

## Commentary

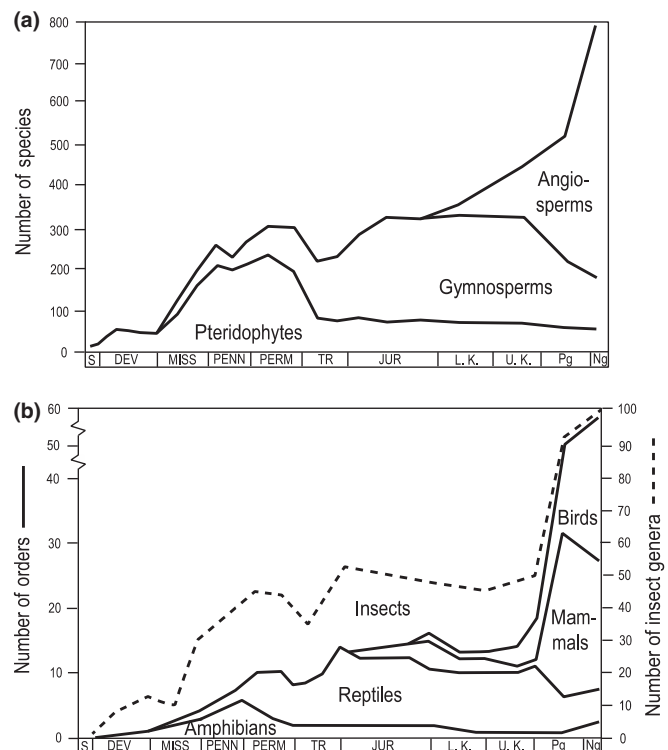
# Measuring the tempo of plant death and birth

Approximately 700 million years ago (Ma), an ancient group of unicellular marine algae evolutionarily diverged and gave rise to the last common ancestor of the predominantly marine Chlorophyta (the green algae) and the last common ancestor of a group of plants that diverged *c.* 450 Ma to give rise to the charophycean algae and the land plants (collectively called the Streptophytes). Subsequent evolutionary innovations on land resulted in four broad groups of land plants distinguished by their structure and reproductive *modus vivendi*. These are represented today by the nonvascular mosses, liverworts, and hornworts (bryophytes), the seedless, free-sporing lycopods, horsetails, and ferns (pteridophytes), the flowerless seed plants (gymnosperms), and by the last to appear in the fossil record, the flowering plants (angiosperms). An early (and by contemporary standards, primitive) analysis of the published literature devoted to their fossil record revealed that each of these four groups once comprised the dominant flora (Niklas *et al.*, 1983). The earliest land plants were undoubtedly nonvascular, bryophyte-like organisms that were ecologically superseded by floras successively dominated by pteridophytes, gymnosperms, and finally angiosperms – a pattern that mimicked the taxonomic dynamics of terrestrial animals (Fig. 1). The same analysis revealed that each successive flora was, on average, more species-rich than its predecessor, indicating that the balance between the origination and extinction of taxa was, on average in favor of origination. In this issue of *New Phytologist*, Silvestro *et al.* (pp. 425–436) present a new and far more masterful analysis of the diversification of the vascular plants, which shows that episodes of high extinction coincided with major floristic transitions and that shifts in origination and extinction rates often coincided with important boundaries and events in the geological column. Silvestro *et al.* also estimate the timing of the origins of the three vascular plant groups, thereby presenting important insights into the complex global process of plant evolution.

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Using a novel hierarchical Bayesian probabilistic method of analysis and a dataset recording 22 415 occurrences of 443 genera of macrofossils (which are more or less evenly distributed among

pteridophytes, gymnosperms, and angiosperms), Silvestro *et al.* focused on the effects of the ‘Big Five’ mass extinctions to gauge the tempo of origination and extinction. They also estimated when each of the three major grades of vascular plants made its first evolutionary appearance by modeling the ‘preservation process’, which infers the origination and extinction rates of each genus based on its multiple occurrences in the geological column. An important aspect of this method of inference is that it does not assume that origination and extinction rates are constant over time, although homogeneous rates are assumed to hold true within discrete time-intervals. These methods of analysis reveal some interesting patterns. For example, origination rates manifest three maxima, one occurring at the Middle Devonian, another in the Early Triassic, and the third in the early Paleogene. The highest extinction rates occur at the Paleozoic–Mesozoic boundary and during the Late Devonian. The authors define diversification rates as being equal to origination rates minus extinction rates. These reached their minimum during the earliest Triassic, but increased during the Middle Triassic. Diversification achieved maxima in the Late Devonian and early Cenozoic. Curiously, diversification rates appear to decline to negative values toward the present day, despite



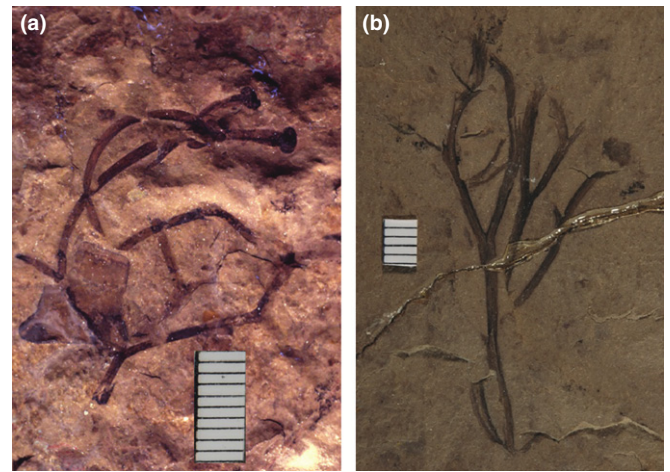
**Fig. 1** Changes in land plant and animal diversity across the Phanerozoic. (a) Number of species attributed to pteridophytes, gymnosperms, and angiosperms plotted against geological age. (b) Number of orders attributed to amphibians, reptiles, mammals, and birds and number of genera of insects plotted against geological age. Redrawn from Niklas (1986).

the rise of the flowering plants that peaked in the Cretaceous. Whether this is an artifact of using genera as the taxon of choice remains problematic (see later).

Of particular interest are the estimates of first occurrences because these give credibility to the analysis. Vascular plants are inferred to first appear during pre-Silurian (late Ordovician) or Early Silurian times, whereas seed plants and flowering plants are estimated to appear first in the Middle Devonian and in the Late Jurassic–Early Cretaceous, respectively. These first occurrences predate the currently oldest known macrofossil for each of the three vascular plant groups. However, each is not particularly far off, thereby emphasizing the fact that the ‘earliest occurrence’ of a taxon in the fossil record is only the ‘minimum oldest age’ because older fossils may yet be found.

There are many questions raised by this study. For example, should not origination and extinction rates be normalized with respect to standing taxonomic diversity? All other things being equal, the greater the number of temporally co-existing taxa, the greater the probability that new taxa can appear or that pre-existing taxa can disappear (Niklas *et al.*, 1980). The addition (or extinction) of a very few taxa in a small flora would have a disproportionate effect relative to their influence in a diverse flora. Are the patterns observed for origination and extinction in any way influenced or biased by abiotic phenomena? An old study based on measurements of paleogeographical maps shows that geological age correlates with total land area, that total land area correlates with the total upland area, and that land plant diversity correlates positively to both (Niklas & Tiffney, 1990). It seems reasonable to speculate that standing taxonomic diversity might increase with increasing land area, and that the probability of being preserved might increase with increasing upland area as vascular land plants adapted to more diverse habitats. Finally, is the genus the appropriate taxonomic level to assess patterns of land plant diversification, and if so are all macrofossil genera equivalent in their reliability? As Silvestro *et al.* correctly note, the oldest most reliable evidence for a vascular flora consists of fossils currently assigned to the genus *Cooksonia* reported from the Wenlock series, early Late Silurian (see Edwards & Richardson, 2004; Wellman, 2014). But are all the fossils placed in this genus really the same thing? Inspection of fossils assigned to *Cooksonia* reveals a range of morphologies with differently shaped sporangia similar to those of extremely disparate plant lineages (i.e. zosterophyllophytes and rhyniophytes). Likewise, some fossils assigned to this genus may not be vascular (Fig. 2). Indeed, some may not even be the remains of land plants (Banks, 1972).

These concerns in no way diminish the importance of the Silvestro *et al.* study, which at the very least serves as a hypothesis to explore other aspects of the fossil record. For example, do trends in vascular plant diversification, origination, and extinction correlate with trends in abiotic factors such as changing sea levels or atmospheric CO<sub>2</sub> concentrations during the Phanerozoic, and if so can these patterns be juxtaposed to enlighten current models for global climate change? Long standing questions of perhaps strictly theoretical interest may also be addressed. For example, do the patterns reported by Silvestro *et al.* help us to better understand plant–animal co-dependencies and interactions, such as pollination or herbivory? Silvestro *et al.* have opened the door to an



**Fig. 2** Compression fossils assigned to the genus *Cooksonia* (a) or credited to have vascular tissue (b), both from the Fiddlers Green member of the Bertie Formation, Cayugan Series, Late Silurian of central New York (scales in millimeters) (Banks, 1972). Yet, neither specimen has recognizable vascular tissues. (a) Group of axes bearing terminal sporangia. Although some axes appear to branch, inspection reveals axes are overlain and unbranched. (b) Branched axes with frayed distal tips lacking sporangia. Cornell University Fossil Plant Collection.

exciting and important era of paleontological investigations, one that could hardly have been imagined 32 years ago.

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