



Angiosperms versus gymnosperms in the Cretaceous

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In a letter to Sir Joseph Hooker dated July 22, 1879, Charles Darwin described the abrupt origin, highly accelerated rate of diversification, and rise to dominance of flowering plants (angiosperms) in the Mid-Cretaceous (100 to 110 Ma) as an “abominable mystery” (1, 2). Knowledge of the paleobotanical record has greatly increased since Darwin’s day. The currently available fossil record clearly documents a sudden and rapid increase in the diversification and geographical extent of angiosperms since the Mid-Cretaceous, resulting in the ecological dominance of flowering plants in almost all terrestrial biomes on Earth today. It has been widely assumed that this major expansion of angiosperms outcompeted other land plants, most particularly the gymnosperms (mainly conifers). As a botany student in the mid-1960s, I was taught this not as a hypothesis but as an “established fact.” In PNAS, Condamine et al. (3) use all of the available fossil and molecular data for conifers to test the competing hypotheses that competition from angiosperms, climate change, or time alone led to the decline of conifers to the benefit of angiosperms. Results from detailed numerical analyses suggest that the increased extinction rates of conifers in the Mid- and Late Cretaceous are most parsimoniously interpreted as a response to the rise of angiosperms, and the alternative hypotheses of climate change or time alone as drivers of the conifer demise are falsified (3).

Within the gymnosperms today (12 families, 79 genera, 985 species), the Pinidae (conifers) is the major group with 6 families, 65 genera, and 627 species (4), such as pines, spruces, and firs. Conifers often occur in relatively harsh environments today such as in boreal areas, at high elevations, and/or on poor or shallow soils. However, conifers were a dominant and widespread component of the Earth’s flora in the Mesozoic, especially in Triassic and Jurassic times (250 to 145 Ma). Rather than concentrating on the rapid rise of angiosperms with their relatively limited fossil record (5), Condamine et al. (3) concentrate on the relatively extensive geological record and well-dated molecular

phylogenies of conifers as a means of evaluating the balance through the Mesozoic and parts of the Cenozoic (Paleogene, Neogene) between gymnosperms and angiosperms and how this balance may have been influenced by tectonism (plate-tectonic movements leading to changes in paleogeography), volcanism, changes in global temperature and atmospheric carbon, sea level fluctuations, and mass extinctions (see figure 1 in ref. 3).

Their study (3) illustrates the problems of much hypothesis testing in earth sciences, whether in Quaternary time or, as in this case, deep time, namely the occurrence of several possible drivers or “predictor variables,” which may, in reality, interact. The geologist Thomas Chamberlin (6) recognized these problems and proposed his “method of multiple working hypotheses” as an invaluable research approach. Condamine et al. (3) adopt this approach. They develop integrated statistical models based on all of the available fossil records of conifers and well-dated molecular phylogenies (“responses”) in relation to climate change (as expressed by changes in global temperature and atmospheric carbon) and of angiosperm diversity (“predictors”) on the diversification and extinction patterns of conifers (see figure 1 in ref. 3). They also incorporate the inherent phylogenetic and dating uncertainties for the molecular data and the uncertainties associated with the age estimates for each fossil record. Their maximum-likelihood and Bayesian methods integrate the possible role of abiotic (climate change) and biotic (relative diversity of angiosperms) factors as possible drivers of conifer patterns. The most probable model is that angiosperms outcompeted conifers during the rapid rise of angiosperms in the Mid-Cretaceous under conditions of long-term global cooling (3). Is this general type of conclusion the likely scenario in the long-term evolutionary history of other plant groups?

Other Plant Groups

Laenen et al. (7) considered the macroevolutionary history of bryophytes (mosses, liverworts, and hornworts)

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that arose soon after the origin of land plants at about 450 Ma (8). They showed that bryophyte overall diversification rates were generally about 50% less than those estimated for ferns and fern allies and 30% less than for angiosperms (7). Time-calibrated phylogenies suggested that bryophytes experienced diversification bursts since the Mid-Mesozoic and that diversification rates in some lineages in the Cenozoic attained values comparable to angiosperms. They concluded that diversification rates do not fully account for the current low bryophyte diversity, and this has probably resulted from frequent extinctions, as in case of the conifers.

Given these findings for conifers (3) and for bryophytes (7), one might expect that the evolutionary histories of both the Polypodiidae (leptosporangiate ferns or so-called “true ferns”) and Lycopodiidae (clubmosses and other fern allies) (4), whose diversity and abundance were high from the Carboniferous to the Jurassic (360 to 145 Ma) and whose fossil records show a sharp decline in the Cretaceous (9), were, in part, a response to the rise of angiosperms in the Cretaceous. However, Schneider et al. (9) showed using molecular data constrained by the limited fossil record that the Polypodiidae (>80% of all extant true ferns) actually diversified in the Late Cretaceous after the major angiosperm diversification, perhaps in response to the increased availability of suitable habitats in the now angiosperm-dominated world. Looking at fern and fern ally diversification over a longer timescale (last 400 Ma), Lehtonen et al. (10) used a Bayesian model to estimate, simultaneously, correlations between diversity patterns and abiotic environmental drivers with an extensive fossil dataset and a detailed molecular phylogeny. Their results suggested that originations depended on within-group diversity and were largely unaffected by environmental change, whereas extinctions were strongly affected by abiotic factors such as climate and geology. Lehtonen et al. (10) concluded that the major drivers of long-term true-fern and fern ally diversity changes were environmentally driven extinctions, whereas originations were opportunistic responses to the availability of appropriate habitats. Angiosperm diversity emerged as a negligible factor in their model. There is thus no support for the hypothesis that the rise of angiosperms in the Mid-Cretaceous drove the replacement of many “old” fern and fern-ally groups by “modern” Polypodiidae true ferns in the Late Cretaceous.

Discussion

A major challenge in all evolutionary biology is to understand what factors regulate the long-term origination and extinction of taxa and thus the rise and fall of entire clades. This challenge is increased further by accumulating evidence that each clade may follow different diversity trajectories through time (3). These

different trajectories may result from the fact that contrasting causes of speciation and extinction may lead to some clades rising, declining, or replacing each other (3). A range of paleontological data shows such biotic replacement, with once-dominant groups disappearing and others appearing to take their place (3).

In PNAS, Condamine et al. use all of the available fossil and molecular data for conifers to test the competing hypotheses that competition from angiosperms, climate change, or time alone led to the decline of conifers to the benefit of angiosperms.

There are two major patterns of clade replacement shown by the fossil record (3): One clade declines while another expands, and mass extinctions. Unlike animal clades, mass extinction events (e.g., the K–Pg event at 66 Ma and the P–T event at 252 Ma) do not appear in general to have had any major evolutionary impacts on land plants (11–13), although they may have impacted some plant diversity and turnover patterns (14–18). Evidence for the clade displacement hypothesis is relatively scarce or, in the case of plants, very rare (3, 10). The study by Condamine et al. (3) demonstrates that clade displacement, previously demonstrated for animals (14, 19, 20), may also apply to plants and highlights the importance of biotic factors in driving long-term diversification patterns as predicted by the “Red Queen” model of evolution (21–24). Detailed paleobotanical studies (3, 7, 9, 10) suggest that long-term biotic and, to some extent, abiotic changes may have played a more important role in plant evolution than mass extinction events have. Assessing the relative role of abiotic changes, the “Court Jester” model of evolution (22, 25), and of biotic changes, the Red Queen model (22, 25), in plant diversification at different spatial and temporal scales (22, 24, 25) remains a major challenge for future studies. Such studies should integrate all available paleobotanical, geological, and molecular phylogenetic data through robust and realistic statistical modeling at a range of scales. Condamine et al. (3) elegantly demonstrates the power of such an approach in their exploration of Darwin’s “abominable mystery.”

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