

The early Eocene equable climate problem revisited

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Abstract. The early Eocene “equable climate problem”, i.e. warm extratropical annual mean and above-freezing winter temperatures evidenced by proxy records, has remained as one of the great unsolved problems in paleoclimate. Recent progress in modeling and in paleoclimate proxy development provides an opportunity to revisit this problem to ascertain if the current generation of models can reproduce the past climate features without extensive modification. Here we have compiled early Eocene terrestrial temperature data and compared with climate model results using a consistent and rigorous methodology. We test the hypothesis that equable climates can be explained simply as a response to increased greenhouse gas forcing within the framework of the atmospheric component of the Community Climate System Model (version 3), a climate model in common use for predicting future climate change. We find that, with suitably large radiative forcing, the model and data are in general agreement for annual mean and cold month mean temperatures, and that the pattern of high latitude amplification recorded by proxies can be largely, but not perfectly, reproduced.

1 Introduction

The early Eocene (~56–48 Ma) encompasses the warmest climates of the past 65 million years. Annual-mean and cold-season continental temperatures were substantially warmer than modern, while meridional temperature gradients were greatly reduced (Wolfe, 1995; Greenwood and Wing, 1995; Barron, 1987). Reconstructions of warm climates on land

are confirmed in the marine realm, with bottom water temperatures ~10°C higher than modern values (Miller et al., 1987; Zachos et al., 2001; Lear et al., 2000). This implies that early Eocene winter temperatures in deep water formation regions, located at the surface in high latitudes, could not have dropped much below 10°C, consistent with the high-latitude occurrence of frost-intolerant flora and fauna (Greenwood and Wing, 1995; Spicer and Parrish, 1990; Hutchison, 1982; Wing and Greenwood, 1993; Markwick, 1994, 1998).

Modelling studies of the early Eocene over the past decades have consistently failed to reproduce the warm continental interior temperatures inferred from paleoclimate proxies, an issue that has come to be known as the “equable climate problem” (Sloan and Barron, 1990, 1992; Sloan, 1994). The model-data mismatch is typically ~20°C for winter temperatures; for mean annual temperature (MAT) the error is typically less, but reaches 10–20°C near the poles (Shellito et al., 2003; Huber et al., 2003; Winguth et al., 2010; Roberts et al., 2009; Shellito et al., 2009). An apparently similar model-data discrepancy exists for the Cretaceous (Spicer et al., 2008; Donnadieu et al., 2006), but we restrict ourselves here to the early Eocene. On the other hand, models have had reasonable success at simulating the cooler intervals of the early Paleogene, such as the middle-to-late Eocene (Roberts et al., 2009; Liu et al., 2009; Eldrett et al., 2009) and Paleocene (Huber, 2009).

The early Eocene equable climate problem, with its suggestion that climate models may lack or misrepresent crucial processes responsible for the warm continental temperatures, has stimulated much innovative thinking in climate modelling (Valdes, 2000). Routes to generating warm early Eocene winter continental interior and polar temperatures that have been explored include: large lakes (Sloan, 1994; Morrill et al., 2001); polar stratospheric clouds (Sloan et al.,



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1992, 1999; Sloan and Pollard, 1998; Kirk-Davidoff et al., 2002; Kirk-Davidoff and Lamarque, 2008); increased ocean heat transport (Berry, 1922; Covey and Barron, 1988; Sloan et al., 1995); finer resolution simulations of continental interiors (Sewall and Sloan, 2006; Thrasher and Sloan, 2009); a permanent, positive phase of the Arctic Oscillation (Sewall and Sloan, 2001); altered orbital parameters (Sloan and Morrill, 1998; Lawrence et al., 2003; Sewall et al., 2004); altered topography and ocean gateways (Sewall et al., 2000); radiative convective feedbacks (Abbot et al., 2009a); altered vegetation (Sewall et al., 2000; Shellito and Sloan, 2006a,b), and changes in sea surface temperature (SST) distributions (Sloan et al., 2001; Huber and Sloan, 1999; Sewall and Sloan, 2004).

Recent work includes interactive ocean-atmosphere coupling; these studies have either failed to reproduce warm winter season temperatures (Roberts et al., 2009; Huber et al., 2003; Shellito et al., 2009) or not presented a comparison of these terrestrial winter temperatures (Tindall et al., 2010; Lunt et al., 2010; Huber and Sloan, 2001; Heinemann et al., 2009; Winguth et al., 2010) with proxies, so it seems important at this point to revisit the current status of the early Eocene equable climate problem.

While the studies described in the previous paragraphs have shown regional improvement in the model-data mismatch, the general outcome of the investigations cited above has been a failure to provide a single, parsimonious, global solution to the equable climate problem. One mechanism (e.g. cloud feedbacks or ocean gateway opening) might explain warmth at polar latitudes but leave temperatures in the western interior of North America unexplained, or vice versa. The failure of these various hypothesized resolutions to the equable climate problem – whether tested individually or in concert – has fostered a sense that they are not the leading order solution and that something major is missing from our understanding of the climate system and its representation in conventional climate models (Zeebe et al., 2009). It is, therefore, important to revisit this problem with the latest generation of models and with an up-to-date proxy data compilation.

One ostensibly straightforward route to resolving the equable climate problem that has not been fully explored to date is simply to raise greenhouse gas forcing sufficiently to yield above-freezing continental temperatures year round. It is known that CO₂ concentrations were above modern during the Eocene (Pearson and Palmer, 2000; Pearson et al., 2009; Pagani et al., 2005; Henderiks and Pagani, 2008; Lowenstein and Demicco, 2006; Doria et al., 2011), and estimates are as high as ~4700 ppmv (Fletcher et al., 2008). In addition to its direct warming effect, increased *p*CO₂ may have primed the climate system to be sensitive to forcing by alterations in other boundary conditions, such as ocean gateways (Sijp et al., 2009) or insolation, or it may have enhanced nonlinear sensitivity through feedbacks, e.g. due to wetland methane emissions (Sloan et al., 1992; Beerling et al., 2009a).

The reluctance to pursue the avenue of enhanced greenhouse gas forcing has clear origins: it is very difficult to simultaneously achieve warm continental interiors without overheating the tropics. Until recently, tropical surface temperature reconstructions indicated early Eocene tropical surface temperatures comparable or even lower than modern (Zachos et al., 1994; Crowley and Zachos, 2000), and climate models easily exceed these temperatures even at CO₂ levels insufficient to give the required mid- to high-latitude terrestrial warming (e.g. Shellito et al., 2003). Thus, the equable climate problem is intimately related to – though distinct from – the “cool tropics paradox” or “low gradient problem” (Barron, 1987; Adams et al., 1990; Huber et al., 2003).

However, the strictures imposed by the low gradient problem have been considerably relaxed recently by the realization that older tropical temperature reconstructions were subject to diagenetic cold bias, and more recent reconstructions using a range of proxies indicate that tropical temperatures may actually have been as high as ~35 °C (see discussion in Sect. 2.1). As suggested by Huber et al. (2003), polar annual mean temperatures of ~15 °C could potentially exist in equilibrium with such warm tropical temperatures without invoking novel climate mechanisms. This opens up the possibility of resolving the equable climate problem by simply raising greenhouse forcing, without recourse to novel mechanisms.

In this paper, we test the hypothesis that the equable climate problem, i.e. warm extratropical annual mean and above-freezing winter temperatures, can be explained simply as a response to increased greenhouse gas forcing within the framework of the Community Climate System Model version 3 (CCSM3). CCSM3 is a climate model in common use for predicting future climate change, used here with standard physics (Collins et al., 2006). The focus is on validation of the model through model-data comparison.

The study is structured as follows. First, Sect. 2 reviews the relevant temperature and CO₂ reconstructions, which guide decisions on the methodology presented in Sect. 3. In Sect. 4, we present a set of Eocene atmospheric general circulation model experiments compared with early Eocene proxy records. We discuss the robustness and limitations of this study in Sect. 5. Finally, Sect. 6 summarizes our conclusions and discusses some implications of the model-data agreement.

2 Interpreting proxy data constraints

Some preliminary considerations must be dealt with before the model-data comparison can be carried out, because proxy records are unavoidably subject to varying interpretations. While there may not be universal agreement on the best interpretative approach, we aim here to at least be clear what our framework is. In this section, we review characterizations of the early Eocene paleotemperature and greenhouse

gas records, with an emphasis on uncertainties and potential biases. Since “Early” and “Middle” have yet to be officially defined for the Eocene, and because some of our data fall just outside of strict stage boundaries, we use “early” and “middle” Eocene. We use early generally to mean Ypresian and include occasionally records that are potentially lowermost Lutetian, but exclude the Paleocene-Eocene Thermal Maximum (PETM) and other identified transient “hyperthermal records” (Nicolo et al., 2007; Lourens et al., 2005; Sluijs et al., 2008). Middle for us generally means Lutetian and its equivalents. All the existing data point to the early Eocene as being a variable world, subject to – and responsive too – orbital forcing, as well as marked by internal variability (having a red-noise like spectrum), distinct transitions (Zachos et al., 2001; Brinkhuis et al., 2006), and persistent modes of variability down to quasi-decadal (Garric and Huber, 2003) and El Niño (Huber et al., 2003) time scales. Consequently, aliasing and undersampling are likely to be important to the analysis we attempt here and also very difficult to avoid or quantify, especially for the terrestrial paleoclimate records that are our focus here. Some attempt is made by utilizing full time series of records for comparison where such are available, but this is a crude and ultimately unsatisfying approach which should eventually be improved upon.

Since this paper focuses on terrestrial records, the discussion of ocean proxies is brief, but it is important for context because SSTs are being interpreted by many to much warmer values than previously thought. We briefly discuss the ocean temperature proxy record in the next section, but given the uncertainties that remain in proxy calibrations and assumptions that go into those proxies, they deserve their own comprehensive treatment and model-data comparison. As described in Sect. 2.2, a factor that has been poorly appreciated by the modelling community is that it is now well acknowledged in the paleobotanical literature that most published terrestrial paleoclimate records have been significantly biased to overly cool values. In this study we focus on annual mean and winter season terrestrial temperatures in order to assess progress in the early Eocene equable climate problem *sensu stricto*.

2.1 Sea surface temperature records

A new characterization of Eocene temperature has recently developed as the product of both a better understanding of diagenetic contamination of older tropical SST records (Schrug et al., 1995; Schrag, 1999; Huber and Sloan, 2000; Pearson et al., 2001b, 2007, 2008) and the development of new proxies such as TEX₈₆ and Mg/Ca (Schouten et al., 2002, 2003; Pearson et al., 2007; Lear et al., 2008; Sexton et al., 2006; Sluijs et al., 2006, 2007, 2008; Liu et al., 2009) for ocean near-surface temperatures. As summarized in Huber (2008), SSTs of ~35 °C are now reconstructed in the early Eocene tropics (Pearson et al., 2001b, 2007; Tripathi et al., 2003; Tripathi and Elderfield, 2004; Zachos et al., 2003). Extratropical

SSTs are also reconstructed to values hotter than previously thought (Bijl et al., 2009; Sluijs et al., 2006, 2009; Zachos et al., 2006; Hollis et al., 2009; Creech et al., 2010; Liu et al., 2009; Eldrett et al., 2009). These hot temperatures have major implications for our understanding of past climate dynamics and of the equable climate problem in particular.

One outgrowth of increasing study of the paleotemperature proxies and improved understanding of the myriad processes and mechanisms that affect proxies has been the unfortunate realization that large and difficult-to-quantify uncertainties persist in proxy interpretations (Shah et al., 2008; Ingalls et al., 2006; Herfort et al., 2006; Kim et al., 2010; Liu et al., 2009; Pearson et al., 2001a; Hugué et al., 2006, 2007, 2009; Wuchter et al., 2004, 2005; Trommer et al., 2009; Turich et al., 2007; Eberle et al., 2010). Of particular concern is the need to extrapolate calibrations out to temperatures and environmental conditions far beyond modern values. This can be a special difficulty in the tropics in which conditions likely were much warmer than the warmest range of core-top calibrations, 30 °C. This either requires extrapolating beyond the core-top calibration or using mesocosm calibrations that extend up to 40 °C. For the Tanzanian TEX₈₆ records of Pearson et al. (2007), peak early Eocene temperatures are either 35.1 °C when extrapolating from the coretop TEX₈₆ (GDGT2-index) calibration or 39.4 °C using the mesocosm based TEX₈₆ (GDGT2-index) calibration (Kim et al., 2010). The warmest values recorded by $\delta^{18}\text{O}$ in planktonic foraminifera of the same age (~49.5 mya) is ~31.5 °C. So at one time and one locality, from what some might consider the best records, reasonable arguments might be made to interpret tropical near-surface temperatures to be 31.5 to 39.4 °C.

On the other hand, sometimes different proxies in a region show a remarkable level of congruence and temporal consistency, for example in the southwest Pacific Ocean (Bijl et al., 2009; Hollis et al., 2009; Liu et al., 2009). But even the congruence of these records may not prove their accuracy, given their arguable lack of consistency with other records. For example, the presence of 11 °C South Atlantic temperatures (Ivany et al., 2008) in the same latitude band as 30 °C temperatures in the South Pacific (Bijl et al., 2009; Hollis et al., 2009) raises questions about the proxy interpretations. The occurrence of ~10 °C deep ocean temperatures (Zachos et al., 2001) requires that some regions see temperatures fall to this value at least in winter, in agreement with the results of Ivany et al. (2008), but South Pacific records seem to preclude temperatures this cold. As recognized in many studies, seasonality and regional variation due to ocean heat transport are important considerations that may help reconcile the different proxies at high latitudes (Hollis et al., 2009), but serious discrepancies persist unexplained at low latitudes (Huber, 2008; Liu et al., 2009).

Reconciling the different approaches and narrowing uncertainty in SSTs is beyond the scope of this paper. Indeed, we believe that focusing on terrestrial temperatures will create a solid benchmark for comparison with SST records in future

work. Furthermore, the terrestrial climate problem is in some senses a better posed one. Fewer mechanisms govern terrestrial temperature, especially in winter. Unlike in the ocean, where mixed layer depth and ocean heat transport changes provide additional complications to the surface energy budget, the terrestrial energy budget – especially in high latitude winter in continental interiors – is more straightforward and well representable in climate models. Since the land surface does not transport heat horizontally and the thermal inertia is negligible, the surface energy budget in winter in high latitude continental interiors reduces to simply atmospheric advection and dominantly longwave radiative processes (since in winter the shortwave processes are negligible).

Prior work has already demonstrated that the advection of heat inland in Eocene simulations is not nearly enough to maintain continental winter warmth, regardless of the imposed warmth of high latitude sea surface temperatures (Sewall et al., 2004; Sloan et al., 2001; Huber and Sloan, 1999). Consequently, the winter season aspect of the equable climate problem is more circumscribed than many of the other interesting problems in Eocene climate since it highlights primarily the role of one mechanism – longwave radiation – which reduces the possible mechanisms to consider relative to, e.g. explaining ocean temperature distributions.

2.2 Terrestrial temperature records

Prior studies have discussed ways in which existing methodologies and sampling approaches introduce warm biases. These include undersampling large regions that were likely cooler than the mean, such as Antarctica, Siberia and north-eastern North America, as well as preferential temporal sampling, e.g. clipping seasonal or orbital scale cycles (Sloan and Barron, 1990; Sloan, 1994; Valdes, 2000). These factors are probably important considerations for developing a better understanding of regional scale climate patterns, but are unlikely to undermine the widespread evidence of continuous warmth in the early Eocene or overwhelm the large cool biases in existing terrestrial reconstructions. On the contrary, many factors conspire to introduce an overall cool bias in the terrestrial paleotemperature record.

Firstly, almost no terrestrial records from the Eocene have been obtained for 30° N to 30° S band, effectively clipping the warmest climatic end-member. Second, where records have been derived, various other factors contribute toward a cool bias. Taphonomic and ecological factors in leaf physiognomic techniques have been shown to lead to systematic cold biases of 2–8 °C (Burnham, 1989; Burnham et al., 2001; Boyd, 1994; Greenwood, 2005, 2007; Spicer et al., 2005; Kowalski, 2002; Kowalski and Dilcher, 2003; Peppe et al., 2010). Further cool biases are introduced by under-sampling the flora, particularly in the early, pioneering studies (Wilf, 1997; Burnham et al., 2005; Wilf et al., 2003). Third, at high latitudes, polar deciduous habits skew high latitude “toothiness” based MAT interpretations to low values (Boyd,

1990, 1994). Fourth, at low latitudes, floral physiognomic techniques are biased to cool values because the proxy becomes insensitive at temperatures much warmer than modern (Head et al., 2009). And finally, many records come from regions with significant paleo-elevation (Wyoming, Okanagan Highlands Wolfe et al., 1998; Smith et al., 2009) and hence may record temperatures cooler than sparsely-sampled low elevation, low relief areas, though this effect may be partially offset by the fact that records are frequently derived from basins within these high-relief regions (Sewall et al., 2000).

If the early Eocene was even warmer than previously thought – as this review of terrestrial and ocean proxies suggests (their large uncertainties notwithstanding) – the mystery of Eocene equable climate deepens unless either the radiative forcing or climate sensitivity were greater than has been typically explored. It also implies that it is very difficult to achieve early Eocene conditions in models and that studies purporting to simulate the early Eocene may instead only be warm enough to match late or middle Eocene conditions. From this perspective, the approach that we utilize in this study, in which various efforts are made to overcome the cold bias of previous proxy compilations, makes the goal of reproducing equable climates harder to reach.

2.3 Greenhouse gases and radiative forcing

Increased radiative forcing, usually ascribed to greenhouse gases, is part of every feasible solution to the equable climate problem tried so far. But, the upper range of plausible greenhouse gas forcing has expanded from prior work. Modeling studies have predominantly explored the low end (520–2000 ppm) of paleo-CO₂ proxy estimates even though the range extends easily up to 4400 ppm in the early Eocene (Pearson and Palmer, 2000). This partly reflects attention to the lower end of CO₂ estimates typically derived from leaf stomatal indices (Royer et al., 2001; Beerling and Royer, 2002a). Yet the calibration of this proxy at high CO₂ is weakly constrained (Beerling and Royer, 2002b; Beerling et al., 2009b) and recent evidence that leaves adapt the size of the stomata and in addition their density at high CO₂ values (Franks and Beerling, 2009) raises questions about the validity of the proxy at high CO₂. Indeed, as recently affirmed by Smith et al. (2010) the stomatal methods should probably be considered semi-quantitative under high CO₂ conditions and may represent CO₂ minima.

Boron and alkenone approaches also have increasing error bars at high CO₂, because their calibrations lose sensitivity at high values (Pagani, 2002; Pearson and Palmer, 2000). The nahcolite approach of Lowenstein and Demicco (2006) only constrains the minimum early Eocene CO₂, and any value above 1125–2985 ppm is possible from that proxy record.

Overall, existing proxy records have much greater accuracy at low CO₂ and once values are significantly higher than modern (somewhere above 560 to 1220 ppm, depending on

the proxy), there is little certainty in the actual value although constraints can be inferred from carbon mass balance models (Zeebe et al., 2009; Panchuk et al., 2008). These constraints currently allow for a wide range of potential early Eocene CO₂ values.

Carbon dioxide is also not the only important source of radiative forcing. Methane concentrations, for example, could have been much higher in the early Eocene (Sloan and Barron, 1992; Sloan et al., 1999; Beerling et al., 2009a). Alternatively, clouds may have functioned differently (Sloan and Pollard, 1998; Kump and Pollard, 2008). We have no proxies for either of these factors, which is one reason why relatively few studies have incorporated them. They represent arguably reasonable, but unconstrained conjectures.

Furthermore, strong radiative forcing in simulations (Shelito et al., 2003; Kump and Pollard, 2008) produces tropical SSTs warmer than traditional reconstructions (Zachos et al., 1994; Crowley and Zachos, 2000) and hotter even than revised reconstructions (Pearson et al., 2007; Huber, 2008). So while it is understood that stronger radiative forcing in models warms extratropical continental interiors, Eocene tropical sea surface temperature constraints provided a primary motivation for not forcing models with greenhouse gas forcing sufficient to maintain extratropical winter warmth (Barron, 1987; Huber and Sloan, 2000).

Finally, it is perhaps an accident of history that much of the Eocene modelling work was performed with the NCAR atmospheric models (CCM, CAM, GENESIS), which have consistently had relatively weak sensitivity of global mean temperature to increased greenhouse gas concentrations (2–3 °C warming per doubling of *p*CO₂) (Kothavala et al., 1999; Otto-Bliesner et al., 2006; Kiehl et al., 2006). Other models, such as the UK models (e.g. HadCM3 and its variants) and ECHAM5/MPI models, have higher sensitivities and have consistently produced temperatures as warm as high-CO₂ CAM simulations with lower radiative forcing (Heinemann et al., 2009; Jones et al., 2010). These more sensitive models run into the same problems with tropical SSTs, though, because climate models have similar (Holland and Bitz, 2003), although not identical (Abbot et al., 2009a), amounts of high-latitude amplification of global warming after normalizing by climate sensitivity. These Eocene studies in models with high sensitivity have not quantitatively examined the issue of continental winter temperatures, which leaves an important gap in evaluating how close we are to solving this long-standing climate problem.

3 Methods

3.1 Proxy records

Various factors must be considered in interpreting climate from proxy records and ambiguity exists in any paleoclimate model-data comparison. Here we describe the methodologies we developed for the model data comparison and the

inclusion of random and biased sources of uncertainty and error. The details of the proxy data used in this study, including original references and calibration information, are summarized in Table 1.

3.1.1 MAT

Macrofloral assemblage data provide many of the quantitative paleotemperature estimates for the Eocene. Different approaches to estimating paleotemperature with macroflora, such as CLAMP (Climate-Leaf Analysis Multivariate Program) (Wolfe, 1995) and LMA (Leaf Margin Analysis) (Wilf, 1997), usually lead to qualitatively similar but quantitatively different MAT estimates. Even within these methodologies, the impacts of differing calibration data sets and approaches can lead to significantly different estimates (Greenwood et al., 2003, 2004; Adams et al., 2008; Spicer et al., 2009). Comparison of different approaches often leads to estimates that differ beyond the stated error estimates of the underlying calibration studies (Uhl et al., 2007). Trends are normally more robust, but since model-data comparison requires aggregating data into “snapshots”, uncertainty in absolute values, rather than trends, is crucial to this study.

For these reasons, it is more important for the purposes of this study to properly account for systematic biases and spatio-temporal sampling uncertainty in proxy records rather than be primarily concerned with the stated random accuracy of the methodologies, which likely substantially underestimate the true uncertainty. Wherever possible in this study, we have chosen to minimize systematic errors while maintaining as consistent an approach in estimating temperature as possible.

To that end, we primarily rely on LMA to estimate MAT, as this approach has a long history and widespread usage in the literature, and it is arguably less sensitive to subjectivity in scoring, sampling, and calibration than other approaches such as CLAMP (Wilf, 1997; Peppe et al., 2010). To offset the well established cool biases in the LMA approach we use the Kowalski and Dilcher (2003) calibration wherever possible unless a compelling reason exists not to. Recently, Peppe et al. (2011) have generated a much more complete and objective calibration study for LMA, which is likely to be the new standard for this field. Yet, as the authors of that study acknowledge, the temperatures generated from that calibration appear to be biased by about 5 °C too cold in Eocene and Cretaceous midlatitude sites and consequently, we believe it is in keeping with the goals of this study to retain a calibration that accounts for this bias as much as possible. In some cases, the only published data available are from taxon-derived transfer functions (such as the coexistence approach, Utescher et al., 2009) or CLAMP-derived temperatures. In another important special case, e.g. Australian flora, there are well-established systematic differences in the relationship between toothiness and temperature that arise from the long isolation of Australia's flora. Consequently, we use

the Australian calibration (Greenwood et al., 2004) for Australian and New Zealand flora. See Table 1 for more details.

More fundamentally, it is unclear how to apply this proxy, or any proxy, outside of its calibration regime, in particular at temperatures much hotter – and with higher $p\text{CO}_2$ and potentially greater rainfall – than those observed in modern vegetated regions (Utescher et al., 2009). Today, MAT above 28 °C does not occur in well-vegetated regions and such techniques are suspect and likely underestimate MAT in regions that are likely to be above that range (Head et al., 2009). Formally a limit exists, since leaves can not be more than 100 % entire-margined. But, more fundamentally, hot (MAT much above 28 °C), wet conditions, with vegetation, have no modern analogue and empirical relationships may break down. We have every reason to think that mean MAT in the tropics was above 30 °C in the early Eocene, but just how much hotter is an unanswered question (Huber, 2008; Jaramillo et al., 2010; Kobashi et al., 2004). We will not be able to address the true warmth of the tropical to subtropical regions with great rigor in this study because of a paucity of terrestrial proxies and the ambiguity of interpreting such records under non-analogue conditions. The only relevant tropical terrestrial MAT constraint we were able to identify from published records was middle Eocene in age (Jacobs, 2004), but we include it in this study for lack of any other available data (see Table 1).

In some regions, where few macrofloral records exist or where LMA or CLAMP have not been applied, other proxies are available and so we rely on them to fill in the large spatial gaps. Especially crucial to constrain are high and low latitude temperatures. Such additional sources of quantitative information include: Nearest Living Relative (NLR) transfer functions, isotopic estimates, and organic geochemical indicators. MAT can be estimated from palynoflora (Eldrett et al., 2009; Greenwood et al., 2010) and from various Nearest Living Relative based empirical correlations with MAT (Utescher and Mosbrugger, 2007; Utescher et al., 2009; Mosbrugger et al., 2005; Poole et al., 2005) and allometric considerations (Head et al., 2009). Oxygen and hydrogen isotopes provide paleotemperature estimates provided certain parameters are well constrained (Eberle et al., 2010; Koch, 1998; Fricke and Wing, 2004; Jähren and Sternberg, 2003, 2008; Jähren, 2007; Jähren et al., 2009).

The MBT-CBT proxy is an organic geochemical proxy for annual mean air temperature derived ultimately from soil bacteria (Weijers et al., 2007b). We use this proxy to provide additional information in the early Eocene, although it is possible that the proxy is biased to summer temperatures at extreme high latitudes (Weijers et al., 2007a; Eberle et al., 2010), or worse, under unusual but difficult-to-rule-out conditions, may not reflect surface temperature at all (Peterse et al., 2009). Attempts to include other information from kaolinite-isotope MAT proxy records (Sheldon and Tabor, 2009) were unsuccessful because suitable age constraints were not available.

3.1.2 Seasonal temperatures

MAT proxies are not the only or even most relevant variable to consider, given that seasonality, or the lack thereof, is the defining characteristic of the equable climate problem (Sloan and Barron, 1990, 1992). The most vexing difficulty in prior work has been in explaining warm winter temperatures. Various approaches to constraining winter temperatures exist. These include using: CLAMP-based cold month mean (CMM) estimates (Wolfe, 1995; Spicer et al., 2009), coldest quarter temp estimates for Australian Eocene floras from nearest living relative transfer functions, which are nearly the same as CCM estimates (Greenwood et al., 2003), the palm/cycad line (Greenwood and Wing, 1995; Wing and Greenwood, 1993; Eldrett et al., 2009), crown crocodilian presence (Hutchison, 1982; Markwick, 1994, 1998, 2007), or isotopic analysis (Eberle et al., 2010). These methodologies provide different kinds of information, e.g., CLAMP provides quantitative, explicit estimates of CMM, whereas the palm/cycad line and crocodilian indicators constrain temperatures to be higher than a threshold value. Differing comparison methodologies are required by the complementary information provided by these different proxies.

The abovementioned studies and others demonstrate that the early Eocene did not experience below freezing temperatures over a huge expanse of the land's surface, except perhaps in the intermontane Canadian Rockies (Wing, 1987; Spicer and Parrish, 1990; McIver and Basinger, 1999; Greenwood et al., 2005; Smith et al., 2009). For some regions (central Antarctica, north central Canada and parts of Eurasia), data coverage is too sparse to state this definitively, but the existing high latitude data indicate temperatures were so warm that it is difficult to physically justify large zones substantially cooler than freezing even in most of the regions with missing data. This is especially true given that inclusion of other potential factors such as higher $p\text{CO}_2$ decreases the tolerance of frost-sensitive flora to cold temperatures (Royer et al., 2002). The presence of crown crocodilians in Kazakhstan and Mongolia also fills in the gaps and argues against temperatures below freezing in the regions we might expect to be the coldest (Markwick, 1998, 2007). The important exceptions to this are in inland Antarctica and at high paleoelevations, where proxy data to constrain temperatures are sparse to non-existent and physical considerations indicate that temperatures may have been cold.

This interpretation does not rely overly on any one proxy being correct as they are independently corroborated by lack of sea ice diatoms Stickley et al. (2009), high latitude occurrence of tropical clays (Robert and Chamley, 1991), warm polar SSTs (Bijl et al., 2009; Sluijs et al., 2006), and ~10 °C bottom water temperatures (Zachos et al., 2001; Lear et al., 2000). These disparate lines of evidence all argue for temperatures remaining above freezing year-round in the regions and seasons expected to be cold, if modern relationships are a guide.

Table 1. Description of Proxy Data Sources and Treatment.

Locality	55 mya (adjusted) paleo- latitude	Mean MAT	upper error	lower error	CMM	cmm error	Primary Reference	Notes
Kisinger Lakes	47.5° N 90.6° W	22.90	3.60	3.60	6.70		Fricke and Wing (2004)	
Chalk Bluffs	44.1° N 102.7° W	20.13	4.57	4.08			Hren et al. (2010)	LMA data from Hren et al. (2010), recalculated with Kowalski and Dilcher calibration.
Chalk Bluffs	44.1° N 102.7° W	20.00	3.60	3.60	5.60		Fricke and Wing (2004)	Values recomputed using Kowalski and Dilcher calibration
Green	45.6° N 88.7° W	24.50	7.20	7.70	7.30	1.5	Fricke and Wing (2004)	Using Kowalski and Dilcher
River/Wind River								calibration
BHB Polecat Bench	47.5° N 88.4° W	21.73	9.05	6.35	4.00	2.5	Wing et al. (2005)/ Wing et al. (2000)	LMA-8 through LMA-4 from Wing et al. (2000). Values recalculated with Kowalski and Dilcher calibration.
Kulthieth	57.8° N 103.8° W	19.40	1.00	1.00	12.60		Wolfe (2004)	This is an old CLAMP number.
Camel's Butte	49.5° N 82.3° W	17.8	3.60	3.60	3.50		Hickey (1977)	This flora with very few specimens, which leads to anomalously low LMA temperatures, instead using the temperature derived in Hickey (1977), which is the preferred number used by later work, such as Wilf et al. (2000).
Yellowstone- Sepulcher	48.8° N 90.8° W	13.10	3.60	3.60	1.90		Fricke and Wing (2004)	Values recalculated using Kowalski and Dilcher calibration.
Republic	53.2° N 98.4° W	11.30	3.60	3.60	4.10	4	Greenwood et al. (2005)	Percent entire margins from Greenwood et al. (2003) (used 8.8° from LMA 1) and used Kowalski and Dilcher calibration.
Princeton	54.6° N 99.8° W	5.00	3.60	3.60	5.30	2.8	Greenwood et al. (2005)	Percent entire margins from Greenwood et al. (2003) and applied Kowalski and Dilcher calibration.
Quilchena	55.1° N 99.8° W	19.03	3.60	3.60	5.80	2	Greenwood et al. (2005)	Percent entire margins from Greenwood et al. (2003) and applied Kowalski and Dilcher calibration. Age from 52 to 51 Mya.
Falkland	55.2° N 98.5° W	8.9	3.60	3.60	5.20	3	Smith et al. (2009)	Percent entire margins from Greenwood et al. (2003) and applied Kowalski and Dilcher calibration gives 11.9 but using the later, better collection of Smith et al. (2009).
McAbee	55.5° N 100.0° W	12.80	3.60	3.60	3.50	4.4	Fricke and Wing (2004)/Greenwood (2005)	As above.
Horsefly	57.5° N 100.0° W	12.86	3.60	3.60	5.30	2.8	Greenwood et al. (2005)	As above.
Driftwood Canyon	60.6° N 105.3° W	8.25	3.60	3.60	2.70	5.6	Greenwood et al. (2005)	As above.
Site 913	64.8° N 5.2° E	14.46	5.22	5.16	7.00	3	Eldrett et al. (2009)	Longitude should be adjusted to 0 for site to be from Greenland. MAT values from 48 to 50 Ma. Error bars are maximum in time series (plus 1 stated error on that value) and the minimum of the time series (minus 1 stated error on that value).
Laguna del Hunco	46.9° S 57.3° W	20.72	5.76	6.63	10.80	3.8	Wilf et al. (2005)	Location adjusted 3° east. Based on the analysis of Wilf et al. (2005), using the Kowalski and Dilcher calibration and using floral data from all the Laguna del Hunco sites.

Table 1. Continued.

Locality	55 mya (adjusted) paleo- latitude	Mean MAT	upper error	lower error	CMM	cmm error	Primary Reference	Notes
Brandy Creek	60.0° S 148.7° E	18.20	2.21	2.21	15.70	2.8	Greenwood et al. (2003, 2004)	Position adjusted 2° N and 3° E. Percent entire margined from Greenwood et al. (2003, 2004), using Australian calibration.
Hotham Heights	58.7° S 149.9° E	17.90	2.33	2.33	15.70	2.6	Greenwood et al. (2003, 2004)	As above.
Dean's Marsh	60.7° S 145.7° E	18.8	2.90	2.90	15.70	2.4	Greenwood et al. (2003, 2004)	As described by Greenwood et al. Dean's Marsh LMA is anomalously low and based on personal communication with Greenwood the "bioclimatic method" MAT derived in those papers is preferred as the the macrofloral collection was poorly characterized and has been subsequently lost in a fire, whereas the bioclimatic estimate is robust and can be verified.
Puryear-Buchanan	37.1° N 70.7° W	35.30	3.60	3.60	16.10		Fricke and Wing (2004)	Values recalculated using the Kowalski and Dilcher calibration. Paleolocation assumes location is near Puryear, TN.
Axel Heiberg	77.5° N 35.3° W	14.70	0.70	0.70	3.70	3.30	Greenwood et al. (2010)	Values directly from Greenwood et al. (2010). These may be middle Eocene (Lutetian).
Axel Heiberg – US 188	77.5° N 35.3° W	12.80	4.30	4.30			Greenwood et al. (2010)	As above.
Ellesmere Island	75.5° N 28.0° W	8.00	7.00	7.00	0.00	7.00	Eberle et al. (2010)	Values directly from Eberle et al. (2010), derived from $\delta^{18}\text{O}$ in biogenic phosphate. Early Eocene in age.
ACEX IODP 302	83.58° N 27.23° E	18.30	1.20	1.90			Weijers et al. (2007)	No land in model near core location, so using nearest land at around 75° N 64° E. GPLATES reconstruction at 55 Ma for the ACEX core is adjusted to paleo-shoreline which is further south than stated. Values taken from Weijers et al. (2007), using Core 29, early Eocene. No meaningful error bars stated in that paper.
Chuckanut, WA	53.6° N 102.4° W	15.50	0.50	0.50	11.50	1.50	Mustoe et al. (2007)	CLAMP MAT from Mustoe et al. (2007).
Harrell Core, Meridian, MS	33.0° N 71.7° W	32.00	2.00	2.00			van Roij (2009)	Location may be adjusted north to match land mask, error around $\pm 2^\circ$. Bashi/Hatchetigbee from van Roij Masters thesis. MBT/CBT temperature is approximate.
Geiselstal, Germany	46.9° N 7.3° E	23.95	1.05	1.05	19.00	2.00	Mosbrugger et al. (2005)	Basal Lutetian age (as old as ~49 Ma). MAT based on CA approach.
Fushun, China	46.8° N 122.2° E	15.85	0.45	0.45	5.00	3.00	Wang et al. (2010)	Values based on macrofloral data, Table 4 of Wang et al. (2010).
Mahenge, Tanzania	18.3° S 30.8° E	36.50	3.60	3.60			Harrison et al. (2001)	Location adjusted by 6° E. Age is ~45 Ma, included for lack of other data. Flora is probably not completely counted and this number is not likely to be robust, but 17 out of 18 members of the flora were entire margined. Kowalski and Dilcher calibration used.
Chermurnaut Bay, Kamchatka	68.0° N 166.7° E	18.20	3.96	3.97			Collinson and Hooker (2003)	Based on Collinson and Hooker summary, based on the work of Budantsev (as cited in Akhmetiev) GPLATES 67.7° N 171.0° E.
Raichikha	54.7° N 127.5° E	18.40	3.60	3.60			Akhmetiev (2010)	Further information on modern location and age/stratigraphy based on van Iiterbeeck (2005) and Akhmetiev (2007). MAT computed from percent entire margin data in text.

Table 1. Continued.

Locality	55 mya (adjusted) paleo- latitude	Mean MAT	upper error	lower error	CMM	cmm error	Primary Reference	Notes
Fossil Hill Flora, King George Island, Antarctica	62.9° S 62.3° W	16.74	3.60	3.60	7.60		Li (1992)	Percent entire margins is from Li (1992). Calculated with Kowalski and Dilcher calibration. Age is considered 49–42 Ma but is subject to varying considerations.
James Ross Basin, Antarctica	64.9° S 61.1° W	16.10	4.00	4.00	7.60		Poole et al. (2005)	JRB averages from Poole et al. (2005) using co-existence approach. Values from Table 3. Age is listed as early Eocene.
Dragon Glacier, King George Island, Antarctica	62.8° S 61.7° W	12.90	3.60	3.60	10.00	0.80	Hunt and Poole (2003)	Values recalculated with Kowalski and Dilcher calibration.
China Gulch	43.3° N 103.38° W	24.51	1.50	1.50			Hren et al. (2010)	5.3 °C km ⁻¹ lapse rate correction applied to MBT/CBT numbers of Hren et al. (2010), with 1.5 “reproducibility” errors.
Camanche Bridge	43.3° N 103.4° W	25.98	1.50	1.50			Hren et al. (2010)	As above.
Pentz	44.8° N 103.8° W	24.00	1.50	1.50			Hren et al. (2010)	As above.
Cherokee Site 1	44.8° N 103.8° W	16.59	1.50	1.50			Hren et al. (2010)	As above.
Fiona Hill	44.1° N 103.1° W	16.70	1.50	1.50			Hren et al. (2010)	As above.
Council Hill	44.7° N 103.2° W	21.63	1.50	1.50			Hren et al. (2010)	As above.
Iowa Hill	44.2° N 103.2° W	22.96	1.50	1.50			Hren et al. (2010)	As above.
You Bet 2	44.3° N 103.1° W	23.80	1.50	1.50			Hren et al. (2010)	As above.
Chalk Bluffs – E	44.3° N 103.2° W	26.75	1.50	1.50			Hren et al. (2010)	As above.
Scotts Flat	44.4° N 103.2° W	24.91	1.50	1.50			Hren et al. (2010)	As above.
Gold Bug	44.5° N 103.2° W	25.08	1.50	1.50			Hren et al. (2010)	As above.
Hidden Gold Camp	44.2° N 103.2° W	18.38	1.50	1.50			Hren et al. (2010)	As above.
Woolsey Flat	44.5° N 103.1° W	24.84	1.50	1.50			Hren et al. (2010)	As above.
Mountain Boy	44.7° N 103.2° W	19.84	1.50	1.50			Hren et al. (2010)	As above.
Pine Grove 1	44.8° N 103.1° W	22.82	1.50	1.50			Hren et al. (2010)	As above.
Otaio	56.1° S 163.7° W	15.97	2.99	2.99	11.00	3.76	Hollis et al. (2011)	Early Eocene of New Zealand, using Australian LMA calibration. Provided by Liz Kennedy.

The published error bars around winter season temperature reconstructions are non-negligible and those around summer temperatures are even larger. More concerning are the conceptual issues involved in using modern floral/climate relationships to estimate past climate regimes with no clear analogue (Utescher et al., 2009), such as subtropical climates in polar night. When strongly restrictive and conserved biophysical-derived traits are involved, such as is clearly the case with freezing temperatures and palm trees and crocodiles, the proxy data provide a stronger constraint than in regions of climate regime space where no clear strong biological constraints exist or which no flora currently occupy. Our approach is that constraints on summer terrestrial

temperatures from paleofloral and faunal records are much weaker than on winter temperature. CLAMP and other multivariate techniques provide some indications but the biophysical constraints on plants on the warm side are poorly understood and probably less strict than those on the cool side. In other words, there is currently no equivalent of a “palm line” for summer temperature and published attempts to estimate summer temps based on assemblages are unlikely to have the same kind of durability as more biophysically constrained numbers. Currently we have no natural ecosystems that persist under temperatures much warmer than ~30 °C, with several meters of rainfall, and with higher than modern $p\text{CO}_2$, so transfer function approaches that

implicitly can only explore climate parameter spaces experienced by modern vegetation are likely to be of limited value. Because of a lack of modern analogue in climate-ecosystem space for these hot, wet conditions, a strong asymmetry exists between the ability to constrain increases in CMM and increases in warm month mean (WMM), except perhaps at high latitudes where WMM conditions may lie within the modern climate envelop (of low latitude conditions). On the other hand, light limitation, in the form of short, but 24-hour growing seasons almost certainly introduces a layer of complexity in interpreting growing season, and hence WMM temperatures at high latitudes.

Based on these considerations, we focus attention on the winter season aspect of the equable climate problem and do not make a quantitative comparison with summer temperature proxy reconstructions. In this study, we find that winter temperatures were above freezing everywhere except for interior Antarctic and small regions of high paleoelevation, primarily restricted to western North America. We adopt a two-pronged approach to model-data comparison for winter temperatures.

First, we show that seasonal-mean modelled temperatures everywhere (with the exceptions mentioned) were above freezing. This broad-strokes approach enables comparison with many of the crucial but qualitative indicators and characterizations of warm winters that are ubiquitous in the early Eocene geological record, including inferences from floral and faunal assemblages and soil and clay types, (Greenwood and Wing, 1995; Markwick, 2007; Pigg and Devore, 2010; Collinson and Hooker, 2003; Valdes, 2000). Such indicators provide important constraints but are difficult to directly compare quantitatively with model output (although see Sellwood and Valdes, 2006 for one excellent approach).

The second approach we employ is to compare CMM temperatures predicted by the models, point by point, with those inferred from paleoclimate proxies. This approach is quantitative and provides explicit error bars, but estimates may not be altogether accurate for all the reasons described previously for MAT. Furthermore, when considering the error bars on CMM estimates, it is important to consider that lower bounds on CMM are more likely to be accurate because those involve strong biological/physical constraints (i.e. palms do not tolerate freezing). The upper error bound on CMM is probably less constrained. Such CMM estimates are not as broadly available as the qualitative records but are as roughly comparable in their extent as the MAT records and often derive from the same analyses. In this study we compile CMM estimates primarily derived from CLAMP but supplemented by other sources, such as isotopic analysis and the co-existence approach. The error estimates are derived from the primary sources and do not account for temporal variation, unlike the MAT error bars. The CMM estimate sources are detailed in Table 1.

3.1.3 Uncertainties in topography, timing, and paleolocation

A major source of ambiguity in model-data comparison is the difference between the modelled elevation and the actual elevation of the proxy locality. Errors of $\sim 6^{\circ}\text{C}$ can be introduced by a 1 km difference in elevation between model and data (Sewall et al., 2000). Every effort has been made to minimize this error by making the most accurate reconstruction of paleoelevation utilizing the available information at the time (Sewall et al., 2000). But, such estimates are controversial and have uncertainty associated with them of at least ± 500 meters in mountainous regions where much of the proxy data are found (Peppe et al., 2010; Hren et al., 2010; Rowley, 2007; Forest, 2007; Meyer, 2007; Molnar, 2010). Paleoelevation scholarship has progressed in the decade since our topography dataset was created and many important details have changed. Nevertheless, little consensus exists on those details (Davis et al., 2009; Mulch et al., 2007; Molnar, 2010) so it is difficult to meaningfully improve the situation at the moment.

Even if the mean elevation of a region was correctly represented by the elevation of a given model grid cell, error can be introduced by the fact that many proxy records are found within basins in high relief regions. This bias in preservation can introduce large errors even when the gross features of topography are fully correct in the model (Sewall et al., 2000). Thus the real errors are probably closer to ± 1000 m in high elevation, high relief regions such as intermontane western North America.

We quantify that uncertainty here by calculating the standard deviation of topography averaged over all elevations greater than 1500 m in a modern high-resolution digital elevation model. Utilizing the average $2\text{-}\sigma$ topographic variation in modern topography (450 m) as an estimate of relief in regions of high mean elevation in the Eocene, we find a $\pm 2.4^{\circ}\text{C}$ uncertainty in temperature introduced as a result of relief, assuming a $5.3^{\circ}\text{C km}^{-1}$ lapse rate based on the work of Hren et al. (2010).

Temporal sampling uncertainty is also a concern since a modelled time slice represents millions of years, whereas substantial evidence exists for climate fluctuations of $\pm 5^{\circ}\text{C}$ at a single location over that time scale (Wilf et al., 1998; Wilf, 2000; Bao et al., 1999; Wing et al., 2000, 2005). Consequently, wherever a time series is available at a locality, we compare the mean as well as the maximum and minimum of the series with the stated random calibration error of the individual proxy data points superimposed. Where a single data point is available, we utilize the stated methodological error although these certainly underestimate the true error range.

Errors are also introduced by various sources of geographic uncertainty, including: uncertainty in the true paleo-latitude and longitude of the fossil locality; uncertainty introduced by differences between the true location of the paleolocality and the location of the paleolocality's position on

the model grid (i.e. differences in reference frame). This is exacerbated by uncertainty in true paleotopography and sea level and the differences between these and the modelled representation of these real-world features. The uncertainty in temperature assignable purely to uncertainty in a locality's true paleolatitude and longitude is relatively small ($<2^{\circ}\text{C}$), both because the position errors themselves are rather small ($\sim \pm 2^{\circ}$ latitude, $\pm 5^{\circ}$ longitude) and because early Eocene temperature gradients were quite small (Greenwood and Wing, 1995). More important is the fact that there can be large differences in absolute paleoposition between two reconstructions, and specifically between the reconstruction that was the basis for the model grid (Sewall et al., 2000) and more recent reconstructions (Markwick, 2007; Mueller et al., 2008).

If, for example, recent reconstructions indicate that North America was 5° further south than the reconstruction in the model, should the model-data comparison be performed at the true paleolatitude and longitude, or at the appropriate model grid paleolatitude and longitude? Or should the temperature estimate from the model grid be corrected back to its correct latitude using an empirical correction? Provided temperature gradients are weak, this is not a large source of uncertainty, introducing perhaps 2.5°C error in the example given, but it has the potential to be a systematic bias.

This can be a more substantial problem in an occasional situation, such as the MBT-CBT record of Weijers et al. (2007a) or the palynological record of Eldrett et al. (2009) which are derived from marine cores and the location of terrestrial source region is primarily conjectural and reflects either a localized source or an integrated signal from regions that are not tightly constrained. As shown below, the potential error associated with this is not estimated to be large.

Further ambiguity and room for error arises when there is a large mismatch between the classification of a locality as land or ocean between the model and reality. For example, near the Gulf Coast of North America or in New Zealand, the true paleolocation of a terrestrial site places it solidly in the ocean on the coarse-resolution model grid. This introduces the problem of deciding to use the nearest available terrestrial grid cell or the nearest grid cell for comparison regardless of whether it is land or ocean. In the case of New Zealand, the South Island was small and barely sub-areal, so it is simple to consider the nearest ocean grid cell as being a reasonable estimator to the terrestrial temperature, but with difficult to quantify error associated with the approximation. For the Gulf Coast data a better approach, given the weak temperature gradients, is to use the nearest land surface grid cell which is more likely to properly account for land-sea temperature contrasts.

It is for these reasons that it is common in model-data comparison studies to compare zonal mean model-derived temperatures with proxy data (Huber and Sloan, 2001; Shellito et al., 2003). It is hoped that many of these errors will cancel out when the data are aggregated and averaged. Whether

or not comparing sparsely-sampled data with zonal means actually leads to a robust characterization of model-data difference has never been quantitatively answered. Pointwise comparison of models and data has been shown to be important in establishing model fidelity in reproducing climate trends in the recent observational record (Duffy et al., 2001) and it seems likely to be a better approach, albeit more challenging, because it requires accounting for random errors and bias in geographic assignment.

3.2 Modelling

As described in previous work, Eocene conditions have been simulated with a fully-coupled general circulation model, the National Center for Atmospheric Research (NCAR) Community Climate System Model version 3 (CCSM3). These simulations span a range of $p\text{CO}_2$ from 560 ppm to 4480 ppm. After synchronous, coupled integration of 2000–5000 years (some simulations equilibrate faster than others), all the simulations equilibrated in terms of surface and global mean ocean temperature and ocean “ideal age” tracers. Aspects of the coupled simulations with a focus on the ocean circulation are described in Liu et al. (2009) and Ali and Huber (2010). The ocean-atmosphere circulation of these simulations are similar to those of Winguth et al. (2010) and Shellito et al. (2009), who utilized the same model with nearly identical boundary conditions, although the simulations were not integrated as long and the solar constant and aerosol treatments were somewhat different. Winguth et al. (2010) provide a good overview of the ocean-atmospheric dynamics simulated by CCSM3 for Eocene conditions that are representative of those in the simulations described here.

The mixed layer depth, sea surface temperature (SST), sea ice fraction, and ocean heat convergence patterns derived from these coupled simulations were utilized to create mixed-layer “slab” oceans for coupling to the atmospheric component of CCSM3, the CAM3. Interesting aspects of the atmospheric dynamics produced in the simulations were described elsewhere (Caballero and Huber, 2010; Williams et al., 2009; Sherwood and Huber, 2010; Eldrett et al., 2009). Of specific importance to this study, an important high latitude feedback in CAM3 was shown to enhance warming near the poles in the Eocene (Abbot et al., 2009b).

Within the context of this large suite of simulations we chose two fixed-SST simulations to provide the first rigorous model-data comparison appropriate to early Eocene continental climates in CAM3/CCSM3. These SSTs are repeating 12-month climatologies derived from the last hundred years of two different fully coupled simulations. Two simulations utilizing the CAM, version 3.1 (Collins et al., 2006) coupled to the standard Community Land Model (CLM3) at T42 spectral resolution ($\sim 2.5^{\circ} \times 2.5^{\circ}$ resolution) incorporating the Eulerian dynamical core, at $p\text{CO}_2$ of 4480 and 2240 ppmv were analyzed. The solar constant was set at

1365 W m^{-2} , aerosol radiative effects were set to zero, and other trace gas concentrations and orbital parameters were set to pre-industrial conditions. The land surface boundary conditions used were the same as described in Sewall et al. (2000) although they have been reinterpolated from the original $2^\circ \times 2^\circ$ data to T42 resolution as opposed to the T31 resolution version that was used in much of the previously described work (Huber and Sloan, 2001; Huber and Caballero, 2003; Shellito et al., 2003, 2009; Winguth et al., 2010). Shorter simulations at resolutions up to T170 ($0.7^\circ \times 0.7^\circ$) were carried out and the results discussed here are robust at higher resolution.

Here we present results of simulations from the NCAR CAM3.1 at T42 resolution driven by these specified SSTs derived from coupled simulations. The fixed SST simulations were carried out for >50 years to ensure equilibrated climatologies and means were calculated over the last 25 years. The main simulation, referred to as EOCENE-4480, was carried out with 4480 ppmv CO_2 and is meant to represent the early Eocene. As described previously, this does not imply that 4480 ppmv is the actual value for the early Eocene; it is merely the radiative forcing necessary for a climate model with a weak sensitivity to achieve climate conditions close to those of the early Eocene. For context and to give an indication of the robustness of these results we, have included results from another case, EOCENE-2240, carried out with 2240 ppm CO_2 and which we have previously shown is a better fit to mid-to-late Eocene climate (El-drett et al., 2009).

In Sect. 4 we present a comparison of zonal mean model results for modern and Eocene conditions, maps of modelled Eocene surface temperatures, and pointwise comparison of proxy data and model results. For this comparison, all proxy records were rotated back to their paleo-locations at approximately 55 mya utilizing the GPLATES software (www.gplates.org) and plate model of Mueller et al. (2008) with some slight adjustments made to accommodate georeferencing differences between the model plate locations and the GPLATES reconstruction.

First, the modern location of the paleo-localities was introduced into GPLATES and then the localities were rotated back to their positions at 55 mya (Fig. 1a). The plate locations determined by GPLATES (<http://www.gplates.org>) were then compared with the paleogeography utilized in the modelling, derived originally from Sewall et al. (2000) in order to determine that they were generally comparable (Fig. 1b–c, 1d–e). In almost all cases, the paleogeography in the model was consistent with the GPLATES 55 mya reconstruction and where adjustments were necessary, they were objectively determined by comparing continental boundaries and making uniform, small adjustments to GPLATES reconstructed latitude and longitude to align correctly with geographic features in the model paleogeography. When this was done, model predictions were compared with proxies at these adjusted locations and inspection of the

results was used to evaluate that the potential errors introduced by differences in true and modelled paleo-location are small (Fig. 1d–e).

Furthermore, a comparison of the model paleogeography we used and the early Eocene paleotopography independently derived by Paul Markwick (Markwick, 2007) revealed that our reconstructions were in general agreement, indicating robustness of general features but differing in important details, for example in intermontane western North America (Fig. 1d–e, 1f). In the subsequent model-data comparison, we accounted for uncertainty in the true paleolocation, its temporal variation over the early Eocene, and the discretization introduced by the model grid by including error bars of $\pm 2.5^\circ$ latitude on both proxy records and the model results. A spreadsheet including the references and values used in the paleotemperature reconstruction has been included as supplemental material. The GPLATES Markup Language (GPML) file used to rotate modern localities is also available as supplemental material.

4 Results

4.1 Modeled zonal-mean surface temperatures

As an overview of the climate changes occurring in the Eocene simulation, Fig. 2 compares modeled zonal-mean surface temperatures from the EOCENE-4480 run with a CAM3 simulation using modern boundary conditions as specified by the Atmospheric Model Intercomparison Project (AMIP). In AMIP simulations, modern, observed SSTs (and other boundary conditions) are specified. The zonal mean includes averaging over both land and ocean. At high latitudes, the Eocene case is $30\text{--}50^\circ\text{C}$ warmer than modern in both MAT and seasonal means. Differences are more muted in the tropics, ranging from $6\text{--}10^\circ\text{C}$ in all seasons. These results qualitatively capture the salient features noted in the proxy temperature record (Barron, 1987): annual mean temperatures much warmer than modern, especially at high latitudes, winter season temperatures generally above freezing, and a much reduced equator-to-pole temperature gradient. The hemispheric asymmetry in temperature increase is consistent with the removal of the Antarctic Ice Sheet and the associated $15\text{--}20^\circ\text{C}$ change associated with the decrease in elevation.

4.2 Maps of modeled surface temperatures

To evaluate the robustness of these climate change patterns to the chosen level of greenhouse gas forcing, we compare the EOCENE-2240 and EOCENE-4480 simulations in Fig. 3. MAT in the EOCENE-4480 case (Fig. 3a) is above freezing everywhere. With the exception of inland Antarctica and a small region in high latitude, mountainous western North America, it is warmer than 10°C everywhere, as required by proxy records (see discussion in Sect. 3.1.2). Maximum

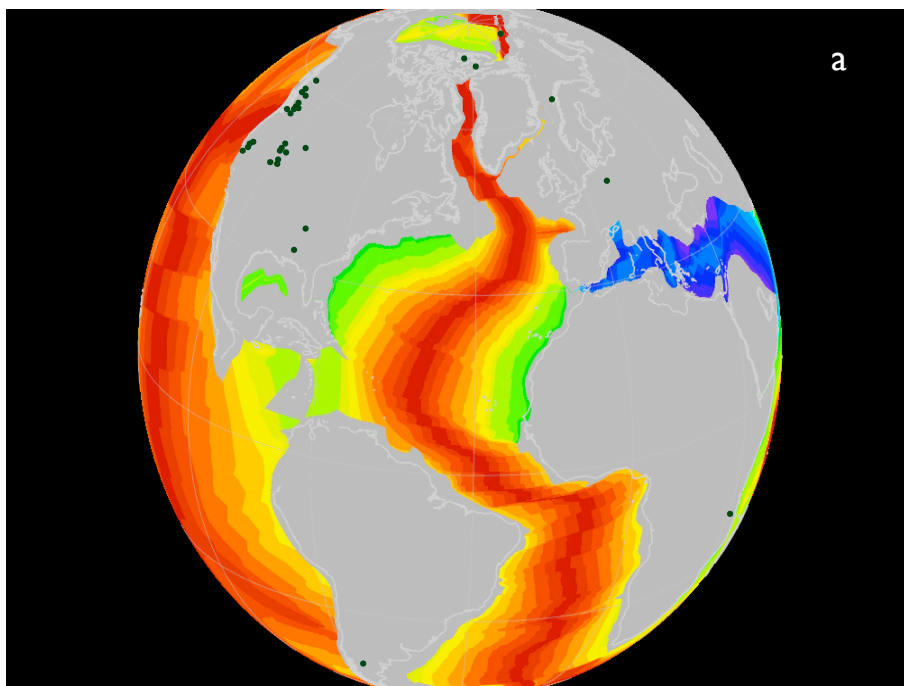


Fig. 1a. Comparison of paleogeographic information used in the simulation with independent reconstructions from Mueller et al. (2008) via the freely available GPLATES software and via personal communication from Paul Markwick. In (a) a plate tectonic reconstruction for 55 mya from GPLATES including sea floor age is shown. Terrestrial paleoclimate proxy localities are indicated on this map with green circles. The modern continental boundaries in their 55 mya positions as reconstructed by GPLATES compared with Markwick's paleogeography are shown in (b, d). The topography used in model (c, e) is compared with the independently derived high resolution early Eocene topography of Markwick (based on Markwick (1998)) (b, d). In these figures, the paleoclimate proxy localities are indicated with magenta circles. The GPLATES derived plate configuration is a reasonable match to the land-sea distribution developed in Sewall et al. (2000) used in the simulations here (c, e). It should be noted that in some cases GPLATES derived paleolocations must be adjusted slightly to fall on land or to be in the right location with respect to topography, as described in the text. In (f) an example of how the pointwise comparison of model and proxy records is performed is shown. Colors are modelled temperatures and the text indicates the abbreviated names of proxy localities. Based on modern latitude and longitudes the localities are rotated back to 55 mya positions using GPLATES, thus enabling the best objective placement of the paleo-positions within the model's reference frame. As (f) shows, errors in paleo-position are unlikely to introduce large errors in inferred temperature except in regions with strong temperature gradients, i.e. in regions of strong elevation variation.

SSTs are about 35 °C, in general agreement with proxies (Pearson et al., 2007; Huber, 2008; Jaramillo et al., 2010; Schouten et al., 2007). The hottest temperatures are on land in the subtropics, where annual mean values are 45 °C. No proxy records currently exist to support or refute this result.

Winter temperatures in the EOCENE-4480 case remain above freezing everywhere except for inland Antarctica. Temperatures in intermontane western North America dip near zero in agreement with the existence of microthermic flora – though with an absence of frost intolerant macroflora – in various upland localities in the region (Smith et al., 2009). Maximum terrestrial temperatures in summer of up to 50 °C are reached in northern and southwestern Africa, southern central South America, southwest North America, central Europe and western central Asia. The interiors of North America and Amazonia are also very hot (>40 °C) in summer. It should be noted that these are seasonal (3-month) means and that temperature extrema on subseasonal

time scales may be substantially higher; we present seasonal means here since they are likely to best reflect the processes that shape the long-term distribution of proxies, flora and fauna. A comparison with the coldest climatological monthly mean temperature is carried out below for strict comparison with CMM proxy records.

Comparison of the two Eocene cases allows the identification of certain regions that are especially sensitive to a globally uniform radiative forcing. The land masses respond roughly homogeneously in the annual mean, though with some enhanced warming in eastern and central North America, central Asia and central South America. Seasonal differences are more pronounced. In boreal winter, the mid-to-high latitude interiors of North America and Asia are loci of focused warming in response to the increase in $p\text{CO}_2$. Northern and central North American and Asian MATs are between −10° and 0 °C in winter in the EOCENE-2240 case, but above freezing everywhere in the EOCENE-4480 case.

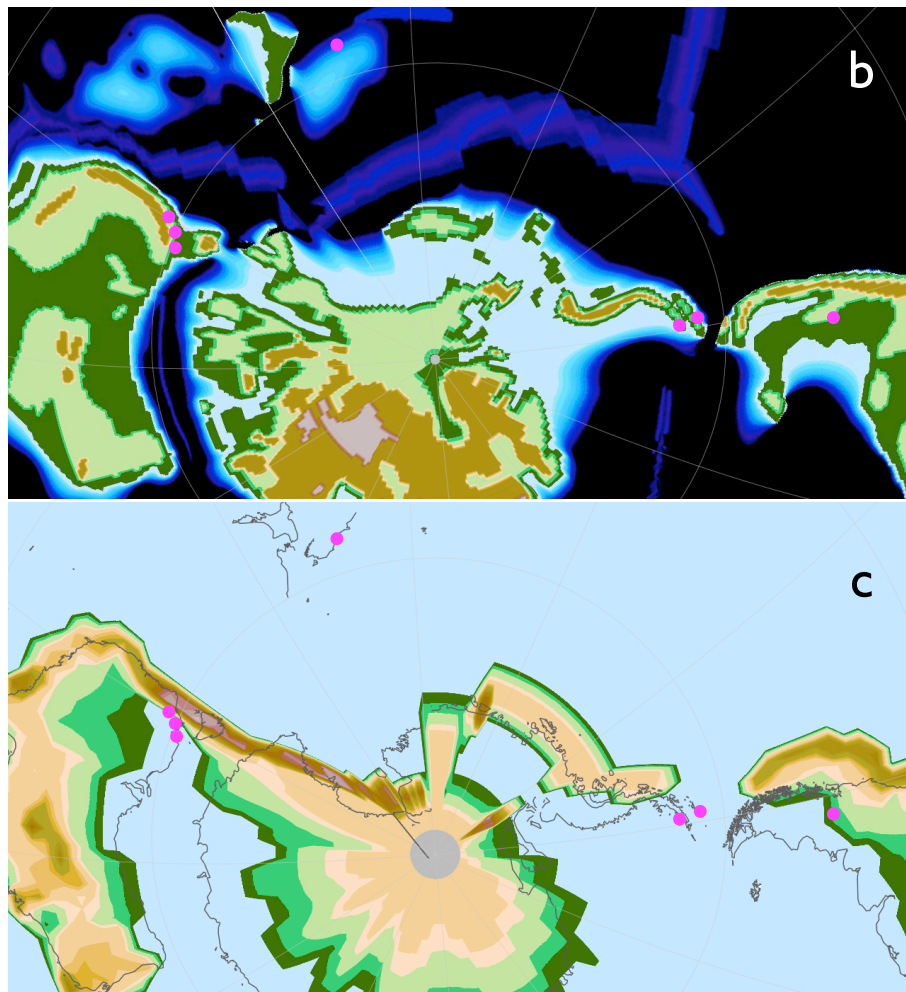


Fig. 1b–c. Figure 1 continued, see Fig. 1a for description.

Localized warming is also evident in austral winter in the interior of Antarctica and in the boreal summer of west central Asia, and in midlatitude North America and Europe. These results show that localized temperature changes of up to 10 °C can occur seasonally even with globally homogeneous forcing and annual-mean SST change of less than 3 °C everywhere. Though the EOCENE-2240 case is very warm and has no sea ice, the additional greenhouse gas forcing in the EOCENE-4480 case yields a polar-amplified warming, with most of the amplification occurring in the winter season. The overall pattern is quite similar to the effect of doubling $p\text{CO}_2$ in modern CAM3/CCSM3 simulations, despite the large differences in continental configuration, background greenhouse gas values, and other boundary conditions. Polar amplification in the absence of sea-ice has been attributed in various studies to increased latent heat transport (Langen and Alexeev, 2007; Caballero and Langen, 2005) and to high-latitude cloud feedbacks (Abbot et al., 2009a,b); the latter have been shown to be especially important in Eocene

CAM3 simulations. Much of the terrestrial winter response seen here (between the two Eocene cases) correlates well with the near complete loss of snow cover and associated albedo decreases in the EOCENE-4480 case.

Most crucially for this study, the fact that winter season temperatures are above freezing in all regions for which quantitative and qualitative proxy data indicate frost intolerance (Greenwood and Wing, 1995; Markwick, 1998; Collinson and Hooker, 2003; Markwick, 2007; Kvacek, 2010) suggests that the EOCENE-4480 simulation does not suffer from the equable climate problem. This comes at the expense of a very large radiative forcing, causing temperatures >40 °C on land over significant regions. However, tropical SSTs in the EOCENE-4480 simulation are in good agreement with what is currently the best tropical proxy temperature records we have, from Tanzania (Pearson et al., 2001b, 2007) and off the coast of Colombia (Jaramillo et al., 2010), though the absolute temperatures inferred from this record are subject to significant uncertainty (Huber, 2008).

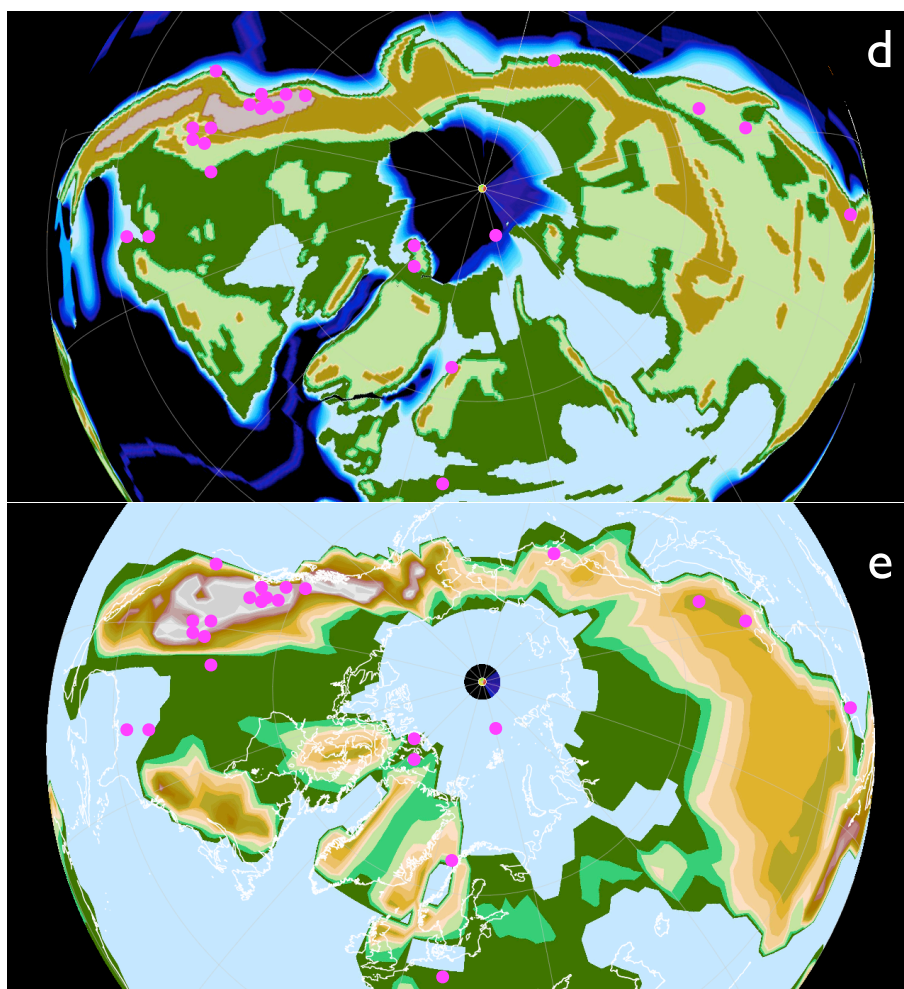


Fig. 1d–e. Figure 1 continued, see Fig. 1a for description.

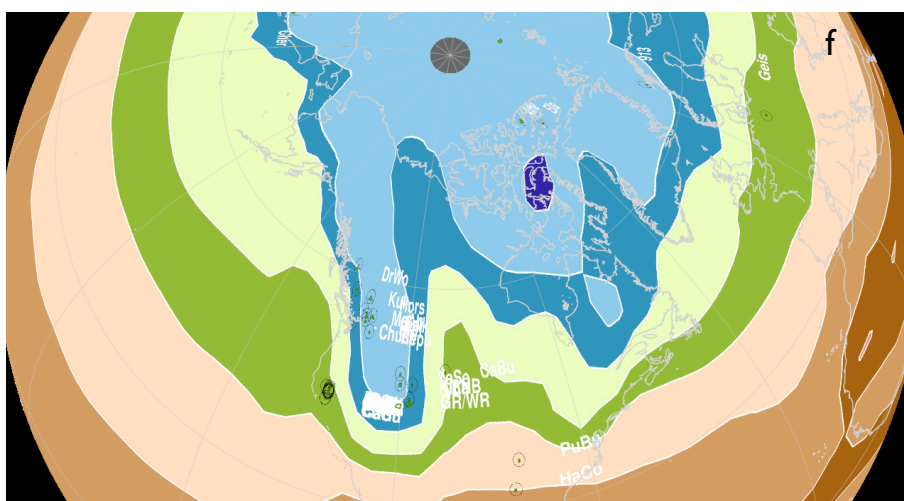


Fig. 1f. Figure 1 continued, see Fig. 1a for description.

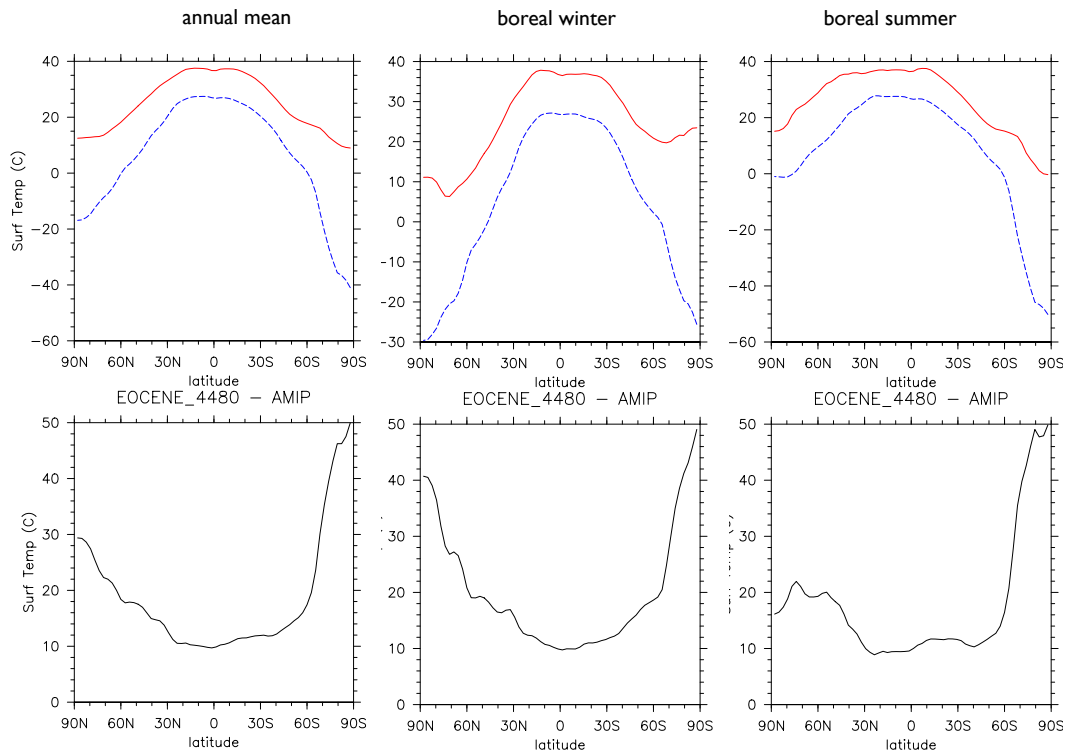


Fig. 2. Zonal mean surface temperature from the EOCENE-4480 (red) and modern, AMIP (blue) simulations as described in the text. In the upper row, the annual (left) boreal winter (middle) and boreal summer (right) means are shown. In the lower row, the anomaly, EOCENE-4480 minus modern, AMIP simulation is shown.

4.3 Pointwise data-model comparison

Pointwise comparison of proxy data and EOCENE-4480 modeled MAT (Fig. 4) reveals reasonably good overall agreement. Substantial scatter in the proxy data is apparent in the Northern Hemisphere midlatitudes, but is due mostly to data from intermontane western North America and likely reflects real gradients in topography and surface temperature that are not well represented in the low resolution topography used in the model (Fig. 5). The model and data generally agree within their respective errors, which include a gross estimate of uncertainty due to modelled versus real elevation in mountainous regions, as discussed in Sect. 3.1.3. Both simulated and proxy data MATs are $\sim 35^{\circ}\text{C}$ at the poleward edge of the subtropics. The model does not appear to capture the peak high latitude temperatures derived from MBT-CBT, although it does capture warm temperatures on Axel Heiberg and Ellesmere Islands. The Axel Heiberg Island proxy records may reflect cooler conditions because they are middle Eocene in age, but the Ellesmere Island data, which is early Eocene in age produces a similar MAT, so the fact that the model matches the data at these high latitude sites is not necessarily attributable to temporal sampling issues. It has been conjectured that the MBT-CBT proxy may be biased to summer values (Weijers et al., 2007a; Eberle et al., 2010), in which case the data and model are more concordant.

Inspection of Fig. 4b suggests that the model does not suffer from a strong bias either to hot or cold temperatures, with roughly equal numbers of points falling on either side of the 1:1 line. The mean data-model difference is 0.7°C , while the standard error is 1.3° (assuming all data points are uncorrelated), implying that there is no statistically significant overall bias. This lack of global bias is qualitatively confirmed on a regional basis by Fig. 5, which shows positive and negative errors scattered randomly with no obvious bias in any region. On the other hand, the 2 largest model-data discrepancies are both on the warm side, with the model overestimating the data by roughly 9°C . Most of the errors lie in regions of steep orography (Figs. 1d–e, 5), with a slight tendency for overprediction of temperatures by the model at lower elevation and underprediction of temperatures along topographic highs; these discrepancies plausibly result from errors in paleolocation of paleoelevation. These nearly bias-free results are a vast improvement over our previous model-data comparison (Huber et al., 2003), which used an older version of the NCAR coupled model with 560 ppmv CO_2 and showed model MATs systematically offset from proxy data by 10°C or more over large parts of the globe.

In Fig. 6 we compare modelled and reconstructed CMM for each locality where quantitative paleoclimate proxy estimates have been compiled. CMM in the model was calculated as the coldest monthly mean value from the 12-month

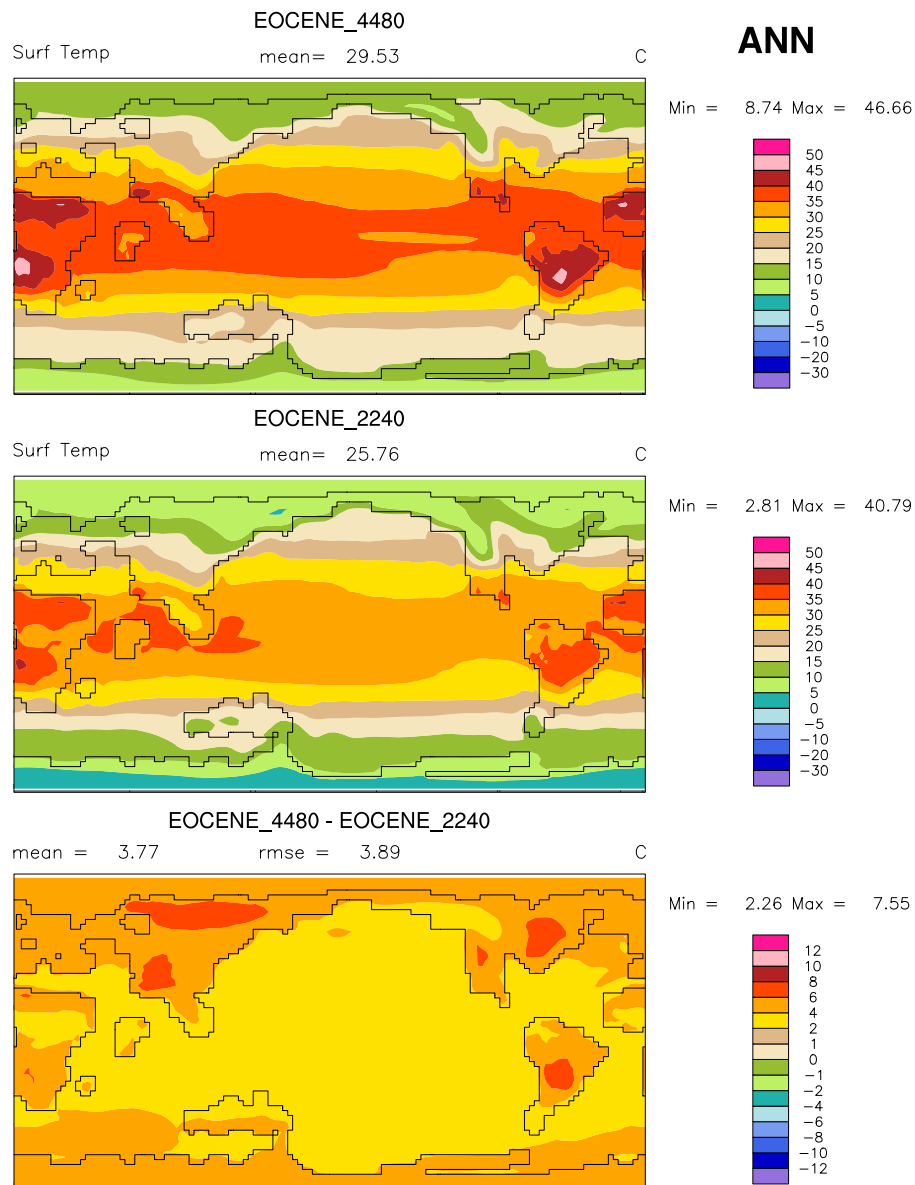


Fig. 3a. Maps of time averaged surface temperature from the EOCENE-4480 and EOCENE-2240 simulations. The annual (a), boreal winter (b), and boreal summer (c) means are shown. The upper row is the EOCENE-4480 case, the middle row is the EOCENE-2240 case, and the bottom row is the anomaly. The range in values is indicated in the color bar in (a) and is the same in (a–c). Units are in °C.

climatology to be as close to possible to the standard definition of CMM employed in paleoclimate reconstructions. Correspondence is excellent, even in mid-to-high latitude regions that have previously been challenging (Shelito et al., 2003). The main remaining discrepancy is at the Puryear-Buchanan site (37.1° N, 70.7° W, see table), where the model produces a CMM of nearly ~25 °C whereas the data are ~16 °C. This may not be too serious given that there is wide uncertainty in the proxy data estimate (Greenwood and Wing, 1995) and other nearby localities, albeit from marine proxies, show winter temperatures of 21.6–24.3 °C

(Kobashi et al., 2004). The model is clearly capable of matching both the general qualitative pattern of a frost-free early Eocene (Fig. 3b), while giving a good quantitative match to winter temperature minima where such data exist (Fig. 6).

Finally, we compare the degree of polar amplification in the data and model simulation. This is a crucial point, as it bears on the long-standing challenge to our ability to predict basic patterns of past climate change (Barron, 1987; Lindzen, 1994; Sloan et al., 1995; Valdes, 2000; Huber and Sloan, 1999; Kirk-Davidoff et al., 2002; Miller et al., 2010;

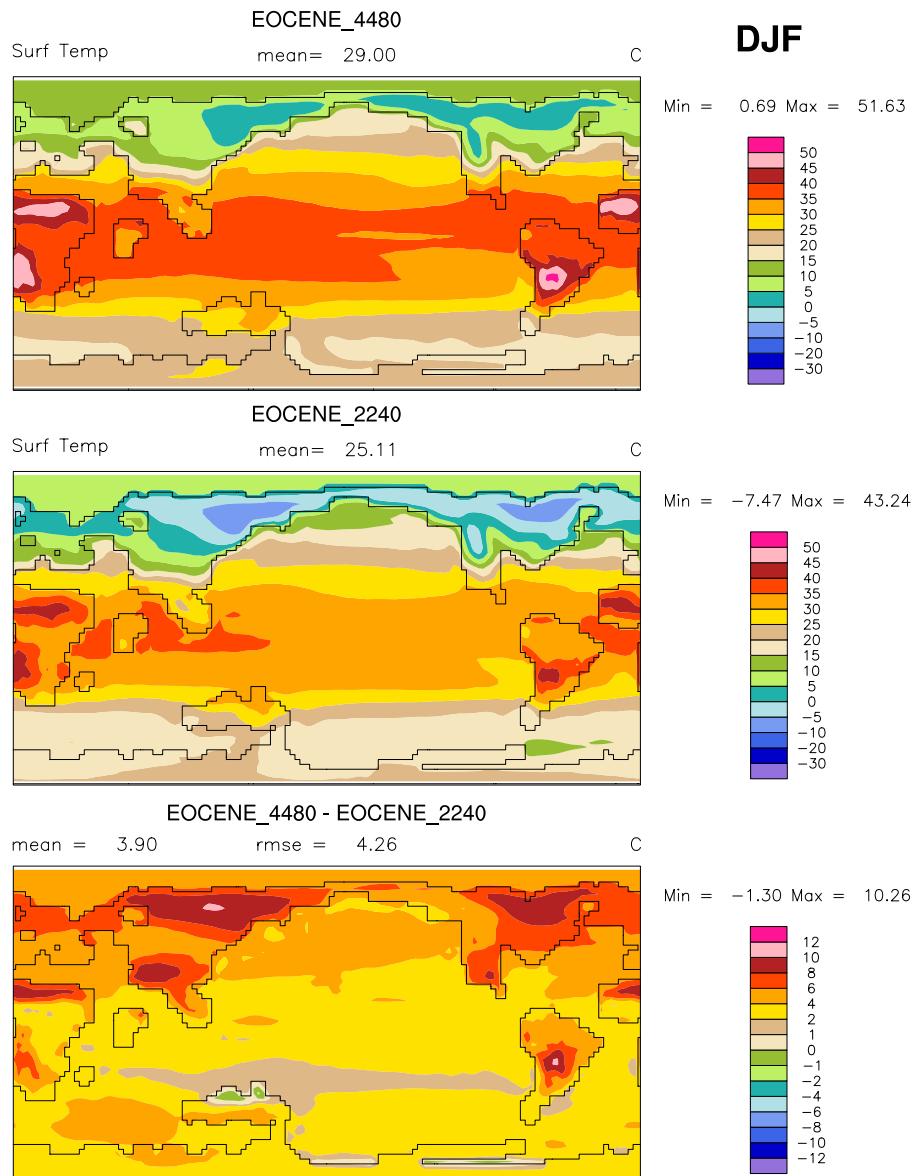


Fig. 3b. Figure 3 continued, see Fig. 3a for description.

Abbot et al., 2009b). To establish the point-by-point degree of temperature change, we take the anomaly of proxy-based Eocene MAT estimates compared to modern observed MAT at the same location. Modern MAT from the European Center for Medium-Range Weather Forecasts 40-Year Reanalysis Project (ERA-40) was used for modern observations. To calculate the pointwise warming of the model with respect to modern, we compare the MAT anomaly point-by-point between the EOCENE-4480 case and the modern CAM3 AMIP simulation discussed in Sect. 4.1. This comparison (Fig. 7) reveals a generally very good correspondence between the modelled and reconstructed warming at all latitudes. The zonal-mean modelled temperature anomaly with respect to

modern conditions gives a good overall agreement with the observational anomalies, though regional and local details introduce significant scatter. Overall, it appears that the model is capable of quantitatively reproducing the polar amplification of terrestrial warming in passing from modern to early Eocene conditions.

5 Discussion

New estimates emerging from improved data coverage, the introduction of new proxies, and reinterpretation of older proxy records, show that temperatures in the early Eocene

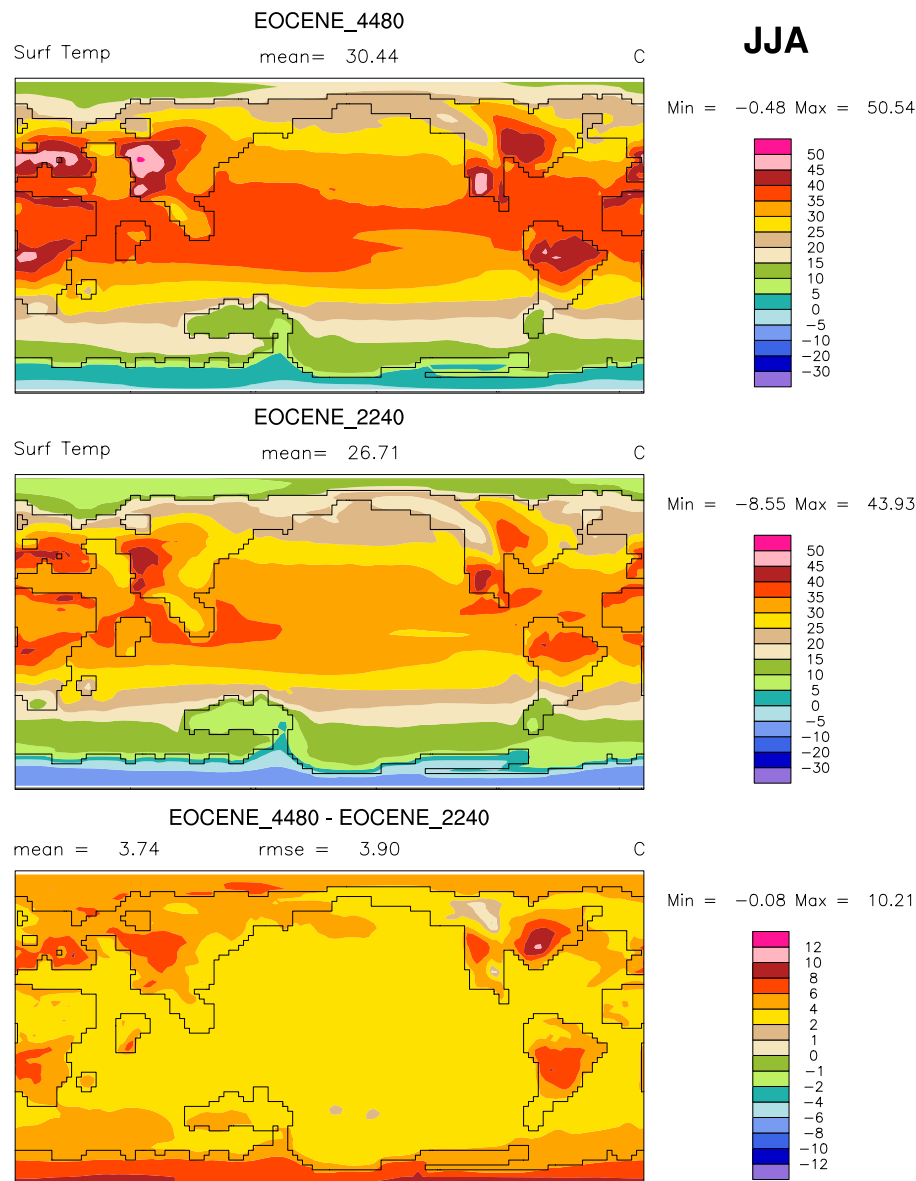


Fig. 3c. Figure 3 continued, see Fig. 3a for description.

were much warmer than previously reconstructed (Covey et al., 1996). Thus, revisiting the equable climate problem requires rethinking how to frame the problem. Most climate model simulations have not investigated temperatures – including tropical temperatures – nor greenhouse gas forcing, in the ranges now considered likely. Our perspective in this paper is that most previous attempts to solve the equable climate problem have suffered from the question being ill-posed. Climate was even warmer than previously reconstructed and the forcing or climate sensitivity were also probably larger. Utilizing these new higher temperature terrestrial reconstructions for comparison makes the model-data comparison more challenging than some prior attempts given

the historical tendency of the models to underestimate extratropical temperatures. Yet our results clearly show that the model makes credible predictions for both the winter season warmth, mean terrestrial temperature change, and the polar amplification of warming in the early Eocene, to our knowledge, for the first time. This was accomplished by incorporating very high values of greenhouse gas radiative forcing. Note that this approach is in a rough sense equivalent to “tuning” climate sensitivity to a higher value, but is much simpler in practice. The 4480 ppm CO₂ concentration used here should not be construed literally: it is merely a means to increase global mean warmth.

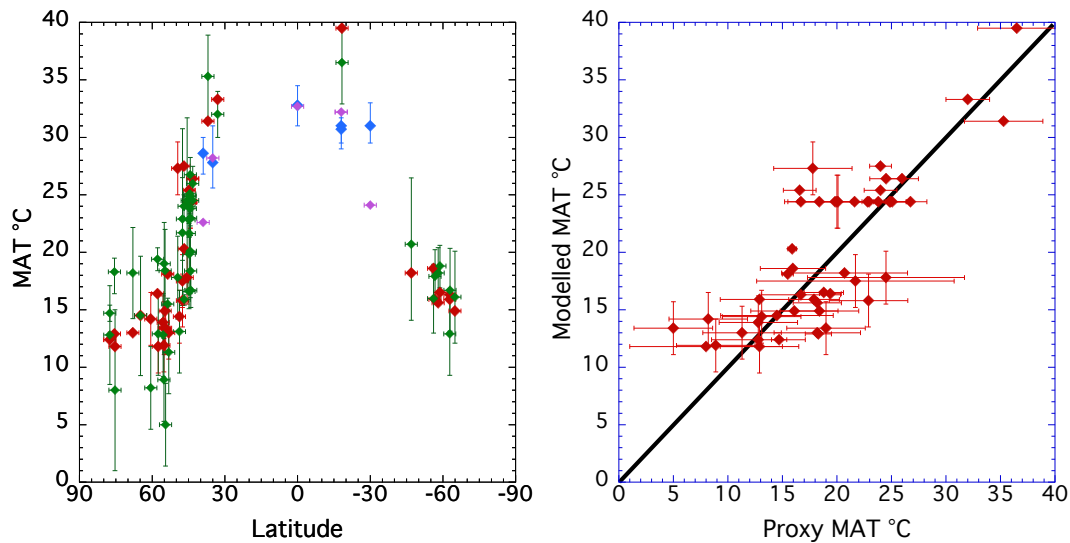


Fig. 4. On the left, a pointwise comparison of annual mean terrestrial surface temperature (MAT) from EOCENE-4480 (red) and proxy data estimates (green) versus latitude. The vertical error bars on the proxies represent the methodological error plus the temporal variation (if a time series) as further described in the text. The model vertical error bars are only included in regions considered to have high elevation and represent topographic uncertainty as described in the text. Horizontal error bars indicate the uncertainty in the position of the paleolocalities and the propagation of that uncertainty onto the discrete model grid (as described in the text). A comparison is also made for reference of tropical SSTs (reconstructed in blue and modelled in magenta). The tropical reconstructions follow those in Huber (2008) with the exception of the Tanzanian (19 South latitude) TEX₈₆ data which were recalculated using the Liu et al. (2009) calibration. It should be noted that the potential uncertainty is underestimated, since only one set of calibrations was used for each proxy and therefore a major source of uncertainty is ignored. On the right, the temperatures reconstructed from terrestrial proxies are plotted versus modelled and the 1-to-1 line is plotted in black. The error bars are the same as previously described.

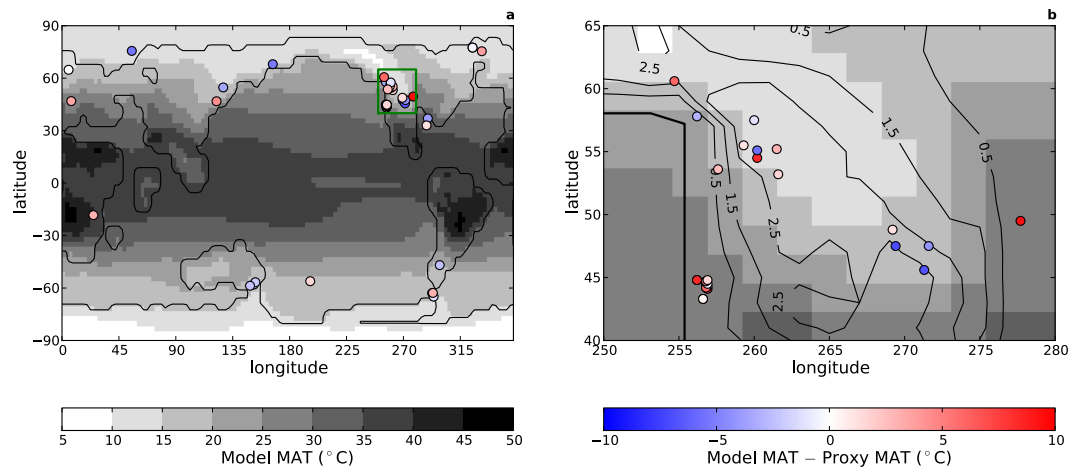


Fig. 5. Difference between modelled and reconstructed MAT as indicated by the color bar (on the right) overlain on the model predicted temperatures (grey scale color bar on left).

Model-data discrepancies remain, however. These do not appear to be of a magnitude that a compelling case for completely “missing physics” can be made, but they do point to many areas that need improvement. But, as described previously in Sects. 2 and 3.1.3 there may be limits to how well we can ever expect the simulations to match observations, given the incompleteness of the record and, of course,

the limitations of the models – we can never expect them to better in the past than they do today, and the weaknesses of modern models are legion. Concrete strategies for continued improvement for the Eocene do exist. There are several factors that should be considered in further refining the model data comparison. These include some concrete refinements described further below: improvements to paleotopography

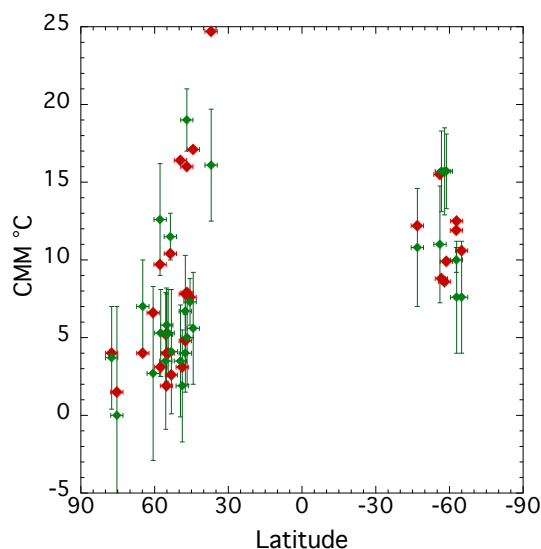


Fig. 6. A pointwise comparison of cold month mean temperature (CMM) from the EOCENE-4480 (red) and proxy data estimates (green) versus latitude. The error bars are as described in the text.

and their representation in the model, exploration of sensitivity to orbital forcing, and improvements to the vegetation boundary conditions.

5.1 Further improvements

5.1.1 Resolution

As discussed by Sewall et al. (2000), the low resolution paleotopography used in this study is probably not only a source of random temperature error (due to random errors in topography) but also probably a source of cold bias. This is because paleoclimate proxies are likely to be warmer than model estimates since they reflect conditions at the bottom of valleys in high relief areas that have a high mean elevation. This systematic bias was not corrected for in this study.

One approach to solving this problem is to use a limited domain atmospheric model at very high resolution (i.e. ~ 50 km), which might enable a full representation of the basin and peak scale orographic details that plague lower resolution, global climate models. This has been attempted over Eocene North America by Sewall and Sloan (2006), and Thrasher and Sloan (2009, 2010) with varying success. These studies clearly demonstrate that modelled temperatures are sensitive to resolving fine scale topographic detail, but little reduction of the model-data mismatch common to lower-resolution global model simulations was noted.

This is probably due to two factors. First, knowledge of the true paleotopographic variation on those length scales is still rudimentary, hence random scatter is introduced. Second, and more importantly, limited area models use dynamics to downscale global model output to finer scales,

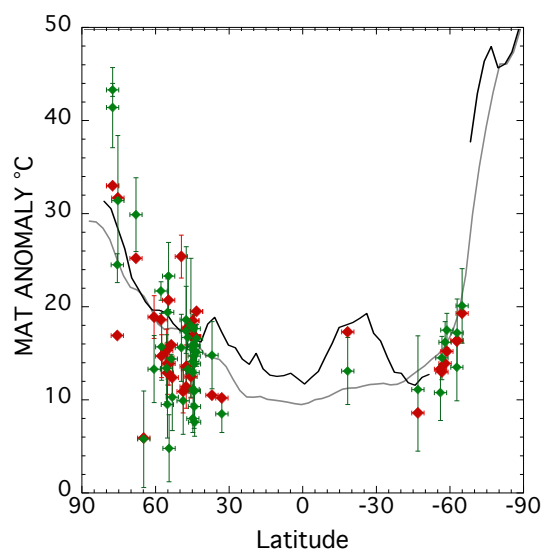


Fig. 7. A pointwise comparison of anomaly of annual mean terrestrial surface temperature (MAT) from the EOCENE-4480 (red) and proxy data estimates (green) minus the modern temperature value at those locations versus latitude. The error bars are the same as described in Fig. 3. The zonal mean anomaly of the EOCENE-4480 case minus the modern AMIP case plotted originally in Fig. 2 is shown in grey on this figure for reference. The land-only zonal mean anomaly is also shown in black.

but they are unlikely to generate temperature results substantially different than the global model used to drive them. In other words, limited domain models such as this, typically produce the same aggregate temperatures as the global models, but with better representations of fine scale variations. Consequently if the global model is biased to too cold values, the limited area model will produce the same result, but at higher resolution (Sloan, 2006; Thrasher and Sloan, 2009, 2010).

Limited domain modeling is likely to be a very effective approach once global models produce results roughly in agreement with proxy data and once high resolution topographic reconstructions are available and are trustworthy. Our results here suggest that this high resolution approach in conjunction with high resolution, accurate paleotopography (and vegetation) may lead to a substantial reduction in the midlatitude scatter between proxy data reconstructions and model output. Building model boundary conditions directly from a properly geo-referenced DEM, such as implemented by Markwick and Valdes (2004), is a clearly better approach than the one originally used in Sewall et al. (2000) and subsequently re-used in the coupled modeling studies of Huber and Sloan (2001), Shellito et al. (2009), Winguth et al. (2010) and in this study.

5.1.2 Orbit

All of these simulations were carried out assuming a modern orbital configuration. Clearly, orbital variations caused fluctuations in temperature patterns in the early Eocene and inclusion of this feature in simulations would alter the seasonal and spatial patterns in detail. Cold summer orbital and hot summer orbit configurations would clearly impact the seasonality in these simulations (Morrill et al., 2001; Sewall et al., 2004; Lawrence et al., 2003). Nevertheless, it is revealing that the relatively crude approach used here of increasing the global radiative forcing due to $p\text{CO}_2$ had a more pronounced impact on reconciling models with data, including seasonally sensitive data, than any orbital approach has so far.

5.1.3 Vegetation

The simulations are likely to be sensitive in their regional details—especially in terms of the localized seasonal temperature extrema—to the vegetation distributions and their representation in land surface models (DeConto et al., 1999; Sewall et al., 2000; Shellito and Sloan, 2006a,b). Cold season, extratropical temperatures are likely to be especially sensitive to vegetation albedo and leaf area index (LAI), whereas peak tropical temperatures are likely to be sensitive to evapotranspirational fluxes, which in turn are controlled by a variety of parameters including LAI, stomatal resistance, leaf phenology, vegetation type fractional coverage, and soil hydrology (Bonan, 2008).

Likely regimes of vegetation albedo are relatively easy to estimate and to test sensitivity to (Upchurch et al., 1999; Otto-Bliesner and Upchurch, 1997; DeConto et al., 1999; Sewall et al., 2000), but the issue of how much latent flux tropical vegetation is capable of in very hot scenarios is a largely unconstrained problem, but very sensitive to the treatment of angiosperm evapotranspiration (Boyce and Lee, 2010). In our view, the least constrained aspect of the modeled temperature distributions is peak subtropical-to-tropical terrestrial warmth, as evidenced by the troubling model prediction of subtropical warmth at the upper limit of proxy error bars. The large, 15 °C differences between localized terrestrial summer maxima surface temperature and the warmest open ocean SSTs is good evidence that a better understanding of the controls on evapotranspiration is necessary to accurately predict tropical-to-subtropical terrestrial temperatures.

5.1.4 Sampling of warm regions

Additional challenges to estimating temperatures in the warmest regions derive from the filter of existing reconstruction methodologies and geographic sampling. At present there are almost no quantitative terrestrial temperature records for the early Eocene from 30° N to 30° S latitude. We have some hints from the late Paleocene (Head et al.,

2009; Huber, 2009) and earliest Eocene (Jaramillo et al., 2010) that tropical conditions were significantly hotter than modern, but in general the early Eocene terrestrial tropics are almost *terra incognita* (Burnham and Johnson, 2004; Jacobs, 2004; Jacobs and Herendeen, 2004; Kaiser et al., 2006). For our analysis, we included one flora from Africa of middle Eocene age, to have at least some tropical information, but given that the early Eocene, as indicated by marine records, was likely somewhat warmer than the middle Eocene, the one tropical estimate shown here likely underestimates the true temperature. Including the tropical SST records of Pearson et al. (2007) or Jaramillo et al. (2010), does not substantially altered our conclusions, given the fact that those studies' reconstructed values are substantially warmer than modern in agreement with our model results and they have large error bars.

Furthermore, floristic approaches to temperature reconstruction are obviously biased to regions with vegetation. We have no idea how hot the arid and semi-arid regions were. Today arid-to-semi-arid regions account for 30 % of terrestrial surface area and this was approximately true in the Eocene as well (Ziegler et al., 2003). So in terms of even approximately reconstructing the mean terrestrial temperature in the early Eocene about one third of the surface area is thoroughly unsampled and it is likely to be the hottest third. Nearby SSTs are not expected to strongly constrain terrestrial temperatures in the subtropical arid regions and deviations between the two as simulated here are expected. Over the oceans, evaporation couples surface temperatures to upper troposphere temperatures through convection and the largeness of the Rossby radius of deformation enforces weak upper atmospheric temperature gradients (Pierrehumbert, 1995; Williams et al., 2009). But this process is inhibited by dry surface conditions and in the presence of large-scale descending atmospheric motions, such very strong surface temperature gradients can exist between oceans and nearby arid regions (Pierrehumbert, 1995). It may be that we must await proxy records utilizing different techniques, such as “clumped isotopes” (Eiler, 2007), to place meaningful constraints on terrestrial temperatures in these areas.

6 Summary and conclusions

In prior work, robust model-data differences within continental interiors, especially in winter, have suggested to many that climate models fail to reproduce the leading order feedbacks in a warmer world. Acknowledging the large error bars in the proxies and the various layers of uncertainty in the model data-comparison we have performed, it appears that the model reproduces the reconstructed MAT, CMM, and the proper degree of terrestrial high latitude amplification. The congruence of models and data in the simulations here and the conditions under which the congruence occurs suggest that the leading order physics are well represented,

but perhaps either radiative forcing or climate sensitivity was near the upper range of plausible values, or some combination of the two. We have shown that increased radiative forcing in the form of very high $p\text{CO}_2$ seems to resolve the equable climate problem without running too far afoul of other constraints, but this does not necessarily mean that $p\text{CO}_2$ was the only major forcing factor. Since the proxy records now allow for warmer temperatures in the tropics, higher water vapor concentrations and a stronger water vapor greenhouse gas forcing (relative to prior simulations with cooler tropical SSTs), help to maintain continental interior warmth. We have not addressed whether the enhanced radiative forcing was due to $p\text{CO}_2$, methane, other greenhouse gases, novel cloud feedbacks, or other “missing” factors. We have also not established whether large forcing is actually necessary, the alternative being high values of climate sensitivity as in the study of Heinemann et al. (2009) and only moderate increases in forcing.

Regardless of which explanation is correct, the model’s ability to capture the reduced seasonality signal and spatial gradients derived from terrestrial paleoclimate proxies provides a validation of CAM3/CCSM3 for climates vastly different from, and warmer than, modern. With the overall modern patterns in good agreement with the proxy data, significant future progress should be possible in understanding the large-scale dynamics of past greenhouse climates within the framework of a validated model.

Substantial work remains to resolve the remaining model-data differences. To us, the most troubling result is extremely hot terrestrial temperatures in the tropics, but sufficient data do not exist to rule this result out at this time. Provided compelling evidence becomes available, ruling out terrestrial temperatures much above 35 °C in the subtropic, then it is likely that improvements in the model’s representation of tropical evapotranspiration and vegetation type can alleviate the problem in future work. It seems likely to us that the remaining model-data discrepancies in mid-to-high latitudes are due to regional and local scale features, such as unresolved topographic and vegetation details, which can be resolved utilizing better boundary condition data sets and higher resolution models.

Our results do not preclude the existence of more exotic forcings and feedbacks (e.g. Kump and Pollard, 2008; Sloan and Pollard, 1998; Emanuel, 2002; Korty et al., 2008) but instead provide a baseline for comparison involving simple and well understood forcing mechanisms. From a reductionist point of view, such novel processes may not be necessary to explain the proxy data patterns, nevertheless enough latitude exists in the proxy interpretations that significant future improvements are possible.

Supplementary material related to this article is available online at:

<http://www.clim-past.net/7/603/2011/cp-7-603-2011-supplement.zip>

<http://roskilde.eas.purdue.edu/~huberm/k.EO4.02.t42-k.EO3.02.t42/>

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References

- Abbot, D. S., Huber, M., Bousquet, G., and Walker, C. C.: High- CO_2 cloud radiative forcing feedback over both land and ocean in a global climate model, *Geophys. Res. Lett.*, 36, L05702, doi:10.1029/2008GL036703, 2009a.
- Abbot, D. S., Walker, C. C., and Tziperman, E.: Can a Convective Cloud Feedback Help to Eliminate Winter Sea Ice at High CO_2 Concentrations?, *J. Climate*, 22, 5719–5731, doi:10.1175/2009JCLI2854.1, 2009b.
- Adams, C., Lee, D., and Rosen, B.: Conflicting isotopic and biotic evidence for tropical sea surface temperatures during the Tertiary, *Palaeogeogr. Palaeoclimatol.*, 77, 289–313, 1990.
- Adams, J. M., Green, W. A., and Zhang, Y.: Leaf margins and temperature in the North American flora: Recalibrating the paleoclimatic thermometer, *Global Planet. Change*, 60, 523–534, doi:10.1016/j.gloplacha.2007.07.001, 2008.
- Akmetiev, M. A.: Paleocene and Eocene floras of Russia and adjacent regions: Climatic conditions of their development, *Paleontolog. J.*, 41, 1032–1039, 2007.
- Akmetiev, M. A.: Paleocene and Eocene floristic and climatic change in Russia and Northern Kazakhstan, *Bull. Geosci.*, 85, 77–94, doi:10.3140/bull.geosci.1145, 2010.

- Ali, J. R. and Huber, M.: Mammalian biodiversity on Madagascar controlled by ocean currents, *Nature*, 463, 653–656, doi:10.1038/nature08706, 2010.
- Bao, H., Koch, P. L., and Rumble, D.: Paleocene-Eocene climatic variation in western North America: Evidence from the $\delta^{18}\text{O}$ of pedogenic hematite, *Geol. Soc. Am. Bull.*, 111, 1405–1415, 1999.
- Barron, E.: Eocene equator-to-pole surface ocean temperatures: A significant climate problem?, *Paleoceanography*, 2, 729–739, 1987.
- Beerling, D. J. and Royer, D. L.: Fossil plants as indicators of the Phanerozoic global carbon cycle, *Annu. Rev. Earth Planet. Sci.*, 30, 527–556, 2002a.
- Beerling, D. J. and Royer, D. L.: Reading a CO_2 signal from fossil stomata, *New Phytol.*, 153, 387–397, 2002b.
- Beerling, D. J., Berner, R. A., Mackenzie, F. T., Harfoot, M. B., and Pyle, J. A.: Methane and the CH_4 -related greenhouse effect over the past 400 million years, *Am. J. Sci.*, 309, 97–113, doi:10.2475/02.2009.01, 2009a.
- Beerling, D. J., Fox, A., and Anderson, C. W.: Quantitative uncertainty analyses of ancient atmospheric CO_2 estimates from fossil leaves, *Am. J. Sci.*, 309, 775–787, doi:10.2475/09.2009.01, 2009b.
- Berry, E.: A Possible Explanation of Upper Eocene Climates, *Proceedings of the American Philosophical Society*, 61, 1–14, 1922.
- Bijl, P. K., Schouten, S., Sluijs, A., Reichert, G.-J., Zachos, J. C., and Brinkhuis, H.: Early Palaeogene temperature evolution of the southwest Pacific Ocean, *Nature*, 461, 776–779, doi:10.1038/nature08399, 2009.
- Bonan, G. B.: Forests and climate change: Forcings, feedbacks, and the climate benefits of forests, *Science*, 320, 1444–1449, doi:10.1126/science.1155121, 2008.
- Boyce, C. K. and Lee, J.-E.: An exceptional role for flowering plant physiology in the expansion of tropical rainforests and biodiversity, *P. Roy. Soc. B-Biol. Sci.*, 277, 3437–3443, doi:10.1098/rspb.2010.0485, 2010.
- Boyd, A.: The Thyra Ø Flora: Toward and understanding of climate and vegetation during the Early Tertiary in the High Arctic, *Rev. Palaeobot. Palyno.*, 62, 189–203, 1990.
- Boyd, A.: Some limitations in using leaf physiognomic data as a precise method for determining paleoclimates with an example from the Late Cretaceous Pautut Flora of West Greenland, *Palaeogeogr. Palaeocl.*, 112, 261–278, 1994.
- Brinkhuis, H., Schouten, S., Collinson, M. E., Sluijs, A., Damsté, J. S. S., Dickens, G. R., Huber, M., Cronin, T. M., Onodera, J., Takahashi, K., Bujak, J., Stein, R., van der Burgh, J., Eldrett, J. S., Harding, I. C., Lotter, A., Sangiorgi, F., Cittert, H., de Leeuw, J., Matthiessen, J., Backman, J., and Moran, K.: Episodic fresh surface waters in the Eocene Arctic Ocean, *Nature*, 441, 606–609, doi:10.1038/nature04692, 2006.
- Burnham, R. J.: Relationships between standing vegetation and leaf litter in a paratropical forest: implications for paleobotany, *Rev. Palaeobot. Palyno.*, 58, 5–32, 1989.
- Burnham, R. J. and Johnson, K.: South American palaeobotany and the origins of neotropical rainforests, *Philos. T. Roy. Soc. B*, 359, 1595–1610, doi:10.1098/rstb.2004.1531, 2004.
- Burnham, R. J., Pitman, N., Johnson, K., and Wilf, P.: Habitat-related error in estimating temperatures from leaf margins in a humid tropical forest, *Am. J. Bot.*, 88, 1096–1102, 2001.
- Burnham, R. J., Ellis, B., and Johnson, K.: Modern tropical forest taphonomy: Does high biodiversity affect paleoclimatic interpretations?, *Palaios*, 20, 439–451, doi:10.2110/palo.2004.P04-60, 2005.
- Caballero, R. and Huber, M.: Spontaneous transition to superrotation in warm climates simulated by CAM3, *Geophys. Res. Lett.*, 37, L11701, doi:10.1029/2010GL043468, 2010.
- Caballero, R. and Langen, P.: The dynamic range of poleward energy transport in an atmospheric general circulation model, *Geophys. Res. Lett.*, 32, L02705, doi:10.1029/2004GL021581, 2005.
- Collins, W., Rasch, P., Boville, B., Hack, J., McCaa, J., Williamson, D., Briegleb, B., Bitz, C., Lin, S., and Zhang, M.: The formulation and atmospheric simulation of the Community Atmosphere Model version 3 (CAM3), *J. Climate*, 19, 2144–2161, doi:10.1175/JCLI3761.1, 2006.
- Collinson, M. E. and Hooker, J.: Paleogene vegetation of Eurasia: framework for mammalian faunas, in: *Distribution and migration of tertiary mammals in Eurasia*, A volume in honour of Hans de Bruijn, edited by: Reumer, J. and Wessels, W., DEINSEA, vol. 10, 41–83, 2003.
- Covey, C. and Barron, E.: The role of ocean heat transport in climatic change, *Earth-Sci. Rev.*, 24, 429–445, 1988.
- Covey, C., Sloan, L. C., and Hoffert, M.: Paleoclimate data constraints on climate sensitivity: The paleocalibration method, *Climatic Change*, 32, 165–184, 1996.
- Creech, J., Baker, J., Hollis, C., Morgans, H., and Smith, E.: Eocene sea temperatures for the mid-latitude southwest Pacific from Mg/Ca ratios in planktonic and benthic foraminifera, *Earth Planet. Sc. Lett.*, 299, 483–495, doi:10.1016/j.epsl.2010.09.039, 2010.
- Crowley, T. J. and Zachos, J. C.: Comparison of zonal temperature profiles for past warm time periods, in: *Warm Climates in Earth History*, edited by: Huber, B., MacLeod, K., and Wing, S., Cambridge University Press, Cambridge, UK, 50–76, 2000.
- Davis, S. J., Mulch, A., Carroll, A. R., Horton, T. W., and Chamberlain, C. P.: Paleogene landscape evolution of the central North American Cordillera: Developing topography and hydrology in the Laramide foreland, *Geol. Soc. Am. Bull.*, 121, 100–116, doi:10.1130/B26308.1, 2009.
- DeConto, R. M., Hay, W., Thompson, S., and Bergengren, J.: Late Cretaceous climate and vegetation interactions: Cold continental interior paradox, in: *Evolution of the Cretaceous ocean-climate system*, edited by: Barrera, E. and Johnson, C., vol. 332, Geological Society of America Special Paper, Boulder, Colorado, 391–406, doi:10.1130/0-8137-2332-9.391, 1999.
- Donnadieu, Y., Pierrehumbert, R. T., Jacob, R., and Fluteau, F.: Modelling the primary control of paleogeography on Cretaceous climate, *Earth Planet. Sc. Lett.*, 248, 426–437, doi:10.1016/j.epsl.2006.06.007, 2006.
- Doria, G., Royer, D. L., Wolfe, A. P., Fox, A., Westgate, J. A., and Beerling, D. J.: Declining atmospheric CO_2 during the late middle Eocene climate transition, *Am. J. Sci.*, 311, 63–75, doi:10.2475/01.2011.03, 2011.
- Duffy, P., Doutriaux, C., Fodor, I., and Santer, B.: Effect of missing data on estimates of near-surface temperature change since 1900, *J. Climate*, 14, 2809–2814, 2001.
- Eberle, J. J., Fricke, H. C., Humphrey, J. D., Hackett, L., Newbrey, M. G., and Hutchison, J. H.: Seasonal variability in Arctic temperatures during early Eocene time, *Earth Planet. Sc. Lett.*, 296,

- 481–486, doi:10.1016/j.epsl.2010.06.005, 2010.
- Eiler, J.: “Clumped-isotope” geochemistry – The study of naturally-occurring, multiply-substituted isotopologues, *Earth Planet. Sc. Lett.*, 262, 309–327, doi:10.1016/j.epsl.2007.08.020, 2007.
- Eldrett, J. S., Greenwood, D. R., Harding, I. C., and Huber, M.: Increased seasonality through the Eocene to Oligocene transition in northern high latitudes, *Nature*, 459, 969–973, doi:10.1038/nature08069, 2009.
- Emanuel, K. A.: A simple model of multiple climate regimes, *J. Geophys. Res.-Atmos.*, 107, 4077, doi:10.1029/2001JD001002, 2002.
- Fletcher, B. J., Brentnall, S. J., Anderson, C. W., Berner, R. A., and Beerling, D. J.: Atmospheric carbon dioxide linked with Mesozoic and early Cenozoic climate change, *Nat. Geosci.*, 1, 43–48, doi:10.1038/ngeo.2007.29, 2008.
- Forest, C. E.: Paleoaltimetry: A review of thermodynamic methods, *Rev. Mineral Geochem.*, 66, 173–193, doi:10.2138/rmg.2007.66.7, 2007.
- Franks, P. J. and Beerling, D. J.: Maximum leaf conductance driven by CO₂ effects on stomatal size and density over geologic time, *P. Natl. Acad. Sci. USA*, 106, 10 343–10 347, doi:10.1073/pnas.0904209106, 2009.
- Fricke, H. C. and Wing, S. L.: Oxygen isotope and paleobotanical estimates of temperature and $\delta^{18}\text{O}$ -latitude gradients over North America during the early Eocene, *Am. J. Sci.*, 304, 612–635, doi:10.2475/ajs.304.7.612, 2004.
- Garric, G. and Huber, M.: Quasi-decadal variability in paleoclimate records: Sunspot cycles or intrinsic oscillations?, *Paleoceanography*, 18, 1068, doi:10.1029/2002PA000869, 2003.
- Greenwood, D. R.: Leaf margin analysis: Taphonomic constraints, *Palaios*, 20, 498–505, doi:10.2110/palo.2004.P04-58, 2005.
- Greenwood, D. R.: North American Leaves and Climates: From Wolfe and Dilcher to Burnham and Wilf, in: *Advances in Mesozoic and Cenozoic Paleobotany: Studies in celebration of David L. Dilcher and Jack A. Wolfe*, edited by: Jarzen, D., Retallack, G., Jarzen, S., and Manchester, S., vol. 258, Courier Forschungsinstitut, Senckenberg, 95–108, 2007.
- Greenwood, D. R. and Wing, S. L.: Eocene continental climates and latitudinal temperature gradients, *Geology*, 23, 1044–1048, 1995.
- Greenwood, D. R., Moss, P., Rowett, A., Vadala, A., and Keefe, R.: Plant communities and climate change in southeastern Australia during the early Paleogene, in: *Causes and Consequences of Globally Warm Climates in the Early Paleogene*, edited by: Wing, S., Gingerich, P., Schmitz, B., and Thomas, E., vol. 369, Geological Society of America Special Paper, Boulder, Colorado, doi:10.1130/0-8137-2369-8.365, 365–390, 2003.
- Greenwood, D. R., Wilf, P., Wing, S. L., and Christophel, D.: Paleotemperature estimation using leaf-margin analysis: Is Australia different?, *Palaios*, 19, 129–142, 2004.
- Greenwood, D. R., Archibald, S. B., Mathewes, R., and Moss, P.: Fossil biotas from the Okanagan Highlands, southern British Columbia and northeastern Washington State: climates and ecosystems across an Eocene landscape, *Can. J. Earth Sci.*, 42, 167–185, doi:10.1139/E04-100, 2005.
- Greenwood, D. R., Basinger, J. F., and Smith, R. Y.: How wet was the Arctic Eocene rain forest? Estimates of precipitation from Paleogene Arctic macrofloras, *Geology*, 38, 15–18, doi:10.1130/G30218.1, 2010.
- Harrison, T., Msuya, C., Murray, A., Jacobs, B., Báz, A., Mundil, R., and Ludwig, K.: Paleontological investigations at the Eocene locality of Mahenge in north-central Tanzania, East Africa, in: *Eocene Biodiversity: Unusual Occurrences and Rarely Sampled Habitats*, edited by: Gunnell, G., Plenum Press, New York, 39–74, 2001.
- Head, J. J., Bloch, J. I., Hastings, A. K., Bourque, J. R., Cadena, E. A., Herrera, F. A., Polly, P., and Jaramillo, C. A.: Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures, *Nature*, 457, 715–717, doi:10.1038/nature07671, 2009.
- Heinemann, M., Jungclaus, J. H., and Marotzke, J.: Warm Paleocene/Eocene climate as simulated in ECHAM5/MPI-OM, *Clim. Past*, 5, 785–802, doi:10.5194/cp-5-785-2009, 2009.
- Henderiks, J. and Pagani, M.: Coccolithophore cell size and the Paleogene decline in atmospheric CO₂, *Earth Planet. Sc. Lett.*, 269, 575–583, doi:10.1016/j.epsl.2008.03.016, 2008.
- Herfort, L., Schouten, S., Boon, J. P., and Damste, J. S. S.: Application of the TEX86 temperature proxy to the southern North Sea, *Org. Geochem.*, 37, 1715–1726, doi:10.1016/j.orggeochem.2006.07.021, 2006.
- Hickey, L.: Stratigraphy and paleobotany of the Golden Valley Formation (Early Tertiary) of western North Dakota, *GSA Memoir*, 150, MB037, 1977.
- Holland, M. and Bitz, C.: Polar amplification of climate change in coupled models, *Clim. Dynam.*, 21, 221–232, doi:10.1007/s00382-003-0332-6, 2003.
- Hollis, C. J., Handley, L., Crouch, E. M., Morgans, H. E. G., Baker, J. A., Creech, J., Collins, K. S., Gibbs, S. J., Huber, M., Schouten, S., Zachos, J. C., and Pancost, R. D.: Tropical sea temperatures in the high-latitude South Pacific during the Eocene, *Geology*, 37, 99–102, doi:10.1130/G25200A.1, 2009.
- Hollis, C. J., Taylor, K. W. R., Pancost, R. D., Creech, J. B., Kennedy, E. M., Strong, C. P., Morgans, H. E. G., Crouch, E. M., Neil, H., Ackerley, D., and Huber, M.: An update on paleoclimate data-model comparisons for the Southwest Pacific, *Berichte Geol. B.-A.*, 85, 92, 2011.
- Hren, M. T., Pagani, M., Erwin, D. M., and Brandon, M.: Biomarker reconstruction of the early Eocene paleotopography and paleoclimate of the northern Sierra Nevada, *Geology*, 38, 7–10, doi:10.1130/G30215.1, 2010.
- Huber, M.: A hotter greenhouse?, *Science*, 321, 353–354, doi:10.1126/science.1161170, 2008.
- Huber, M.: CLIMATE CHANGE Snakes tell a torrid tale, *Nature*, 457, 669–671, doi:10.1038/457669a, 2009.
- Huber, M. and Caballero, R.: Eocene El Niño: Evidence for robust tropical dynamics in the “hothouse”, *Science*, 299, 877–881, doi:10.1126/science.1078766, 2003.
- Huber, M. and Sloan, L. C.: Warm climate transitions: A general circulation modeling study of the Late Paleocene thermal maximum (about 56 Ma), *J. Geophys. Res.-Atmos.*, 104, 16633–16655, doi:10.1029/1999JD900272, 1999.
- Huber, M. and Sloan, L. C.: Climatic responses to tropical sea surface temperature changes on a “greenhouse” Earth, *Paleoceanography*, 15, 443–450, doi:10.1029/1999PA000455, 2000.
- Huber, M. and Sloan, L. C.: Heat transport, deep waters, and thermal gradients: Coupled simulation of an Eocene Greenhouse Climate, *Geophys. Res. Lett.*, 28, 3481–3484, doi:10.1029/2001GL012943, 2001.

- Huber, M., Sloan, L. C., and Shellito, C.: Early Paleogene oceans and climate: A fully coupled modeling approach using the NCAR CCSM, in: *Causes and Consequences of Globally Warm Climates in the Early Paleogene*, edited by: Wing, S., Gingerich, P., Schmitz, B., and Thomas, E., vol. 369, Geological Society of America Special Paper, Boulder, Colorado, 25–47, doi:10.1130/0-8137-2369-8.25, 2003.
- Huguet, C., Cartes, J. E., Damste, J. S. S., and Schouten, S.: Marine crenarchaeotal membrane lipids in decapods: Implications for the TEX86 paleothermometer, *Geochemistry Geophysics Geosystems*, 7, Q111010, doi:10.1029/2006GC001305, 2006.
- Huguet, C., Schimmelmann, A., Thunell, R., Lourens, L. J., Damste, J. S. S., and Schouten, S.: A study of the TEX86 paleothermometer in the water column and sediments of the Santa Barbara Basin, California, *Paleoceanography*, 22, PA3203, doi:10.1029/2006PA001310, 2007.
- Huguet, C., Kim, J.-H., de Lange, G. J., Damste, J. S. S., and Schouten, S.: Effects of long term oxic degradation on the U-37(K'), TEX86 and BIT organic proxies, *Org. Geochem.*, 40, 1188–1194, doi:10.1016/j.orggeochem.2009.09.003, 2009.
- Hunt, R. J. and Poole, I.: Paleogene West Antarctic climate and vegetation history in light of new data from King George Island, edited by: Wing, S., Gingerich, P., Schmitz, B., and Thomas, E., vol. 369, Geological Society of America Special Paper, Boulder, Colorado, 395–412, doi:10.1130/0-8137-2369-8.395, 2003.
- Hutchison, J. H.: Turtle, crocodilian, and champsosaur diversity changes in the Cenozoic of the north-central region of western United States, *Palaeogeogr. Palaeoclimatol.*, 37, 149–164, 1982.
- Ingalls, A., Shah, S., Hansman, R., Aluwihare, L., Santos, G., Druffel, E., and Pearson, A.: Quantifying archaeal community autotrophy in the mesopelagic ocean using natural radiocarbon, *P. Natl. Acad. Sci. USA*, 103, 6442–6447, doi:10.1073/pnas.0510157103, 2006.
- Ivany, L. C., Lohmann, K. C., Hasiuk, F., Blake, D. B., Glass, A., Aronson, R. B., and Moody, R. M.: Eocene climate record of a high southern latitude continental shelf: Seymour Island, Antarctica, *Geol. Soc. Am. Bull.*, 120, 659–678, doi:10.1130/B26269.1, 2008.
- Jacobs, B. and Herendeen, P.: Eocene dry climate and woodland vegetation in tropical Africa reconstructed from fossil leaves from northern Tanzania, *Palaeogeogr. Palaeoclimatol.*, 213, 115–123, doi:10.1016/j.palaeo.2004.07.007, 2004.
- Jacobs, B. F.: Palaeobotanical studies from tropical Africa: relevance to the evolution of forest, woodland and savannah biomes, *Philos. T. Roy. Soc. B*, 359, 1573–1583, doi:10.1098/rstb.2004.1533, 2004.
- Jahren, A. H.: The Arctic Forest of the Middle Eocene, *Annu. Rev. Earth Planet. Sci.*, 35, 509–540, doi:10.1146/annurev.earth.35.031306.140125, 2007.
- Jahren, A. H. and Sternberg, L.: Humidity estimate for the middle Eocene Arctic rain forest, *Geology*, 31, 463–466, 2003.
- Jahren, A. H. and Sternberg, L. S. L.: Annual patterns within tree rings of the Arctic middle Eocene (ca. 45 Ma): Isotopic signatures of precipitation, relative humidity, and deciduousness, *Geology*, 36, 99–102, doi:10.1130/G23876A.1, 2008.
- Jahren, A. H., Byrne, M. C., Graham, H. V., Sternberg, L. S. L., and Summons, R. E.: The environmental water of the middle Eocene Arctic: Evidence from δD , δO^{18} and δC^{13} within specific compounds, *Palaeogeogr. Palaeoclimatol.*, 271, 96–103, doi:10.1016/j.palaeo.2008.09.016, 2009.
- Jaramillo, C. A., Ochoa, D., Contreras, L., Pagani, M., Carvajal-Ortiz, H., Pratt, L. M., Krishnan, S., Cardona, A., Romero, M., Quiroz, L., Rodriguez, G., Rueda, M. J., de la Parra, F., Morón, S., Green, W., Bayona, G., Montes, C., Quintero, O., Ramirez, R., Mora, G., Schouten, S., Bermudez, H., Navarrete, R., Parra, F., Alvarán, M., Osorno, J., Crowley, J. L., Valencia, V., and Vervoort, J.: Effects of rapid global warming at the Paleocene-Eocene boundary on neotropical vegetation, *Science*, 330, 957–961, doi:10.1126/science.1193833, 2010.
- Jones, T. D., Ridgwell, A., Lunt, D. J., Maslin, M., Schmidt, D. N., and Valdes, P. J.: A Palaeogene perspective on climate sensitivity and methane hydrate instability, *Philos. T. Roy. Soc. A*, 368, 2395–2415, doi:10.1098/rsta.2010.0053, 2010.
- Kaiser, T., Ansorge, J., Arratia, G., Bullwinkel, V., Gunnell, G. F., Herendeen, P., Jacobs, B. F., Mingram, J., Msuya, C., and Musolf, A.: The maar lake of Mahenge (Tanzania) unique evidence of Eocene terrestrial environments in sub-Saharan Africa, *Z. Dtsch. Ges. Geowiss.*, 157, 411–431, doi:10.1127/1860-1804/2006/0157-0411, 2006.
- Kiehl, J., Shields, C., Hack, J., and Collins, W.: The climate sensitivity of the Community Climate System Model version 3 (CCSM3), *J. Climate*, 19, 2584–2596, doi:10.1175/JCLI3747.1, 2006.
- Kim, J.-H., van der Meer, J., Schouten, S., Helmke, P., Willmott, V., Sangiorgi, F., Koc, N., Hopmans, E. C., and Damste, J. S. S.: New indices and calibrations derived from the distribution of crenarchaeal isoprenoid tetraether lipids: Implications for past sea surface temperature reconstructions, *Geochim. Cosmochim. Acta*, 74, 4639–4654, doi:10.1016/j.gca.2010.05.027, 2010.
- Kirk-Davidoff, D. B. and Lamarque, J.-F.: Maintenance of polar stratospheric clouds in a moist stratosphere, *Clim. Past*, 4, 69–78, doi:10.5194/cp-4-69-2008, 2008.
- Kirk-Davidoff, D. B., Schrag, D., and Anderson, J.: On the feedback of stratospheric clouds on polar climate, *Geophys. Res. Lett.*, 29, 1556, doi:10.1029/2002GL014659, 2002.
- Kobashi, T., Grossman, E., Dockery, D., and Ivany, L.: Water mass stability reconstructions from greenhouse (Eocene) to icehouse (Oligocene) for the northern Gulf Coast continental shelf (USA), *Paleoceanography*, 19, PA1022, doi:10.1029/2003PA000934, 2004.
- Koch, P. L.: Isotopic reconstruction of past continental environments, *Annu. Rev. Earth Planet. Sci.*, 26, 573–613, doi:10.1146/annurev.earth.26.1.573, 1998.
- Korty, R., Emanuel, K. A., and Scott, J.: Tropical cyclone-induced upper-ocean mixing and climate: Application to equable climates, *J. Climate*, 21, 638–654, doi:10.1175/2007JCLI1659.1, 2008.
- Kothavala, Z., Oglesby, R., and Saltzman, B.: Sensitivity of equilibrium surface temperature of CCM3 to systematic changes in atmospheric CO₂, *Geophys. Res. Lett.*, 26, 209–212, doi:10.1029/1998GL900275, 1999.
- Kowalski, E. A.: Mean annual temperature estimation based on leaf morphology: a test from tropical South America, *Palaeogeogr. Palaeoclimatol.*, 188, 141–165, doi:10.1016/S0031-0182(02)00550-3, 2002.
- Kowalski, E. A. and Dilcher, D. L.: Warmer paleotemperatures for terrestrial ecosystems, *P. Natl. Acad. Sci. USA*, 100, 167–170, doi:10.1073/pnas.232693599, 2003.

- Kump, L. R. and Pollard, D.: Amplification of Cretaceous warmth by biological cloud feedbacks, *Science*, 320, 195–195, doi:10.1126/science.1153883, 2008.
- Kvacek, Z.: Forest flora and vegetation of the European early Palaeogene – a review, *Bull. Geosci.*, 85, 63–76, doi:10.3140/bull.geosci.1146, 2010.
- Langen, P. and Alexeev, V.: Polar amplification as a preferred response in an idealized aquaplanet GCM, *Clim. Dynam.*, 29, 305–317, doi:10.1007/s00382-006-0221-x, 2007.
- Lawrence, K. T., Sloan, L. C., and Sewall, J. O.: Terrestrial climatic response to precessional orbital forcing in the Eocene, in: *Causes and Consequences of Globally Warm Climates in the Early Paleogene*, edited by: Wing, S., Gingerich, P., Schmitz, B., and Thomas, E., vol. 369, Geological Society of America Special Paper, Boulder, Colorado, 65–77, doi:10.1130/0-8137-2369-8.65, 2003.
- Lear, C., Elderfield, H., and Wilson, P.: Cenozoic deep-sea temperatures and global ice volumes from Mg/Ca in benthic foraminiferal calcite, *Science*, 287, 269–272, doi:10.1126/science.287.5451.269, 2000.
- Lear, C. H., Bailey, T. R., Pearson, P. N., Coxall, H. K., and Rosenthal, Y.: Cooling and ice growth across the Eocene-Oligocene transition, *Geology*, 36, 251–254, doi:10.1130/G24584A.1, 2008.
- Li, H. M.: Early Tertiary paleoclimate of King George Island, Antarctica – evidence from the Fossil Hill Flora, in: *Recent Progress in Antarctic Earth Science*, edited by: Yoshida, Y., Kaminuma, K., and Shiraishi, K., Terra Scientific Publishing Company, Tokyo, Japan, 371–375, 1992.
- Lindzen, R.: Climate dynamics and global change, *Annu. Rev. Fluid Mech.*, 26, 353–378, 1994.
- Liu, Z., Pagani, M., Zinniker, D., DeConto, R. M., Huber, M., Brinkhuis, H., Shah, S. R., Leckie, R. M., and Pearson, A.: Global Cooling During the Eocene-Oligocene Climate Transition, *Science*, 323, 1187–1190, doi:10.1126/science.1166368, 2009.
- Lourens, L. J., Sluijs, A., Kroon, D., Zachos, J. C., Thompson, E., Roehl, U., Bowles, J., and Raffi, I.: Astronomical pacing of late Palaeocene to early Eocene global warming events, *Nature*, 435, 1083–1087, doi:10.1038/nature03814, 2005.
- Lowenstein, T. K. and Demicco, R. V.: Elevated Eocene atmospheric CO₂ and its subsequent decline, *Science*, 313, 1928, doi:10.1126/science.1129555, 2006.
- Lunt, D. J., Valdes, P. J., Jones, T. D., Ridgwell, A., Haywood, A. M., Schmidt, D. N., Marsh, R., and Maslin, M.: CO₂-driven ocean circulation changes as an amplifier of Paleocene-Eocene thermal maximum hydrate destabilization, *Geology*, 38, 875–878, doi:10.1130/G31184.1, 2010.
- Markwick, P. J.: “Equability”, continentality, and Tertiary “Climate”: The crocodilian perspective, *Geology*, 22, 613–616, 1994.
- Markwick, P. J.: Fossil crocodilians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data in reconstructing palaeoclimate, *Palaeogeogr. Palaeoclimatol.*, 137, 205–271, 1998.
- Markwick, P. J.: The palaeogeographic and palaeoclimatic significance of climate proxies for data-model comparisons, in: *Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies*, edited by: Williams, M., Haywood, A., Gregory, F., and Schmidt, D., The Micropalaeontology Society, Special Publication, The Geological Society of London, London, 251–312, 2007.
- Markwick, P. J. and Valdes, P.: Palaeo-digital elevation models for use as boundary conditions in coupled ocean-atmosphere GCM experiments: a Maastrichtian (late Cretaceous) example, *Palaeogeogr. Palaeoclimatol.*, 213, 37–63, doi:10.1016/j.palaeo.2004.06.015, 2004.
- McIver, E. and Basinger, J. F.: Early Tertiary floral evolution in the Canadian high arctic, *Ann. Mo. Bot. Gard.*, 86, 523–545, 1999.
- Meyer, H. W.: A review of paleotemperature – Lapse rate methods for estimating paleoelevation from fossil floras, *Rev. Mineral Geochem.*, 66, 155–171, doi:10.2138/rmg.2007.66.6, 2007.
- Miller, G., Alley, R., Brigham-Grette, J., Fitzpatrick, J., Polyak, L., Serreze, M., and White, J.: Arctic amplification: can the past constrain the future?, *Quaternary Sci.*, 29, 1779–1790, doi:10.1016/j.quascirev.2010.02.008, 2010.
- Miller, K. G., Fairbanks, R., and Mountain, G.: Tertiary oxygen isotope synthesis, sea level history, and continental margin erosion, *Paleoceanography*, 2, 1–19, 1987.
- Molnar, P.: Deuterium and oxygen isotopes, paleoelevations of the Sierra Nevada, and Cenozoic climate, *Geol. Soc. Am. Bull.*, 122, 1106–1115, doi:10.1130/B30001.1, 2010.
- Morrill, C., Small, E., and Sloan, L. C.: Modeling orbital forcing of lake level change: Lake Gosiute (Eocene), North America, *Global Planet. Change*, 29, 57–76, doi:10.1016/S0921-8181(00)00084-9, 2001.
- Mosbrugger, V., Utescher, T., and Dilcher, D. L.: Cenozoic continental climatic evolution of Central Europe, *P. Natl. Acad. Sci. USA*, 102, 14964–14969, doi:10.1073/pnas.0505267102, 2005.
- Mueller, R. D., Sdrolias, M., Gaina, C., Steinberger, B., and Heine, C.: Long-term sea-level fluctuations driven by ocean basin dynamics, *Science*, 319, 1357–1362, doi:10.1126/science.1151540, 2008.
- Mulch, A., Teyssier, C., Cosca, M. A., and Chamberlain, C. P.: Stable isotope paleoaltimetry of Eocene core complexes in the North American Cordillera, *Tectonics*, 26, TC4001, doi:10.1029/2006TC001995, 2007.
- Mustoe, G. E., Dillhoff, R. M., and Dillhoff, T. A.: Geology and paleontology of the early Tertiary Chuckanut Formation, in: *Floods, Faults, and Fire: Geological Field Trips in Washington State and Southwest British Columbia*, edited by: Stelling, P. and Tucker, D. S., Geological Society of America Field Guide, 9, 121–135, doi:10.1130/2007.fld009(06), 2007.
- Nicolo, M. J., Dickens, G. R., Hollis, C. J., and Zachos, J. C.: Multiple early Eocene hyperthermals: Their sedimentary expression on the New Zealand continental margin and in the deep sea, *Geology*, 35, 699, doi:10.1130/G23648A.1, 2007.
- Otto-Bliesner, B. L. and Upchurch, G.: Vegetation-induced warming of high-latitude regions during the late Cretaceous period, *Nature*, 385, 804–807, 1997.
- Otto-Bliesner, B. L., Tomas, R., Brady, E., Ammann, C., Kothavala, Z., and Clauzet, G.: Climate sensitivity of moderate- and low-resolution versions of CCSM3 to preindustrial forcings, *J. Climate*, 19, 2567–2583, doi:10.1175/JCLI3754.1, 2006.
- Pagani, M.: The alkenone-CO₂ proxy and ancient atmospheric carbon dioxide, *Philos. T. Roy. Soc. A*, 360, 609–632, doi:10.1098/rsta.2001.0959, 2002.
- Pagani, M., Zachos, J. C., Freeman, K. H., Tipple, B., and Bohaty, S. M.: Marked decline in atmospheric carbon dioxide

- concentrations during the Paleogene, *Science*, 309, 600–603, doi:10.1126/science.1110063, 2005.
- Panchuk, K., Ridgwell, A., and Kump, L. R.: Sedimentary response to Paleocene-Eocene Thermal Maximum carbon release: A model-data comparison, *Geology*, 36, 315–318, doi:10.1130/G24474A.1, 2008.
- Pearson, A., McNichol, A., Benitez-Nelson, B., Hayes, J., and Eglinton, T.: Origins of lipid biomarkers in Santa Monica Basin surface sediment: A case study using compound-specific $\delta^{13}\text{C}$ -14 analysis, *Geochim. Cosmochim. Acta*, 65, 3123–3137, doi:10.1016/S0016-7037(01)00657-3, 2001a.
- Pearson, P. N. and Palmer, M.: Atmospheric carbon dioxide concentrations over the past 60 million years, *Nature*, 406, 695–699, doi:10.1038/35021000, 2000.
- Pearson, P. N., Ditchfield, P., Singano, J., Harcourt-Brown, K., Nicholas, C., Olsson, R., Shackleton, N. J., and Hall, M.: Warm tropical sea surface temperatures in the Late Cretaceous and Eocene epochs, *Nature*, 413, 481–487, doi:10.1038/35097000, 2001b.
- Pearson, P. N., van Dongen, B. E., Nicholas, C. J., Pancost, R. D., Schouten, S., Singano, J. M., and Wade, B. S.: Stable warm tropical climate through the Eocene Epoch, *Geology*, 35, 211–214, doi:10.1130/G23175A.1, 2007.
- Pearson, P. N., McMillan, I. K., Wade, B. S., Jones, T. D., Coxall, H. K., Bown, P. R., and Lear, C. H.: Extinction and environmental change across the Eocene-Oligocene boundary in Tanzania, *Geology*, 36, 179–182, doi:10.1130/G24308A.1, 2008.
- Pearson, P. N., Foster, G. L., and Wade, B. S.: Atmospheric carbon dioxide through the Eocene-Oligocene climate transition, *Nature*, 461, 1110–1113, doi:10.1038/nature08447, 2009.
- Peppe, D. J., Royer, D. L., Wilf, P., and Kowalski, E. A.: Quantification of large uncertainties in fossil leaf paleoaltimetry, *Tectonics*, 29, TC3015, doi:10.1029/2009TC002549, 2010.
- Peppe, D. J., Royer, D. L., Cariglino, B., Oliver, S. Y., Newman, S., Leight, E., Enikolopov, G., Fernandez-Burgos, M., Herrera, F., Adams, J. M., Correa, E., Currano, E. D., Erickson, J. M., Hinojosa, L. F., Hoganson, J. W., Iglesias, A., Jaramillo, C. A., Johnson, K. R., Jordan, G. J., Kraft, N. J. B., Lovelock, E. C., Lusk, C. H., Niinemets, Ü., Peñuelas, J., Rapson, G., Wing, S. L., and Wright, I. J.: Sensitivity of leaf size and shape to climate: global patterns and paleoclimatic applications, *New Phytol.*, 190, 724–739, doi:10.1111/j.1469-8137.2010.03615.x, 2011.
- Peterse, F., Kim, J.-H., Schouten, S., Kristensen, D. K., Koc, N., and Damsté, J. S. S.: Constraints on the application of the MBT/CBT palaeothermometer at high latitude environments (Svalbard, Norway), *Org. Geochem.*, 40, 692–699, doi:10.1016/j.orggeochem.2009.03.004, 2009.
- Pierrehumbert, R. T.: Thermostats, radiator fins, and the local runaway greenhouse, *J. Atmos. Sci.*, 52, 1784–1806, 1995.
- Pigg, K. B. and Devore, M. L.: Floristic composition and variation in late Paleocene to early Eocene floras in North America, *Bull. Geosci.*, 85, 135–154, doi:10.3140/bull.geosci.1136, 2010.
- Poole, I., Cantrill, D., and Utescher, T.: A multi-proxy approach to determine Antarctic terrestrial palaeoclimate during the Late Cretaceous and Early Tertiary, *Palaeogeogr. Palaeoclimatol.*, 222, 95–121, doi:10.1016/j.palaeo.2005.03.011, 2005.
- Robert, C. and Chamley, H.: Development of early Eocene warm climates, as inferred from clay mineral variations in oceanic sediments, *Global Planet. Change*, 89, 315–331, 1991.
- Roberts, C. D., Legrande, A. N., and Tripathi, A. K.: Climate sensitivity to Arctic seaway restriction during the early Paleogene, *Earth Planet. Sc. Lett.*, 286, 576–585, doi:10.1016/j.epsl.2009.07.026, 2009.
- Rowley, D. B.: Stable isotope-based paleoaltimetry: Theory and validation, *Rev. Mineral Geochem.*, 66, 23–52, doi:10.2138/rmg.2007.66.2, 2007.
- Royer, D. L., Wing, S. L., Beerling, D. J., Jolley, D. W., Koch, P. L., Hickey, L. J., and Berner, R. A.: Paleobotanical evidence for near present-day levels of atmospheric CO_2 during part of the tertiary, *Science*, 292, 2310–2313, doi:10.1126/science.292.5525.2310, 2001.
- Royer, D. L., Osborne, C. P., and Beerling, D. J.: High CO_2 increases the freezing sensitivity of plants: Implications for paleoclimatic reconstructions from fossil floras, *Geology*, 30, 963–966, 2002.
- Schouten, S., Hopmans, E., Schefuß, E., and Damsté, J. S.: Distributional variations in marine crenarchaeotal membrane lipids: a new tool for reconstructing ancient sea water temperatures?, *Earth Planet. Sc. Lett.*, 204, 265–274, doi:10.1016/S0012-821X(02)00979-2, 2002.
- Schouten, S., Hopmans, E., Forster, A., van Breugel, Y., Kuypers, M., and Damsté, J.: Extremely high sea-surface temperatures at low latitudes during the middle Cretaceous as revealed by archaeal membrane lipids, *Geology*, 31, 1069–1072, doi:10.1130/G19876.1, 2003.
- Schouten, S., Forster, A., Panoto, F. E., and Damsté, J. S. S.: Towards calibration of the TEX₈₆ palaeothermometer for tropical sea surface temperatures in ancient greenhouse worlds, *Org. Geochem.*, 38, 1537–1546, doi:10.1016/j.orggeochem.2007.05.014, 2007.
- Schrag, D.: Effects of diagenesis on the isotopic record of late paleogene tropical sea surface temperatures, *Chem. Geol.*, 161, 215–224, 1999.
- Schrag, D., Depaolo, D. J., and Richter, F.: Reconstructing past sea surface temperatures: correcting for diagenesis of bulk marine carbonate, *Geochim. Cosmochim. Acta*, 59, 2265–2278, 1995.
- Sellwood, B. and Valdes, P. J.: Mesozoic climates: General circulation models and the rock record, *Sediment Geol.*, 190, 269–287, doi:10.1016/j.sedgeo.2006.05.013, 2006.
- Sewall, J. and Sloan, L. C.: Less ice, less tilt, less chill: The influence of a seasonally ice-free Arctic Ocean and reduced obliquity on early Paleogene climate, *Geology*, 32, 477–480, doi:10.1130/g20295.1, 2004.
- Sewall, J. and Sloan, L. C.: Come a little bit closer: A high-resolution climate study of the early Paleogene Laramide foreland, *Geology*, 34, 81–84, doi:10.1130/G22177.1, 2006.
- Sewall, J. O. and Sloan, L. C.: Equable Paleogene climates: The result of a stable, positive Arctic Oscillation?, *Geophys. Res. Lett.*, 28, 3693–3695, doi:10.1029/2001GL013776, 2001.
- Sewall, J. O., Sloan, L. C., Huber, M., and Wing, S.: Climate sensitivity to changes in land surface characteristics, *Global Planet. Change*, 26, 445–465, doi:10.1016/S0921-8181(00)00056-4, 2000.
- Sewall, J. O., Huber, M., and Sloan, L. C.: A method for using a fully coupled climate system model to generate detailed surface boundary conditions for paleoclimate modeling investigations: an early Paleogene example, *Global Planet. Change*, 43, 173–182, doi:10.1016/j.gloplacha.2004.03.004, 2004.

- Sexton, P. F., Wilson, P. A., and Pearson, P. N.: Microstructural and geochemical perspectives on planktic foraminiferal preservation: “Glassy” versus “Frosty”, *Geochem. Geophys. Geos.*, 7, Q12P19, doi:10.1029/2006GC001291, 2006.
- Shah, S. R., Mollenhauer, G., Ohkouchi, N., Eglinton, T. I., and Pearson, A.: Origins of archaeal tetraether lipids in sediments: Insights from radiocarbon analysis, *Geochim. Cosmochim. Acta*, 72, 4577–4594, doi:10.1016/j.gca.2008.06.021, 2008.
- Sheldon, N. D. and Tabor, N. J.: Quantitative paleoenvironmental and paleoclimatic reconstruction using paleosols, *Earth-Sci. Rev.*, 95, 1–52, doi:10.1016/j.earscirev.2009.03.004, 2009.
- Shellito, C. and Sloan, L. C.: Reconstructing a lost Eocene Paradise, Part II: On the utility of dynamic global vegetation models in pre-Quaternary climate studies, *Global Planet. Change*, 50, 18–32, doi:10.1016/j.gloplacha.2005.08.002, 2006a.
- Shellito, C. and Sloan, L. C.: Reconstructing a lost Eocene paradise: Part I. Simulating the change in global floral distribution at the initial Eocene thermal maximum, *Global Planet. Change*, 50, 1–17, doi:10.1016/j.gloplacha.2005.08.001, 2006b.
- Shellito, C. J., Sloan, L. C., and Huber, M.: Climate model sensitivity to atmospheric CO₂ levels in the Early-Middle Paleogene, *Palaeogeogr. Palaeocl.*, 193, 113–123, doi:10.1016/S0031-0182(02)00718-6, 2003.
- Shellito, C. J., Lamarque, J.-F., and Sloan, L. C.: Early Eocene Arctic climate sensitivity to pCO₂ and basin geography, *Geophys. Res. Lett.*, 36, L09707, doi:10.1029/2009GL037248, 2009.
- Sherwood, S. C. and Huber, M.: An adaptability limit to climate change due to heat stress, *P. Natl. Acad. Sci.*, 107, 9552–9555, doi:10.1073/pnas.0913352107, 2010.
- Sijp, W., England, M., and Toggweiler, J.: Effect of ocean gateway changes under greenhouse warmth, *J. Climate*, 22, 6639–6652, doi:10.1175/2009JCLI3003.1, 2009.
- Sloan, L. C.: Equable climates during the early Eocene: Significance of regional paleogeography for North American climate, *Geology*, 22, 881–884, 1994.
- Sloan, L. C.: A framework for regional modeling of past climates, *Theor. Appl. Climatol.*, 86, 271–279, doi:10.1007/s00704-005-0207-3, 2006.
- Sloan, L. C. and Barron, E.: “Equable” climates during Earth history, *Geology*, 18, 489–492, 1990.
- Sloan, L. C. and Barron, E.: A comparison of Eocene climate model results to quantify paleoclimatic interpretations, *Palaeogeogr. Palaeocl.*, 93, 183–202, doi:10.1016/0031-0182(92)90096-N, 1992.
- Sloan, L. C. and Morrill, C.: Orbital forcing and Eocene continental temperatures, *Palaeogeogr. Palaeocl.*, 144, 21–35, doi:10.1016/S0031-0182(98)00091-1, 1998.
- Sloan, L. C. and Pollard, D.: Polar stratospheric clouds: A high latitude warming mechanism in an ancient greenhouse world, *Geophys. Res. Lett.*, 25, 3517–3520, doi:10.1029/98GL02492, 1998.
- Sloan, L. C., Walker, J., Moore, T. C., Rea, D., and Zachos, J. C.: Possible methane-induced polar warming in the early Eocene, *Nature*, 357, 320–322, doi:10.1038/357320a0, 1992.
- Sloan, L. C., Walker, J., and Moore, T. C.: Possible role of oceanic heat transport in early Eocene climate, *Paleoceanography*, 10, 347–356, doi:10.1029/94PA02928, 1995.
- Sloan, L. C., Huber, M., and Ewing, A.: Polar stratospheric cloud forcing in a greenhouse world, in: *Reconstructing Ocean History: A Window Into the Future*, edited by Abrantes, F., and Mix, A. C., Kluwer Academic, New York, New York, 273–293, 1999.
- Sloan, L. C., Huber, M., Crowley, T., Sewall, J. O., and Baum, S.: Effect of sea surface temperature configuration on model simulations of “equable” climate in the Early Eocene, *Palaeogeogr. Palaeocl.*, 167, 321–335, doi:10.1016/S0031-0182(00)00245-5, 2001.
- Sluijs, A., Schouten, S., Pagani, M., Woltering, M., Brinkhuis, H., Damste, J., Dickens, G., Huber, M., Reichert, G., Stein, R., Matthiessen, J., Lourens, L., Pedentchouk, N., Backman, J., and Moran, K.: Subtropical arctic ocean temperatures during the Palaeocene/Eocene thermal maximum, *Nature*, 441, 610–613, doi:10.1038/nature04668, 2006.
- Sluijs, A., Bowen, G., Brinkhuis, H., Lourens, L., and Thomas, E.: The Palaeocene-Eocene Thermal Maximum super greenhouse: biotic and geochemical signatures, age models and mechanisms of global change, in: *Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies*, edited by: Williams, M., Haywood, A., Gregory, F., and Schmidt, D., The Micropalaeontology Society, Special Publication, The Geological Society of London, London, UK, 323–349, 2007.
- Sluijs, A., Roehl, U., Schouten, S., Brumsack, H.-J., Sangiorgi, F., Damste, J. S. S., and Brinkhuis, H.: Arctic late Paleocene-early Eocene paleoenvironments with special emphasis on the Paleocene-Eocene thermal maximum (Lomonosov Ridge, Integrated Ocean Drilling Program Expedition 302), *Paleoceanography*, 23, PA1S11, doi:10.1029/2007PA001495, 2008.
- Sluijs, A., Schouten, S., Donders, T. H., Schoon, P. L., Roehl, U., Reichert, G.-J., Sangiorgi, F., Kim, J.-H., Damsté, J. S. S., and Brinkhuis, H.: Warm and wet conditions in the Arctic region during Eocene Thermal Maximum 2, *Nat. Geosci.*, 2, 777–780, doi:10.1038/NGEO668, 2009.
- Smith, R. Y., Basinger, J. F., and Greenwood, D. R.: Depositional setting, fossil flora, and paleoenvironment of the Early Eocene Falkland site, Okanagan Highlands, British Columbia, *Can. J. Earth Sci.*, 46, 811–822, doi:10.1139/E09-053, 2009.
- Smith, R. Y., Greenwood, D. R., and Basinger, J. F.: Estimating paleoatmospheric pCO₂ during the Early Eocene Climatic Optimum from stomatal frequency of Ginkgo, Okanagan Highlands, British Columbia, Canada, *Palaeogeogr. Palaeocl.*, 293, 120–131, doi:10.1016/j.palaeo.2010.05.006, 2010.
- Spicer, R. A. and Parrish, J.: Late Cretaceous-early Tertiary palaeoclimates of northern high latitudes: a quantitative view, *J. Geol. Soc.*, 147, 329–341, 1990.
- Spicer, R. A., Herman, A., and Kennedy, E.: The sensitivity of CLAMP to taphonomic loss of foliar physiognomic characters, *Palaos*, 20, 429–438, doi:10.2110/palo.2004.P04-63, 2005.
- Spicer, R. A., Ahlberg, A., Herfort, A. B., Hofmann, C.-C., Raikovich, M., Valdes, P. J., and Markwick, P. J.: The Late Cretaceous continental interior of Siberia: A challenge for climate models, *Earth Planet. Sc. Lett.*, 267, 228–235, doi:10.1016/j.epsl.2007.11.049, 2008.
- Spicer, R. A., Valdes, P. J., Spicer, T. E. V., Craggs, H. J., Srivastava, G., Mehrotra, R. C., and Yang, J.: New developments in CLAMP: Calibration using global gridded meteorological data, *Palaeogeogr. Palaeocl.*, 283, 91–98, doi:10.1016/j.palaeo.2009.09.009, 2009.
- Stickley, C. E., John, K. S., Koc, N., Jordan, R. W., Passchier, S., Pearce, R. B., and Kearns, L. E.: Evidence for middle Eocene

- Arctic sea ice from diatoms and ice-rafted debris, *Nature*, 460, 376–379, doi:10.1038/nature08163, 2009.
- Thrasher, B. L. and Sloan, L. C.: Carbon dioxide and the early Eocene climate of western North America, *Geology*, 37, 807–810, doi:10.1130/G30090A.1, 2009.
- Thrasher, B. L. and Sloan, L. C.: Land cover influences on the regional climate of western North America during the early Eocene, *Global Planet. Change*, 72, 25–31, doi:10.1016/j.gloplacha.2010.02.002, 2010.
- Tindall, J., Flecker, R., Valdes, P. J., Schmidt, D. N., Markwick, P. J., and Harris, J.: Modelling the oxygen isotope distribution of ancient seawater using a coupled ocean-atmosphere GCM: Implications for reconstructing early Eocene climate, *Earth Planet. Sc. Lett.*, 292, 265–273, doi:10.1016/j.epsl.2009.12.049, 2010.
- Tripathi, A. and Elderfield, H.: Abrupt hydrographic changes in the equatorial Pacific and subtropical Atlantic from foraminiferal Mg/Ca indicate greenhouse origin for the thermal maximum at the Paleocene-Eocene Boundary, *Geochim. Geophys. Geos.*, 5, Q02006, doi:10.1029/2003GC000631, 2004.
- Tripathi, A. K., Delaney, M., Zachos, J. C., Anderson, L., Kelly, D., and Elderfield, H.: Tropical sea-surface temperature reconstruction for the early Paleogene using Mg/Ca ratios of planktonic foraminifera, *Paleoceanography*, 18, 1–13, doi:10.1029/2003PA000937, 2003.
- Trommer, G., Siccha, M., van der Meer, M. T. J., Schouten, S., Damsté, J. S. S., Schulz, H., Hemleben, C., and Kucera, M.: Distribution of Crenarchaeota tetraether membrane lipids in surface sediments from the Red Sea, *Org. Geochem.*, 40, 724–731, doi:10.1016/j.orggeochem.2009.03.001, 2009.
- Turich, C., Freeman, K. H., Bruns, M. A., Conte, M., Jones, A. D., and Wakeham, S. G.: Lipids of marine Archaea: Patterns and provenance in the water-column and sediments, *Geochim. Cosmochim. Acta*, 71, 3272–3291, doi:10.1016/j.gca.2007.04.013, 2007.
- Uhl, D., Klotz, S., Traiser, C., Thiel, C., Utescher, T., Kowalski, E. A., and Dilcher, D. L.: Cenozoic paleotemperatures and leaf physiognomy – A European perspective, *Palaeogeogr. Palaeoclimatol.*, 248, 24–31, doi:10.1016/j.palaeo.2006.11.005, 2007.
- Upchurch, G., Otto-Bliesner, B., and Scotese, C.: Terrestrial vegetation and its effects on climate during the latest Cretaceous, in: *Evolution of the Cretaceous ocean-climate system*, edited by: Barrera, E. and Johnson, C., vol. 332, Geological Society of America Special Paper, Boulder, Colorado, 407–426, 1999.
- Utescher, T. and Mosbrugger, V.: Eocene vegetation patterns reconstructed from plant diversity – A global perspective, *Palaeogeogr. Palaeoclimatol.*, 247, 243–271, doi:10.1016/j.palaeo.2006.10.022, 2007.
- Utescher, T., Mosbrugger, V., Ivanov, D., and Dilcher, D. L.: Present-day climatic equivalents of European Cenozoic climates, *Earth Planet. Sc. Lett.*, 284, 544–552, doi:10.1016/j.epsl.2009.05.021, 2009.
- Valdes, P. J.: Warm climate forcing mechanisms, in: *Warm Climates in Earth History*, edited by: Huber, B., MacLeod, K., and Wing, S., Cambridge University Press, Cambridge, UK, 3–20, 2000.
- van Itterbeeck, J., Bolotsky, Y., Bultynck, P., and Godefroit, P.: Stratigraphy, sedimentology and palaeoecology of the dinosaur-bearing Kundur section (Zeya-Bureya Basin, Amur Region, Far Eastern Russia), *Geol. Mag.*, 142, 735–750, doi:10.1017/S0016756805001226, 2005.
- van Rooij, L.: The Paleocene Eocene Thermal Maximum in the Gulf of Mexico: a low latitude paleoenvironmental reconstruction, Master's thesis, University of Utrecht, <http://igitur-archive.library.uu.nl/student-theses/2010-0107-200136/UUindex.html> (last access: 6 June 2011), 2009.
- Wang, Q., Ferguson, D. K., Feng, G.-P., Ablae, A. G., Wang, Y.-F., Yang, J., Li, Y.-L., and Li, C.-S.: Climatic change during the Palaeocene to Eocene based on fossil plants from Fushun, China, *Palaeogeogr. Palaeoclimatol.*, 295, 323–331, doi:10.1016/j.palaeo.2010.06.010, 2010.
- Weijers, J. W. H., Schouten, S., den Donker, J. V., Hopmans, E., and Damsté, J. S.: Environmental controls on bacterial tetraether membrane lipid distribution in soils, *Geochim. Cosmochim. Acta*, 71, 703–713, doi:10.1016/j.gca.2006.10.003, 2007a.
- Weijers, J. W. H., Schouten, S., Sluijs, A., Brinkhuis, H., and Damsté, J. S. S.: Warm arctic continents during the Palaeocene-Eocene thermal maximum, *Earth Planet. Sc. Lett.*, 261, 230–238, doi:10.1016/j.epsl.2007.06.033, 2007b.
- Wilf, P.: When are leaves good thermometers? A new case for leaf margin analysis, *Paleobiology*, 23, 373–390, 1997.
- Wilf, P.: Late Paleocene-early Eocene climate changes in southwestern Wyoming: Paleobotanical analysis, *Geol. Soc. Am. Bull.*, 112, 292–307, 2000.
- Wilf, P., Beard, K. C., Davies-Vollum, K., and Norejko, J.: Portrait of a late Paleocene (early Clarkforkian) terrestrial ecosystem: Big Multi Quarry and associated strata, Washakie Basin, Southwestern Wyoming, *Palaio*, 13, 514–532, 1998.
- Wilf, P., Labandeira, C. C., Kress, W. J., Staines, C. L., Windsor, D. M., Allen, A. L., and Johnson, K. R.: Timing the radiations of leaf beetles: hispinids on gingers from latest Cretaceous to recent, *Science*, 289, 291–4, doi:10.1126/science.289.5477.291, 2000.
- Wilf, P., Cuneo, N., Johnson, K., Hicks, J., Wing, S. L., and Obradovich, J.: High plant diversity in Eocene South America: Evidence from Patagonia, *Science*, 300, 122–125, doi:10.1126/science.1080475, 2003.
- Wilf, P., Labandeira, C. C., Johnson, K. R., and Cuneo, N. R.: Richness of plant-insect associations in Eocene Patagonia: A legacy for South American biodiversity, *P. Natl. Acad. Sci. USA*, 102, 8944–8948, doi:10.1073/pnas.0500516102, 2005.
- Williams, I. N., Pierrehumbert, R. T., and Huber, M.: Global warming, convective threshold and false thermostats, *Geophys. Res. Lett.*, 36, L21805, doi:10.1029/2009GL039849, 2009.
- Wing, S., Bao, H., and Koch, P. L.: An early Eocene cool period? Evidence for continental cooling during the warmest part of the Cenozoic, in: *Warm Climates in Earth History*, edited by: Huber, B., MacLeod, K., and Wing, S., Cambridge University Press, Cambridge, UK, 197–237, 2000.
- Wing, S., Harrington, G., Smith, F., Bloch, J., Boyer, D., and Freeman, K.: Transient floral change and rapid global warming at the Paleocene-Eocene boundary, *Science*, 310, 993–996, doi:10.1126/science.1116913, 2005.
- Wing, S. L.: Eocene and Oligocene floras and vegetation of the Rocky Mountains, *Annals of the Missouri Botanical Garden*, 74, 748–784, 1987.
- Wing, S. L. and Greenwood, D. R.: Fossils and fossil climate: The case for equable continental interiors in the Eocene, *Philos. T. Roy. Soc. B*, 341, 243–252, 1993.

- Winguth, A. M. E., Shellito, C. J., Shields, C., and Winguth, C.: Climate Response at the Paleocene-Eocene Thermal Maximum to Greenhouse Gas Forcing-A Model Study with CCSM3, *J. Climate*, 23, 2562–2584, doi:10.1175/2009JCLI3113.1, 2010.
- Wolfe, J.: Paleoclimatic estimates from Tertiary leaf assemblages, *Annu. Rev. Earth Planet. Sci.*, 23, 119–142, 1995.
- Wolfe, J., Forest, C. E., and Molnar, P.: Paleobotanical evidence of Eocene and Oligocene paleoaltitudes in midlatitude western North America, *Geol. Soc. Am. Bull.*, 110, 664–678, 1998.
- Wuchter, C., Schouten, S., Coolen, M., and Damste, J.: Temperature-dependent variation in the distribution of tetraether membrane lipids of marine Crenarchaeota: Implications for TEX₈₆ paleothermometry, *Paleoceanography*, 19, PA4028, doi:10.1029/2004PA001041, 2004.
- Wuchter, C., Schouten, S., Wakeham, S., and Damste, J.: Temporal and spatial variation in tetraether membrane lipids of marine Crenarchaeota in particulate organic matter: Implications for TEX₈₆ paleothermometry, *Paleoceanography*, 20, PA3013, doi:10.1029/2004PA001110, 2005.
- Zachos, J. C., Stott, L., and Lohmann, K. C.: Evolution of early Cenozoic marine temperatures, *Paleoceanography*, 9, 353–387, 1994.
- Zachos, J. C., Pagani, M., Sloan, L. C., Thomas, E., and Billups, K.: Trends, rhythms, and aberrations in global climate 65 Ma to present, *Science*, 292, 686–693, doi:10.1126/science.1059412, 2001.
- Zachos, J. C., Wara, M., Bohaty, S. M., Delaney, M. L., Petrizzo, M., Brill, A., Bralower, T., and Premoli-Silva, I.: A transient rise in tropical sea surface temperature during the Paleocene-Eocene Thermal Maximum, *Science*, 302, 1551–1554, doi:10.1126/science.1090110, 2003.
- Zachos, J. C., Schouten, S., Bohaty, S., Quattlebaum, T., Sluijs, A., Brinkhuis, H., Gibbs, S. J., and Bralower, T. J.: Extreme warming of mid-latitude coastal ocean during the Paleocene-Eocene Thermal Maximum: Inferences from TEX₈₆ and isotope data, *Geology*, 34, 737–740, doi:10.1130/G22522.1, 2006.
- Zeebe, R. E., Zachos, J. C., and Dickens, G.: Carbon dioxide forcing alone insufficient to explain Palaeocene–Eocene Thermal Maximum warming, *Nat. Geosci.*, 2, 576–580, doi:10.1038/ngeo578, 2009.
- Ziegler, A., Eshel, G., Rees, P., Rothfus, T., Rowley, D., and Sunderlin, D.: Tracing the tropics across land and sea: Permian to present, *Lethaia*, 36, 227–254, doi:10.1080/00241160310004657, 2003.