

Climate and vegetational regime shifts in the late Paleozoic ice age earth

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ABSTRACT

The late Paleozoic earth experienced alternation between glacial and non-glacial climates at multiple temporal scales, accompanied by atmospheric CO₂ fluctuations and global warming intervals, often attended by significant vegetational changes in equatorial latitudes of Pangaea. We assess the nature of climate–vegetation interaction during two time intervals: middle–late Pennsylvanian transition and Pennsylvanian–Permian transition, each marked by tropical warming and drying. In case study 1, there is a catastrophic intra-biomic reorganization of dominance and diversity in wetland, evergreen vegetation growing under humid climates. This represents a threshold-type change, possibly a regime shift to an alternative stable state. Case study 2 is an inter-biome dominance change in western and central Pangaea from humid wetland and seasonally dry to semi-arid vegetation. Shifts between these vegetation types had been occurring in Euramerican portions of the equatorial region throughout the late middle and late Pennsylvanian, the drier vegetation reaching persistent dominance by Early Permian. The oscillatory transition between humid and seasonally dry vegetation appears to demonstrate a threshold-like behavior but probably not repeated transitions between alternative stable states. Rather, changes in dominance in lowland equatorial regions were driven by long-term, repetitive climatic oscillations, occurring with increasing intensity, within overall shift to seasonal dryness through time. In neither case study are there clear biotic or abiotic warning signs of looming changes in vegetational composition or geographic distribution, nor is it clear that there are specific, absolute values or rates of environmental change in temperature, rainfall distribution and amount, or atmospheric composition, approach to which might indicate proximity to a terrestrial biotic-change threshold.

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INTRODUCTION

The objective of this paper is to assess the nature of responses of late Paleozoic terrestrial vegetation to changes in abiotic attributes of the earth–climate system and to evaluate the geologic record for evidence of warning signs that biotic changes may be imminent. The focus is on late Paleozoic equatorial terrestrial ecosystems from two time periods that experienced major environmental change: the middle–late Pennsylvanian transition during the Carboniferous, and the Carboniferous–Permian transition. The changes during these two time intervals are fundamentally different in nature. The older represents an internal reorganization of wetland vegetation throughout the western and central parts of Pangaea, and was associated with a relatively brief interval of significantly

decreased effective moisture and possibly with radiatively forced global warming. The latter involves a shift in the dominant lowland vegetation from humid wetland plant assemblages to seasonally dry assemblages. It was associated with large-scale climate changes associated with the transition from a possibly ice-free interval of generally warm global climate to the onset of the most extensive glaciation of the entire Late Paleozoic Ice Age. Both of these examples have specific biogeographic footprints, largely restricted to central and western equatorial Pangaea.

In the course of evaluating these patterns we first examine the underlying assumptions that are used to infer associations between vegetation and environmental factors on geologic time scales. These processes include the recognition of spatio-temporal relationships between vegetation and environmental

factors and the identification of mechanistic linkages between these elements. The analyses and inferences drawn from them are complicated by the vagaries of the stratigraphic record and our own difficulties in comprehending that for which we have no modern analogues. However, through the combination of empirical approaches and modeling, similar to those used with modern vegetation, this system can begin to be understood more fully.

Additionally, evaluation of these ancient systems against various first-principles explanatory frameworks helps us to refine our thinking. In these two case studies, we examine the vegetational responses to changing physical conditions in light of explicit model-driven expectations. In particular, we attempt to discriminate between conceptual models involving regime shifts or state changes through analysis of whether vegetational responses were gradual or catastrophic, reversible or irreversible.

BASIC PATTERNS

Synchronous changes in climate, as inferred from various kinds of proxy data, and vegetational composition have been documented from many times in pre-Pleistocene geologic history (Beerling & Woodward, 2001). Most of these major biotic changes are associated with widespread changes in sedimentary and resultant lithologic patterns. A few of the more high-profile examples include the Paleocene–Eocene Thermal Maximum (Wing & Harrington, 2001; Zachos *et al.*, 2005), and boundary events associated with the Cretaceous–Tertiary (Johnson, 1992), Triassic–Jurassic (McElwain *et al.*, 1999; but see Lucas & Tanner, 2008), and Permian–Triassic (Looy *et al.*, 2001; Erwin *et al.*, 2002; Rees *et al.*, 2002). Less attention has been paid to similar events within the late Paleozoic (Phillips & Peppers, 1984; Montañez *et al.*, 2007), even though some of these are well documented, due to difficulties with dating and because the taxonomic composition and ecologic structure differ significantly from modern systems. Recent advances in our understanding of the dynamics of the atmosphere and climate during this period now make linkages possible between terrestrial ecosystems and climate change (Montañez *et al.*, 2007). These late Paleozoic cases are doubly important because they occur during an interval of cold global climates, with large ice masses at the south and, perhaps, at times, the north polar regions (Fielding *et al.*, 2008a). Thus, this biotic–abiotic system is the closest analogue we have to our modern icehouse Earth (Gastaldo *et al.*, 1996). We will focus on two examples. The first, and oldest, occurred around the middle–late Pennsylvanian boundary, approximately 306 Ma, across the Euramerican equatorial coal belt and was a time of reorganization of the humid, wetland biome. The other occurred near the Carboniferous–Permian boundary in western equatorial Pangaea, approximately 299 Ma (Gradstein *et al.*, 2004), and recorded the establishment of seasonally dry vegetation in the tropical lowlands.

CONCEPTUAL FRAMEWORK

The problem of correlation-causation

Searching for a causal mechanism or driver of patterns in the fossil record can suffer from conflation of correlation with causation. Within the comparative method, the basis/mainstay of hypothesis framing lies in (a) the identification of patterns in a dataset of interest, (b) statistical analysis and characterization thereof, (c) identification of recurrent instances of the pattern at other times and places, and (d) establishment of correlations between the patterns of interest with patterns in different kinds of data. Great reliance often is placed on modern, actualistic data to interpret both fossil and proxy environmental patterns. In addition, physical/dynamic modeling can be used to determine whether an association between two properties should be expected/is consistent with the physical/theoretical framework.

This process begins with detection of patterns of change in a biologic or geologic variable of interest, usually a change of large magnitude occurring as either an incremental directional trend or a threshold-like change. Detection of temporal changes is followed by a search for changes in other variables as independent confirmation that ‘something is happening’ (e.g. Erwin, 2006; Montañez *et al.*, 2007). In particular, patterns are sought in variables that can be assessed independently of the one(s) in which the change was first detected.

The correlation of patterns in independent data sources follows the identification of trends. It is facilitated by high resolution stratigraphic correlation on several temporal scales. Most importantly, as in the examples used in this paper, all of the proxy time series should come from the same set of successions/samples. Thus, even if absolute time control cannot be well established, excellent constraints can be placed on relative age assignments. Broader regional and global correlations, to standard geologic time series, can greatly expand understanding of the patterns in question by linking them to other well-constrained studies (for example: linking ‘near field’ polar glacial records to ‘far field’ equatorial sedimentary patterns and climate proxies – papers in Martini, 1997; Fielding *et al.*, 2008b).

When comparing data from different locations, it is necessary to evaluate the spatiotemporal scope of the patterns and processes under investigation in order to avoid scale mismatches when pairing data from different sources. This certainly must precede inference of a causal link when moving from a pattern of correlation to a hypothesis of causation. Temporal-scale considerations in particular are essential in the comparison of biotic and abiotic patterns: do the supposed cause and effect variables match up temporally and spatially – do they occur at the same rates, over the same intervals of time, or have effects of similar spatial scope? One also must ask if there is a logical link between the biologic and the physical variables that have been identified as of interest; i.e. from our understanding of

the world, is there a plausible reason to expect cause and effect? This usually will be based on reasoning from actualistic patterns and uniformitarian assumptions, which undergird inference at the level of causation; however, knowledge of unusual events in geologic history also helps us to imagine possible scenarios outside of modern experience. Usually, variables initially are divided into dependent and independent, i.e. they are ordered relative to one another as ‘driver’ and ‘response’. Most often, one class of variables (here physical factors) is considered to be ‘independent’ and another class (here biotic conditions, and certain physical climate variables) ‘dependent’, though this will be blurred by feedbacks, which likely exist in the systems under consideration here. Many studies of extant ecosystems show strong, and often non-linear, plant and animal responses to the distribution of and changes in physical conditions, both climatic and substrate/soil related (Webb *et al.*, 2006).

In the end, based solely on this comparative approach, we are still left with the matter of estimating the likelihood of association between an observed change (effect) and the presumed driving force or forces (cause). Any studies based in the geologic record will suffer from this problem. The only way around it is to introduce an experimental dimension, which is where modeling becomes important as a means to examine hypotheses of cause and effect independently (see below).

In the instances considered here, we wish to match changes in the proportions of various plants (dominance), in taxonomic richness (‘biodiversity’), or in the distribution of different vegetation types (biomes) in a biogeographic region, with coincident changes in climatically sensitive geologic variables, such as stable isotopes, paleosol morphologies, or relative sea-level. This is done under the assumption, based on modern examples, that the physical factors are most likely to be drivers of biotic change, but that there may be detectable feedbacks. We consider the hypotheses in light of experimental approaches using global climate models, where appropriate by integrating existing climate simulations for tropical Pangaea during the late Paleozoic. We also compare data and model results in each example to several possible explanatory frameworks or working hypotheses.

The best-of-field fallacy

The great population geneticist, J.B.S. Haldane once said that: ‘The universe is not only queerer than we suppose, it is queerer than we *can* suppose’. This statement could be a motto for those working in paleoecology and climatology. The distant past may contain physical and biologic systems that are outside of the experience of those working in the modern world or the recent ice ages.

In historical science, our experience and imagination constrains what we choose as explanations for the patterns we see. In what was described as the ‘best of field fallacy’ (Macbeth, 1971), we choose between explanations ‘a’, ‘b’, and ‘c’, when,

in fact, the correct answer is ‘d’. Just how we envision or create ‘d’ *de novo* is a matter for philosophers and students of neurobiology (e.g. Feyerabend, 1993). In the best-of-field context, we should expect that our causal explanations of patterns will be, potentially, incorrect, and subject to improvement as new data or new ideas and insights intrude into the explanatory framework.

Reconstructing past system behavior may have to allow for conditions unlike those of today. We must, however, assume that the underlying physical principles do not change. Thus, bio- and geophysical first principles allow the interpretation of the state of, or trends in, proxies by which we estimate many of the variables of interest. These proxies can be mainly physico-chemical (paleosol morphology, mineralogy, geochemistry) or biomechanical (e.g. functional morphology; metabolic scaling relationships). First principles permit a more straightforward interpretation of the meaning of these proxies and of changes therein.

Perhaps the only means of escape from the limitations imposed by absence of modern analogues for particularly peculiar ancient situations, and for lack of imagination or understanding as applied to them, is to undertake modeling. Models, through the systematic use of physical principles, can elucidate possibilities that are not perceptible/conceivable by other means and serve as ways to sidestep both uniformitarian and correlation-causation constraints. Models require explicit description of the system from first principles, so that all the parameters are known and the states of all the variables specified at the outset. This provides for the possibility of experimentally manipulating the system (assuming it has been reconstructed reasonably accurately), even to the point where conditions that lie outside of the realm of modern experience can be specified. In this manner, hypotheses can be tested explicitly and model outputs can be tested directly against empirical data. Models also may fall prey to the best of field fallacy. Inasmuch as a system can be described from first principles, a model may escape this syndrome. However, the incorporation of processes and/or dynamics that are not known or cannot be described from first principles, but are rather determined from empiricism, opens the possibility that the model may be biased toward the modern. This can be a particular problem when using models, such as general circulation models, that have been optimized for the present climate.

VEGETATION–CLIMATE RELATIONSHIPS

Vegetation closely reflects climate at any given time and place in earth history. That this is so led Köppen (1936, translated in Claussen, 1998) to describe vegetation as ‘crystallized, visible climate’, which though a bit hyperbolic expresses the essence of biogeography. This close relationship between plants and the global environment has permitted the development of biogeographic frameworks, such as the dynamic biome system

of Walter (1985), the descriptive life-zones of Holdridge (1967), or more recent attempts to describe the distribution of plants on the basis of their physiologic and structural attributes (e.g. Prentice *et al.*, 1992; Woodward *et al.*, 2004). The most recent examples aim their systems to feed squarely into land surface models coupled to atmospheric general circulation models (GCMs), so that vegetation responses to climate change can be predicted under various future-climate scenarios (e.g. Woodward & Lomas, 2004). Past climates, too, have been modeled and used to predict patterns in extinct vegetation (Beerling & Woodward, 2001), mainly using climate (e.g. temperature, precipitation) as the driver with the plants responding (e.g. the tandem papers of Gibbs *et al.*, 2002 and Rees *et al.*, 2002 for the Permian). Ziegler *et al.* (2003) made the strong case for a link between air mass dynamics, consequent climate patterns, and vegetational distribution, beginning with the Permian and advancing to the present day.

Plant–climate patterns must be looked at from a hierarchical perspective. Many of the more descriptive systems can be described as ‘correlative’ or ‘static’, and produce climate envelopes by which vegetation is circumscribed. Other approaches, described as ‘dynamic’ or ‘process based’ (Shugart, 1997), attempt to link plant physiologic and distributional patterns (Cramer *et al.*, 2001) to particular vegetational traits. These more dynamic models reduce the complexity of vegetational characterization, if for no other reason than to make the models computationally tractable. Bonan *et al.* (2003), for example, have reduced tree-dominated vegetation to seven types globally, Woodward & Lomas (2004) to five, and have focused on the identification of ‘functional types’ (see papers in Smith *et al.*, 1997; Bonan *et al.*, 2002). Such dynamic models are expressly individualistic (Gleasonian) in their mechanistic underpinnings (Prentice *et al.*, 1992), assuming that larger spatial patterns emerge from the dynamic responses of individual plants, conditioned evolutionarily by their species identities. This is certainly supported by the patterns of vegetational recovery following the last glacial maximum, which have been well documented by Quaternary paleoecologists (e.g. Huntley & Webb, 1989), often resulting in so-called non-analogue communities (Overpeck *et al.*, 1992; Williams & Jackson, 2007). The question is this, however: Are there scale breaks in or spatial limits to these individualistic vegetational dynamics, resulting in higher order spatial patterns that converge on/are effectively the same as the vegetation–climate envelopes identified by the static approaches (DiMichele *et al.*, 2005a)? In other words, are individualistic dynamics spatially bounded, occurring mainly within larger vegetational units, such as biomes, between which there is limited species overlap?

Dynamic interactions among individual plants, appearing stochastic at the lowest spatial levels, may manifest themselves within bounded and persistent species-pools or biomes at larger spatial scales. In such a hierarchy, composition becomes

increasingly more subject to static characterization at the larger spatial scales. Consider the recently proposed Unified Theory of Biodiversity and Biogeography of Hubbell (2001), in which plant species are considered, at the smallest spatio-temporal scales, to be effectively ecologically identical in terms of their resource requirements. This may have applicability within a species pool, which one might broadly construe as a biome. For example, can one realistically differentiate a particular ‘maple-only’ versus ‘beech-only’ spot on a hillside in the central Appalachian mountains? Yet, one can differentiate, in terms of likelihood, areas and habitats more conducive to colonization by maple, beech or other members of that species pool, than by spruce or larch or members of that species pool. Such higher-level spatial-scale vegetational boundaries, or ecotones, may reflect physical controls, deriving from plant evolutionary responses to the discontinuous distribution of physical factors (rainfall, temperature).

Work with wholly extinct fossil plant groups and the species pools or biomes they constitute, is much more restricted in its flexibility than investigations of fossil plant groups and floras closely related to those living today (the nearest living relative approach of Mosbrugger & Utescher, 1997; Mosbrugger, 1999). For the most part, studies of late Paleozoic biomes have had to rely on the description of recurrent plant associations in light of climatic proxy variables, or by mapping such plant associations onto the results of GCM simulations. Ziegler (1990), for example, used the Walter (1985) biome model to divide the Permian into an on-average series of climate-based biomes paralleling those of the present day. Rees (2002) and Rees *et al.* (2002) modified this approach by assigning statistically identified groups of plant taxa to biomes based on Walter’s scheme. They assembled global plant-assemblage data for several Permian geologic stages, which are large time bins of temporal durations that exceed the temporal scale of climatic fluctuations, thus introducing significant time averaging into the data. The statistically identified plant associations were located paleogeographically and then compared to climate simulations (Gibbs *et al.*, 2002), and biomes identified by linking the plants to modeled climate parameters.

Incorporating feedbacks

It seems intuitive that vegetation does more than respond to changes in climate – it actively affects climate through feedbacks (e.g. Woodward *et al.*, 1998; Webb *et al.*, 2005, 2006; Bonan, 2008). Feedbacks are not well understood, though such understanding is improving, primarily through modeling studies that link GCMs to various kinds of dynamic vegetation models (six of which are compared in Cramer *et al.*, 2001), generally studied in the context of changing atmospheric CO₂ concentrations. For a brief, concise review of vegetation–climate feedback, see Feddema *et al.* (2005); Brovkin (2002) and Bonan (2008) provide longer, more comprehensive reviews.

Feddema *et al.* (2005) divide feedbacks into two categories, biogeochemical and biogeophysical. The former are effects of vegetation on biogeochemical cycles, such as the carbon cycle or hydrologic cycles (see Zeng *et al.*, 2004 for discussion of possible positive feedbacks between atmospheric CO₂ and the carbon cycle). The latter is a broader category in which vegetational structure and abundance affect aspects of the physical climate such as reflectivity of the earth's surface (albedo), partitioning of heat transfer from the earth to the atmosphere into sensible versus latent components, and land-surface roughness. Ultimately, these physical aspects influence cloud cover, local temperatures, the position of rising versus descending circulating air currents, and rainfall patterns. One of the simplest positive correlations is between rainfall, measured as 'rain days' and vegetation cover (Webb *et al.*, 2006). Thus factors that increase vegetation cover will tend to increase rainfall, and vice versa, resulting in positive feedback loops, though such effects may be very local and not translate from small to large spatial scales (Webb *et al.*, 2005). Tropical rain forests, for example, have low albedo, which leads to an increase in net radiative heating and rising air masses. This ascending air causes low pressure to develop near the surface, increasing the local water vapor flux, enhancing precipitation and leading to greater soil moisture, greater latent heat flux and greater forest growth (Lofgren, 1995). Conversely, reduction of vegetation can lead to an increase in surface albedo and a decrease in net radiative heating. These radiative changes, along with a decrease in soil moisture and latent heat flux, promote subsidence of dry air. This further reduces vegetation and increases albedo, resulting in another positive feedback that is particularly strong in desert areas and tends to maintain them (Lofgren, 1995; Brovkin, 2002; Foley *et al.*, 2003). In snow-covered arctic environ-

ments, increases in global temperatures result in increased vegetation cover, reduced albedo, elevated temperatures, and further expansion of vegetation (Woodward *et al.*, 1998).

Such feedbacks likely existed on the Paleozoic earth as well and have been incorporated into some modeling approaches. Poulsen *et al.* (2007), for example, modeled late Paleozoic climate using a GCM coupled to an equilibrium vegetation model based on the modern earth; the vegetation model was modified, however, to eliminate grasses, which had not yet evolved. Unlike a static modeling approach, the coupled climate-vegetation modeling approach attempts to capture biogeophysical interactions between climate and vegetation. Nonetheless, it still relies on modern climate-biome relationships that may or may not be appropriate for the distant past. Coupled climate-vegetation models of the late Paleozoic predict profound changes in vegetation and continental climate with an increase in atmospheric CO₂ from modern (355 ppmv) to high (2800 ppmv) levels (Poulsen *et al.*, 2007). Changes in atmospheric CO₂ concentrations in the past could have acted as initiators of changes in the distribution and dynamics of vegetation (e.g. Montañez *et al.*, 2007), resulting in positive feedback loops similar to those linked to modeled shifts in landcover associated with rising CO₂ in our current world (DeFries *et al.*, 2002; Feddema *et al.*, 2005).

System thresholds and multiple stable states

The character of vegetational change in response to changing climate may follow several different dynamic pathways, with or without vegetation feedbacks (Fig. 1). In the conceptually simplest, local and regional species composition change

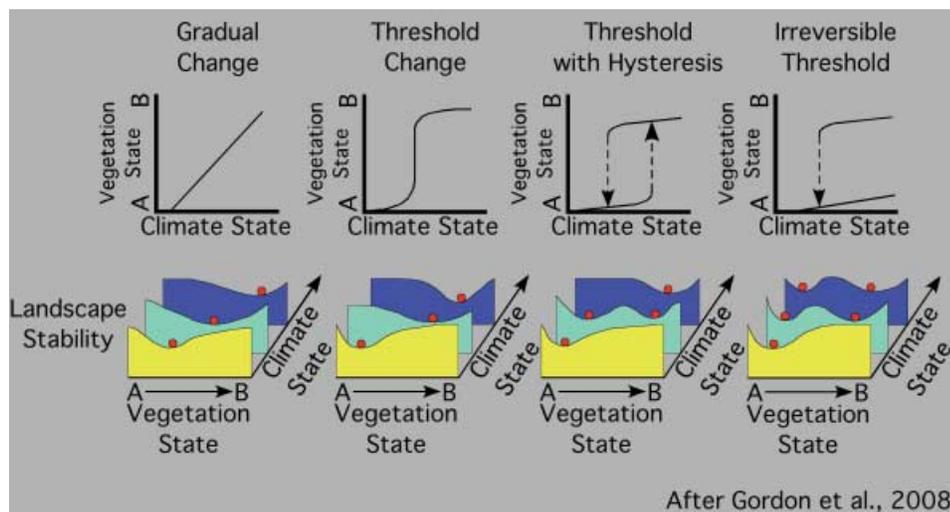


Fig. 1 Four conceptual models of the relationship between environmental change (Climate State) and vegetation response (Vegetation State). See text for details. Modified from Gordon *et al.* (2008).

gradually through time, tracking a gradual change in climate. More difficult to study are changes that happen at threshold points. In these instances, vegetation resists gradual changes in climate only to respond with a catastrophic change in state once a climatic threshold is passed. In the simplest case, the threshold divides two distinct states with different environmental tolerances. More difficult to document is the instance of multiple or alternative stable states that can exist under a range of identical climatic conditions. In this case, the shift from one state to another may occur at a threshold, however, the transition points between states lie at different points in climate space. For example, a unit change in climate parameter X may lead to a vegetational change, but a unit change in parameter X in the opposite direction will not reverse the transition. This path-dependent behavior in a system is referred to as 'hysteresis'. A third possibility for a threshold response is irreversibility, where change from state 1 to state 2 cannot be reversed under any circumstances. These response patterns are summarized by Scheffer *et al.* (2001), Foley *et al.* (2003), and Gordon *et al.* (2008). Positive feedbacks between climate and vegetation can play a role in any of these response types, but are implicated most strongly as drivers in the alternative/multiple-stable-state systems. The problem for neoecology has been documenting these systems, because one must be able to isolate environmental variables, which is difficult in a field-based study (e.g. Sousa & Connell, 1985; Petraitis & Methratta, 2006).

In a modern example, it has been argued by several authors (Claussen, 1998; Brovkin, 2002; Foley *et al.*, 2003) that an apparently rapid shift from a vegetated to a nearly unvegetated state in the modern Sahara, about 5500 years ago represents a catastrophic, alternative stable state response. In this situation, the switch between a green and a desert Sahara was driven by positive feedbacks between vegetation cover, albedo, and rainfall patterns. Once vegetation cover dropped to some threshold point, the change from a vegetated to an unvegetated state is proposed to have happened rapidly. This is not a universally accepted conclusion, however, and recent papers have challenged this both through empirical study of palynologic data (Kröpelin *et al.*, 2008) and modeling studies (Liu *et al.*, 2006), the latter implying a threshold-like response but one driven strictly by vegetational tracking of climate change, without positive feedbacks between vegetation and climate. In the strictest conception of the alternative state concept, the physical conditions under which the alternative states exist should be effectively the same.

Variations on any or all of these possible response profiles may belong among the multiple working hypotheses that form the spectrum of explanatory models for vegetation change in the deep past. We believe that a threshold model, possibly one of alternative stable states or irreversible change, may apply to our first case study. In the second case study, a threshold-like response or a more gradual change seem to be called for.

CASE STUDIES

Case study 1: The middle–late Pennsylvanian transition

A change in terrestrial tropical wetland vegetation has been documented across the middle–late Pennsylvanian transition (Fig. 2) (Phillips *et al.*, 1974; Pfefferkorn & Thomson, 1982; Phillips & Peppers, 1984; Phillips *et al.*, 1985; DiMichele & Phillips, 1996; Kosanke & Cecil, 1996; Peppers, 1996, 1997; Cleal & Thomas, 2005). In other publications this boundary is variously identified as the Desmoinesian–Missourian, Westphalian–Stephanian, or Moscovian–Kasimovian, as well as the middle–late Pennsylvanian. These boundaries are, however, not temporally equivalent, even though they have often been treated as such (e.g. see Gradstein *et al.*, 2004; Fielding *et al.*, 2008a; Heckel, 2008; Ogg *et al.*, 2008). We have chosen to call this simply the middle–late Pennsylvanian transition and await final biostratigraphic placement of the stage boundaries, against which the biotic and geophysical changes can then be assessed.

The biotic pattern is a rapid, essentially catastrophic change from wetland vegetation rich in, or dominated by, giant lycopsid trees, seed ferns and tree ferns, to one dominated by tree ferns, with subdominant seed ferns; the change also includes significant turnover in species and genera within the major evolutionary lineages involved (DiMichele & Phillips, 1996; Peppers, 1996) (Fig. 3). The change did not encompass the entire Pangaeon tropics, extending through Euramerica but not into China, where middle Pennsylvanian-type vegetation persisted well into the Permian in wetland environments (Hilton & Cleal, 2007; Pfefferkorn & Wang, 2007).

This vegetational change occurred during a time of dynamic climatic change. First of all, much of the Pennsylvanian was a time of glacial–interglacial oscillations probably on time scales approximating those of the Pleistocene (Wanless & Shepard, 1936; Heckel, 1994, 2002; Horton *et al.*, 2007; Heckel in Ogg *et al.*, 2008). Thus, environmental conditions in the tropics were changing regularly, on orbital frequencies (e.g. Heckel, 1986; Drummond & Wilkinson, 1993; Cecil *et al.*, 2003; Perlmutter & Plotnick, 2003). Theoretical climate models (GCMs) support this connection between fluctuating high-latitude ice sheets and tropical climate. Peyser & Poulsen (2008) and Poulsen *et al.* (2007), using late Paleozoic GCM simulations, demonstrate that the glaciation/deglaciation of polar regions on Gondwana could have substantially altered precipitation levels and the seasonal distribution thereof, as well as surface temperatures over low-latitude Pangaea.

As a consequence of these environmental oscillations on orbital time scales, the wetland vegetation of the Pennsylvanian, which has led to its characterization as the 'coal age', was but one phase of the linked ice volume/climate/sea-level cycles. Such wetland vegetation was present only periodically in lowland Pennsylvanian basins with other kinds of floras, typical of seasonally dry conditions, often present between the times

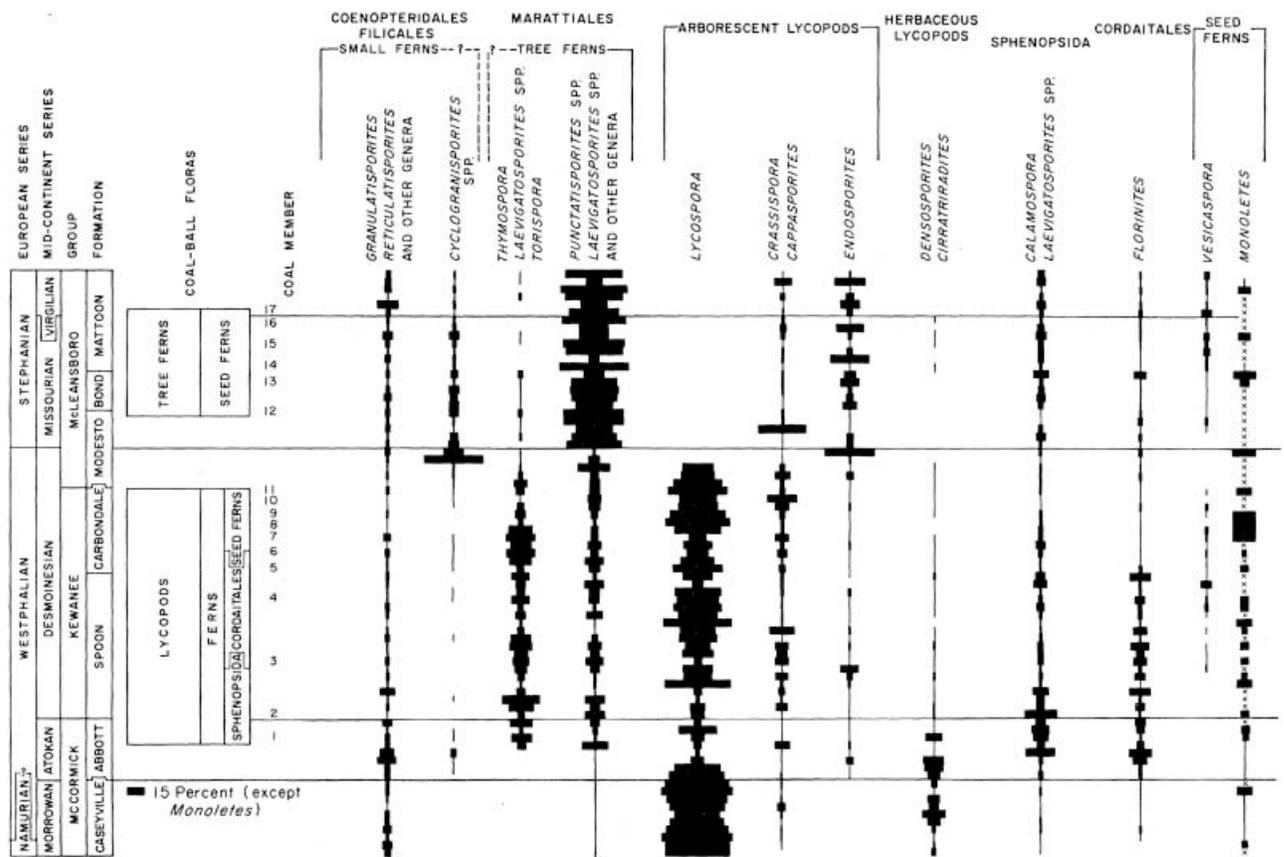
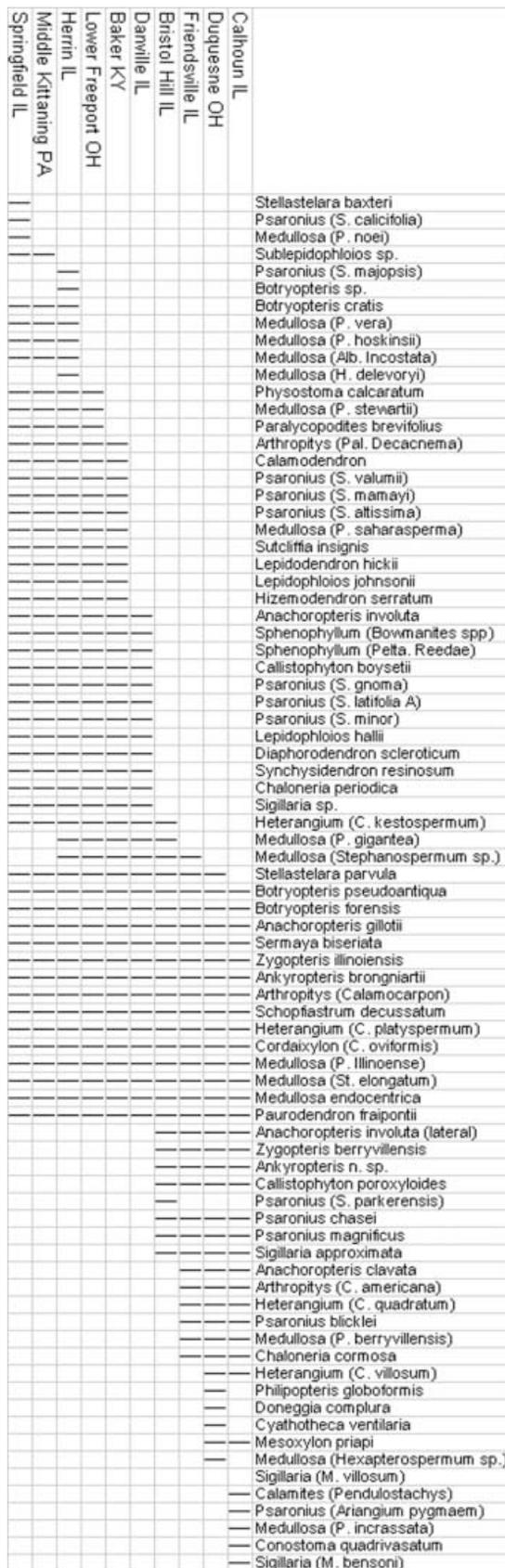


Fig. 2 Changes in major groups of fossil plants during the middle-late Pennsylvanian transition based on palynologic analyses of coal beds from the Illinois Basin, USA. Diagram from Phillips *et al.* (1974) Fossil plants and coal: patterns of change in Pennsylvanian coal swamps of the Illinois Basin. *Science*, **184**, 1367–1369, reprinted with permission of AAAS.

of peat formation. Delta-switching models that would have peats (of the type leading to economic coal beds) forming in some delta lobes while clastic sedimentation occurred nearby on some other lobe, and limestones formed elsewhere nearby (e.g. Horne *et al.*, 1978) have been largely abandoned. Such models fail to account for the differential climatic and physicochemical conditions attending the formation of *in situ* thick beds of terrestrial organic matter versus carbonate and evaporite precipitation from seawater, and how these differ further from climates suitable for transport and deposition of clastics (Cecil, 1990; Cecil *et al.*, 2003). Coal beds represent ancient peat-forming mires, which require moisture input to exceed evapotranspiration nearly year-round, conditions that Cecil (1990; see also Cecil *et al.*, 2003) has labeled ‘humid’ or ‘perhumid’. This same basic flora, differing slightly in species composition and dominance patterns from that of the peat-forming mires, is preserved in clastic rocks deposited above and below the coal beds. The plants of this flora likely grew in mineral-soil flood basins also under humid conditions (Gastaldo, 1996), though with slightly more seasonality than that needed for peat accumulation. Periods of transport of large amounts of clastics into the basinal lowlands is a sedimentary

characteristic requiring some seasonality of rainfall (Cecil, 1990; Cecil & Dulong, 2003).

Alternating with these wetter times were intervals when the basinal lowlands experienced seasonality of rainfall. Moisture seasonality is indicated by the presence of vertic paleosols (frequently representing the immediate seat earths/underclays of coal beds – indicative of seasonal climates), or marine rocks of various types. In addition, there is both palynologic (e.g. Peppers, 1997; Dimitrova & Cleal, 2007) and macrofossil (e.g. Lyons & Darrah, 1989; DiMichele & Aronson, 1992; Plotnick *et al.*, 2008) evidence between the coal beds that an entirely different assemblage of plants lived in the basinal lowlands, dominated by species tolerant of seasonal moisture regimes (see case study 2). Where the wetland plants went when the seasonally dry vegetation occupied the lowland basins is unknown – they could have migrated out as an intact unit, later to migrate back in, or they might have disassembled into isolated refugial pockets in wet areas, to reassemble during the next period of wet tropical conditions (DiMichele *et al.*, 2002). This dynamic is different from that seen in the modern Amazonian forest that appears to persist intact, even if there are some changes in species composition, forest extent,



and structure between Pleistocene–Holocene glacial maxima and minima (e.g. Bush *et al.*, 2007).

This cannot be overstressed, and so we repeat it: Pennsylvanian humid-to-perhumid climate, the wetlands that climate engendered, and the flora that grew under that climate, came and went repeatedly as sea-level and climate in the tropics fluctuated, presumably in response to changes in ice volume. Other kinds of plants dominated the basinal environments when the vast wetlands were not there (e.g. Cridland & Morris, 1963; Broutin *et al.*, 1990; DiMichele & Aronson, 1992; Kerp, 1996; Falcon-Lang *et al.*, 2004), and these non-wetland plants belonged to a distinct biome, representing a different climatic regime from that under which the wetlands predominated (DiMichele *et al.*, 2008).

Our understanding of the dynamics of the vegetation during this time period must be framed by this intermittent appearance of peat forming and clastic wetlands during the Pennsylvanian, and through the middle–late Pennsylvanian transition.

Vegetational patterns

In abstract, the middle–late Pennsylvanian changes are these: middle Pennsylvanian wetland environments were dominated for over 9 million years by a complex of plants consisting, by the end of the middle Pennsylvanian, of numerous species and genera of arborescent lycopsids, seed ferns, cordaitalean seed plants, calamitean sphenopsids and marattialean tree ferns. During the middle–late Pennsylvanian transition, the dominance patterns in wetland vegetation changed dramatically throughout the European and North American equatorial basins. Well over half the species typical of middle Pennsylvanian wetlands went extinct, based on both adpression and coal-ball macrofossil data (e.g. DiMichele & Phillips, 1996; Blake *et al.*, 1999). In the late Pennsylvanian, tree ferns dominated most wetland settings (e.g. Falcon-Lang, 2006; Willard *et al.*, 2007); they were both diverse and abundant. On average seed ferns were subdominant, with only one major genus of lycopsid tree, *Sigillaria*, remaining as a significant element. Calamiteans continued to play a relatively minor role, as did cordaitaleans. This change did not happen in wetland basins of far eastern Pangaea, on the Chinese microcontinents, where middle Pennsylvanian type floras persisted until the later Permian (Hilton & Cleal, 2007).

The morphology and basic ecology of the wetland plant groups is reviewed in a number of papers (e.g. DiMichele & Phillips, 1994; Cleal, 2007).

During the latter part of the middle Pennsylvanian, in the coal basins of Euramerica, the flora of the wettest areas was dominated by many species of giant lycopsid trees belonging

Fig. 3 Changes in taxonomic composition of coal beds based on macrofossils preserved in coal balls during the middle–late Pennsylvanian transition. The boundary between the middle and late Pennsylvanian lies between the Danville and Bristol Hill Coals. Based on the data in DiMichele & Phillips, 1996.

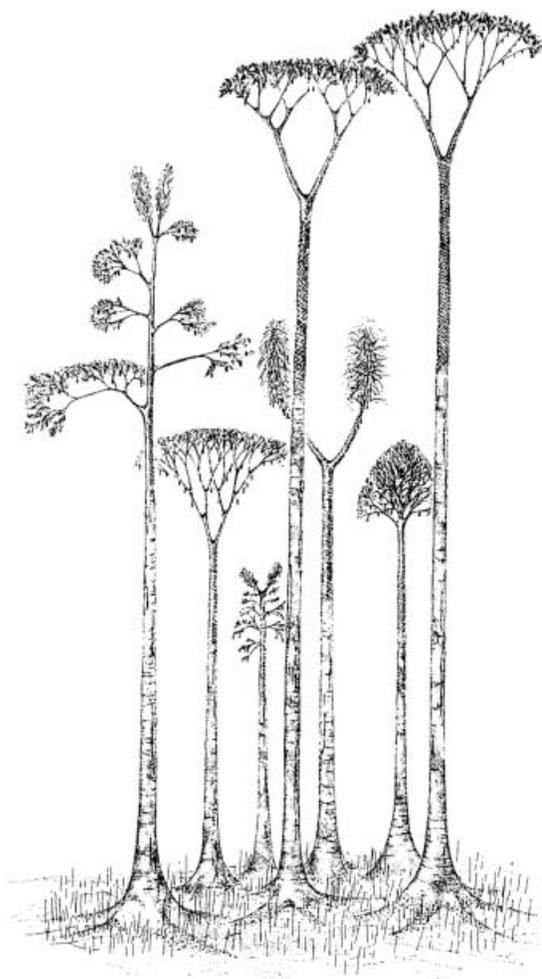


Fig. 4 Reconstructions of giant lycopsid trees. Left-to-right: *Diaphorodendron scleroticum*, *Lepidophloios hallii**, *Paralycopodites brevifolius*, *Synchronidendron dicentricum**, *Sigillaria approximata**, *Diaphorodendron phillipsii*, *Lepidodendron hickii**. All trees are shown in their mature, reproductive states and architectures. Those names above marked with an asterisk (*) are monocarpic, producing all cones in the crowns; the plants would have grown as unbranched poles until near the end of life when the crowns and accompanying reproductive organs were produced, followed by tree death. Reproduced from Bateman *et al.* (1992) Experimental cladistic analysis of anatomically preserved arborescent lycopsids from the Carboniferous of Euramerica: An essay on paleobotanical phylogenetics. *Annals of the Missouri Botanical Garden*, **79**, 500–599, reprinted with permission of the Missouri Botanical Garden Press.

to several genera – this group is extinct (Fig. 4). Lycopsid trees varied in height from several meters to over 40 m (Thomas & Watson, 1976). Intermixed to varying degrees with these trees, and dominating other parts of the wetlands on their own, were tree ferns belonging to the order Marattiales – this group is still extant but modern examples are not trees. Middle Pennsylvanian marattiales were relatively small trees compared to those of the late Pennsylvanian, which were much larger (Lesnikowska, 1989; Falcon-Lang, 2006). All were of extremely ‘cheap’ construction, the stems and roots consisting

largely of air spaces (Ehret & Phillips, 1977; Baker & DiMichele, 1997). Also locally abundant to dominant in clastic substrate wetlands, less so in peats, were medullosan seed ferns, a diverse group of trees, shrubs and vines (Pfefferkorn *et al.*, 1984; Krings *et al.*, 2003; DiMichele *et al.*, 2006a). Calamitean sphenopsids and cordaitalean seed plants also were present in lowland settings as less abundant components.

During the late middle Pennsylvanian the tree ferns underwent a gradual increase in abundance in lowland, wetland environments of all types. In clastic substrate settings they increased both within floras dominated by other groups of plants, and in their dominance of landscape patches (Pfefferkorn & Thomson, 1982; Peppers, 1997; Dimitrova *et al.*, 2005). In peat-forming habitats, tree ferns became generally more abundant, though this abundance appears to have been concentrated in assemblages of mixed species composition, probably not the wettest subenvironments within these settings (Phillips & DiMichele, 1981; Phillips *et al.*, 1985; DiMichele & Phillips, 1988; Peppers, 1996; DiMichele *et al.*, 2002). In addition, the patterns across Euramerica suggest that the proportion of tree ferns to lycopsids was strongly affected by local conditions, including water tables within accumulating mires (Dimitrova & Cleal, 2007), thus indicating regional variability that was to continue into the earliest post-turnover period.

In the late Pennsylvanian, tree ferns became the dominant elements during the wetter intervals of the climate/sea-level cycles in many kinds of lowland habitats of the equatorial region. Palynologic analyses of coal beds (e.g. Peppers, 1985, 1996; Willard & Phillips, 1993; Kosanke & Cecil, 1996) indicate that specific patterns of tree fern dominance varied greatly from coal to coal in the late Pennsylvanian, even though tree ferns as a group were dominant in peat-forming settings. Macrofossil coal-ball analyses (Phillips *et al.*, 1985; Willard & Phillips, 1993; Willard *et al.*, 2007) also indicate considerable variation in the particular tree ferns that were abundant in any given peat mire. Variability in tree-fern composition of mire forests also occurred in the late middle Pennsylvanian, but involved different tree fern species from those of the late Pennsylvanian (Mahaffy, 1988; Willard, 1993). Tree fern diversity in clastic wetlands during the late Pennsylvanian, as determined from adpression fossils, also was considerable (e.g. Knight, 1983).

The floristic changes detected in the Euramerican portion of the tropics do not occur in the far eastern regions in the Chinese microcontinents (Hilton & Cleal, 2007). The Chinese floras are dominated by arborescent lycopsids, cordaitaleans, and other groups similar to those from the middle Pennsylvanian of Euramerica, and also include other elements, such as Noeggerathiales (Pfefferkorn & Wang, 2007) in some deposits. The persistence of many elements of the middle Pennsylvanian wetland flora, similar at the taxonomic level of family and perhaps genus, in the eastern microcontinents probably reflects the persistence of wet conditions there across

the middle–late Pennsylvanian transition and beyond; certainly a threshold in environmental conditions was not crossed in the Chinese microcontinents. This will not be discussed further in this paper.

Structure of lycopsid versus tree-fern-dominated vegetation

As a final point, the basic architecture of middle and late Pennsylvanian wetland arborescent vegetation may have differed considerably. These differences could have had profound effects on the relationships between the vegetation and the local-to-regional climates. There is considerable evidence that large tracts of late middle Pennsylvanian lycopsid tree-dominated vegetation were extremely open, compared to what we think of as tropical forests today. This inference is based on two lines of evidence. (1) Morphologic studies suggest that many common and abundant giant lycopsids grew for most of their lives as unbranched poles, probably covered with leaves, adding the branched, so-called crown only in the final phase of determinate growth (Fig. 4). Appearance of the crown in these growth forms was associated with the end of individual tree life and the formation of reproductive organs (Andrews & Murdy, 1958; Eggert, 1961; DiMichele & Phillips, 1985; Phillips & DiMichele, 1992). Thus, the crown of these trees was not a light-intercepting device, and a treed landscape, which we hesitate to call a forest, could have, at stages, been composed of a mass of large poles. (2) Studies of the distribution of lycopsid tree stumps preserved in coal mines suggest such stands varied greatly in the amount of subcanopy, understory, or ground-cover vegetation associated with them, that the trees were effectively randomly distributed in space, and that in flooded environments they may have formed low diversity lycopsid-only stands (Gastaldo, 1986a,b; DiMichele & DeMaris, 1987; Wnuk & Pfefferkorn, 1987; DiMichele *et al.*, 1996; Gastaldo *et al.*, 2004). Consequently, large tracts of lycopsid-tree wetlands may have had exposed, unshaded surfaces, apparently flooded for much of the time. In contrast, post-change, late Pennsylvanian tree fern vegetation appears much more likely to have formed closed canopies (Fig. 5), at least in patches. For example, Falcon-Lang (2006) reports *in situ* tree fern forests with standing trees much more densely packed than has been inferred for lycopsid trees based on *in situ* tree stumps in the middle Pennsylvanian. Furthermore, morphologic studies of marattialean tree ferns (e.g. Morgan, 1959; Lesnikowska, 1989) show them to have had canopies of large fronds that likely shaded substrates (Fig. 6). However, tree-fern-dominated forests also are richer in vines and ground cover, suggesting open areas likely resulting from higher disturbance frequencies than in lycopsid-dominated vegetation.

Environmental conditions and changes

In many parts of Euramerica, there are distinct differences in the character of middle and late Pennsylvanian rocks, when similar stratigraphic increments of the inferred climate/



Fig. 5 Contrasting canopy structure between late middle Pennsylvanian and early late Pennsylvanian peat mire vegetation at approximately the same scale. Note the greater overall height, but much greater openness of the middle Pennsylvanian, lycopsid tree-dominated assemblage, with locally closed canopy patches comprised of tree ferns and pteridosperms. The late Pennsylvanian tree fern canopy is closed, with a few emergent lycopsids.

sea-level cycles are compared. The sea-level lowstand component of middle Pennsylvanian cyclothem is composed of highly weathered sands, siltstones and mudstones, including histosols, Fe-oxide nodule and rhizolith-bearing spodosols, ultisols and subordinate amounts of vertisols lacking carbonate (Cecil *et al.*, 1985; personal observations of the authors based on core and outcrop from the Donetz, Appalachian, and Illinois basins). The matrices of those gleyed spodosols and ultisols underlying coal beds, conventionally referred to as ‘underclays’, are Al-oxide- and kaolinite-rich with low base saturation, indicative of deep leaching under wet conditions (Montañez *et al.*, 2008a).

In late Pennsylvanian cyclothem, sandstone deposits are significantly less weathered and exhibit gleyed colors reflecting the presence of Fe-Mg-rich minerals. Coal beds (histosols) are fewer and less well developed. Reddened siltstones and mudstones reappear abundantly in the succession for the first

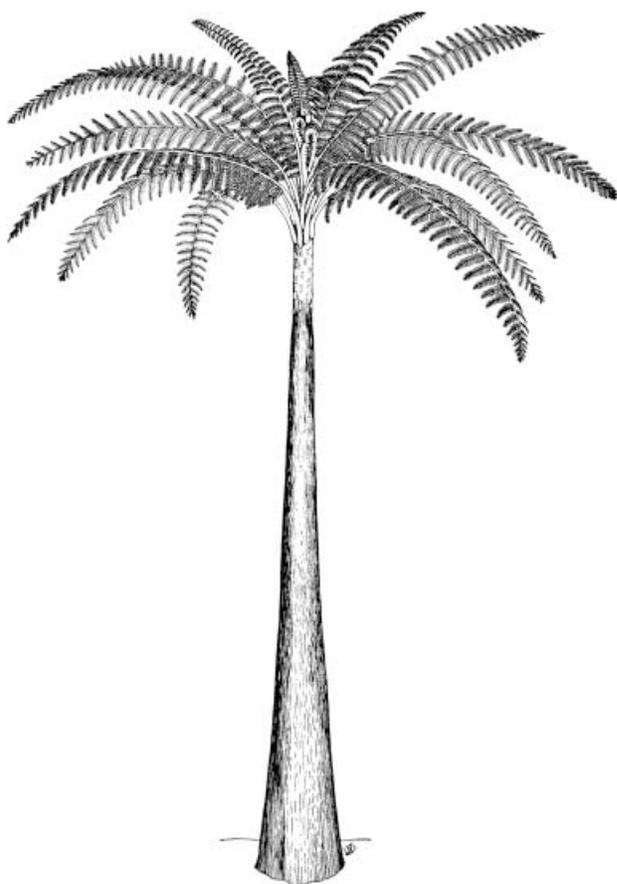


Fig. 6 Reconstruction of the marattialean tree fern *Psaronius*. Reproduced from Morgan (1959) The morphology and anatomy of American species of the genus *Psaronius*. *Illinois Biological Monographs*, 27, 1–108, reprinted with permission of the University of Illinois Press.

time since the upper Mississippian succession. Late Pennsylvanian paleosols exhibit macromorphologic indications of being better drained than those of the middle Pennsylvanian and are dominated by vertisols and calcic vertisols, and subordinate calcisols. Morphologic characteristics of these paleosols are clearly indicative of strong seasonality and a predominance of months when evaporation exceeded precipitation, including both well-developed vertic features (e.g. clastic dikes, slickensides, mukara subsurface bedding) and development of calcareous horizons (as carbonate rhizoliths and nodules), indicative of high evapotranspirative loss of moisture (e.g. Jenny, 1941; Arkley, 1963; Royer, 1999; Nordt *et al.*, 2006). There also is minimal pedogenic clay accumulation. Shifts in $\delta^{18}\text{O}$ values of pedogenic calcites and meteoric calcite cements in limestones within the same cyclothem indicate a significant drop in effective moisture across the boundary, presumably due to a decrease in precipitation. This suite of characteristics indicates formation of earliest late Pennsylvanian paleosols under strongly seasonally dry climates. Thus, overall, there appears to have been a geologically rapid shift in climate from

more humid conditions in the middle Pennsylvanian to moist subhumid-to-semiarid conditions in the late Pennsylvanian. Superimposed on this shift was the continuation of the shorter-term (10^4 to 10^5 year) climate/sea-level cycles recorded by individual cyclothem.

Notably, in the latest part of the middle Pennsylvanian, coal beds indicative of the wetter end-member of the climate cycles become progressively thinner and of lower quality, including increases in clastic partings, suggesting a reduction in the duration of climatic conditions favorable for peat formation. In North America this applies to the Appalachian Basin (Cecil *et al.*, 1985; Winston, 1990; Kosanke & Cecil, 1996), and the mid-continent regions of the Illinois and Western Interior basins (Kosanke *et al.*, 1960; Phillips & Peppers, 1984; Peppers, 1997). In the early late Pennsylvanian, coal beds continue to be thin and rarely of economic quality (the so-called 'Lower Barren Measures' in the Appalachians, see Condit, 1909). These facies trends indicate that initially sea-level lowstands within late Pennsylvanian short-term cycles (cyclothem) continued to be the most humid parts of those cycles, times at which peats formed, as has been inferred for the middle Pennsylvanian (Cecil *et al.*, 2003). Effective moisture during interglacials appears to have been significantly lower, however, than during middle Pennsylvanian interglacials, and precipitation more seasonal. Note, however, the suggestion of Olszewski & Patzkowsky (2003) that during the latest late Pennsylvanian (Virgilian–Gzhelian) the wettest periods may correspond to high stands of sea-level (interglacials?).

The record of sea-level changes in the equatorial regions during the middle–late Pennsylvanian transition (Rygel *et al.*, 2008; Bishop *et al.*, in review) indicates a reduction in the amplitude of cyclothem-scale, sea-level fluctuations in the late Pennsylvanian possibly associated with an overall global high-stand of sea-level (Haq & Schutter, 2008). This is broadly consistent with findings in the Gondwanan record of significant reduction in the volume of polar ice during the later middle Pennsylvanian and into the late Pennsylvanian, possibly even the elimination of polar ice caps (Fielding *et al.*, 2008a,b).

The ultimate driver of these long-term changes is unknown. Suggestions include the rise/fall of the Central Pangaea Mountains (Ziegler *et al.*, 1997; Otto-Bliesner, 2003) or development of a mega-monsoonal climate (Kutzbach & Gallimore, 1989; Kessler *et al.*, 2001). However, the wide geographic breadth of climate and vegetation changes across equatorial Pangaea, and their relatively abrupt transition between states, require a driver with broader impacts and faster response times. Both modeling studies (Poulsen *et al.*, 2007) and empirical studies (Montañez *et al.*, 2008a) point to CO_2 as a primary cause, although several factors may have contributed (Cleal & Thomas, 2005; Peyser & Poulsen, 2008; Tabor & Poulsen, 2008). Significantly, evidence exists for a relatively rapid shift from humid to semi-arid–arid conditions in the Paganzo Basin, northwestern Argentina at the end of

the Moscovian (Gulbranson *et al.*, 2008), suggesting that the tropical drying trend may have extended to higher latitude southern Gondwana. Climate simulations for a range of atmospheric $p\text{CO}_2$ and ice volume on southern Gondwana suggest CO_2 -forcing of drying across the middle–late Pennsylvanian transition (Poulsen *et al.*, 2007; Montañez *et al.*, 2008a). These emerging proxy records come from throughout Pangaea and point to a mechanistic link between ice-volume, sea-level amplitudes, precipitation levels and atmospheric $p\text{CO}_2$. In other words, when inferred $p\text{CO}_2$ goes up, ice appears to disappear at higher latitudes (Fielding *et al.*, 2008a), the amplitude of high-frequency sea-level events goes down (significantly) (Heckel, 2008; Rygel *et al.*, 2008; Bishop *et al.*, in review), and continental effective moisture is significantly reduced.

Working hypotheses

The middle-late Pennsylvanian vegetational change appears to be an ‘intra-biomic’ event. That is, the vegetational changes involve evolutionary lineages (clades) that have their ecologic centroids in physically similar wetland habitats, particularly those that existed under humid conditions. As such, it was a state change from vegetation type A to vegetation type B, both of which, in modern terms, might be referred to as having an evergreen-broadleaf physiognomy (e.g. Woodward *et al.*, 2004; though this appellation might not fit exactly to Pennsylvanian vegetation – see comments by Johnson (2007) and DiMichele *et al.* (2009) on use of the term ‘rainforest’ for Pennsylvanian-age vegetation).

Wetland habitats of the late middle Pennsylvanian saw a rise in weedy species of tree ferns, both interstitially and as dominants of parts of the landscape, possibly in response to changing physical conditions brought about by rising atmospheric CO_2 and warming global temperatures. Such changes suggest somewhat more seasonality during the wettest parts of climate cycles, resulting in dominantly planar peat-forming environments, increasing vegetational patchiness, and greater physical disturbance. The more seasonal climate periods, which predominated between the wetter climatic intervals, also began to become progressively drier. This indicates an average shift of global tropical climates to greater seasonality at all phases of climate/sea-level cycles, whatever the average yearly rainfall at that part of the cycle.

A large change in dominant vegetation occurred across the middle–late Pennsylvanian boundary, contrasting with the relatively stable coal bed-to-coal bed patterns of the late middle Pennsylvanian. This change appears to have been accompanied by a significantly greater overall shift of the extremes of the climate spectrum than that of the later middle Pennsylvanian to still greater seasonal dryness. The reappearance of peat-forming environments within each cycle, however, indicates that climate cycling remained and included conditions wet enough for the formation of thick peats. Early late Pennsylvanian rocks appear to record a greater range of

climatic variation within any given climate/sea-level cycle than in the late middle Pennsylvanian.

Thus, both sides of this middle–late Pennsylvanian boundary are marked by repeated appearances of wetlands, and within each the (different) vegetational structures were remarkably persistent, returning with each reappearance of basinal wetland habitats (e.g. DiMichele *et al.*, 1996; Pfefferkorn *et al.*, 2000; DiMichele *et al.*, 2002; Cleal, 2007). Despite the rises and falls of sea-level and associated changes in climate in the lowland basins, the vegetation characteristic of the middle Pennsylvanian or late Pennsylvanian wetlands returned over and over again for millions of years. The period of disruption during the middle–late Pennsylvanian transition acts as a separator. Many lines of evidence indicate that lycopsid-rich vegetation (mixed with tree ferns and pteridosperms) disappeared from the basins during what would seem to have been just another in the long series of wet-dry, glacially driven oscillations. What returned in its place, however, during the wettest interval of the next cycle of peat accumulation, was a new order, dominated by tree ferns and pteridosperms, with lycopsids represented only by a paltry selection of sigillarian lycopsids.

We consider four conceptual models to explain this change (Fig. 1). These are based on the models presented graphically in Scheffer *et al.* (2001), and subsequently modified in Scheffer & Carpenter (2003), Foley *et al.* (2003) and Gordon *et al.* (2008). (1) A gradual change from vegetation type A to vegetation type B during which there is significant mixing of species. (2) A threshold-type regime shift from type or state A to B, which happens rapidly once a certain set of conditions is crossed during a directional environmental change. (3) A threshold-type regime shift involving multiple stable states with hysteresis in which more than one vegetational state can exist under a given set of conditions, though not simultaneously. In this latter case, if the change is reversible, the state A-to-state B threshold will lie at a different point in climate space than a state B-to-state A shift. (4) A multiple stable state system involving an irreversible change of state.

We reject model (1) as a possible explanation. The vegetational patterns show an abrupt change in composition that does not track the inferred more gradual changes in atmospheric composition and changing moisture regimes. Temporal resolution of the vegetation through this interval is good (e.g. Peppers, 1997). And the vegetation of the middle Pennsylvanian differs vastly in species composition from that of the late Pennsylvanian, including major changes in the lycopsids (DiMichele & Phillips, 1996), which disappear as dominants, and different tree ferns (Lesnikowska, 1989; DiMichele & Phillips, 1996; Peppers, 1996; Blake *et al.*, 1999) and pteridosperms, which rise to positions of dominance. In addition, the character of the vegetation in the late Pennsylvanian is very different from that of the middle Pennsylvanian in terms of the numbers and diversity of climbing plants and ground cover, changes that were not occurring gradually during the later middle Pennsylvanian (Krings *et al.*, 2003).

Consideration of the threshold models requires rejection of a large stratigraphic gap as the cause of the great vegetational differences between the middle and late Pennsylvanian. Correlations based on conodonts and cyclothem stratigraphic relationships between the American mid-continent, Appalachians, and eastern Europe, do not support an interval of extensive missing time in the North American geologic section, as has been asserted (Wagner & Lyons, 1997; Wagner, 2004), based mainly on plant fossil occurrences. Paleobotanical patterns in the Appalachians (Blake *et al.*, 1999) and the mid-continent (Peppers, 1997) indicate a nearly continuous record of sedimentation across the middle–late Pennsylvanian boundary. In the North American mid-continent coal basins, the time hiatus represented across this boundary does not appear to be detectably different from that found between other coal beds within typical cyclothem sequences. Although a paleosol is present, there is no indication of significant downcutting, which might be expected if there were lowered sea-level and a long temporal hiatus in deposition on the craton.

Model (2) is a one-way threshold response in which the vegetation potentially could reverse its state were the driving physical conditions to reverse. This model must be viewed as unlikely, given that wetland conditions suitable for the development of peat-forming and humid floodplain vegetation are present in both the middle and the late Pennsylvanian. Thus, as far as we can resolve the environmental component, the late Pennsylvanian wetlands represent a return to physical conditions similar to those of the late middle Pennsylvanian, but without a return to the earlier type of vegetation. In this case, it could be argued that middle Pennsylvanian-type vegetation persisted outside of the region (it did – in China), or in a fragmentary, marginalized state within the region, but that wetland conditions in Euramerica were, in fact, different from those of the late middle Pennsylvanian in ways that we have been unable to resolve at present.

There are significant taxonomic compositional differences between middle and late Pennsylvanian wetland floras. These floras also differed in structure as well as in composition. That of the middle Pennsylvanian not only contained the bizarre lycosid pole forests, but was highly heterogeneous spatially. Several different kinds of plant associations have been identified within peat-forming landscapes and there are regional differences across Euramerica in the vegetation (Cleal, 2007). In addition, the peat-substrate and clastic-substrate floras were distinct at a variety of levels. In some instances, for example, such as the lycosid trees, different species and even some genera may have characterized the different kinds of wetlands, perhaps reflecting differences in nutrient conditions (Willard, 1989a,b). In other instances, the representation of pteridosperm foliage for example, the suite of species reported from peat-forming vegetation (based on coal balls) is a lower diversity subset of that known from adpressed foliage, where the diversity of pteridosperms was much higher (see citations in DiMichele *et al.*, 2006a). In

contrast, late Pennsylvanian peat-forming environments and those of clastic-substrate wetlands were significantly similar in many ways. Marattialeen tree ferns of many different species dominated much of both kinds of settings and the surviving lycosids were the same in both (basically *Sigillaria brardii*). And earlier late Pennsylvanian vegetational structure, as mentioned above, also differed in a variety of ways from that of the middle Pennsylvanian in many habitats.

A final bit of data that might be seen as consistent with, if not definitive of, this one-way model is the period of high compositional variance in wetland vegetation between successive intervals of recurrence during the earliest late Pennsylvanian. This implies a return of environments suitable for occupancy by wetland plants, but a regional absence of the former occupants. Thus, the system took perhaps as many as 300 000 to 1 million years and several orbital cycles of environmental/climatic/sea-level fluctuations for the new, dominant vegetation type to become emplaced.

Model (3) is very similar to model (2) in that it requires crossing a threshold, likely of an environmental nature. The major difference between these latter two models is the presence in model (3) of different threshold points for the transitions from state A to state B and the reverse. Why consider this model? It is clear that in the late Pennsylvanian, physical conditions conducive to the development of wetlands returned periodically in a manner similar to that occurring during the early and middle Pennsylvanian. In addition, these conditions were sufficient to support vegetation composed of plants similar in basic evolutionary affinity to those that dominated later middle Pennsylvanian wetlands. Furthermore, within the equatorial tropics, in far eastern Pangaea, there continued to exist wetlands populated by plants and vegetation similar in many ways to that of the middle Pennsylvanian (Hilton & Cleal, 2007) – thus, populations existed from which restocking of the late Pennsylvanian wetlands could have taken place.

It can be argued, in favor of model (3), that despite redevelopment in the late Pennsylvanian of conditions presumably suitable for many middle Pennsylvanian-type wetland plants, the dominant elements failed to return from potential source areas. One possibility for this is the fragmentation of wetland landscapes in the Variscan region of Europe (Oplustil & Cleal, 2007). The shrinkage of wetlands, the demise of paralic swamp habitats, and the separation of wetlands into small, isolated basins, would have presented a significant barrier to the back migration of displaced middle Pennsylvanian floral elements. Another potential explanation is incumbency of the standing vegetation, which may be one of the underlying reasons for different threshold points. Occupancy being 9/10 of the law, conditions would have to change sufficiently to dramatically reduce the ability of the incumbent vegetation to replace itself. In this instance, a significant increase in climatic wetness and long-term flooding would have been required to suppress tree-fern recruitment and favor the penetration of a

diverse array of lycopsid trees from distant areas such as the eastern equatorial regions. In a world of reduced ice volume, the tropical belt would have witnessed a general reduction of precipitation, and thus of long-lived wetland corridors, in all parts of the long-term climate cycle. Under such generally drier climates the lycopsid-rich vegetation may not have been able to replace or displace the tree ferns.

The irreversible model (4) cannot be rejected as a potential explanation. It is possible, given the scenario above, that the shift to tree fern and pteridosperm dominated vegetation could not have been displaced at all by vegetation similar to that of the late middle Pennsylvanian. There is much we do not understand about environmental or biologic dynamics in the long term, due to the nature of the geologic record, especially the lack of preservation of fossils outside of basinal areas. Consider, for example, that the drier end of late Pennsylvanian climate/sea-level cycles was considerably drier than a similar point in the climate curve in late middle Pennsylvanian cycles, as evidence suggests. Under such conditions, it may have been impossible for the lycopsid-rich vegetation, tied strongly to wetlands, to survive in spatially diminished and disconnected local refugia during the dry, inter-peat-formation periods. Similarly, the opportunistic life histories of tree ferns, with their massive spore production and attendant colonization potential, may have made it impossible for plants with larger, water-borne propagules, such as the giant lycopsid trees, to recover as quickly when wetlands returned in abundance. Irreversibility also could result mostly as a simple matter of population sizes. Once tree ferns became established in large numbers, and if relative proportions of major groups stayed roughly constant during drier periods of population shrinkage, each group would have recovered in approximately the same proportions during the return of wet periods, from one climate/sea-level cycle to the next (which fits certain aspects of the neutral model of Hubbell [2001]). Without another major environmental disruption of some type, this system would have certain self-maintaining qualities.

In all of these models, but particularly model (3), we continue to face the problem of where the wetland vegetation hides when it is not dominant in the basinal lowlands. If it disassembles into isolated refugia during the drier intervening intervals, then a model in which the effects of incumbency are important and in which there are one or more threshold points separating different kinds of wetland vegetation from dominance gains further appeal.

Case study 2: The Pennsylvanian–Permian transition

Vegetational patterns

Wetlands are abundantly represented in the basinal lowlands of the Pennsylvanian – thus the moniker ‘coal age’, reflecting the abundant deposits of peat that formed during that time. However, over the same time period, the basinal lowlands or their margins (depending on the extent to which the sea

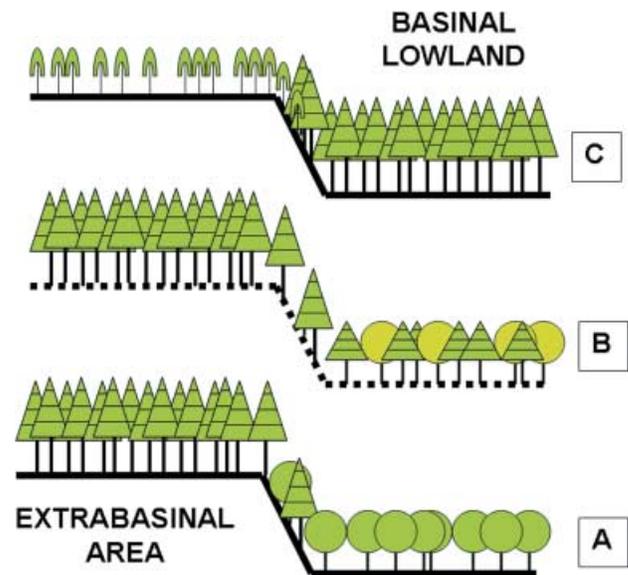


Fig. 7 Space-time transitional dynamic relationship between three distinct biomes – species pools in the late Paleozoic tropics. (A) Humid–perhumid climate in the basinal lowlands. Wetland vegetation dominates, with occasional preservation of allochthonous plant remains from the nearest extrabasinal areas. (B) Transition from humid climate to seasonally dry climate in the basinal lowlands. Extrabasinal elements move into the basin as recruitment begins to decline for formerly dominant wetland elements. (C) Seasonally dry climate in the basinal lowlands. Formerly remote vegetation now dominates lowlands, with occasional preservation of allochthonous elements from yet another vegetation type, attuned to yet more moisture-stressed conditions.

extended onto the craton) were also home to vegetation of an entirely different morphologic character and taxonomic composition, plants typical of seasonally moisture-limited climates. These two vegetation types (or more – there likely was more than one kind of seasonal-climate vegetation) occupied the basins at different times in the covariant ice/sea-level/climate cycles that characterized the Pennsylvanian and Early Permian (Fig. 7).

The type of seasonally dry vegetation that eventually came to prominence in the basinal lowlands of the Permian – one rich in conifers and other kinds of seed plants – appeared at the margins of equatorial basinal lowlands as early as the middle Pennsylvanian (Scott & Chaloner, 1983; Galtier *et al.*, 1992; Plotnick *et al.*, 2008). Most of these early occurrences are allochthonous macrofossils or pollen, and entirely conifers, probably transported in from surrounding upland areas (Lyons & Darrah, 1989; Zhou, 1994; Peppers, 1997). In rare cases, the fossil material seems to have been captured in place by unusual preservational circumstances (e.g. in sink holes on a karst landscape at the basin margin – Plotnick *et al.*, 2008). In contrast, late Pennsylvanian, conifer-rich floras fully occupied parts of the basinal lowlands and are preserved as typical parautochthonous adpression assemblages (there are many examples of these – see Broutin *et al.*, 1990, and

DiMichele & Aronson, 1992; a few of the more well-characterized deposits from western Pangaea, all of which are Missourian in American terminology [early late Pennsylvanian], are the 7–11 flora of Ohio [McComas, 1988], the Garnett flora of Kansas [Cridland & Morris, 1963], the Hamilton Quarry flora of Kansas [Rothwell & Mapes, 1988], and the Kinney Quarry of New Mexico [Mamay & Mapes, 1992]).

What kind of vegetation was this and how does it compare and contrast with that of humid–perhumid conditions? The tropical plants typical of seasonally dry climates might be characterized broadly as a mixture of broadleaf evergreen, broadleaf deciduous and needleleaf evergreen (in the terminology of Woodward *et al.*, 2004, for modern vegetation). Even the needleleaf trees, walchian conifers, bore plagiotropic lateral branches (Hernandez-Castillo *et al.*, 2001), which they appear to have shed in much the same way that broadleaf evergreen plants shed long-lived compound leaves. All of the broadleaf taxa, callipterids, taeniopterids, comioids, gigantopterids, and supaioids, appear to have been deciduous. However, it is not certain that this deciduousness was seasonal, and in some instances almost certainly was not (given thick woody tissue in the petiole bases of the leaves of some taxa – e.g. Chaney *et al.* 2009). Many of these plants had compound leaves, but of sizes considerably smaller and of heavier construction than the large fronds of medullosan pteridosperms or marattialean tree ferns that dominated most wetland vegetation. The conditions under which this ‘new’ flora flourished certainly were not extremely dry, although its elements probably exhibited a range of drought tolerance and most were more tolerant than the dominant plants of the equatorial lowland coal swamps.

There was little compositional overlap at the levels of species or major clades between the wetland and seasonally dry floras. The two floras are intercalated within the lowlands of the late Pennsylvanian, occurring in different horizons from different times, even on the fine scale of single outcrops, where they may occur in separate beds (Kerp & Fichter, 1985; DiMichele *et al.*, 2005b). This long transitional interval ended in the Early Permian when wetland vegetation greatly contracted, and reappeared only during momentary expansions, perhaps during brief pluvial periods (Montañez *et al.*, 2007; Rhodes *et al.*, 2007). Aside from these brief pluvial intervals, the seasonally dry vegetation dominated Permian basinal lowlands throughout the Euramerican part of Pangaea (Kerp, 1996; DiMichele *et al.*, 2006b).

It is difficult to determine which of these vegetation types was more common in the equatorial lowland basins over time. This is especially true during the late Pennsylvanian, where peats and typical wetland plant assemblages are well preserved in fossil deposits, but the seasonally dry flora, though less commonly found, is preserved in many deposits. Basinal paleosols of the later Pennsylvanian indicate much drier conditions than those of the middle Pennsylvanian, including calcic Vertisols that may reside immediately beneath coal beds, suggesting strong climatic oscillation. The floras that occupied

these paleosols, sometimes represented by deep, straight roots, are suggested to be large trees, possibly cordaitalean or coniferous seed plants (based on the rooting morphologies and the composition of seasonally dry macrofloras from the same time interval). Based on such lines of evidence, it seems quite possible that seasonally dry vegetation could have occupied basinal lowlands for longer periods of time than the wetland vegetation of humid climate periods, especially during the late Pennsylvanian.

In western-most Pangaea, the final disappearance of widespread, humid, wetland vegetation appears to have occurred very rapidly. In north-central Texas (Montañez *et al.*, 2007; Tabor *et al.*, unpublished data) (Fig. 8) and in New Mexico (DiMichele *et al.*, 2004, 2007), there is a very short interval of interdigitated or mixed floras that is followed by (i.e. overlain by) complete dominance of the lowlands by seasonally dry vegetation, a pattern that persists (based on current stratigraphic understanding) through the Sakmarian. Wetter elements begin to reappear in the early Artinskian, in mixed to entirely distinct floras, possibly representing pluvial intervals, within rocks that otherwise contain seasonally dry plant assemblages. In a sense, this is the opposite of what was seen in the late Pennsylvanian; in the early Artinskian, the seasonally dry flora predominates in the fossil record, with occasional, scattered occurrences of the wetter flora.

Timing of the transition

The Pennsylvanian–Permian boundary is poorly defined in a string of terrestrial basins that stretch across equatorial Pangaea, which has led to continued debates about correlation, the ages of rocks, and the significance of various kinds of fossil data. These include east-central New Mexico (Lucas *et al.*, 2002), north-central Texas (Hentz, 1988; Montañez *et al.*, 2007), the Dunkard basin of the Appalachians (Barlow, 1975; Wagner & Lyons, 1997; Blake *et al.*, 1999), and the Rotliegendes of Germany and Britain (Kerp & Fichter, 1985). Within each basin there is an excellent lithostratigraphic framework and high fidelity correlation. Thus, it is possible to link biologic and physical patterns, such as proxies for climate variables, at the basinal scale. The basic pattern of change is the same in all of these basins. However, the timing of biotic, lithostratigraphic and geochemical changes is not clearly correlated between basins, and there are several reasons to believe that this will remain refractory. Even though the climatic events or shifts were likely to have been synchronous, these changes may have been manifested differently, in terms of climatic effects, due to regionally unique conditions (elevation, degree of continentality, latitude, etc.). Consequently, vegetational responses would have varied across the Pangaeian equatorial region (Montañez *et al.*, 2008b; Tabor & Poulsen, 2008).

The major points are these: (1) The plants are facies controlled, and the facies strongly reflect the climates under which they accumulated. Thus, we can presume that the plants were tied strongly to climate, as they are today. This limits

peat formation varies, being generally less in the first half of the late Pennsylvanian and becoming greater in the second half (e.g. the massive, latest Pennsylvanian age Pittsburgh coal bed of the central Appalachians, Repine *et al.*, 1993). Thus, the wetter parts of cycles may have been getting wetter, or lasting longer, through the late Pennsylvanian due to some combination of climatic amelioration and the return to glacial conditions in the latest Pennsylvanian (Isbell *et al.*, 2003; Fielding *et al.*, 2008a; Montañez *et al.*, 2008a).

The volume of grounded ice in the Southern Hemisphere may have been significantly reduced in the early part of the late Pennsylvanian (Fielding *et al.*, 2008a; J. Isbell, pers. comm. 2008). Thus, glacial drivers of sea-level and climate change likely were significantly reduced at this time, as recently suggested (Bishop *et al.*, in review), raising the question of what was driving cyclic patterns of sedimentation. During the early Pennsylvanian and through most of the middle Pennsylvanian, these climate oscillations were driven mainly by glacial–interglacial cyclicity. Short-term sea-level fluctuations are not necessarily driven exclusively by the dynamics of ice sheets or continental glaciers, however. Sea-level fluctuations of 5 to 10+ m may occur on the 10⁵- to 10⁶-year scale in response to filling and draining of continental reservoirs (Jacobs & Sahagian, 1995). The progressive accretion of Pangaea also could have had an effect on global sea-level – albeit at much longer timescales ($\geq 10^6$ year) through thermal buoyancy and associated tectonic isostasy, which would have been accompanied by withdrawal of inland seas from large parts of the craton, factors independent of ice volume. The timescales on which such tectonic processes operate, however, are much longer than those of orbitally driven glacioeustasy, thus rendering them (tectonic processes) unlikely candidates for driving short-term stratigraphic stacking and inferred periodicity.

Short-term climate oscillations are superimposed on a longer term trend of drying in equatorial Pangaea during the later Pennsylvanian and Early Permian (Cecil *et al.*, 1985; Montañez *et al.*, 2007). This trend led to the dominance of the seasonally dry floras that predominate in most of western and central Pangaea until the end of the Permian (Schweitzer, 1986). This drying may have been driven by a combination of long-term changes in atmospheric CO₂ and changes in polar ice volume (Peyser & Poulsen, 2008). These underlying drivers affect the strength of the Hadley circulation cells near the equator, with strongest effects in the southern hemisphere. Proximate effects on wind patterns (Tabor & Montañez, 2002; Soreghan *et al.*, 2008) control the distribution of moisture in the western parts of the Pangaea, where this vegetational shift is most pronounced and happens most abruptly (Tabor *et al.*, unpublished data).

Working hypotheses

The oscillation between vegetation typical of humid and seasonally dry conditions can be evaluated in terms of the same

models applied to case study 1. In case study 2, however, the vegetation types represent different biomes growing under very different kinds of prevailing climate. The four models are (1) a gradual change from wetland to seasonally dry vegetation, (2) a threshold response from wetland to seasonally dry vegetation, (3) a threshold response with hysteresis, implying that there are climatic conditions under which either vegetation type could exist, and (4) an irreversible threshold response from one state to the other. There is no reason to consider an irreversible threshold model (model 4) because these two vegetation types clearly demonstrate repeated spatial replacement over a long time interval. In fact, the Pennsylvanian–Permian transition is simply one instance of the oscillatory replacement of wetland by seasonally dry vegetation, or vice versa, perhaps the most exemplary and clearly developed, but still one of many in the late Pennsylvanian through Middle Permian.

Unlike the intrabiomic vegetational restructuring that occurred at the middle–late Pennsylvanian boundary, the wet–dry vegetational transition involves a spatial change of plant species on the landscape, much like that documented following Pleistocene deglaciation in the north temperate zone. Thus, at some scale of space and time, model (1) is possible, as plant range zones change. Some compositional overlap between these two vegetation types has been documented during transitions from one type to the other near the boundary (Tabor *et al.*, unpublished data), and in several, short-term examples of oscillations between these two vegetation types later, in the Artinskian/Early Permian of north-central Texas (Rhodes *et al.*, 2007). In light of the fact that individual plants cannot ‘pickup and move’ like vagile animals, spatial changes in vegetation driven by climatic change involve propagule dispersal, the differential establishment and growth to maturity of juveniles (recruitment), and the differential death of adult plants. These are the factors that affect changing distributions at the most fundamental level – on the ground, so to speak. In such instances there nearly always will be an overlap between some remnant of the prior vegetation and the incoming elements of the new. This was described for pluvial intervals during the Pleistocene of the American Southwest as ‘vegetational inertia’ (Cole, 1985). In this scenario, as climate changes, plants of the indigenous vegetation at a local site undergo progressively declining recruitment while, at the same time, new species, more suited to changed climatic conditions, move in around them. Depending on the life spans of the prior occupants, there will be a variable period of overlap of the two vegetation types. In such a scenario, physical climate change is a strong independent driver, with the vegetation mainly responding to climate changes.

Indeed, in a transitional pattern of this kind, the two forms of vegetation really are little more than ships passing in the night. Whereas there may be overlap for some period of time during the change from one climatic end point to the other, such overlap will generally be brief and transitory, forming what might be considered a non-analogue vegetation relative

to the most commonly represented states (Overpeck *et al.*, 1992; Williams & Jackson, 2007). The vast majority of known examples of these kinds of vegetation indicate strong differentiation between them. Through millions of years, at each reappearance in the fossil record during the Permian, the Euramerican tropical wetland flora becomes ever more depauperate in terms of species richness. And when it appears, it is mainly represented by weedy opportunistic species, such as tree ferns (DiMichele *et al.*, 2007).

Models (2) and (3) involve a threshold-like state change from wetland to seasonally dry vegetation. There certainly seems to be some sort of threshold involved in this transition, indicated by the very limited compositional overlap between the two types of floras and their dominance under different kinds of physical conditions, according to proxy climate indicators. These two discrete floras constitute different biomes, with considerably different vegetational structure and phenology, and probably stature and degree of canopy openness. Most biome boundaries in the modern world are defined by ecotones of varying width, in which there can be some overlap in composition. However, due to the fairly sharp climatic breaks created by atmospheric dynamics (Ziegler *et al.*, 2003), vegetation also will tend to reflect those physical patterns. A threshold-like response does not preclude some limited overlap as described above.

If model (2) is applied, invoking a simple reversible threshold response, there does appear to be a climatic breakpoint, probably related to moisture availability and its seasonal distribution. Wetland, broadleaf evergreen vegetation exists on one side of this threshold, seasonally dry evergreen needleleaf and evergreen broadleaf to broadleaf deciduous vegetation on the other. It appears to have been possible, based mainly on the patterns of oscillation between these vegetation types during the Pennsylvanian, to reverse local and regional dominance.

Model (3) involves a threshold response with hysteresis, in which the climatic conditions under which a change from one state to the other lie at different points in the continuum of moisture availability and temperature depending on whether the transition involves wet-to-dry or dry-to-wet. In such a case, there would be a range of physical conditions under which either vegetation type could exist locally, though not together in the same landscape mosaic. Modern examples of this kind of dynamic, especially involving switching between biomes, are most likely in environments with extreme climates, such as a desert (e.g. Foley *et al.*, 2003) or in snow-covered sub-polar regions (Chapin *et al.*, 2005; Foley, 2005). Multiple stable states have been argued to exist on a smaller scale of structural difference between end members in a variety of settings including temperate grasslands (Baker & Walford, 1995; Seabloom & Richards, 2003), marshes (Dong *et al.*, 2002), and a variety of marine environments (Knowlton, 2004; Petraitis & Dudgeon, 2004, 2005; Petraitis & Methratta, 2006), including reefs (Knowlton, 1992; Aronson *et al.*, 2004). We cannot rule

out this type of response. However, the occasional overlap of elements of wetland and seasonally dry vegetation suggests that if there were a range of conditions compatible to both, it was narrow and frequently involved some sort of floristic overlap, a pattern more consistent with the simple threshold type (2) model.

In any of these scenarios, the potential for positive feedbacks in this system is considerable, though the effects will be manifested locally, likely accelerating vegetational change put in motion by broader climatic effects. The gradual fragmentation of evergreen broadleaf vegetation will reduce latent heat effects and thus moisture transfer to the atmosphere, reducing rainfall. The percentage of insolation reaching the ground also will increase. Such changes should increase the extent of heating of the soil surface, and increase sensible heating of the atmosphere, resulting directly in surface drying, and indirectly by reducing the effects vegetation will have on rainfall enhancement. All such effects will facilitate the change of local vegetation to one characterized by broadleaf deciduous and needleleaf evergreen architectures and phenologies.

Looking specifically at the Pennsylvanian–Permian transition, the data suggest that the biologic changes are ‘driven’ by the physical changes with which they can be correlated (e.g. Montañez *et al.*, 2007). The plant response most likely reflects changes in regional temperature and in rainfall abundance and distribution, changes likely radiatively forced by large fluctuations in atmospheric $p\text{CO}_2$. The initial trigger to the vegetational change was likely extrinsically driven by changes in physical conditions. Once these changes were set in motion, once a positive inertia was established, changes in the vegetation, such as canopy openness, relative amount of evapotranspiration, and so forth, may, in turn, have impacted many components of the physical system leading to positive feedbacks on drying and warming.

Taken to its logical extreme, we suggest that the climate–plant relationship we document in case study 2 may have occurred to some degree during each transition from wetter to more seasonally dry periods throughout the middle and late Pennsylvanian and Early Permian in response to climate/sea-level cycles. Thus, the Permo–Carboniferous transition is but one, particularly dramatic example of this dynamic. On top of this, the climatic mean may have been shifting progressively to drier during this time, particularly in the Euramerican portion of the equatorial region. These dynamics may have ended in Middle Permian time when the overall increase in tropical aridity throughout central and western Pangaea brought about the demise of many of the vegetation types involved in these transitions.

DISCUSSION

We have focused on framing, in terms of models developed on the basis of modern systems, vegetational change during times of major climate change in the deep past. This has been done

with an acute awareness of the distinct differences between the late Paleozoic and the present. For example: (a) The existence of the Pangaeon supercontinent and (b) the unique climatic consequences thereof. (c) The enormous areas of low lying continental surfaces leading to the development of vast, shallow seas. (d) Vegetation different in taxonomic composition and, to some degree, structure from that of today. Even so, there also are important similarities between the late Paleozoic and the modern world, the most significant of which is a shared cold-earth (icehouse) climate, with the attendant cycles of glacial waxing and waning of different magnitudes (considered in both case study 1 and 2, though from different perspectives). The Paleozoic also offers several examples of complete transitions from ice-dominated periods of glacial–interglacial cyclicality to possibly ice-free times of global warming, one of which we examined here (case study 1), and times of the rapid and extensive onset of ice from extended times of warm conditions (case study 2). Thus, the glacial earth of the Paleozoic offers an excellent, and in fact unique, point of comparison to the modern world.

The times of vegetational change discussed here were identified completely independently of changes in the physical environmental proxies with which they correlate closely, including indications of changing atmospheric CO₂, sea-level fluctuation and extent, and climatic data inferred from morphologic and chemical analysis of paleosols, coal quality data, and data on coal resource abundance. Linkage of patterns of change in climate proxy and biologic data to climate models has further tied all these together into a large-scale framework. In this study we have not attempted to use climate models experimentally to force certain kinds of vegetational changes and thus assess their likelihood or even their possibility, but such models nonetheless closely underpin our understanding and interpretation of the physical changes and the potential for vegetation–climate feedbacks.

The explicit ecologic models considered here emerged from conceptual and experimental studies of alternative stable states in natural ecosystems (Lewontin, 1969; Sutherland, 1974) and have recently received growing attention and application. They are general enough in scope and construction to have been applied to many kinds of ecosystems, terrestrial and marine, composed of many different kinds of organisms and ranges of interactions. At this time, at least, we believe they are encompassing enough to use as the explanatory universe, though we are cognizant of the best-of-field possibility. We have not included, for example, the potential role of natural selection; considerable evolutionary opportunity could have accompanied the release of resources associated with environment disruptions and extinction (such as that at the middle–late Pennsylvanian transition). We will address this below.

The models for vegetational response to changing environmental conditions offer a comparative framework against which empirical data can be evaluated. Several outcomes are possible, recognizing that the fossil record has many limitations

that must be considered. For example, much information about vegetational dynamics on the landscape scale is hidden from us in the terrestrial fossil record. Consider the persistence of a middle Pennsylvanian-type flora in China into the Permian, or the repeated ‘disappearance’ and ‘reappearance’ of the wetland vegetation in the basinal lowlands as sea-level and climate fluctuated (where did it go?), or the initially spotty occurrence of seasonally dry vegetation in basinal lowlands between peat-forming periods, telling us it was ‘out there’ somewhere beyond our sampling window (a pattern we see elsewhere in the record when vegetation types adapted to yet drier conditions make their incursions into basinal lowlands in the Early Permian). All of these patterns point to a fossil record that will not produce an understandable historical story simply from an empiric reading of the data in stratigraphic order. Rather, the data make sense only when placed within conceptual explanatory frameworks or models. In the best of situations, the data would prove sufficient in both spatial and temporal density/coverage and quality to permit comparison against the models and clear selection of a best fit. Alternatively, and much more likely, there will be temporal gaps in the fossil record that limit aspects of comparison and permit the possibility of more than one explanatory model, as was found here in each case study. Even so, there often are grounds for preferring one possible model over another, and grounds for outright rejection of others, which we also have done.

Table 1 presents a comparison of the two case studies. Some of the physical drivers appear to be similar in each case and show similar spatio-temporal trends. In each instance, changes in vegetation are associated with major drying and warming trends. Differences between the proxy records in each case study reflect the incomplete nature of the analyses at this time, such that *p*CO₂ has been inferred from paleosols in case study 1, whereas for case study 2 terrestrial temperatures have been inferred but only indirect estimates of *p*CO₂. *p*CO₂ estimates based on latest Pennsylvanian pedogenic carbonates from Utah and Arizona suggest that CO₂ was higher then (~1000 ppmv or so ±300 ppmv) than in the earliest Permian when *p*CO₂ falls to present-day levels (Montañez *et al.*, 2007), a trend that has been suggested by Saltzman (2003) based on marine calcite δ¹³C values. So, in case study 2, we can infer that changes in *p*CO₂ were taking place, but their scale and even their direction are uncertain at this time. Unpublished marine microfossil data (V. Davydov, pers. comm., 2007) also suggest a significant global warming of the oceans in the very latest Pennsylvanian, possibly reflecting a short-lived interval of global sea-level rise and likely warmer conditions worldwide (González, 1990; López Gamundí *et al.*, 1992; Scheffler *et al.*, 2006). Thus, the existing data suggest many similarities in atmospheric and environmental conditions during each of the time intervals evaluated and that these climate–vegetation relationships repeated themselves over and over again throughout the Permo–Carboniferous. The difference is the scale of the biologic system under examination. In case study

Table 1 Comparison of vegetation, potential drivers of change, and the biotic responses in case studies 1 and 2

	Case study 1: Middle–Late Pennsylvanian transition	Case study 2: Pennsylvanian–Permian transition
Vegetational scale	Intrabiome	Interbiome
Vegetation type	Entirely broadleaf evergreen	Broadleaf evergreen-to-mixed needleleaf evergreen/ broadleaf deciduous/broadleaf evergreen
Vegetational responses	<ol style="list-style-type: none"> 1. Threshold change with hysteresis – Model (3) (possible to most probable) 2. Threshold change without hysteresis – Model (2) (possible) 3. Irreversible threshold change with hysteresis – Model (4) (possible) 4. Gradual change – Model (1) (not likely) 	<ol style="list-style-type: none"> 1. Threshold change without hysteresis – Model (2) (possible to most probable) 2. Gradual change – Model (1) (possible) 3. Threshold change with hysteresis – Model (3) (possible, not likely) 4. Irreversible threshold change with hysteresis – Model (4) (not likely)
Climate proxies and physical factors	<ul style="list-style-type: none"> – Increasing CO₂ – Climate spectrum shifts to drier throughout Euramerica and likely southern Gondwana – Diminishment or loss of southern hemisphere continental ice – Rise of central European mountain ranges 	<ul style="list-style-type: none"> – Precipitation decrease in tropics – Development of E-to-W patterns of continental aridity Increased continentality
Vegetation–climate feedbacks	<ul style="list-style-type: none"> – Tree ferns rise gradually in abundance within wetlands during late middle Pennsylvanian due to ability to reproduce under conditions of reduced moisture – Local wetland vegetation climate feedbacks only throughout interval because of intrinsically high rainfall during peat-forming intervals 	<ul style="list-style-type: none"> – Positive feedbacks develop as vegetation becomes sparser, resulting in acceleration of increased atmospheric heating and reduced rainfall

1, the changes documented lie within a single vegetation type or biome, and involve disruption, disassembly and reassembly patterns within a single species pool. Case study 2 documents a change in spatial coverage of two distinct biomes that flourished under different climatic conditions.

Time gaps and ecological turnover

Perhaps the most problematic aspect of evaluating process-based hypotheses against fossil data is the intermittent temporal nature of the fossil record and, thus, the intercalated time gaps. During such gaps, it is difficult or impossible to determine what was happening to the organisms or the ecological systems they comprised. In the examples considered here, this problem is most serious for case study 1, the middle–late Pennsylvanian transition where a single environmental type is the focus.

By restricting analysis to a single physical environment (wetland mires and swamps in case study 1), we are able to hold constant (or as constant as one can with natural systems) a wide range of variables, including many aspects of fossil preservation (what Behrensmeyer *et al.* (2000) call isotaphonomy, controlling for the similarity of deposition and preservational biases). However, for case study 1, we know very little about what happened to the vegetation and its species components from one appearance in the record to the next. There are many indications that the climates prevailing between times of coal-roof shale couplet deposition were seasonal to semi-arid, given evidence of rock types and paleosols (Cecil, 1990; Cecil *et al.*, 2003). The presence of deeply weathered paleosols through the middle–late Pennsylvanian transition in the Appalachian Basin was one of the reasons Wagner & Lyons (1997) suggested significant missing time there, an assertion

that has been addressed, and not substantiated, by a number of different authors looking at both terrestrial and marine rocks (Peppers, 1997; Blake *et al.*, 1999; Heckel, 2008).

If examined on a regional scale, even as broad as Euramerica, it might be argued that the middle–late Pennsylvanian transition does not represent alternative possibilities for vegetational organization, but rather two distinct vegetation types separated by an extinction event. Expanding the spatial scale, however, reveals that middle-Pennsylvanian-type vegetation, rich in lycopsids, continued to exist in the microcontinental areas of eastern Tethys but did not manage to re-establish in central and western Pangaea after conditions suitable for its occupation returned. We propose two factors that may have contributed to the spatially separate co-existence of these two species pools. First geographic barriers may have blocked species exchanges between central and eastern Pangaea. These barriers include the fragmentation of wetlands and elevational changes in Europe, brought on by the Variscan orogeny (Cleal & Thomas, 2005; Oplustil & Cleal, 2007), as well as the general isolation by Tethyan seaways of the Chinese microcontinents on which the middle-Pennsylvanian-type wetland floras survived (Hilton & Cleal, 2007). Secondly, the younger, tree-fern-dominated species pool may have evolved as a consequence of environmental disruption, but ultimately it was through recruitment, establishment, and successful occupation of resource space that it kept the earlier dominant elements from returning in a show of what is known as incumbent advantage. That the tree-fern-dominated floras did not invade the eastern Pangaeian wetlands also may reflect these same phenomena. To have a multiple stable state system, both species pools need to be able to exist under the same environmental conditions in the same region so that species

dispersal events can occur (even if establishment is not successful) (e.g. Shurin *et al.*, 2004; Urban *et al.*, 2008). Thus, through the examination of spatial patterns, it may be possible to understand more effectively the signals of ecologic and evolutionary change preserved in gappy temporal patterns.

Evolutionary considerations

There is an evolutionary component to each of these biologic turnover events, something that may be easier to examine empirically in the fossil record than in modern ecosystems. Recognizing that the fossil record is not without significant biases, it nonetheless can be used judiciously, by examination of the data in the context of multiple working hypotheses that recognize as many of the flaws as we can think of! We will not develop these models extensively in this paper, but they should be noted because, ultimately, they may expand the realm of possible ecological explanations that should be considered for evaluating vegetation–climate feedbacks and responses.

During the middle–late Pennsylvanian transition there appears to have been a temporally abrupt biologic change within one major kind of environment, abrupt even by geologic record standards (e.g. the record documented by Peppers, 1997). Up to two-thirds of the species reported from latest middle Pennsylvanian peat-forming environments do not reappear in the earliest late Pennsylvanian (DiMichele & Phillips, 1996) (Fig. 3). Ultimately, tree ferns gain ascendancy in late Pennsylvanian wetlands, but not before a period of what can be described as vegetational heterogeneity that lasted for several hundred thousand years and involved several climate/sea-level cycles. Understood almost exclusively through palynology, this heterogeneity was both spatial (Kosanke & Cecil, 1996; Peppers, 1996; Dimitrova & Cleal, 2007) and temporal (Peppers, 1985) within peat-forming swamps and mires of the earliest late Pennsylvanian. Several successive earliest late Pennsylvanian coals show highly variable composition and dominance–diversity patterns: small isoetoid lycopsids, calamitean sphenopsids, sigillarian lycopsids, and various tree ferns, dominate large parts of these wetlands, with tree ferns finally emerging ascendant (Phillips *et al.*, 1974; Peppers, 1985). This clearly was a time when long-standing patterns of dominance and diversity were swept away rapidly and resources of space and nutrients were opened up for new species. A new kind of vegetation emerged, even though systems retaining a middle Pennsylvanian aspect continued to exist in far eastern Pangaea (Cleal & Wang, 2002; Pfefferkorn & Wang, 2007; Hilton & Cleal, 2007).

The persistence of the prior system for several million years in the middle Pennsylvanian, and the subsequent persistence of the late Pennsylvanian replacement flora for several millions more, both through regular cyclothemetic sea-level/climate oscillations, raise the question of incumbent advantage – Why certain taxa remain dominant from one coal to the next despite the environmental changes between consecutive coal

beds? How is this played out environmentally and evolutionarily? One possible scenario is this, applicable to case study 1, in which climate change and evolution of innovation are integrally linked. This scenario presumes the survival of the wetland vegetation in regional refugia, within or proximate to basinal lowlands during periods of seasonal dryness between times of widespread peat formation. (a) A particular kind of vegetation (the wetland vegetation in this case) gets established within a climate–resource space. (b) Climate fluctuates such that the area covered by this vegetation also fluctuates. (c) The vegetation persists during the least favorable climate periods in approximately the same species abundance proportions, though with greatly reduced overall numbers, as during the favorable periods, as long as climate stays within some window of tolerance and refugia of some adequate size exist. (d) The reappearance of favorable conditions is accompanied by a species-wise proportional expansion of the plant populations, maintaining the basic vegetation from one cycle of most favorable climate to the next. (e) If climate changes more than some-to-many of the species of this vegetation can tolerate, by greatly reducing the area and/or number of refugia, major changes in proportion occur by a variety of means, including simply stochastically. A high degree of fragmentation into small refugia, potentially creates happenstance opportunities for the reshuffling of dominance patterns, including survival and rise to proportional dominance of newly evolved forms.

Late Pennsylvanian fern-dominated wetland landscapes offer yet another twist on this model. Given the increased strength of seasonal dryness between times of widespread wetland development during the late Pennsylvanian, tree-fern-dominated vegetation may indeed have been subject to greater fragmentation and spatial displacement than was typical during cyclic climate/sea level changes in the middle Pennsylvanian. In this scenario, such repeated fragmentation may underlie the considerable tree-fern species heterogeneity that has been documented spatially and temporally. Basic weedy habit, high dispersibility and inferred rapid growth rates (based on ‘cheap’ construction, low carbon allocation to stems and roots per unit volume) of these plants, may have made recolonization of wetlands with each cycle of renewal much more of a lottery or land rush than in the middle Pennsylvanian, where many of the dominant trees appear to have been more closely tied to water ways for dispersal and to have dispersed and grown more slowly.

The evolutionary component of case study 2 is entirely different in character. The seasonally dry vegetation was ‘out there’ but poorly represented in the fossil record for millions of years prior to its regular appearance in typical adpression floras. This strongly suggests that evolution was going on apace in areas that the record did not sample adequately. Preservation of this vegetation required fortuitous special circumstances (given that it was mostly represented by paleosols and coarse sandstones deposited under high-energy and high-sediment yield conditions, i.e. river avulsion, braided

stream deposits laid down under flashy flood conditions) at times when the basinal lowlands were seasonally dry. Or, evidence of it could come from proximity of well-drained uplands to humid basinal lowlands, such that bits and pieces of the hinterland elements could be transported into the wetland basins (such as in most middle Pennsylvanian examples of this flora). Furthermore, there is increasing evidence that the plants of the ever more environmentally stressful extrabasinal areas may also be more phylogenetically derived, suggesting that low occupancy/low incumbency habitats may have permitted the survival of divergent evolutionary novelties (DiMichele & Aronson, 1992; Kerp, 1996; Rothwell & Mapes, 2001; Looy, 2007). Ultimately, strong and long-persistent climate changes in the equatorial lowlands brought this vegetation type down into these basins where it replaced the prior wetland occupants. If dry basinal conditions lasted long enough to extinguish most of the prior wetland taxa, as seems to have happened in the early Permian of Euramerica, new wetland species ultimately evolved in place, in the lowland basins, from elements of these seasonally dry floras. This, again, involves the survival of evolutionary innovation in areas of low resource utilization/expropriation, either through evolution in areas that were not yet exploited or were underexploited by vascular plants (in increasingly high stress settings) or through the exploitation of resources made available by physical extirpation of the prior occupants (in some cases, space being the equivalent of resources).

Essentially both case studies demonstrate the same underlying principle: evolution of novel forms is not driven by the ever watchful eye of natural selection, but by the happenstance intersection of the blind generation of variation and the opportunity to survive in areas with little or no resource competition – created by climate-driven extinctions such as those discussed for case study 1, or by the movement of plants into ever more peripheral areas of the earth, which underlies the origin of the seasonally dry vegetation discussed in case study 2. Such areas may be vast unoccupied physical spaces or they may be resource pools created by ecosystem engineering when organisms evolve traits that permit them to exploit or even to create new resources (Erwin, 2008). In the end, many of these novelties are called (by the processes underlying the generation of variation) but few are chosen (because they usually confront unsuitable physical conditions or incumbents) . . . which is why we ought not to ask why there are so many forms of life, but why there are so few.

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