Bayesian multi-proxy reconstruction of the early Eocene latitudinal temperature gradient

Kilian Eichenseer[[1]](#footnote-20) and Lewis A. Jones[[2]](#footnote-21)

# Abstract

Geochemical data such as oxygen isotopes (d18O), tetraether indices (TEX86) and magnesium calcium ratios (Mg/Ca) are routinely used to reconstruct ocean temperatures in deep time. However, limited spatial coverage and disagreements between geochemical proxies compromise the accuracy of these reconstructions. Geological data such as coral reefs, mangroves, and evaporites have the potential to supplement geochemical data by improving spatial coverage and constraining temperature estimates. Historically, these data have been used to qualitatively inform upon palaeoclimatic conditions at broad spatial scales, yet no transfer functions exist to convert geological data into temperature estimates. Quantitative temperature reconstructions have therefore not made use of these data. Here, we present a Bayesian hierarchical model to integrate geological data–with established temperature proxies–into a unified quantitative framework. We apply this approach to the early Eocene climatic optimum (EECO), the interval with the warmest sustained temperatures of the Cenozoic. Assuming the conservation of thermal tolerances of modern coral reefs and mangrove taxa, we establish broad sea surface temperature ranges for EECO coral reef and mangrove sites. We integrate these temperature estimates with the EECO geochemical shallow marine proxy record to model the latitudinal temperature gradient and its uncertainty. Our results confirm the presence of a flattened latitudinal temperature gradient and unusually high polar temperatures during the EECO. We show that the inclusion of ecological data can substantially reduce the uncertainty on temperature estimates in climate zones lacking geochemical data.

# Introduction

The geological record holds evidence for episodes in Earth history with fundamentally different climates than our current (Scotese *et al.* 2021). Some episodes, for example the early Eocene, are thought to have been significantly warmer than the modern (Pross *et al.* 2012), potentially representing an analogue for extreme climate warming scenarios (Burke *et al.* 2018). Reconstructions of palaeoclimate commonly use 1) geochemical proxy data, 2) ecological or lithological climate indicators, or 3) earth system modelling.

Geochemical proxies such as oxygen isotopes (d18O), tetraether indices (TEX86) and magnesium calcium ratios (Mg/Ca) are used to derive palaeotemperature estimates for individual locations using experimentally derived transfer functions (e.g. Liu *et al.* 2009). To generate regional or global average estimates, the mean of multiple local estimates is taken (e.g. Veizer & Prokoph 2015). This approach has the advantage of being transparent and easy to reproduce, modify or expand with new data, but is prone to sampling bias (Jones & Eichenseer 2022). Ecological and lithological climate data provide an alternative method of reconstructing palaeotemperatures, using e.g. leaf physiognomy and floral assemblages to derive palaeotemperature proxies (Greenwood *et al.* 2003), or using lithological indicators to determine the range of palaeoclimatic belts (Scotese *et al.* 2021). Despite some recent advances (Chandra *et al.* 2021), ecological and lithological climate indicators are still rarely used in quantitative palaeoclimate reconstructions, particularly for the marine realm. Earth system models take a fundamentally different approach by modelling the climate-generating processes directly, reconstructing spatially resolved climate estimates for the entire globe [@???]. However, this approach still relies on proxy data to constrain the large number of possible model setups and ground truth the model output [@???] It also requires substantial computing resources and technical expert knowledge, and is thus difficult to implement or modify for most palaeoclimate researchers.

Spatially resolved climate reconstructions provide an alternative that can be employed more readily by a broad range of workers. Examples of this approach include the visualisation of proxy compilations along a latitudinal gradient Vickers *et al.* (2021). Interpolation is sometimes used to bridge spatial gaps in palaeoclimate data (Taylor *et al.* 2004), taking advantage of the autoregressive nature of climatic data: much of the information on the climate of any given location is contained in the climate data of nearby locations (Reynolds & Smith 1994). Adding to this, some proxy-based reconstructions use statistical modelling to infer climatic patterns. For example, polynomial regression has been used to reconstruct latitudinal temperature gradients (Bijl *et al.* 2009), and 2D-reconstructions of surface temperatures have been created with Gaussian process regression (Inglis *et al.* 2020).

Here, we present a Bayesian, hierarchical model for inferring sea surface temperatures (SST) that expands upon existing, spatial reconstructions of palaeoclimate by allowing for the integration of 1) prior information based on physical principles and the observed, modern SST distribution, and of 2) geochemical and ecological climate proxies in a common, quantitative framework. We apply this approach to the early Eocene climatic optimum (EECO), the interval with the warmest sustained temperatures of the Cenozoic. Assuming the conservation of thermal tolerances of modern coral reefs and mangrove taxa, we establish broad temperature ranges for EECO coral reef and mangrove sites. We integrate these temperature estimates with the EECO geochemical, shallow marine proxy record to model the latitudinal SST gradient and its uncertainty.

# Materials & Methods

## Geochemical data

Geochemical climate proxy data were extracted from a latest Paleocene and early Eocene compilation (**hollis2019?**). This compilation provides four different geochemical proxies for reconstructing seawater temperature: *47*, Mg/Ca and TEX\_86\_. For our analyses, this dataset was restricted to the EECO and samples from the continental shelf. Recrystallised $18O samples were also excluded as secondary diagenetic calcite precipitated after deposition can bias isotope measurements and offset temperature values (**schrag1999?**). This resulted in most $18O samples being excluded from the dataset (x out of x). After data filtering, x geochemical proxy samples remained. For a detailed description of each proxy see (**hollis2019?**).

## Ecological data

**Coral reefs.** Today, shallow warm-water coral reefs are limited to tropical and subtropical latitudes (~34°N–32 degS), with minimum sea surface temperature (~18 degC) tolerances being the primary constraint on this distribution (Johannes *et al.* 1983; Kleypas *et al.* 1999; Yamano *et al.* 2001). As coral reefs reside at the upper thermal limit of the oceans today, their maximum sea surface temperature tolerance is less well-constrained with some studies suggesting up to 35.6 degC in the geological past (Jones *et al.* 2022). Nevertheless, the distribution of coral reefs have frequently been recognised as tracers of past (sub-)tropical conditions (Ziegler *et al.* 1984; Kiessling 2001). During the Eocene, coral communities and reefs expanded across tropical and temperate latitudes, with some communities found up to palaeolatitudes of 43 degC N (Zamagni *et al.* 2012). Using a compilation of Paleocene–early Eocene coral reefs and community localities (Zamagni *et al.* 2012), we generate quantitative sea surface temperature estimates for the ECCO. To do so, we extract localities inferred to be Ilerdian (early Eocene) coral reefs from the compilation, and that can be confidently assigned to the EECO. We exclude coral knobs and coral-bearing mounds which might have broader climatic limits than coral reef ecosystems. This filtering resulted in four unique coral reef localities remaining for the EECO, all of which conform to the modern latitudinal range of coral reefs (<34 deg N). Subsequently, we use statistically derived temperature limits (minimum = 21 degC, average = 27.6 degC, maximum = 29.5 degC) from the published literature (Kleypas *et al.* 1999) to define a normal probability distribution of potential temperature values for coral reef localities. This normal probability distribution was defined with a mean of 27.6 and a standard deviation of 2.125, placing 97.5% of the probability density above the minimum. As the distribution of modern corals is skewed towards warmer temperatures, this approach results in 16.5% of the probability being placed on temperatures > 29.5 degC, allowing for the possibility that Eocene coral reefs were adapted to warmer conditions than modern-day coral reefs.

**Mangroves.** Mangroves are distributed throughout the tropics and subtropics today. While factors beside SST influence the distribution of mangroves, empirical, lower temperature limits have been established for the genera *Avicennia* (15.6 degC) and *Rhizophora* (20.7 degC) (Quisthoudt *et al.* 2012). Both *Avicennia* and members of the Rhizophoraceae family were widespread in the early Eocene, but only *Avicennia* occurred at polar latitudes (Suan *et al.* 2017; Popescu *et al.* 2021). Assuming that Eocene members of these mangrove taxa conform to the same climatic requirements as their modern relatives, the presence and absence of *Avicennia* and Rhizophoraceae pollen can be used as a palaeotemperature indicator. For this analysis, published mangrove occurrence data were taken from Popescu *et al.* (2021), and converted to quantitative temperature estimates. From this data, we identify two types of pollen assemblages which we ascribe different temperature distributions:

1. *Avicennia*-only assemblages (): the absence of Rhizophoraceae is indicative of temperatures being between 15.6 degC (lower temperature limt of *Avicennia*) and 20.7 (lower temperature limit of *Rhizophora*). However, a value of 22.5 degC is ascribed as the upper temperature limit here as *Rhizophora* is rare below this temperature. We define the *Avicennia*-only temperature distribution as a normal distribution with a mean of 19.05 degC and a standard deviation of 1.725, resulting in 95% of the probability density being placed within the temperature limits.
2. *Avicennia* and Rhizophoraceae assemblages (): the presence of both groups suggests that the locality should have a minimum temperature of 20.7 degC (lower temperature limit of *Rhizophora*). As the upper thermal limits of *Aviciennia* and *Rhizophora* are not well established in Quisthoudt *et al.* (2012), we assign the same maximum temperature limits (29.5 degC) as coral reef localities as mangroves are also widely distributed throughout tropical regions. Consequently, we define the temperature distribution for this locality as a normal distribution with a mean of 25.1 and a standard deviation of 2.2, with 95% probability density within the temperature limits.

[Fig 1: Map and distribution of proxy data and ecological data]

## Palaeogeographic reconstruction

The palaeogeographic distribution of geochemical and ecological data was reconstructed using the Merdith *et al.* (2021) plate rotation model via the palaeoverse R package ver. XXX (REF). The midpoint age of the EECO (51.2 Ma), along with the present-day coordinates of geochemical and ecological data, were used for palaeorotation.

## Bayesian framework

**Model structure (Fig 2).** We model the mean temperature () at location as a function of absolute latitude () with a logistic regression (growth curve or Richard's curve) of the form:

where and denote the lower and upper asymptote, respectively, specifies the latitude of maximal growth, the most quickly with latitude, denotes the growth rate (Fig. 2), denotes the residual standard deviation, and denotes the number of locations.

We infer from individual temperature observations , derived from geochemical data, at location as

where is the number of observations at each location, and is the estimated standard deviation of the temperatures at location .

Similarly, is inferred for locations with ecological proxies from the associated normal temperature distributions with a given mean and standard deviation, and , as

This structure implies that is not fixed at the mean proxy temperature at location , , but is drawn towards the overall logistic regression curve, i.e. towards . The pull towards tends to be high when is low, when the observations are scattered, i.e.  is high, and/or when the overall standard deviation is low. In practice, this has the desirable consequence that locations with few observations and large temperature differences between observations have less influence on the overall regression than well-sampled locations with consistent temperature observations.

**Priors (Fig2x).** In the Bayesian framework, priors need to be placed on the unknown parameters of a model. We placed weakly informative, conjugate inverse-gamma priors on and :

We set , allowing these priors to be quickly overwhelmed by the data as and increase, as we have little *a priori* knowledge of these parameters.

In contrast, we put informative priors on the regression coefficients , , and , based on physical principles, and vaguely based on the modern climate system:

**A.** Predicted seawater surface temperatures are not allowed to be , the freezing point of sea water. The highest prior density of is placed around , and it slowly tapers off towards higher temperatures. This shape is achieved by placing a skew-normal prior on the lower asymptote, specified as

where , , and are the location, scale and shape parameters.

**K.** Input of solar energy decreases from the tropics to the poles. Hence, the latitudinal temperature gradient is broadly negative, i.e. temperature decreases with absolute latitude. This is achieved by setting . The prior on the upper asymptote is a truncated normal distribution with the mean set to of the modern SST gradient, with a broad standard deviation:

The distribution is truncated to the left at , but not truncated to the right ().

**M.** The steepness of the gradient is presumed to be highest in mid-latitudes; this is expressed with a normal prior on with the mean set to of the modern SST gradient:

**B.** The steepness or growth rate of the gradient is constrained to be and to not be exceedingly high, as oceanic and atmospheric heat transfer is bound to prevent very abrupt SST changes across latitudes. A gamma-distributed prior of the form

was placed on . The shape and rate parameters and were chosen such that the highest prior density is at of the modern SST gradient, .

[Fig. 2: Model structure and visualisation of parameters and priors]

## Model validation

[Fig. 3]

To test whether our logistic regression model can adequately describe latitudinal temperature gradients, we applied a simplified version of the model to modern sea surface temperatures from Bio-Oracle [@…]. As these modern, annual sea surface temperatures estimates are associated with little uncertainty, there is no need for a hierarchical model structure, and we substituted temperature () for in eq. ? and ?. To verify that the modern gradient can be approximated with limited sampling, we resampled modern sea surface temperatures at modern latitudes corresponding the palaeolatitudes of the Eocene samples. This process was repeated 100 times, randomly chosing a longitude for each latitude in each repetition. The parameters of the non-hierarchical temperature model were estimated for each of the 100 samples, and the iterations after burn-in from the posterior of the parameters were pooled to generate the resulting median temperature gradient with 95 % credible intervals ( to percentile).

## Parameter estimation

We estimated the posterior distributions of the model parameters using a Markov chain Monte Carlo (MCMC) algorithm, written in R. Specifically, we sampled the unknown parameters , , and with Metropolis-Hastings, and used Gibbs sampling to estimate all other unknown parameters. Posterior inference on the modern gradient is based on four chains with 60,000 iterations each, 10,000 of which were discarded as burn-in, and keeping every 10th iteration, resulting in a total of 20,000 iterations. The modern temperature gradient with the Eocene sampling distribution was estimated in one chain with 25,000 iterations for each of the 100 temperature samples. 5,000 iterations each were discarded as burn-in, and every 10th iteration was kept, resulting in a total of 200,000 iterations across all 100 model runs. For the Eocene model, we ran four chains with 600,000 iterations each, discarding 100,000 as burn-in and keeping every 100th iteration, as the hierarchical model structure results in higher autocorrelation of the chains. The Eocene posterior inference is thus based on a total of 20,000 iterations with low autocorrelation (effective multivariate sample size for , , and is > 18,000).

## Processing of model results

Modelled sea surface temperature estimates were generated with eq. ?, calculating the sea surface temperatures at any latitude with the parameter estimates of each iteration from the posterior. The median, and percentile of temperatures where then taken from all temperature estimates obtained at the latitude of interest.

Differences between Eocene and modern temperatures at a certain latitude were calculated by randomly pairing all iterations of the posterior from the Eocene and modern temperature gradient model, calculating the Eocene and modern temperature using the respective iterations, taking the difference, and then calculating the median (, percentile) from all pairs of iterations.

Global average temperatures were calculated by taking the weighted mean of the median (, percentile) temperature estimates in 1 degree latitudinal bins. The weights were set to the proportion of global surface area in each latitudinal bin, i.e. decreasing with increasing latitude as:

where is the upper, and is the lower latitudinal boundary of bin .

# Results

## Model validation

[Fig 3 - Modern gradient] The average modern temperature gradient can be closely approximated with our model when using the full modern SST dataset (Fig. 3a). Degrading the amount and distribution of data points to match the early Eocene sampling distribution () still results in a close match of the modelled gradient with the empirical gradient (Fig 3b). A noticable, but minor offset is apparent in high latitudes, where sampling is most incomplete (Fig 3b).

## EECO reconstruction

The modelled Eocene temperature gradient is starkly different from the modern (Fig 4). Modelled, median equatorial temperatures are 4.2 (95% CI: 0.2 - 8.3) degC higher for the Eocene, and polar temperatures are higher by 25.0 (95% CI: 17.0 - 29.1) degC. This results in a strongly flattened latitudinal temperature gradient of 9.0 (95% CI: 2.5 - 17.8) degC for the Eocene, as opposed to 29.6 degC for the modern.

The high variability of early Eocene palaeotemperature proxies, particularly in the mid-latitudes, and the scarcity of high-latitude data, results in substantial uncertainties in the modeled temperature gradient. This is reflected in the residual standard deviation () of the early Eocene gradient, 4.9 (95% CI: 3.8 - 6.5) degC, more than twice as high than of the modern gradient, resampled at early Eocene latitudes, 2.2 (95% CI: 1.6 - 3.1) degC. The inclusion of ecological proxy data only slightly reduces the overall model standard deviation, but helps constrain polar temperature estimates (Supplementary materials).

The global Eocene mean sea surface temperature is estimated at 28.8 (95% CI: 25.7 - 31.7) degC, significantly higher than the modern (17.6 degC).

## Fig 4 - compare Eocene gradient with modern gradient, also with previous reconstructions / ES models?

* x1 Draw samples from the posterior gradient to get a latitudinal gradient of deg C / deg lat with uncertainty (intercept gradient at 0 and 90 deg lat)
* x2 generate global average temperature, and tropical, temperate, polar temperatures in a similar way, accounting for area

# Discussion

**Comparison to existing methods.** Latitudinal temperature gradients have been estimated with a variety of parametric and non-parametric statistical techniques. Parametric methods include polynomials (Greenwood & Wing 1995; Bijl *et al.* 2009) and a cosine function (Inglis *et al.* 2020). Whilst some of those functions are flexible enough to model a range of empirical temperature gradients, the logistic function used herein has the added advantage of an easily understandable relationship between each of the model parameters and the shape of the latitudinal gradient (Fig. 2). Non-parametric models can very flexibly follow the shape of an unknown temperature gradient Zhang *et al.* (2019), but have the disadvantage of having no model parameters that can be compared between data sets. Parametric methods should therefore be preferred to non-parametric temperature gradient models, as long as very broad prior information on the shape of the gradients exists. The ease with which such prior information can be integrated is perhaps the major advantage of our method: The Bayesian framework allows to specify arbitrary priors on the four parameters that control the upper and lower temperature limits, the steepness of the gradient, and the latitudinal position of the steepest point in the gradient (see Methods). A further improvement to existing methods is that the hierarchical structure of our model explicitly accounts for variation of temperature estimates at individual localities, and for uncertainty associated with the ecological temperature proxies. An extension of the model additionally accounts for measurement uncertainty of the geochemical proxies (Supplementary Materials).

**Comparison to Eocene proxy and modelling studies**.

A major theme of the discussions on the early Eocene greenhouse climate has been the discrepancy between proxy records, particularly ecological climate indicators such as macrofloral assemblage data, have

* x1 compare lat gradient to literature estimates, e.g. Zhang2019
* compare lat gradient to climate models and the “early EECO problem”
* discuss insufficiency of proxies (high variability, …)
* discuss utility of the model and future applications

# Conclusions

# Acknowledgements

# Author contributions

# Data accessibility

# References

BIJL, P. K., SCHOUTEN, S., SLUIJS, A., REICHART, G.-J., ZACHOS, J. C. and BRINKHUIS, H. 2009. [Early Palaeogene temperature evolution of the southwest Pacific Ocean](https://doi.org/10.1038/nature08399). *Nature*, **461**, 776–779.

BURKE, K. D., WILLIAMS, J. W., CHANDLER, M. A., HAYWOOD, A. M., LUNT, D. J. and OTTO-BLIESNER, B. L. 2018. [Pliocene and Eocene provide best analogs for near-future climates](https://doi.org/10.1073/pnas.1809600115). *Proceedings of the National Academy of Sciences*, **115**, 13288–13293.

CHANDRA, R., CRIPPS, S., BUTTERWORTH, N. and MULLER, R. D. 2021. [Precipitation reconstruction from climate-sensitive lithologies using Bayesian machine learning](https://doi.org/10.1016/j.envsoft.2021.105002). *Environmental Modelling & Software*, **139**, 105002.

GREENWOOD, D. R. and WING, S. L. 1995. [Eocene continental climates and latitudinal temperature gradients](https://doi.org/10.1130/0091-7613(1995)023<1044:ECCALT>2.3.CO;2). *Geology*, **23**, 1044.

———, MOSS, P. T., ROWETT, A. I., VADALA, A. J. and KEEFE, R. L. 2003. [Plant communities and climate change in southeastern Australia during the early Paleogene](https://doi.org/10.1130/0-8137-2369-8.365). *In* *Causes and Consequences of Globally Warm Climates in the Early Paleogene*, Geological Society of America.

HOLLIS, C. J., DUNKLEY JONES, T., ANAGNOSTOU, E., BIJL, P. K., CRAMWINCKEL, M. J., CUI, Y., DICKENS, G. R., EDGAR, K. M., ELEY, Y., EVANS, D. and OTHERS. 2019. The DeepMIP contribution to PMIP4: Methodologies for selection, compilation and analysis of latest paleocene and early eocene climate proxy data, incorporating version 0.1 of the DeepMIP database. *Geoscientific Model Development*, **12**, 3149–3206.

INGLIS, G. N., BRAGG, F., BURLS, N. J., CRAMWINCKEL, M. J., EVANS, D., FOSTER, G. L., HUBER, M., LUNT, D. J., SILER, N., STEINIG, S., TIERNEY, J. E., WILKINSON, R., ANAGNOSTOU, E., DE BOER, A. M., DUNKLEY JONES, T., EDGAR, K. M., HOLLIS, C. J., HUTCHINSON, D. K. and PANCOST, R. D. 2020. [Global mean surface temperature and climate sensitivity of the early Eocene Climatic Optimum (EECO), Paleocene (PETM), and latest Paleocene](https://doi.org/10.5194/cp-16-1953-2020). *Climate of the Past*, **16**, 1953–1968.

JOHANNES, R., WIEBE, W., CROSSLAND, C., RIMMER, D. and SMITH, S. 1983. Latitudinal limits of coral reef growth. *Marine ecology progress series. Oldendorf*, **11**, 105–111.

JONES, L. A. and EICHENSEER, K. 2022. [Uneven spatial sampling distorts reconstructions of Phanerozoic seawater temperature](https://doi.org/10.1130/G49132.1). *Geology*, **50**, 238–242.

JONES, L. A., MANNION, P. D., FARNSWORTH, A., BRAGG, F. and LUNT, D. J. 2022. Climatic and tectonic drivers shaped the tropical distribution of coral reefs. *Nature communications*, **13**, 1–10.

KIESSLING, W. 2001. Paleoclimatic significance of phanerozoic reefs. *Geology*, **29**, 751–754.

KLEYPAS, J. A., MCMANUS, J. W. and MEÑEZ, L. A. 1999. Environmental limits to coral reef development: Where do we draw the line? *American zoologist*, **39**, 146–159.

LIU, Z., PAGANI, M., ZINNIKER, D., DECONTO, R., HUBER, M., BRINKHUIS, H., SHAH, S. R., LECKIE, R. M. and PEARSON, A. 2009. [Global Cooling During the Eocene-Oligocene Climate Transition](https://doi.org/10.1126/science.1166368). *Science*, **323**, 1187–1190.

MERDITH, A. S., WILLIAMS, S. E., COLLINS, A. S., TETLEY, M. G., MULDER, J. A., BLADES, M. L., YOUNG, A., ARMISTEAD, S. E., CANNON, J., ZAHIROVIC, S. and OTHERS. 2021. Extending full-plate tectonic models into deep time: Linking the neoproterozoic and the phanerozoic. *Earth-Science Reviews*, **214**, 103477.

POPESCU, S.-M., SUC, J.-P., FAUQUETTE, S., BESSEDIK, M., JIMÉNEZ-MORENO, G., ROBIN, C. and LABROUSSE, L. 2021. [Mangrove distribution and diversity during three Cenozoic thermal maxima in the Northern Hemisphere (pollen records from the Arctic regions)](https://doi.org/10.1111/jbi.14238). *Journal of Biogeography*, **48**, 2771–2784.

PROSS, J., CONTRERAS, L., BIJL, P. K., GREENWOOD, D. R., BOHATY, S. M., SCHOUTEN, S., BENDLE, J. A., RÖHL, U., TAUXE, L., RAINE, J. I., HUCK, C. E., VAN DE FLIERDT, T., JAMIESON, S. S. R., STICKLEY, C. E., VAN DE SCHOOTBRUGGE, B., ESCUTIA, C. and BRINKHUIS, H. 2012. [Persistent near-tropical warmth on the Antarctic continent during the early Eocene epoch](https://doi.org/10.1038/nature11300). *Nature*, **488**, 73–77.

QUISTHOUDT, K., SCHMITZ, N., RANDIN, C. F., DAHDOUH-GUEBAS, F., ROBERT, E. M. R. and KOEDAM, N. 2012. [Temperature variation among mangrove latitudinal range limits worldwide](https://doi.org/10.1007/s00468-012-0760-1). *Trees*, **26**, 1919–1931.

REYNOLDS, R. W. and SMITH, T. M. 1994. Improved global sea surface temperature analyses using optimum interpolation. *Journal of climate*, **7**, 929–948.

SCOTESE, C. R., SONG, H., MILLS, B. J. W. and VAN DER MEER, D. G. 2021. [Phanerozoic paleotemperatures: The earth’s changing climate during the last 540 million years](https://doi.org/10.1016/j.earscirev.2021.103503). *Earth-Science Reviews*, **215**, 103503.

SUAN, G., POPESCU, S.-M., SUC, J.-P., SCHNYDER, J., FAUQUETTE, S., BAUDIN, F., YOON, D., PIEPJOHN, K., SOBOLEV, N. N. and LABROUSSE, L. 2017. [Subtropical climate conditions and mangrove growth in Arctic Siberia during the early Eocene](https://doi.org/10.1130/G38547.1). *Geology*, **45**, 539–542.

TAYLOR, S. P., HAYWOOD, A. M., VALDES, P. J. and SELLWOOD, B. W. 2004. [An evaluation of two spatial interpolation techniques in global sea-surface temperature reconstructions: Last Glacial Maximum and Pliocene case studies](https://doi.org/10.1016/j.quascirev.2003.12.003). *Quaternary Science Reviews*, **23**, 1041–1051.

VEIZER, J. and PROKOPH, A. 2015. [Temperatures and oxygen isotopic composition of Phanerozoic oceans](https://doi.org/10.1016/j.earscirev.2015.03.008). *Earth-Science Reviews*, **146**, 92–104.

VICKERS, M. L., BERNASCONI, S. M., ULLMANN, C. V., LODE, S., LOOSER, N., MORALES, L. G., PRICE, G. D., WILBY, P. R., HOUGÅRD, I. W., HESSELBO, S. P. and OTHERS. 2021. Marine temperatures underestimated for past greenhouse climate. *Scientific reports*, **11**, 1–9.

YAMANO, H., HORI, K., YAMAUCHI, M., YAMAGAWA, O. and OHMURA, A. 2001. Highest-latitude coral reef at iki island, japan. *Coral Reefs*, **20**, 9–12.

ZAMAGNI, J., MUTTI, M. and KOŠIR, A. 2012. The evolution of mid paleocene-early eocene coral communities: How to survive during rapid global warming. *Palaeogeography, palaeoclimatology, palaeoecology*, **317**, 48–65.

ZHANG, L., HAY, W. W., WANG, C. and GU, X. 2019. [The evolution of latitudinal temperature gradients from the latest Cretaceous through the Present](https://doi.org/10.1016/j.earscirev.2019.01.025). *Earth-Science Reviews*, **189**, 147–158.

ZIEGLER, A., HULVER, M., LOTTES, A. and SCHMACHTENBERG, W. 1984. Uniformitarianism and palaeoclimates: Inferences from the distribution of carbonate rocks. *Geological journal. Special issue*, 3–25.

1. Department of Earth Sciences, Durham University, South Road, DH1 3LE, Durham, United Kingdom [↑](#footnote-ref-20)
2. Centro de Investigación Mariña, Grupo de Ecoloxía Animal, Universidade de Vigo, 36310 Vigo, Spain [↑](#footnote-ref-21)