / (0+1+2+3+cren+cren′+5)
R² = 0.12
n = 46
*iso*GDGT-5
5 / (0+1+2+3+cren+cren′+5)
R² = 0.78
n = 12
peat pH
2
4
6
8
10

Figure S7

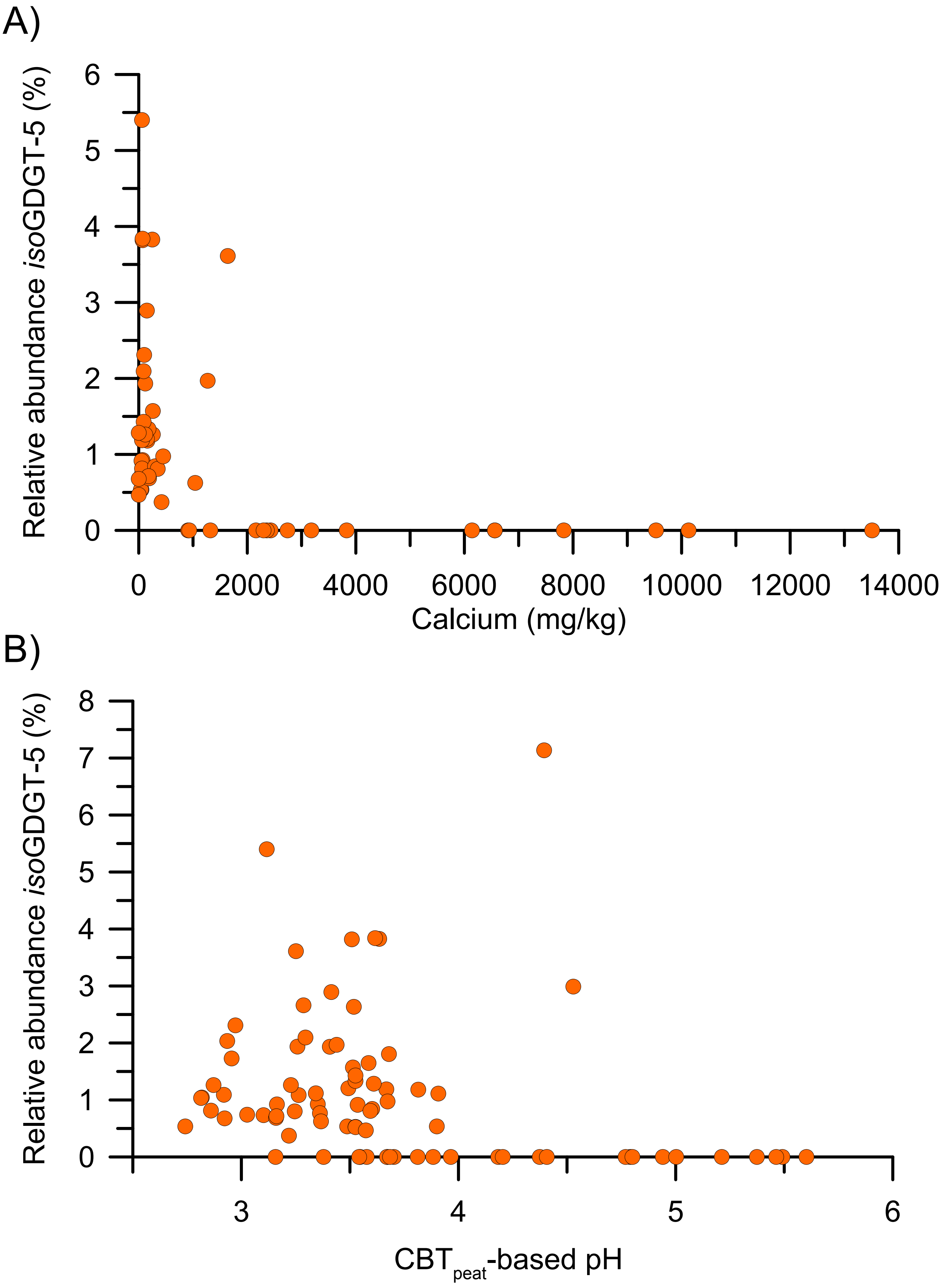

A)
Relative abundance *iso*GDGT-5 (%)
0
1
2
3
4
5
6
0
2000
4000
6000
8000
10000
12000
14000
Calcium (mg/kg)
B)
Relative abundance *iso*GDGT-5 (%)
0
1
2
3
4
5
6
7
8
3
4
5
6
CBT$_{peat}$-based pH

Figure S8

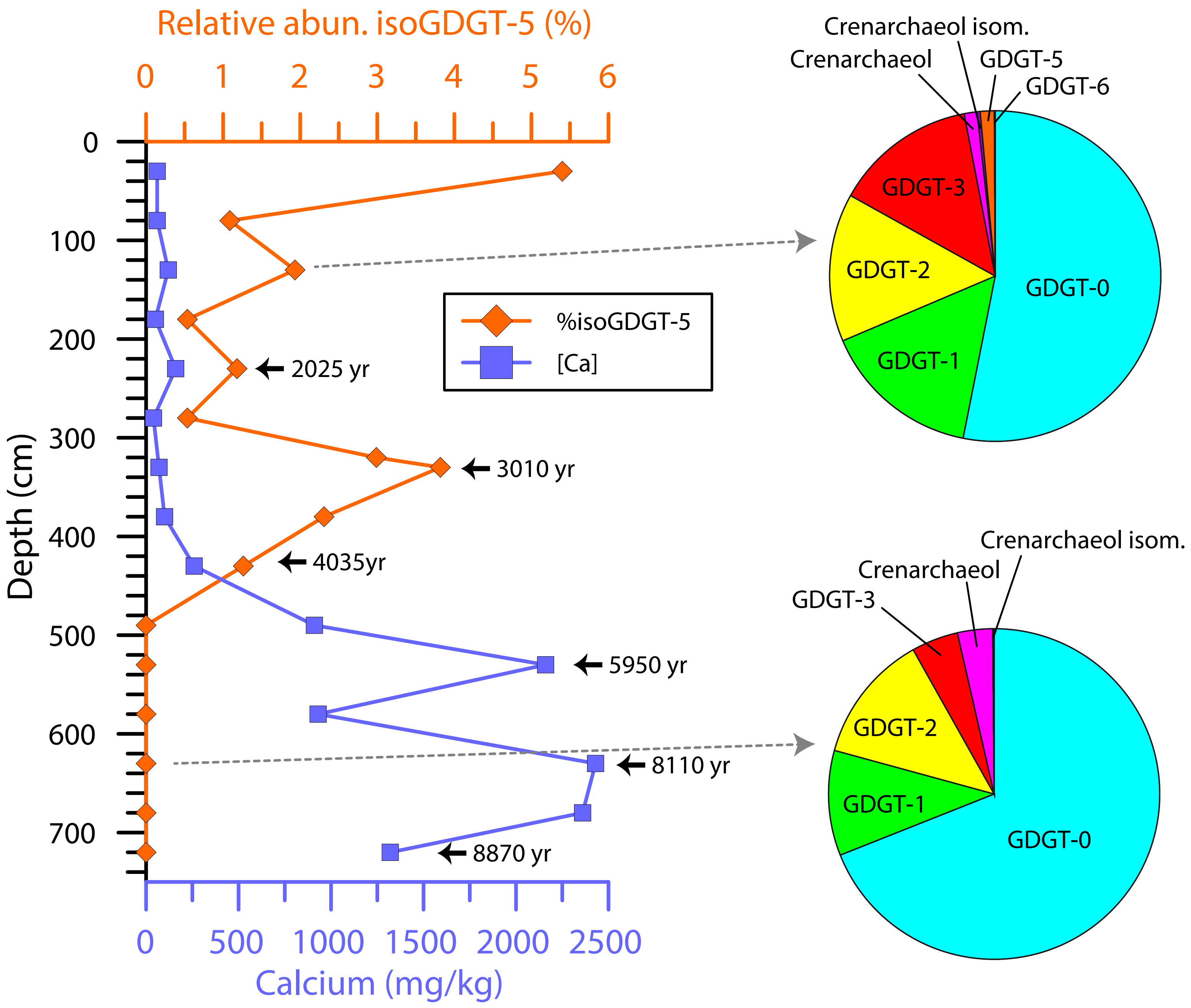

Relative abun. isoGDGT-5 (%)
0
1
2
3
4
5
6
Depth (cm)
0
100
200
300
400
500
600
700
2025 yr
3010 yr
4035yr
5950 yr
8110 yr
8870 yr
%isoGDGT-5
[Ca]
0
500
1000
1500
2000
2500
Calcium (mg/kg)
Crenarchaeol isom.
Crenarchaeol
GDGT-5
GDGT-6
GDGT-3
GDGT-2
GDGT-1
GDGT-0
Crenarchaeol isom.
Crenarchaeol
GDGT-3
GDGT-2
GDGT-1
GDGT-0

Figure S9

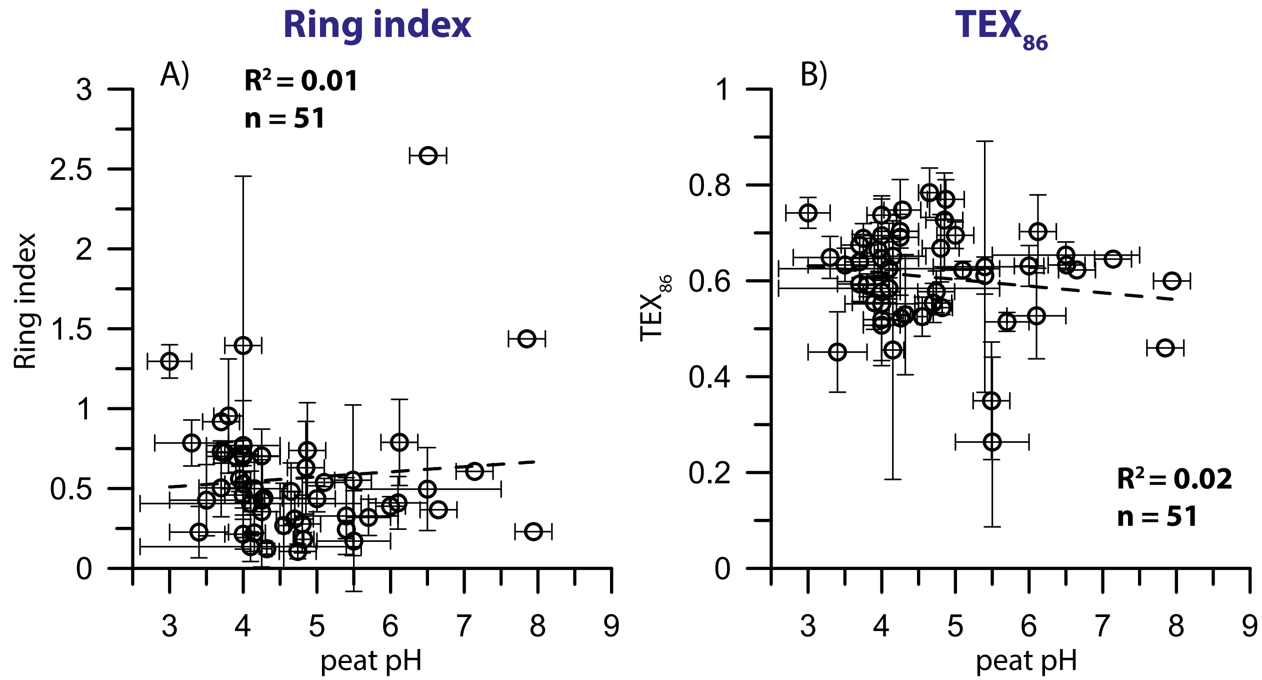

Ring index
A)
$R^2 = 0.01$
$n = 51$
Ring index
0
0.5
1
1.5
2
2.5
3
3
4
5
6
7
8
9
peat pH
TEX_{86}
B)
$R^2 = 0.02$
$n = 51$
TEX_{86}
0
0.2
0.4
0.6
0.8
1
3
4
5
6
7
8
9
peat pH

Figure S10

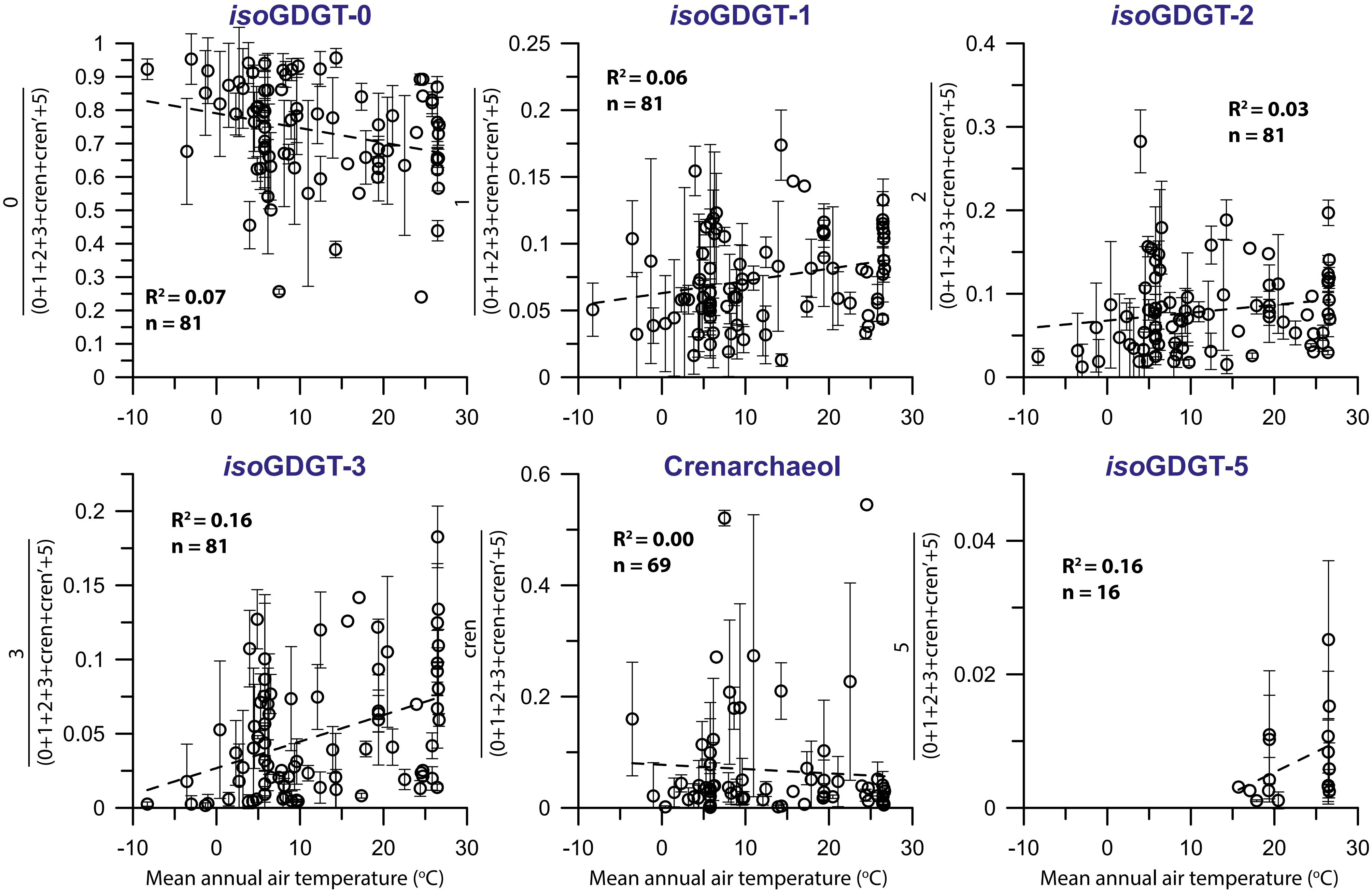

isoGDGT-0
R² = 0.07
n = 81
0 / (0+1+2+3+cren+cren′+5)
isoGDGT-1
R² = 0.06
n = 81
1 / (0+1+2+3+cren+cren′+5)
isoGDGT-2
R² = 0.03
n = 81
2 / (0+1+2+3+cren+cren′+5)
isoGDGT-3
R² = 0.16
n = 81
3 / (0+1+2+3+cren+cren′+5)
Crenarchaeol
R² = 0.00
n = 69
cren / (0+1+2+3+cren+cren′+5)
isoGDGT-5
R² = 0.16
n = 16
5 / (0+1+2+3+cren+cren′+5)
Mean annual air temperature (°C)
Mean annual air temperature (°C)
Mean annual air temperature (°C)
-10
0
10
20
30

Figure S11

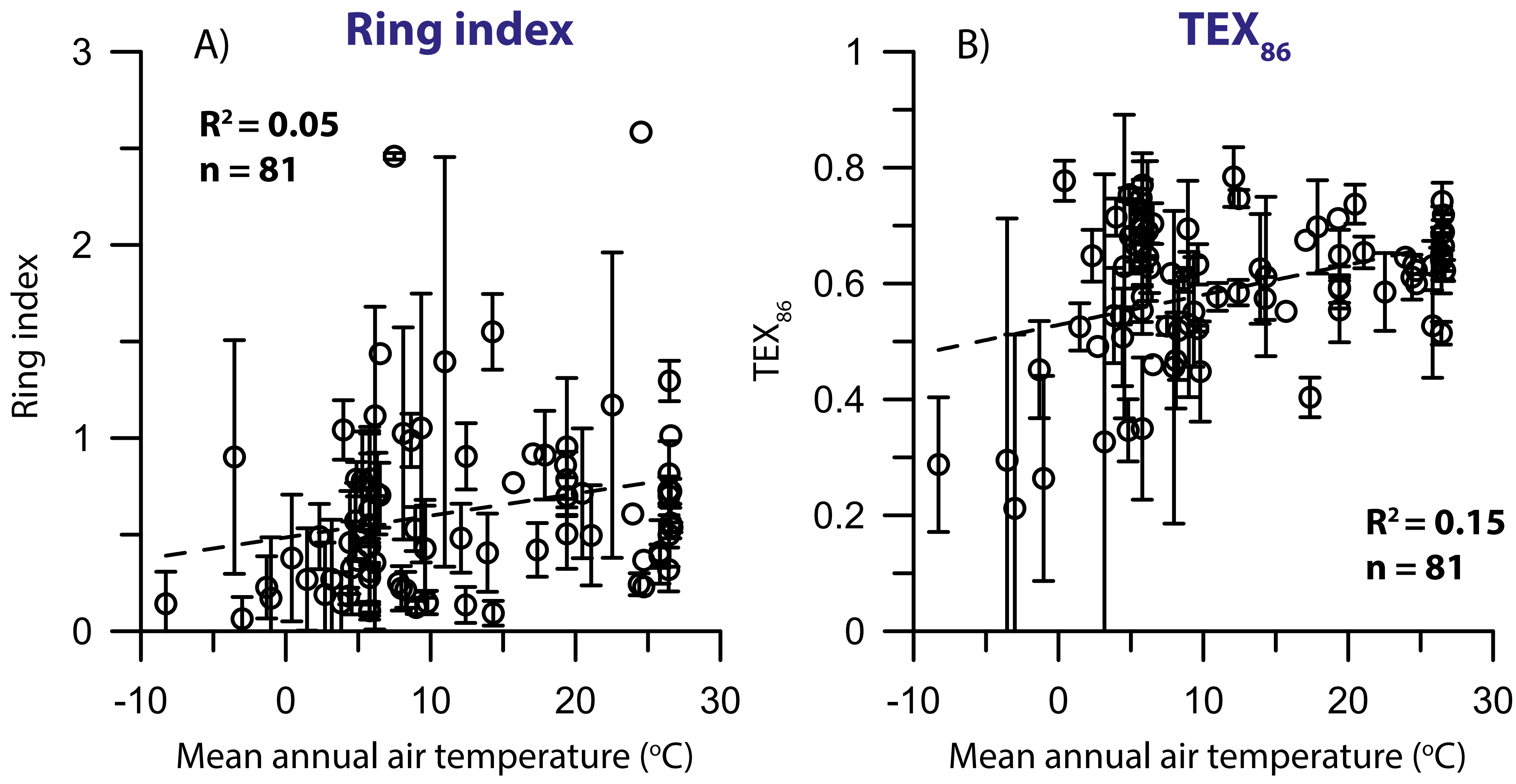

A)
Ring index
R² = 0.05
n = 81
Ring index
0
1
2
3
-10
0
10
20
30
Mean annual air temperature (°C)
B)
TEX86
R² = 0.15
n = 81
TEX86
0
0.2
0.4
0.6
0.8
1
-10
0
10
20
30
Mean annual air temperature (°C)

Figure S12

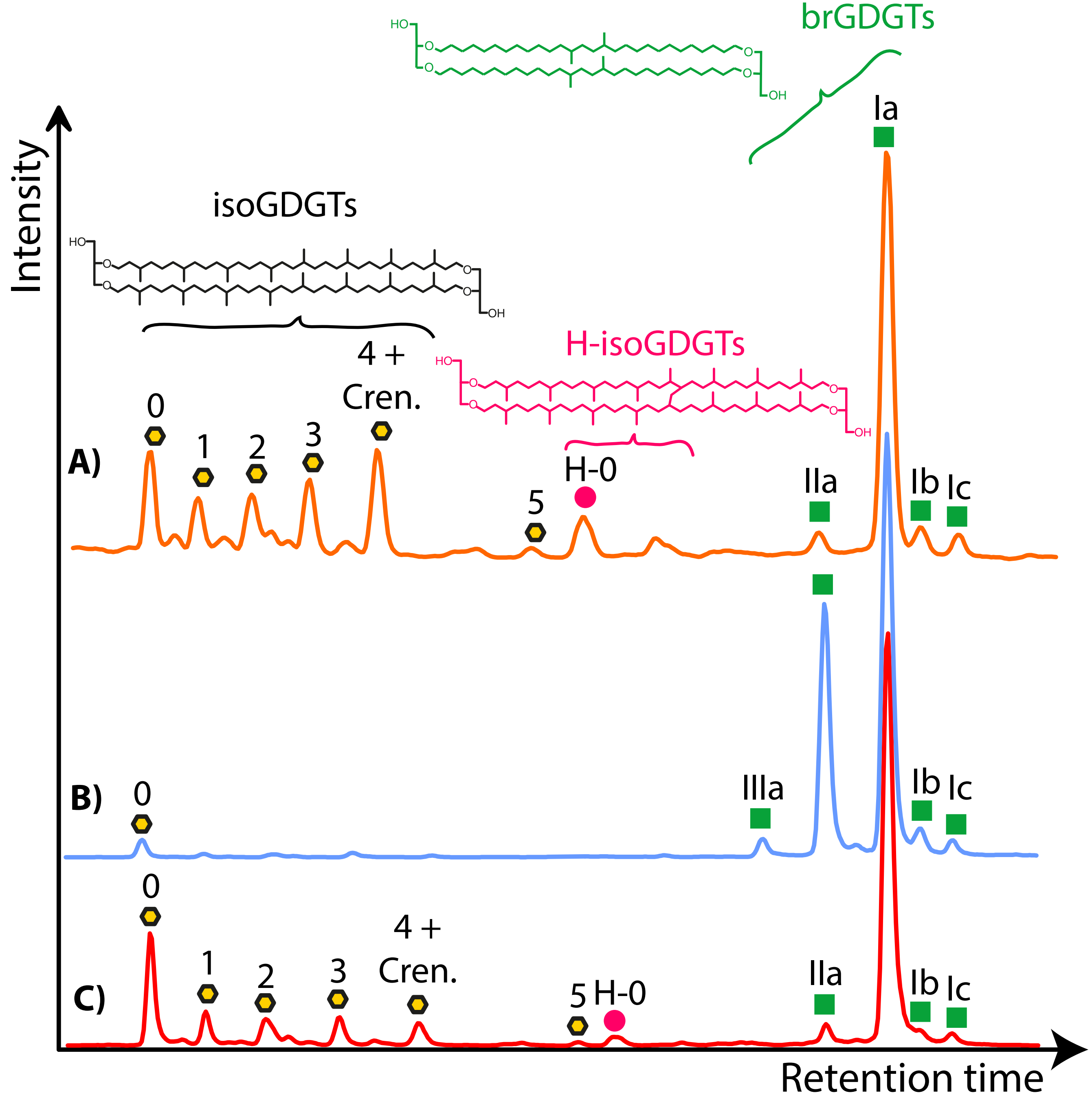
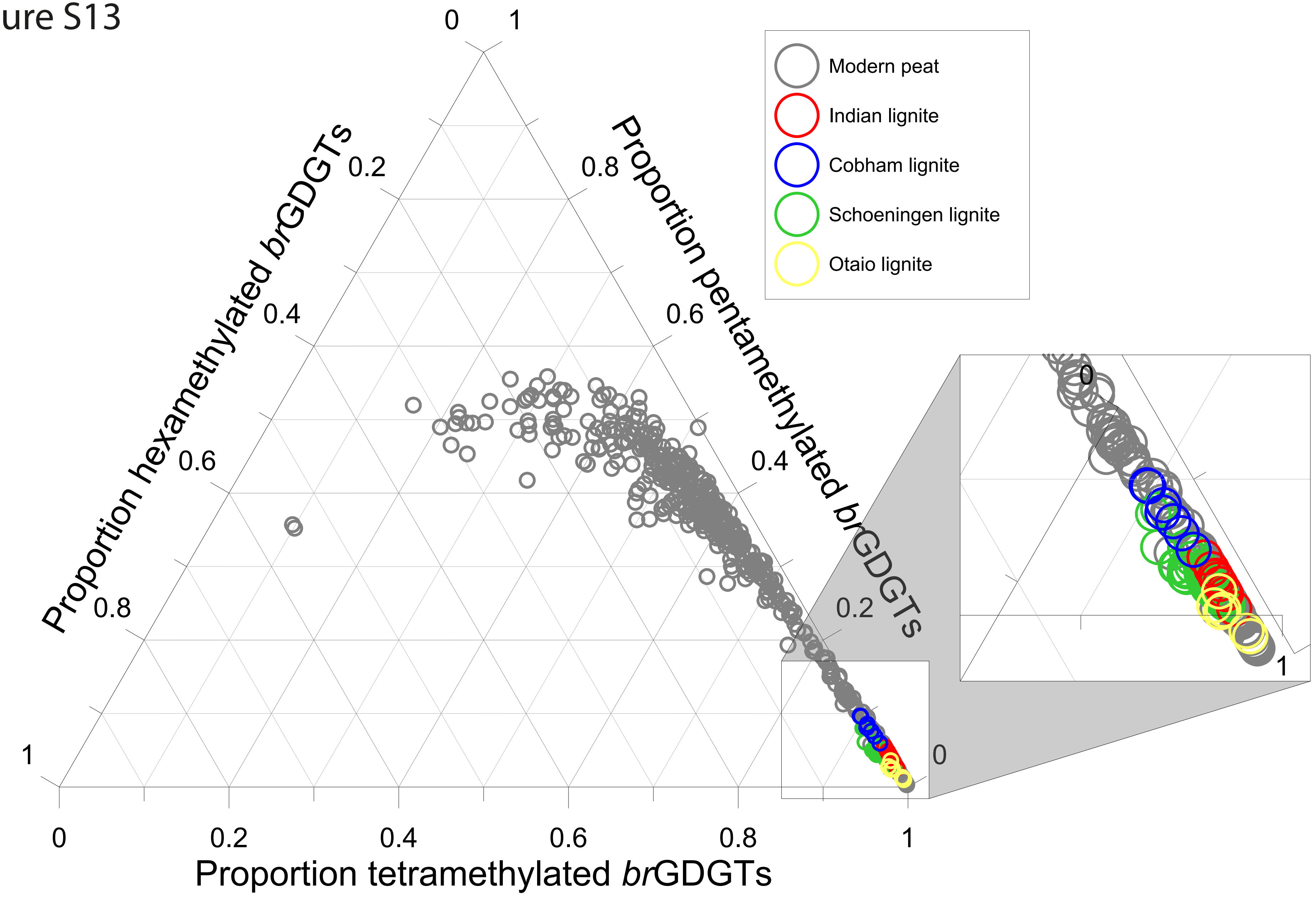

brGDGTs
HO
O
O
O
O
OH
Ia
isoGDGTs
HO
O
O
O
O
OH
4 +
Cren.
H-isoGDGTs
HO
O
O
O
O
OH
Intensity
A)
0
1
2
3
5
H-0
IIa
Ib
Ic
B)
0
IIIa
Ib
Ic
C)
0
1
2
3
4 +
Cren.
5
H-0
IIa
Ib
Ic
Retention time

Figure S13



0
1
0.2
0.4
0.6
0.8
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
Proportion hexamethylated *br*GDGTs
Proportion pentamethylated *br*GDGTs
Proportion tetramethylated *br*GDGTs
Modern peat
Indian lignite
Cobham lignite
Schoeningen lignite
Otaio lignite
0
1

Figure S14

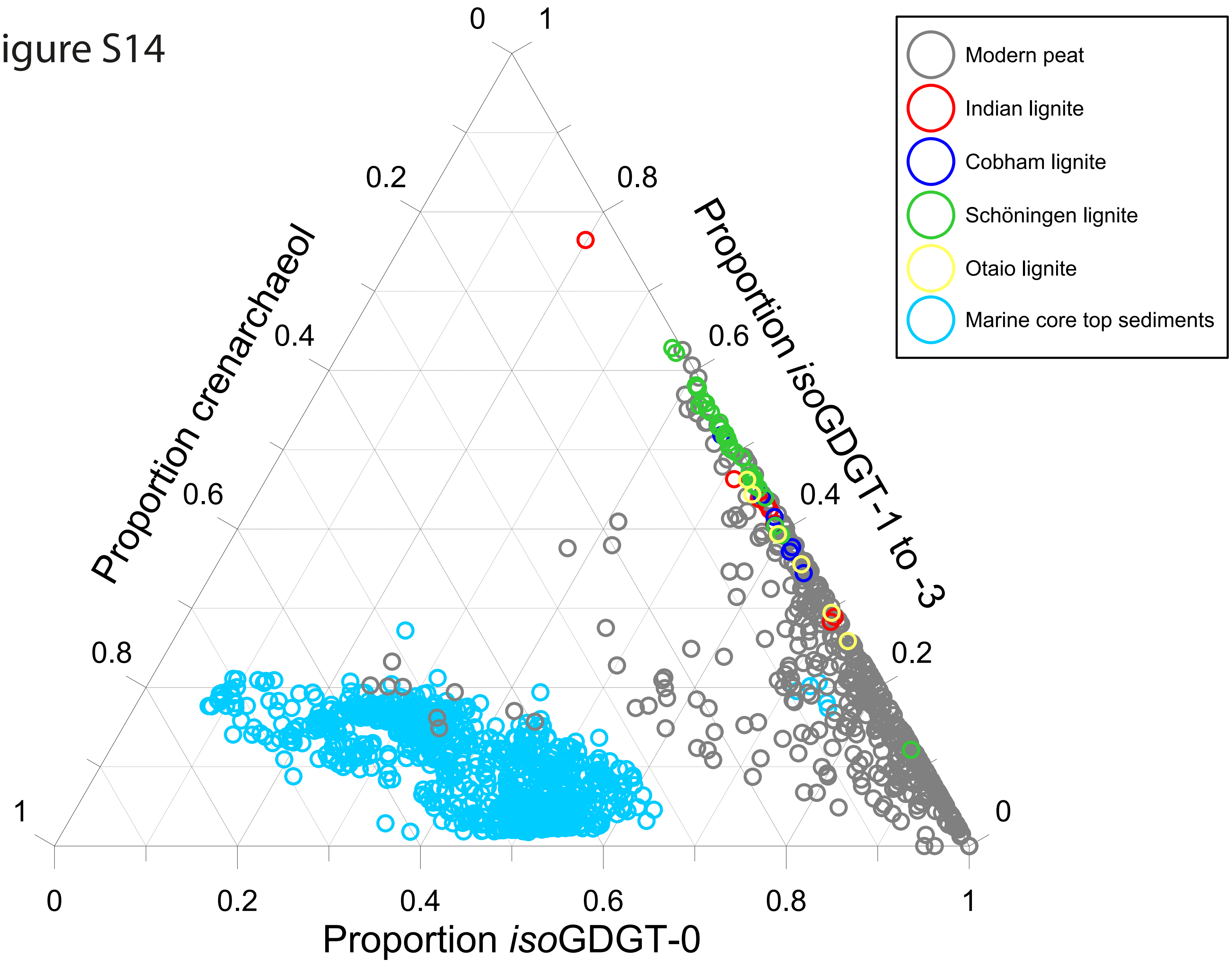

0
1
0.2
0.8
0.4
0.6
0.6
0.4
0.8
0.2
1
0
0
0.2
0.4
0.6
0.8
1
Proportion crenarchaeol
Proportion *iso*GDGT-1 to -3
Proportion *iso*GDGT-0
Modern peat
Indian lignite
Cobham lignite
Schöningen lignite
Otaio lignite
Marine core top sediments

Figure S15

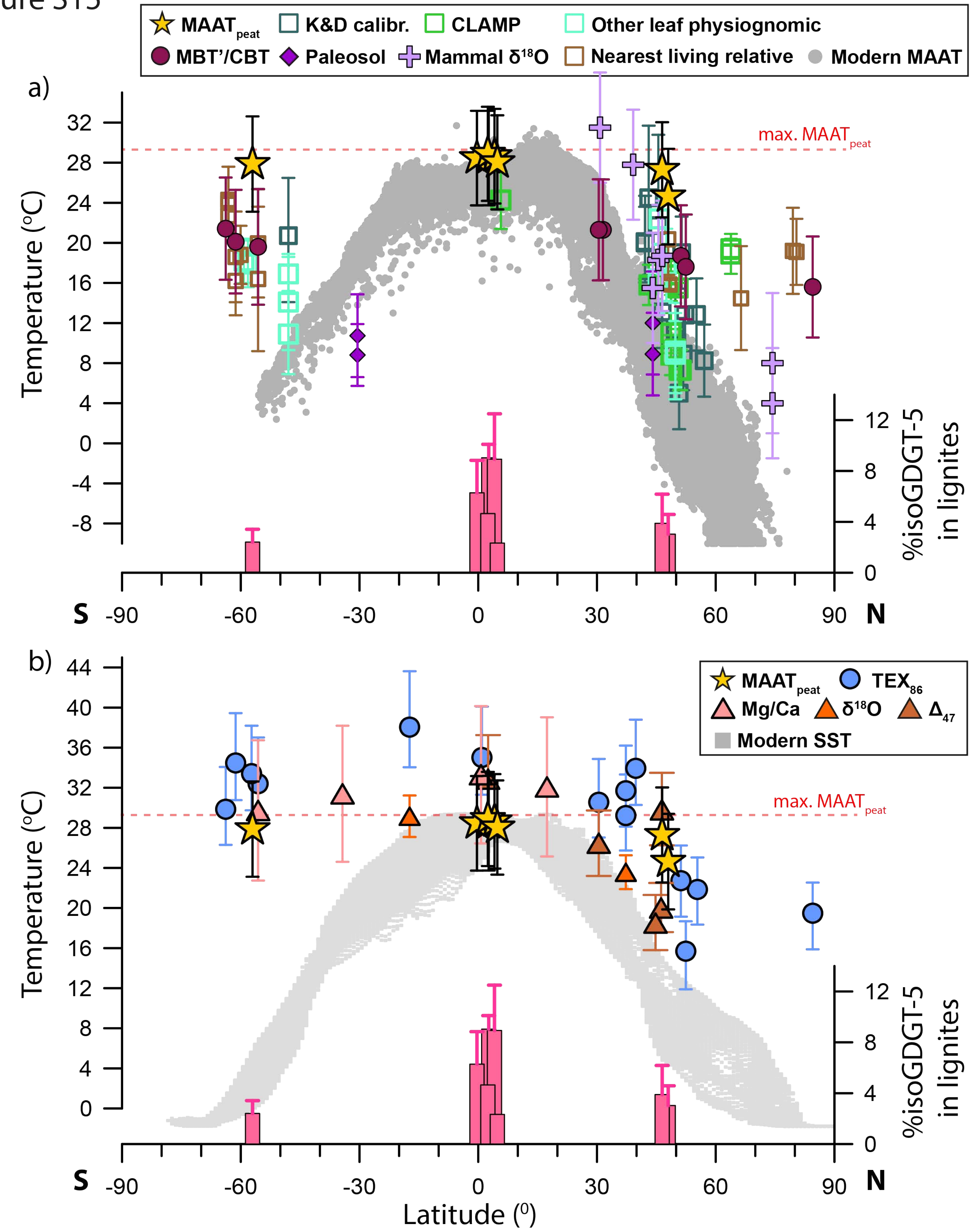

MAAT$_{peat}$
K&D calibr.
CLAMP
Other leaf physiognomic
MBT'/CBT
Paleosol
Mammal δ^{18}O
Nearest living relative
Modern MAAT
a)
max. MAAT$_{peat}$
Temperature (°C)
32
28
24
20
16
12
8
4
0
-4
-8
12
8
4
0
%isoGDGT-5 in lignites
S
-90
-60
-30
0
30
60
90
N
b)
MAAT$_{peat}$
TEX$_{86}$
Mg/Ca
δ^{18}O
Δ$_{47}$
Modern SST
max. MAAT$_{peat}$
44
40
36
32
28
24
20
16
12
8
4
0
Temperature (°C)
12
8
4
0
%isoGDGT-5 in lignites
S
-90
-60
-30
0
30
60
90
N
Latitude (°)

Figure S16

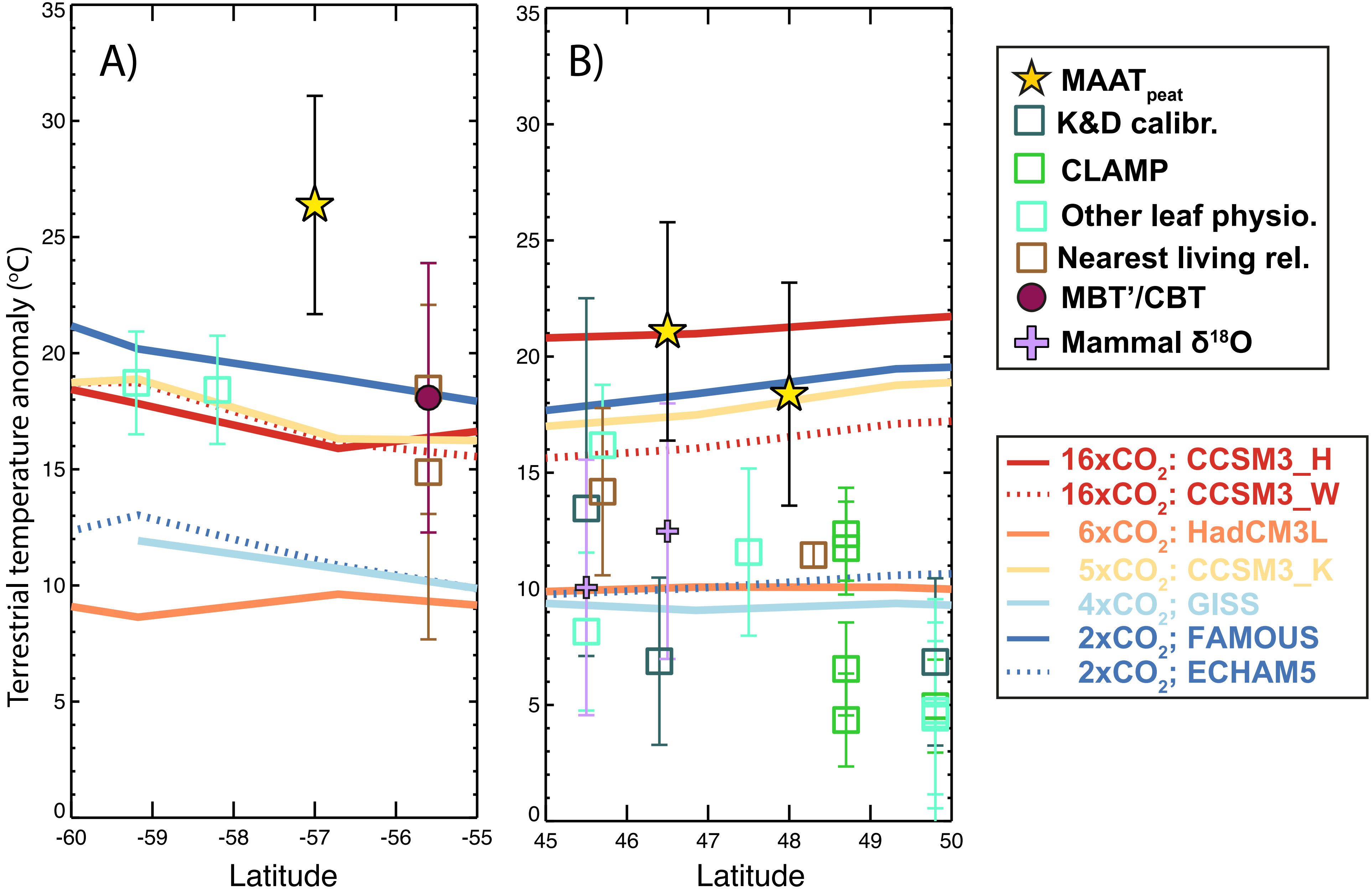
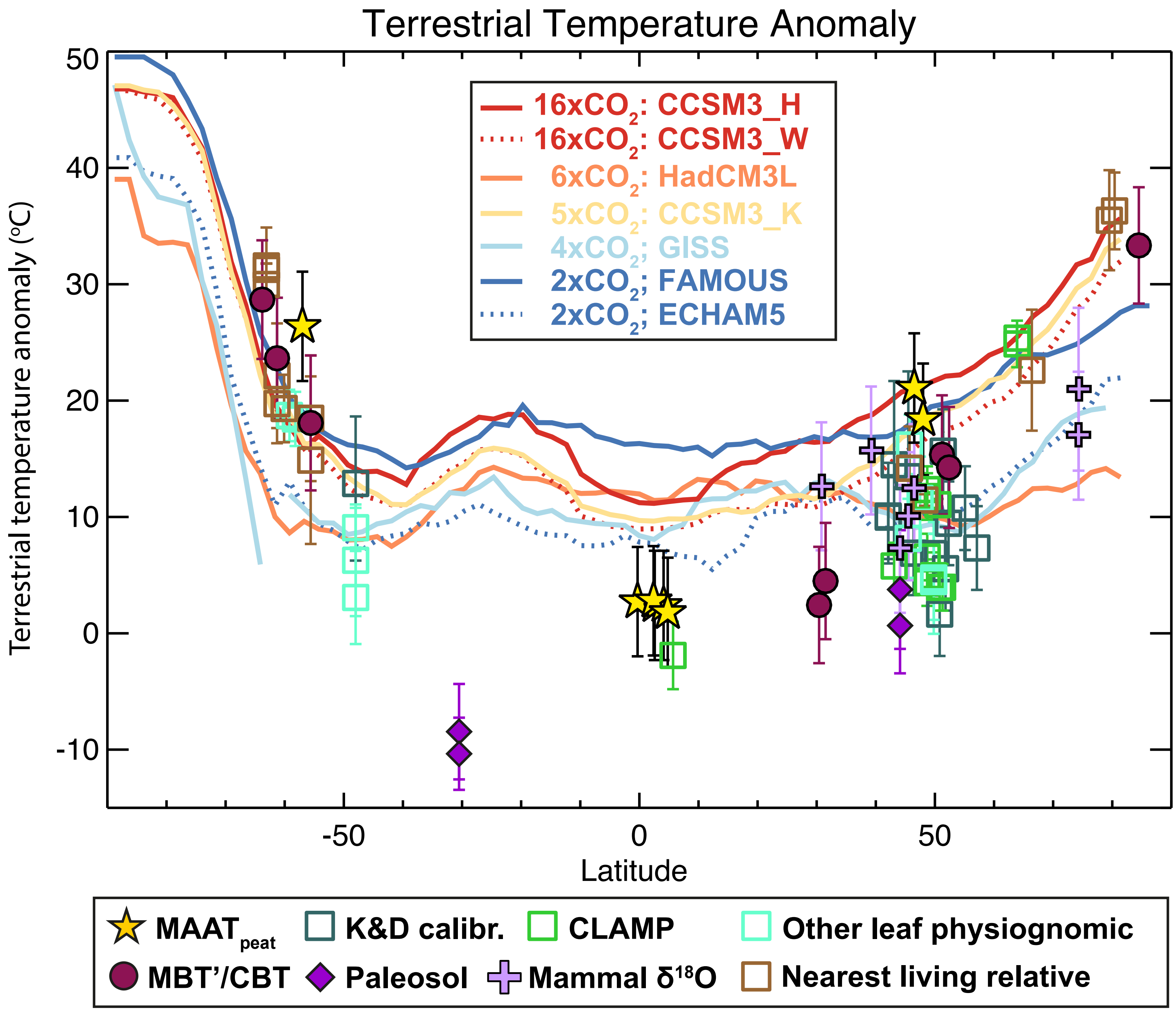

A)
B)
Terrestrial temperature anomaly (°C)
0
5
10
15
20
25
30
35
-60
-59
-58
-57
-56
-55
45
46
47
48
49
50
Latitude
Latitude
MAAT$_{peat}$
K&D calibr.
CLAMP
Other leaf physio.
Nearest living rel.
MBT'/CBT
Mammal $\delta^{18}O$
16xCO_2: CCSM3_H
16xCO_2: CCSM3_W
6xCO_2: HadCM3L
5xCO_2: CCSM3_K
4xCO_2; GISS
2xCO_2; FAMOUS
2xCO_2; ECHAM5

Figure S17


Terrestrial Temperature Anomaly
16xCO$_2$: CCSM3_H
16xCO$_2$: CCSM3_W
6xCO$_2$: HadCM3L
5xCO$_2$: CCSM3_K
4xCO$_2$; GISS
2xCO$_2$; FAMOUS
2xCO$_2$; ECHAM5
Terrestrial temperature anomaly (°C)
50
40
30
20
10
0
-10
-50
0
50
Latitude
MAAT$_{peat}$
K&D calibr.
CLAMP
Other leaf physiognomic
MBT'/CBT
Paleosol
Mammal δ^{18}O
Nearest living relative