

# Clades, ecological amplitudes, and ecomorphs: phylogenetic effects and persistence of primitive plant communities in the Pennsylvanian-age tropical wetlands

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## Abstract

Pennsylvanian-age wetland plant communities and landscape gradients exhibit persistent species composition and ecomorphic structure. Such patterns are attributable in large part to strong phylogenetic partitioning of ecological resource space at the level of higher taxa. Each of four major class-rank clades in tropical wetlands was centered in a physically distinct part of the lowland ecosystem. Once established in these physical settings clades tended to resist displacement until removed by physically driven extinction. Lycopsid trees were the principal dominants of the wettest habitats and had subpartitioned these environments along generic lines. Seed plants were the dominants on well to poorly drained clastic substrates, a diverse set of habitats reflected in high diversity of species and architectures. Sphenopsids were most abundant in aggradational environments subject to high levels of physical stress. Ferns initially were interstitial opportunists and colonizers of disturbed areas in a variety of environments. These ecological patterns were established in concert with the architectural radiation of the vascular plants, which occurred during the Devonian–Mississippian transition and established the major classes. Within the wetlands, the replacement of species by close relatives drawn from the same families or genera contributed significantly to persistence of communities and landscape gradients. Replacement was more likely to occur from within a clade where similar ecologies already existed, than from across major clades between which the basic ecologies were different. Possibly interacting with the phylogenetic factors were community and landscape level multispecies effects that may have placed limits on species replacement patterns. The existence of such emergent properties of multispecies assemblages is suggested by a breakdown of the system beginning with major, climatically induced extinctions at the Middle–Late Pennsylvanian transition. Following extinctions of the major Middle Pennsylvanian trees, opportunistic ferns gave rise to dominants in many parts of the wetlands, perhaps due to loss of some aspects of system self-regulation. As climatic drying continued seed plants began their largely passive rise to dominance in most kinds of habitats.

*Keywords:* palaeobotany; palaeoecology; Pennsylvanian; tropical; extinction

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## 1. Introduction

Pennsylvanian-age plants of tropical wetlands formed assemblages that recurred repeatedly in similar physical settings over time spans of millions of years. Patterns of repetition were both quantitative and qualitative (DiMichele and Phillips, 1995; DiMichele et al., 1996), manifested mainly as landscape gradients (terminology of Allen and Hoekstra, 1992) composed of “communities” with persistent species composition and ecomorphic structure. Species turnover generally did not disrupt the ecomorphic characteristics of the communities because replacement most often involved members of the same or closely related genera.

Modern plant communities in most of the world are dominated by the plants from one, albeit diverse, twig of the phylogenetic tree of Tracheophyta, the angiosperms. In contrast, Carboniferous plant communities, particularly those older than Late Pennsylvanian age, were dominated by elements from each of four major classes of vascular plants: Lycopsidea, Sphenopsida, Pteropsida, and Spermatopsida. These clades/classes are distinct architecturally, and represent widely divergent ways to reproduce, develop tree habits, and add secondary tissues to the primary plant body, among other attributes. Partly as a consequence of architectural and life-history differences, these clades have distinct ecological distributions. This phylogenetically deep, class-level partitioning of terrestrial ecological space originated with the radiation of modern vascular-plant lineages during the Late Devonian and Early Mississippian; it persisted in the tropics until the Late Pennsylvanian when extinctions began to reduce or eliminate the dominant tree forms of the different classes. With continued climatic changes seed plants diversified extensively and passively became the dominant tree forms in most ecosystems (Knoll, 1984).

The ecological patterns in Pennsylvanian coal-swamp plant communities can be described broadly as conforming to the descriptions of coördinated stasis, described as “evolutionary stasis among numerous unrelated lineages within communities” (Brett and Baird, 1995, p. 285; see also

Brett et al., 1990). Paralleling the patterns described by Brett and his colleagues for Silurian–Devonian marine faunas, background species turnover in coal swamps was minor throughout most of the Pennsylvanian, and ecological reorganization was concentrated in times following major extinctions. The issue considered herein is the degree to which Pennsylvanian tropical pattern, namely persistence of community organization over geological time, was a consequence of the high level phylogenetic partitioning of ecological resource space that originated during the Devonian–Mississippian, class-level radiation of vascular plants.

## 2. Pieces of the puzzle

### 2.1. Theoretical considerations

There are several concepts in ecology that overlap with or describe ecological characteristics of relevance to the concept of coördinated stasis; a good summary of these terms can be found in Pimm (1984) or Perry (1994). Of greatest interest is “persistence”, which describes the long-term dominance-diversity dynamics of a species assemblage. Persistence is a geological time analogue of the concept of “stability”, which describes the response of a species assemblage to disturbance. Stability and persistence of fossil assemblages can be considered from the viewpoint of recurrent species composition or recurrent structural attributes, and are central to the coördinated stasis concept. Related to stability and persistence are “resilience” and “resistance”, which describe, respectively, the ability of a species assemblage to return to its former dominance-diversity state following a disturbance, and the degree to which a species assemblage retains its dominance-diversity structure in the face of perturbation. Resistance can be treated as the degree to which a species assemblage remains little or unchanged on geological time scales, reflecting the degree to which species from outside the system successfully infiltrate and establish as components. Contributing to stability is “redundancy” or the

degree to which several species in the system have the same functional roles. The concept of ecomorphic equivalence has been used to examine the use of structural attributes of species as proxy for a broader suite of ecological characteristics (Wing et al., 1992). The sessile life mode of vascular plants, combined with shared requirements for basic resources (light, water, mineral nutrients) has led to numerous broad convergences in growth habit and life history. Such convergences underlie attempts to find ecomorphic equivalence among phylogenetically disparate groups of plants.

Prior to the work of May (1972, 1973), intuitive theory dictated that the more complex a system became, that is the more species that composed the assemblage and the greater the interactions among them, the more stable that system would be. The mathematical studies of May (1973) demonstrated that the more complex a system became the more susceptible it was to disintegration should some species be removed by local extirpation or global extinction. This inverse relationship between complexity and stability has been controversial since its introduction, although it is generally, if in some circles grudgingly, accepted. Modifying May's concepts are new views that place ecological organization within a hierarchical framework. For example, the concept of "home-field-advantage" (Pimm, 1991) states that the incumbent species has an advantage over invaders in the exploitation of a regional resource; this is supported by studies of animal introductions to oceanic islands (e.g., Pimm, 1991; Schoener and Spiller, 1995). On a geological time frame such resistance behavior may be manifested as "incumbent advantage" (Gilinsky and Bambach, 1987). An existing species may exclude new forms from a resource through interaction of random extirpation and the probability of occupancy of randomly appearing patches through time; new isolates or small populations of invading species are at a numerical disadvantage in locating resources and are more likely than established widespread species to be eliminated entirely by local density-independent perturbations. This is, in effect, metapopulation theory of Levins (1969) expanded to geological time (see also McKinney and Allmon, 1995). Additionally, all species may not be of

equal importance to the long term stability or persistence of an ecosystem; particular "keystone" species may be linked more strongly to the functional aspects of the larger species assemblage. Such properties are emergent, group-level characteristics that depend on context — where and with what others is the species of interest growing. Hierarchical concepts have been extended and formalized (Allen and Hoekstra, 1992; O'Neill et al., 1986; Perry, 1994) and suggest that distinct properties of species assemblages may be revealed only by consideration of spatial scale.

As a descriptor of pattern in the fossil record coördinated stasis is as much an ecological as an evolutionary concept. It fundamentally reflects the long-term persistence of species assemblages, presumably in the face of minor perturbations. The periodic reorganization of assemblage structure and composition may reflect threshold-like disintegration of the interactions among species, what in terrestrial systems has been called "loss of biotic regulation" (Bormann and Likens, 1979). Loss of regulation results from the increasing propagation of potentially small system perturbations, such as the loss of a few key species to extinction. While it may never be possible to identify the particular taxa or physical disturbance of importance, the patterns seen at some points in the fossil record are consistent with modern ecological models of rapid system deterioration and reorganization (e.g., DeAngelis, 1992; but see comments by Valentine and Jablonski, 1993, Buzas and Culver, 1994, or Overpeck et al., 1992).

## 2.2. *The origin of vascular-plant classes*

All major body plans of vascular plants originated during the Late Devonian and Early Mississippian (Niklas, 1994; DiMichele and Bateman, 1996), elaborating on simpler architectural themes present in their ancestors. Although there is dispute over how these vascular plants should be classified, the clades represented by each of these groups are generally treated as classes, the characteristics of which are summarized in Table 1. The exception to this scheme is the angiosperms, which in traditional Linnaean classification have been granted class-level rank, generally resulting

Table 1  
Characteristics of the post-Devonian classes of vascular plants

Class	Protoxylem	Stele	Leaf type	Life cycle	Sporangium
Lycopsida	exarch	protostele	microphyll	homosporous	lateral, nonfoliar
Pteropsida	mesarch	proto/siphono	megaphyll	homosporous	terminal, foliar
Sphenopsida	mesarch	node-internode	megaphyll	homosporous	terminal, on sporangiophore
Progymnosp.	mesarch	eustele	megaphyll	homosporous	terminal, non-foliar
Spermatop.	mesarch	eustele	megaphyll	heterosporous	terminal, non-foliar

in the inflation of other orders of seed plants to class or even phylum rank in order to maintain a balanced classification (e.g., Bold, 1973, which has become a standard for many vascular plant classifications). A spate of recent phylogenetic analyses are broadly consistent with the traditional, non-inflated classifications (e.g. Crane, 1990). Thus, for the purposes of this paper, class is shorthand for maximally distinctive architecture and its use should be seen as a way to simplify communication not as an intrinsic belief in the objective existence of the class rank.

The Devonian ancestors of the Mississippian–Pennsylvanian flora were structurally simple, but accrued complexity incrementally from the Late Silurian through the Middle Devonian (Chaloner and Sheerin, 1979; Knoll et al., 1984). Beginning in the Middle Devonian and continuing into the Early Mississippian, there was a rapid increase in structural complexity, measured as number of organs, and diversity of kinds of structural organization.

These events are important for understanding the dynamics of Pennsylvanian tropical forests because they established the elements of the ecosystems. In addition to architectures, each of the classes became centered in a different part of the tropical-lowland environment. The “breadth” of ecological opportunity in each of these parts of the terrestrial realm then limited the relative diversities of the class centered there (DiMichele and Bateman, 1996). The ecological partitioning that characterized the Pennsylvanian tropics thus originated during the class-level radiation. Allowing for overlap, the ecological patterns that would characterize most of the late Paleozoic had emerged by the early Mississippian (DiMichele and Hook, 1992).

The most significant dichotomy involved the lycopsids and the seed plants. The wettest parts of the lowlands were dominated by lycopsids, which were tolerant of low nutrient, flooded, swampy conditions, including organic-rich substrates (Scheckler, 1986a, b). Seed plants (Spermatopsida) were emerging as dominants in environments that experienced periodic moisture limitation, but within the broader wetland setting (Retallack and Dilcher, 1988). Terra firma settings offered great ecological opportunity and, as a result, the seed plants diversified into several ecologically distinct orders.

Sphenopsids were abundant in a relatively narrow set of habitats characterized by sedimentary aggradation, disturbance, and mechanical stress, often along stream and lake margins or flood basins. Success in these environments may be attributable to the clonal habit of arborescent sphenopsids, the only Paleozoic group to evolve trees of this growth form (Tiffney and Niklas, 1985).

Ferns appear to have evolved as opportunists, tolerant of or perhaps dependant upon disturbances at various scales (Scott and Galtier, 1985); this appears to be true particularly of small, ground cover ferns and the early marattialeans of small stature. Some ferns also may have preferred physically stressful environments such as swamps.

On a geological time scale, the termination of the radiation seems to have been controlled by two principal factors. As the ecospace was progressively occupied the likelihood of origination of any new class was diminished, a pattern described for marine invertebrates by Valentine (1980), whose model seems equally applicable to the terrestrial realm. This “incumbent occupancy” (Gilinsky and Bambach, 1987) may be seen as a

geological-time manifestation of ecological home-field-advantage (Pimm, 1991); once one of the major clades was established within a particular subset of the environment other groups had a lower probability of establishing in that resource space. On a smaller scale, this phenomenon is illustrated by the partitioning of the wettest parts of the lowlands by the lycopsid trees, where patterns of ecological partitioning persisted for over nine million years of the Westphalian (Phillips and Peppers, 1984). Secondly, and of equal importance, was increasing developmental limitation on the breadth of evolutionary innovation. As plants became more complex their organ systems became progressively more developmentally interdependent (the developmental ratchet of Levinton, 1988), and existing architectures placed constraints on subsequent morphological changes. High taxonomic diversity within the seed plant clade demonstrates this phenomenon well. Differences among major orders (considering the angiosperms to be an order) reflect changes in position or degree of fusion of reproductive organs, and coöptation of sterile parts into reproductive functions. But, basic construction and reproductive organization of orders within classes are conserved and differ much less profoundly than among classes.

### 2.3. *Ecological partitioning and persistence in Pennsylvanian-age wet lowlands*

The ecological partitioning of the tropics during the Early and Middle Pennsylvanian continued patterns developed in the Mississippian. The major players in this partitioning were trees, and each of the major groups in the lowlands had distinctive construction (Table 2). Extensive documentation demonstrates continuation of the principal dichotomy between the lycopsids and seed plants (Scott, 1978; Pfefferkorn and Thomson, 1982; DiMichele and Phillips, 1994), the continued location of sphenopsids in aggradational settings (e.g., Gastaldo, 1992), and the role of groundcover filicalean ferns largely as interstitial weeds. Marattialean ferns seem to have originated as small opportunists and colonizers (Lesnikowska, 1989), with larger forms appearing in the late Westphalian as site occupiers in physically stressful

sites (Pfefferkorn, 1976). Major changes in dominance-diversity patterns took place between the Middle and Late Pennsylvanian in the Euramerican part of Amerosinia following disappearance of over half the species, including most of the tree species, in wetland environments (Phillips et al., 1974; DiMichele and Phillips, 1996); many genera survived in North and South China (Cathaysia) into the Permian but did not recolonize the western regions of the tropics (Guo, 1990). In the Late Pennsylvanian lowlands of Euramerica tree ferns of the order Marattiales dominated many assemblages both in peat-forming and mineral soil wetlands (Phillips et al., 1974, 1985).

The wetlands constituted a biome that can be divided into two major landscapes, characterized respectively by peat and clastic substrates (e.g., Scott, 1977, 1978; Pfefferkorn and Thomson, 1982). Westphalian clastic floras were dominated by pteridospermous seed plants until near the end of the epoch when tree ferns began to rise in prominence. Thus, during the Westphalian patterns on peat and clastic substrates were quite different. Tree ferns began a steep rise in importance in both kinds of landscape during the latest Westphalian, and by Stephanian were dominant throughout the wet lowlands. The wetland biome remained largely distinct from a contemporaneous dryland biome that is rarely seen in Westphalian lowland deposits. The dryland biome included conifers and was largely seed-plant dominated (Mapes and Gastaldo, 1986; Lyons and Darrah, 1989; Broutin et al., 1990; DiMichele and Aronson, 1992). It begins to be well represented in the fossil record during the Late Pennsylvanian, evidently signalling climatic fluctuations that brought drier conditions to the lowland basins.

Overprinting the ecological patterns of the Pennsylvanian were polar glaciations that strongly influenced global climate (Frakes et al., 1992). The wetland floras that make up most of the Pennsylvanian record of plant fossils reflect apparently disjunct recurrences of wet climates in the lowland tropics. Climatic and eustatic fluctuations permitted the repeated development of wetlands and peat formation in lowland basins (Cecil, 1990). Climatic fluctuations during the late Tertiary and

Table 2  
Architectural features of trees in vascular-plant classes

Class	Dominant organs	Stem organization	Support tissue	2nd vascular tissue
Lycopsida	stem	bark and wood both structurally important	periderm (bark)	unifacial cambium
Pteropsida	stem and fronds	Primary stem with complex siphonostele	adventitious roots	no secondary phloem no secondary tissues
Sphenopsida	stem	node-internode construction	wood—parenchyma rich	unifacial cambium
Progymnospermopsida	stem and fronds	woody stem	wood—dense	bifacial cambium
Spermatopsida (Pteridospermales)	stem and fronds	polystelic, highly parenchymatous	wood and cortical sclerenchyma	bifacial cambium
Spermatopsida (Cordaitales)	stem and leaves	woody stem	wood	bifacial cambium
	Growth habit	Life history	Reproductive output	
Lycopsida	pole trees with rapid growth, shallow rooted	determinate, often monocarpic colonists of disturbed sites	high production of aquatic propagules wide dispersal in wet habitats	
Pteropsida	trees with large crown of fronds	indeterminate, homosporous opportunists-site occupants	mass production of small, highly dispersible isospores	
Sphenopsida	clonal small trees	clones indeterminate, most species homosporous	moderate cone production vegetative reproduction important on site	
Progymnospermopsida	large trees	intermediate, site occupants, heterosporous	?high output of mega- and microspores	
Spermatopsida (Pteridospermales)	medium trees	indeterminate, water-animal dispersed seeds and pollen	low production of large, energy-rich seeds and pollen	
Spermatopsida (Cordaitales)	large trees; possibly some mangroves	indeterminate, wind and water pollination—seed dispersal	high output of medium-sized seeds	

Pleistocene parallel those of Pennsylvanian Period, and require that vegetation either was repeatedly disrupted and reassembled, or was able to persist mostly intact in isolated refugia, or migrate regionally as tropical climate varied in temperature and rainfall patterns. Each of these alternatives has interesting and important consequences for long-term ecological dynamics.

### 3. Ecosystem persistence in peat swamps

#### 3.1. Patterns

Studies of coal-ball concretions, which preserve the litter and root systems of peat-forming forests (Phillips et al., 1976), demonstrate several key characteristics of peat-swamp vegetational dynamics.

##### 3.1.1. Landscape gradients

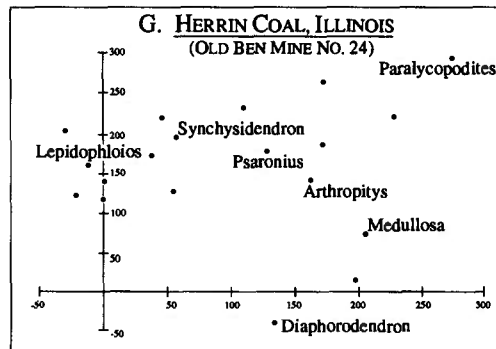
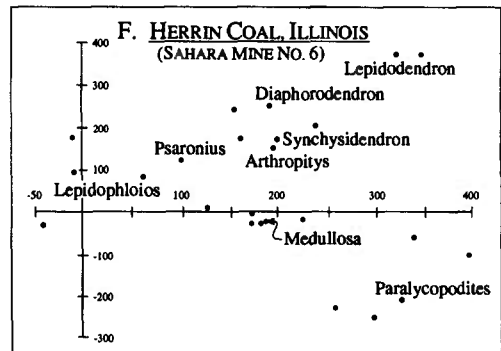
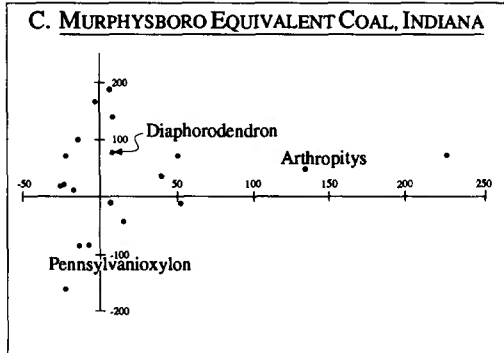
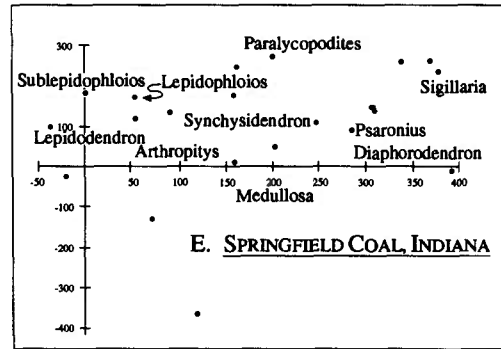
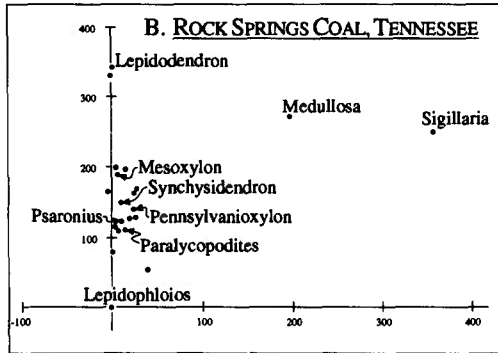
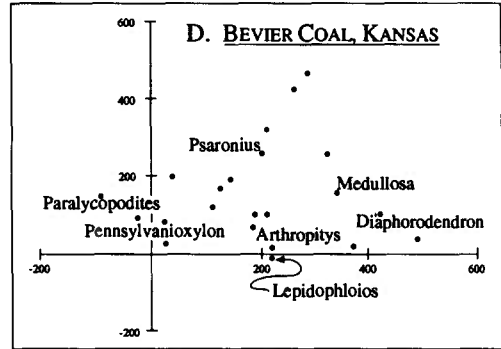
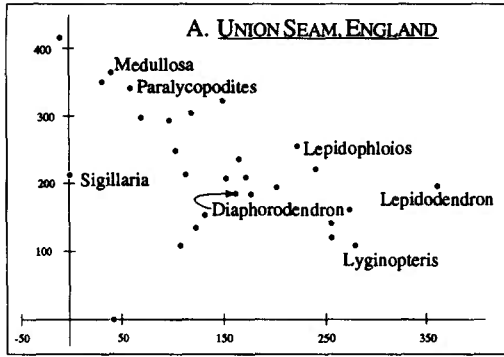
Landscape gradients persisted for millions of years, reappearing through numerous consecutive coal beds. These recurrent gradients are associated with persistent dominance-diversity patterns, best documented for the nine million years of the Westphalian (DiMichele and Phillips, 1995; DiMichele et al., 1996). In a paper written in 1989 but only published recently, we (DiMichele and Phillips, 1995) argued that the end-point communities of gradients within Pennsylvanian coal swamps were the main elements of persistence. Here we wish to modify this and look more at the resource gradients these recurrent assemblages comprise. Persistence can be recognized at two levels. On shorter time scales of one to two million years, such as the Carbondale (Illinois Basin) and Allegheny (Appalachian Basin) Formations equivalent to the Westphalian D stage, species composition of landscape gradients is conserved (DiMichele et al., 1996). Such patterns come closest to documenting stability at the species dominance-diversity level. On longer time scales up to 10 m.y., such as the entire Westphalian, structural aspects of assemblages persist even in the face of nearly complete species turnover during the interval. The conservation of structure is closely tied to ecomorphic replacement by close relatives.

Fig. 1 illustrates the distribution of species centroids in ordinations of coal balls or coal-ball zones from selected coals of the Westphalian. The relative positions and proximities of species reflect the degree of association in the samples. Several gradients are represented, and those of the Westphalian A and late Westphalian D are remarkably similar. Most noteworthy are three recurrent associations: those dominated or greatly enriched in monocarpic lycopsids, particularly species of *Lepidophloios*, those dominated or codominated by medullosan pteridosperms and *Paralycopodites brevifolius* and by cordaites during the Westphalian B through early D, and those with abundant polycarpic lycopsids of the genus *Diaphorodendron*. Groundcover ferns and pteridosperms tend to occur rarely in association with the monocarpic lycopsids, independently interpreted as occurring in standing water areas (Phillips and DiMichele, 1992; DiMichele and Phillips, 1994).

The complete spectrum of assemblages occurred in the Westphalian A and late Westphalian D. During the mid-Westphalian, into the early Westphalian D, intraswamp gradients were simplified and various combinations of end-point assemblages characterize the coal beds sampled. These “incomplete” landscapes may reflect changes in the scale of the gradients, caused by variations in the intensity and distribution of recurrent wet climates. Resulting greater regionalism thus may have limited the complexity detected by our often geographically restricted samples. Palynological evidence suggests this, for example, in the Sumnum coal of Illinois (Peppers, 1970). The reappearance of a Westphalian A-type landscape in the late Westphalian D, and the periodic appearance of all parts of the more complex landscapes throughout the Westphalian B through early D, suggests that all major end-point assemblage types (communities) persisted throughout the interval.

##### 3.1.2. Species turnover

Measured with either microfossils or megafossils, species turnover occurred continually throughout the Pennsylvanian, mostly at a level of <5% of total species from one coal seam to the next (Peppers, 1985; DiMichele et al., 1996) (Fig. 2). Despite this turnover, the ecomorphic structure of



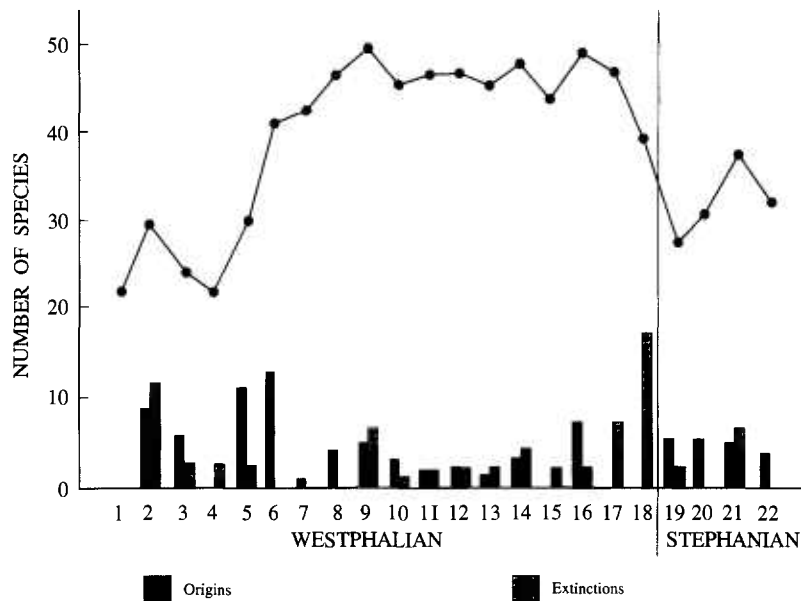


Fig. 2. Species diversity, origination and extinction through time. Curve represents total species diversity, based on range-through data. Histograms denote first (origin) and last (extinction) occurrences at any coal horizon. Coals numbered in stratigraphic order from oldest to youngest: Westphalian A: 1 = Union Seam, England, 2 = Bouxharmont Seam, Belgium. Westphalian B: 3 = Lower Elkhorne coal, Kentucky, 4 = Hamlin coal, Kentucky. Westphalian C: 5 = Rock Springs coal, Tennessee. Westphalian D: 6 = Urbandale locality, Iowa, 7 = Buffaloville coal, Indiana, 8 = Murphysboro equivalent coal, Indiana, 9 = Secor coal, Oklahoma, 10 = Fleming coal, Kansas, 11 = Bevier coal, Kansas, 12 = Sumnum (Houchin Creek) coal, Illinois, 13 = Iron Post coal, Oklahoma, 14 = Springfield coal, Indiana, 15 = Middle Kittanning coal, Pennsylvania, 16 = Herrin coal, Illinois, 17 = Upper Freeport coal, Ohio, 18 = Baker coal, Kentucky. Stephanian: 19 = Bristol Hill coal, Illinois, 20 = Friendsville coal, Illinois, 21 = Duquesne coal, Ohio, 22 = Calhoun coal, Illinois. Vertical line marks the Westphalian–Stephanian boundary.

communities on landscape gradients remained substantially the same for millions of years; species replacement was largely on ecomorphic themes and was mostly among species within the same genera or families (Phillips, 1980), i.e. strongly phylogenetically constrained (Figs. 3 and 4).

### 3.1.3. Extinction and recovery patterns

A major extinction occurred during the Westphalian–Stephanian transition in the Euramerican tropics (excluding Cathaysia). In coal swamps, two-thirds of the species, and nearly 90% of the trees, disappeared at this time (DiMichele

Fig. 1. Detrended correspondence analysis of ordinations of species in coal-ball profiles and random samples from seven coals of Westphalian age (Lower and Middle Pennsylvanian). Each point represents a single species. Ordinations of species assemblages are not shown (see DiMichele and Phillips, 1995, for ordinations of species assemblages). Coals represented in stratigraphic order are: A. Union Seam, Westphalian A of England, random sample. B. Rock Springs coal, Westphalian C of Tennessee, random sample. C. Murphysboro equivalent coal, early Westphalian D of Indiana, profiles. D. Bevier coal, middle Westphalian D of Kansas, random sample. E. Springfield coal, late Westphalian D of Indiana, profiles. F. Herrin coal, Sahara Mine No. 6, late Westphalian D of Illinois, profiles. G. Herrin coal, Old Ben No. 24 Mine, late Westphalian D of Illinois, profile. For further stratigraphic and locality information see Phillips et al. (1985). Generic names are shown for the major tree taxa with the greatest quantitative abundances. The end points of the major gradients are marked by *Medullosa* (a pteridosperm associated with mineral matter and fusain), *Paralycopodites* (a polycarpic lycopsid associated with mineral matter and fusain), *Lepidophloios* (a monocarpic lycopsid associated with low diversity assemblages that lack groundcover), and *Diaphorodendron* (a polycarpic lycopsid associated with high diversity assemblages). In some coals the calamite *Arthropitys* is abundant and generally widespread. *Psaronius* tree ferns are common beginning in the Westphalian D and are rarely found in close association with monocarpic lycopsids. The cordaitan gymnosperms *Pennsylvanioxylon* and *Mesoxylon* occur in abundance from the Westphalian B through the early Westphalian D mainly in association with medullosans or *Paralycopodites* in highly decayed peats with abundant fusain or mineral matter.

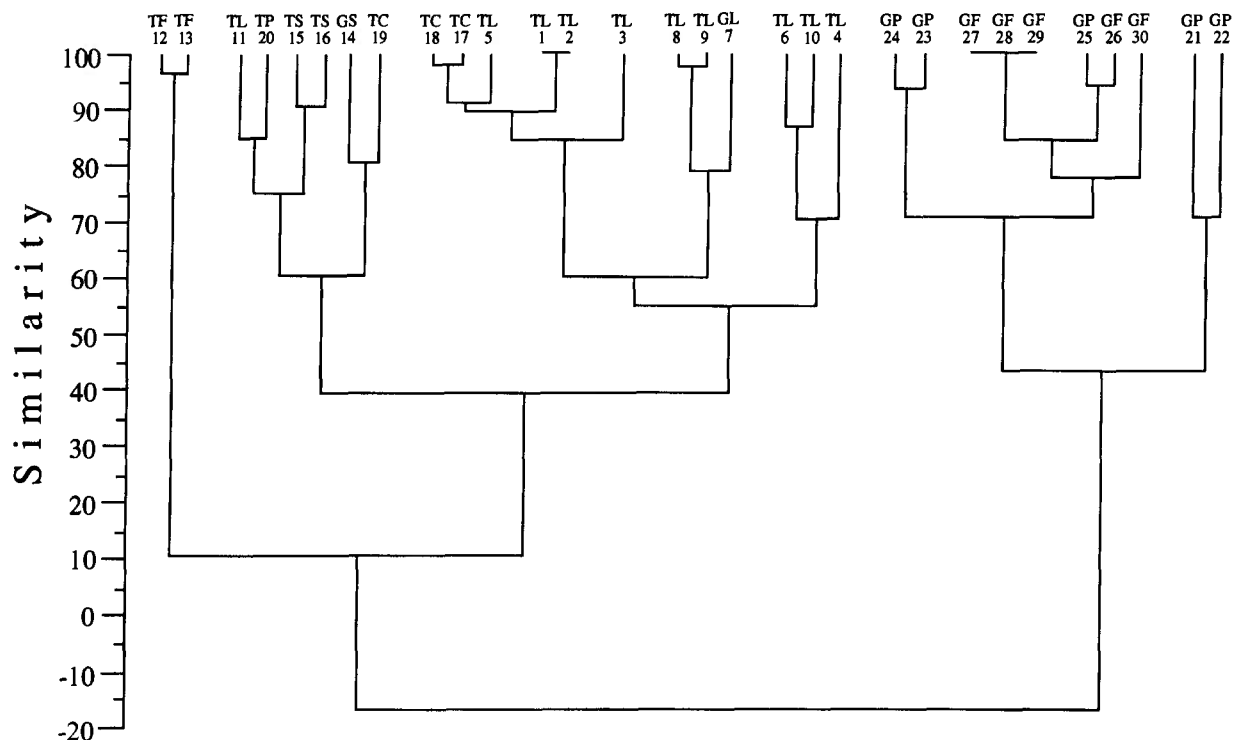


Fig. 3. Unweighted pair groups cluster analysis of species of Pennsylvanian coal swamp plants. Similarity is measured by Spearman's Rank correlation using characters described in Table 3. *TL* = tree lycopsid, *TF* = tree fern, *TC* = tree cordaite, *TS* = tree sphenopsid, *TP* = tree pteridosperm, *GP* = groundcover pteridosperm, *GF* = groundcover fern, *GL* = groundcover lycopsid. Species are keyed to the following numbers: 1 = *Diaphorodendron vasculare* (polycarpic lycopsid), 2 = *Diaphorodendron phillipsii* (polycarpic lycopsid), 3 = *Diaphorodendron scleroticum* (polycarpic lycopsid), 4 = *Synchysidendron resinosum* (monocarpic lycopsid), 5 = *Paralycopodites brevifolius* (polycarpic lycopsid), 6 = *Lepidodendron hickii* (monocarpic lycopsid), 7 = *Hizemodendron serratum* (probable monocarpic lycopsid), 8 = *Lepidophloios hallii* (monocarpic lycopsid), 9 = *Lepidophloios harcourtii* (monocarpic lycopsid), 10 = Stephanian *Sigillaria* sp. (polycarpic lycopsid), 11 = Westphalian *Sigillaria* sp. (polycarpic lycopsid), 12 = Stephanian *Psaronius* sp. (tree fern), 13 = Westphalian *Psaronius* sp., 14 = *Sphenophyllum* sp. (sphenopsid), 15 = *Arthropitys* (sphenopsid), 16 = *Calamodendron americanum* (sphenopsid), 17 = *Mesoxylon* sp. (cordaite), 18 = *Pennsylvanioxylon birame* (cordaite producing *Cardiocarpus spinatus*), 19 = *Pennsylvanioxylon/Cordaixylon dumusum* (cordaite producing *Cardiocarpus oviformis*), 20 = *Medullosa* sp. (pteridosperm), 21 = *Lyginopteris oldhamia* (pteridosperm), 22 = *Callistophyton boysettii* (pteridosperm), 23 = *Schopfiasstrum decussatum* (pteridosperm), 24 = *Heterangium lintonii* (pteridosperm), 25 = *Heterangium* sp. (pteridosperm), 26 = *Anachoropteris involuta* (fern), 27 = *Zygopteris* spp. (fern), 28 = *Ankyropteris bronngiartii* (fern), 29 = *Botryopteris* spp. (fern), 30 = *Botryopteris cratis* (fern).

and Phillips, 1996). Stephanian floras of Euramerica were dominated by tree ferns, with major changes in the importance of ground cover pteridosperms and ferns (Phillips et al., 1974) and a substantial decrease in diversity (Fig. 2). Virtually all fern vines disappeared, for example, leaving only climbing pteridosperms. The landscape gradients and community types of the Westphalian did not reappear in the Stephanian, despite the survival of typically Westphalian assemblages in the Permian of Cathaysia (Guo, 1990).

The rise of tree ferns both in peat and clastic wetland landscapes resulted in homogenization of structural and dynamic patterns throughout the wet lowlands. This type of organization persisted into the Early Permian.

### 3.2. Ecomorphs and ecomorphic replacement

Central to our arguments of persistent structural and clade level ecological organization is the observation of ecomorphic replacement. Moreover, eco-

morphs are drawn largely from the same class-level phylogenetic groups, indicating a strong overprint of phylogeny on ecological dynamics. One objective, therefore, is to demonstrate the overlap of phylogenetic affinity and ecomorphic characters, keeping in mind that these patterns underlie the landscape gradients that characterize the Pennsylvanian lowlands. Three approaches are described, including two that proved largely to partly unsatisfactory, illustrating the nature of the problem and the difficulty of escaping the phylogenetic overprint on ecological patterns.

By inspection we first classified coal-swamp plants into sixteen ecomorphic groups based on architecture and life history. Trees, however, were strongly segregated into phylogenetic groups. Furthermore, most of the tree groups are composed of lycopsids, which are the most studied and best known from the perspective of life history and ecological distribution (e.g., Phillips, 1979; DiMichele and Phillips, 1985; Wnuk, 1985; Gastaldo, 1987; Phillips and DiMichele, 1992). Small plants, largely ground cover and vines, sorted out clearly into groups independently of phylogenetic relationships.

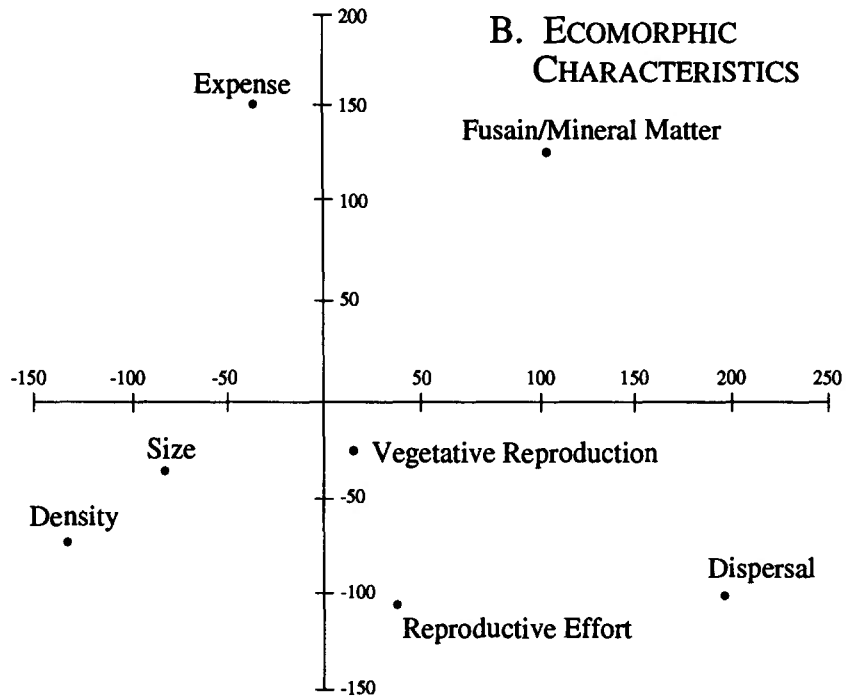
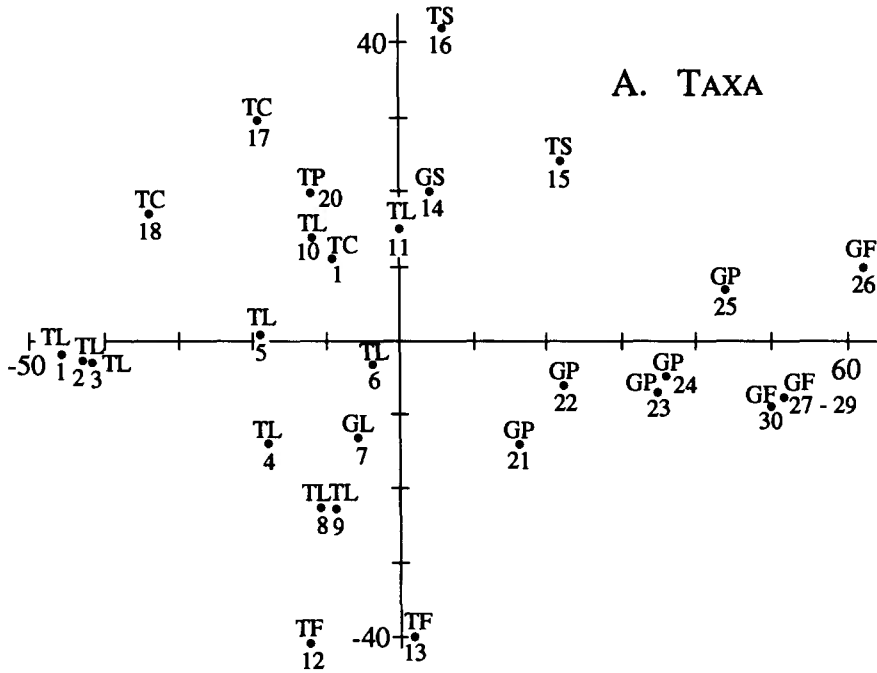
In order to refine the patterns observed by inspection and attempt to reduce the effects of phylogeny, we next attempted to order coal-swamp plants into ecomorphic groups objectively based on shared, ecologically interpretable, morphological features. Thirty taxa ranging in gross habit from large trees to ground cover (Table 4) were each characterized on the basis of 20 directly observable aspects of morphology, such as diameter of largest known axes, height of largest known individuals, tracheid diameter, wood parenchyma concentration, root system density, disseminule size, etc. Cluster and ordination analyses of these morphological character sets failed to produce groups that we could interpret, either ecologically or morphologically; the morphological patterns were inconsistent with the patterns of ecological distribution within coal-swamp landscapes. Analyses of character correlation indicate much covariation among traits and suggest that many of the traits individually have limited ecological significance but are part of larger multi-character syndromes.

As a next step we identified eight attributes of potential ecological importance (Table 3) and ranked each taxon relative to the others, using our experience with the plants to determine the ranking. While this approach admittedly has a strongly subjective element, the characters on which the rankings are based and the placement of taxa have been made explicit. Characters and the bases for determining them are listed in Table 3; the scorings for various taxa are shown in Table 4. A matrix of taxon rankings was used for cluster and ordination analyses of taxa. Cluster analyses were performed in SPSS PC+ for DOS using UPGMA with Spearman's Rank correlation as the metric. Taxa and ecomorphic attributes were simultaneously ordinated in a Detrended Correspondence Analysis using 26 segments for detrending of the data. Regressions were performed on all possible character pairs in SPSS PC+ in order to identify possible redundancy in our choice and scoring of characters; as a result "habit" was eliminated from the analyses because of its strong correlation with size. This method produced interpretable clusters, although a number of ambiguities remain. Until more detailed autecological studies are produced for many of the plants such ambiguities will remain unresolved. Nonetheless, both UPGMA and ordination analyses produced groups that continue to reflect strong phylogenetic overprints on ecological patterns (Figs. 3 and 4).

### 3.3. *Ecomorphic distribution of coal-swamp taxa*

#### 3.3.1. *Ground cover*

Plants classified as ground cover are those growing at or just above the soil/atmosphere interface. Nearly all such taxa in peat-forming environments appear to have had a trailing, or largely recumbent, scrambling habit that contributed to space occupation. The distribution of stems and rachises in coal-ball peats suggests tolerance of partial burial in litter. In general, ground cover is poorly represented in most coal-ball assemblages and rarely exceeds 3–4% of total peat biomass; the average coal-swamp community usually contained no more than two or three species. However, a dense mixture of numerous species of small ferns, sphenopsids and pteridosperms can be found on occasion



covering exposure horizons within large coal balls. All of the groundcover species could form dense cover, deduced from great abundance of foliar members and stems in some peat layers. However, in light of the irregular occurrence of such dense, often multispecies patches, they probably were irregularly distributed in space and probably represent the early stages of recovery from disturbance in areas under open canopy. Given that analyses of coal demonstrate frequent fires and floods, the typical rarity of groundcover-rich floras may be a preservational happenstance.

Patterns of distribution in coal-swamp assemblages (Phillips and DiMichele, 1981; DiMichele and Phillips, 1988; Pryor, 1993) suggest some segregation of seed-plant and lower-vascular plant ground cover, with large areas of overlap. Woody seed plants and sphenopsids, such as some or all species of *Callistophyton*, *Microspermopteris*, *Heterangium*, *Cordaixylon*, *Sphenophyllum*, and perhaps *Lyginopteris* had robust construction but probably had rapid enough growth and sufficient branching to cover substrates rapidly and recover from disturbances (Rothwell, 1981; Rothwell and Warner, 1984; Pigg et al., 1987; Taylor and Stockey, 1976; Batenburg, 1982). The many species of small gymnospermous seed plants with adventitious roots, vegetative propagation, and sprawling habit in Pennsylvanian forests stands in marked contrast to forests of today where virtually all the gymnosperms are upright, centrally rooted trees or shrubs. Ground-cover seed plants face life-history challenges in pollination and seed dispersal.

During the Pennsylvanian, most were wind pollinated (Rothwell, 1981) and many had winged, presumably wind-dispersed seeds. For successful sexual reproduction, such low growing seed plants must have occupied open areas, subject to wind currents.

In contrast to seed-plant ground cover, homosporous lower vascular plants produced highly dispersible spores and potentially bisexual gametophytes, probably requiring less wind current than seed plants. The herbaceous ferns were cheaply constructed and probably had rapid growth. Many species of *Botryopteris* and *Anachoropteris*, produced epiphyllous shoots (Phillips, 1974), permitting development of large clones that, presumably, could recover rapidly from burial by sediment or detritus.

Conspicuously less common than scramblers within peat swamps were centrally rooted groundcover plants with procumbent habit. Such plants would have been unable to escape burial by litter or sediment, and could not control access to resources by expropriating space. Lycopside such as *Hizemodendron serratum* (Baxter, 1965) and *Paurodendron fraipontii* (Phillips and Leisman, 1966) had morphologically inflexible centralized root systems, reflective of their rhizomorphic lycopsid ancestry. However, such lycopsids probably were tolerant of water saturated and-or nutrient poor substrates. They often occur in great abundance, suggesting local development of dense patches.

Fig. 4. Detrended correspondence analysis ordination of species (A) scored on Spearman rank correlation of ecomorphic characteristics (B). DCA simultaneously ordines taxa and traits. Labels in A: TL= tree lycopsid, TF= tree fern, TC= tree cordaite, TS= tree sphenopsid, TP= tree pteridosperm, GP= groundcover pteridosperm, GF= groundcover fern, GL= groundcover lycopsid. Species are keyed to the following numbers: 1 = *Diaphorodendron vasculare* (polycarpic lycopsid), 2 = *Diaphorodendron phillipsii* (polycarpic lycopsid), 3 = *Diaphorodendron scleroticum* (polycarpic lycopsid), 4 = *Synchysidendron resinum* (monocarpic lycopsid), 5 = *Paralycopodites brevifolius* (polycarpic lycopsid), 6 = *Lepidodendron hickii* (monocarpic lycopsid), 7 = *Hizemodendron serratum* (probable monocarpic lycopsid), 8 = *Lepidophloios hallii* (monocarpic lycopsid), 9 = *Lepidophloios harcourtii* (monocarpic lycopsid), 10 = Stephanian *Sigillaria* sp. (polycarpic lycopsid), 11 = Westphalian *Sigillaria* sp. (polycarpic lycopsid), 12 = Stephanian *Psaronius* sp. (tree fern), 13 = Westphalian *Psaronius* sp., 14 = *Sphenophyllum* sp. (sphenopsid), 15 = *Arthropityx* (sphenopsid), 16 = *Calamodendron americanum* (sphenopsid), 17 = *Mesoxylon* sp. (cordaite), 18 = *Pennsylvanioxylon birame* (cordaite producing *Cardiocarpus spinatus*), 19 = *Pennsylvanioxylon/Cordaixylon dumosum* (cordaite producing *Cardiocarpus oviformis*), 20 = *Medullosa* sp. (pteridosperm), 21 = *Lyginopteris oldhamia* (pteridosperm), 22 = *Callistophyton boysettii* (pteridosperm), 23 = *Schopfiastrum decussatum* (pteridosperm), 24 = *Heterangium lintonii* (pteridosperm), 25 = *Heterangium* sp. (pteridosperm), 26 = *Anachoropteris involuta* (fern), 27 = *Zygopteris* spp. (fern), 28 = *Ankyropteris brongniartii* (fern), 29 = *Botryopteris* spp. (fern), 30 = *Botryopteris cratis* (fern).

Table 3  
Pennsylvanian coal-swamp plant ecological patterns. Criteria for ranking taxa

1. Expense of plant construction per unit biomass: (1) lowest to (7) highest. Based on: amount and type of primary support tissue; amount and type of accessory support tissue; amount and type of secretory tissue; size of photosynthetic array and support branches
2. Size of plant: (1) small to (6) large. Based on: estimate relative to other plants in analysis of height, girth, and foliage, biomass of the mature plant. Includes data from compression fossils, where whole plants are found occasionally; six categories
3. Habit: (1) small trailing ground cover, (2) shrubs, (3) vines, (4) small trees, (5) large trees. Based on: comparative morphology of the plant; ordered by size
4. Reproductive effort: (1) low to (5) high for for polycarpic plants (multiple reproduction during life of individual), (6) for monocarpic plants (one reproduction in life of an individual). Based on: relative abundance of reproductive organs encountered in analysis of random samples of coal balls, normalized for abundance of parent plant. Estimate of seasonal fecundity, not lifetime fecundity.
5. Dispersal potential: (1) local dispersal, (2) extra-local dispersal, (3) uniformly wide dispersal. Based on: distribution of the disseminule vs. distribution of the parent plant in profiles and random samples of coal balls; for homosporous plants, based on the distribution of the isospore in palynological profiles.
6. Vegetative reproduction: (1) vegetative reproduction predominates, (2) sexual reproduction predominates. Based on: habit of plant and frequency of occurrence of reproductive organs (in some groups reproductive organs are rare and habit suggests high spreading rates)
7. Density: (1) clumped, low abundance, (2) uniform occurrence, low abundance, (3) clumped occurrence, moderate abundance, (4) uniform abundance, moderate occurrence, (5) clumped occurrence, high abundance, (6) uniform occurrence, high abundance. Based on: median abundance of taxon in zones of profiles of coal balls, modified by other information on tree stands, packing and relative distribution (largely from compression fossils).
8. Relationship to mineral matter and fusain (mineral charcoal): (1) low to (2) high. Based on: quantitative analysis of coal-ball profiles; the relative proportions of a taxon preserved as fusain; the frequency of occurrence of a taxon in fusain-rich zones; the association of a taxon with clastic partings, seat earth, or dispersed inert materials in the coal determined by petrographic analysis.

### 3.3.2. Vines

Climbing habit has been proposed for relatively few species of coal-swamp plants, mostly ferns and pteridosperms. Among ferns, *Botryopteris cratis*

(Millay and Taylor, 1980) is perhaps the best documented. This species frequently is found embedded in the root mantle of *Psaronius* tree fern trunks. In addition, long internodes and adaxial rather than lateral origin of epiphyllous shoots suggest a climbing morphology. Among the seed plants, most species of *Heterangium* and *Schopfiastrum decussatum* may have been lianas. Most of the numerous *Heterangium* species (Pigg et al., 1987) have small stems, a parenchyma-rich stele, irregular secondary xylem production, and little or no adventitious rooting. *Heterangium* species are found commonly preserved as fusain (mineral charcoal), which is inert and thus resists decay; possibly burned during crown fires, such preservation suggests that our record of these plants would be quite poor without such special preservational circumstances. The sphenopsid *Arthropitys deltoides* was suggested to be a vine (Cichan and Taylor, 1983) based on small stem diameters, tracheids with thin walls and large diameters, and wood with broad parenchymatous zones. Among medullosan pteridosperms, the only candidate for liana habit is *Medullosa endocentrica* (Hamer and Rothwell, 1988).

A number of plants may have been "facultative" climbers, sprawling across the surface until a substrate suitable for climbing was encountered. J.E. Mickle (pers. comm., 1987) has described these as "poison ivy"-like plants. Included are *Ankyropteris brongniartii*, which is often associated with tree-fern root mantles, has long internodes, and abundant stem aphanopores (Mickle, 1980), *Lyginopteris oldhamia*, *Microspermopteris aphyllum*, and, possibly, *Schopfiastrum decussatum*. As with *Heterangium*, these putative lianas often are preserved as fossil charcoal.

The apparent rarity of vines may reflect our inability to distinguish this habit clearly, and common preservation of vines as decay-resistant fusain suggests strong biases otherwise against their incorporation into the fossil record. However, present evidence suggests that vines were not common in peat-swamp forests. Pole trees, such as lycopsids, may have presented little opportunity for lianas, due to the lack of a highly branched crown through which a liana could extend. In addition, those lycopsids with crowns shed lateral

Table 4  
Summary of taxon rankings by ecomorphic criteria

	Exp.	Sz.	Hb.	RE	Dis.	V/S	Den.	F/MM
<i>Lepidophloios hallii</i>	4	5	4	5	3	2	6	2
<i>Lepidophloios harcourtii</i>	4	4	4	5	3	2	6	2
<i>Lepidodendron hickii</i>	5	6	5	5	2	2	3	3
<i>Diaphorodendron scleroticum</i>	5	6	5	2	1	2	5	1
<i>Diaphorodendron vasculare</i>	5	4	4	2	1	2	6	1
<i>Diaphorodendron phillipsii</i>	5	4	4	2	1	2	6	1
<i>Synchysidendron resinosum</i>	4	6	5	5	1	2	2	1
<i>Paralycopodites brevifolius</i>	5	4	4	4	1	2	5	3
Stephanian <i>Sigillaria</i> spp.	5	6	5	3	1	2	3	4
Westphalian <i>Sigillaria</i> spp.	5	4	4	1	2	2	3	4
<i>Hizemodendron serratum</i>	2	2	1	3	1	1	3	2
<i>Arthropitys (Calamocarpon)</i>	6	4	4	3	3	1	1	4
<i>Calamodendron</i> sp.	6	3	4	1	1	1	1	4
<i>Sphenophyllum</i> spp.	3	2	1	2	1	1	3	4
Westphalian <i>Psaronius</i> spp.	1	5	4	4	3	2	4	2
Stephanian <i>Psaronius</i> spp.	1	6	4	4	3	2	6	2
Medullosan pteridosperms	6	4	4	3	1	2	4	4
<i>Heterangium</i> spp.	3	2	3	3	3	2	1	4
<i>Heterangium lintonii</i>	3	2	1	3	3	1	1	2
<i>Callistophyton</i> spp.	3	2	1	3	3	1	3	3
<i>Lyginopteris oldhamia</i>	3	2	3	3	3	2	3	2
<i>Schopfiastrum decussatum</i>	3	2	3	3	3	2	1	2
<i>Botryopteris</i> spp.	2	1	1	2	3	1	1	2
<i>Botryopteris cratis</i>	2	1	3	2	3	2	1	2
<i>Anachoropteris</i> spp.	2	1	3	2	3	1	1	4
<i>Zygopteris</i> spp.	2	1	1	2	3	1	1	2
<i>Ankyropteris bronngiartii</i>	2	1	1	2	3	1	1	2
<i>Pennsylvanioxylon (C. spinatus)</i>	7	3	2	4	2	2	6	4
<i>Pennsylvanioxylon (C. oviformis)</i>	7	3	2	2	1	2	6	2
<i>Mesoxylon (Mitrospermum)</i>	7	3	2	2	1	2	3	2

branches (DiMichele and Phillips, 1985), which would have selected against lianas by removing crown branches as a stable support platform. Medullosans and probably *Psaronius* formed dense skirts of recurved, dead leaves (Pfefferkorn et al., 1984; Wnuk and Pfefferkorn, 1984), a habit that is thought to help some modern trees shed lianas, even if only a fortuitous byproduct of tree construction. Vines are most abundant in assemblages that also have diverse and abundant ground cover, perhaps due to disturbance and open canopies.

### 3.3.3. Trees

Trees were the major biomass contributors to Pennsylvanian peat deposits, and, by inference, the dominant elements of peat-swamp forests. They also imparted most of the structure and dynamics

to these forests. The ecomorphic classification of Pennsylvanian trees (Table 3) still strongly reflects evolutionary relationships (Figs. 3 and 4). When compared to phylogenies, tree ecomorphotypic groups are almost always monophyletic or paraphyletic rather than polyphyletic, indicating a strong overlap between phylogeny and ecology. The class-level clades represent different architectural “solutions” to arborescence, and have very different life histories and reproductive biologies. This pattern creates minimal taxonomic overlap among a broad spectrum of ecological strategies. The pattern may reflect the early radiation of class-level groups into largely “empty” resource space in the Late Devonian and Early Mississippian. Many lineages were diversifying rapidly at this time (Knoll et al., 1984; Niklas, 1994; DiMichele

and Bateman, 1996) and the result was extensive colonization of the land surface. It was not until extinctions in the Late Pennsylvanian and Early Permian that some of these primordial groups were reduced in importance or eliminated, ultimately permitting seed plants to expand greatly in ecological importance as tropical drying took place. In the context of Pennsylvanian ecology, the seed plants were “extinction resistant”, many species capable of surviving moisture stress and adapting to a wide variety of conditions. Thus, the Westphalian (Early and Middle Pennsylvanian) represents the zenith of the primeval forest and its type of resource partitioning with maximum delineation of ecomorphic variation among dominant groups.

Most Pennsylvanian-age trees were monoaxial in construction. The arborescent lycopsids were true “pole trees” (Thomas and Watson, 1976; DiMichele and Phillips, 1985; Wnuk, 1985; Phillips and DiMichele, 1992). Monocarpic species spent most of their lives as unbranched poles with reproductive organs borne in the branches of the crown, which formed only once, late in the life of an individual (*Lepidophloios* spp., *Lepidodendron* spp., *Synchysidendron* spp., many *Sigillaria* spp.). Polycarpic species had columnar trunks on which was produced a sparse crown of deciduous, cone-bearing lateral branches in two or more rows (*Paralycopodites brevifolius*, most species of *Diaphorodendron*). Lycopsid trees varied from site occupying forms with self-replacing populations to opportunists that colonized areas of severe disturbance (Thomas, 1981; Gastaldo, 1986; DiMichele and DeMaris, 1987).

Also columnar in basic form were calamite trees of the genera *Arthropitys* and *Calamodendron*. Some calamite trees produced whorls of branches much smaller in diameter than the parent axis, and others were unbranched (Crookall, 1969, gives examples from compression preservation). The variety of patterns described from compressions has not been correlated with coal-ball specimens. The calamites combined pole habit with clonal growth (Tiffney and Niklas, 1985), the only clonal Pennsylvanian trees, which gave them the ability to recover from repeated burial (Gastaldo, 1992). The ability to spread vegetatively evidently con-

ferred some advantage in coal-swamp habitats, where calamites usually were of minor quantitative significance but were widespread (at the Sahara locality in the Herrin coal bed, for example, sphenopsids account for <5% of the biomass but occur in 55% of the coal balls). Peppers (1985) suggests a brief period of quantitative importance during the Westphalian B (early Middle Pennsylvanian) based on palynological patterns.

Most species of *Psaronius* tree ferns and medullosan pteridosperms were monoaxial trees with large apical crowns. Through the development of complex, often highly branched fronds these trees were able to have an extensive photosynthetic array without branching of the trunk. Neither group ever produced species with the great size of the arborescent lycopsids. Although broadly similar in aspects of habit the ecologies of these groups appear to have been different, especially in the Westphalian.

*Psaronius* species varied in size from elfin, lacking substantial root mantle support for the stem, to large, robust trees perhaps up to 10–15 m in height (Morgan, 1959; Lesnikowska, 1989). Their highly dispersible isospores and broad distribution in Westphalian D (late Middle Pennsylvanian) and Stephanian (Late Pennsylvanian) swamps suggest a colonizing potential possessed by no other trees in the forest. Yet they appear to have been uncommon in Westphalian habitats dominated by *Lepidophloios* trees. Large trees evolved during the late Westphalian in clastic substrate habitats (Pfefferkorn, 1976); during the Stephanian large tree ferns became the dominant forms in swamps from which most kinds of trees had been eliminated by abiotically induced extinctions (Phillips and Peppers, 1984). Thus, it is possible that the *Psaronius* species that dominated the Stephanian swamps moved into peat-forming environments from surrounding habitats.

Medullosan pteridosperms encompassed a range of growth architectures, from slender and flexulous to robust with straight trunks (Pfefferkorn et al., 1984; Wnuk and Pfefferkorn, 1984). Stem and leaf tissues were highly invested with resins and sclerenchyma, making these among the most costly trees per unit biomass. Coal swamp species represent a subset of the numerous foliage types known from

compression preservation; no lineages confined exclusively to peat substrates have been described. Fronds of some species were extremely large, many meters in length (Laveine, 1986), but it is not certain that peat-substrate forms attained such size, at least not until the Stephanian (Galtier and Phillips, 1985). Medullosan species in coal swamps probably exploited patchy, open areas; foliage varies in thickness and different species have characteristics found today in sun-loving and shade-loving plants (Reihman and Schabillion, 1985; Beeler, 1983; Mickle and Rothwell, 1982). Common ovules and foliage indicate that several important species had distributions that did not overlap significantly. However, few “whole plant” species have been reconstructed at present. We have treated medullosans as a single category in multivariate analyses of coal ball profiles (noting ovule and foliage distributions) and abundances were highly variable.

Cordaitean trees, *Pennsylvanianoxylon/Cordaixylon* and *Mesoxylon*, had branched crowns and general habit more like that found in modern conifers and most dicotyledonous trees. *Pennsylvanianoxylon birame* was a small tree, 3–4 m in height (Costanza, 1985). Based on the presence of a stilt root system and association with marine invertebrates in coal balls, it has been suggested to be a mangrove (Cridland, 1964; Raymond and Phillips, 1983), but evidence is equivocal. This species or complex of species, all producing *Cardiocarpus spinatus* ovules, apparently could tolerate extremes of physical stress and may have colonized areas subject to regular, severe disturbance, and low substrate moisture. Reproductive output was high. Other species of *Pennsylvanianoxylon* or *Cordaixylon* appear to have had similar habits and physical tolerances (Rothwell and Warner, 1984; DiMichele and Phillips, 1995). *Mesoxylon* species, in contrast, appear to have been larger than *Pennsylvanianoxylon* (Costanza, 1985; Trivett and Rothwell, 1985). Species of *Mesoxylon* are most abundant in peats with high root to shoot ratios, indicating high levels of peat decay. Growth rings occur in some roots probably indicating seasonal variations in substrate moisture. Dense pycnoxylic wood in all cordaiteans suggests slow growth relative to the

large lycopsid trees and the cheaply constructed tree ferns.

## 4. Discussion

### 4.1. Patterns in Pennsylvanian wetlands

The maintenance of ecological gradients in the wet, lowland tropics over millions of years during the Pennsylvanian appears to have resulted in part from strong phylogenetic constraints. The resource requirements of species and the patterns of species replacement through time reflect distinct ecological centroids for each of several major lineages of plants. These ecological differences originated during the Late Devonian–Early Mississippian radiation of vascular plants, in which the major architectural groups (classes) originated. Such patterns persisted broadly in the tropics until the Early Permian. Unlike the world that followed the demise of this “primeval forest”, Mississippian and Pennsylvanian wet tropical landscapes were dominated to various degrees by four classes of plants, within which there were a number of highly distinctive orders. After the climatically mediated, major vegetational change that characterized the “Paleophytic”–“Mesophytic” transition in the Early Permian (Frederiksen, 1972; Knoll, 1984), one class, seed plants, dominated most of the landscapes. And since the Cretaceous, one group of seed plants, the angiosperms, has been predominant in most of the world’s terrestrial ecosystems.

During the Carboniferous and Early Permian the global diversity of terrestrial plants was considerably lower than during the post-Cretaceous (Niklas et al., 1980; Niklas and Tiffney, 1994). Ecological “redundancy” (sensu Perry, 1994) was confined mostly to class-level clades, and, as illustrated by the lycopsids, to families and genera within these classes. Following late Paleozoic extinctions, the dominant phylogenetic spectrum was simplified. The degree of ecological separation of the major clades during the zenith of the primeval forest must not be overstated, however. The centers of distribution, dominance, and diversity were distinct but there certainly was overlap, leading to the multispecies community types that

recurred during the Pennsylvanian on peat and clastic substrates.

Is phylogenetic partitioning of the ecological landscape the single key to patterns of persistence of both species composition and ecomorphic characteristics of Pennsylvanian plant assemblages? Are the patterns from this time interval thus unique and of no importance for broader debates in ecology? Consider that species turnover in a wholly Gleasonian, ecologically individualistic world should contribute to much mixing of assemblages through geologic time, especially in a world like that of the Pennsylvanian, dominated by glacial climatic dynamics (Cecil, 1990; Frakes et al., 1992). Even if the likelihood of species replacement in a particular ecological context is strongly skewed to close relatives, the migrations and floristic changes engendered by pulses of glacially driven climate change within a topographically heterogeneous tropical world should have created numerous opportunities for the development of non-analogue floras (sensu Overpeck et al., 1992). Such opportunities would have been both ecological and evolutionary, whereby members of one clade would be able to move into resources vacated by extinction of members of another, or give rise to descendant forms capable of exploiting available resources.

Stratigraphic patterns of species replacement and turnover suggest that there remains an important role for interspecific interactions and emergent ecosystem properties in the dynamics of species replacement. Few patterns of cross-clade replacement in ecological kind can be identified during the times of relatively stable ecosystem structure in the Pennsylvanian. Yet, there is indisputable evidence of species turnover at low levels between coals, which occurred during the cycles of climate and sea-level change separating major, widespread coal beds. Replacement species seem to be derived from within swamp habitats, for those clades that are centered in peat and clastic swamps, during times of background turnover. During times of major extinction, however, a different pattern occurs, one in which new ecological structure emerges following elimination of dominant groups from broad regions of the tropics (these patterns are similar to those identified by Brett and Baird, 1995, in marine ecosystems). At such times remain-

ing groups expand the breadth of their resource use, demonstrating the latent ability to move beyond the phylogenetic limits apparent earlier.

Patterns such as these suggest that when extinction levels are low, the system retains an element of ecological “fabric” created by the remaining species, a group-level expression of incumbent/home-field advantage. As a consequence the resource hyperspace vacated by extinction remains to some extent; it is most likely to be occupied by a species with resource requirements and utilization patterns similar to the prior occupant. For most of the Pennsylvanian, this replacement is most likely to be a species drawn from the same clade as the prior occupant, reflecting primeval phylogenetic patterns of ecological partitioning. Elevated levels of extinction disrupt this evolved fabric of interactions and permit competition among a broader spectrum of organisms for the less structured resource pool. With most incumbents eliminated, at least regionally, resources become available for use by any remaining forms that can exploit them. This is seen during the Stephanian, when groups that were more narrowly distributed in Westphalian ecosystems expand their ecological roles. Resulting assemblages have structure and dynamics distinct from those of earlier ecosystems; remaining species create a new system. In effect, a period of strongly individualistic dynamics may commonly follow a time of elevated extinction, as suggested by Vermeij (1987).

#### 4.2. *Coordinated stasis and ecosystem persistence*

The fossil record presents a mixed picture of persistence and hyperindividualism, which raises the ever present issue of scale. In dispute is whether landscapes and communities are dominated by individual species movements and repeated reassembly after major, particularly climatic, disruption, or whether they migrate or move into isolated refugia, intact to some large degree, as climates change regionally. Most neoecologists accept Gleasonian individualism as a scale independent process that accounts for the structure of ecosystems, landscapes, and biomes. Miller (1990) presents cogent arguments for the predominance of reassembly following environmental disruption.

tions, in the fossil record of marine invertebrate assemblages. Studies of Pleistocene terrestrial (e.g. Webb, 1988) and marine (e.g. Valentine and Jablonski, 1993) records suggests the predominance of individual migration and reassembly, although there may be biogeographic limits to the species pool (Roy et al., 1995). Buzas and Culver (1994) demonstrate reassembly of near shore benthic foraminiferal assemblages from a common species pool during successive shelf flooding events, and argue against system-level properties based on variable levels of species turnover between temporally distinct assemblages. Bennington and Bambach (1996) also argue for reassembly based on statistical analysis of successive faunas; although the same basic species pool is involved from one fauna to the next, they maintain that statistically different dominance-diversity and compositional patterns require an individualistic response model. Clearly, there is strong evidence of individualism in these studies, although there also is an emerging sense that such dynamics may be spatio-temporally bounded and that we must identify clearly the bounds of the species pool and seek causes at that level.

Other times in the fossil record demonstrate the long-term persistence of multispecies assemblages. Most notable is the work of Brett et al. (1990) and Brett and Baird (1995), which identified and brought into sharp focus the issue of coöordinated stasis. These authors document persistent assemblages of marine invertebrates punctuated by brief intervals of collapse and rapid reorganization. Within stable blocks small scale anagenetic change can be identified, but large scale evolutionary and ecological changes correspond to periods of maximum species turnover. Based initially on their work in the Hamilton Group (Devonian) of New York, they have extended the documentation of these patterns to other areas of the Paleozoic Appalachian Basin, and suggest that the classic trilobite biomes of Palmer (1965) represent a similar type of dynamic system (Brett and Baird, 1995). In the terrestrial realm, Wing (1984) identified persistent plant assemblages in the Eocene of Wyoming, although the stratigraphic section in which he worked did not include a major period of turnover and recovery. The basic patterns found

in these investigations are quite similar in whole or part to those of the Pennsylvanian tropical wetlands.

Neocology, presently, is beginning to develop a framework in which to describe and understand hierarchical organization of natural systems that extends rather than replaces reductionist models (e.g. Pimm, 1991; Allen and Hoekstra, 1992; Perry, 1994). Included are investigations of "assembly rules" for natural communities (e.g., Drake, 1990; Graves and Gotelli, 1993; Wilson and Whittaker, 1995), which seek regularities and restrictions on membership in multispecies assemblages of plants and animals. These analyses suggest that guild membership, especially when close phylogenetic relationship is involved, may preclude coöccurrence of species in the same community. Recent studies also have demonstrated the persistence of rainforest fragments in refugia within the Amazon basin during the height of the last glaciation, when dry forests were predominant throughout much of the area (Oliveira-Filho and Ratter, 1995); such investigations support models, at least for tropical terrestrial systems, that favor persistence over breakup and reassembly of wetland assemblages.

The presently available data on Pennsylvanian tropical wetland forests do not reveal directly whether long-term persistence of species assemblages and landscape architecture were due to climatic tracking, restriction to refugia or breakup and reassembly between times of everwet climate in basinal lowlands. Considering modern tropical analogues, we favor persistence as a result of migration of qualitatively intact assemblages, or restriction of remnant assemblages to refugia, rather than breakup and reassembly over some large, effectively limitless, geographic region. The Stephanian, in particular, was a time when climate oscillations increased in tropical areas. Terrestrial fossils record the existence of two biome types in the tropics, one dominated by wetland plants, the other by dryland plants, each occurring independently in lowland basins. The species composition of these two biomes overlaps minimally (Cridland and Morris, 1963; Broutin et al., 1990; DiMichele and Aronson, 1992), which strongly suggests that wetland plants "moved" or were relegated to dispersed patches as seasonal and everwet climates

began to oscillate in the tropics. Within this framework, the patterns of persistence and turnover in Westphalian–Stephanian swamp communities, which were described in the body of this paper, are an internal reorganization of the wetland biome. The ultimate demise of this entire system was driven by ever greater extremes of physical stress, which ultimately permitted the passive rise of the dry biome as the tropical depositional basins became seasonal.

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