

PALEOBOTANY

Reproductive innovations and pulsed rise in plant complexity

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Morphological complexity is a notable feature of multicellular life, although whether it evolves gradually or in early bursts is unclear. Vascular plant reproductive structures, such as flowers, are familiar examples of complex morphology. In this study, we use a simple approach based on the number of part types to analyze changes in complexity over time. We find that reproductive complexity increased in two pulses separated by ~250 million years of stasis, including an initial rise in the Devonian with the radiation of vascular plants and a pronounced increase in the Late Cretaceous that reflects flowering plant diversification. These pulses are associated with innovations that increased functional diversity, suggesting that shifts in complexity are linked to changes in function regardless of whether they occur early or late in the history of vascular plants.

Whether measured as complexity (1) or disparity (2, 3), morphological diversity is often thought to have been established early in evolutionary history through pulses such as the Cambrian explosion (4, 5), which are characterized by developmental or ecological innovations (4, 5). The generality of this pattern is unclear, however, as lineages may also show continued diversification (6). Green plants represent an independent radiation of multicellular life in which to explore large-scale patterns in morphological evolution, especially given that the tempo and mode of plant evolution differ from those of evolution in animals (7). The reproductive structures of land plants in particular are familiar examples of morphological diversity and biological complexity; flowers can be intricate structures with many specialized parts in precise arrangements (8–10). At the same time, diverse groups such as ferns produce simple reproductive structures consisting of little more than sporangia. This wide variation underlies many attempts to understand the evolution of land plants and terrestrial ecosystems given that reproductive characters are a core component of phylogenetic analyses (11, 12); reproductive traits have been linked to diversification (13); and propagules such as pollen, seeds, and fruits play fundamental roles in ecology (14).

The plant fossil record suggests that reproductive complexity has generally increased over evolutionary history; the earliest groups produced simple structures (15, 16) whereas those of some derived clades are highly differentiated (8–10). But understanding exactly

when and how reproductive complexity increased is challenging because it requires consistent measurement of complexity across disparate groups (17). In this study, we developed a simple approach for analyzing morphological complexity on the basis of the diversity and arrangement of the basic parts that compose plant reproductive structures, which can be applied to any plant group. We focused on vascular plants—the most diverse and ecologically dominant land plant group from the late Silurian (~420 million years ago) onward.

We divided vascular plant reproductive structures into their basic morphological components and tallied the number of distinctive types of parts in any given taxon (similar to analyses of cell types) (18). These types consist of various kinds of sporangia (including the pollen sacs and nucellus of seed plants) and what we term morphological element types (METs), defined as geometrically distinct regions that occur between sporangia and vegetative leaves or shoots. METs encompass much of what botanists would recognize as reproductive diversity, including organ-level features such as bracts, petals, and carpels, as well as differentiated subregions of these organs (e.g., petal spurs or stigmas; see supplementary materials and methods for discussion of character scoring). After identifying basic part types, we scored how many hierarchical orders of clustering each exhibited. For example, if multiple sporangia were borne on a sporophyll and the sporophylls were reiterated around a fertile axis, the sporangia would show two orders of clustering (once on the sporophyll and once around the axis), whereas the sporophyll would show only one order of clustering (fig. S2 and supplementary methods). We use METs as our primary measure of morphological complexity and use the degree to which both sporangia and METs were reiterated as an additional measure of organizational complexity.

Using this approach, we scored a dataset of 1504 extant and fossil reproductive structures from 1338 taxa, including 866 fossil and 472 extant samples (see supplementary materials and methods for sampling details). Morphological complexity as measured by METs increased in two pulses associated with important periods of structural and ecological innovation (Fig. 1A). The first pulse corresponds to the initial radiation of vascular plants during the Devonian (16), culminating in the appearance of nonflowering seed plants (referred to as “gymnosperms”), and the second reflects diversification of derived lineages within one seed plant group (angiosperms, or flowering plants) during the Late Cretaceous (Fig. 1A) (19). Lineages with lower complexity persist throughout, but pulses increase variance (fig. S3 and table S1). Complexity patterns among extant taxa mirror those of fossils (Fig. 1A), although better sampling of angiosperms results in a higher maximum (see supplementary text). Differences in reproductive biology among groups help structure this basic pattern; average complexity in free-sporing vascular plants, which exhibit the ancestral reproductive biology of land plants (20), rises through the initial pulse but plateaus at a relatively low level thereafter (Fig. 1B and table S2). Within seed plants, dedicated pollen-producing structures (e.g., pollen cones and staminate flowers) are more similar in complexity to free-sporing reproductive structures (Fig. 1C and table S3), whereas seed-producing structures define the upper bounds and are responsible for major shifts and peaks (Fig. 1D and table S4).

These patterns are consistent across lineages; free-sporing plants have independently evolved varying levels of complexity (see discussion of homology in supplementary text) but have consistently few METs, comparable to many pollen-producing structures (Fig. 2). By contrast, seed-producing structures show notably high MET numbers in various gymnosperms (e.g., certain conifers, Gnetales, Bennettitales) and extremely high numbers in some derived angiosperms (Fig. 2) within magnoliids, monocots, and eudicots. Our data also show an expected relationship between complexity and pollination syndrome; animal pollination is associated with the highest complexity among both pollen and seed-producing structures, whereas abiotic pollination is associated with lower complexity (Fig. 2). These temporal and lineage-specific patterns of complexity remain similar when a different scoring approach is used—one based on the number of organ-level part types rather than METs (supplementary materials and methods and figs. S4 and S5)—which suggests that they are robust.

Diversity in the organization and arrangement of parts shows patterns similar to those

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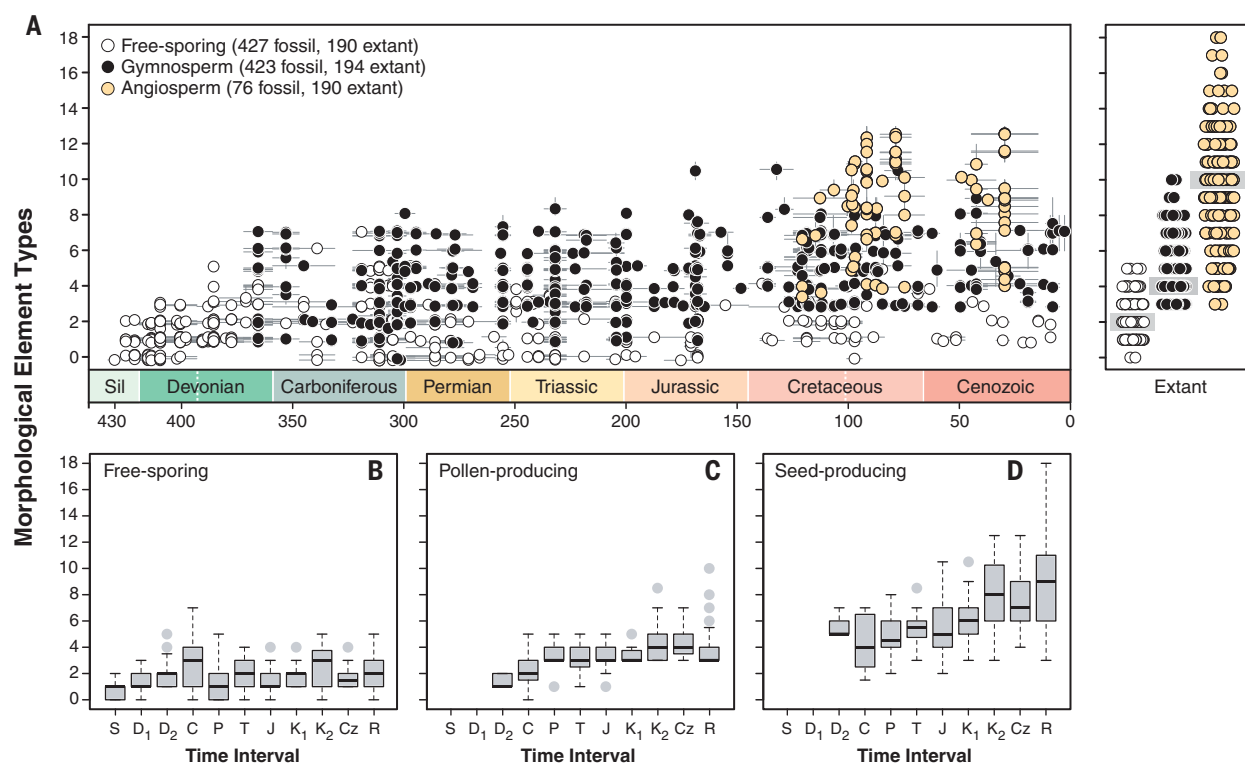


Fig. 1. Complexity patterns in vascular plant reproductive structures

through time. (A) Number of METs through time. Free-sporing plants reproduce through spores, whereas both gymnosperms and angiosperms produce seeds; “gymnosperm” refers to any nonflowering seed plant. A small amount of random noise was added to integer MET values to better visualize patterns. Error bars represent uncertainty in age and MET count; for taxa with potential MET variation, data points represent the average between minimum and maximum. Reproductive structures from extant taxa are shown as stripcharts (right), with median values indicated by gray boxes. (B to D) Boxplots of free-

sporing (B), pollen-producing (C), and seed-producing (D) structures over binned geologic time intervals. The boxes indicate interquartile ranges of aggregate MET counts with outlier taxa shown as points. The Devonian and Cretaceous periods were divided into subintervals corresponding to Early and Middle-Late Devonian and Early and Late Cretaceous; these subintervals are shown on the geologic time scale in (A) by dotted lines. S, Silurian; D₁, Early Devonian; D₂, Middle-Late Devonian; C, Carboniferous; P, Permian; T, Triassic; J, Jurassic; K₁, Early Cretaceous; K₂, Late Cretaceous; Cz, Cenozoic; R, Recent.

of MET counts (Fig. 3). We used a rarefaction approach to account for differences in sampling intensity among groups (see supplementary materials and methods), where the steeper rarefaction curves of seed-producing structures indicate that they have a greater number of unique part arrangements than either free-sporing reproductive structures or dedicated pollen-producing structures in gymnosperms regardless of sampling (Fig. 3). The relative paucity of distinct arrangements in these latter two types of structures is not because their parent lineages have completely explored character space but rather because the observed number of specialized arrangements is well below expectations based on sampling theoretical space at a comparable intensity (fig. S6). Even among seed-producing structures, only those of angiosperms are consistent with a random sampling of theoretical space (fig. S6), suggesting that all other vascular plant groups have evolved a restricted set of part arrangements. The extremely steep slope of angiosperm rarefaction curves (both in pollen- and seed-producing structures) relative to those

of other seed plants is not surprising, as they are undersampled relative to their extreme diversity, but it is noteworthy that even our current dataset includes more part arrangements than in all other seed plant groups combined over their entire history.

Our results suggest a straightforward explanation for the evolution of plant reproductive complexity, where higher levels are associated with greater functional diversity or increased specificity in functional performance, particularly with regard to pollination. Free-sporing and wind-pollinated pollen-producing structures have few parts and change little through time because they perform a limited suite of functions with optimal biomechanical solutions (21). METs in these structures primarily package and protect developing sporangia or pollen sacs (see discussion in supplemental text). Seed-producing structures, by contrast, perform more diverse functional roles, from pollination to protecting and dispersing seeds. Simultaneously optimizing diverse functions can generate disparity (4), and seed-producing structures have evolved

specialized parts for specific functions (e.g., micropylar arms for capturing pollen, interlocking scales to protect seeds, and seed wings for dispersal). This process has reached notably high levels in angiosperms, where a basic innovation (a carpel that encloses seeds) allowed for the development of more specific pollination mechanisms—namely, a single reception surface (the stigma) whose precise morphology and placement relative to other organs underlies specialized animal pollination syndromes (8–10). Such syndromes often involve different floral parts functioning in concert to accommodate specific pollinators, resulting in the evolution of the complicated perianth and androecium morphologies that are largely responsible for the extremely high MET numbers (>11) in derived angiosperms (see Data S1). The carpel also increased the hierarchical organization of angiosperm flowers, and the high number of part arrangements in angiosperms reflects this increased clustering (fig. S7).

That vascular plant reproductive complexity increased over time in some clades as they

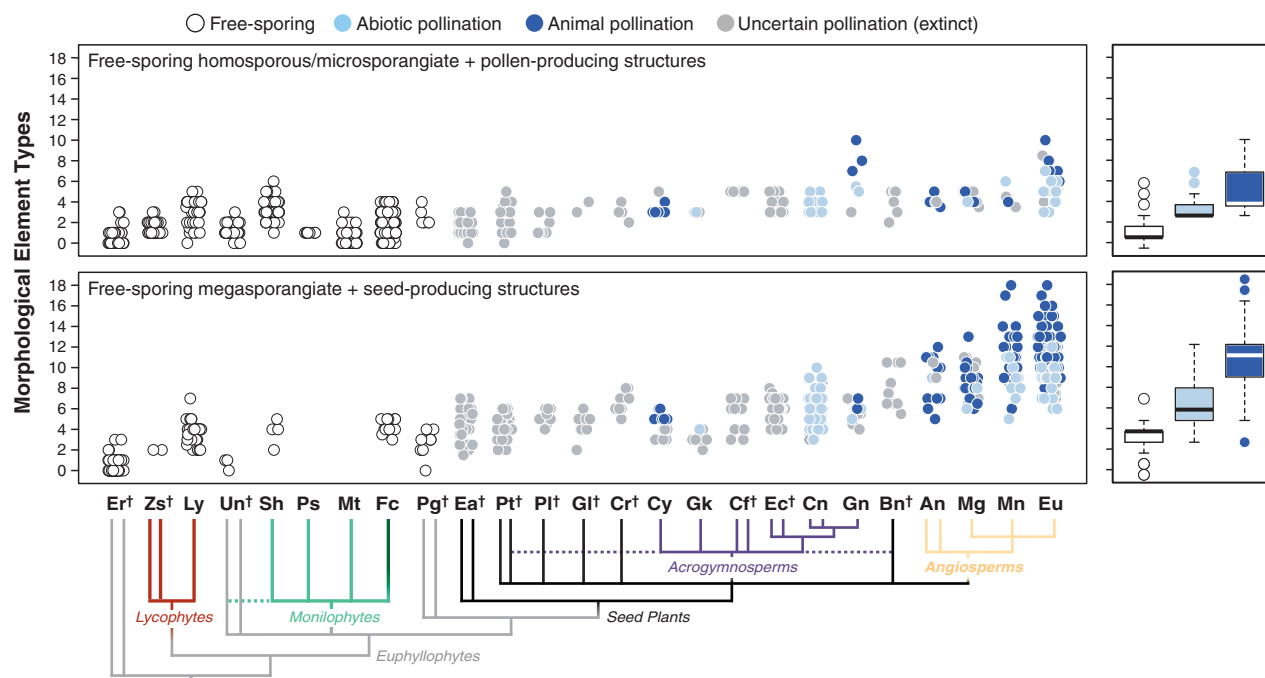


Fig. 2. Complexity patterns in vascular plant reproductive structures

across groups. (Top) Stripcharts of MET number for free-sporing homosporous and microsporangiate structures, and seed plant pollen-producing structures. (Middle) Free-sporing megasporangiate and seed-producing structures; the latter may also produce pollen if bisexual. For taxa with uncertain MET number, average value is shown. Abiotic pollination includes wind and water vectors. (Bottom) Provisional phylogeny based on previous studies is shown (11, 12, 32–34) with major crown clades labeled. Acrogymnosperms and monilophytes are based on extant taxa and may include unresolved fossil groups (shown by dotted lines).

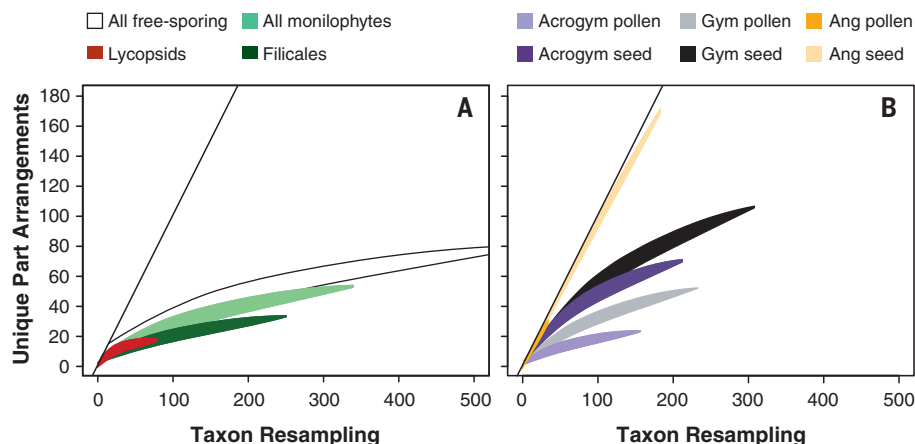
Multiple branches leading to a group indicate potential paraphyly or polyphyly; extinct groups are indicated by a dagger. Er, early plants; Zs, zosterophylls; Ly, lycophytes; Un, unlabeled early euphyllophytes; Sh, sphenophylls; Ps, Psilotales and Ophioglossales; Mt, Marattiales; Fc, Filicales; Pg, progymnosperms; Ea, early “pteridosperms”; Pt, later “pteridosperms”; Pl, Peltaspermales; Gl, Glossopteridales; Cr, Corystospermales; Cy, Cycadales; Gk, Ginkgoales; Cft, early coniferophytes; Ec, early conifers (walchians, voltziales, unlabeled stem); Cn, crown conifers; Gn, Gnetales; Bn, Bennettitales; An, ANA grade angiosperms; Mg, magnoliids; Mn, monocots; Eu, eudicots.

evolved specialized functions is not surprising, although it is important to emphasize that complexity does not always increase. For example, *Ginkgo* reproductive structures are less complex than those of the earliest seed plants, and wind-pollinated angiosperms often evolve reduced, simple flowers (Fig. 2). What is notable in our data, however, is how the total range in reproductive complexity expanded in pulses separated by nearly 250 million years of relative stasis (Fig. 1A and fig. S3). This period, which lasted from the Carboniferous through the Early Cretaceous, is surprising given the obvious potential for higher complexity in seed-producing structures. Surviving members of seed plant lineages that were abundant during this period are known for large genomes and slow rates of evolution that might lead to morphological conservatism (22), but Paleozoic and Mesozoic gymnosperms nonetheless evolved disparate reproductive structures, including those with specialized insect pollination syndromes [e.g., (23)]. Gymnosperms are evidently capable of producing morphologically and functionally diverse structures, but the long plateau in their complexity suggests that levels seen in angiosperms were simply not accessible to seed plants before

the novel geometric and functional possibilities created by the carpel. Carpel evolution does not appear to have immediately led to enhanced complexity, however; the earliest angiosperms in our dataset were no more complex than contemporary gymnosperms (Fig. 1A), and early-diverging extant lineages (with the exception of some derived Nymphaeales) have MET numbers similar to those of gymnosperm groups such as Bennettitales (Fig. 2) (Kolmogorov-Smirnov test $P = 0.52$). This offset would only be more pronounced if crown angiosperms substantially predate their first fossil appearance (24), as we see no evidence of shifts toward higher complexity until the well-documented radiation of more derived lineages from the mid-Cretaceous onward (19). Although we have emphasized the role of function, genomic and developmental innovations may also be important; for example, the origins of seed plants and angiosperms are associated with whole-genome duplication events (25), and angiosperms have characteristically small genome sizes and high modularity (26, 27) that may have enabled lineages within angiosperms to exploit new functional possibilities created by the evolution of the carpel.

Plant evolution and animal evolution are often described as “dancing to a different beat” (7), and our study provides a window into the macroevolutionary history of plants that complements other large-scale analyses, such as those based on compilations of taxic richness (28). Both highlight the importance of the initial Devonian radiation of vascular plants and the Cretaceous diversification of flowering plants in transforming the ecological and morphological space occupied by land plants. Number of part types is only one aspect of complexity; other important aspects of reproductive diversity include fusion among parts, internal anatomy, nutritive reserves (e.g., endosperm), and specific reproductive growth patterns [e.g., phenology, pollen tube growth (29)]. However, our approach allows us to simplify the huge range of vascular plant reproductive morphology, identify key temporal patterns in the evolution of that diversity, and address long-standing ideas relating to its evolution [e.g., (30)]. As in many studies of animal morphological disparity or complexity (2–4), vascular plants show an early rise, achieving levels comparable to those of modern gymnosperms by the latest Devonian (~365 million years ago) as lineages evolve

Fig. 3. Rarefaction curves comparing the number of part arrangements in vascular plant groups at different subsampling intensities. (A) Free-sporing plants and major subclades. **(B)** Seed plants and major subclades. Each cloud represents 95% confidence intervals based on 1000 subsampling replicates. “Gym Pollen,” “Gym Seed,” and “all free-sporing” do not represent clades, but we include them for comparative purposes. Seed-producing structures have steeper slopes than free-sporing and pollen-producing structures in most groups of plants, indicating more part arrangements regardless of sampling. Acrogym, Acrogymnospermae; Gym, all gymnosperms; Ang, angiosperms. “Pollen” and “seed” in the key refers to pollen-producing and seed-producing structures, respectively.



the basic suite of reproductive functions that persist to the present day. In contrast to macro-evolutionary patterns among many animal groups, however, the most pronounced and substantial shift in plant reproductive complexity occurred much later, after the emergence of a distinctive clade whose innovations allowed them to explore a much more expansive functional and phenotypic space, one characterized by the intricate interactions with pollinating animals that have long made flowers objects of fascination (8, 37).

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SUPPLEMENTARY MATERIALS

<https://science.org/doi/10.1126/science.abi6984>
Materials and Methods
Supplementary Text
Figs. S1 to S7
Tables S1 to S4
References (36–49)
Data S1

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Evolutionary pulses of complexity

The evolution of land plants has been marked by an increase in the complexity of reproductive structures. Leslie *et al.* analyzed the temporal pattern of this increase in a study of fossil and extant land plants across the entire paleontological record. Reproductive complexity increased in two widely separated pulses corresponding to key innovations in reproductive biology: the origin of seeds in the very late Devonian and the origin of flowering plants in the mid-Cretaceous almost 250 million years later. After the origin of flowers, there was a rapid expansion in the morphological complexity of flowering plants. In contrast to many aspects of animal morphological diversity, which expanded early in evolutionary history, most complexity in plants was achieved relatively late. —AMS

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