

On The Record

The preservation of cause and effect in the rock record

Michael P. D'Antonio^{*†} , Daniel E. Ibarra^{*†}, and C. Kevin Boyce

Abstract.—Evolutionary events may impact the geological carbon cycle via transient imbalances in silicate weathering, and such events have been implicated as causes of glaciations, mass extinctions, and oceanic anoxia. However, suggested evolutionary causes often substantially predate the environmental effects to which they are linked—problematic when carbon cycle perturbations must be resolved in less than a million years to maintain Earth's habitability. What is more, the geochemical signatures of such perturbations are recorded as they occur in widely distributed marine sedimentary rocks that have been densely sampled for important intervals in Earth history, whereas the fossil record—particularly on land—is governed by the availability of sedimentary basins that are patchy in both space and time, necessitating lags between the origination of an evolutionary lineage and its earliest occurrence in the fossil record. Here, we present a simple model of the impact of preservational filtering on sampling to show that an evolutionary event that causes an environmental perturbation via weathering imbalance should not appear earlier in the rock record than the perturbation itself and, if anything, should appear later rather than simultaneously. The Devonian Hangenberg glaciation provides an example of how evolutionary events might be more fruitfully considered as potential causes of environmental perturbations. Just as the last samplings of species lost in mass extinction are expected to come before the true environmental event, first appearance should be expected to postdate the geological expression of a lineage's environmental impact with important implications for our reading of Earth history.

Michael P. D'Antonio and C. Kevin Boyce. Department of Geological Sciences, Stanford University, Stanford, California 94305, U.S.A. E-mail: michaeldantonio22@gmail.com, chkenboy@stanford.edu.

Daniel E. Ibarra[‡]. Department of Earth and Planetary Science, University of California, Berkeley, Berkeley, California 94720, U.S.A. E-mail: daniel_ibarra@brown.edu. [‡]Present address: Institute at Brown for Environment and Society and the Department of Earth, Environmental and Planetary Science, Brown University, Providence, Rhode Island 02912, U.S.A.

Accepted: 11 August 2022

*Corresponding author.

†These authors contributed equally.

Introduction

A variety of evolutionary innovations in the ecophysiology of land plants and other components of the terrestrial biota are proposed to have been transformative for the carbon cycle as the relevant clade became widespread and ecologically dominant, but how the carbon cycle can be transformed is highly constrained. The reaction of silicate minerals and CO₂—both introduced to Earth's surface via volcanism—forms clays and releases ions to solution to be later precipitated as marine carbonates (Berner 1991). This net chemical weathering reaction modulates atmospheric CO₂ concentration and regulates Earth's climate over geological

time (Urey 1952). The input of carbon to Earth's surface environment via volcanic and metamorphic outgassing is balanced by the output of carbon from Earth's surface environment via burial in rocks as carbonate or organic carbon. This balance must be maintained on ~10⁶ yr timescales to avoid deterioration of Earth's climate to either a Mars-like (carbon removal outstrips introduction) or Venus-like (carbon introduction outstrips removal) state (Walker et al. 1981; Berner and Caldeira 1997; D'Antonio et al. 2020; Isson et al. 2020). Because weathering consumes CO₂, a permanent or prolonged (>10⁵ yr) change in weathering rate without a corresponding proportional change in

carbon inputs would represent a scenario in Earth's exogenic carbon cycle with clear catastrophic consequences extreme enough (e.g., a Snowball Earth episode) that they demonstrably have not happened over the Phanerozoic.

Evolutionary events may be associated with perturbations of the carbon cycle that occur when a new equilibrium atmospheric CO₂ concentration is established. These perturbations can provoke sharp changes to weathering-derived nutrient fluxes and climate until steady state is reached, but such imbalances must be resolved within ~1 Myr (Algeo and Scheckler 2010; Bachan et al. 2017; D'Antonio et al. 2020). For example, the Frasnian/Famennian (Late Devonian) Kellwasser events each lasted ~100 kyr, calibrated to the short eccentricity Milankovitch cycle (Schindler [1990] as cited in House 2002; De Vleeschouwer et al. 2013, 2017; Pier et al. 2021), and the end-Famennian (Devonian/Carboniferous) Hangenberg crisis lasted 50–100 kyr, calibrated to precise U-Pb zircon dates from bounding ash beds (Myrow et al. 2014)—both appropriate durations of short-term perturbations potentially arising from transiently elevated weathering fluxes. These perturbations can involve dramatic impacts, including glaciation, marine anoxia, and mass extinction, but their transience and rapid resolution require a close coupling of cause and effect on geological timescales. This presents a problem when the attributions of environmental events to evolutionary causes are often associations separated by tens of millions of years, such as Late Ordovician glaciation following the Middle Ordovician appearance of land plants and the Late Devonian black shale events following the Middle Devonian appearance of deep-rooting trees (Bernier 1997; Algeo and Scheckler 1998; Lenton et al. 2012). (Here, we note that not all environmental events fit this <1 Myr context of carbon cycle perturbations. For example, the 10 Myr timescales of tectonics-driven changes to paleogeography and ocean circulation patterns are more relevant for explaining the longer Phanerozoic glaciations [Scher and Martin 2006; Pohl et al. 2014], and the 100 Myr timescales of the rock cycle [Bachan and Kump 2015; Boyce et al. 2022] become relevant for considering the longest events, such as the

Paleoproterozoic Lomagundi-Jatuli event [Prave et al. 2021].)

For carbon cycle perturbations, cause and effect are required to be near simultaneous over million-year timescales; however, the geological expression of this cause and effect may then be distorted by differential preservation in the rock record. The global ocean is well mixed on 1–5 kyr timescales, far shorter than the 150 kyr residence time of carbon in the system, so that the potential preservation of carbon cycle perturbations in the geological record should be globally distributed. These perturbations can then be intensively sampled with carbon isotopic composition from the abundance and temporal continuity of near-shore marine carbonates (e.g., Caplan and Bustin 1999; Zachos et al. 2005; Hull 2015). For example, thousands of $\delta^{13}\text{C}$ measurements have been taken within 100 kyr both of the Paleocene–Eocene thermal maximum (PETM) and of mass extinctions such as the Cretaceous/Paleogene and Permian/Triassic extinction events (e.g., Payne et al. 2004; Hull 2015; Hull et al. 2020).

The fossil record behaves differently. Just as the last appearance of a fossil will precede the actual extinction of that taxon (Signor and Lipps 1982), the first appearance of a fossil will lag the actual origination (Sepkoski 1998; Kirchner and Weil 2000), with range offset spanning anywhere from a few hundreds of thousands of years to several million years (Holland and Patzkowsky 2002). In addition to this phenomenon inherent to the structure of stratigraphic architecture, incomplete sampling has been shown to lengthen lags between origination and first appearance, or last appearance and extinction (Kirchner and Weil 2000). Statistical analyses of the fossil record have been conducted with marine strata and taxa (Marshall 1990, 1994), but ecological gradients, stratigraphic architecture, and facies effects are all important hurdles for inferring taxon range (Holland and Patzkowsky 2002; Patzkowsky and Holland 2012; Holland 2020). The complications of incomplete preservation and sampling are compounded for terrestrial fossils due to the extreme patchiness of fossiliferous strata requiring a basin to have been present at the right place and at the right time, with elevation, relief, burial rate, and erosion rate likely playing important roles (Holland 1995, 2016,

2022; Kidwell and Holland 2002; Peters and Husson 2017). This patchiness can be seen in the outsized importance of Euramerican foreland basins for our understanding of Pennsylvanian forests (Nelsen et al. 2016), followed by the specific importance of South Africa in understanding evolution of the land biota in the Permian and Triassic (Anderson and Anderson 1983, 1997; Gastaldo et al. 2005, 2015).

Together, these factors are likely to lead to an inversion of our basic expectations regarding cause and effect in the rock record. Given the resolution limits of geological time, evolutionary events should be essentially simultaneous with any resulting weathering-mediated carbon cycle perturbations they might have caused. This simultaneity—once filtered through the differential preservation potential and sampling intensity of the geochemical record of environmental perturbation versus the fossil record of potential biotic causes—should result in the earliest record of environmental effect preceding the record of its biotic cause (Fig. 1). Here, this hypothesis is explained with a simple model, and its potential implications are explored in the context of Paleozoic land plant evolution.

Methods

For illustrative purposes, land plant evolution occurring in the terrestrial realm is modeled; however, this logic would similarly apply to any other evolutionary event and an environmental effect argued to be related via causality, such as the impact of earthworm evolution on soil carbon storage, of shallow-marine burrowers on sedimentary geochemistry, or of cyanobacterial evolution and atmospheric oxygenation. The expected number of samples per unit time that will capture either a carbon cycle perturbation or an appropriate fossil of the biotic trigger of the perturbation, $E(x)$, is approximated by the equation:

$$E(x) = A * B * C * D \quad (1)$$

where A is the number of samples per unit time, B is the probability that appropriate sediments are available for geochemical or biological preservation, C is the probability that the geochemical or biological signal was regionally present,

and D is the probability that an entirely appropriate sample will have captured the relevant geochemistry or biology. For carbon cycle perturbations, A_{geo} was set to 100,000 samples per 2 Myr, B_{geo} was set to 1 to reflect the relative abundance of marine limestones, C_{geo} was set to 1 to reflect the well-mixed nature of the ocean on relevant timescales, and D_{geo} was set to 0.95 to reflect the signal of some samples being lost to vital effects or to diagenesis and other postdepositional alteration.

Fossils—especially terrestrial fossils—are preserved and distributed differently than marine carbonates and are also subject to differences in sampling intensity, leading to divergent value assignments for A_{bio} through D_{bio} . For biological fossils, A_{bio} was set to 1000 samples per 2 Myr—purposely set as being 100 times less than A_{geo} of the carbon cycle sampling; B_{bio} was set to 0.05 to reflect the availability of floodplain, mire, and lake deposits (the relevant land plant fossil record archives) relative to the abundance of marine deposits; C_{bio} was set to 0.25 to reflect relevant available land surface; and D_{bio} was set to 0.3 to reflect the fossil needing to be of the correct lineage. These values are order of magnitude estimates and no precision is implied; however, it is unambiguous that each of the A – D values should be substantially lower for the terrestrial fossil record than for the shallow-marine carbonate record, and the preservational disadvantages of terrestrial fossils are magnified by the multiplication of these factors.

A uniform distribution with $\text{min} = 0$ yr and $\text{max} = 2$ Myr was then sampled A times for both the geochemical and biological samples (Fig. 2). These graphs represent spatial distributions of geochemical data points and fossils. The simulated data were then filtered progressively through sampling, without replacement, of factors B , C , and D (Fig. 2). The perturbation is assumed to last 100 kyr, with an onset 100 kyr after the initial appearance of its evolutionary cause. The expected frequency that the earliest fossil sampling of an evolutionary event will appear either before the onset of the environmental perturbation (i.e., within 100 kyr of the evolutionary origin) or simultaneous with the environmental perturbation (i.e., between 100 and 200 kyr of the evolutionary origin) was then calculated by dividing the number of

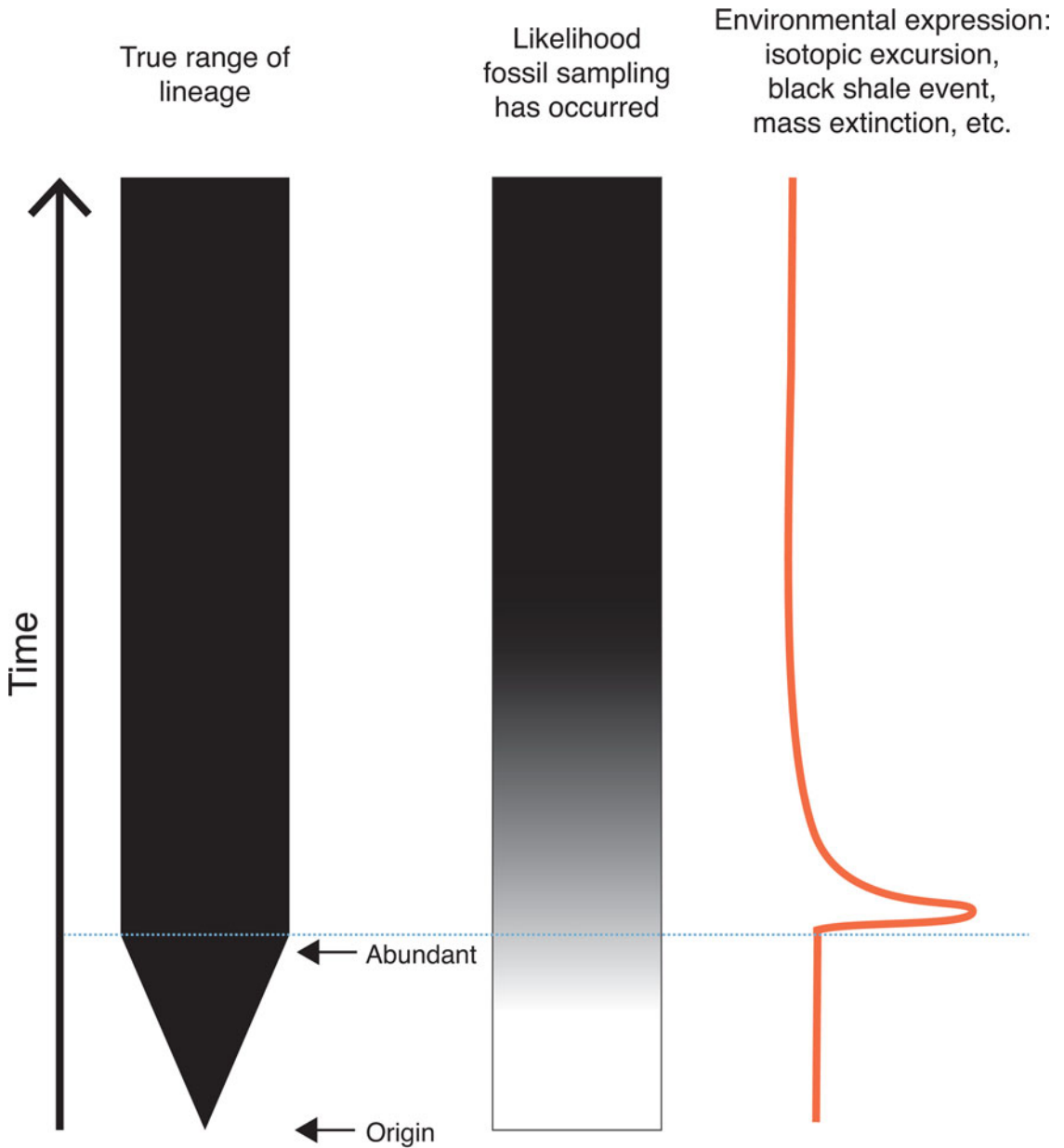


FIGURE 1. Schematic of how cause and effect will be presented in the rock record. An evolutionary event—i.e., origination of a clade with a trait of biogeochemical importance—occurs, and its abundance increases over time until it has broad expression over the landscape. Its rise to environmental abundance can trigger a carbon cycle perturbation, e.g., through a transient imbalance in global weathering, nutrient fluxes, or organic carbon burial rates. Depending on the environmental impact, such a carbon cycle perturbation may be expressed as an isotopic excursion, a black shale horizon, and/or a mass extinction—all of which can be preserved in the rock record without delay relative to their true timing due to their global character and wide environmental expression. A substantial carbon cycle perturbation must be resolved within 1 Myr, but the return to equilibrium will often take much less time, related to the ~150 kyr residence time of carbon in Earth's surface reservoirs (atmosphere, ocean, and biosphere). At the same time, a significant lag is expected between the true origin and the first fossil sampling of an evolutionary lineage with expected time lags lasting into the millions of years. This suggests that the cause of a carbon cycle perturbation will most often appear in the rock record after the geochemical perturbation itself.

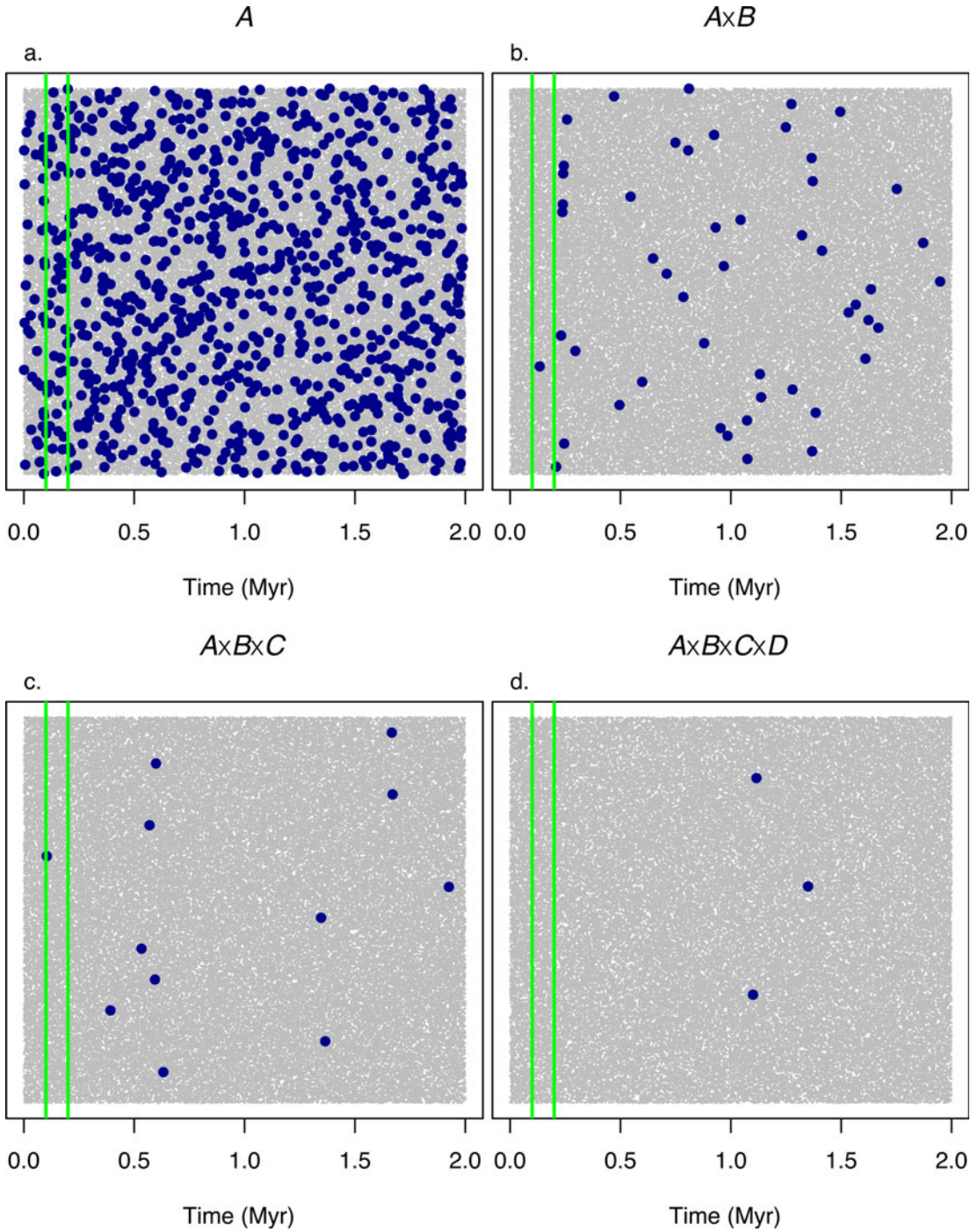


FIGURE 2. Effect of differential taphonomic filtering on preserving cause and effect in the rock record. In all panels, an environmental perturbation lasting 100 kyr (bounded by the two green lines) lags the true origin (time 0) of its biotic cause by 100 kyr, allowing for the establishment and spread of the lineage before the resulting environmental effects. Geochemical sampling through the time interval can be expected to be effectively continuous (small gray circles, abundant enough to be individually indistinguishable in the graph), but the potential for fossil sampling (blue circles) of the biotic cause before or simultaneous with the resulting perturbation decreases drastically given the parameterization of A , B , C , and D from equation (1) in the text. Thus, the expected frequency of environmental perturbation sampling being earlier than the evolutionary event in the fossil record increases with each step in the data-filtration pipeline. a, Before filtration, 1000 paleontological vs. 100,000 geochemical sampling opportunities are available (i.e., $A_{\text{bio}} = 0.01A_{\text{geo}}$) within the first 2 Myr following the true first appearance of the relevant evolutionary lineage. b–d, Fossil data points filtered successively through the probability of sampling being of an appropriate environment ($B_{\text{bio}} = 0.05$), that the relevant lineage was regionally present ($C_{\text{bio}} = 0.25$), and that an otherwise appropriate fossil is of the correct lineage ($D_{\text{bio}} = 0.3$). Geochemical sampling remains steady through this filtration of the fossil record (i.e., $A_{\text{geo}} = B_{\text{geo}} = C_{\text{geo}} = 1$), other than a slight drop in sampling ($D_{\text{geo}} = 0.95$) in d, reflecting the possibility of diagenetic alteration of isotopic geochemistry.

biological data remaining after filtration through B , C , and D by the original biological data sample size ($A_{\text{bio}} = 1000$). This filtration of the original uniform distribution was then repeated 1000 times. The code used for calculations is included as an R file in the Supplementary Material.

Results and Discussion

Given our assumptions, a new lineage of novel ecophysiological importance will be sampled as a fossil before its ecological spread and induction of a carbon cycle perturbation (i.e., before the leftmost vertical green line in Fig. 2) only 0.015% of the time. Thus, if our approximations of A – D are reasonable to a first order, then only once or twice out of 10,000 events would the fossil cause appear before the effect of a carbon cycle perturbation. Considering also the expected frequency of earliest fossil appearance simultaneous with the carbon cycle perturbation it caused (i.e., between the vertical green lines in Fig. 2) only adds an additional 0.015%.

Although crude, these simple calculations highlight that it is highly unlikely that the earliest fossil would come before an environmental perturbation it caused; rather, the opposite is the case and, most often, the earliest record of the perturbation should appear in the rock record before the earliest fossil of the relevant lineage. The assumptions made in our calculation are conservative where possible. For example, the likelihood of finding a relevant fossil is not uniform but should increase through time as the new lineage increases in abundance and geographic range; therefore,

the expected frequency of early fossil finds close to the origination of the taxon or trait should be lower than coded here (Marshall 1990; Holland 2016). Furthermore, the D_{bio} in our formulation assumes any fossil documentation of a lineage is equally adequate when more specific information may be required. As an example, most fossils of a plant lineage may be of leaves with relatively few specimens documenting a habit of large, deep-rooting trees.

Even in an extreme parameterization of the three biological values amplifying preservation potential ($B_{\text{bio}} = 0.25$, $C_{\text{bio}} = 0.5$, and $D_{\text{bio}} = 0.5$, vs. the original $B_{\text{bio}} = 0.05$, $C_{\text{bio}} = 0.25$, and $D_{\text{bio}} = 0.3$, with A_{bio} held the same as in the “Methods”), the expected frequency of the earliest fossil of an evolutionary event appearing earlier than the carbon cycle perturbation it caused only rises to 0.3%. Alternate parameterizations might include a much longer lag between the origins of the relevant trait and its rise to ecological dominance and perturbation of the system (Fig. 1). If the lineage remained rare enough not to impact the system, however, then it is expected to have a more limited opportunity for fossil preservation.

There is a wider parameter space to consider, but the outcome of evolutionary cause generally appearing after environmental effect in the rock record may be inescapable. Certainly, much of Earth history is poorly sampled, but there can be no lag in the sampling of a carbon cycle perturbation: either it has been sampled from the rock record before its resolution or it has not. And if it has not been sampled, then it is simply an unknown for which no explanation will be sought. A longer carbon cycle

perturbation lasting >1 Myr can be constructed to allow greater likelihood of its evolutionary cause being sampled before its resolution. However, this would require small imbalances of ~1% (Berner and Caldeira 1997; D'Antonio et al. 2020) that are unlikely to be recognized as a perturbation in need of explanation—far from the 100%–10,000% imbalances that are considered and implemented into carbon cycle models, for example, in weathering capacity increases between barren and vegetated substrates (Moulton and Berner 1998; Lenton et al. 2012).

At the other extreme, this exercise illustrates how far removed from the actual particulars are various suggestions in the literature that biotic events led to environmental perturbations millions or tens of millions of years later. These scenarios would require the routine capture as fossils of the earliest examples of a lineage when still found only in localized populations of low abundance—contrary to expectations of preservation potential—followed by prolonged suppression of any dispersal across the broader landscape so as to delay environmental impact, despite vegetation being capable of migrating thousands of kilometers on 10 kyr timescales, as documented both in the last deglaciation and during the PETM (Wing et al. 2005; Zanon et al. 2018). Such a scenario would then culminate with a rapid spread at the time of the actual perturbation. Some suggestions in the earlier literature of geobiological impact long after a first appearance can be recognized to have been reasonable in their original context of poor temporal precision regarding the events involved. In this way, it was reasonable in decades past to wonder whether Pangea formation was relevant to end-Permian extinctions, as the temporal constraints were not there to be confident the events were separated by tens of millions of years (Erwin 1993). However, these suggestions must be recognized as artifacts from the history of our science for which continuing citation as viable possibilities is not warranted.

Land Plants and Paleozoic Glaciations: A Case Study.—The appearance of land plants was perhaps the most consequential geobiological event in the Phanerozoic. Today, the group

represents ~80% of total global biomass (Bar-On et al. 2018) and is responsible for ~50% of net primary productivity (Field et al. 1998). Land plants are often implicated in changes in the Earth's surface, as they possess high potential for ecosystem and Earth system engineering. This includes their ability both to transport water deep into continental interiors via transpirational recycling (Shukla and Mintz 1982; Boyce and Lee 2017; Ibarra et al. 2019) and to impact weathering on micro- (Drever 1994) and macroscale scales (Berner 1992; Winnick and Maher 2018), as well as ecological (Moulton and Berner 1998; Moulton et al. 2000) and geological temporal scales (Algeo and Scheckler 2010; D'Antonio et al. 2020; Boyce et al. 2022). Over the Paleozoic, the appearances of land plants, vascular plants, and deep-rooting vascular plant trees in the lowlands followed by colonization of the dry well-drained uplands have each been thought to have increased weathering capacity, with potential impacts including glaciations of varying duration, marine anoxia driven by increased nutrient fluxes, and mass extinction (Berner 1992; Algeo and Scheckler 1998, 2010; Lenton et al. 2012).

The evolution of terrestrial vegetation and successive innovations in plant physiology and how plants interact with their substrate, such as deep rooting and mycorrhizal associations, can enhance weathering capacity at any given atmospheric CO₂ concentration, leading to lower equilibrium levels of atmospheric CO₂, as borne out both by modeling and proxy data (Berner 1992, 2006; Royer et al. 2014; Ibarra et al. 2019). Because CO₂ is a greenhouse gas, the permanent lowering of its baseline concentrations can correctly be viewed as a contributing factor in all later glaciations. In this sense, it is logically correct to view the Devonian evolution of trees as contributing to the late Paleozoic glaciations (Berner 1997); however, it would be equally correct to view Devonian tree evolution as contributing to our Cenozoic glaciation, because atmospheric CO₂ has never returned to the concentrations that existed before the Devonian. In both cases, these glaciations that each spanned tens of millions of years would have been rendered more likely to occur with lower equilibrium CO₂

concentrations but would also have been highly dependent on favorable continental configurations and other factors.

Where prior studies have suggested that an evolutionary innovation in the terrestrial biota, including several different land plant lineages, arbuscular mycorrhizal and ectomycorrhizal fungi, lichens, and cryptobiotic soil crusts, was the cause of a carbon cycle perturbation or long-term trend, these studies have done so either by identifying a perturbation or trend and scanning backward in time until reaching a suitable evolutionary origin or by identifying an evolutionary origin and scanning forward in time until reaching a suitable perturbation or trend (e.g., Berner 1992, 2006; Algeo et al. 2001; Heckman et al. 2001; Kennedy et al. 2006; Lenton et al. 2012, 2016; Kump 2014). When operating under this paradigm, the evolutionary origin coming before the effect in the rock record becomes an unavoidable outcome, because it is already assumed in the first place. Our findings suggest that a different, counterintuitive logic may be more accurate: one should look after the effect for the cause. In practice, this would involve recognizing the geochemically recorded timing of the perturbation to be accurate and then identifying evolutionary causes that might have been plausibly simultaneous with the perturbation while recognizing that the first record of that cause can be expected to come later in the stratigraphic record—perhaps by a few million years.

The glacial pulse associated with the Hangenberg crisis serves as a useful case study to apply this logic in Earth history. This glacial pulse was terminal-Devonian (~359 Ma) and lasted >100 kyr (Myrow et al. 2014), and its timing and duration are now well understood globally (Caplan and Bustin 1999; Kaiser et al. 2015; Becker et al. 2016). The duration and directionality of climate deterioration are consistent with a pulse of globally elevated weathering fluxes relative to volcanic outgassing as atmospheric CO₂ declined to a new equilibrium concentration (D'Antonio et al. 2020). Although the cause of the perturbation remains uncertain and may have been abiotic (Caplan and Bustin 1999), it has been suggested that plant evolution played a role (Pawlik et al.

2020). If the perturbation was caused by a land plant evolutionary event, then the question should be, what could have happened at the same time as the event? On their own, the evolution of seed plants is removed from possibility, because they first appear as fossils within the Famennian (specifically, Fa2c miospore biozone) (Gillespie et al. 1981; Rothwell et al. 1989), approximately 363 Ma (House and Gradstein 2005)—roughly 4 Myr too early to have been a cause of the Hangenberg glacial episode. Likewise, on their own, the evolution of deep robust rooting systems is removed from possibility, because they appear as fossils in the mid-Devonian (Stein et al. 2020)—25–30 Myr before the Hangenberg glacial episode—much too early to have been relevant. If these earlier land plant evolutionary events in the Devonian (i.e., the origin of seeds and several independent originations of deep rooting systems) did represent carbon cycle perturbations, then they would most likely have been manifested as some of the Devonian black shale horizons, although with existing age constraints and the patchiness of the geological record it may be difficult to match specific evolutionary events with specific periods of widespread black shale deposition (Algeo and Scheckler 1998, 2010).

For the Hangenberg glaciation, the most realistic contender for a biotic cause might be the evolution of the first abundantly woody trees specifically among the seed plants. Large, deep-rooting trees had been present in proximal settings since the Middle Devonian among free-sporing vascular plants, but the severing of dependence on environmental water for reproduction may have allowed seed plant trees to spread inland more broadly, including to the uplands, and could have led to a meaningful pulse of elevated weathering fluxes on a global scale. Seed plants are first known earlier in the Late Devonian as smaller shrubs that would have been more shallowly rooting; the first massively woody seed plant trunks appear as fossils in the earliest Carboniferous (Galtier and Meyer-Berthaud 2006; Decombeix et al. 2011; Chen et al. 2021). Thus, it is these trees that might have plausibly spread at the time needed to have induced the global perturbation that is the Hangenberg.

For decades, we have recognized that the victims of mass extinction should last appear in the fossil record before the geological record of the environmental event (Signor and Lipps 1982; Marshall 1990; Marshall and Ward 1996). In a parallel way, the first appearance of a fossil lineage should postdate any global environmental disruption caused by the lineage, as with the carbon cycle. Of course, the evolution and spread of those seed plant trees seen in the earliest Carboniferous may instead have been a response to the climate change inherent in the Hangenberg glacial event, rather than being the cause of that event. A basic consequence of the logic advocated here is that effect and true cause should be difficult to distinguish. The record requires a complex reading that may always be ambiguous. However, there is still value in understanding the limits of what can be known and eliminating from contention all the traditional suspects that evolved millions of years too early.

Acknowledgments

We thank M. Patzkowsky, S. Holland, and A. Bush for their helpful comments during the review process, including the suggestion from A. Bush to add Fig. 1. D.E.I. was supported by the University of California Berkeley Miller Institute for Basic Research and University of California President's Postdoctoral Fellowships. The authors declare no competing interests.

Data Availability Statement

The R code used in this project is available as Supplementary Material in Dryad: <https://doi.org/10.5061/dryad.fbg79cnxw>.

Literature Cited

- Algeo, T. J., and S. E. Scheckler. 1998. Terrestrial-marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events. *Philosophical Transactions of the Royal Society of London B* 353:113–130.
- Algeo, T. J., and S. E. Scheckler. 2010. Land plant evolution and weathering rate changes in the Devonian. *Journal of Earth Science* 21(Suppl.):75–78.
- Algeo, T. J., S. E. Scheckler, and J. B. Maynard. 2001. 12. Effects of the Middle to Late Devonian spread of vascular land plants on weathering regimes, marine biotas, and global climate. Pp. 213–236 in P. G. Gensel and D. Edwards, eds. *Plants invade the land: evolutionary and environmental perspectives*. Columbia University Press, New York.
- Anderson, J. M., and H. M. Anderson. 1983. *Palaeoflora of southern Africa*, Vol. 1. CRC Press, Rotterdam, Netherlands.
- Anderson, J. M., and H. M. Anderson. 1997. Towards new paradigms in Permo-Triassic Karoo palaeobotany (and associated faunas) through the past 50 years. *Palaeontologia Africana* 33:11–21.
- Bachan, A., and L. R. Kump. 2015. The rise of oxygen and siderite oxidation during the Lomagundi Event. *Proceedings of the National Academy of Sciences USA* 112:6562–6567.
- Bachan, A., K. V. Lau, M. R. Saltzman, E. Thomas, L. R. Kump, and J. L. Payne. 2017. A model for the decrease in amplitude of carbon isotope excursions across the Phanerozoic. *American Journal of Science* 317:641–676.
- Bar-On, Y. M., R. Phillips, and R. Milo. 2018. The biomass distribution on Earth. *Proceedings of the National Academy of Sciences USA* 115:6506–6511.
- Becker, R. T., S. I. Kaiser, and M. Aretz. 2016. Review of chrono-, litho- and biostratigraphy across the global Hangenberg Crisis and Devonian–Carboniferous Boundary. *Geological Society of London Special Publication* 423:355–386.
- Berner, R. A. 1991. A model for atmospheric CO₂ over Phanerozoic time. *American Journal of Science* 291:339–376.
- Berner, R. A. 1992. Weathering, plants, and the long-term carbon cycle. *Geochimica et Cosmochimica Acta* 56:3225–3231.
- Berner, R. A. 1997. The rise of plants and their effect on weathering and atmospheric CO₂. *Science* 276:544–546.
- Berner, R. A. 2006. GEOCARBSULF: a combined model for Phanerozoic atmospheric O₂ and CO₂. *Geochimica et Cosmochimica Acta* 70:5653–5664.
- Berner, R. A., and K. Caldeira. 1997. The need for mass balance and feedback in the geochemical carbon cycle. *Geology* 25:955–956.
- Boyce, C. K., and J.-E. Lee. 2017. Plant evolution and climate over geological timescales. *Annual Review of Earth and Planetary Sciences* 45:61–87.
- Boyce, C. K., D. E. Ibarra, M. P. Nelsen, and M. P. D'Antonio. 2022. Nitrogen-based symbioses, phosphorus availability, and accounting for a modern world more productive than the Paleozoic. *Geobiology*. doi:10.1111/gbi.12519.
- Caplan, M. L., and R. M. Bustin. 1999. Devonian–Carboniferous Hangenberg mass extinction event, widespread oceanic-rich mudrock and anoxia: causes and consequences. *Palaeogeography, Palaeoclimatology, Palaeoecology* 148:187–207.
- Chen, B., J. Chen, W. Qie, P. Huang, T. He, M. M. Joachimski, M. Regelous, P. A. E. Pogge von Strandmann, J. Liu, X. Wang, I. P. Montañez, and T. J. Algeo. 2021. Was climatic cooling during the earliest Carboniferous driven by expansion of seed plants? *Earth and Planetary Science Letters* 565:116953.
- D'Antonio, M. P., D. E. Ibarra, and C. K. Boyce. 2020. Land plant evolution decreased, rather than increased, weathering rates. *Geology* 48:29–33.
- Decombeix, A.-L., B. Meyer-Berthaud, and J. Galtier. 2011. Transitional changes in arborescent lignophytes at the Devonian–Carboniferous Boundary. *Journal of the Geological Society, London* 168:547–557.
- De Vleeschouwer, D., M. Rakociński, G. Racki, D. P. G. Bond, K. Sobień, and P. Claeys. 2013. The astronomical rhythm of Late-Devonian climate change (Kowala section, Holy Cross Mountains, Poland). *Earth and Planetary Science Letters* 365:25–37.
- De Vleeschouwer, D., A.-C. Da Silva, M. Sinnesael, D. Chen, J. E. Day, M. T. Whalen, Z. Guo, and P. Claeys. 2017. Timing and pacing of the Late Devonian mass extinction event regulated by eccentricity and obliquity. *Nature Communications* 8:2268.
- Drever, J. I. 1994. The effect of land plants on weathering rates of silicate minerals. *Geochimica et Cosmochimica Acta* 58:2325–2332.
- Erwin, D. H. 1993. *The great Paleozoic crisis*. Columbia University Press, New York.

- Field, C. B., M. J. Behrenfeld, J. T. Renderson, and P. Falkowski. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281:237–240.
- Galtier, J., and B. Meyer-Berthaud. 2006. The diversification of early arboreous seed ferns. *Journal of the Torrey Botanical Society* 133:7–19.
- Gastaldo, R. A., R. Adendorff, M. Bamford, C. C. Labandeira, J. Neveling, and H. Sims. 2005. Taphonomic trends of macrofloral assemblages across the Permian–Triassic Boundary, Karoo Basin, South Africa. *Palaios* 20:479–497.
- Gastaldo, R. A., S. L. Kamo, J. Neveling, J. W. Geissman, M. Bamford, and C. V. Looy. 2015. Is the vertebrate-defined Permian–Triassic boundary in the Karoo Basin, South Africa, the terrestrial expression of the end-Permian marine event? *Geology* 43:939–942.
- Gillespie, W. H., G. W. Rothwell, and S. E. Scheckler. 1981. The earliest seeds. *Nature* 293:462–464.
- Heckman, D. S., D. M. Geiser, B. R. Eidell, R. L. Stauffer, N. L. Kardos, and S. B. Hedges. 2001. Molecular evidence for the early colonization of land by fungi and plants. *Science* 293:1129–1133.
- Holland, S. M. 1995. The stratigraphic distribution of fossils. *Paleobiology* 21:92–109.
- Holland, S. M. 2016. The non-uniformity of fossil preservation. *Philosophical Transactions of the Royal Society of London B* 371:20150130.
- Holland, S. M. 2020. The stratigraphy of mass extinctions and recoveries. *Annual Review of Earth and Planetary Sciences* 48:75–97.
- Holland, S. M. 2022. The structure of the nonmarine fossil record: predictions from a coupled stratigraphic-paleoecological model of a coastal basin. *Paleobiology* 48:372–396.
- Holland, S. M., and M. E. Patzkowsky. 2002. Stratigraphic variation in the timing of first and last occurrences. *Palaios* 17:134–146.
- House, M. R. 2002. Strength, timing, setting and cause of mid-Palaeozoic extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 181:5–25.
- House, M. R., and F. Gradstein. 2005. The Devonian Period. Pages 202–221 in F. Gradstein, J. Ogg, and A. Smith, eds. *A geologic time scale 2004*. Cambridge University Press, Cambridge.
- Hull, P. M. 2015. Life in the aftermath of mass extinctions. *Current Biology* 25:R941–R952.
- Hull, P. M., A. Bornemann, D. E. Penman, M. J. Henehan, R. D. Norris, P. A. Wilson, P. Blum, L. Alegret, S. J. Batenburg, P. R. Brown, T. J. Bralower, C. Cournede, A. Deutsch, B. Donner, O. Friedrich, S. Jehle, H. Kim, D. Kroon, P. C. Lippert, D. Lorocho, I. Moebius, K. Moriya, D. J. Peppe, G. E. Ravizza, U. Röhl, J. D. Schueth, J. Sepúlveda, P. F. Sexton, E. C. Sibert, K. K. Śliwińska, R. E. Summons, E. Thomas, T. Westerhold, J. H. Whiteside, T. Yamaguchi, and J. C. Zachos. 2020. On impact and volcanism across the Cretaceous–Paleogene boundary. *Science* 367:266–272.
- Ibarra, D. E., J. K. Caves Rügenstein, A. Bachan, A. Baresch, K. V. Lau, D. L. Thomas, J.-E. Lee, C. K. Boyce, and C. P. Chamberlain. 2019. Modeling the consequences of land plant evolution on silicate weathering. *American Journal of Science* 319:1–43.
- Isson, T. T., N. J. Planavsky, L. A. Coogan, E. M. Stewart, J. J. Ague, E. W. Bolton, S. Zhang, N. R. McKenzie, and L. R. Kump. 2020. Evolution of the global carbon cycle and climate regulation on Earth. *Global Biogeochemical Cycles* 34(2):e2018GB006061.
- Kaiser, S. I., M. Aretz, and R. T. Becker. 2015. The global Hangenberg Crisis (Devonian–Carboniferous transition): review of a first-order mass extinction. *Geological Society of London Special Publication* 423:387–437.
- Kennedy, M., M. Droser, L. M. Mayer, D. Pevear, and D. Mrofka. 2006. Late Precambrian oxygenation: inception of the clay mineral factory. *Science* 311:1446–1449.
- Kidwell, S. M., and S. M. Holland. 2002. The quality of the fossil record: implications for evolutionary analyses. *Annual Review of Ecology and Systematics* 33:561–588.
- Kirchner, J. W., and A. Weil. 2000. Delayed biological recovery from extinctions throughout the fossil record. *Nature* 404:177–180.
- Kump, L. R. 2014. Hypothesized link between Neoproterozoic greening of the land surface and the establishment of an oxygen-rich atmosphere. *Proceedings of the National Academy of Sciences USA* 111:14062–14065.
- Lenton, T. M., M. Crouch, M. Johnson, N. Pires, and L. Dolan. 2012. First plants cooled the Ordovician. *Nature Geoscience* 5:86–89.
- Lenton, T. M., T. W. Dahl, S. J. Daines, B. J. W. Mills, K. Ozaki, M. R. Saltzman, and P. Porada. 2016. Earliest land plants created modern levels of atmospheric oxygen. *Proceedings of the National Academy of Sciences USA* 113:9704–9709.
- Marshall, C. R. 1990. Confidence intervals on stratigraphic ranges. *Paleobiology* 16:1–10.
- Marshall, C. R. 1994. Confidence intervals on stratigraphic ranges: partial relaxation of the assumption of randomly distributed fossil horizons. *Paleobiology* 20:459–469.
- Marshall, C. R., and P. D. Ward. 1996. Sudden and gradual molluscan extinctions in the latest Cretaceous of western European Tethys. *Science* 274:1360–1363.
- Moulton, K. L., and R. A. Berner. 1998. Quantification of the effect of plants on weathering: studies in Iceland. *Geology* 26:895–898.
- Moulton, K. L., J. West, and R. A. Berner. 2000. Solute flux and mineral mass balance approaches to the quantification of plant effects on silicate weathering. *American Journal of Science* 300:539–570.
- Myrow, P. M., J. Ramezani, A. E. Hanson, S. A. Bowring, G. Racki, and M. Rakociński. 2014. High-precision U–Pb age and duration of the latest Devonian (Famennian) Hangenberg event, and its implications. *Terra Nova* 26:222–229.
- Nelson, M. P., W. A. DiMichele, S. E. Peters, and C. K. Boyce. 2016. Delayed fungal evolution did not cause the Paleozoic peak in coal production. *Proceedings of the National Academy of Sciences USA* 113:2442–2447.
- Patzkowsky, M. E., and S. M. Holland. 2012. Stratigraphic paleobiology: understanding the distribution of fossil taxa in time and space. University of Chicago Press, Chicago.
- Pawlik, L., B. Buma, P. Šamonil, J. Kvaček, A. Galazka, P. Kohout, and I. Malik. 2020. Impact of trees and forests on the Devonian landscape and weathering processes with implications to the global Earth's system properties—a critical review. *Earth-Science Reviews* 205:103200.
- Payne, J. L., D. J. Lehrmann, J. Wei, M. J. Orchard, D. P. Schrag, and A. H. Knoll. 2004. Large perturbations of the carbon cycle during recovery from the end-Permian extinction. *Science* 305:506–509.
- Peters, S. E., and J. M. Husson. 2017. Sediment cycling on continental and oceanic crust. *Geology* 45:323–326.
- Pier, J. Q., S. K. Brisson, J. A. Beard, M. T. Hren, and A. M. Bush. 2021. Accelerated mass extinction in an isolated biota during Late Devonian climate changes. *Scientific Reports* 11:24366.
- Pohl, A., Y. Donnadieu, G. Le Hir, J. F. Buoncristiani, and E. Vennin. 2014. Effect of the Ordovician paleogeography on the (in)stability of the climate. *Climate of the Past* 10:2053–2066.
- Prave, A. R., K. Kirsinmäe, A. Lepland, A. E. Fallick, T. Kreitsmann, Yu. E. Deines, A. E. Romashkin, D. V. Rychanchik, P. V. Medvedev, M. Moussavou, K. Bakakas, and M. S. W. Hodgskiss. 2021. The grandest of them all: the Lomagundi–Jatuli Event and Earth's oxygenation. *Journal of the Geological Society* 179:jgs2021-036.
- Rothwell, G. W., S. E. Scheckler, and W. H. Gillespie. 1989. *Elkinsia* gen nov., a late Devonian gymnosperm with cupulate ovules. *Botanical Gazette* 150:170–189.
- Royer, D. L., Y. Donnadieu, J. Park, J. Kowalczyk, and Y. Goddérès. 2014. Error analysis of CO₂ and O₂ estimates from the long-term

- geochemical model GEOCARBSULF. *American Journal of Science* 314:1259–1283.
- Scher, H. D., and E. E. Martin. 2006. Timing and climatic consequences of the opening of the Drake Passage. *Science* 312:428–430.
- Schindler, E. 1990. Die Kellwasser-Krise (hohe Frasn-Stufe, Ober-Devon). Selbstverlag der Geologischen Institute der Georg-August-Universität Göttingen, Göttingen.
- Sepkoski, J. J., Jr. 1998. Rates of speciation in the fossil record. *Philosophical Transactions of the Royal Society of London B* 353:315–326.
- Shukla, J., and Y. Mintz. 1982. Influence of land-surface evapotranspiration on the Earth's climate. *Science* 215:1498–1501.
- Signor, P. W., III, and J. H. Lipps. 1982. Sampling bias, gradual extinction patterns and catastrophes in the fossil record. In L. T. Silver and P. H. Schultz, eds. *Geological implications of impacts of large asteroids and comets on the Earth*. Geological Society of America Special Paper 190:291–296.
- Stein, W. E., C. M. Berry, J. L. Morris, L. V. A. Hernick, F. Mannolini, C. Ver Straeten, E. Landing, J. E. A. Marshall, C. H. Wellman, D. J. Beerling, and J. R. Leake. 2020. Mid-Devonian *Archaeopteris* roots signal revolutionary change in earliest fossil forests. *Current Biology* 30:421–431.e2.
- Urey, H. C. 1952. On the early chemical history of the Earth and the origin of life. *Proceedings of the National Academy of Sciences USA* 38:351–363.
- Walker, J. C. G., P. B. Hays, and J. F. Kasting. 1981. A negative feedback mechanism for the long-term stabilization of Earth's surface temperature. *Journal of Geophysical Research* 86:9776–9782.
- Wing, S. L., G. J. Harrington, F. A. Smith, J. I. Bloch, D. M. Boyer, and K. H. Freeman. 2005. Transient floral change and rapid global warming at the Paleocene–Eocene boundary. *Science* 310:993–996.
- Winnick, M. J., and K. Maher. 2018. Relationships between CO₂, thermodynamic limits on silicate weathering, and the strength of the silicate weathering feedback. *Earth and Planetary Science Letters* 485:111–120.
- Zachos, J. C., U. Röhl, S. A. Schellenberg, A. Sluijs, D. A. Hodell, D. C. Kelly, E. Thomas, M. Nicolo, I. Raffi, L. J. Lourens, H. McCarren, and D. Kroon. 2005. Rapid acidification of the ocean during the Paleocene–Eocene Thermal Maximum. *Science* 308:1611–1615.
- Zanon, M., B. A. S. Davis, L. Marquer, S. Brewer, and J. O. Kaplan. 2018. European forest cover during the past 12,000 years: a palynological reconstruction based on modern analogs and remote sensing. *Frontiers in Plant Science* 9:253.