

Annual Review of Earth and Planetary Sciences

Plant Evolution and Climate Over Geological Timescales

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Annu. Rev. Earth Planet. Sci. 2017. 45:61–87

First published as a Review in Advance on May 15,
2017

The *Annual Review of Earth and Planetary Sciences* is
online at earth.annualreviews.org

<https://doi.org/10.1146/annurev-earth-063016-015629>

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Keywords

evolution of plants, transpiration, albedo, land plants, angiosperms, forests

Abstract

The terrestrial vegetation is unambiguously an important factor in the climate system, modulating the exchange of energy, momentum, water vapor, and other trace gases between land and atmosphere. Here, we review the evolution of the terrestrial flora from the Proterozoic through to the Neogene at three distinct scales—the overall evolution of floral composition, the evolution of plant physiology, and the evolution of landscape occupation both spatially and seasonally—all in the context of how the vegetation may have influenced climate through time and which deep-time evolutionary transitions may have had the greatest effect. Our focus is upon the direct impacts of the vegetation on temperature and precipitation, but we also consider the indirect impacts of plants on climate via atmospheric composition. We argue that the times of greatest change in plant climate feedbacks are likely to have been the Carboniferous and the early Paleogene.



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1. INTRODUCTION

Temperature, precipitation, and their seasonal variability strongly constrain the potential vegetation of an area, but the vegetation itself can also influence the local climate. As such, the evolution of plant morphology and physiology is a key consideration in understanding climate during important environmental and evolutionary events, such as the Devonian evolution of deep rooting, the Cretaceous evolution of flowering plants, or the Paleocene–Eocene Thermal Maximum. However, these research directions are subject to important challenges. Vegetation simulations become increasingly unreliable the further they are removed from the modern conditions and floral compositions for which they have been tuned. Furthermore, the climate impacts of evolutionary transitions and environmental events in Earth history are often considered in inappropriately hermetic isolation without the larger context of what came before and after.

Climate has at its foundation a series of physical parameters—solar influx, atmospheric composition, land-ocean distributions, topography, etc.—but the actual resultant climate is the outcome of feedbacks between these abiotic parameters and the biota. In particular, plants affect the exchange of energy, momentum, water vapor, and other trace gases between land and atmosphere by modifying albedo, evapotranspiration, surface roughness, and a host of more detailed climate parameters (Bonan 2015) (see the sidebar titled *How Vegetation Alters Climate: Primary Mechanisms*). The energy output of the Sun has changed through time (Feulner 2012). Plate tectonics can alter climate via the impact of the latitudinal distribution of continents on global albedo (Kirschvink 1992), the volcanic output of greenhouse gases (McKenzie et al. 2016), and the consumption of greenhouse gases in the weathering of silicate rocks exposed in tectonic uplift (Waldbauer & Chamberlain 2005). How might evolutionary changes in the vegetation matter over geological timescales?

HOW VEGETATION ALTERS CLIMATE: PRIMARY MECHANISMS

- **Albedo:** This is the proportion of solar energy that is reflected rather than absorbed relative to the total solar influx, or insolation.
- **Surface roughness:** Wind speeds are reduced in proximity to a surface, creating turbulence that transports energy, momentum, and water vapor between the surface and the atmosphere (turbulence is also created by buoyant motions driven by surface heating during the daytime). Surface roughness varies depending on the height and spacing of deviations from a flat surface. Tall forests with high roughness create more turbulence and enhance the efficiency of land-atmosphere interaction. This zone of reduced wind speeds and turbulent exchange at the bottom of the atmosphere is the planetary boundary layer.
- **Transpiration:** As the CO₂ used in photosynthetic carbon fixation diffuses into a vascular plant via its stomata (epidermal pores), water simultaneously diffuses out to the atmosphere from the leaf. The water lost during this process of transpiration is typically supplied to the leaf by the plant's vasculature from the substrate and thus represents groundwater that would otherwise largely be shielded from evaporation.
- **Evaporation:** Independent of transpiration, any expansion of wettable surface area at or above the substrate—such as leaves and stems—provides some capacity to store water before it can be lost to groundwater that is less available for re-evaporation.
- **Evapotranspiration:** Evaporation and transpiration are often lumped together as evapotranspiration when the relative proportion of moisture sources either is immaterial or cannot be readily distinguished.

As a significant boundary condition for the exchange of energy, momentum, and water vapor between land and atmosphere (Dickinson et al. 1986, Sellers et al. 1986), the vegetation is typically a component of climate models—including those in deep-time Earth history (Poulsen et al. 2007, Upchurch et al. 2015)—although it is included most often as a necessary component rather than a particular focus. Recent research (e.g., Friedlingstein et al. 2006) has begun to put more emphasis on modeling of the biosphere itself, largely in order to provide predictive understanding of future carbon cycle dynamics. Perhaps more relevant to considering the geological past, the specific importance of the presence or absence of plants has also received attention in terms of the impact of plants at the edges of their distribution, notably of forested landscapes at high latitude (Betts 2000, Bonan et al. 1992, Upchurch et al. 1999), in semiarid landscapes (Hoffmann & Jackson 2000, Levis et al. 2004), and in human-induced land-use change (Lawrence & Vandecar 2015 and references therein). Other work has focused on theoretical extremes, such as wet versus dry land surfaces with or without the potential for evapotranspiration (Shukla & Mintz 1982) or vegetated versus unvegetated landscapes (Kleidon et al. 2000). This latter “desert world” simulation found a doubling of precipitation when terrestrial vegetation was present. See **Figures 1** and **2** for comparable simulations.

The above work is largely indirect or nonspecific regarding the role of plant evolutionary history in deep-time climate dynamics. The radiation of flowering plants during the Cretaceous provides an example of how specific evolutionary events can directly impact climate. As discussed in more detail below, fossil leaf traits in conjunction with the physiological diversity of living plants suggest that flowering plants have greatly increased physiological capacities for transpirational water loss to the atmosphere and for photosynthetic carbon gain relative to all other plants, living or extinct. Transpirational recycling of precipitation plays an important role in rainforest climates, so that the possible geographic extent of tropical rainforests might have been much smaller prior to the fourfold increase in transpiration capacity believed to have accompanied flowering plant evolution (Boyce et al. 2009). When this potential impact is explored via climate modeling (Boyce & Lee 2010, Lee & Boyce 2010), the overall result—although geographically heterogeneous—is a substantially hotter, drier, and more seasonal tropics with a great reduction in everwet rainforest area (results reproduced in **Figure 1** and **2**).

Angiosperm evolution likely increased precipitation; however, that relatively simple statement becomes far more complex and convoluted when considered in its more detailed biological and paleontological context. First, the relevant evolutionary traits are not shared by all flowering plants, but have been derived more or less independently in at least three separate angiosperm lineages: the monocots, the eudicots, and the magnoliids (Boyce et al. 2009, Brodribb & Feild 2010, Zwieniecki & Boyce 2014). (See **Figure 3** for the evolutionary relationships of all lineages mentioned in the text.) Second, the geographic spread of flowering plants from tropical to higher latitudes was a protracted process not entirely complete even by the end of the Cretaceous (Crane & Lidgard 1989, Wing et al. 2012). Third, the full range of angiosperm leaf traits associated with high physiological capacities is not found in the fossil record until after the Cretaceous, in the early Paleogene (Feild et al. 2011). Thus, the Early Cretaceous first appearance of flowering plants is unlikely to bear any particular climatological significance. Rather, any climate modification by flowering plant evolution would reflect a far more complex radiation across space, time, and phylogeny. Given these complexities, are there other transitions in plant evolution that also might have had significant climatological impact, and if so, what might they have looked like? After exploring the various climate parameters that might have been altered by plant evolution, we consider the radiation of the major land plant lineages and their overall structure, the evolution of their hydraulic physiology, and the likely time course of their geographic and environmental occupation of the landscape.

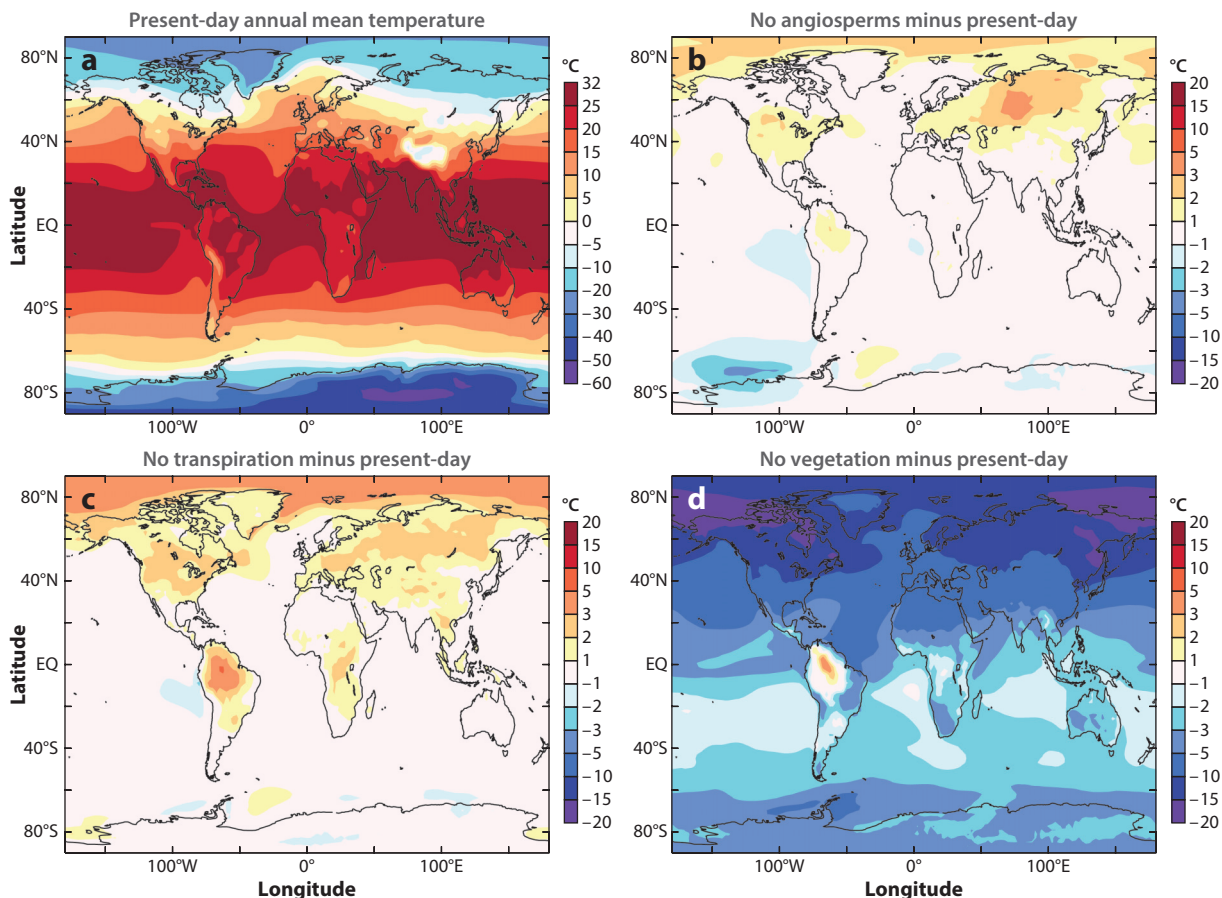


Figure 1

Dissection of the impact of vegetation on temperature. (a) Calculated temperatures with full modern vegetation and (b–d) temperature responses to a modified terrestrial biome. (b) Modern vegetation with maximum transpiration reduced by a factor of four; comparable to previous simulations of the reduced physiological capacities of nonangiosperm vascular plants (Boyce & Lee 2010, Lee & Boyce 2010). (c) Modern vegetation as far as albedo and structure, but with all transpirational capacity removed. (d) All vegetation removed; comparable to previous bare ground simulations (Kleidon et al. 2000). All runs were reproduced using the National Center for Atmospheric Research Community Earth System Model (NCAR CESM) 1.2.2 (Neale et al. 2013), coupled to a slab ocean in calculations, with present-day solar energy, atmospheric composition, and land-ocean configuration.

2. THE RANGE OF POTENTIAL PLANT FEEDBACKS ON CLIMATE

Plants harvest sunlight, CO_2 , and water to generate chemical energy and organic material, influencing the terrestrial environment physically, chemically, and biologically. During this process they could modulate the CO_2 concentration in the atmosphere, the amount of solar energy reflected versus absorbed (i.e., albedo), the boundary layer structure, and the transfer of energy, momentum, water vapor, and trace constituents [for detailed explanations, see Bonan (2015)].

2.1. Energy

Expansion of vegetation coverage in general increases the absorption of solar energy because vegetation tends to absorb more energy compared with bare ground or a snow-covered surface. The

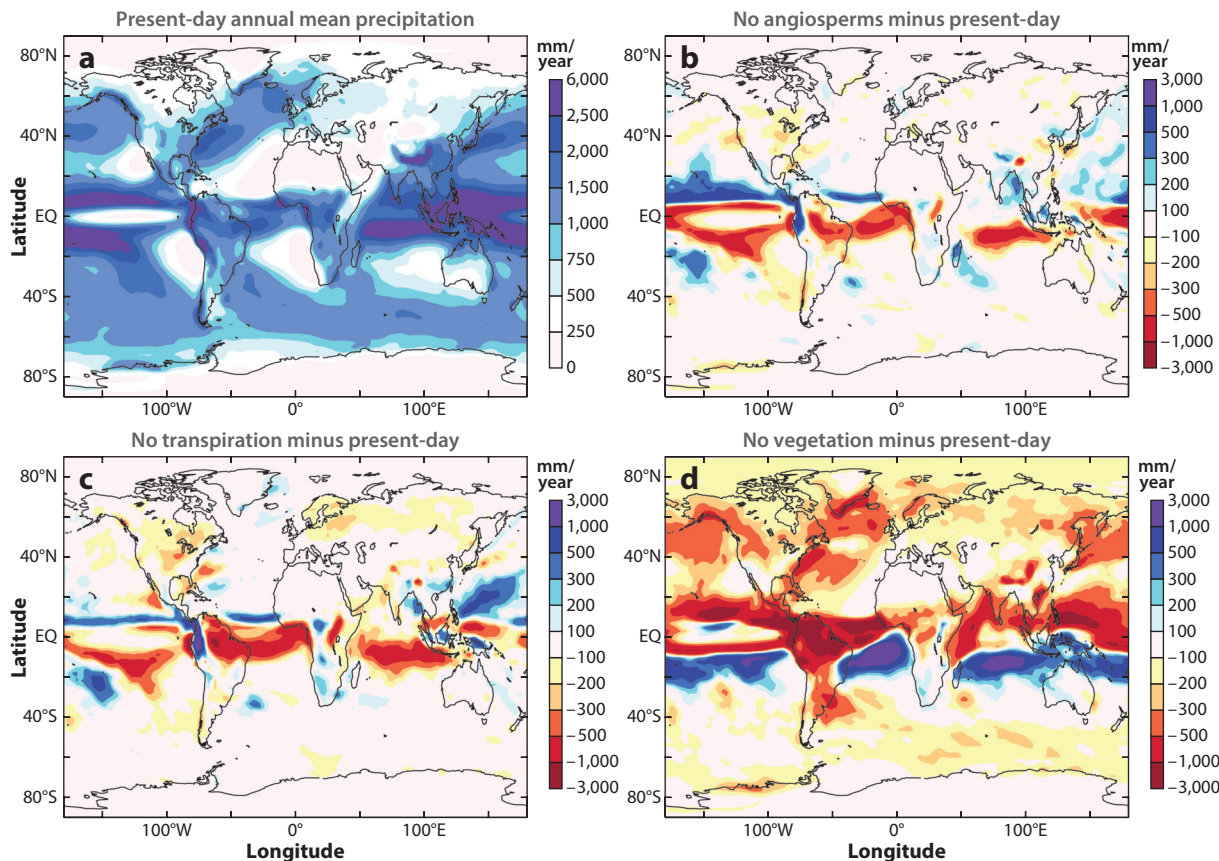


Figure 2

Dissection of the impact of vegetation on precipitation. (a) Calculated precipitation with full modern vegetation and (b–d) precipitation responses to a modified terrestrial biome. (b) Modern vegetation with maximum transpiration reduced by a factor of four; comparable to previous simulations of the reduced physiological capacities of nonangiosperm vascular plants (Boyce & Lee 2010, Lee & Boyce 2010). (c) Modern vegetation as far as albedo and structure, but with all transpirational capacity removed. (d) All vegetation removed; comparable to previous bare ground simulations (Kleidon et al. 2000). All runs were reproduced using the National Center for Atmospheric Research Community Earth System Model (NCAR CESM) 1.2.2 (Neale et al. 2013), coupled to a slab ocean in calculations, with present-day solar energy, atmospheric composition, and land-ocean configuration.

effect of vegetation on surface temperature is highest in boreal forest (Bonan 2008)—the evergreen forests protruding over snow absorb more sunlight compared with snow-covered treeless areas (Lorant et al. 2011). According to climate model simulations, boreal forest could increase seasonal surface temperature by more than 10°C, particularly in April when the incoming solar energy is high yet the surface is still covered by snow (Betts 2000, Bonan et al. 1992). Another climate modeling study showed that high-latitude regions became warmer in the mid-Holocene partly because of the increased tree coverage, originally triggered by an increase at high latitudes of solar input, or insolation (Foley et al. 1994). In a much warmer climate period such as the Cretaceous, tree coverage in high latitudes is also thought to have contributed to global warmth (Otto-Bliesner & Upchurch 1997). Under a scenario with no vegetation, global temperature decreases by 5°C, with particularly colder temperatures in Northern Hemispheric high-latitude regions (Figure 1),

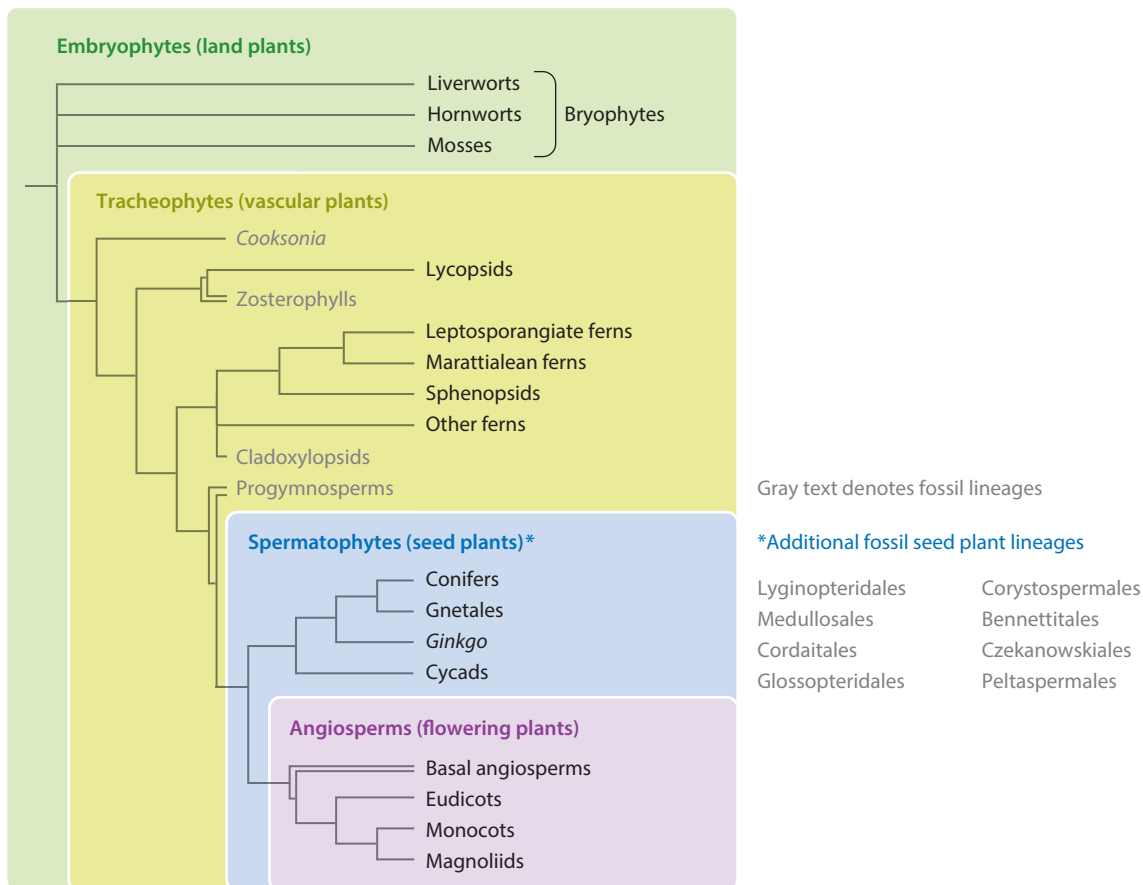


Figure 3

Simplified evolutionary relationships of the land plants mentioned in this article. Topology of the phylogeny is based on living plants with the addition of fossils (in gray text and with truncated branches). Although *Cooksonia* is assigned a single location here, different fossils that have been described as *Cooksonia* are likely to have different phylogenetic positions, such as basal to the zosterophyll/lycopsid line or basal to the lineage including ferns and seed plants. The relationships of the different extinct seed plant groups are too tenuous for direct inclusion in the phylogeny beyond being recognized as seed plants. For sources see Boyce (2008), Boyce et al. (2009).

suggesting that the expansion of trees in high latitudes probably increased global temperature (cf. Bala et al. 2007).

2.2. Water

When plants open their stomatal pores for CO_2 uptake, water vapor is transpired out to the atmosphere, cooling the near-surface air, as illustrated by the sudden increase of moisture and leveling off of temperature increase after leaf emergence in deciduous forests (Fitzjarrald et al. 2001). Plants influence soil development (Crocker & Major 1955), and the presence of organic matter increases a soil's water-holding capacity (Kramer & Boyer 1995). In low-latitude regions and during the warm seasons in higher-latitude regions, the net effect of vegetation via albedo and transpiration is to decrease temperature, because of the increased transfer of energy from sensible to latent heat (**Figure 1**). Modeling studies show that complete deforestation of the tropics would

be expected to increase global temperature by 0.1°C to 0.7°C (Bala et al. 2007, Findell et al. 2006), but global deforestation lowers global temperature because the response in high latitudes is dominant (Bala et al. 2007).

The water pumped back to the atmosphere by transpiration is previous precipitation extracted from the soil. This recycling of moisture constitutes approximately two-thirds of precipitation on land (Dai & Trenberth 2002); thus, the evolution of terrestrial vegetation capable of carrying out this process should have increased global precipitation. As described above, the complete removal of tropical forest would decrease precipitation in general (**Figure 2**), although the magnitude of the decrease differs depending on the specifics of the location and the parameterization of the model used (Lawrence & Vandecar 2015). The moistening of the low-level atmosphere through evapotranspiration also plays a significant role in initiating convection (Fu et al. 1999, Lee & Boyce 2010). The wet season relies on moisture transport from the ocean, but the timing of its onset can be dependent on the persistence of evapotranspiration through until the end of the dry season—which is only possible when plants have deep roots that can access the soil moisture reservoir (Lee et al. 2005, Nepstad et al. 1994, Oliveira et al. 2005). Analysis of summertime evapotranspiration and precipitation over the continental United States showed that evapotranspiration increases the frequency of convection by moistening the boundary layer but does not increase the intensity of convection (Findell et al. 2011). Evapotranspiration over tropical rainforest has similarly been shown to play a buffering role, decreasing precipitation variability by maintaining relatively high moisture content in the lower atmosphere (Lee et al. 2012).

2.3. Circulation

Although evapotranspiration could provide the moisture that is required for the onset of convection, how it influences local precipitation remains elusive. Evapotranspiration decreases near-surface temperature and could potentially decrease upward motion. Gentine et al. (2013) demonstrated the counterintuitive result that convection could be favored over dry surfaces. Increased cloud formation over dry soil could happen when the air above the boundary layer is humid and unstable because the increased sensible heating deepens the boundary layer. In other words, the temperature at the top of the boundary layer becomes colder when the soil is drier because the air mass cools over a greater altitude with a deep boundary layer as it moves up and expands, reaching condensation when moisture becomes available above the boundary layer (Gentine et al. 2013, Westra et al. 2012). In line with this argument, deforestation can indeed increase precipitation in some cases (Chagnon & Bras 2005, Negri et al. 2004).

Evapotranspiration changes the temperature and moisture profile of the boundary layer, and this local change can feed back onto the ~1,000-km-scale synoptic circulation (Betts & Viterbo 2005) and regulate the position of the convective margin—the transition between nonconvective and convective regions (Lintner et al. 2013, Lintner & Neelin 2009). The redistribution of energy by plants can further influence the global circulation pattern. Increased tree cover in the northern mid- to high latitudes increases Northern Hemispheric temperature, which displaces the Intertropical Convergence Zone (ITCZ) tropical rainy belt northward (Swann et al. 2012, 2014), yielding more rainfall in the Asian and African monsoon regions and less rainfall in South America, because the ITCZ tends to be offset more toward a warmer hemisphere (Chiang & Friedman 2012, Schneider et al. 2014). Complete removal of vegetation shifts the ITCZ southward (**Figure 2**) because the Northern Hemisphere becomes much colder than the Southern Hemisphere without boreal trees protruding above snow (**Figure 1**).

Although the local response to evapotranspiration can vary depending on the local climatic conditions, increased evapotranspiration by plants should enhance total precipitation, which includes

precipitation downstream. By calculating where local air masses had traveled over the previous 10 days, Spracklen et al. (2012) found that air that had traveled over densely forested area in the preceding few days produced more than twice as much rain as air that had traveled over less forested area. Along this line, the decrease in snowfall on Mt. Kilimanjaro has been partly attributed to upstream deforestation in East Africa (Fairman et al. 2011) and the decrease in precipitation in montane cloud forests in Costa Rica to upstream lowland deforestation (Lawton et al. 2001).

Plants, particularly tall trees, increase the roughness of land surfaces, decreasing wind near the surface. The regrowth of forests in the Northern Hemisphere has been suggested to contribute to a decrease in observed wind speeds and evaporative demand there (Vautard et al. 2010); however, the increased stability associated with global warming has also been proposed as the mechanism behind these effects (Reijmer et al. 2004, Ren 2010). Roughness influences the turbulent mixing between land surface and atmosphere (Bonan 2015) and could contribute to large-scale circulation patterns (Hoffmann & Jackson 2000), although the pure dynamic effect of roughness on climate is much smaller compared with albedo or evapotranspiration (Zeng et al. 1996).

2.4. A Caveat

The terrestrial vegetation also has the potential to alter climate in ways for which the assessment of evolutionary change is difficult. For example, plants emit chemical compounds that eventually become aerosols, small particles suspended in the atmosphere (Jaenicke 2005). Aerosols absorb or scatter atmospheric radiation, directly affecting climate, and have other indirect effects such as modifying cloud properties and the chances of precipitation. A majority of aerosols are biogenic in extensively vegetated areas (Martin et al. 2010); fungal spores and bacteria in particular contribute to cloud condensation nuclei (Pöhlker et al. 2012, Spracklen & Heald 2014).

3. A FRAMEWORK OF LAND PLANT EVOLUTIONARY HISTORY AND THE PASSIVE INTERACTION OF PLANT STRUCTURE WITH CLIMATE

The antecedent of our modern terrestrial vegetation is typically taken to be bare earth. Prior to the advent of the now-dominant land plant lineage, however, the land surface would not have been barren: Evidence of terrestrial microbial activity extends back more than 2 Gyr into the Precambrian (Gutzmer & Beukes 1998). This oldest evidence is sparse, but understandably so given that both terrestrial environments and the Precambrian are independently underrepresented in the rock record relative to marine rocks and the Phanerozoic. In any case, freshwater environments appear to be important in the early phylogenetic history of the cyanobacteria (Dagan et al. 2013), and there is no clear need to reject the notion that cyanobacteria-based microbial ecosystems would have existed on exposed soils more than 2 Gyr ago, once atmospheric oxygen had reached the minimal levels needed to support a UV-shielding ozone layer (Wellman & Strother 2015). The modern equivalents of these microbial surfaces are often heavily pigmented, with albedos comparable to land plant-based vegetations (Belnap 1995). They can also alter runoff, slowing infiltration and providing some slight capacity for transient water storage directly at the substrate surface where it would be available for re-evaporation. Thus, though the impact on climate of early terrestrial microbial activity is likely to be relatively minor, the bare earth of desert world simulations (e.g., Kleidon et al. 2000) (**Figure 1**) is more extreme than strictly necessary. A truly barren terrestrial landscape surely did exist at some point, but it would likely require going back to at least the Archean to find it.

3.1. The Early Paleozoic

Aside from limited environments where cyanobacteria-based microbial soil crusts and/or lichens can be important, modern terrestrial vegetation is almost exclusively composed of the land plants, or embryophytes. The land plants are a single distinct lineage of related plants comprising four sublineages, including the three nonvascular bryophyte groups (the mosses, hornworts, and liverworts) and the vascular plants (**Figure 3**). Spores diagnostic for the embryophytes are known from the Ordovician, and other spores more ambiguously associated with the land plants are known from the Cambrian (Wellman & Strother 2015). These oldest embryophytes would have been of a bryophyte grade of construction—small, rootless, with little capacity to modulate their own water status or resist desiccation. Modern moss can form thick turfs with abundant internal surface area generating considerable water storage capacity, but this tends to occur in environments that are already subject to poor drainage. Regardless, there has been no direct evidence for the formation of bryophyte peats during the early history of terrestrial vegetation; peat moss itself appears to have diversified in the Neogene (Shaw et al. 2010).

3.2. The Devonian and Carboniferous

Vascular plants, or tracheophytes, are first recorded with macrofossils of the later Silurian, followed by a substantial radiation in the Devonian encompassing all of the major vascular plant lineages: lycopsids (including the extant club mosses and quillworts), sphenopsids (including the extant horsetails), the various fern groups, and seed plants (**Figure 3**). Tracheophytes include multiple convergent evolutions of leaves, roots, wood, and large trees (Boyce 2010). Nearly all carefully regulate their water balance via stomatal leaf pores that can be shut to limit water loss. Most of these plants are capable of extracting water from the soil under considerably negative pressures with their roots, and they amplify the surface area for environmental exchange several-fold via their leaves. These traits, however, were largely absent from early vascular plants; aside from a relatively precocious zosterophyll/lycopsid lineage that could bear tiny leaves and simple roots, they were absent from Silurian tracheophytes. Even the more robust plants continuing through the Early Devonian were no more than a few centimeters in axial diameter and approximately a meter in height, while also lacking leaves, wood, and often roots (Boyce 2008). Thus, even traits universally associated with members of the modern tracheophyte vegetation were initially lacking. These early vascular plants would have accumulated more biomass per individual than bryophytes, but that biomass tended to consist of surface area—minimizing cylinders invested with hydrophobic cuticles. Thus, with neither the capacity to mobilize soil water (as found in later deep-rooting tracheophytes) nor the increase in surface water storage available for re-evaporation of local precipitation (as provided by the extensive hydrophilic surface area of many bryophytes), vascular plants would have largely been passive recipients of their local climate through the Early Devonian.

Over the later Devonian and Early Carboniferous, more derived characteristics were acquired progressively and often independently in different vascular plant groups, including the evolution of the distinct primary growth organography of stem, leaf, and root, as well as the derivation of secondary growth, such as wood and bark. Trees and forests were present by the Middle Devonian with four or five independent derivations of both woody and nonwoody tree habits appearing already by the end of the Devonian. Forests could be dense (Stein et al. 2012) and canopy heights would have been in the 5- to 10-m range, although Late Devonian *Archaeopteris* may have approached 20 or 30 m in some cases (Decombeix & Meyer-Berthaud 2013, Meyer-Berthaud et al. 2010). The earliest trees included both woody branching forms, such as the progymnosperm *Archaeopteris*, and rosette forms with a distal tuft of fronds borne on a pole-like trunk (although the

earliest of these did not yet have proper leaves, and the “fronds” were abscising branch complexes), such as some cladoxyloids (Meyer-Berthaud et al. 2010). Thus, not only is the later Devonian the first time that groundwater would have been made available for evapotranspiration via the action of deep roots, but it represents the first time that the vegetation may have substantially changed the surface roughness of the landscape, at least in some environments.

By the later Carboniferous, the full modern complement of overall vascular plant architectures was present (**Figure 4**), ranging from small herbs and shrubs to climbers to large trees including

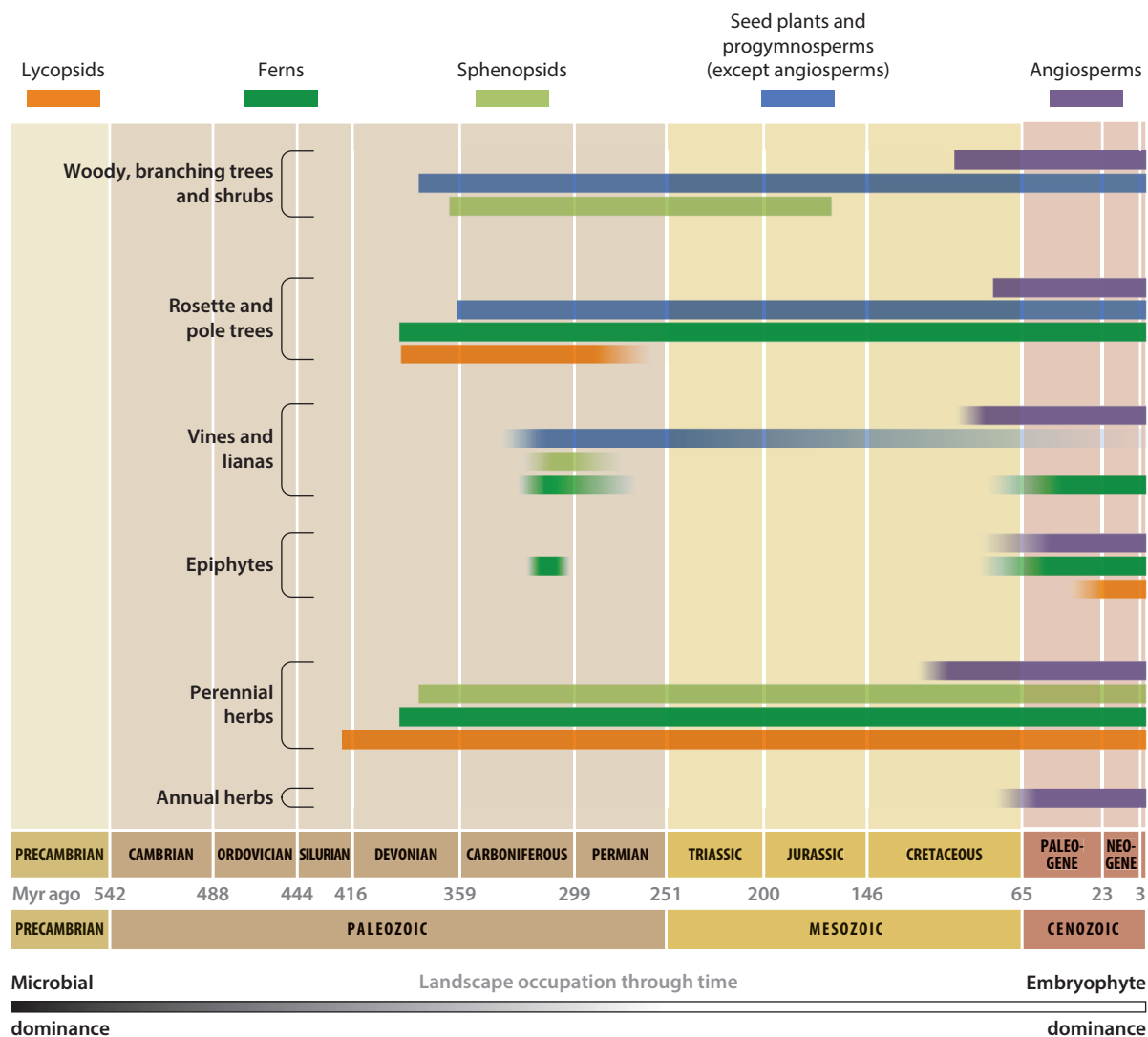


Figure 4

Ecological diversity and landscape occupation through time. Plots represent qualitative summaries of the literature and syntheses of the arguments advanced in this article. Beyond the color-coded vascular plant lineages shown, some other plants of the early fossil record, predominantly herbaceous, do not fit comfortably in one of the lineages tracked here and are excluded from the ecology plots. “Ferns” as used here is an aggregate of several lineages that may not all be closely related.

both woody and nonwoody forms—albeit with certain caveats, such as that lianas were present, but with relatively limited evidence of true epiphytes, and that herbs were present, but only perennial herbs rather than annuals (Boyce & Leslie 2012). Forest canopies may have routinely been more than 20 m tall, and the tallest trees were at least 50 m tall. Also important was the increasing floral heterogeneity; the reason that the possible impacts of Early Devonian vascular plants on climate can be concisely summarized is, in part, because those plants were all very similar. In contrast, the Carboniferous represents a high watermark for vegetative disparity: Lycopsiids, sphenopsids, ferns, and seed plants each produced trees of wildly different construction that were all important elements of forest canopies, and each dominated at least some environments. As a comparison, modern trees are exclusively seed plants with the exception of a few, ecologically restricted, leptosporangiate tree ferns.

The heterogeneity and structural complexity of Carboniferous plants present an enormous challenge given that the vegetation characteristics deemed important enough to include in climate models are complex, multifarious, and subtle: precipitation interception and trickle-down potential, radiative fluxes between canopy elements and the ground, wet versus dry fractions for albedo calculations, shade versus sunlit fractions, etc. Thus, whereas changes in individual aspects of form can be recognized (DiMichele et al. 2009, Wilson et al. 2015), the overall complexity among Carboniferous plants is such that the safest strategy presently available may be to recognize that the modern envelope of parameter values would have been achieved for most characteristics describing plant structure. Even where evolutionary perturbations present clear alternatives, the climatic impacts of those alternatives cannot be readily assessed. For example, at the Kasimovian–Gzhelian (i.e., Westphalian–Stephanian) boundary of the Late Carboniferous, lycopsiids (e.g., *Lepidodendron*, *Sigillaria*, *Lepidophloios*) were sharply and overwhelming replaced by marattialean tree ferns (e.g., *Psaronius*) as the dominant canopy element in the lowland swamp forests of Euramerica.

The arborescent lycopsiids possessed more structural diversity than can be described here (Boyce & DiMichele 2016), but generally speaking they included pole trees, up to 40 or 50 m tall, that could be relatively widely spaced canopy emergents extending 20 m or more above lower canopy elements. They had densely packed linear leaves up to a meter long that would have presented an enormous leaf area index (LAI; the amount of leaf area for a given amount of ground area) for an individual tree, although expressed over small and widely spaced footprints for each tree. Long, grassy, flexuous leaves likely shed most of the precipitation they intercepted distally via drops rather than channeling it to the stem, and furthermore, that trunk was invested either in cuticle-covered leaf bases or, after the leaf bases were shed, in a periderm tissue that was likely to have been equally hydrophobic (Boyce et al. 2010a). As a result, the surfaces of the trees would have typically been dry.

In contrast, the tree ferns that replaced the lycopsiids as canopy dominants would have presented a much lower and more even canopy height. Their distal rosette of highly compound fronds would have yielded a much lower LAI per plant, but expressed over a much larger footprint per tree and likely with considerable overlap between the footprints of adjacent trees. Their fronds likely channeled more intercepted precipitation to their trunk, and that trunk was largely a thick mantle of roots investing a relatively thin stem. This spongy mantle of largely dead and hollow roots would have held a great deal of precipitation available for re-evaporation. Indeed, the root mantles of analogous living tree ferns are routinely used as a horticultural substrate for growing epiphytic orchids because of this water storage capacity, and the root mantles of Paleozoic tree ferns were a substrate for epiphytes otherwise rare prior to the Cenozoic (Rößler 2000). As a final difference, the thick single-veined leaves of the lycopsiids likely transpired less water per unit leaf area than the thinner leaf lamina of the ferns, which had a somewhat higher leaf vein density (as discussed

in more depth in Section 4.2). We hazard no guess as to how all those disparate characteristics of lycopsids versus tree ferns might have summed up to a differential impact on climate—all the more so when the stratigraphic boundary of their ecological turnover itself appears to represent an important climate transition related to extensive glaciation in Gondwana coinciding with the filling of many of the tectonic basins that allowed such extensive lowland swamps in the first place (Nelsen et al. 2016).

3.3. The Permian and Earlier Mesozoic

The Carboniferous lowland forests were dominated by lineages now extinct (e.g., lyginopterid, medullosan, and cordaitalean seed plants), in some cases involving architectures now absent from the related lineages that have survived to the present (e.g., arborescence among the lycopsids, sphenopsids, and marattialean ferns), but the Carboniferous also represented the first appearance of various more derived lineages that would dominate at later times. The leptosporangiate lineage that makes up the bulk of modern fern diversity first appeared in the Carboniferous. Among the seed plants, or spermatophytes, the conifers first appeared in the Late Carboniferous and, depending on the ambiguous affinity of potential early relatives, the cycad (e.g., *Taeniopteris*, *Phasmatocycas*) and *Ginkgo* (e.g., *Trichopitys*) lineages may also have first appeared at this time as well. However, the functional and architectural diversity exhibited by the modern representatives of these lineages would not have been fully present until at least the Mesozoic, and lineages now extinct still dominated the Permian and, to a lesser extent, the Triassic. For example, conifers were of increasing importance in the Permian but were represented only by archaic forms now extinct; all modern conifer families, aside from the Cretaceous Pinaceae, first appeared in the Triassic. The basal extant leptosporangiate fern families appeared in the Permian and Triassic, but the polypods that make up most living leptosporangiate diversity did not radiate until the Cenozoic. Cycadophytes and ginkgophytes similarly diversified in the Mesozoic. [For details regarding the form, anatomy, and history of any of the fossils mentioned here or elsewhere in the text, we recommend Taylor et al. (2009).]

The emphasis of the preceding paragraph is on lineages with living representatives because of their links to modern ecophysiological diversity, but there was also a continual turnover of lineages now extinct throughout the later Paleozoic and Mesozoic. For example, Cordaitales and Glossopteridales seed plants were important canopy trees in the Permian (in the Northern and Southern Hemispheres, respectively) but, along with the gigantopterids, were both extinct by the end of the Permian. Corystosperm seed plants were overwhelmingly dominant, but only in the Triassic and only in Gondwana. Bennettitales, Czekanowskiales, and Caytoniales seed plants may all have been relatively common floral elements, but only in the Mesozoic. However, the origin and extinction of each of these lineages—along with a variety of others—are unlikely to have meaningfully expanded or contracted the overall range of plant structure and architecture that may have influenced climate. For example, Bennettitales fossils can be so similar to cycads as to require details of stomata anatomy in order to be distinguished from them. The other lineages all present more or less overlapping iterations of lianas, shrubs, unbranched rosette trees, and tree architectures that branched more frequently. For example, seed plant lianas and vines have been more or less continually in existence since the Carboniferous; however, this continuity likely occurred without any direct evolutionary connection between iterations of the climbing habit among some members of each lineage in the Lyginopteridales, Medullosales, Gigantopteridales, Peltaspermales, Bennettitales, and a few other seed plant groups—as well as several lineages of sphenopsids and ferns—prior to the evolution of the modern seed plant climbers in the Gnetales and diverse flowering plants (Burnham 2009).

3.4. The Cretaceous and Cenozoic

Although flowering plants may have changed the world in many other ways, their evolutionary radiation during the Cretaceous and Cenozoic did not change the basic range of plant architectures at the coarse scale relevant to climate feedbacks. For example, the first evidence of herbaceous eudicot angiosperms is Early Cretaceous (Jud 2015) and of grasses is Late Cretaceous (with the spread of grasslands delayed until the later Cenozoic; Strömberg 2011), but systems that were equivalent to grasslands—i.e., dominated by herbaceous plants with a large proportion of subterranean biomass—were likely already present in the form of fern savannahs and prairies in the mid-Cretaceous and presumably earlier (Skog & Dilcher 1994). Thus, to whatever extent flowering plants changed terrestrial climates, it was likely a result of their internal physiology, not their external form.

4. EVOLUTION OF PLANT HYDRAULICS AND ACTIVE PHYSIOLOGICAL INVOLVEMENT WITH CLIMATE

Like the microbial mats with which they coexisted, the earliest bryophyte-grade land plants likely represented a passive reflection of their current local water balance—that is, active when water was available and dead or dormant when it was not (i.e., poikilohydry) and with no capacity to draw water from any depth in the soil except, perhaps, via mycorrhizal fungal symbionts (Taylor et al. 2009). In contrast, the vast majority of extant vascular plants are homoiohydric, capable of maintaining a relatively stable internal water status via the drawing up of water from the soil with their roots, transporting water throughout the plant with their vasculature, and limiting water loss by lining external surfaces with a hydrophobic cuticle traversed by stomatal pores that can be opened to allow CO₂ uptake for photosynthesis or shut when necessary to limit further the loss of water. As discussed in Sections 2 and 3, the mere presence of large plants as passive objects may impact flow of air currents, albedo, and surface water storage and evaporation, but plant evolution is likely to have had the greatest impact on climate via the active physiological involvement of vascular plants in the redistribution and transpiration of soil water to increase photosynthesis.

4.1. The Early Fossil Record: Homoiohydric Traits in Poikilohydric Plants?

Many of the traits associated with vascular plant homoiohydricity—the cuticle, stomata, and vascular cells—appeared first in poikilohydric bryophytes but often function in ways directly contradictory to expectations based on living vascular plants [see the sidebar titled Alternation of Generations (and Water)]. The photosynthetic tissues of a variety of bryophytes do have a waxy hydrophobic cuticle, but one that is either punctured by large, freely open holes or is otherwise discontinuous, exposing wet living cells directly to the atmosphere. Under such circumstances, a hydrophobic cuticle may retard water loss to some degree, but such a cuticle may be directed as much or more to promoting the shedding of excess surface water films rather than to preventing water loss—important in damp environments because diffusion of CO₂ is 10⁵ times slower in water than in air. Angiosperms can provide analogous examples of such counterintuitive uses of the cuticle (Feild et al. 1998).

Stomata are also present in some bryophytes, where they are limited to the diploid sporophyte generation. This sporophyte is primarily involved in spore production, is scantily photosynthetic at most, and is physiologically dependent on the actively photosynthetic haploid gametophyte generation to which it is physically attached. In the absence of substantial photosynthesis, why have stomata for gas exchange? These stomata tend to be concentrated near the base of the sporangia, and one idea is that this pattern serves not to decrease water loss but rather to increase

ALTERNATION OF GENERATIONS (AND WATER)

Animals are typically multicellular only in the diploid phase of their life cycle, when they have two sets of chromosomes. The haploid phase, with a single set of chromosomes, is typically limited to the sexual sperm and egg—although bees, among other animals, can depart from this generality. In contrast, land plants always have two multicellular generations, both haploid gametophyte and diploid sporophyte, a life cycle known as the alternation of generations. The haploid gametophyte that is dominant in bryophytes is progressively reduced in vascular plants. In many ferns, the haploid remains an independent photosynthetic plant, but on a millimeter scale. In other cases, the gametophyte is a nonphotosynthetic parasite of soil fungi. In seed plants, the haploid phase is further restricted to a few cells within the seeds and pollen grains.

This trend of sporophyte dominance is relevant to water relations. In the bryophytes, the haploid that conducts most or all of the photosynthesis and all of the substrate interaction is poikilohydric, with a water status that fluctuates freely with the environment. In tracheophytes, the diploid that conducts the photosynthesis and substrate interaction is almost always homoiohydric—that is, capable of maintaining a stable water status and carrying on physiological activity in a drying environment. (The haploid phases of many of the above-mentioned ferns maintain the capacity for photosynthesis and substrate interaction, but those diminutive structures are of little environmental importance and are poikilohydric.) Homoiohydry is achieved both by resisting desiccation via a hydrophobic cuticle and the activity of stomatal pores—with very few fossil exceptions, stomata are typically found only in the diploid sporophyte, even in bryophytes—and by replacing water lost to the atmosphere via uptake of groundwater by roots, often reaching the water table at considerable depths, followed by transport from the roots via the vasculature to the sites of transpirational loss, primarily in the leaves. Thus, the transition from haploid to diploid dominance also represents a transition to more active involvement in the hydrological cycle, although the anatomical and physiological details spanning the actual evolutionary transition can be complex and counterintuitive.

it in order to drive the flow of soluble micronutrients from the soil specifically to the sites of spore production (Edwards et al. 1996). Another equally counterintuitive possibility is the active promotion of sporangial drying for spore dispersal (Duckett et al. 2009).

Finally, conducting cells also can be present—including analogs to both the water-conducting xylem and sugar-transporting phloem of vascular plants—but their role is far less central in bryophyte physiology than in tracheophytes: Transport can actually be faster externally along the surface of a moss due to capillary action between leaf bases than internally through the dedicated conducting cells of the same moss (Héban 1977). Thus, the oldest fossil record of stomata-bearing cuticles and potential conducting cells (Taylor & Wellman 2009, Wilson 2016) should not be taken as heralding the immediate commencement of extensive active plant involvement in the hydrological cycle. Indeed, the diploid sporophytes of many of the earliest vascular plants of the later Silurian and Early Devonian were so small—often much less than 1 mm in axial diameter—as to have crowded out basic aspects of photosynthetic function, requiring a more bryophyte-like physiology with sporophyte dependence on a photosynthetic gametophyte (Boyce 2008).

4.2. Homoiohydric Vascular Plants: Vasculature

Other early vascular plants—beginning with the Silurian and Early Devonian zosterophyll relatives of modern lycopsids and joined later in the Devonian by other vascular plants more closely related to modern ferns and seed plants—would begin to follow more of the expectations of vascular plant physiology. These include the mobilization of groundwater to maintain homoiohydry despite the transpirational water loss associated with photosynthetic gas exchange, particularly given the

increases in maximum rooting depth that occurred over the Devonian and the multiple convergent evolutions of wood and leaves in the Devonian and Carboniferous. It is these vascular plants that could have first taken an active physiological role in the hydrological cycle (**Figure 4**), although caveats regarding landscape occupation are discussed in Section 5.

Surveys of leaf vein densities across extant vascular plants and their almost 400-Myr-long leaf fossil record indicate that flowering seed plant evolution represented a unique escalation of physiological capacities (Boyce et al. 2009, Feild et al. 2011, Sack & Scoffoni 2013, Walls 2011). Even in large trees, at least one-third and up to four-fifths of the total hydraulic resistance of a vascular plant is concentrated in the last few centimeters represented by the leaf (Sack & Holbrook 2006) because it is in the leaf that water must leave dedicated conducting tissue and traverse the living mesophyll tissue dedicated to photosynthesis en route to the stomata and transpiration. The resistance to transport across the mesophyll is orders of magnitude higher than the resistance to transport through the conducting tissue, and thus shortening the path length of transport through the mesophyll greatly reduces the overall resistance of the plant. The most direct route to shortening the mesophyll path length is to increase the density of veins, and flowering plants have both mean and maximum values approximately four times higher than all other plants, living or extinct.

This evolutionary innovation of angiosperm leaf structure is expected to have brought an approximately fourfold increase in transpiration capacity, with substantial impact on climate (**Figure 2**). With the potential impact of shifting atmospheric CO₂ concentrations on productivity being the key complication (Beerling & Woodward 1997, Brodribb & Feild 2010, Franks & Beerling 2009a), the stability of vein density differences through time has also been used to argue that the elevated photosynthetic capacity of extant angiosperms relative to other plants was maintained in the geological past, even at times when CO₂ levels were higher (Boyce & Zwieniecki 2012). Thus, terrestrial productivity would have been consistently low prior to angiosperm evolution. High vein density is an important but not the sole prerequisite for high angiosperm productivity; even considering just hydraulic physiology, angiosperms are also distinct in possessing high conductivity vessel elements as well as differences in individual leaf vein structure, vein placement, and even behavioral hydraulic safety margins (Brodribb & Holbrook 2004, Feild & Brodribb 2013, Zwieniecki & Boyce 2014). Vein density serves as a proxy integrating these various differences that is readily measurable in the fossil record.

4.3. Homoiohydric Vascular Plants: Stomata

Notably, the preceding section is focused on the evolution of hydraulic physiology and the leaf vascular network, but the evolution of stomatal characteristics is also unavoidably important. Veins and stomata are at either end of leaf hydraulics, yet whereas the range of vein densities was stable for 300 Myr prior to the evolution of derived angiosperms, maximum stomata densities fluctuated over more than an order of magnitude (Boyce et al. 2010b). This disjunct presents a challenge. For example, much of the ground covered here has been reviewed previously and with much more detail regarding the role of the evolution of plant physiology in climate models (Berry et al. 2010), but there the focus was exclusively on stomata, and as a result, the expectation of angiosperms enhancing the hydrological cycle was registered but could be no more than a suspicion.

One complication is that information regarding stomata in the fossil record has largely been collected as a proxy for past atmospheric CO₂ concentrations with the evolution of plant physiology being only a secondary application. The stomatal index that has been widely useful as a proxy for paleo-CO₂ (McElwain & Chaloner 1995) has no direct relevance to photosynthetic or transpirational characteristics, and stomatal density alone is not physiologically informative unless stomatal pore sizes are also known (Franks & Beerling 2009a,b). Increasingly, the physiologically

relevant data are being collected, but understanding of how the relevant parameters interact is still in flux (Assouline & Or 2013, Boyce & Zwieniecki 2012, Brodribb & Feild 2010, Franks & Beerling 2009b, Zwieniecki et al. 2016). Where vein, stomata, and physiological data have been collected in parallel, vein density appears to be a good predictor of physiology (McElwain et al. 2016). Even just the continued diversification of how fossil cuticle and epidermal traits are considered in the context of paleoenvironmental work (e.g., Dunn et al. 2015) could pay future dividends regarding understanding climate evolution and the role of plant physiology in it.

4.4. C₄ Photosynthesis?

C₃ photosynthesis-based grasslands became prominent in the Oligocene and earlier Miocene, followed by the rise to dominance of C₄ photosynthesis in lower-latitude grasslands in the later Miocene and Pliocene. C₄ photosynthesis is advantageous at higher temperatures and lower CO₂ concentrations (Edwards et al. 2010), which means that any discussion of the evolution of C₄ photosynthesis is unavoidably tied to climate evolution. However, the radiation of C₄ photosynthesis in different regions lagged important Neogene climate change, framing its evolution as a response to climate change rather than a driver of it. This view is supported by the convergent evolution of C₄ photosynthesis in many separate Neogene flowering plant lineages, including a variety of grasses and nongrasses (Sage et al. 2011), although it has been hypothesized that grass evolution reinforced the climate trends that had allowed for their initial spread (Beerling & Osborne 2006), a phenomenon that can be generalized to other landscapes that are fire prone (Bond & Scott 2010).

5. EVOLUTION OF LANDSCAPE OCCUPATION IN SPACE AND TIME

Once vascular plants did appear, their spread was subject to both geographic and environmental gradients. The earliest macrofossils are widespread in the tropics, but largely found only in the tropics (Raymond et al. 2006). However, the scant high-latitude record that does exist for the Late Silurian (e.g., Bolivia at 60–75°S; Edwards et al. 2001) and Early Devonian (e.g., Brazil at ~80°S; Gerrienne et al. 2001) suggests a tropical preservational bias; the likely culprit for this bias is the erosional loss of potential high-latitude records with the subsequent glaciation of Gondwana in the Carboniferous and Permian (coupled with scant land mass in the Northern Hemisphere). High-latitude deciduous forests were certainly well established in both hemispheres by the Permian, with the *Cordaites* and *Glossopteris* seed plants dominating the Northern and Southern Hemispheres, respectively (Rees et al. 2002).

5.1. Spatial Occupation of Landscapes

Since its inception, the vascular flora was geographically widespread in the tropics where—in theory—it could have had the largest potential impact via evapotranspiration and related processes, and this tracheophyte vegetation may already have been equally widespread across higher-latitude Gondwana in the Late Silurian. However, a cosmopolitan distribution likely did not initially translate to widespread abundance or environmental impact: The early record of vascular plants is overwhelmingly dominated by wet lowland environments (e.g., Hotton et al. 2001). The sedimentary record itself is, of course, biased toward lowlands, but the environmental restrictions of the earliest tracheophytes are widely expected to be real and accurate for several reasons. First, beyond the fact that the minute earliest members of the vascular plant lineage (e.g., *Cooksonia*) were likely to have resembled poikilohydric bryophytes in their physiology, the other Silurian and Early Devonian plants possessed no or little roots (Gensel et al. 2001), no wood, and

water-conducting cells poorly adapted for withstanding strongly negative pressures (Wilson 2016) and were reliant on turgor water pressure for hydrostatic mechanical support of their upright axes (Bateman et al. 1998)—an inauspicious combination for thriving anywhere except a reliably wet environment. Second, carbon isotopic records of fossil heterotrophs (i.e., the potential fungus *Prototaxites*) indicate consumption of substrates other than C₃ vascular plants, most likely microbial soil crusts and bryophytes (Hobbie & Boyce 2010). Thus, though early tracheophytes may have lined waterways, the broader landscape would have still largely been dominated by an older, simpler flora. Despite evolutionary changes, the vegetation through the earlier Devonian would have represented a passive expression of near-surface water availability, whether transient (areas dominated by poikilohydric microbial crusts and bryophytes) or more permanent (areas dominated by homoiohydric vascular plants). As such, the vegetation should have had little direct impact on climate beyond any albedo effects in the limited areas newly occupied by vascular plants, although the directionality of any albedo changes associated with floral replacement would be unclear given the heavy pigmentation possible in microbiotic crusts.

Trees, abundant wood production, and deeper rooting all first appeared in the Middle Devonian, and floodplain forests were extensive by the Late Devonian (Algeo & Scheckler 1998). The presence of large trees dramatically changed sedimentology and the surface flow of water, giving rise to the appearance of meandering and anastomosing rivers and more surface ponding (Gibling & Davies 2012). Thus, more free water would have been exposed to surface evaporation, although it is unclear whether this would have any large climatic impact given that surface freshwater remains a small proportion of the overall landscape. Evidence for upland vegetation first comes in the form of allochthonous material washed into lowland environments in the earliest Carboniferous (Bateman & Rothwell 1990) followed by more direct preservation of upland flora in the Late Carboniferous (DiMichele & Aronson 1992, Falcon-Lang & Bashforth 2004), particularly in karst sinkholes (Plotnick et al. 2009). The Carboniferous, therefore, may represent the first time that vascular plants substantially altered the hydrological cycle via the mobilization of groundwater with the full occupation of large contiguous regions by deep-rooting plants. Fossil preservation of desert floras is typically unavailable, but occupation by terrestrial vascular plants of their full modern environmental range is likely to have occurred by the time of the Permian–Triassic radiations of conifers and cycads, given the distributions of these lineages in modern arid and semiarid environments.

Full landscape occupation by vascular plants was likely established near the end of the Paleozoic; however, flowering plants are physiologically distinct from other vascular plants, as discussed in Section 4, so that the specific time course of their landscape occupation and physiological evolution is also relevant to climate. The oldest securely identified angiosperm microfossil and macrofossil material is of Barremian to Aptian age (130–125 Myr ago). The more abundant palynological record indicates that the early distribution of angiosperms was overwhelmingly tropical (Crane & Lidgard 1989) and their spread to higher latitudes did not occur until their Cenomanian radiation at the beginning of the Late Cretaceous (100 Myr ago). However, their geographic spread did not immediately result in ecological dominance. Where preservation permits ecological censusing, angiosperms may have represented a majority of the species, but those species were individually rare and the majority of the biomass still consisted of ferns and gymnosperms—even at mid-latitudes in the latest Cretaceous (Wing et al. 2012). Just as vascular plants may have become geographically widespread in the Devonian despite remaining environmentally restricted until the Carboniferous, flowering plants radiated in the Cretaceous but may not have achieved their full modern environmental dominance until the Paleogene. The potential for delayed ecological dominance is also reflected in the proxies available for photosynthetic physiology: Angiosperm fossil leaf vein densities are exclusively low and fully overlap with those of nonangiosperms in

the Early Cretaceous (Feild et al. 2011). This is in concordance with the basal extant lineages of flowering plants being drought-intolerant, scanty woody shrubs found on the shaded floor of wet tropical forests that have vegetative physiology more comparable to that of modern ferns than to that of more derived angiosperms (Brodribb & Feild 2010, Feild & Arens 2007, Zwieniecki & Boyce 2014). Angiosperm vein densities rose over the Late Cretaceous, but the higher extremes of the range seen in modern flowering plants were not recorded in the fossil record until the Early Paleogene (Feild et al. 2011).

5.2. Temporal Occupation

As is the case for the changing geographic and environmental distribution of plants through time, the short-term temporal occupation of landscapes—whether reflecting seasonality or response to frequent disturbance—may also have been subject to evolutionary change. In temperate forests, for example, annual angiosperm herbs may extend the period of transpiration and alter albedo both before the forest canopy is active and after canopy leaves have senesced. Angiosperm herbs such as grasses can also be the dominant vegetation in environments where seasonal restrictions in water availability, in conjunction with fire and herbivory, limit the potential viability of larger woody perennial plants. As discussed above, however, perennial herbaceous ferns can occupy similar roles and did so prior to angiosperm evolution, so that any impact would be due to the specific increased physiological capacities of flowering plant herbs rather than to the general presence or absence of nondormant plants. In more extreme cases of frequent disturbance, the rapid growth and accelerated reproduction unique to flowering plants may be essential for the completion of a life cycle and establishment of a self-sustaining population. However, rapid colonization by ferns of postdisturbance landscapes via propagule dispersal is well established in the modern world (Walker & Sharpe 2010) and can be inferred in the fossil record (Vajda et al. 2001). Thus, from a climatological perspective, most frequently disturbed landscapes would likely have been occupied by at least an incipient vegetation, regardless of whether that vegetation had a chance to set seed and become self-propagating before the next round of disturbance. One possible exception may be the transient occupation of arid environments, when precipitation is sporadically available, by fast-growing, stress-avoiding angiosperm ephemerals; it seems unlikely that nonangiosperms capable of dormancy, such as geophytes with subterranean storage organs and resurrection plants, could somehow have provided a perennial equivalent to make up for the rapid recycling via transpiration of transiently available desert rainfall prior to angiosperm evolution.

5.3. The Density of Occupation: Leaf Area

Physiological capacities, such as transpiration, are typically measured and expressed in terms of unit leaf area. Thus, a final caveat that must be considered regarding landscape occupation through time is whether the density of leaf area has changed: In theory, the higher transpiration capacity of angiosperms per unit leaf area could be at least partially offset if plants existing prior to the angiosperm radiation had more leaves (Bond 1989). Indeed, living conifers can have very high LAIs (Asner et al. 2003), as, presumably, could some extinct lineages for which fossil stems can bear a high density of leaves (e.g., arborescent lycopods, *Czekanowskia*; Miller & Hickey 2010). However, angiosperms can also have a high density of leaf area (Dunn et al. 2015). In any case, light absorption approaches saturation at a landscape LAI of 5.5, and various modern tropical and temperate forest biomes each average between 4 and 6, with all achieving at least 90% attenuation of photosynthetically active light (Asner et al. 2003). If anything, the upper bound of leaf area has likely increased in the time since angiosperm evolution: Cenozoic polypod ferns

have evolved phytochromes that can work at uniquely low light levels (Watkins & Cardelús 2012), allowing their radiation as rainforest epiphytes and likely slightly increasing the maximum LAI seen in rainforests. However, under the microenvironmental circumstances of polypod fern leaves operating just above a depressed light compensation point, their addition can hardly be expected to have much of an environmental impact. Leaves at the top of the canopy have the highest transpirational and photosynthetic rates and determine the albedo of the system; the effects of any additional leaves necessarily must be added to the low-light environments at the bottom of the canopy, where the least physiological work can be done. Thus, although there is no obvious reason to expect the leaf area of a particular biome type to have changed dramatically over the past several hundred million years, even if dramatic changes in leaf area occurred, the environmental impact should be less dramatic: Doubling the LAI of a particular forest type from 4–5 to 8–10 would have some effect but would not be expected to double rates of photosynthesis or transpiration because the extra leaves would be added deeper and deeper in the shadows.

6. INDIRECT FEEDBACK OF PLANTS ON CLIMATE THROUGH ATMOSPHERIC COMPOSITION

6.1. The Chemical Weathering of Silicates

In addition to direct feedbacks on precipitation and temperature, plant evolution also has influenced climate indirectly by altering atmospheric composition and the abundance of greenhouse gases. The need for some kind of chemostat feedback to keep atmospheric CO₂ concentrations within a reasonable range has been recognized (e.g., Berner & Caldeira 1997), and the drawdown of CO₂ by the chemical weathering of silicate rocks has been seen as the key candidate (Berner et al. 1983). When CO₂ is high, both the warmer temperatures and the resulting enhanced hydrological cycle increase the rate of CO₂ consumption by the chemical weathering of feldspars and other silicate minerals to clays. The cold temperatures associated with low CO₂ concentrations slow this process, allowing more CO₂ to accumulate in the atmosphere. Land plants—specifically the deep-rooting vascular plants that first appeared in the Devonian—have been proposed to play a key role in this process (Berner 1992). Plants produce soluble organic acids that, alongside CO₂, can contribute to chemical weathering. Furthermore, the respiration and eventual decay of roots provide a direct source of CO₂ at depth, so that soil CO₂ concentrations can be high even when atmospheric CO₂ is relatively low. These processes are modeled to have led to a pronounced drop in atmospheric CO₂ concentrations suggested as a cause for subsequent glaciations (Berner 2004).

The pervasive impact of Berner's work (Berner 1992, 2004), however, has generated some problems. A similar plant-based increase in chemical weathering has subsequently been evoked for a whole series of earlier environmental events: the end-Ordovician glaciation (Lenton et al. 2012), a late Neoproterozoic increase in oxygen (Kennedy et al. 2006; but see Tosca et al. 2010), and even the earlier Proterozoic abundance of chemically mature, highly pure quartz arenite sandstones (Dott 2003). It is reasonable to think that land plants did lower atmospheric CO₂ levels by increasing the weathering rates of continental silicates; however, all of the various alternative claims should probably be recognized as mutually exclusive. If microbial soil crusts are argued to have already dramatically increased chemical weathering in the Proterozoic, then that is implicitly an argument against such a weathering increase with the evolution of Devonian vascular plants. If the impact of the modern vegetation is atomized and allowed to accrue incrementally—for example, with production of soluble organic acids appearing with Ordovician bryophytes but elevated soil CO₂ concentrations not appearing until the respiration of deep roots in the Devonian—then the impact on atmospheric CO₂ might also be expected to be incremental and without the singular,

dramatic Devonian drop seen in models of the long-term carbon cycle (Bernier 2006). Indeed, the initial evolution of deep-rooting vascular plants was in the Devonian (Algeo & Scheckler 1998), but evidence for their spread out of the distal lowland floodplains across the larger landscape comes more from the Carboniferous, as discussed in Section 5, so their impact on CO₂ concentrations should perhaps not be assumed to be a step function associated with their first appearance. We advocate no particular position here other than the recognition that there is more work to be done (e.g., Morris et al. 2015) and that the current conventional expectations may not be the final word.

6.2. Biomass Accumulation and Preservation

Plant evolution may also be expected to impact CO₂ concentrations more directly through the photosynthetic sequestration of atmospheric CO₂ as biomass: The terrestrial biosphere, including soil, currently contains approximately three times more carbon than the atmosphere (Stocker et al. 2013). Biomass is, nonetheless, still small relative to crustal reservoirs of carbon, and biomass production and decay should be in steady state over geological timescales; thus, biomass turnover is of minimal relevance to the long-term carbon cycle (Bernier 2004, Bernier et al. 1983). The initial forestation of the planet could have been an important perturbation, but the protracted spread of that vegetation would likely have rendered imperceptible the change in atmospheric CO₂ levels that was specific to the original biomass accumulation. Still, perturbations of atmospheric CO₂ concentration might be possible with large-scale but short-term perturbations of terrestrial vegetation (Bernier 2004), such as the globally widespread forest fires that might have been associated with the Cretaceous–Paleogene extinction or the Paleocene–Eocene Thermal Maximum (e.g., Vajda et al. 2001). Indeed, disruption of canopy transpiration during these events may also have impacted the hydrological cycle and temperature, more so after angiosperm evolution than in earlier events, such as the Permian–Triassic extinction (Boyce & Lee 2010).

More relevant to the long-term carbon cycle is the burial in sedimentary deposits of a small fraction of photosynthetic production, thereby preventing reoxidation. Besides silicate weathering, organic matter burial is the other major sink of CO₂ in the long-term carbon cycle, and it was of particular importance early in the evolution of forested ecosystems; an outsized proportion of all coal comes from the Carboniferous. This pattern of coal accumulation has commonly been attributed to the delayed evolution of fungi capable of degrading lignin, the recalcitrant cell wall constituent that is abundant in woody vascular plants (e.g., Meyer-Berthaud et al. 2010); however, this hypothesis has been found to be broadly inconsistent with the fossil and sedimentary record (Nelsen et al. 2016). Preservation of any terrestrial organic matter, whether lignified or not, is dependent on proximity to a depositional system where waterlogging promotes anoxia. Thus, land plant evolution has been essential in that plants provide the source of organic matter being preserved, but coal deposition is ultimately dictated by tectonics and climate, with the details of plant biochemical evolution having no special relevance.

7. DISCUSSION: PLANTS CHANGED CLIMATE, BUT WHEN EXACTLY?

Discretely segregating plant evolution into architecture, physiology, and landscape occupation is not strictly appropriate because these properties clearly interact. For example, evolution of physiological characteristics that allow for tolerance of strongly negative xylem water pressures (Pittermann 2010) was surely relevant to the colonization by seed plants of more arid habitats. As a second example, we argue that it is important to keep in mind the pigmentation of microbial soil crusts and mats; however, these features have no capacity to be emergent above snow. Thus, the late Paleozoic spread of forests might have had a large seasonal impact on albedo at high latitudes

and altitudes even if the replacement of a microbial flora by forests had a more muted impact on albedo at low latitudes and altitudes. In this context, some evolutionary changes may even be expected to have opposite effects depending on scale. For example, the structural, biochemical, and behavioral changes associated with crassulacean acid metabolism photosynthesis in succulents as diverse as desert cacti and euphorbs as well as epiphytic orchids and bromeliads (Lüttge 2004) provide for increased water use efficiency, thus leading to less transpiration for a given amount of photosynthesis. However, these changes also may contribute to greater occupation of drier environments than might otherwise be permissible. Thus, an individual plant's capacity for water conservation might lead to more transpiration overall at the landscape scale.

Despite these issues, the goal of separately considering different aspects of the land plant evolutionary radiation is to emphasize that the first appearance of an evolutionary lineage or anatomical characteristic does not necessarily herald an immediate climatological or geobiological impact. Despite the considerable scientific attention that has been directed to the Devonian evolution of vascular plants and the Cretaceous evolution of flowering plants, it may well be the Carboniferous and the Paleogene that represent the maximum expression of environmental impact for those two radiations.

Such temporal offsets between evolutionary origins and environmental occupation might have real manifestations. The mid-Devonian evolution of deep-rooting vascular plants and accompanying shifts in silicate weathering are often evoked as a potential causal mechanism for the Late Carboniferous glaciation (e.g., Berner 2004). Given the time lag of 70 Myr, this would be analogous to linking the modern glaciation to Cretaceous angiosperm evolution. A focus instead on the more recently discovered end-Devonian glaciation (Brezinski et al. 2010) would still only shorten the gap to 30 Myr. However, consideration of the timing of full landscape occupation might make a link more tenable. Regarding angiosperm evolution, both the Late Cretaceous and the Early Cenozoic represent warm intervals in Earth history. As with earlier warm periods (Ziegler et al. 2003), at least seasonal aridity was common at both low and mid-latitudes in the Cretaceous—despite the presence of continental seaways that would have reduced the distances of moisture transport. In the Early Cenozoic, high-precipitation forests extended from the tropics well up into the temperate zones (Morley 2000). The Late Cretaceous and Paleogene both came after the initial appearance and evolutionary diversification of the flowering plants. Along with further physiological innovation, what came in between was their geographic and environmental spread.

DISCLOSURE STATEMENT

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

ACKNOWLEDGMENTS

We thank R. Pierrehumbert, M. Foote, and P. Chamberlain for helpful discussion and encouragement. This work was supported by NSF-EAR-1415464.

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Errata

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