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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

Volume 56, Supplement I, No. 4, pp. 24–41, 6 figs. April 20, 2005

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Terrestrial ecosystems of the late Paleozoic form a distinct global hierarchy of organizational levels, paralleling that seen in the modern world. At the highest level are at least three biotic provinces delimited by geographic and very broad scale climatic factors. Within each province are several biomes, reflecting substrate and climatic controls. Biomes are roughly equivalent to plant "species pools," those plants capable of colonizing available resource spaces within the physical area of the biome, and within which many species are roughly ecologically equivalent. Biome boundaries tend to be rather sharp. Within biomes are recurrent species associations, or communities, among which there is significant overlap in composition but that differ in dominance-diversity patterns. These patterns are examined here primarily in ancient tropical systems. The patterns of spatial partitioning of Permo-Carboniferous landscapes conform broadly to those predicted by the unified neutral theory of Hubbell (2001). However, species ecological equivalence is not "global" but rather appears to be restricted to biomes/species pools. The complexity of this hierarchical organization appears to have increased and deepened from the time vascular plants appeared on the land surface in the Late Silurian through the late Paleozoic and beyond. This may be related, in part, to increased "energy" input into the system, driving spontaneous organization of complexity and progressively restricting the spatial scale of species equivalence.

The Late Carboniferous and Early Permian time interval (~ 325–280 million years ago) was the first cold climate interval (glacial age, *sensu lato*) in Earth history where the continents were covered by vascular plants. A time of low atmospheric carbon dioxide, possibly high oxygen, and continental glaciation paralleling that of our modern Earth (Berner 1994; Gastaldo et al. 1996), the Paleozoic is an excellent analogue to the present. As a consequence, the spatial patterns of vegetational distribution during this period are remarkably similar to those of today (Ziegler 1990).

The objective of this paper is to examine broadly these patterns of plant distribution at several different scales, from global biotic provinces to the nature of plant response to differences in local habitat conditions. Such patterns underlie a core debate in ecology about ecosystem assembly: Are there such things as assembly rules? Are plants distributed in what would be, under ideal conditions, an essentially unbroken landscape gradient, reflective only of the individualistic tolerances of particular species, or are there interaction rules among species that lead to patterns of structure at different scales of resolution? Whereas this is in part a question of dynamics, which might be seen as difficult to derive from the fossil record, even the dynamics of extant ecosystems are largely inferred from the analysis of patterns in very short-term data with high levels of background "noise" (see any of numerous ecological studies, e.g., Hilborn and Mangel 1997, or Hayek and Buzas 1997 for overviews). Thus, the Carboniferous lends itself to the detection of significant patterns just about as well as modern systems. Plus it permits aspects of these systems to be studied over time as well as space, lending an extra dimension to pattern recognition. Thus, the basis to infer process and to test models is greatly enhanced by fossil data.

What follows is an initial examination of these patterns at multiple *spatial* scales. It is in space that these ecological patterns are expressed. The addition of a time dimension extends the analysis in a way that ecological studies of modern systems cannot approach. Temporal data allow a system resolved at a particular scale to be tracked through an extended period of time, such as repetitive examination of interglacial vegetation from one cycle to the next (e.g., Schoonmaker 1998).

THE LATE CARBONIFEROUS FLORA

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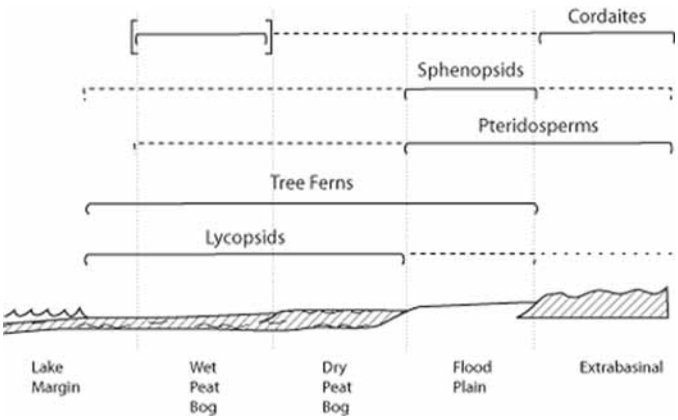

FIGURE 1. Landscape partitioning by major plant groups during the Late Carboniferous. Based on data from the Illinois Basin collected by Pfefferkorn (compression-impression fossils), Phillips and colleagues (coal-balls) and Peppers (palynofloras), from various publications.

Landscapes of the Late Carboniferous were dominated by entirely different plant groups from those that comprise most of the biomass in modern ecosystems. This is important and adds to the significance of the analysis because we can generalize even more strongly if we see patterns that **affect** taxonomically different but ecologically comparable groups of plants. At the highest taxonomic level, there were four Linnaean classes of vascular plants that were important components of Late Carboniferous ecosystems: lycopsids, sphenopsids, ferns, and seed plants. Within these groups were several subgroups, some of which persist to the present. The ecological distributions of these plant groups are summarized in Figure 1.

The lycopsids were composed of three orders, all three of which are still extant. The Isoetales, which were represented by the giant lepidodendrid "scale trees," were dominant biomass producers, particularly in wetland habitats, especially those in which peat accumulated (Phillips and DiMichele 1992). Like extant flowering plants, these ancient lycopsids could tolerate both freshwater and brackish water settings, allowing them to colonize all coastal and interior wet areas, forming marshes (DiMichele et al. 1979; Gastaldo et al. 2004a) as well as forested wetlands (Gastaldo 1986). The Lycopodiales and Selaginellales are herbaceous groups today and appear to have had similar roles in the Paleozoic (Thomas 1992). Although accounting for enormous amounts of biomass, the lycopsids were not a particularly diverse group, reflecting their growth in a very homogeneous, if extensive, range of habitats — wetlands. Some tree lycopsids, however, most notably *Sigillaria*, did grow on drier sandy soils within the broader wetlands, such as those formed by point bars, that could experience dry intervals. Lycopsids were present in each of the major floristic provinces, although different evolutionary lineages are present in each province with little cross occurrence (Meyen 1982; Archangelsky 1984; DiMichele and Phillips 1994).

The seed plants dominated *terra ferma* habitats, but were also widespread in wetlands. The most commonly encountered dominant tree groups include the medullosan pteridosperms (seed ferns) in the wet tropics (Phillips 1981; Pfefferkorn and Thomson 1982), and the cordaites (sister group of the conifers) in both the wet and seasonally dry tropics and north temperate zone (Meyen 1982; Raymond 1988; Falcon-Lang and Scott 2000; Falcon-Lang 2003). Less commonly found in basinal lowlands were the conifers (Lyons and Darrah 1989) and the peltasperms (Kerp 1988) in the seasonally dry tropics. In the south temperate zone several distinct groups are found including the pteridosperm *Nothorhacopteris*, ginkgophytes, cordaites, and conifers, though of types distinct from the walchians of the equatorial region (Archangelsky 1984; Archangelsky and Cuneo 1991). The glossopterid floras did not develop in the south temperate regions until the Permian (Cuneo 1996). There are many other groups of seed plants that were not trees but were important ecosystem components, such as the lyginopterids in the wet tropics and a whole array of unique taxa in the seasonally dry tropics.

Important ferns of the Late Carboniferous are divisible into several groups. The most conspicuous of these were the marattialean tree ferns. The Marattiales are still extant, although none of the modern forms are trees. This group dominated tropical wetlands in the latest Carboniferous. These trees were inexpensively constructed in terms of carbon biomass allocation, with stems, leaves, and especially the roots of the trunk-supporting root mantle, rich in airspaces. Inexpensive construction, combined with massive reproduction, permitted the earliest species of this clade to play the ecological role of opportunists though they later rose to ecological prominence to the status of dominant forest trees following extinctions within the Late Carboniferous (Phillips et al. 1974; Pfefferkorn and Thomson 1982; Lesnikowska 1989; DiMichele and Phillips 2002). Marattiales appear in the south temperate regions in the Permian (Cuneo and Archangelsky 1987). Small ferns are assignable to the Filicales (though with organization quite different from extant members of that group, Phillips 1974) and the Zygopteridales, a wholly extinct group (Dennis 1974), in the tropics. The small ferns occupied a wide range of ecological roles, including ground cover and vines, and many were opportunists responding to local disturbance (LePage and Pfefferkorn 2000).

Calamitean sphenopsids of the Carboniferous are very similar in gross structural organization to modern Equisetales, except for the presence of secondary xylem, permitting the Carboniferous forms to grow much larger. This group occupied a very narrow range of habitats, primarily those of aggradational or disturbed settings where their clonal growth habit would permit recovery from burial by sediment accumulation (Gastaldo 1992; Pfefferkorn et al. 2001). Possibly reflective of the narrowness of their habitat, they appear to be depauperate in species diversity throughout their geological history. These plants also were a constituent of the swamps, coexisting in space and time with everything from the “wettest” to the “driest” lycopsids. (Gastaldo et al. 2004b).

Many of these Carboniferous plant groups have relatively closely related modern descendents, although these descendents are very dissimilar architecturally and therefore ecologically (in the sense of Hallé et al. 1978). From reproductive and anatomical points of view, the giant lycopsid trees, in particular have no comparable morphological analogues, and no close phylogenetic relatives still important in modern ecosystems. Modern *Equisetum*, although not woody or arborescent, is very similar to the ancient calamites in basic architecture, including narrow ecological breadth. However, today’s floras have architecturally similar plants that use ecospace in a similar manner to the extinct forms (Hallé et al. 1978; Pfefferkorn et al. 2001). This similarity allows us to compare the reaction of flora and vegetation over long time intervals on a “taxon-free,” ecomorphic basis.

BIODIVERSITY PARTITIONING

Global Provinces

The largest geographical scale of biological partitioning is the province, which has both spatial and temporal ranges (Wagner 1993). There have long been considered to be three fundamental Carboniferous plant biogeographic provinces (Fig. 2), following the terminology of Raymond et al. (1985; Raymond 1996), with more traditional terms in parentheses (Gothan 1937; Halle 1937; Chaloner and Lacey 1973; Chaloner and Meyen 1973): Equatorial (Euramerican-Cathaysian), Northern High Latitudes (Angaran) and Southern High Latitudes (Gondwanan). In addition, a southern Paratropical floral zone has been recognized recently in the Early Carboniferous (Paracan realm; Iannuzzi and Pfefferkorn 2002). The small number of biogeographic provinces recognized in the Permo-Carboniferous is likely a consequence of the continental configuration of the time. The aggregation of most of the Earth's continental landmasses into a single, nearly continuous region provided opportunities for lateral extensions of plant ranges within, and occasionally between, paleoenvironmentally suitable regions. In the modern world, by contrast, the hyperdispersion of the continents presents many natural barriers to plant dispersal and range extension, isolating climatically similar regions. This leads to the evolutionary independence of such areas and the development of distinct floras.

The Equatorial Province frequently has been subdivided (Fig. 2) to account for persistent differences between eastern areas (Cathaysian), western floras of everwet climates (Euramerican), and western floras of seasonally dry climates (western North American). Clearly, this is a heterogeneous way of dividing up the equatorial region; the two western divisions are cast better as biomic differences within the larger province. In addition, there is clear evidence of spread through time of certain distinctive taxa within the tropics (Fig. 3), indicating that migration routes were present intermittently, permitting taxa to spread over vast geographic areas within environmental

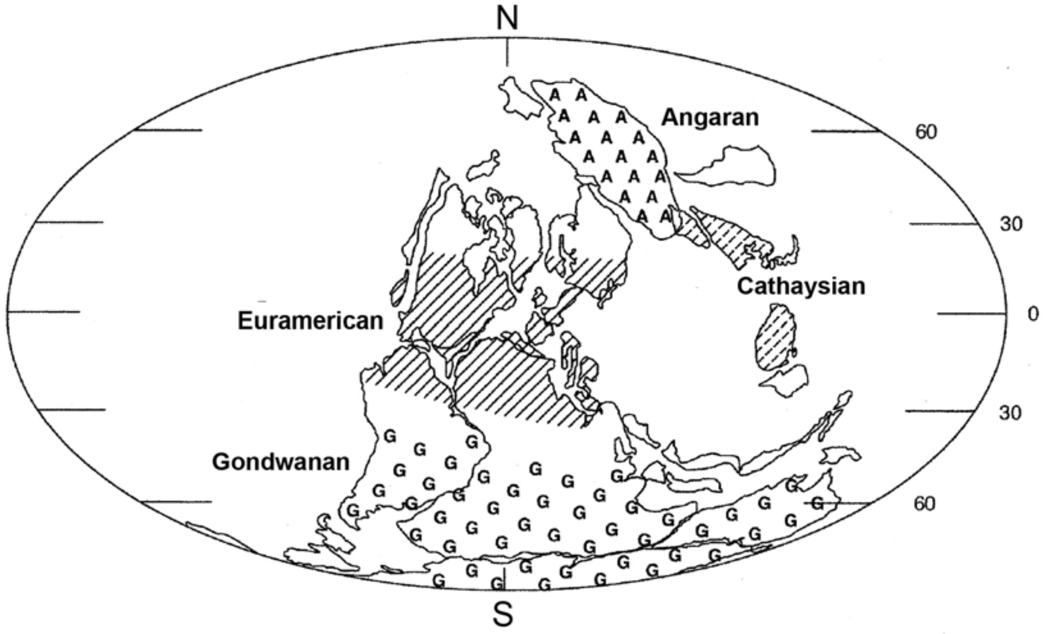

FIGURE 2. The world of the Carboniferous-Permian boundary showing continental positions and distribution of major floristic provinces (base map modified from Eldridge, et al. 2000).

constraints (Laveine et al. 2000). The Cathaysian flora also contains seasonally dry and everwet biomes. Both have many generic level similarities to those of Euramerica at the generic level but differ considerably at the level of species. This illustrates the persistent confusion of scale of resolution of these biological patterns. The basic global subdivisions of the Carboniferous persist into the Permian, although more subzonation frequently has been recognized (Chaloner and Meyen 1973; Ziegler et al. 1981; Rees 2002; Rees et al. 2002)

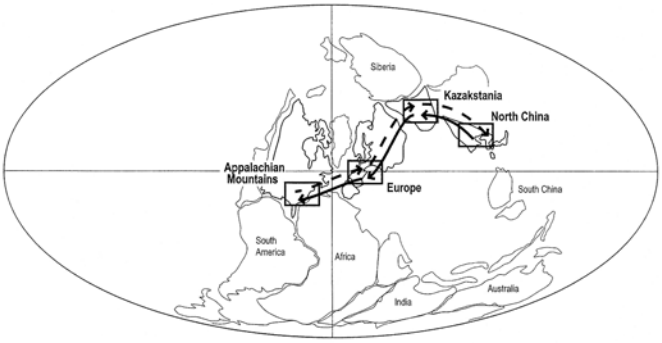

FIGURE 3. Sweepstakes migration route within the Late Carboniferous tropical wetlands. Migration occurred in both directions and included several taxa. Geographic barriers on the route often delayed migration of specific taxa for millions of years whereas others passed through "instantaneously" in geological terms. The four boxes show the areas from which extensive data sets have been published (modified after Laveine, et al. 2000).

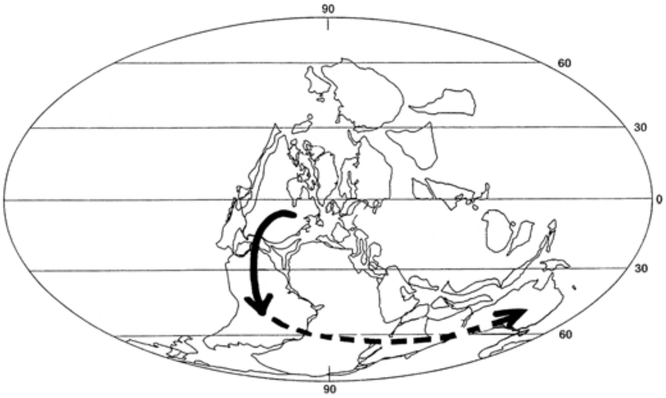

FIGURE 4. Migration route of Late Carboniferous tropical Euramerican plants into the southern temperate Gondwanan realm, suggested for the *Lesleya-Megalopteris-Glossopteris* complex, near the Carboniferous-Permian boundary (reconstructed from interpretations of Leary 1998).

Regions of overlap between these provinces occurred along their contact zones and have been well documented in the Permian. These overlaps occur primarily along the margins of the Tethys Ocean and in other parts of the margin of the Equatorial Province (e.g., Wagner 1959, 1962; Broutin et al. 1995; Broutin et al. 1998). In these areas, mixtures of plants common to seasonally dry areas of the different provinces appear to be the most commonly intermixed taxa and to penetrate most deeply into adjacent provinces. One of the most significant interprovincial migrations (Fig. 4) may be the movement of the ancestors of *Glossopteris*, a dominant in Early Permian age temperate floras of the Southern Hemisphere, from their sites of tropical origin in better drained, extrabasinal floras (Leary 1998).

Provincial regions differed in botanical composition at the level of orders and families, with class-level evolutionary lineages having similar ecological patterns of distribution in each area. The Equatorial Province is by far the best studied, a consequence of the concentration of workers and the accessibility of plant fossils exposed in the course of mining Carboniferous coals. Although the same basic classes of plants are dominant in each of the provinces, the orders and families that dominate ecosystems are considerably different. Members of the class Lycopsida are most abundant in wet habitats in all three regions, with seed plants of the Spermatopsida dominating in *terra ferma* environments. Small ferns, mostly Filicales, can be found as opportunists, particularly in *terra ferma* settings. And the Marratiales begin as small, probably opportunistic forms, later becoming dominants in wetlands. The calamitean Sphenopsida are of low diversity and most common in stream-and-lake margin deposits.

The specific lineages of these plants are generally quite different in each province. For example, the stigmarian (rhizomorphic) lycopsids, *sensu* DiMichele and Bateman (1996), are the dominant elements in most Equatorial Carboniferous wetlands, especially those that accumulated peat, up to the end of the Westphalian. Dominant lycopsids in the higher latitude provinces (including the Paracan realm) were primarily cormose isoetaleans, even if of tree stature. Equatorial seed plant lineages of the Carboniferous include the medullosan pteridosperms, the lyginopterids, the callistophytaleans, the Euramerican cordaites and their sister group, the walchian conifers, the latter groups demonstrating abundance in seasonally dry habitats. (Cunningham et al. 1993) In contrast, ruflorian cordaites rose to dominance in the Northern High Latitudes beginning in the mid-Carboniferous (Meyen 1982). In the Southern High Latitudes the appearance of glossopterid seed plants did not occur until the Permian (Cuneo 1996). Among the sphenopsids, the sphenophylls were most common and diverse in the Equatorial Province. Ferns were opportunists in all three provinces, and the marattialean tree ferns (*Psaronius*) are known from the Equatorial Province in the Carboniferous and Permian but also appear in the Southern High Latitude Province in the Permian.

Thus, at the highest levels, the floras of these Late Paleozoic provinces appear to be distinct at a deep evolutionary level with rare crossover taxa, such as the proposed *Lesleya-Megalopteris-Glossopteris* complex. Perhaps this represents different radiations from common Late Devonian or earliest Carboniferous ancestral species lineages.

Biomes within Provinces

The floras that characterize different floral provinces (different physical parts of the globe) can be broken down into sub-floras, or biomes, that characterize different climatic regimes and, possibly, different substrate conditions (Ziegler 1990; Rees 2002). The best example of this is found in the western part of the Equatorial Province (i.e., present day western North America). In this area, three distinct vegetation types have been identified that have few species in common. Two of these, in particular, are well known and characterized. We will refer to these as the wetland biome and the seasonally dry biome (DiMichele and Aronson 1992). The third biome, one of xeric areas with limited soil moisture, is known from a few Permian deposits formed during times of extreme drying in basinal lowlands (DiMichele et al. 2000). This flora probably was present in the equatorial regions during the Carboniferous but in areas remote from basinal lowlands, where preservation was not likely (Lyons and Darrah 1989).

Ziegler (1990), following Walter's (1985) concept of modern biomes, hypothesized that the Permian world was divided in much the same way as today. Using climatically sensitive sediments, Ziegler (1990) identified climate zones and mapped floras onto these. Although his analysis is focused on the Early Permian, the basic patterns described probably would apply equally well throughout much of the Carboniferous. Ziegler et al. (2003) argued that patterns of atmospheric and oceanic circulation created global climatic patterns much like those seen today, and, most importantly, that the boundaries between these climatic zones were relatively sharp. As a consequence of the abrupt climatic discontinuities, there are relatively sharp biomic boundaries.

Continued studies demonstrate that floristic zonation was geographically complex, especially during the Permian (Rees 2002; Rees et al. 2002). Such zonational complexities may reflect the geographical evolutionary roots of floras at the provincial scale (Broutin et al. 1990; DiMichele and Aronson 1992), thus, constraining biomes within specific floristic provinces. The concept of a floral province is primarily biogeographic. Biomes, on the other hand reflect the climatic-edaphic restrictions on species distributions within provinces, a consequence of both evolutionary and ecological processes.

The plants of the Wetland Biome (everwet biome of Ziegler 1990) comprise the best known Carboniferous flora, and may be one of the best known fossil floras from any time interval in Earth history. Knowledge of this flora derives from its close association with coal beds and, therefore, its exposure in the course of coal mining throughout Europe, North America, and China. The wetland biome includes locally dominant tree forms from five plant lineages in four classes: (1) the lepidodendrid lycopsids of the class Lycopsida; (2) the calamitean sphenopsids of the class Sphenopsida; (3) the marattialean tree ferns of the class Pteropsida; and (4) the cordaitean seed plants and medullosan seed plants of the class Spermatopsida. In addition, there are many species of ground cover and vines drawn from these same classes. These are the plants so often pictured in classic dioramas of Late Carboniferous lowland, tropical forests.

The Seasonally Dry Biome (summer wet biome of Ziegler 1990) was first described in detail by Cridland and Morris (1963) during a study of plants of the Kansas Pennsylvanian-age coal measures. From the Late Pennsylvanian (Stephanian) Garnett locality, they described a flora dominated by seed plants, most notably conifers, with an admixture of other seed plants. Since that time, there have been reports of a number of other such floras, generally enriched in and dominated by seed plants, including conifers and other genera not found in the wetland biome. The best described of these include the Late Pennsylvanian floras of the Hamilton Quarry of Kansas (Rothwell and Mapes 1988; Cunningham et al. 1993) and the Kinney Quarry of New Mexico (Mamay and Mapes 1992); there are numerous sites that have been collected less intensively but that preserve similar floras in both Europe and North America (Broutin et al. 1990; DiMichele and Aronson 1992). Evidence of the Seasonally Dry Biome is found in Middle Pennsylvanian (Westphalian) coastal wetland deposits well before its more fully developed appearance in the Late Pennsylvanian. The early appearances are diverse in composition. For example, early, Westphalian-age conifer occurrences all occur as rare fragmentary remains apparently transported from better-drained uplands into adjacent basins (Lyons and Darrah 1989). These occurrences indicate, however, that this vegetation existed outside of the window of preservation for perhaps as much as 6 million years before the discovery of extensive conifer-dominated macrofossil deposits. On the other hand, there are fossil assemblages from the Early Westphalian dominated by groups that do not appear to be part of the Seasonally Dry biome, which appears in the later Pennsylvanian. These include floras that have clear substrate/edaphic differences, such as the limestone soil floras described from the Spencer Farm site in Illinois (Leary, 1973, 1974, 1980; Leary and Pfefferkorn 1977), which are dominated by the broad-leaved seed plants of uncertain affinity, *Lesleya* and *Megalopteris* (Fig. 5). Other floras are dominated by cordaites (Falcon-Lang 2003; **?????** in press), which were a group that had both lowland, wetland species and extrabasinal species (Fig. 6). None of these floras include a

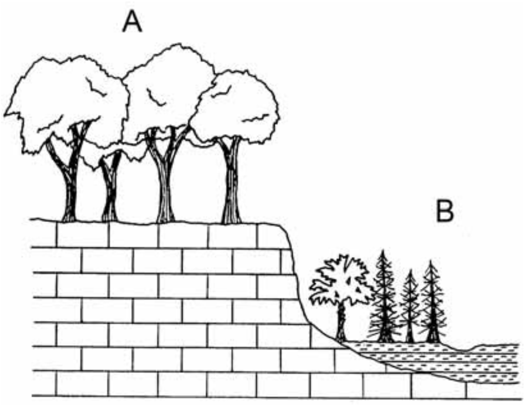

FIGURE 5. Cross section through a reconstructed landscape in western Illinois during the Early Pennsylvanian. A: Extrabasinal, rarely preserved flora growing on limestone soil and experiencing water stress. The trees shown represent *Lesleya* and *Megalopteris*, the presumed tropical ancestors of the south temperate *Glossopteris*. B: Wetland flora here represented by medullosan pteridosperms and *Calamites* (reconstructed after Leary and Pfefferkorn 1977).

conifer component. This indicates that extra-basinal floras (sensu Pfefferkorn 1980) were compositionally diverse, indicative of distinct microhabitat differences, possibly reflective of very subtle differences in substrate moisture of even temperature regimes.

The xeric biome was characterized by long periods of dryness and short periods of moisture, based on paleosols and general sedimentary environments (DiMichele et al., in press~~/wet spots~~). Thus, we refer to it as the Seasonally Wet biome. These floras occur in association with bedded gypsums, oolitic limestones, and weakly developed paleosols. It is probable that plants grew along streamsides and significant portions of interfluves were weakly vegetated or, at times, even un-vegetated. The flora was composed entirely of seed plants, including conifers, cycads, and putative ginkgophytes (DiMichele et al. 2000, 2004). DiMichele et al. (2000) found this flora in rocks of late Early to earliest Middle Permian age in small channel-form deposits of North Central Texas. In taxonomic composition it compares most closely to floras of the Late Permian "Zechstein" flora of Germany and England (Schweitzer 1986) and paleotropical Mesozoic floras of Late Triassic and Early Jurassic age. Consequently, its appearance is precocious and unexpected in rocks as old as Early Permian. A similar Early Permian "precocious" flora has been reported by LePage et al. (2003) that includes elements from both the Angaran and Euramerican floral provinces, which indicates that this kind of biomic partitioning occurred independently in different provinces.

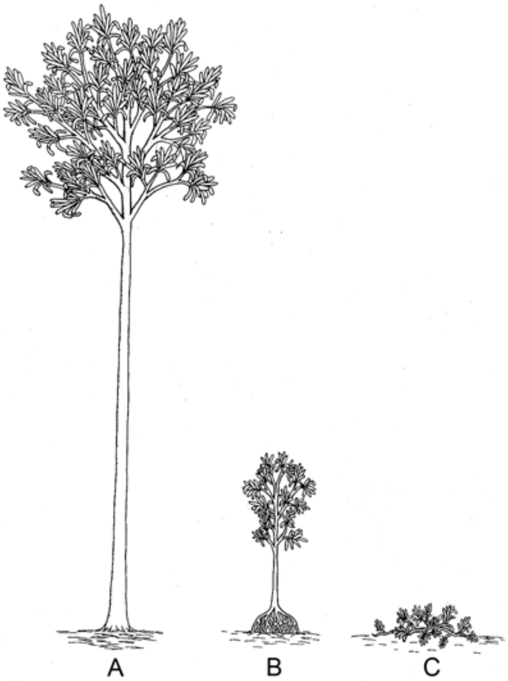

Figure 6. Reconstructions of the three life forms of cordaitalean gymnosperms from the Late Carboniferous. A: Species from extrabasinal settings on seasonally dry soils (after Grand 'Eury 1877). B: Middle Pennsylvanian species in coastal mangrove environments, often associated with peat formation (after Cridland 1964). C: Late Pennsylvanian species living in peat-forming, nutrient poor wetlands (after Rothwell and Warner 1984).

The three tropical biomes share few species in common (Broutin et al. 1990; DiMichele and Aronson 1992). The most prominent crossover species between the Wetland and Seasonally Dry biomes are primarily opportunistic weedy forms of wet soils, such as marattialean tree ferns (Lesnikowska 1989), or streamside specialists adapted to the rigors of periodic catastrophic disturbance, such as calamites (Barthel and Rössler 1996; Gastaldo 1992). The environments these kinds of plants inhabited occurred in nearly all landscapes, but changing climatic conditions reduced the areal extent considerably, from "wetlands" to "wet spots" (DiMichele et al. in press). Between the Seasonally Dry and xeric Seasonally Wet biomes, the common species are primitive groups of conifers. By the time the Seasonally Dry biome appears in the rock record, the western tropical region appears to have been sufficiently dry to exclude virtually all elements from the former Wetland Biome.

Recurrent Assemblages/Communities within Biomes

Within any given biome there are recurrent habitat-specific assemblages that share to a varying extent species from the larger biome-level species pool. It is at this level that questions of body size also become prominent influences on how community-level dynamics are understood. For example, very small organisms, such as bryophytes and small ferns, may perceive the resource space as more heterogeneous than larger organisms such as trees, shrubs and vines. Here we will concentrate on the larger organisms, those more likely to be preserved in the fossil record in sufficient numbers to be understood in a quantitative sense (Scheihing 1980). In order to elucidate these kinds of distributional patterns, a great deal of collecting and quantitative study is necessary. Consequently, the Wetland Biome of the tropics is best suited to serve as an example.

At the broadest spatial scale, tropical wetlands can be divided into two major landscape types (see Allen 1998, for a discussion of the concept of "landscape"): mostly flooded, swamp environments, and *terra ferma* habitats with wet substrates but short or no periods of standing water (Gastaldo 1987). The dominant elements in these two landscape types are very different. During the Early and Middle Pennsylvanian (Westphalian), swamp habitats, often autothonous or parautothonous in preservation, were dominated on average by lycopsid trees, with subdominant pteridosperms (Pfefferkorn and Thomson 1982; Phillips et al. 1985; Wnuk and Pfefferkorn **1989 ?? 1987 in biblio**; Gastaldo et al., in press). In contrast, *terra ferma* assemblages, preserved largely as allochthonous accumulations, were dominated by pteridosperms with subdominant sphenopsids and, late in the Westphalian, tree ferns (Pfefferkorn and Thomson 1982; Scott 1979). During the Late Pennsylvanian (Stephanian), following major extinctions at the Westphalian-Stephanian boundary (Phillips et al. 1974), tree ferns dominated various habitats in both the swampy and *terra ferma* parts of the Wetland Biome, with pteridosperms in a subdominant role (Willard and Phillips 1993).

Within each of these broad landscape types a number of species assemblages can be recognized by broad recurrence of dominance-diversity patterns. In the swampy parts of the landscape, peat substrates and clastic substrates, had different suites of dominant lycopsid trees (Willard 1989a, 1989b). And in peat substrates themselves, both within and between coals, distinctive recurrent assemblages have been recognized statistically (Phillips and DiMichele 1981; DiMichele and Phillips 1988; Raymond 1988; Willard and Phillips 1993; Pryor 1993). Depending where in time, such communities may be characterized by low diversity and high dominance of specific lycopsids, such as *Lepidophloios*, presumably on flooded sites. In contrast, other communities are rich in ground cover and vines, dominated by a mixture of lycopsids, such as *Diaphorodendron* and *Synchysidendron*, pteridosperms and tree ferns. These plants apparently grew in areas with periodic substrate exposure and associated with elevated levels of charcoal and clastic matter in the coal.

Similar broad plant-by-environment patterns ("biofacies") have been recognized in floodbasin settings (Scott 1978, 1979; Gastaldo 1986). In clastic swamps, dominance by *Lepidodendron*, pteridosperms, and calamites was most common (Pfefferkorn and Thomson 1982; Gastaldo 1987, 1992). Lycopsids were much less abundant in less swampy areas. In nearly all instances, however, there is a great deal of overlap in specific taxonomic composition among wetland habitat clastic deposits. The amount of overlap is variable. Undersampling spatially will make assemblages appear more distinctive whereas, in other instances, local transport of plant parts within flooded wetlands will tend to homogenize assemblages. For example, DiMichele and Nelson (1989) found a sharp contact zone between plant assemblages in the roof shale of the Springfield coal of Indiana, one dominated by pteridosperms, the other by sigillarian lycopsids. On the other hand, Gastaldo et al. (2004b) identified spatial co-occurrence of most of the major plant groups, including different kinds of lycopsids and pteridosperms, in an *in situ* forest in the underclay of the Blue Creek coal of Alabama.

If this discussion appears undefined and lacking in clear structure it is because the degree of species overlap in physical distribution is much greater within biomes, at the scale of communities, than between biomes. Although there are general patterns of recurrence, there also are degrees of overlap in species distribution patterns that put most in combination at some time and place. The publications cited above document both the local and landscape patterns of differentiation.

DISCUSSION

Where the Action Is

When examined in space, and over a limited interval of geological time, it is apparent that species distributions can be recognized at several hierarchical levels. Our ability to create such organizational spheres, however, begs an important question. Are there processes that operate only at one level or another of the hierarchy? In other words, does the existence of several global species provinces, or of several different biome-level species pools within each province, imply the existence of causation at that same hierarchical level? Are there emergent processes with limited spheres of operation or are their processes that operate at different rates at different spatial scales? The correct answer to these questions might be "perhaps, but not likely."

The alternative is to suggest that processes operating at the level of individual-plant interactions dictate the entire structural hierarchy (Hubbell 2001). In this case, the dominant processes would be inter-individual competition (as opposed to interspecific competition), colonization of temporarily available resource space (following disturbance), and changes in the biogeographic range of populations in response to changes in ambient climatic factors such as rainfall and temperature. In the end, this comes back to the inter-individual factors of differential and directional spatial establishment mediated by competition and opportunity.

It is difficult to demonstrate a need for higher-level processes to create the higher-level spatial patterns. Examine the instance of biomes within provinces, for example. A biome is a collection of organisms with similar climatic and substrate requirements. The limits of those conditions in space will mark the boundaries of the ranges of those species broadly "adapted" to such conditions. And studies of plant geography indicate that climate zones change relatively abruptly in space, not over long gradients (Walter 1985), dictating reasonably sharp boundaries between biomes.

Superimpose on biomes the combined constraints imposed by natural barriers, such as oceans, and major climatic zones, both latitudinal/longitudinal and those created by mountain ranges, and the result is provincialization. Regions with Mediterranean climate, such as southern Europe and coastal California, have been isolated for so long that completely separate species pools developed in each, despite similar physical conditions. This is the interaction of evolution with resource opportunity writ over millions of years. Provincialization may appear spontaneously as the global flora becomes more complex and as natural barriers change over time.

To the extent that there are "emergent properties" of species or individual interactions, these may be found in the controls on community assembly at any given point in space. As Weiher and Keddy (1999) or Belyea and Lancaster (1999) have pointed out in developing models of ecosystem assembly, there are three major components controlling a local flora or fauna. (1) Can individuals of a species get to a site of available resources? Thus, is that species a member of the regional species pool, which is approximately the same as biome? (2) Once dispersed to the site, can those individuals germinate and then utilize the resources effectively, and can they withstand the physical rigors of the particular site? (3) If (1) and (2) are affirmative, can the individuals colonize the site in the face of competition for resources with other individuals, either those that might be there already or others that might enter the site later? This latter point is probably one of population dynamics related both to the efficiency of resource exploitation (e.g., Tilman 1988), and simple likelihood related to numbers of individuals able to find available resources (e.g., Hubbell 2001). Once established, a species mixture may persist locally simply due to relative proportions of reproductive output by the individuals within a given area. The dominance-diversity hierarchy may be difficult to change without a catastrophic local or regional disturbance because the more abundant species will be the most likely to capture/colonize available space, assuming a general stochastic equivalence among competitors in the face of minor changes in climate and disturbance regime.

As Ulanowicz (1997) has argued, however, once higher levels of system organization appear, these may exert constraints on the dynamics at lower levels. Perturbations, for example, may occur at spatio-temporal scales that are invisible when examined at certain levels of the spatial hierarchy but that, nonetheless, constrain what may or will happen particularly at levels below those where their impact is seen. For example, a climate change may affect the physical distribution of conditions that set the boundaries of a species pool (biome) but may not affect the dynamics of recovery from a local disturbance within that biome. At the same time, changed climatic conditions may greatly change the frequency or magnitude of disturbances at lower ecological organizational levels in the spatial hierarchy.

Self-regulating Properties of Late Paleozoic Ecosystems

It is possible that Late Carboniferous ecosystems had a peculiar form of cybernetic (self) regulation, or one that was more visible in these systems than in those from later periods of geological time (should it prove to be a general ecosystem property, see Drake et al. 1999). This property has been recognized only in the tropical wetland biome where most late Paleozoic paleoecological investigations have focused. In brief, it has been asserted (DiMichele and Phillips 1996; DiMichele et al. 1996; Pfefferkorn et al. 2000; DiMichele et al. 2000) that Late Carboniferous coal-swamp ecosystems retained certain clade-by-environment patterns of dominance, despite a constant background of species turnover of a few percent per 100,000 years, between successive peat-forming wetland ecosystems in geological time (successive glacial-interglacial events). The pattern was first recognized by classifying species according to their ecomorphic characteristics rather than by taxonomically specific characteristics (DiMichele and Phillips 1996), e.g., relative reproductive output, propagule dispersal potential, resource allocation patterns, tree versus shrub versus vine versus ground cover growth habit, and so forth.

There is a clear pattern of ecomorphic replacement within a biome following low level background extinction during the Carboniferous-Permian. This appears to result from ecological limitations imposed by a much older Devonian phylogenetic radiation in which the major plant clades (taxonomic class-level groups) first evolved and developed distinctive ecological centroids (broad environmental tolerances, e.g., wetlands vs. seasonally dry *terra ferma* settings) as the evolutionary radiation proceeded (Peppers and Pfefferkorn 1970; DiMichele and Bateman 1996; DiMichele et al. 2000). In this early radiation, all the major body plans of vascular plants appeared — Lycopsida (in wetlands), Pteropsida (as opportunists in *terra ferma* environments), Sphenopsida (in aggradational environments), and Spermatopsida (in *terra ferma* environments) — each body plan the equivalent of a traditional Linnaean class. Every group was represented to greater or lesser degrees within each of these broad physical settings, but the dominant clade further subdivided the resource space in a similar manner among lower taxonomic groups, resulting in a kind of fractal pattern. The result was that dominant lineages tended to continue in their particular ecological roles. Extinct ancestors were replaced by structurally and ecologically similar descendant forms within the environments in which they were dominant — such species replacement by close relatives, in response to background extinction, led to conservatism in ecosystem architecture.

The Spatial Limits of Species Substitutability

In a recent book, Stephen Hubbell (2001) developed a new null model for the controls on species assemblage composition. In his model, all species are ecologically substitutable at a global level, interactions are modeled among individual plants rather than among species, and the proportional abundances of species dictate the likelihood of resource capture in response to the disturbances that create opportunities for colonization. The model considers dynamics at the level of both local and regional species pools. The assumption of species substitutability has come under criticism (e.g., Terborgh et al. 1996) because it is clearly incorrect, especially when viewed at a global level. However, Hubbell's thinking developed from years of observing the tree-species composition of tropical forests in which species turnover appeared to be slow and generally non-directional, a pattern he and Robin Foster described as "community drift" (Hubbell and Foster 1986). And when one walks through a forest, even in the temperate zone, it is not clear that a tree on any one spot is competitively favored by the conditions at that point in space. It might be asked if indeed species are not substitutable — but at what spatial scale?

Applicable to this problem is the yet older question of how local species assemblages are structured. Is a local assemblage a happenstance association of species with similar resource requirements under the prevailing climatic conditions, what has been labeled the "individualistic" model? Or are there predictable interactions among species that control the structure of a local assemblage, such that there are distinct emergent properties of the group not present in any of the individual species? The touchstones of this debate are Henry Alan Gleason (1926) and Frederick E. Clements (1916), although the debate has been recast in a variety of terms since, including and extensive debate during the 1970s and 1980s, largely among animal ecologists, about ecosystem assembly (see Diamond 1975). Students of North-temperate Quaternary palynology have strongly reaffirmed the individualistic model by noting that tree species recover from deglaciation at independent rates, resulting in "non-analogue" communities (e.g., Overpeck et al. 1996).

The question becomes, then, is there a scale at which Hubbell's assumption of species substitutability, basic species individuality, applies (given that it cannot apply globally — what are the spatial limits)? The deep fossil record may provide an answer to this question. From our analysis, it appears that the biome is the best approximation of a regional species pool. The regional species pool will contain those species that will be stochastically capable of colonizing a given patch in a local area, allowing for fluctuations in temperature and rainfall and associated disturbance frequency, on a time-averaged basis. We suggest that such species pools might be called "Hubbell cells" in analogy with the Bénard convection cells that develop spontaneously in an open pot of water when heated at the bottom. Species pools may develop more or less spontaneously across an ecological landscape. This may reflect increased "energy" input to systems over time, created by evolutionary advances in photosynthetic biochemistry, the evolution of complex root systems, and the elaboration of leaves and tree stature.

Such organization of ecological systems in the modern time plane was suggested by Weiher and Keddy (2001), in which they developed a verbal model of ecosystems as thermodynamically dissipative systems, extending to communities concepts previously applied at higher levels of ecological organization (e.g., Ulanowicz 1997). In such systems, levels of hierarchical organization form spontaneously as energy input to the system is increased.

"Hubbell cells" may indeed represent some form of spontaneous ecological organization formed by the interaction of higher-level geographic barriers and lower level, individual processes of competition and dispersal in response to disturbance. "Energy" input to the Earth's global ecological system through time might be conceived as increased efficiency of such things as photosynthesis, nutrient cycling, and organismal-Earth system buffering, all of which have changed directionally over geological time. All would increase both the organic and inorganic nutrient pools available to plants. The result has been increasing provincialization through time, there initially being very few global provinces with few and very widespread taxa. This provincialization at the highest level was accompanied by increasing complexity within provinces (biomes) and increasing complexity of plant distribution within biomes. It is at the biome boundaries that most plant ranges appear to truncate and it is within biomes that "individualism" seems to operate to some spatiotemporally variable degree.

ACKNOWLEDGMENTS

We thank Nina Jablonski for the invitation to participate in the symposium from which this paper is an outgrowth. We thank Richard Bateman, Kay Behrensmeyer, Douglas Erwin, Roberto Iannuzzi, Tom Olsezwski, Tom Phillips, Bill Stein, and Scott Wing for sharing their ideas in various discussions. This publication is based in part on work supported by the National Science Foundation under grants EAR-0207848 to Hermann Pfefferkorn and EAR-0207359 to Robert Gastaldo. William DiMichele acknowledges the Walcott Funds of the Smithsonian Institution for support.

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