

*Ecological Sorting of Vascular
Plant Classes During the Paleozoic
Evolutionary Radiation*

William A. DiMichele, William E. Stein,
and Richard M. Bateman

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THE DISTINCTIVE BODY PLANS of vascular plants (lycopsids, ferns, sphenopsids, seed plants), corresponding roughly to traditional Linnean classes, originated in a radiation that began in the late Middle Devonian and ended in the Early Carboniferous. This relatively brief radiation followed a long period in the Silurian and Early Devonian during which morphological complexity accrued slowly and preceded evolutionary diversifications confined within major body-plan themes during the Carboniferous. During the Middle Devonian–Early Carboniferous morphological radiation, the major class-level clades also became differentiated ecologically: Lycopsids were centered in wetlands, seed plants in terra firma environments, sphenopsids in aggradational habitats, and ferns in disturbed environments. The strong congruence of phylogenetic pattern, morphological differentiation, and clade-level ecological distributions characterizes plant ecological and evolutionary dynamics throughout much of the late Paleozoic. In this study, we explore the phylogenetic relationships and realized ecomorphospace of reconstructed whole plants (or composite whole plants), representing each of the major body-plan clades, and examine the degree of overlap of these patterns with each other and with patterns of environmental distribution. We conclude that

ecological incumbency was a major factor circumscribing and channeling the course of early diversification events: events that profoundly affected the structure and composition of modern plant communities.

Paleoecological studies of Carboniferous terrestrial environments consistently have revealed distinct ecological centroids for those major architectural groups traditionally described as taxonomic classes. Although the ecological spectra encompassed by the constituent species of these clades overlapped, each predominated in a distinct, broadly construed environmental type, irrespective of whether dominance is assessed by species richness or percentage biomass. In modern landscapes, one of these primordial architectural groups, the seed plants, dominate most habitats, and among seed plants, the angiosperms are now most prominent over most of the Earth's surface. The roots of the modern pattern first appeared at the end of the Paleozoic, when the breadth of ecologically dominant taxa narrowed at the class level, and one class, seed plants, began their rise to prominence in all types of environments. The rise of angiosperms from within the seed plants further narrowed the phylogenetic breadth of ecologically dominant clades. Viewed over geological time, the patterns of clade replacement within major environmental types suggest a self-similar pattern, each new radiation bringing to dominance an even more narrow portion of phylogenetic diversity.

The primordial Carboniferous pattern appears to have become progressively established during the Middle to Late Devonian, when major architectural groups of vascular plants originated from the structurally simple ancestral forms predominant from the Late Silurian to the late Early Devonian (Scott 1980; Gensel and Andrews 1984). This radiation has come under increasing phylogenetic scrutiny (Crane 1990; Kenrick and Crane 1991, 1997; Gensel 1992; Bateman in press). Much still remains to be learned, however, regarding the early evolution of major bauplans (represented by modern classes), which were largely in place by the Early Carboniferous, and of the paleoecological preferences of these groups. The paleoenvironmental distribution of the major clades is well enough known to lead us to conclude that the radiation of architectural types (bauplans) coincided with partitioning of ecological resources, the latter playing an important role in both channeling and constraining the radiation.

The interplay between evolution and ecology, the understanding of which is a primary objective of evolutionary paleoecology, is well illustrated by these mid-Paleozoic events. The evolution of large-scale architectural (and hence taxonomic) discontinuities was made possible in large part by the (evolving) patterns of resource occupation in what was initially an ecologically undersaturated terrestrial world. We believe the basic dynamics of ecological control of

plant diversification and morphology are probably general rather than unique to this major radiation (for a parallel pattern in modern seed plants see Lord, Westoby, and Leishman 1996). The architectural results and taxonomic consequences of the mid-Paleozoic radiation, however, are unique, due to both unique environmental opportunities available at the time and the relatively simple morphologies (and by inference low developmental complexity) of the ancestral forms (Stein 1993; DiMichele and Bateman 1996).

The Scenario

Prior to the Middle Devonian, vascular plants were, in structural and developmental terms, relatively simple compared with later forms (e.g., Knoll et al. 1984). Organ, tissue, and cell types were few and such innovations were added piecemeal, gradually building structural complexity in the various lineages (Chaloner and Sheerin 1979). Furthermore, the ecological spectrum encompassed by these plants was limited largely to the wetter parts of lowland environments (Andrews et al. 1977; Edwards 1980; Gensel and Andrews 1984; Beerbower 1985; Edwards and Fanning 1985). The variety of environments colonized through time clearly increased, although relatively slowly, and likely was limited more by constraints produced by primitive vegetative and reproductive morphology (e.g., inadequate root systems, few types of dispersal modes, limited photosynthetic arrays, reproductive phenotypes linked to the need for free water) than by basic physiology, the core aspects of which were probably in place (e.g., photosynthetic pathways, water transport, nutrient use; for discussion of major phases in plant evolution see Bateman 1991). The possible phenotypic disparity (*sensu* Foote 1994) between ancestor and descendant species was small, although the aggregate spectrum of variation was gradually expanding through time. Clearly, morphological and physiological behavior (capacity) are linked, and as structural complexity increased so did the capacity for energy acquisition and utilization.

During the late Middle and Late Devonian, the vascular plants attained an aggregate "critical mass" of morphological complexity regulated by increasingly complex developmental systems (Niklas, Tiffney, and Knoll 1980; Rothwell 1987; Wight 1987; Stein 1993; DiMichele and Bateman 1996). This permitted an increase in the maximum ancestor–descendant disparity; phenotypic "experimentation" became greater simply because of greater complexity of the starting forms. The unfilled nature of ecological resource space at this time created a permissive, abiotic selective regime that allowed many of these "hopeful monsters" to locate adequate resources where there was minimal competition from well entrenched incumbent species (Scheckler 1986a;

Bateman 1991; Bateman and DiMichele 1994a). Thus, even though the earliest derivatives would not have been optimally functional, distinctive new plant architectures appeared and, more critically, some established historically persistent ecologically delimited clades.

The radiation was relatively brief for two reasons (DiMichele and Bateman 1996): (1) Nonaquatic plants have a limited range of resource acquisition and exploitation strategies (Niklas 1997), and the number of major resource pools available to vascular plants is rather limited, so the effects of incumbent advantage (Gilinsky and Bambach 1987; Rosenzweig and McCord 1991) in different parts of the ecological landscape developed very rapidly as resources were expropriated; (2) as morphological complexity accrued, the effects of the "epigenetic ratchet" (Levinton 1988) began to limit the size of ancestor-descendant evolutionary disparity—developmental interdependencies progressively limited functional morphological combinations. Moreover, with greater structural and developmental complexity, the evolution of new architectures requires "escape" from the structural organization of complex ancestral forms (Bateman 1996a). This does not mean that speciation rate declined. Rather, the average morphological difference between ancestor and descendant declined, and new species fitted into the existing architectural types (bauplans).

Relative species diversities of class-level clades that evolved during the Middle Devonian radiation, particularly tree forms, appear to have been limited strongly by the resource breadth of the environment into which the clade radiated. Terra firma habitats, the favored territory of seed plants, were the most physically diverse and were thus capable of supporting the most species and the most variation on the basic architectural aspects of the clade. Wetlands, the ecological centroid of the rhizomorphic lycopsids, were much less diverse edaphically and consequently supported fewer architectural types and fewer species. Aggradational and disturbed habitats, the narrowest of all adaptive zones, were occupied by the rhizomatous sphenopsids, which evolved proportionally the fewest variations on their basic tree architecture and also were the group with the lowest species diversity. Early ferns were opportunists that exploited interstitial disturbance in many kinds of environments, permitting them to radiate in significant numbers in ecotonal settings. Tree-fern dominance did not appear until much later, after environmentally induced extinctions created opportunities to exploit previously occupied resources (Pfefferkorn and Thomson 1982; Phillips and Peppers 1984).

We examine this scenario from three perspectives, each of which is usually examined independently as a central attribute of an evolutionary radiation. Only through examination of all three is it possible to evaluate interrelated

causal factors for this important period in vascular plant history (Bateman, in press). First is the pattern of phylogenetic diversification that began in the Middle Devonian and substantially terminated by the Early Carboniferous. Second is the nature of the ecophenotypic morphospace that evolved during this radiation and the degree to which it was congruent with the phylogenetic pattern. Third is the ecological preferences of the major lineages and the degree to which such preferences constrained the species diversities of class-level clades.

The Vascular Plant Radiation: Phylogeny

Extant vascular plants can be organized into two major complexes based on their ancestry. The basal groups of the vascular plant phylogenetic tree are represented by the zosterophylls and the trimerophytes, apparently descended from common ancestors among the earliest vascular plants, the rhyniophytes (Banks 1968; Gensel 1992). This fundamental basal dichotomy took place no later than Early Devonian (Banks 1975).

Derivatives of the zosterophylls include at least one and possibly two distinct clades (Kenrick and Crane 1997). The older and more diverse clade is the lycopsids. Within this group are three subclades, likely successively derived from one another in the sequence Lycopodiales, Selaginellales, Isoetales. The other clade is the barinophytes, which may be zosterophylls or derived from a zosterophyll ancestor (Brauer 1981).

Most extant plants are derivatives of the trimerophytes, encompassing several complexes of structurally similar groups. Perhaps least derived are the ferns, first appearing in the Late Devonian (Phillips and Andrews 1968; Rothwell 1996), consisting of several architecturally distinct subgroups, the zygopterids, marattialeans, and filicaleans. The sphenopsids include the equisetophytes and sphenophylls, and may be derived from morphologically intermediate groups in the Middle Devonian that include the iridopterids (Stein, Wight, and Beck 1984) or one or more groups of cladoxylopsids (Skog and Banks 1973; Stein and Hueber 1989). The seed plants and their ancestors, the progymnosperms, form another distinct group. There are two major sublineages of progymnosperms, the archaeopterids and aneurophytes, and there has been considerable debate over which of these groups included the seed-plant ancestor (Rothwell 1982; Meyen 1984; Beck and Wight 1988).

Clearly, classical Linnean taxonomy has not successfully encapsulated this early radiation. Groups with distinctive body plans form a nested hierarchy of relationships, rendering some paraphyletic (e.g., progymnosperms in their possible relationship to seed plants). Crane (1990) and Kenrick and Crane

(1991, 1997) examined this radiation cladistically and compared it with traditional Linnean grouping. Although the nested hierarchy means that some architectural groups are more closely related to one another than to other groups, the basic architectures clearly are distinct, especially when viewed retrospectively in the light of subsequent radiations. Since the Early Carboniferous, speciation largely has taken place within the confines of these existing body plans. Surviving to the present are all three of the lycopsid groups, the filicalean and marattialean ferns, the equisetophyte sphenopsids, and numerous groups of seed plants (although none that were present in the Carboniferous). Here, we view the angiosperms as a subset of the seed plants.

We present a cladistic representation of this early radiation (figure 11.1), noting the points of origin of modern plant body plans. This cladistic phylogeny is an authoritarian composite based on several separate analyses (see figure caption). Placed in the context of geologic time, phylogenetic analysis demonstrates the relative temporal compression of the radiation. It makes no claim for nor does it require unique rates of speciation or evolutionary mechanisms operating only during this time interval. It does emphasize, however, that the outcomes of the evolutionary process appear to have changed in breadth, with ancestor–descendant disparity apparently decreasing in a nonlinear fashion through time (Gould 1991; Erwin 1992).

The Angiosperm Problem

The flowering plants are the only group traditionally given high taxonomic rank (i.e., class rank or above) that did not originate during the Middle Devonian–Early Carboniferous radiation. Some mention of them is necessary because the question will arise: Is not the origin and diversification of the angiosperms, the most species-rich groups of vascular plants ever to inhabit the Earth, indeed a radiation as profound structurally as that of the Late Devonian? Angiosperms have been ranked most often between phylum (equivalent to division) and class. This high rank was deemed necessary to accommodate the great species diversity within the group. It reflects a historical accident in plant systematics, where classification systems were initially developed and based upon extant plants, overwhelmingly angiosperms, with the less derived groups subsequently incorporated into the classification in only a quasi-phylogenetic manner. During the past 25 years, it has become traditional to distort this problem even further by treating the angiosperms as a phylum. In attempts to justify this taxonomic strategy, nearly all nonangiospermous seed plant and lower vascular plant orders were inflated to the rank of phylum, simply in order to accommodate the large number of Linnean ranks needed to encapsulate the diversity of the angiosperms (leaving most of these “phyla” encompassing only

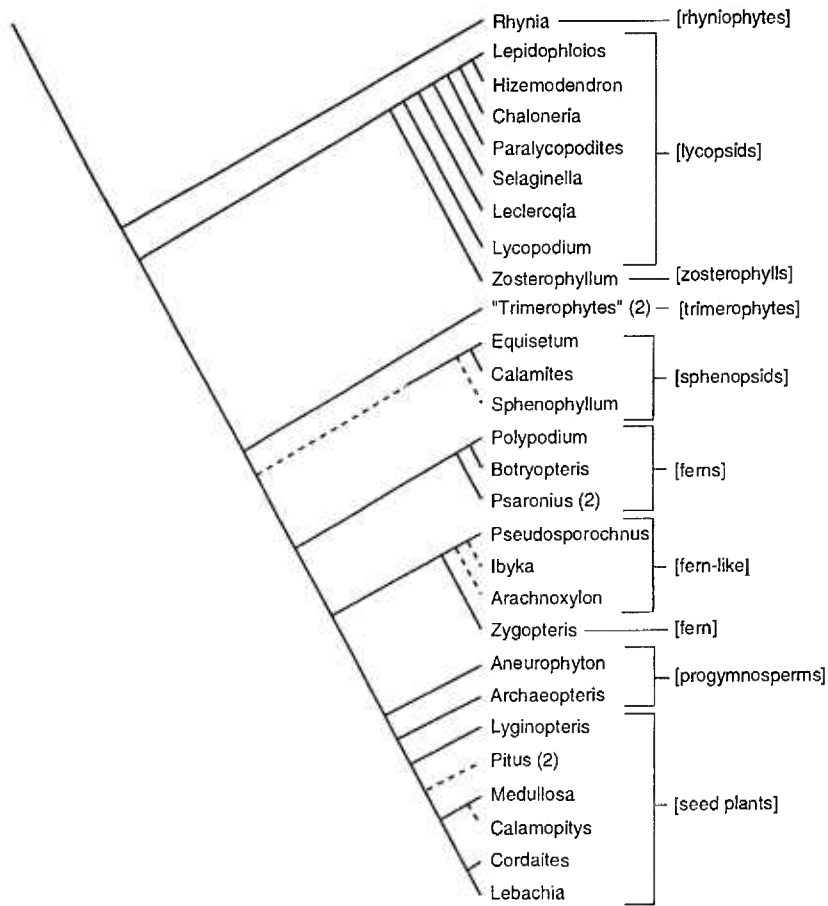


FIGURE 11.1. Tentative phylogeny of representative composite and whole-plant taxa, compiled by synthesizing an amalgam of recent phylogenetic studies. Main framework of the phylogeny is extrapolated from Rothwell (1996, figure 1), also with reference to Crane (1990), Kenrick and Crane (1991, 1997), Pryer, Smith, and Skog (1995), and Stevenson and Loconte (1996). Lycophyte clade (A) follows Bateman (1996a,b, figure 1), also with reference to Kenrick and Crane (1991, 1997) and Bateman, DiMichele, and Willard (1992). Lignophyte clade (B) follows Rothwell and Serbet (1994, figure 1), also with reference to Doyle and Donoghue (1992) and Nixon et al. (1994).

one class and one order). This approach obscures evolutionary relationships among the supposed phyla, the evolutionary significance of morphologies observed within each group, and the morphological disparity among them.

Numerous phylogenetic analyses of seed plants have appeared in recent years (Crane 1985; Doyle and Donoghue 1992; Nixon et al. 1994; Rothwell and

Serbet 1994). All of these demonstrate clearly that the angiosperms are a derived group within the seed-plant body plan that, like all other basic body plans, was a product of the great Devonian radiation. Furthermore, from a morphological perspective, the basics of angiosperm design are no more distinct from any of the traditional seed plant "orders" than any of these "orders" are from one another (cf., Lyginopteridales, Medullosales, Cycadales, Coniferales, Ginkgoales, Peltaspermales, Pentoxylales, Caytoniales, Bennettitales, Gnetales). It cannot be denied that many more variations on the seed-plant architectural theme have evolved among the more derived angiosperms than within any other seed-plant group. Even the most divergent forms, however, are largely confined within the seed plant–progymnosperm bauplan. Consequently, allowing for the implicit phylogenetic outlook of the Linnean perspective, the angiosperms should be ranked as an order (Bateman 1991; DiMichele and Bateman 1996); a very species-rich order, but an order nonetheless. Rather than indicating a later escape from the constraints of development and body plan that were emplaced in the Middle Devonian–Early Carboniferous radiation, they are, in fact, one of the best indications of the inescapability of such constraints. Body plans evolved early and entrained subsequent evolution of form.

The Vascular Plant Radiation: Ecomorphospace

The major clades that originated in the Late Devonian appear by inspection to represent different body plans, or at least different styles of structural organization. In order to test this hypothesis we undertook an analysis of the structure–function morphospace relationships realized by the major lineages. Philosophically, our objective was not to identify an idealized (or Raupian) morphospace, one circumscribed by theoretical limits on plant architectures (e.g., Niklas 1977, 1982), but rather to examine the morphospace as delimited by the plants that actually existed at different times (Foote 1993, 1994). Coded taxa were chosen so that each major lineage (class-level clade) would be represented by several placeholders or (if no single species was fully reconstructed) by composite taxa from different sublineages within each class. In this way, we hope to examine the degree to which each class formed a distinct functional morphological entity that might be termed an ecomorphic group. *Ecomorphic characters* are units of structure–function that will be compared analytically to the results of the ecological analysis; consequently, they were chosen to emphasize shared aspects of functional morphology largely separate from phylogeny, in several instances they are not necessarily homologous (i.e., synapomorphous) between or even within groups. Although characters were

chosen to minimize repetition, we recognize that they are not fully independent. The numerical analyses used do not require that character axes be orthogonal. Indeed, we were seeking characters that are nonorthogonal due to covariance, reflecting developmental or ecological associations but not necessarily phylogenetic relatedness. Wherever clear duplication (as opposed to convergent patterns of expression) of structural or functional attributes was identified, one of the overlapping characters was excluded from the analysis. Our intention in constructing the ecomorphospace was to determine the degree of congruence between the phylogenetic relationships of groups based on cladistic analysis (figure 11.1) and their similarity as measured by distance in the multivariate space of structure–function (ecomorphic) characters.

Plants were scored for each of 22 ecomorphic characters listed in table 11.1 and discussed in the following section; a best guess, based on nearest known relatives or functionally related morphological features, was made for matrix cells lacking direct observations. The plants and scores of states for particular ecomorphic characters are listed in table 11.2. Analyses were carried out with NTSYS, version 1.8 (Applied Biostatistics, Inc.), written by James Rolf. Analyses were exploratory and visual in nature, as no explicit hypotheses of similarity or difference were tested statistically. Techniques utilized included principal components analysis (PCA) on the correlation matrix of ecomorphic characters, unweighted pair group cluster analysis (UPGMA), and complete linkage cluster analysis (CLCA), the latter two utilizing the Euclidean distance metric. Results are shown in figures 11.2 and 11.3.

Ecomorphic Characters

The following aspects of structure–function were used in the analysis. For convenience of analysis, each ecomorphic character was divided into alternative discrete structure–function “states” by analogy with phenetic or cladistic characters. In most instances, more than two states have been identified for each ecomorphic character; if a linear sequence was hypothesized, the endpoint states were considered to be more distinct from each other than either was from any of the intermediate states. In other instances, where linear chains of states were not inferred (ecomorphic characters 2–3, 11–12, 14–16, 19–20), multistate ecomorphic characters were converted to two-state or multistate, allowing for several possible proximity relationships among states.

Ecomorphic character 1 expresses the growth capacity of the axis/shoot apex. The growth dynamics of both the root and shoot system in vascular plants are regulated by the meristems, which are places where cell division takes place and from which much of the internal and external architecture is

TABLE 11.1. Features of Morphology used in the Analysis of Ecomorphospace^a

- 1 - Growth capacity of the apex - shoot apex:
 - 0 = only more-or-less isodichotomous apex [rhyniophytes]
 - 1 = distinctly anisodichotomous apex organization present [in addition to isodichotomous; trimerophytes]
 - 2 = large central apex producing much smaller lateral appendages/leaves [herbaceous lycopsids]
 - 3 = relatively small central apex producing large lateral appendages [seed plants, ferns]
- 2 - Capacity for light reception by appendicular laminar surfaces:
 - 0 = low: cylindrical axes only responsible for light reception
 - 1 = medium: capacity enhanced by small scales/leaves providing laminar photosynthetic surfaces
 - 2 = high: photosynthetic capacity mostly by laminar photosynthetic surfaces
- 3 - Capacity for light reception by branch ramification:
 - 0 = none: dichotomous axes [rhyniophytes]
 - 1 = significant ramification but not filling of all the space [conifers]
 - 2 = space-filling ramifications
- 4 - Degree of apical dominance over lateral branch systems:
 - 0 = none or very little
 - 1 = moderate, anisodichotomous
 - 2 = strong apical dominance [conifers, lycopsids, *Equisetum*]
- 5 - Main shoot (apex) geotropism:
 - 0 = ascendant
 - 1 = main axis prostrate with ascendent lateral axes
 - 2 = fully upright main axis
- 6 - Support mechanisms of main axis:
 - 0 = minimal supporting structures
 - 1 = "semi-self supporting" (Rowe et al. 1993)
 - 2 = fully self-supporting
- 7 - Reproduction - life cycle:
 - 0 = homosporous, free-sporing
 - 1 = heterosporous, free-sporing
 - 2 = heterosporous, retained megaspores
 - 3 = heterosporous, single functional megaspores, retained
- 8 - Fructification display:
 - 0 = solitary or paired sporangia
 - 1 = small clusters of terminal or lateral sporangia, borne on lateral branch systems
 - 2 = "cones" (= masses of sporangia), either as separate structures or periodically as part of main or lateral shoot development
- 9 - Growth habit - rooting:
 - 0 = adventitious roots/rootlets
 - 1 = functional central root
- 10 - Cortical - ground tissue specialization for air flow:
 - 0 = none present
 - 1 = well developed aerenchyma or schizogeneous air channels
- 11 - Stelar architecture:
 - 0 = solid protosteles

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TABLE 11.1. (continued)

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- 1 = solid but distinctly ribbed protosteles
 - 2 = dissected primary vascular system
 - 12 - Pith or ground parenchyma - both stem and petiole/rachis:
 - 0 = center of stem with well developed primary xylem tracheids
 - 1 = pith or ground parenchyma present
 - 13 - Secondary growth:
 - 0 = absent
 - 1 = present, unifacial or otherwise limited in extent (developmental capacity)
 - 2 = present, unlimited developmental capacity and potential extent
 - 14 - Support tissues - internal physiology:
 - 0 = distributed or undifferentiated support
 - 1 = cortical support / limited internal physiology
 - 2 = peripheral bark support of unlimited extent / limited internal physiology
 - 15 - Root mantle support:
 - 0 = distributed or undifferentiated support
 - 1 = root mantle support including peripheral vascular support
 - 16 - Support tissues - external physiology:
 - 0 = distributed or undifferentiated support
 - 1 = wood support / external physiology
 - 17 - Separation of sexes in sporophyte population:
 - 0 = plants showing no separation or homosporous
 - 1 = plants monoecious, but with spatial or temporal separation of megasporangiate and microsporangiate structures
 - 18 - Capacity for continued vegetative growth following reproduction:
 - 0 = determinate sporangial structures terminate axial/lateral branch shoots of crown
 - 1 = sporangial structures periodic; vegetative growth continues on main axis of lateral shoots of the crown
 - 19 - Cortical or ground tissue specialization:
 - 0 = none present
 - 1 = massive, not in discrete bundles
 - 2 = discrete bundles at periphery of cortex ['sparganum', 'dictyoxyton', etc.]
 - 20 - Cortical specialization involving a periderm:
 - 0 = none present
 - 1 = 'secondary modification' of cortex by means of continued cell division, but not organized in tissue systems [*Triloboxylon* (Stein, Wight, and Beck 1983)]
 - 2 = periderm - all kinds - involving discrete zones of cell proliferation
 - 3 = massive permanent covering periderm [rhizomorphic lycopsids]
 - 21 - Secondary xylem architecture:
 - 0 = no secondary xylem
 - 1 = manoxylic or intermediate secondary xylem
 - 2 = distinctly pycnoxylic secondary xylem [conifers]
 - 22 - Propagule size:
 - 0 = small
 - 1 = medium/small
 - 2 = medium/large
 - 3 = large
-

^aDefined states of ecomorphic characters used in the ecomorphospace analysis. In some instances, exemplar taxa are included in brackets.

TABLE 11.2. Taxa and States of Features Used in Analysis of Ecomorphospace

TAXON	CODE	ECOMORPHIC CHARACTERS																					
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Aneurophytes	ANE	1	0	1	1	1	1	0	1	0	0	1	0	2	0	0	1	0	0	2	1	1	0
Aneurophytes	ANE	1	0	1	2	1	1	0	1	0	0	1	0	2	0	0	1	0	0	2	1	1	0
Aneurophytes	ANE	1	0	1	1	2	1	0	1	0	0	1	0	2	0	0	1	0	0	2	1	1	0
Aneurophytes	ANE	1	0	1	2	2	1	0	1	0	0	1	0	2	0	0	1	0	0	2	1	1	0
Archaeopterids	ARC	3	2	1	2	2	2	1	2	1	0	2	1	2	0	0	1	0	0	2	2	2	1
Botryopteris	BOT	3	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calamites	CAL	3	2	2	2	1	2	0	2	0	1	2	1	2	0	0	1	0	0	2	1	0	0
Calamopitys	CPS	3	2	0	2	2	1	3	2	1	0	2	1	1	1	0	0	2	0	2	1	1	2
Chaloneria	CHA	2	2	0	2	2	2	1	2	1	1	0	1	1	1	0	0	1	1	0	3	1	1
Cladoxylopsids	CLA	1	0	2	2	2	2	0	2	1	0	2	0	1	0	0	1	0	0	0	0	0	0
Coniferales	CON	3	1	1	2	2	2	3	2	1	0	2	1	2	0	0	1	1	0	2	2	2	2
Cordaitales	COR	3	2	1	2	2	2	3	2	1	0	2	1	2	0	0	1	1	0	0	2	2	3
Equisetum	EQU	2	0	2	2	1	1	0	2	0	1	2	1	0	2	0	0	0	0	1	0	1	0
Filicales	FIL	3	2	0	1	1	1	0	2	0	0	2	0	0	1	0	0	0	0	0	0	0	0
herbaceous lycopsids	HLY	2	1	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
herbaceous lycopsids	HLY	2	1	0	1	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hizemodendron	HIZ	2	1	1	2	2	2	3	2	1	1	0	1	1	0	0	0	2	0	0	1	2	2
Iridopteridales	IRI	1	0	1	1	1	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0
Lepidophloios	LEP	2	2	0	2	2	2	3	2	1	1	0	1	1	2	0	0	1	1	0	3	1	3
Lyginopteris	LYG	3	1	1	1	0	1	3	1	1	0	2	1	1	1	0	0	2	0	2	2	1	2
Marattiales	MAR	3	2	0	2	1	2	0	2	0	1	2	1	0	0	1	0	0	0	0	0	0	0
Marattiales	MAR	3	2	0	2	2	2	0	2	0	1	2	1	0	0	1	0	0	0	0	0	0	0
Medullosa	MED	3	2	0	2	2	1	3	2	1	0	2	1	1	1	0	0	2	0	1	2	1	3
Paralycopodites	PAR	2	1	1	2	2	2	2	2	1	1	0	1	1	2	0	0	0	0	0	3	1	1
Pitrus	PIT	3	2	0	2	2	2	3	2	1	0	2	1	2	0	0	1	1	0	2	2	2	2

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TABLE 11.2. (continued)

TAXON	CODE	ECOMORPHIC CHARACTERS																					
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>Pinus</i>	PIT	3	2	0	2	2	2	3	2	1	0	2	1	2	0	0	1	2	0	2	2	2	2
Rhyniophytes	RHY	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Selaginella</i>	SEL	2	1	0	1	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sphenophyllum</i>	SPH	2	1	1	1	0	1	0	2	0	0	0	1	0	0	1	0	0	0	0	2	1	0
Trimerophytes	TRI	1	0	1	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Trimerophytes	TRI	1	0	1	1	1	2	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Zosterophylls	ZOS	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Zygopteris</i>	ZYG	3	1	1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0

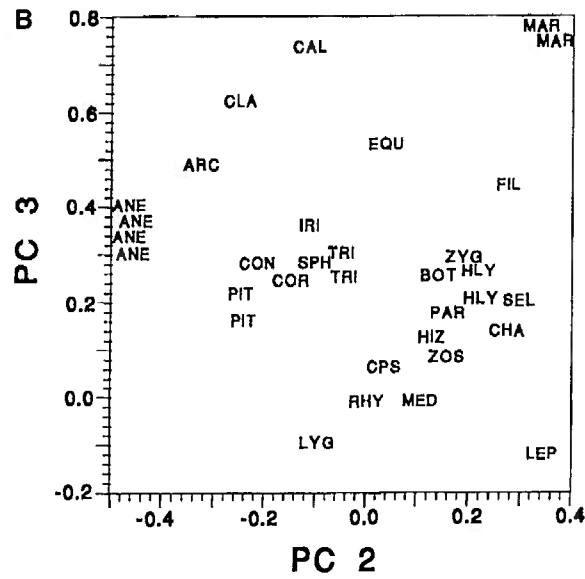
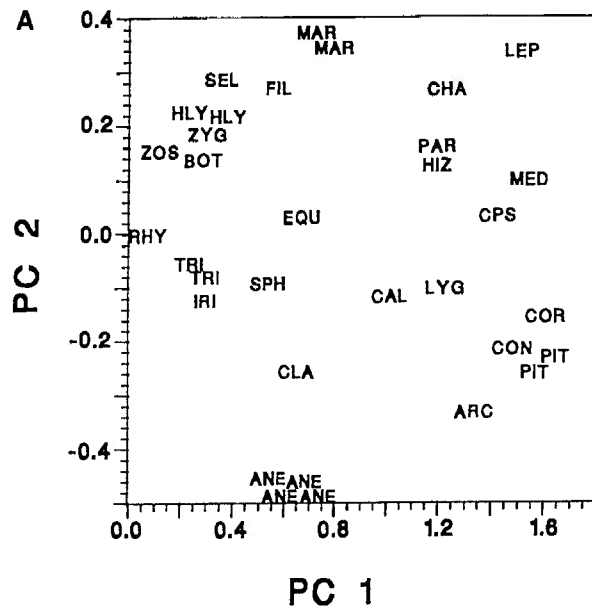


FIGURE 11.2. Principal components analysis of representative composite and whole-plant taxa. Analysis based on data matrix presented in table 11.2. See table 11.2 for key to acronyms: (A) Axis 1 vs. Axis 2; (B) Axis 2 vs. Axis 3. See text for details.

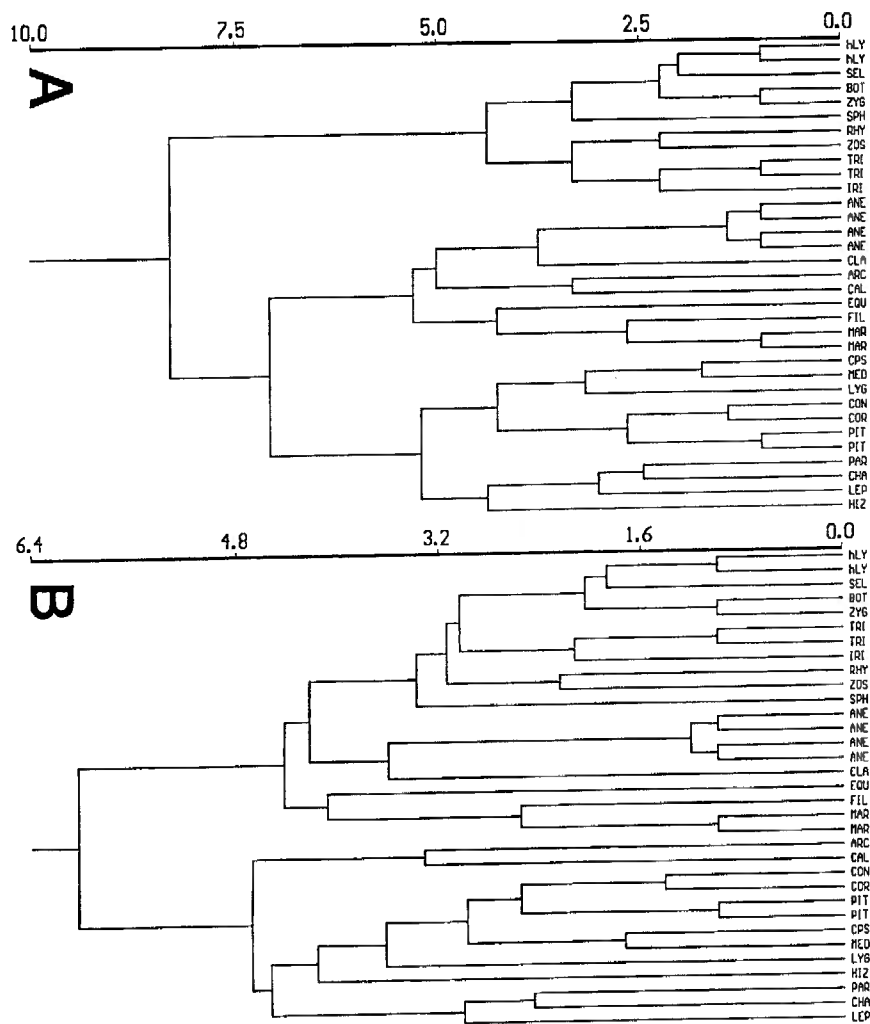


FIGURE 11.3. Cluster analyses of representative composite and whole-plant taxa. Analysis based on data matrix presented in table 11.2. See table 11.2 for key to codes. (A) Unweighted Pair Group Method of Analysis (UPGAC); (B) Complete Linkage Cluster Analysis (CLCA). See text for details.

controlled (e.g., Bateman, in press). This ecomorphic character attempts to capture the developmental interaction between the apex of the central axis and the lateral appendages. Simple, bifurcating apices (states 0 and 1) contrast with apices that produce appendicular organs, notably leaves (states 2 and 3). Appendicular organs may have minimal developmental impact on axis organization (state 2) or may have a strong feedback effect on further development of the axis (state 3).

Ecomorphic characters 2 and 3 express the potential of the aerial shoot system to capture light, either through appendicular organs or through the organization of the branch system. Light is a primary resource, needed for growth, development, and reproduction in all plants. Architecture of the photosynthetic array does not capture all dimensions of the means by which plants sequester light, most obviously missing physiological trade-offs for dealing with temperature, water stress, and variations in light intensity. Even at the basic level examined here, however, construction of the array clearly differs among major clades.

Ecomorphic character 2 expresses the capacity for light reception by appendicular laminar surfaces.

Ecomorphic character 3 expresses the enhancement of the capacity for light reception by branch arrangement through the support of appendicular organs, or by density of branching, increasing axis surface area.

Ecomorphic characters 4, 5, and 6 describe, in various combinations, the aerial growth form of a plant. They include the mechanisms by which a plant branches and the degree to which the lateral branching morphology is regulated by the apex, the vertical or horizontal position of the shoot axis, and the ability of the plant to support itself. Ecomorphic characters 13–16, the nature of support tissues, also contribute to growth form, particularly the ability to grow upright and the potential to achieve considerable height. Height further enhances light interception and propagule dispersal, emphasizing the functional interrelatedness of many architectural features.

Ecomorphic character 4 expresses the degree of apical dominance over the lateral branching system. This character identifies the extent to which the plant developed a main axis and either wholly suppressed lateral branches or relegated them to a subordinate, lateral growth position.

Ecomorphic character 5 expresses main-shoot (apex) geotropism. This character seeks to identify the developmental basis of growth habit. In ascendant growth forms (state 0) the apex is elevated dynamically as the axis “unrolls” along a substrate. Other shoot systems of clonal organisms differentiate into strictly prostrate and strictly vertical stems (state 1). A fully upright

plant (state 2) may be centrally rooted or may be supported by adventitious roots, but is fundamentally unitary in construction and vertical in orientation.

Ecomorphic character 6 describes the support mechanism of main axis. It describes the degree to which the main axis was capable of supporting itself in an upright (vertical) position. Some plants with upright structure are not capable of standing vertically without leaning against or climbing on other plants (i.e., "semi-self supporting" *sensu* Rowe, Speck, and Galtier 1993; Speck 1994).

Ecomorphic character 7 describes reproduction and life cycle. This character focuses on the ability of a plant to disseminate its reproductive organs and gain control over the vagaries of environmental conditions. Each of the basic life histories in plants places different constraints on the likelihood of reproductive success and dispersal to suitable habitats. Homosporous plants, for example, often have great dispersal abilities and can produce a new population from a single propagule. They must, however, accommodate two independent life history phases (gametophyte and sporophyte) during evolution of habitat tolerance (Bateman and DiMichele 1994b). Seed plants, in contrast, greatly compress the life cycle, almost into one life history phase, the sporophyte, but must contend with the necessity for pollination and special mechanisms to disperse seeds. Using the major life cycles as short-hand, this character differentiates homosporous, heterosporous, and seed-bearing plants, considering degree of heterospory to represent a structure-function morphocline. "Seeds" are considered to be any integumented megasporangium; consequently, the "aquacarp" of the rhizomorphic lycopsids (Phillips and DiMichele 1992) are coded as functional seeds, even though, in phylogenetic terms, they were not borne by seed plants.

Ecomorphic character 8 expresses fructification display. Reproductive effort, both in any single reproductive event and over the entire lifetime of the individual, is an important ecological characteristic related to energy allocation patterns. Reproductive effort can be measured in various ways for fossil plants, although, unfortunately, not by the precise dry weight measurements preferentially made for extant plants. Here we used the degree of aggregation of sporangia as a measure of reproductive effort put into any one, short-term event. Note that fern fronds bearing abundant sporangial clusters (sori) are coded as "cones," reflecting shared high reproductive output per reproductive event (state 3).

Ecomorphic character 9 expresses growth habit and rooting. This ecomorphic character is intended to separate centrally rooted plants from those in which adventitious roots are the main fluid absorbing and/or support organs. Plants with central rooting have limited potential to spread from the point of

rooting. The root system and shoot system in such plants must remain continually connected by live tissue. Adventitious roots provide flexibility in point of growth through time if combined with a prostrate growth habit, but also limit the ability of the plant to undergo extended vertical growth.

Ecomorphic character 10 describes ground tissue specialization for gaseous flow within the plant body. The presence of aerenchyma tissues is most frequently associated with growth under conditions of periodic flooding or standing water. In some plants (e.g., some species of *Psaronius* tree ferns), aerenchymatous tissues provide structural strength with limited carbon input and may have permitted attainment of tree habit with minimal energetic outlay.

Ecomorphic characters 11 and 12 differentiate the primary vascular architecture of the plant. Vascular architecture influences both support of the primary body and water conducting capacity. This is especially important in herbaceous plants with little or no secondary vascular tissues, but is also important in many groups that achieve tree habit using support mechanisms other than wood. The combination of ecomorphic characters 11 and 12 permits specialized types of nonlobed steles to be identified (e.g., siphonosteles are coded as protosteles in ecomorphic character 11 and as having a pith in ecomorphic character 12).

Ecomorphic character 11 describes the stelar architecture of main axis. States are differentiated by the degree of stelar surface area created by xylary lobing: smooth, ribbed, or dissected.

Ecomorphic character 12 describes the pith or ground parenchyma in main axis or leaves. Pith parenchyma has been shown to be a mechanism of water storage and a means to reduce the energetic cost of vascular support of an axis (a cylinder is a more effective means of support than a solid rod).

Ecomorphic character 13 expresses presence and mode of secondary vascular growth. It reflects the potential of the vascular cambium (if present) to produce a cylinder of secondary xylem and phloem. Plants with unifacial cambia have limited growth potential (Cichan and Taylor 1984), as do some plants with bifacial cambia.

Ecomorphic characters 14, 15, and 16 differentiate contrasting means of support of the shoot system and the effects these means of support have on location of the major physiological processes of the plant. Plants with states 1 or 2 of ecomorphic character 14 have cortical or peripheral bark support. Such plants retain much of their physiology within the support tissues, most notably water and nutrient transport. Plants with state 1 of ecomorphic character 15 have peripheral support from mantles of adventitious roots. Such root mantles are functionally analogous to wood, transporting water and nutrients

to active leaves and meristems. In such systems, water transport, although external, is compartmentalized within the individual roots. Most other stem-based physiology resides within the support tissue. Ecomorphic character 16 identifies those plants supported by secondary xylem. In such cases, vascular tissue development confines all the active physiology outside of or marginal to the main locus of support of the plant: the periphery of the vascular cylinder.

Ecomorphic character 17 describes separation of the sexes in the sporophyte population. The distribution of male and female sex organs in plant populations is a complex phenomenon that would benefit from greater detail than can be obtained from most fossil taxa. For example, many homosporous plants (state 0) with potentially bisexual gametophytes regulate sex organ production through complex chemical regulation, creating distinct male and female plants; in other cases, male and female sex organs function on the same gametophyte. Many heterosporous plants produce both microspores ("male") and megaspores ("female") in the same cone, but when dispersed, the mature sex organs from the same plant, borne on different gametophytes, may not be in close proximity. Unfortunately, this character can be identified for few taxa; in fossils its level of refinement is far below that possible for extant plants. In our matrix, where the state in the fossil could not be determined, scoring was based on comparison with the nearest living relative.

Ecomorphic character 18 describes the capacity of the plant to continue vegetative growth following sexual reproduction. This character separates those plants that are monocarpic (semelparous) from those that are polycarpic (iteroparous). In the case of rhizomatous and other clonal plants (e.g., *Equisetum*), reproductive capacity was considered for the whole clone rather than just the "individual" upright shoots.

Ecomorphic character 19 describes cortical ground tissue specialization. Some plants have specialized sclerenchyma bundles or regions of the cortex that can serve as support tissues. Such tissues offer flexible support in young stems of plants with limited secondary support tissues in all or part of the plant, or in vine-like stems.

Ecomorphic character 20 describes cortical specialization involving a periderm. Periderms are secondary nonvascular tissues developing at the periphery of the stem. In certain lycopsids, the periderm was a permanent, largely supportive tissue (state 2). In most woody plants periderm is strictly protective, given the peripheral position of the active physiological attributes of the plant. In such plants new layers of periderm form during each increment of growth, reorganized within the secondary phloem of the previous increment (state 3).

Ecomorphic character 21 describes secondary xylem architecture. It is intended to separate plants that produce dense, pycnoxylic wood from those that have more parenchymatous wood or produce larger diameter, thinner walled tracheids.

Ecomorphic character 22 expresses propagule size. It distinguishes plants by the size of their female disseminules (see Bateman and DiMichele 1994b). Homosporous plants are routinely small, generally less than 160–180 μm (state 0). Heterosporous plants are apportioned between the two medium states (1 and 2), generally between 160–180 μm and 1 mm, or 1 mm to 5 mm. State 3 is for propagules greater than 5 mm in diameter. Seeds may fall in states 1, 2, or 3, although all the seeds scored for Paleozoic plants were of medium-large or large size.

Numerous potential ecomorphic characters could not be evaluated satisfactorily in the suite of fossils under consideration. Examples include epiphytic habit, parasitism or saprophytism, the nature of the relationships of root systems with mycorrhizal fungi, and of course numerous physiological features. In many cases there are grounds to speculate on certain of these characters for a few, exceptionally well-known species, but provide no basis for assessing the vast majority of species. At this juncture, therefore, we present this list of ecomorphic characters as a preliminary examination of the ecomorphospace created by the Middle Devonian–Early Carboniferous evolutionary radiation.

Coded Taxa

The following vascular land plants were selected for the analysis. Our objective was to include as many growth forms as possible in the analysis, including different variants within the major groups. Where unavoidable, composite taxa were constructed to permit combination of anatomical, morphological, and reproductive features, generally not all known from a single “species” (it is possible that different fossil species actually may represent the same plant preserved differently).

Rhyniophytes

Rhyniophytes are the basal plexus from which the two major Early Devonian clades are thought to have evolved (Banks 1968). The rhyniophytes are represented by a generalized composite plant similar in character to *Rhynia gwynne-vaughnii* (Kidston and Lang 1917; D. S. Edwards 1980). This is the most phylogenetically primitive plant in the analysis.

Trimerophyte Lineage

TRIMEROPHYTES. Two types of generalized trimerophytes are represented, based on *Psilophyton dawsonii* (Banks, Leclercq, and Hueber 1975) and *Pertica* spp. (Kaspar and Andrews 1972; Granoff, Gensel, and Andrews 1976). They differ according to the form of growth of the axis (ecomorphic character 5), either ascendant or with inferred upright axes borne on a prostrate axis system.

IRIDOPTERIDS. These are represented by the genera *Ibyka* (Skog and Banks 1973: gross morphology) and *Arachnoxylon* (Stein 1981; Stein, Wight, and Beck 1983: anatomy).

CLADOXYLOPSIDS. These are represented by the genus *Pseudosporochnus* (Leclercq and Banks 1962; Stein and Hueber 1989; Berry and Fairon-Demaret 1997).

SPHENOPSIDS. Herbaceous equisetophytes are represented by the modern genus, *Equisetum*. Woody tree-equisetophytes are represented by a generalized, homosporous calamitean; all members of this group shared common basic architectural features (Andrews and Agashe 1965; Barthel 1980). Sphenophylls are represented by the prostrate, but woody, *Sphenophyllum plurifoliatum* (Williamson and Scott 1894).

FERNS. Three major variants of fern architecture are included in the analysis. The Filicales include two taxa, a generalized filicalean based on the modern polypodiaceous ferns and *Botryopteris antiqua* from the Late Carboniferous (Phillips 1974). The Zygopteridales are represented by *Zygopteris illinoensis* (Dennis 1974), a form very similar to the filicalean types but differing phylogenetically rather than in gross architecture; both botryopterids and zygopterids are known from the Early Carboniferous. The Marattiales are represented by two generalized forms of Late Carboniferous *Psaronius*. The more primitive is of scrambling habit and lacks a well developed root mantle; the more derived is arborescent with a large supportive root mantle (Lesnikowska 1989).

PROGYMNOSPERMS. There are two widely recognized types of progymnosperms, the aneurophytes and archaeopterids. Four alternative interpretations of aneurophyte morphology are presented, based on different interpretations and combinations of ecomorphic characters 4 and 5 (degree of apical dominance and main shoot geotropism), both contributing to general growth habit. The concept of aneurophytes is based on *Rellimia* (Bonamo 1977), *Triloboxylon* (Matten and Banks 1966; Scheckler 1976), and *Tetraxylopteris* (Bonamo and Banks 1967). Archaeopterids are represented as a composite, combining information from petrified stem remains and compressions of foliage and reproductive organs (Beck and Wight 1988; Trivett 1993).

SEED PLANTS. Included in the analysis are several kinds of seed plants, which can be grouped broadly into two lineages. "Cycadophytic" seed plants share radially symmetrical seeds, manoxylic wood, and limited secondary vascular development, and include *Calamopitys* (Rowe and Galtier 1988; Galtier and Meyer-Berthaud 1989), *Medullosa primaeva* (Delevoryas 1955; Stidd 1980), and *Lyginopteris oldhamia* (Oliver and Scott 1904). "Coniferophytic" seed plants share more dense, pycnoxylic wood with unlimited potential for secondary growth, bilaterally symmetrical seeds, and generally small leaves; included are two variations of *Pitus* that differ on uncertainty in ecomorphic character 17 (dioecy or monoecy), a generalized cordaitalean (Costanza 1985; Trivett and Rothwell 1985), a generalized primitive conifer (Clement-Westerhoff 1988).

Zosterophyll Lineage

ZOSTEROPHYLL. Generalized zosterophyll are based on *Rebuchia*, *Serrulacaulis*, and *Gosslingia* (Niklas and Banks 1990; Lyon and Edwards 1991; Hueber 1992).

LYCOPODIOPSIDS. These are represented by an herbaceous lycopod similar in form to extant *Huperzia* and by the Middle Devonian *Leclercqia* (Banks, Bonamo, and Grierson 1972). The two types of lycopodioid morphology included here differ in degree of inferred apical dominance (ecomorphic character 4).

SELAGINELLIDS. Most evidence for the presence of selaginellids in the Devonian and Early Carboniferous is equivocal (Thomas 1992; although see Rowe 1988). However, the phylogeny of the lycopsids (Bateman 1996b) suggests that selaginellids evolved prior to the isoetoids, which have an excellent Late Devonian and Carboniferous record. Consequently, we scored a modern *Selaginella* of the *S. kraussiana* type.

ISOETALEANS. The isoetalean lycopsids were a far more diverse group in the Paleozoic than they are today. Many fossil forms are known in exceptional detail, and whole plants have been reconstructed. We used as exemplars the best known extinct tree forms, *Lepidophloios hallii* (the most derived species) and *Paralycopodites brevifolius* (the most primitive species), the pseudoherb *Hizemodendron serratum*, and the more typically isoetalean *Chaloneria* (Bateman, DiMichele, and Willard 1992).

Analysis Results

Principal Components Analysis

The principal components analysis (figure 11.2) reveals a pattern that is strongly, but not perfectly, congruent with the phylogeny. In other words, the

clusters of taxa based on ecomorphic characters, and the relative proximity of these clusters, are similar to the grouping of taxa in the phylogenetic analysis. Ninety percent of the variance is accounted for by the first eight axes and 66% by the first three, indicating (perhaps expected) high dimensionality of the morphospace. The basic pattern shows clearly when the coded taxa are plotted on the first two axes (figure 11.2A). The seed plants and their pteridophytic ancestors, the progymnosperms, are largely distinct from the rest of the lower vascular plants. There is some overlap among the cycadophytic seed plants and the woody equisetophyte and cladoxylopsid lower vascular plants. Differentiated along the first axis are forms with centralized root systems and upright growth habits (wood or bark supported) versus those with trailing habit. This latter gradient in habit is anchored at one end by the phylogenetically basal rhyniophytes and at the other by plants with tree habit, divided into two major groups: the lycopsids plus ferns and the progymnosperms plus seed plants. Various other groups, mostly pteridophytes, occupy the middle ground. Most differentiated by a third axis (figure 11.2B) are the marattialean tree ferns, the calamites (tree sphenopsids), and, to a lesser extent, the cladoxylopsids, indicating that these groups represent different ways to build a tree and may share some similarities in detail, despite significant, including phylogenetic, differences.

The following aspects of this analysis are noteworthy:

1. Using rhyniophytes as a basis for comparison, isoetoid lycopsids are the most ecologically-structurally divergent members of the zosterophyll lineage. They form a fairly tight cluster in the PCA. Members of this group have a distinctive basic body plan. They are bark-supported, have strong apical dominance, specialized root systems, and heterosporous reproduction. Branches play little or no role in the construction of their photosynthetic array, and leaves and branches are based on different developmental programs, resulting in few architectural similarities such as those found in leaves and shoots of groups descended from trimerophytes. Bark support permits them to separate support and water transport functions in different specialized tissues; Cichan (1986), in model studies, found lycopsid wood to have high efficiency in water transport. The structural and developmental similarity of the rhizomorphic rootlets to the microphyllous leaves, and the lack of identifiable secondary phloem to permit transport of photosynthate from the shoot to the root systems, suggest that root systems may have been photosynthetically self-supporting (Phillips and DiMichele 1992). Thus, these plants may come closer than any other vascular plant trees to a colonial growth habit, similar to that seen in metazoans such as bryozoans.

2. The seed plants represent the evolutionary pinnacle of the trimerophyte lineage. Although diverse, they form four distinct clusters on the PCA plot, clearly separated from all pteridophytes except the archaeopterid progymnosperms, which are virtually identical to seed plants in vegetative architecture. Of course, except for the archaeopterids, the seed plants are united by the presence of their specialized reproductive apparatus, which permits them to escape free-water constraints during critical phases of the life cycle. All woody members of this group have distinctly bifacial vascular cambia, although many have limited wood development. Leaves are primitively large and share many developmental and structural characteristics with branches. The stems tend to be centrally rooted. Most of the plants included here are trees, except for the scrambling or semi-self supporting *Calamopitys* and *Lyginopteris*, which plot away from the other seed plants. The medullosans and lyginopterids converge with the lycopsids in some design aspects, particularly in their nonwoody peripheral support and consequent high flow capacity in the specialized secondary xylem (Cichan 1986).

3. The aneurophyte progymnosperms do not cluster with the archaeopterid progymnosperm-seed plant group. Aneurophytes are similar to other Middle Devonian plants on PCA axis 1. They occupy an intermediate position, possibly indicating the general progression of many lineages toward larger size and greater phenotypic complexity than Early Devonian ancestors, while being less divergent than Late Devonian forms. PCA axis 2 indicates that aneurophytes, although the most divergent, are nevertheless most like their cousins, the archaeopterids and (to a lesser extent) the early seed plants. The overall isolation of the aneurophytes probably signifies a divergent ecological role for these plants in the Middle Devonian, perhaps reflecting movement into the better drained habitats more fully exploited later by archaeopterids and seed plants.

4. The sphenopsids and their potential ancestors, iridopterids, sphenophylls, and herbaceous and woody equisetophytes (Stein, Wight, and Beck 1984), form a loose cluster that is closer than any other lineage to the ancestral trimerophytes. The relationship is closest between the trimerophytes and iridopterids, with the sphenophylls somewhat more distant. All share trailing or rhizomatous growth habits. *Equisetum* and the calamites are considerably less similar in the ecomorphospace than would be expected, given their clear phylogenetic and structural similarities, including shared nodal whorls of leaves, branches, and reproductive organs, and unique attributes of the reproductive organs (notably sporangia borne on "sporangiohores" of uncertain homology to reproductive organs in other plants).

Perhaps the relatively small, nonwoody *Equisetum* is not a particularly close ecological analogue of the ancient woody, arborescent calamites.

5. Filicalean and zygopterid ferns plus lycopsids, all of generalized trailing morphology, form a distinct group that is more phylogenetically heterogeneous than the other clusters. In contrast, ground cover plants with sprawling, thicket-forming, or climbing habits (e.g., *Hizemodendron* among the rhizomorphic lycopsids, *Sphenophyllum* among the sphenopsids, and *Lyginopteris* among the primitive seed plants) appear closer to the tree forms of the respective taxonomic groups. The cluster of ferns and primitive lycopsids may reflect phylogenetically retained (i.e., plesiomorphic) structural simplicity, whereas the other groups with sprawling habit have converged by secondary morphological simplification from relatively derived architectures (Bateman 1994, 1996a). Thus, specialization followed by simplification actually may have created more ways to exploit the resources available to ground cover than were available to the more primitive ancestral forms.

Cluster Analyses

Several ecomorphic groups appear in both the CLCA and UPGMA cluster analyses (Figure 11.3). Because CLCA uses the most distant relationship of taxa in constructing clusters, this method tends to suggest clusters of greater compactness, but lower similarity, than UPGMA. The latter assesses relationships of unlinked taxa with the arithmetic means of clusters that have already been formed. Both methods use the full dimensionality of the data in calculating distances between taxa. Thus, the methods serve as a useful comparison with the more incomplete, but highly suggestive, patterns observed in PCA.

1. As with the PCA, there remains a distinction between ground cover and the more structurally complex trees. The first dichotomy in the complete linkage dendrogram, and the second in the UPGMA dendrogram, separate ground cover from tree forms. Forming one group are primitive rhyniophytes, trimerophytes, zosterophylls, lycopodiopsids, sellaginellopsids, filicalean and zygopterid ferns, iridopterids, and *Sphenophyllum*. Missing from this group are the ground cover rhizomorphic lycopsids, the ground cover pteridosperms, and, interestingly, both the trailing filicalean and the marattialean ferns.

2. Another feature also seen in the PCA is evident in the dendrograms. The tree-sized groups show strong concordance with phylogeny. The following architectural groups are distinct in both CLCA and UPGMA analyses:

the woody seed-plants, the bark-supported isoetalean lycopsids, and the relatively primitive aneurophytes plus cladoxylopsids. More difficult to interpret are two consistent associations: (1) the marattialeans (both tree and trailing habits) plus *Equisetum* plus the advanced filicaleans, and (2) the archaeopterids plus calamites.

3. In UPGMA, which, compared to CLCA, de-emphasizes highly divergent taxa, the first dichotomy separates woody taxa from those that generate little if any woody tissue. Unsurprisingly, most of the nonwoody forms are also nontrees. Of the woody forms, the rhizomorphic lycopsids are the only group not supported primarily by wood. In contrast, the CLCA separates most ground cover, including clonal mats, from tree and shrub habits.

Patterns of Ecological Distribution of Major Vascular Plant Clades

Clade Distributions

The major vascular plant classes appear to occupy distinct ecological centroids soon after their appearance, their divergence continuing through the Late Devonian and Early Carboniferous. This assertion is borne out not only by the previous ecomorphospace analysis but by numerous paleoecological studies that relate fossil plant species to sedimentary environments and thereby reconstruct ancient plant communities. In the most generalized terms the clades differentiate as follows.

Isoetalean lycopsid trees became dominant elements in the wettest parts of the lowlands. Beginning as important elements in minerotrophic (clastic substrate) swamps (Scheckler 1986a,b), they quickly became the dominant elements in peat-forming habitats as well (Daber 1959; Phillips and Peppers 1984; Scott, Galtier, and Clayton 1985). Scott (1979) documented their occurrence in a broad spectrum of wetland habitats well into the Late Carboniferous, including swamps, mires, point bars, and the wetter parts of flood plains.

Calamitean tree sphenopsids appeared in stream and lakeside settings as early as the Late Devonian (Scheckler 1986a) and continued in these types of aggradational environments throughout the Carboniferous and into the Permian (Teichmüller 1962; Scott 1978, 1979; Bateman 1991; Gastaldo 1992). Their success in habitats with high clastic influx reflects their clonal, rhizomatous growth habit and the ability it confers to recover from burial (Potonié 1909; Gastaldo 1992). The literature suggests that calamites became relatively widespread in wetlands but were only truly abundant in environments marginal to water bodies, a narrow "adaptive zone."

The progenitors of the seed plants, the progymnosperms, appear to have become tolerant of soil moisture deficits early in their evolutionary history. Beck (1964) and Retallack (1985) suggested that archaeopterid progymnosperms exploited a wide range of habitats in the Late Devonian, including better drained interfluves. Although such environments may not have been "dry" by later standards, they appear to have been among the drier settings colonized by Middle and Late Devonian vascular plants. Substrate-penetrating centralized root systems may have been a key morphological feature permitting this ecology (Bateman and DiMichele 1994b; Algeo et al. 1995; Retallack 1997; Elick, Driese, and Mora 1998; Driese et al. 1997), along with the moderate reproductive diapause offered by heterospory, where spores of some species can persist in a pregermination state without water.

Seed plants appear to have arisen in wetland settings, possibly in habitats similar to those occupied by heterosporous progymnosperms (Scheckler 1986a,b). Of course, early seed habit may have been very similar in its functional attributes to heterospory and have worked most effectively in habitats with regularly available free water (Bateman and DiMichele 1994b). In the Early Carboniferous, however, seed plants radiated in terra firma habitats (Bridge, Van Veen, and Matten 1980; Matten, Tanner, and Lacey 1984; Retallack and Dilcher 1988), a resource zone made available to them by their reproductive biology, basically through reproductive preadaptation (or exaptation in the terminology of Gould and Vrba 1982) to survive moisture stress. Terra firma settings offer a wider array of environmental variations and a vastly greater physical space than that colonized by either the isoetalean lycopsids or the sphenopsids.

Late Devonian ferns and fernlike plants are not particularly well understood ecologically. *Rhacophyton*, a fernlike possible zygopterid, was a dominant element in organic-rich swamps (Scheckler 1986a,b). Certainly, by the Early Carboniferous there is excellent documentation of ferns occupying a variety of habitats, especially those subject to significant disturbance. Scott and Galtier (1985) described volcanigenic landscapes in which ferns are common elements, often preserved as fusain (mineralized charcoal), suggesting growth in habitats frequently swept by ground fires. In the Late Carboniferous, both ground-cover and larger marattialean ferns occurred in a wide range of habitats, except those that appear to have been flooded for long periods of time (Mickle 1980; Lesnikowska 1989; Rothwell 1996). The ground cover elements often are found in highly diverse assemblages within coal-ball deposits from coal seams (Phillips and DiMichele 1981; DiMichele and Phillips 1988), suggesting colonization of short-lived areas of disturbance within mire and swamp forests. Marattialean tree ferns, on the other hand, appear to have

arisen in terra firma settings and from there began a penetration of forests dominated by seed plants, perhaps as weedy elements in more disturbed parts of landscapes. Following extinctions of tree lycopsids in the Late Pennsylvanian of the western tropical belt (not in China, however), tree ferns became dominants in many lowland, wetland habitats throughout the later part of the Late Carboniferous and into the Permian.

Timing of Origination of the Patterns

The most comprehensive analyses of Paleozoic plant ecology focus on the Carboniferous. Certainly, for the Late Carboniferous, dominance of class-level groups has been documented in distinctive sedimentological settings in the tropics, reflecting original resource partitioning. There is considerable literature, extending back into the early part of the twentieth century, that documents the occurrence of plants in coal measures environments in particular. Scott (1977, 1978, 1979, 1980, 1984) summarized this literature, particularly as it relates to compression-impression (adpression) floras from the coal measures, and provided extensive quantitative data documenting plant distribution by sedimentological setting. Eble and Grady (1990) and DiMichele and Phillips (1994) also summarized general patterns of distribution, focusing mostly on floristic associations within peat swamps. Many studies (e.g., Chaloner 1958; Cridland and Morris 1963; Havlena 1970; Pfefferkorn 1980; Lyons and Darrah 1989) documented the coeval existence of lowland-wetland and extrabasinal, more xeric floras in the Late Carboniferous tropics. Little is known of the extrabasinal floras until the last stage of the Late Carboniferous (Stephanian). At that time periodic climatic oscillations created intermittent drier conditions in the lowlands, which permitted immigration of extrabasinal elements (e.g., Winston 1983; Mapes and Gastaldo 1984; Rothwell and Mapes 1988; Mamay and Mapes 1992), providing the earliest unequivocal evidence of conifers and other more derived seed plant groups.

The distributional patterns of Late Carboniferous plants raised our awareness of the broadly distinct ecological centroids of the major clades (e.g., Scott 1980; DiMichele and Bateman 1996; DiMichele and Phillips 1996). Because the pattern already existed and was well differentiated in the Late Carboniferous, it became clear that its origin lay deeper in time.

Early Carboniferous floras have received extensive study recently, largely by Scott, Galtier, and colleagues (Scott and Galtier 1985; Scott, Galtier, and Clayton 1985; Scott et al. 1986; Rex 1986; Rex and Scott 1987; Bateman and Scott 1990; Scott 1990; Bateman 1991), who documented sedimentary environments and revised the systematics of the plants. During the Early Carbonifer-

ous, Europe and most of North America were outside the tropical rainy belt (Raymond, Parker, and Parrish 1985). Consequently, the paleoclimate and spectrum of habitats represented in the fossil record differs from that found in the Late Carboniferous. Yet, the basic patterns of clade-by-habitat distribution revealed by these recent studies appear fundamentally similar to later times. All major body plans, except marattialean ferns, are recorded in the Early Carboniferous. It is in rocks of this age that the early ecological role of ferns as interstitial opportunists is most evident (Scott and Galtier 1985). By the early Namurian, floral assemblages similar to those of the later Carboniferous coal measures began to appear intermittently in wetland habitats (Jennings 1984, 1986; Raymond 1996).

The Carboniferous studies point squarely back to the Devonian as the time of origin of the ecological patterns that would persist directly for the next 30 million years and beyond through influencing patterns of clade replacement through time. Although there are relatively few paleoecological studies of Late Devonian plants, some are quite comprehensive. For example, Scheckler (1986a) provided a thorough examination of the major lineages and their ecological distributions. The basic patterns of partitioning can be detected quite readily in these floras. However, the spectrum of environments occupied and the details of distribution vary from the more prominent patterns that would follow. It thus appears that this was a time of sorting out. The seed plants and their early occurrences in swampy habitats, the dominance of fern-like plants in organic-rich swamps, the occurrence of isoetalean lycopsids in peri-swamp wetlands, and the commonness and numerical dominance of progymnosperms in many floras all are patterns that are close, but not identical, to those that would be more firmly established by the Early Carboniferous. Ecological differentiation can be recognized much earlier still, among the more primitive plants of the Early and Middle Devonian (e.g., Matten 1974; Stein, Wight, and Beck 1983; Edwards and Fanning 1985; Hotton et al. in press). These patterns, however, have yet to be linked clearly to those found in younger vegetation.

Demise of the Primeval Ecosystem

The ecological patterns that evolved in the Late Devonian and earliest Early Carboniferous persisted until the Westphalian, the middle of the Late Carboniferous, throughout most of the world. During the early to middle part of the Late Carboniferous extinctions began, evidently driven by global climatic changes related to the dynamics of polar glaciations (Frakes, Francis, and Sytka 1992). These floristic changes were globally asynchronous but everywhere had

the effect of breaking up the primitive clade-by-habitat patterns of resource partitioning. Seed plants rose to prominence as resources were vacated, and long-term patterns of clade incumbency ended. Climatic changes took place earlier and to a greater extent in the northern and southern temperate zones, driving extinctions and permitting the rise of seed plants in these parts of the world (Meyen 1982; Cúneo 1996). The pattern of disassembly of the tropical wetland biome began later. Its ultimate replacement by a seed-plant dominated biome was hierarchical, beginning first within the wetlands, followed later by replacement of the whole wetland biome on a larger scale (Fredericksen 1972; Broutin et al. 1990; DiMichele and Aronson 1992). In parts of China, Westphalian-type floras persisted well into the Permian (Guo 1990) but ultimately disappeared. Within the subsequent Mesozoic ecosystems there is evidence that subgroups of seed plants and ferns partitioned ecospace along phylogenetic lines and that such patterns of partitioning can be found among angiosperm groups in modern ecosystems (Lord, Westoby, and Leishman 1996).

Diversity Patterns: Did Breadth of Resource Space Constrain the Species Diversity of the Major Clades?

The major clades differ considerably in species and generic diversity. Although species from different clades co-occurred and their aggregate ecological amplitudes overlapped, each clade nonetheless had a distinct ecological centroid. We are led to speculate, then, whether differences in overall species diversity may have been controlled in part by the ecological opportunities available within the core environment colonized by each clade. Do these opportunities reflect not only the physical variability of the habitat but also the simple area available for colonization, which Rosenzweig (1995) suggests as the most important regulator of diversity patterns?

Quantification of past diversity is a problem, however. Two approaches have been used: global species diversity and average floristic diversity. The only comprehensive global database was compiled by Niklas, Tiffney, and Knoll (Knoll, Niklas, and Tiffney 1979; Niklas, Tiffney, and Knoll 1980, 1985), which indicates considerable differences in the diversity of the major clades through time. In the Niklas et al. (1985) compilation, Late Carboniferous arborescent lycopsids are the most diverse group, with over 100 species reported, followed by approximately 50 species of ferns, 40 seed plants, and 20 sphenopsids. In contrast, Knoll (1986) reported diversity of major groups as average floristic diversity. In this latter compilation, during the Early and Middle Pennsylvanian, seed plants were the most diverse group, accounting for approximately 55% of the species; ferns and sphenopsids account for somewhat less than 20% each; and lycopsids account for just 7%.

We determined to follow the method of Knoll (1986) because his results paralleled our direct experiences with Carboniferous tropical floras at local and regional scales, which suggest that seed plants are most diverse, followed in order by ferns, lycopsids, and sphenopsids. Raymond (1996) also reported patterns similar to those of Knoll (1986) on the basis of a regional stage-level compilation. After examination of numerous "local" Late Carboniferous floras (narrow time intervals and uniform depositional environments) and several large monographic treatments of regional floras (longer time intervals and mixed depositional settings), we selected eight examples from tropical Euramerica, confining our analysis to floras Namurian and Westphalian in age. The objective was to examine taxonomic diversity of each major clade in several different kinds of environments or taphonomic settings, representing time windows of different durations. Confining analyses to monographic treatments of floras enabled us to minimize problems of form taxonomy (different names for parts of the same whole plant) and the vagaries of taxonomic use. Finally, by working only with Namurian and Westphalian floras, the confounding effects of major extinctions and ecosystem reorganizations in the later Late Carboniferous were avoided. No attempt was made to combine the floras into a single database because of the problems of inconsistent taxonomic use. Following Knoll (1986), our intent is to seek diversity averages across a representative sampling of locales and environments.

We also examined modern environments as "actualistic" analogues to the Carboniferous, to investigate how patterns of species diversity were constrained by broad environmental types; specifically, wetlands versus terra firma. If our assertions are correct, basic patterns of species packing should vary among these two broad environments. Even though modern taxonomic composition is very different from that of the past, relative diversity patterns should reflect underlying, taxonomically independent controls. The existing numbers for modern environments were obtained from many different sources; studies had a variety of objectives and thus used many different sampling strategies and methods of reporting data. Hence, our compilation is of necessity neither complete nor rigorously statistical. Campbell (1993) provided an excellent summary comparing flooded and terra firma forest diversity in the Amazon basin, which we discovered after undertaking our compilation.

Diversity Patterns in Late Carboniferous Floras

The floras examined can be divided broadly into two landscape types within the wetland biome: peat-forming mires and floodplains. Within each of these there are clearly differentiable subenvironments that have recurrent, distinctive species composition; however, we wish to examine only relative diversities of the major clades and so have chosen to average spatially across subenvironments

TABLE 11.3. Species Diversity of Selected Pennsylvanian Floras^a

		<i>Leary & Pfef 1977</i> <i>Compression Flora</i> <i>Spencer Farm Flora</i> Average spp. #	<i>Scott 1977</i> <i>Compression Flora</i> <i>Annbank-Coal Roof</i> Single Site	<i>DiMichele et al. 1991</i> <i>Coal-Ball Flora</i> <i>Secor Coal</i> Single Site
Lycopsids	8.8	1	1	7 (74.4)
Ferns	15.8	3	2	10 (5.9)
Sphenopsids	7.1	4	5	2 (7.4)
Pteridosperm	22.25	9	9	10 (3.9)
Cordaites	2	5	1	3 (8.3)
Unident. Seed Plant	0.4	0	0	1 (0.1)
Total Seed Plant	24.6	14	10	14 (12.3)

^aNumbers in parentheses are percent abundance values based on quantitative analyses of respective floras. For each flora the citation, compressed versus coal ball, locality, and single or multisite origin are noted. If all groups of seed plants are combined, average species number is 26.4.

within each of the landscape types. The patterns are clear. Without exception, seed plants are the most species-rich group in all floras, generally two to three times as diverse as lycopsids (table 11.3). This is the case even in those habitats where lycopsids dominate in terms of biomass. Fern diversity rarely exceeds that of seed plants but generally is slightly lower. Sphenopsids are the least diverse major clade. Diversity pattern should not be confused with ecological dominance (Wing, Hickey, and Swisher 1993). Lycopsids have been shown clearly to dominate many Late Carboniferous swamps and mires (Phillips, Peppers, and DiMichele 1985), whereas pteridosperms and sphenopsids dominate most Westphalian and Namurian compression floras from floodplain habitats (Pfeferkorn and Thomson 1982).

Similar patterns prevail in both the Southern Hemisphere Gondwana floras (Cúneo 1996) and the Northern Hemisphere Angara floras (Meyen 1982). Although lycopsids are major elements of the landscape and dominate many environments, in overall diversity at either the generic or species level, seed plants are two to three times more diverse than lycopsids.

Modern Diversity Patterns

Our goal was to contrast the species diversity of modern wetlands with that of terra firma environments, expecting that species diversity would be lower in wetlands. Obtaining robust data proved to be as difficult as for fossils but for different reasons. Few regional studies break floras down by habitat, and diver-

TABLE 11.3. (continued)

<i>DiMichele et al. 1991</i> <i>Compression Flora</i> <i>Secor Coal Roof</i> <i>Single Site</i>	<i>Pfefferkorn 1979</i> <i>Compression Flora</i> <i>Mazon Creek</i> <i>Multisite</i>	<i>Willard et al. 1995</i> <i>Compression Flora</i> <i>Springfield Coal</i> <i>Split</i> <i>Single Site</i>	<i>Josten 1991</i> <i>Compression Flora</i> <i>NW German Coal</i> <i>Measure</i> <i>Multisite</i>	<i>DiMichele and</i> <i>Phillips 1996</i> <i>Coal Ball Flora</i> <i>Eastern USA Coal</i> <i>Measures</i> <i>Multisite</i>
1 (0.1)	15	5	32	10
7 (28.2)	37	3	48	16
4 (14.0)	9	3	25	5
11 (57.8)	33	6	82	18
0 (0)	2	1	3	1
0 (0)	0	0	0	2
11 (57.8)	35	7	85	21

sity patterns remain poorly known in many parts of the world. Furthermore, where diversity has been reported by habitat type, the size of the area sampled varies greatly. Without the original data it is not possible to normalize for differences in sampling area. So, once again, a general impression must be gained by inspection rather than by rigorous statistical analysis.

The data we compiled are summarized in table 11.4. Clearly, well-drained, terra firma habitats are more diverse than wetlands, both in total species numbers and in range of variation (Peters et al. 1989; Campbell 1993). In Brazil, for example, a 0.5 ha area of seasonally flooded varzea forest contains 37 tree species, whereas the same area of nearby terra firma forest contains 165 tree species (Prance 1994). Compilation of species by habitat type in Costa Rican forest preserves (Hartshorn and Poveda 1983) demonstrates much lower diversity in swamps and riparian habitats than in terra firma environments. Organic-rich wetlands (peat swamps, bogs, and fens) are lower in species diversity than the surrounding areas, both in temperate and tropical environments (Best 1984; Kartawinata 1990; Westoby 1993; Wheeler 1993). Even in arctic habitats, where species diversity is low in general, the wettest habitats are the least diverse (Muc and Bliss 1977).

The closest approximation to a global summary is given by Gore (1983) in *Ecosystems of the World 4B*. An appendix summarizes all families and genera referenced in the aforementioned volume, a total of 489 genera from 161 families of vascular plants. These are probably gross underestimates, given the

TABLE 11.4. Species Diversity of Selected Extant Floras, Divided by Geographic Region and Terra Firma or Wetland Environment within Region

Sampling Region	Environment or Flora	Sample	Diversity	Geographic Location	Citation
Southeast Asian Floras					
TERRA FIRMA					
		10.5 h	406	E. Kalimantan lowland forest	Kartawinata 1990
		1.6 h	239	E. Kalimantan lowland forest	Kartawinata 1990
		25 plots'	332	N. Sumatra lowland forest	Kartawinata 1990
		1 h	62	lowland Indonesian forest	Kartawinata 1990
		1 h	70	lowland Indonesian forest	Kartawinata 1990
		1 h	95	lowland Indonesian forest	Kartawinata 1990
		1 h	100	lowland Indonesian forest	Kartawinata 1990
		1 h	108	lowland Indonesian forest	Kartawinata 1990
		1 h	110	lowland Indonesian forest	Kartawinata 1990
		1 h	120	lowland Indonesian forest	Kartawinata 1990
		1 h	175	lowland Indonesian forest	Kartawinata 1990
		1 h	208	lowland Indonesian forest	Kartawinata 1990
WETLANDS					
		0.5 h	20	Semboja kerangas (swamp) forest	Kartawinata 1990
		0.5 h	10	Semboja kerangas (swamp) forest	Kartawinata 1990
		1 h	70	Indonesian freshwater swamp	Kartawinata 1990
		0.2 h	29	Indonesian peat swamp	Kartawinata 1990
		0.2 h	35	Indonesian peat swamp	Kartawinata 1990
		0.2 h	40	Indonesian peat swamp	Kartawinata 1990
		0.2 h	45	Indonesian peat swamp	Kartawinata 1990
		0.2 h	50	Indonesian peat swamp	Kartawinata 1990
FLORAS					
		flora	14500	Malaysia—angiosperms	
		flora	650	Malaysia—ferns	

TABLE 11.4. (continued)

Sampling Region	Environment or Flora	Sample	Diversity	Geographic Location	Citation
<i>Southeast USA Floras</i>					
	FLORAS				
		flora	9	Okefenokee swamp trees	Best 1984
			18	Cypress domes—trees	Best 1984
			27	Bayhead swamps—trees	Best 1984
			30	Mixed hardwoods wetland—trees	Best 1984
			71	Mesic mixed hardwood forest—trees	Best 1984
		flora	101	Okefenokee swamp	Lowe & Jones 1984
			65	forb and grass spp.	Lowe & Jones 1984
			6	vines	Lowe & Jones 1984
			21	shrubs	Lowe & Jones 1984
			9	trees	Lowe & Jones 1984
		flora	33 tree / 100 total	River floodplain	Lugo 1984
			13 tree / 99 total	Old fields	Lugo 1984
			5 tree / 179 total	Pine barrens	Lugo 1984
			7 tree / 23 total	Sand scrub	Lugo 1984
<i>Floras of Great Britain</i>					
	FLORAS				
		flora	3354	Total vascular plant species	Kent 1992
		flora	464	Total fern species	Wheeler 1993
		flora	109	Total bog species	Wheeler 1993

Floras of Australia

FLORAS

flora	approx. 25,000	Angiosperm species	Westoby 1993
flora	37	Tropical mangrove forests	Gore 1983
flora	55	Tidal salt marshes	Gore 1983

Floras of the Arctic

TERRA FIRMA

flora	15.2	Average spp. diversity of 10 sites	Muc & Bliss 1977
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WETLAND

flora	12	Wet sedge meadow	Muc & Bliss 1977
flora	4	Tidal salt marsh	Muc & Bliss 1977

Global Patterns

TOTAL DIVERSITY

15,000	Angiosperm genera	Takhtajan 1997
383	Angiosperm families	Takhtajan 1997
127	Nonangiosperm genera	Tryon and Tryon 1982
41	Nonangiosperm families	Tryon and Tryon 1982

WETLAND DIVERSITY

450	Angiosperm genera	Gore 1983
147	Angiosperm families	Gore 1983
39	Nonangiosperm genera	Gore 1983
24	Nonangiosperm families	Gore 1983

poor state of our knowledge of diversity in many parts of the tropics. Even so, they pale by comparison with global estimates of total vascular plant diversity of more than 15,000 genera and 424 families (Takhtajan 1997; Tryon and Tryon 1982), a gap that is unlikely to be bridged by greater sampling (which should also add proportionally more terra firma taxa).

Wetlands account for between 5,570,000 and 8,558,000 km² of a total world land area (approximately 6%: Mitsch and Gosselink 1993). In the United States and Canada, for example, total land area is 18,616,960 km² (Hofstetter 1983; Zoltai and Pollett 1983; Ian Davidson, personal communication, 1997). Of this area, wetlands account for between 1,970,000 and 2,370,000 km² (10–13%), depending on the chosen definition of *wetland*. Peatlands in Southeast Asia account for only 50,000 km² of nearly 2,250,000 km² of total land area (about 2%). In 29 temperate countries, peatlands account for approximately 5% of total land area (Gore 1983). Clearly, the possibility that habitable area is an important constraint on wetland diversity must be considered seriously (Rosenzweig 1995). This should be qualified by the realization that not only is significantly more of the earth's surface terra firma than wetland, but the variation in edaphic conditions in that terra firma area is much greater than in the wetlands.

Overview

The "tesserae model" of Valentine (1980) provides a framework for the origin of "higher taxa" that may be the best single descriptor for the dynamics of the origin of vascular plant classes and, more generally, provides a clear link between ecology and the evolutionary process. In brief, the model suggests that unexploited or underexploited resource space is highly permissive of large morphological discontinuities early in an evolutionary radiation. Resource space is visualized in three dimensions as a field of tesserae similar to a checkerboard, with time along the vertical axis and niche space along the horizontal axes. Space filling begins at the bottom and, through time, the niche space (squares on the checkerboard) is progressively filled. Valentine considered body plans that differ significantly from ancestral forms to be less well integrated developmentally than the ancestral forms, and thus in need of a large, low-competition resource space in which to stabilize. Forms that were small modifications of ancestral body plans were assumed to be able to survive in resource pools of narrower breadth. As space fills, the likelihood of successful establishment of major morphological innovations declines because resources become increasingly scarce and thus more difficult for highly divergent forms to locate, especially if large targets of opportunity are needed. In

effect, this aspect of selection acts as a filter that becomes finer and thus more restrictive as the radiation proceeds. Yet forms only slightly divergent from the ancestors will continue to be able to locate resources because they are more readily accommodated within existing resource limitations.

Using the categorization of Erwin (1992), the spectrum of modern vascular-plant architectures originated in a "novelty radiation," where the limits of the morphological envelope were described early and filling of the adaptive space with a broad spectrum of increasingly specialized species followed later. Incumbent or "home-field" advantage (Gilinsky and Bambach 1987; Pimm 1991; Rosenzweig and McCord 1991) provides ecological bounds to such radiations; in theory, once resource space is occupied, incumbents impede invasions of new species (DiMichele and Bateman 1996).

Whether or not such equilibrium models accurately describe patterns in the short term, studies of the origin of plant morphological features during the Devonian (Chaloner and Sheerin 1979; Knoll et al. 1984; Bateman in press) suggest that complexity initially accrued gradually and that the appearance of major architectures was concentrated in a relatively narrow time interval conforming fundamentally to equilibrium models (e.g., Valentine 1980). The paleobotanical studies of diversity patterns were not linked explicitly to either ecological or phylogenetic patterns, but they mesh well with subsequent data.

Although all aspects of this model still need considerable refinement, the general patterns seem fairly clear. High level phylogeny and morphospace conform well. Patterns of ecological distribution map with a high level of consistency onto the pattern of phylogenetic relationships. The Middle Devonian–Early Carboniferous radiation rapidly became highly channeled ecologically, resulting in an exceptional degree of high-level phylogenetic partitioning of ecological resources that continued to influence ecological dynamics through the middle of the Late Carboniferous (DiMichele and Phillips 1996). It was not until this system began to break down under the influence of major changes in global climate that seed plants began their rise to prominence in the late Paleozoic. The seed plant rise appears to have been globally asynchronous (Knoll 1984) but driven by similar dynamics in temperate as well as tropical regions. These linked patterns suggest a strong role for incumbent advantage in mediating major evolutionary replacements. As cautioned by Valentine (1980), however, radiations following breakdown of the primordial system are less likely to generate new body plans. Rather, they are fueled by innovations from ever more restricted (i.e., less inclusive) parts of the phylogenetic tree, representing modifications of existing forms rather than radically new solutions to the age-old problems of evolutionary opportunity.

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