Annual Review of Plant Biology

Paleobotany and Global Change: Important Lessons for Species to Biomes from Vegetation Responses to Past Global Change

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Abstract

Human carbon use during the next century will lead to atmospheric carbon dioxide concentrations ($pCO_2$) that have been unprecedented for the past 50–100+ million years according to fossil plant-based CO$_2$ estimates. The paleobotanical record of plants offers key insights into vegetation responses to past global change, including suitable analogs for Earth’s climatic future. Past global warming events have resulted in transient poleward migration at rates that are equivalent to the lowest climate velocities required for current taxa to keep pace with climate change. Paleobiome reconstructions suggest that the current tundra biome is the biome most threatened by global warming. The common occurrence of paleoforests at high polar latitudes when $pCO_2$ was above 500 ppm suggests that the advance of woody shrub and tree taxa into tundra environments may be inevitable. Fossil pollen studies demonstrate the resilience of wet tropical forests to global change up to 700 ppm CO$_2$, contrary to modeled predictions of the future. The paleobotanical record also demonstrates a high capacity for functional trait evolution as an additional strategy to migration and maintenance of a species’ climate envelope in response to global change.

Keywords

CO$_2$, polar amplification, migration, adaptation, resilience, leaf traits, extinction, leaf mass per area, paleoclimate, paleoatmosphere
INTRODUCTION

Paleobotany is the study of fossil plants in deep geological time. It is concerned with the history of the Earth’s vegetation on evolutionary time scales, encompassing on a global scale both long periods of relative climatic stability and episodes of intense atmospheric and climatic upheaval. During Earth’s geological history, there have been many episodes of global climate change that were of a similar magnitude to the anthropogenically forced climate change that has occurred during the past century. Equally, there are climatic and atmospheric events in the pre-Quaternary past that have been identified as good analogs of Earth’s climatic future under a doubling of atmospheric carbon dioxide concentrations ($p$CO$_2$) and our aspirational global warming target of no more than 2°C above preindustrial temperatures. What the paleobotanical record offers in abundance to the study of global change is the dimension of time coupled with a combined set of Earth system boundary conditions, which are more representative of our climate future than any interval during the past approximately 2 million years (the Quaternary period). However, the limitation of using the pre-Quaternary climate record to better understand biological response to global change is also related to time. The temporal resolution available in the geological record of fossil plants is on the order of tens of thousands of years at best, but more often, it is on the order of hundreds of thousands to millions of years. Therefore, the paleobotanical record is imperfect, as it offers a window onto individual species, communities, and biome-level responses to global change, in particular to elevated CO$_2$ and global mean surface terrestrial temperature, yet this view is blinkered by irregular snapshots taken every 10,000 to 100,000 years. This review synthesizes studies in paleobotany that provide important insights into plant and vegetation responses to past global change, from the species to the biome scale, with a particular focus on times in Earth’s history that represent climatic transitions from icehouse to greenhouse states and from mild greenhouse to super-greenhouse states, as it is these intervals that are most representative of Earth’s climate future.

GEOLOGICAL CONTEXT FOR CONTEMPORARY GLOBAL CHANGE

The primary drivers of climatic change on a global scale are solar forcing, atmospheric composition, plate tectonics, and the Earth’s biota (25, 56, 129). The relative position of Earth in
relation to the sun and the age of the sun (51) determines the total solar irradiance at any point in Earth’s geological history. On geological timescales, atmospheric composition is determined by the carbon, oxygen, sulfur, and phosphorous cycles (16, 18), and how they are influenced by Earth system processes. Constituents of the atmosphere that have changed dramatically on geological timescales include CO₂ and O₂, both of which force global climate (116, 129). In the geological past, intense episodes of global cooling and warming have been linked, respectively, to the massive release of SO₂ from volcanism (158) and CH₄ from marine clathrates (70, 91), and thermogenically to volcanic intrusions (59, 152). These gasses, too, have shaped global climate and had an impact on Earth’s biota, particularly at faunal mass-extinction boundaries (99, 159), but on much shorter timescales than CO₂ and O₂. Both SO₂ and CH₄ are relatively short lived in the atmosphere; SO₂ rains out within years of release and CH₄ is highly unstable, soon oxidizing to CO₂, but both have left their signatures in the fossil record of plants via isotopic (133) and physiognomic and cellular signatures in leaves (4, 44). However, they are not considered further in this review. Perhaps the most valuable understanding that has come from a deep-time perspective on global climate change is that current Earth system models likely underestimate the sensitivity of the global mean temperature to atmospheric CO₂ (52, 129). Climate sensitivity refers to the change in global mean temperature in response to a doubling of CO₂ over the preindustrial concentration of 280 ppm (113). Most climate and Earth system models use a climate sensitivity of approximately 3 Kelvin (reviewed in 129); however, analyses of climate sensitivities on longer geological timescales have concluded that these sensitivities are likely to be underestimated when considering global temperature and proxy or model CO₂ estimates for greenhouse intervals in the geological past (52, 129). This is of considerable concern for policy-makers because knowledge of the deep-time record argues for much more severe increases in future global temperature than any current climate model predicts under a doubling of CO₂. According to Foster et al.’s (52, p. 1) assessment of greenhouse forcing through time, “If CO₂ continues to rise further into the twenty-third century, then the associated large increase in radiative forcing, and how the Earth system would respond, would likely be without geological precedent in the last half a billion years.”

**VASCULAR PLANTS AND ATMOSPHERE EVOLUTION**

Broadly, the evolution of vascular plants during the past 420 million years can be subdivided into three distinct evolutionary phases: Paleophytic (old plants), Mesophytic (middle plants), and Cenophytic (young plants). The evolutionary phases are temporally offset to those of the evolutionary faunas that define three stratigraphic eras: Paleozoic, Mesozoic, and Cenozoic, which subdivide the Phanerozoic Eon (155, 166). Plant extinctions at the taxonomic levels of family and order do not coincide with all of the faunal mass-extinction boundaries that characterize the start and end of eras and tend to be more protracted in their nature and more difficult to pinpoint in geological history (30, 99). Traditionally, the evolutionary floras defined intervals of reproductive dominance (30, 110).

Paleophytic ecosystems are typically dominated by vascular spore-bearing plants (pteridophytes), including extant lineages such as lycophytes and monilophytes (ferns and Equisetales) and extinct groups, such as progymnosperms. The Mesophytic era ushered in the dominance of seed-over spore-based reproduction for the first time, with gymnosperms typically having greater relative abundance in fossil floras than pteridophytes. Extant gymnosperm lineages that had an important role in the Mesophytic era include conifers, cycads, and ginkgos. Finally, the Cenophytic era represents a time in Earth’s history when flowering plants (angiosperms) underwent rapid diversification and became dominant within terrestrial ecosystems, ultimately giving rise to the modern flora. It is now recognized that plant evolutionary eras are not only characterized by

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**Clathrate**: an ice-like solid compound composed of methane trapped in the crystal structure of water

**Thermogenesis**: the process by which hydrocarbon gasses, including methane, are released from kerogens or organic-rich sediments due to high temperatures and pressure

**Physiognomy(ic)**: the architecture of a leaf, including shape traits of the leaf base, tip and margin, characteristics of venation, and leaf size

**Paleophytic**: the time in geological history when spore-bearing vascular plants (pteridophytes) were ecologically dominant in the majority of terrestrial ecosystems; often considered from mid-Silurian to late Carboniferous

**Mesophytic**: the time in geological history when nonangiosperm seed plants (gymnosperms) were ecologically dominant in most terrestrial ecosystems; usually considered from late Carboniferous to mid-Cretaceous
Cenophytic: the time in geological history when angiosperms were ecological dominant; usually considered from mid-Cretaceous to present
Monilophytes: spore-bearing plant evolutionary group comprising all ferns, horsetails, and whisk ferns
Progymnosperms: an extinct group of woody spore-bearing plants from which all seed plants likely arose
Pennsylvanian: a subperiod of the Carboniferous dating between 323.2 and 298.9 Mya according to the International Commission on Stratigraphy

The Paleophytic era of plant evolution occurred against a backdrop of strongly fluctuating atmospheric CO₂ and global climate at multiple different temporal scales. The earliest vascular plants belonging to the Paleophytic era evolved approximately 423 Mya (139) in an atmosphere of strongly elevated CO₂ that was more than 10 times higher than preindustrial levels (57, 95, 126), which then declined by the Carboniferous to levels similar to those of our contemporary icehouse world (10, 106), as plant diversity and geographical coverage increased (Figure 1). In turn, the radiation of land plants resulted in increased carbon sequestration through the chemical weathering of silicates and the burial of organic matter in the great coal swamps of the Carboniferous (3, 106). New high-resolution, multiproxy records for the late Pennsylvanian document glacial–interglacial atmospheric [CO₂] fluctuations of between approximately 200 and 800 ppm, which coincided with ice sheet contraction and expansion and resultant sea level rise (106). In large part, the Mesophytic era was characterized by CO₂ concentrations above 500 ppm (11, 12, 29, 43, 57, 94, 100, 114, 124, 145, 151, 178) and as high as 2,000 ppm or greater at the boundary of the Triassic and Jurassic periods (23, 135, 143, 177). The Cenophytic era was characterized by a pattern of long-term decline in CO₂ and by global cooling leading to our current icehouse conditions (Figure 2) (7, 52, 57, 63, 65, 68, 82, 93, 119, 122, 132, 140, 144, 149, 160, 162, 180). It has been suggested that the evolution and rise to ecological dominance of flowering plants may have contributed to the long-term decline in CO₂ of the Cenophytic by increasing carbon sequestration through impacts on the long-term carbon cycle (17); however, this hypothesis has not been rigorously tested and, therefore, remains speculative. CO₂ was not the only atmospheric constituent gas to change dramatically throughout Earth history; O₂ likely also fluctuated wildly, according to some models (16, 19, 61, 105) from lows of <10% to peaks as high as 30%. O₂ has an important role in forcing global climate (116) and likely plant evolutionary patterns as well (67, 166, 179). However, as it will not change considerably during the next two centuries, only CO₂ and its impact on plant biology are considered in this review.

THE FOSSIL PLANT RECORD AND PAST GLOBAL CHANGE
The Earth’s vegetation has undoubtedly been shaped by climatic and atmospheric evolution during millions of years of geological time. Climate, specifically the mean annual temperature (MAT) and mean annual precipitation (MAP), defines the geographical extent of our modern biomes and plays a fundamental part in defining the ecological niche of species. Often, views of the vegetated Earth
Figure 1
Time line of plant evolution demonstrating the estimated first occurrences of major plant groups (bryophytes, based on the time of origin of land plants, >450 Mya (139); pteridophytes, based on the time of origin of vascular plants, 433.5 Mya (139); gymnosperms, based on the time of origin of seed plants, 373.8 Mya; angiosperms, 143.8 Mya (139); and grasses, 65 Mya (148)), biomes through time (166), and the timing of the phases of plant evolutionary floras (Paleophytic, Mesophytic, and Cenophytic), modified from Reference 30. Plant illustrations from Reference 166 by Marlene Hill-Donnelly; used with permission. Geological timescale from the 2013 update by the International Commission on Stratigraphy. Abbreviations: Mio., Miocene; O., Oligocene; P., Paleocene.
McElwain & Chaloner, 1995; 407 to 400 Mya (1)
Franks et al., 2014; 409 to 13 Mya (15)
Roth & Konrad, 2003; 409 Mya (1)
Beierling, 2002; 324 to 270 Mya (24)
Montanez et al., 2016; 312 to 303 Mya (25)
McElwain et al., 1999; 202 to 199 Mya (8)
Steinthorsdottir et al., 2011; 202 to 199 Mya (17)
Beierling et al., 1998; 205 to 168 Mya (4)
Wu et al., 2016; 205 to 171 Mya (3)
Bonis et al., 2010; 203 Mya (1)
Chen et al., 2001; 187 to 135 Mya (3)
Steinthorsdottir & Vajda, 2015; 186 Mya (1)
Sun et al., 2007; 186 to 139 Mya (7)
McElwain et al., 2005; 183 to 182 Mya (6)
Beierling & Royer, 2002; 168 Mya (1)
Yan et al., 2009; 168 Mya (5)
Haworth et al., 2005; 133 to 104 Mya (9)
Du et al., 2016; 121 to 112 Mya (1)
Passalia, 2009; 121 to 101 Mya (16)
Mays et al., 2015; 97 Mya (1)
Barclay et al., 2010; 94.5 to 93.9 Mya (17)
Quan et al., 2009; 81 to 72 Mya (9)
Steinthorsdottir et al., 2016b; 57 to 60 Mya (4)
Beierling et al., 2002; 66 to 63 Mya (5)*
Royer, 2003; 61 to 54 Mya (2)*
Royer et al., 2000b; 60 to 15 Mya (24)*
Smith et al., 2010; 50 Mya (3)
Greenwood et al., 2003; 49.9 Mya (9)
McElwain, 1999; 47.8 to 44.5 Mya (5)
Grein et al., 2011; 47 Mya (1)
Kürschner et al., 2001; 44.5 Mya (1)
Maxbauer et al., 2014; 43 Mya (1)
Doria et al., 2011; 38 Mya (1)
Steinthorsdottir et al., 2016a; 36 to 23 Mya (5)
Roth-Nebelsick et al., 2012; 25 Mya (1)
Grein et al., 2013; 33 to 17 Mya (6)**
Roth-Nebelsick et al., 2014; 33 Mya (1)
Erdei et al., 2012; 30 Mya (5)
Sun et al., 2017; 28.5 Mya (1)
Kürschner et al., 2008; 26 to 12 Mya (18)*
Reichgelt et al., 2016; 23 Mya (2)
Wang et al., 2015; 13.8 to 1 Mya (7)
von der Burch et al., 1993; 10 to 2 Mya (5)***
Wan et al., 2011; 8.5 Mya (3)
Stults et al., 2011; 8.3 to 6.1 Mya (2)
Kürschner et al., 1996; 6.6 to 2.8 Mya (4)
Retallack, 2009a; 233 to 3.9 Mya (17)

Caption appears on following page
Figure 2. (Figure appears on preceding page)
(a) A record of atmospheric carbon dioxide concentration (\(pCO_2\)) in parts per million (ppm) during the Phanerozoic based on 47 independent, stomatal-based \(pCO_2\) proxy studies (7, 10, 12, 14, 21, 29, 34, 42, 43, 46, 52, 57, 65–67, 68, 82, 83, 92–95, 100, 106, 114, 119, 122, 123, 125–128, 132, 135, 140, 141–145, 149–151, 160–162, 177, 178, 180). See Reference 52 for a compilation of raw data from all of these studies, with the exception of 106, which is added here to produce the Lowess regression (heavy blue line) and upper and lower uncertainty bounds. The number in parentheses after each citation refers to the number of \(pCO_2\) estimates generated from each study together with the age range of fossils used to reconstruct \(pCO_2\). Asterisks indicate use of updated data: single asterisk (*) for data updated by Beerling et al. (2009); double asterisk (**) for data updated by Roth-Nebelsick et al. (2004); and triple asterisk (***) for data updated by Kürschner et al. (1996). Blue dots represent mean \(pCO_2\) levels from individual studies listed in the figure. Small green dots represent the minimum and maximum \(pCO_2\) estimates from the same studies. The inset graph plots the projected \(pCO_2\) rise during the next two centuries based on different Representative Concentration Pathways (RCPs) (104) with the anticipated rise in global mean temperature (113). Red boxes highlight the intervals that are a focus of this review. (b) Paleogeographic maps illustrate the occurrence of fossil plant localities (colored dots) possessing evidence for woody fossil taxa (tracheophytes) in time and space derived from the Paleobiology Database (https://paleobiodb.org). Occurrence data were plotted using the Paleobiology Database on June 15, 2017, using the group name tracheophyta. Note the high proportion of exceptionally high-latitude sites with trees through time. Inset graph in panel a has a noncontinuous scale. Abbreviation: Mya, million years ago.

and how it will respond under anthropogenic global change are biased by a contemporary-only view that has insufficient consideration for deep evolutionary history. However, because our climate future will likely be more similar to the Eocene of approximately 50 Mya or stages within the Jurassic or Cretaceous (203 to 65 Mya), it has been argued that we should look back and have greater appreciation for the origin of the modern flora. Many in-depth reviews (25, 30, 99, 139) and books (31, 35, 147, 154) have been dedicated to paleobotany and the evolution of plants. The aim of this section is to provide a brief overview of the past 420 million years of vascular plant evolution that have relevance for, and should be considered in the context of, vegetation responses to contemporary global change. The following six lessons have been gleaned from the deep-time fossil record.

1. All living species, with the exception of those that originated during the past century, naturally or through human intervention, have survived an approximately 20-million-year window of time when the atmospheric \(CO_2\) concentration has been at its lowest level (less than approximately 300 ppm)—that is, during the past 304 million years since the Late Pennsylvanian ice age (Figures 1 and 2). Unsurprisingly, this 20-million-year window of low atmospheric \(CO_2\) was accompanied by the lowest mean global temperatures recorded during the past 400 million years (52, 180). Therefore, our contemporary global flora are adapted to low \(CO_2\) in relative terms and, remarkably, have survived global cooling and declines in atmospheric \(CO_2\) since the Eocene–Oligocene boundary (approximately 34 Mya.) without exceeding normal background levels of extinction (99, 117, 166). This suggests that the vast majority of plant species are resilient and adaptable to climate and atmospheric changes, given sufficient time.

2. Among modern flora are families, genera, and species that have exceptionally long evolutionary histories dating back to the Mesophytic era of plant evolution (Figure 1) when elevated \(CO_2\) and equable global temperatures prevailed (Figure 2). These are predominantly vascular seed plants within the gymnosperms. However, this grouping also includes vascular spore-bearing taxa, which although they may have originated during the icehouse climate of the Carboniferous and early Permian, are lineages that have survived up to the present. All these lineages experienced nearly 230 million years of Earth’s history when \(CO_2\) was considerably elevated above present levels (e.g., > 500 ppm). Thus, despite the fact that all of the longest-lived lineages have survived the past 20 million years of relatively low \(CO_2\), they are likely more adapted to a high \(CO_2\) atmosphere, such as that predicted to occur during the next few centuries, than are very recently evolved lineages (such as many angiosperms) that lack the
Genetic memory of super-greenhouse conditions. It is highly likely that many gymnosperms and pteridophytes with the oldest geological origins are preadapted to our climate future (45, 102, 179). These include taxa in which the carbon assimilation rates today (<400 ppm) are strongly limited by CO₂ diffusion from the atmosphere to the site of carboxylation at the chloroplast, due to either low stomatal or mesophyll conductance (102, 108, 109). Both theoretical studies (109) and experimental observations (102) project that diffusion-limited taxa will benefit more significantly from future increases in CO₂ and will have strong increases in carbon assimilation rates than those with high stomatal or mesophyll conductance.

3. The grass family, Poaceae, to which all grass-based food crops (such as wheat, barley, and rice) belong, originated relatively recently, approximately 65 Mya during the Late Cretaceous (148). Grass-dominated biomes—such as steppes, prairies, and savannahs—have an exceptionally recent origin in the context of land plant evolution, expanding globally in the majority of continents during the Late Eocene to Oligocene (<35 Mya) (148), concurrently with falling CO₂ levels (Figure 2 and references therein), declining global temperature, and increasing continental aridity. Therefore, in relative terms and in the context of long-term climatic and atmospheric history, the evolutionary success of grasses occurred under the declining atmospheric CO₂ that led to our current icehouse. Prior to the origin of grass-dominated ecosystems, savannahs of pteridophytes (ferns and Equisetales) prevailed where climate conditions did not support fully wooded vegetation.

4. It is clear from a wealth of paleobotanical studies (69, 97, 120, 121, 148, 166) that paleobiomes have waxed and waned in lockstep with global climate over geological time (Figure 1). A few observations from these studies stand out. First, during times of high atmospheric CO₂ concentrations and global warmth, the temperature gradient between the equator and pole is shallow (Figure 3), which results in fewer (<5) distinct vegetation biomes compared with today’s 10 biomes in an icehouse climate (Figure 1). Second, based on current understanding of atmospheric composition using stomatal proxy records, it appears that a tropical rainforest biome was absent from the low latitudes when atmospheric CO₂ was higher than approximately 700 ppm (Figures 1 and 2, and references therein). According to the future carbon use projections in Representative Concentration Pathway (RCP) 6, CO₂ will reach 700 ppm by 2150, and RCP 8.5 projects that this level will be reached well within this century (Figure 2) (113). Further paleobotanical studies are urgently required to establish whether such an apparent CO₂ threshold for the existence of a tropical everwet biome (tropical rainforest) is robust or whether its absence for much of the Mesophytic was due to the fact that the traits that are used to define our understanding of a modern tropical rainforest, such as high leaf-vein density (25), had not yet evolved in the gymnosperm-dominated taxa of the Mesophytic. Alternatively, there is also a chance that a tropical rainforest biome was present in the Mesophytic but remains undetected because of an absence of fossils, localities, or both in the low tropical latitudes (Figure 2) or because existing fossil plant assemblages have been wrongly classified in terms of their biome characterization.

Palynological (or palynomorph, meaning pollen and spore) studies of low-latitude tropical rainforests with modern characteristics have shown that they date back to the Paleocene (75, 78, 174). It appears that these forests survived the extreme global warming event of approximately 5 to 8°C MAT during more than 200,000 years at the Paleocene–Eocene thermal maximum (PETM) (103) 56 Mya, with little evidence of extinction, but instead showed a strong signal of resilience. In the tropics of Colombia and western Venezuela, a palynological study suggested that tropical rainforest vegetation increased diversity in response to global warming at the PETM (76). This finding strongly contradicts
Figure 3

(a) Comparison of modern (blue dashed line) versus Eocene (red solid line) model of the mean annual temperature (MAT) profile from Huber & Caballero (73), demonstrating the marked polar amplification of MAT under an extreme Eocene CO₂ greenhouse forcing of >4,000 ppm. Eocene MAT records according to latitude are based on paleo MAT proxy data compiled by Huber & Caballero (73). Forcing the model with >4,000 ppm is currently the only mechanism for achieving a good match between data and model, suggesting that the climate sensitivity of current Earth system models is not sufficiently sensitive to CO₂ (52) or that other greenhouse forcing variables that are not included, such as methane or water vapor, had important roles in equable Eocene climates. (b) There is generally good agreement between proxy data and model estimates of MAT when a high CO₂ forcing of 4,000 ppm is used. (c) The reconstruction of a high-latitude (75 to 80°N) Eocene-aged *Metasequoia glyptostroboides* forest is based on fossil tree stumps found in situ on Axel Heiberg Island, Canada, from Reference 165. Fossil forests at two nearby sites were discovered, including a slightly older forest (fossil forest 1) and a slightly younger forest (fossil forest 2). Adapted with permission from References 165 and 73.

future-model projections of ecosystem collapse in the tropics (33). The record of atmospheric CO₂ change associated with this warming event remains unconstrained, however, so it cannot yet be determined whether 700 ppm (Figure 1) is a CO₂ threshold for tropical rainforest survivability.

5. The tundra biome was absent for much of Earth’s vegetated history (Figure 1). This startling observation will be elaborated on in further detail in the section Polar Amplification and Past Vegetation Responses.
6. Finally, the current differentiation of biomes into 10 distinctive vegetation units is a distinctly modern phenomenon that likely had its origin in the Miocene, only 11 Mya (Figure 1) (166).

**POLAR AMPLIFICATION AND PAST VEGETATION RESPONSES**

Greenhouse gas–induced global change will not result in equivalent warming levels in all parts of the world. Due to a phenomenon referred to as polar amplification, the Earth’s poles have warmed (72) and will continue to warm at a faster rate and reach a higher magnitude of relative warming than the average planetary warming (138). This is because heat is readily transported poleward by oceans and the atmosphere due to positive feedback effects involving snow cover, albedo, vegetation, soot, and algal cover in the Arctic and Antarctic, and to many other Earth system phenomena that appear to amplify polar warming as the greenhouse gas concentration in the atmosphere rises (for a detailed review, see 138). The question is, Will global change have a disproportionate impact on plant biology, ecosystem function, ecology, and feedback in the highest latitudes of our planet due to the phenomenon of polar amplification?

Recent, historical satellite data sets document the greening of the tundra biome (79), the range expansion of woody shrub (107) and tree taxa (reviewed in 28) into tundra systems, and a general increase in woody plant biomass and relative abundance (107). Considerable scientific effort is focusing on how such vegetation changes will feed back to the Arctic climate system via changes in carbon sequestration and the water cycle and changes to surface irradiance (reviewed in 107). Increasing shrubiness has likely already had an unexpected negative impact on herbivore populations, such as caribou, by decreasing browse quality (48). Furthermore, field-based evidence for woody plant responses to amplified Arctic warming is not all positive. Reduced tree growth has been observed for some taxa due to drought-induced stress (6) and negative biotic interaction, such as bark beetle infestation. Satellite normalized difference vegetation index data have recorded areas of browning that indicate productivity loss as well as greening in Arctic vegetation (79). Furthermore, a large percentage of Arctic vegetation among all plant functional types has shown no perceptible change in productivity in response to contemporary global change (79). Owing to the fact that shifts in ecological composition, the ecophysiological function of vegetation, or both can have a large impact on the climate and on the biotic system as a whole, it is important to predict whether short-term temporal trends in Arctic vegetation change will continue under CO₂-induced global warming. The paleobotanical record of high Arctic floras may provide broad insight into these questions.

The geological record is replete with high polar fossil floras demonstrating fully wooded ecosystems at paleolatitudes as high as 79°N (62, 142, 163, 165) and 75°S (36, 47, 53, 80, 115, 118), ranging in age from 290 Mya in the Permian Antarctic (153) to approximately 23 Mya (early Miocene) in the Arctic (71) and to approximately 37 Mya in the Antarctic (late Eocene) (Figure 2) (156). Collectively, these polar fossil forests demonstrate that fully wooded terrestrial ecosystems with tree densities similar to modern forests, occurring today at temperate and tropical latitudes (115, 165), can be sustained in the high Arctic and Antarctic when the global atmospheric CO₂ concentration is >500 ppm (Figure 2 and references therein) and greenhouse-induced forcing of 5 W/m² is evident (52). The presence of high-latitude forests in the geological past also highlights the extreme vulnerability of the contemporary tundra biome, which is notable for its apparent absence for millions of years of Earth history during times of high global warmth and elevated CO₂ concentrations (Figures 1 and 2). Based on biome reconstructions (Figure 1) (166) and the documented presence of polar forests (Figure 2), it appears that the tundra biome as defined today did not exist for the majority of the Mesophytic era of vascular plant evolution and the early
Cenophytic up to the time of the inception of Antarctic ice sheets at around the Eocene–Oligocene boundary, approximately 34 Mya (180).

Paleobotanical studies have demonstrated that during the early Eocene (56 to 49 Mya), a time of peak sustained global warmth during the past 65 million years (Figure 3) (73), the Arctic Ocean was ice free (Figure 1) and fringed by a mosaic of mixed deciduous (Carya, Liquidambar, Ulmus, Larix), evergreen (Picea, Pinus), and swamp (Metasequoia, Glyptostrobus) forests (62), and teeming with high densities of the aquatic fern Azolla (8). Estimated canopy heights of between 25 and 40 m have been reconstructed for Metasequoia forests at 79°N, with aboveground paleoproductivity estimates ranging from 2.8 to 5.5 Mg/(ha·year) (Figure 3), which is thought to be similar to that observed today in old growth temperate rain forests in the north Pacific (165). The presence of Azolla is attributed to high levels of runoff into the Arctic Ocean resulting in a sufficient freshening of the seawater or the development of a freshwater cap suitable for its survival and proliferation (27, 32). Substantially higher precipitation in the Arctic than modern levels is also supported by isotopic analyses of fossil tree rings (136) and leaf physiognomy studies (163), although the definition of the seasonal pattern of rainfall remains disputed—that is, whether it was predominantly summer wet (136) or year round (163). The eventual demise of Azolla in the Arctic Ocean is attributed to reduced runoff and a slight salinity increase (8).

The presence of a freshwater fern in the Eocene Arctic Ocean is a remarkable demonstration of the possible consequences of global change in Arctic terrestrial ecosystems and of threshold behavior linking terrestrial and ocean systems via runoff (27). Numerous Earth system models predict increased global runoff under future elevated concentrations of CO₂ as a direct response to reduced transpiration of global vegetation (60). Although the Eocene Azolla studies have not considered that physiological forcing of the climate by Arctic vegetation affected fluctuations in runoff and, instead, attributed changes to altered precipitation patterns and amount alone, such a study is warranted and possible through the examination of fossil cuticle archives in Arctic fossil floras. Such studies are discussed later in this review, with a case example from the late Triassic mass-extinction event (approximately 200 Mya). An interesting side note is that Azolla is now considered a potential candidate taxa for negative carbon emission measures because of its phenomenal growth rate and carbon sequestration potential.

Based on overwhelming paleobotanical evidence, it is highly likely that the current northward migration of woody tree and shrub taxa into the Arctic, along with the general greening (reviewed in 28, 107), will continue and, in doing so, will drive positive feedback of the climate system that will further accelerate the warming and wetting of the Arctic (74, 163). In the past, high polar forests had carbon sequestration potentials (13, 115, 131, 165) equivalent to those of the much lower temperate latitudes, and they impacted the hydrological cycle sufficiently to alter ecological dominance patterns within oceans (8, 27). These findings from paleobotanical studies suggest that the role of Arctic vegetation in the global biogeochemical cycling of water and carbon will become increasingly important if we continue on a path of intense petroleum use.

PAST GLOBAL CHANGE AND IMPACTS ON PLANT COMMUNITY COMPOSITION

Future global change is predicted to alter the ecological composition of plant communities because species are highly individualistic in their responses to climate change. Species differences in migration rate, invasive capacity, resilience in the face of climate change, and extinction tolerance will all result in the emergence of plant communities that have no past or modern analogs and that occupy climate envelopes or niches that may not have a historical or modern precedent. What will these future communities look like? This complex question can be addressed using different
Free-air CO₂ enrichment (FACE): in situ open-air elevated CO₂ experiments where mature established native vegetation or crops are exposed to elevated CO₂ treatments over long durations and compared with ambient CO₂ controls.

Extinction, Migration, and Past Global Change

The deep-time fossil record paints a picture of remarkable resilience in the face of extreme climate change that surpasses in magnitude both contemporary and future predicted mean global terrestrial temperature rises (76, 99, 166, 170). However, one important distinction is that the rate of anthropogenic climate change far exceeds that of any well-characterized greenhouse-induced global warming event in the deep geological past. Plant family- and generic-level extinctions are rare in the fossil record even at the big five mass extinction boundaries, which recalibrated the evolutionary clock of the animal kingdom with family-level extinctions of more than 50% (166). Some of the best-studied intervals of global change in the fossil plant record include the Triassic–Jurassic boundary, 201.36 ± 0.17 Mya (175); the PETM, 56 Mya; and the Eocene–Oligocene boundary, 33.9 Mya. The first two events represent rapid greenhouse gas–induced global warming episodes; the last coincides with the initiation of the Antarctic ice sheet and global cooling leading to our current icehouse. Therefore, I focus on the first two events and the common patterns that have emerged from studying them, despite the fact that they are separated by millions of years of plant evolution and, thus, are characterized by vastly different phylogenetic landscapes from each other and from the modern world.

Analyses of the Triassic–Jurassic boundary and the PETM have documented clear evidence of local extinction, but not global extinction, and both intra- and intercontinental-scale migration resulting in dramatically altered plant community composition and dominance patterns (76, 90, 98, 103). During the PETM, compositional shifts in terrestrial vegetation were marked but transient in temperate latitudes (103) and long-lived in the tropics (76). High temperatures and likely increased aridity in the North American temperate biomes resulted in geologically rapid compositional changes as local mixed deciduous and evergreen forest taxa—such as Betula, Laurus, Ulmus, Cercidiphyllum, Carya, and Taxodium—decreased in relative abundance, and southern subtropical Leguminosae expanded their range northward by up to 1,000 km (103). A somewhat surprising finding in the tropics was an increase in standing diversity as global temperatures rose by 5°C within 10,000 to 20,000 years but tropical precipitation remained at least stable, resulting in only muted levels of extinction and a large increase in originations (103). However, despite low extinction rates, significant compositional shifts are evident in the tropical pollen and spore records at the PETM (76) and during the End-Triassic (90). These paleo examples strongly suggest that global warming has a marked effect on the composition of terrestrial plant communities that is driven predominantly by migration rather than extinction. Admittedly, it is difficult to draw parallels with Anthropocene warming and vegetation responses because they are occurring at a minimum of 20 times faster than any past warming episode in Earth’s history (reviewed in 40). A rough comparison of climate velocities (the distance per unit of time that a species needs to migrate to keep within its existing climate envelope) for the PETM (0.05 to 0.1 km/year, based on...
and that predicted for the end of this century under an RCP 8.5 scenario (0.5 to 128 km/year (40, 88)) identifies a stark mismatch between what the fossil record demonstrates is possible and what future predictions indicate will be necessary for taxa to remain within their climate niches. Closer examination of an alternative future scenario with less elevated CO₂ concentrations (and climate velocities of 0.01 to 12 km/year) (40, 88) provides some hope, however, as PETM climate velocities at least map onto the lower range of future predictions.

Paleobotany, Adaptation, and Past Global Change

Plants have alternative strategies for surviving global change beyond migrating and maintaining their existing climate envelope, including acclimation and adaptation. However, investigating the adaptive capacity of individual species is complex because it requires observations of multiple generations and, therefore, requires experiments of long duration, which are rarely feasible. Alternatively, space-for-time studies are often employed using the spatial gradients in MAT, MAP, or both as surrogates for climate change; however, these studies are limited because they cannot account for the impact of anthropogenic CO₂ rise. Paleobotanical studies offer a means of examining plants’ capacity to adapt to global change on timescales of tens of thousands to millions of years and, perhaps more importantly, help to define the limits of species’ environmental tolerance in the geological past. An important set of prerequisites for such fossil-based studies is that (a) the magnitude and pace of paleoenvironmental change is well characterized from plant-based proxies and independently verified with nonplant-based proxy approaches so that circularity is avoided, and (b) multiple fossil plant beds are preserved in the same geological sections, thus offering regular snapshots of plant community composition, paleophysiology, and diversity from before, during, and after the global change interval. Such fossil localities provide rare study systems where species-, generic-, and community-level attributes that provide measures of ecosystem stability and resilience can be tracked in response to past global change. They can also be examined to elucidate traits that increase extinction risk and those likely to confer resilience in the face of global change, both of which may have relevance for current conservation efforts. One study system that has yielded a wealth of data relevant to contemporary issues of climate change and vegetation responses occurs at a field locality called Astartekløft in East Greenland. This fossil plant locality preserves sediments and fossil plant beds within the Kap Stewart Group that span the End-Triassic mass extinction event (ETE) and the ensuing recovery interval that occurred in the Earliest Jurassic (Figure 2).

The End-Triassic Mass Extinction Event

The ETE, dated at 201.56 Mya (175), was the third greatest faunal mass extinction event in Earth’s history (137). It is characterized by an episode of intense CO₂-induced global warming (98) that was triggered by both intrusive and extrusive volcanism (reviewed in 38) associated with the Central Atlantic Magmatic Province. Atmospheric CO₂ and global temperature changes associated with the ETE are well characterized from multiple proxy sources, and they document a geologically rapid trebling of CO₂ concentrations from pre-excursion levels of approximately 600 ppm to levels >2,000 ppm (Figures 2 and 4) (23, 94, 135, 143, 177). These paleo CO₂ estimates were made using the stomatal-based proxy method applied to Triassic and Jurassic fossil cuticles from Greenland (94, 143), Sweden (94), Germany (23), Northern Ireland (143), and China (177), and they were independently verified from fossil soil–based proxies (135). The End-Triassic global change event occurred at a substantially slower pace than contemporary anthropogenic CO₂ increases, and it was initiated at a time when the pre-excursion atmospheric CO₂ concentration was higher than
Figure 4
Compilation of global change and biological responses recorded at Astartekloft, East Greenland, associated with the End-Triassic extinction event. (a) CO₂ change (pCO₂) (143). CO₂ estimates based on calibrations using a transfer function of Barclay & Wing (2016) (gray triangles) and the Carboniferous standardization (gray diamonds) and recent standardization (gray squares) of McElwain (1998). (b) Plant compositional response as indicated by detrended correspondence analysis (DCA) axis 1 scores from relative abundance data (98) (green diamonds). Note that the numerical scale plots fossil plant communities (assemblages), which are compositionally similar in terms of their relative abundance distributions, closely together and those that are compositionally distinct further apart. (c) Plant migration responses in relation to paleolatitude (°N) (98) (brown diamonds) and plant generic diversity trends (blue squares) based on relative abundance distributions of fossil plant taxa (101). The x-axis refers to the height of the geological cliff section from which fossil plants were sampled, with time going from older to younger with height. Landscape visualizations by Marlene Hill-Donnelly; used with permission. Abbreviation: ppm, parts per million.
today (approximately 600 ppm). However, the total estimated magnitude of CO₂ increase that prevailing plants were exposed to (e.g., an addition of approximately, 1,740 ppm) is similar to that expected by the year 2250 under RCP 8.5 (e.g., an addition of approximately 1,660 ppm between preindustrial years and the year 2100) (Figure 4). If more conservative estimates of Late Triassic CO₂ rise are considered (e.g., an addition of 990 ppm to the Late Triassic atmosphere), an equivalent magnitude of CO₂ rise will occur well before 2150 under an RCP 8.5 scenario (Figure 4).

Therefore, the Late Triassic global warming event occurred at a considerably slower pace (12 times slower than RCP 2.6 and a whopping 280 times slower than RCP 8.5) than modern global warming, but the event had a greater overall magnitude than contemporary anthropogenic forcing. Although it is an imperfect analog, it highlights the acuteness of current global change and provides a window through which to study the adaptive capacity of plant traits, species, and whole communities in the past.

Case Study of Past Global Change: Astartekloft, East Greenland

Paleobotanical studies indicate that forested, gymnosperm-dominated ecosystems at Astartekloft, East Greenland, underwent rapid compositional shifts during the Late Triassic as atmospheric CO₂ reached 1,000 ppm (94), which was followed by 85% species-level turnover coincident with a further CO₂ rise to 1,500 ppm (94, 143). Although only one plant family suffered global extinction, extirpation was marked at the species level (98, 158, 159), on the basis of detailed study of macrofossils (mainly fossil leaves), and at the generic level (112), on the basis of detailed study of palynomorphs (fossil pollen and spores). The extinction of reproductive specialists ranged from regional extinction (Bennettitales) to global extinction (Lepidopteris), whereas wind-pollinated generalists proliferated in the aftermath of the species turnover event (ferns and fern allies, Ginkgoales) in East Greenland and Southern Sweden (90, 98). In other regions of the supercontinent Pangea and in East Greenland, the ETE is marked by a geologically transient ecological dominance of ferns and fern allies (87) belonging to extant fern families, many of which today have exclusively tropical and subtropical biogeographical distributions. Thermophilic conifers belonging to the extinct Cheirolepidiaceae family became dominant in the continental interiors in many global localities (22), perhaps aided by widespread fire disturbance (15) and their likely capacity for whole-genome duplication (81), which is generally rare in gymnosperms. However, the total estimated magnitude of CO₂ increase that prevailing plants were exposed to (e.g., an addition of approximately, 1,740 ppm) is similar to that expected by the year 2250 under RCP 8.5 (e.g., an addition of approximately 1,660 ppm between preindustrial years and the year 2100) (Figure 4).
Climate velocity: the estimated rate at which a species must migrate along the Earth’s surface to maintain a constant mean annual temperature under global climate change.

Maximum stomatal conductance ($g_{\text{max}}$): calculated as a function of stomatal density and pore size; measures the maximum rate at which CO$_2$ can diffuse into a leaf and water can diffuse out.

0.02 km/year) represents a climate velocity at the very lowest estimated rates required by modern floras to keep pace with anthropogenic climate change under an A1B future CO$_2$ scenario (88).

Despite evidence for a strong pattern of northward migration in the Northern Hemisphere, immigrants accounted for only a small percentage of early Jurassic floras, and within approximately 200,000 years, stable forested ecosystems had been reestablished and were predominantly made up of species that were already present in the forest communities of the latest Triassic (90, 98).

Therefore, the major ecological pattern to emerge from both fossil leaf and palynomorph studies of Astartekloft is generic-level resilience to extreme global warming with lower environmental and ecological tolerances at the species level. Furthermore, although migration is evident, suggesting that species moved to maintain their climate envelope as global and regional temperatures warmed, there is also strong indirect evidence for in situ adaptation in leaf functional traits (4, 5, 15, 94, 141, 146) and speciation (66, 98) on 100,000-year timescales in response to the ETE global warming event. This is a facet of vegetation response to climate change that is not well accounted for in climate niche, physiological, or dynamic vegetation models because the prevailing paradigm based on Quaternary palynological studies assumes climate niche conservatism (164).

**TRAIT ADAPTATION AND PHYSIOLOGICAL FEEDBACK**

DNA is not preserved in the deep-time fossil record (166). So how can pre-Quaternary-aged fossil plants or parts of them be used to investigate the capacity of a species to adapt to global change? This is particularly complicated by the paleobotanical species concept, which is based on morphological or anatomical traits, or both, which may not be plastic. For example, two fossil plant species defined using aspects of their leaf morphology may represent ecotypes providing evidence for adaptation in response to global change or two separate species in which the speciation event is completely unrelated to the prevailing global change. Trait-based paleobotanical studies offer one method of addressing this limitation.

Paleoecological studies of important traits relating to the leaf economics spectrum (176) demonstrate the adaptation of leaf mass per area (LMA) in response to CO$_2$-induced global warming associated with the ETE (141), PETM (37), and the Cretaceous–Tertiary (21) mass extinction event. Soh et al.’s (141) study showed that global warming selected for fossil plant taxa with high LMA following the ETE, thus providing the first evidence on evolutionary timescales that high CO$_2$ selects for an ecological stress tolerance strategy. The widespread dominance of evergreen taxa during the Eocene (157), which likely had high LMA, provides further support for this pattern. Soh et al.’s study (141) determined that high plasticity in leaf economics traits, such as LMA, was a clear advantage for the longevity of the genus *Ginkgo*, a living-fossil taxon that has survived to the present.

Other examples of important ecophysiological traits that have been tracked in response to past global change include water-use efficiency (11, 39, 54, 168), maximum stomatal conductance ($g_{\text{max}}$) (55, 84, 102, 169), and xylem conductive capacity (24, 167). Although studies of these types of traits are in their infancy, results suggest that plants have adapted to past elevated CO$_2$-induced global change by decreasing stomatal conductance (54) and increasing their water-use efficiency, which on geological timescales has had a positive feedback effect on the regional hydrological cycle by increasing runoff (146, 168) and on the carbon cycle by changing the sink strength of the terrestrial biosphere (106). Differences in the magnitude of the water-use efficiency response to CO$_2$ among fossil taxa have also significantly impacted the competitive landscape at critical climatic thresholds, such as the transitions from interglacial to glacial in the Late Pennsylvanian (168) and elevated to super-elevated CO$_2$ climate states during the ETE (146).
Predictions from general circulation models (GCM) that have proposed dramatic increases in future global runoff in response to a doubling of CO$_2$ (20, 60) have been strongly criticized based on results from FACE studies at mature temperate forest sites (86, 134). Schäfer et al. (134) argued that forest feedback on the hydrological cycle under elevated CO$_2$ concentrations would be highly dependent on species composition because the directionality and magnitude of canopy transpiration responses to elevated CO$_2$ following 3.5 years of exposure were found to be species specific. Leuzinger & Körner (86) suggested that the physiological effect of elevated CO$_2$ concentrations on transpiration was much lower than expected from theory and from leaf-level observations of stomatal conductance responses to CO$_2$. They argue that the seasonal pattern of precipitation was a much more important predictor or determinant of flood risk than physiological forcing of the hydrological cycle via reduced transpiration in temperate forests. However, when the potential physiological forcing of climate and the hydrological cycle are viewed through the lens of paleobotany, the global predictions of enhanced runoff using GCMs are by no means extreme. A change in river architecture in the Jameson Land basin in East Greenland—from slow-moving and meandering in the Late Triassic to fast, erosive braided systems in the earliest Jurassic—was likely driven by an estimated 50% reduction in canopy-level transpiration under intense CO$_2$-induced global warming (146). Geological evidence of increased runoff associated with the ETE includes changes in stream current directions and transient oceanic anoxia in marine sediments (146). Furthermore, within-genus reductions in leaf-level stomatal conductance were accompanied by ecosystem-level shifts in community composition that resulted in community-weighted reduction in overall canopy transpiration. Specifically, Late Triassic forests dominated by Bennettitales with high leaf-level transpiration rates (146) and low LMA (141) were replaced by dominants from within the Ginkgoales family that had higher LMA and lower leaf-level transpiration. This is an example in which exposure to CO$_2$ over hundreds of thousands of years resulted in both species-level adaptation (a reduction in stomatal density and pore size and hence $g_{\text{max}}$) and community-level compositional changes (98), which altered the function of the vegetation as a whole toward more conservative water use, less recycling of water through the vegetation, and, hence, enhanced runoff. These observations on more than 100,000-year timescales support predictions from general circulation models of increased runoff due to a reduction in canopy-level transpiration resulting from elevated CO$_2$ concentrations (60), and they are contrary to findings from some FACE studies that have been too short to account for community composition changes as well as leaf-level adaptation of functional and economic traits (86, 134).

**PALEOBOTANICAL INSIGHTS ON CO$_2$ FERTILIZATION OF PHOTOSYNTHESIS**

FACE studies on crops and both maturing temperate forests and those that have achieved full canopy closure have shown a strong and sustained CO$_2$ fertilization effect on net primary production (2, 85, 111) due to an increase in leaf-level photosynthetic carbon gain (1), despite downregulation of RuBisCO activity (85). However, the typical elevation of CO$_2$ of >200 ppm above ambient concentrations in FACE studies is subtle when considered in the context of future projections, such as RCPs 6.5 and 8.5. Will CO$_2$ fertilization be maintained in an ambient atmosphere of ≥500 ppm, or is it more likely that photosynthetic carbon gain will saturate? This is an important question with regard to budgeting the future carbon sequestration potential of forests and vegetation as a whole in a high CO$_2$ world. CO$_2$ has been ≥500 ppm for the majority of the past 500 million years. Theoretically, therefore, species with RuBisCO-limited photosynthesis and high
resistance to CO₂ diffusion (102, 109) likely had much higher leaf-level saturation of photosynthetic rates for much of the past than their ancestors do today in a comparatively CO₂-starved world.

There is no clear consensus on the deep-time evolution of photosynthesis in vascular plants from studies using proxy estimates from fossil leaves (26, 96, 102) or model estimates derived from fossil leaf traits (54). Similarly, there remains a wide range of opinions on the evolution of the productivity of terrestrial ecosystems through time and whether modern systems are the most productive (24, 25) or less so than those of the geological past (such as the Eocene), assuming a positive correlation between diversity and productivity (77, 130). What is clear, however, is that the total area of forested ecosystems expands dramatically poleward during greenhouse intervals (Figures 1 and 2), which on evolutionary timescales enabled a greater speciation rate during the Cenophytic era and likely higher productivity in many biomes because of a species-area effect (77). Therefore, the fossil record of Mesophytic and Cenophytic paleobiome distribution suggests that the carbon sequestration potential may increase under moderate greenhouse climates of between 500 and 700 ppm CO₂ (Figure 1). However, a detailed carbon stock assessment of the Paleophytic era has highlighted the switching of carbon sequestration potential between the glacial and interglacial climate, with glacially surprisingly sequestering more carbon in the tropics than during the interglacials (106). Thus, the jury remains out on the CO₂ fertilization effect at concentrations >500 ppm. It is essential and possible, now that boundary atmospheric conditions are better constrained than ever (Figure 2), to undertake a quantitative inventory of the carbon sequestration potential of the terrestrial biosphere through geological time using a combination of paleo leaf economics traits and dynamic vegetation modeling to address this critical question further.

**SUMMARY POINTS**

1. The majority of extant plant species, with the exception of those that originated during the Anthropocene, have survived a period of approximately 20 million years when the atmospheric CO₂ concentration was exceptionally low (<300 ppm) as viewed in the context of atmospheric composition during the past 400 million years of Earth’s history.

2. Paleobotanical studies of the tropical rainforest biome suggest that it is much more resilient to global change than predicted by Earth system models.

3. The widespread occurrence of fully forested ecosystems at high polar latitudes in the geological past during conditions of elevated CO₂ concentrations confirms that the tundra biome is the biome most threatened by future global changes.

4. Paleoclimate data and the presence of polar forests support the concept of the polar amplification of climate during elevated CO₂ concentrations.

5. Evidence for enhanced runoff into the Arctic during episodes of past global warmth, such as the Eocene, support suggestions that high Arctic vegetation will have a much more important role in the biogeochemical cycling of carbon and water toward the end of this century if we continue on a path of profligate fossil fuel use and changes in land use.

6. The estimated climate velocities for plant migration associated with the PETM and ETE global warming events were much slower than those that are believed to be required for extant taxa to keep pace with future climate change based on future worst-case carbon-use scenarios, such as RCP 8.5.
7. The pace of Anthropocene climate change is without geological precedent, yet past global change events of much greater overall magnitude are evident in the fossil plant record.

8. Catastrophic predictions of a future dead zone planet Earth and direct climate-driven extinctions are unfounded based on evidence from the plant fossil record; however, dramatic ecological shifts in dominance patterns should be expected.

9. Trends in paleoproductivity based on evidence from the plant fossil record and the evolution of photosynthesis remain hotly debated and are important areas for future research.

10. Overall, the Earth’s vegetation is much more resilient to global change than many contemporary-only studies would predict because the fossil record demonstrates that many taxa are preadapted to our climate future and others can adapt in situ, and many that have unchangeable climatic envelopes likely have climate velocities that are just about sufficient to keep pace with future global change as long as we take a more sustainable path of future carbon use.

DISCLOSURE STATEMENT

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

ACKNOWLEDGMENTS

Shanan E. Peters is thanked for generating the fossil plant occurrence maps through time for Figure 2 from The Paleobiology Database (https://paleobiodb.org/#/). Funding from Science Foundation Ireland is gratefully acknowledged (grant number 11/PI/1103). Joseph White and Isabel Montañez are thanked for discussions on the subject of this invited review.

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**Errata**

An online log of corrections to *Annual Review of Plant Biology* articles may be found at http://www.annualreviews.org/errata/arplant