Uplands, lowlands, and climate: Taphonomic megabiases and the apparent rise of a xeromorphic, drought-tolerant flora during the Pennsylvanian-Permian transition

William A. DiMichele[a*], Arden R. Bashforth[b], Howard J. Falcon-Lang[c], and Spencer G. Lucas[d]

[a]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560 USA, dimichel@si.edu, corresponding author; [b]Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5-7, 1350 Copenhagen K, Denmark, bashforth@snm.ku.dk; [c]Department of Earth Sciences, Royal Holloway, University of London, Egham, Surrey TW20 0EX, UK, Howard.Falcon-Lang@rhul.ac.uk; [d]New Mexico Museum of Natural History and Science, Albuquerque, NM 87104, USA, spencer.lucas@state.nm.us*

ABSTRACT – The Late Mississippian and Pennsylvanian have been referred to as the Coal Age due to enormous paleotropical peat accumulations (coal beds). Numerous fossil floras have been collected from these coals, and their associated seatearth paleosols and roof shales, over more than two centuries, leading to the inference of vast swampy wetlands covering the Pangean tropics during the Pennsylvanian. In contrast, the Permian tropics are characterized as more arid, with sparser and more heterogeneous vegetation than inferred for the Pennsylvanian. In the tropics, the Pennsylvanian to Permian transition has been described as a changeover from a pteridophyte-dominated “Paleophytic flora”, to a seed-plant dominated “Mesophytic flora”. This view notwithstanding, floras dominated by xeromorphic seed plants also are well known from the Pennsylvanian tropics. Some authors have characterized these plants as being occupants of uplands, , subsequently transported into basinal-lowland, preservational environments. In this model, uplands are well drained, causing areas of drought under otherwise everwet climates. In this paper, we present an alternative interpretation: that the apparent transition in Pennsylvanian-Permian tropical vegetation reflects two types of megabias. First is a taphonomic megabias, strongly favoring the vegetation of humid climates over that of seasonally dry climates. Accordingly, tropical-plant preservational potential fluctuated in concert with Late Paleozoic Ice Age glacial-interglacial oscillations, and contemporaneous sea-level and climatic changes. Second is an analytical megabias, strongly favoring the discovery and collection of the wetland biome from Pennsylvanian strata, overlooking the less frequently and more poorly preserved drought-tolerant biome. By Permian times, vast wetlands, and their fossil record, had largely disappeared from central Pangea (although continuing in Cathaysia), making drought-tolerant vegetation more "visible" to searchers, without changing its preservational circumstances. We demonstrate that the upland model is untenable, being inconsistent with the principles of plant biogeography and with geological aspects of the fossil record.

Key words: wetland; dryland; Paleophytic; Mesophytic; late Paleozoic

1. Introduction

Contra negantem principia non est disputandum (Against one who denies the principles, there can be no debate). -- Arthur Schopenhauer, Eristische Dialektik (1831)

It has long been recognized that the Pennsylvanian wetland flora of Pangea's Euramerican tropical latitudes differed significantly from the drought-tolerant, xeromorphic flora that later typified those tropical regions during the early Permian. This change in the most commonly found types of plant fossils has been attributed, we believe correctly, to a long-term drying trend in the tropics, which began at the end of the Early Pennsylvanian and continued, in a long-wavelength, oscillatory manner, into the Permian (e.g., McKee and Crosby, 1975; Cecil et al., 1985; Joeckel, 1995; Roscher and Schneider, 2006; Schneider et al., 2006; Schneider and Romer, 2010; Rosenau et al., 2013; DiMichele et al. 2011; Opluštil et al., 2013a; Martino, 2017). For many years, there has been a sense that these long-term climatic changes were accompanied by the rise of a distinctive kind of vegetation, the so-called Mesophytic Flora (e.g. Gothan, 1912; Gothan and Gimm, 1930; von Bülow, 1942; Fredericksen, 1972; DiMichele et al., 2008; Cleal and Cascales- Miñana, 2014) that typified the Permian, an emergence that could be used as a biostratigraphic guide. The line of reasoning is that even if the exact Pennsylvanian-Permian boundary were fuzzy in terms of lithological and biotic composition, one could discern the difference between these time periods by the on-average compositional aspects of their floras. This argument can be found in discussions about the age of floras dominated by more xeromorphic elements, such as conifers, callipterids, *Taeniopteris*, and others (e.g., Fredericksen, 1972; Bode comments following Gillespie et al., in Barlow, 1975; Wagner and Lyons, 1997;

DiMichele et al., 2008; van Hoof et al., 2013), which differ greatly from the wetland floras found in association with coal beds, primarily from partings, roof-shales, seat-earths, and fossils from the coal beds themselves (palynomorphs and coal-balls).

Kerp (1996, 2000) and later DiMichele et al. (2008) argued that these terms had significant problems, noting that there was a major conceptual change between their original definitions and subsequent use. In essence, the terms had moved from representing stratigraphically-diagnostic floras to representing distinct biomes. With that shift, although the new concept filled a clear need, it also conflicted with the original sense of the terms, which were now largely incongruent.

Before going further in our exploration of this matter, some terms that we use in this paper must be defined. We broadly demarcate the different regions of equatorial (or, interchangeably, tropical) Pangea into its western, central, and eastern parts. The areas envisioned do not have formal, latitudinal boundaries, and are outlined both spatially, and in terms of prevailing aspects of their environment, particularly climate. Western equatorial Pangea is considered to stretch from the Panthalassan coast line, present-day western United States and northern Mexico, into the regions of the western Midcontinent, approximately West Texas, and western portions of Kansas, Nebraska, and Iowa. Central equatorial Pangea encompasses those regions characterized by extensive coal-bearing strata, located in a string of basins from North-Central Texas, eastern parts of Oklahoma, Kansas, Nebraska, and Iowa (the Midcontinent region of the U.S.), through the eastern U.S. (Illinois and Appalachian basins), the Maritime basins of eastern Canada, the Variscan regions of Europe, and into the Donets Basin of the Ukraine. Eastern equatorial Pangea includes regions of the Middle East, southern Russia, and China.

We also employ various terms to describe assemblages of plants, both alone and in their environmental context. The terminology is somewhat hierarchical, reflecting the fact that ecological terminology is notoriously non-quantitative, conceptual, and often scaled to the problem being addressed. The term "vegetation" is used in a very general sense, and refers to the plants growing in an area of unspecified size, with possible consideration of their physiognomy, or relative abundances. A "biome" means an assemblage of plants with particular physiognomic characteristics, associated with certain soil and climatic conditions. The term has broad taxonomic implications, mainly at higher taxonomic levels, such as arborescent lycopsids, conifers, tree ferns, or callipterids. By "habitat", we refer to the physical-environmental, abiotic variables that predominate in an organism's site of growth. Although not scale-free, the concept of habitat does depend on the size of the organisms in question. There may be a variety of different habitats and microhabitats (differentiated inexactly by spatial scale) within a biome, and they may harbor quantitatively different proportions of species from place to place, and differ compositionally from one another. The concept of "niche" is frequently used side-by-side with habitat, and captures the multidimensional life-history strategy of an organism. Thus, a niche includes biotic interactions and the physical environment in which an organism lives. A "flora" is taxonomically specific, but non-quantitative, and refers to the plant taxa, at the finest resolution possible, for a particular area, or within a biome. A "species pool" refers to the suite of species in a particular geographic area that potentially could colonize any portion of that region, even if the plants might not be able to survive under the particular local conditions at any given moment; in other words, these are the species for which there is no dispersal limitation. A "community" is an assemblage of species living under a common set of physical and climatic conditions, and is characterized quantitatively by a particular dominance-diversity profile. We use “ecosystem” to include both plants and animals in an expanded version of the community concept, recognizing both internal factors such as nutrient cycling, soil chemistry and microbiome, organism interactions, and external factors such as climate. A “landscape” is a dynamic mixture of variably interconnected populations, communities, and/or ecosystems over an unspecified area.

In order to understand the spatio-temporal patterns of the equatorial vegetation during the Pennsylvanian and early Permian,, it is necessary first to understand the environmental conditions experienced by the Earth’s tropical regions during this time interval. For much of the late Paleozoic, the Earth experienced a millions-of-years long, complex, cool-climate mode that is now termed the Late Paleozoic Ice Age (LPIA), the basic physical attributes of which are well documented (e.g., Fielding et al., 2008; Isbell et al., 2012; Montañez and Poulsen, 2013). This interval was characterized by regular glacial-interglacial fluctuations, superimposed on longer-term variations in ice volume, including times when Earth was nearly ice free. Although the LPIA encompassed a long-term, Pennsylvanian-Permian drying trend, intermediate-term fluctuations, millions of years long (e.g., Roscher and Schneider, 2006; Schneider, 2008; Fielding et al., 2008; Isbell et al., 2012), of more or less ice were superimposed on this trend, in addition to much shorter term glacial-interglacial cycles on the scale of 100,000 to 400,000 years (Heckel et al., 2007; Isbell et al., 2012). These latter, glacial-interglacial oscillations are closely linked to attendant, covariant changes in ice volume, sea-level, and global climate (Heckel, 2008; Cecil et al., 2003a; Tabor and Poulsen, 2008). The combination of paleosol studies (e.g., Joeckel, 1995; Driese and Ober, 2005; Rosenau et al. 2013), coal quality analyses (Mastalerz et al., 2004; Neuzil et al., 2005), isotopic examination of plant remains (Montañez et al., 2017; Richey et al., 2018), and sedimentological studies (Martino, 2017; Bashforth et al., 2016a, b; Falcon-Lang et al., 2015) suggests that the environmental fluctuations on glacial-interglacial, and perhaps even shorter time scales may reflect the influence of orbital variations, within the spectrum of Milankovich cycles (Falcon-Lang, 2004a; van den Belt et al., 2015).

Thus, the Pennsylvanian Coal-Age tropics did not exist under a uniformly humid, high-rainfall, warm climate (Gastaldo, 1996; Falcon-Lang et al., 2009, 2011a). Rather, climate varied both spatially and temporally in an oscillatory manner (Cecil et al., 2003a). The Euramerican coal basins of Central Pangea, in particular, experienced fluctuations in moisture distribution and abundance, and probably also temperature (Tabor et al., 2013), on time scales of approximately 100,000 and 400,000 years (Heckel, 2008; Cecil et al., 2014). These time frames are of much high-frequency (shorter wave-length) than the longer-term decline in average tropical moisture through the Pennsylvanian and into the Permian. In the central regions of the Pangean tropics, it appears that, the longer-term drying pattern was expressed on glacial-interglacial time frames by the wet intervals becoming less wet, and the dry intervals becoming more dry (e.g., Schutter and Heckel, 1985; Joeckel, 1999; Roscher and Schneider, 2006).

As more data have emerged, both from western equatorial Pangea and from those strata in coal basins not directly associated with (i.e., between, but not in contact with) the coals, it has become clear that plant biogeographic patterns and environmental events of the time were complex, and that climate was not ever-wet throughout the tropical regions of central Pangea. In brief, it appears that the western regions of Euramerican Pangea were drier, on average, than the central parts of the continent throughout all of the Pennsylvanian, and harbored permanently resident drought-tolerant plant populations (White, 1912; Arnold, 1941; Rothwell and Mapes, 1988; Mamay and Mapes, 1992; Tidwell and Ash, 2003; DiMichele et al., 2017; Tabor et al., 2013; Falcon-Lang et al., 2015). Populations of drought-tolerant plants also existed in portions of the Variscan/Appalachian mountain complex, also known as the Central Pangean or the Trans-Pangean Mountains (e.g., Roscher and Schneider, 2006; Peyser and Poulsen, 2008), where, at times, there may have been rain-shadow effects (Broutin et al., 1990; Kerp, 2000; van Hoof et al., 2013). The iconic swampy wetlands that have come to symbolize the Pennsylvanian were primarily located in the central parts of the continent, which today are the Midcontinent through Appalachian regions of North America, the Canadian Maritimes, and much of Europe. These wetlands persisted as periodic, widespread environments in the eastern part of Pangea, present-day China, continuing in the Permian (e.g., Guo, 1990; Hilton and Cleal, 2007; Pfefferkorn and Wang, 2007). However, central Pangea, and later eastern Pangea, experienced strong swings in climate from humid/perhumid to subhumid/semi-arid, on glacial-interglacial-orbital time frames of hundreds of thousands of years (e.g., Cecil et al., 2003a). Consequently, the wetland biome was periodically fragmented and reduced to survival in refugial areas (Falcon-Lang et al. 2009; Looy et al., 2014b). Climate models (e.g., Poulsen et al., 2007; Peyser and Poulsen, 2008; Horton et al., 2012) suggest that there were no permanently widespread wet belts within or peripheral to the equatorial regions, within which large expanses of such vegetation resided permanently, nor did such areas appear during times of spreading aridity to which such vegetation might have dispersed *en masse* (DiMichele et al., 2010; Falcon-Lang and DiMichele, 2010; Wilson et al., 2017). Thus, it is possible that the Pennsylvanian tropics were dominated by drought-tolerant plants for longer periods of time than they were dominated by peat-forming and associated wetland vegetation (Falcon-Lang et al., 2009). However, the much lower likelihood of preservation of the drought-tolerant vegetation (Gastaldo and Demko, 2011) leaves us with a strongly biased impression of the Pennsylvanian tropical region.

In this paper, we examine various aspects of plant taphonomy in the late Paleozoic tropical region. We argue that the diminished fossil record of wetland vegetation, and the coincident increase in the proportional representation of xeromorphic, drought-tolerant vegetation at the Pennsylvanian-Permian transition does not coincide with the origin of drought-tolerant vegetation. Rather, one or more xeromorphic, drought-tolerant biomes existed long beforehand and covered vast areas of tropical Pangea. during the Pennsylvanian The perceived rise to dominance of drought-tolerant vegetation in the tropics near the Pennsylvanian--Permian boundary reflects a series of taphonomic factors that, in combination, constitute what Behrensmeyer et al. (2000) term a " preservational megabias" and an "analytical megabias". In undertaking this analysis, we also consider an assertion, which may be unique to the literature involving late Paleozoic paleobotany, that elevation results in drainage, and that drainage causes drought. This assertion clearly assumes, either implicitly or explicitly, an unchanging humid, high-rainfall "tropical" climate; thus the occurrence of xeromorphic floral elements is simply considered to be an indicator of nearby uplands, even of modest elevation (Cridland and Morris, 1963; Pfefferkorn, 1980).

2. The Late Paleozoic Ice Age

The late Paleozoic Era was the last extensive period of polar glaciation experienced by the Earth prior to the late Cenozoic (Gastaldo et al., 1996). The so-called Late Paleozoic Ice Age (LPIA) consisted of several, distinct 10^6-year periods of more intense glaciation separated by similarly long intervals of warmth (Fielding et al. 2008; Isbell et al., 2012). Arguably, the LPIA began with a short period of glaciation during the latest Devonian (Brezinski et al., 2008, 2010;

Isaacson et al., 2008) that may have continued at a variable intensity through the Early Mississippian (Mii et al. 1999; Buggisch et al., 2008; Kammer and Matchen, 2008). A long warm period intervened and was terminated by renewed glaciation, which persisted from the Late Mississippian (e.g., Roscher and Schneider, 2006; Gastaldo et al., 2009a), through the Pennsylvanian (e.g., Falcon-Lang, 2004a; Heckel et al., 2007; Heckel, 2008; Montañez and Cecil, 2013; Cecil et al., 2014), and into the early Permian (e.g., Beerbower, 1961; Miller et al., 1996; Olszewski and Patzkowsky, 2003; Montañez and Poulsen, 2013). As noted above, this long interval witnessed 10^6-year oscillations in ice volume, and attendant fluctuations of sea-level and climate. Furthermore, superimposed on these fluctuations was a long-term drying trend in the Pangean tropics that extended from the Early Pennsylvanian, perhaps Late Mississippian, into the Permian (Schutter and Heckel, 1985; Roscher and Schneider, 2003; Tabor and Poulsen, 2008; DiMichele et al., 2011; Opluštil et al., 2013a). This trend was accompanied by significant changes in the vegetation (Kerp and Fichter, 1985; Šimůnek and Martínek, 2009; Opluštil et al., 2013a; Wagner and Álvarez-Vázquez, 2010), particularly that of the tropical peat-forming wetlands (e.g., Phillips et al., 1974; Pfefferkorn and Thomson, 1982; Phillips and Peppers, 1984; Kosanke and Cecil, 1996; Montañez, 2016).

The tropical wetland biome of the Carboniferous is one of the best known and most intensely studied plant assemblages of the Phanerozoic, due to the association of the plant fossils with coal, where, for more than two centuries, they have been exposed by mining operations (DiMichele and Falcon-Lang 2011). Thus, wetland plant fossils, collected mostly in active mines from roof-shales and seat-earths, and sometimes from the coal bed itself, dominate the late Paleozoic paleobotanical collections in many museums in Europe and North America. The plant fossils form the basis of thousands of scientific books and papers, and underpin the conventional viewpoint of the Pennsylvanian terrestrial tropics. Indeed, the image of the Carboniferous world as an omnipresent wet, tropical jungle began with some of the earliest paleobotanical studies in the 1800s. This firmly entrenched perspective of the Coal Age is reflective of the abundance and excellence of preservation of wetland plant fossils, and frequent encounters with them by paleobotanists, made possible by an Industrial Revolution fueled by coal mining.

The geologic record of Pennsylvanian strata in the Euramerican regions of tropical Pangea provides an enormous amount of evidence for glacial-interglacial cycles, reflected in regular oscillations of sea-level and climate. These oscillations have a periodicity of roughly 100,000 to 400,000 years or less (e.g., Heckel et al., 2007; van den Belt et al., 2015), broadly similar to those seen in the Pleistocene and Holocene world. The oscillations are recorded in parts of the Euramerican tropics by stratigraphic sequences described as “cyclothems” (see Langenheim and Nelson, 1992, for a full history of the concept), particularly from where the landscape was broad and flat over millions of hectares. In the central United States, where the concept originated (Shepard and Wanless, 1935; Wanless and Shepard, 1936), the term cyclothem describes a package of strata that usually contains a marine and a terrestrial phase (Figure 1). The degree to which these phases are developed depends on the regional topography, distance from the contemporaneous shelf edge, and the extent of accommodation space created by a combination of regional tectonism, sea-level dynamics, and sediment compaction (e.g., Kvale et al., 2004; Opluštil et al., 2013b). In some parts of the Pangean tropics, such cycles are preserved in almost entirely marine successions, with the terrestrial phases represented only by exposure surfaces (e.g., Elrick and Scott, 2010). In other regions, cyclothems consist of mixed marine and terrestrial successions, including the arid parts of western Pangea (the Paradox Basin of Utah; Jordan and Mountney, 2012), and the American Midcontinent and Illinois Basin

(Heckel et al., 2007; Heckel, 2008; Falcon-Lang et al. 2018). In regions relatively distant from the continental margin, such as the Appalachian Basin, largely terrestrial successions are characteristic, with only occasional marine beds (Klein and Willard, 1989; Heckel et al., 1998; Greb et al., 2008). In Europe, within what were mountainous regions of Central Pangea, such successions are less well developed, although cyclic sequences have been identified (Gastaldo et al., 2009a, b; Opluštil et al., 2013b; Opluštil and Sýkorová, 2018), recording changes in climate and associated sedimentation patterns.

For our purposes, it is important to recognize the nature of Late Mississippian through early Permian changes in the amount and nature of environmental complexity, which had a major effect on the changing vegetational patterns in the paleo-equatorial region. Climatic changes on many different spatio-temporal scales occurred throughout the Pangean tropics, causing repeated changes in physical conditions, frequently over vast areas of thousands of kilometers, and on a variety of time scales. The Pennsylvanian and Permian were not times of environmental quiescence. The Pennsylvanian was not simply "wet", nor was the Permian "dry". Rather, during the Pennsylvanian long intervals of nearly aseasonal rainfall, on time scales ranging from roughly 1000 to 10,000 years, regularly transitioned to similarly long or longer intervals of seasonal aridity. As noted above, the balance between these two extremes trended, on average, toward greater aridity in a time-transgressive, west-to-east direction across the Pangean supercontinent (Schutter and Heckel, 1985; Roscher and Schneider, 2006; Cecil et al. 2003a). By the Permian, although fluctuations on various time scales still occurred, the balance in Euramerica had shifted to less rainfall overall. Such environmental change was an important driver of ecological changes on the broad scale of the Euramerican tropical landscape.

3. The preservation of terrestrial organic matter

In order to interpret the plant fossil record in evolutionary or ecological terms, it is necessary to understand the variables that affect the preservation of plant remains, as organic compressions, impressions, or trace fossils, encompassed by the discipline of taphonomy (see, for summary, Behrensmeyer et al., 2000). The most important observation is that most plant remains have almost no chance of preservation, or of leaving even a trace of their former existence. To be preserved, either as an organic compression, or as an impression from which the organic matter has decayed, plant remains must be buried under conditions that inhibit decay, are unlikely to be disturbed by bioturbation, and, ultimately, are unlikely to be removed by erosion too quickly.

3.1 A model for terrestrial organic matter preservation

One of the most cogent analyses of the preservational biases affecting the plant fossil record is that of Gastaldo and Demko (2011), as further modified by Looy et al. (2014). The discussion below primarily is drawn from these two sources. Mainly focused on the preservation of organic matter, this model applies to most forms of preservation, and thus can be generalized. We consider there to be three stages of preservation in order for plant remains to become part of the geological record (Figure 2).

The first condition is short-term preservation, usually on the time scale of hours to months, but of years in some instances. Organic matter will be destroyed rapidly if not removed from the zone of oxidation, and particularly away from the activities of microorganisms (fungi and bacteria) and detritivorous arthropods. This requirement can be achieved through burial under dysoxic to anoxic conditions, either in oxygen-depleted parts of the water column, or below the vadose zone. Such preservation also may be facilitated by ash falls or other volcanogenic sediments (e.g., Burnham, 1993; Wang et al., 2012; Opluštil et al., 2014), but these instances still must conform with the strictures requiring non-oxidative conditions.

The second stage, intermediate-term preservation, entails conditions that remove organic matter from the effects of erosion, or from other destructive effects resulting from changes in landscape hydrological features. Spanning hundreds to thousands of years, this intermediate stage requires the creation of accommodation space. This process can be accomplished by sea-level rise that drowns coastal areas, including the areas that flank rivers/estuaries or lakes, accompanied by the accumulation of siliciclastic or carbonate sediments (e.g. Falcon-Lang and DiMichele, 2010; Cecil et al., 2014; Falcon-Lang et al, 2016; Nelson et al., 2020). Preservation may be further facilitated by the compaction of sediment or peat, which also can create intermediate-term accommodation space (e.g., Kvale and Archer, 1990).

The final stage is long-term preservation. This phase relies on the plant-bearing deposit being located in an area that is undergoing subsidence (i.e., in a depositional basin). Thus, there are very few documented examples of anything other than basinal, lowland, often coastal settings preserved in the Paleozoic fossil record. In the younger geological record, there are examples of floras preserved in fully terrestrial, intracontinental basins. In the context of upper Paleozoic deposits, however, there has been ample time for erosion to do its work, and hence inland or high-elevation basins are unlikely to be preserved. Exceptions are noteworthy, and, for the Pennsylvanian and Permian equatorial zone, come primarily from the mountainous regions of Central Pangea (Roscher and Schneider, 2006; Opluštil and Cleal, 2007) where complex tectonics ocassionally created conditions that enabled the preservation of vegetation that grew in elevated areas; under most circumstances, the record of vegetation from such settings has little chance of preservation in the long-term geological record. The first, and by far the most common, instance occurs when plant remains are transported to the floor of a narrow valley from the surrounding slopes, and buried there (e.g., Opluštil and Cleal, 2007, p. 237; Stárková et al., 2016; Libertín et al., 2009; Cleal et al., 2017). Very rarely, true upland areas may be buried below the zone of erosion, due to particular tectonic circumstances. Opluštil (2005) provided one such example, from the Czech Republic, where sediments were deposited in a network of relatively narrow valleys that were bounded by ridges up to 200 m high, and incorporated plant remains that originated from the valley walls. More importantly, the intramontane setting was interpreted to have been initially at an elevation of ca. 1000 m within the Variscan mountains.

The end result of this series of short-, intermediate-, and long-term preservational events, is a highly biased paleobotanical record, one that favors the preservation of plants that lived under humid climates, near a body of water, and in lowland, actively subsiding basins. Preservation is enhanced if the plant-bearing deposits were proximate to shorelines, either in coastal areas subject to flooding during sea-level rise, in peri-marine areas, or in off-shore brackish to shallow marine coastal waters or lagoons (e.g., the famous Middle Pennsylvanian Mazon Creek biota – Schellenberg, 2002; Clements et al., 2018). If burial occurred in areas that were not proximate to marine conditions, such as in intracratonic basins or basins within mountainous regions, active tectonic subsidence and thick sedimentary accumulations were essential for the preservation of plant fossils.

3.1.1 A climate modifier

In those areas of central Pangea with extensive coal deposits, the concept of the Pennsylvanian tropics being ever-wet with a persistent humid-to-perhumid climate (sensu Cecil, 2003) has been the default interpretation for most of the history of its study. This presumption is revealed by reading the last 200 years of paleobotanical literature on Pennsylvanian plants, supplemented by peat/coal formation models from much of the last 50 years. However, as recognized nearly a century ago (e.g., Elias 1933; Elias in Moore, 1936), and as a large amount of evidence from physical geology indicates, equatorial coal basins of central and western Pangea alternated between “wet” and “dry” conditions, reflecting climatic fluctuations tied to glacial-interglacial cycles on a scale of 10^4 - 10^5 years. During the drier parts of these cycles, the short-term preservational potential of organic matter was severely curtailed.

Within the context of an ever-wet Pennsylvanian tropics, basinal areas are envisioned as having been perpetually water-saturated lowlands, thus always favorable to the short-term preservation of organic matter. Soil-moisture deficits are considered to be have been induced by elevation. Thus, it is hypothesized that only in upland regions, which are purported to have been much drier due to elevation-induced drainage, was a distinct biome to be found, composed of xeromorphic, drought-tolerant plants. However,, even a cursory examination of modern tropical rainforest areas demonstrates the falsity of this model. Where high, nearly aseasonal rainfall exceeds evapotranspiration for 10-12 months a year, areas of even several hundred meters of elevation harbor much the same species pool as those at lower elevations (e.g., Voromisto et al., 2004; Kenfack et al., 2014); differences in species composition under such conditions are primarily quantitative rather than qualitative. This does not to imply that elevation has no effect on the water table and species composition in tropical rainforest areas, as elevation certainly can play a role (e.g. Rennó et al, 2008), and we do not wish to overstate the case. We assert, however, that wholesale differences in species pools sufficient to distinguish unique biomes are not caused by topographic differences in rainforest landscapes under humid-to-perhumid climates. If there are major species pool changes caused by elevational effects within a tropical region characterized mainly by rainforest, those effects may reflect temperature changes with altitude, slope instability, etc. Biome scale differences thus tend to be caused by significant climatic differences within or between regions, or by climatic changes within a given region over time.

The controls on plant preservation, in conformance with the Gastaldo and Demko (2011) and Looy et al., 2014) models, indicate that climatic fluctuations dictated the contents of the species pools that occupied lowland, subsiding basins, rather than local, small scale elevational changes of 10s of meters. Furthermore, even if conditions for intermediate- and long-term preservation were present, the likelihood of short-term preservation was greatly reduced during intervals of seasonal drought, especially where the water table fell below the level of the buried plant remains during the dry season.

3.1.2 A sedimentology-by-climate modifier

Comment is warranted about sedimentation in tropical environments, and its relationship to climate. It is obvious that for macroscopic plant remains to be preserved, even in the short term, they must be buried in a sediment catchment. Actualistic studies of various modern sedimentary environments provide insight into the dynamics of such accumulations of plant remains (e.g., Spicer, 1981; Scheihing and Pfefferkorn, 1984; Gastaldo, 1986b; Spicer and Greer, 1986; Rich, 1989; Ricardi-Branco et al., 2009, 2020). Importantly, however, virtually all of these studies were performed in environments where active transport and deposition of siliciclastic sediments was taking place. There are, however, other riverine settings where streams carry little or no sediment. Both kinds of environments have direct relationships to climate.

Cecil and Dulong (2003) specifically examined the relationship between sediment transport from terrestrial environments into streams and rivers, and thence into downstream depositional settings. They found (Figure 3A) that sediment transport is greatest under subhumid to semi-arid, seasonal climate regimes, and declines significantly under both humid-to-perhumid and arid climates. In very wet habitats, plant canopy cover and rooting combine to reduce soil erosion. The more dense and closed the canopy, the greater the interception of rain and reduction of its impact on the soil surface (e.g., Brandt, 1988); and the more dense the root, and associated mycorrhizal, network, the greater the coherence of the soil (Gyssels et al., 2005; Baets et al., 2007; Li et al., 2017). Canopy cover and density of rooting are expected to be higher in humid terra firma forests than in seasonally dry forested habitats (e.g., Murphy and Lugo, 1986; Green et al., 2005; Rosado et al., 2011), possibly represented by lower turnover rates of fine roots in the wetter sites (Santantonio and Hermann, 1985). At the other end of the spectrum, there is less fluvial transport of siliciclastic sediment out of arid environments due to greatly attenuated surface runoff. The primary siliciclastic output from these environments is in the form of dust (Cecil et al., 2018) and occasional flash floods.

The projections of Cecil and Dulong (2003) were tested directly by Cecil et al. (2003b; see also Harris et al., 2008), who examined sediment discharge in a selection of tropical rivers, and found a strong relationship between the distribution (seasonality) of rainfall and sediment load. A similar relationship was reported by Latrubesse et al. (2005, see particularly their fig.6, reproduced here as Figure 3B), who examined a larger number of rivers than did Cecil et al. (2003b), and found that those in the tropics under largely aseasonal, high-rainfall climates generally carried very low sediment loads, despite often having high discharge volumes. Archer and Kvale (1994) and Nelson et al. (2020) described estuarine settings in which a similar climatic scenario was invoked to explain the development of siliciclastic tidalite deposits associated with coal beds in the Middle Pennsylvanian of the Illinois Basin, and sedimentological studies suggest this to be a general and widespread phenomenon by Pennsylvanian time (e.g., Gibling et al., 2014). An interesting modern analogue is the effect of human activities on the sediment load of rivers. In effect, deforestation and intense agriculture mimic the effects of decreased rainfall by removing tree canopies and rooting, resulting in increased sediment loads (e.g., Bruijnzeel, 2004), whereas the damming of rivers may have effects on sediment load similar to high, aseasonal rainfall. These relationships have been documented for modern deltas (Nienhuis et al., 2020).

This piece of the preservation puzzle is important because it suggests that, during the wettest periods, when peat was accumulating in lowland settings (see below), the regional drainage system likely carried a very low sediment load. Not until climate began to shift to greater seasonality, but was still within the wet subhumid to humid range sensu Cecil (2003), did streams begin to carry more sediment. Thus, the environmental conditions under which peat-substrate floras accumulated – those represented by coal balls and coal palynology – likely were different from those under which adpression floras in siliciclastic seat-earth and roof-shale deposits formed, or those that formed offshore of coastal wetlands that developed following intervals of peat accumulation. Hence, the typical roof-shale flora above a coal bed is not entombed in flood-deposited sediments laid down during high-intensity, periodic storms under an otherwise unchanging climate (e.g., Thomas and Cleal, 2015). Rather, most roof-shales record larger scale events that involved a change in environmental conditions toward greater seasonality of rainfall, and thus less favorable conditions for peat accumulation, concomitant with increased sediment transport and rising sea-level in paralic regions (e.g., Kvale et al., 1994; Archer et al., 2016; Elrick et al., 2017a).

3.1.3 A peat formation-by-climate modifier

In assessing the environment of Pennsylvanian and Permian landscapes, coal is understood to be the "wet" end member of a wet-dry gradient. Representing a former peat swamp, a coal bed is presumed, for the reasons outlined in the Gastaldo-Demko/Looy et al. model, to indicate the most extreme example of the convergence of short-, intermediate-, and long-term preservational conditions. There remain, however, matters regarding peat accumulation and coal formation that require additional comment, based on observations of modern-day physical settings, or the physical and chemical conditions attending various kinds of environments.

We begin with the caveat that when discussing "peat", we are referring to widespread blanket peats that are low in ash content. As peat compaction and the processes that attend coalification take place, the ash content of the original peat will become magnified and rise proportionally relative to the percentage of fixed carbon (e.g., Shearer and Moore, 1996). If the siliciclastic content of the original peat is too high an organic-rich shale will result, rather than a coal.. For example, the U.S. Geological Survey excludes from its coal resource estimates organic rich rocks with ash weight-% ash content of > 33% (Wood et al., 1983). The objective here, therefore, is to consider those modern environments in which peat of coal-grade quality is accumulating, and in that aspect are analogues for Pennsylvanian and Permian peat swamps.

It is often presumed that peat formation is driven by rising sea-level, which causes coastal paludification, and the conversion of large, formerly well drained coastal areas to wetlands (e.g., Bohacs and Suter, 1997). Modern data indicate, rather, that peat formation is driven by climate, particularly by humid to perhumid conditions (terminology of Cecil, 2003), which, in the tropics, translates to 10-12 months per year during which rainfall exceeds evapotranspiration. Modern peat swamps, whether tropical, temperate, or boreal, are found only under these climatic conditions. In the tropics, some of the best examples of such peats are found in coastal Sumatra (possibly initiated by sea-level damming along river courses, but not by turning the coastal landscapes into vast wetlands) (Takahashi, 2002; Page et al., 2004; Domaine et al., 2010), intermontane Malaysia (where sea-level is not a factor) (Wüst and Bustin, 2001), or the Cuvette Centrale, an elevated inland region of the Congo (again, where sea-level is not a factor) (Dargie et al., 2017). To our knowledge, there are no extensive peat bodies today that appear to have formed as time transgressive belts advancing landward ahead of rising sea-level; there are abundant peaty, clastic-rich deposits forming in many coastal areas around the world, but these are not precursors to coal. Consider, if sea-level rise were the driver of peat formation, given the sustained sea-level increase since the last glaciation, coastal regions of the modern world should be blanketed in thick, low-ash peat, not by the thin organic mucks or banded high and low ash peats that occur only locally today.

If further proof is needed of the inefficacy of sea-level rise as the primary driver of peat formation, one also may turn to the geological record. Were rising sea level the cause of peat formation, then coal beds should be found throughout the Pennsylvanian geological record in western Pangea. They are not. Yet numerous episodes of sea-level rise and fall, accompanied by surface exposure, are documented in the western reaches of Pangea (e.g., Goldhammer et al., 1994; Cecil et al., 2003a; Elrick and Scott, 2010; Brand et al., 2012), and elsewhere in the world (e.g. Liu et al., 2017). Furthermore, given that sea-level has risen and fallen throughout geological history, one should expect coal beds to be associated with every event in the geological record recording a transgression of the sea over the land surface. This clearly is not the case.

There have been, and still are, widely promulgated and influential, models that place peat accumulation in environments close to areas of active siliciclastic sedimentation, such as in high-constructive deltas, and even lateral to carbonate lakes (e.g., Horne and Ferm, 1978; Valero Garcés et al, 1997; Thomas and Cleal, 2015) (Figure 4). In order for such landscapes to exist, the peat swamp and the carbonate lakes would foremost need to be protected from siliciclastic input. Second, the swamp would need to be forming in an environment with a climate that was equally favorable to the movement and transport of siliciclastics, the accumulation of peat, and the precipitation of carbonate, all in close proximity. And third, the pH distributions across the landscape would need to vary abruptly in order for peat and carbonate to be forming side-by-side. We cannot rule out that two or all three of these conditions could, in fact, sometimes coincide and permit low-ash peat to accumulate on a landscape with nearby significant siliciclastic deposition, and even carbonate lakes. In our opinion, however, such hypothetical environmental situations fail to account for the full range of data from sedimentology, geochemistry, and the known conditions promoting peat accumulation.

There also are suggestions that the siliciclastics between any two coal beds represent short-term flood deposits, from which the peat swamp rapidly recovered to recolonize the landscape, with most of the time in a coal-bearing section thus being represented by the coal (e.g. Thomas and Cleal, 2015; Thomas et al., 2019). However, the siliciclastic intervals between coal beds, however, rarely can be characterized as solitary floods, or even sequential floods over a brief time interval. Rather, the siliciclastic successions frequently contain paleosols, including Calcisols and Vertisols that take thousands of years to form, and both siliciclastic and carbonate marine strata, and it is not uncommon for some inter-coal siliciclastic deposits, or parts of them, to evidence strong overprinting by tidal forces (Kvale and Archer, 1990), all of which indicate dramatic environmental changes between one coal bed and the next. Furthermore, the thickness of strata between coal beds is not an indicator of the time encapsulated between those coals. Importantly, the siliciclastic portions of strata separating coal beds are most frequently characterized by numerous hiatuses (including paleosols), which account for the great majority of the time (Miall, 2014; Scott and Stephens, 2015).

Siliciclastic and carbonate deposits between coals are potentially very different in their significance than siliciclastic partings within single coal beds. Partings in coal beds may result from a wide variety of processes, from effectively instantaneous volcanic ash deposits (e.g., Greb et al., 1999a; Opluštil et al., 2007; Wang et al., 2012), to hiatuses of relatively short duration (e.g., Gresley, 1894; Fisher, 1925). Some thin layers of clay or siltstone separating two distinct benches of coal, when followed laterally for many kilometers, thicken and become fully developed intervals of siliciclastic, marine, and pedogenically altered strata (e.g., Jacobson, 1987, 1993).

In summary, it is imperative to consider climate as a variable when interpreting the sedimentological conditions under which peat accumulation and coal formation took place. There are conflicts in the conditions needed for peat to form and persist, for rivers to carry high sediment loads, and for carbonates to form. These incompatibilities may be resolved when climatic conditions favorable to those particular physical and chemical conditions are considered.

3.2 Modern environments as models for vegetational distribution

Modern tropical environments provide analogues for understanding the past and should be consulted to formulate models for the organization of ancient landscapes, ecosystems, and habitats. However, modern tropical landscapes can be extremely complex, with significant habitat heterogeneity, tracked by vegetation, as indicated for tropical rainforests (e.g., Salovaara et al., 2004, 2005) and rainforest wetlands (Junk et al., 2011). Similarly, tropical dry forest can demonstrate an even greater amount of habitat heterogeneity, with the differences between flats, slopes, and ridge crests accentuated by drainage effects (e.g., Roy and Singh, 1994; Balvanera et al., 2002; Balvanera and Aguirre, 2006; Ferreira-Nunes eet al., 2014). We emphasize that these drought-tolerant forests are known from areas of distinctly seasonal climate (Sanchez-Azofeifa, 2003; Santos et al., 2011; Dryflor, 2016), not from elevated areas in the midst of rainforests.

There are significant differences in the composition, biodiversity, and prevailing life histories between floras of the modern tropical world and those of the late Paleozoic. Despite these differences, however, many of the most basic patterns of plant distribution, and the factors controlling them, would have been the same: soil-moisture levels and changes in those levels throughout the year, temperature, especially the lowest temperature encountered, light regime, and the nature and frequency of disturbance agents, such as wind, floods, fire. All of these factors will be affected to some degree by elevation, slope, and aspect, but the nature of those effects will be strongly controlled by the prevailing climate. Important to our purposes here, the effects of slope and aspect also should have been much the same in the Pennsylvanian and Permian as they are today.

A major factor affecting comparisons between the Paleozoic and modern worlds is the difference in biodiversity and the variables that underlie that disparity. The much lower vegetational biodiversity of late Paleozoic may have resulted in sharper demarcations in species-by-environment segregation than in the modern world, leading to clearer boundaries between species pools, and to more obvious mapping of phylogenetic lineages onto habitat and niche spaces. Close mapping between phylogenetic lineages and ecological preferences has been labelled “phylogenetic niche conservatism” in modern ecological studies (e.g., Webb, 2000; Prinzing et al., 2001; Webb et al., 2004; Wiens and Donoghue, 2004; Losos, 2008; Wiens et al., 2010; Crisp and Cook, 2012; Prinzing et al., 2017; Saupe et al., 2018), and also has been examined in the geological record (e.g., DiMichele and Phillips, 1996; Hotton et al., 2001; Holland and Zaffos, 2011; Stigall, 2012; Brett et al., 2016). Pennsylvanian and Permian ecosystems appear to have been composed of significantly fewer plant species than compose modern ecosystems under similar climates and physical conditions; late Paleozoic plant diversities are at least an order of magnitude lower (Cleal et al., 2012; Moore et al., 2014). This lower diversity may reflect the predominant wind pollination and/or dispersal of the vast majority of species, permitting large, interconnected populations to exist, even where habitat space was fragmented (DiMichele, 2014, and citations therein). As a consequence, one might expect to find less variation in community-level composition across space because there were fewer possible component combinations. In effect, within any one Paleozoic species pool there were fewer species to divide up the resources than one would find in a modern ecosystem. One prediction, therefore, is that the niche-breadth of late Paleozoic plants would have been greater than that of plants in similar environments today. Alternatively, there may have been significant types of physical conditions that Paleozoic plants did not, or could not, occupy, including many in lowland, humid climate, basinal areas, where Paleozoic diversity is best documented and is strikingly lower than in similar modern settings. However, to our knowledge, no evidence supports this latter, alternative, hypothesis. Finally, the great extent of coastal areas occupied by lowland wetland habitats immediately prior to and during periods of peat accumulation in many parts of Euramerican Pangea may have no parallel in the modern world. If these were environments of considerable physical uniformity, they may have presented strong selective barriers to evolutionary innovation by virtue of the power of large-population incumbency effects (Knoll, 1985). Furthermore, distinctive microhabitats surrounding the basin margins (e.g., Leary, 1975; Leary and Pfefferkorn, 1977; Opluštil and Cleal, 2007; Stárková et al., 2016), harboring a larger species pool than that typical of basin centers, even under the same basic climatic background, have a comparatively low likelihood of survival into the geological record due to the effects of erosion.

Perhaps the most important observation to be made in the context of this article is that elevation, in and of itself, does not cause drought. Indeed surface runoff may be greater on steep slopes than in flatter terrain, and there will be downhill movement of water both across the surface and through the soil. However, as studies of tropical rivers show, high rainfall areas with low seasonality, and seasonally equable distributions of rainfall (humid to perhumid climates), typically have very low sediment loads, a reflection of the intense rooting and closed canopies that limit soil surface disturbance, sediment entrainment, and sediment runoff (Bruijnzeel, 2004). Elevation, by itself, does not guarantee low soil moisture, high levels of erosion, or sparse, drought-stricken vegetation (e.g., Figure 5). Furthermore, as indicated unequivocally by blanket-peat distribution in temperate regions (e.g., Gorham, 1957; Bragg and Tallis, 2001; Evans and Warburton, 2011), or, similarly, by high elevation inland-upland peat accumulations in the modern tropics (Amazon – Lähteenoja et al., 2013; Malaysia – Wüst and Bustin, 2001; Africa – Dargie et al., 2017), uplands are not necessarily, and certainly not obligately, dry. Rather, elevated areas are subject to periodic drought if the prevailing climate is seasonally dry, but they may experience little or no drought if the regional climate is aseasonally humid. As a case in point, the largest peatland on earth is found in the Cuvette Central of the Congo, in an interior, upland region (Dargie et al., 2017).

Consider also areas at temperate latitudes where there is considerable elevational change but little change in the species pool – climate is, once again, the controlling variable. For example, Figure 6 A-D illustrates both true upland and coastal lowland vegetation clothed in Eastern Deciduous Forest at various localities in east-central USA. These images show the remains of drought-tolerant species potentially being incorporated in shore-line sediments at present-day sea-level (Figure 6 A-B), under a subhumid, seasonal climate. Neither these plants, nor the other drought tolerant plants growing nearby, can be characterized as upland species. The coastal lowland region of the Chesapeake Bay (Figure 6C) affords a much greater opportunity for organic matter preservation than the upland region of the Central Appalachians in western Virginia (Figure 6D). Figure 6E illustrates a wetland at Caddo Lake, Texas, where the area immediately beyond the lake is dominated by drought-tolerant vegetation, thereby demonstrating how wetland vegetation can exist within a landscape dominated by seasonally dry plants. Note that, at 50 m surface elevation, this wetland has high short-term preservation potential, but, without significant sea-level rise or tectonically driven subsidence, likely poor prospects for intermediate or long-term preservation.

In many areas of the world today, where there is elevational change, such as in mountainous regions, there also is a broadly positive correlation between elevation and rainfall. Orographic cooling of moist air masses may result in increasing rainfall, and decreased drought, at intermediate to higher elevations. Thus, under many circumstances, uplands will receive greater volumes of rainfall than do lower elevation sites (e.g., Dhar and Rakhecha, 1981; Garcia-Martino et al., 1996), or greater moisture through fog and clouds, leading to the development of cloud forests (Bruijnzeel et al., 2011). We note that the relationship between these factors can be non-linear, and can vary in complex ways, both within mountainous terrain (e.g., Fleming, 1986; Chavez and Takahashi, 2017), and over broad continental regions.

Given the complexity and difficulties of making measurements and modeling rainfall in the present-day world (e.g., Goovaerts, 2000), however, when studying the Paleozoic, it is prudent to focus on the most general conclusions, and to allow for exceptions, but not to make the exceptions the rule. Perhaps the simplest generality is that regional climate is the most important variable controlling plant distribution. Under a given climate regime, whatever it may be, uplands may be subject to greater moisture stress than regionally nearby lowlands due to drainage, but also may receive the same or perhaps even greater moisture than the adjacent lower elevation sites. This generalization implies that, if the prevailing regional climate were humid to perhumid, the upland soils would probably also have high levels of soil moisture, including sufficient moisture to support upland swamps and lakes. In contrast, under sub-humid to semi-arid climates, the same uplands, depending on elevation, airflow patterns, nearby moisture sources, etc., may be far more heterogeneous compared to lower elevation sites, including the possibility of receiving more rainfall than the seasonally dry lowland regions. Thus, as seasonality increases into the realm of subhumid to semi-arid, the habitat heterogeneity of the landscape also may be expected to increase.

The literature on modern vegetation and its relationship to climate and habitat factors is enormous. In addition, we do not wish to oversimplify the matter – landscape slope and aspect, elevational change, winds, soil types, etc., have a great effect on vegetation in local areas. However, we are considering here whether or not elevational change of < 10 to a few hundred meters, under a regionally humid to perhumid climate, should be expected to yield completely different biomes that have few or no species in common.

As an example, consider the Kenfack et al. (2014) study of a Cameroonian rain forest, whichh has a climate at the borderline between wet sub-humid and humid in the categorization of Cecil (2003). A single species pool characterizes the 50 ha study area, within which there is nearly 100 m of elevational variation. The elevation of the study area varies from 150 to 240 m. More than 60% of the species have distributional centroids related to elevation, but of 489 tree species, 101 (21%) have no significant habitat preference, and only 171 (35%) were more dense in one of the five identified habitats than expected at random. For our purposes here, the key findings of the Kenfack et al. (2014) study are that the species pool was the same throughout the elevationally variable study area, and, although there were species differences associated with habitat, those differences could not be explained by better performance of the specialists under their "home" habitat conditions. This finding suggests that episodic droughts (caused by rainfall deficits, not by drainage per se) in this wet sub-humid environment may exert control over long-term patterns of plant distribution.

4. Sampling megabias of the Pennsylvanian plant fossil record

The Euramerican plant-fossil record of the Pennsylvanian Subperiod, as is clear from examination of more than 200 years of scientific literature, is overwhelmingly typified by plants from environments with persistently high levels of soil moisture, especially from swamps and other types of wetlands. This is particularly the case in areas where coal mining exposed great quantities of easily accessible rock strata for collecting plant fossils, particularly in mainland Europe, Great Britain, the Canadian Maritimes, and the eastern half of the United States. For the most part, the fossiliferous strata occur immediately above or below a coal bed.

Floras typical of seasonally dry habitats, however, also are present in what were the Pangean tropics. Although much less common than wetland floras, such drought-tolerant plants actually are not all that rare in coal basins. Rather, these fossils tend to be found only in natural outcrops, or in strata poorly exposed in surface coal mines, or not exposed at all in underground mines. Such floras, though uncommon, are the most frequently encountered in the Pennsylvanian and Permian strata of western Pangea, where there is little or no coal, and where the fossiliferous beds are mainly exposed on natural outcrops, road cuts, and, occasionally, in stone quarries.

4.1 Why are wetland floras so common?

The abundance of wetland floras stems, in part, from the fortuitous combination of the conditions best suited for the preservation of organic matter, as detailed by Gastaldo and Demko (2011) and Looy et al. (2014a), and summarized above. In the tropics, humid climatic conditions (sensu Cecil, 2003), in which rainfall exceeds evapotranspiration for 9-11 months of the year contribute not only to high soil moisture, but to the development of standing bodies of water in both coastal regions and floodplains, thus providing sites for short-term preservation. With only rare exceptions, virtually all floras collected from Pennsylvanian equatorial environments are from former depositional basins. Furthermore, in the absence of concrete sedimentological and structural evidence to suggest long-distance transport, it is most probable that the great majority of the plants actually lived in the basinal regions where they are found (DiMichele et al., 2010), thus increasing their likelihood of long-term preservation. In addition, and importantly, a great number of those basins were coastal, and thus subject to periodic marine inundation, or, if intramontane, were in settings subject to periodic influx of high sediment volumes during intervals of seasonal climate, when sediment mobility was greatest (see Cecil and Dulong, 2003). These situations provide conditions that enhance intermediate-term preservation. As a result, there is what Behrensmeyer et al. (2000) called an original "taphonomic megabias" favoring the proportional preservation of wetland plants above all others. We use the term "proportional" because we do not wish to imply that plants of seasonally dry landscapes cannot also grow in basinal lowlands, and also be preserved due to fortuitous combinations of taphonomic variables. Rather, we wish to imply that, from the perspective of likelihood, the preservation of wetland plant assemblages from certain geographic and tectonic settings is going to predominate in the plant fossil record, reflecting favorable original conditions for the burial and preservation of organic matter.

Also contributing to an over-representation of wetlands in our vision of Pennsylvanian landscapes is what Behrensmeyer et al. (2000) referred to as an "analytical megabias", a taphonomic factor that originates with the scientific procedures used, rather than necessarily resulting from original preservational conditions. For the Pennsylvanian, this megabias could be described as “seeing the world through coal-colored glasses” (Figure 7). In underground mining, the only fossiliferous beds typically seen are those immediately adjacent to the coal bed being extracted, or from mineral partings in the coal bed itself. Typically, accumulations of aerial plant remains in coal seat-earths represent early stages of swamp development (e.g., Gastaldo, 1986a; Stull et al., 2012), prior to the onset of peat formation. In contrast, roof-shales may form in a variety of ways (Gastaldo et al., 1995), but mostly preserve the final vegetation of the peat-swamp, or that of the mineral-soil swamps and wetlands that developed immediately after peat accumulation ceased. In some cases, these plants, which grew late in the wetter phase of a glacial-interglacial cycle, during coastal flooding, may have been transported from the fringing coastal plain and preserved in nearshore marine environments, where they then were preserved. One of the best examples of this process is represented by the well known Mazon Creek flora from the Francis Creek Shale, one of several roof-shale facies of the Colchester (No. 2) Coal bed of the Illinois Basin (Baird et al., 1985).

Surface mining also offers access to strata between coals, deposits that are not genetically associated with peat accumulation in swamps, or in the immediately preceding or following wetlands (e.g., Winston, 1983; Carpenter et al., 2011; Bashforth et al., 2016b; DiMichele et al., 2016). However, in surface mines, the plant-bearing strata between coal beds are rarely searched for, or their environmental context is lost when such fossils are collected from mine spoils. Thus, as a consequence of what might be called a “coal-mine perspective”, the image of the Pennsylvanian repeatedly presented in most illustrations and museum dioramas is that of vast wetlands, under an everwet climate (Figure 8A, B), a perspective derived from the fact that most fossils have been extracted from deposits formed during the wettest parts of glacial-interglacial cycles.

4.2 Where are floras of seasonally dry habitats found?

Within the coal fields of Europe and North America, there are deposits containing floras that are compositionally distinct from those found in or immediately above or below coals. The discovery of these plant fossils often is fortuitous, and occurs in surface coal mines, quarries, and other natural or artificial exposures. In these situations, plant remains tend to be found first by geologists carrying out mineral surveys, or doing stratigraphic studies or bedrock mapping. Some recent examples of these floras include discoveries in surface coal mines (McComas, 1988; Falcon-Lang et al., 2009; Carpenter et al., 2011; Bashforth et al., 2016b), in sinkholes in limestone quarries (Leary, 1975; Plotnick et al., 2009), from a gas-pipeline excavation (Martino, 2017), and from natural exposures (Leary and Pfefferkorn, 1977; Falcon-Lang et al., 2011a; Bashforth et al., 2014; Šimůnek, 2018, see description of *Cordaites olneyensis* from among several others). The elements of these floras include a variety of xeromorphic plants, typically associated with habitats that experienced periodic moisture stress (Figure 8C). Most noteworthy of these are conifers, cordaitaleans (an ecologically highly diverse group with members living in a variety of habitats, stretching from swamps to uplands), taeniopterids, certain noeggerathialeans (especially in western Pangea), and presumed seed-plants, such as *Lesleya* and *Megalopteris*. Various mesomorphic forms also characterize these floras, some of which also occur in more typical wetland assemblages, including certain odontopterids, mixoneurids, neurodontopterids, and, in some instances, callipterids. The composition of these floras varies with time and location. Furthermore, the floras frequently are what can be described as being "mixed", meaning that they also contain wetland components to varying degrees, particularly marattialean tree ferns and calamitalean sphenopsids, but also commonly certain medullosan pteridosperms. In our experience with late Middle and Late Pennsylvanian floras of the USA, *Macroneuropteris scheuchzeri* and *Neuropteris ovata* are the most common of these medullosans, both of which probably represent species complexes rather than single taxa. In the Late Pennsylvanian and early Permian, odontopterids, mixoneurids, *Neurodontopteris*, and *Reticulopteris* also become regularly encountered pteridosperm components of mixed assemblages.

4.2.1 Drought-tolerant floras in western Pangea

The western portions of tropical Pangea, in the present-day western USA, were, on-average, drier throughout the entire Pennsylvanian and Permian, meaning more seasonally dry and subject to lower overall annual precipitation, than central regions of the supercontinent. This observation is documented by the study of paleosols, by the presence of sedimentary environments typical of arid climates, by models of atmospheric circulation and rainfall patterns (McKee, 1975; Cecil et al., 2003a; Tabor and Montañez, 2002; Tabor and Poulsen, 2008), and by the paleobotanical composition of Pennsylvanian and Permian floras. Paleosols in western Pangea, for example, typically are Vertisols that frequently are calcic, even trending to calcretes (e.g., Goldhammer and Elmore, 1984; Joeckel, 1989, 1991, 1994; Cecil et al., 2003a; Feldman et al., 2005; Tabor et al., 2008; Goldberg and Miller, 2019; Tanner and Lucas, 2019). In the far western regions, such as present day New Mexico, Arizona and Utah, even where plant fossils characteristic of wetland environments have been found (e.g., Tidwell, 1967; Tidwell et al., 1992; Lucas et al., 2009), the fossil assemblages are not associated with coal beds, indicating that rainfall was sufficiently seasonal to preclude peat formation (Cecil, 2003). Furthermore, sedimentary settings in western Pangea include, as climate end members, evaporites and eolian deposits (e.g., Soreghan, 1992; Soreghan et al., 2002; Cecil et al., 2003a; Scott, 2005; Falcon-Lang et al., 2011a; Jordan and Mountney, 2012), which were contemporaneous with peat swamps, swampy wetlands, and seasonally wet habitats farther east in central Pangea.

Mixed floras containing, enriched in, or dominated by xeromorphic plants are the prevalent Pennsylvanian assemblages encountered in western Pangea. Early Pennsylvanian age floras from Colorado, Utah, Arizona, and Oregon (Read, 1934; Mamay and Read, 1956; Tidwell, 1967; Jennings, 1980; Tidwell et al., 1992; Tidwell and Ash, 2003) are not associated with coal beds; some even come from red-bed deposits. These Early Pennsylvanian assemblages are composed predominantly of wetland-species, which conforms to the inference of McKee (1975) that the tropics of the Early Pennsylvanian (his “Interval A”) experienced widespread humidity, including in the western regions of the Pangean continent. However, several of these floras also contain unusual elements that are not typical of floras found in association with coal beds, such as the noeggerathialean *Charliea*, the coniferophyte *Dicranophyllum*, ginkgophyte-like plants, and rare sphenopsids, such as *Phyllotheca*. These outlier taxa indicate close proximity of periodically moisture-stressed habitats to those with more stable water tables, although not wet enough for peat accumulation. These mixed assemblages occur because the existence of climatic seasonality creates enough habitat heterogeneity to permit drought-tolerant plants in areas of periodic moissture stress to live side-by-side with areas of persistently high soil moisture. Given the great distances between these Early Pennsylvanian deposits in western Pangea, and from what is known of the tectonic regime of the region during this time, there is little reason to believe that the Early Pennsylvanian drought-tolerant elements were transported from uplands.

Physical evidence indicates that the overall climate was more seasonal in the west than in more central regions of the supercontinent, creating general conditions of periodic moisture stress, within which patchy areas of higher soil moisture existed, a not-uncommon condition in many parts of the world today, including coastal regions of basins, which cannot be characterized as uplands.

From the Middle Pennsylvanian into the early Permian, the predominant kinds of floras found in western Pangea were a mixture of wetland taxa and those tolerant of seasonal drought, with the latter often dominant. An extreme example is represented by in situ tree stumps of a conifer-dominated flora from an early Late Pennsylvanian (Missourian) arid coastal habitat in New Mexico (Figure 9), hence clearly not an upland (Falcon-Lang et al., 2016). Several similar floras have been described (e.g., Sellards, 1908; Elias in Moore, 1936; Cridland and Morris, 1963; Rothwell and Mapes; 1988; Tidwell, 1988; Mamay and Mapes, 1992; Falcon-Lang et al., 2015; DiMichele et al., 2017, 2019). These floras, in addition to many others, indicate that populations of drought-tolerant plants were apparently permanently resident in the western portions of Pangea throughout the Pennsylvanian. They are found intermixed with wetland plants because it is possible, as noted above, to have wetland areas within a region subject to a sub-humid, seasonal climate. In contrast, it is improbable that large, persistent populations of drought-tolerant plants would be found in regions of widespread, persistent humid to perhumid climatic conditions.

Several of these western Pangean floras have caused considerable stratigraphic confusion because the xeromorphic elements were considered to be indicative of a Permian age. The most notable example may be that from Garnett, Kansas (Figure 10), found in the Rock Lake Shale, of Late Pennsylvanian (Missourian/Kasimovian) age (Elias in Moore et al., 1936; Cridland and

Morris, 1963; Winston, 1983). This flora is found in a channel fill, demonstrably in lateral facies association with a calcic Vertisol (Joeckel, 1989; Feldman et al., 2005), and in no way represents an upland. Although embedded within the Pennsylvanian coal measures of Kansas, and with the age of the enclosing strata determined independently of the plants, disagreements about the age continued into the 1970s (see comments on the paper of Remy, 1975, p. 345-352). Such confusion also can be found elsewhere. For example, consider the assessment of an Appalachian Basin flora from the Middle-Late Pennsylvanian boundary, in the midst of the Appalachian coal measures, deemed latest Pennsylvanian or even Permian in age (Wagner and Lyons, 1997) based on its fossil flora. This interpretation prompted the assertion of a 6-million-year gap in the fossil record, for which there is no geological evidence and conflicting, independent marine biostratigraphic evidence (see commentary by Falcon-Lang et al., 2011b).

4.2.2 Drought-tolerant floras within the coal measures

The spatio-temporal relationships of wetland and drought-tolerant species pools in the central Pangean coal basins are different from those in western Pangea. The central regions of the supercontinent periodically hosted widespread swamps in which thick, low-ash peat accumulated, the precursor of economic coal. Such accumulations, as we have discussed above, are direct indications of humid-to-perhumid climates (sensu Cecil, 2003), those in which rainfall exceeds evapotranspiration for 10 or more months of the year, conditions necessary for peat to accumulate and persist in a relatively warm, frost-free, tropical environment. We restate that the distribution of rainfall, relative to evapotranspiration, is more important than mean annual rainfall, not only for peat to accumulate, but for it to resist complete destruction by oxidation, or consumption by micro- and macro-organisms. Immediately before, and immediately after, intervals of peat accumulation, the tropical lowland regions also appear to have been occupied by a wetland biome composed of the well known species pool, based on allochthonous floras from nearshore settings (e.g., Mazon Creek; Wittry, 2006), and primarily parautochthonous remains from floodplains (e.g., Scott, 1977, 1979) and swamps (e.g., Gastaldo, 1987).

During the intervals of humid climate, the species pool that constituted the drought-tolerant biome was mostly absent from the vast area of the central Pangean tropical lowlands. Where elements of the biome did exist in these regions, some evidence suggests survival in areas of rain shadow (e.g., van Hoof et al., 2013). In other instances, assemblages asserted to be preserved in or proximate to uplands (e.g., Lyons and Darrah, 1989; Falcon-Lang, 2004b, 2006; Falcon-Lang and Bashforth, 2004, 2005) merit reevaluation in the light of more recent finds (e.g. Martino, 2017), which suggest a climatic cause and actual occurrence in a lowland basin.

Within the humid parts of glacial-interglacial cycles, both peat and clastic substrates in the lowlands supported plants with growth habits and anatomical structures indicating physiological requirements for nearly unflaggingly high soil-moisture levels (Cichan, 1986; Wilson, 2013; Wilson et al., 2017). These plant fossils represent the classic Pennsylvanian Coal Age vegetation (Figure 8A, B), which was characterized by a diversity of arborescent vegetation; the modern relatives of these plants, where there are any, generally are small and of limited ecological importance, particularly true of the pteridophyte groups. The pteridophytes included the gigantic lepidodendroid and sigillarian lycopsids, woody calamitalean sphenopsids, and marattialean tree ferns. The arborescent seed-producing plants included the medullosan pteridosperms (seed ferns), which have no close modern descendent groups, and certain sub-lineages of the cordaitaleans, a coniferophytic group with broad leaves and loosely organized strobili. The cordaitaleans have been a point of confusion that only recently appears to have been clarified, with many arguing that they were indicators of "uplands" (e.g., Chaloner, 1958). In fact, these plants might be called "the oaks of the Paleozoic", in that various species occurred in nearly every kind of environment, from lowland peat swamps and wetlands (e.g., Cridland, 1964; Rothwell and Warner, 1984; Costanza, 1985; Falcon-Lang, 2005; Hilton et al., 2009; Šimůnek et al., 2009; Raymond et al., 2010), in which they displayed a variety of growth habits, to seasonally dry areas, sometimes, but not necessarily, in inferred uplands (Figure 8C), where large, woody trees predominated (e.g., Falcon-Lang and Bashforth, 2004, 2005; Falcon-Lang, 2006; Gibling et al., 2010; Bashforth et al., 2014; Ielpi et al., 2014; Trümper et al., 2020). In addition, there appears to have been much greater diversity among the cordaitaleans than recognized on the basis of their conservative morphology. Such diversity has been revealed by studies of leaf cuticles (e.g., Šimůnek, 2000), and is consistent with the great ecological breadth of the group. It is important to emphasize that, based on their biomass contribution to the peat, cordaitaleans were one of the dominant groups in Middle Pennsylvanian peat-forming swamps (e.g., Phillips and Peppers, 1984; Montañez, 2016). The large biomass of these plants found in coal balls clearly was not transported in from "uplands", given both the abundance and common occurrence of cordaitalean roots (assigned to the genus *Amyelon*) found in permineralized peat (e.g., Cridland, 1964; Greb et al., 1999b).

Despite the overwhelmingly more common occurrence of the wetland biome in basins that contain coal-rich stratigraphic successions, a different species pool also occurs in these basins. The plants of this other species pool are similar to the assemblages found in western Pangea, and are predominantly of mixed composition, often being dominated by xeromorphic plants considered by most paleobotanists to be characteristic of moisture-stressed habitats. These mixed floras typically occur in strata between coal beds, where they frequently are preserved in channel-fill deposits (Figure 11), which in many cases record intermittent stream discharge, suggesting seasonality of flow volume (e.g., Bashforth et al., 2014; Fielding et al., 2020). In case there are doubts about the existence of thousands-of-years-long seasonally dry intervals in coal basins, there is now a large body of evidence from fossil soils that points to the predominance of such climatic periods between times of peat formation. These climatic intervals varied from sub-humid to semi-arid, deduced from the presence of Vertisols and calcic Vertisols (Figure 12), some with thick, caliche-like carbonate layers or with carbonate-encrusted, vertically disposed, deeply penetrating roots (Figure 12A). These vertic soils have been reported from intervals spanning the entire Pennsylvanian in areas from the central U.S. to the Canadian Maritimes, which was on the European side of the central Pangean mountainous area (Joeckel, 1979, 1995; Tandon and Gibling, 1994; Cecil et al., 2003a; Martino, 2004; Falcon-Lang et al., 2009; Carpenter et al., 2011; Catena and Hembree, 2012; Rosenau et al., 2013; Bashforth et al., 2014). Perhaps of more interest, however, are recent descriptions of Vertisols within coal-bearing sequences from intramontane regions in the Variscan belt (Opluštil et al., 2015, 2019). These paleosols record the existence of climatic fluctuations similar to those that took place in paralic areas of Euramerica. Amplifying the paleosol data, sedimentological studies also indicate seasonality in sediment dispersion patterns (e.g., Kvale, et al.1994; Carpenter et al., 2011; Cecil et al., 2014; DiMichele, 2014, fig. 17; Opluštil et al., 2015, 2019; Bashforth et al., 2016b; Fielding et al., 2020). Sedimentological data also suggest, on a larger spatio-termporal scale, that the long-term drying trend from the Early Pennsylvanian into the Permian proceeded from west to east in a time-transgressive manner across the Euramerican portion of Pangea (e.g., Schutter and Heckel, 1985; Roscher and Schneider, 2006; Schneider and Romer, 2010; DiMichele et al., 2011).

As noted below, there are a number of coal-basin floras that contain variable amounts of drought-tolerant elements. In the USA and Canada, these studies include floras from the Early Pennsylvanian (e.g., Leary, 1975; Leary and Pfefferkorn, 1977; Bashforth et al., 2014), Middle Pennsylvanian (e.g., Falcon-Lang et al., 2009; Plotnick et al., 2009; Dolby et al., 2011 – a palynofloral example; Bashforth et al., 2016b), and Late Pennsylvanian (e.g., Carpenter et al., 2011; Martino, 2017), in addition to older descriptions of individual occurrences of xeromorphic, drought-tolerant species from coal measures strata (e.g., Bassler, 1916; Darrah, 1935, 1936). In Europe, such floras are numerous, and most common in the Upper Pennsylvanian (e.g. Šimůnek and Martínek, 2009), although they also are reported from Lower Pennsylvanian (e.g., Opluštil et al., 2007) and Middle Pennsylvanian deposits (e.g., van Hoof et al., 2013 – a palynoflora).

The resulting pattern in the central portions of Pangea is the temporal and stratigraphic intercalation of wetland and drought-tolerant plant assemblages. This intercalation mirrors changes in climate that are covariant with fluctuations in sea-level, driven proximately by changes in southern polar ice volume, which probably were controlled by a combination of changes in atmospheric composition (Peyser and Poulsen, 2008; Horton et al., 2012; Heavens et al., 2015) and orbital forcing (Heckel et al., 2007; van den Belt et al., 2015). Only rarely are any indications of drought-tolerant elements found in association with assemblages from coal seat-earths or roof-shales. This pattern conforms with observations of modern tropical regions with a humid-to-perhumid climate, where the species pool covers a great areal extent, varying in complex ways with habitat type, but with large amounts of compositional overlap. In contrast, the floras from between coal beds are associated with paleosols that imply seasonal-drought, and sedimentological indicators of seasonal variation in flow regimes; such floras are highly variable in composition, and most often are a mixture of xeromorphic taxa and wetland elements, the latter most commonly tree ferns and calamitaleans. The humid-climate floras are, of course, well understood when compared with those from drought-prone times and places. A detailed comparison of these two floras is almost impossible, due to the vast numbers and intense study of wetland assemblages, and the relative rarity, often fragmented condition, and relatively poor preservation of many drought-tolerant assemblages. Furthermore, until recently, there have been few systematic searches for drought-tolerant assemblages within coal-measures strata. Thus , as a consequence, the actual abundance of such assemblages remains a quantitative mystery.

5. Taphonomic megabias and the Pennsylvanian-Permian transition

We have attempted to document the assertion that the apparent rise of the drought-tolerant biome during the Pennsylvanian to Permian transition is an illusion created by taphonomic factors. A tropical, drought-tolerant flora existed in Euramerica at least as far back as the Mississippian, and was periodically widespread in tropical Pangea. During the Permian, the drought-tolerant biome became more continuously present on many parts of the Pangean landscape as plants with requirements for high soil-moisture became constricted in space and time. The floristic characteristics of the transition from the Pennsylvanian to the Permian, therefore, depend upon where on the Earth this transition is observed, including where in the tropical realm.

In the western parts of Pangea, nearly all floras, even those of Early Pennsylvanian age, which was the wettest interval in the Pennsylvanian, contain drought-tolerant elements. By the Middle Pennsylvanian, these drought-tolerant plants were common components of all western Pangean assemblages, and can be found as the dominant elements in many fossil floras from the region. During the Late Pennsylvanian, and into the Permian, drought-tolerant assemblages became the most commonly encountered fossil-plant assemblages in the terrestrial, and even parts of the marine geological record of western Pangea (e.g., DiMichele et al., 2000; Baumgardner et al., 2016; Kvale et al., 2020). There was little peat accumulation in western Pangea at any time during the late Paleozoic, despite extensive evidence, from many different geographic areas, of regular sea-level fluctuations and associated climatic changes. In the extreme, consider the Paradox Basin of the southern Colorado Plateau, USA, where, near the Pennsylvanian-Permian boundary, the deposits of a meandering river system bearing a mixed floral assemblage of tree ferns, calamitaleans, and conifers (DiMichele et al., 2014) are found sandwiched between deposits of eolian dunes. The climate simply never became wet enough to support peat accumulation at most times in western Pangea, meaning that the conditions necessary to inhibit the decay of organic matter and/or preserve such accumulations in the long term were not being met (Gastaldo and Demko, 2011, as described above). The western Pangean landscape most likely harbored a widespread drought-tolerant flora with more mesic, drought-intolerant elements confined to microhabitats with high soil moisture; in other words, proximate to water bodies where the preservation of organic matter was most likely.

It is in the coal basins of central Pangea that the relationship between the drought-tolerant biome and the wetland biome becomes the most difficult to interpret, due to extreme taphonomic megabiases. Two prominent megabiases exist. The first, operating in the late Paleozoic, is a fundamental difference in the likelihood of preservation. The second, operating today, is a difference in “discoverability”, and has an analytical cause. In the central portions of tropical Pangea (present day Midwestern and Eastern USA, Eastern Canada, and Europe from Britain to the Urals), the swings in prevailing climate associated with glacial-interglacial cycles oscillated between a humid and a subhumid-to-semiarid phase (Falcon-Lang, 2004a; Cecil et al., 2003a). During a portion of any given cycle, the climate was humid-to-perhumid over vast areas of the tropics. This type of climate led to high levels of soil moisture and the accumulation of peat in physically suitable areas (e.g., Cecil et al. 1985), and thus was characterized by the wetland species pool of the wetland biome. During other parts of any individual cycle, the climate shifted to seasonally dry (subhumid to perhaps semi-arid) and actually may have been of longer duration than the humid phase (Falcon-Lang et al., 2009); this seasonally dry climate created conditions suitable for a drought-tolerant species pool (Figures 13, 14). Because of the strong relationship between plants and climate (the famous comment of Wladimir Köppen [1936, p. 6] that vegetation is “materialized, visible climate” – see original and translation in Looy et al., 2014a), the mixing of these two species pools was complex and asymmetrical. As is the case today, the likelihood of finding taxa that require periodic soil-moisture deficits in a tropical rainforest is low. In contrast, however, the likelihood of finding taxa with an obligate requirement for high soil-moisture is relatively great, under a seasonally dry climate, due to more microhabitat and soil-moisture heterogeneity under such climatic conditions. This contrast was amplified by the much lower species diversity during the late Paleozoic, compared to that of today; resources were partitioned among fewer species, and the wind dispersal and pollination of most forms means that there would have been significant taxonomic similarity across microhabitats on the landscape scale.

As a consequence of glacial-interglacial contrasts, during the humid/perhumid portions of cycles, the high volumes of rainfall, and more importantly, the negligible seasonality of its distribution, created conditions suitable for the wetland species pool to blanket the Central Pangean landscape (Figure 13). In areas where peat did not form, there nonetheless would still have been high soil-moisture, and dense, sediment-binding and erosion-inhibiting vegetation covering nearly all of the regional landscape. Under such conditions, even with expected microhabitat heterogeneity, the effects of elevational variation would have been blunted by the generally high water tables, made so by the volume and temporal distribution of rainfall. In other words, the drainage effects of elevation would have been muted significantly in the central Pangean tropics under a humid climate mode. This muting made it unlikely for large areas of drought-tolerant vegetation to persist at lower elevations, in mountainous regions, other than in rain-shadow areas (e.g., van Hoof et al., 2013), or perhaps as patches at higher elevation (e.g., Broutin et al., 1990), such as occurs in parts of the modern Andes due to regional geological effects on airflow patterns (Chavez and Takahashi, 2017). And if elevation increases enough, the confounding effects of temperature are introduced, which may exert a considerable effect on species-pool composition even in tropical regions if the mountain belts are high enough. However, as studies of Variscan tectonics have indicated (Roscher and Schneider, 2006; Kroner and Romer, 2013), there almost certainly was never, at any one time, a significant mountain range across the entire central area of Pangea. Rather much of the eastern and central Variscan region was eroded to low hills by the Late Pennsylvanian.

During the drier parts of cycles, when climate was subhumid to semi-arid, there would have been months-long periods of soil-moisture deficits, the existence of which is indicated by the characteristics of paleosols and sedimentary patterns in the strata between coal beds. The imposition of seasonality on a tropical landscape does not, however, increase the degree of homogeneity to the extent that high rainfall and weak seasonality do. There are, therefore, areas of higher soil moisture where plants requiring such conditions can survive (e.g., Looy et al., 2014b).

We conclude, therefore, that the two megabias factors, in combination, create the illusion of a major rise of a drought-tolerant tropical flora at the time of the Pennsylvanian-to-Permian transition. Without question, the dry flora did become the predominant flora of the Permian throughout much of central and western Pangea. However, the biome also was present, and covered large areas, during the Pennsylvanian (e.g., Gastaldo, 1996). During the transition to the Permian, the residence time of the seasonally dry biome in the lowlands of central Pangea increased until it became permanent, although the sedimentological conditions under which it was preserved did not change.

The Pennsylvanian-Permian shift in floras is magnified by taphonomic biases to make it look more dramatic than it actually was, particularly in those areas where peat accumulation occurred during wetter climate phases; the apparent transition is less dramatic, or even minor in areas of western Pangea, which were rich in drought-tolerant vegetation for nearly all of the Pennsylvanian. To parse this out: (1) Drought-tolerant floras appear to have been present in the Pangean tropics from the earliest Carboniferous. (2) The drought-tolerant flora is most often preserved in deposits of channels and lakes, most generally being of limited areal extent, and not associated with economically viable coal beds. (3) Therefore, without a concerted and targeted search, drought-tolerant floral elements usually are not likely to be found in the strata of Pennsylvanian-age coal basins, because they are rare to start with, and becausee they occur in strata that generally are poorly exposed. (4) In contrast, the wetland flora is found within, immediately above, and immediately below coal beds, and is, therefore, extensively revealed in the course of mining activity. (5) The wetland flora is, therefore, easily found and collected. (6) In addition, for taphonomic reasons, the wetland flora was much more likely to be preserved where and when it occurred during the Pennsylvanian than was the drought-tolerant flora, so it is, a priori, much more abundantly represented in the geological record. (7) A long-term drying trend in the Euramerican Pangean tropics began in the Early Pennsylvanian, and continued, with fluctuations, into the Permian. (8) By the Permian, the frequency of peat-swamp development (and resulting coal beds) in Euramerica had dropped significantly, signaling the demise of vast wetland areas, but not eliminating the wetland biome entirely. (9) The disappearance of coal beds removes the easy access to abundant plant-fossil material via mine exposures, and it also reflects a significant change in the predominant form of plant preservation from widespread, swampy wetlands to smaller channel- and lake-fill sequences. (10) All that remains in the drier Permian of Euramerica are the smaller deposits containing mixed floras, or even floras entirely composed of drought-tolerant elements (Figure 15). These are the same kind of deposits in which the drought- biome was preserved during the Pennsylvanian. In the Permian, however, these are the only remaining sources of plant-fossil remains.

The result of this pattern is that the visibility of deposits that contain seasonally dry plants increases significantly; they are all that remains, giving the false impression that drought-tolerant vegetation took over the tropics of Euramerica. Rather, what actually took place was a shift in the prevailing climatic spectrum, from one favoring the preservation (and later discovery) of wetland vegetation, to one in which wetland vegetation no longer periodically dominated the landscape, and was no longer widely preserved. Thus, the drought-tolerant biome did not take over (neither did the whole tropical world become a well drained upland). Rather the wetland biome simply was removed from the equation. This change left drought-tolerant and mixed floras as “the only game in town”, as the old saying goes.

This transition is summed up in Figure 16, a schematic illustration that attempts to capture the complexity of this transition as it occurred in the central regions of Pangea. It is in that region where there were regular oscillations between dominance by the wetland and drought-tolerant biomes during the Pennsylvanian, before becoming increasingly dry at all phases of glacial-interglacial oscillations into the early Permian. The pattern would look considerably different were a similar representation made for western Pangea, where elements of the drought-tolerant biome were permanently resident in basinal areas. Our data indicated that changes there were quantitative, with the relative proportions of wetland and drought-tolerant plants varying in different parts of cycles (e.g. DiMichele et al., 2017).

6. Do uplands cause drought?

This paper was prompted, in part, by the need to address a long-standing belief that, during the Pennsylvanian Coal Age, the tropics were subject to a widespread and prevailing wet climate *all of the time*. A corollary to this viewpoint is that the only way to explain the appearance of xeromorphic, presumably drought-tolerant plants, which are not found among the plants characteristic of coal roof-shales, seat-earths, or in the coal itself, is to place them in uplands (Figure 17). Under this scenario, these uplands supposedly were well drained, resulting in soil-moisture deficits, even though the prevailing tropical climate is envisioned to have been everwet throughout the entire Pennsylvanian, even in these tropical uplands. The minimum elevations required of such uplands have been proposed to be quite modest, sometimes just a few meters, with locations varying from the margins of peat-forming or mineral-substrate swamps, to a presence on higher ground in the midst of landscapes otherwise covered by wetlands. For example, Cridland and Morris (1963) proposed that as little as 6 m of elevation would have caused enough drainage to induce the colonization of the envisioned (but undocumented) hills by an entirely different suite of species from that in the supposedly surrounding, immediately adjacent, peat-forming and siliciclastic-substrate, swampy wetland areas (Figure 10).

Tracing the literature back in time, the concept appears in various indirect forms early in the 20th century, mainly as an assumption that extrabasinal areas would experience drier conditions than would be found in basins (e.g., Gothan and Gimm, 1930; White, 1931), but likely goes back even farther (Stopes and Watson, 1909). The idea appears to have been firmly established by the mid-20th century (e.g., Chaloner, 1958; Havlena, 1961; Cridland and Morris, 1963). Pfefferkorn (1980) argued for restriction of the term "uplands" to mountainous regions, and introduced the concept of "extrabasinal lowlands" to account for hilly elevated areas that proximately fringed basins, and were 100-200 m above the basin floor. He envisioned such areas as a more likely source of exotic plants than distant mountainous regions. We note that there was no consideration of climate in this suggested solution, however.

In elevated areas of the modern tropics, including in mountainous terrain, not all uplands or extrabasinal lowlands are colonized by drought-tolerant plants, although where those drought-tolerant upland plants are found, the background climate is generally seasonally dry. Floristic distribution and composition are determined far more by prevailing climate than by elevation, the main effect of which, in the tropics, is on temperature (Figure 18). However, we recognize that steep slopes, particularly in mountainous regions, present a special case, although these habitats also can become stabilized by vegetational cover under very wet climates, as indicated by studies (cited above) that find low sediment loads in rivers draining areas of rugged terrain under high, aseasonal rainfall regimes. Slope and elevation alone do not guarantee high rates of erosion.

The relationship between sediment load in rivers and climate is important for another reason. It has been suggested that the siliciclastic sediments between coal beds are the result of short-duration floods, which periodically, perhaps due to the influence of catastrophic storms, engulfed and buried peat swamps. The swamps then recovered rapidly and recolonized the landscape (e.g., Thomas and Cleal, 2015). This explanatory model is similar to one that prevailed in coal geology, which placed peat-forming swamps within active deltas, amidst shifting loci of sediment deposition (Horne et al., 1978). The short-term-flood model does not take into account the extensive evidence for the presence of paleosols among the siliciclastic deposits between coals, most of which (the paleosols) show evidence of seasonal climates. Nor does the model acknowledge the presence of marine beds in many coal-bearing sequences, among the strata between coals, indicating significant, long-term changes in environmental conditions. But, perhaps most critically, the short-term-flood model does not take into consideration the hiatuses between various siliciclastic units, which dominate the temporal record, particularly in terrestrial strata. Most of the time represented by a stratigraphic section is taken up by temporal gaps, not by actual beds of rock (including coal), reflecting the dynamics of terrestrial sedimentary systems. The evidence indicates large amounts of time, tens of thousands of years or more, tied up in the intervals that typically separate successive coal beds. Regardless of these features, the unlikelihood of this flood model also comes from the fact that the extrabasinal lowlands, and perhaps even more distant uplands, surrounding the vast peat-covered landscape would have experienced the same kind of climate, namely a humid to perhumid climate, which was favorable for tropical peat accumulation. Under such conditions, river sediment loads would be expected to be low. This is further amplified by the fact that siliciclastic input is anathema to peat formation, creating instead conditions for the development of organic-rich mucks, which become organic shale beds. Various lines of evidence point to a black-water character for many rivers passing through Pennsylvanian peat swamps, carrying low sediment loads (Gibling et al., 2014; Elrick et al., 2017; Nelson et al., 2020), consistent with observations of modern environments in humid-perhumid climate areas, where landscapes are densely vegetated and rivers have low sediment loads, despite high discharge volumes.

Returning again to uplands, consider areas of peat accumulation in modern upland, inland areas, removed from the effects of sea-level rise or coastal climates, but forming under the effects of humid climates today. Lakes also are frequently present at high elevation; for an extreme example there is Lake Titicaca of Peru and Bolivia at 3800 m (e.g., Paduano et al., 2003), or the many other Andean lakes, with surrounding vegetation reflective of local climate. In fact, the Andean Altiplano has undergone repeated expansions and contractions of wetlands in response to climate changes since the last glacial maximum (e.g., Rigsby et al., 2005). In the late Paleozoic geological record, there also are some wetland deposits hypothesized to have formed within the region of the Variscan mountainous areas of Central Europe, at >1000 m elevation with >100 m of relief along the walls of river valleys (Becq-Giraudon, et al., 1996; Opluštil, 2005; Opluštil and Cleal, 2007). The generality of this inference, that of high altitude basins, has been challenged on the combined basis of radiometric dating, and considerations of erosion and uplift rates in the Recent (Roscher and Schneider, 2006; Schneider and Romer, 2010), and on detailed studies of Variscan tectonics and the stratigraphic sequences in intramontane basins (e.g., Schneider et al., 2005; Kroner and Romer, 2013; Trümper et al., 2020). That any examples of such higher elevation wetlands can be found directly indicates that during the Pennsylvanian, there were upland regions that supported typical wetland vegetation.

The Late Paleozoic Ice Age was accompanied by numerous, covariant changes in sea level and climate in the Euramerican tropical regions of Pangea. The geological evidence of this is abundant, of a variety of types, and entirely independent of plant fossils. Plants track climate relatively closely today, and there is no reason to believe they did not do so in the Pennsylvanian and Permian. Wetlands, including peat-forming swamps, can be found wherever climate and substrate conditions are suitable, both at high or low elevations. However, high-elevation peat accumulations (coal), if they occurred during the late Paleozoic, would have had relatively low long-term preservation potential because of the long expanses of time for erosion to do its work. That any coals are present, even rarely, indicates that high elevation areas could be wet, and not invariably well drained and plagued by drought.

In answer to prescient observations such as that of Wagner and Álvarez-Vázquez (2010, p. 305), who noted: "…it seems surprising that the presence of upstanding relief with alluvial fan deposits in the Peñarroya Basin (Westphalian) has not led to any conifer finds. There are also very few conifer records in the Stephanian B of NW Spain, despite the evidence for palaeovalleys associated with a rugged landscape in the near vicinity of the basin", we respond that elevation does not uniformly and invariably cause "drought". The drainage effects caused by elevational changes will be damped under humid-to-perhumid climates, and become accentuated as climate becomes more seasonally dry. The vegetational differences and changes in time and space, recorded in the upper Paleozoic rock record, reflect the primary influence of climate on habitat and habitat heterogeneity, just as occurs in the modern world.

7. A suggested rationale for addressing the upland vs. climate question

Philosopher Willard V. Quine was a 20th century proponent of the idea of "underdetermination" of scientific hypotheses. In its simplest terms, this means that two or more competing hypotheses might have equivalent outcomes, and thus be undifferentiable based on empirical data. This could be restated to say that a unitary hypothesis cannot be deduced from the observations made in nature (see further discussions of this in, e.g., Bergström, 1993, or Stanford, 2017). Thus, in evaluating competing explanations for data, there is no "Elementary, my dear Watson" moment, where all the observations point unwaveringly and without question to a single conclusion. Rather, there are competing hypotheses. A subset of this is an idea set forth by Macbeth (1971), the Best in Field Fallacy, which simply states that we may choose among competing hypotheses, only to discover later that none were correct; one hypothesis with more explanatory power may exist and be unknown to us, it may not yet have been thought of by anyone and so will be unavailable for consideration, or it may only emerge with the addition of new empirical evidence. Thus, when faced with patterns in nature that demand conceptual explanation, an investigator must make an intuitive, inductive leap. One may invent a hypothesis, or have strong preferences for a particular existing hypothesis, based on what is known and how it is interpreted, in combination with other factors, such as preferring the simplest explanation. However, also important is the so-called Principle of Total Available Evidence, which has been attributed to Carnap (1947), but originated conceptually much earlier. This principle states that evidence relevant to the phenomenon under consideration cannot be ignored, and that additional evidence should be sought in areas that would appear to shed light on a problem of interest.

This is not a new understanding. Alfred Wegener (1966, p. vii) stated "Scientists still do not appear to understand sufficiently that all earth sciences must contribute evidence toward unveiling the state of our planet in earlier times, and that the truth of the matter can only be reached by combing all this evidence. . . It is only by combing the information furnished by all the earth sciences that we can hope to determine 'truth' here, that is to say, to find the picture that sets out all the known facts in the best arrangement and that therefore has the highest degree of probability. Further, we have to be prepared always for the possibility that each new discovery, no matter what science furnishes it, may modify the conclusions we draw."

Certainly, the geological sciences, including paleontology, face a severe problem when it comes to total evidence. The geological record is made up only of glimpses of the past. Missing time vastly exceeds the time recorded by geological strata. And, in the case of terrestrial life, we likely see far less than 10% of the habitats on the earth at any given time, and preserve far less than 1% of the organisms that ever lived. That we deal with so many unknowns means that we cannot deny the matter of underdetermination of many of our hypotheses, and with that, the problem of many possible explanations for the patterns we observe. Thus, we must use total available evidence to the extent we are able, and almost all studies, including the present one (!), that are attempting to explain complex phenomena will likely fall short in this regard. This may be especially true in the case of the patterns described and commented on in this essay; there is an overwhelming scientific literature of observation, both of the modern world and that of the geological past, relevant to the matter of factors controlling the distribution of plants on any particular landscape, at varying spatial and temporal scales. Thus, it is correspondingly difficult to find even a fraction, let alone all, of the relevant work.

Here, we have attempted to bring together as many different lines of evidence as we are able, in order to evaluate the controls on the spatial distribution of vegetation in the equatorial regions of the Pangean supercontinent during the late Paleozoic. These lines of evidence include both patterns from the geological record, and relevant patterns from the modern record, wherein direct measurement of environmental variables, and broader, more complete spatial observations, are possible. We have combined these observations with considerations of taphonomy, particularly the likelihood and nature of preservation of terrestrial plant remains, and how those processes might have worked in the deep past. From this attempt at a synthesis, we believe the hypothesis best supported by the data is that climate was a first-order controlling variable in the habitat distribution of late Paleozoic plants, as it is for the plants of today. This is not to deny the effects of variability in the elevation of the land surface, which certainly is a second-order factor of considerable importance, but one that actually is more difficult to assess than the effects of climate.

Finally, we have tried to bring to bear several considerations to explain the seeming rise of a drought-tolerant flora during the Carboniferous-Permian transition. These include: the patterns of vegetational distribution over different spatial scales and their underlying controlling factors, the conditions under which remains of that vegetation are most likely to be preserved in the modern world and in the geological record, and, finally, where those remains are most likely to be discovered today. We conclude that the rise of drought-tolerant vegetation during the Carboniferous-Permian transition is an illusion, created by taphonomic happenstance, and that both wetland and drought-tolerant plants, and the biomes they constituted, existed across the Pangean interior for virtually all of the Carboniferous. The strata that enclose the drought-tolerant biome became a proportionally larger part of the fossil record during the later

Pennsylvanian and into the Permian, as the wetland biome began to shrink and disappear from the tropical landscape. At the same time, the drought-tolerant flora became ensconced more permanently across much of the tropics, where previously it had oscillated in dominance with the wetland flora. However, the actual geological abundance of deposits containing the drought-tolerant flora may have changed little through time. Rather, the loss of the strata in which wetland floras were dominant made the deposits with plant fossils from seasonally dry settings more “visible” to researchers, thus making it more likely for the plant remains to be found, collected, and characterized.

8. Summary

The Late Paleozoic Ice Age (LPIA) was a time of orbitally forced glacial-interglacial fluctuations, which were the proximate drivers of coincident sea-level and climatic changes. In tropical Pangea (Euramerica, Cathaysia), vegetation tracked these periodic environmental fluctuations, marked by changes in the spatial distributions of wetland and drought-tolerant biomes, or floras, each of which was characterized by largely distinct species pools. The glacial-interglacial fluctuations were superimposed on a long-term drying trend in the Euramerican portion of the Pangean tropics, which became drier (on average) during the Pennsylvanian, continuing into the Permian. The cause of this drying trend is not fully understood. Howwever, the process ultimately resulted in the loss of extensive wetlands as cyclically wet periods became less wet and dry periods became drier.

The floristic changes accompanying the long-term drying trend frequently have been characterized as the rise of a so-called Mesophytic flora. Examination of biogeographic patterns, climate models, and sedimentary environments suggests that drought-tolerant species pools, collectively constituting one or more biomes, were permanently resident in western Pangea and possibly in parts of the Variscan mountains of central Pangea long before the Permian. During the Pennsylvanian, coinciding with the periodic appearance of seasonally dry climates, drought-tolerant plants dispersed from these areas of stable, large populations into central Pangea, reaching those basinal areas in which peat had been accumulating during wetter parts of glacial-interglacial cycles. In contrast to this pattern of expansion from large, stable population centers, the wetland species pool remained centered in central Pangea, and fragmented into refugial pockets during the periods of seasonal climate. Therefore, rather than simple range expansion during the return of humid conditions, the wetland biome expanded from numerous disconnected refugial areas, and repeatedly reassembled with each glacial cycle into the vast Coal-Age wetland ecosystems. Thus, during the Pennsylvanian, drought-tolerant biome biogeography was dominated mainly by spatial expansion from and contraction back into large geographic areas in which populations were permanently interconnected. The wetland-biome spatial patterns, in contrast, were characterized by dominance over vast areas during humid intervals, contraction in place into fragmented, small, disconnected refugia during intervals of climatic seasonality, followed by reassembly sourced from those refugia upon the return of humid conditions.

Significant taphonomic “megabiases” affect our understanding of the dynamics and spatial distributions of these biomes: (1) The Late Mississippian through Pennsylvanian Coal Age tropics often are misinterpreted as invariably wet. In reality, they experienced demonstrably wet-dry oscillations, and in some areas (western Pangea, rain-shadow areas in the Central Pangean Mountains, perhaps at very high elevation within mountainous regions) were perpetually seasonally dry. The tropics were nowhere everwet throughout, or even for significant parts of, the Coal Age. (2) An ancient preservational megabias: The physical conditions under which the wetland tropical biome thrived gave it a relatively good chance of preservation. Consequently, the wetland biome is well represented in the rock record. In contrast, there was a huge negative preservational bias against the drought-tolerant flora, making it much rarer than the wetland flora in the geological record. (3) A modern analytical megabias: As a result of its association with coal beds, and thus coal mining, the wetland flora is far more likely than the drought-tolerant flora to be exposed and readily found today. Strata containing the drought-tolerant biome generally are not readily exposed, accessed, or searched for, especially in strata of Pennsylvanian age, where vast amounts of wetland plant fossils are readily available, not only due to their originally superior preservational potential, but because of their exposure during coal mining. (4) As the Euramerican tropics became drier into the Permian, the loss of extensive wetlands resulted in a greatly diminished fossil record of the wetland plants, but did not result in a significant change in the absolute abundance of plant-fossil accumulations formed under seasonally dry conditions, or a change in the sedimentary environments in which those plant fossils are found. Therefore: (5) A modern search-image megabias: The largely fortuitous pattern of drought-tolerant plant preservation changed little in mode or frequency as wetland deposits declined, but appears to have been similar in form and likelihood during both the Pennsylvanian and early Permian within Euramerica. What did change, however, is the "geologic visibility" of the drought-tolerant biome, as the strata in which it is preserved became the only source of plant-fossil remains in much of the later Pennsylvanian and Permian.

During the Pennsylvanian, in central Pangea (Midcontinent US through the Donets Basin), the wetland and drought-tolerant biomes were intercalated through time, as major climate swings between humid/perhumid and subhumid/semi-arid occurred in conjunction with glacial-interglacial cycles. During the humid-to-perhumid phases of these swings, when wetlands covered vast stretches of interior Pangea, populations of seasonally dry plants did not persist in wetland landscapes in patchy microhabitats, but rather were excluded nearly entirely. In contrast, during the seasonal periods in the central Pangean coal basins, and in the seasonally dry areas of western Pangea and parts of the central Pangean mountainous regions, wetland and drought-tolerant elements were mixed, with wetland patches existing in various microhabitats in otherwise seasonally dry landscapes. Over time, in these seasonally dry times and/or regions, as overall aridity increased in the Euramerican tropics during the Pennsylvanian and early Permian, the fossil floras also became increasingly dominated by xeromorphic elements, although some wetland elements, most commonly marattialean tree ferns and calamitaleans, continued to exist within these seasonally dry tropical landscapes. During the early Permian, drought-tolerant biomes, similar to and derived from those of the Pennsylvanian, dominated Euramerica. Included within these landscapes were areas of habitat wet enough to support a suite of wetland species, albiet much reduced in diversity from their Pennsylvanian zenith. By that time, widespread wetland floras had shifted to eastern Pangea (Cathaysia), where they continued to appear intercalated with drought-tolerant floras.

Acknowledgments

We thank Robyn Burnham, University of Michigan, Scott Wing, Smithsonian Institution, Scott Elrick and W. John Nelson, Illinois State Geological Survey, and Joerg Schneider, TU Bergakademie Freiberg, for sharing illustrations and discussions about some of the ideas expressed in this paper. WD thanks Stewart Umphrey, St. John’s College (ret.), for sharing his thoughts about the nature of the relationship between scientific data and hypotheses. Comments and suggestions provided by Benjamin Bomfleur, University of Münster, Stanislav Opluštil, Charles University, an anonymous reviewer, and Editor Thomas J. Algeo resulted in significant changes to the final version of this paper; they are thanked for their time and effort.

References

Archer, A.W., Feldman, H.R., Kvale, E.P. and Lanier, W.P., 1994. Comparison of drier-to wetter-interval estuarine roof facies in the Eastern and Western Interior coal basins, USA. Palaeogeography, Palaeoclimatology, Palaeoecology, 106, 171-185.

Archer, A.W., Elrick, S., Nelson, W.J. and DiMichele, W.A., 2016. Cataclysmic burial of Pennsylvanian Period coal swamps in the Illinois Basin. In: Tessier, B. and Reynaud, J.-Y. (Eds.), Contributions to Modern and Ancient Tidal Sedimentology. International Association of Sedimentologists Special Publication 47, 217-231.

Arnold, C.A., 1941. Some Paleozoic plants from central Colorado and their stratigraphic significance. Contributions from the Museum of Paleontology University of Michigan, 6, 59-70.

Baets, S.D., Poesen, J., Knapen, A. and Galindo, P., 2007. Impact of root architecture on the erosion- reducing potential of roots during concentrated flow. Earth Surface Processes and Landforms, 32, 1323-1345.

Baird, G.C., Sroka, S.D., Shabica, C.W. and Beard, T.L., 1985. Mazon Creek-type fossil assemblages in the US midcontinent Pennsylvanian: their recurrent character and palaeoenvironmental significance. Philosophical Transactions of the Royal Society of London B, Biological Sciences, 311, 87-99.

Balvanera, P. and Aguirre, E., 2006. Tree Diversity, Environmental Heterogeneity, and Productivity in a Mexican Tropical Dry Forest 1. Biotropica, 38, 479-491.

Balvanera, P., Lott, E., Segura, G., Siebe, C. and Islas, A., 2002. Patterns of β- diversity in a Mexican tropical dry forest. Journal of Vegetation Science, 13, 145-158.

Bashforth, A.R. and Nelson, W.J., 2015. A Middle Pennsylvanian macrofloral assemblage from below the Rock Island (No. 1) Coal Member, Illinois: resolving the Bolsovian–Asturian boundary in the Illinois Basin. Review of Palaeobotany and Palynology, 222, 67-83.

Bashforth, A.R., Cleal, C.J., Gibling, M.R., Falcon-Lang, H.J. and Miller, R.F., 2014. Paleoecology of early Pennsylvanian vegetation on a seasonally dry tropical landscape (Tynemouth Creek Formation, New Brunswick, Canada). Review of Palaeobotany and Palynology, 200, 229-263.

Bashforth, A.R., DiMichele, W.A., Eble, C.F. and Nelson, W.J., 2016a. A Middle Pennsylvanian macrofloral assemblage from wetland deposits in Indiana (Illinois Basin): a taxonomic contribution with biostratigraphic, paleobiogeographic, and paleoecologic implications. Journal of Paleontology, 90, 589-631.

Bashforth, A.R., DiMichele, W.A., Eble, C.F. and Nelson, W.J., 2016b. Dryland vegetation from the Middle Pennsylvanian of Indiana (Illinois Basin): the dryland biome in glacioeustatic, paleobiogeographic, and paleoecologic context. Journal of Paleontology, 90, 785-814.

Bassler, H., 1916. A cycadophyte from the North American coal measures. American Journal of Science, Series 4, 42, 21-26.

Baumgardner Jr, R.W., DiMichele, W.A. and de Siqueira Vieira, N., 2016. An early Permian coastal flora dominated by *Germaropteris martinsii* from basinal sediments in the Midland Basin, West Texas. Palaeogeography, Palaeoclimatology, Palaeoecology, 459, 409-422.

Becq-Giraudon, J.-F., Montenat, C. & van den Driessche, J. 1996. Hercynian high-altitude phenomena in the French Massif Central: tectonic implications. Palaeogeography, Palaeoclimatology, Palaeoecology, 122, 227–241.

Beerbower, J.R., 1961. Origin of cyclothems of the Dunkard group (upper Pennsylvanian-lower Permian) in Pennsylvania, West Virginia, and Ohio. Geological Society of America Bulletin, 72, 1029-1050.

Behrensmeyer, A.K., Kidwell, S.M. and Gastaldo, R.A., 2000. Taphonomy and paleobiology. Paleobiology, 26(S4), 103-147.

Bergström, L., 1993. Quine, underdetermination, and skepticism. Journal of Philosophy, 90, 331-358.

Bode, H. Comments. In: Barlow, J.A., ed., 1975. The Age of the Dunkard. Proceedings of the 1st I.C. White Memorial Symposium (1972). Morgantown: West Virginia Geologic and Economic Survey.

Bohacs, K. and Suter, J., 1997. Sequence stratigraphic distribution of coaly rocks: fundamental controls and paralic examples. AAPG Bulletin, 81, 1612-1639.

Brand, U., Jiang, G., Azmy, K., Bishop, J. and Montañez, I.P., 2012. Diagenetic evaluation of a Pennsylvanian carbonate succession (Bird Spring Formation, Arrow Canyon, Nevada, USA) — 1: Brachiopod and whole rock comparison. Chemical Geology, 308, 26-39.

Brandt, J., 1988. The transformation of rainfall energy by a tropical rain forest canopy in relation to soil erosion. Journal of Biogeography, 15, 41-48.

Bragg, O.M. and Tallis, J.H., 2001. The sensitivity of peat-covered upland landscapes. Catena, 42, 345-360.

Brett, C.E., Zaffos, A. and Miller, A.I., 2016. Niche conservatism, tracking, and ecological stasis. In: Eldredge, N, Pievani, T., Serrelli, E. and Temkin, I. (Eds.), Evolutionary Theory: A Hierarchical Perspective, p. 282-306.

Brezinski, D.K., Cecil, C.B., Skema, V.W. and Stamm, R., 2008. Late Devonian glacial deposits from the eastern United States signal an end of the mid-Paleozoic warm period. Palaeogeography, Palaeoclimatology, Palaeoecology, 268,143-151.

Brezinski, D.K., Cecil, C.B. and Skema, V.W., 2010. Late Devonian glacigenic and associated facies from the central Appalachian Basin, eastern United States. GSA Bulletin, 122, 265-281.

Broutin, J., Doubinger, J., Farjanel, G., Freytet, P., Kerp, H., Langiaux, J, Lebreton, M.-L, Sebban, S and Satta, S., 1990. Le renouvellement des flores au passage Carbonifère Permien: approches stratigraphique, biologique, sédimentologique. Comptes rendus de l'Académie des Sciences. Série 2, Mécanique, Physique, Chimie, Sciences de l'Univers, Sciences de la Terre, 311, 1563-1569.

Bruijnzeel, L.A., 2004. Hydrological functions of tropical forests: not seeing the soil for the trees?. Agriculture, Ecosystems and Environment, 104, 185-228.

Bruijnzeel, L.A., Mulligan, M. and Scatena, F.N., 2011. Hydrometeorology of tropical montane cloud forests: emerging patterns. Hydrological Processes, 25, 465-498.

Buggisch, W., Joachimski, M.M., Sevastopulo, G. and Morrow, J.R., 2008. Mississippian $\delta^{13}C_{carb}$ and conodont apatite $\delta^{18}O$ records — their relation to the late Palaeozoic glaciation. Palaeogeography, Palaeoclimatology, Palaeoecology, 268, 273-292.

Burnham, R.J., 1993. Plant deposition in modern volcanic environments. Earth and Environmental Science Transactions of The Royal Society of Edinburgh, 84, 275-281.

Carnap, R., 1947. On the application of inductive logic. Philosophy and Phenomenological Research, 8, 133-148.

Carpenter, D., Falcon-Lang, H.J., Benton, M.J. and Nelson, W.J., 2011. Fishes and tetrapods in the Upper Pennsylvanian (Kasimovian) Cohn Coal Member of the Mattoon formation of Illinois, United States: systematics, paleoecology, and paleoenvironments. Palaios, 26, 639-657.

Catena, A. and Hembree, D., 2012. Recognizing vertical and lateral variability in terrestrial landscapes: a case study from the paleosols of the Late Pennsylvanian Casselman Formation (Conemaugh Group) southeast Ohio, USA. Geosciences, 2, 178-202.

Cecil, C.B., 2003. The concept of autocyclic and allocyclic controls on sedimentation and stratigraphy, emphasizing the climatic variable. SEPM Special Publication, 77, 13-20.

Cecil, C.B. and Dulong, F.T., 2003. Precipitation models for sediment supply in warm climates. SEPM Special Publication, 77, 21-27.

Cecil, C.B., Stanton, R.W., Neuzil, S.G., Dulong, F.T., Ruppert, L.F. and Pierce, B.S., 1985. Paleoclimate controls on late Paleozoic sedimentation and peat formation in the central Appalachian Basin (USA). International Journal of Coal Geology, 5, 195-230.

Cecil, C.B., Dulong, F.T., West, R.R., Stamm, R., Wardlaw, B.A. and Edgar, N.T., 2003a. Climate controls on the stratigraphy of a Middle Pennsylvanian cyclothem in North America. SEPM Special Publication, 77, 151-180.

Cecil, C.B., Dulong, F.T., Harris, R.A., Cobb, J.C., Gluskoter, H.G. and Nugroho, H., 2003b. Observations on climate and sediment discharge in selected tropical rivers, Indonesia. SEPM Special Publication, 77, 29-50.

Cecil, C.B., DiMichele, W.A. and Elrick, S.D., 2014. Middle and Late Pennsylvanian cyclothems, American Midcontinent: Ice-age environmental changes and terrestrial biotic dynamics. Comptes Rendus Geoscience, 346, 159-168.

Cecil, C.B., Hemingway, B.S. and Dulong, F.T., 2018. The chemistry of eolian quartz dust and the origin of chert. Journal of Sedimentary Research, 88, 743-752.

Chaloner, W.G., 1958. The Carboniferous upland flora. Geological Magazine, 95, 261-262.

Chavez, S.P. and Takahashi, K., 2017. Orographic rainfall hot spots in the Andes- Amazon transition according to the TRMM precipitation radar and in situ data. Journal of Geophysical Research: Atmospheres, 122, 5870-5882.

Cichan, M.A., 1986. Conductance in the wood of selected Carboniferous plants. Paleobiology, 12, 302-310.

Cleal, C.J. and Cascales- Miñana, B., 2014. Composition and dynamics of the great Phanerozoic Evolutionary Floras. Lethaia, 47, 469-484.

Cleal, C.J., Opluštil, S., Thomas, B.A., Tenchov, Y., Abbink, O.A., Bek, J., Dimitrova, T., Drábková, J., Hartkopf-Fröder, C., Van Hoof, T. and Kędzior, A., 2009. Late Moscovian terrestrial biotas and palaeoenvironments of Variscan Euramerica. Netherlands Journal of Geosciences, 88, 181-278.

Cleal, C.J., Uhl, D., Cascales-Miñana, B., Thomas, B.A., Bashforth, A.R., King, S.C. and Zodrow, E.L., 2012. Plant biodiversity changes in Carboniferous tropical wetlands. Earth-Science Reviews, 114, 124-155.

Cleal, C.J., Scanu, G.G., Buosi, C., Pittau, P. and Kustatscher, E., 2017. Middle Pennsylvanian vegetation of the San Giorgio Basin, southern Sardinia (Italy). Geological Magazine, 154, 1155-1170.

Clements, T., Purnell, M. and Gabbott, S., 2019. The Mazon Creek Lagerstätte: a diverse late Paleozoic ecosystem entombed within siderite concretions. Journal of the Geological Society, 176, 1-11.

Costanza, S.H., 1985. *Pennsylvanioxylon* of Middle and Upper Pennsylvanian coals from the Illinois Basin and its comparison with *Mesoxylon*. Palaeontographica Abteilung B, 197, 81-121.

Cridland, A.A., 1964. *Amyelon* in American coal balls. Palaeontology, 7, 186-209.

Cridland, A.A. and Morris, J.E., 1963. *Taeniopteris, Walchia* and *Dichophyllum* in the Pennsylvanian system in Kansas. University of Kansas Science Bulletin, 44, 71-85.

Dargie, G.C., Lewis, S.L., Lawson, I.T., Mitchard, E.T., Page, S.E., Bocko, Y.E. and Ifo, S.A., 2017. Age, extent and carbon storage of the central Congo Basin peatland complex. Nature, 542, 86-90.

Darrah, W.C., 1935. Permian elements in the fossil flora of the Appalachian Province. I. *Taeniopteris*. Harvard University Botanical Museum Leaflets, 3(9), 137-148.

Darrah, W.C., 1936. Permian elements in the fossil flora of the Appalachian Province. II. *Walchia*. Harvard University Botanical Museum Leaflets, 4(2), 9-19.

Dhar, O.N. and Rakhecha, P.R., 1981. The effect of elevation on monsoon rainfall distribution in the central Himalayas. In: Lighthill, J. and Pearce, R.P. (Eds.), Monsoon dynamics. Cambridge University Press, Cambridge, p. 253-260.

DiMichele, W.A., 2014. Wetland-dryland vegetational dynamics in the Pennsylvanian ice age tropics. International Journal of Plant Sciences, 175, 123-164.

DiMichele, W.A., and Falcon-Lang, H.J., 2011. Fossil forests in growth position (T^0 assemblages): origin, taphonomic biases and palaeoecological significance. Journal of the Geological Society, 168, 585–605.

DiMichele, W.A. and Philips, T.L., 1996. Clades, ecological amplitudes, and ecomorphs: phylogenetic effects and the persistence of primitive plant communities in the Pennsylvanian-age tropics. Palaeogeography Palaeoclimatology Palaeoecology, 127, 83-105.

DiMichele, W.A., Chaney, D.S., Dixon, W.H., John Nelson, W. and Hook, R.W., 2000. An Early Permian coastal flora from the central basin platform of Gaines County, west Texas. Palaios, 15, 524-534.

DiMichele, W.A., Kerp, H., Tabor, N.J. and Looy, C.V., 2008. The so-called “Paleophytic–Mesophytic” transition in equatorial Pangea—multiple biomes and vegetational tracking of climate change through geological time. Palaeogeography, Palaeoclimatology, Palaeoecology, 268, 152-163.

DiMichele, W.A., Cecil, C.B., Montañez, I.P. and Falcon-Lang, H.J., 2010. Cyclic changes in Pennsylvanian paleoclimate and effects on floristic dynamics in tropical Pangaea. International Journal of Coal Geology, 83, 329-344.

DiMichele, W. A., Cecil, C. B., Chaney, D. S., Elrick, S. D., Lucas, S. G., Lupia, R., Nelson, W. J., and Tabor, N. J., 2011. Pennsylvanian-Permian vegetational changes in tropical Euramerica. In: Harper, J. A. (Ed.), Geology of the Pennsylvanian-Permian in the Dunkard Basin. Guidebook, 76th Annual Field Conference of Pennsylvania Geologists, Washington, PA, p. 60-102.

DiMichele, W.A., Cecil, C.B., Chaney, D.S., Elrick, S.D. and Nelson, W.J., 2014. Fossil floras from the Pennsylvanian-Permian Cutler Group of southeastern Utah. Utah Geological Association Publication, 43, 491–504.

DiMichele, W.A., Chaney, D.S., Lucas, S.G., Nelson, W.J., Elrick, S.D., Falcon-Lang, H.J. and Kerp, H., 2017. Middle and Late Pennsylvanian fossil floras from Socorro County, New Mexico, USA. In: Lucas, S.G., DiMichele, W.A. and Krainer, K. (Eds.), Carboniferous-Permian transition in Socorro County, New Mexico. New Mexico Museum of Natural History and Science Bulletin, 77, 25-100.

DiMichele, W.A., Hotton, C.L., Looy, C.V. and Hook, R.W., 2019. Paleoecological and paleoenvironmental interpretation of three successive macrofloras and palynofloras from the

Kola Switch locality, lower Permian (Archer City Formation, Bowie Group) of Clay County, Texas, USA. Paläontologische Zeitschrift, 93, 423-451.

Dolby, G., Falcon-Lang, H.J. and Gibling, M.R., 2011. A conifer-dominated palynological assemblage from Pennsylvanian (late Moscovian) alluvial drylands in Atlantic Canada: implications for the vegetation of tropical lowlands during glacial phases. Journal of the Geological Society, 168, 571-584.

Dommain, R., Couwenberg, J. and Joosten, H., 2010. Hydrological self-regulation of domed peatlands in south-east Asia and consequences for conservation and restoration. Mires and Peat, 6, 1–17

Driese, S.G. and Ober, E.G., 2005. Paleopedologic and paleohydrologic records of precipitation seasonality from Early Pennsylvanian "underclay" paleosols, USA. Journal of Sedimentary Research, 75, 997–1010.

Dryflor (Latin American and Caribbean Seasonally Dry Tropical Forest Floristic Network), 2016. Plant diversity patterns in neotropical dry forests and their conservation implications. Science, 353, 1383-1387.

Elias, M.K. 1933. Late Paleozoic plants of the Midcontinent region as indicators of time and of environment. Report of the XVI International Geological Congress 1, 691-700.

Elrick, M. and Scott, L.A., 2010. Carbon and oxygen isotope evidence for high-frequency (104–105 yr) and My-scale glacio-eustasy in Middle Pennsylvanian cyclic carbonates (Gray Mesa Formation), central New Mexico. Palaeogeography, Palaeoclimatology, Palaeoecology, 285, 307-320.

Elrick, S.D., Nelson, W.J., Ames, P.R. and DiMichele, W.A., 2017a. Floras characteristic of Late Pennsylvanian peat swamps arose in the late Middle Pennsylvanian. Stratigraphy 14, 123-141.

Elrick, S.D., Nelson, W.J. and Lucas, S.G., 2017b. Fossil wood from Late Pennsylvanian sabkhas in Socorro County, New Mexico. New Mexico Museum of Natural History and Science Bulletin 77, 101-108.

Evans, M. and Warburton, J., 2011. Geomorphology of upland peat: erosion, form and landscape change. John Wiley and Sons,Ltd., Chichester, U.K. 288 p.

Falcon-Lang, H.J., 2004a. Pennsylvanian tropical rain forests responded to glacial-interglacial rhythms. Geology, 32, 689-692.

Falcon-Lang, H.J., 2004b. Pennsylvanian upland vegetation and its implications for the demise of the peat-forming tropical biome. Geological Balcanica, 34, 39-45.

Falcon-Lang, H.J., 2005. Small cordaitalean trees in a marine-influenced coastal habitat in the Pennsylvanian Joggins Formation, Nova Scotia. Journal of the Geological Society, 162, 485-500.

Falcon-Lang, H.J., 2006. Vegetation ecology of Early Pennsylvanian alluvial fan and piedmont environments in southern New Brunswick, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology, 233, 34-50.

Falcon-Lang, H.J. and Bashforth, A.R., 2004. Pennsylvanian uplands were forested by giant cordaitalean trees. Geology, 32, 417–420.

Falcon-Lang, H.J. and Bashforth, A.R., 2005. Morphology, anatomy, and upland ecology of large cordaitalean trees from the Middle Pennsylvanian of Newfoundland. Review of Palaeobotany and Palynology, 135, 223-243.

Falcon-Lang, H.J. and DiMichele, W.A., 2010. What happened to the coal forests during Pennsylvanian glacial phases?. Palaios, 25, 611-617.

Falcon-Lang, H.J., Nelson, W.J., Elrick, S., Looy, C.V., Ames, P.R. and DiMichele, W.A., 2009. Incised channel fills containing conifers indicate that seasonally dry vegetation dominated Pennsylvanian tropical lowlands. Geology, 37, 923-926.

Falcon-Lang, H.J., Jud, N.A., Nelson, W.J., DiMichele, W.A., Chaney, D.S. and Lucas, S.G., 2011a. Pennsylvanian coniferopsid forests in sabkha facies reveal the nature of seasonal tropical biome. Geology, 39, 371-374.

Falcon-Lang, H.J., Heckel, P.H., DiMichele, W.A., Blake Jr., B.M., Easterday, C.R., Eble, C.F., Elrick, S., Gastaldo, R.A., Greb, S.F., Martino, R.L., Nelson, W.J., Pfefferkorn, H.W., Phillips, T.L. and Rosscoe, S.J., 2011b. No major stratigraphic gap exists near the Middle–Upper Pennsylvanian (Desmoinesian–Missourian) boundary in North America. Palaios, 26, 125–139.

Falcon-Lang, H.J., Lucas, S.G., Kerp, H., Krainer, K., Montañez, I.P., Vachard, D., Chaney, D.S., Elrick, S.D., Contreras, D.L., Kurzawe, F. and DiMichele, W.A., 2015. Early Permian (Asselian) vegetation from a seasonally dry coast in western equatorial Pangea: Paleoecology and evolutionary significance. Palaeogeography, Palaeoclimatology, Palaeoecology, 433, 158-173.

Falcon-Lang, H.J., Kurzawe, F. and Lucas, S.G., 2016. A Late Pennsylvanian coniferopsid forest in growth position, near Socorro, New Mexico, USA: Tree systematics and palaeoclimatic significance. Review of Palaeobotany and Palynology, 225, 67-83.

Falcon-Lang, H.J., Nelson, W.J., Heckel, P.H., DiMichele, W.A. and Elrick, S.D. 2018., New insights on the stepwise collapse of the Carboniferous Coal Forests : Evidence from cyclothems and coniferopsid tree-stumps near the Desmoinesian–Missourian boundary in Peoria County, Illinois, USA. Palaeogeography, Palaeoclimatology, Palaeoecology, 490, 375-392.

Feldman, H.R., Franseen, E.K., Joeckel, R.M. and Heckel, P.H., 2005. Impact of longer-term modest climate shifts on architecture of high-frequency sequences (cyclothems), Pennsylvanian of Midcontinent USA. Journal of Sedimentary Research, 75, 350-368.

Ferreira-Nunes, Y.R., da Luz, G.R., Rebleth, S., de Souza, D.L.D.S., das Dores Magalhães-Veloso, M., do Espírito-Santo, M.M. and dos Santos, R.M., 2014. Floristic, structural, and functional group variations in tree assemblages in a Brazilian Tropical Dry Forest: effects of successional stage and soil properties. Tropical dry forests in the Americas: Ecology, conservation and management. Taylor and Francis, p. 325-346.

Fielding, C.R., Frank, T.D. and Isbell, J.L., 2008. The late Paleozoic ice age—A review of current understanding and synthesis of global climate patterns. Geological Society of America Special Papers, 441, 343-354.

Fielding, C.R., Nelson, W.J. and Elrick, S.D., 2020. Sequence stratigraphy of the late Desmoinesian to early Missourian (Pennsylvanian) succession of southern Illinois: Insights into controls on stratal architecture in an icehouse period of Earth history. Journal of Sedimentary Research, 90, 200-227.

Fisher, D.J., 1925. Structure of Herrin (no. 6) Coal seam near Duquoin. Illinois State Geological Survey Report of investigations, 5, 1-34.

Fleming, T.H., 1986. Secular changes in Costa Rican rainfall: correlation with elevation. Journal of Tropical Ecology, 2, 87-91.

Frederiksen, N.O., 1972. The rise of the Mesophytic flora. Geoscience and Man, 4, 17-28.

Garcia-Martino, A.R., Warner, G.S., Scatena, F.N. and Civco, D.L., 1996. Rainfall, runoff and elevation relationships in the Luquillo Mountains of Puerto Rico. Caribbean Journal of Science, 32, 413-424.

Gastaldo, R.A., 1986a. Implications on the paleoecology of autochthonous lycopods in clastic sedimentary environments of the Early Pennsylvanian of Alabama. Palaeogeography, Palaeoclimatology, Palaeoecology, 53, 191-212.

Gastaldo, R.A., 1986b. Selected aspects of plant taphonomic processes in coastal deltaic regimes. Paleotonological Society Papers, 15, 27-44.

Gastaldo, R.A., 1987. Confirmation of Carboniferous clastic swamp communities. Nature, 326, 869-871.

Gastaldo, R.A., 1996. Flöznah and Flözfern assemblages: Potential predictors of Late Carboniferous biome replacement? In: Leary, R.L. (Ed.), Patterns in Paleobotany: Proceedings of a Czech-U.S. Carboniferous Paleobotany Workshop. Illinois State Museum Scientific Papers, 26, 19-27.

Gastaldo, R.A. and Demko, T.M., 2011. Long term hydrology controls the plant fossil record. In: Allison, P. A., and Bottjer, D. J. (Eds.), Taphonomy: processes and bias through time, 2nd edition, New York. Topics in Geobiology, 32, 249–286.

Gastaldo, R.A., Pfefferkorn, H.W. and DiMichele, W.A., 1995. Taphonomic and sedimentologic characterization of roof-shale floras. Geological Society of America Memoir 185, 341-352.

Gastaldo, R.A., DiMichele, W.A. and Pfefferkorn, H.W., 1996. Out of the icehouse into the greenhouse: a late Paleozoic analogue for modern global vegetational change. GSA Today 6(10), 1-7.

Gastaldo, R.A., Purkynova, E., Simunek, Z. and Schmitz, M.D., 2009a. Ecological persistence in the Late Mississippian (Serpukhovian, Namurian A) megafloral record of the Upper Silesian Basin, Czech Republic. Palaios, 24, 336-350.

Gastaldo, R.A., Purkynova, E. and Simunek, Z., 2009b. Megafloral perturbation across the Enna Marine Zone in the Upper Silesian Basin attests to Late Mississippian (Serpukhovian) deglaciation and climate change. Palaios, 24, 351-366.

Geißler, C., Kühn, P., Böhnke, M., Bruelheide, H., Shi, X. and Scholten, T., 2012. Splash erosion potential under tree canopies in subtropical SE China. Catena, 91, 85-93.

Gibling, M.R., Bashforth, A.R., Falcon-Lang, H.J., Allen, J.P. and Fielding, C.R., 2010. Log jams and flood sediment buildup caused channel abandonment and avulsion in the Pennsylvanian of Atlantic Canada. Journal of Sedimentary Research, 80, 268-287.

Gibling, M.R., Davies, N.S., Falcon-Lang, H.J., Bashforth, A.R., DiMichele, W.A., Rygel, M.C. and Ielpi, A., 2014. Palaeozoic co-evolution of rivers and vegetation: a synthesis of current knowledge. Proceedings of the Geologists' Association, 125, 524-533.

Goldberg, K. and Miller, K.B., 2019. Geology of the Flint Hills, Kansas: Sea-level and climate changes in the Permian. Geological Society of America Field Guide, 52, 1-24.

Goldhammer, R.K. and Elmore, R.D., 1984. Paleosols capping regressive carbonate cycles in the Pennsylvanian Black Prince Limestone, Arizona. Journal of Sedimentary Research, 54, 1124-1137.

Goldhammer, R.K., Oswald, E.J. and Dunn, P.A., 1994. High-frequency, glacio-eustatic cyclicity in the Middle Pennsylvanian of the Paradox Basin: an evaluation of Milankovitch forcing. International Association of Sedimentologists Special Publication, 38, 243-281.

Goovaerts, P., 2000. Geostatistical approaches for incorporating elevation into the spatial interpolation of rainfall. Journal of Hydrology, 228, 113-129.

Gorham, E., 1957. The development of peat lands. The Quarterly Review of Biology, 32, 145-166.

Gothan, W., 1912. Paläobotanik. In: Korschelt, E., Linck, G., Schaum, K., Simon, H. Th., Verworn, M., Teichmann, E. (Eds.), Handwörterbuch der Naturwissenschaften. Gustav Fischer Verlag, Jena, pp. 408–460.

Gothan, W. and Gimm, O., 1930. Neuere Beobachtungen und Betrachtungen über die Flora des Rotliegenden in Thüringen. Arbeiten aus dem Institut für Paläobotanik und Petrographie der Brennsteine, 2, 39-74.

Greb, S.F., Eble, C.F. and Hower, J.C., 1999a. Depositional history of the Fire Clay coal bed (Late Duckmantian), eastern Kentucky, USA. International Journal of Coal Geology, 40, 255-280.

Greb, S.F., Eble, C.F., Chesnut, D.R., Phillips, T.L. and Hower, J.C., 1999b. An in situ occurrence of coal balls in the Amburgy coal bed, Pikeville Formation (Duckmantian), central Appalachian Basin, USA. Palaios, 14, 432-450.

Greb, S.F., Pashin, J.C., Martino, R.L. and Eble, C.F., 2008. Appalachian sedimentary cycles during the Pennsylvanian: Changing influences of sea level, climate, and tectonics. In: Fielding, C.R., Frank, T.D., and Isbell, J.L. (Eds.), Resolving the Late Paleozoic Ice Age in Time and Space. Geological Society of America Special Paper, 441, 235-248.

Green, J.J., Dawson, L.A., Proctor, J., Duff, E.I. and Elston, D.A., 2005. Fine root dynamics in a tropical rain forest is influenced by rainfall. Plant and Soil, 276, 23-32.

Gresley, W.S., 1894. The "slate binders" of the "Pittsburg" coal bed. American Geologist, 14, 356-365.

Guo Y., 1990. Paleoecology of flora from coal measures of Upper Permian in western Guizhou. Journal of the China Coal Society, 15, 48-54.

Gyssels, G., Poesen, J., Bochet, E. and Li, Y., 2005. Impact of plant roots on the resistance of soils to erosion by water: a review. Progress in Physical Geography, 29, 189-217.

Harris, R., Cecil, C.B., Dulong, F.T. and Nugroho, H., 2008. Is sediment discharge controlled more by climate or tectonics? Studies of suspended and dissolved loads from rivers in active orogens of Indonesia. Himalayan. Geology, 29, 32-33.

Havlena, V., 1961. Die flöznahe und flözfremde Flora des oberschlesischen Namurs A und B. Palaeontographica Abt B, 180, 22- 38.

Heavens, N.G., Mahowald, N.M., Soreghan, G.S., Soreghan, M.J. and Shields, C.A., 2015. A model-based evaluation of tropical climate in Pangaea during the late Palaeozoic icehouse. Palaeogeography, Palaeoclimatology, Palaeoecology, 425, 109-127.

Heckel, P.H., 2008. Pennsylvanian cyclothems in Midcontinent North America as far-field effects of waxing and waning of Gondwana ice sheets. In: Fielding, C.R., Frank, T.D., and Isbell, J.L. (Eds.), Resolving the Late Paleozoic Ice Age in Time and Space. Geological Society of America Special Paper 441, 275–289.

Heckel, P.H., Gibling, M.R. and King, N.R., 1998. Stratigraphic model for glacial-eustatic Pennsylvanian cyclothems in highstand nearshore detrital regimes. Journal of Geology, 106, 373-384.

Heckel, P.H., Alekseev, A.S., Barrick, J.E., Boardman, D.R., Goreva, N.V., Nemyrovska, T.I., Ueno, K., Villa, E. and Work, D.M., 2007. Cyclothem ["digital"] correlation and biostratigraphy across the global Moscovian-Kasimovian-Gzhelian stage boundary interval (Middle-Upper Pennsylvanian) in North America and eastern Europe. Geology, 35, 607-610.

Hilton, J. and Cleal, C.J., 2007. The relationship between Euramerican and Cathaysian tropical floras in the Late Palaeozoic: palaeobiogeographical and palaeogeographical implications. Earth-Science Reviews, 85, 85-116.

Hilton, J., Shi-Jun, W., Galtier, J. and Bateman, R.M., 2009. Cordaitalean seed plants from the Early Permian of North China. II. Reconstruction of *Cordaixylon tianii*. International Journal of Plant Sciences, 170, 400-418.

Holland, S.M. and Zaffos, A., 2011. Niche conservatism along an onshore-offshore gradient. Paleobiology, 37, 270-286.

Horne, J.C., Ferm, J.C., Caruccio, F.T. and Baganz, B.P., 1978. Depositional models in coal exploration and mine planning in Appalachian region. AAPG Bulletin, 62, 2379-2411.

Horton, D.E., Poulsen, C.J., Montañez, I.P. and DiMichele, W.A., 2012. Eccentricity-paced late Paleozoic climate change. Palaeogeography, Palaeoclimatology, Palaeoecology, 331, 150-161.

Hotton, C.L., Hueber, F.M., Griffing, D.H., Bridge, J.S., Gensel, P.G. and Edwards, D., 2001. Early terrestrial plant environments: an example from the Emsian of Gaspé, Canada. In: Edwards, D. and Gensel, P.G. (Eds.), Plants invade the land: evolutionary and environmental perspectives. Columbia University Press, New York, p. 179-212.

Ielpi, A., Gibling, M.R., Bashforth, A.R., Lally, C., Rygel, M.C. and Al-Silwadi, S., 2014. Role of vegetation in shaping Early Pennsylvanian braided rivers: Architecture of the Boss Point Formation, Atlantic Canada. Sedimentology, 61, 1659–1700.

Isaacson, P.E., Diaz-Martinez, E., Grader, G.W., Kalvoda, J., Babek, O. and Devuyst, F.X., 2008. Late Devonian–earliest Mississippian glaciation in Gondwanaland and its biogeographic consequences. Palaeogeography, Palaeoclimatology, Palaeoecology, 268, 126-142.

Isbell, J.L., Henry, L.C., Gulbranson, E.L., Limarino, C.O., Fraiser, M.L., Koch, Z.J., Ciccioli, P.L. and Dineen, A.A., 2012. Glacial paradoxes during the late Paleozoic ice age: evaluating the equilibrium line altitude as a control on glaciation. Gondwana Research, 22, 1-19.

Jacobson, R.J., 1987. Stratigraphic correlations of the Seelyville, DeKoven, and Davis coals of Illinois, Indiana, and Western Kentucky. Illinois State Geological Survey Circular 539, 1-27.

Jacobson, R.J., 1993. Coal Resources of the Dekoven and Davis Members (Carbondale Formation) in Gallatin and Saline Counties, Southeastern Illinois. Illinois State Geological Survey Circular, 551, 1-41.

Jennings, J.R., 1980. Fossil plants from the Fountain Formation (Pennsylvanian) of Colorado. Journal of Paleontology, 54, 149-158.

Joeckel, R.M., 1989. Geomorphology of a Pennsylvanian land surface: Pedogenesis in the Rock Lake Shale Member, southeastern Nebraska. Journal of Sedimentary Petrology, 59, 469-481.

Joeckel, R.M., 1991. Paleosol stratigraphy of the Eskridge Formation; Early Permian pedogenesis and climate in southeastern Nebraska. Journal of Sedimentary Research, 61, 234-255.

Joeckel, R.M., 1994. Virgilian (Upper Pennsylvanian) Paleosols in the upper Lawrence Formation (Douglas Group) and its Snyderville Shale Member (Oread Formation, Shawnee Group) of the northern Midcontinent, USA; pedologic contrasts in a cyclothem sequence. Journal of Sedimentary Research, 64, 853-866.

Joeckel, R.M., 1995. Paleosols below the Ames Marine Unit (Upper Pennsylvanian, Conemaugh Group) in the Appalachian Basin, USA; variability on an ancient depositional landscape. Journal of Sedimentary Research, 65, 393-407.

Joeckel, R.M., 1999. Paleosol in Galesburg Formation (Kansas City Group, Upper Pennsylvanian), northern Midcontinent, USA; evidence for climate change and mechanisms of marine transgression. Journal of Sedimentary Research, 69, 720-737.

Jordan, O.D. and Mountney, N.P., 2012. Sequence stratigraphic evolution and cyclicity of an ancient coastal desert system: the Pennsylvanian–Permian Lower Cutler Beds, Paradox Basin, Utah, USA. Journal of Sedimentary Research, 82, 755-780.

Junk, W.J., Piedade, M.T.F., Schöngart, J., Cohn-Haft, M., Adeney, J.M. and Wittmann, F., 2011. A classification of major naturally-occurring Amazonian lowland wetlands. Wetlands, 31, 623-640.

Kammer, T.W. and Matchen, D.L., 2008. Evidence for eustasy at the Kinderhookian-Osagean (Mississippian) boundary in the United States: response to late Tournaisian glaciation. Geological Society of America Special Paper, 441, 261-274.

Kenfack, D., Chuyong, G.B., Condit, R., Russo, S.E. and Thomas, D.W., 2014. Demographic variation and habitat specialization of tree species in a diverse tropical forest of Cameroon. Forest Ecosystems, 1: 22, https://doi.org/10.1186/s40663-014-0022-3.

Kerp, H., 1996. Post-Variscan late Paleozoic northern hemisphere gymnosperms: the onset to the Mesozoic. Review of Palaeobotany and Palynology, 90, 263–285.

Kerp, H., 2000. The modernization of landscapes during the Late Paleozoic-Early Mesozoic. The Paleontological Society Papers, 6, 79-114.

Kerp, H. and Fichter, J., 1985. Die Makrofloren des saarpfälzischen Rotliegenden (? Ober-Karbon-Unter-Perm; SW-Deutschland). Mainzer Geowissenschaftliche Mitteilungen, 14, 159-286.

Klein, G.D. and Willard, D.A., 1989. Origin of the Pennsylvanian coal-bearing cyclothems of North America. Geology, 17, 152-155.

Knoll, A.H., 1985. Exceptional preservation of photosynthetic organisms in silicified carbonates and silicified peats. Philosophical Transactions of the Royal Society of London. B, Biological Sciences, 311, 111-122.

Köppen, W., 1936. Das Geographisches System der Klimate. In: Köppen, W. and Geiger, R. (Eds.), Handbuch der Klimatologie, Vol. 1 Part C. Gebrüder Borntraeger, Berlin, p. 1–46.

Kosanke, R.M. and Cecil, C.B., 1996. Late Pennsylvanian climate changes and palynomorph extinctions. Review of Palaeobotany and Palynology, 90, 113-140.

Kroner, U. and Romer, R.L., 2013. Two plates—many subduction zones: the Variscan orogeny reconsidered. Gondwana Research, 24, 298-329.

Kvale, E.P. and Archer, A.W., 1990. Tidal deposits associated with low-sulfur coals, Brazil Fm. (Lower Pennsylvanian), Indiana. Journal of Sedimentary Research, 60, 563-574.

Kvale, E.P., Fraser, G.S., Archer, A.W., Zawistoski, A., Kemp, N. and McGough, P., 1994. Evidence of seasonal precipitation in Pennsylvanian sediments of the Illinois Basin. Geology, 22, 331-334.

Kvale, E.P., Mastalerz, M., Furer, L.C., Engelhardt, D.W., Rexroad, C.B. and Eble, C.F., 2004. Atokan and early Desmoinesian coal-bearing parasequences in Indiana, U.S.A., Sequence stratigraphy, paleoclimate, and tectonics of coal-bearing strata. AAPG Studies in Geology, 51, 71–88.

Kvale, E.P., Bowie, C.M., Flenthrope, C., Mace, C., Parrish, J.M., Price, B., Anderson, S. and DiMichele, W.A., 2020. Facies variability within a mixed carbonate-siliciclastic sea-floor fan (upper Wolfcamp Fm., Permian, Delaware Basin, New Mexico). AAPG Bulletin, 104, 525–563.

Lähteenoja, O., Flores, B. and Nelson, B., 2013. Tropical peat accumulation in Central Amazonia. Wetlands, 33, 495-503.

Langenheim, R.L., Jr. and Nelson, W.J., 1992. The cyclothemic concept in the Illinois Basin: a review. Geological Society of America Memoir, 180, 55-72.

Latrubesse, E.M., Stevaux, J.C. and Sinha, R., 2005. Tropical rivers. Geomorphology, 70, 187-206.

Leary, R.L., 1975. Early Pennsylvanian paleogeography of an upland area, western Illinois, USA. Bulletin de la Société belge de géologie, 84, 19-31.

Leary, R.L. and Pfefferkorn, H.W., 1977. An Early Pennsylvanian flora with *Megalopteris* and Noeggerathiales from west-central Illinois. Illinois State Geological Survey Circular, 500, 1-46.

Li, Q., Liu, G.B., Zhang, Z., Tuo, D.F., Bai, R.R. and Qiao, F.F., 2017. Relative contribution of root physical enlacing and biochemistrical exudates to soil erosion resistance in the Loess soil. Catena, 153, 61-65.

Libertín, M., Dašková, J., Opluštil, S., Bek, J. and Edress, N., 2009. A palaeoecological model for a vegetated early Westphalian intramontane valley (Intra-Sudetic Basin, Czech Republic). Review of Palaeobotany and Palynology, 155, 175-203.

Liu, C., Jarochowska, E., Du, Y., Vachard, D. and Munnecke, A., 2017. Stratigraphical and $\delta^{13}C$ records of Permo-Carboniferous platform carbonates, South China: Responses to late Paleozoic icehouse climate and icehouse–greenhouse transition. Palaeogeography, Palaeoclimatology, Palaeoecology, 474, 113-129.

Looy, C.V., Kerp, H., Duijnstee, I.A.P and DiMichele, W.A., 2014a. The late Paleozoic ecological-evolutionary laboratory, a land-plant fossil record perspective. The Sedimentary Record, 12(4), 4-18.

Looy, C.V., Stevenson, R.A., Van Hoof, T.B. and Mander, L., 2014b. Evidence for coal forest refugia in the seasonally dry Pennsylvanian tropical lowlands of the Illinois Basin, USA. PeerJ, 2, p.e630.

Lucas, S.G., DiMichele, W.A., Krainer, K., Chaney, D.S. and Spielmann, J.A., 2009. A coal-measure forest near Socorro, New Mexico. New Mexico Geological Society Field Conference Guidebook, 60, 235-242.

Lyons, P.C. and Darrah, W.C., 1989. Earliest conifers of North America: upland and/or paleoclimatic indicators?. Palaios, 4, 480-486.

Macbeth, N. 1971. Darwin retried: An appeal to reason. Gambit Incorporated, Boston, MA.

Mamay, S.H. and Mapes, G., 1992. Early Virgilian plant megafossils from the Kinney Brick company quarry, Manzanita Mountains, New Mexico. New Mexico Bureau of Mines and Mineral Resources Bulletin, 138, 61-85.

Mamay, S.H. and Read, C.B., 1956. Additions to the flora of the Spotted Ridge Formation in central Oregon. U.S. Geological Survey Professional Paper, 274-I, 211-226.

Martino, R. L., 2004. Sequence stratigraphy of the Glenshaw Formation (Middle–Late Pennsylvanian) in the Central Appalachian Basin. In: Pashin, J.C. and Gastaldo, R.A. (Eds.), Sequence stratigraphy, paleoclimate, and tectonics of coal-bearing strata. AAPG Studies in Geology, 51, 1–28.

Martino, R.L., 2017. Walchian conifers from the Mid-Late Pennsylvanian Conemaugh Group in the Appalachian Basin: Stratigraphic and depositional context, and paleoclimatic significance. International Journal of Coal Geology, 171, 153-168.

Mastalerz, M., Drobniak, A., Rupp, J.A. and Shaffer, N.R., 2004. Characterization of Indiana's coal resource: availability of the reserves, physical and chemical properties of the coal, and present and potential uses. Indiana Geological Survey, Open File Study 04-02.

McCann, T., Pascal, C., Timmerman, M.J., Krzywiec, P., López-Gómez, J., Wetzel, L., Krawczyk, C.M., Rieke, H. and Lamarche, J., 2006. Post-Variscan (end Carboniferous-Early Permian) basin evolution in western and central Europe. Geological Society, London, Memoirs, 32, 355-388.

McComas, M.A., 1988. Upper Pennsylvanian compression floras of the 7-11 mine, Columbiana County, northeastern Ohio. Ohio Journal of Science, 88, 48-52.

McKee, E.D., 1975. Interpretation of Pennsylvanian history. In: McKee, E.D. and Crosby, E.J. (Eds.), Paleotectonic investigations of the Pennsylvanian System in the United States. Part II. Interpretive summary and special features of the Pennsylvanian System. U.S. Geological Survey Professional Paper, 853, 1-21.

Miall, A., 2014. The emptiness of the stratigraphic record: a preliminary evaluation of missing time in the Mesa Verde Group, Book Cliffs, Utah, U.S.A. Journal of Sedimentary Petrology, 84, 457-469.

Mii, H.S., Grossman, E.L. and Yancey, T.E., 1999. Carboniferous isotope stratigraphies of North America: implications for Carboniferous paleoceanography and Mississippian glaciation. Geological Society of America Bulletin, 111, 960-973.

Miller, K.B., McCahon, T.J. and West, R.R., 1996. Lower Permian (Wolfcampian) Paleosol-bearing cycles of the US Midcontinent; evidence of climatic cyclicity. Journal of Sedimentary Research, 66, 71-84.

Montañez, I.P., 2016. A Late Paleozoic climate window of opportunity. Proceedings of the National Academy of Sciences, 113, 2334-2336.

Montañez, I.P. and Cecil, C.B., 2013. Paleoenvironmental clues archived in non-marine Pennsylvanian–lower Permian limestones of the Central Appalachian Basin, USA. International Journal of Coal Geology, 119, 41-55.

Montañez, I.P. and Poulsen, C.J., 2013. The Late Paleozoic ice age: an evolving paradigm. Annual Review of Earth and Planetary Sciences, 41, 629-656.

Moore, R.C., Elias, M.K. and Newell, N.D., 1936. A "Permian" flora from the Pennsylvanian rocks of Kansas. Journal of Geology, 44, 1-31.

Moore, L.C., Wittry, J. and DiMichele, W.A., 2014. The Okmulgee, Oklahoma fossil flora, a Mazon Creek equivalent: Spatial conservatism in the composition of Middle Pennsylvanian wetland vegetation over 1100 km. Review of Palaeobotany and Palynology, 200, 24-52.

Murphy, P.G. and Lugo, A.E., 1986. Ecology of tropical dry forest. Annual Review of Ecology and Systematics, 17, 67-88.

Nelson, W.J., Elrick, S.D., DiMichele, W.A. and Ames, P.R. 2020. Evolution of a peat-contemporaneous channel: The Galatia channel, Middle Pennsylvanian, of Illinois Basin. Illinois State Geological Survey Circular. IN PRESS.

Neuzil, S.G., Dulong, F.T. and Cecil, C.B., 2005. Spatial trends in ash yield, sulfur, selenium, and other selected trace element concentrations in coal beds of the Appalachian Plateau region, USA. U.S. Geological Survey, Open File Report No. 2005-1330.

Nienhuis, J.H., Ashton, A.D., Edmonds, D.A., Hoitink, A.J.F., Kettner, A.J., Rowland, J.C. and Törnqvist, T.E., 2020. Global-scale human impact on delta morphology has led to net land area gain. Nature, 577, 514-518.

Olszewski, T.D. and Patzkowsky, M.E., 2003. From cyclothems to sequences: the record of eustasy and climate on an icehouse epeiric platform (Pennsylvanian-Permian, North American Midcontinent). Journal of Sedimentary Research, 73, 15-30.

Opluštil, S., 2005. Evolution of the Middle Westphalian river valley drainage system in central Bohemia (Czech Republic) and its palaeogeographic implication. Palaeogeography, Palaeoclimatology, Palaeoecology, 222, 223– 258.

Opluštil, S. and Cleal, C.J., 2007. A comparative analysis of some Late Carboniferous basins of Variscan Europe. Geological Magazine, 144, 417-448.

Opluštil, S. and Sýkorová, I., 2018. Early Pennsylvanian ombrotrophic mire of the Prokop Coal (Upper Silesian Basin); what does it say about climate?. International Journal of Coal Geology, 198, 116-143.

Opluštil, S., Pšenička, J., Libertín, M. and Šimůnek, Z., 2007. Vegetation patterns of Westphalian and Lower Stephanian mire assemblages preserved in tuff beds of the continental basins of Czech Republic. Review of Palaeobotany and Palynology, 143, 107–154.

Opluštil, S., Šimůnek, Z., Zajíc, J. and Mencl, V., 2013a. Climatic and biotic changes around the Carboniferous/Permian boundary recorded in the continental basins of the Czech Republic. International Journal of Coal Geology, 119, 114-151.

Opluštil, S., Edress, N.A. and Sýkorová, I., 2013. Climatic vs. tectonic controls on peat accretion in non-marine setting; an example from the Žacléř Formation (Yeadonian–Bolsovian) in the Intra-Sudetic Basin (Czech Republic). International Journal of Coal Geology, 116, 135-157.

Opluštil, S., Pšenička, J., Bek, J., Wang, J., Feng, Z., Libertín, M., Šimůnek, Z., Bureš, J. and Drábková, J., 2014. T^0 peat-forming plant assemblage preserved in growth position by volcanic ash-fall: A case study from the Middle Pennsylvanian of the Czech Republic. Bulletin of Geosciences, 89, 773-818.

Opluštil, S., Lojka, R., Rosenau, N.A., Strnad, L. and Sýkorová, I., 2015. Middle Moscovian climate of eastern equatorial Pangea recorded in paleosols and fluvial architecture. Palaeogeography, Palaeoclimatology, Palaeoecology, 440, 328-352.

Opluštil, S., Lojka, R., Rosenau, N., Strnad, L. and Kędzior, A., 2019. Climatically-driven cyclicity and peat formation in fluvial setting of the Moscovian–Early Kasimovian Cracow

Sandstone Series, Upper Silesia (Poland). International Journal of Coal Geology, 212, Article No. 103234,

Paduano, G.M., Bush, M.B., Baker, P.A., Fritz, S.C. and Seltzer, G.O., 2003. A vegetation and fire history of Lake Titicaca since the Last Glacial Maximum. Palaeogeography, Palaeoclimatology, Palaeoecology, 194, 259-279.

Page, S.E., Wüst, R., Weiss, D., Rieley, J.O., Shotyk, W. and Limin, S., 2004. A record of Late Pleistocene and Holocene carbon accumulation and climate change from an equatorial peat bog (Kalimantan, Indonesia): implications for past, present and future carbon dynamics. Journal of Quaternary Science, 19, 625–635.

Peyser, C.E. and Poulsen, C.J., 2008. Controls on Permo-Carboniferous precipitation over tropical Pangaea: a GCM sensitivity study. Palaeogeography, Palaeoclimatology, Palaeoecology, 268, 181-192.

Pfefferkorrn, H.W., 1980. A note on the term "upland flora". Review of Palaeobotany and Palynology, 30, 157-158.

Pfefferkorn, H.W. and Thomson, M.C., 1982. Changes in dominance patterns in Upper Carboniferous plant-fossil assemblages. Geology, 10, 641-644.

Pfefferkorn, H.W. and Wang, J., 2007. Early Permian coal-forming floras preserved as compressions from the Wuda District (Inner Mongolia, China). International Journal of Coal Geology, 69, 90-102.

Phillips, T.L. and Peppers, R.A., 1984. Changing patterns of Pennsylvanian coal-swamp vegetation and implications of climatic control on coal occurrence. International Journal of Coal Geology, 3, 205-255.

Phillips, T.L., Peppers, R.A., Avcin, M.J. and Laughnan, P.F., 1974. Fossil plants and coal: patterns of change in Pennsylvanian coal swamps of the Illinois Basin. Science, 184, 1367-1369.

Plotnick, R.E., Kenig, F., Scott, A.C., Glasspool, I.J., Eble, C.F. and Lang, W.J., 2009. Pennsylvanian paleokarst and cave fills from northern Illinois, USA: a window into late Carboniferous environments and landscapes. Palaios, 24, 627-637.

Poulsen, C.J., Pollard, D., Montañez, I.P. and Rowley, D., 2007. Late Paleozoic tropical climate response to Gondwanan deglaciation. Geology, 35, 771-774.

Prinzing, A., Durka, W., Klotz, S. and Brandl, R., 2001. The niche of higher plants: evidence for phylogenetic conservatism. Proceedings of the Royal Society of London. Series B: Biological Sciences, 268, 2383-2389.

Prinzing, A., Ozinga, W.A., Brändle, M., Courty, P.E., Hennion, F., Labandeira, C., Parisod, C., Pihain, M. and Bartish, I.V., 2017. Benefits from living together? Clades whose species use similar habitats may persist as a result of eco- evolutionary feedbacks. New Phytologist, 213, 66-82.

Raymond, A., Lambert, L., Costanza, S., Slone, E.J. and Cutlip, P.C., 2010. Cordaiteans in paleotropical wetlands: an ecological re-evaluation. International Journal of Coal Geology, 83, 248-265.

Read, C.B., 1934. A flora of Pottsville age from the Mosquito Range, Colorado. U.S. Geological Survey Professional Paper, 185-D, 79-96.

Remy, W. 1975. The floral changes at the Carboniferous-Permian boundary in Europe and North America. In: Barlow, J.A. (Ed.), The Age of the Dunkard. West Virginia Geological and Economic Survey, Morgantown, p. 305-344.

Rennó, C.D., Nobre, A.D., Cuartas, L.A., Soares, J.V., Hodnett, M.G. and Tomasella, J., 2008. HAND, a new terrain descriptor using SRTM-DEM: Mapping terra-firme rainforest environments in Amazonia, 112, 3469-3481.

Ricardi-Branco, F., Branco, F.C., Garcia, R.J., Faria, R.S., Pereira, S.Y., Portugal, R., Pessenda, L.C. and Pereira, P.R., 2009. Plant accumulations along the Itanhaém River basin, southern coast of São Paulo state, Brazil. Palaios, 24, 416-424.

Ricardi-Branco F., Rios F.S., Pereira S.Y., 2020. Actualistic taphonomy of plant remains in tropical forests of southeastern Brazil. In: Martínez S., Rojas A. and Cabrera F. (Eds,). Actualistic Taphonomy in South America. Topics in Geobiology (Springer), 48, 111-138.

Rich, F.J., 1989. A review of the taphonomy of plant remains in lacustrine sediments. Review of Palaeobotany and Palynology, 58, 33-46.

Richey, J.D., White, J.D., Montañez, I.P., Wilson, J.P. and DiMichele, W.A., 2018. Physiological functioning of seasonally dry adapted floras in response to changes in late Paleozoic atmospheric composition. Geological Society of America Abstracts with Programs, 50 (6), Final Paper Number 235-5. doi: 10.1130/abs/2018AM-321954

Rigsby, C.A., Bradbury, J.P., Baker, P.A., Rollins, S.M. and Warren, M.R., 2005. Late Quaternary palaeolakes, rivers, and wetlands on the Bolivian Altiplano and their palaeoclimatic implications. Journal of Quaternary Science, 20, 671-691.

Rosado, B.H.P., Martins, A.C., Colomeu, T.C., Oliveira, R.S., Joly, C.A. and Aidar, M.P.M., 2011. Fine root biomass and root length density in a lowland and a montane tropical rain forest, SP, Brazil. Biota Neotropica, 11, 203-209.

Roscher, M. and Schneider, J.W., 2006. Permo-Carboniferous climate: Early Pennsylvanian to Late Permian climate development of central Europe in a regional and global context. Geological Society, London, Special Publications, 265, 95-136.

Rosenau, N.A., Tabor, N.J., Elrick, S.D. and Nelson, W.J., 2013. Polygenetic history of paleosols in middle–upper Pennsylvanian cyclothems of the Illinois basin, USA: Part II. Integrating geomorphology, climate, and glacioeustasy. Journal of Sedimentary Research, 83, 637-668.

Rothwell, G.W. and Mapes, G., 1988. Vegetation of a Paleozoic conifer community. In: Mapes, G. and Mapes, R.H. (Eds), Regional geology and paleontology of upper Paleozoic Hamilton quarry area in southeastern Kansas. Kansas Geological Survey Guidebook, 6, 213-223.

Rothwell, G.W. and Warner, S., 1984. *Cordaixylon dumusum* n. sp.(Cordaitales). I. Vegetative structures. Botanical Gazette, 145, 275-291.

Roy, S. and Singh, J.S., 1994. Consequences of habitat heterogeneity for availability of nutrients in a dry tropical forest. Journal of Ecology, 82, 503-509.

Salovaara, K.J., Cárdenas, G.G. and Tuomisto, H., 2004. Forest classification in an Amazonian rainforest landscape using pteridophytes as indicator species. Ecography, 27, 689-700.

Salovaara, K.J., Thessler, S., Malik, R.N. and Tuomisto, H., 2005. Classification of Amazonian primary rain forest vegetation using Landsat ETM+ satellite imagery. Remote Sensing of Environment, 97, 39-51.

Sanchez-Azofeifa A., Kalacska M.E., Quesada M., Stoner K.E., Lobo J.A., Arroyo-Mora P., 2003. Tropical Dry Climates. In: Schwartz M.D. (Ed.), Phenology: An Integrative Environmental Science. Tasks for Vegetation Science, Springer, Dordrecht, 39, 121-137.

Santantonio, D. and Hermann, R.K., 1985. Standing crop, production, and turnover of fine roots on dry, moderate, and wet sites of mature Douglas-fir in western Oregon. Annales des Sciences Forestieres, 42, 113-142.

Santos, J.C., Leal, I.R., Almeida-Cortez, J.S., Fernandes, G.W. and Tabarelli, M., 2011. Caatinga: the scientific negligence experienced by a dry tropical forest. Tropical Conservation Science, 4, 276-286.

Saupe, E.E., Barve, N., Owens, H.L., Cooper, J.C., Hosner, P.A. and Peterson, A.T., 2018. Reconstructing ecological niche evolution when niches are incompletely characterized. Systematic Biology, 67, 428-438.

Schellenberg, S.A., 2002. Mazon Creek: preservation in late Paleozoic deltaic and marginal marine environments. In: Bottjer, D.J., Etter, W., Hagadorn, J.W. and Tang, C.M. (Eds.), Exceptional fossil preservation: a unique view on the evolution of marine life. New York: Columbia University Press, p. 185-203.

Schneider, J. and Romer, R.L., 20 I0. The Late Variscan molasses (Late Carboniferous to Late Permian) of the Saxo-Thuringian Zone. In: Linnemann, U. and Romer, R.L. (Eds.), Pre-Mesozoic Geology of Saxo-Thuringia - From the Cadomian Active Margin of the Variscan Orogen. Schweizerbart, Stuttgart, p. 323-346.

Scott, A.C., 1977. A review of the ecology of Upper Carboniferous plant assemblages, with new data from Strathclyde. Palaeontology, 20, 447-473.

Scott, A.C., 1979. The ecology of Coal Measure floras from northern Britain. Proceedings of the Geologists' Association, 90, 97-116.

Scott, A.C. and Stephens, R.S., 2015. British Pennsylvanian (Carboniferous) coal-bearing sequences: where is the time?. Geological Society, London, Special Publications, 404, 283-302.

Scott, K.M., 2005. Cohesion, water vapor, and floral topography: Significance for the interpretation of the depositional mechanisms of the late Paleozoic Halgaito Formation, Cutler Group, southeastern Utah. New Mexico Museum of Natural History and Science Bulletin, 30, 296-299.

Shearer, J.C. and Moore, T.A., 1996. Effects of experimental coalification on texture, composition and compaction in Indonesian peat and wood. Organic Geochemistry, 24, 127-140.

Scheihing, M.H. and Pfefferkorn, H.W., 1984. The taphonomy of land plants in the Orinoco Delta: a model for the incorporation of plant parts in clastic sediments of Late Carboniferous age of Euramerica. Review of Palaeobotany and Palynology, 41, 205-240.

Schneider, J.W., Hoth, K., Gaitzsch, B.G., Berger, H.J., Steinborn, H., Walter, H. and Zeidler, M.K., 2005. Carboniferous stratigraphy and development of the Erzgebirge Basin, East Germany. Zeitschrift der deutschen Gesellschaft für Geowissenschaften, 156, 431-466.

Schneider, J.W., Körner, F., Roscher, M. and Kroner, U., 2006. Permian climate development in the northern peri-Tethys area—the Lodève basin, French Massif Central, compared in a European and global context. Palaeogeography, Palaeoclimatology, Palaeoecology, 240, 161-183.

Schneider, J.W. 2008. Hradec Kralove 1988, Schneider, J.: “Basic problems of biogeography and biostratigraphy of the Upper Carboniferous and Rotliegendes”. Twenty years after - anything new? In: Štamberg, S. and Zajíc, J. (Eds.), Faunas and palaeoenvironments of the Late Palaeozoic. Special Publication to 5th Symposium on Permo-Carboniferous Faunas, Museum of Eastern Bohemia at Hradec Králové, p. 35-37.

Schutter, S.R. and Heckel, P.H., 1985. Missourian (early Late Pennsylvanian) climate in Midcontinent North America. International Journal of Coal Geology, 5, 111-140.

Sellards, E.H., 1908. Chapter X, Fossil plants of the upper Paleozoic of Kansas. The University Geological Survey of Kansas (Special report on oil and gas), 9, 386-499.

Shepard, F.P. and Wanless, H.R. 1935. Permo-Carboniferous coal series related to Southern Hemisphere glaciation. Science, 81, 521-522.

Simon, S.S., Gibling, M.R., DiMichele, W.A., Chaney, D. and Koll, R., 2018. An exhumed fine- grained meandering channel in the lower Permian Clear Fork Formation, north- central Texas: Processes of mud accumulation and the role of vegetation in channel dynamics. International Association of Sedimentologists Special Publication 48, 149-172.

Šimůnek, Z., 2000. Cuticles of *Cordaites* from the Westphalian, Stephanian and Autunian of the Bohemian Massif (Czech Republic)(a preliminary study). Acta Palaeobotanica-Krakow, 40, 25-34.

Šimůnek, Z., 2018. Cuticular analysis of new Westphalian and Stephanian *Cordaites* species from the USA. Review of Palaeobotany and Palynology, 253, 1-14.

Šimůnek, Z. and Martínek, K., 2009. A study of Late Carboniferous and Early Permian plant assemblages from the Boskovice Basin, Czech Republic. Review of Palaeobotany and Palynology, 155, 275-307.

Šimůnek, Z., Opluštil, S. and Drábková, J., 2009. *Cordaites borassifolius* (Sternberg) Unger (Cordaitales) from the Radnice Basin (Bolsovian, Czech Republic). Bulletin of Geosciences, 84, 301-336.

Soreghan, G.S., 1992. Preservation and paleoclimatic significance of eolian dust in the Ancestral Rocky Mountains province. Geology, 20, 1111-1114.

Soreghan, G.S., Elmore, R.D. and Lewchuk, M.T., 2002. Sedimentologic-magnetic record of western Pangean climate in upper Paleozoic loessite (lower Cutler beds, Utah). Geological Society of America Bulletin, 114, 1019-1035.

Spicer, R.A., 1981. The sorting and deposition of allochthonous plant material in a modern environment at Silwood Lake, Silwood Park, Berkshire, England. U.S. Geological Survey Professional Paper, 1143, 1-77.

Spicer, R.A. and Greer, A.G., 1986. Plant taphonomy in fluvial and lacustrine systems. Paleontological Society Papers, 15, 10-26.

Stanford, K., 2017. Underdetermination of Scientific Theory. In: Zalta, E.N. (Ed.), The Stanford Encyclopedia of Philosophy (Spring 2017 Edition) URL = https://plato.stanford.edu/archives/spr2017/entries/scientific-underdetermination/.

Stárková, M., Šimůnek, Z. and Drábková, J., 2016. Geology of Carboniferous outlier between Lísek and Hýskov in paleobotanical and palynological context (Westphalian, Duckmantian). Czech Geological Survey, Geological Research Reports, 49, 215-224. (In Czech with English abstract).

Stigall, A.L., 2012. Using ecological niche modelling to evaluate niche stability in deep time. Journal of Biogeography, 39, 772-781.

Stopes, M.C. and Watson, D.M.S., 1909. On the present distribution and origin of the calcareous concretions in coal seams known as ‘coal balls’. Philosophical Transactions of the Royal Society, B200, 167–218.

Stull, G.W., DiMichele, W.A., Falcon-Lang, H.J., Nelson, W.J. and Elrick, S., 2012. Palaeoecology of *Macroneuropteris scheuchzeri*, and its implications for resolving the paradox of ‘xeromorphic’plants in Pennsylvanian wetlands. Palaeogeography, Palaeoclimatology, Palaeoecology, 331, 162-176.

Tabor, N.J. and Montañez, I.P., 2002. Shifts in late Paleozoic atmospheric circulation over western equatorial Pangea: Insights from pedogenic mineral $\delta^{18}O$ compositions. Geology, 30, 1127–1130.

Tabor, N.J. and Montañez, I.P., 2004. Permo-Pennsylvanian alluvial paleosols (north-central Texas): High-resolution proxy records of the evolution of early Pangean paleoclimate. Sedimentology, 51, 851–884.

Tabor, N.J. and Poulsen, C.J., 2008. Palaeoclimate across the Late Pennsylvanian–Early Permian tropical palaeolatitudes: a review of climate indicators, their distribution, and relation to palaeophysiographic climate factors. Palaeogeography, Palaeoclimatology, Palaeoecology, 268, 293–310.

Tabor, N.J., Montañez, I.P., Scotese, C.R., Poulsen, C.J. and Mack, G.H., 2008. Paleosol archives of environmental and climatic history in paleotropical western Pangea during the latest Pennsylvanian through Early Permian. In: Fielding, C.R., Frank, T.D., and Isbell, J.L. (Eds.), Resolving the Late Paleozoic Ice Age in Time and Space. Geological Society of America Special Paper, 441, 291–303.

Tabor, N.J., DiMichele, W.A., Montañez, I.P. and Chaney, D.S., 2013. Late Paleozoic continental warming of a cold tropical basin and floristic change in western Pangea. International Journal of Coal Geology, 119, 177-186.

Takahashi, H., Shimada, S., Ibie, B., Usup, A. and Yudha, L.S., 2002. Annual changes of water balance and a drought index in a tropical peat swamp forest of Central Kalimantan, Indonesia. In: Rieley, J.O., Page, S.E. and Setiadi, B. (Eds.), Peatlands for People, Natural Resources Function and Sustainable Management. Proceedings of the International Symposium on Tropical Peatland. BPPT and Indonesian Peat Association, Jakarta, p. 63–67.

Tandon, S.K. and Gibling, M.R., 1994. Calcrete and coal in Late Carboniferous cyclothems of Nova Scotia, Canada: Climate and sea-level changes linked. Geology, 22, 755–758.

Tanner, L.H. and Lucas, S.G., 2017. Paleosols of the upper Paleozoic Sangre de Cristo Formation, north-central New Mexico: Record of early Permian palaeoclimate in tropical Pangaea. Journal of Palaeogeography, 6, 144-161.

Thomas, B.A. and Cleal, C.J., 2015. Cyclones and the formation of plant beds in late Carboniferous tropical swamps. Palaeobiodiversity and Palaeoenvironments, 95, 531-536.

Thomas, B.A., Appleton, P., Cleal, C.J. and Seyfullah, L.J., 2020. The distribution of plant fossils and their palaeoecology in Duckmantian (Bashkirian, Lower Pennsylvanian) strata at Brymbo, North Wales, UK. Geological Journal, 55, 3179-3207.

Tidwell, W.D., 1967. Flora of Manning Canyon Shale. Part I. A lowermost Pennsylvanian flora from the Manning Canyon Shale, Utah, and its stratigraphic significance. Brigham Young University Geology Studies, 14, 3-66.

Tidwell, W.D., 1988. A new Upper Pennsylvanian or Lower Permian flora from Southeastern Utah. Brigham Young University Geology Studies, 35, 33-56.

Tidwell, W.D. and Ash, S.R., 2003. Revision and description of two new species of *Charliea* Mamay from Pennsylvanian strata in New Mexico and Utah, USA. Review of Palaeobotany and Palynology, 124, 297-306.

Tidwell, W.D., Jennings, J.R. and Beus, S.S., 1992. A Carboniferous flora from the Surprise Canyon Formation in the Grand Canyon, Arizona. Journal of Paleontology, 66, 1013-1021.

Trümper, S., Gaitzsch, B., Schneider, J.W., Ehling, B.C., Kleeberg, R. and Rößler, R., 2020. Late Palaeozoic red beds elucidate fluvial architectures preserving large woody debris in the seasonal tropics of central Pangaea. Sedimentology, 67, 1973-2012.

Valero Garcés, B.L., Gierlowski-Kordesch, E. and Bragonier, W.A., 1997. Pennsylvanian continental cyclothem development: no evidence of direct climatic control in the Upper Freeport Formation (Allegheny Group) of Pennsylvania (northern Appalachian Basin). Sedimentary Geology, 109, 305-319.

Van den Belt, F.J., van Hoof, T.B. and Pagnier, H.J., 2015. Revealing the hidden Milankovitch record from Pennsylvanian cyclothem successions and implications regarding late Paleozoic chronology and terrestrial-carbon (coal) storage. Geosphere, 11, 1062-1076.

Van Hoof, T.B., Falcon-Lang, H.J., Hartkopf-Fröder, C. and Kerp, H., 2013. Conifer-dominated palynofloras in the Middle Pennsylvanian strata of the De Lutte-6 borehole, The Netherlands: implications for evolution, palaeoecology and biostratigraphy. Review of Palaeobotany and Palynology, 188, 18-37.

Von Bülow, K.,1942. Die Florengeschichte als Motor der tierischen Entwicklung: V Bülow, K., 1942. Die Florengeschichte als Motor der tierischen Entwicklung. Zeitschrift der Deutschen Geologischen Gesellschaft, 94, 338-357.

Vormisto, J., Tuomisto, H. and Oksanen, J., 2004. Palm distribution patterns in Amazonian rainforests: What is the role of topographic variation?. Journal of Vegetation Science, 15, 485-494.

Wagner, R.H. and Álvarez-Vázquez, C., 2010. The Carboniferous floras of the Iberian Peninsula: A synthesis with geological connotations. Review of Palaeobotany and Palynology, 162, 239–324.

Wagner, R.H. and Lyons, P.C., 1997. A critical analysis of the higher Pennsylvanian megafloras of the Appalachian region. Review of Palaeobotany and Palynology, 95, 255-283.

Wang, J., Pfefferkorn, H.W., Zhang, Y. and Feng, Z., 2012. Permian vegetational Pompeii from Inner Mongolia and its implications for landscape paleoecology and paleobiogeography of Cathaysia. Proceedings of the National Academy of Sciences, 109, 4927-4932.

Wanless. H.R. and Shepard, F,P., 1936. Sea level and climate changes related to late Paleozoic cycles. Geological Society of America Bulletin, 47, 1177–1206.

Wegener, A., 1966. The Origin of Continents and Oceans. 4th Edition. Translated from the original German by J. Birham. Dover Publications, Inc., New York.

Webb, C.O., 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. American Naturalist, 156, 145-155.

Webb, C.O., Ackerly, D.D., McPeek, M.A. and Donoghue, M.J., 2002. Phylogenies and community ecology. Annual Review of Rcology and Systematics, 33, 475-505.

White, D., 1912. The characters of the fossil plant *Gigantopteris* Schenk and its occurrence in North America. Proceedings of the United States National Museum, 41, 493-516.

White, D., 1931. Climatic implications of Pennsylvanian flora. Illinois State Geological Survey Bulletin, 60, 271-281.

Wiens, J.J. and Donoghue, M.J., 2004. Historical biogeography, ecology and species richness. Trends in Ecology and Evolution, 19, 639-644.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Jonathan Davies, T., Grytnes, J.A., Harrison, S.P. and Hawkins, B.A., 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology letters, 13, 1310-1324.

Willard, D.A., Phillips, T.L., Lesnikowska, A.D. and DiMichele, W.A., 2007. Paleoecology of the Late Pennsylvanian-age Calhoun coal bed and implications for long-term dynamics of wetland ecosystems. International Journal of Coal Geology, 69, 21-54.

Wilson, J.P., 2013. Modeling 400 million years of plant hydraulics. The Paleontological Society Papers, 19, 175-194.

Wilson, J.P., Montañez, I.P., White, J.D., DiMichele, W.A., McElwain, J.C., Poulsen, C.J. and Hren, M.T., 2017. Dynamic Carboniferous tropical forests: new views of plant function and potential for physiological forcing of climate. New Phytologist, 215, 1333-1353.

Winston, R.B., 1983. A Late Pennsylvanian upland flora in Kansas: systematics and environmental implications. Review of Palaeobotany and Palynology, 40, 5-31.

Wittry, J., 2006. The Mazon Creek Fossil Flora. ESCONI Associates, Downers Grove, Illinois.

164 p.

Wood, G.H., Kehn, T.M., Carter, M.D. and Culberston, W.C., 1983. Coal resource classification of the U.S. Geological Survey. U.S. Geological Survey Circular, 891, 1-65.

Wüst, R.A. and Bustin, R.M., 2001. Low-ash peat deposits from a dendritic, intermontane basin in the tropics: a new model for good quality coals. International Journal of Coal Geology, 46, 179-206.

Figure 1. Cyclothem. A., Idealized Midcontinent USA cyclothem divided into a terrestrial and marine phase reflecting a single glacial-interglacial cycle. B., Portions of a cyclothem in the field. Strata associated with the Middle Pennsylvanian, Springfield Coal of the Illinois Basin.

Figure 2. The Gastaldo and Demko (2011) Model modified for a peat-forming landscape, in accordance with the model of Elrick et al. (2017a). A – B., Short-term preservation. A., Peat forms and is preserved during the humid climate phase of a glacial-interglacial cycle. River is black-water and no remains are preserved there. B., The river is converted to an estuary during sea-level rise. The peat swamp is buried in areas flanking the river as mudflats form. Plant remains also are incorporated into both the mudflat and channel sediments, where preservation is possible below the water table. C., Intermediate-term preservation of the peat and associated organic matter in the siliciclastic deposits occurs as sea level continues to rise, and associated marine sediments are deposited on the former coastal lowlands. D., Long-term preservation of the wetland landscape facilitated by basinal subsidence. E., Short-term preservation. Renewed landscape incision occurs in association with sea-level fall under seasonally dry climatic conditions. Organic matter becomes entombed only in some channels and floodplain lakes, where preservation is possible only if it remains below the water table. F., Long-term preservation of seasonally dry floral remains depends on continued accumulation of sediment due to sea-level rise and basinal subsidence.

Figure 3. Sediment load as a function of rainfall regime. A., General relationship between rainfall volume and annual distribution, and the volume of sediment transport, based on measurements from selected tropical rivers (Originally Figure 1A of Cecil and Dulong, 2003,

reproduced in accordance with the permissions guidelines of the Society for Sedimentary Geology [SEPM]). B., Empirical relationship between selected rivers comparing sediment load to drainage-basin size differentiated by climate regime (Base graph originally published in Latrubesse et al., 2005, as Figure 6, used with permission of Elsevier Scientific Publishers license number 4797720592053).

Figure 4. Model that envisions a Middle Pennsylvanian landscape with contemporaneous close proximity of peat formation, siliciclastic deposition, and non-marine carbonate lake formation. (Modified from part of figure 2 of Valero Garcés et al., 1997).

Figure 5. Amazonian tropical rainforest, in the vicinity of Manaus, Brazil, Amazon River Basin, under humid climate. Images A–C taken along the Rio Negro, west of Manaus, the largest blackwater river in the world; elevation of the river at its juncture with the Amazon is ~30 m, reaching >200 m at its source. A., River margin with fring of flooded forest; note elevated areas in distant background, covered with rainforest. B., River edge vegetation, some in, or falling into, the water. C., River margin, with vegetation along bank being incorporated into river-borne sediment. D., 70 km north of Manaus. Local elevation 40-120 m. Photos A-C courtesy of Scott L. Wing, Smithsonian Institution. Photo D courtesy of Robyn J. Burnham, University of Michigan.

Figure 6. Temperate drought-tolerant vegetation of east-central North America under seasonally dry climate. A., Shoreline of Rhode River, a Chesapeake Bay estuary, effectively at sea-level. B., Shoreline of Rhode River. Drought-tolerant, deciduous hardwood tree, portions of which are

being incorporated into shoreline sediments, without being transported from an “upland”. C., Chesapeake Bay estuaries south of Baltimore, Maryland, high summer humidity, approximately at sea-level, covered in drought-tolerant Eastern Deciduous Forest Biome vegetation. D., Appalachian Mountains in western Virginia, view to east from Skyline Drive, covered in drought-tolerant Eastern Deciduous Forest vegetation. E., Caddo Lake, the margins of which are colonized by *Taxodium distichum*, inland of which the landscape is covered by drought-tolerant vegetation. Surface elevation of lake is ~ 50 m. All photographs by the authors.

Figure 7. Underground and surface coal mine exposures and wetland flora. A., Roof-shales and base of lycopsid tree rooted in the top of the Springfield Coal, Middle Pennsylvanian, Indiana. B., *Sigillaria* tree stump rooted in thin, unnamed Middle Pennsylvanian coal, Indiana, for contrast with stump seen in underground exposure. C., Large lycopsid tree trunk (measured at 2 m diameter and 30 m length with minimal taper, and no crown or roots), Herrin Coal, Illinois. D., Rare example of coal seat-earth containing adpression fossils, Murphysboro Coal, Illinois. E., The difficulties of surface mine collecting, Winslow-Henderson Channel above Baker Coal, Indiana. F., Coal balls, which are permineralized peat-stages of the coal, formed early in peat diagenesis, prior to peat compaction and coalification. Coal balls preserve the vegetation that grew during peat formation under a humid-to-perhumid climate; Herrin Coal, Illinois. All photographs by the authors.

Figure 8. Pennsylvanian landscape reconstructions. A., Late Pennsylvanian wetland landscape, Calhoun Coal, Illinois. B., Middle Pennsylvanian wetland landscape, Herrin Coal, Illinois. C., Middle Pennsylvanian seasonally dry landscape, idealized, Illinois Basin. All reconstructions

created by Mary Parrish, Smithsonian Institution. Image A originally published in Willard et al. (2007) used with permission of Elsevier Scientific Publishers license number 4798850608829. Image C originally published in DiMichele (2014), open access.

Figure 9. Upper Pennsylvanian (Missourian) exposure, interpreted as coastal environment, in central New Mexico. Carbonate-gypsum dunes entomb a forest of coniferophytes rooted in a micritic mudstone. A., Carbonate-gypsum dune exposure. B., Upright tree trunk (T, to right of staff, scale in 1 foot increments), buried in carbonate-gypsum dune deposit (G); LS = micritic limestone at base of exposure into which the tree is rooted. C., Exumed large coniferophyte tree stump, rooted in micritic mudstone. For details see Falcon-Lang et al., 2011a, 2015; Elrick et al., 2017b.

Figure 10. The “upland” model of Cridland and Morris (1963), which proved influential in promoting the idea that a few meters of elevation, within a landscape otherwise dominated by swampy wetlands, could support a species pool entirely distinct from that of the surrounding vegetation. The figure has been modified to be in accordance with their text; elevation is shown as 6 m and the elevated area is shown as surrounded by swamps. Figure modified from Cridland and Morris (1963) (Copyright (c) 1963. University of Kansas. Museum of Natural History. Used with permission).

Figure 11. Channel cut-and-fill features between coal beds. A., Channel below Baker Coal, upper Middle Pennsylvanian, Indiana. White arrow marks channel axis. Note truncated horizontal beds on flanks. Described in Falcon-Lang et al. (2009). B., Channel below Cottage Coal, upper

Middle Pennsylvanian, Indiana. White arrow marks channel axis. Note truncated horizontal beds on flanks. Described in DiMichele (2014, fig. 17), and Fielding et al. (2020, fig. 10). C., Upright stump of *Sigillaria* (white arrow) preserved in the channel illustrated in (B). Several additional channels of this kind are illustrated and described in Fielding et al. (2020). All photographs by the authors.

Figure 12. Paleosols below coal beds, recording seasonally dry climatic conditions, distinctly different from those under which peat accumulated. A., Stacked calcic Vertisols below the Harlem Coal and Ames Marine Zone, lower Upper Pennsylvanian, West Virginia. Note vertical root casts, encased in $CaCO_3$, in lower paleosol. The stacking of these paleosols also indicates significant "missing time" in the hiatus between them. B., Calcic Vertisol below the Cohn Coal, lower Upper Pennsylvanian, Illinois. Photograph A by authors. Photograph B by Scott Elrick, Illinois State Geological Survey, used with permission.

Figure 13. Spatial oscillation of the equatorial wetland (green) and drought-tolerant (red) biomes during glacial-interglacial cycles, tracking climatic changes. A-D represent changes in the central, Euramerican portion of Pangea. During the humid phase (A & D), the wetland biome dominates vast areas of the central continent; the drought-tolerant biome is resident in western Pangea and in portions of the mountainous regions of central Pangea. During the onset of seasonal drought (B), the drought-tolerant biome expands and the wetland biome contracts into patchy, isolated refugia; mixed drought-tolerant floras dominate central Pangea. With the onset of the next humid cycle, the wetlands reassemble from isolated refugia, and the drought-tolerant

flora contracts into areas where it is permanently resident. Base map created by Ron Blakey, used with permission.

Figure 14. Central Pangean coal basins: Coordinated oscillations in sea-level and climate, tracked by vegetation during a single glacial-interglacial cycle. A., Basin under marine high-stand, seasonal climate, drought-tolerant vegetation dominant. Low preservation potential. B., Basin during marine regression, climate remains seasonal, channel incision initiated, drought-tolerant vegetation dominant. Low to moderate preservation potential. C., Late glacial and early interglacial, sea-level near lowstand, craton broadly exposed, high humidity and peat formation, wetland vegetation dominant. High short-term preservation potential. D., Marine transgression of low lying cratonic regions, burying wetland deposits. High intermediate-term preservation potential.

Figure 15. Lower Permian channel fill formed under semi-arid conditions, north-central Texas, described by Simon et al. (2018). A., View down channel axis. A mixed flora including conifers, gigantopterids, and tree ferns occurred within the channel fill. Channel is incised into and flanked by a vertic paleosol, indicating climatic seasonality. Photograph by the authors. B., Reconstruction of the channel. [A = Vertic paleosol overprinting floodplain mudstone; B = Channel-lag deposits; C = Point bar deposits with inclined strata accumulating by lateral and oblique accretion; D = Abandoned channel deposits (massive and weakly laminated mudstone); E = Plant remains (foliage, seeds), bivalves, fish(?) coprolites]. Modified from Simon et al. (2018).

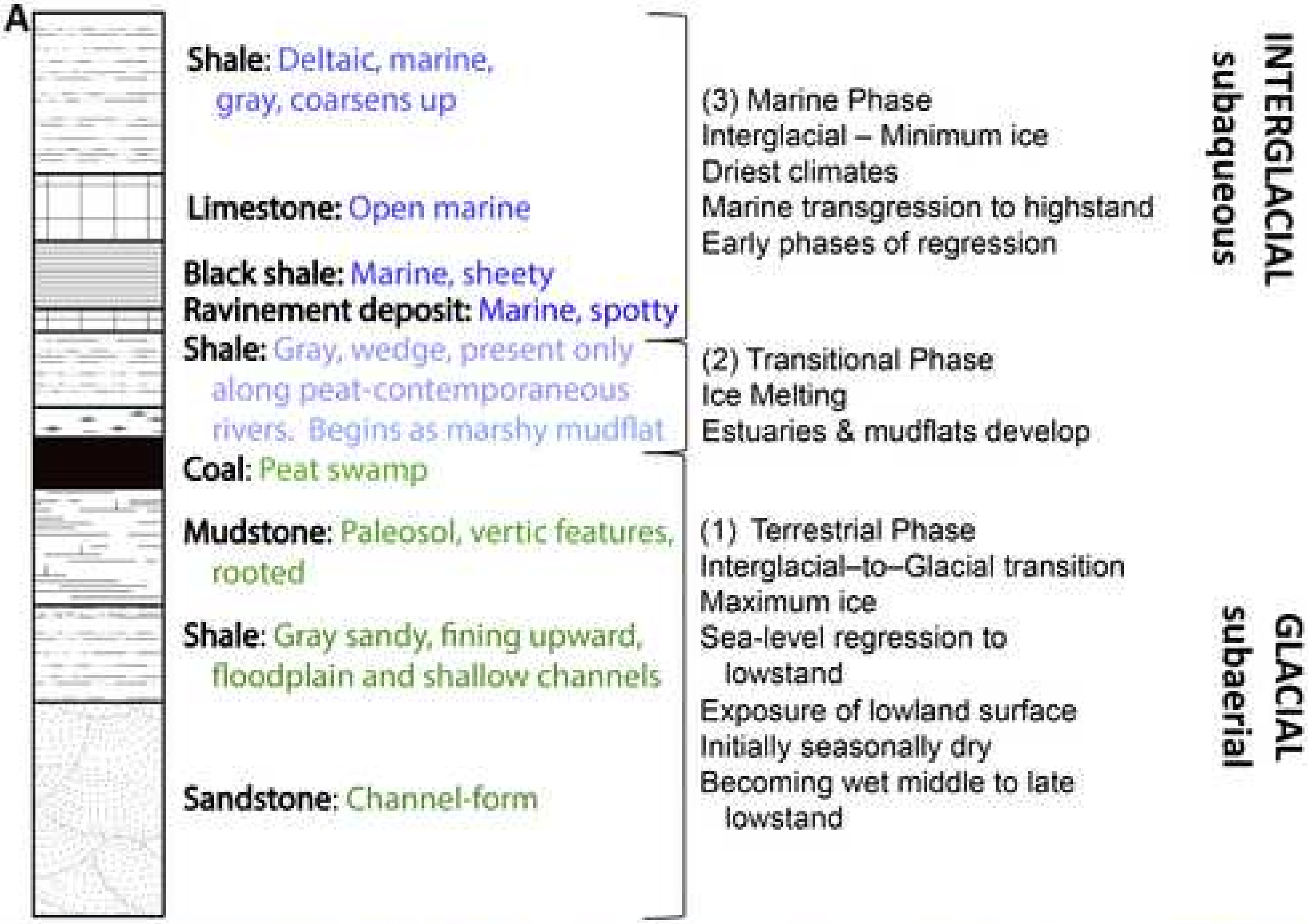
Figure 16. Taphonomic megabias and the Pennsylvanian-Permian vegetational transition. During the Pennsylvanian, plants of the wetland biome (green) were abundantly preserved in association with peat formation and generally widespread in landscapes with high soil moisture. In between periods of peat formation, when climate shifted to seasonally dry the preservation potential of organic matter dropped precipitously. During these periods, the drought-tolerant biome (red) appeared in basins, but was mixed to varying degrees with elements of the wetland biome, living in refugial pockets (green between red stripes). In the transition to and during the early Permian, the wettest intervals became seasonally dry and preserved mainly drought-tolerant vegetation, with variable numbers of wetland species, dominantly marattialean tree ferns and calamitalean sphenopsids. The drier intervals during the early Permian had effectively no short-term preservation potential. During the Pennsylvanian, the great predominance of wetland vegetation, exposed during coal mining, permits large collections of such plants to be made; at the same time, there is much less exposure of deposits containing drought-tolerant plants, and neither are such deposits actively searched for. During the Permian, the small, more isolated, mainly channel-fill deposits bearing plant fossils are more actively searched for, leading to the false appearance of the “rise” of a drought-tolerant flora at that time. In fact, the drought-tolerant flora had been there all along, during the entire Pennsylvanian, but becomes much more apparent or “visible” during the Permian.

Figure 17. The Upland Model. The basic assumptions of this model: (1) Pennsylvanian climate was everwet, all the time. (2) Elevation causes drainage, which causes drought, which brings with it xeromorphic vegetation tolerant of moisture deficits. (3) Preservation of organic matter

occurs in basinal lowlands, but not in the upland, elevated regions. There is no temporal component in this model.

Figure 18. The Climate Model. This model has significantly more moving parts than the Upland Model and, thus, is more difficult to present simplistically. (1) It explicitly recognizes climate as the most important factor controlling the distribution of vegetation and the preservation likelihood of organic matter. (2) It acknowledges that the Pennsylvanian was an ice age and that tropical climate and sea-level fluctuated in concert with glacial-interglacial cycles. (3) It recognizes that the effects of climate will be differentially expressed on landscapes of different elevational complexity. (4) It recognizes that climate will be different across the Pangean landscape, leading to different patterns in different basins, but that climatic oscillation still can be recognized. A. The expression of climate change where mountainous terrain adjoins a sedimentary basin. B. The effects of change in climate across the central portion of Euramerica, west to east, in separate, widely separated basins. The areas to the left of the margin of each depositional basin can be considered extrabasinal lowlands (sensu Pfefferkorn, 1980).

Figure 1 Click here to access/download;Figure;Figure 1 Cyclothem.jpg



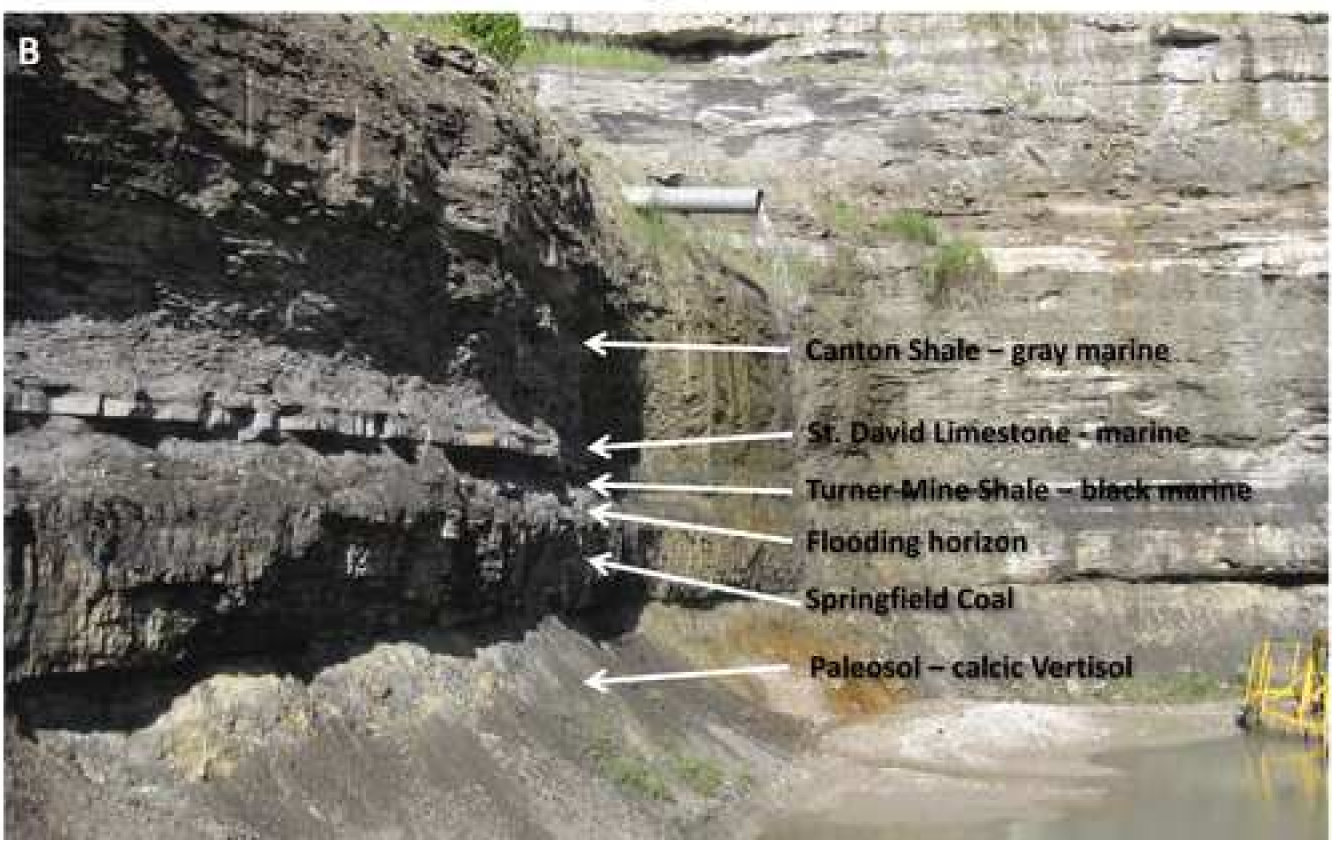
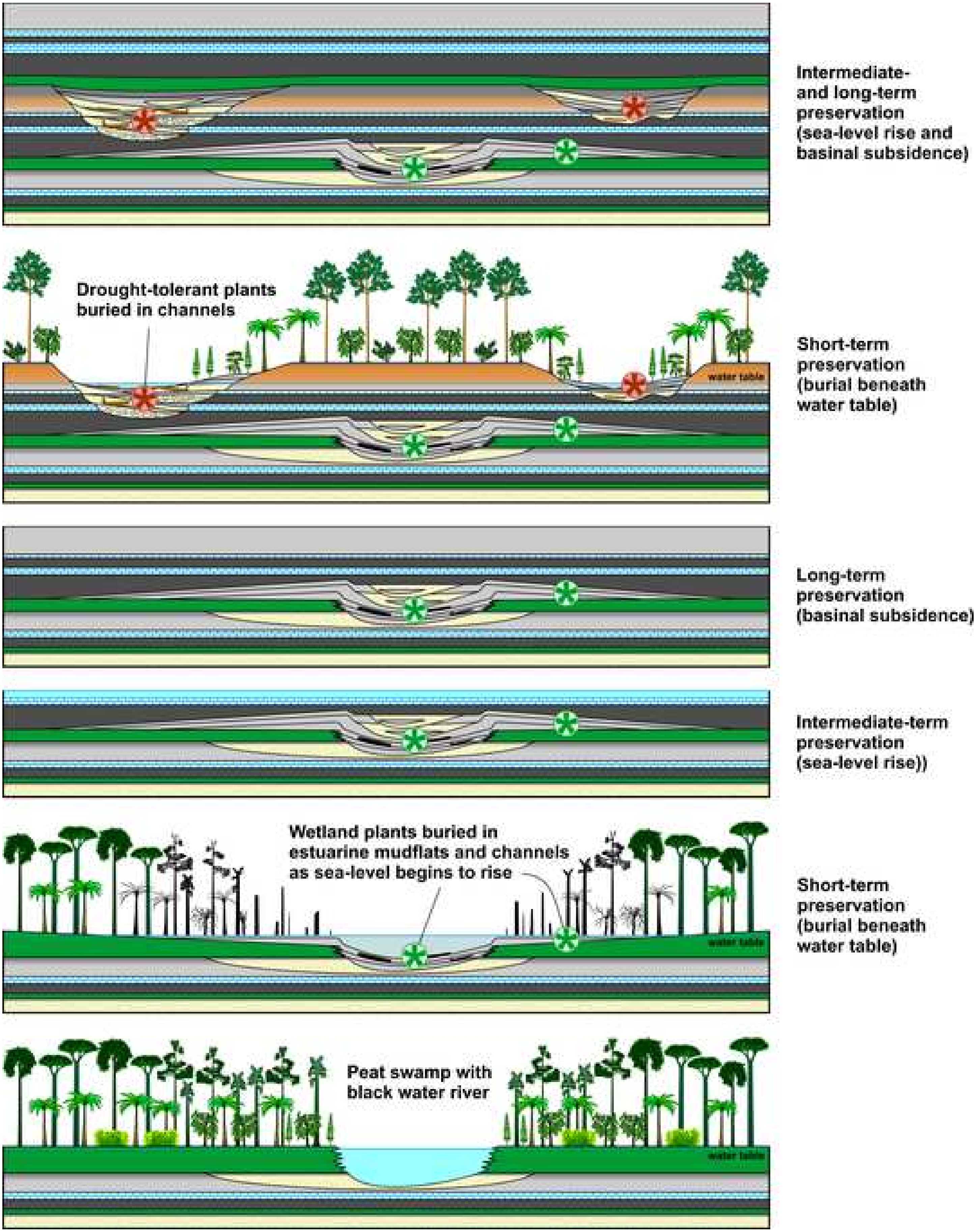


Figure 2 REVISED



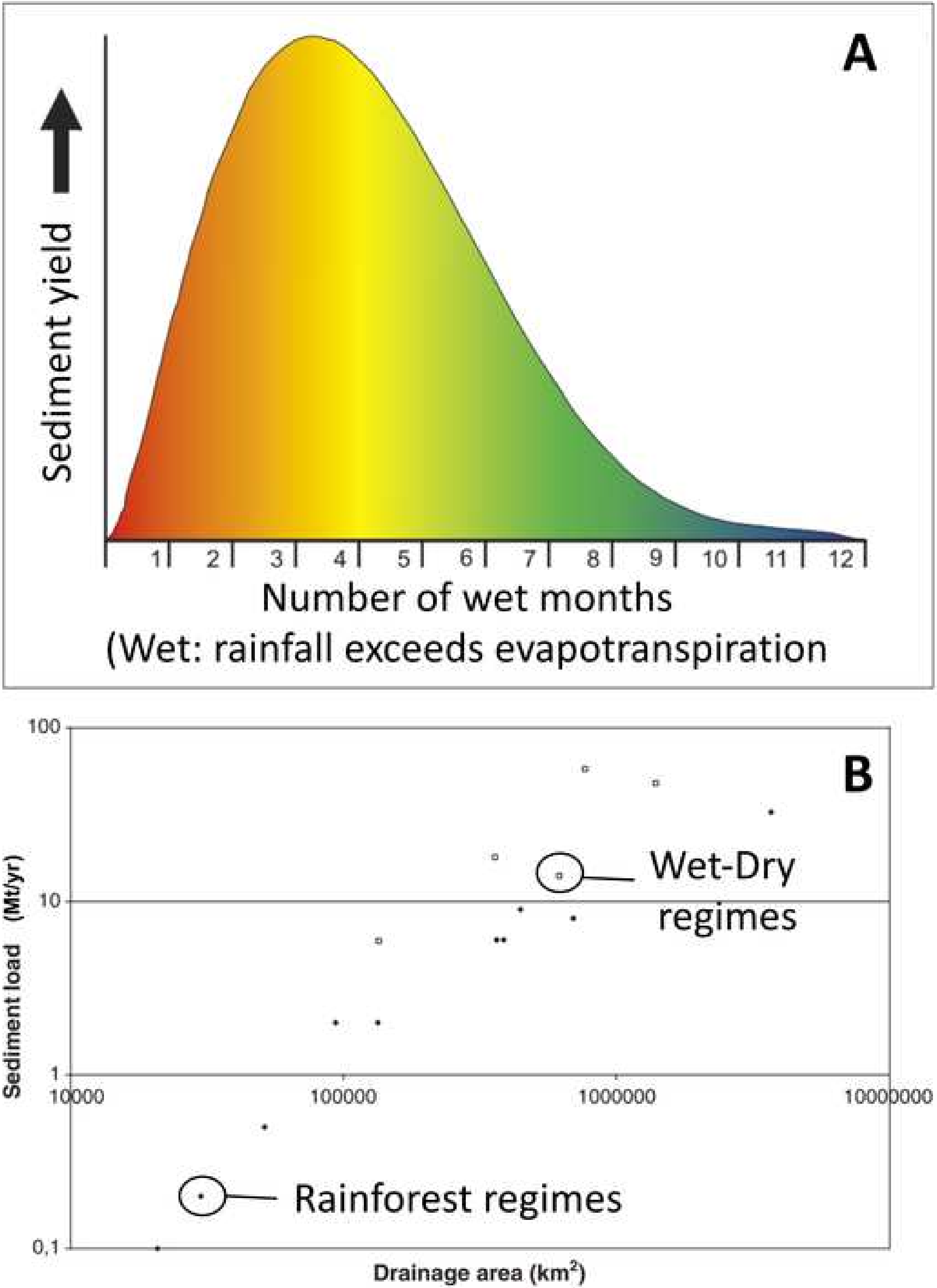
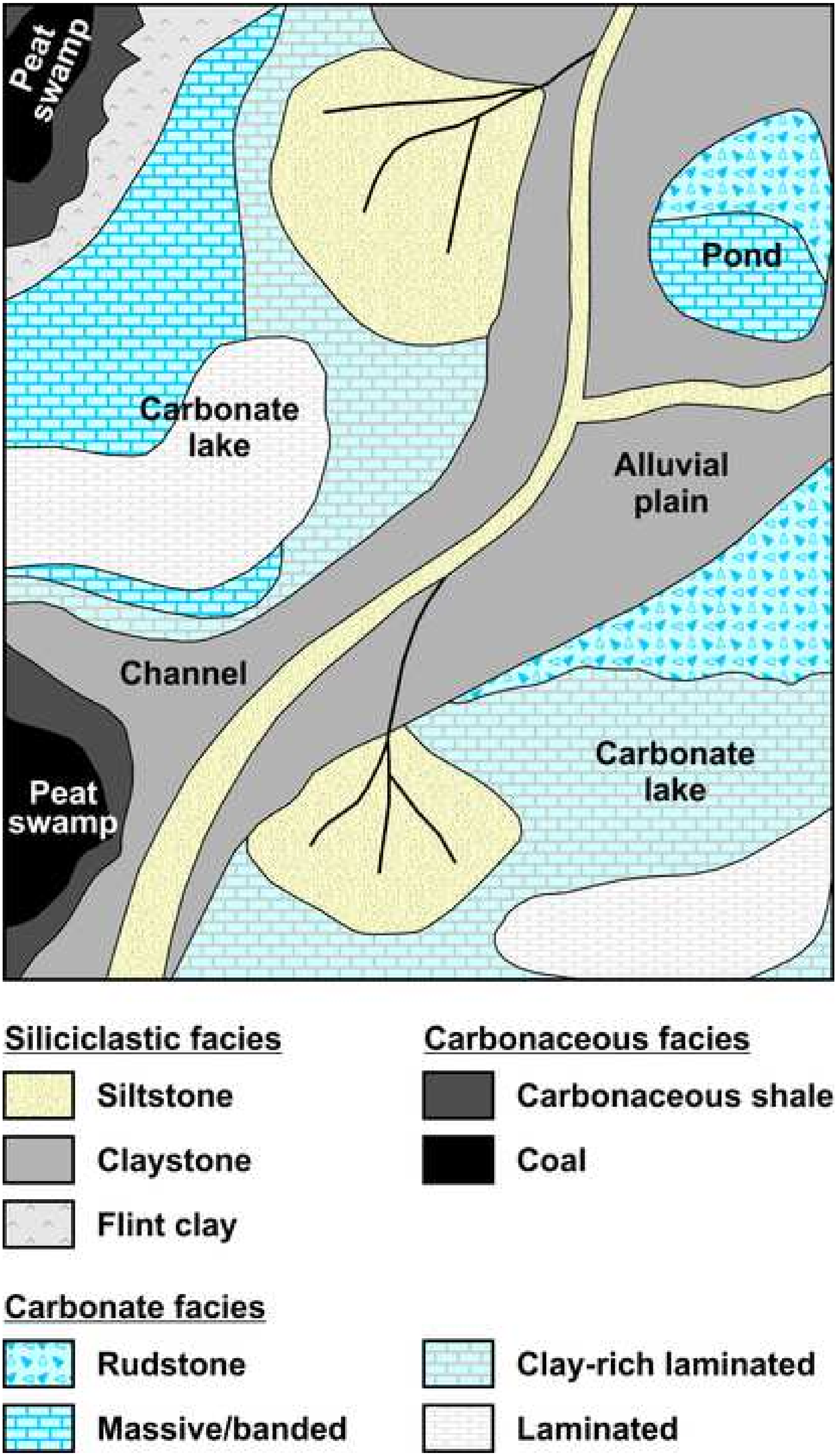

A
Sediment yield
1
2
3
4
5
6
7
8
9
10
11
12
Number of wet months
(Wet: rainfall exceeds evapotranspiration
B
100
10
1
0,1
Sediment load (Mt/yr)
10000
100000
1000000
10000000
Drainage area (km²)
Wet-Dry regimes
Rainforest regimes

Figure 4 REVISED



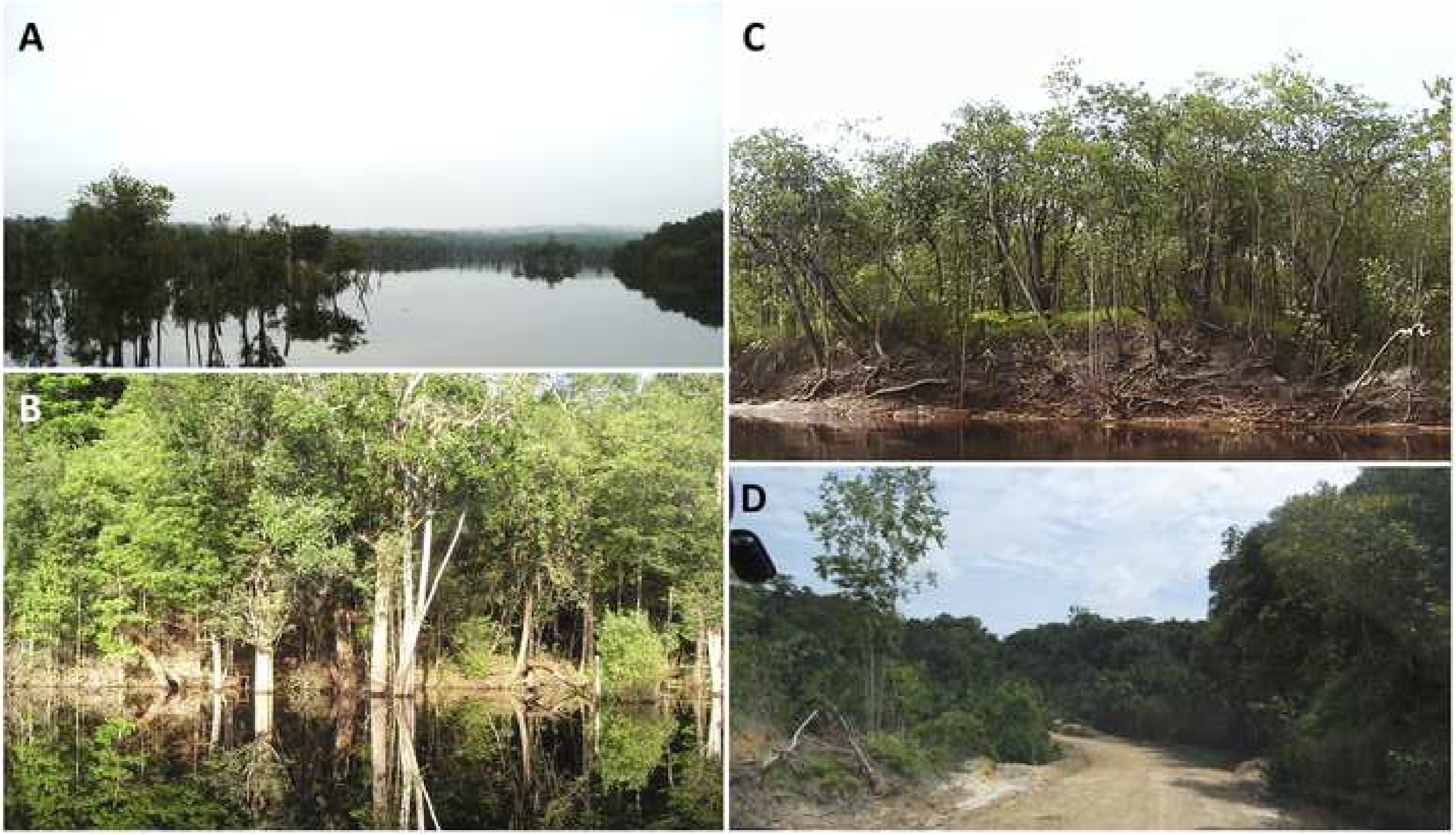
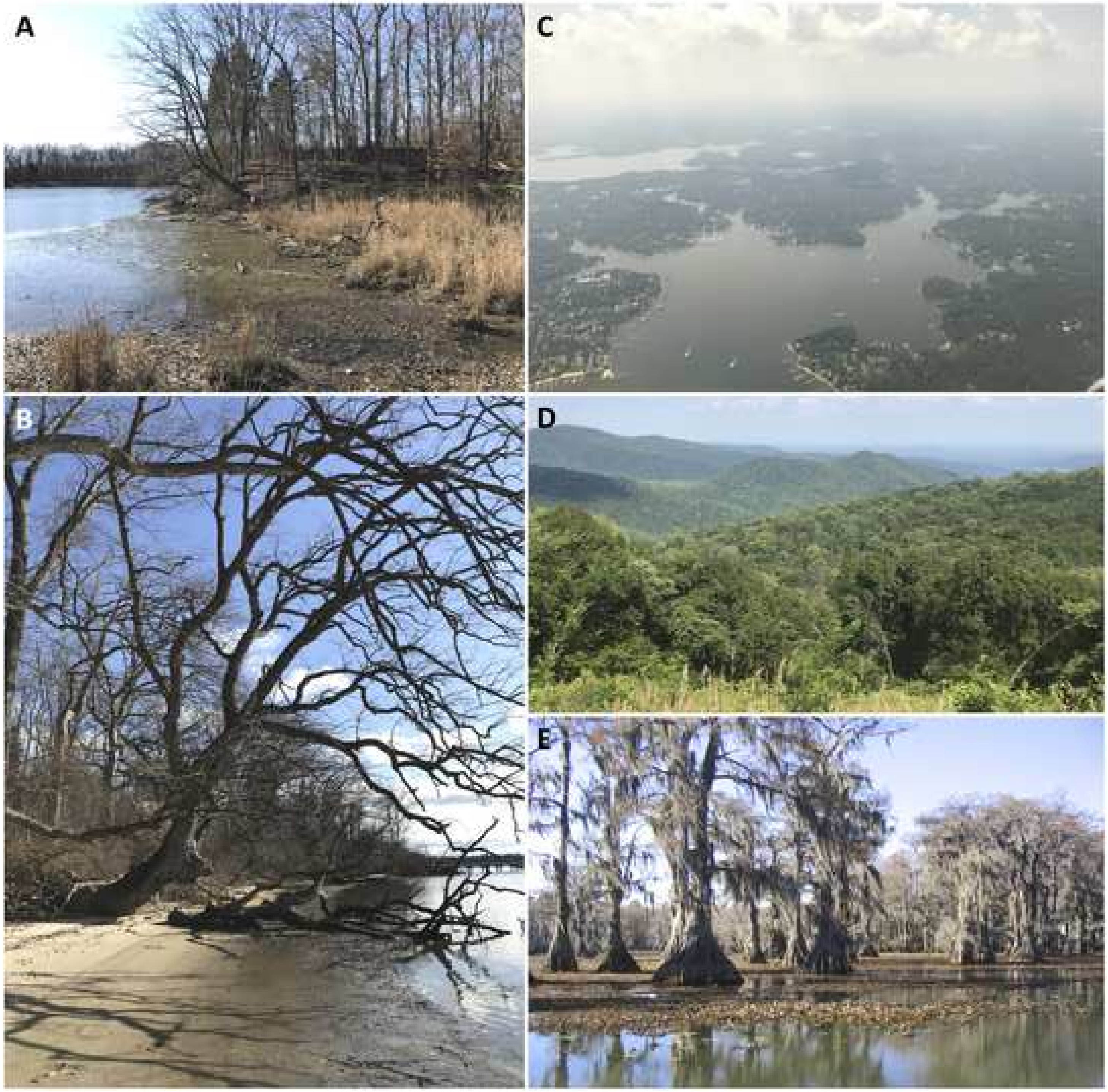

A
B
C
D

Figure 6




A
coal
B
coal
F
coal
coal balls
C
coal
D
coal
E
river channel deposits
coal

Figure 8

Click here to access/download;Figure;Figure 8 Landscapes.jpg

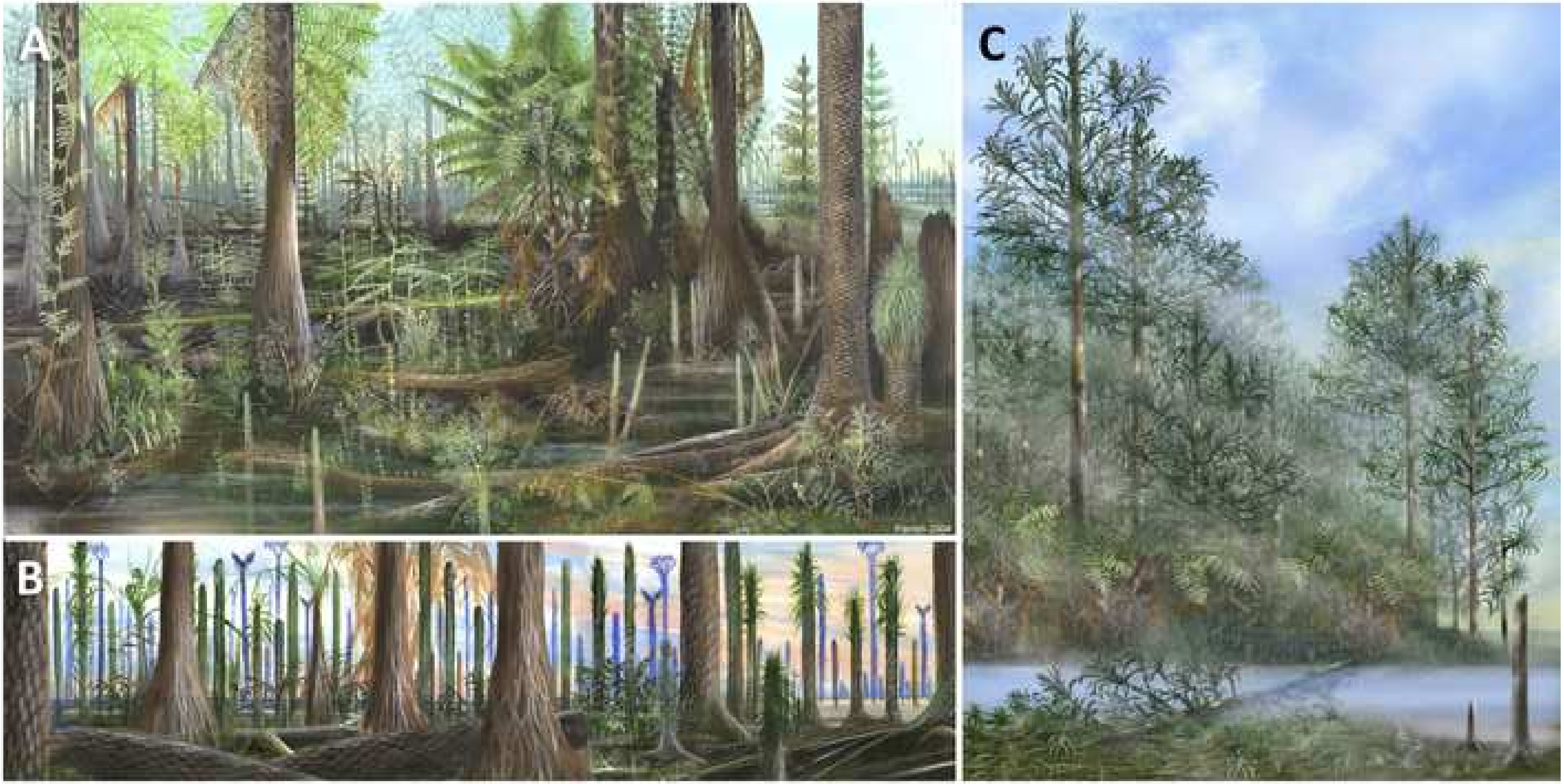


Figure 9 REVISED

Click here to access/download;Figure;Figure 9 SabkhaNMLatePenn REVISED.jpg

Figure 10 REVISED

Click here to access/download;Figure;Figure 10 CridlandMorrisUpland REVISED.jpg

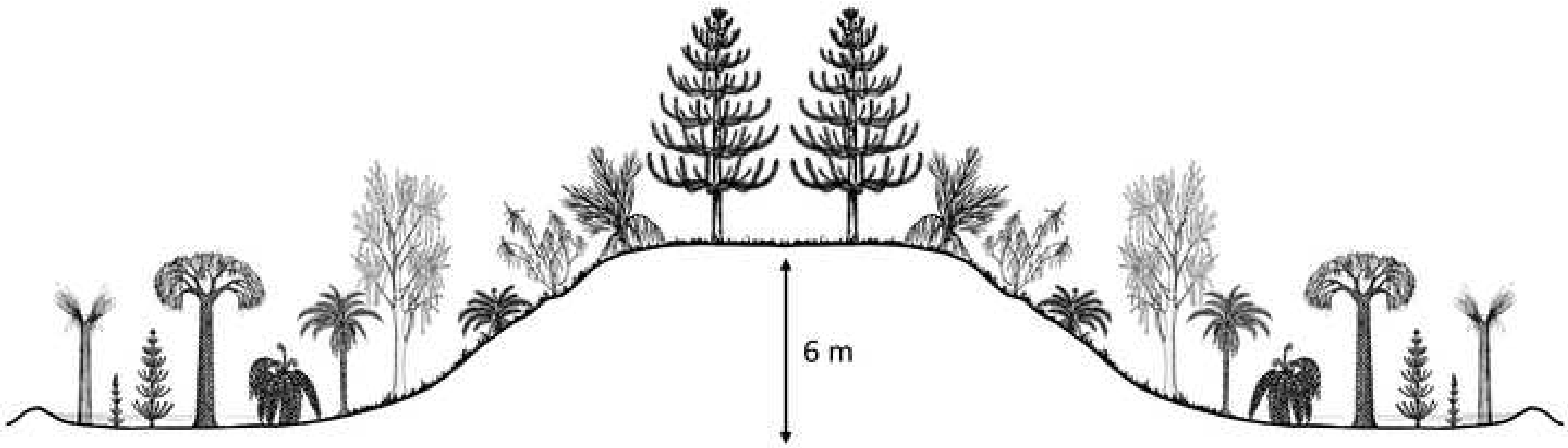


Figure 11 REVISED

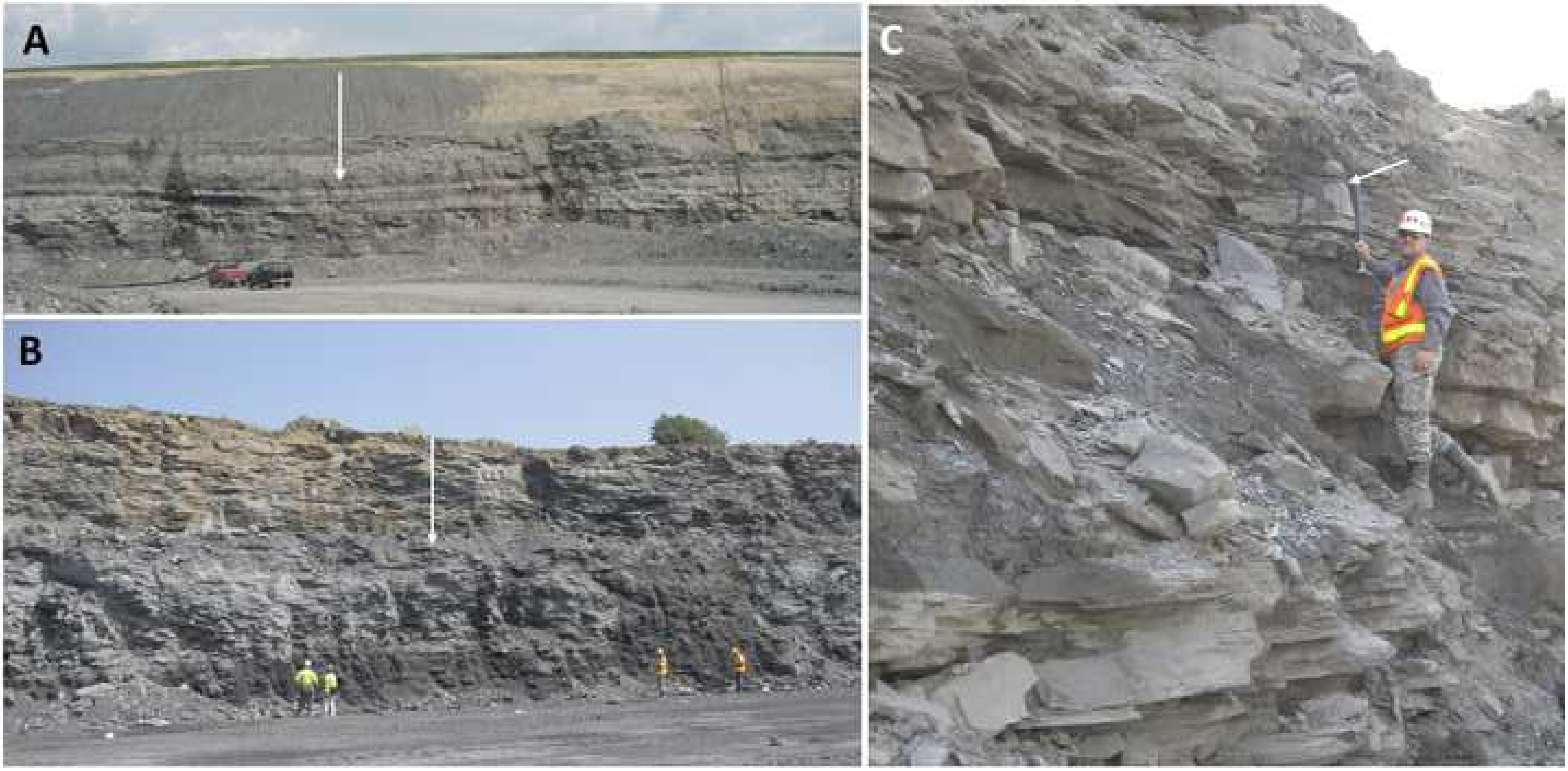


Figure 12 REVISED

Click here to access/download;Figure;Figure 12 CoalMeasuresPaleosols REVISED.jpg

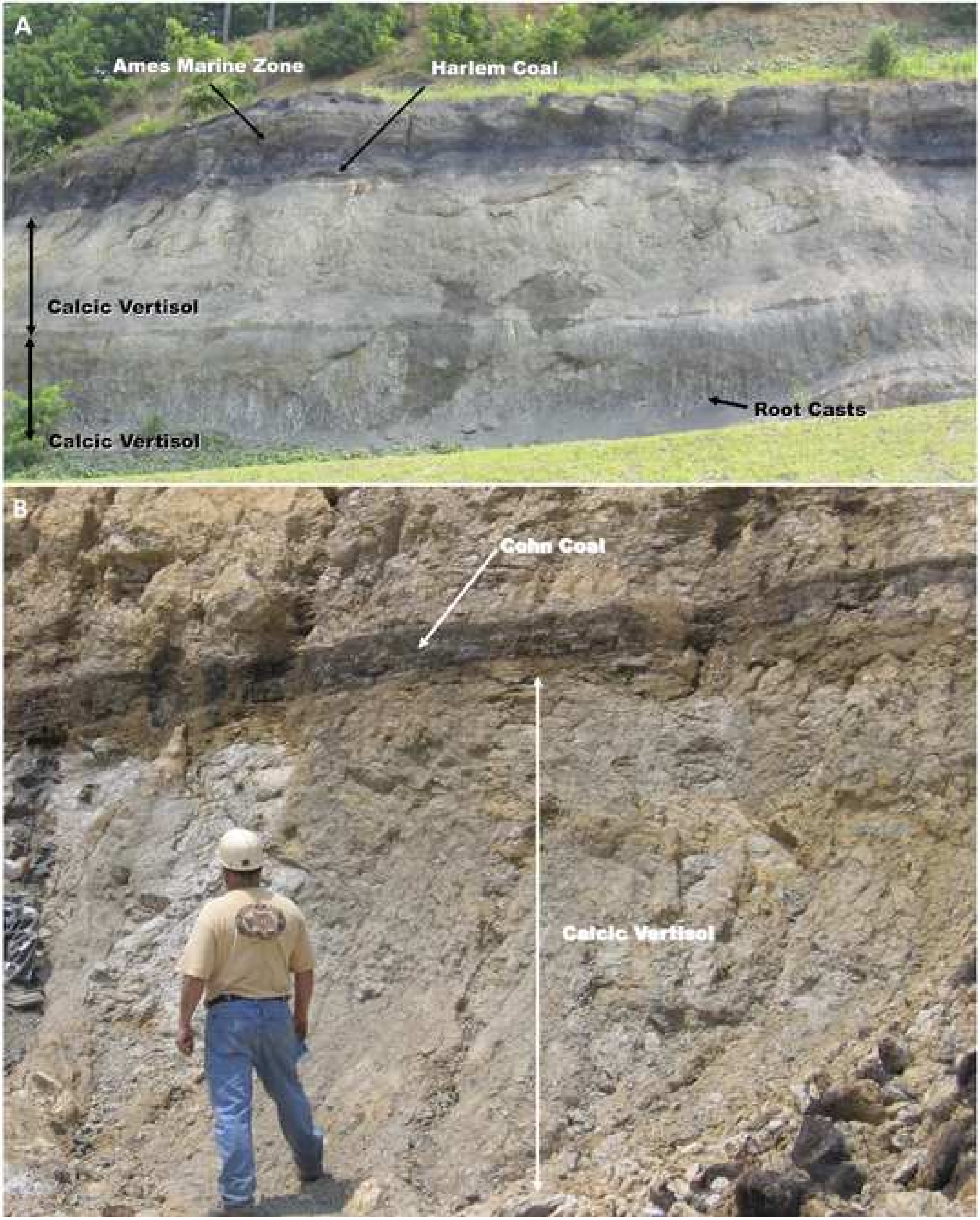


Figure 13

Click here to access/download;Figure;Figure 13 Biogeography.jpg

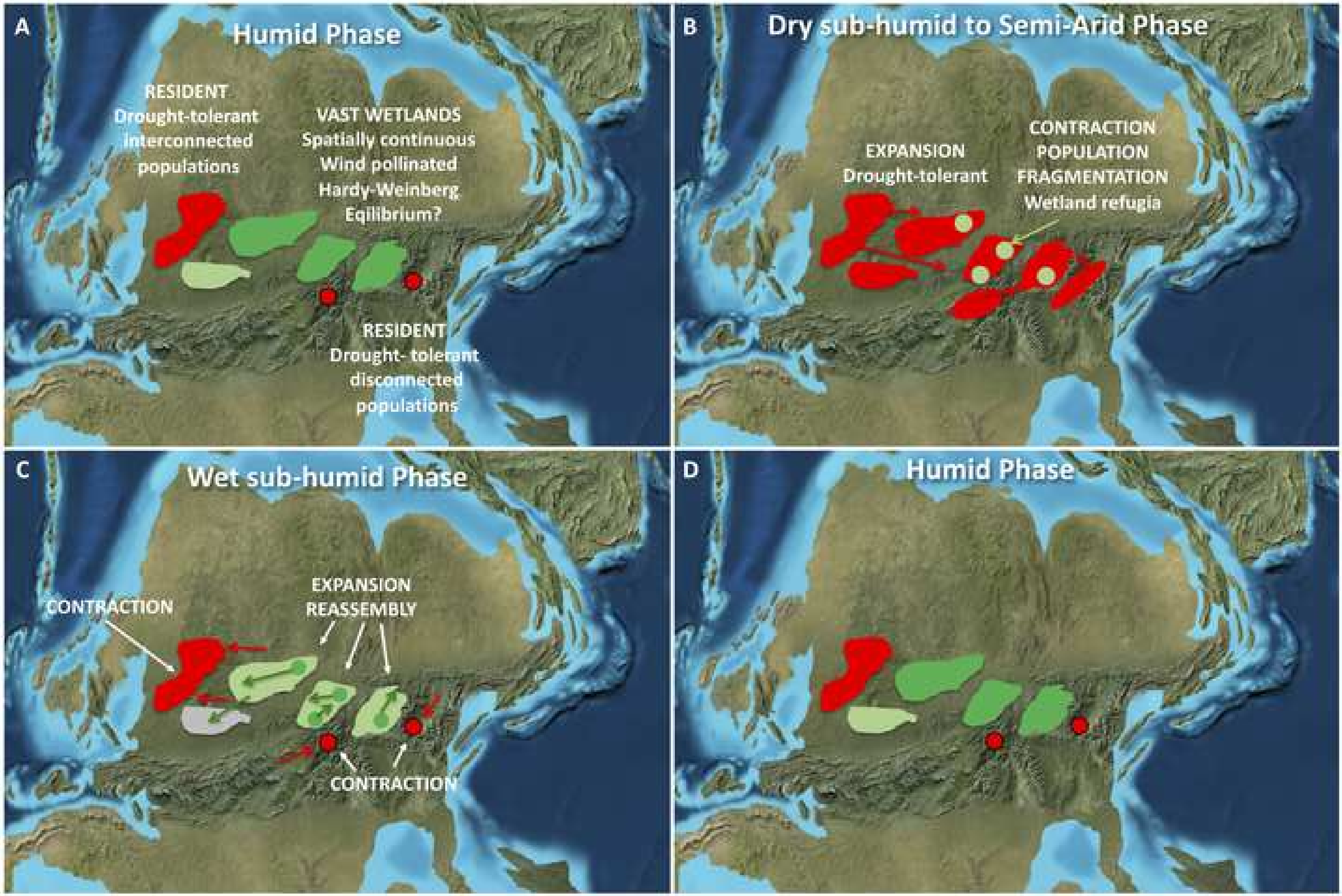


Figure 14

Click here to access/download;Figure;Figure 14 SLClimateCycle.jpg

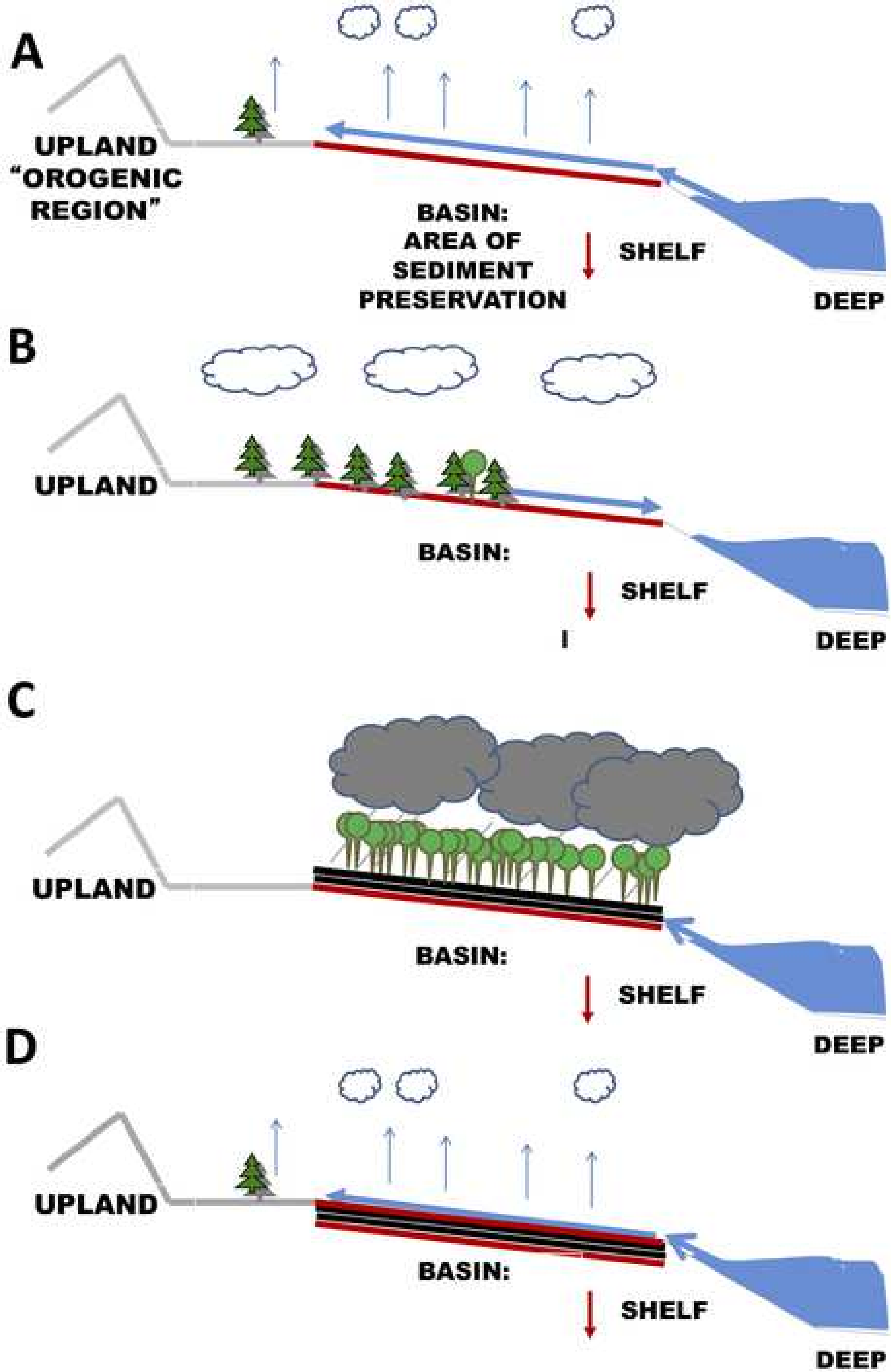


Figure 15 REVISED

Click here to access/download;Figure;Figure 15 Semi-aridChannelFill REVISED.jpg

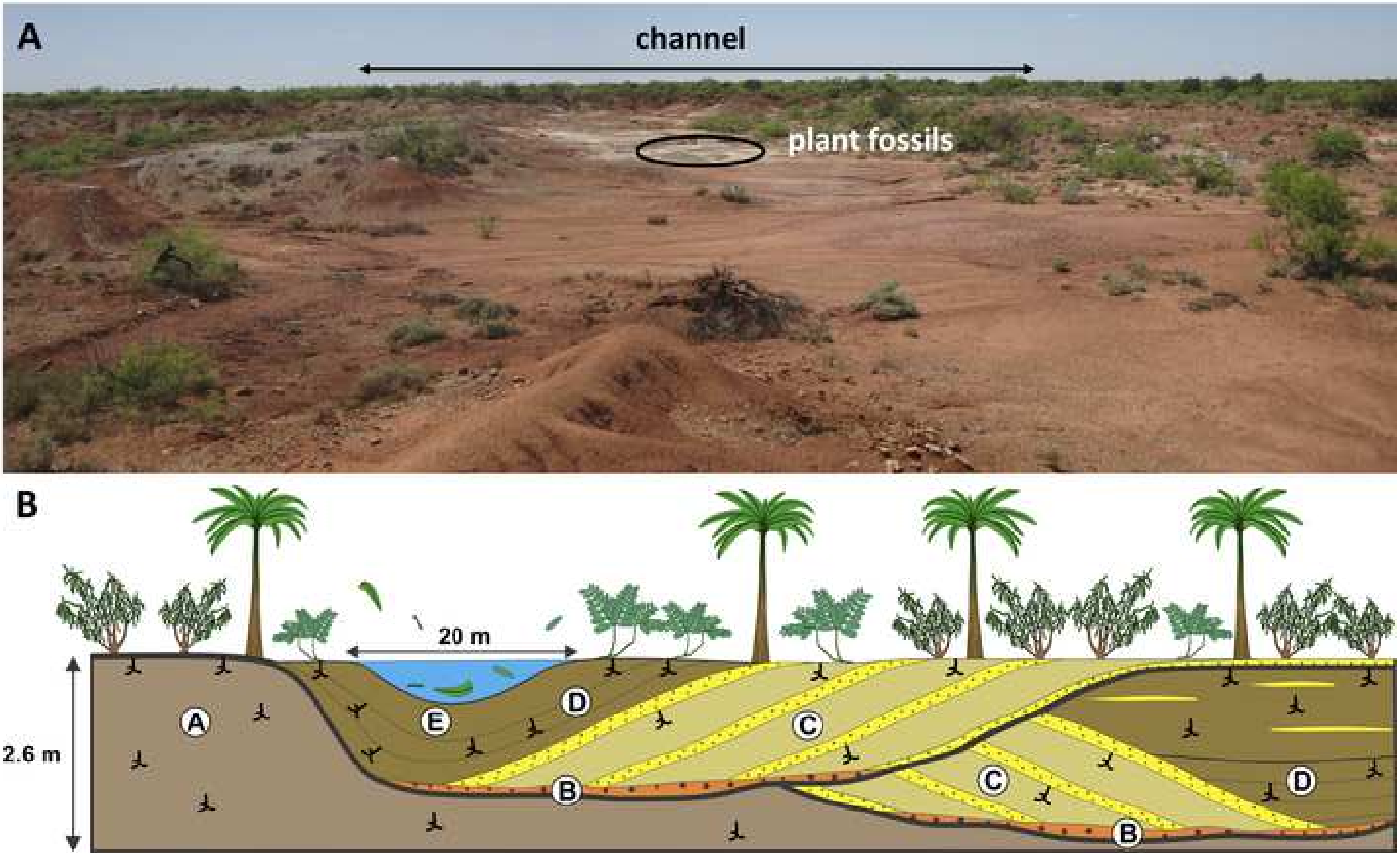


Figure 16 REVISED

Click here to access/download;Figure;Figure 16 REVISED.tif

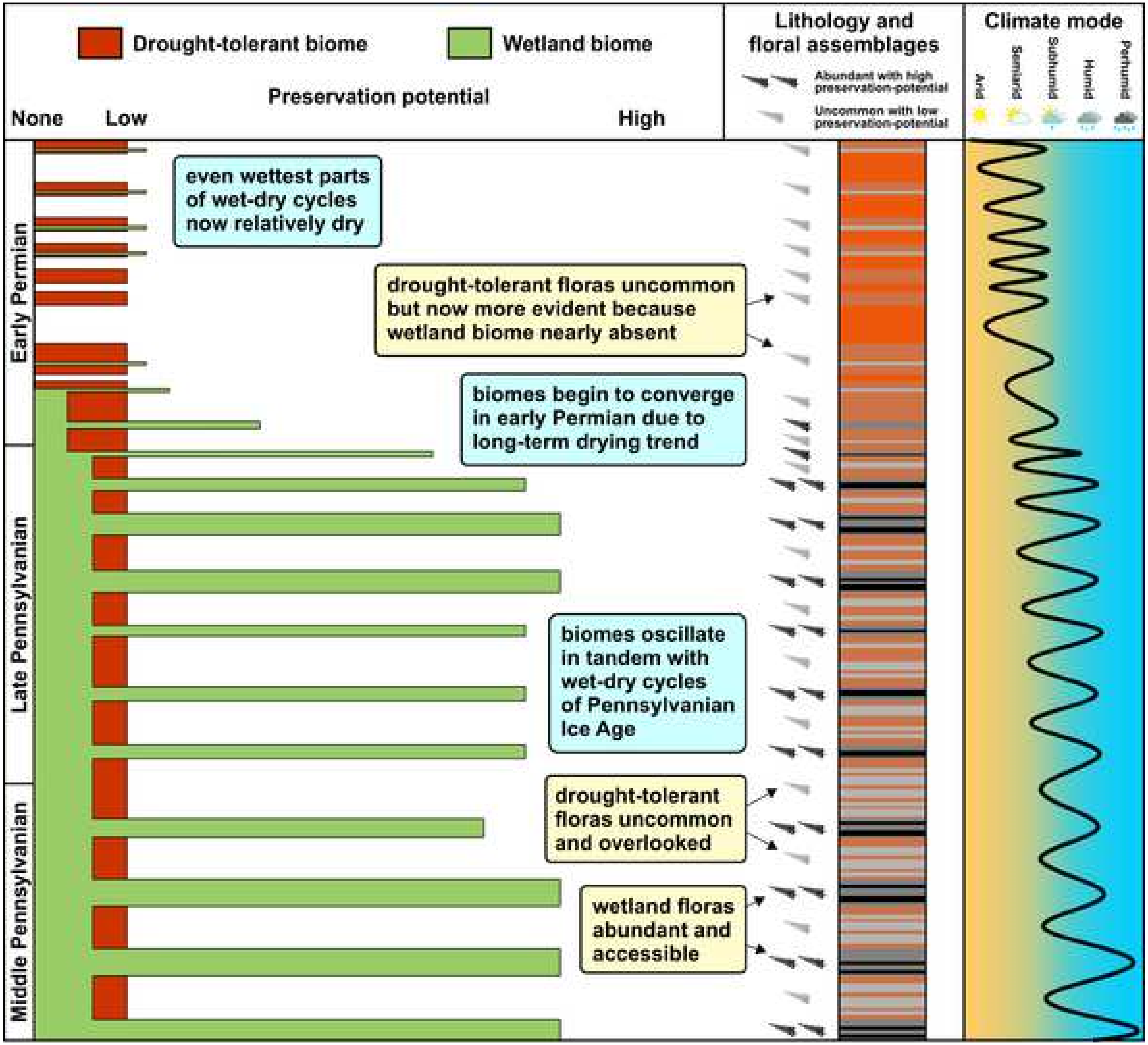


Figure 17

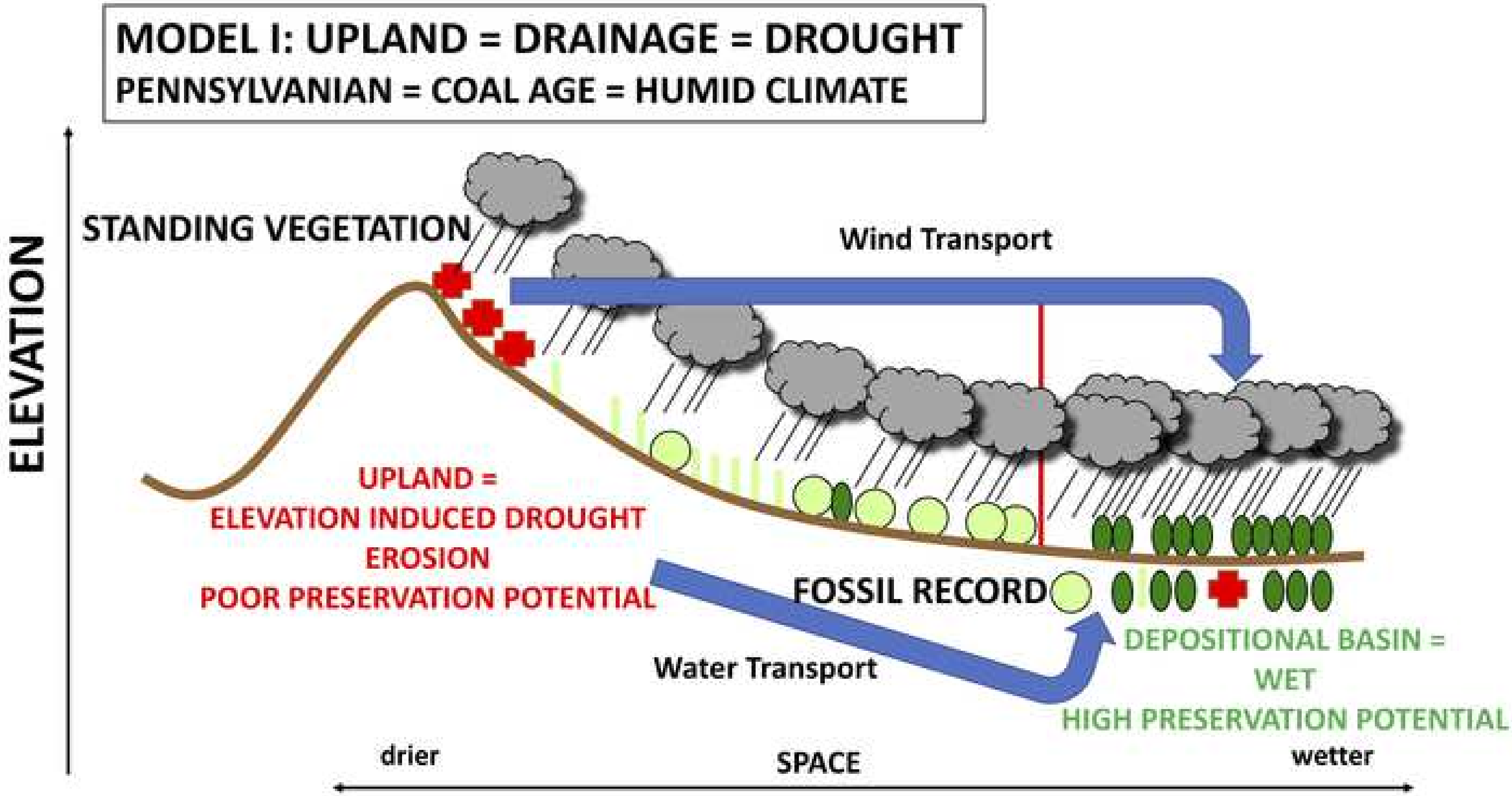

MODEL I: UPLAND = DRAINAGE = DROUGHT
PENNSYLVANIAN = COAL AGE = HUMID CLIMATE
ELEVATION
STANDING VEGETATION
Wind Transport
UPLAND =
ELEVATION INDUCED DROUGHT
EROSION
POOR PRESERVATION POTENTIAL
FOSSIL RECORD
Water Transport
DEPOSITIONAL BASIN =
WET
HIGH PRESERVATION POTENTIAL
drier
SPACE
wetter

Figure 18

Click here to access/download;Figure;Figure 18 ClimateModel.jpg