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Towards a Cenozoic History of Atmospheric CO₂
The Cenozoic CO₂ Proxy Integration Project (CenCO₂PIP) Consortium

Abstract: The geological record encodes the relationship between climate and atmospheric carbon dioxide (CO₂) over long and short timescales, as well as potential drivers of evolutionary transitions. However, reconstructing CO₂ beyond direct measurements requires the use of paleo-proxies and herein lies the challenge, as proxies differ in their assumptions, degree of understanding, and even reconstructed values. Here we critically evaluate, categorize, and integrate available proxies to create a high-fidelity and transparently constructed atmospheric CO₂ record spanning the past 66 million years. This provides clearer evidence for higher Earth System Sensitivity in the past and for the role of CO₂ thresholds in biological and cryosphere evolution.
The contribution of atmospheric CO$_2$ to Earth’s greenhouse effect and the potential for variations in the global carbon cycle to cause climate change has been known for more than a century (1), but it was only in 1958 that direct measurements of the concentration of CO$_2$ in the atmosphere (or molar mixing ratio - the mole fraction of a gas in one mole of air) were systematically collected. Alongside reconstructions of the historical rise in Earth’s surface temperature (2), this record has become one of the most influential and scientifically valuable environmental time-series, documenting the continuous rise in annual mean CO$_2$ from 315 parts per million (ppm) in 1958 to 419 ppm in 2022 (3). Projecting beyond these records to estimate how Earth’s climate will respond to further increases in CO$_2$ requires global climate models (4). However, while successful in explaining observed historical climate change (2), models leave doubt as to whether global mean temperature will rise linearly as a function of future doubling of CO$_2$ (i.e., an invariant ‘climate sensitivity’) or whether climate feedbacks will lead to an increasing (or ‘state-dependent’) sensitivity of climate to CO$_2$ in the future (5, 6).

We can turn to the geological record to help constrain models and improve our understanding of non-linearities in the climate system (e.g., 7), as it documents a variety of global climate changes and critically, climate states warmer than today. Leveraging this record, however, requires the paired quantification of both past atmospheric CO$_2$ and temperature. In parallel with recent efforts to compile and vet paleo-temperature estimates (8), here we focus on paleo-CO$_2$ estimates. Samples of ancient air can be extracted and analyzed from bubbles preserved in ancient polar ice (9, 10), but continuous ice core records currently only extend our knowledge of CO$_2$ back about 800 thousand years (kyr) (for a compilation, see 11), with isolated time slices extending to ~2 Ma (million years ago) (12, 13). Importantly, at no point during the Pleistocene (2.58 Ma to 11,700 years ago) did CO$_2$ come close to present-day values (419 ppm, year 2022), with 300 ppm being the highest value measured to date (14). In contrast, depending on the extent of future human emissions, atmospheric CO$_2$ could reach 600–1000 ppm by the year 2100 (2). Feedbacks between changing climate and the carbon cycle may also amplify or diminish emissions from surficial carbon reservoirs (e.g., thawing permafrost, adjustments in size and composition of the terrestrial biosphere and marine carbon pool), creating additional uncertainty in future CO$_2$ projections (15, 16). Past changes in CO$_2$ inherently include the role of these feedbacks, and their study could help reduce uncertainty in Earth system models (17).

A solid understanding of atmospheric CO$_2$ variation through geological time is also essential to deciphering and learning from other features of Earth’s history. Changes in atmospheric CO$_2$ and climate are suspected to have caused mass extinctions (e.g., 18, 19) as well as evolutionary innovations (20, 21). During the Cenozoic, long-term declines in CO$_2$ and associated climate cooling have been proposed as the drivers of changing plant physiology (e.g., carbon-concentrating mechanisms), species competition and dominance, and associated with this, mammalian evolution. A more refined understanding of past trends in CO$_2$ is therefore central to understanding how modern species and ecosystems arose and may fare in the future.

Extending the CO$_2$ record beyond the temporally restricted availability of polar ice requires the use of ‘proxies’. In essence, a CO$_2$ proxy could be any biological and/or geochemical property of a fossil or mineral that responds to the concentration of ambient CO$_2$ when it is formed. Unfortunately, unlike in the case of bubbles of ancient air trapped in polar ice, this response is invariably indirect. The connection between a proxy signal and atmospheric CO$_2$ is
often strongly mediated via biological 'vital effects' (e.g., concentration of or discrimination against certain molecules, elements or isotopes due to physiological processes such as biomineralization, photosynthesis, respiration), may be indirectly connected to the atmosphere via dissolution of carbon in seawater or lakes, may involve isotopic or other chemical fractionation steps, or a combination of these. When preserved in terrestrial or marine sediments, proxy substrates can also be impacted by post-depositional ('diagenetic') processes that must be accounted for. Relationships between proxies and CO$_2$ are typically calibrated using observations or laboratory experiments; in biological systems, these calibrations are often limited to modern systems (e.g., modern organisms or soils), and applications to the distant past focus on physiologically or physically similar systems preserved in the sediment and rock record (e.g., similar fossil organisms or fossil soils). Most CO$_2$ proxies also require estimation of one or more additional environmental parameters and hence depend on additional proxy records. The complexity of proxy-enabled paleoclimate reconstructions thus presents a major challenge for creating a self-consistent estimate of atmospheric CO$_2$ through geological time and requires careful validation.

One of the first paleo-CO$_2$ proxies to be devised was based on the observation that vascular plants typically optimize the density, size, and opening/closing behavior of stomatal pores on their leaf surfaces to ensure sufficient CO$_2$ uptake while minimizing water loss (e.g., 22). A count of stomatal frequencies then provides a simple proxy for the CO$_2$ concentration experienced by the plant (23). Changes in ambient CO$_2$ can also drive a cascade of interrelated effects on photosynthesis, the flux of CO$_2$ into the leaf (largely determined by stomatal size and density), and the carbon isotopic fractionation during photosynthesis ($\Delta^{13}C$, 22, 23, 24). While lacking functional stomata, non-vascular plants like liverworts also exhibit isotopic fractionation during photosynthesis, and their $\delta^{13}C$ values are thus similarly controlled by ambient CO$_2$. The list of terrestrial paleo-CO$_2$ proxies also includes inorganic carbonate nodules precipitated in ancient soils (i.e., paleosols) as well as sodium carbonate minerals precipitated in continental lacustrine evaporites. While the paleosol proxy uses the carbon isotope composition of carbonate nodules and deconvolves the mixture of atmospheric and soil-respired CO$_2$ in soil porewaters using models of soil CO$_2$ (25, 26), the nahcolite proxy is based on the CO$_2$ dependence of sodium carbonate mineral equilibria (27, 28). Analogous to non-vascular plants on land, phytoplankton fractionate carbon isotopes during photosynthesis in response to the concentration of dissolved CO$_2$ in seawater, creating an isotopic signal stored in organic biomolecules that can be retrieved from ocean sediments (29). Boron proxies recorded in fossil shells of marine calcifying organisms are related to seawater pH, which in turn can be related back to atmospheric CO$_2$ (30, 31). A detailed discussion of the analytical details, entrained assumptions, and inherent uncertainties of currently available CO$_2$ proxies, plus summaries of recent advances and opportunities for further validation, is presented in the Supplemental Material and in Table S1.

Although each of these proxies has been validated extensively, comparing reconstructions from different proxies often reveals discrepancies. Prior compilations of paleo-CO$_2$ and explorations of the CO$_2$-climate linkage already exist (32-34), however, those studies applied limited proxy vetting, include CO$_2$ estimates that predate major innovations in some methods, and use rather basic data interpolation to assess broad CO$_2$ trends. Earlier CO$_2$ reconstructions are also often insufficiently constrained by ancillary data (e.g., concomitant
temperature, isotopic composition of seawater or atmosphere) to be consistent with modern
proxy theory, have incomplete or missing uncertainty estimates for CO₂ and/or sample age, and
may exhibit fundamental disagreement with other proxies, leaving our current understanding of
past CO₂ incomplete.

In this study we present the results of a 7-year endeavor by an international consortium
of researchers whose collective expertise spans the reconstruction of paleo-CO₂ from all available
terrestrial and marine archives. We have jointly created a detailed, open-source database of
published paleo-CO₂ estimates including all raw and ancillary data together with associated
analytical and computational methods. Each record was vetted and categorized in view of the
most recent proxy understanding, with calculations adopting a common methodology including
full propagation of uncertainties. We focus our efforts here on the Cenozoic, when the spatial
distribution of continents and ocean basins, as well as the structure of marine and terrestrial
ecosystems, was similar to the modern, yet profound changes in CO₂ and climate occurred.
Identifying the most reliable Cenozoic CO₂ estimates published to date allows us to quantify
important physical (e.g., temperature, ice volume) and biological (i.e., physiological, ecosystem)
thresholds and tipping points.

We structure this investigation as follows: First we summarize the methodology by which
we assessed the CO₂ proxies and associated estimates. We then apply these methods to derive
a series of paleo CO₂ compilations comprised of data with different levels of quality or
confidence, and statistically integrate the ‘top-tier’ data to create a realization of the Cenozoic
variability in atmospheric CO₂. This is followed by a discussion of the climatic implications
(including climate sensitivity) of the paleo-CO₂ curve, and a presentation of an evolutionary
perspective. We finish with a roadmap for further advances in understanding past changes in
atmospheric CO₂.

Critical assessment of atmospheric CO₂ proxies

The basis of our synthesis is a set of comprehensive data templates documenting all types
of proxy data and their corresponding CO₂ estimates (a total of 6,247 data points). The completed
data sheets for each study can be accessed as the paleo-CO₂ 'Archive' in NOAA's National Climatic
Data Center (NCDC). These 'Archive' sheets report all underlying data at face value from the
original publications, but their unprecedented level of detail is designed to facilitate critical
evaluation and recalculation of each CO₂ estimate.

From the 'Archive', published CO₂ estimates were evaluated by teams of experts who are
active in validating and applying these proxies, and often included the original authors of the
respective data. No new proxy data were collected as part of this effort, but estimates were
recalculated where needed and possible, and age models were revised where new evidence was
readily accessible. Additionally, CO₂ and age uncertainties were updated, as necessary, to
consistently reflect propagated 95% confidence intervals. The vetting criteria are summarized in
Supplementary Table S1 and detailed in paleo-CO₂ 'Product' sheets. These CO₂ estimates are
categorized as follows: 'Category 1' estimates (Fig. 1a, 1,673 data points or ~27% of the original
total) are based on data whose uncertainty is fully documented and quantifiable in view of
current proxy understanding. 'Category 2' estimates (Fig. 1b, 1,813 data points) contain sources of uncertainty that are not yet fully constrained. These uncertainties vary between proxies and datasets, and include, e.g., insufficient replication, poorly constrained proxy sensitivity to parameters other than CO$_2$, or extrapolation of calibration curves. 'Category 3' estimates (the residual 2,761 data points or ~44% of the Cenozoic paleo-CO$_2$ estimates published to date) are either superseded by newer, independently published evaluations from the same raw data, are considered unreliable due to factors such as incomplete supporting datasets that prevent full quantification of uncertainties, or outdated sample preparation methods.

Although objective criteria are applied throughout, the vetting process was particularly challenging for the paleosol- and phytoplankton-based proxies because multiple approaches are currently in use for interpreting these proxy data (35-41). Given the lack of a universally agreed-upon method, we compare multiple approaches for treating the data of these two proxies whenever possible. For the paleosol proxy, the greatest source of uncertainty is in the estimation of paleo-soil CO$_2$ concentration derived from respiration. Two different approaches are commonly used to do this. The first method is based on proxy-estimated mean annual rainfall, while the second is based on soil order (i.e., the most general hierarchical level in soil taxonomy, comparable to kingdom in the classification of biological organisms). However, few records in the database allow for a direct comparison between the two approaches. An opportunity for comparison exists with two Eocene records (37, 42), where re-calculation using each of the two different methods leads to CO$_2$ estimates that do not overlap within 95% confidence intervals for most stratigraphic levels (Fig. S6). This implies that the uncertainty in estimating paleo-soil CO$_2$ concentration derived from respiration cannot be fully quantified with either of these approaches. Thus, most paleosol-based CO$_2$ estimates were designated as Category 2. For the phytoplankton proxy, routinely applied methods differ in how algal cell size and growth rate are accounted for, as well as the assumed sensitivity of algal $\delta^{13}$C values to aqueous CO$_2$ concentration (see Supplementary Materials for details). Where data are available, we compare both newer and traditional methods, finding that although there are deviations between the resulting CO$_2$ estimates, they do agree within 95% confidence intervals. We hence assign many phytoplankton CO$_2$ estimates to Category 1 and present mean CO$_2$ and uncertainty values that reflect the range of results from the different methods.

Towards a Cenozoic history of atmospheric CO$_2$

Our composite Category 1 and 2 realizations of Cenozoic CO$_2$ (Figs. 1a and b) display much better agreement among proxies than does the ‘raw’, un-curated collection ('Archive', Fig. 1c). Encouragingly, objective criteria applied to the original data products automatically placed the earlier-reported estimates of ‘negative’ CO$_2$, as well as some unusually high values, into Category 3, and without subjective intervention to otherwise filter them. We note that the Category 1 composite is now largely dominated by marine proxy estimates, with some intervals (e.g., the middle Paleocene, ~63-57 Ma) very sparsely sampled. Furthermore, some intervals (e.g., Oligocene, Miocene) still exhibit significant differences between proxies; for instance, marine-based CO$_2$ estimates start high and decline during the Oligocene (~34-23 Ma), whereas plant-based estimates suggest overall lower and constant CO$_2$ (Fig. 1a). Estimates of global
temperature (Fig. 2b) during this time interval are largely invariant, which leaves us with the questions of whether CO$_2$ and climate were decoupled during this interval, or whether there is a systematic bias in the marine or plant-based CO$_2$ proxies and/or in the temperature proxies. All proxies become more uncertain further back in time as our knowledge of vital effects in biological proxy carriers, secular changes in the elemental and isotopic composition of ocean and atmosphere, as well as proxy sensitivity to environmental parameters that change along with CO$_2$ (e.g., temperature, rainfall, see Supplementary Materials for details) becomes less certain. In some cases, ancillary constraints and uncertainties are shared across multiple proxies (e.g., assumed atmospheric δ$^{13}$C is common to proxies based on land plant δ$^{13}$C, leaf gas exchange, and paleosols), creating interdependence of estimates from seemingly independent proxies. More robust paleo-CO$_2$ reconstruction thus requires not only continued application of all proxies but also replication from different locations.

Although some uncertainties and proxy disagreements remain, the much-improved agreement within the vetted paleo-CO$_2$ compilation gives us confidence that a quantitative reconstruction of Cenozoic CO$_2$ based on the combined Category 1 data is possible. To do so, we statistically model mean CO$_2$ values at half-million-year intervals, together with uncertainties in age and proxy CO$_2$ estimates (Fig. 2a, see Supplementary Materials for details). Our choice of a 500-kyr resolution interval reflects a compromise driven by the proxy data compilation. Although parts of the Cenozoic, particularly the Plio-Pleistocene, are sampled at higher temporal resolution, the density of records remains relatively sparse throughout much of the Paleogene (1 datum per 190 kyr on average). As a result, the data (and in some cases the underlying age models) are not suited to interpreting higher-frequency (e.g., Milankovitch-scale) variations in atmospheric composition, and we focus here on low-frequency (e.g., multi-million year) trends and transitions. Proxy sampling within some intervals may be biased toward conditions that deviate from the 500-kyr mean (most notably here, the Paleocene-Eocene Thermal Maximum, PETM). We do not attempt to remove this bias but recommend caution in interpreting any features expressed at sub-million-year timescales.

This curve (Fig. 2a) allows us to constrain Cenozoic paleo-CO$_2$ and its uncertainty with greater confidence than earlier efforts. The highest CO$_2$ values of the past 66 Myr appear during the Early Eocene Climatic Optimum (EECO, ~53-51 Ma), while the lowest values occur during the Pleistocene. In contrast to earlier compilations, which suggested early Cenozoic CO$_2$ concentrations <400 ppm (e.g., 33), rigorous data vetting and newly published records place early Paleocene mean CO$_2$ in our reconstruction between 650 and 850 ppm. However, the Paleocene remains data poor, and uncertainty in the curve remains large. Although the Paleocene record is predominantly based on the boron isotope proxy (Fig. 1a), inclusion of other (non-marine) proxy data does influence and refine the reconstruction through this epoch, supporting the value of the multi-proxy approach (Fig. S10). Following the rapid CO$_2$ rise and fall associated with the PETM at 56 Ma, mean CO$_2$ steadily rose to peak values of ~1600 ppm around 51 Ma during the EECO. The middle and late Eocene recorded slightly lower values (800-1100 ppm). Mean CO$_2$ dropped to <600 ppm across the Eocene-Oligocene transition (EOT, 33.9 Ma) and reached values that generally fall between ~400 and 200 ppm during the Miocene through Pleistocene, except for a notable increase during the Middle Miocene (~17-15 Ma) to a mean of ~500 ppm. Uncertainty in the mean CO$_2$ values drops substantially in the Plio-Pleistocene (see also Fig. S11),
as expected given a dramatic increase in data density. Our analysis suggests that ~14.5-14 Ma was the last time 500-kyr-mean CO₂ value was as high as the present (Fig. S11), and that all Plio-Pleistocene peak interglacial CO₂ concentrations were exceptionally likely less than those of the modern atmosphere (Fig. S12). In contrast, prior to the Miocene, there is very little support (<2.5% probability) for Cenozoic 500-kyr-mean CO₂ values reaching or falling below pre-industrial levels.

Climatic implications of the revised CO₂ curve

Relationship with global temperature change and climate sensitivity

Our reconstructed Cenozoic CO₂ trends are broadly coherent with those for global temperature as inferred, e.g., from the oxygen isotopic composition (δ¹⁸O) of fossil benthic foraminifera shells (43, 44) and compilations of global surface temperature (45) (Fig. 2b). The Paleocene and Eocene epochs display overall higher temperatures and atmospheric CO₂ concentrations as compared to the later Oligocene, Miocene, and Pliocene - consistent with a predominantly greenhouse-gas regulated global energy budget. More specifically, the slow rise and subsequent fall of CO₂ over the course of the Paleocene and Eocene are mirrored by global temperatures, just as a transient Miocene CO₂ rise coincides with a period of warming at the Miocene Climatic Optimum (MCO). The EOT is identifiable in both the CO₂ and temperature records, despite the smoothing introduced by the curve fitting and 500-kyr binning interval.

Despite this overall agreement, rates and timing of CO₂ vs. temperature changes in the two records are not always synchronized (Fig. 2a,b). For example, CO₂ appears broadly static or even rising during the late Eocene (37-34 Ma) and late Miocene (11-5 Ma) despite global cooling (see also 46) at these times. Conversely, decreasing CO₂ during the early Oligocene corresponds with relatively stable global temperatures (Fig. 2b, but see also 47, 48) and ice volume (Fig. 2c) at that time. We note that the reconstructed Oligocene CO₂ decrease is driven by the contribution of marine proxies to the composite curve, whereas estimates from leaf gas exchange proxies are low and broadly static (Fig. 1c), a discrepancy that cannot be resolved without further experimentation and data collection. We caution that, even at the 500-kyr resolution of our study, the relative timing of CO₂ and temperature change might be unresolved in poorly sampled intervals (i.e., middle Paleocene), but should be well resolved during more recent, well sampled intervals (i.e., late Miocene through present, Fig. S8). Is the occasional divergence of temperature and CO₂ change evidence for occasional disconnects between CO₂ forcing and climate response? Although one might posit bias in the CO₂ reconstruction, the strength of our multiproxy approach is the reduced likelihood that multiple proxies exhibit common bias during particular periods of the Cenozoic. We suggest that some cases of divergence between temperature and CO₂ could reflect non-CO₂ effects on climate (e.g., changes in paleogeography affecting ocean circulation, albedo and heat transport, 49), or the temperature reconstructions used herein could be biased by non-thermal influences (e.g., uncertain elemental and isotopic composition of paleo-seawater, physiological or pH effects on proxies, 48, 50).

Our updated CO₂ curve, in conjunction with existing global temperature reconstructions, gives us the opportunity to reassess how climate sensitivity might have evolved through the
Cenozoic. The most commonly reported form of climate sensitivity is equilibrium climate sensitivity (ECS), which focuses on fast feedback processes (e.g., clouds, lapse rate, snow, sea ice) and is therefore best suited for predicting present-day warming (~3°C for a doubling of CO₂ above the pre-industrial condition). Because the average temporal resolution of our CO₂ database is coarser than 1000 years, we cannot estimate ECS directly. Instead, our data are most appropriate for interpreting an Earth System Sensitivity (ESS[CO₂], following the taxonomy of 51) – the combination of short-term climate responses to doubling CO₂ plus the effects of slower, geological feedback loops such as the growth and decay of continental ice sheets. We compare our reconstructed 500-kyr-mean CO₂ values with two different estimates of global surface temperature. We apply the same Bayesian inversion model used in the CO₂ reconstruction to derive 500-kyr-mean surface temperatures from the benthic foraminiferal δ¹⁸O compilation of Ref. (43), which we convert to temperatures using the methodology of Ref. (44) (Fig. 2b). In addition, we pair a set of multiproxy global surface temperature estimates for eight Cenozoic time intervals (Fig. 2b, 45) with posterior CO₂ estimates from time bins corresponding to each interval. The two temperature reconstructions are broadly similar, although the benthic record suggests relatively higher temperatures during the hothouse climate of the Paleocene and Eocene, whereas the multiproxy reconstruction is elevated relative to the benthic record during the Oligocene and Neogene.

The co-evolution of atmospheric CO₂ and global mean surface temperature (GMST) over the Cenozoic is shown in Fig. 3. Because CO₂ is on a log scale, the slopes of lines connecting two adjacent points in time reflect the average intervening ESS[CO₂]. Benthic δ¹⁸O-derived temperatures suggest early Paleocene warming occurs with a very high ESS[CO₂] (>8°C per CO₂ doubling), although CO₂ uncertainties are large during this time interval. ESS[CO₂] steadily declines towards the peak of Cenozoic warmth ~50 Ma, then steepens again to ~8°C per CO₂ doubling for much of the cooling through to the EOT at ~34 Ma. In contrast, the multiproxy global temperature record suggests a lower ESS[CO₂] of ~5°C between the early Eocene and earliest Oligocene. During the Oligocene and early part of the Miocene, both temperature records imply a near-zero ESS[CO₂], i.e., CO₂ values appear to decline with no appreciable global cooling. ESS[CO₂] implied by both temperature reconstructions steepens again from the middle Miocene (~16 Ma) to present, averaging 8°C per CO₂ doubling over the past 10 Myr.

An alternative perspective on early Cenozoic climate forcing was introduced by Ref. (44), who hypothesized that all pre-Oligocene climate change was the response of direct and indirect CO₂ radiative forcing plus long-term change in solar output (i.e., constant albedo). Given this, they converted Paleocene and Eocene benthic δ¹⁸O-derived GMST to estimates of CO₂ change required to explain the temperature record. Our reconstruction offers a direct test of this hypothesis, and although it compares well with the δ¹⁸O approach of Ref. (44) throughout much of the early Cenozoic, our curve suggests that the late Eocene decline in CO₂ was less severe than expected under the constant albedo assumption (Fig. 513). This result is consistent with a growing contribution of glacier and sea ice albedo effects (e.g., 52, 53) and the opening of Southern Ocean gateways (e.g., 54) to climate cooling preceding the Eocene-Oligocene boundary.
In summary, the Cenozoic compilation confirms a strong link between CO$_2$ and GMST across timescales from 500 kyr to tens of Myr, with ESS$_{[CO2]}$ generally within the range of 5-8°C – patterns consistent with most prior work (32-34, 45, 51, 55-60), and considerably higher than the present-day ECS of ~3°C. Both temperature reconstructions imply relatively high ESS$_{[CO2]}$ values during the last 10 Myr of the Cenozoic, when global ice volumes were highest. This agrees with expectations of an amplified ESS$_{[CO2]}$ due to the ice-albedo feedback (61). However, even during times with little-to-no ice (Paleocene to early Eocene), we find elevated values of ESS$_{[CO2]}$ (approaching or exceeding 5°C per CO$_2$ doubling). This implies that fast, non-ice feedbacks, such as clouds or non-CO$_2$ greenhouse gases (60, 62-65) were probably stronger in the early Paleogene than they are in the present-day climate system (see also 5). The Oligocene to early Miocene is the most enigmatic interval, with an apparent decrease in CO$_2$ despite relatively stable temperature, implying near zero ESS$_{[CO2]}$. It should be noted that this is one interval where different CO$_2$ proxies disagree on CO$_2$ change (Fig. 1a), with relatively stable values from plants but a decline in values from alkenones. More work is needed to confirm these CO$_2$ and temperature findings, but if these estimates are correct, this could partly reflect transition from a climate state too cold to support the strong fast feedbacks (e.g., clouds) of the early Eocene (5), but not cold enough to generate strong ice-albedo feedback. Tectonic changes in the arrangement of continents and the opening of critical ocean gateways may also be confounding derivation of ESS$_{[CO2]}$ at that time (e.g., 49, 54).

Relationship with the evolution of the cryosphere

Our composite CO$_2$ record also enables reexamination of the evolution of Earth’s cryosphere (Fig. 2c) in relation to CO$_2$ radiative forcing. We use the sea level estimation of Ref. (66) for this comparison because it covers the entire Cenozoic and is somewhat independent of the benthic $\delta^{18}O$ stack (43) used for the GMST derivation in Fig. 2b and also of the more recent sea level reconstruction of Ref. (67). Although there are significant differences between the two sea level estimates, the main features discussed herein are broadly consistent between them. The establishment of a permanent, continent-wide Antarctic ice shield at the EOT (~34 Ma) comes at the end of a ~10-Myr period of generally slowly decreasing CO$_2$. There is evidence for isolated, unstable Antarctic glaciers at various points over the 10-Myr interval prior to the EOT (50, 53, 66, 68), which is consistent with the increasing paleogeographic isolation of Antarctica and Southern Ocean cooling (54), and CO$_2$ may have been sufficiently low to enable the repeated crossing of a glaciation threshold by periodic orbital forcing. Tectonic cooling of Antarctica would have progressively raised the CO$_2$ glaciation threshold, which has been modeled to be within 560-920 ppm (69, 70). Our composite CO$_2$ record allows us to further assess this glaciation threshold but requires determining the point during glacial inception when strong positive feedbacks (e.g., ice-albedo and ice sheet elevation) commenced and ice sheet growth accelerated (71). Using the sea level curve of Ref. (66), we determine this point as 33.75 ±0.25 Ma, where our composite CO$_2$ record suggests 719 $^{+180}_{-152}$ ppm (95% CIs). Once established, the land-based Antarctic ice sheet likely persisted for the remainder of the Cenozoic, although significant retreat of land-based ice has been modeled (30-36 m sea level equivalent, 72) and estimated from proxies (Fig. 2c) for the Miocene Climatic Optimum (MCO). 500-kyr-mean CO$_2$ values increased to ~500 ppm during the MCO (Figs. 2a, S10), and benthic foraminiferal $\delta^{18}O$ (Fig. 2b, 43) and clumped isotopes (50).
indicate warming. While the stability of the land-based Antarctic ice sheet depends on many factors in addition to CO$_2$-induced global warming (e.g., hysteresis (73), bed topography (74)), our composite record indicates that significant retreat of land-based ice did not occur below 441-480 ppm (2.5-50 percentiles), and some land-based ice may have persisted up to 563 ppm (97.5 percentile) during the MCO. Excepting the MCO, atmospheric CO$_2$ has remained below our current value of 419 ppm since the late Oligocene (Figs. 2a, S10), with relatively small sea-level variations (up to ~20m, Fig. 2c and 67) being driven by orbitally-forced melting of the marine-based ice sheet (e.g., 72, 75). Finally, at ~2.7 Ma, the transition to intensified northern hemisphere glaciation and orbitally-driven glacial cycles coincided with CO$_2$ values that began decreasing after a relative high during the Pliocene (Fig. 2a).

Evolutionary implications of the revised CO$_2$ curve

While geologic trends in terrestrial floral and faunal habitat ranges (e.g., 76, 77) and diversity (e.g., 78, 79, 80) are largely thought to be controlled by temperature and associated climate patterns, atmospheric CO$_2$ has been hypothesized to drive the evolution of biological carbon concentrating mechanisms and their subsequent diversification in terrestrial plants (CCMs, Fig. 2d, 81, 82). Our realization of how atmospheric CO$_2$ has varied through the Cenozoic allows us to re-examine this hypothesis. The two primary CCMs in terrestrial plants are the crassulacean acid metabolism (CAM) and C$_4$ photosynthetic syndromes. CCMs in terrestrial C$_4$ and CAM plants confer competitive advantages over the ancestral C$_3$ pathway under higher growing season temperatures, low rainfall, and lower atmospheric CO$_2$. As a result, C$_4$ photosynthesis contributes about 23% of today's global terrestrial gross primary production (GPP, 83).

Plant clades with the C$_4$ pathway first emerged in the early Oligocene (84, 85), yet did not expand to ecological significance until the late Miocene (i.e., <5% GPP before ~10 Ma, Fig. 2d, 86, 87, 88). CAM plants (e.g., cacti, ice plants, agaves, and some orchids) underwent significant diversification events around the late Oligocene and late Miocene (89-91). Taken together, two general biological thresholds emerge based on our CO$_2$ record: (1) All known origins of C$_4$ plants occurred when atmospheric CO$_2$ was lower than ~550 ppm (i.e., after 32 Ma, Fig. 2a,d, 84), which is in agreement with theoretical predictions (92, 93). (2) All major Cenozoic CAM diversification events coincided with intervals when CO$_2$ was lower than ~430 ppm (i.e., after 27 Ma, 89, 90).

Our record is thus consistent with decreasing atmospheric CO$_2$ (< 550 ppm) being a critical threshold for the Cenozoic origin, diversification, and expansion of C$_4$ and CAM plants within grasslands, arid habitats (such as deserts), and habitats (such as epiphytes), and provides strong data support for previous hypotheses (20, 84, 86, 88, 89, 92, 94, 95). Importantly, following their origin in the early Oligocene, C$_4$ plants did not immediately proliferate. By ~24 to ~18 Ma, open habitat grasslands are evident on most continents (96), yet widespread dispersal of C$_4$ plants was delayed until the late Miocene, and without any apparent decline in CO$_2$ (Fig. 2d). Therefore, the rise of C$_4$ plants to their dominance in many tropical and subtropical ecosystems was likely driven (and maintained today) by other factors such as fire, seasonality of rainfall, and herbivory (i.e., grazing that keeps landscapes open) (97, 98). The temporal evolution of these factors warrants further study as we move towards a future where CO$_2$ may rise above the 550-ppm threshold that was key to the origin, taxonomic diversification, and spread of C$_4$ plants.
Terrestrial mammals evolved and adapted to the changing and more open floral ecosystems of the late Cenozoic (99-101), and are thus indirectly linked to the 550-ppm atmospheric CO$_2$ threshold discovered herein. In particular, dental wear patterns (such as the shape of the chewing surface of a tooth, i.e., mesowear) and tooth morphology, such as crown height, reflect an increasingly abrasive and tough diet (102, 103), and can be traced across many herbivore lineages during this period. For instance, mesowear in North American Equidae (horses and their ancestors, Fig. 2d) began to increase in the late Eocene, and steadily continued into the Quaternary. Similarly, equids evolved high-crowned (hypododont) teeth in the Miocene (103-105), and their body size increased to accommodate higher intake of more abrasive, grassy vegetation (Fig. 2d).

Evolutionary trends are a little less clear in the ocean, because marine algal CCMs are ubiquitous and diverse in form (106) and are believed to have an ancient origin. Moreover, the large spatial and seasonal variance of dissolved CO$_2$ in the surface ocean (as compared to the relatively uniform seasonal and spatial concentration of CO$_2$ in the air) may somewhat decouple their evolution from geologic trends in atmospheric CO$_2$. Evidence exists that marine algae, and in particular the coccolithophores (i.e., the source of the alkenone biomarkers), express CCMs to greater extent when CO$_2$ is lower (e.g., 107, 108, 109), with estimates of cellular carbon fluxes suggesting enhanced CCM activity in coccolithophores began ~7-5 Ma (110). However, our revised CO$_2$ curve displays mean atmospheric CO$_2$ broadly constant at 300-350 ppm since at least ~14 Ma (Figs. 2a, S10), suggesting that increased CCM activity may reflect other proximal triggers, perhaps involving changes in ocean circulation and nutrient supply.

Perspectives and opportunities for further advances

Our community-assessed composite CO$_2$ record and statistically modelled time-averaged CO$_2$ curve exhibit greater clarity in the Cenozoic evolution of CO$_2$ and its relationship with climate than was possible in previous compilations, and furthermore highlight the value of cross-disciplinary collaboration and community building. Generating a paleo-CO$_2$ record with even greater confidence requires targeted efforts using multiple proxies to fill in data gaps, higher resolution and replication from multiple locations, and novel approaches to resolve remaining differences between CO$_2$ proxy estimates. Specifically: although the number and diversity of paleo-CO$_2$ proxy records continues to grow, data remain relatively sparse during several key parts of the Cenozoic record (e.g., middle Paleocene, Oligocene). Moreover, records from the Paleocene and Eocene are dominated by estimates from the boron isotope proxy, increasing potential for bias. Targeted efforts are hence needed to expand the number and diversity of data through these intervals and to refine multi-proxy reconstructions. Secondly, despite substantial progress, there remains a lack of consensus regarding the identity and/or quantification of some of the factors underlying each of the proxy systems analyzed here. New experimental and calibration studies, particularly those that isolate and quantify specific mechanistic responses and/or their interactions, need to be undertaken in order to reduce potential biases and uncertainty for each method. For instance, the emerging fields of genomics, evolutionary and developmental biology, and proteomics provide exciting new opportunities for improving and
understanding paleo-proxy systematics. Thirdly, and associated with improved experimental quantification, refining our theoretical and mechanistic understanding of how proxies are encoded will allow us to create explicit and self-consistent representations of the processes involved. The development of proxy system forward models provides a promising leap in this direction (e.g., 111). Bayesian statistical methods can then enable the full suite of models and data to be integrated and constrain the range of environmental conditions, including atmospheric CO\textsubscript{2} and other variables that are consistent with the multiproxy data (112, 113). Finally, development of new proxies is also a realistic and desirable aim. For instance, while this study focuses on more established proxies, new proxies such as coccolith calcite stable isotopes (114) and mammalian bone and teeth oxygen-17 anomalies (115) show promising results for reconstructing paleo-CO\textsubscript{2}, but perhaps require further validation before they can be assessed with confidence.

Proxies and proxy-based reconstructions of how atmospheric CO\textsubscript{2} has varied through deep time have improved immeasurably over the past few decades. While they will never allow us to reconstruct past CO\textsubscript{2} with the same fidelity as direct air measurement, our study shows how community-based consensus assessment, together with a critical reanalysis of proxy models and assumptions, can progressively move us towards a quantitative history of atmospheric CO\textsubscript{2} for geological time.


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Data and materials availability: The completed data sheets for each study can be accessed as the paleo-CO$_2$ 'Archive' at NOAA's National Center for Environmental Information (NCEI). The specific choice of category, as well as the updated CO$_2$ and age estimates, are documented in 'Product' sheets for each data set and proxy. In contrast to the 'Archive', which will grow with new publications but will otherwise remain passive, the paleo-CO$_2$ 'Product' is a living database that will be updated when newly published data or ancillary data constraints become available, and/or methodological improvements are developed that enable modernization ofunderconstrained datasets. The 'Product' sheets created for this study can be accessed in NCEI, and this is also the place where future data updates will be made available in consecutive versions of the data 'Product'.

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823 Supplementary Text, Sections 1-10, Figs. S1 to S13
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Fig. 1. Documentation and assessment of all Cenozoic paleo-CO$_2$ estimates published to date. Individual proxy estimates are defined by colored symbols in legends. (a) Vetted Category 1 estimates with their fully developed uncertainty estimates (95% CIs); age uncertainties have been updated or established to the best of current understanding. (b) Vetted Category 2 estimates whose uncertainty is not yet fully constrained. Category 1 data are shown in grey for reference. (c) Archive compilation of all CO$_2$ estimates in their originally published quantification. To toggle view of individual proxy records in panels (a) and (c), please go to paleo-co2.org (Note: panel (a) visualization will be published on the website after acceptance of the manuscript for publication).
**Fig. 2. Category 1 paleo-CO₂ record compared to global climate signals.** The vertical dashed line indicates the onset of continent-wide glaciation in Antarctica. (a) Atmospheric CO₂ estimates (symbols) and 500-kyr mean statistical reconstructions (median and 50 and 95% credible intervals - dark and light-blue shading, respectively). Major climate events are highlighted (K-PG - Cretaceous/Paleogene boundary, PETM - Paleocene Eocene Thermal Maximum, EECO - Early Eocene Climatic Optimum, MECO - Middle Eocene Climatic Optimum, EOT - Eocene/Oligocene Transition, MCO - Miocene Climatic Optimum, NHG - onset of Northern Hemisphere Glaciation, MPT - Mid Pleistocene Transition). The 2022 annual average atmospheric CO₂ of 419 ppm is indicated for reference. (b) Global mean surface temperatures estimated from benthic δ¹⁸O data after Westerhold et al. (43) (solid line, individual proxy estimates as symbols, and statistically reconstructed 500-kyr mean values shown as the continuous curve, with 50 and 95% credible intervals) and from surface temperature proxies (45) (grey boxes). (c) Sea level after Ref. (66) with gray dots displaying raw data; the solid black line reflects median sea level in a 1-Myr running window. High- and lowstands are defined within a running 400-kyr window, with lower and upper bounds of highstands defined by the 75th and 95th percentiles, and lower and upper bounds of lowstands defined by the 5th and 25th percentiles in each window. Globes depict select paleogeographic reconstructions and the growing presence of ice sheets in polar latitudes from Ref. (116). (d) Crown ages show C₄ clades, with CCMs adapted to low CO₂, initially diversified in the early Miocene and then rapidly radiated in the late Miocene (117). Flora transition from dominantly forested and woodland to open grassland habitats based on fossil phytolith abundance data (96). North American equids typify hoofed animal adaptations to new diet and environment (103), including increasing tooth mesowear (black line, note inverted scale), hypsodonty (blue line), and body size.
Fig. 3. Application of the Category 1 CO₂ record to determine ESS[CO₂]. GMST deviation (K) from preindustrial global average surface temperature of 14.15°C is displayed versus paleo-CO₂ doublings relative to the preindustrial baseline of 280 ppm (upper x-axis) and paleo-CO₂ estimates on a log scale (lower x-axis). The slopes between two points in time reflect the average ESS[CO₂]. Circles reflect 500-kyr binned 'Category 1' CO₂ estimates paired with corresponding GMST-means from Ref. (43), squares pair CO₂ and GMST means from compilations of sea surface temperature (45) in seven coarsely resolved time intervals. Note that this figure omits the Pliocene temperature estimate of (45) because it samples too short a time interval (cf. Fig. 2) to be comparable with mean CO₂. Data from Cenozoic epochs are color coded and shift from red (Paleocene) to yellow (Pleistocene); labels indicate specific age bins (Ma). Dashed lines indicate reference ESS[CO₂] lines of 8 and 5°C warming per doubling of CO₂.