

Annual Review of Marine Science

The Balance of Nature: A Global Marine Perspective

Constantin W. Arnscheidt and Daniel H. Rothman

Lorenz Center, Department of Earth, Atmospheric, and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139, USA; email: cwa@mit.edu, dhr@mit.edu

Annu. Rev. Mar. Sci. 2022. 14:49–73

First published as a Review in Advance on
June 11, 2021

The *Annual Review of Marine Science* is online at
marine.annualreviews.org

<https://doi.org/10.1146/annurev-marine-010318-095212>

Copyright © 2022 by Annual Reviews.
All rights reserved

**ANNUAL
REVIEWS CONNECT**

www.annualreviews.org

- Download figures
- Navigate cited references
- Keyword search
- Explore related articles
- Share via email or social media

Keywords

carbon cycle, paleoclimate, environmental stability, mass extinctions

Abstract

The ancient idea of the balance of nature continues to influence modern perspectives on global environmental change. Assumptions of stable biogeochemical steady states and linear responses to perturbation are widely employed in the interpretation of geochemical records. Here, we review the dynamics of the marine carbon cycle and its interactions with climate and life over geologic time, focusing on what the record of past changes can teach us about stability and instability in the Earth system. Emerging themes include the role of amplifying feedbacks in producing past carbon cycle disruptions, the importance of critical rates of change in the context of mass extinctions and potential Earth system tipping points, and the application of these ideas to the modern unbalanced carbon cycle. A comprehensive dynamical understanding of the marine record of global environmental disruption will be of great value in understanding the long-term consequences of anthropogenic change.

See, thro' this Air, this Ocean, and this Earth,
 All Nature quick, and bursting into birth.
 Above, how high progressive life may go?
 Around how wide? how deep extend below?
 Vast Chain of Being! which from God began,
 Ethereal Essence, Spirit, Substance, Man,
 Beast, Bird, Fish, Insect! what no Eye can see,
 No Glass can reach! from Infinite to Thee!
 From Thee to Nothing!—On superior Pow'rs
 Were we to press, inferior might on ours;
 Or in the full Creation leave a Void,
 Where one step broken, the great Scale's destroy'd:
 From Nature's Chain whatever Link you strike,
 Tenth or ten thousandth, breaks the chain alike.
 —Alexander Pope (1733, lines 233–46)

If nature is in balance, how did we get here in the first place?
 —Per Bak (1996, p. 29)

1. INTRODUCTION

The ancient notion of the balance of nature is essentially a statement of static equilibrium. Nature is perceived as life and the environment—in modern terms, the Earth system—and is imagined to not change significantly over time. The idea of balance continues today in assumptions of stable steady states. Studies seeking to reconstruct past environmental conditions from analyses of ancient sediments are often based on this premise (e.g., Berner 2004).

Geochemical time series, however, often tell an ostensibly different story. For example, the isotopic composition of carbon in Earth's oceans during the Eocene (56–34 Mya) appears to change abruptly at intermittent times. Somehow, the system occasionally reaches a turning point where small changes rapidly become large. The well-known Paleocene–Eocene Thermal Maximum (PETM) (Zachos et al. 2001, McInerney & Wing 2011) is but one of many hyperthermal events (Sexton et al. 2011) that behave in this fashion. Some of the most dramatic events in the marine carbon isotope record coincide with periods of mass extinction (Walliser 1996, Stanley 2010, Rothman 2017). In these cases, both life and the environment evolved catastrophically.

Understanding the conditions responsible for such disruptions is one of the most important objectives of paleoclimate studies. It is also of contemporary relevance. These events may indicate unstable dynamics. The present-day carbon cycle and Earth system contain many mechanisms via which amplifying feedbacks could lead to instability (Lenton et al. 2008, Hofmann & Schellnhuber 2009, Riebesell et al. 2009). If instability is possible, it follows that the modern perturbation of the carbon cycle may be sufficient to excite mechanisms of self-amplification (Rothman 2019). The question of balance then becomes existential.

To provide a basis for addressing such questions, here we review the dynamics of the marine carbon cycle and its interactions with climate and life over geologic time. There is an extensive literature on the history of the geologic carbon cycle. Berner (2004) provided a book-length review of key processes in the long-term carbon cycle and changing CO₂ and O₂ levels throughout the Phanerozoic. Cramer & Jarvis (2020) and Grossman & Joachimski (2020) reviewed the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ records, respectively, throughout Earth history. Zeebe & Westbroek (2003), Ridgwell (2005), and Ridgwell & Zeebe (2005) focused on the evolution of the global carbonate cycle as a powerful regulator of the Earth system. Westerhold et al. (2020) provided a continuous high-resolution record of geochemical analyses of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ for the Cenozoic, which updated the earlier, highly influential paper by Zachos et al. (2001) on the evolution of the Cenozoic climate.

Hyperthermal event:
 a geologically abrupt
 warming event
 characterized in part
 by increasing
 atmospheric CO₂
 levels

Phanerozoic: the
 geologic eon from
 542 Mya to the present

Cenozoic: the
 geologic era from
 66 Mya to the present

Compared with these earlier efforts, our review concentrates less on inferring past environmental conditions; instead, we feature the consistency of the carbon cycle's fluctuations with stable or unstable behavior.

2. NATURE'S BALANCE: A HISTORY OF THE IDEA

Early explicit assumptions of balance are mostly ecological. Egerton (1973) credited the first use of the word in this context to William Derham, an English clergyman and naturalist, in 1713:

The Balance of the Animal World is, throughout all Ages, kept even, and by a curious Harmony and just Proportion between the increase of all Animals, and the length of their Lives, the World is through all Ages well, but not over-stored. (Derham 1713, p. 171)

The Western origin of the concept extends back at least two millennia further, to ancient Greece. Two ideas are of particular interest here (Egerton 1973). One is the myth of the supraorganism in Plato's *Timaeus*—the idea that different living beings are actually the organisms of a super-being. The other is Aristotle's idea that the world's species filled a graded continuum, the *scalae naturae*. Along with other concepts of Plato and Aristotle, the *scalae naturae* formed the foundation of the idea of the Great Chain of Being, in which an effectively infinite number of hierarchically ordered links, ranging from minerals to humans, describes the intrinsic order of the natural world (Lovejoy 1936). Alexander Pope's *Essay on Man*, quoted in the epigraph above, envisions the chain as being so perfect that the destruction of any single link would lead to “a general dissolution of the cosmical order” (Lovejoy 1936, p. 60). In modern terms, we might say that Pope envisions the chain as an exquisitely balanced, perfect equilibrium that would lose its stability if, say, a particular species became extinct. But, following the kind of theological reasoning common at the time, that could not happen because then the chain would no longer be perfect. Although the continuous gradations of the great chain were decisively disproved in the early nineteenth century by the *embranchement* theory of the French naturalist Georges Cuvier (Mayr 1982), the notion of balance was far more durable.

The possibility of extinction nevertheless posed problems. Cuvier's study of fossil mammals, most famously the mastodon, made the reality of extinction clear (Rudwick 2014). But why did extinctions occur? Cuvier pointed to sudden environmental changes—“catastrophes”—in which “living organisms without number have been the victims” [Cuvier 1812 (1997), p. 190]. During such events, “the thread of operations is broken; nature has changed course, and none of the agents she employs today would have been sufficient to produce her former works” [Cuvier 1812 (1997), p. 193]. The possibility of an unbalanced world famously provoked a backlash from the Scottish geologist Charles Lyell. The clash between Cuvier's catastrophism and Lyell's notion of a balanced steady state—uniformitarianism—was one of the great scientific controversies of the first half of the nineteenth century (Sepkoski 2020). For Lyell, extinctions resulted from environmental change, but life and the environment were never out of balance: “The Author of Nature [has] ordained that the fluctuations of the animate and inanimate creation should be in perfect harmony with each other” (Lyell 1832, p. 159).

Darwin (1859) embraced Lyell's idea. As Sepkoski (2020) described in detail, Darwin viewed the extinction and origination of species as a gradual process that maintained a dynamic equilibrium, in which the total number of species remained constant: “‘Balance,’ for Darwin, meant that while the actors may be constantly entering and departing the stage, broadly speaking the play remains the same” (Sepkoski 2020, p. 50). As a result of Darwin's immense influence, catastrophism effectively vanished from serious science for the next century.

The paleontologist Norman Newell was partly responsible for its resurgence. Whereas Cuvier had argued (incorrectly) that “no slow cause can have produced sudden effects” [Cuvier 1812 (1997), p. 198], Newell (1963) suggested that gradual changes in sea level could lead to discrete episodes of widespread extinction. The discovery that the end-Cretaceous extinction was immediately preceded by a bolide impact (Alvarez et al. 1980) made sudden global catastrophe a reality. Moreover, twentieth-century advances in nonlinear dynamics have made clear the manifold ways in which slowly changing conditions can lead to abrupt system-wide responses (Strogatz 1994, Bak 1996). Nature, it seems, is deceiving: It appears to be in balance until the moment arrives when it clearly is not. But it is precisely those episodes of apparent instability that have determined the co-evolution of Earth and life. And another may determine our future (Barnosky et al. 2011, Ceballos et al. 2015).

Thus, the question of the balance of nature—which has never been well defined (Simberloff 2014)—now gives way to asking whether the Earth system is stable.

3. THE RECORD OF GLOBAL MARINE CHANGE

3.1. Mass Extinctions: Earth System Instability?

The question of life’s stability over geologic time can be directly investigated using the fossil record. **Figure 1** shows a graph of Phanerozoic extinction rates for marine animal genera. Five distinct peaks rise substantially over background extinction rates—the so-called Big Five mass extinction events (Bambach 2006).

Determining the causes of mass extinctions remains one of the great challenges in Earth science (Hallam & Wignall 1997). Even the end-Cretaceous event, once solely identified with the aforementioned impact, is now known to have coincided with massive volcanism (Schoene et al. 2019, Sprain et al. 2019), which also accompanied the end-Permian (Burgess & Bowring 2015) and

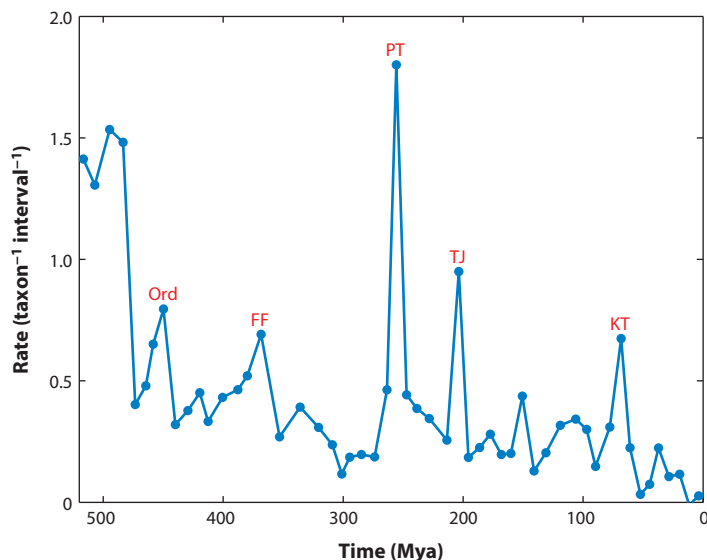


Figure 1

Extinction rates for marine animal genera during the Phanerozoic. The five labeled peaks indicate the end-Ordovician (Ord), Frasnian–Famennian (FF), end-Permian (PT), end-Triassic (TJ), and end-Cretaceous (KT) mass extinction events. Data are from Alroy (2014).

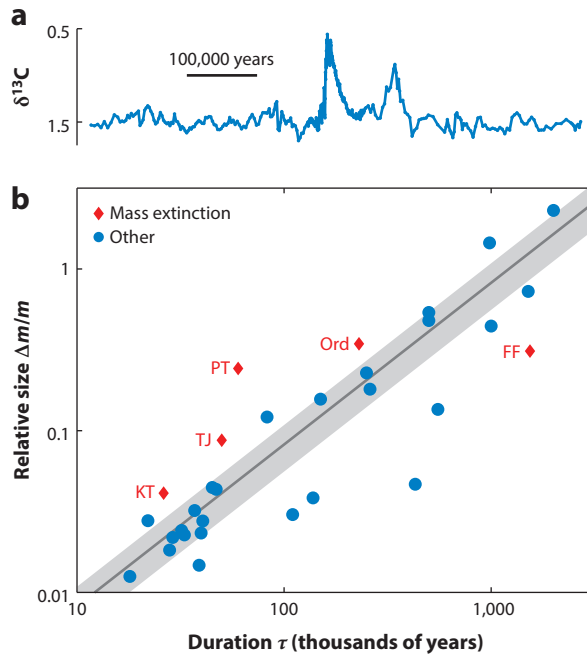


Figure 2

Disruptions of the marine carbon cycle. (a) Time series of the geochemical proxy $\delta^{13}\text{C}$ during the Eocene, around 54 Mya. Here and elsewhere in this review, time advances to the right and the geochemical axis decreases upward. The prominent bursts are the Eocene events H1 and H2. Data are from Westerhold et al. (2017). (b) Relative sizes versus durations of 31 disruptions of the Phanerozoic carbon cycle (Rothman 2017). The straight line denotes a characteristic rate of change discussed in Section 5. Abbreviations: FF, Frasnian–Famennian; KT, end-Cretaceous; Ord, end-Ordovician; PT, end-Permian; TJ, end-Triassic.

end-Triassic (Blackburn et al. 2013) events. Coincidence, however, does not by itself indicate why great numbers of species disappeared. Possible mechanisms include ocean acidification (Knoll et al. 2007, Payne & Clapham 2012), marine anoxia (Wignall & Twitchett 1996), methane hydrates (Brand et al. 2016), and climate warming (Joachimski et al. 2012). These mechanisms are not mutually exclusive, nor may we assume that the arrow of causality points only one way. Consequently, attempting to identify a single cause of a mass extinction event is analogous to trying to specify a single cause of World War I or the 2008 financial crisis. Preexisting conditions and proximal events may be identified, but the fundamental problem lies in the synergistic interactions of the system's components. In other words, mass extinctions likely result from amplifying feedbacks within the Earth system and unstable evolution of the system as a whole.

We can gain a quantitative understanding of the problem by complementing the record of marine animal extinctions with the record of changes in the marine carbon cycle. **Figure 2a** shows a geochemical time series that varies as fluxes within the cycle change. We discuss the interpretation of such data in Section 3.2. Now, however, let it suffice to say that anomalous bursts in such time series can be converted to fluxes of CO_2 into the oceans. Integration over the duration τ of a particular influx then yields an estimate of the amount by which the oceans' store of inorganic carbon increases (Rothman 2017). The result is expressed as the change Δm relative to the initial carbon mass m .

Figure 2b plots $\Delta m/m$ versus τ for events dispersed throughout the Phanerozoic along with a straight line that marks a characteristic flux. Four of the five mass extinction events plot above the

diagonal line, while nearly all other events plot near or below it. During these four events, the flux of CO₂ into the oceans was greater than it was in all other cases. Mass extinction events therefore distinguish themselves not only in terms of catastrophic losses of life but also as anomalously rapid changes in the marine carbon cycle.

Does this mean that mass extinctions result from instability in the Earth system? If so, how would we know? The remainder of this review focuses on ideas and concepts that help address such questions. We begin with pertinent aspects of the carbon cycle and the geochemical data that probe it.

3.2. The Marine Carbon Cycle

The carbon cycle is life's expression at a global scale (Sarmiento & Gruber 2006, Emerson & Hedges 2008, Archer 2010, Williams & Follows 2011, Rothman 2015). Fueled by solar energy, autotrophs such as phytoplankton and land plants use photosynthesis to convert carbon dioxide to organic carbon, in the form of carbohydrates. Further up the food chain, other organisms use organic carbon as an energy source, converting it back to inorganic CO₂ via the process of respiration. Respectively, these processes constitute the forward and backward directions of the reaction



where CH₂O is a schematic carbohydrate. A small fraction of the organic carbon escapes respiration and is buried in sediments, which allows accumulation of atmospheric oxygen and provides a source of fossil fuels (Berner 2004). Geologic processes normally return this carbon to the atmosphere on timescales of many millions of years; the human extraction and burning of fossil fuels amounts to a hundredfold increase in this rate of reinjection.

Figure 3 summarizes key fluxes and processes in the global carbon cycle. Because CO₂ dissolves in water, CO₂ concentrations in the atmosphere and ocean approach equilibrium; largely as a consequence of ocean carbonate chemistry, the ocean contains approximately 50 times as much carbon as the atmosphere. Marine biota, together with aspects of the ocean circulation, further contribute to inhomogeneity in the spatial distribution of carbon in the oceans (Sarmiento & Gruber 2006, Williams & Follows 2011). Inorganic carbon is removed from the surface climate system on timescales of tens of thousands of years through the burial of precipitated carbonates in ocean sediments (Zeebe & Westbroek 2003) and returned on much longer timescales through the weathering of exposed rocks, mantle degassing, or metamorphism in subduction zones (Caldeira 1991, Edmond & Huh 2003). The apparent dependence of weathering rates on surface temperatures and CO₂ concentrations is widely thought to lead to a stabilizing feedback on the surface climate system (Walker et al. 1981, Berner et al. 1983); we discuss this further in Section 4.4. Detailed quantification of the various fluxes and reservoir sizes can be found in works by Berner (2004), Ridgwell & Edwards (2007), and Ciais et al. (2013).

Changes in the carbon cycle critically affect Earth's climate through the atmospheric CO₂ concentration, which traps heat via the greenhouse effect (Foote 1856, Tyndall 1863, Arrhenius 1896; for a modern exposition, see Pierrehumbert 2010). The temperature increase resulting from the doubling of the atmospheric CO₂ concentration is a critical quantity of interest: a recent assessment reports a 90% confidence interval of 2.3–4.7 K (Sherwood et al. 2020). Past events of abrupt marine carbon cycle change, such as those in **Figure 2**, have frequently included abrupt CO₂-driven global warming; indeed, events such as the PETM are often considered analogs to modern-day anthropogenic climate change (Zachos et al. 2008, Dunkley Jones et al. 2010, Zeebe & Zachos 2013).

Reservoir: a distinct grouping of carbon, typically based on geography, geology, chemistry, or function

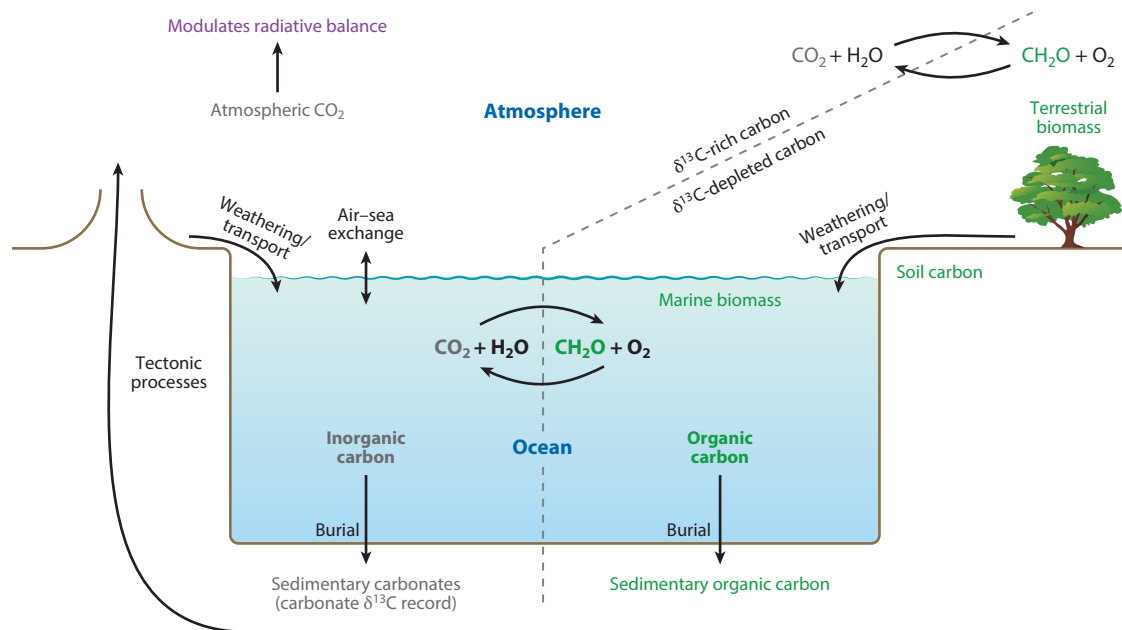


Figure 3

Key fluxes and processes in the global carbon cycle. In particular, we highlight the effective partitioning into organic and inorganic reservoirs (Equation 1) and that the organic reservoir is substantially depleted in $\delta^{13}\text{C}$.

The marine component of the carbon cycle is of further independent significance because it provides our principal record of past carbon cycle changes. Carbon has two stable isotopes, ^{12}C and ^{13}C (the former is by far predominant). The mass of each is conserved, but processes within the carbon cycle alter their relative abundance in distinct reservoirs. Most importantly, photosynthesis favors the lighter isotope; consequently, organic carbon is isotopically lighter—i.e., its $^{13}\text{C}/^{12}\text{C}$ ratio is smaller—than inorganic carbon. On timescales greater than the ocean circulation time ($\sim 1,000$ years), dissolved inorganic carbon may be considered well mixed within the deep ocean. Thus, its burial in rocks as carbonate minerals provides a record, via its isotopic composition, of the relative global fluxes of photosynthesis and respiration. Carbon isotopic compositions are typically reported as the deviation $\delta^{13}\text{C}$ of the $^{13}\text{C}/^{12}\text{C}$ ratio from a standard value, R_{std} , in parts per thousand (per mil, or ‰):

$$\delta^{13}\text{C} = \left(\frac{^{13}\text{C}/^{12}\text{C}}{R_{\text{std}}} - 1 \right) \times 1,000. \quad 2.$$

This is the quantity plotted in **Figure 2a**. Upswings in the time series (whose vertical axis is reversed in the figure) may be interpreted as disruptions in which respiration rates increase relative to photosynthesis. Such events would occur, for example, when a previously unreactive organic reservoir is converted to CO_2 by microorganisms.

Figure 4 provides relevant examples of past $\delta^{13}\text{C}$ variability. The data in the figure are from Westerhold et al. (2020), who have compiled a high-resolution composite record spanning the entire Cenozoic from the preserved shells of benthic foraminifera. **Figure 4a** makes clear that the marine carbon cycle has exhibited substantial variability on timescales of many tens of millions of years, and also that the background variability has seemingly been punctuated

Benthic foraminifera: seafloor-based single-celled organisms with carbonate shells

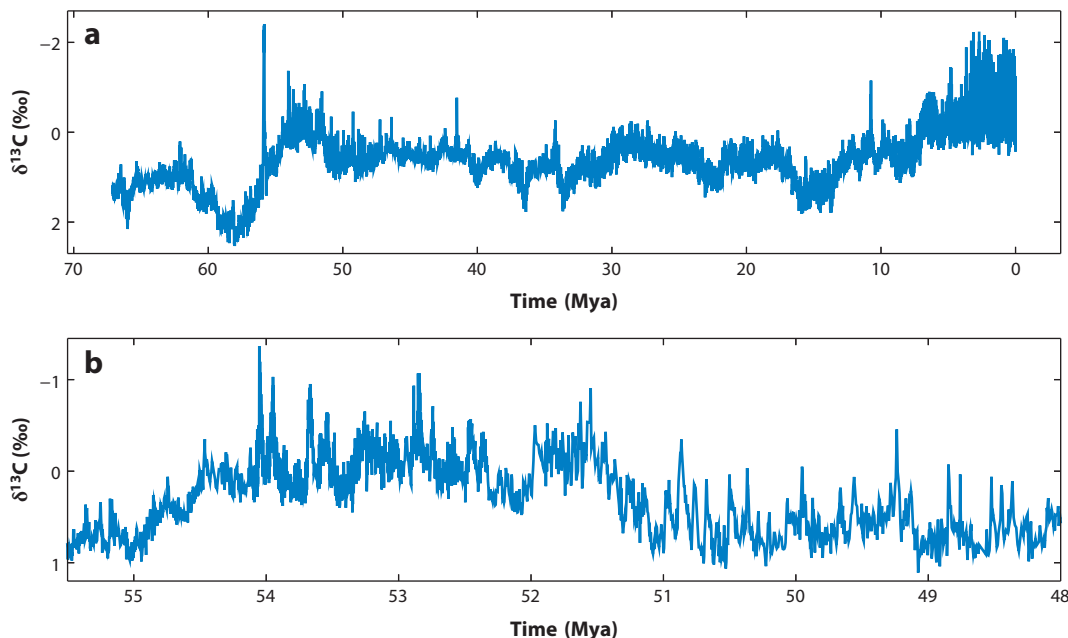


Figure 4

Examples of past $\delta^{13}\text{C}$ variability from the Cenozoic benthic foraminiferal composite record of Westerhold et al. (2020). Panel *a* makes clear that the marine carbon cycle has exhibited substantial variability on timescales of many tens of millions of years and that the background variability has been repeatedly punctuated by seemingly abrupt negative excursions. Panel *b* highlights a period during the early Eocene in which negative excursions (hyperthermals) occurred repeatedly in a seemingly intermittent fashion.

by multiple abrupt upswings (i.e., negative excursions in $\delta^{13}\text{C}$). **Figure 4b** focuses on a period when such excursions occurred in a repeated, intermittent fashion, as described in Section 1; these are examples of the Eocene hyperthermals. The above reasoning already suggests that such disruptions represent injections of $\delta^{13}\text{C}$ -depleted carbon into the ocean–atmosphere system, and this idea is further confirmed by other proxy records. For example, the sedimentary $\delta^{18}\text{O}$ record reveals that the negative $\delta^{13}\text{C}$ excursions coincided with abrupt global warming (Sexton et al. 2011, Kirtland Turner et al. 2014)—an expected consequence of CO_2 injection.

Nevertheless, the interpretation of the isotopic record is rarely if ever free of ambiguity. One obvious problem is the determination of the age of the sample. A less obvious problem is whether the observed isotopic fluctuations truly reflect changes in the global carbon cycle rather than local conditions. Indeed, local fluctuations can be literally granular, resulting from diagenetic processes uncoupled to the global cycle. The possibility that significant isotopic fluctuations are due to authigenic carbonate—i.e., carbonate that precipitated in the sedimentary pore space rather than in the ocean—has received much attention recently (Schrag et al. 2013, Dyer et al. 2015, Husson et al. 2015, Cui et al. 2017, Higgins et al. 2018, Mitnick et al. 2018, Davis Barnes et al. 2020, Husson et al. 2020), including a major review (Fantle et al. 2020). The issue is important, but its quantitative significance remains unclear. Because we focus here on global processes, featuring concepts that are independent of the interpretation of individual data sets, we implicitly assume that the carbon-isotopic record reflects fluctuations of the global carbon cycle (see the sidebar titled Converting Non-Steady-State $\delta^{13}\text{C}$ Changes to Carbon Fluxes).

4. STABILITY OF THE GLOBAL CARBON CYCLE

4.1. The Steady-State Assumption

Understanding changes in the global carbon cycle on geologic timescales requires an accounting of the input and output fluxes in **Figure 3**. With m denoting the total mass of carbon in the ocean–atmosphere system, a mass balance equation is given simply by

$$\frac{dm}{dt} = F_{\text{in}} - F_{\text{out}}, \quad 3.$$

where F_{in} denotes carbon input due to geologic processes, and F_{out} denotes the output flux due to inorganic and organic carbon burial (**Figure 3**).

The ubiquitous steady-state assumption postulates that $dm/dt \approx 0$ on timescales much greater than approximately 100,000 years (Berner 2004). This assumption is motivated by consideration of the residence time of carbon in the ocean–atmosphere system (Kump & Arthur 1999), theory and observations that suggest $F_{\text{in}} \approx F_{\text{out}}$ throughout much of Earth's history (Berner & Caldeira 1997, Zeebe & Caldeira 2008), and the stabilizing weathering feedback (Section 4.4). However, even if the steady-state assumption is valid on multimillion-year timescales, it is not valid for many of the disruption events shown in **Figure 2**. Indeed, as noted by Sundquist (1985), the accuracy of any steady-state assumption depends on the timescale; this is as true for the total surface carbon cycle as it is for any of its subsystems. Approaches for steady-state and non-steady-state $\delta^{13}\text{C}$ modeling are described in the sidebar titled Converting Non-Steady-State $\delta^{13}\text{C}$ Changes to Carbon Fluxes.

Closely related to the steady-state assumption is the assumption that the long-term carbon cycle is stable. Since, for example, F_{in} in Equation 3 may change over time, a steady state can be maintained only if there exist processes that act to bring F_{out} back into balance. In this sense, stability is a dynamical prerequisite for the existence of steady states. However, the interpretation

CONVERTING NON-STEADY-STATE $\delta^{13}\text{C}$ CHANGES TO CARBON FLUXES

When $\delta^{13}\text{C}$ changes on timescales shorter than the residence time of carbon in the oceans ($\sim 100,000$ years), steady-state interpretations of the isotopic changes may be inapplicable. To see why, let j_i and δ_i be the flux and isotopic composition of carbon input to the ocean, respectively; similarly, let j_o and δ_o be the burial flux and isotopic composition of organic carbon. Then the isotopic composition of carbonate, δ_a , varies as (Rothman et al. 2014, equation S8)

$$m \frac{d\delta_a}{dt} = j_i(\delta_i - \delta_a) + j_o(\delta_o - \delta_a),$$

where m is the mass of inorganic carbon in the ocean. The first term on the right-hand side encodes changes in the composition of inorganic carbon due to the inputs; the second shows how the burial of organic carbon increases δ_a by a factor proportional to $\varepsilon = \delta_o - \delta_a > 0$, which is predominantly attributable to photosynthetic isotope fractionation (Hayes et al. 1999). In a balanced steady state, the two terms on the right-hand side sum to zero and the left-hand side vanishes. We then find (Hayes et al. 1999)

$$\delta_a = \delta_i + f\varepsilon,$$

where $f = j_o/j_i$ is the organic fraction of the carbon burial flux. In the unsteady, unbalanced case, the magnitude of the left-hand side of the first equation above may be commensurate with that of the terms on the right-hand side. Nevertheless, the input flux j_i , for example, may be obtained when the other terms are known or assumed. For more details, see works by Kump & Arthur (1999) and Rothman (2017).

of stability in terms of a tendency for input and output fluxes to remain balanced is a very narrow one. For example, important quantities such as atmospheric CO₂ and surface temperature can vary substantially at long timescales while the steady-state approximation holds (Berner 2004). Furthermore, this notion of stability does not naturally generalize to the interpretation of geochemical records such as $\delta^{13}\text{C}$, as these record concentrations, not fluxes. We therefore devote some time to discussing the meaning of global environmental stability.

4.2. Environmental Stability: The Mathematical View

In a similar manner to the balance of nature itself, the first attempts to formalize environmental stability were made in the context of ecology, on much shorter timescales than those of carbon cycle change. These efforts go back to the classic works of Lotka (1925) and Volterra (1926) and were well summarized by May (1973). In this approach, we define a system vector $\mathbf{x}(t)$ whose elements are all the variables that we care about. In ecology, these are most frequently the populations of the different species in the ecosystem, but for our purposes we can consider $\mathbf{x}(t)$ to contain all relevant carbon cycle quantities, such as atmospheric $p\text{CO}_2$ or sedimentary $\delta^{13}\text{C}$. Then, broadly speaking, a mathematical model of $\mathbf{x}(t)$ is considered stable if, for some wide range of values of $\mathbf{x}(0)$,

$$\lim_{t \rightarrow \infty} \|\mathbf{x}(t) - \mathbf{x}^*\| = 0, \quad 4.$$

where \mathbf{x}^* is a fixed point, or equilibrium, and the vertical bars denote a measure of the distance between \mathbf{x} and \mathbf{x}^* . Equation 4 states that when the system is perturbed from its equilibrium \mathbf{x}^* , it will return precisely to this equilibrium if given infinite time. Note that, for simplicity, this definition omits the possibility of stable attractors with dimension higher than zero, which will not be an issue here.

Despite its precision, Equation 4 is of limited utility in interpreting geochemical time series. **Figure 5**, which displays the $\delta^{13}\text{C}$ data spanning the PETM, illustrates why. The inset shows that the $\delta^{13}\text{C}$ signal undergoes a clear disruption that decays quasi-exponentially back to its prior value. This decay is in line with the intuitive conception of stability as the system's ability to recover from perturbation; moreover, it is broadly consistent with Equation 4. However, the main plot shows that the total $\delta^{13}\text{C}$ change ($\sim 2.5\%$) between 58 and 54 Mya spans a range commensurate with the PETM excursion itself. Such variation on multiple timescales is not contained in Equation 4.

One way to reconcile this with notions of stability is to argue that stabilizing feedbacks drive the system toward a fixed point $\mathbf{x}^*(t)$ that itself changes in time (e.g., due to tectonic processes). In this view, the quasi-exponential decay in the inset axis in **Figure 5** reflects the action of the stabilizing feedbacks, and the variability on multimillion-year timescales reflects the changing position of the fixed point. If the system tends to stay near the moving fixed point, this is referred to as quasi-static evolution. In the context of long-term carbon cycle change, quasi-static change is essentially the basis of the steady-state assumption (Rothman et al. 2003, Berner 2004). Constantly moving fixed points can be mathematically formalized using the framework of pullback attractors (Dijkstra 2013).

4.3. A Practical Definition of Stability

The fundamental issue with any definition of stability that requires the observables $\mathbf{x}(t)$ to converge fully to some $\mathbf{x}^*(t)$ as a limit of infinite time is approached is that this is applicable only to mathematical models and not to the real-world systems they represent. The Earth system exhibits fluctuations on all timescales (Lovejoy 2015); thus, this kind of convergence is not possible. Furthermore, we are not interested in the limit of very long times. Indeed, if any asymptotic equilibrium awaits us there, it will be the heat death of the universe. On the other hand, if the observables

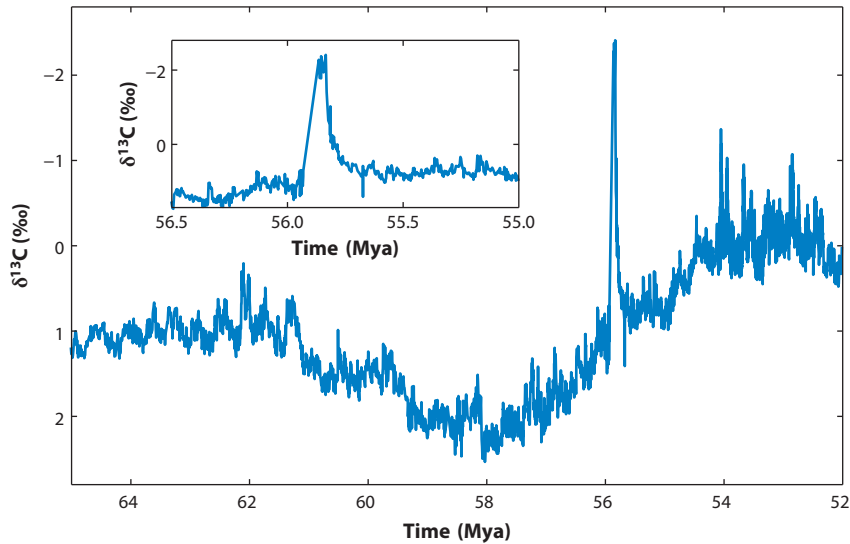


Figure 5

The Paleocene–Eocene Thermal Maximum (PETM), as expressed in the orbitally tuned benthic $\delta^{13}\text{C}$ compilation of Westerhold et al. (2020). The PETM constitutes an intuitively obvious disruption above the background variability. However, it is worth noting that the roughly 2.5‰ change in $\delta^{13}\text{C}$ between 58 and 54 Mya is similar to that of the PETM itself; the latter stands out due to its much faster timescale. The inset shows the abrupt onset and subsequent decay in detail.

$\mathbf{x}(t)$ arrive in the vicinity of some \mathbf{x}^* and stay there with only small fluctuations, one would consider the system to be stable for all practical purposes. This motivates a definition of practical stability:

$$\lim_{t \rightarrow T} \|\mathbf{x}(t) - \mathbf{x}^*\| < X, \quad 5.$$

where X and T are specifically chosen x scales (i.e., magnitudes) and timescales, respectively, and $\mathbf{x}(0)$ can again take some wide range of starting values. In other words, we consider a system to be stable if, upon perturbation, it returns to within a distance X of some system state \mathbf{x}^* on a timescale T . **Figure 6** summarizes the distinction between mathematical stability (Equation 4) and practical stability (Equation 5).

The identification of the concept of practical stability has important implications. It suggests that, in general, issues regarding the stability of the Earth system (and, indeed, many other systems) can be meaningfully discussed only if the scales X and T are identified. The concept of practical stability also allows us to formally define disruption events. A disruption event, such as the PETM in **Figure 5**, is a fluctuation that anomalously violates Equation 5 for some X and T that typical fluctuations do satisfy. In other words, disruptions are events that are large for their timescale. For example, the PETM in **Figure 5** exhibits the same $\delta^{13}\text{C}$ variability over tens of thousands of years that the background signal exhibits over millions of years. Indeed, the idea that large disruptions are events in which typical background rates of change are exceeded also applies to the identification of mass extinction events (Bambach 2006, Alroy 2008).

We consider the dynamical origins of carbon cycle disruptions and their relationships to mass extinctions in Section 5. Before we get there, we first discuss the mechanisms responsible for stability.

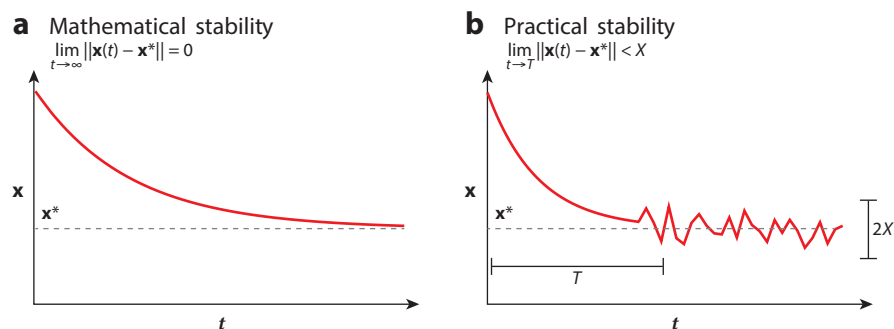


Figure 6

The distinction between (a) mathematical stability (Equation 4) and (b) practical stability (Equation 5). In the former definition, the system state \mathbf{x} converges to some fixed point \mathbf{x}^* as time t becomes infinite. In the latter definition, which we argue is the one of interest for most real-world systems, the system state \mathbf{x} converges to within a distance X of the fixed point on a timescale T . We suggest that, in general, issues of environmental stability can only be meaningfully discussed if \mathbf{x} , X , and T have been identified.

4.4. Stabilizing Mechanisms in the Carbon Cycle

It has long been argued that stabilizing mechanisms of some kind are required to explain essential aspects of Earth's evolution. For example, early in Earth's history, the incoming solar energy flux was approximately 25% lower than it is today, but there is still abundant evidence for the presence of surface liquid water and even life at this time; this is referred to as the faint young Sun paradox (Sagan & Mullen 1972, Feulner 2012). In terms of Equation 5, the question is essentially why the system $\mathbf{x}(t)$ has always stayed within some finite range that permitted the continued existence of life. In terms of the carbon cycle, a related insight is that input fluxes of CO_2 into the ocean–atmosphere system on geologic timescales must have remained largely equal to the output fluxes (Bernier & Caldeira 1997). Nevertheless, the idea that these observations necessarily imply a stabilizing feedback has been challenged (Tyrrell 2020).

The primary stabilizing feedback that has been proposed to explain the above observations is the weathering feedback (Walker et al. 1981, Bernier et al. 1983). Silicate weathering removes CO_2 from the ocean–atmosphere system, and the weathering flux depends on temperature and atmospheric CO_2 levels. Therefore, if temperature increases, weathering would draw down CO_2 , counteracting this increase, and vice versa. Based on these considerations, model estimates for the characteristic e -folding response time of this feedback are in the range of 200,000–400,000 years (Sundquist 1991, Colbourn et al. 2015).

Although the silicate weathering feedback can in principle balance the input and output carbon fluxes into and out of the ocean–atmosphere system over geologic time, it does not necessarily maintain a specific temperature or atmospheric CO_2 level. The weathering flux is affected by many tectonic (Edmond & Huh 2003) and hydrologic (Maher & Chamberlain 2014) processes that vary over long timescales. Recently, Macdonald et al. (2019) have shown a strong correlation between Phanerozoic glacial periods and the extent of low-latitude arc–continent collisions, suggesting that tectonically driven changes in global weatherability have been a major control on Earth's climate state. Life also plays an important role in the weathering flux. For example, land plants increase weathering rates via a number of processes and may strengthen the feedback on atmospheric CO_2 (Bernier 1992). Nevertheless, the effect of land plant evolution on the total weathering flux may have been outweighed by a coincident increase in the organic burial fraction (D'Antonio et al. 2020).

e -folding time: the time required for a perturbation to decay to $1/e$ of its initial value

On shorter timescales, another important stabilizing mechanism is ocean carbonate compensation (Broecker & Peng 1987, Sarmiento & Gruber 2006). The ocean's concentration of carbonate ions (CO_3^{2-}) is set by a balance between the input flux from weathering of carbonate rocks and burial of precipitated carbonates in sediments (**Figure 3**). Because the carbonate burial flux is an increasing function of the deep-sea carbonate concentration (Zeebe & Westbroek 2003), an anomalous increase in carbonate concentration leads to excess burial, counteracting this increase (and vice versa). Through its effect on the carbonate concentration, this process acts as a significant but incomplete feedback on atmospheric CO_2 ; modeling indicates that it has an e -folding timescale on the order of 10,000 years (Sundquist 1990, Archer et al. 1998, Archer 2005, Ridgwell & Hargreaves 2007, Zeebe & Zachos 2013). This relatively fast response timescale originated with the development of pelagic biogenic calcification in the mid-Mesozoic (Ridgwell 2005, Ridgwell & Zeebe 2005), making it an interesting case study for how life itself has been involved in stabilizing the Earth system.

These stabilizing feedbacks describe how the carbon cycle may recover from a large perturbation such as those in **Figure 2**, but not how life in the Earth system may recover from large perturbations such as a mass extinction. While individual species of course cannot return from extinction, life's recovery from large Earth system perturbations can be quantified in terms of global biodiversity. The recovery of global biodiversity after mass extinction events is driven by two important processes: a drop in background extinction rates immediately afterward and a much larger origination rate as new species expand into empty ecological niches (Alroy 2008). For mass extinctions such as those highlighted in **Figure 1**, recovery in terms of biodiversity occurs on timescales of tens of millions of years (Alroy 2008).

From the above discussion, it is clear that life is intimately involved in the processes that act to stabilize the global carbon cycle (and thus the Earth system) on long timescales. The most ambitious conception of life's role in stabilizing the Earth system, the Gaia hypothesis, takes this further. In its original form, it postulates that planetary-scale self-regulation occurs "by and for the biosphere" (Lovelock & Margulis 1974)—a modern rendition (Simberloff 2014) of Plato's supraorganism (Section 2). Criticism of this idea has focused on the issues in defining it as a testable hypothesis and on questioning how planetary-scale homeostasis could arise from organism-scale natural selection (Kirchner 1989, 2002). By contrast, modern arguments in favor of the Gaia hypothesis highlight that self-regulation could arise from many possible selection mechanisms beyond classical natural selection (Lenton et al. 2018). Recapitulating the full extent of this discussion is beyond the scope of this review. For our purposes, we simply conclude that life has played an important role in the mechanisms stabilizing the long-term carbon cycle, and that in some instances, such as carbonate compensation, life has contributed to tighter planetary regulation than there would be otherwise; we remain neutral as to whether this was an inevitable or contingent outcome.

5. INSTABILITY, MASS EXTINCTIONS, AND CRITICAL RATES OF CHANGE

5.1. Intrinsic Instability or Forced Response?

Past disruptions of the marine carbon cycle and life (**Figure 2**) have been explained as possible consequences of a wide range of physical causes. Large injections of carbon into the ocean-atmosphere system could arise from many sources, including volcanic emissions (Gutjahr et al. 2017, Clapham & Renne 2019, Schoene et al. 2019), oceanic dissolved organic carbon (Rothman et al. 2003, Sexton et al. 2011), sedimentary methane hydrates (Dickens 2003), high-latitude

Pelagic biogenic calcification: precipitation of carbonates by organisms living in the open ocean

Mesozoic: the geologic era from 252 to 66 Mya

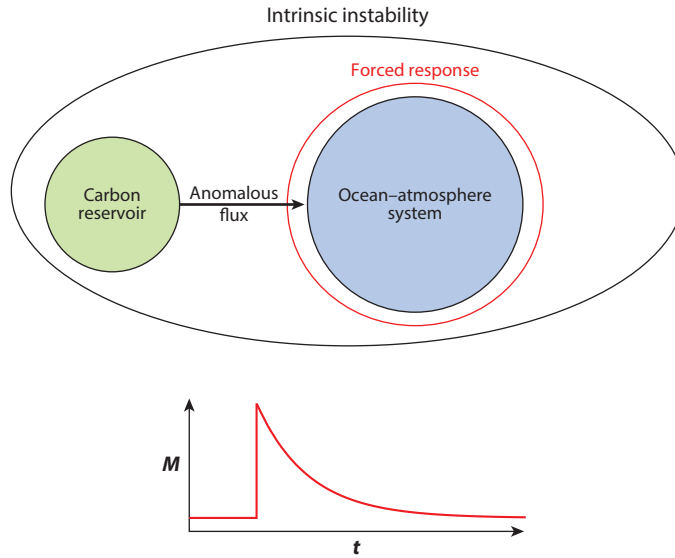


Figure 7

Example of how the distinction between a forced response and an intrinsic instability depends on how one defines the system of interest. We consider an event of rapid carbon injection into the ocean and atmosphere, in which the mass M of surficial inorganic carbon increases abruptly. If the source reservoir is considered separate from the system (*red boundary*), the system is forced and then responds to that forcing. If the reservoir is considered a part of the system, on the other hand (*black boundary*), the disruption occurs due to intrinsic instability.

permafrost deposits (DeConto et al. 2012), and terrestrial organic carbon (Kurtz et al. 2003). Pathways via which such a disruption could lead to mass extinction were discussed in Section 3.1 and include global warming, ocean acidification, and marine anoxia.

Beyond identifying the source, however, we would also like to understand the dynamical mechanisms responsible—namely, to what extent are disruptions consequences of external forcing (such as volcanic carbon release) or intrinsic amplifying feedbacks that lead to instability (Section 3.1)? In terms of Equation 5, we ask how the system $\mathbf{x}(t)$ may come to be far away from \mathbf{x}^* in the first place. If the system departs from the neighborhood of \mathbf{x}^* due to an extrinsic cause and subsequently recovers to \mathbf{x}^* on a timescale T , we consider the system to have been forced and then to have recovered stability. However, if the system moved far away from \mathbf{x}^* due to mechanisms intrinsic to the system, the system experienced a period of instability. The distinction between extrinsic and intrinsic causes allows a clearer differentiation than classical dichotomies between uniformitarianism (or gradual change) and catastrophism (or rapid change) (Section 2; see also Sepkoski 2020). Nevertheless, we shall see that the issue of timescale remains pertinent.

Note first, however, that the distinction between a forced response and intrinsic instability depends on the system that is being considered. **Figure 7** illustrates a rapid carbon injection into the ocean and atmosphere that leads to global warming and ocean acidification (as described above) and originates from some well-defined reservoir. If we define the system of interest to include this reservoir, then the disruption event arises from intrinsic instability; if we define the system to exclude this reservoir, then the event is instead a forced response. This illustrates an important point: Whether we consider a disruption event to be primarily a forced response or a consequence

of intrinsic instability depends on a seemingly arbitrary choice of where the boundaries of the system are drawn.

Of course, the dichotomy between intrinsic and extrinsic causes is not perfect. For example, small extrinsic perturbations can be amplified into large disruptions due to intrinsic amplifying feedbacks, which is the basis of climate tipping points (Lenton et al. 2008). The observation that many past climate–carbon cycle disruptions appear to be paced by changes in Earth’s orbital parameters [e.g., the Eocene hyperthermals (Lourens et al. 2005, Sexton et al. 2011, Kirtland Turner et al. 2014)] suggests that small extrinsic forcings (i.e., orbital changes) have indeed been amplified in this manner, providing further evidence for the importance of amplifying feedbacks in generating past Earth system disruptions. Indeed, from the potential carbon sources listed at the start of this section, only volcanic emissions can be reasonably considered to have no coupling with the rest of the surface environment. For disruptions stemming from any other source, amplifying feedbacks of some kind must have been involved.

The above reasoning suggests that in many cases we may be free to adopt either the forced response or intrinsic instability perspective, depending on where we choose to draw the boundary of the system we consider (**Figure 7**). This is important to recognize because the perspective we choose determines the scientific questions we are able to ask. The vast majority of efforts to model past carbon cycle disruptions have employed the forced response view. In this scenario, the response of an ocean–atmosphere carbon cycle model to a fixed carbon input is analyzed; comparing this response with proxy data then yields inferences about the magnitude, rate, and source of the carbon release responsible (e.g., Dunkley Jones et al. 2010, Kirtland Turner 2018). However, the forced response approach does not allow us to investigate important aspects of a disruption’s dynamical origin: How was the disruption initiated, and how did feedbacks contribute to amplifying it? These questions are critical for understanding the Earth system’s response to the anthropogenic carbon cycle perturbation (Section 5.4), suggesting that a greater focus on intrinsic instability is needed. This perspective has notably been applied to understanding Pleistocene glacial cycles (see the sidebar titled *Intrinsic Feedbacks and Pleistocene Glacial Variability*). Studies that have addressed the dynamics of intrinsic amplifying feedbacks in climate–carbon cycle disruptions of the deeper past include those by Lunt et al. (2011), Rothman (2019), and Wallmann et al. (2019).

Pleistocene: the geologic epoch from 2.58 to 0.01 Mya

INTRINSIC FEEDBACKS AND PLEISTOCENE GLACIAL VARIABILITY

The role of intrinsic feedbacks in observed climate–carbon cycle dynamics has received much attention in the context of the Pleistocene epoch, which has seen repeated sawtooth-like oscillations in glacial ice volume, temperature, atmospheric CO₂, and $\delta^{13}\text{C}$ on an apparent timescale of 100,000 years (Emiliani 1955, Shackleton 1977, Broecker 1982, Petit et al. 1999, Archer et al. 2000, Sigman & Boyle 2000, Lisiecki & Raymo 2005, Westerhold et al. 2020). The early suggestion that orbital changes played a key role in driving these cycles (Milanković 1941) was supported by the discovery that the record of glacial variability exhibits peaks at orbital frequencies (Hays et al. 1976); nevertheless, because these peaks contribute only a small fraction of the total variance (Wunsch 2004), intrinsic processes must also be important. Low-order models incorporating a range of plausible positive feedbacks generate free oscillations or limit cycles [Le Treut & Ghil 1983, Saltzman et al. 1984, Ghil & Childress 1987, Gildor & Tziperman 2000, Saltzman 2002, Paillard & Parrenin 2004; see also the reviews by Crucifix (2012) and Alexandrov et al. (2021)], which can then be synchronized or phase locked to the orbital forcing (Ghil & Childress 1987, Tziperman et al. 2006). While the glacial cycle problem remains far from solved, such work sheds light on the ways in which extrinsic forcing could modulate powerful intrinsic mechanisms to generate large-scale global change.

5.2. Characteristic Disruptions: Evidence for Instability?

The behavior of the disruptions in **Figure 2** may provide further evidence for carbon cycle disruptions having been a consequence of intrinsic instability. Following an argument outlined by Rothman (2019), we consider once again the relationship between the sizes and timescales of disruptions depicted in **Figure 2**. The gray region enclosing the line in **Figure 2** contains roughly half of the events in the database. These events each exhibit a size proportional to their timescale and thus a characteristic rate. If carbon cycle disruptions are extrinsically caused, the multitude of potential forcing mechanisms would be unlikely to exhibit a characteristic rate. A characteristic rate would be expected, however, in a system capable of intrinsic instability. Instabilities result from self-amplification. Nonlinearities within the system define how fast the system changes and at what point self-amplification is arrested by damping. For example, the amplitude and period of nonlinear oscillations—also called limit cycles—are determined by the system’s parameters rather than its initial conditions (Strogatz 1994).

The existence of these events does not uniquely determine the mechanisms that generate them. However, an important feature of nearly all carbon cycle disruptions is that the system returns more or less to its original state after the disruption terminates, roughly as indicated in **Figure 7**. This suggests that the nonlinear amplification of characteristic events follows a perturbation that exceeds a particular type of threshold. Below the threshold, the system simply relaxes back to its stable equilibrium. Exceedance of the threshold, however, causes the system to behave as if it were on a limit cycle for one cycle only, after which it returns to the stable equilibrium. Such behavior is characteristic of systems that are said to be excitable (Izhikevich 2007). In an excitable carbon cycle, the amplitude and duration of the disruption (and thus the rate of growth) are independent of the size of the initiating perturbation (Rothman 2019).

5.3. Critical Rates of Change and Mass Extinctions

As summarized in Section 2, Cuvier’s catastrophism hypothesized that extinction followed rapid environmental change. But how fast is fast? Newell’s revival of catastrophism provided an answer: “Extinction. . . is not simply a result of environmental change but is also a consequence of failure of the evolutionary process to keep pace with changing conditions in the physical and biological environment” (Newell 1963, p. 86). In other words, extinction follows when environmental change exceeds a critical rate.

This reasoning can be applied to changes in the carbon cycle by considering the evolution of the mass m of dissolved inorganic carbon in the oceans (Rothman 2017). As indicated in **Figure 2**, we focus on the relative change or reduced mass $M = \Delta m/m^*$, where m^* is the steady-state mass. Then, if T is the time over which M grows, Newell’s statement envisions a critical rate

$$r_c = M/T \tag{6}$$

above which extinction follows. The diagonal line in **Figure 2** represents a constant rate of change, and the fact that it separates four mass extinction events from nearly all other carbon cycle disruptions suggests not only that it marks r_c but also that it confirms Newell’s hypothesis. We consider how Equation 6 relates to the anthropogenic perturbation of the modern carbon cycle in Section 5.4.

The identification of a critical rate of environmental change as the likely threshold for initiating mass extinctions is profound. First, we note that this criterion is essentially equivalent to the criterion for identifying significant disruptions (Section 4.1): Because the Earth system exhibits fluctuations across a wide range of magnitudes and timescales, fluctuations rise above the

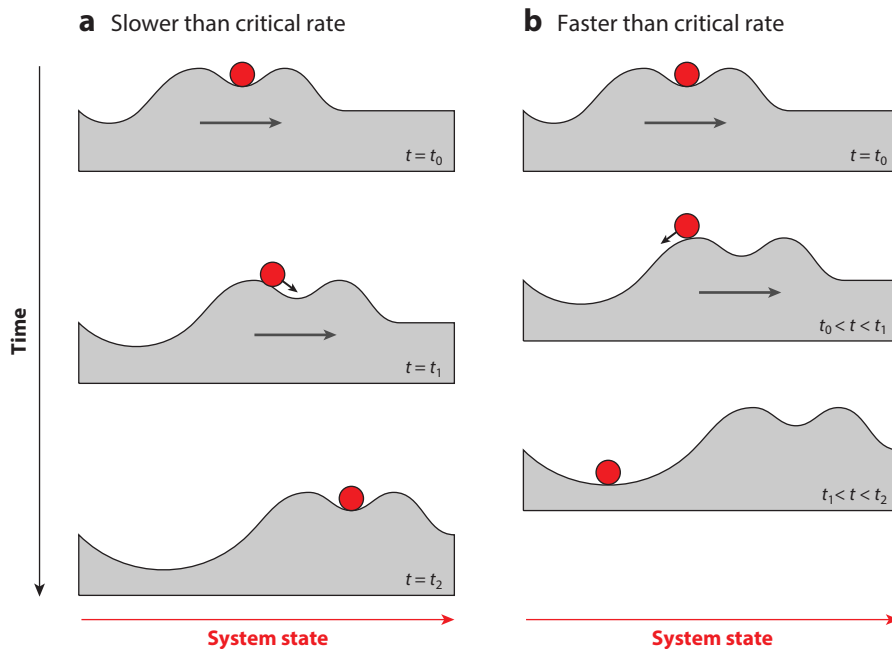


Figure 8

The dynamics of rate-induced tipping. We consider a system whose state (the position of the red ball) evolves under the influence of a changing potential well (grey). The system is initially stable within a potential well. If this well moves slowly, the system is able to recover its equilibrium within the well (panel *a*). If it moves faster, on the other hand, the system cannot keep up and tips into a very different state (panel *b*).

background signal only if they are large for their timescale (i.e., if they exceed a critical rate). Furthermore, the above statement essentially describes an instance of rate-induced tipping, which describes how a system may be altered dramatically when the forcing exceeds a critical rate of change (Wieczorek et al. 2010).

Figure 8 illustrates the dynamics of rate-induced tipping. We consider an initially stable system whose state evolves under the influence of a moving potential well. If the potential well moves slowly enough, the system is able to track the fixed point—this is the quasi-static evolution discussed in Section 4.1. If the potential well moves faster, on the other hand, the system state cannot keep up and tips into a very different state. Rate-induced tipping has been recognized as relevant in various climate and Earth system contexts (Wieczorek et al. 2010, Ashwin et al. 2012, Arnscheidt & Rothman 2020). As **Figure 8** suggests, it is likely to arise generally in any complex system with stabilizing feedbacks in which forcing parameters change faster than the rate at which those feedbacks resist such changes.

Figure 2 and the above discussion suggest that mass extinction occurs when a critical rate of carbon cycle change is exceeded (Equation 6). Beyond this, similar principles are likely to be relevant for the initiation of carbon cycle disruptions in the first place. Sections 5.1 and 5.2 suggest that small perturbations to the carbon cycle can, under the right circumstances, be amplified into large disruptions by intrinsic feedbacks. Many of the associated tipping points are likely to take the form of critical rates. This is the case, for example, for the characteristic disruptions produced in the model described by Rothman (2019).

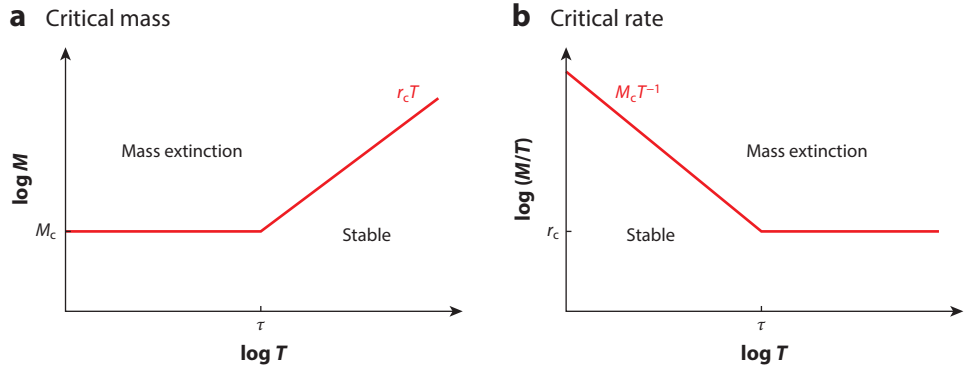


Figure 9

The origin of Equation 8. (a) Thresholds for mass extinction may be expressed in terms of a critical mass M_c of carbon at timescales short with respect to the principal damping timescale τ , and a critical rate r_c of carbon injection at long timescales. (b) Formulating the short-timescale critical mass as a critical rate of change, we find that this rate is proportional to $1/T$.

5.4. The Consequences of Modern Carbon Cycle Change

Human activities are drastically altering the carbon cycle as well as the larger Earth system. Our injection of fossil fuel CO_2 into the atmosphere constitutes a global Earth system forcing unprecedented for many tens or even hundreds of millions of years (Zeebe et al. 2016, Foster et al. 2017); intrinsic feedbacks are likely to further amplify it in a nonlinear fashion (Steffen et al. 2018). The potentially catastrophic consequences of such change are highlighted by the beginning of a human-caused sixth mass extinction (Barnosky et al. 2011, Ceballos et al. 2015), which has also captured the popular imagination (Kolbert 2014). How can we use our emerging understanding of past catastrophic carbon cycle disruptions and their relationship to mass extinctions to understand the potential consequences of modern, geologically fast change?

As shown in **Figure 2**, the critical rate expressed in Equation 6 applies on timescales greater than 10,000 years, which is also approximately the dominant timescale τ on which perturbations to the marine CO_2 reservoir are damped (Section 4.4). Injections of carbon on shorter timescales $T \ll \tau$ are essentially unaffected by damping; in this case, the threshold would take the form of a T -independent critical (reduced) mass of carbon M_c (Rothman 2017). One way to see this is to consider **Figure 8**: When the potential well moves much faster than the damping timescale, all that matters is how far the well moves.

If we specify the duration T of the carbon influx, we can convert the critical mass M_c to the T -dependent critical rate

$$r'_c = M_c/T, \quad T \ll \tau. \quad 7.$$

Because the long-timescale critical rate expressed by Equation 6 must approximately equal r'_c when $T \sim \tau$, we find that $r_c \sim M_c/\tau$. Therefore (Rothman 2019),

$$r'_c \sim \begin{cases} r_c \tau/T, & T \ll \tau, \\ r_c, & T \gg \tau. \end{cases} \quad 8.$$

This is summarized schematically in **Figure 9**.

The fact that the critical rate is proportional to $1/T$ on timescales shorter than τ is significant because it suggests a way to directly compare the slow events of the geologic past with the much faster event of the present century. Projections indicate that human activities will result in

an injection of roughly $1.8\text{--}4.2\text{ Gt C y}^{-1}$ into the oceans during the twenty-first century (Ciais et al. 2013). Meanwhile, the critical rate in **Figure 2** corresponds to $r_c = 0.06 \pm 0.02\text{ Gt Cy}^{-1}$. Consequently, the twenty-first-century injection rate will exceed r_c by a factor that ranges from approximately 20 to 100. While this is alarming on its own, we can use Equation 8 to compare this rate with those of past disruptions. Given $T = 100$ years and $\tau \sim 10,000$ years, we find that $r'_c \sim 100r_c$, which coincides with the upper end of the twenty-first-century projections. Thus, the projected carbon injection is approximately commensurate with the historical threshold for mass extinction (Rothman 2019).

A more specific comparison can be drawn. Recall from Section 3.1 that at least three mass extinction events were associated with episodes of massive volcanism. Averaged over a typical duration of approximately 1 million years, the rate at which CO_2 degasses from the erupted magma is negligible; however, the eruptions are likely episodic, resulting in more significant rates localized in time (Self et al. 2005, Courtillot & Fluteau 2014, Clapham & Renne 2019). In particular, Schoene et al. (2019) found a significant magma pulse shortly before the end-Cretaceous extinction that lasted for approximately 10,000 years. Arithmetic conversion to a CO_2 degassing rate (Self et al. 2005) suggests that as much as roughly $0.02\text{--}0.04\text{ Gt C y}^{-1}$ were injected into the oceans over 10,000 years. Given similarities among flood basalt events (Clapham & Renne 2019), we identify this rate with r_c . Equation 8 with $T = 100$ years and $\tau = 10,000$ years again yields $r'_c = 100r_c = 2\text{--}4\text{ Gt C y}^{-1}$. This suggests that humanity's perturbation of the modern carbon cycle may be equivalent, in terms of its potential to induce a mass extinction, to past episodes of massive volcanism on geological timescales (Rothman 2019).

This reasoning can likely be generalized further. The above analysis assumes that the anthropogenic CO_2 pulse will not be further amplified by intrinsic carbon cycle feedbacks; by contrast, the reasoning in Sections 5.1–5.3 suggests that it will be. If global tipping points due to amplifying feedbacks indeed exist, then the $1/T$ scaling of the threshold on timescales shorter than τ likely also applies to them, because this scaling arises naturally in systems with a rate-induced tipping point and a well-defined damping timescale. The balance of nature is thus inextricably tied to time. As we learn more about the dynamical origins of past disruptions, the $1/T$ scaling may allow us to further constrain global tipping point thresholds by direct comparison with the geologic past, allowing humanity to better avoid crossing them in the future.

SUMMARY POINTS

1. The ancient notion of the balance of nature takes its modern form in the assumptions of stable steady states and linear responses to perturbation that are widely employed in the interpretation of geochemical records.
2. Due to its centrality with respect to climate and life, the record of marine carbon cycle change provides a way to empirically assess the degree to which the Earth system has been stable or unstable in the past.
3. The notions of a steady state and stability depend on the timescales being considered, in part because the Earth system exhibits variability on a vast range of scales.
4. Disruptions of Earth's carbon cycle are damped by carbonate compensation on a timescale of approximately 10^4 years and by weathering on timescales of $10^5\text{--}10^6$ years, while biotic recovery after a mass extinction (in terms of biodiversity) occurs on a timescale of approximately 10^7 years.

5. Whether an observed disruption constitutes a forced response or intrinsic instability depends strongly on where the boundaries of the system are drawn.
6. Self-amplifying feedbacks have likely contributed substantially to many past carbon cycle disruptions.
7. The carbon cycle disruptions coincident with past mass extinctions are separated from other disruptions by a critical rate of change; the related concept of rate-induced tipping may be of wide general relevance for global environmental change.
8. For a perturbation of duration T , the critical rate of change scales as $1/T$ for $T \ll 10^4$ years; thus, the anthropogenic perturbation to Earth's carbon cycle may be equivalent, in terms of its potential to induce mass extinction, to episodes of massive volcanism in the geologic past.

FUTURE ISSUES

1. Improving our understanding of stability and instability in Earth's geologic past requires long, well-calibrated proxy records with high temporal precision and resolution, focused on periods of disruption.
2. Modeling of carbon cycle disruptions has emphasized a forced response perspective, in which fixed masses of carbon are injected into an ocean–atmosphere model; expanding the conceptual boundaries of the model and adopting the intrinsic instability perspective may lead to a better understanding of the underlying dynamics.
3. Once the dynamics leading to past carbon cycle disruptions are better understood, we will be in a better position to identify dangerous tipping points and to predict the long-term consequences of the anthropogenic perturbation to the Earth system.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

This work was supported in part by the Lorenz Center and the School of Science at the Massachusetts Institute of Technology.

LITERATURE CITED

- Alexandrov DV, Bashkirtseva IA, Crucifix M, Ryashko LB. 2021. Nonlinear climate dynamics: from deterministic behavior to stochastic excitability and chaos. *Phys. Rep.* 902:1–60
- Alroy J. 2008. Dynamics of origination and extinction in the marine fossil record. *PNAS* 105(Suppl. 1):11536–42
- Alroy J. 2014. Accurate and precise estimates of origination and extinction rates. *Paleobiology* 40:374–97
- Alvarez LW, Alvarez W, Asaro F, Michel HV. 1980. Extraterrestrial cause for the Cretaceous–Tertiary extinction. *Science* 208:1095–108

- Archer D. 2005. Fate of fossil fuel CO₂ in geologic time. *J. Geophys. Res. Oceans* 110:C09S05
- Archer D. 2010. *The Global Carbon Cycle*. Princeton, NJ: Princeton Univ. Press
- Archer D, Khesghi H, Maier-Reimer E. 1998. Dynamics of fossil fuel CO₂ neutralization by marine CaCO₃. *Glob. Biogeochem. Cycles* 12:259–76
- Archer D, Winguth A, Lea D, Mahowald N. 2000. What caused the glacial/interglacial atmospheric pCO₂ cycles? *Rev. Geophys.* 38:159–89
- Arnscheidt CW, Rothman DH. 2020. Routes to global glaciation. *Proc. R. Soc. A* 476:20200303
- Arrhenius S. 1896. On the influence of carbonic acid in the air upon the temperature of the ground. *Lond. Edinb. Dublin Philos. Mag. J. Sci.* 41:237–76
- Ashwin P, Wieczorek S, Vitolo R, Cox P. 2012. Tipping points in open systems: bifurcation, noise-induced and rate-dependent examples in the climate system. *Philos. Trans. R. Soc. A* 370:1166–84
- Bak P. 1996. *How Nature Works: The Science of Self-Organized Criticality*. New York: Springer
- Bambach RK. 2006. Phanerozoic biodiversity mass extinctions. *Annu. Rev. Earth Planet. Sci.* 34:127–55
- Barnosky AD, Matzke N, Tomiya S, Wogan G, Swartz B, et al. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471:51–57
- Berner RA. 1992. Weathering, plants, and the long-term carbon cycle. *Geochim. Cosmochim. Acta* 56:3225–31
- Berner RA. 2004. *The Phanerozoic Carbon Cycle: CO₂ and O₂*. New York: Oxford Univ. Press
- Berner RA, Caldeira K. 1997. The need for mass balance and feedback in the geochemical carbon cycle. *Geology* 25:955–56
- Berner RA, Lasaga AC, Garrels RM. 1983. The carbonate-silicate geochemical cycle and its effect on atmospheric carbon dioxide over the past 100 million years. *Am. J. Sci.* 283:641–83
- Blackburn TJ, Olsen PE, Bowring SA, McLean NM, Kent DV, et al. 2013. Zircon U-Pb geochronology links the end-Triassic extinction with the Central Atlantic Magmatic Province. *Science* 340:941–45
- Brand U, Blamey N, Garbelli C, Griesshaber E, Posenato R, et al. 2016. Methane hydrate: killer cause of Earth's greatest mass extinction. *Palaeoworld* 25:496–507
- Broecker WS. 1982. Glacial to interglacial changes in ocean chemistry. *Prog. Oceanogr.* 11:151–97
- Broecker WS, Peng TH. 1987. The role of CaCO₃ compensation in the glacial to interglacial atmospheric CO₂ change. *Glob. Biogeochem. Cycles* 1:15–29
- Burgess SD, Bowring SA. 2015. High-precision geochronology confirms voluminous magmatism before, during, and after Earth's most severe extinction. *Sci. Adv.* 1:e1500470
- Caldeira K. 1991. Continental-pelagic carbonate partitioning and the global carbonate-silicate cycle. *Geology* 19:204–6
- Ceballos G, Ehrlich PR, Barnosky AD, Garca A, Pringle RM, Palmer TM. 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. *Sci. Adv.* 1:e1400253
- Ciais P, Sabine C, Bala G, Bopp L, Brovkin V, et al. 2013. Carbon and other biogeochemical cycles. In *Climate Change 2013: The Physical Science Basis; Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, ed. TF Stocker, D Qin, G-K Plattner, M Tignor, SK Allen, et al., pp. 465–570. Cambridge, UK: Cambridge Univ. Press
- Clapham ME, Renne PR. 2019. Flood basalts and mass extinctions. *Annu. Rev. Earth Planet. Sci.* 47:275–303
- Colbourn G, Ridgwell A, Lenton T. 2015. The time scale of the silicate weathering negative feedback on atmospheric CO₂. *Glob. Biogeochem. Cycles* 29:583–96
- Courtillot V, Fluteau F. 2014. A review of the embedded time scales of flood basalt volcanism with special emphasis on dramatically short magmatic pulses. In *Volcanism, Impacts, and Mass Extinctions: Causes and Effects*, ed. G Keller, AC Kerr. Boulder, CO: Geol. Soc. Am. [https://doi.org/10.1130/2014.2505\(15\)](https://doi.org/10.1130/2014.2505(15))
- Cramer B, Jarvis I. 2020. Carbon isotope stratigraphy. In *Geologic Time Scale 2020*, ed. FM Gradstein, JG Ogg, M Schmitz, G Ogg, pp. 309–43. Amsterdam: Elsevier
- Crucifix M. 2012. Oscillators and relaxation phenomena in Pleistocene climate theory. *Philos. Trans. R. Soc. A* 370:1140–65
- Cui H, Kaufman AJ, Xiao S, Zhou C, Liu XM. 2017. Was the Ediacaran Shuram Excursion a globally synchronized early diagenetic event? Insights from methane-derived authigenic carbonates in the uppermost Doushantuo Formation, South China. *Chem. Geol.* 450:59–80

- Cuvier G. 1812 (1997). Preliminary discourse. Translated in *Georges Cuvier, Fossil Bones, and Geological Catastrophes: New Translations and Interpretations of the Primary Texts*, ed. MJS Rudwick, pp. 183–252. Chicago: Univ. Chicago Press
- D’Antonio MP, Ibarra DE, Boyce CK. 2020. Land plant evolution decreased, rather than increased, weathering rates. *Geology* 48:29–33
- Darwin C. 1859. *On the Origin of Species*. London: Murray
- Davis Barnes B, Husson JM, Peters SE. 2020. Authigenic carbonate burial in the Late Devonian–Early Mississippian Bakken Formation (Williston Basin, USA). *Sedimentology* 67:2065–94
- DeConto RM, Galeotti S, Pagani M, Tracy D, Schaefer K, et al. 2012. Past extreme warming events linked to massive carbon release from thawing permafrost. *Nature* 484:87–91
- Derham W. 1713. *Physico-Theology; or, A Demonstration of the Being and Attributes of God, from His Works of Creation*. London: Innys
- Dickens GR. 2003. Rethinking the global carbon cycle with a large, dynamic and microbially mediated gas hydrate capacitor. *Earth Planet. Sci. Lett.* 213:169–83
- Dijkstra HA. 2013. *Nonlinear Climate Dynamics*. Cambridge, UK: Cambridge Univ. Press
- Dunkley Jones T, Ridgwell A, Lunt D, Maslin M, Schmidt D, Valdes P. 2010. A Palaeogene perspective on climate sensitivity and methane hydrate instability. *Philos. Trans. R. Soc. A* 368:2395–415
- Dyer B, Maloof AC, Higgins JA. 2015. Glacioeustasy, meteoric diagenesis, and the carbon cycle during the Middle Carboniferous. *Geochem. Geophys. Geosyst.* 16:3383–99
- Edmond JM, Huh Y. 2003. Non-steady state carbonate recycling and implications for the evolution of atmospheric PCO_2 . *Earth Planet. Sci. Lett.* 216:125–39
- Egerton FN. 1973. Changing concepts of the balance of nature. *Q. Rev. Biol.* 48:322–50
- Emerson SR, Hedges JI. 2008. *Chemical Oceanography and the Marine Carbon Cycle*. Cambridge, UK: Cambridge Univ. Press
- Emiliani C. 1955. Pleistocene temperatures. *J. Geol.* 63:538–78
- Fantle MS, Barnes BD, Lau KV. 2020. The role of diagenesis in shaping the geochemistry of the marine carbonate record. *Annu. Rev. Earth Planet. Sci.* 48:549–83
- Feulner G. 2012. The faint young Sun problem. *Rev. Geophys.* 50:RG2006
- Foote E. 1856. Circumstances affecting the heat of the sun’s rays. *Am. J. Sci. Arts* 22:382–83
- Foster GL, Royer DL, Lunt DJ. 2017. Future climate forcing potentially without precedent in the last 420 million years. *Nat. Commun.* 8:14845
- Ghil M, Childress S. 1987. *Topics in Geophysical Fluid Dynamics: Atmospheric Dynamics, Dynamo Theory, and Climate Dynamics*. New York: Springer
- Gildor H, Tziperman E. 2000. Sea ice as the glacial cycles’ climate switch: role of seasonal and orbital forcing. *Paleoceanography* 15:605–15
- Grossman E, Joachimski M. 2020. Oxygen isotope stratigraphy. In *Geologic Time Scale 2020*, ed. FM Gradstein, JG Ogg, M Schmitz, G Ogg, pp. 279–307. Amsterdam: Elsevier
- Gutjahr M, Ridgwell A, Sexton PF, Anagnostou E, Pearson PN, et al. 2017. Very large release of mostly volcanic carbon during the Palaeocene–Eocene Thermal Maximum. *Nature* 548:573–77
- Hallam A, Wignall PB. 1997. *Mass Extinctions and Their Aftermath*. Oxford, UK: Oxford Univ. Press
- Hayes JM, Strauss H, Kaufman AJ. 1999. The abundance of ^{13}C in marine organic matter and isotopic fractionation in the global biogeochemical cycle of carbon during the past 800 Ma. *Chem. Geol.* 161:103–25
- Hays JD, Imbrie J, Shackleton NJ. 1976. Variations in the Earth’s orbit: pacemaker of the ice ages. *Science* 194:1121–32
- Higgins JA, Blättler C, Lundstrom E, Santiago-Ramos D, Akhtar A, et al. 2018. Mineralogy, early marine diagenesis, and the chemistry of shallow-water carbonate sediments. *Geochim. Cosmochim. Acta* 220:512–34
- Hofmann M, Schellnhuber HJ. 2009. Oceanic acidification affects marine carbon pump and triggers extended marine oxygen holes. *PNAS* 106:3017–22
- Husson JM, Higgins JA, Maloof AC, Schoene B. 2015. Ca and Mg isotope constraints on the origin of Earth’s deepest $\delta^{13}\text{C}$ excursion. *Geochim. Cosmochim. Acta* 160:243–66
- Husson JM, Linzmeier BJ, Kitajima K, Ishida A, Maloof AC, et al. 2020. Large isotopic variability at the micron-scale in ‘Shuram’ excursion carbonates from South Australia. *Earth Planet. Sci. Lett.* 538:116211

- Izhikevich EM. 2007. *Dynamical Systems in Neuroscience: The Geometry of Excitability and Bursting*. Cambridge, MA: MIT Press
- Joachimski MM, Lai X, Shen S, Jiang H, Luo G, et al. 2012. Climate warming in the latest Permian and the Permian–Triassic mass extinction. *Geology* 40:195–98
- Kirchner JW. 1989. The Gaia hypothesis: Can it be tested? *Rev. Geophys.* 27:223–35
- Kirchner JW. 2002. The Gaia hypothesis: fact, theory, and wishful thinking. *Clim. Change* 52:391–408
- Kirtland Turner S. 2018. Constraints on the onset duration of the Paleocene–Eocene Thermal Maximum. *Philos. Trans. R. Soc. A* 376:20170082
- Kirtland Turner S, Sexton PF, Charles CD, Norris RD. 2014. Persistence of carbon release events through the peak of early Eocene global warmth. *Nat. Geosci.* 7:748–51
- Knoll AH, Bambach RK, Payne JL, Pruss S, Fischer WW. 2007. Paleophysiology and end-Permian mass extinction. *Earth Planet. Sci. Lett.* 256:295–313
- Kolbert E. 2014. *The Sixth Extinction: An Unnatural History*. London: A&C Black
- Kump LR, Arthur MA. 1999. Interpreting carbon-isotope excursions: carbonates and organic matter. *Chem. Geol.* 161:181–98
- Kurtz A, Kump L, Arthur M, Zachos J, Paytan A. 2003. Early Cenozoic decoupling of the global carbon and sulfur cycles. *Paleoceanography* 18:1090
- Le Treut H, Ghil M. 1983. Orbital forcing, climatic interactions, and glaciation cycles. *J. Geophys. Res. Oceans* 88:5167–90
- Lenton TM, Daines SJ, Dyke JG, Nicholson AE, Wilkinson DM, Williams HT. 2018. Selection for Gaia across multiple scales. *Trends Ecol. Evol.* 33:633–45
- Lenton TM, Held H, Kriegler E, Hall JW, Lucht W, et al. 2008. Tipping elements in the Earth's climate system. *PNAS* 105:1786–93
- Lisiecki LE, Raymo ME. 2005. A Pliocene–Pleistocene stack of 57 globally distributed benthic $\delta^{18}\text{O}$ records. *Paleoceanography* 20:PA1003
- Lotka AJ. 1925. *Elements of Physical Biology*. Baltimore, MD: Williams & Wilkins
- Lourens LJ, Sluijs A, Kroon D, Zachos JC, Thomas E, et al. 2005. Astronomical pacing of late Palaeocene to early Eocene global warming events. *Nature* 435:1083–87
- Lovejoy AO. 1936. *The Great Chain of Being*. Cambridge, MA: Harvard Univ. Press
- Lovejoy S. 2015. A voyage through scales, a missing quadrillion and why the climate is not what you expect. *Clim. Dyn.* 44:3187–210
- Lovelock JE, Margulis L. 1974. Atmospheric homeostasis by and for the biosphere: the Gaia hypothesis. *Tellus* 26:2–10
- Lunt DJ, Ridgwell A, Sluijs A, Zachos J, Hunter S, Haywood A. 2011. A model for orbital pacing of methane hydrate destabilization during the Palaeogene. *Nat. Geosci.* 4:775–78
- Lyell C. 1832. *Principles of Geology, Being an Attempt to Explain the Former Changes of the Earth's Surface, by Reference to Causes Now in Operation*, Vol. 2. London: Murray
- Macdonald FA, Swanson-Hysell NL, Park Y, Lisiecki L, Jagoutz O. 2019. Arc-continent collisions in the tropics set Earth's climate state. *Science* 364:181–84
- Maher K, Chamberlain C. 2014. Hydrologic regulation of chemical weathering and the geologic carbon cycle. *Science* 343:1502–4
- May RM. 1973. *Stability and Complexity in Model Ecosystems*. Princeton, NJ: Princeton Univ. Press
- Mayr E. 1982. *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Cambridge, MA: Harvard Univ. Press
- McInerney FA, Wing SL. 2011. The Paleocene–Eocene Thermal Maximum: a perturbation of carbon cycle, climate, and biosphere with implications for the future. *Annu. Rev. Earth Planet. Sci.* 39:489–516
- Milanković M. 1941. *Kanon der Erdbestrahlung und seine Anwendung auf das Eiszeitenproblem*. Belgrade: K. Serb. Akad.
- Mitnick EH, Lammers LN, Zhang S, Zaretskiy Y, DePaolo DJ. 2018. Authigenic carbonate formation rates in marine sediments and implications for the marine $\delta^{13}\text{C}$ record. *Earth Planet. Sci. Lett.* 495:135–45
- Newell ND. 1963. Crises in the history of life. *Scientific American*, Feb., pp. 76–95
- Paillard D, Parrenin F. 2004. The Antarctic ice sheet and the triggering of deglaciations. *Earth Planet. Sci. Lett.* 227:263–71

- Payne JL, Clapham ME. 2012. End-Permian mass extinction in the oceans: an ancient analog for the twenty-first century? *Annu. Rev. Earth Planet. Sci.* 40:89–111
- Petit JR, Jouzel J, Raynaud D, Barkov NI, Barnola JM, et al. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399:429–36
- Pierrehumbert RT. 2010. *Principles of Planetary Climate*. Cambridge, UK: Cambridge Univ. Press
- Pope A. 1733. *An Essay on Man: In Epistles to a Friend*, Part I. London: Wilford. 2nd ed.
- Ridgwell A. 2005. A Mid Mesozoic Revolution in the regulation of ocean chemistry. *Mar. Geol.* 217:339–57
- Ridgwell A, Edwards U. 2007. Geological carbon sinks. In *Greenhouse Gas Sinks*, ed. D Reay, CN Hewitt, K Smith, J Grace, pp. 74–97. Wallingford, UK: CABI
- Ridgwell A, Hargreaves J. 2007. Regulation of atmospheric CO₂ by deep-sea sediments in an Earth system model. *Glob. Biogeochem. Cycles* 21:GB2008
- Ridgwell A, Zeebe RE. 2005. The role of the global carbonate cycle in the regulation and evolution of the Earth system. *Earth Planet. Sci. Lett.* 234:299–315
- Riebesell U, Körtzinger A, Oschlies A. 2009. Sensitivities of marine carbon fluxes to ocean change. *PNAS* 106:20602–9
- Rothman DH. 2015. Earth's carbon cycle: a mathematical perspective. *Bull. Am. Math. Soc.* 52:47–64
- Rothman DH. 2017. Thresholds of catastrophe in the Earth system. *Sci. Adv.* 3:e1700906
- Rothman DH. 2019. Characteristic disruptions of an excitable carbon cycle. *PNAS* 116:14813–22
- Rothman DH, Fournier GP, French KL, Alm EJ, Boyle EA, et al. 2014. Methanogenic burst in the end-Permian carbon cycle. *PNAS* 111:5462–67
- Rothman DH, Hayes JM, Summons RE. 2003. Dynamics of the Neoproterozoic carbon cycle. *PNAS* 100:8124–29
- Rudwick MJS. 2014. *Earth's Deep History: How It Was Discovered and Why It Matters*. Chicago: Univ. Chicago Press
- Sagan C, Mullen G. 1972. Earth and Mars: evolution of atmospheres and surface temperatures. *Science* 177:52–56
- Saltzman B. 2002. *Dynamical Paleoclimatology: Generalized Theory of Global Climate Change*. San Diego, CA: Academic
- Saltzman B, Hansen AR, Maasch KA. 1984. The late Quaternary glaciations as the response of a three-component feedback system to Earth-orbital forcing. *J. Atmos. Sci.* 41:3380–89
- Sarmiento JL, Gruber N. 2006. *Ocean Biogeochemical Dynamics*. Princeton, NJ: Princeton Univ. Press
- Schoene B, Eddy MP, Samperton KM, Keller CB, Keller G, et al. 2019. U-Pb constraints on pulsed eruption of the Deccan Traps across the end-Cretaceous mass extinction. *Science* 363:862–66
- Schrag DP, Higgins JA, Macdonald FA, Johnston DT. 2013. Authigenic carbonate and the history of the global carbon cycle. *Science* 339:540–43
- Self S, Thordarson T, Widdowson M. 2005. Gas fluxes from flood basalt eruptions. *Elements* 1:283–87
- Sepkoski D. 2020. *Catastrophic Thinking: Extinction and the Value of Diversity from Darwin to the Anthropocene*. Chicago: Univ. Chicago Press
- Sexton PF, Norris RD, Wilson PA, Pälike H, Westerhold T, et al. 2011. Eocene global warming events driven by ventilation of oceanic dissolved organic carbon. *Nature* 471:349–52
- Shackleton NJ. 1977. Carbon-13 in Uvigerina: tropical rainforest history and the equatorial Pacific carbonate dissolution cycles. In *The Fate of Fossil Fuel CO₂ in the Oceans*, ed. NR Andersen, A Malahoff, pp. 401–27. New York: Plenum
- Sherwood S, Webb MJ, Annan JD, Armour K, Forster PM, et al. 2020. An assessment of Earth's climate sensitivity using multiple lines of evidence. *Rev. Geophys.* 58:e2019RG000678
- Sigman DM, Boyle EA. 2000. Glacial/interglacial variations in atmospheric carbon dioxide. *Nature* 407:859–69
- Simberloff D. 2014. The “balance of nature”—evolution of a panchreston. *PLOS Biol.* 12:e1001963
- Sprain CJ, Renne PR, Vanderkluysen L, Pande K, Self S, Mittal T. 2019. The eruptive tempo of Deccan volcanism in relation to the Cretaceous–Paleogene boundary. *Science* 363:866–70
- Stanley SM. 2010. Relation of Phanerozoic stable isotope excursions to climate, bacterial metabolism, and major extinctions. *PNAS* 107:19185–89

- Steffen W, Rockström J, Richardson K, Lenton TM, Folke C, et al. 2018. Trajectories of the Earth system in the Anthropocene. *PNAS* 115:8252–59
- Strogatz S. 1994. *Nonlinear Dynamics and Chaos*. New York: Addison-Wesley
- Sundquist ET. 1985. Geological perspectives on carbon dioxide and the carbon cycle. In *The Carbon Cycle and Atmospheric CO₂: Natural Variations Archean to Present*, ed. ET Sundquist, WS Broecker, pp. 55–59. Washington, DC: Am. Geophys. Union
- Sundquist ET. 1990. Influence of deep-sea benthic processes on atmospheric CO₂. *Philos. Trans. R. Soc. Lond. A* 331:155–65
- Sundquist ET. 1991. Steady-and non-steady-state carbonate-silicate controls on atmospheric CO₂. *Quat. Sci. Rev.* 10:283–96
- Tyndall J. 1863. On radiation through the earth's atmosphere. *Lond. Edinb. Dublin Philos. Mag. J. Sci.* 25:200–6
- Tyrrell T. 2020. Chance played a role in determining whether Earth stayed habitable. *Nat. Commun. Earth Environ.* 1:61
- Tziperman E, Raymo ME, Huybers P, Wunsch C. 2006. Consequences of pacing the Pleistocene 100 kyr ice ages by nonlinear phase locking to Milankovitch forcing. *Paleoceanography* 21:PA4206
- Volterra V. 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Mem. R. Accad. Lincei* 2:31–113
- Walker JC, Hays P, Kasting JF. 1981. A negative feedback mechanism for the long-term stabilization of Earth's surface temperature. *J. Geophys. Res. Oceans* 86:9776–82
- Walliser OH, ed. 1996. *Global Events and Event Stratigraphy in the Phanerozoic*. Berlin: Springer
- Wallmann K, Flögel S, Scholz F, Dale AW, Kemena TP, et al. 2019. Periodic changes in the Cretaceous ocean and climate caused by marine redox see-saw. *Nat. Geosci.* 12:456–61
- Westerhold T, Marwan N, Drury AJ, Liebrand D, Agnini C, et al. 2020. An astronomically dated record of Earth's climate and its predictability over the last 66 million years. *Science* 369:1383–87
- Westerhold T, Röhl U, Frederichs T, Agnini C, Raffi I, et al. 2017. Astronomical calibration of the Ypresian timescale: implications for seafloor spreading rates and the chaotic behavior of the solar system? *Clim. Past* 13:1129–52
- Wieczorek S, Ashwin P, Luke CM, Cox PM. 2010. Excitability in ramped systems: the compost-bomb instability. *Proc. R. Soc. A* 467:1243–69
- Wignall PB, Twitchett RJ. 1996. Oceanic anoxia and the End Permian mass extinction. *Science* 272:1155–58
- Williams RG, Follows MJ. 2011. *Ocean Dynamics and the Carbon Cycle: Principles and Mechanisms*. Cambridge, UK: Cambridge Univ. Press
- Wunsch C. 2004. Quantitative estimate of the Milankovitch-forced contribution to observed Quaternary climate change. *Quat. Sci. Rev.* 23:1001–12
- Zachos JC, Dickens GR, Zeebe RE. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* 451:279–83
- Zachos JC, Pagani M, Sloan L, Thomas E, Billups K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292:686–93
- Zeebe RE, Caldeira K. 2008. Close mass balance of long-term carbon fluxes from ice-core CO₂ and ocean chemistry records. *Nat. Geosci.* 1:312–15
- Zeebe RE, Ridgwell A, Zachos JC. 2016. Anthropogenic carbon release rate unprecedented during the past 66 million years. *Nat. Geosci.* 9:325–29
- Zeebe RE, Westbroek P. 2003. A simple model for the CaCO₃ saturation state of the ocean: the “Strangelove,” the “Neritan,” and the “Cretan” Ocean. *Geochem. Geophys. Geosyst.* 4:1104
- Zeebe RE, Zachos JC. 2013. Long-term legacy of massive carbon input to the Earth system: Anthropocene versus Eocene. *Philos. Trans. R. Soc. A* 371:20120006