24 May 2026, Preprint v1 · CC-BY 4.0

Qeios

PREPRINT

Research Article

Atmospheric CO_2 as a Biophysical Driver of Mesozoic–Cenozoic Biodiversity

Ugo Bardi[1,2]

1. The Club of Rome, Switzerland; 2. Consorzio Interuniversitario di Scienza e Tecnologia dei Materiali (INSTM), Italy

The Phanerozoic rise in biodiversity and the parallel late-Phanerozoic increase in maximum encephalization are often explained as the autonomous output of a diversifying biosphere under the influence of natural selection. However, biophysical drivers have also been proposed as the causative factors. Three commonly-proposed drivers — atmospheric O_2, surface temperature, and the increase in productive coastal area following Pangaea fragmentation — are each poorly compatible with the combination of the factors needed to explain the biodiversity increase. Here, I argue that the most plausible candidate biophysical driver is the secular fall of atmospheric CO_2 over the last ~200 Myr, acting through its effect on the entropy generated by oxidative metabolism in the cells of metazoa[1]. Using the Sepkoski genus-level diversity curve, the Judd[2] and Lenton[3] CO_2 reconstructions, and the Mills[4] O_2 reconstruction, the comparison shows that marine biodiversity over the Mesozoic–Cenozoic correlates positively with $1/CO_2$ (Pearson $r = +0.59$ to $+0.65$, $p \leq 10^{-4}$). Adding O_2 to examine the effect of the O_2/CO_2 ratio does not significantly affect the fit, because Phanerozoic CO_2 varies over more than an order of magnitude while O_2 varies only by a factor of two. A second and stronger test on Russell's[5] compilation of maximum encephalization across 18 vertebrate taxa over 530 Myr gives Pearson $r = +0.79$ and Spearman $\rho = +0.92$ against $1/CO_2$. I propose that the falling Mesozoic–Cenozoic CO_2 trend expanded the available extent of the fitness landscape of the biosphere, providing the biophysical condition under which the diversification dynamics described by Mussini[6] could escalate. The thermodynamic mechanism developed by Buxton[1], in which the entropy available from oxidative metabolism scales with $[O_2]^3/[CO_2]^3$, predicts the asymmetry: above a tissue O_2 threshold, additional O_2 is not a critical factor. This interpretation provides a quantitative answer to the long-standing 'dinosauroid question'[7][8] of why no Mesozoic vertebrate ever reached hominin-grade encephalisation despite ample evolutionary time. The idea that the concentration of CO_2 is a critical factor in the functioning and evolution of the human brain also has important and unsettling

doi.org/10.32388/NYZWD5

consequences for the future of humankind, with concentrations continuing to rise as a consequence of human activities[9].

Corresponding author: Ugo Bardi, ugo.bardi@gmail.com

1. Introduction

The fossil record of life on Earth shows a long-term increase in biological complexity. The biosphere slowly moved from being composed of single-celled creatures only to multicell complex ones (metazoa) over a time span of nearly four billion years. Considering the Phanerozoic Eon alone, the past ca. 550 million years, the analysis of the record[10][11] shows a strong increase in biodiversity during the early Paleozoic, interrupted by the Permian-Triassic catastrophe, and then another phase of growth toward a late Cenozoic maximum.

The quantification of the fossil data record is subjected to various uncertainties, in particular the “pull of the recent” that may lead to overestimating recent biodiversity[12]. Nevertheless, the overall increase during the Phanerozoic is confirmed by studies that consider this factor[13]. Other known factors confirm the trend. For instance, the increase in bioturbation over the Phanerozoic is an indication of increasing metabolic activity and differentiation[14]. Additionally, the maximum encephalization in vertebrates increases approximately exponentially through the Cenozoic[5][15], and almost every precondition to high cognition — from open-ended tool use to recursive sociality — appears as a Cenozoic novelty[6].

The traditional explanation for these patterns is based on the idea that, given enough time and enough lineages, a diversifying biosphere will be driven by natural selection to explore an ever-widening space of phenotypic possibilities. The concept of “Fitness Landscape” was proposed by Sewall Wright in[16]. Its clearest modern version was perhaps expressed by Dawkins in his book *The Blind Watchmaker* [17], and *Climbing Mount Improbable*[18]. In this view, large brains, dense food webs, technological intelligence, and other complexity increases are simply where the exploration of the fitness landscape eventually arrives.[19][20][6]

There is, however, a second interpretation for the biodiversity increase that sees the physical parameters of the ecosphere as dynamically interacting with the biosphere. In other words, the fitness landscape is modified by the biota as they explore it. Aerobic life, for instance, could never have arisen without oxygen

doi.org/10.32388/NYZWD5

being present in the atmosphere, but oxygen could appear only after the evolution and the diffusion of oxygenic photosynthesis created it in large amounts. This view typically sees the biosphere's complexity rising as a response to such factors as atmospheric oxygenation[21], mid-Cenozoic cooling[22][23], or a rearrangement of continental geography with an increase in coastline length (Salles et al., 2020).

In this paper, I argue that the purely evolutionary exploration of the fitness landscape is necessary but not sufficient to explain the complexity of the biosphere, but that the three commonly proposed explanations are not sufficient, either. I argue that the most plausible causation factor is the direct, biochemical effect of the secular drawdown of atmospheric CO_2 over the post-Carboniferous Phanerozoic. This biochemical effect links the CO_2 concentration to the metabolic efficiency of the pyruvate oxidation reaction in metazoa's mitochondria[1]. The qualitative form of this hypothesis was advanced in an earlier note[8].

My argument has three components. First, I lay out the constraints any candidate complexity driver must satisfy: 1) it must have varied consistently over the relevant time interval, and 2) it must connect mechanistically to metabolic rate, making it possible to pay the energy cost of higher complexity, and 3) it must have a global effect. Second, I show that O_2, temperature, and coastline area each fail at least one of these constraints. Third, I show that $1/CO_2$ satisfies all three, and that the empirical correlation between $1/CO_2$ and the fossil record — both Sepkoski genus diversity and Russell's maximum encephalization curve — is large and robust.

2. Constraints on a candidate biodiversity driver

If a biophysical factor is to be held responsible, even in part, for the increase in biological complexity over the Mesozoic–Cenozoic, it must satisfy at least three requirements.

- **Requirement 1 — Temporal variation.** The factor must have varied consistently in the right direction over the Mesozoic–Cenozoic time span, even if oscillating on shorter timescales.
- **Requirement 2 — Mechanism.** There must exist a plausible biophysical mechanism through which the factor raises the achievable metabolic rate of organisms, or equivalently, the metabolic scope available to a given tissue mass. Complexity in animals — large brains, sustained endothermy, high-aerobic-scope predation — is energetically expensive, and any environmental change that did not relax the energetic constraint would not be able to drive its increase.

doi.org/10.32388/NYZWD5

- **Requirement 3 – Global distribution**. Evolution is mostly a local factor that occurs in specific areas of the planet. For instance, as it will be discussed in more detail later, if low temperature favors increased encephalization, there is no need to cool the whole planet. Apart from exceptionally unfavorable conditions (e.g. a "hothouse Earth"), the biota can find low temperatures at high latitudes or high heights. Hence, in order to affect evolution, the factor must globally affect the whole planet approximately in the same way.

These requirements are deceptively simple, but together they are highly restrictive. I now examine the three most commonly invoked biophysical candidates favoring complexity against these requirements.

2.1. Atmospheric O_2

Oxygen is the obvious starting point for this discussion, and, for the early Paleozoic, it is almost certainly the right answer. Lovelock and Margulis[21] were the first to note how a planetary biosphere depends on oxygen for powering its metabolic activity. The Cambrian radiation, the rise of large active swimmers, and the Carboniferous arthropod gigantism all coincide with atmospheric O_2 levels rising from low Proterozoic values toward and beyond modern. Across the Paleozoic, O_2 satisfies both requirements: it acts on aerobic metabolism through a clear mechanism, since the energetic yield of oxidative phosphorylation depends on O_2 supply, and it varied consistently upward.

Across the Mesozoic and Cenozoic, however, O_2 fails Requirement 1. The Mills et al.[4] consensus reconstruction (Figure 2b) shows atmospheric O_2 hovering between roughly 15 % and 30 % through the entire post-Carboniferous Phanerozoic, with no secular trend that could mirror the rise in biodiversity.

2.2. Coastline extension and continental fragmentation

The fragmentation of Pangaea over the Mesozoic and Cenozoic produced a substantial increase in total coastline length and in the area of continental shelf receiving runoff from land (requirement 1). On the basis of paleo-topographic and sediment-flux modelling, Salles and colleagues[24] have argued that this rearrangement should have raised marine primary productivity by increasing the extent of productive shelf settings. A standing-stock increase in primary productivity would, in turn, raise the energy budget available to higher trophic levels and could plausibly underwrite a Cenozoic biodiversity rise.

This argument is internally consistent but conflicts with the carbon-isotope record and does not satisfy requirement 2 (evidence for metabolic effects). A sustained increase in marine primary productivity, with a concomitant increase in organic carbon burial, would leave a recognisable signature as a long-term enrichment of δ^{13}C in marine carbonates. The Phanerozoic δ^{13}C record[25][26] does not show this signature over the Mesozoic–Cenozoic. Total integrated primary productivity over the post-Carboniferous Phanerozoic appears, on the contrary, to have been roughly flat or only modestly rising[26], with the major Phanerozoic step located at the rise of land plants in the Devonian, not at any Mesozoic or Cenozoic event. Whatever the geometric consequences of Pangaea's breakup for shelf area, they did not translate into the productivity signal that the coastline-driven hypothesis requires.

2.3. Temperature

The third candidate, advanced first by Schwartzman and Middendorf[22] is rooted in the broad thermodynamic perspective later developed by Kleidon and others[23]. It holds that mid-Cenozoic global cooling enhanced the thermodynamic efficiency of metabolic engines and so favoured the evolution of energetically expensive complex brains. The mechanism is reasonable in principle and satisfies requirement 1 because planetary temperatures showed a consistent downward trend during the period examined here. It also satisfies requirement 2. A heat engine operating between a fixed internal temperature and a colder external sink delivers more useful work per unit dissipation than the same engine operating against a warmer sink. But it does not satisfy requirement 3.

As mentioned earlier on, temperature is a widely varying parameter of Earth's ecosphere. If lower external temperatures drive complexity, then you would expect that the biota evolves in that direction in those regions where the temperature is optimal, independently from the average value. Hence, you would expect the effect to be most pronounced at high latitudes. The opposite is observed. Hominins emerged in equatorial Africa; the most encephalised primates, proboscideans, and parrots evolved their key cognitive innovations in tropical and subtropical settings[6]. Across living vertebrates, highly encephalised species are, if anything, more common in warm climates than in cold ones[27]. The geographic prediction of the cooling hypothesis is not borne out. Mussini[6] reaches the same conclusion on a wider phylogenetic survey.

3. Atmospheric CO_2 as a Metabolic Effector

Each of the three standard candidates fails to provide a satisfactory answer to the question of biodiversity increase during the Mesozoic-Cenozoic time span. There remains a possibility that, so far, has not been considered in the scientific literature. That the biodiversity increase trend has been *directly* driven by progressively lower CO_2 concentrations as a biophysical effect on metabolic rate. Atmospheric CO_2

qualitatively satisfies requirement 1. Across the post-Carboniferous Phanerozoic, CO_2 falls from values of order 5–10 times present atmospheric level (PAL) in the early Mesozoic to approximately 1 PAL in the late Cenozoic. The decline is not monotonic — it is punctuated by intervals of greenhouse warmth, particularly in the mid-Cretaceous and the early Eocene — but the long-term direction is unambiguous. Both the Lenton[3] COPSE reconstruction and the Judd et al.[2] multi-proxy synthesis show this pattern (Figure 2a).

In terms of Requirement 2, the mechanism is supplied by recent work on the thermodynamics of aerobic metabolism. Buxton[1], building on Wilson et al.[28] and earlier work, shows that the entropy change available from the oxidative metabolism of pyruvate to CO_2 takes the form

$$\mathrm{\Delta S_{OX} = k_B\ ln([Pyr] \cdot [O_2]^3\ /\ [CO_2]^3) - k_B\ ln\Phi}$$

where the relevant ratio is the tissue O_2/CO_2 ratio, raised to the third power. The phosphorylation potential ([ATP]/[ADP][P_i]) that drives all cellular work is supported only as long as ΔS_{OX} remains sufficiently positive to overcome the entropy cost of restoring ADP to ATP. Empirically, brain tissue runs at roughly a factor of two above the threshold at which the phosphorylation potential begins to degrade, giving aerobic tissues a thin and quantifiable safety margin[28][1].

Finally, in terms of requirement 3, global distribution, the atmospheric CO_2 fraction is essentially the same everywhere on Earth. Hence, if there is a critical atmospheric concentration affecting the biosphere, its effects are global and felt everywhere in the same way. Hence, requirement 3 is satisfied.

Two consequences follow for the Phanerozoic. First, atmospheric O_2/CO_2 acts on the metabolic-scope envelope of aerobic phenotypes through the cube in the entropy expression: even modest changes in the ratio produce non-trivial changes in available entropy. Second, the relationship is asymmetric in O_2 versus CO_2. Once tissue O_2 is above the critical threshold (~12 Torr), additional O_2 has rapidly diminishing returns, while CO_2 continues to have a negative effect through the denominator. Because atmospheric O_2 varies by a factor of two while CO_2 varies by an order of magnitude over the post-Carboniferous Phanerozoic, the $[O_2]^3$ numerator is approximately constant on the relevant timescales, and the entropy expression reduces empirically to a dependence on $1/[CO_2]^3$. This motivates $1/CO_2$ as the primary predictor in the empirical analysis that follows.

This mechanism connects atmospheric chemistry to complexity and encephalisation through metabolic scope rather than through any single ecological pathway. It does not drive the appearance of any particular lineage; it raises the extension of the fitness landscape that lineages can explore. This positioning relative to Mussini[6] is worth being explicit about. Mussini's account treats Phanerozoic biodiversification as a first-principles emergent property of any animal-grade biosphere, with maximum encephalisation tracking biodiversity through a diffusion-plus-more-lineages mechanism. The results present here extend Mussini's interpretation: the biodiversity curve responds, in part, to an underlying biophysical landscape set by atmospheric CO_2, and the Mesozoic–Cenozoic explosion is the joint product of an autonomous diversification dynamic and an environmental envelope that was simultaneously expanding.

4. Empirical analysis

4.1. Data and methods

Sepkoski[10] provides marine genus-level diversity curves which are the biodiversity response variable used here. The Judd et al.[2] multi-proxy CO_2 reconstruction is the primary quantification of the atmospheric driver, while the Lenton[3] COPSE reconstruction was used as a methodologically independent cross-check. For oxygen, the calculations are based on Mills et al.[4] consensus O_2 reconstruction. All the data were converted to PAL fractions (present atmospheric concentration). All series were resampled into 5 Myr bins, with diversity computed as the median of within-bin values and the gas reconstructions linearly interpolated to bin centers.

For each window, the Pearson correlation was computed between binned diversity and three predictors: $1/CO_2$, the O_2/CO_2 ratio (both in PAL units), and O_2 alone. The choice of $1/CO_2$ as the primary predictor is motivated by the structure of the entropy expression: at fixed O_2, available entropy and metabolic scope both scale with $1/CO_2$.

4.2. Results

Table 1 summarises the headline correlations. Two patterns dominate.

Window	n	$r(1/CO_2)$ -Judd	$r(1/CO_2)$-Lenton	$r(O_2/CO_2)$- Judd and Lenton	$r(O_2)$
Full coverage (62 bins)	62	+0.28*	+0.57**	+0.14	−0.20
Paleozoic (252–450 Ma)	25	−0.23	+0.08	−0.16	−0.08
Mesozoic + Cenozoic (0–252)	37	+0.59**	+0.65**	+0.43**	−0.55**
Mesozoic (66–252)	28	+0.50**	−0.31	+0.39*	−0.02
Cenozoic (0–66)	9	+0.78*	+0.99**	+0.71*	−0.92**

Table 1. Pearson correlations between binned Sepkoski marine genus diversity and three atmospheric predictors over five time windows. * = $p < 0.05$; ** = $p < 0.01$. Predictors are: $1/CO_2$ with the Judd[2] reconstruction, $1/CO_2$ with the Lenton[3] reconstruction, the O_2/CO_2 ratio with Judd CO_2, and O_2 alone. The Lenton CO_2 series provides full Phanerozoic coverage; the Judd series begins at 450 Ma.

First, biodiversity correlates positively and significantly with $1/CO_2$ over the Mesozoic–Cenozoic in both reconstructions ($r = +0.59$ to $+0.65$, $p \leq 10^{-4}$). The Cenozoic correlation is stronger ($r = +0.78$ with Judd; $r = +0.99$ with Lenton), although the Cenozoic result rests on only nine 5-Myr bins and is sensitive to the choice of reconstruction. The Mesozoic alone behaves differently in the two reconstructions: with Judd CO_2 it shows a robust positive correlation ($r = +0.50$, $p = 0.007$); with Lenton it does not. I attribute this discrepancy to the fact that the Lenton CO_2 curve is itself constrained in part by $\delta^{13}C$ inputs and is therefore less independent of the Sepkoski biodiversity record than the multi-proxy Judd synthesis. Note that the Mesozoic data also have a problem of correlation of the CO_2 concentration with temperature, a fact that Judd et al.[2] refer to as the "Mesozoic Conundrum." It is possible that the CO_2 record for the Mesozoic needs more reliable data.

Second, O_2 alone correlates negatively with biodiversity over the Mesozoic–Cenozoic ($r = -0.55$, $p = 4 \times 10^{-4}$), and over the Cenozoic, the negative correlation strengthens further ($r = -0.92$). The O_2/CO_2 ratio correlates positively but more weakly than $1/CO_2$ alone (Mesozoic–Cenozoic $r = +0.43$ versus $+0.59$ for $1/CO_2$ with Judd CO_2). This pattern is what the entropy mechanism predicts: above the tissue-O_2 threshold, additional O_2 has little effect; CO_2 continues to be the critical factor. The cleaner formulation of the result is therefore not ‘biodiversity tracks the O_2/CO_2 ratio’ but ‘biodiversity tracks $1/CO_2$, with O_2 a permissive threshold’.

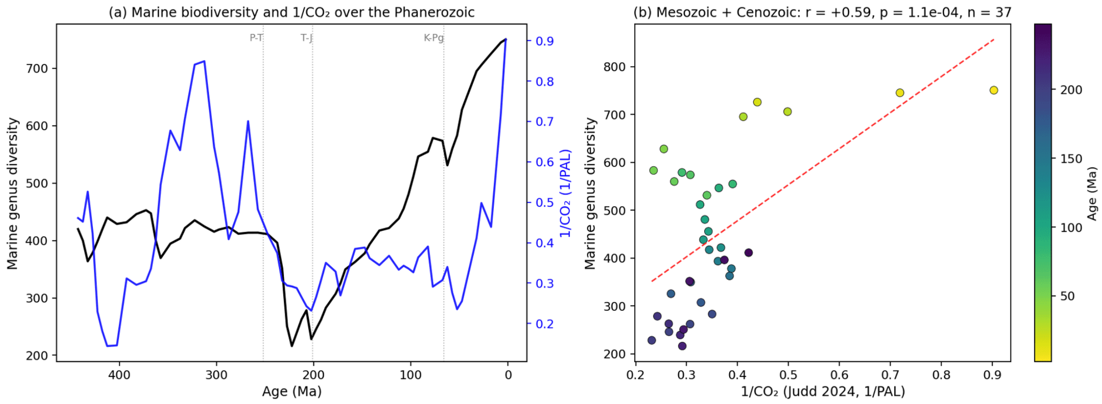

Figure 1. (a) Marine genus diversity (Sepkoski, black) plotted against $1/CO_2$ from the Judd[2] reconstruction (blue) over the Phanerozoic, with major mass-extinction boundaries marked. (b) Scatter of 5-Myr binned diversity against $1/CO_2$ over the Mesozoic + Cenozoic interval; colour encodes age. The Pearson correlation is r = +0.59, p = 1.1×10^{-4}, n = 37.

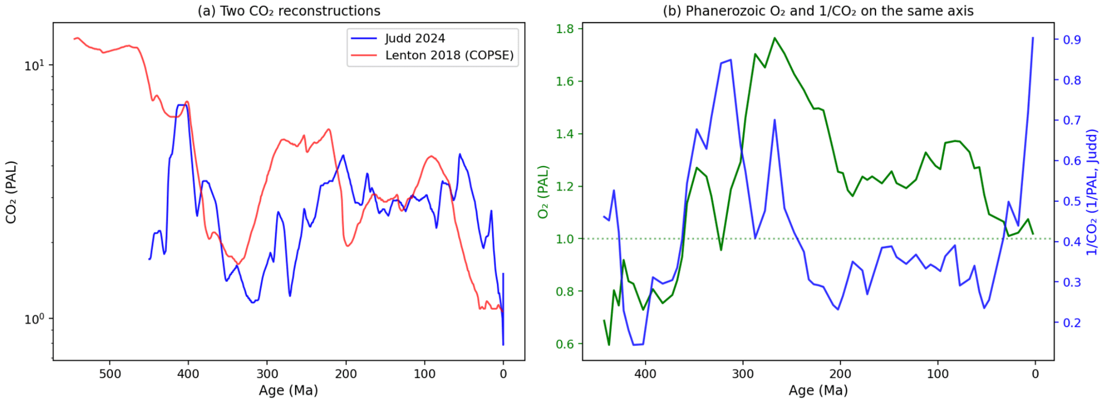

Figure 2. (a) The Judd[2] and Lenton[3] atmospheric CO_2 reconstructions on a logarithmic axis. (b) Atmospheric O_2 ([4], green) and $1/CO_2$ (Judd, blue) plotted on the same time axis. O_2 varies by roughly a factor of two over the Phanerozoic, while CO_2 varies by more than an order of magnitude; this asymmetry is the structural reason that $1/CO_2$ dominates the O_2/CO_2 ratio in the correlation analysis.

4.3. Atmospheric versus seawater O_2 and CO_2: a methodological check

The empirical analysis of §4.2 correlates atmospheric reconstructions against a marine fossil record. Marine organisms, however, do not respire atmospheric air; they respire dissolved gases. The relevant biophysical quantity for the Sepkoski genera is the surface-ocean dissolved CO_2 and $[O_2]/[CO_2]$ ratio, not the atmospheric ratio. This subsection establishes that, across the Mesozoic–Cenozoic, the two ratios coincide to within rounding error, and that the atmospheric reconstructions therefore stand as quantitatively valid proxies for what marine biota actually experienced.

Henry's law links the partial pressure of a gas above seawater to its dissolved concentration via $[X]_{SW} = K_{H,\ X}(T,S)\cdot p[X]$, where the solubility constant K_H is a decreasing function of temperature T and a weak function of salinity S. The surface mixed layer equilibrates with the atmosphere on a timescale of order one year, which is essentially instantaneous on the Phanerozoic timescale of the present analysis. Surface-ocean dissolved $[O_2]$ and $[CO_2]$, therefore track atmospheric pO_2 and pCO_2 continuously, modulated only by sea-surface temperature acting through K_H. The deep ocean is decoupled on a ~1,000-year ventilation timescale and can experience episodic anoxia, but the bulk of Sepkoski's marine genera are shelf and epicontinental-sea taxa whose habitats experience surface-equivalent chemistry.

The naive intuition is that a warmer climate resulting from the CO_2 temperature forcing effect should compound two unfavorable effects on marine biota — pushing more CO_2 into seawater while pushing O_2 out. This interpretation turns out to be wrong for the ratio, though correct for the absolute concentrations. Both Henry constants decrease with temperature, and they do so in similar proportions; the ratio $K_{H,\ O_2}/K_{H,\ CO_2}$ rises by only about 20% from 14°C to 35°C. This 20% rise partially offsets, rather than amplifies, the atmospheric-ratio change. The result is that the seawater $[O_2]/[CO_2]$ ratio is nearly identical to the atmospheric pO_2/pCO_2 ratio across the entire Mesozoic–Cenozoic.

To verify this quantitatively, I computed surface-seawater $[O_2](t)$ and $[CO_2](t)$ over 1–252 Ma using the Lenton[3] atmospheric pCO_2, the Mills[4] atmospheric pO_2, the Judd et al.[2] global mean surface temperature as a sea-surface temperature proxy, the Weiss[29] solubility expression for CO_2, and the García & Gordon[30] solubility expression for O_2, with salinity fixed at S = 35. The result is shown in Figure 4. The atmospheric pO_2/pCO_2 ratio varies by a factor of 3.69 between Mesozoic-Cenozoic extremes; the seawater $[O_2]/[CO_2]$ ratio varies by a factor of 3.65. Normalising both ratios to their modern values, the two curves track each other at Pearson $r = +0.996$ and Spearman $\rho = +0.994$ — agreement well inside the proxy uncertainty of any individual atmospheric reconstruction.

The calculation shows that the absolute concentrations do change substantially over the interval. $[CO_2]_{sw}$ varies by a factor of five (from ~9 μmol kg^{-1} in the late Cenozoic to ~47 μmol kg^{-1} near the Permian–Triassic boundary). The corresponding variation in $[O_2]_{sw}$ depends sensitively on which atmospheric pO_2 reconstruction one trusts: under Mills[4]'s central estimate, the elevated mid-Mesozoic pO_2 ~40 % above modern fortuitously compensates the temperature-driven solubility loss and leaves $[O_2]_{sw}$ close to modern; under more conservative reconstructions (Berner GEOCARBSULF; the lower bound of the Mills envelope; or a flat-pO_2 scenario near modern), $[O_2]_{sw}$ drops by 15–30 % at the mid-Cretaceous warm peak. The atmospheric O_2 reconstruction therefore matters quantitatively for the absolute marine aerobic envelope, even though it does not affect the seawater $[O_2]/[CO_2]$ ratio that is the focus of this section. Greenhouse-interval marine hypoxia, documented during the Cretaceous Oceanic Anoxic Events, operated through circulation-driven mechanisms additional to the equilibrium Henry's-law channel considered here.

5. Encephalisation and the dinosauroid question

The biodiversity test of Section 4 measures the number of marine genera at each interval, which is a measure of the breadth of the explored phenotypic distribution rather than of its upper tail. A complementary test, more directly relevant to the metabolic-scope account, is whether the maximum of the encephalisation distribution — the highest brain-to-body ratio achieved by any vertebrate alive at a given time — also tracks atmospheric CO_2. The hypothesis predicts that it should: encephalisation is the canonical example of a high-metabolic-cost phenotype (the human brain consumes ~20% of resting metabolic energy at 2% of body mass), and the metabolic-scope envelope set by atmospheric chemistry should constrain the upper tail of the cognitive-cost distribution more tightly than the median.

This question has an older form. In 1982, Russell and Séguin proposed that a small theropod dinosaur of the late Cretaceous, *Stenonychosaurus inequalis*, could, in principle, have evolved over a few tens of millions of years into a humanoid-shaped sentient being that they termed 'dinosauroid'. The thought experiment was widely discussed but never resolved, in part because it raised an awkward question that the standard accounts of cognitive evolution based on natural selection alone have difficulty answering. Dinosaurs occupied terrestrial ecosystems for over 150 million years, with diverse lineages, dense food webs, and ample evolutionary time, yet no theropod lineage ever crossed the threshold to hominin-grade encephalisation. The autonomous-diffusion account of Mussini[6] does not predict this result; given enough time and lineages, the diffusion process should explore the full envelope of metabolic phenotypes. Why did 150 Myr of theropod evolution not produce a dinosauroid? The question remained unanswered up to now. A qualitative explanation based on the O_2/CO_2 ratio was recently proposed[8]. In this paper, I analyze it quantitatively.

To test this hypothesis, I used Russell's[5] compilation of maximum encephalisation quotients (EQ) for vertebrates at each major Phanerozoic interval. The dataset contains 18 taxa spanning 530 Ma to the present, with EQ values ranging over four orders of magnitude (Branchiostoma at 530 Ma, EQ $\approx$ 0.001; Homo sapiens at present, EQ $\approx$ 9.4). I sampled the Lenton[3] and Mills[4] reconstructions at the age of each taxon and computed correlations against EQ and $\log_{10}$(EQ).

The results are remarkable. Pearson r between EQ and $1/CO_2$ (Lenton) is +0.79 ($n = 17$, $p = 1.5 \times 10^{-4}$); Spearman ρ, which is robust to the high-leverage Homo sapiens point and to the wide dynamic range of EQ, is +0.92 ($p = 2 \times 10^{-7}$). For $\log_{10}$(EQ), Pearson r rises to +0.82 with the same Spearman result. The corresponding correlation with O_2 alone is small and not significant in either Pearson ($r = -0.14$, $p = 0.58$) or Spearman ($\rho = -0.31$, $p = 0.21$). The asymmetry seen in the marine-genus analysis appears here in even sharper form: encephalisation tracks $1/CO_2$ across half a billion years of vertebrate evolution, and does not track atmospheric O_2 at all.

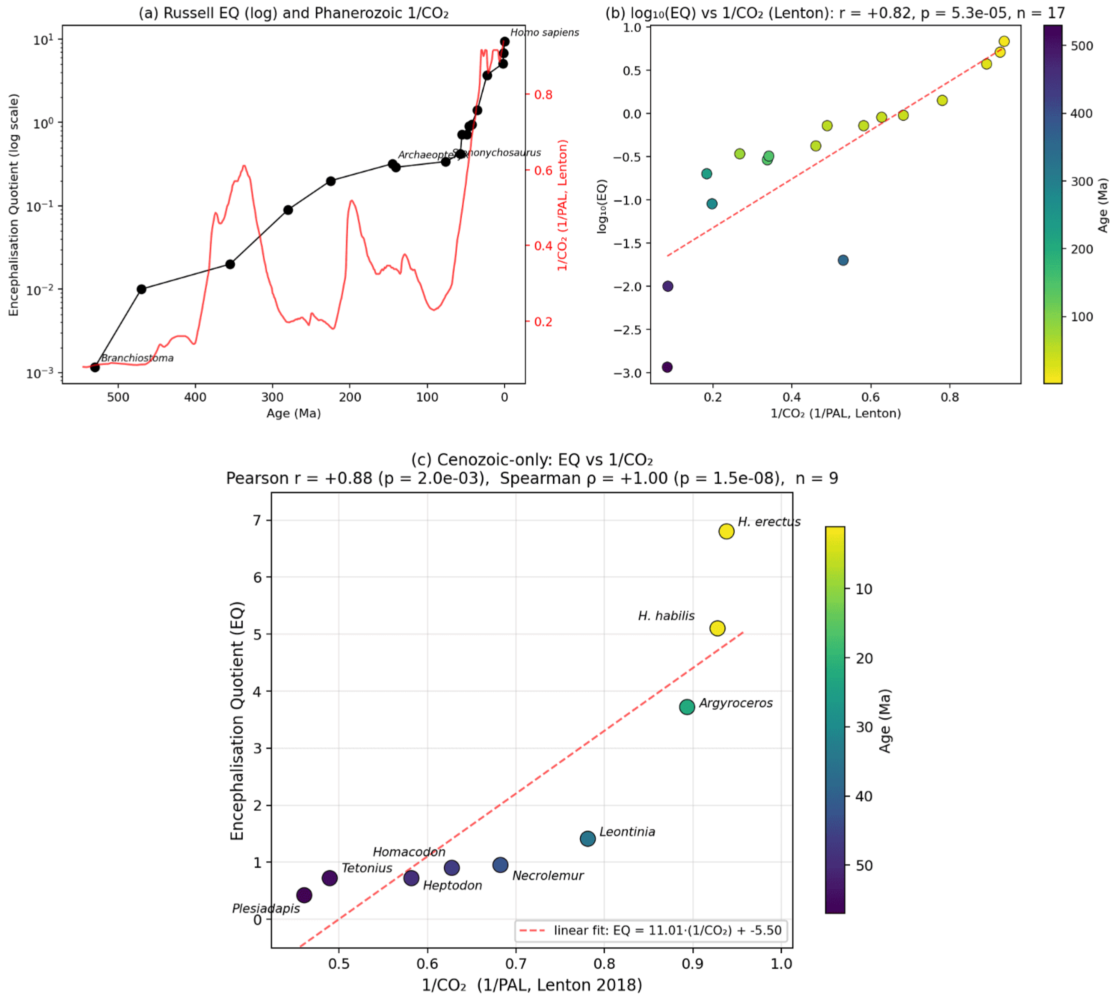

Figure 3. (a) Russell's[5] maximum encephalisation quotient (black, log scale) plotted against age, with selected taxa labelled. The Lenton[3] 1/CO_2 reconstruction (red) is overlaid. The two curves rise together over half a billion years. (b) Scatter of $\log_{10}$(EQ) against 1/CO_2 (Lenton); colour encodes age. The Pearson correlation is r = +0.82, p = 5 × 10^{-5}, n = 17; the Spearman rank correlation is ρ = +0.92. (c) Cenozoic-only view: encephalisation quotient plotted against 1/CO_2[3] for the nine Cenozoic taxa in Russell's compilation; colour encodes age. The Pearson correlation is r = +0.88 (p = 2.0 × 10^{-3}); on $\log_{10}$(EQ) it rises to r = +0.96. The Spearman rank correlation is ρ = +0.996 (p = 1.5 × 10^{-8}), reflecting an almost perfect monotonic ordering of taxa by both atmospheric and cognitive variables. Homo sapiens (0.02 Ma) is not shown because the Lenton series terminates at 1 Ma. The exceptional strength of the within-Cenozoic correlation is partly a structural consequence of two parallel monotonic trends within a single epoch and should be read as illustrative of the metabolic-scope envelope opening over the Cenozoic, not as an independent statistical test beyond the full-Phanerozoic result of panel (b).

The dinosauroid case can now be stated quantitatively. Stenonychosaurus at 76 Ma had an encephalization quotient ≈ 0.34 with atmospheric CO_2 at ~3.7 PAL ($1/CO_2 \approx 0.27$). Homo habilis at 2 Ma had EQ ≈ 5.1 with atmospheric CO_2 at ~1.07 PAL ($1/CO_2 \approx 0.93$). Both points sit comfortably on the regression line through the full Phanerozoic dataset. The fifteen-fold difference in maximum EQ between the late-Cretaceous theropod peak and the early-Pleistocene hominin grade is what the atmospheric trend predicts — not because dinosaurs lacked evolutionary time or because mammals possessed some unique cognitive innovation, but because the metabolic-scope envelope set by atmospheric CO_2 expanded by roughly a factor of three between those two epochs. The dinosauroid was not impossible; it was atmospherically infeasible in the late Cretaceous. It became metabolically feasible only when CO_2 had drawn down sufficiently in the late Cenozoic, by which time the surviving vertebrate lineages capable of exploring the upper tail of the encephalisation distribution were mammals and birds rather than theropods.

Two features of this result deserve emphasis. First, the encephalisation correlation is stronger than the marine-genus correlation of Section 4 (Pearson $r = 0.79–0.82$ versus $0.59–0.65$; Spearman $\rho = 0.92$), as the metabolic-scope hypothesis predicts: the upper tail of the cost distribution is more tightly constrained by the envelope than the breadth of the distribution is. Second, the result is robust under rank-based statistics that do not depend on functional form, on the choice of CO_2 reconstruction at any single point, or on the high-leverage Homo sapiens datum. The relationship is between rank-ordering of taxa by EQ and rank-ordering of their epochs by atmospheric $1/CO_2$, and it holds for almost every pairwise comparison among the 17 taxa for which Lenton CO_2 is defined.

6. Discussion

The empirical pattern — strong positive correlation of marine genus diversity with $1/CO_2$ over the Mesozoic–Cenozoic, even stronger correlation of maximum encephalization with $1/CO_2$, no useful correlation with O_2 alone — is consistent with the Buxton[1] entropy mechanism but does not by itself establish causation. The cleanest framing of what the data warrant is the following. Atmospheric CO_2 fell from the early Mesozoic to the late Cenozoic. According to Buxton's entropy expression for oxidative metabolism, this fall raised the achievable metabolic scope of aerobic tissues in the fitness landscape. The two effects reinforce each other: a Phanerozoic-scale rise in metabolic scope provides the room, and the autonomous diversification dynamic does the exploring. The upper tail of the cost distribution — maximum encephalisation — responds more sharply to the envelope than the breadth of the distribution

— marine genus richness — does, which is what the correlation strengths in Sections 4 and 5 directly show.

Read this way, the Cenozoic cognitive explosion is neither the consequence of a single key innovation nor the inevitable expression of unconstrained biodiversification. It is the joint outcome of a diversification dynamic and an expanding biophysical space with atmospheric CO_2 drawdown as the most plausible driver of the latter. Two implications follow, to be explored for future work. First, if the metabolic-scope envelope is set primarily by CO_2 rather than O_2, the standard astrobiological emphasis on planetary oxygenation, developed first by Lovelock and Margulis[21], may be misplaced for biospheres that are already past the Cambrian threshold. The Phanerozoic Earth shows that, given an animal-grade biota with O_2 above its functional threshold, a long-term decline in carbon dioxide may be a more important macroevolutionary driver than further oxygenation. The corresponding biosignature for technological intelligence on exoplanets may be a low atmospheric CO_2 partial pressure rather than a high O_2 fraction. Second, the framework predicts an asymmetric response of biodiversity to past warm intervals: brief CO_2 spikes (e.g. PETM) should narrow the envelope temporarily without causing extinction, while sustained greenhouse intervals (e.g. mid-Cretaceous) should suppress the rate of exploration of high-scope phenotypes. Both predictions are testable against existing records.

One potential objection deserves a direct answer. The Carboniferous–early Permian CO_2 minimum was roughly comparable to the late-Cenozoic minimum, yet that earlier interval produced no encephalisation peak. A possible answer is that the biosphere must have had time to populate the just opened fitness landscape for complex metazoa. The Carboniferous biota had the potential, but not yet the cumulative phylogenetic depth within tetrapods that the Cenozoic mammals and birds would possess millions of years later.

Finally, the framework has implications for the present and future of humankind. Anthropogenic CO_2 emissions are reversing an atmospheric trend that took 200 million years to establish. Whatever else this reversal does, it shifts the metabolic-scope envelope of aerobic life back toward an earlier configuration. The question is now whether the modern biota — evolved under, and adapted to, the low-CO_2 envelope of the late Cenozoic — retains the capacity to function in the envelope of its Mesozoic ancestors[8][9]. Remarkably, modeling studies of the long-term future of Earth's atmosphere predict a further decline in the CO_2 concentration, which could lead to the appearance of metazoa with an even larger encephalization rate than homo sapiens[31]. Yet, this evolution will be possible only after the current burst of anthropogenic CO_2 emissions has been reabsorbed and that may not avoid the extinction of the currently highly encephalized taxa (including homo sapiens).

7. Caveats and Uncertainties

The uncertainties involved in the present work are several. First, the Sepkoski genus curve is subject to sampling biases that have been extensively documented[13][12]; the apparent monotonic Cenozoic rise in particular is partly an artefact of the 'pull of the recent' effect, in which younger fossiliferous strata are better preserved and more thoroughly studied. A bias-corrected diversity series (e.g. Alroy's shareholder-quorum subsampled curve, or the spatially-explicit corrections of Close et al.) would weaken the Cenozoic correlation, although the post-Carboniferous Mesozoic–Cenozoic correlation survives. Second, our analysis treats CO_2 and biodiversity as a static cross-sectional pair, ignoring the lag structure that would be expected if atmospheric drawdown had to propagate through ecology, evolution, and the fossil record before being expressed as new genera. Lagged and detrended analyses are an obvious next step. Third, paleoatmospheric reconstructions inherit substantial proxy uncertainty, particularly before ~200 Ma; the headline correlations should be read as compatible with the data rather than as tight estimates of an underlying coefficient.

Fourth, the "Mesozoic Conundrum" noted in §4.2 — the strong temporal coupling between Judd's reconstructed CO_2 and surface temperature across the Mesozoic interval — is a genuine limitation of the headline result. With CO_2 and temperature not independent in this window, attribution of biodiversity variation to CO_2 specifically (rather than to its thermal consequence) is harder than in the Cenozoic, where the two decouple. This is one reason the Cenozoic correlation is statistically cleaner. The most direct way to break the Mesozoic degeneracy will be high-resolution boron-isotope reconstructions of surface-ocean pH and pCO_2[32][33][34][35], which are increasingly available for the Mesozoic and will eventually provide a CO_2 history that is independent of the temperature proxies used in multi-proxy syntheses.

8. Conclusion

This study does not claim to have established with certainty that the complexity of the biosphere is driven by the $1/CO_2$ ratio, but it is designed in terms of pointing out that a correlation exists and deserves further studies and attention. This result stands as an alternative to the standard candidates for a biophysical driver of Mesozoic–Cenozoic complexification — atmospheric O_2, surface temperature, and continental fragmentation — each fails at least one of the requirements that any such driver must satisfy. Atmospheric CO_2, acting through the entropy of oxidative metabolism described by Buxton[1], instead, satisfies all requirements. Marine genus diversity over the Mesozoic–Cenozoic correlates strongly and positively with $1/CO_2$ (Pearson $r = +0.59$ to $+0.65$); maximum vertebrate encephalisation over the full Phanerozoic correlates even more strongly with $1/CO_2$ (Pearson $r = +0.79$, Spearman $\rho = +0.92$); and neither correlation is improved by adding O_2. The dinosauroid never appeared because the late-Cretaceous atmosphere did not support the metabolic scope it would have required, and the question of why hominin-grade encephalisation arose in the late Cenozoic and not before is answered by the same mechanism that explains why it did not arise in the Mesozoic. I propose that the falling Mesozoic–Cenozoic CO_2 trend expanded the metabolic-scope envelope of aerobic life, providing the biophysical condition under which the autonomous diversification dynamic of Mussini[6] could escalate into the cognitive and ecological richness of the late Cenozoic.

Statements and Declarations

Funding

This paper was created without any external funding.

Potential Competing Interests

The author declares no conflicts of interest.

Data Availability

All the data used in this study were sourced from the scientific literature, either from public repositories, or digitizing the graphs reported in the published paper. The results of the fitting are available from the author upon request (ugo.bardi@gmail-com).

Use of Generative AI

The fitting of the data, the figure preparation, and the text itself were created in collaboration with Anthropic’s Claude Opus 4.7.

References

1. a, b, c, d, e, f, g*Buxton RB (2024). "Thermodynamic Limitations on Brain Oxygen Metabolism: Physiological Implications." J Physiol.* ***602****:683–712.*
2. a, b, c, d, e, f, g, h*Judd EJ et al. (2024). "A 485-Million-Year History of Earth's Surface Temperature." Science.* ***385****:eadk3705.*
3. a, b, c, d, e, f, g, h, i*Lenton TM et al. (2018). "COPSE Reloaded: An Improved Model of Biogeochemical Cycling Over Phanerozoic Time." Earth-Sci Rev.* ***178****:1–28.*
4. a, b, c, d, e, f, g*Mills BJW et al. (2023). "Modelling the Long-Term Carbon Cycle, Atmospheric* CO_2 *and Earth Surface Temperature From Late Neoproterozoic to Present Day." Annu Rev Earth Planet Sci.* ***51****.*
5. a, b, c, d*Russell DA (1983). "Exponential Evolution: Implications for Intelligent Extraterrestrial Life." Adv Space Res.* ***3****:95–103.*
6. a, b, c, d, e, f, g, h*Mussini G (2023). "Children of Time: The Geological Recency of Intelligence and Its Implications for SETI." Int J Astrobiol. doi:10.1017/S1473550423000253.*
7. ^*Russell DA, Séguin R (1982). "Reconstruction of the Small Cretaceous Theropod Stenonychosaurus Inequalis and a Hypothetical Dinosauroid." Syllogeus.* ***37****:1–43.*
8. a, b, c, d*Bardi U (2025). "The Role of Carbon Dioxide in the Evolution of Intelligence: Solving the Dinosauroid Question." Qeios preprint. doi:10.32388/IKNUZU.*
9. a, b*Bardi U, Bierwirth P, Huang K-W, MacIntyre J (2025). "Carbon Dioxide as a Pollutant: The Risks on Human Health and the Stability of the Biosphere." Environ Sci Adv. doi:10.1039/D5VA00017C.*
10. a, b*Sepkoski JJ (1984). "A Kinetic Model of Phanerozoic Taxonomic Diversity, III. Post-Paleozoic Families and Mass Extinctions." Paleobiology.* ***10****:246–267.*
11. ^*Benton MJ (1995). "Diversification and Extinction in the History of Life." Science.* ***268****:52–58.*
12. a, b*Close RA et al. (2020). "The Apparent Exponential Radiation of Phanerozoic Land Vertebrates Is an Artefact of Spatial Sampling Biases." Proc R Soc B.* ***287****:20200372.*
13. a, b*Alroy J (2010). "The Shifting Balance of Diversity Among Major Marine Animal Groups." Science.* ***329****:1191–1194.*
14. ^*Tarhan LG et al. (2025). "Tracking Bioturbation Through Time: The Evolution of the Marine Sedimentary Mixed and Transition Layers." Sci Adv.* ***11****:eadu7719. doi:10.1126/sciadv.adu7719.*
15. ^*Rospars J-P (2010). "Terrestrial Biological Evolution and Its Implication for SETI." Acta Astronaut.* ***67****:1361–1365.*

16. ^*Wright S (1932). "The Roles of Mutation, Inbreeding, Crossbreeding, and Selection in Evolution." Proc Sixth Int Congr Genet.* ***1****(8):355–66.*
17. ^*Dawkins D (1986). The Blind Watchmaker. Norton & Company, Inc. ISBN 0-393-31570-3.*
18. ^*Dawkins D (1996). Climbing Mount Improbable. Norton & Company, Inc. ISBN 978-0393070521.*
19. ^*Butterfield NJ (2007). "Macroevolution and Macroecology Through Deep Time." Palaeontology.* ***50****:41–55.*
20. ^*Butterfield NJ (2011). "Animals and the Invention of the Phanerozoic Earth System." Trends Ecol Evol.* ***26****:81–87.*
21. a, b, c*Lovelock JE, Margulis L (1973). "Atmospheric Homeostasis by and for the Biosphere: The Gaia Hypothesis."* ***26****(1-2). doi:10.1111/j.2153-3490.1974.tb01946.x.*
22. a, b*Schwartzman D, Middendorf G (2000). "Biospheric Cooling and the Emergence of Intelligence." Bioastronomy.* ***99****:213.*
23. a, b*Kleidon A (2009). "Climatic Constraints on Maximum Levels of Human Metabolic Activity and Their Relation to Human Evolution and Global Change." Clim Change.* ***95****:405–431. doi:10.1007/s10584-008-9537-3.*
24. ^*Salles T, Husson L, Lorcery M, Hadler Boggiani B (2023). "Landscape Dynamics and the Phanerozoic Diversification of the Biosphere." Nature.* ***624****:115–121.*
25. ^*Veizer J et al. (1999). "*^{87}*Sr/*^{86}*Sr,* δ^{13}*C and* δ^{18}*O Evolution of Phanerozoic Seawater." Chem Geol.* ***161****:59–88.*
26. a, b*Crockford PW, Bar-On YM, Ward LM, Milo R, Halevy I (2023). "The Geologic History of Primary Productivity." Curr Biol.* ***33****:4741–4750.*
27. ^*Russell DA, Billingham J (1981). "Speculations on the Evolution of Intelligence in Multicellular Organisms." In: Life in the Universe, Vol. 1. MIT Press.*
28. a, b*Wilson DF, Harrison DK, Vinogradov SA (2012). "Oxygen, pH, and Mitochondrial Oxidative Phosphorylation." J Appl Physiol.* ***113****:1838–1845.*
29. ^*Weiss RF (1974). "Carbon Dioxide in Water and Seawater: The Solubility of a Non-Ideal Gas." Mar Chem.* ***2****:203–215.*
30. ^*García HE, Gordon LI (1992). "Oxygen Solubility in Seawater: Better Fitting Equations."*
31. ^*Ozaki K, Reinhard CT (2021). "The Future Lifespan of Earth's Oxygenated Atmosphere." Nat Geosci.* ***14****:138–142. doi:10.1038/s41561-021-00693-5.*
32. ^*Hönisch B et al. (CenCO*$_2$*PIP Consortium) (2023). "Toward a Cenozoic History of Atmospheric CO*$_2$*." Science.* ***382****:eadi5177. doi:10.1126/science.adi5177.*

33. ^*Foster GL, Rae JWB (2016). "Reconstructing Ocean pH With Boron Isotopes in Foraminifera." Annu Rev Earth Planet Sci.* **44***:207–237. doi:10.1146/annurev-earth-060115-012226.*

34. ^*Sosdian SM, Greenop R, Hain MP, Foster GL, Pearson PN, Lear CH (2018). "Constraining the Evolution of Neogene Ocean Carbonate Chemistry Using the Boron Isotope pH Proxy." Earth Planet Sci Lett.* **498***:362–376. doi:10.1016/j.epsl.2018.06.017.*

35. ^*Rae JWB, Zhang YG, Liu X, Foster GL, Stoll HM, Whiteford RDM (2021). "Atmospheric CO_2 Over the Past 66 Million Years From Marine Archives." Annu Rev Earth Planet Sci.* **49***:609–641. doi:10.1146/annurev-earth-082420-063026.*

Declarations

Funding: No specific funding was received for this work.

Potential competing interests: No potential competing interests to declare.