Bayesian multi-proxy reconstruction of latitudinal temperature gradients applied to the Early Eocene

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# Abstract

Accurately reconstructing large-scale palaeoclimate patterns from sparse local records is critical for understanding the evolution of Earth’s climate. Challenges arise particularly from the patchiness and uneven sampling of palaeoclimate data, and from the disparate nature of the proxy data. Geochemical data usually provide temperature estimates via transfer functions informed by experiments, and transfer functions based on the climatic requirements of modern taxa exist for some fossil plant assemblages. In contrast, most ecological and lithological data, e.g. coral reefs and evaporites, only convey information on broad climatic requirements. Historically, most large-scale proxy-based reconstructions have been based on either geochemical or ecological data, but few approaches exist for combining multiple proxy types into a single, quantitative reconstruction. Large spatial gaps in existing proxy records have often been bridged by simple averaging, without taking into consideration the spatial distribution of the samples, leading to biased temperature reconstructions. Here, we present a Bayesian hierarchical model to integrate ecological data with established geochemical proxies into a unified quantitative framework, bridging gaps in the latitudinal coverage of proxy data. 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 sea surface temperature gradient and global average temperatures. Our results confirm the presence of a flattened latitudinal temperature gradient and unusually high polar temperatures during the EECO, which is supported by high-latitude ecological data. We show that the inclusion of ecological data and adequate prior information can substantially reduce uncertainty in palaeoclimate reconstructions, and allow for unbiased temperature estimates from sparse data.

# Introduction

The increasing availability of large compilations and databases of deep-time climate data now offers the opportunity for empirical palaeoclimate reconstructions of unprecedented scope (e.g. Veizer & Prokoph 2015; Hollis *et al.* 2019; Scotese *et al.* 2021; Grossman & Joachimski 2022; Judd *et al.* 2022). To exploit the full potential these data sets offer, two fundamental challenges need to be overcome: Disparate types of proxy data need to be integrated to inform a single climate reconstruction, and large-scale scale climate patterns need to be inferred from localised, often sparse observations. To address these challenges, we present a novel Bayesian model that combines quantitative proxies and palaeoecological constraints into a fully quantitative model of the latitudinal gradient of sea surface temperatures, bridging spatial gaps in sparsely sampled climate data.

Existing palaeoclimate reconstructions are generally based on one of three approaches (see Burgener *et al.* 2023): 1) Geochemical proxies such as oxygen isotopes (d18O), tetraether indices (TEX86) and magnesium calcium ratios (Mg/Ca) provide quantitative palaeotemperature estimates using transfer functions based on experimental work and field observations (Wuchter *et al.* 2004; e.g. Liu *et al.* 2009). 2) Palaeobiological, ecological and lithological proxy data provide climate constraints, but no experimentally determined transfer functions exist to directly infer quantitative climate parameters from these records (e.g. Wolfe 1995; Kvaček 2007; Cao *et al.* 2019). Instead, palaeoclimate signals are inferred based on the climatic conditions of analogous, modern sediments (Chandra *et al.* 2021), or based on the premise that the climatic requirements of ancient taxa, plant traits or ecological communities were similar to those of their nearest modern relatives (Peppe *et al.* 2011; Royer 2012; Salonen *et al.* 2019). 3) Earth system models offer the most highly resolved and complete climate reconstructions, but ultimately rely on constraints provided by the geological and fossil record (Lunt *et al.* 2021).

Even when using the full range of available records, proxy-based climate reconstructions beyond the Holocene are inevitably patchy (e.g. Hollis *et al.* 2019), and global temperature reconstructions based on those records alone are prone to bias (Jones & Eichenseer 2022). Inferring regional or global-scale patterns from an incomplete record relies on the bridging of spatial gaps. A common approach that requires no additional computation is the spatial visualisation of proxy-derived temperatures against latitude, showing broad latitudinal temperature trends (Hollis *et al.* 2019; 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 (Bijl *et al.* 2009) and cosine functions (Inglis *et al.* 2020) have been used to reconstruct latitudinal temperature gradients, and 2D-reconstructions of surface temperatures have been created with Gaussian process regression (Inglis *et al.* 2020). These approaches work well for interpolating relatively well-sampled data, but the absence of constraints on the modeled parameters means that such models can produce unrealistic temperature estimates when extrapolating from sparsely sampled data. Statistical modelling in the Bayesian framework helps overcome this problem by requiring the explicit specification of priors for the model parameters, which can be used to express physical constraints (Chandra *et al.* 2021).

Here, we present a Bayesian, hierarchical model for inferring the latitudinal gradient of sea surface temperatures (SSTs) that expands upon existing, spatially explicit reconstructions of palaeoclimate by allowing for the integration of 1) prior information based on physical principles and on the observed, modern SST distribution, and of 2) geochemical and ecological climate proxies in a common, quantitative framework. We use a generalised logistic function to infer the shape of the temperature gradient despite a patchy latitudinal coverage, and test the robustness of this method using a down-sampled record of modern SSTs. We apply this model to the record of the early Eocene climatic optimum (EECO), combining a compilation of geochemical proxies (Hollis *et al.* 2019), mangrove communities (Popescu *et al.* 2021), and coral reefs (Zamagni *et al.* 2012), using a nearest-living-relative approach (see e.g. Greenwood *et al.* 2017) to establish broad temperature ranges for the ecological data.

The early Eocene is the focus of a substantial body of palaeoclimate literature (e.g. Berggren *et al.* 1998; Thomas *et al.* 2000; Hyland *et al.* 2017; Lunt *et al.* 2021), as it is the interval with the warmest sustained temperatures of the Cenozoic (Pross *et al.* 2012), and potentially represents an analogue for extreme climate warming scenarios (Burke *et al.* 2018). For palaeoclimate modelers, the early Eocene presents a challenge: Geochemical proxy data (Hollis *et al.* 2019) and ecological data (Markwick 1994; Greenwood & Wing 1995) indicate tropical to subtropical conditions up to high latitudes, but early climate models have not been able to model warm polar temperatures and a shallow latitudinal temperature gradient under realistic conditions (Sloan & Barron 1990). Although more recent climate models have been able to better align their simulations with the proxy record (Huber & Caballero 2011), the nature of the early Eocene temperature gradient remains a matter of debate (Tierney *et al.* 2017). The shape and magnitude of the inferred EECO latitudinal gradient depends on the selection of proxies, on the method for dealing with spatial gaps and uneven sampling, on the inclusion or exclusion of terrestrial, shallow and deep marine data, while differential reporting of the results complicates comparisons of different approaches (Evans *et al.* 2018; Hollis *et al.* 2019; Inglis *et al.* 2020). Our goal is to provide a robust, yet simple method for inferring and comparing temperature gradients that can be readily used with different proxy types and with patchy records. We use this model to quantify the latitudinal SST gradient and the global mean SST of the early Eocene, but the unspecific design of our method means it can be readily applied to other time intervals and proxy records.

# Materials & Methods

## Modern sea surface temperatures

## Geochemical data

Geochemical climate proxy data were extracted from a latest Paleocene and early Eocene compilation (Hollis *et al.* 2019). This compilation provides four different geochemical proxies for reconstructing seawater temperature: , , Mg/Ca and . For our analyses, this dataset was restricted to the EECO and samples from the continental shelf. Recrystallised samples were also excluded as secondary diagenetic calcite precipitated after deposition can bias isotope measurements and offset temperature values (Schrag 1999). 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 (Hollis *et al.* 2019).

## 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

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). Trace plots of the MCMC chains indicate convergence and good mixing of the chains (Supplementary Figure S1).

## 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.

The latitudinal gradient is calculated as the difference between the modeled temperature at the equator (0 deg latitude) and at the poles (90 deg absolute latitude). Given the sigmoidal shape of the modern as well as the Eocene gradient (see Fig. 4), this results in only slightly higher estimates of the gradient than when comparing e.g. the zonal average of equatorial and high-latitude temperatures, as is done in some earlier studies (e.g. Evans *et al.* 2018).

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); almost all of the variation in the empirical median temperatures in bins of 1 deg absolute latitude is explained by the modeled gradient (). Reducing the amount and the spatial coverage of data points to match the early Eocene sampling distribution () still results in a close match of the modeled gradient with the empirical gradient (Fig. 3b). The 95% credible interval (CI) of reconstructed gradients (Fig. 3b) is noticeably narrower than the spread of empirical temperature values (Fig. 3a). The modern, latitudinal gradient, modeled with all data, spans 29.6 degC from the equator to the poles. When modeled with only the early Eocene sampling locations, the median temeprature gradient is 29.3 (95% CI: 27.0 - 31.6) degC. A random sampling of modern temperatures at latitudes corresponding to the sampled Eocene palaeolatitudes would thus allow the reconstruction of the modern latitudinal temperature gradient with good accuracy, with expected deviations from the actual gradient as low as -2.6 to 2.1 degC (95 % CI).

Additional model runs with simulated SST data show that latitudinal gradients following a flat, linear or quadratic function can also be adequately reconstructed by our model (Fig. S4). The generalised logistic function underlying the reconstruction leads to the inferred gradient being pushed towards a sigmoidal shape in the absence of proxies (see very high latitudes in Fig. S4a,c). This is intended, as in the absence of data, the shape of the reconstructed gradient should be broadly similar to the sigmoidal shape of the modern SST gradient, as it is the only empirically observed SST gradient.

Modeling the latitudinal temperature gradient facilitates accurate reconstruction of global mean surface temperatures (GMST). The modern, global mean sea surface temperature (GMsST) estimate is 17.6 degC when using the full, modern data set. When reduced to the early Eocene sampling distribution, the modern GMsST is estimated at 17.8 (16.8 - 18.8) degC. The deviations from the full modern estimate are again very low, with a 95 % credible interval of -0.8 to 1.3 degC.

## EECO reconstruction

The modeled Eocene temperature gradient is starkly different from the modern (Fig 4). Modelled, median equatorial temperatures are 4.2 (0.2 - 8.3) degC higher for the EECO, and polar temperatures are higher by 25.0 (17.0 - 29.1) degC. This results in a flattened latitudinal temperature gradient of 9.0 ( 2.5 - 17.8) degC for the EECO, as opposed to 29.6 degC for the modern. To facilitate the comparison with latitudinal gradients reported in the literature, which sometimes do not report temperatures in very high latitudes, we report also the EECO gradient between the equator and the modern-day polar circle (66.6 deg), which is slightly lower at 7.8 ( 2.2 - 13.7).

The high variability of EECO palaeotemperature proxies, particularly in the mid-latitudes, and the scarcity of high-latitude data, result in substantial uncertainties in the modeled temperature gradient. This is reflected in the residual standard deviation () of the EECO gradient, 4.9 (3.8 - 6.5) degC, more than twice as high than of the modern gradient, 2.2. This signifies that the early Eocene data fit less well to the logistic, latitudinal gradient model, which can also be seen from the drastic departure of some of the proxy data from the gradient estimates (Fig. 4).

The early Eocene GMsST is estimated at 28.7 (26.7 - 30.7) degC, 11.1 degC higher than the modern. A model run excluding the ecological proxies results in a GMsST that is higher by 1.6 (-1.8 - 4.8) degC. The median latitudinal gradient is similar when excluding the ecological proxies, with a median of 9.2 degC, but with a 20% wider 95% CI (Supplementary materials). This indicates that the ecological proxy data are broadly in agreement with the geochemical proxies, while providing additional constraints on the shape of the early Eocene temperature gradient.

Due to the limited spatial coverage of the early Eocene proxy record, and due to the added model complexity of simultaneously estimating a model across both hemispheres, we pooled the proxy data across both hemispheres. Applying the model separately to each hemispheres results in substantial differences in hemispherical, average temperatures, with the southern hemisphere being warmer by 6.5 (3.5 - 9.4) degC. The inferred latitudinal gradient is somewhat steeper in the northern hemisphere ( 4.8 degC, although the 95% CI spans -6.6 to 14.3 degC), but the large uncertainties associated with both gradients, and the lack of polar proxy data in the southern hemisphere preclude a more precise statement (Fig. S3).)

## 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

## Improved reconstruction of temperature gradients and global average temperatures

The Bayesian model presented herein accurately reconstructs the modern, latitudinal SST gradient from a patchy and relatively small (n = 34) sample of temperature data. This is an advancement over previously used linear or quadratic approximations (e.g. **Refs?**), which are inherently unable to capture the sigmoidal shape of the modern SST gradient. Our generalised logistic function is flexible enough to approximate the shapes of all of those functions. As such, our model presents an alternative to non-parametric methods for inferring latitudinal temperature gradients, which are sometimes favoured as they can very flexibly follow the shape of an unknown temperature gradient (e.g. Zhang *et al.* 2019; Jones & Eichenseer 2022). However, when used for interpolation or prediction outside the proxy range, non-parametric methods such as Gaussian process regression strictly respond to the data (e.g. Inglis *et al.* 2020), and the resulting large-scale patterns are informed by the idiosyncracies of a patchy proxy record.

In our Bayesian, parametric model, informative priors on the model parameters improve the prediction of sea surface temperatures in the unsampled, very high latitudes: Notice that the upper limit of the credible interval does not increase beyond the range of the data, whereas unconstrained approaches such as splines, Gaussian processes or even standard linear regression could lead to unrealistically high upper bounds in this case (see Rasmussen & Williams 2004). Prior information on the shape of latitudinal temperature gradients on Earth exists for all geological time periods, and should be used in any palaeoclimate reconstruction. For example, the greater amount of solar radiation per unit area in low latitudes causes Earth’s latitudinal temperature gradient to be broadly negative (Beer *et al.* 2008). The ease with which such prior information can be integrated is a major advantage of our method, as the shape of the modeled gradient is controlled by four parameters which clearly relate to its magnitude, steepness and the latitude of its greatest steepness.

Palaeoclimate reconstructions are often summarised as global mean surface temperatures (GMST), providing a standardised metric for characterising the state of the Earth’s climate (Royer *et al.* 2004; Inglis *et al.* 2020). However, the calculation of global mean surface temperatures from sparse proxy data is susceptible to bias (Jones & Eichenseer 2022). By modeling the temperature variation across latitudes, a complete temperature distribution is obtained, filling in gaps in the proxy record through inter- or extrapolation. This eliminates the problem that specific climate zones may dominate the proxy record, as intersecting the modeled temperature gradient at narrow latitudinal intervals and accounting for the varying sizes of latitudinal bands by weighting provides unbiased GMST estimates. Some deep-time GMST reconstructions account for differential sampling by calculating zonal averages, but do not use the full latitudinal range of temperatures (Inglis *et al.* 2020). We anticipate that applying this improved will significantly alter Phanerozoic, proxy-based temperature curves, particularly when applied to intervals with small or biased samples of temperature proxies. (Royer *et al.* 2004; Veizer & Prokoph 2015; Jones & Eichenseer 2022).

## Incorporating ecological constraints in palaeoclimate reconstructions

Our results exemplify how incorporating quantified ecological temperature constraints can provide more precise temperature reconstructions than geochemical proxies alone, adding to the advances in palaeoclimate reconstructions achieved by integrating lithological data (Scotese *et al.* 2021). Combining the occurrences of climate-sensitive plant communities (Greenwood & Wing 1995), reptiles (**Marwick2007?**), leaf shapes (Peppe *et al.* 2011), with geochemical proxies offers substantial potential for improving quantitative palaeoclimate reconstructions across the Phanerozoic. Our modelling framework offers a straightforward way of integrating ecological climate data with other proxy data: The hierarchical model structure accounts for variation of temperature estimates from proxies at individual localities, which is treated equivalent to the uncertainty associated with the ecological temperature proxies. A local temperature estimate, based on multiple geochemical proxies, thus has the same weight as a local temperature estimate obtained from the occurrence of a climate-sensitive plant community, whilst preserving the uncertainty associated with each estimate.

Our approach for deriving fully quantitative climate reconstructions from ecological data is borrowed from nearest living relative methods, commonly employed in terrestrial, Cenozoic climate reconstructions (Fauquette *et al.* 2007; Pross *et al.* 2012). These methods have the problem that the thermal preferences of taxa may have changed over time. More significantly, in the early Eocene, sea surface temperatures may have reached heights unknown in the modern world, and nearest living relative methods based on the modern are inherently unable to predict such elevated temperatures. This is especially true for taxa that inhabit the warmest part of the ocean today, e.g. coral reefs [@]. Although coral reefs are threatened by warming sea surface temperatures today [@], it is conceivable that Eocene reef corals were adapted to a warmer climate. The fossil record indicates that reef development may have been stunted in the early Eocene, but the few early Eocene coral reefs occur in low latitudes (Zamagni *et al.* 2012). Tropical temperatures predicted by the geochemical proxy record indicate hotter-than-modern tropical temperatures (Fig. S2), suggesting that the modern climate range of coral reefs may underestimate the early Eocene thermal niche for coral reefs. We have tried to account for that possibility by widening the temperature probability distribution for reef corals, but the predicted temperatures for the reef and mangrove sites still lie below the temperatures indicated by the geochemical proxy record (Fig. 4, Fig. S2).

This dilemma could be resolved in future studies by applying machine learning approaches to inferring quantitative temperatures from ecological and lithological proxies: If geochemical proxies and ecological or lithological data are derived from the same location and time interval, the climatic requirements of these taxa or sediments can be learned by using palaeotemperatures from that time interval, instead of or in addition to modern modern temperatures. This approach would ultimately rely on geochemical proxies providing absolute temperature estimates, but the resulting information could be exported to other locations lacking good coverage of geochemical proxies via their fossil or sedimentary record.

## Early Eocene climate

The geochemical proxy record and ecological data indicate that the latitudinal SST gradient of the early Eocene climatic optimum was significantly shallower than the modern (Huber & Caballero 2011), but beyond that, there is little agreement. Evans *et al.* (2018) estimate the SST gradient at 32+-10% of the modern, which would correspond to ~20+- 3degC, using the difference between the mean tropical and deep ocean data. The modeled SST of Tierney *et al.* (2017) using TEX86 is ~ 12 degC, when taking the difference between temperatures at the polar circles and the equator. Inglis *et al.* (2020) include both terrestrial air temperature and SST estimates in their model of the latitudinal temperature gradient in their Figure S4a; they model a polar circle to equatorial gradient of ~ 13degC. All of those estimates are significantly lower than the SST gradient predicted by an EECO climate model ensemble Tierney *et al.* (2017), which predicts a polar circle to equatorial gradient of 26degC. Keating-Bitonti *et al.* (2011) show a proxy-based SST gradient of ~ 13degC, and Bijl *et al.* (2009) model a gradient of ~9degC in the northern and only ~5degC in the southern hemisphere for the early Eocene. Our polar circle to equatorial gradient is lower than most previous estimates at 7.8degC, although the 95% credible interval overlap with several of the listed gradient estimates.

[Table 1: Early Eocene latitudinal temperature gradients from the literature]

In latitudes beyond the polar circle, the discrepancy between our model predictions and those of earlier, proxy-based models increases, as those predict almost linearly decreasing SSTs towards the poles, whereas our median model prediction suggests only a slight decrease beyond the polar circle. However, the scarcity of temperature records in this range leads to widening credible intervals, including the possibility of stronger temperature decreases. Polar temperature estimates from our model are thus conservative in that they admit large uncertainty where data is absent, which is desirable. However, the presence of high proxy-derived temperature estimates at ~ 60 deg latitudes forces the modeled median temperature curve to be too high at ~ 24 degC, relative to the temperatures indicated by the high-latitude mangrove communities (15.6 - 22.5 degC). In contrast, the extrapolated polar temperatures of most previous proxy-based models are likely too low, given the abundance of ecological data indicating temperate or subtropical high-latitude climates during the EECO (Pross *et al.* 2012; Popescu *et al.* 2021)

The very high variability of the proxy record in mid-latitudes results in large uncertainties on the shape of temperature gradient and on the GMsST. Biases and errors in the proxy reconstructions likely contribute to the observed variability, as geochemical proxies reflect many other factors besides seawater temperature (Hollis *et al.* 2019). Despite excluding d18O measurements from recrystallised fossils, systematic offsets remain between mostly warm temperatures derived from TEX86, and cooler temperatures derived from d18O, delta47, and the ecological proxies. Seasonality [Keating-Bitonti *et al.* (2011) and temporal changes within the EECO (Westerhold *et al.* 2018) may also contribute to the large variability of the EECO proxy data.

Recent GMsST estimates of the EECO and of the early Eocene range from 23.4 to 37.1 degC, with the lowest GMSTs being derived from d18O, and the higher estimates including TEX86 (Inglis *et al.* 2020). Many studies include both marine and terrestrial proxies to derive GMST estimates, but despite great differences in proxy selection and in the calculation of global average temperatures, many recent estimates fall in the range of 27 - 29.5 degC (Caballero & Huber 2013; Hansen *et al.* 2013; Cramwinckel *et al.* 2018; Zhu *et al.* 2019), similar to our GMsST estimate of 28.7 degC.

# Conclusions

The Bayesian hierarchical model presented herein is able to reconstruct latitudinal gradients from both geochemical and ecological proxy data, whilst reflecting the uncertainty associated with the ecological temperature proxies, and accounts for the variation of multiple temperature estimates at individual localities. Using informative prior information allows for accurate temperature reconstructions from records with geographically incomplete sampling. By providing temperature estimates across the entire latitudinal range, this method also facilitates the reconstruction of unbiased global average temperatures. Application of our model to the EECO confirms the existence of latitudinal temperature gradients that were flatter than predicted by most Earth system models and by the majority of proxy-based work. High-latitude pollen records support this interpretation. Our GMsST estimate is in good agreement with most existing estimates, indicating that broadly accurate GMsST reconstructions are possible even with substantial deviations in the shape of the latitudinal temperature gradient. Our new method opens the door for improving the accuracy of proxy-based palaeoclimate reoncstructions and Phanerozoic temperature curves, particularly in intervals with a patchy record, and mitigates the biases incurred from uneven sampling.

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# Author contributions

# Data accessibility

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