

Impact of an icehouse climate interval on tropical vegetation and plant evolution

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ABSTRACT: Complex plant ecosystems first experienced the effects of major glaciation during the Late Paleozoic Ice Age. The general response of Carboniferous tropical vegetation to these climatic fluctuations, especially the transitions from greenhouse to icehouse conditions (ice age *sensu lato*) and a return to warm times, now can be characterized based on large paleobotanical data sets originally collected to solve stratigraphic and paleoecologic questions. These data come primarily from North America and central Europe, which at the time were part of a single continental mass situated in the tropics. At the onset of icehouse conditions, innovation (speciation leading to novel forms and ecologies) occurred in environments subjected to perhumid (everwet) climates, while floras in better drained, drier, and more seasonal conditions remained dominated by holdovers/survivors from older biomes. This pattern is termed the ‘Havlena effect’. During the height of the ice age, glacial-interglacial cycles produced large sea-level fluctuations and concomitant climatic changes, such that significant areas of continents in the tropics were alternately covered by shallow seas or densely vegetated terrestrial coastal plains. In spite of the repeated destruction of wet lowland habitats during each marine transgression and their further fragmentation that accompanied a climate change from humid to sub-humid, seasonally dry conditions, most of the species and the basic configuration of the plant communities in the wetland biome remained stable. This resilience demonstrates that glacial-interglacial cycles by themselves are not responsible for either extirpation or extinction of these biomes. At the transition from icehouse-to-greenhouse conditions, dry-biome forms, which had been evolving outside of the taphonomic preservational window, became dominant across basinal landscapes while wet landscapes retained their ‘conservative’ species composition. This pattern is termed the ‘Elias effect’. Thus, environmental threshold-crossing marked both the beginning and end of this cold interval, with the loci of response in different environmental settings. In contrast, the minor systematic changes that occurred during glacial-interglacial cycles did not influence the composition or structure of tropical lowland vegetation substantially.

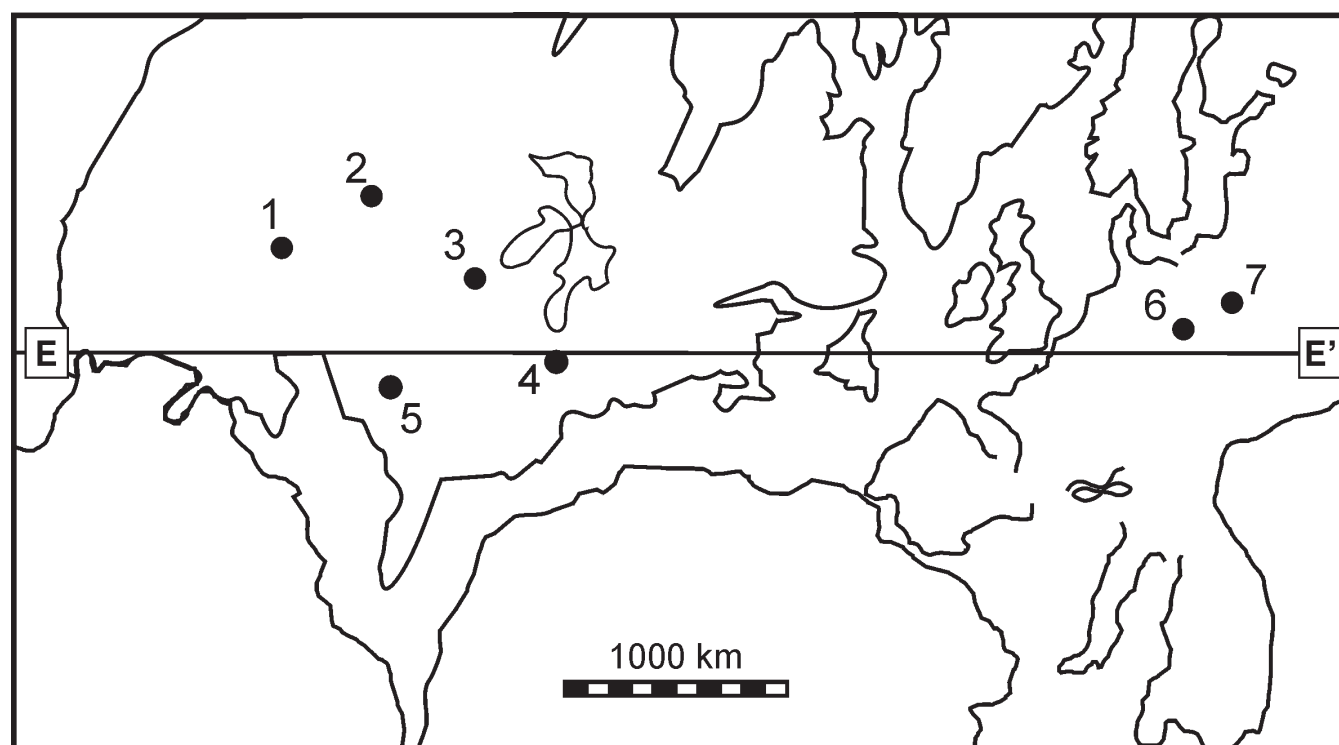
INTRODUCTION

The latest Mississippian–Pennsylvanian–Permian (Late Paleozoic Ice Age or LPIA of Montañez and Poulson 2013) and the Neogene–Quaternary are the only times in Earth history when complex vegetation characterized by large, arborescent plants covered the land during icehouse conditions (= ice age *sensu lato*). In addition, the Late Paleozoic is the only interval in Earth history during which the responses of vegetation to shifts and transitions between these various climate states (greenhouse to icehouse and icehouse to greenhouse) can be studied (Gastaldo, DiMichele and Pfefferkorn 1996), leaving the LPIA as the time interval where its effect on terrestrial plant cover provides a model system. Currently, the planet has not experienced an icehouse-to-greenhouse transition, but it can be expected sometime in the future. Thus, paleobotanical investigations into the biotic responses to these abiotic transitions have important implications for understanding the current icehouse climate and the resultant changes in vegetation and agriculture should human activity trigger the onset of greenhouse conditions.

Late Paleozoic paleobotanical data are most complete for the paleotropics (Gastaldo, DiMichele and Pfefferkorn 1996) for several reasons. Widespread Carboniferous tropical peats

formed the coal deposits that fueled the industrial revolution and are still utilized to produce significant amounts of electricity today. Macrofloral and palynological remains are well preserved in the peat deposits themselves and in the associated siliciclastic and carbonate sediments that envelope these organic accumulations (e.g., Scott and Rex 1985; Gastaldo, Pfefferkorn and DiMichele 1995). Numerous paleobotanical publications based on data from these widespread and intensively mined beds and associated strata form the basis of the current contribution (text-fig. 1).

Three kinds of vegetational transitions between climate states are considered in this paper. Although glacial deposits are known from the latest Devonian (e.g., Isaacson et al. 2008; Brezinski et al. 2009) and earliest parts of the Mississippian, we focus our attention on the vegetational response during the LPIA. The LPIA began in the earlier Visean (Middle Mississippian) and experienced a second pulse of glaciation in the Serpukhovian (Late Mississippian), when ice caps formed around the South Pole in Gondwana (Ziegler 1989; Crowley and Baum 1992; Grossman et al. 2008; Gulbranson et al. 2010). The first example (text-fig. 2, A) highlights the transition from greenhouse-to-icehouse conditions at the initiation of the LPIA. Subsequently, glacial-interglacial cycles at the height of that ice age (text-fig. 2, B and C) are



TEXT-FIGURE 1

Partial palinspastic map of the tropical area during the Pennsylvanian (Carboniferous, 310 Ma), modified after Crowley and Baum 1992, showing areas where data were generated, used, or cited: 1-Texas, 2-Kansas, 3-Illinois, 4-West Virginia, and 5-Alabama in the United States, 6-Upper Silesian Coal Basin in the Czech Republic and Poland, and 7-Lublin-Volhynian Basin in Poland and Ukraine. Paleo-equator (E–E') is shown against the present-day continental outline for ease of orientation.

considered based on two examples. Finally the icehouse-to-greenhouse transition in the latest Pennsylvanian is evaluated (text-fig. 2, D).

Vegetational changes accompanying these climate-state transitions commonly are recorded by the succession of tropical lowland paleofloras in the very thick sections of Euramerica. Milankovitch-type glacial-interglacial cycles are well documented in many Carboniferous basins (Wanless and Shepard 1936; Heckel 1995, 2008; Gastaldo, Purkyňová and Šimůnek 2009; Eros et al. 2012; Cecil, DiMichele and Elrick 2014; van den Belt, van Hoof and Pagnier 2015), and associated vegetational changes have been studied intensively. Visean–Serpukhovian records are found in the Upper Silesian and Lublin-Volhynian basins that straddle the borders between the Czech Republic and Poland and Poland and Ukraine, respectively (Purkyňová 1970; Kmiecik 1995; Kotasowa and Migier 1995; Gastaldo et al. 2009; Gastaldo, Purkyňová and Šimůnek 2009). Temporal changes in paleofloras in these basins can be compared with similar patterns found in correlative basins across the Late Paleozoic paleo-equatorial region. These include Morrowan–Wolfcampian (Bashkirian–Asselian) successions in the Appalachian (Gillespie and Pfefferkorn 1979; Wagner and Lyons 1997; Blake et al. 2002; Gastaldo et al. 2004) and Illinois basins (Phillips et al. 1974; DiMichele, Pfefferkorn and Phillips 1996; DiMichele, Phillips and Nelson 2002) in the USA and later Langsettian–Sakmarian (Bashkirian–Sakmarian) successions in a number of European basins

(e.g., Kerp and Fichter 1985; Cleal and Thomas 2005; Opluštil and Cleal 2007; Wagner and Álvarez-Vázquez 2010; Cleal et al. 2012; Opluštil et al. 2016). In addition, late in the Middle Pennsylvanian (~Moscovian–Kasimovian; Westphalian–Stephanian; text-fig. 2), a period of major warming occurred accompanied by ice melting and sea-level rise (Fielding, Frank and Isbell 2008; Heckel 2008; Rygel et al. 2008). This interval was marked by a major floral turnover and has been investigated intensively, particularly in North America (Phillips and Peppers 1984; DiMichele and Phillips 1996a; Kossack and Cecil 1996; Peppers 1996, 1997; Falcon-Lang et al. 2011), and can be compared with patterns in Europe. Hence, the extensive literature on Carboniferous paleobotany and biostratigraphy and its linkage to independently documented environmental changes provide the database on which the patterns discussed herein are built and framed in a paleoclimatic and evolutionary perspective.

CHANGES DURING THE ONSET OF ICEHOUSE CONDITIONS: HAVLENA EFFECT

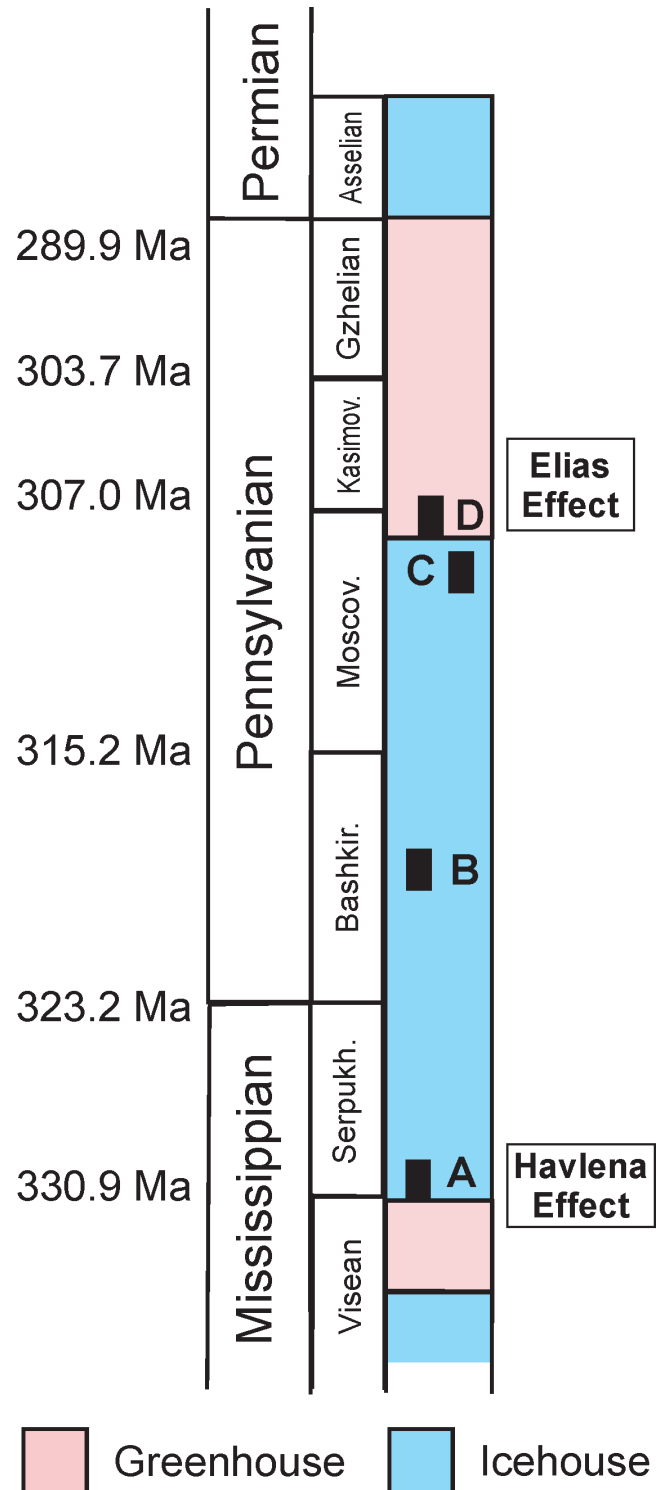
The onset of icehouse conditions in the earliest Serpukhovian after the late Visean warm interval (Iannuzzi and Pfefferkorn 2002; Pfefferkorn, Alleman and Iannuzzi 2014) was marked in the paleotropics by a transition from semiarid-to-subhumid, wet/dry climatic cyclicity to a predominantly everwet, humid-to-perhumid climate (following the terminology of Cecil 2003). Although terrestrial facies from this stratigraphic interval are present in many parts of the world, the thickest sections

are preserved in the USCB (Upper Silesian Coal Basin), part of a fore-deep basin that straddles the boundary between Poland and the Czech Republic (Gastaldo et al. 2009; Gastaldo, Purkyňová and Šimůnek 2009). The LCB (Lublin Coal Basin) in Poland and Ukraine also preserves a virtually complete, even though condensed, succession of intercalated marine and terrestrial beds at this transition.

Purkyňová (1959a, b) and Havlena (1961) identified a pattern in plant-macrofossil distribution in stratigraphic sections of the Czech part of the USCB that appeared contradictory at the time. The roof shale floras preserved directly above a coal seam, which in Havlena's terminology in German is *flöz nah* or 'stratigraphically near the seam,' represented the wettest environments and were comprised of species similar to those occurring in younger, overlying strata (e.g., Westphalian). However, fossil floras recovered from the siliciclastic-dominated parts of the successions higher above coal seams (*flöz fern* or 'stratigraphically distant from the seam') consisted of species known from older parts of the stratigraphic section (e.g., Visean). These latter floras represent somewhat drier environments as shown by their autoecological features and their sedimentologic context (Gastaldo 1996). Hence, the more mesic 'flöz nah' floras were populated by survivors from earlier times, giving them a late Visean aspect; in contrast, the 'flöz fern' assemblages were of a younger aspect. Thus, collections made in ice-house strata but deposited during more seasonally dry time intervals within a single Milankovitch cycle consist of floras that appear to be 'old', due to close evolutionary linkages with forms that were dominant during the prior greenhouse interval (text-fig. 3, A). It is clear that the everwet and seasonally dry biomes and their respective floras occupied climatically or ecologically disparate environments within the same broad, geographic region (Gastaldo 1996). The phylogenetic relationships of taxa in these two separate floras indicate that the wet environments were the loci of evolutionary innovation, when earlier it had been concentrated in seasonally dry settings. Here, we name this pattern the Havlena effect (text-fig. 2, A) after Vaclav Havlena (1928–1984).

At the onset of the icehouse climate, the plants of the seasonally dry biome survived in abundance in environments characterized by periodic drought stress, which remained part of the tropical lowlands. Later, as icehouse conditions became more fully developed, the lowlands experienced long-term oscillations between humid/perhumid climates and seasonally drier climates, reflecting oscillations in polar ice volume (Montañez and Poulson 2013). These oscillations were tracked by their respective biomes; however, there were significant extinctions of the older elements of the seasonally dry flora during the first few glacial-interglacial oscillations of the early Serpukhovian (Gastaldo et al. 2009).

At the same time, wetland assemblages persisted with the same systematic composition and diversity through multiple glacial-interglacial cycles, clustered into several separate, successive intervals of ~1.8-myr duration. Species turnover during these times was ≤10% between successive glacial-interglacial cycles and involved the less common taxa (Gastaldo et al. 2009); replacement species were derived from within the coastal lowlands. Species turnover exceeded 30% during two stratigraphic intervals and appears to have happened 'rapidly' in each case. However, Gastaldo, Purkyňová and Šimůnek (2009) demonstrated that species extirpation and extinction



TEXT-FIGURE 2

Time intervals (A–D) under consideration in relation to intervals of cold climate (= icehouse conditions or ice age *sensu lato*) and warm climate (= greenhouse conditions). Strong but different effects on tropical lowland floras are seen in intervals A and D, while vegetation during the glacial-interglacial cycles at the height of the ice age (intervals B and C) shows only minimal effects. Boundaries of icehouse and greenhouse times and nature of glaciation after Isbell et al. (2003a, b) and Fielding, Frank and Isbell (2008). Ages from the International Chronostratigraphic Chart (IGC 2016.04).

during these intervals of elevated turnover were coincident with widespread tropical warming, occurring during Southern Hemisphere deglaciation, and reflected in the deposition of thick marine zones (201 m maximum thickness). Each marine zone consists of multiple, condensed maximum flooding surfaces (e.g., Naneta and Enna marine zones), identified using gamma-ray logs and representing upwards of 500 kyr per marine zone (Gastaldo, Purkyňová and Šimůnek 2009).

As the ice age intensified towards maximum glacial coverage at the Mississippian-Pennsylvanian boundary, plants of the Early–Middle Mississippian seasonally dry biome continued to survive in tropical latitudes. Their biogeographic range likely was pushed to the western margin of Pangea during glacials and returned to more central regions during interglacials, when equatorial Mean Annual Temperature stabilized and seasonal rainfall conditions returned. Much of the biome underwent extinction, although many taxa survived into the Pennsylvanian and perhaps even the Permian. Some of the taxa that seemingly disappeared from seasonally dry paleofloras apparently survived in extrabasinal refugia. These species reappear as Lazarus taxa in the latest Carboniferous and earliest Permian, as climates dried in the western tropics.

The increasing dominance of the wet facies in tropical basins during glacial phases of Milankovitch-controlled cycles agrees with the prediction that climate belts contract towards the equator at the onset of an ice age, due to restriction and a much better defined ITCZ (inter-tropical convergence zone; Pfefferkorn 1995; Cecil et al. 2003; Peyser and Poulsen 2008). As the everwet tropical environments spread rapidly to dominance during these phases of glacial-interglacial cycles, evolutionary innovation occurred in this newly created, unoccupied ecological space. Competition was minimal for the taxa that could live in this new habitat and new morphological innovations survived to dominate the landscape. This Havlena effect conforms to what Erwin (1992) termed a ‘novelty radiation’, one that occurs under reduced competition for resources and permits major body plan innovation.

PERSISTENCE OF VEGETATION DURING THE HEIGHT OF THE ICEHOUSE INTERVAL

The Black Warrior Basin, Alabama, is a foreland basin with a very thick section of Morrowan age strata (Bashkirian; Langsettian, lowermost Westphalian; text-fig. 2, B). Through thirteen glacial-interglacial depositional cycles representing ~1.3 myr (Pashin and Gastaldo 2009), megaflores and palynological assemblages of the wetland portion of each cycle do not exhibit any systematic differences and do not allow the succession to be subdivided biostratigraphically (Gillespie and Rheams 1985; Eble and Gillespie 1989). This is in spite of the complexity of spatial distribution shown by the floras in any given wetland landscape (Gastaldo et al. 2004). The vegetational persistence at this temporal scale is similar to that reported by Gastaldo et al. (2009) for Serpukhovian floras in the Silesian Basin.

The Carbondale Formation of the Illinois Basin is of late Desmoinesian age (late Moscovian; Asturian, latest Westphalian; text-fig. 2, C). It also exhibits a pattern of vegetational persistence in the face of repetitive changes in climate and sea level. A minimum of 10 intervals of sea-level rise/fall and accompanying climatic changes are recorded by recurring packages of marine and terrestrial rocks (cyclothem), attributed to

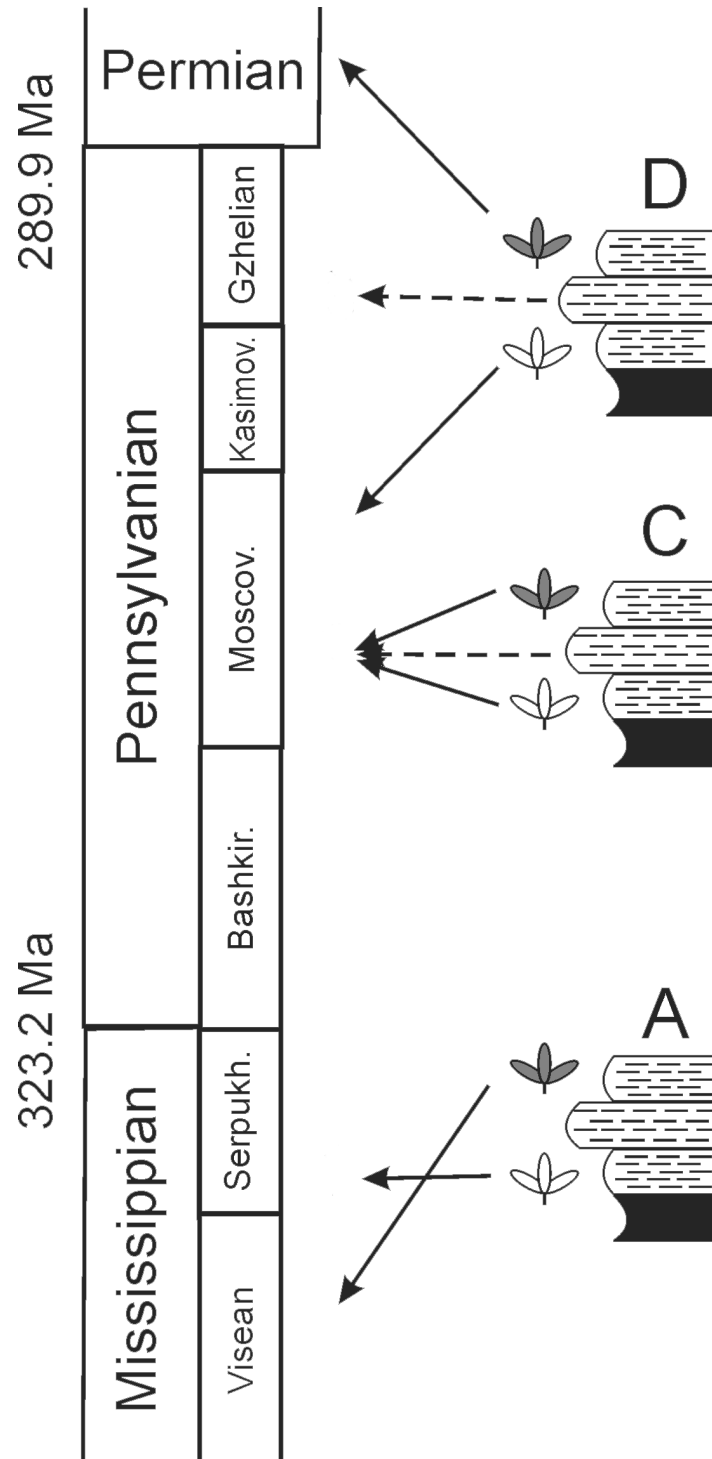
glacial eustasy (Wanless and Shepard 1936; Heckel 1986; Archer and Kvale 1993). These Pennsylvanian terrestrial wetland deposits are rich in plant fossils. They are preserved as coal balls (concretions formed during peat stage; Phillips, Avcin and Berggren 1976) or as dispersed pollen and spores in coals, as well as adpressions in roof shales of coal beds and in floodplain deposits preserved below coal beds, laterally equivalent to paleosols (Gastaldo, Pfefferkorn and DiMichele 1995). Thus, patterns of change are well documented at several levels of detail, and the overall pattern is one of persistence of vegetational structure (DiMichele, Phillips and Nelson 2002; Pfefferkorn et al. 2008). This is particularly true of patterns in taxonomic dominance, patterns of species co-occurrence, and in the centering of species abundance in particular habitats (DiMichele, Pfefferkorn and Phillips 1996; DiMichele and Phillips 1996a, b; DiMichele, Phillips and Nelson 2002). Wetland species turnover during this time was <10% between successive cycles and generally involved the less common taxa; the dominant tree forms recur from one cycle to the next.

There is a strong correlation between climate and sedimentary depositional patterns, which can be used to infer several drivers of change in this system. At a coarse scale, indicators of wet (coals and bauxites) vs dry (evaporites, vertisols, and caliches) conditions have been used to configure paleogeographic maps and infer prevailing climates (Cecil 1992). At a finer scale of resolution, climate can be inferred from the relationship between rainfall and sediment-transport potential, with low sediment transport predominating during the wettest (coals) and driest (chemical rocks) periods and maximum transport occurring during times of seasonality (clastic rocks; Cecil 1992; Cecil and Dulong 2003) or at the inflection points between climate states (Gastaldo and Demko 2011). In addition, increasingly finer resolution of climate dynamics is emerging from studies of paleosols (Driese and Ober 2005; Catena and Hembree 2012; Rosenau et al. 2013 a, b) and the association of floral evidence with specific depositional environments in a sequence-stratigraphic context (Bashforth et al. 2014, 2016; Archer et al. 2016; DiMichele et al. 2016). Such patterns are used to infer changes in climate associated with particular vegetation types.

It is clear from such lithologic-climatic linkages that tropical vegetation was affected by both periodic marine transgressions over large parts of the continent and by associated climatic changes involving rainfall patterns and seasonality, along with possible temperature regimes. The wetlands, in particular, were severely fragmented and restricted in extent by these climate and sea-level oscillations (text-fig. 4). Nonetheless, wetland biomes reassembled regularly during the wettest phase of each glacial-interglacial cycle during the height of the LPIA.

CHANGES DURING WANING OF ICEHOUSE CONDITIONS: ELIAS EFFECT

A pronounced change from, on-average, a wetter to a drier climate occurred at the Desmoinesian-Missourian boundary (~Moscovian-Kasimovian, text-fig. 2, D; Phillips et al. 1974; Mapes and Gastaldo 1986; Cecil 1992; DiMichele and Phillips 1996a). This interval signals a period of extensive deglaciation and global warming (Crowley and Baum 1992; Isbell et al. 2003a), marking the end of an icehouse interval. During this change in climate state, entire taxonomic groups of land plants disappeared from the Euramerican tropics, and wetland ecosystems were extensively reorganized (DiMichele and Phillips 1996a; Pfefferkorn et al. 2008). Concomitantly, many of these



TEXT-FIGURE 3

Patterns of apparent ages (indicated by oblique arrows) recognized in tropical wetland floras (white leaves) and somewhat better drained and seasonably drier, tropical mesic habitats (gray leaves) in local stratigraphic sections of the Carboniferous at three different times: A (greenhouse to icehouse transition), C (during glacial intervals of icehouse conditions), and D (icehouse to greenhouse transition; see also text-fig. 2, A, C, D); dates in Ma from International Chronostratigraphic Chart, IGC 2016.04. Apparent biostratigraphic discrepancies of tropical Carboniferous vegetation at the beginning and end of an icehouse interval demonstrate several key features. Innovation (i.e., origination of new taxa) occurred in wetlands at the initiation of the icehouse conditions (Havlena effect at A, early Namurian = Serpukhovian). During the height of the icehouse (C), floras preserved in the different tropical lowland settings do not show any distinct differences. At the beginning of the next greenhouse interval (D), innovation occurs in the more seasonably drier settings with the appearance of floras with a more modern (i.e., Permian) composition (Elias effect). The situation in A can be compared to the tropics at the beginning of our present icehouse interval in the Tertiary (beginning of Neogene); the situation in C is comparable to the Pleistocene and the Recent, whereas the situation at D models the consequences of the possible, and often predicted, transition from icehouse to greenhouse conditions in the future.

major groups survived in peat-forming wetlands of the Cathaysian tropical microcontinents where high rainfall prevailed (Tian et al. 1996; Hilton and Cleal 2007; Wang et al. 2012). Following the transition to greenhouse conditions, glacial episodes returned, albeit with smaller ice volumes in near-field records across the Southern Hemisphere continents (Crowley and Baum 1992; Isbell et al. 2003b). These episodes are reflected in higher sea levels and lower variance in cyclothemic deposits of the North American Midcontinent (Heckel 2008; Rygel et al. 2008). Paleobotanical patterns in the western tropics exhibit a return to a wetland flora, albeit of different taxonomic composition, along with the occasional preservation of a seasonally dry biome in the lowland basins (Elias 1936; Moore, Elias and Newell 1936; Mapes and Gastaldo 1986; Broutin et al. 1990; DiMichele and Aronson 1992; Tabor et al. 2013b; Looy and Hotton 2014; DiMichele et al. 2016). These latter plants possibly extended their biogeographic range from areas in western Pangea, where permanent populations resided (Falcon-Lang, Kurzwane and Lucas 2016).

Prior to the end of the icehouse climate, vegetation in peat-forming mires of Europe and North America was dominated by six or more species of lycopsid trees, with subordinate tree fern and pteridosperm (gymnosperm) species. The change at the Desmoinesian-Missourian boundary (Phillips et al. 1974) is marked by a regional extirpation/extinction in Euramerica that claimed nearly two-thirds of the existing mire species, including 87% of the tree forms and 33% of the ground cover (DiMichele and Phillips 1996a). For a short stratigraphic interval after the extinction, palynological analyses (Kosanke and Cecil 1996; Peppers 1996, 1997) indicate that dominance patterns varied from coal-to-coal in the local succession, with changing dominant groups that included small lycopsids (*Polysporia*), previously rare tree lycopsids (*Sigillaria*), sphenopsids, and tree ferns (DiMichele and Phillips 1996b). We refer to this time as a ‘species lottery’. After several cycles of peat deposition and sea-level fluctuation, a variety of opportunistic tree-fern species became the dominant mire elements (Willard and Phillips 1993; Willard et al. 2007). Similar patterns occurred in flood-basin vegetation as identified from roof-shale floras (Pfefferkorn and Thomson 1982). This constitutes a reorganization of the ecological landscape within the broader context of the lowland-wetland biome. The dominant species of Late Pennsylvanian wetlands, although different from those found stratigraphically below, were drawn from the same evolutionary lineages that occurred in these habitats during the Middle Pennsylvanian.

Prior to this Desmoinesian-Missourian wetland vegetational reorganization, assemblages had begun to appear in the lowlands that were quite distinct in their species composition. Dominated by gymnosperms, particularly cordaitaleans, the Middle Pennsylvanian assemblages included taxa that were not to become dominant floristic elements until the Late Pennsylvanian and Permian. These included such things as conifers (Falcon-Lang et al. 2009; Plotnick et al. 2009; van Hoof et al. 2013) and *Taeniopteris* (Brongn.) (Bashforth et al. 2016), and possible *Sphenopteris germanica* Weiss or a similar form (DiMichele et al. 2016). They occurred in areas quite distant from contemporaneous high-elevation loci, indicating the presence of these plants in the basinal lowlands during dry parts of glacial-interglacial cycles. Conifer-rich floras are found more commonly and more fully developed in the Late Pennsylvanian lowlands, invading normally wet areas during episodes of more intensive

seasonal dryness and often associated with lithologies near the clastic-to-chemical rock transition; the plants associated with these floras often are of kinds more typical of the later Pennsylvanian and Permian, such as callipterids and *Taeniopteris*. These latter deposits are interpreted to have formed under drier climatic conditions (Cecil and Dulong 2003). Examples include the 7-11 flora of Ohio (McComas 1988), the Garnett flora of Kansas (Cridland and Morris 1963; Winston 1983, 1985), the Hamilton Quarry flora of Kansas (Rothwell and Mapes 1988; Cunningham et al. 1993), and the Kinney Quarry flora of New Mexico (Mamay and Mapes 1992). Numerous other dryland floras have been reported from North America and Europe (e.g., White 1912; Arnold 1941; Kerp and Fichter 1985; Broutin et al. 1990; DiMichele and Aronson 1992). Beginning in the Middle Pennsylvanian, the seasonally dry biome (following Ziegler 1990) contained a higher percentage of evolutionarily derived taxa than did the wetland biome. In addition, Lazarus taxa, known previously only from seasonally dry floras of the Late Mississippian, reappear in these Late Pennsylvanian and early Permian drier environments after a long history of unseen existence outside of the preservational window (DiMichele and Gastaldo 2008; Gastaldo and Demko 2011). One such taxon is *Archaeocalamites* Stur (Mamay and Bateman 1991). Until recently, the reappearance of *Sphenopteridium* Schimper (Mamay 1992) also was believed to be evidence for a Lazarus taxon. Systematic re-evaluation, however, has concluded that Mamay’s (1992) figured material conforms to another taxon, *Sphenopteris germanica*, which is an element of Middle Pennsylvanian, seasonally dry floras in New Mexico (DiMichele 2014) and occurs throughout western Pangea in the Pennsylvanian (Pfefferkorn and Resnik 1984). Ultimately, the seasonally dry biome rose to dominance in Permian deposits throughout most of the tropics (Kerp and Fichter 1985; Kerp 1996; Tabor et al. 2013a; Looy et al. 2014). The exception to this is in China, where the proximity of microcontinents to oceanic and atmospheric circulation conditions permitted the everwet biome to persist (Rees et al. 2002; Wang and Pfefferkorn 2013). This pattern of appearance of new taxa in successively more seasonally dry environments continued into the Permian, where additional dryland biomes have been recognized, each consisting of new kinds of conifers and associated plants (Looy et al. 2014).

In Late Pennsylvanian and early Permian stratigraphic successions, floras ascribed to wet-climate and drier-climate conditions often occur in alternating beds that contain sedimentological indicators of wetter or drier climates (Feldmann et al. 2005; DiMichele et al. 2013; Tabor et al. 2013b; Looy and Hotton 2014). Elias (1936; Moore, Elias and Newell 1936) was one of the first to report this observation from the Midcontinent sequences in Kansas. He noted that wet-climate floras, having affinities with Carboniferous taxa including *Neuropteris ovata* Hoffmann and *Macroneuropteris scheuchzerii* (Hoffmann) Cleal et al. were found in strata that are clearly of Permian age. In contrast, the drier-climate floras were dominated by taxa thought to be typical of the Permian, especially the foliage of *Callipteris*-type pteridosperms (gymnosperms) and conifers. These stratigraphically alternating floras represented the overlap of elements that, otherwise, were dominant in lowland basins and of which, ultimately, the latter biome progressively expanded over the landscape under an increasingly dry seasonal climate (Montañez et al. 2007; Looy et al. 2014). This is in contrast to the earlier Havlena effect. The latest Pennsylvanian records a drier-climate flora, the features of which are of a stratigraphically younger aspect. Thus, the dynamics represent a

reversal of the effect noted at the beginning of the LPIA. We call this set of conditions the Elias effect (text-figs. 2, D and 3, D) after Maxim Konrad Elias (1889–1982). Here, innovation occurs in extrabasinal settings and plants from those areas expand non-competitively into the depositional lowlands during more seasonally dry times.

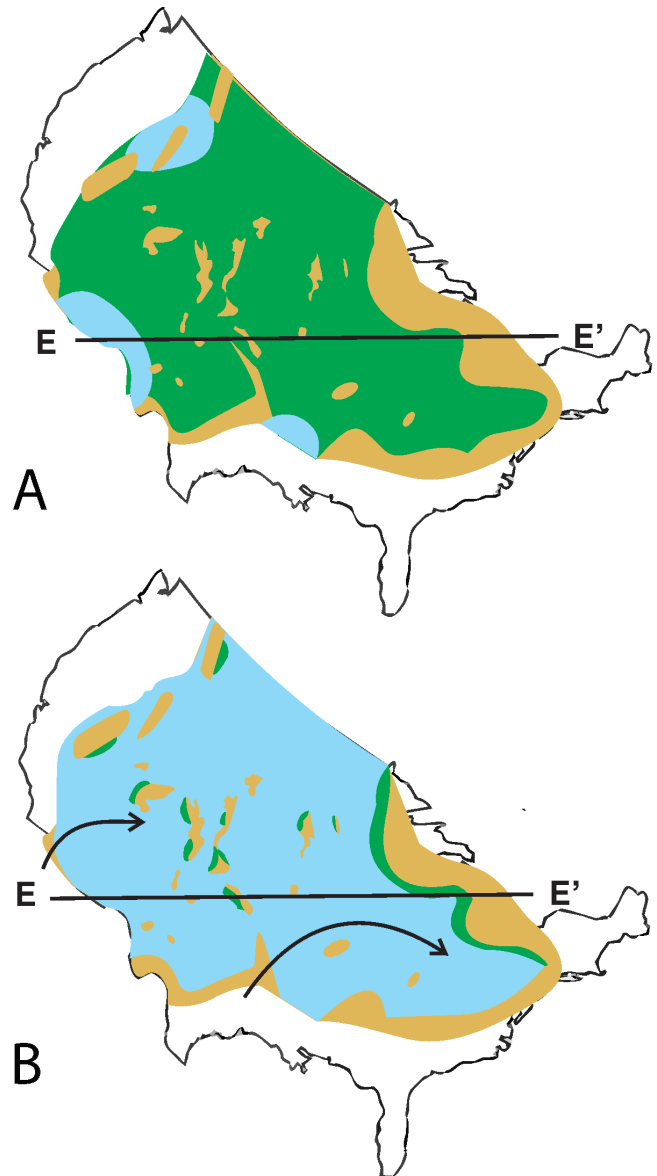
CONCLUSIONS

The major patterns of paleotropical vegetational change during icehouse conditions of the Late Paleozoic Ice Age are now apparent. Distinctly different patterns and dynamics constitute the onset, height, and waning of this particular icehouse interval. Megafloras preserved during the onset of the LPIA exhibit evolutionary innovations in those areas most affected by changes in soil moisture (swamps and mires) under increasingly humid-to-perhumid, everwet conditions. In contrast, habitats wherein better drained soils persisted, influenced by more seasonal conditions during this time, were occupied by plant taxa that were holdovers from a similar, previous climate state. Broad vegetational patterns during the height of the Carboniferous icehouse are similar to those of the Pleistocene, as evidenced during our own icehouse interval. Wetland biomes reorganized with the same systematic diversity and composition following biogeographic range contraction and subsequent expansion, in response to the waxing and waning of continental ice sheets and the effect of that on global sea level and climate. The pattern documented at the transition out of the Pennsylvanian cannot be compared with anything in the Recent or Anthropocene, because we have yet to experience this directional climate shift. We, thus, suggest the following generalities.

Vegetational persistence or reoccurrence is the dominant pattern during the height of an ice age. Glacial advance and retreat and associated sea-level and climatic changes appear to have minimal effects on vegetational structure or dominance-diversity patterns. This is true as long as overall extinction levels are low between subsequent glacial and interglacial periods and no other thresholds exist. These findings are similar to those described for our current ice age (Bennett 1997).

Major extinctions and vegetational restructuring occur at the transitions between globally warm and globally cool conditions. Within a species pool, weedy taxa (ruderals) have advantages in capturing resource space and attaining ecological dominance during times of significant restructuring following extinctions. Opportunist advantage has been described following other extinctions in both the terrestrial and marine realms (Tschudy et al. 1984; Fraiser, Twitchett and Bottjer 2005). However, these changes do not involve major body-plan evolutionary innovations. Evolutionary innovation that results in major new body plans appears to be confined to those times and places where extrinsic drivers either create new habitats or cause extinctions, thus opening major resource spaces to colonization (Valentine 1980; Bateman and DiMichele 2003) and enhancing the likelihood of pulses of niche construction (Erwin 2008). These events are generally rare, and conform to periods of ‘escalation’ (Vermeij 1987). It appears that once such resource spaces are filled, innovation is suppressed (Valentine 1980; DiMichele and Bateman 1996).

In the context of the ice-age tropics, innovation is most likely to occur in wetland habitats at the onset of glaciation. This is due to the initial creation of everwet habitats in the tropical regions,



TEXT-FIGURE 4

Maps of the United States (current outline shown to aid in orientation) with paleo-equator (E–E') indicated for the Carboniferous ~310 Ma during the height of icehouse conditions. A, North America during maximum regression (lowest sea level = glacial interval of icehouse conditions), which is associated with the maximum extent of ice in the Southern Hemisphere. Green indicates extent of lowland floras, blue represents marine conditions, and brown indicates areas of higher elevation characterized by erosion. B, North America during marine transgression associated with maximum deglaciation in an interglacial period, when lowland floras were restricted to marginal refugia. Epicontinental seas covered large parts of the continent. The arrows indicate the generalized direction of the transgression. These two states (A and B) alternated regularly as evidenced by the cyclostratigraphic record. Plants and plant communities persisted through these repeated cycles even though they were extirpated over large areas of the continent during each sea-level highstand. This persistence of floras was demonstrated (e.g., DiMichele, Phillips and Nelson 2002) for 11 glacial-interglacial cycles in the Illinois Basin (interval C of text-figs. 2 and 3). Transgressions did not always have the same maximum extent shown here (see Heckel 2008). Map modified after Cecil and Dulong (2003).

while tropical seasonally dry habitats become refugia for older taxa (the Haylena effect). At the end of glaciation, innovation is seen more clearly in seasonally dry habitats. This is a consequence of seasonally dry areas increasing their spatial distribution (spreading) during the beginning of extensive periods of seasonal dryness, while increasingly patchy wetlands become refugia for the older wetland elements (the Elias effect).

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