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Special Section:

Climatic and Biotic Events of the Paleogene: Earth Systems and Planetary Boundaries in a Greenhouse World

Key Points:

- Multiproxy studies increase confidence in paleoclimate reconstructions; we present the first such study for land-based CO₂ proxies
- Our study highlights relatively new, more widely applicable proxy methods based on robust models of gas exchange in C₃ photosynthesis
- Our CO₂ estimates are more congruent with the current understanding of Earth system sensitivity than are previous lower estimates

Supporting Information:

- Supporting Information S1
- Data Set S1
- Data Set S2
- Data Set S3
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Multiple Proxy Estimates of Atmospheric CO₂ From an Early Paleocene Rainforest

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Abstract Proxy estimates of atmospheric CO₂ are necessary to reconstruct Earth's climate history. Confidence in paleo-CO₂ estimates can be increased by comparing results from multiple proxies at a single site, but so far this strategy has been implemented only for marine-based techniques. Here we present CO₂ estimates for the well-studied early Paleocene Castle Rock site in Colorado using four paleobotanical proxies. Median estimates range from 470 to 813 ppm, demonstrating fair correspondence. The synthesis yields a median of 616 ppm (352–1110 ppm at 95% confidence), considerably higher than previous early Paleocene CO₂ estimates (~300 ppm). Ash bed geochronology by the high-precision U-Pb method places the Castle Rock assemblage at 63.844 ± 0.097 Ma (fully propagated 2σ error). When these results are placed into the broader context of other Cenozoic CO₂ estimates from plant-gas-exchange approaches and coeval estimates of global mean surface temperature, a pattern emerges of an Earth system sensitivity around 3 °C per CO₂ doubling during the Paleocene and Eocene, a time with little land ice, then steepening to >7 °C after the Eocene once land ice was present on Antarctica.

Plain Language Summary As atmospheric CO₂ continues to increase, we enter a climate state whose analog in terms of CO₂ concentration is found millions of years ago. Information about climate from such distant times is only available to us via proxy methods (i.e., indicators of climate recorded in ancient rocks and fossils); increasing confidence in proxy results is therefore a high priority. Here we compare four different CO₂ proxy methods using plant fossils from an exceptionally diverse rainforest that existed near present-day Denver, Colorado, 63.8 million years ago. Estimates are largely congruent and higher than previously thought (~600 ppm). The higher CO₂ levels during this warm period are in better agreement with the current understanding of long-term Earth system climate sensitivity, and results from the newer gas-exchange proxy methods paint a coherent picture of Earth system sensitivity evolution over the Cenozoic.

1. Introduction

Long-term surface temperature is primarily controlled by the abundance of the greenhouse gas carbon dioxide (Lacis et al., 2010). Atmospheric CO₂ varied between ~180 to ~280 ppm over the past 800 kyr before the Industrial Revolution (Luthi et al., 2008), but accelerating anthropogenic carbon emissions since then have pushed it to ~400 ppm. Projections show concentrations reaching >720 ppm by the end of the century unless emission rates are lowered (Intergovernmental Panel on Climate Change, 2014), a level perhaps not seen in over 30 million years (Beerling & Royer, 2011). To understand the response of climate to our current increase in atmospheric CO₂ and to predict what climatic conditions future generations may face, reconstructions of Earth's pre-Pleistocene paleoclimate history—accessible only via proxy—are critical (Montañez et al., 2011).

Proxies for estimating a climate variable such as CO₂ are based on responses of natural systems to the variable in a way that is preserved in the geologic record (Beerling & Royer, 2011). A compilation of CO₂ estimates

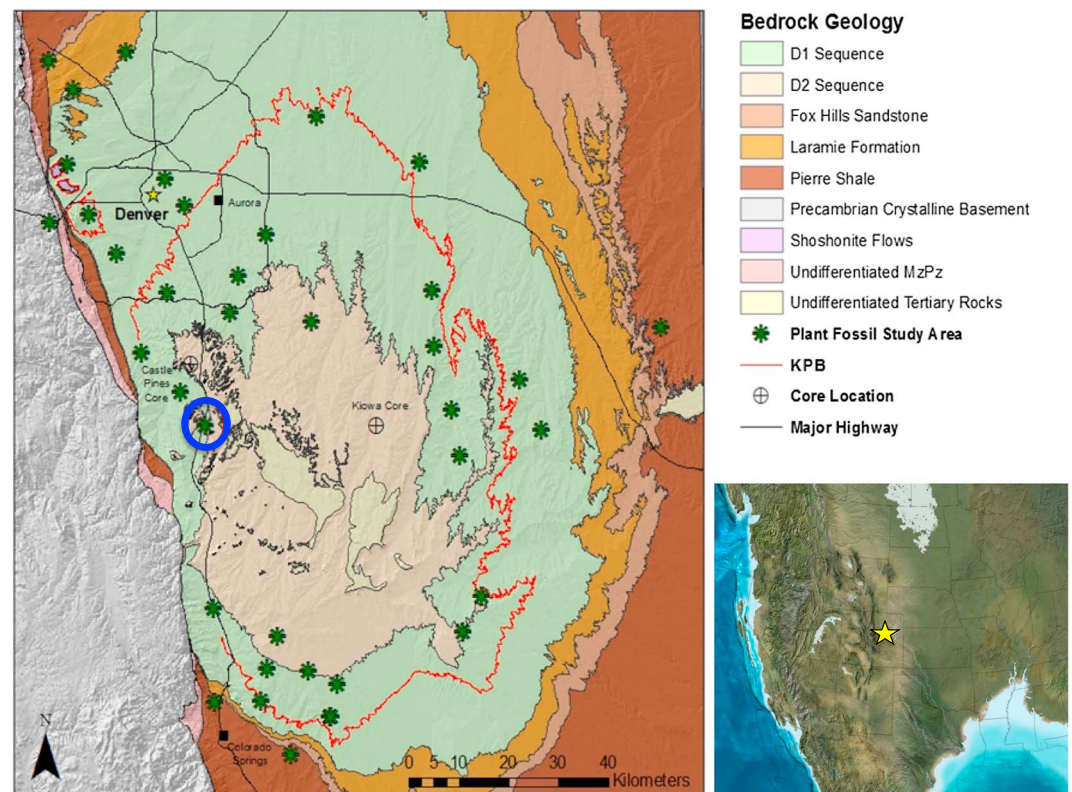


Figure 1. Bedrock geology and plant fossil study areas in the Denver Basin, Colorado. Fossil study areas, shown by the green asterisks, are georeferenced from Johnson et al. (2003); all other map data come from Dechesne et al. (2011). The western edge of the Denver Basin is bounded by exposed Precambrian crystalline basement. Moving towards the center of the basin, sedimentary bedrock layers decrease in age, from the Cretaceous Pierre Shale to the Eocene D2 Sequence (Dechesne et al., 2011). The Cretaceous-Paleogene Boundary (KPB), shown in red, is located approximately midway through the D1 Sequence. The wheel crosses mark the locations of the Castle Pines and Kiowa cores, used to correlate subsurface geology in the basin. The hillshade raster shows present-day elevation. The Castle Rock study area is circled in blue. Inset: Paleogeography of the North America Western Interior at the KPB, from Ron Blakely, Colorado Plateau Geosystems, Arizona, USA (<http://cpgeosystems.com/paleomaps.html>). The Denver Basin is marked by the gold star, with the Rocky Mountain Front Range nearby to the west and the Mississippi Embayment to the southeast (present-day Louisiana and Mississippi).

over the Cenozoic from multiple methods shows considerable scatter (>2 -fold) for most time intervals (Beerling & Royer, 2011). The best way to distinguish whether this scatter represents real, short-term CO_2 variation or limitations of particular methods is to generate CO_2 estimates from multiple methods at single sites (Montañez et al., 2011).

Previous multiproxy studies have been limited to the marine alkenone and boron methods for the low- CO_2 world (<400 ppm) of the Miocene (Badger et al., 2013) and Pliocene (Seki et al., 2010). Here we estimate CO_2 for the exceptional early Paleocene fossil plant site Castle Rock (Ellis et al., 2003) with four different paleobotanical proxies. The Castle Rock section is located on the western edge of the Denver Basin in Colorado (Figure 1) with a direct radioisotopic age of 63.844 ± 0.060 Ma (± 0.097 including all sources of uncertainty), ~ 2.2 (± 0.06) Myr after the Cretaceous-Paleogene boundary (KPB) mass extinction event (see Text S1 for more information about the site and Text S3.11 for details of U-Pb isotopic analyses). Castle Rock contains the abundant remains of a rainforest preserved in situ over a short time period (<3 m in stratigraphic section) by successive overbank flooding (Ellis et al., 2003). The species richness at Castle Rock is several times higher than other post-KPB extinction sites in North America (Ellis et al., 2003; Johnson et al., 2003; Johnson & Ellis, 2002). The diversity of taxa, morphology of fossil leaves, and estimates of temperature and rainfall indicate that Castle Rock was similar to present-day tropical or paratropical rainforests (Ellis et al., 2003). Despite being well studied, no estimates of atmospheric CO_2 have yet been published from the site.

The four proxies applied here are the stomatal index (SI) and three newer methods based on C_3 photosynthesis: the BRYOCARB model for the asexual nonvascular liverworts (Fletcher et al., 2006) and two others for stomatal-bearing plants, which we refer to here as the Franks (Franks et al., 2014) and Konrad (Konrad et al., 2008) models. The widely used (e.g., Barclay et al., 2010; Doria et al., 2011; Kürschner et al., 2008; Royer et al., 2001) SI method (Salisbury, 1927) derives from the inverse relation between atmospheric CO_2 and the fraction of leaf epidermal cells that are stomata, the pores on the leaf surface that allow for gas exchange with the atmosphere (Royer, 2001; Woodward, 1987). A drawback of this proxy is that the quantitative SI- CO_2 relationship is empirical and species-dependent, limiting its use to fossil taxa with very close living relatives (Beerling & Royer, 2002b; Royer, 2001). The newer, more complex gas-exchange models minimize this shortcoming. Nonetheless, all of the described plant-based proxy methods have produced reliable estimates of atmospheric CO_2 concentration in different settings. Our goals here were (i) to estimate atmospheric CO_2 concentration for the early Paleocene with greater confidence by applying multiple plant-based proxies to a single fossil site and (ii) to use this information to gain greater insight into long-term Earth system climate sensitivity.

2. Methods

2.1. Proxy Models

The gas-exchange models (Franks, Konrad, and BRYOCARB) are based on a simple, well-validated model for C_3 photosynthesis, where the rate of carbon assimilation is equal to the product of total leaf conductance to CO_2 and the atmospheric-to-leaf-internal CO_2 concentration gradient (Farquhar & Sharkey, 1982); we refer to this as the Farquhar model. Additionally, in each of these models the carbon isotope discrimination during photosynthesis ($\Delta^{13}C$) is used to reconstruct the ratio of leaf-internal-to-atmospheric CO_2 concentration (c_i/c_a). This fractionation, which occurs due to discrimination against ^{13}C during CO_2 diffusion into leaf (or thallose) intercellular spaces (4.4‰) and during carbon fixation by Rubisco (20–27‰), can be determined from measurements of plant tissue carbon isotope composition ($\delta^{13}C$; corrected for diagenesis) and an estimate of paleo-atmospheric CO_2 $\delta^{13}C$ (corrected for soil respiration in the case of the BRYOCARB model). Although photorespiration may affect the relationship between leaf $\delta^{13}C$ and c_i/c_a (Schubert & Jahren, 2018), including this effect would increase our CO_2 estimates from the Franks model by <50 ppm. A brief description of each gas-exchange model is given below; full details of these models and our methods are given in Texts S2 and S3.

For each proxy method, 95% confidence intervals for estimated CO_2 were determined using 10,000 Monte Carlo simulations (Data Set S5) to propagate uncertainties in all input parameters.

2.1.1. Franks Model

The Franks model for stomatal-bearing vascular plants (Franks et al., 2014) consists of two main equations that are iteratively solved for two unknowns: paleo-photosynthetic rate and paleo-atmospheric CO_2 concentration. Key input parameters come from stomatal morphology and carbon isotopic composition measurements on fossil leaf tissue and from gas-exchange measurements on present-day relatives. The first of the iteratively solved equations is the Farquhar model, where total leaf conductance to CO_2 is determined largely by stomatal density and morphology. The second equation, derived from an expression for RuBP regeneration-limited photosynthesis (Farquhar et al., 1980), describes the long-term change in photosynthetic rate due to changing atmospheric CO_2 concentration relative to known values in a nearest living relative. We updated the equation presented by Franks et al. (2014) by incorporating the present-day c_i/c_a (see Data Sets S1 and S2); this change improves the accuracy of the estimated photosynthetic rate (see Text S2.2). An updated version of the model (v2) is available as R code in the supporting information.

2.1.2. Konrad Model

The Konrad model (Konrad et al., 2008) is also appropriate for stomatal-bearing vascular plants and is based on iteratively solving two main equations, the first of which is the Farquhar model. The Konrad model differs from the Franks model in the second main equation: here, paleo-photosynthetic rate is estimated based on the assumption that it is optimized with respect to water loss under given environmental conditions (Konrad et al., 2008). Thus, the model requires estimates of paleo-environmental parameters such as temperature and relative humidity and estimates of photosynthetic parameters for the given taxon such as the maximum RuBP-saturated rate of carboxylation at 25 °C (V_{c_max25}) (Konrad et al., 2008). The code is available in Maple

and Mathematica in the supporting information; also available is an updated Mathematica version including Monte Carlo error propagation (used for this study).

2.1.3. BRYOCARB Model

The BRYOCARB model (Fletcher et al., 2006) is for nonvascular liverworts, which lack stomata. Thus, thallus conductance to CO_2 either scales with atmospheric CO_2 (for liverworts with fixed pores, such as *Marchantia* spp.; Green & Snelgar, 1982; Raven, 1993) or is fixed (for liverworts without pores). The BRYOCARB model works by inverting the dependence of $\Delta^{13}\text{C}$ on atmospheric CO_2 (c_a ; Fletcher et al., 2006). The model first calculates $\Delta^{13}\text{C}$ values for a range of c_a values (Fletcher et al., 2006). This calculation includes an estimate of the corresponding photosynthetic rate based on environmental parameters such as temperature, irradiance, and c_a , and physiological parameters such as dark respiration rate, maximum rate of carboxylation by Rubisco, and maximum rate of electron transport (Fletcher et al., 2006). A smooth interpolation is then fit to the ($\Delta^{13}\text{C}$, c_a) pairs. Finally, this function is used to find the c_a value corresponding to the measured $\Delta^{13}\text{C}$ (Fletcher et al., 2006).

In the supporting information we present updated R code for the BRYOCARB model (v2), modified from Fletcher et al. (2008) to include the calculation of $\Delta^{13}\text{C}$ and paleo-irradiance (based on latitude, age, cloud cover, and leaf area index); these calculations were made off-line in the original model.

2.2. Fossil Analysis

The stomatal-bearing fossil species used in this study were *Ginkgo* sp. (CR 125; $N = 15$), cf. *Sassafras* sp. (CR 10; $N = 4$), and a Lauraceae morphotype (CR 20; $N = 10$). Cuticle from the latter two taxa was separated from the rock matrix with polyester overlays then treated in HCl and HF to remove mineral debris (Kouwenberg et al., 2007). The *Ginkgo* cuticle required no pretreatment because it was already separated from the rock matrix.

Morphological measurements were made under epifluorescence microscopy. Stomatal density (and SI for *Ginkgo*) was measured in three fields-of-view on each leaf fragment, and pore length was measured on 8–15 stomata per fragment. Guard cell width was estimated from pore length using scalings derived from measurements on extant relatives (see Data Sets S3 and S4). Photographs documenting each measurement are available on Figshare (Kowalczyk, 2018).

Carbon isotope compositions ($\delta^{13}\text{C}$) for *Sassafras* and *Marchantia* were measured at the UC Davis Stable Isotope Facility. Castle Rock *Ginkgo* and Lauraceae morphotype CR 20 $\delta^{13}\text{C}$ measurements were provided by A. Hope Jahren. Fossil cuticle $\delta^{13}\text{C}$ values for the stomatal-bearing taxa were corrected for diagenesis to reconstruct bulk leaf $\delta^{13}\text{C}$ based on the isotopic difference between bulk leaf and cuticle that we measured on extant relatives; the equivalent offset for liverwort fossil tissue was taken from Fletcher et al. (2008).

2.3. Paleo-environmental Estimates

The Konrad model (Konrad et al., 2008) requires estimates of paleo-temperature, relative humidity, and average wind speed. Mean annual temperature for Castle Rock ($21.8 \pm 1.5^\circ\text{C}$) was estimated using leaf-margin analysis (Wilf, 1997) by Ellis et al. (2003). Relative humidity ($77 \pm 5\%$) and wind speed ($2.5 \pm 0.5\text{ m/s}$) were estimated from typical values in extant rainforests (Richards, 1996).

BRYOCARB model parameters include paleo-temperature and irradiance. We calculate tree-top irradiance using solar luminosity at 63.8 Ma (Gough, 1981) and the paleolatitude of Castle Rock (44°N ; van Hinsbergen et al., 2015). The irradiance at ground level (the presumed habitat of the nonepiphytic *Marchantia*) is reduced as an exponential function of leaf area index (LAI) according to the Lambert-Beer extinction law (Larcher, 1995). In a review of global literature, Asner et al. (2003) find a mean and standard deviation LAI of 4.8 ± 1.7 for evergreen broadleaf forests. Because extant tropical *Marchantia* species are typically found in semishaded to open spaces in rainforests such as river banks or roadsides (Bischler & Boisselier-Dubayle, 1993; Das & Sharma, 2012; Fuselier & McLetchie, 2004; Siregar et al., 2013), we adopt the lower end of the Asner et al. (2003) range (mean LAI = 3.95) for the Castle Rock *Marchantia* sp. Irradiance uncertainty is estimated as 12.5% of the mean value, following Fletcher et al. (2008).

All proxy models except SI require an estimate of paleo-atmospheric CO_2 carbon isotopic composition ($\delta^{13}\text{C}_{\text{atm}}$) to calculate discrimination ($\Delta^{13}\text{C}$). We adopt a value of $-5.0 \pm 0.32\text{‰}$ from the Tipple et al. (2010) record. For the BRYOCARB model, we apply a correction of -1.5‰ to account for a more negative $\delta^{13}\text{C}_{\text{atm}}$ near ground level due to soil respiration (see Text S3.10.3).

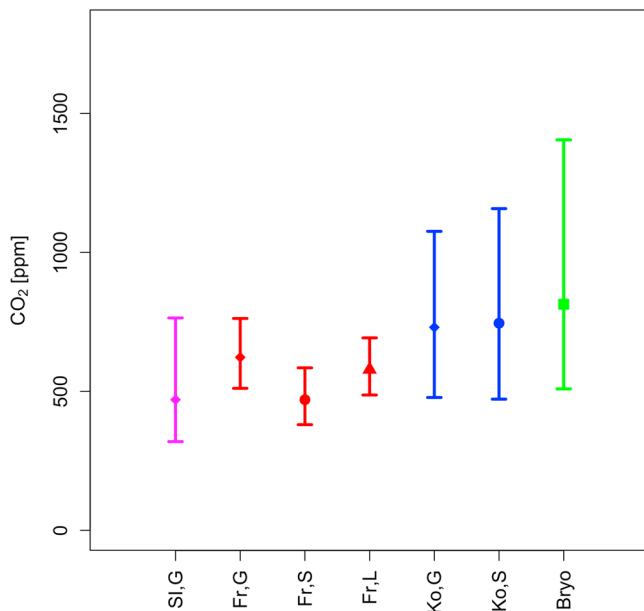


Figure 2. Atmospheric CO₂ estimates from Castle Rock, colored according to proxy method (magenta = stomatal index [SI], red = Franks model [Fr], blue = Konrad model [Ko], green = BRYOCARB [Bryo]) with plotting symbols indicating fossil morphotype (diamond = *Ginkgo* sp. [CR 125; G], circle = cf. *Sassafras* sp. [CR 10; S], triangle = Lauraceae morphotype [CR 20; L], and square = *Marchantia* sp.). The error bars indicate the 95% confidence interval for each CO₂ estimate.

model to growth paleo-temperature (Figure S25 and Text S5.3), a parameter that is difficult to estimate with high precision and that is not explicitly included in the Franks model. In contrast, the Franks model shows greater variability across species than the Konrad model. We consider this a result of tuning the Konrad model such that present-day CO₂ estimates from the nearest living relatives are correct (following the recom-

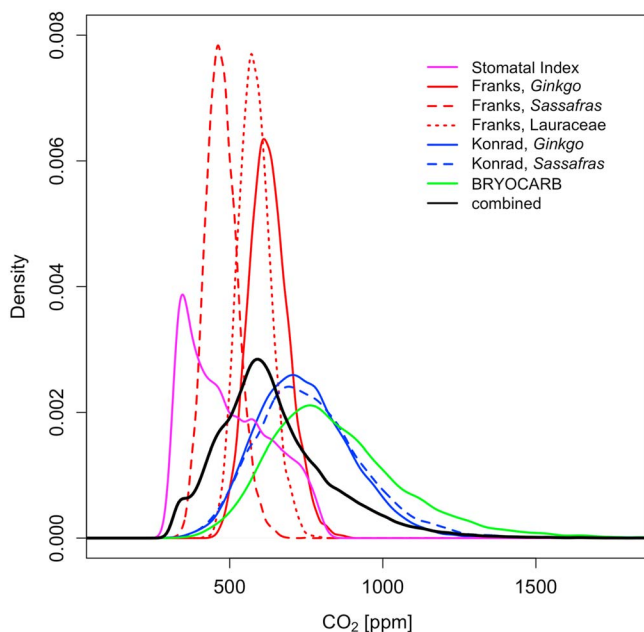


Figure 3. Probability distributions from all proxy estimates. The solid black line shows the combined distribution (median = 616 ppm, 95% CI = 352–1110 ppm).

3. Results and Discussion

3.1. Comparison Across Methods

Median CO₂ estimates for the early Paleocene from Castle Rock range from 470 to 813 ppm (Figures 2 and 3, see also Data Set S1). All pairwise 95% confidence intervals overlap, increasing confidence in the reconstructed CO₂. The magnitude of scatter in the Castle Rock median CO₂ estimates is close to that seen for many time-slices in the CO₂ proxy compilation of Beerling and Royer (2011), suggesting that some of the scatter in the compilation is due to methodological biases rather than true short-timescale CO₂ variations.

The combined CO₂ probability density function for Castle Rock has a median of 616 ppm and a 95% confidence interval of 352–1,110 ppm (Figure 3). The combined estimate from Castle Rock is approximately double previous estimates from roughly coeval studies using SI (Beerling et al., 2009) and paleosols (Huang et al., 2013), which range from 212 to 367 ppm (Figure S23 and Text S4).

The CO₂ estimate from the SI proxy (470 ppm) is lower than most of the estimates from the gas-exchange methods for stomatal-bearing plants (Figure 2). We attribute this to the flattening of the *Ginkgo* SI response curve at elevated CO₂ (Beerling et al., 2009). We note that using the new SI power law calibration from Barclay and Wing (2016) yields an even lower estimate of 352 ppm (Text S5.1).

CO₂ estimates from the Konrad model have larger uncertainty than those of the Franks model. This is likely due to the high sensitivity of the Konrad model to growth paleo-temperature (Figure S25 and Text S5.3), a parameter that is difficult to estimate with high precision and that is not explicitly included in the Franks model. In contrast, the Franks model shows greater variability across species than the Konrad model. We consider this a result of tuning the Konrad model such that present-day CO₂ estimates from the nearest living relatives are correct (following the recom-

ended protocol for this proxy), whereas no such tuning was done for the estimates from the Franks model (Text S3.2). The Franks model overpredicts present-day CO₂ for *Ginkgo biloba* by ~100 ppm (Data Set S2). If a similar bias affects fossil *Ginkgo*, then early Paleocene CO₂ could be overestimated somewhat. Conversely, the fossil *Ginkgo* estimate is partly based on measured inputs from living *G. biloba* for the photosynthetic parameters A_0 and ζ (Text S3.2). If instead we use the recommended values from Franks et al. (2014) for these two inputs ($A_0 = 5.85 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; $\zeta = 0.23$; see Data Set S2 for details), then the estimated CO₂ for fossil *Ginkgo* increases by ~70 ppm; this illustrates the sensitivity of the model to these parameters (Text S5.2) and suggests that our estimate may be falsely low.

Finally, we note that the BRYOCARB model estimate has a larger 95% confidence interval than the others; this site-specific result occurs because the atmosphere-to-leaf carbon isotope discrimination ($\Delta^{13}\text{C}$) inferred for the Castle Rock liverwort lies on a high-sensitivity region of the CO₂ response curve for this model (Figure S26 and Text S5.4).

3.2. Cenozoic Earth-System Sensitivity

Earth system sensitivity (ESS) is a measure of climate sensitivity that includes short- and long-term feedback (Hansen et al., 2008; Lunt et al., 2010; Pagani et al., 2010). Following Royer et al. (2012), we conservatively estimate a minimum Paleocene-to-preindustrial ESS by considering a

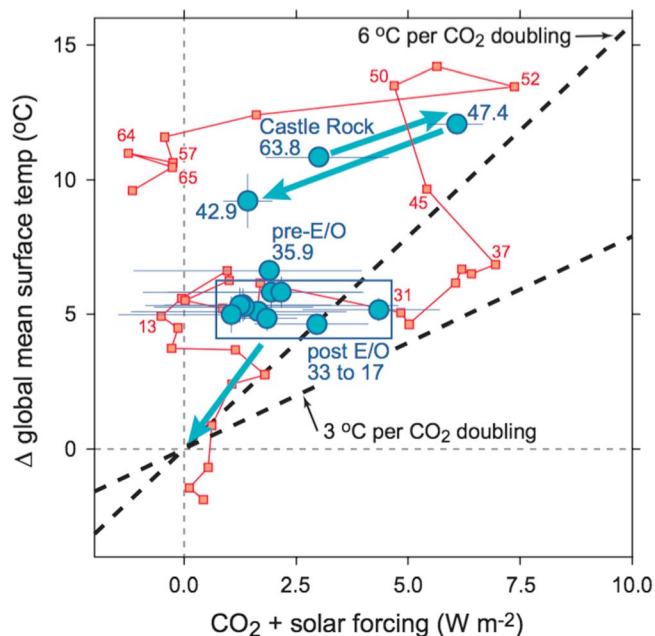


Figure 4. Earth system sensitivity (ESS) over the Cenozoic, modified from Figure 2b in Royer (2016). ESS is shown as the change in global mean surface temperature (Hansen et al., 2013) versus the change in radiative forcing due to atmospheric CO₂ and solar luminosity evolution, both relative to pre-industrial conditions. The red squares show data from a variety of CO₂ proxy methods (see Royer, 2016) averaged over 1-Myr intervals, while the larger blue circles show data only from gas-exchange CO₂ proxies (i.e., the Franks and Konrad models; Franks et al., 2014; Konrad et al., 2008), where each symbol is an individual estimate. The blue box summarizes the range of gas-exchange estimates between 33 and 17 Ma. For both data sets, the error bars represent ± 1 standard deviations. E/O is the Eocene/Oligocene boundary.

minimum global surface temperature change of $\sim 7^\circ\text{C}$ (Hansen et al., 2013; Zachos et al., 2008) and a maximum forcing, first including atmospheric CO₂ and solar luminosity ($F_{\text{CO}_2,\text{SOL}}$) and second including the additional radiative effect of continental positions ($F_{\text{CO}_2,\text{SOL,GEO}}$); for the latter, we assume a paleogeographic effect equivalent to 1 CO₂ doubling, a likely overestimate (Royer et al., 2012).

The highest early Paleocene atmospheric CO₂ estimate from previous studies, 367 ppm (Beerling et al., 2009), implies an unrealistic ESS of $>100^\circ\text{C}$ per CO₂ doubling associated with $F_{\text{CO}_2,\text{SOL}}$ (i.e., a decoupling between CO₂ and temperature) or, including the additional forcing from continental positions ($F_{\text{CO}_2,\text{SOL,GEO}}$), 6.8°C . The higher CO₂ estimates from Castle Rock (616 ppm, 95% CI = 352–1,110 ppm) give more reasonable average Cenozoic ESS values of 9.3°C ($F_{\text{CO}_2,\text{SOL}}$; 95% CI = 4.3– $>100^\circ\text{C}$) and 4.0°C ($F_{\text{CO}_2,\text{SOL,GEO}}$; 95% CI = 2.7– 7.2°C). These are likely minimum estimates; for example, the temperature change of 7°C used in the calculation is at the lower end of the proxy constraints; a value of 10–11 $^\circ\text{C}$ is more likely (Hansen et al., 2013). By comparison, the fast-feedback climate sensitivities associated with most climate models tuned to the early Cenozoic are $\sim 3^\circ\text{C}$ (Lunt et al., 2012). Our minimum constraints on ESS thus reinforce the notion that some additional positive feedback (either fast or slow) are probably needed to explain early Cenozoic warmth; these *missing* feedback factors may be related to clouds (Abbot et al., 2009; Caballero & Huber, 2013; Hansen et al., 2013; Sagoo et al., 2013), aerosols (Kiehl & Shields, 2013; Kump & Pollard, 2008; Upchurch et al., 2015), or vegetation (Beerling et al., 2011; Loptson et al., 2014).

Our ESS calculation is the mean between 63.8 Ma and the preindustrial era; it is likely masking temporal variability, for example, higher values during times when large ice sheets are present (e.g., Hansen et al., 2008). Royer (2016) partly addressed this concern by tracking the evolution of ESS over the Cenozoic using CO₂ estimates from a variety of proxy methods and the

global mean surface temperature model from Hansen et al. (2013) but found some anomalous patterns. For example, ESS is unreasonably high from 52 to 37 Ma but very low or negative from 33 to 13 Ma (see red squares in Figure 4). These patterns may be due to inaccurate CO₂ estimates (Royer, 2016). Here we modify this analysis by using only CO₂ estimates from the Franks (Franks et al., 2014) and Konrad (Konrad et al., 2008) gas-exchange models. These results give a more coherent picture of ESS (blue circles in Figure 4): values of $\sim 3^\circ\text{C}$ during the early Cenozoic hothouse period, then transitioning to higher values ($>7^\circ\text{C}$) sometime between 42.9 and 33 Ma and continuing until the present-day. This is consistent with studies estimating a lower ESS for ice-free climates and a higher ESS in the presence of large ice sheets such as those that begin to develop near the Eocene–Oligocene boundary ~ 34 Ma (e.g., PALAEOSENS, 2012). Additional gas-exchange CO₂ estimates at times not presently covered will be needed to confirm this result, but this preliminary analysis suggests that the greater reliability of the gas-exchange proxy methods may help us to understand ESS under different climate states.

4. Summary

Our multiproxy study using fossils from an exceptionally diverse early Paleocene rainforest constrains atmospheric CO₂ to ~ 350 – 1100 ppm at 95% confidence. This estimate is approximately double previous coeval CO₂ estimates and is more in keeping with the known warmth of the early Paleocene. The broad agreement among methods increases confidence in the proxies and underscores the value of a multiproxy framework. The new gas-exchange models highlighted here retain sensitivity at high CO₂ and have the potential to be widely applied to more fossil taxa than the SI. Critically, the gas-exchange CO₂ estimates from this and other studies over the Cenozoic paint a more coherent picture of Earth system sensitivity across the hothouse-icehouse transition than that drawn by CO₂ estimates from other proxy methods.

References in Supporting Information

These references contributed to the supporting files: Arnott (1959), Bahcall et al. (2001), Barclay et al. (2003), Barclay and Wing (2016), Beerling et al. (1998), Beerling et al. (2002), Beerling and Royer (2002a), Beerling et al. (2009), Beerling and Royer (2002b), Benner et al. (1987), Bowring et al. (2011), Boyce (2009), Breecker and Retallack (2014), Broadmeadow et al. (1992), Buchmann et al. (1997), Burnham and Johnson (2004), Burnham et al. (2001), Burnham et al. (1992), Carpenter et al. (2007), Chater et al. (2011), Chen et al. (2001), Clyde et al. (2016), Collister et al. (1994), Condon et al. (2015), Crifò et al. (2014), Critchfield (1970), Dechesne et al. (2011), Diefendorf et al. (2010), Dilcher (1973), Dinarès-Turell et al. (2014), Dow et al. (2014), Dunn et al. (2015), Edwards et al. (1998), Edwards (1990), Ellis et al. (2003), Ellis et al. (2004), English and Johnston (2004), Evans and Von Caemmerer (1996), Farquhar and Von Caemmerer (1982), Farquhar et al. (1980), Farquhar et al. (1989), Farquhar et al. (1982), Farquhar and Sharkey (1982), Ferguson (1985), Fletcher et al. (2005), Fletcher et al. (2004), Fletcher et al. (2008), Fletcher et al. (2006), Francey et al. (1985), Franks and Farquhar (1999), Franks et al. (2013), Franks and Beerling (2009a), Franks and Beerling (2009b), Franks et al. (2001), Franks and Farquhar (2007), Franks et al. (2014), Gardner (1975), Givnish (1988), Gradstein et al. (2012), Graham et al. (2014), Green and Snelgar (1982), Greenwood (1992), Grein et al. (2011), Haworth et al. (2011), Haworth et al. (2013), Hicks et al. (2003), Hoke et al. (2014), Holtum and Winter (2001), Huang et al. (2013), Jaffey et al. (1971), Jahren and Sternberg (2003), Johnson and Ellis (2002), Johnson et al. (2003), Kao et al. (2000), Konrad et al. (2008), Kouwenberg et al. (2007), Kürschner (1997), Larcher (1995), Leigh et al. (2011), LI-COR (2011), Lockheart et al. (1997), Long and Bernacchi (2003), Mattinson (2005), Maxbauer et al. (2014), McElwain and Chaloner (1996), McElwain et al. (2016), McLean et al. (2011), McLean et al. (2015), Medina et al. (1986), Niinemets et al. (2009), Pagani et al. (2005), Peppe et al. (2011), Ramezani et al. (2011), Raschke and Dickerson (1973), Raven (1993, 2002), Raynolds (2002), Raynolds and Johnson (2002), Richardson et al. (2009), Roth-Nebelsick (2007), Royer (2001, 2003), Royer and Hren (2017), Royer et al. (2001), Rudall et al. (2012), Sack et al. (2006), Sack and Scoffoni (2013), Salisbury (1927), Sewall and Sloan (2006), Sharkey et al. (2007), Shobe and Lersten (1967), Smith et al. (2010), Spicer (1980), Sprain et al. (2015), Sternberg et al. (1989), Sun et al. (2003), Taylor (1999), Uhl and Mosbrugger (1999), Vanderpoorten and Goffinet (2009), Vitousek and Howarth (1991), Warren and Adams (2006), Wilf and Johnson (2004), Woodward (1987), Wullschlegler (1993), Zaiss et al. (2014), and Zeiger et al. (1987).

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