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Title: Reproductive innovations and pulsed rise in plant complexity

One Sentence Summary: Plant reproductive complexity rises in two widely separated pulses associated with major evolutionary innovations.

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1 **Abstract:**

2 Morphological complexity is a notable feature of multicellular life, although whether
3 it evolves gradually or in early bursts is unclear. Vascular plant reproductive
4 structures, such as flowers, are familiar examples of complicated morphology, and
5 here we analyze changes in complexity over time using a simple approach based on
6 the number of part types. We find that reproductive complexity increased in two
7 pulses separated by nearly 250 million years of stasis, including an initial Devonian
8 rise with the radiation of vascular plants and a dramatic Late Cretaceous increase
9 reflecting flowering plant diversification. These pulses are associated with
10 innovations that increased functional diversity, suggesting that shifts in complexity
11 are linked to changes in function regardless of whether they occur early or late in
12 the history of vascular plants.

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

18 The plant fossil record suggests that reproductive complexity has generally
19 increased over evolutionary history: the earliest groups produced simple structures
20 (15, 16) while those of at least some derived clades are highly differentiated (8-10).
21 But understanding exactly when and how reproductive complexity increased is
22 challenging because it requires consistently measuring complexity across disparate
23 groups (17). Here we develop a simple approach for analyzing morphological

1 complexity based on the diversity and arrangement of the basic parts that compose
2 plant reproductive structures, which can be applied to any plant group. We focus on
3 vascular plants, the most diverse and ecologically dominant land plant group from
4 the Late Silurian (~420 million years ago) onwards.

5 We divided vascular plant reproductive structures into their basic
6 morphological components and tallied the number of unique types of parts in any
7 given taxon (akin to analyses of cell types; 18). These types consist of various kinds
8 of sporangia (including the pollen sacs and nucellus of seed plants) and what we
9 term morphological element types (METs), defined as geometrically distinct regions
10 that occur between sporangia and vegetative leaves or shoots. Morphological
11 element types encompass much of what botanists would recognize as reproductive
12 diversity, including organ-level features like bracts, petals, and carpels, as well as
13 differentiated subregions of these organs (e.g., petal spurs or stigmas; see
14 Supplementary Materials and Methods for discussion of character scoring). After
15 identifying basic part types, we then scored how many hierarchical orders of
16 clustering each exhibited; for example, if multiple sporangia were borne on a
17 sporophyll and sporophylls were reiterated around a fertile axis, sporangia would
18 show two orders of clustering (once on the sporophyll and once around the axis)
19 while the sporophyll only one (Fig. S2 in Supplementary Methods). We use METs as
20 our primary measure of morphological complexity and the degree to which both
21 sporangia and METs were reiterated as an additional measure of organizational
22 complexity.

1 Using this approach, we scored a dataset of 1504 extant and fossil
2 reproductive structures from 1338 taxa, including 866 fossil and 472 extant (see
3 Supplementary Materials and Methods for sampling details). Morphological
4 complexity, as measured by METs, increased in two pulses associated with
5 important periods of structural and ecological innovation (Fig. 1A). The first pulse
6 corresponds to the initial radiation of vascular plants over the Devonian (16),
7 culminating in the appearance of non-flowering seed plants (referred to broadly
8 here as ‘gymnosperms’), while the second reflects diversification of derived lineages
9 within one seed plant group (angiosperms, or flowering plants) over the Late
10 Cretaceous (Fig. 1A; 19). Lineages with lower complexity persist throughout, but
11 pulses increase variance (Fig. S3; Table S1). Complexity patterns among extant taxa
12 mirror those of fossils (Fig. 1A), although better sampling of angiosperms results in
13 a higher maximum (see Supplemental Text). Differences in reproductive biology
14 among groups structure this basic pattern; average complexity in free-sporing
15 vascular plants, which exhibit the ancestral reproductive biology of land plants [20],
16 rises through the initial pulse but plateaus at a relatively low level thereafter (Fig.
17 1B; Table S2). Within seed plants, dedicated pollen-producing structures (e.g.,
18 pollen cones, staminate flowers) are more similar in complexity to free-sporing
19 reproductive structures (Fig. 1C; Table S3), whereas seed-producing structures
20 define the upper bounds and are responsible for major shifts and peaks (Fig. 1D;
21 Table S4).

22 These patterns are consistent across lineages; free-sporing plants have
23 independently (see discussion of homology in Supplementary Text) evolved varying

1 levels of complexity but have consistently few METs, comparable to many pollen-
2 producing structures (Fig. 2). In contrast, seed-producing structures show notably
3 high MET numbers in various gymnosperms (e.g., certain conifers, Gnetales,
4 Bennettitales) and extremely high numbers in some derived angiosperms (Fig. 2),
5 especially various lineages magnoliids, monocots, and eudicots. Our data also show
6 an expected relationship between complexity and pollination syndrome; animal
7 pollination is associated with the highest complexity among both pollen and seed-
8 producing structures while abiotic pollination is associated with lower complexity
9 (Fig. 2). These broad temporal and lineage-specific complexity patterns remain
10 similar when using a different scoring approach based on the number of organ-level
11 part types rather than METs (Supplementary Materials and Methods; Figs. S4, S5),
12 suggesting that they are robust.

13 Diversity in the organization and arrangement of parts shows similar
14 patterns as MET counts (Fig. 3). Here we used a rarefaction approach to account for
15 differences in sampling intensity among groups (see Supplementary Materials and
16 Methods), where the steeper rarefaction curves of seed-producing structures
17 indicate that they have more unique part arrangements than either free-sporing
18 reproductive structures or dedicated pollen-producing structures in gymnosperms
19 regardless of sampling (Fig. 3). The relative paucity of unique arrangements in these
20 latter two structures is not because their parent lineages have completely explored
21 character space; the observed number of unique arrangements is well below
22 expectations based on sampling theoretical space at comparable intensity (Fig. S6).
23 Even among seed-producing structures, only those of angiosperms are consistent

1 with a random sampling of theoretical space (Fig. S6), suggesting that all other
2 vascular plant groups have evolved a restricted set of part arrangements. The
3 extremely steep slope of angiosperm rarefaction curves (both in pollen and seed-
4 producing structures) relative to other seed plants is not surprising because they
5 are undersampled relative to their extreme diversity, but it is noteworthy that even
6 our current data set includes more unique part arrangements than in all other seed
7 plant groups, combined, over their entire history.

8 Our results suggest a straightforward explanation for the evolution of plant
9 reproductive complexity, where higher levels are associated with greater functional
10 diversity or increased specificity in functional performance, particularly with
11 regards to pollination. Free-spring and wind-pollinated pollen-producing
12 structures have few parts and change little through time because they perform a
13 limited suite of functions with optimal biomechanical solutions (21); METs in these
14 structures primarily package and protect developing sporangia or pollen sacs (see
15 discussion in Supplemental Text). Seed-producing structures, in contrast, perform
16 more diverse functional roles from pollination to protecting and dispersing seeds.
17 Simultaneously optimizing diverse functions can generate disparity (4), and seed-
18 producing structures have clearly evolved specialized parts for specific functions
19 (e.g., micropylar arms for capturing pollen, interlocking scales to protect seeds, and
20 seed wings for dispersal). This process has reached extreme levels in angiosperms,
21 where a basic innovation (a carpel that encloses the seeds) allowed for the
22 development of more specific pollination mechanisms; namely, a single reception
23 surface (the stigma) whose precise morphology and placement relative to other

1 organs underlies specialized animal pollination syndromes (8-10). Such syndromes
2 often involve different floral parts functioning in concert to accommodate specific
3 pollinators, resulting in the evolution of the complicated perianth and androecium
4 morphologies that are largely responsible for uniquely high MET numbers (>11) in
5 derived angiosperms (see Supplemental Data). The carpel also increased the
6 hierarchical organization of angiosperm flowers, and the high number of unique
7 part arrangements in angiosperms reflects this increased clustering (Fig. S7).

8 That vascular plant reproductive complexity increased over time in some
9 clades as they evolved specialized functions is not surprising, although it is
10 important to emphasize that complexity does not always increase; *Ginkgo*
11 reproductive structures are less complex than those of the earliest seed plants and
12 wind-pollinated angiosperms often evolve reduced, simple flowers (Fig. 2). What is
13 most striking in our data, however, is how the total range in reproductive
14 complexity expanded in pulses separated by nearly 250 million years of relative
15 stasis (Fig. 1A; S3). This period, lasting from the Carboniferous through the Early
16 Cretaceous, is especially notable given the obvious potential for higher complexity
17 in seed-producing structures. Surviving members of seed plant lineages that were
18 abundant during this period are known for large genomes and slow rates of
19 evolution that might lead to morphological conservatism (22), but Paleozoic and
20 Mesozoic gymnosperms nonetheless evolved disparate reproductive structures,
21 including those with specialized insect pollination syndromes (e.g., 23).
22 Gymnosperms are evidently capable of producing morphologically and functionally
23 diverse structures, but the long plateau in their complexity suggests that levels seen

1 in angiosperms were simply not accessible to seed plants before the novel
2 geometric and functional possibilities created by the carpel. Carpel evolution does
3 not appear to have immediately led to unprecedented complexity, however; the
4 earliest angiosperms in our dataset were no more complex than contemporary
5 gymnosperms (Fig. 1A), and early-diverging extant lineages (with the exception of
6 some derived Nymphaeales) have similar MET numbers to gymnosperms groups
7 like Bennettitales (Fig. 2; Kolmogorov-Smirnov test $p = 0.52$). This offset would only
8 be more pronounced if crown angiosperms substantially predate their first fossil
9 appearance (24), as we see no evidence of shifts towards higher complexity until the
10 well-documented radiation of more derived lineages from the mid-Cretaceous
11 onwards (19). Although we have emphasized the role of function, genomic and
12 developmental innovations may also be important; for example, the origin of seed
13 plants and angiosperms is associated with whole-genome duplication events (25)
14 and angiosperms have characteristically small genome sizes and high modularity
15 (26, 27) that perhaps enabled lineages within angiosperms to exploit new functional
16 possibilities created by the evolution of the carpel.

17 Plant and animal evolution are often described as “dancing to a different
18 beat” (7), and our study provides a new window into the macroevolutionary history
19 of plants that complements other large-scale analyses, such as those based on
20 compilations of taxic richness (28). Both highlight the importance of the initial
21 Devonian radiation of vascular plants and the Cretaceous diversification of
22 flowering plants in transforming the ecological and morphological space occupied
23 by land plants. Although the number of part types is of course only one aspect of

1 complexity - fusion among parts, internal anatomy and nutritive reserves (e.g.
2 endosperm), and specific reproductive growth patterns (e.g., phenology, pollen tube
3 growth [29]) are other important aspects of reproductive diversity - our approach
4 allows us to simplify the huge range of vascular plant reproductive morphology,
5 identify key temporal patterns in the evolution of that diversity, and address long-
6 standing ideas relating to its evolution (e.g., 30). As in many studies of animal
7 morphological disparity or complexity (2-4), vascular plants show an early rise,
8 achieving levels comparable to modern gymnosperms by the latest Devonian (~365
9 Ma) as lineages evolve the basic suite of reproductive functions that persist to the
10 present day. In contrast to macroevolutionary patterns among many animal groups,
11 however, the most pronounced and substantial shift in plant reproductive
12 complexity occurred much later, following the emergence of a unique clade whose
13 innovations allowed them to explore a much more expansive functional and
14 phenotypic space, one characterized by the intricate interactions with pollinating
15 animals that have long made flowers objects of fascination (8, 31).

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15 **Author contributions** ABL, CS, and LM designed and conducted the analyses. ABL
16 collected the data and scored taxa for complexity characters. All authors contributed
17 to writing the manuscript.

18
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20 **Competing interests** The authors declare no competing interests.

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22
23 **Data Availability** Complexity scorings for all taxa and reproductive structures are
24 described in shorthand notation in the Supplementary Information. Full scoring
25 data for all reproductive structures with citations and references for literature
26 sources are available on Dryad: <https://doi.org/10.5061/dryad.w0vt4b8qx>.

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33 **Supplementary Materials**

34 Materials and Methods

35 Supplementary Text

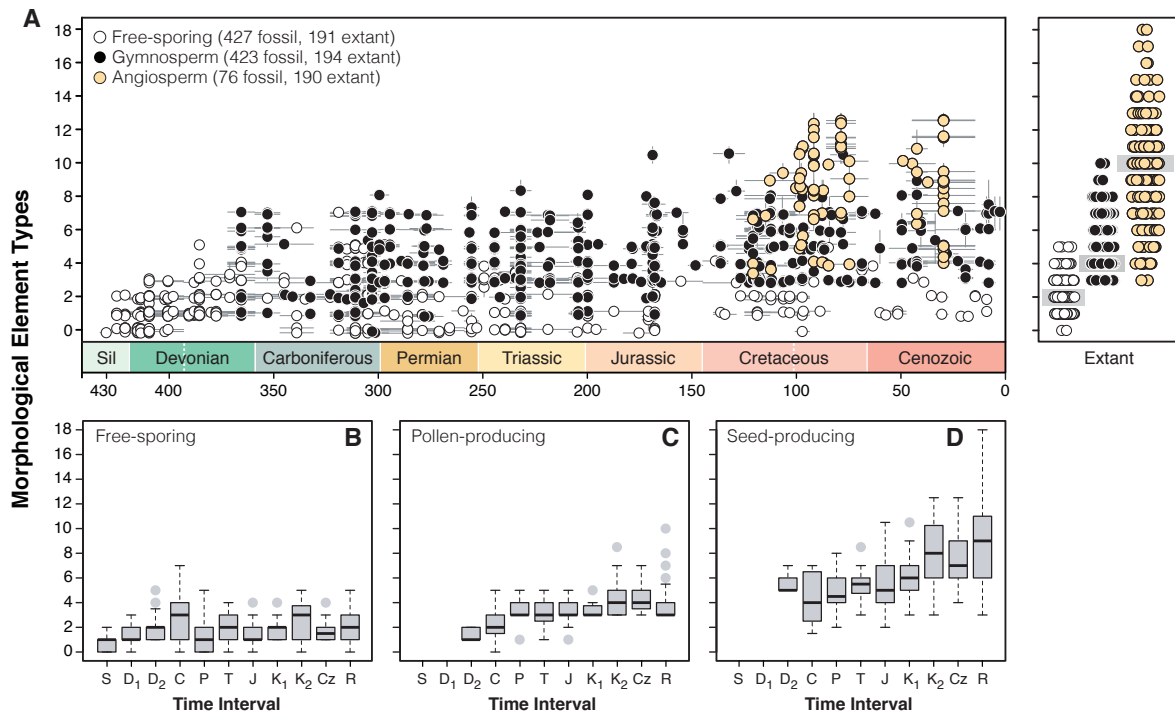
36 Figs. S1 to S7

37 Tables S1 to S4

38 Supplementary Data

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Fig 1. Complexity patterns in vascular plant reproductive structures through

time. (A) Number morphological element types (METs) through time. Free-sporing

plants reproduce through spores, while both gymnosperms and angiosperms

produce seeds; ‘gymnosperm’ refers to any non-flowering seed plant. A slight 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 represents average between minimum and maximum.

Reproductive structures from extant taxa are shown as stripcharts in the panel on the

right, with median values indicated by gray boxes. **(B-D)** Boxplots of free-sporing **(B)**,

pollen-producing **(C)**, and seed-producing **(D)** structures over binned geologic time

intervals. Boxes indicate interquartile range of aggregate MET counts with outlier

taxa shown as points. Devonian and Cretaceous periods were divided into

subintervals corresponding to Early (D₁) and Middle-Late Devonian (D₂), and Early

(K₁) and Late Cretaceous (K₂); 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.

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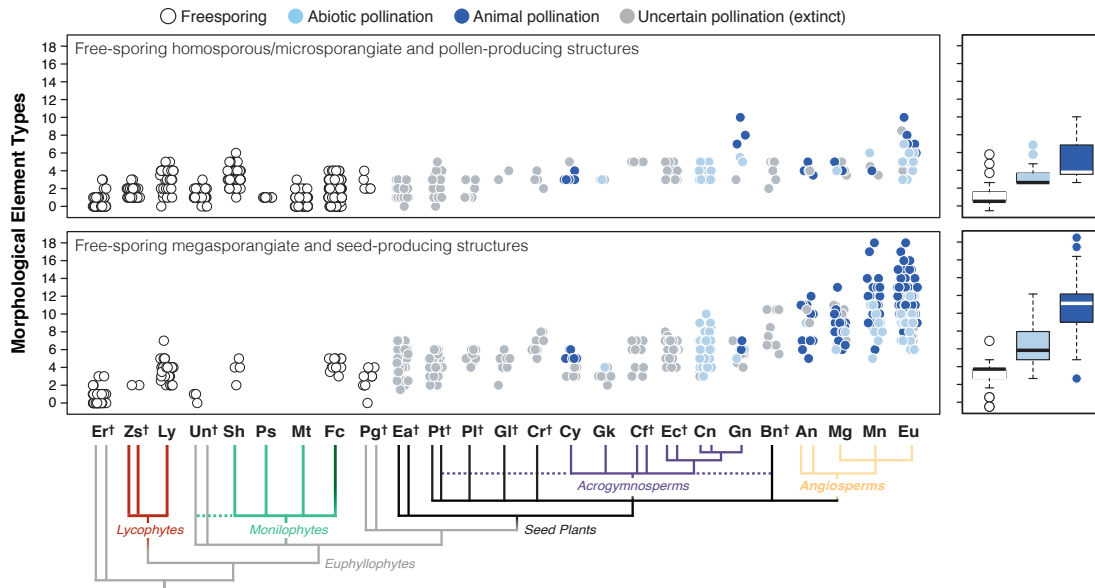
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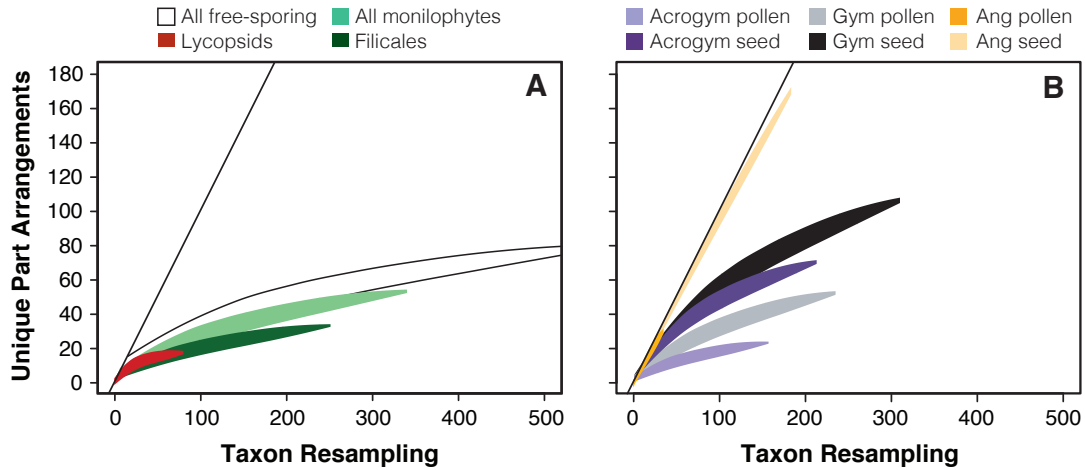
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Fig 2. Complexity patterns in vascular plant reproductive structures across groups. Stripcharts of MET number for free-sporing homosporous and microsporangiate structures, and seed plant pollen-producing structures (upper panel), and for free-sporing megasporangiate and seed-producing structures (lower panel); seed-producing structures may also produce pollen if bisexual. For taxa with uncertain MET number, average value is shown. Abiotic pollination includes wind and water vectors. Provisional phylogeny based on previous studies (11,12,38-40) 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 = lycopsids, Un = unplaced early euphyllophytes, Sh = sphenophylls, Ps = Psilotales + Ophioglossales, Mt = Marattiales, Fc = Filicales, Pg = progymnosperms, Ea = early “pteridosperms”, Pt = later “pteridosperms”, Pl = Peltaspermales, Gl = Glossopteridales, Cr = Corystospermales, Cy = Cycadales, Gk = Ginkgoales, Cf = early coniferophytes, Ec = early conifers (walchians, voltziales, unplaced stem), Cn = crown conifers, Gn = Gnetales, Bn = Bennettitales, An = ANA grade angiosperms, Mg = magnoliids, Mn = monocots, Eu = eudicots.

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Fig 3. Rarefaction curves comparing the number of unique 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. “Gymnosperms” 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 unique part arrangements regardless of sampling. Acrogym = Acrogymnospermae, Gym = all gymnosperms, Ang = angiosperms. “Pollen” and “seed” in the legend refers to pollen-producing and seed-producing structures.