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# Evolutionary Floras – revealing large-scale patterns in Palaeozoic vegetation history

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## Abstract

The overarching trajectory of Palaeozoic vegetation history can be interpreted as the sequential replacement of the Eotracheophytic, Eophytic, Palaeophytic and Mesophytic evolutionary floras. Each evolutionary flora was characterised by a group of co-existing supra-generic plant taxa (families and orders) that formed relatively coherent communities in time and space. In most cases, the transition between floras was relatively brief and usually reflected the appearance of evolutionary adaptations (e.g. seeds, robust steles) that favoured the plants of the new flora. The main exception was the diachronous appearance of the Mesophytic Flora during the late Carboniferous and Permian, apparently the result of the invasion by upland or extra-basinal vegetation pre-adapted to the drier substrates that were developing then in the lowlands. The mass extinctions that had such a major effect on Sepkoski's evolutionary faunas had little effect on the dynamics of the evolutionary floras.

**Keywords:** Evolutionary floras, Palaeozoic

## Introduction

Since the start of scientific palaeobotany, it has been recognised that different fossil floras occur in different parts of the stratigraphical column (e.g., Brongniart, 1828a; Unger, 1845). For a time, this tended to be explained as the result of climate change (e.g., Sternberg, 1823; Brongniart, 1829), in some ways foreshadowing current interests in the link between climate and vegetation in deep time (Beerling, 2017). However, following the development of Darwinism in the mid-19<sup>th</sup> century, changes in the palaeobotanical record became increasingly interpreted in terms of plant phylogeny. By the early 20<sup>th</sup> century, the evolutionary relationships of many of the major plant clades had been established, with most major groups (except the angiosperms) having lineages extending deep into geological time.

Nevertheless, some palaeobotanists continued to look for broader-scale vegetational patterns in the fossil record (e.g., Brongniart, 1849; Schimper, 1869; Saporta, 1879). This gave rise to the idea that Phanerozoic vegetation history occurred in distinct phases and could be interpreted as a succession of large-scale floras (e.g., Potonié & Gothan, 1921). Whilst there is today general agreement that vegetation has changed in character through geological time, this punctuated model of global vegetation history has been more contentious. In this paper, we will briefly explore the background to some of these ideas, especially how they relate to Palaeozoic vegetation history.

## Historical background

### *19<sup>th</sup> century ideas*

The earliest systematic attempts to document the distribution of plant fossil taxa (e.g., Sternberg 1825; Brongniart, 1828a) clearly showed that strata of different ages contained quite different fossil floras. Initially, the history of vegetation was divided into distinct intervals or phases according to the palaeobotanical content of the different stratigraphical units (e.g., Sternberg, 1825; Brongniart 1829): for instance, Brongniart (1828b) recognised four “*periodes de végétation*”, broadly corresponding to the Carboniferous, the Permian – Triassic, the Jurassic – Cretaceous, and the Cenozoic. The evidence initially suggested that vegetation change was following a broadly similar pattern to that seen in the faunas but, as more palaeobotanical data were collated (e.g., Unger, 1845, 1850; Brongniart, 1849; Bronn, 1849) discrepancies began to be revealed and alternative models were proposed to explain these new data (Table 1). Although the different schemes differed in detail, there was general agreement on four broad points: vegetation history could be interpreted as a succession of

distinct, large-scale floras; each flora was characterised by a combination of major plant groups; the transitions between successive floras were relative brief (i.e., there was a punctuated-equilibrium-like pattern to the floras); and the transitions between the floras did not coincide with the major changes in the faunas.

Although it became increasingly evident that these large-scale floras represented in the palaeobotanical record were reflecting the true pattern of vegetation history (Arber, 1912; Clements, 1916; Wieland, 1925) there were sometimes problems with delineating the floras, and therefore in distinguishing them, especially in the transitional phases. This was partly because the floras had been developed using data that had been “binned” into stratigraphical intervals (systems, series), which were defined using palaeozoological criteria; it is now well-known that using such binned data can significantly distort taxonomic diversity patterns in the fossil record (Raup, 1972). Also, the stratigraphical relationships and therefore relative dating of some floras were sometimes wrong: for instance, recognisably Carboniferous floras were dated as Silurian by Saporta (1879) and so included in his Eophytic Flora, which made little palaeobotanical sense.

This ambiguity in the definitions of these floras meant that they tended not to be used in discussions on the history of vegetation through geological time (e.g., Renault, 1888; Potonié, 1897, 1899; Seward, 1898; Zeiller, 1900). Potonié (1897, p. 8) figured the then-accepted stratigraphical timescale with intervals marked as “Zeitalter der Zooidogamen” (Cambrian to middle Permian) and “Zeitalter der Dicotyledonen” (Cretaceous and Cenozoic), and it has been suggested that these were intended to designate distinct floras (e.g. DiMichele *et al.*, 2008). However, they in fact merely represented the times when these groups of plants were thought to be particularly abundant; in his more detailed analysis of vegetation history, Potonié (1899) made no reference to either these terms or the Saporta floras.

### *Gothan floras*

An alternative way of revealing the broad pattern of Phanerozoic vegetation history was used by Gothan (1912). Adopting an approach pioneered by Bronn (1849), Gothan produced a bar chart showing the stratigraphical ranges of what he regarded as the most important taxonomic plant groups (Fig. 1a). Although this was still showing the ranges against the standard stratigraphical scale, the ranges were not being constrained by the boundaries of the stratigraphical units. Gothan (1912) did not discuss the consequences of his range chart but it seemed to indicate that there were three separate stratigraphical intervals, each clearly

characterised by floras dominated by particular major plant groups. He labelled these intervals as “Palaeozoikum der Pflanzenwelt”, “Mesozoikum der Pflanzenwelt” and “Kaenozoikum der Pflanzenwelt” (i.e., Palaeozoic, Mesozoic and Cenozoic floras), despite that their ranges did not coincide with those stratigraphical intervals.

These ideas were developed in greater detail by Potonié & Gothan (1921), who on their p. 430 presented a very similar range-chart to that in Gothan (1912), but with the intervals now labelled Palaeophyticum, Mesophyticum and Kaenophyt[icum] (adapting the terms introduced by Saporta, 1879). These were now clearly described as large evolutionary phases (“große Entwicklungsabschnitte”) in vegetation history, characterised by co-existing major groups of plants (Fig. 1b). The Cenophytic was the most clearly defined, identified by the dominance of the angiosperms. The Mesophytic was identified mainly by the dominance of conifers, cycadaleans, bennettitaleans and ginkgophytes, and matoniacean and dipteridacean ferns. The Palaeophytic was less-clearly defined but was based mainly on the upper Devonian to middle Permian fossil floras dominated by lycopsids, sphenopsids, ferns (notably marattialeans), pteridospermous gymnosperms and cordaitanthaleans. However, the earlier Devonian floras were also included in the Palaeophytic, largely because Potonié & Gothan suggested that they were transitional with the Late Devonian floras (although this was not really borne out by their range chart). There was little empirical evidence at this time, but Potonié & Gothan (1921) suspected that there must also have been Silurian or even earlier vegetation. These hypothetical Silurian floras were provisionally included within the Palaeophytic, but Potonié & Gothan suggested that they might eventually merit being assigned to a fourth vegetation phase, referred to as the “Algenzeit”.

There was some ambiguity in the way that Potonié & Gothan (1921) interpreted these vegetation phases. At one level, they were defined purely on what would today be regarded as biostratigraphical criteria – the co-occurrences of major plant groups in the palaeobotanical record. However, they also seemed to regard them as analogous to the three major time-divisions (now known as eras) of the Phanerozoic chronostratigraphical time that had been developed using the palaeozoological record, the Palaeozoic, Mesozoic and Cenozoic (e.g., Phillips, 1841). But this ambiguity must be understood in the context of the lack of differentiation between chronostratigraphy and biostratigraphy in the early 20<sup>th</sup> century. That biozones should not be conflated with time had been demonstrated, such as through the work on Jurassic ammonites by Buckman (1902; for a review see Callomon, 1995) but most palaeontologists tended to ignore the distinction; it was not until much later that chronostratigraphy and biostratigraphy were strictly segregated (Hedberg, 1954, 1965, 1976).

Nevertheless, it is clear that Potonié & Gothan (1921) had defined the Palaeophytic, Mesophytic and Cenophytic using the stratigraphical distribution of high-ranked taxa of plant fossils, and not when the different types of vegetation were growing – in today's stratigraphical framework, they were biostratigraphical and not chronostratigraphical concepts.

#### *Later developments*

For some time, the Potonié & Gothan (1921) floras were not widely used, at least partly because most palaeobotanists were still concerned mainly with plant fossil taxonomy rather than seeking broad patterns of vegetation history (e.g., Bertrand, 1926; Hirmer, 1927). However, even when the history of vegetation through geological time was being reviewed (e.g., Seward, 1933; Walton, 1940; Arnold, 1947) no mention was made of these floras. At least part of the problem seems to have been that these floristic concepts had been rather subjectively developed through the personal experience of palaeobotanists (mainly Gothan), making them difficult to test in a scientific sense.

It was not until the 1950s that the ideas discussed by Potonié & Gothan (1921) re-surfaced, initially by Gothan & Weyland (1954) and then through the work of the Russian school of palaeobotany. For instance, the palaeobotanical textbook by Kryshtofovich (1957) included a modified set of floras in the discussion of vegetation history: the Palaeophytic, Mesophytic and Cenophytic floras were interpreted in essentially the same way as Potonié & Gothan (1921) except that each was divided into two sub-floras, and the pre-Devonian floras were referred to as Phycomycophytic. A broadly similar approach was also taken by Vakhrameev *et al.* (1978) and Meyen (1987) in their floristic analyses of the palaeobotanical record; Meyen (1987) in particular argued for their value in interpreting the broad pattern of Phanerozoic vegetation history.

Banks (1964, p. 116) produced a stratigraphical range chart for the major plant groups, similar to that published by Gothan (1912). From this, he recognised four “levels of evolution”, each dominated by a particular major plant group. Although Banks did not refer to the Potonié & Gothan (1921) model, there are clear similarities between his levels of evolution and their floras: Level I – Algae ( $\equiv$  “Algenzeit”); Level II – Lower Vascular plants ( $\equiv$  Palaeophytic); Level III – Gymnosperms ( $\equiv$  Mesophytic); and Level IV – Angiosperms ( $\equiv$  Cenophytic). The boundaries between these “levels of evolution” were interpreted as reflecting the replacement of one flora by another, with the transitional phases being

significantly shorter than the times of equilibrium. The Banks model therefore agrees broadly with the views of Potonié & Gothan (1921) – vegetation history can be seen in terms of long intervals of relative stasis separated by briefer intervals of change.

Niklas *et al.* (1983, 1985) illustrated a diversity curve for plant fossil-species through the Phanerozoic and divided the history of vegetation into “Evolutionary Phases”. On the face of it, these phases seemed analogous to the Potonié & Gothan (1921) floras, and the chart in their 1983 paper has been widely reproduced in the literature as representing the underlying pattern of Phanerozoic vegetation history. However, the Niklas *et al.* phases were in fact just the species diversity curves of informal taxonomic groups chosen *a priori*: (1) early vascular plants; (2) other pteridophytes; (3) gymnosperms; and (4) angiosperms. Despite comments by subsequent authors (e.g., Sepkoski, 1990) they cannot really be compared with the Potonié & Gothan (1921) floras.

#### *Sepkoski model*

The idea that fossil faunas (especially the marine invertebrates that dominate the fossil record) show large-scale changes through the stratigraphical column has also had a long history (e.g., Cuvier, 1825; Phillips, 1860), and was part of the underpinning of the division of Phanerozoic time into Palaeozoic, Mesozoic and “Tertiary” eras (e.g., Phillips, 1841). But testing these ideas scientifically was hindered by the absence of sufficiently comprehensive data on the detailed distribution of all of the faunal taxa.

This changed in the late 1970s when the first such datasets for marine faunal families started to be compiled (Sepkoski, 1982, 1992). Sepkoski (1981) analysed these data using factor analysis – a numerical ordination method that aims to identify the underlying factors (in this case faunas) that most efficiently describe the patterns in multivariate data. Sepkoski resolved the data into three large-scale factors that he called evolutionary faunas, which reflected more than 90% of the total variance: a Cambrian Fauna, a Palaeozoic Fauna (Ordovician to Permian) and a Modern Fauna (Triassic to Quaternary). Although the model was the subject of some criticism (reviewed by Alroy, 2004) the results seem to reflect a real pattern within the Phanerozoic marine fossil record (Stigall, 2017; Brayard *et al.*, 2017; Colmenar & Rasmussen, 2018; Rojas *et al.*, 2019, 2021).

Applying a similar approach to the palaeobotanical record was also hindered by the lack of suitable taxonomic data. Some data were given in Harland (1967) but not with sufficient stratigraphical resolution, and a suitable dataset did not become available until the publication

of *Fossil Record 2* (Benton, 1993). The latter was supplemented by revised data for the ferns (Collinson, 1996) and gymnosperms (Anderson *et al.*, 2007), and then subjected by Cleal & Cascales-Miñana (2014) to the same type of factor analysis as used by Sepkoski (1981). The result was a five-factor model that explained 95% of the variance in the plant family data and were referred to as evolutionary floras (Fig. 2). The three largest factors (explaining nearly 90% of the variance) were similar to the Palaeophytic, Mesophytic and Cenophytic floras of Potonié & Gothan (1921), and so these names were adopted. In addition, the analysis resolved a mainly Devonian flora that was named Eophytic (adopting the term used by Saporta, 1875), and a mainly pre-Devonian flora initially named Rhyniophytic but since renamed Eotracheophytic (following the nomenclature of Gray, 1993: see Servais *et al.*, 2019).

A later factor analysis of the Silurian – Devonian floras was undertaken by Capel *et al.* (2021) using a dataset of fossil-genera. This revealed essentially the same pattern as in the Cleal & Cascales-Miñana (2014) study, with Eotracheophytic, Eophytic and Palaeophytic floras, supporting the general robustness of the evolutionary floras model (Fig. 3). The only notable difference was that the Eophytic appeared to be divided into two distinct sub-floras that were not resolved at the family rank.

### **Evolutionary floras**

The following brief review will only deal with the evolutionary floras represented in the Palaeozoic fossil record (Figs 4, 5). The post-Palaeozoic evolutionary floras are relatively straightforward, with the Mesophytic replacing the Cenophytic flora during the Cretaceous, reflecting the rise of the angiosperms (e.g. Cascales-Miñana *et al.*, 2016a). Further discussions on the Palaeozoic evolutionary floras can be found in Cleal & Thomas (2019) and Cleal (2021a).

#### *Eotracheophytic Flora*

This reflects the transition from aquatic to terrestrial vegetation, mainly during the Ordovician and Silurian (Gerrienne *et al.*, 2016; Servais *et al.*, 2019). The fossil record reveals a progressive change from cryptospores, to cuticle and tracheid mesofossils, to slender, bifurcating axes with possible terminal sporangia, to identifiable paratracheophytes (“rhyniophytes”) and then eutracheophytes such some *Cooksonia* (Edwards & Feehan, 1980; Edwards *et al.*, 2001; Strother *et al.*, 2004; Salamon *et al.*, 2018). Gray (1993) distinguished



the non-vascular, rhyniophytoid plants as a separate Eoembryophytic Flora (see also Kenrick & Crane, 1997) but, as this seems to grade into the subsequent Eotracheophytic Flora, it has not been differentiated here. Gerrienne *et al.* (2016) also suggested the green algal ancestors of the rhyniophytoids should be referred to as the Proembryophytic Flora but we know little about these plants other than the dispersed cryptospores.

The Eotracheophytic Flora consisted of plants that were constrained in size to a few millimetres by their internal anatomy (especially the very slender stele), and the resulting vegetation has been described as a turf-like community (Baars, 2017). However, there is in fact little evidence of the lower parts of these eotracheophytic plants and it possible that many were in fact not fully subaerial – the lower parts may still have been subaqueous, with only the upright, sporangium-bearing stems extending out of the water (Servais *et al.*, 2019).

### *Eophytic Flora*

Although the Eotracheophytic Flora persisted into the Early Devonian, by the Pragian it was almost completely replaced by the Eophytic Flora. The new flora consisted of significantly larger and more complex plants. The increase in stature was the result of a thicker stele that provided more support to the stem (Strullu-Derrien *et al.*, 2013; Decombeix *et al.*, 2019), whilst the development of more diverse cauline branching patterns resulted in parts of the plant becoming segregated into specialised photosynthetic and reproductive structures (e.g., Bonacorsi & Leslie, 2019; Szövényi *et al.*, 2019). The greater morphological complexity is reflected in increased taxonomic diversity (Cascales-Miñana, 2016) which in turn expanded the range of habitats that could be vegetated.

Cleal & Cascales-Miñana (2014) characterised the Eophytic Flora as being dominated by zosterophylloids, basal lycopsids and basal euphyllophytes, but the analysis of genera by Capel *et al.* (2021) suggested that there are in fact two distinct subfloras. The early Eophytic Flora found in the Lower Devonian is dominated by zosterophylloids (Zosterophyllaceae, Gosslingiaceae), barinophytoids, basal euphyllophytes (Trimerophytaceae) and rhyniophytoids. These included the first plants to be fully adapted to a terrestrial life with well-documented rhizomorphic structures. They also represent the oldest plants that can be directly related to the two tracheophyte subdivisions – the Lycophytina and Euphyllophytina.

The early Eophytic Flora was progressively replaced during the Middle Devonian by subarborescent lycopsids (Protolepidodendraceae, Haskinsiaceae), cladoxylloids, rhacophytoids and archaeopteridoids (“progymnosperms” – Aneurophytaceae,

Archaeopteridaceae), which Capel *et al.* (2021) assigned to a late Eophytic Flora. The increase in stature in these new groups of plants was largely a consequence of a more complex cauline anatomy including the development of secondary growth, and resulted in the first forests (Berry, 2019), which had wide-ranging consequences for climate and landscape (Morris *et al.*, 2015). Increasing stature of plants was driven by competition for light to enhance photosynthesis, which was further improved through the development of planate and webbed leaves (Harrison & Morris, 2018). More complex reproductive strategies were also developing, as evidenced by the appearance of heterospory (Bateman & DiMichele, 1994; Petersen & Burd, 2017), although the pteridophytic reproduction strategies were probably still constraining vegetation to the mainly wetter habitats.

### *Palaeophytic Flora*

The rise of the Palaeophytic Flora in the Late Devonian and early Mississippian had a profound effect on the physical environment as well as the trajectory of vegetation history. It not only saw a significant increase in both taxonomic diversity (Cascales-Miñana, 2016) and plant biomass: plants were not only growing larger (mainly through increased cauline secondary growth) but were also expanding into a wider range of habitats (mainly through the evolution of the seed). The expansion of forests significantly altered landscapes and river flow (Gibling & Davies, 2012) and the resulting change in water chemistry caused marine anoxia through encouraging algal blooms (Algeo *et al.* 1995; Carmichael *et al.* 2019), which in turn caused a biotic crisis in marine habitats (the Frasnian/Famennian extinction – McGhee, 1996). The enhanced carbon sequestration by the expanding forests may also have contributed to the start of the Late Palaeozoic Ice Age – one of the most extensive glacial episodes in Earth history (Berner 2003).

The lycopsids continued to be major components especially of wetland vegetation, diversifying into the arborescent families (e.g., Lepidocarpaceae, Flemingiaceae, Sigillariostroboaceae). There was also a significant diversification of early ferns (Botryopteridaceae, Corynepteridaceae, Psalixochlaenaceae, Stauropteridaceae, Tedeleaceae, Zygopteridaceae – e.g., Galtier & Scott, 1985; DiMichele & Phillips, 2002). In the Pennsylvanian, marattialean ferns (principally the Psaroniaceae) became major components of the Palaeophytic Flora, forming tree-fern forests over large areas of lowland tropical Pangaea.

The most significant change, however, was the appearance of seed-plants (Anderson *et al.*, 2007). This enabled vegetation to expand into a much greater range of habitats as their gametophytes no longer needed surface moisture for fertilisation to occur (Meyer-Berthaud *et al.*, 2018). The earliest seed-plants were pteridosperms with large, fern-like fronds of the Lyginopteridales, followed later in the Carboniferous by the Medullosales and then Callistophytales. Pinopsid seed-plants also appear in Palaeophytic floras in the Pennsylvanian or possibly late Mississippian, mainly represented by the Cordaitanthaleans (a probable sister group of the Pinales).

The Palaeophytic Flora is best represented in the Carboniferous of Euramerica and then extended into Cathaysia in the latest Carboniferous and Permian (Hilton & Cleal, 2007; Wang, 2010; Cleal, 2021a,b; Opluštil *et al.*, 2021). During the Carboniferous, the higher palaeolatitudes of Gondwana and Angara mostly had relatively low-diversity vegetation dominated by subarborescent lycopsids (e.g., Meyen, 1982; Iannuzzi & Pfefferkorn, 2002; Mosseichik, 2018). The phylogenetic relationship between these and the better-understood arborescent lycopsids of the palaeotropical belt is still unclear, but it is probably reasonable to regard them all as being essentially part of the Palaeophytic Flora. In the Permian, following the end of the Late Palaeozoic Ice Age, the higher palaeolatitudes supported more diverse vegetation often dominated by seed-plants, notably the Glossopteridales in Gondwana (McLoughlin, 2011) and the Vojnovskiales (“ruflorias”) in Angara (Meyen, 1982); in Gondwana, lycopsids also remain important components of the vegetation (Spiekermann *et al.*, 2021). As the diversity dynamics of these higher-latitude seed-plant-dominated communities appear to follow broadly similar patterns to the palaeotropical vegetation especially of Cathaysia (Cleal, 2018), for the time being it seems reasonable to include them also within the Palaeophytic Evolutionary Flora.

### *Mesophytic Flora*

A major change in the palaeobotanical record starts in the upper Carboniferous and continues through the Permian, with the appearance of floras dominated by Pinales, Peltaspermales, cycadopsids and ginkgopsids. This is the Mesophytic Flora in the Cleal & Cascales-Miñana (2014) model. The replacement of the Palaeophytic by the Mesophytic Flora reflects one of the most important changes to terrestrial vegetation in Earth history and was interpreted by Wing (2004) as being equivalent to a mass extinction. Unlike the other biotic crises sometimes interpreted as mass extinctions, however, this was a long, drawn-out

vegetational change that occurred in different parts of the world over a period of some 50 Ma. The appearance of Mesophytic fossil floras often coincides with the development of red-beds caused by better-drained substrates (e.g., Kerp, 1996, 2000; Wang, 1996; DiMichele *et al.*, 2008, 2009). It seems to have been the result of upland (or at least extra-basinal – Thomas & Cleal, 2017) vegetation that was pre-adapted to the somewhat drier conditions, spreading into the lowlands as conditions there changed due to a combination of orogenic and climatic changes (Frederiksen, 1972).

Vegetation history underwent significant disruption during the late Permian and Early Triassic. Known as the Permian – Triassic mass extinction (Cascales-Miñana *et al.*, 2016b; Cleal, 2018) it was caused by massive eruptions of mainly basaltic magma in the Emeishan and Siberian large igneous provinces (Bond *et al.*, 2010; Stevens *et al.*, 2011; Hochuli *et al.*, 2016). Vegetation remained impoverished across the world for some 5 Ma in the Early Triassic, mainly dominated by shrubby lycopsids and conifers, and c. 55% of plant families became extinct (Cascales-Miñana & Cleal, 2014; Cascales-Miñana *et al.*, 2016b), and plant life did not start to properly recover until the Middle Triassic (Vajda & McLoughlin 2007). Nevertheless, despite the number of plant families that disappeared during this biotic crisis, Late Triassic and Jurassic vegetation had an essentially similar taxonomic structure to the Permian Mesophytic Flora, and the numerical analysis by Cleal & Cascales-Miñana (2014) did not distinguish them; as with the Potonié & Gothan (1921) model, the Mesophytic Flora extended from the Permian through to the Cretaceous.

### Discussion

The debate as to whether the overall history of vegetation change has been gradual or punctuated can be traced back to the late 19<sup>th</sup> century, and largely has its origins in whether the data are being viewed from a “top-down” or “bottom-up” perspective. When the palaeobotanical record has been viewed as a whole (i.e., “top-down”) most authors have seen patterns, especially in the distribution of supra-generic taxa. This might be dismissed simply as the natural, human tendency to see patterns in complex data, irrespective of whether or not a pattern actually exists (sometimes referred to as apophenia). The reality of these patterns appeared to be supported by the numerical analyses of plant taxa through time (Cleal & Cascales-Miñana, 2014; Capel *et al.*, 2021) but, again, this on its own does not provide objective verification of the revealed patterns. The numerical method used (factor analysis) is an ordination technique that can reveal patterns in highly complex multivariate data –

patterns that will otherwise be difficult to see – but provides no measure of the statistical robustness of the results; the results still have to be independently validated. There are post-hoc numerical methods that can test the statistical significance of the groupings suggested by ordination, such as bootstrapping or multivariate analysis of variation (Hammer & Harper, 2006), but these will just show whether or not the results could be the result of chance, not whether they are botanically meaningful. In the case of the evolutionary floras model, the best test is whether they make sense to the experienced palaeobotanist. Cleal & Cascales-Miñana (2014) argued that they did: paraphrasing Sepkoski (1981), “...the results should be of no real surprise to any palaeobotanist...who has walked out a variety of stratigraphical sections or picked through a number of museum drawers.” The main thing was not so much the analytical method used, but that the results made intuitive sense, and that they had been based on robust and testable data.

If, in contrast, a “bottom-up” approach is taken, identifying such large-scale floras in a particular bed or locality can be difficult. Especially in transitional phases, the exact delineation of the floras is often not sharp; it may not be possible always to say that an individual plant fossil assemblage belongs to this flora or that flora; this was, for instance, found to be a problem with the Palaeophytic – Mesophytic transition (DiMichele *et al.*, 2008). But this is misunderstanding what the evolutionary floras are intended to show: they are not classificatory concepts into which each and every assemblage can be slotted. Rather, they are intended to provide a sense of the overarching pattern of vegetation change through the Phanerozoic.

The evolutionary floras are characterised by co-existing groups of plant families that formed coherent communities in time and space. The Eotracheophytic, Eophytic and Palaeophytic floras can also be characterised at the rank of class (Fig. 5). This is probably because these floras at least partly reflect the major evolutionary innovations that partly help circumscribe the classes (e.g., cuticles, seeds, increasingly complex vascular structures and cauline branching). This is in contrast to the rise of the Mesophytic Flora, which was at least partly caused by family changes within classes; there are, for instance both typically Palaeophytic and typically Mesophytic families of pteropsids, cycadopsids and pinopsids. This is probably because of the fundamentally different nature of the Palaeophytic – Mesophytic transition, which was the result of global environmental changes, rather than the appearance of major, class-defining evolutionary innovations.

Hoffman & Fenster (1986) suggested that the evolutionary faunas of Sepkoski (1981) were reflecting the biotic crises known as mass extinctions, but this does not seem to be the

case with the evolutionary floras. In one case, in fact, there is evidence that the rise of the Palaeophytic Flora and the consequential expansion of forest cover may have been partly responsible for the Frasnian – Famennian mass extinction in the marine faunas (Algeo *et al.*, 1995). Only the rise of the Mesophytic Flora seems to be reflecting a global ecological crisis but this significantly pre-dated the late Permian – Early Triassic (P / T) event. There was significant disruption to vegetation at about the Permian –Triassic boundary (Hochuli *et al.*, 2010, 2016) and many families became extinct (Cascales-Miñana *et al.*, 2018), but the fundamental taxonomic structure of vegetation was little altered: the Mesophytic Flora continued from the Permian through to the Triassic and later.

### Conclusion

Empirical evidence suggests that Palaeozoic vegetation dynamics can be interpreted as a succession of large-scale floras. The existence of such floras has been suggested since the early 19<sup>th</sup> century and numerical analyses of large databases of plant fossil distributions (Cleal & Cascales-Miñana, 2014; Capel *et al.*, 2021) have now given a solid foundation to these ideas. It is now possible to identify distinct evolutionary floras (analogous to the evolutionary faunas of Sepkoski, 1981), which reflect either major evolutionary innovations or global ecological changes. In contrast to the evolutionary faunas, however, the biotic crises known as mass extinction had little effect on the dynamic pattern of the evolutionary floras.

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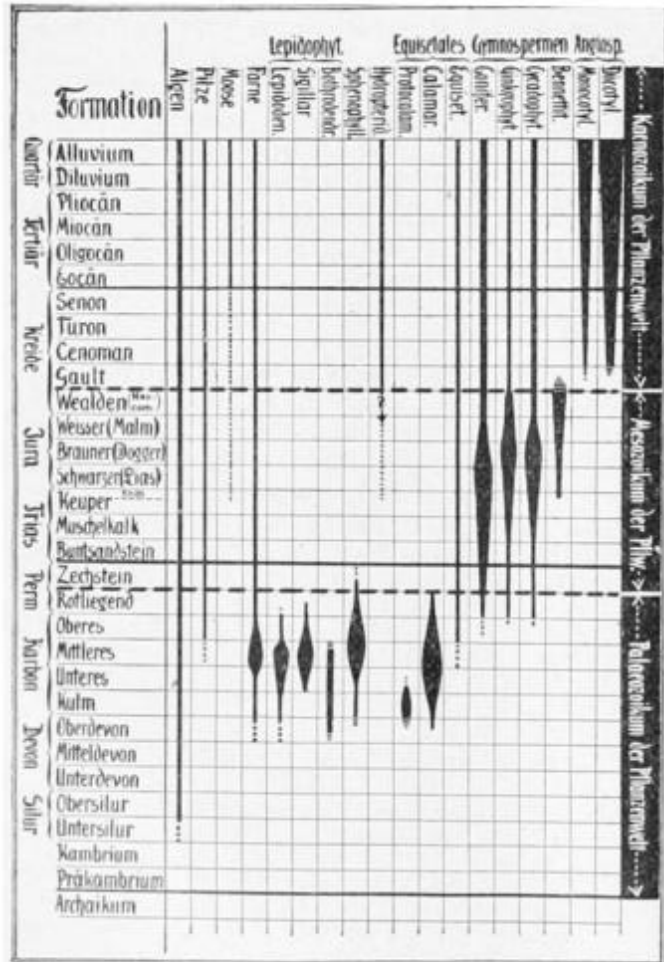
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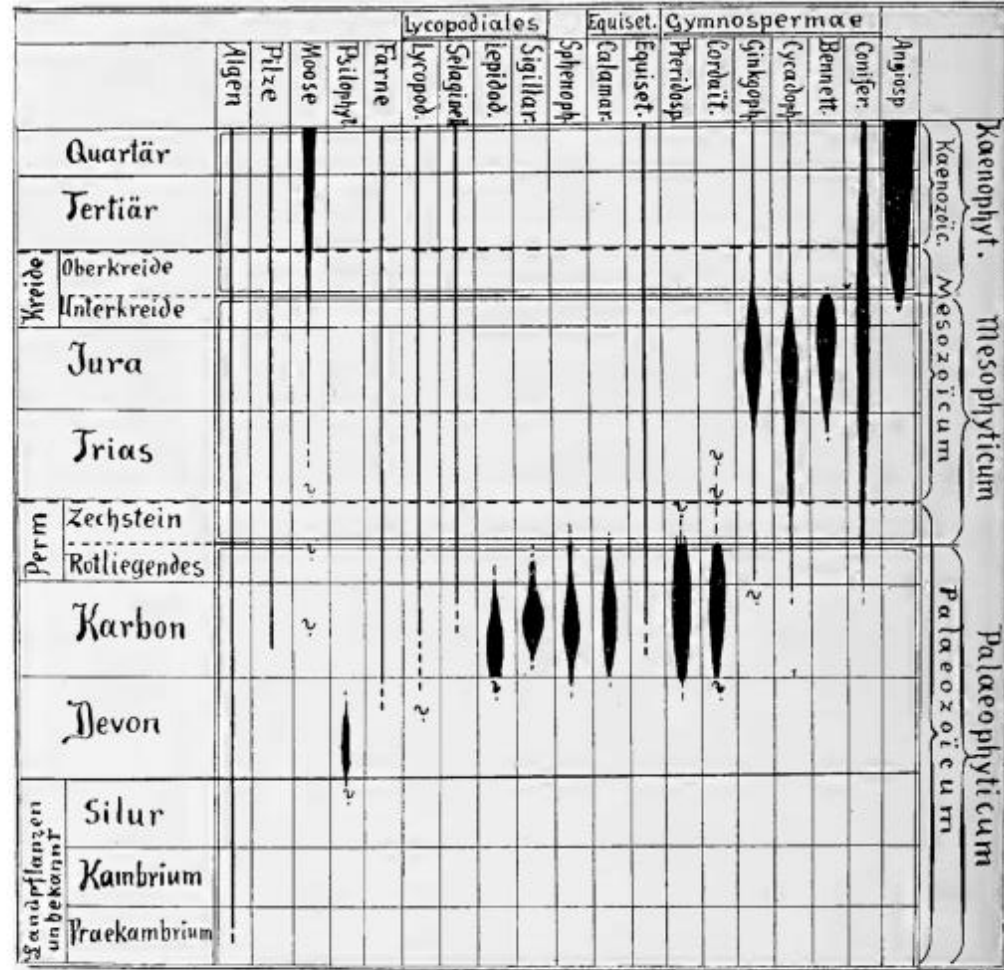
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Table 1. Various proposals for large-scale floras to explain the broad patterns of Phanerozoic vegetation history

	Brongniart (1828b)	Brongniart (1849)	Schimper (1869)	Saporta (1879, 1890)	Gothan (1912)	Potonié & Gothan (1921)
Neogene	Quatrième Période	Règne des Angiospermes	Règne des Angiospermes	Neophytic	Cenozoikum der Pflanzenwelt	Cenozoic
Palaeogene						
Cretaceous	Troisième Période	Règne des Gymnospermes	Règne des Gymnospermes	Mesophytic	Mesozoikum der Pflanzenwelt	Mesophytic
Jurassic						
Triassic						
Permian	Seconde Période	Règne des Acrogène	Règne des Cryptogames vasculaires	Palaeophytic	Palaeozoikum der Pflanzenwelt	Palaeophytic
Carboniferous						
Devonian	??????	??????	Règne des Thalassophyte	Eophytic		“Algenzeit”
Silurian						



(a) Gothan (1912)



(b) Potonié & Gothan (1921)

Fig. 1. The tables given by Gothan (1912) and Potonié & Gothan (1921) showing the evidence being used to define large-scale patterns in the plant fossil record. Note the change in nomenclature used in the two papers.



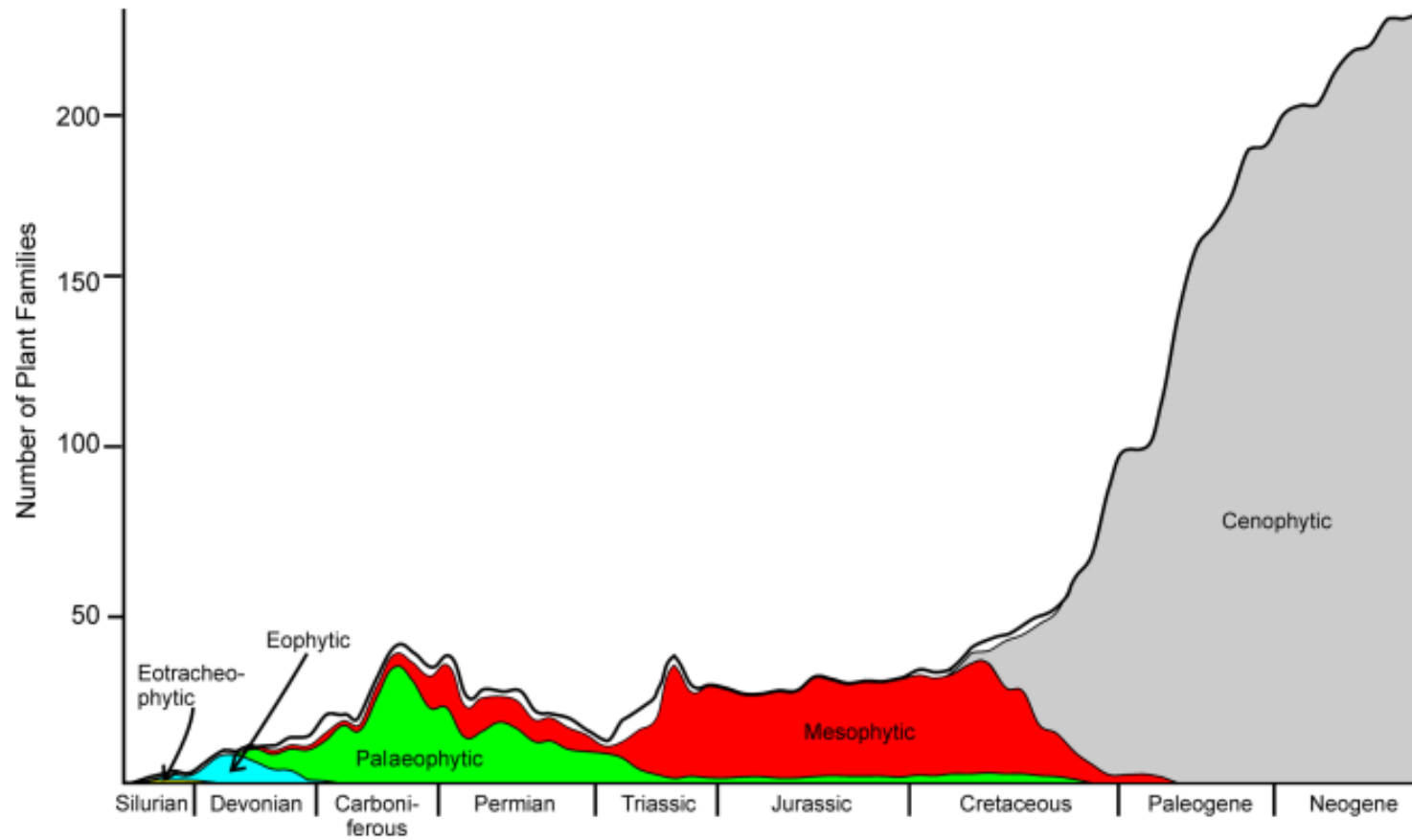


Fig. 2. The Evolutionary Floras model developed by Cleal & Cascales-Miñana (2024) based on a factor analysis of a dataset representing the stratigraphical distribution of plant families and classes.

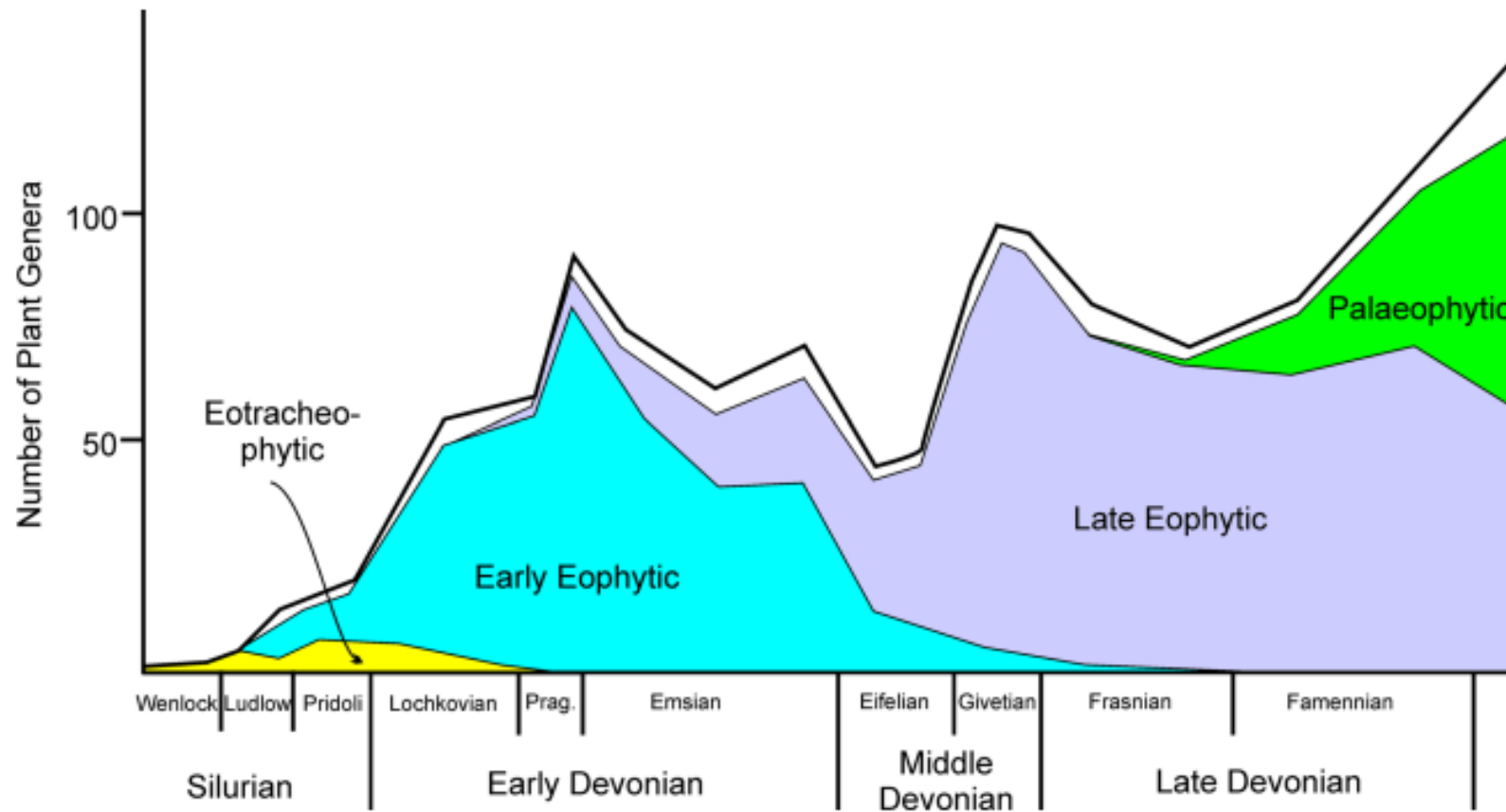


Fig. 3. Results of a factor analysis by Capel *et al.* (2020) of a dataset representing the distribution of plant genera through the Silurian and Devonian. This broadly agreed with the results of the Cleal & Cascales-Miñana (2024) evolutionary floras except for the division of the Eophytic into two subfloras.

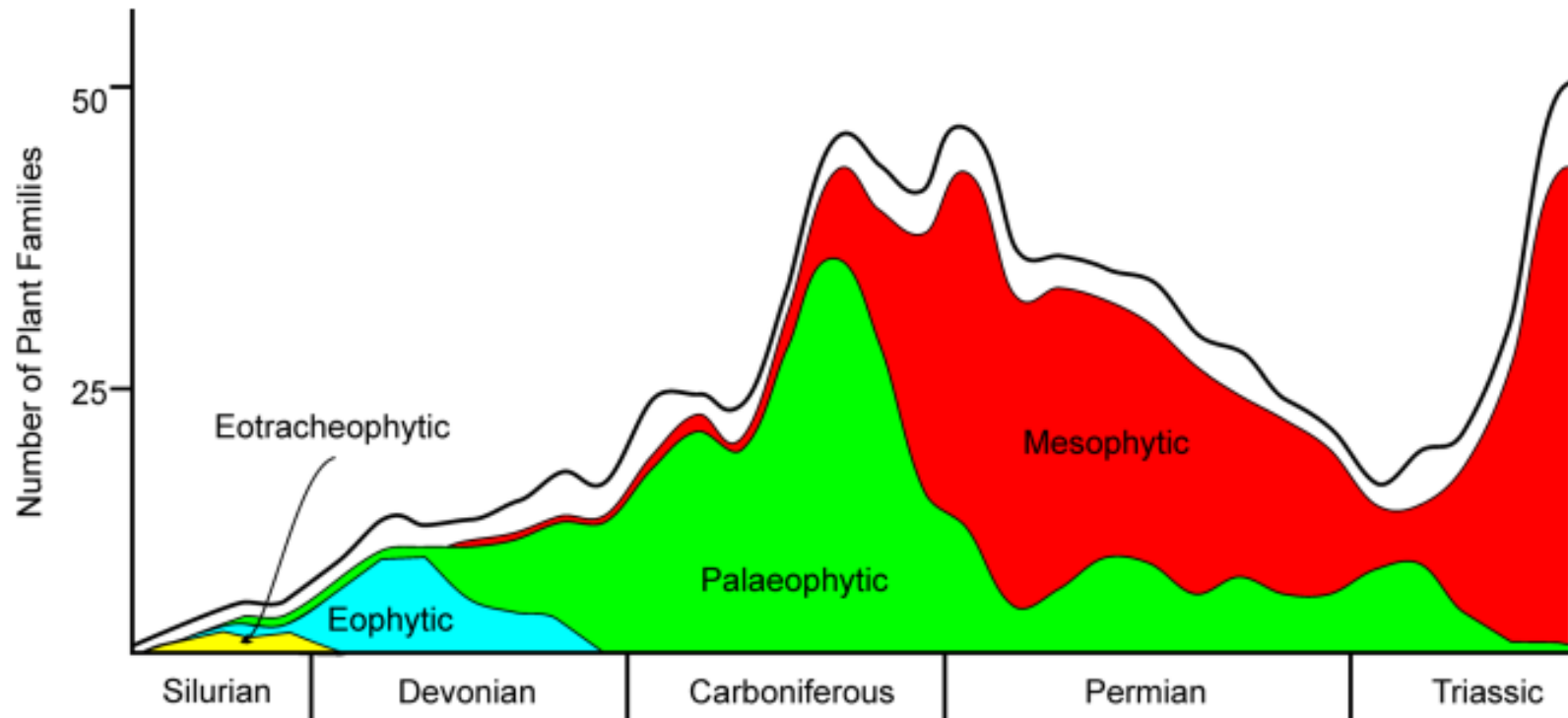


Fig. 4. The evolutionary floras of the Palaeozoic, integrating data from Cleal & Cascales-Miñana (2024) and Capel *et al.* (2021).

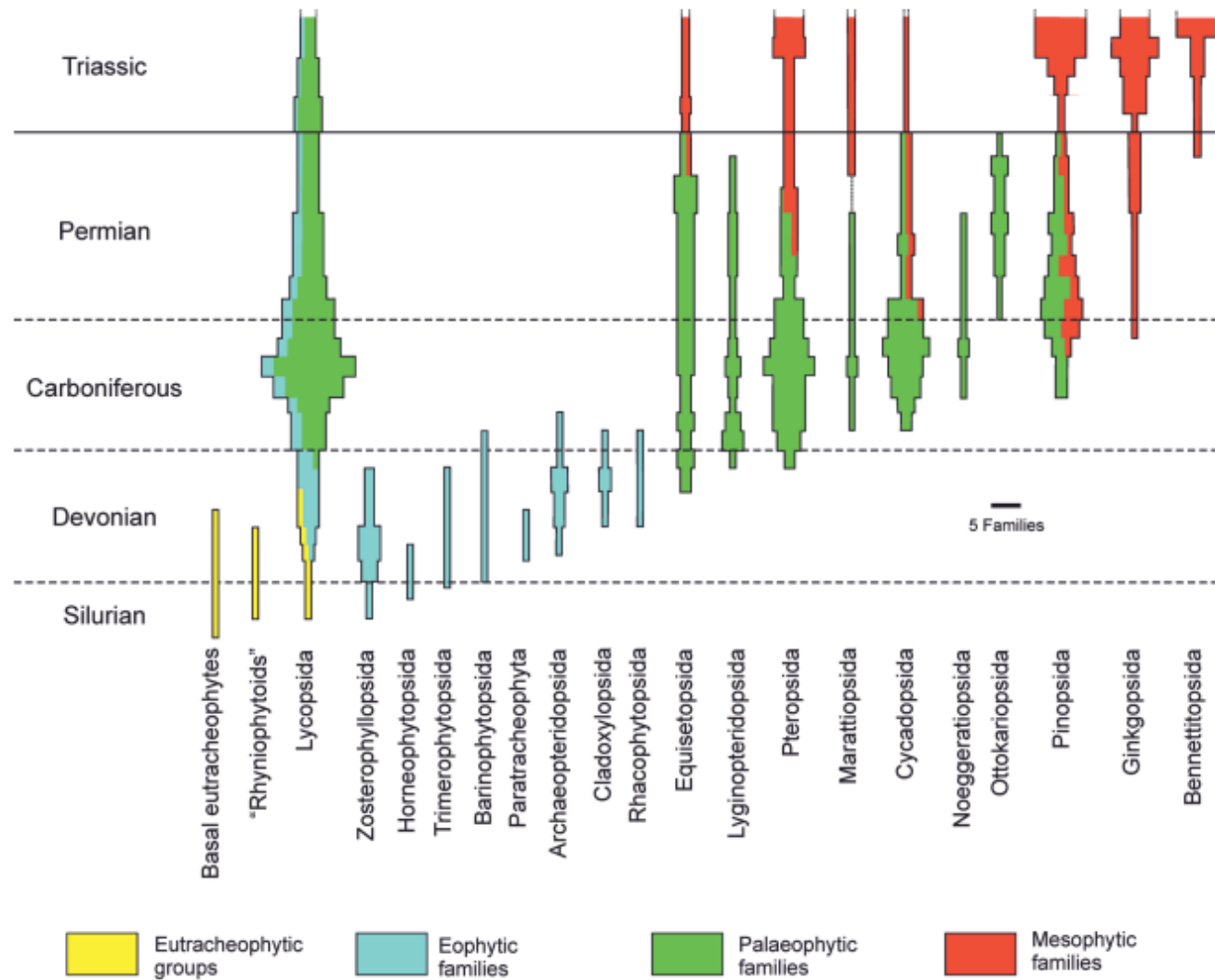


Fig. 5. Spindle diagram showing changing family diversities within the main classes of plants found in Palaeozoic floras. Each spindle shows the relative representation of Eophytic, Palaeophytic and Mesophytic families. The data have been updated from Cleal & Cascales-Miñana (2024).