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Review Article

The Silurian–Devonian terrestrial revolution: Diversity patterns and sampling bias of the vascular plant macrofossil record

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ABSTRACT

During the mid-Palaeozoic, vascular land plants (i.e., tracheophytes) underwent a great radiation that triggered the development of the land biosphere – the so-called Silurian–Devonian terrestrial revolution. However, little is known about how different plant groups impacted this process. A newly constructed dataset of plant macrofossil genera is used to characterize the tempo and mode of development of Silurian–Devonian vegetation and how it spread out over subaerial habitats. Important fluctuations of diversity and evolutionary rates of vegetation are linked to the diversity dynamics of particular tracheophyte groups. Despite a general increase of taxonomic richness through the Devonian, there was a clear stepwise pattern of origination and extinction events that resulted in the main floral transitions over time, such as the change to a forested landscape. To test if sampling bias may be affecting the observed diversity patterns, the latter were compared with the number of plant macrofossil localities as a proxy for sampling effort. This suggested a highly significant correlation between observed diversity and sampling effort, but it was not homogeneous, suggesting that at least some diversity fluctuations have a potential biological explanation. The sampling-corrected pattern of standing diversity suggests a clear increase of plant richness in the Pragian (Early Devonian) and Givetian (Middle Devonian), which may be related to the early expansion of the tracheophyte clades and the initial diversification of forested ecosystems, respectively. Further works should be focused on elucidate the impact of rock record on our understanding of Devonian plant diversification.

1. Introduction

The early development of the land biosphere has been affected by landmark events in the evolution and diversification of plants (Tomescu, 2009; Cascales-Miñana et al., 2010; Kenrick et al., 2012; Cleal and Cascales-Miñana, 2014, 2021; Gerrienne et al., 2016; Morris et al., 2018b; Xue et al., 2018; Bowles et al., 2020; Gensel et al., 2020; Puttick et al., 2020). This was notably through the earliest radiation of land plants (embryophytes), from the Middle Ordovician to the early Silurian (~470–430 Ma), the origin and early diversification of vascular plants (tracheophytes), from the middle Silurian to the Middle Devonian (~430–385 Ma), and the expansion of early forests in the Middle to Late Devonian (~390–358 Ma) (Edwards and Davies, 1990; Edwards and Selden, 1992; Edwards et al., 2000; Steemans et al., 2009; Prestianni and

Gerrienne, 2010; Wellman, 2010, 2014; Xiong et al., 2013; Edwards et al., 2014; Wellman and Strother, 2015; Strother et al., 2017; Morris et al., 2018a, 2018b; Salamon et al., 2018; Servais et al., 2019; Gensel et al., 2020; Stein et al., 2007, 2012, 2020; Capel et al., 2021; Strother and Foster, 2021).

Plants colonized the land through a series of distinct phases representing changes in composition and type of vegetation, and an increase in complexity of subaerial ecosystems (see Gerrienne et al., 2016 for details; Fig. 1). The Silurian–Devonian plant macrofossil record provides a major resource for assessing the relationship between this process (see Meyer-Berthaud et al., 2016a, 2016b, and references therein), and how it both helped cause and was affected by major environmental changes. For instance, Silurian vegetation consisted of small, simple plants (e.g., Raymond et al., 2006; Wellman et al., 2013; Libertín et al., 2018; Gensel

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et al., 2020; Gensel, 2021), which were replaced in the Devonian by floras characterized by an "explosion" in morphological disparity (Fig. 1). This Devonian plant radiation, comparable to the "Cambrian explosion" of marine faunas (*sensu* Bateman et al., 1998), triggered a radical transformation of continental landscapes, from coasts with only localized vegetation to widespread inland forests (Algeo and Scheckler, 1998; Algeo et al., 2001; Morris et al., 2015; Xue et al., 2015a, 2016, 2018; Shen et al., 2020; Stein et al., 2020). This was the so-called Silurian–Devonian terrestrial revolution, which was crucial for the development of the Earth geo-biosphere, causing major global changes through feedback effects on the evolution of the physical environment, such as major transitions in atmospheric composition and climate (Le Hir et al., 2011; Xue et al., 2015a, 2018; Gerrienne et al., 2016; Qie et al., 2019; Servais et al., 2019; Dahl and Arens, 2020).

Silurian–earliest Devonian polysporangiophyte diversity mainly consisted of small rhyniophytic plants (Edwards et al., 2014; Morris and Edwards, 2014; Morris et al., 2018a) – the Eotracheophytic Flora of Cleal and Cascales-Miñana (2021). Subsequently, zosterophylloids and basal euphyllophytes began gradually becoming substantial components of Early Devonian floras (Tomescu, 2009; Cascales-Miñana and Meyer-Berthaud, 2014, 2015; Toledo et al., 2018; Xue et al., 2018;

Bickner and Tomescu, 2019; Fig. 1). In the Middle and Late Devonian, arborescent forms developed in multiple clades, including cladoxyloids (Stein et al., 2007, 2012; Giesen and Berry, 2013), lycopsids (Gensel and Berry, 2001; Xu et al., 2012; Gerrienne et al., 2018) and progymnosperms (Cressler, 2006; Decombeix et al., 2011; Stein et al., 2020), which triggered the diversification of early forest vegetation (Fig. 1).

Tracheophytes evidently underwent a massive taxonomic radiation during the Devonian, alongside an increase in complexity of tissues, reproductive and photosynthetic organs, including innovations such as leaves, wood and seeds, allowing the progressive colonization of terrestrial environments (Gerrienne et al., 2011; Steemans et al., 2012; Strullu-Derrien et al., 2013; Xue et al., 2015a, 2018; Gerrienne and Gensel, 2016; Cascales-Miñana et al., 2019a; Crepet and Niklas, 2019; Bonacorsi et al., 2020; Niklas and Crepet, 2020). The influence of plant terrestrialization on the physical environment including atmospheric CO₂ and O₂ levels, climate, and weathering rates, among others (Algeo et al., 1995), further demonstrates the decisive importance of vegetation development to Earth’s landscapes (Kenrick et al., 2012; Lenton et al., 2012; Xue et al., 2016; Dahl and Arens, 2020).

Recent reinvestigations of collection data (e.g., Gutak et al., 2011;

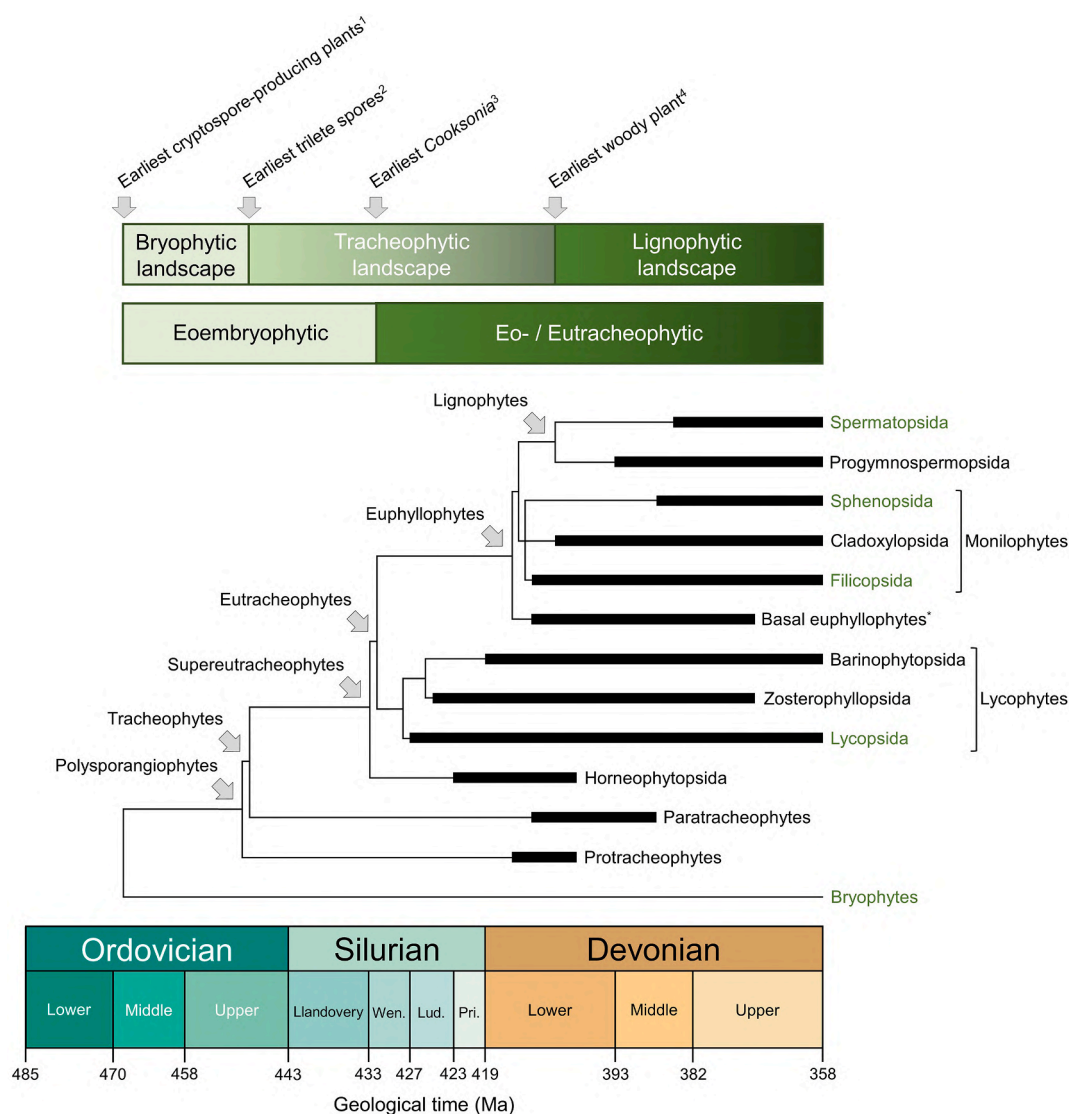


Fig. 1. Early evolutionary framework of embryophytes. Bryophytic, tracheophytic and lignophytic landscapes *sensu* Strother et al. (2010). Eoembryophytic and Eutracheophytic steps of plant evolution *sensu* Gray (1993). Data from Gerrienne et al. (2016, and references therein). Modified from Servais et al. (2019). References: 1. Rubinstein et al. (2010); 2. Steemans et al. (2009); 3. Libertín et al. (2018); 4. Gerrienne et al. (2011). *Former Trimerophytosida.

Orlova et al., 2016), revisions and descriptions of numerous different taxa (e.g., Hao and Xue, 2013; Berry and Gensel, 2019; Xu et al., 2020), alongside refined age range constraints and synthetic works (e.g., Wellman et al., 2012, 2013; Xue et al., 2015a, 2018; Barrett, 2016; Cascales-Miñana et al., 2019c; Kraft et al., 2019; Shen et al., 2020; Lu et al., 2021), now renders it feasible to compile new comprehensive and more detailed datasets of the early land plant macrofossil record (e.g., Capel et al., 2021). However, important uncertainties persist about (i) whether the diversity dynamics of early plants follow comparable trajectories between different major groups, (ii) whether some plant groups were more affected by major environmental change than others, or (iii) whether the uneven sampling of the early plant fossil record hampers accurate reconstructions of these fundamental vegetation dynamics.

Here, we aim to (1) revisit the global-scale macrofossil-based diversity trajectories and macroevolutionary patterns of Silurian–Devonian floras, (2) reconstruct the early diversity variations within main taxonomic groups, and (3) quantify the impact of sampling bias on the early land plant fossil record. From this, we attempt to provide a revised model of plant diversification in early terrestrial ecosystems.

2. Taxonomic and evolutionary context of Silurian–Devonian floras

Multiple factors such as homoplasy and the incompleteness of the fossil record have rendered the phylogeny of early land plant groups as still controversial (see e.g., Niklas and Crepet, 2020, and references therein). However, phylogenetic reconstructions using gene sequence data have significantly increased our understanding of plant evolutionary history, despite showing some discrepancies with analyses based on morphological characters (Rothwell and Nixon, 2006; Rothwell et al., 2018). Likewise, numerous cladistic approaches using morphological/anatomical characters on fossil taxa (e.g., Decombeix et al., 2011; Hao and Xue, 2013; Toledo et al., 2018, 2021; Durieux et al., 2021) or using both extant and fossil taxa (e.g., Rothwell, 1999; Kenrick and Crane, 1997a; Elgorriaga et al., 2018; Crepet and Niklas, 2018, 2019; Niklas and Crepet, 2020) have resulted in phylogenies where the position of certain groups is still controversial (e.g., cladoxylopsids). Further studies will contribute to a better resolution of such groups in the phylogenetic tree. Nevertheless, a phylogenetic framework, which summarizes much consensus and provides the evolutionary context to this study, is presented in Fig. 1.

The monophyly of embryophytes is unequivocally accepted, with all extant and extinct land plants most likely sharing a last common ancestor in one of the different lineages of streptophyte algae (Niklas and Kutschera, 2010; Servais et al., 2019). The bryophytes have been identified as either paraphyletic (e.g., Qiu et al., 2006; Chang and Graham, 2011) or monophyletic (e.g., Cox et al., 2014; Puttick et al., 2018; Morris et al., 2018b), within the Embryophyta. All extant vascular plants are polysporangiophytes (i.e., plants with independent branched sporophyte bearing multiple sporangia; Kenrick and Crane, 1997a), which also include non-vascular fossil plants such as the eophytes (Edwards et al., 2022) and the protracheophytes, the latter being represented by *Aglaophyton/Teruelia* (Edwards, 1986; Cascales-Miñana and Gerrienne, 2017; Fig. 1). Kenrick and Crane's (1997a) analysis included the Horneophytosida within the protracheophytes, although subsequent investigations have suggested the presence of irregular wall thickenings in *Horneophyton*, resolving Horneophytosida as a sister clade to the eutracheophytes (i.e., true vascular plants; Cascales-Miñana et al., 2019b; Fig. 1).

Whilst tracheophytes are considered monophyletic (Gerrienne et al., 2016 and references therein; Puttick et al., 2018), its most basal members lack clear synapomorphies beside their tracheophytic affinity and are referred to as basal eutracheophytes, e.g., *Cooksonia* (Gonez and Gerrienne, 2010; Libertín et al., 2018, and references therein). Paratracheophytes (former Rhyniaceae *sensu* Kenrick and Crane, 1991) are distinguished from other basal eutracheophytes most notably by their S-

type tracheids (Gerrienne et al., 2006), whereas the latter usually possesses C-, G- and P-type tracheids (Edwards, 2003; Cascales-Miñana et al., 2019a; Decombeix et al., 2019; Fig. 1).

The two main lineages of eutracheophytes living today, lycophytes and euphyllophytes, are considered monophyletic (Kenrick and Crane, 1997b; Qiu et al., 2006; Crepet and Niklas, 2018, 2019). Lycopsidea and Zosterophyllopsida are the two main classes usually recognized in the Lycophytina *sensu* Kenrick and Crane (1997a), while the sister-group relationship of these two groups has been questioned by other analyses (Hao and Xue, 2013; Fig. 2). Lycopsidea are monophyletic, characterized by features including the presence of microphylls, a stellate xylem strand and a close association between sporangia and sporophylls (Gensel and Berry, 2001; Figs. 3–4). Zosterophyllopsids in contrast are leafless and bear reniform sporangia (Banks, 1968; Hueber, 1972; Cascales-Miñana and Meyer-Berthaud, 2014; Fig. 2). Barinophytosida are an enigmatic group overall characterized by alternatively arranged appendages and sporangia arranged in two rows on a one-sided spike and were probably among the first heterosporous tracheophytes (Bonacorsi et al., 2020, 2021). Different circumscriptions of the Zosterophyllopsida have been put forward: for instance, Kenrick and Crane (1997a) found them paraphyletic to other lycophytes and excluded taxa lacking circinate veneration and showing a helical arrangement of the sporangia but included Barinophytaceae. Nonetheless, Hao and Xue (2013) found zosterophylls to be monophyletic by including taxa bearing their sporangia helically, as we show here (Figs. 1–2).

The taxa traditionally assigned to trimerophytes, such as *Psilophyton* and *Pertica*, and other basal euphyllophytes such as *Eophyllophyton* and *Polythecophyton*, are thought to be a complex plexus from which emerged derived clades of euphyllophytes (Hao and Beck, 1993; Kenrick and Crane, 1997a; Tomescu, 2009; Hao and Xue, 2013; Crepet and Niklas, 2019); we thus temporarily assign these basal euphyllophytes into the same 'clade' only for convenience of analyses (Fig. 1). Monilophytes, i.e., modern ferns and horsetails, as well as their fossil relatives, are regarded as the sister group of spermatophytes according to molecular and fossil data (Pryer et al., 2001, 2004; Tomescu, 2009; Wang et al., 2015; Puttick et al., 2018; Figs. 1, 4, 5). Devonian monilophytes include cladoxylopsids, sphenopsids, and fern-like groups such as Rhacophytales and Stauropteridales here included within filicophytes. Compared with the basal euphyllophytes, the cladoxylopsids, generally considered as basal fern-like plants, are defined by a more complex vascular system with numerous vascular strands (Meyer-Berthaud and Decombeix, 2007, 2009); a more recent review of this group was presented by Durieux et al. (2021). The position of the sphenopsids, i.e., plants characterized by ribbed stems, small leaves in whorls distributed in stem nodes and internodes, remains unclear (Rothwell, 1999; Tomescu, 2009; Elgorriaga et al., 2018).

Lignophytes are characterized by their bifacial vascular cambium, and encompass both progymnosperms and spermatophytes (Crane, 1985; Steemans et al., 2012; Momont et al., 2016; Decombeix et al., 2019). Progymnosperms (Aneurophytales, Archaeopteridales, Protopytales, and probably Noeggerathiales) are generally considered to be a sister group to seed plants (Crane et al., 2004; Hilton and Bateman, 2006; Niklas and Crepet, 2020; Wang et al., 2021; Figs. 1, 4). The Aneurophytales are homosporous and are assumed to be a sister clade to the heterosporous Archaeopteridales and spermatophytes, although these relationships are not yet resolved (Gerrienne et al., 2010; Toledo et al., 2018; Wang et al., 2021). Spermatophytes are strongly resolved as a monophyletic group (Kenrick and Crane, 1997a, 1997b; Magallón and Hillu, 2009; Toledo et al., 2018; Fig. 1). Earliest spermatophytes in the Devonian are generally recognized by the presence of cupulate ovules with an integumented megasporangium containing a single megaspore (Gerrienne et al., 2004; Gerrienne and Meyer-Berthaud, 2007; Wang et al., 2014; Liu et al., 2017; Fig. 5), but some do not show any cupules (e.g., *Guazfia*; Wang et al., 2022). This clade later greatly diversified and is today's most important plant lineage.

To fully describe the Silurian–Devonian diversity changes, data

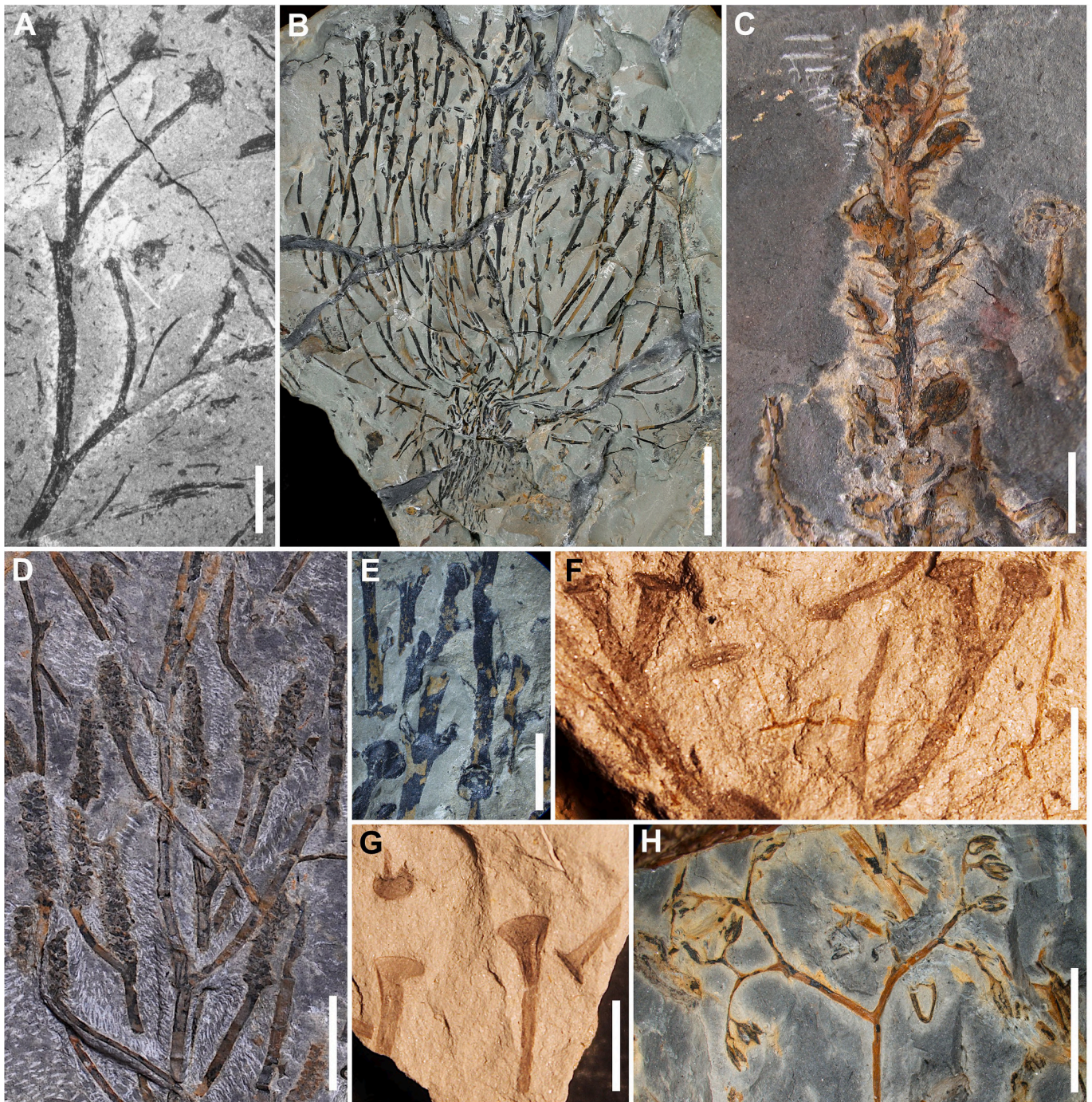


Fig. 2. Morphological diversity of Silurian–Devonian floras (I). (A) *Eocooksonia sphaerica* (Senkevitch) Doweld (Basal eutracheophytes). Axis showing pseudo-monopodial branching and terminal sporangia. Specimen PKUB14902, upper Silurian (Pridoli) Wutubulake Formation of Xinjiang, China (Xue et al., 2015b, fig. 1a). Scale bar = 0.5 cm. (B, E) *Zosterophyllum shengfengense* Hao et al. (Zosterophyllopsida). (B) An entire, uprooted specimen showing shallow rooting system and fertile axes with terminal spikes. Specimen PUH-QXI01-1, Lower Devonian (Lochkovian) Xitun Formation of Yunnan (Hao et al., 2010, fig. 2a). Scale bar = 2 cm. (E) Enlarged view of lateral sporangia of same specimen (Hao et al., 2010, fig. 2b). Scale bar = 0.5 cm. (C) *Discalis longistipa* Hao (Zosterophyllopsida). Fertile axis with lateral sporangia and spines. Specimen PUH-Dis.1, Lower Devonian (Pragian) Posongchong Formation of Yunnan, China (Hao and Xue, 2013, fig. 4.26). Scale bar = 0.5 cm. (D) *Adoketophyton parvulum* Zhu et al. (Barinophytopsida). Axes with terminal strobili. Specimen PKU-ZH01a, Lower Devonian (Pragian) Posongchong Formation of Yunnan, China (Zhu et al., 2011, plate I, fig. 1) Scale bar = 1 cm. (F) *Pertonella* sp. A sensu Gerrienne et al., 2001 (Rhyniophytoids). Two isotomous axes ending in terminal sporangia. Specimen ULg 13521, Lower Devonian (Lochkovian) Furnas Formation of Paraná Basin, Brazil (Gerrienne et al., 2001, plate III, fig. 4). Scale bar = 0.5 cm. (G) *Cooksonia paranensis* Gerrienne et al. (Basal eutracheophytes). Axes terminating in sporangia. Specimen ULg 1351SP, Lower Devonian (Lochkovian) Furnas Formation of Paraná Basin, Brazil (Gerrienne et al., 2001, plate II, figs. 4–5, 7). Scale bar = 0.5 cm. (H) *Pauthecohyton gracile* Xue et al. (Basal euphyllphytes). Lateral branch terminating in fertile units with sporangia. Specimen PKU-XH244a, Lower Devonian (Pragian) Posongchong Formation of Yunnan, China (Xue et al., 2012, plate I, fig. 1). Scale bar = 0.5 cm. (A–E, H) Specimens housed at the School of Earth and Space Sciences, Peking University. (F, G) Specimens housed at the palaeobotanical collections of the University of Liege.

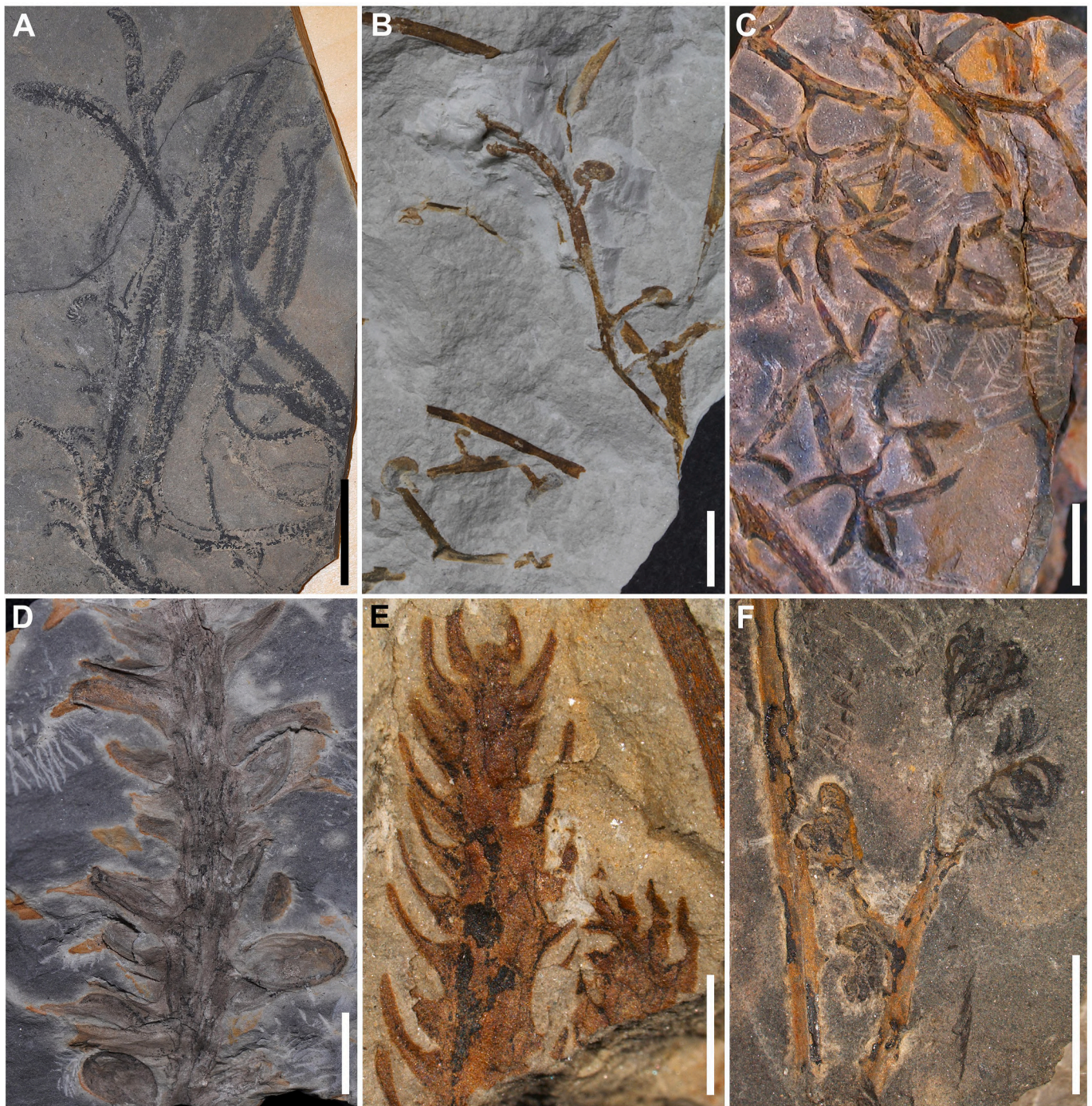


Fig. 3. Morphological diversity of Silurian–Devonian floras (II). (A) *Bathurstia denticulata* Hueber (Zosterophyllopsida). Fertile axes with terminal spikes. Specimen US704-8326, Lower Devonian (Pragian) Bathurst Island Formation of Nunavut, Canada (Kotyk and Basinger, 2000, fig. 3). Scale bar = 3 cm. (B) *Danziella artesiana* (Danzé-Corsin) Edwards (Zosterophyllopsida). Smooth axes with lateral sporangia subtended by straight stalks. Specimen USTL 3595b, Lower Devonian (Pragian–Emsian) Grès de Rebreuve Formation, France (Edwards, 2006, plate I, figs. 1 and 6). Scale bar = 0.5 cm. (C) *Psilophyton primitivum* Hao et Gensel (Basal euphyllophytes). Pairs of sporangia terminating lateral branches. Specimen PUH.09-Psi.1, Lower Devonian (Pragian) Posongchong Formation of Yunnan, China (Hao and Xue, 2013, fig. 4.59a). Scale bar = 0.5 cm. (D) *Dibracophyton acrovatum* Hao et al. (Barinophytosida). A part of strobilus with lateral fertile units. Specimen PKU-Ch. Di-01a, Lower Devonian (Pragian) Posongchong Formation of Yunnan, China (Hao et al., 2012, plate II, fig. 8). Scale bar = 0.5 cm. (E) *Hueberia zhichangensis* Yang et al. (Lycopsida). Terminal parts of two leafy axes. Specimen PKU-XH383, Lower Devonian (Pragian) Posongchong Formation of Yunnan, China (Xue, 2013, fig. 1G). Scale bar = 0.2 cm. (F) *Eophyllophyton bellum* Hao (Basal euphyllophytes). Axes with small laterals terminating in leaf pairs. Specimen BUPb137, Lower Devonian (Pragian) Posongchong Formation of Yunnan, China (Hao, 1988, plate III, fig. 1). Scale bar = 0.5 cm. (A) Specimens housed at the palaeobotanical collections of the University of Saskatchewan. (B) Specimens housed at the palaeontological collections of the University of Lille. (C–F) Specimens housed at the School of Earth and Space Sciences, Peking University.

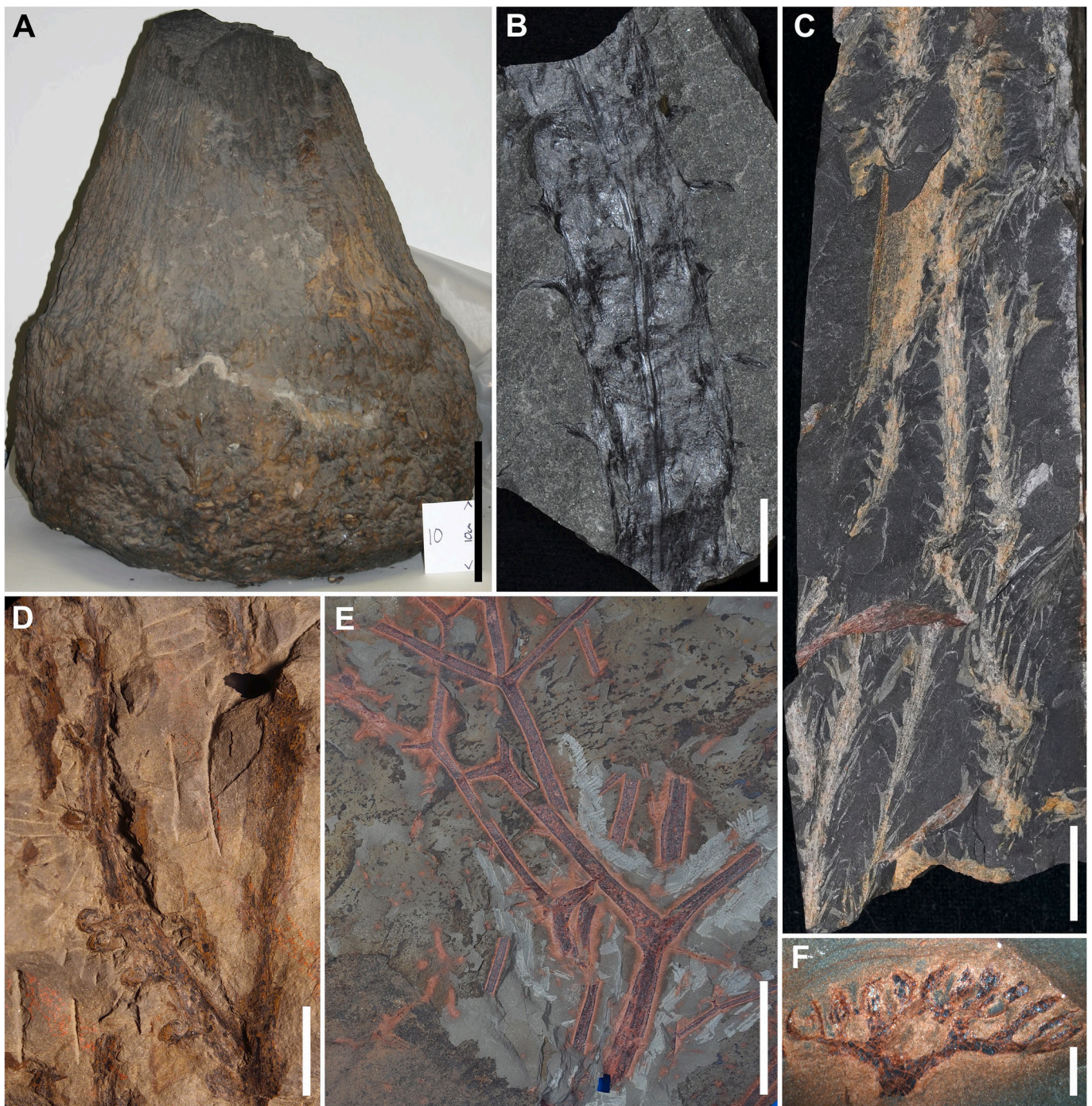


Fig. 4. Morphological diversity of Silurian–Devonian floras (III). (A) *Eospermatopteris* (Cladoxylopsida) cast. Photo by Chris Berry, courtesy of William E. Stein. Scale bar = 20 cm. (B) *Drepanophycus qujingensis* Li et Edwards (Lycopsida). Leafy axis. Specimen PKUB18299, Lower Devonian (Pragian–Emsian) Xujiachong Formation of Yunnan, China. Scale bar = 1 cm. (C) *Leclercqia* cf. *complexa* Banks et al. emend. Bonamo et al. (Lycopsida). Leafy axes. Specimen PKUB20504, Middle-Upper Devonian of Inner Mongolia, China (Bai et al., 2021a, fig. 4a). Scale bar = 1 cm. (D) *Sawdonia deblondii* (Gerrienne) Gensel et Berry (Zosterophyllopsida). Axis with sporangia arranged on one side. Specimen ULg E 13404E (Gerrienne, 1996, plate I, figs. 1–6, 8). Scale bar = 1 cm. (E–F) *Melvillipteris sonidia* Bai et al. (Filicopsida). (E) Main axes and lateral branches. Specimen PKUB18801a, Upper Devonian of Inner Mongolia, China (Bai et al., 2021b, fig. 7a). Scale bar = 3 cm. (F) Fertile structure showing an initial dichotomy, producing two major sporangial clusters. Specimen PKUB18830, same location of previous one (Bai et al., 2021b, fig. 12a). Scale bar = 1 cm. (A) Specimen housed at the New York State Museum. (B–C, E–F) Specimens housed at the School of Earth and Space Sciences, Peking University. (D) Specimens housed at the palaeobotanical collections of the University of Liege.

analysis (see below) was conducted using both phylogenetic and taxonomic criteria, i.e., analyzing macroevolutionary variations from both monophyletic clades and morphological groups. The studied clades include, firstly, lycophytes, and euphyllophytes, and secondly, lycopsids, zosterophylloids, as well as monilophytes and lignophytes

(Fig. 1). Regarding the considered groups, we tested major class-level categories, which include barinophytopsids, filicopsids, cladoxyloids, progymnosperms, sphenopsids and spermatopsids (Fig. 1).

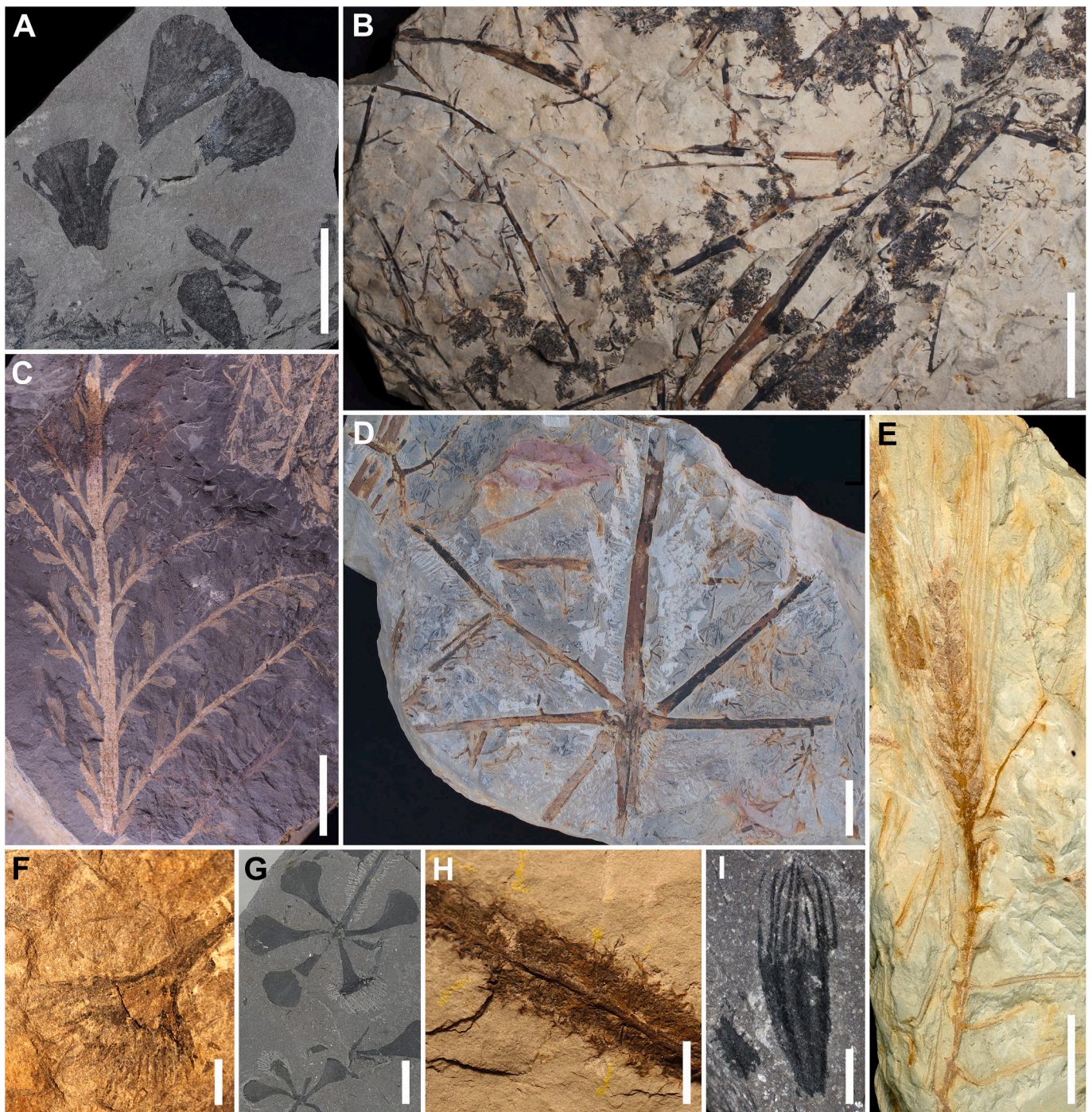


Fig. 5. Morphological diversity of Silurian–Devonian floras (IV). *Xituphyllum megalofolium* (Wu) Chen emend. Huang et al. (Sphenopsida). Detached leaves. Specimen PKUB13606a, Upper Devonian (Famennian) Wutong Formation of Zhejiang, China (Huang et al., 2017, fig. 6A). Scale bar = 50 mm. (B) *Rhacophyton condrusorum* Crépin (Filicopsida). Fronds with fertile structures, which are shown as dense clusters of sporangia. Specimen USTL 3594, Upper Devonian (Famennian) Evieux Formation of Belgium. Scale bar = 5 cm. (C) *Archaeopteris halliana* (Goepfert) Lesquereux (Progymnospermopsida). Penultimate and ultimate branches and sterile leaves. Specimen PB11728, Upper Devonian (Famennian) Dawushi Formation of Guangdong, China (Cai et al., 1987, plate I, fig. 2). Scale bar = 2 cm. (D) *Denglongia hubeiensis* Xue et Hao (Cladoxylopsida). Main axis with a whorl of first-order branches. Specimen PKUXH110, Upper Devonian (Frasnian) Huangjiadeng Formation of Hubei, China (Xue and Hao, 2008, fig. 2h). Scale bar = 15 mm. (E) *Lilingostrobus chaloneri* Gerrienne et al. (Lycopsida). Unbranched stem terminating in a strobilus. Specimen 0901, Upper Devonian (Famennian) Xikuangshan Formation of Hunan, China (Gerrienne et al., 2018, fig. 2A). Scale bar = 1 cm. (F) *Thorezia vezereensis* Gerrienne et Prestianni (Spermatopsida). Cupulate seed borne terminally on a short axis. Specimen ULg 1375, Upper Devonian (Famennian) Evieux Formation, Belgium. Scale bar = 0.5 cm. (G) *Sphenophyllum fanwanense* Huang et al. (Sphenopsida). Axes with whorls of leaves. Specimen PB23804, Upper Devonian (Famennian) Wutong Formation of Zhejiang, China (Huang et al., 2021, fig. 3H). Scale bar = 1 cm. (H) *Eviostachya hoegii* Stockmans (Sphenopsida). Strobilus with dense sporangia. Specimen ULg 1521, Upper Devonian (Famennian) Evieux Formation, Belgium. Scale bar = 0.5 cm. (I) *Calycosperma qii* Liu et al. (Spermatopsida). Cupule showing distal linear tips. Specimen PKUB15302b, Upper Devonian (Famennian) Wutong Formation of Zhejiang, China (Liu et al., 2018, plate I, fig. 3). Scale bar = 0.5 cm. (A, D, G, I) Specimens housed at the School of Earth and Space Sciences, Peking University. (B) Specimens housed at the palaeontological collections of the University of Lille. (C) Specimens housed at Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences. (E–F) Specimens housed at the palaeobotanical collections of the University of Liege.

3. Materials and methods

3.1. Data compilation

The analysis described here uses both diversity and sampling data. Diversity data came from the Capel et al. (2021, table S1) plant macrofossil-based compilation, with slight modifications (Table S1). The employed dataset consists of the first and last appearance datum (FAD–LAD) for each plant fossil-genus (*sensu* Cleal and Thomas, 2010, 2021) in the interval ranging from Sheinwoodian (middle Silurian) to Famennian (Upper Devonian). The temporal distribution of taxa was tabulated assuming FADs–LADs reflected continuous ranges (i.e., the range-through method; Boltovskoy, 1988). In total, more than 400 fossil-genera were involved which captures a comprehensive overview of major Silurian–Devonian floral changes (see Capel et al., 2021, fig. 1). FADs–LADs were based on maximum observed diversity, i.e., including both genus- and species-level occurrences in open nomenclature (e.g., cf. *Tarrantia* and *Archaeopteris* sp., respectively). The resulting temporal ranges showed a high heterogeneity of taxonomic longevities. This is mainly due to the age uncertainties of certain genera, which were tabulated from more than one time bin, even if they occur at just a single locality, e.g., *Danziella* (Pragian–Emsian; Edwards, 2006) or *Parazosterophyllum* (Pridoli–Pragian; McSweeney et al., 2020). As noted by Brocklehurst et al. (2013), however, if the stratigraphical uncertainties are randomly distributed, the diversity signal is reliable and is preferable to attempting to improve resolution and possibly producing an artificial signal (see e.g., Smith, 2001, and reference therein).

We prioritized the use of fossil-genera rather than the species-level for plant diversity studies. This is because species data are more sensitive to floristic variations due to the number of synonyms, endemism and the uncertainties of some identifications based on highly fragmentary specimens, which could artificially inflate plant diversity (Knoll et al., 1984; Silvestro et al., 2015; Cascales-Miñana, 2016). Another issue stems from the distinctive nature of plant fossil taxonomy, in which different parts of one plant (e.g., leaves and/or reproductive organs) can belong to different fossil-species, and this will distort the species diversity signal (Cleal and Thomas, 2010, 2021; Cleal et al., 2021, and references therein). It is known that these inflation-related problems may also occur at the generic rank, but this taxonomic level seems to be less sensitive to these biases (Knoll et al., 1984; Wang et al., 2010; Xiong et al., 2013). To minimize these biases, “artificial fossil-genera” (*sensu* Cleal and Thomas, 2021), synonyms, and gametophytes were excluded, and known plants representing the same palaeobiological entity were linked (e.g., *Calamophyton/Duisbergia*, Giesen and Berry, 2013), to get the most accurate representation of plant diversity dynamics. Each entry in the dataset consists of a genus name, biological affinity, stratigraphical age, and outcrop location (Table S1). Importantly, while some taxa have a highly detailed temporal assignment (e.g., Gutak et al., 2011), others present a less precise resolution (e.g., Prestianni et al., 2012). Hence, in an attempt to minimize overestimating plant diversity, FADs–LADs were traced at the stage and sub-stage levels according to temporal resolution given by original data sources (Table S1, Text S1). Absolute ages are according to the International Chronostratigraphic Chart 2020 (v2020/03; Cohen et al., 2013, updated).

It is well-documented that fossil-derived diversity patterns can be influenced by a series of biases including both geological constraints (e.g., availability of fossiliferous outcrops), and collecting factors (e.g., variation in sampling effort) (Crampton et al., 2003; Smith and McGowan, 2007; Barrett et al., 2009; Brocklehurst et al., 2013; Dunhill et al., 2014a, 2014b, 2018; Walker et al., 2017a). Indeed, since Raup (1972) first observed an apparent correlation between Phanerozoic marine diversity and the fluctuations in the volume of sedimentary rock, many researchers have put emphasis on discerning the reliability of the fossil record when studying changes of past diversity over time (see e.g., Smith et al., 2012; Benton, 2015, and references therein). From this, several ways to assess, and compensate for this problem, have been tested using

the so-called sampling proxies, i.e., a metric representing “collecting effort” (Benton et al., 2011). It is generally agreed that a good sampling proxy must consider all aspects of collecting data that are influenced by geological and anthropogenic factors, and ideally should be independent of the palaeobiodiversity signal it is seeking to correct (Benton et al., 2011; Dunhill, 2011). However, an ongoing debate still exists about what is the most appropriate sampling proxy (see discussion below). For instance, recent studies claim that the strong observed association between formation counts and raw diversity is mainly due to information redundancy (see e.g., Dunhill et al., 2018, and references therein). In this study, we have attempted to reduce this and other related problems by using the plant-bearing fossil localities per time unit as a measure of sampling effort through time. Locality compilation, which is based on species occurrences within each genus range, provides direct insights into sampling and is, therefore, a reliable basis for developing integrated model-based approaches (e.g., Lloyd et al., 2008; Benton et al., 2011; Butler et al., 2011; Fröbisch, 2013; Xiong et al., 2013; Cascales-Miñana and Meyer-Berthaud, 2014, 2015; Brown et al., 2019). The locality list is given in Table S2. Raw diversity and sampling data are also available on request.

3.2. Processing methods

3.2.1. Temporal patterns of diversification

To characterize the observed diversity dynamics (i.e., the apparent diversity changes taken at face value from the fossil record; Foote, 2001) of Silurian–Devonian tracheophytes, we firstly calculated the total and standing diversity per time unit. Total diversity (N_{tot}) is the total number of plant genera within a given time interval, which can be used as a first descriptor of encountered diversity. Following Foote (2000a), N_{tot} was calculated by:

$$N_{\text{tot}} = N_{\text{FL}} + N_{\text{bL}} + N_{\text{Ft}} + N_{\text{bt}} \quad (1)$$

where for a given time interval t_i , N_{FL} is the number of single-interval taxa (i.e., taxa whose FAD and LAD are both within the interval t_i), N_{bL} is the number of bottom-only boundary crossers (i.e., taxa crossing the lower boundary of interval t_i and become extinct during that interval), N_{Ft} is the number of top-only boundary crossers (i.e., taxa that make their FAD during the interval t_i and cross the upper boundary of that interval) and N_{bt} is the number of taxa ranging through the entire interval t_i (i.e., crossing both the lower and upper boundaries of the interval).

We also traced the boundary-crossing diversity (N_{b}), which is the only measure of actual standing diversity that allows a comparison of the diversity at the start of different intervals (Bambach et al., 2004). N_{b} is based on the equation (Foote, 2000a, table 1):

$$N_{\text{b}} = N_{\text{bL}} + N_{\text{bt}} \quad (2)$$

We further calculated the mean-standing diversity (MSD), which estimates the diversity at a specific point of time. MSD corresponds to the equation (Foote, 2000a, table 1):

$$\text{MSD} = (N_{\text{bL}} + N_{\text{Ft}} + 2 N_{\text{bt}})/2 \quad (3)$$

The dynamics of floral changes were evaluated from a set of evolutionary metrics using both per-taxon rates and boundary-crosser method (Foote, 2000a; Cascales-Miñana et al., 2013; Warnock et al., 2020). We calculated the per-taxon and per-capita origination (λ) and extinction (μ) rate measures as descriptors of diversity changes. Per-taxon rates are based on the FADs–LADs proportions observed during a given interval t_i , according to the equations (Foote, 2000a, table 1):

$$\lambda = (N_{\text{FL}} + N_{\text{Ft}})/(N_{\text{tot}})^* 1/\Delta t_i \quad (4)$$

$$\mu = (N_{\text{FL}} + N_{\text{bL}})/(N_{\text{tot}})^* 1/\Delta t_i \quad (5)$$

Per-taxon rates normalize observed FADs–LADs by total diversity and

by the interval length (Δt_i) to obtain an estimate of the instantaneous, origination-extinction rates per lineage-million-years (Foote, 2000a). In contrast, per-capita rates, are based on the following equations (Foote, 2000a, table 1), which are directly derived from Raup's (1985) branching theory:

$$\lambda = -\ln(N_{\text{bt}}/N_{\text{Ft}} + N_{\text{bt}})^* 1/\Delta t_i \quad (6)$$

$$\mu = -\ln(N_{\text{bt}}/N_{\text{bL}} + N_{\text{bt}})^* 1/\Delta t_i, \quad (7)$$

Per-capita rates are singleton-free metrics based on the assumption that the number of lineages extending through the interval depends only on the taxonomic rates for such an interval and provides a true rate regardless of the origination-extinction magnitude (Foote, 2000a). To complement this, the amount of change in floral composition was evaluated via per-capita turnover rates expressed by $\lambda + \mu$.

Sepkoski (1978, 1979, 1984) kinetic model predicted that Phanerozoic marine diversity changes were controlled by the balance between origination and extinction. This model also postulated that diversification rate is diversity dependent. In plants, Knoll et al. (1984) used these assumptions to explain the early phase of Silurian–Devonian plant diversification by plotting total origination-extinction rates against diversity per time unit. Here, we revisit Knoll et al.'s (1984) approach by comparing change in origination-extinction per-taxon and per-capita rates against total and boundary-crossing standing diversity per time unit, respectively (see Foote, 2000b, figs. 1–2 for details). This double check attempts to compensate for the Lagerstätten effect on global diversity trends, which, in some intervals (e.g., Pragian, see Hao and Xue, 2013; Cascales-Miñana and Meyer-Berthaud, 2015), is caused by a high proportion of single-interval (and endemic) taxa. Following Benton et al. (2013), correlation between variables was evaluated via Spearman's rank correlation tests to determine whether any substantial correlation revealed could explain the observed variance.

Niklas et al. (1983) argued that a high degree of correlation exists between origination rates and plant longevities. They further commented that the initial diversification of successive floras is characterized by high origination rates but short taxon longevities. This idea was originally tested by contrasting the mean of origination rates and taxa duration among major plant groups through the Phanerozoic (see Niklas et al., 1983, fig. 2). However, when the algorithm used was described, they referred to diversification rates instead of origination metrics, as well as sometimes to summed *versus* averaged rates. Hence, to test Niklas et al.'s (1983) assumptions on the early land plant fossil record, we plotted both the per-taxon origination and diversification rates, i.e., the net rate of increase between origination and extinction values, against mean taxon longevity. Also, in both cases, the mean and summed rate values were tested. Correlation was again evaluated via Spearman's rank correlation tests.

Finally, as biostratigraphic data are by essence occurrences collated into chronostratigraphic units of unknown and unequal duration, we tested the impact of using "unequal time bins" on the resulting patterns. This was done by applying the method described by Gibert and Escarguel (2017), which allow reconstructed diversity curves to be obtained from intervals of equal duration. In our case, we computed a total diversity curve based on equal time bins of 3.1 Myr, value corresponding to the mean duration of used interval lengths. In addition, to investigate whether uneven time-bin length distorts the observed diversity signal, the correlation between raw diversity and time-bin length was also tested by Spearman rank correlation.

3.2.2. Sampling intensity and corrected diversity estimates

We plotted total and standing diversity data against a sampling signal (i.e., the number of sampled localities per time unit) and evaluated the fit between them. We followed the identical strategy adopted by Cascales-Miñana and Meyer-Berthaud (2015) and used Pearson's product-moment correlation coefficients, and Spearman's and Kendall's

rank correlation coefficients that provide complementary views of the major data variations through time. Pearson's coefficient measures the strength of a correlation between two variables, while Spearman's and Kendall's measures whether peaks and troughs follow comparable trajectories (Fröbisch, 2013). To avoid inconsistencies of false positives we ran a two-time data analysis from raw and generalized-differenced (detrended) data for comparisons, which removes general background trends caused by autocorrelation (McKinney, 1990; Benson and Butler, 2011). Transformed data were obtained via Lloyd's 'functions.2.r' script (see <http://www.graemetlloyd.com/methgd.html>) in R (R Core Team, 2020; v.3.6.3), which has been used in many previous similar studies (e.g., Lloyd et al., 2011; Dunhill et al., 2012; Benton et al., 2013; Cascales-Miñana et al., 2016). P-values lower than 0.05 were considered as significant.

To correct diversity estimates, we applied Lloyd's (2012) implementation of the Smith and McGowan (2007) method, which has been widely used for evaluating sampling impact on apparent diversity (e.g., Mannion et al., 2012; Smith et al., 2012; Brocklehurst et al., 2013; Fröbisch, 2013; Walter and Fröbisch, 2013; Newham et al., 2014; Minter et al., 2017). The Smith and McGowan (2007) method was developed to remove potential bias caused by variations in rock-availability for sampling per time interval, by calculating modelled (or predicted) diversity estimates assuming a linear relationship between apparent diversity and a correction measure. From this, the predicted diversity (i.e., the diversity correlated to sampling) is then subtracted from the apparent diversity, leaving the residual, or sampling-corrected diversity estimate. Lloyd (2012) refined this method by avoiding the assumption of a linear relationship between diversity and sampling proxy. Prior to calculation of the predicted values of diversity, the most appropriate model is chosen by following the Akaike Information Criterion (AIC) (Johnson and Omland, 2004). But most importantly, Lloyd's (2012) method further allows extending confidence intervals around the data to identify diversity fluctuations that are significantly greater and/or lower than those predicted from the sampling proxy, and so have a potential biological explanation beyond rock record noise. See <http://www.graemetlloyd.com/methscd.html> for analysis implementation.

4. Results

4.1. Taxonomic diversity estimates

Large-scale diversity patterns of Silurian–Devonian tracheophytes, including dynamics of major taxonomic groups, are shown in Figs. 6–8. From this, we see that the total diversity of tracheophytes increases steadily from the Ludlow (late Silurian) to the Lochkovian (earliest Devonian) (Fig. 6), caused mainly by increases in the lycophytes (Fig. 7A), notably basal lycopsids (Fig. 7B) and zosterophylloids (Fig. 7C). Thereafter, taxonomic diversity reached a brief plateau during the Lochkovian (Fig. 6), likely due to the stratigraphically-constrained occurrences of basal eutracheophytes and rhyniophytoid taxa. A subsequent, "explosive" peak is seen at the end-Pragian, mainly because of high zosterophylloids and barinophytoid diversities (Figs. 7C, 8A), and to a lesser extent, a minor lycopsid diversity peak (Fig. 7B). Subsequently, tracheophyte diversity begins to decline in the Emsian, followed by a minor increment towards the end of the Early Devonian (Fig. 6) caused by lycopsids and basal euphyllphytes (Fig. 7A–B, D).

The Middle Devonian trends of tracheophyte diversity are characterized by a drastic reduction at the base of the Eifelian (earliest Middle Devonian; Fig. 6). This is principally due to a strong decline in zosterophylloids (Fig. 7C). Interestingly, the Eifelian diversity of tracheophytes reaches levels not seen since Lochkovian times (Fig. 6). After that, a second diversity peak is observed during the Givetian (late Middle Devonian) (Fig. 6), triggered by an important pulse of both lycophyte (Fig. 7A) and euphyllphyte diversity (Fig. 7D). More specifically, the Givetian diversification involves lycopsids (Fig. 7B), and almost all major groups of monilophytes (Fig. 7E), such as filicopsids

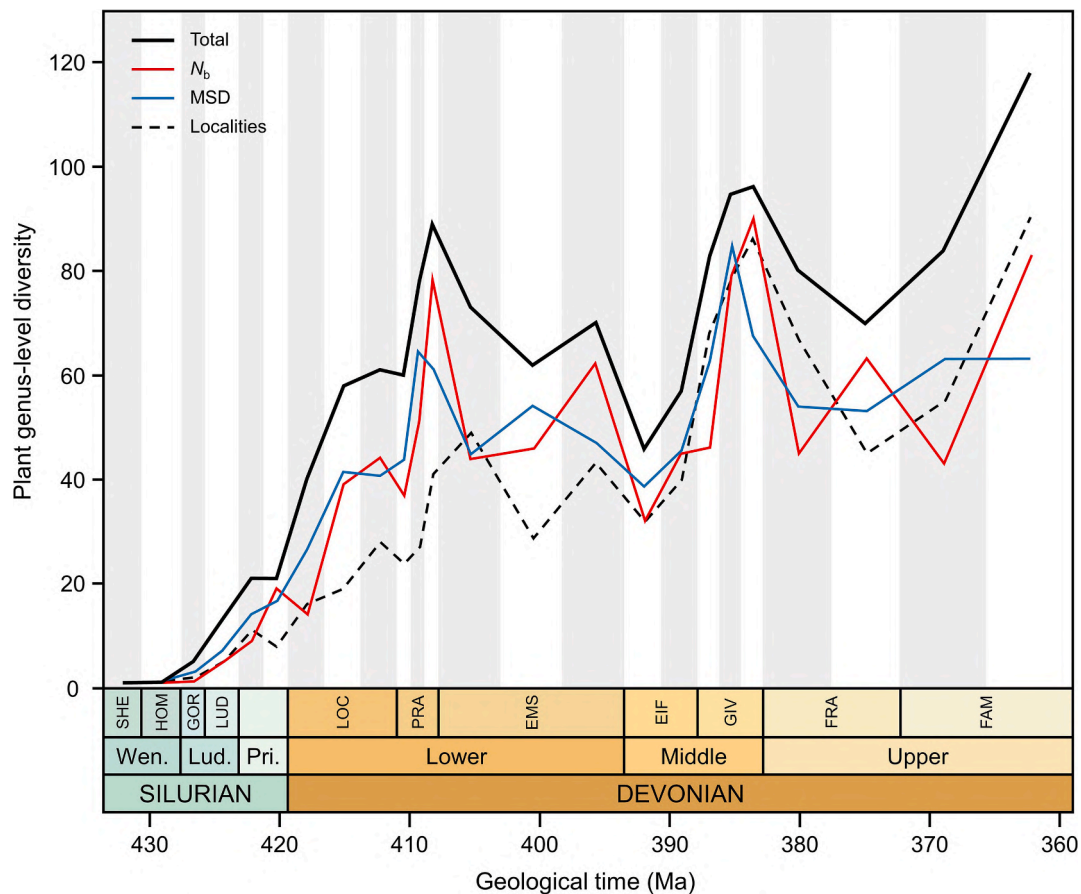


Fig. 6. Silurian–Devonian diversity patterns of tracheophytes. Bold, red and blue lines show total, boundary-crossing (N_b) and mean-standing (MSD) diversity of plant genera per time unit, respectively. Dashed line shows the sampled localities per time unit. Alternation of white and grey boxes represent the different used time units (stage to sub-stage level). Abbreviations: SHE, Sheinwoodian; HOM, Homeric; GOR, Gorstian; LUD, Ludfordian; Pri., Pridoli; LOC, Lochkovian; PRA, Pragian; EMS, Emsian; EIF, Eifelian; GIV, Givetian; FRA, Frasnian; FAM, Famennian.

(Fig. 8B) and especially cladoxylopsids (Fig. 8C), as well as lignophytes, notably progymnosperms (Fig. 8D).

This second maximum peak of diversity is followed by an important depletion in the Frasnian (Late Devonian), mainly linked to a reduction of cladoxylopsid and progymnosperm taxa (Fig. 8C–D). Tracheophyte diversity steadily increases again throughout the Famennian (latest Devonian), where the highest values are observed (Fig. 6), triggered mainly by a diversification of lycophytes (Fig. 7A), euphyllophytes (Fig. 7D) and lignophytes (Fig. 7F). It is further sustained by the diversity increase of sphenopsids (Fig. 8E), and spermatopsids (Fig. 8F), and results in an overall exponential increase in diversity.

The N_b and MSD metrics follow the same trends as total diversity (Fig. 6), which suggests that the observed apparent pattern is not critically distorted by single-interval taxa. Perhaps, the most notable difference is in the boundary-crossing diversity during the Late Devonian (Fig. 6), which shows some discrepancies from the observed MSD changes (Fig. 6); indeed, the MSD pattern does not capture a late Frasnian diversity peak recorded in boundary-crossing fluctuations (Fig. 6). This discrepancy is also seen in the diversity curves for each of the major clades (Fig. 7A, D), and is probably due to the succession of longer time units in the Late Devonian. Moreover, the fact that the MSD pattern displays similar variations to the other two metrics (Total and N_b), within individual clades (Fig. 7), and in each different plant group (Fig. 8) highlights the robustness of these apparent diversity signals.

Data analysis based on equal time bins did not show major differences concerning the total pattern of apparent diversity shown in Fig. 6 (Fig. S1A). Likewise, results show that there is no significant correlation between the plant richness and used interval lengths ($\rho = 0.03$, $p >$

0.05; Fig. S1B).

4.2. Origination, extinction, and turnover rates

Fig. 9 shows some of the broad macroevolutionary trends in tracheophytes during the Silurian–Devonian. Highest origination values are observed from the Silurian to the Early Devonian with notable peaks in the Pridoli, and at the beginning of the Lochkovian and of the Pragian (Fig. 9A). After that, an important origination pulse occurs at the base of the Givetian (Middle Devonian) (Fig. 9A). In contrast, the extinction pattern shows highest values at the end-Pragian and the end-Givetian (Fig. 9B). There are no major differences observed between per-taxon and per-capita rate measures for originations or extinctions (Fig. 9A–B), showing that single-interval taxa and unequal time units were having little impact.

For taxonomic turnover, the difference between per-taxon and per-capita rates is small and they generally follow similar trajectories. However, while per-taxon pattern shows no major fluctuation through the Silurian–Devonian transition, per-capita values show a series of turnover peaks in the Pridoli and the Lochkovian (Fig. 9C). After that, highest turnover pulses are observed in the Pragian and the Givetian (Fig. 9C), indicating an important amount of change in floristic composition during these intervals.

Within clades and groups (Figs. 10–11), Early Devonian origination-extinction pulses are shared by the major clades then existing. For instance, highest origination-extinction values are observed in the Pragian from lycophytes (Fig. 10A–B), including lycopsids (Fig. 10D–E), zosterophylloids (Fig. 10G–H), and barinophytoids (Fig. 11A–B), as

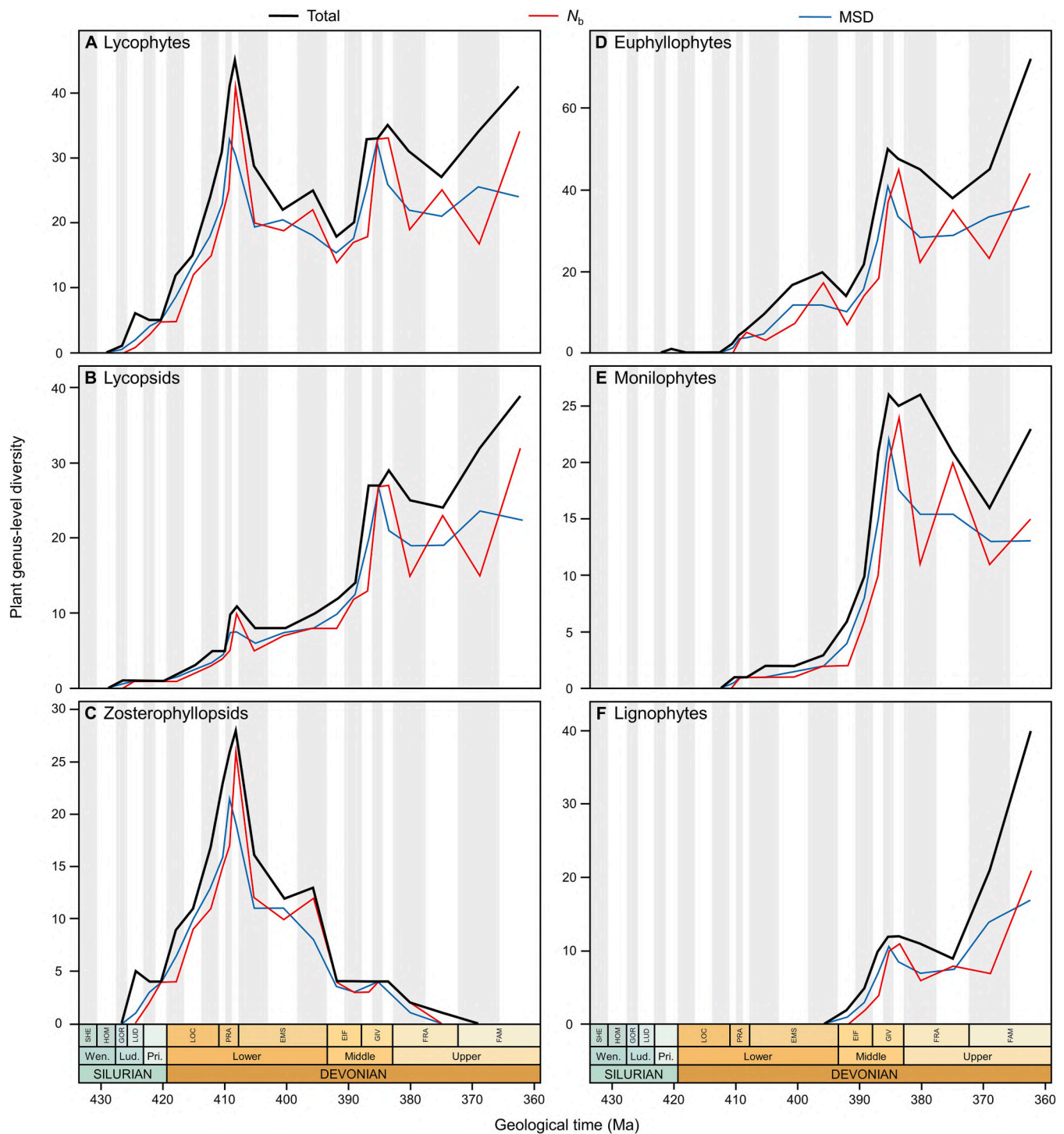


Fig. 7. Silurian–Devonian diversity patterns of main tracheophyte clades. Bold, red and blue lines show total, boundary-crossing (N_b) and mean-standing (MSD) diversity of plant genera per time unit, respectively. (A) Lycophytes; (B) Lycopside; (C) Zosterophylloids; (D) Euphylllophytes; (E) Monilophytes; (F) Lignophytes. Abbreviations, same as in Fig. 6.

well as from basal euphylllophytes (Fig. 10J–K). Likewise, Middle Devonian (Givetian) origination–extinction peaks are shared by all tested clades, including monilophytes (Fig. 10M–N), filicopsids (Fig. 11D–E), cladoxyloids (Fig. 11H) and sphenopsids (Fig. 11M–N), as well as lignophytes (Fig. 10P–Q), such as progymnosperms (Fig. 11J–K). Results further show an isolated origination increment driven by Middle Devonian (Eifelian) cladoxyloids (Fig. 11G). Moreover, the turnover rate shows two major pulses: one in the Pragian mainly concerning lycophytes (Figs. 10C, 10F, 10I, 11C), and a second

one in the Givetian involving euphylllophytes (Figs. 10–11L, 10–11O, 10R, 11F, 11I). Finally, evolutionary patterns of spermatopsids show a clear diversification towards the end of the Devonian (Fig. 11P–R).

Fig. 12 shows the relationships between the changes in total and boundary-crossing diversity and origination–extinction values for all Silurian–Devonian vascular plants. It is known that diversity is controlled by the balance of origination and extinction rates (Sepkoski, 1978, 1979, 1984; Knoll et al., 1984; Foote, 2000a, 2000b; Bambach et al., 2004; Alroy, 2008, 2010a, 2010b; Cascales-Miñana and Cleal,

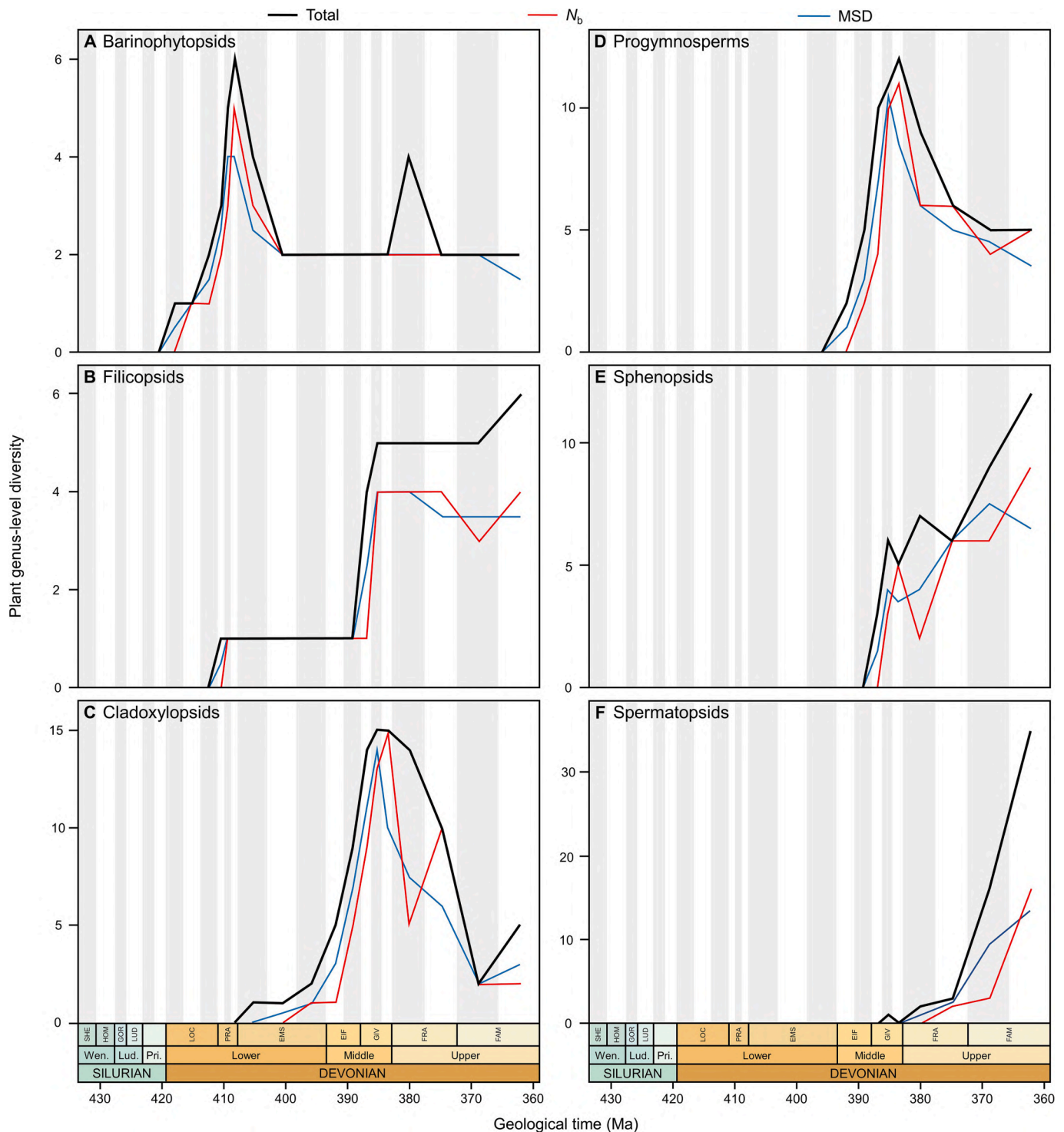


Fig. 8. Silurian–Devonian diversity patterns of main tracheophyte groups. Bold, red and blue lines show total, boundary-crossing (N_b) and mean-standing (MSD) diversity of plant genera per time unit, respectively. (A) Barinophytopsids; (B) Filicopsids; (C) Cladoxylopsids; (D) Progymnosperms; (E) Sphenopsids; (F) Spermatopsids. Abbreviations, same as in Fig. 6.

2012). Foote (2000b) commented that larger increases in origination rate tend to be associated with larger increases in diversity, and larger decreases in origination rate with larger decreases in diversity. Likewise, larger increases in extinction rate are associated with larger reductions in diversity, and larger decreases in extinction rate with larger rises in diversity. We find partial correlations between changes in origination-extinction levels and total diversity values (Fig. 12A–B). But importantly, results show significant correlation values in both cases from

standing metrics (Fig. 12C–D). Results further show stronger correlation levels between changes in extinction values and changes in diversity ($\rho = -0.60$, $p < 0.01$; Fig. 12D), which suggests that for Silurian–Devonian floras, variations in extinction rate may be more important than variations in origination rate to explain short-term fluctuations in the apparent dynamics of plant diversity.

In plants, it has been suggested that the overall patterns of increasing origination rates and decreasing observed longevities between major

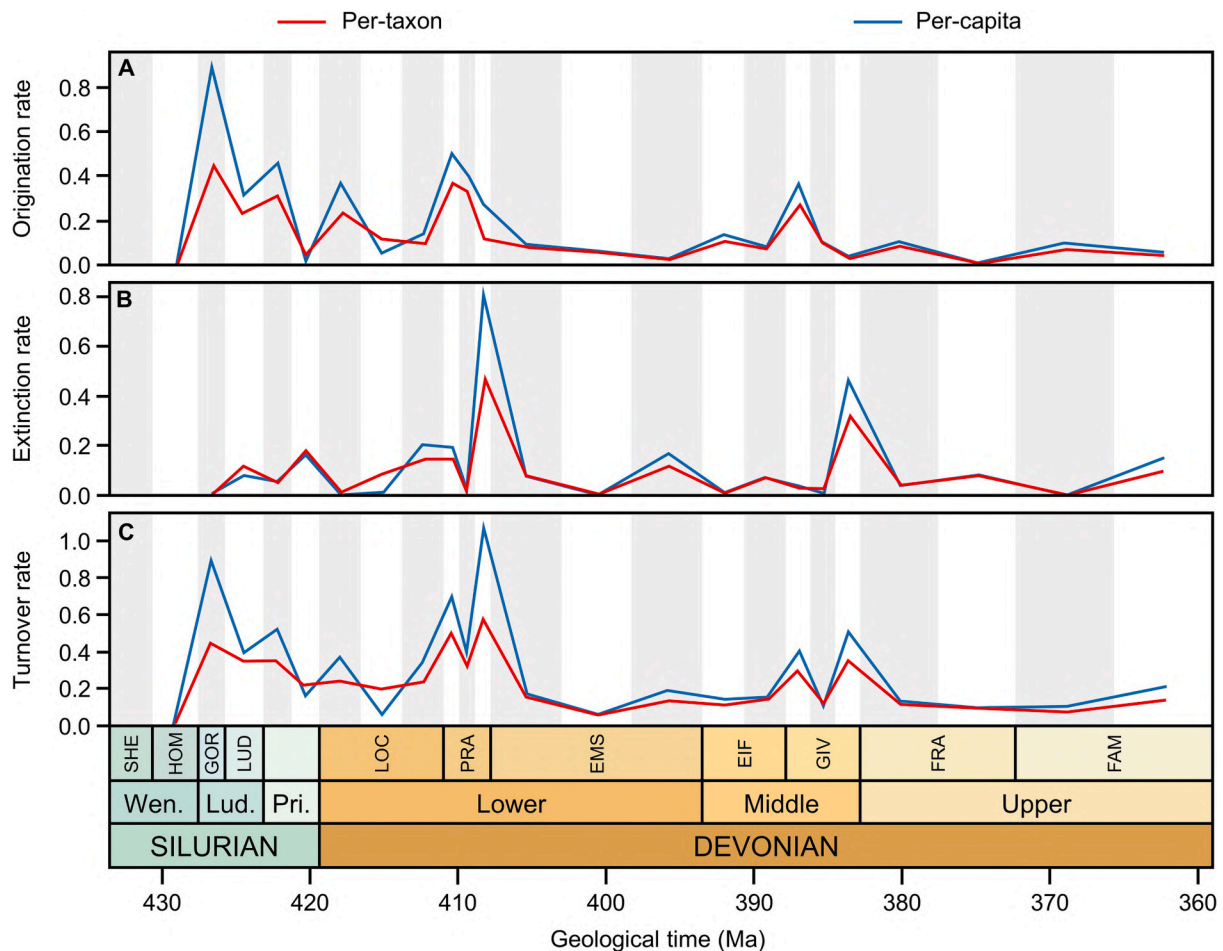


Fig. 9. Silurian–Devonian macroevolutionary patterns of tracheophytes. Red and blue lines show per-taxon and per-capita origination (A), extinction (B) and turnover (C) rates of plant genera, respectively. Abbreviations, same as in Fig. 6.

groups are significantly correlated (Niklas et al., 1983). However, we find no correlation between the mean origination and longevity at the genus-level for the tested Silurian–Devonian plant groups ($\rho = -0.15$, $p > 0.05$; Fig. 13A), probably due to the high volatility observed both within and among groups (Fig. S2). In contrast, results show significant correlation between diversification rates and observed longevity of each group ($\rho = 0.69$, $p < 0.05$; Fig. 13B), which would support the key role of extinction patterns on observed turnover dynamics (Figs. 10–11). Complementary analysis based on summed origination and diversification rate values provided identical results (Fig. S3).

4.3. Sampling bias and corrected diversity estimates

It would seem reasonable that increases in sampling intensity would increase apparent diversity both within floral assemblages and within stratigraphical intervals. Fig. 6 plots the number of sampled localities per time unit and confirms that high diversity values tend to be associated with high sampling intensities (e.g., in the Givetian) and diversity declines with reduced sampling intensities (e.g., in the Emsian). For that reason, it is not surprising that fewer plant genera are registered through the Early–Middle Devonian transition, because fewer sampled localities are recognized in that interval compared with previous time intervals (Table S2, Text S1). A regression analysis shows significant positive correlations between the observed number of plant macrofossil taxa (both raw and detrended data) and the number of localities (Fig. 14A–B). However, MSD is only significantly correlated with site numbers when raw MSD data are used (Fig. 14C–D), suggesting that MSD is less sensitive to bias by sampling intensity than total diversity

and so provides a better picture of Silurian–Devonian plant diversity dynamics.

Fig. 15 compares observed and predicted patterns of Silurian–Devonian diversity of tracheophytes. There is a similarity between patterns from both the total diversity and MSD patterns, except that latter tends to be a little smoother (Fig. 15A–B). The residual differences between these observed and predicted data were used to plot the sampling-corrected curves for observed diversity and MSD shown in Fig. 15C–D. These sampling-corrected data mainly fall within the 95% confidence interval suggesting that the trends are mainly being driven by sampling (Fig. 15C–D); this seems to be particularly so for the Silurian–early Lochkovian diversity data. However, there are significant positive excursions in the observed residual observed (raw) data during the Early Devonian (Lochkovian and Pragian) and negative excursions in the Middle Devonian (Eifelian), and at the end-Givetian (Fig. 15C), which are likely to have biological (rather than sampling) causes. The MSD residuals data follow a broadly similar pattern except for additional positive excursions in the middle Emsian and middle Givetian (Fig. 15D).

5. Discussion

5.1. Apparent patterns of early plant diversity

Early work on land plant diversification (Niklas et al., 1980, 1983, 1985; Knoll et al., 1984; Niklas, 1988; Niklas and Tiffney, 1994) based on the macrofossil record suggested diversity followed a general increasing trend in the late Silurian and Early Devonian, until it reached

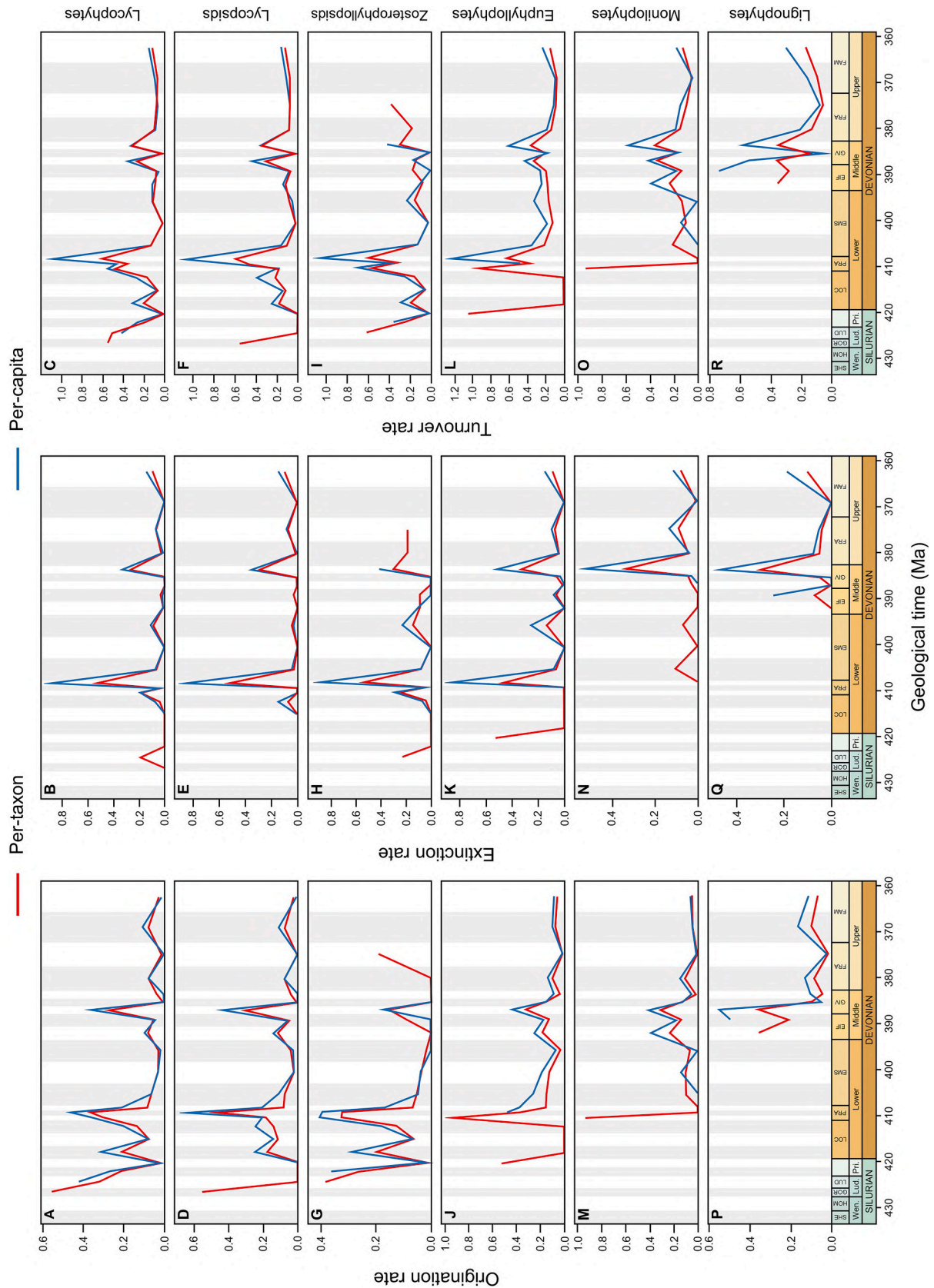


Fig. 10. Silurian-Devonian macroevolutionary patterns of main tracheophyte clades. Red and blue lines show per-taxa and per-capita origination (left column), extinction (central column) and turnover (right column) rates of plant genera, respectively. (A-C) Lycophytes; (D-F) Lycopsids; (G-I) Zosterophylloids; (J-L) Euphyllophytes; (M-O) Monilophytes; (P-R) Lignophytes. Abbreviations, same as in Fig. 6.

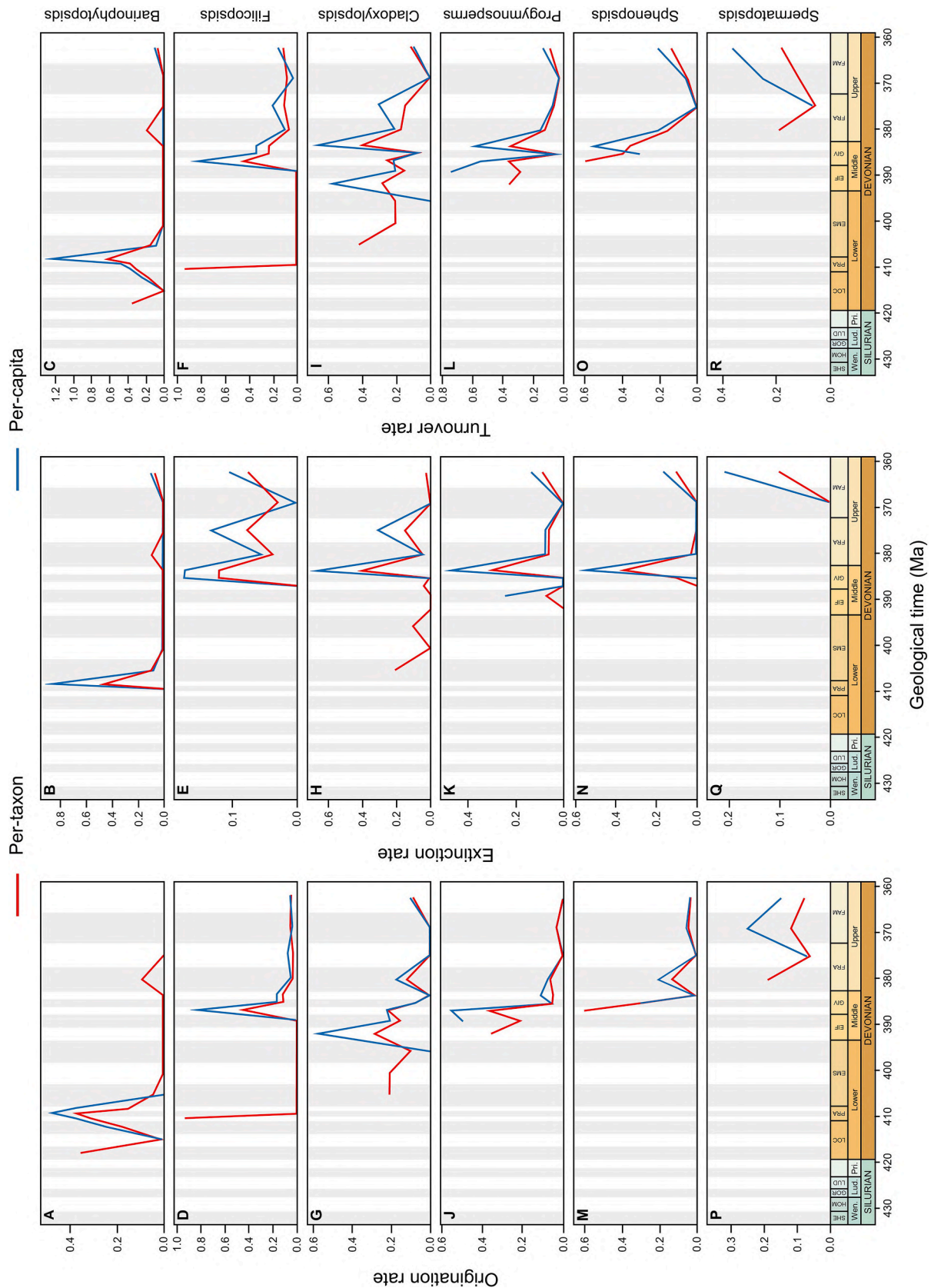


Fig. 11. Silurian–Devonian macroevolutionary patterns of main tracheophyte groups. Red and blue lines show per-taxa and per-capita origination (left column), extinction (central column) and turnover (right column) rates of plant genera, respectively. (A–C) Barinophytopsids; (D–F) Filicopsids; (G–I) Cladoxylopsids; (J–L) Progymnosperms; (M–O) Sphenopsids; (P–R) Spermatopsids. Data analysis conducted at the genus-level. Abbreviations, same as in Fig. 6.

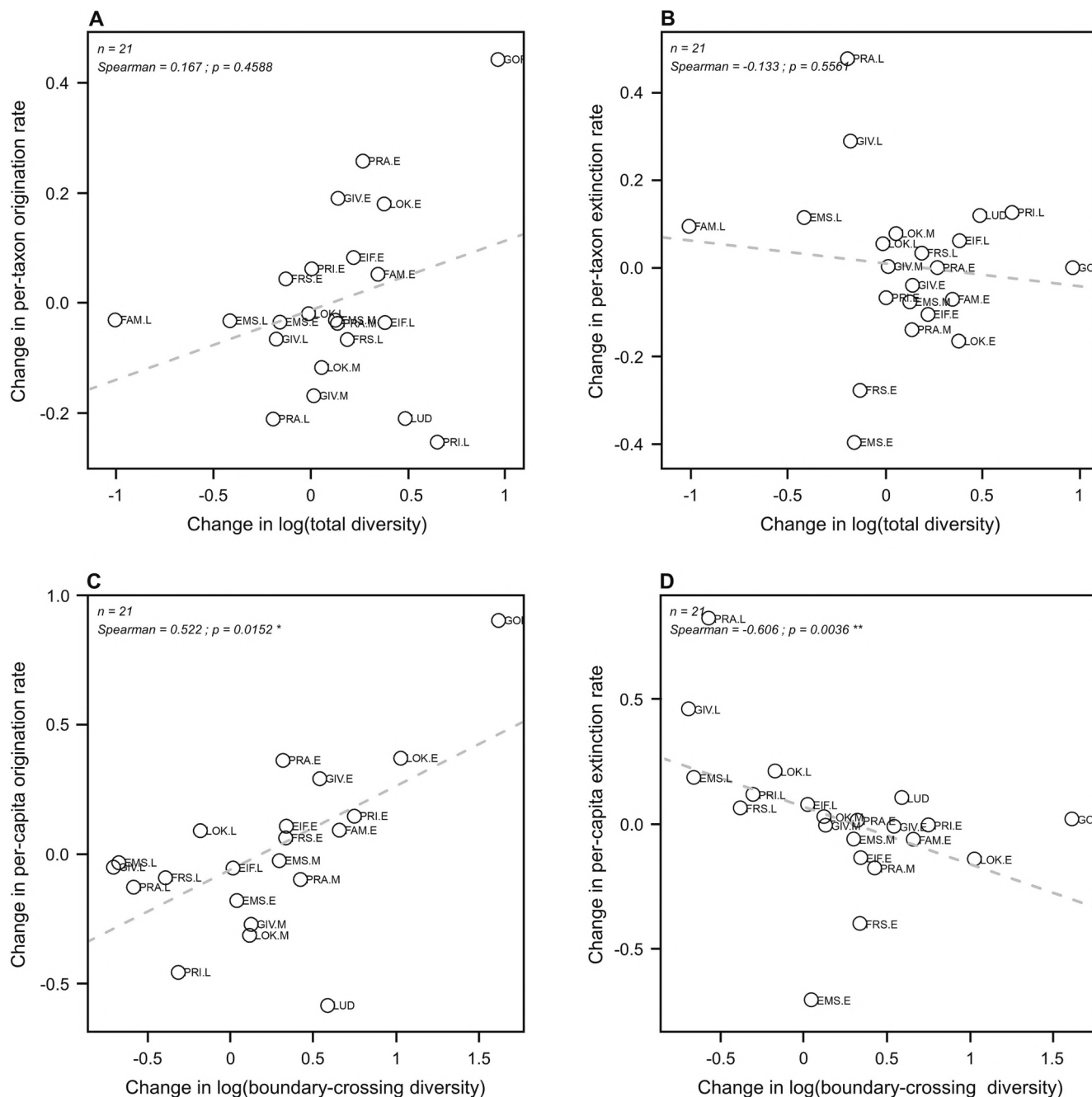


Fig. 12. Comparison between change in total (A–B) and boundary-crossing (C–D) diversity and change in per-taxon and per-capita origination–extinction rates of tracheophyte genera, respectively. Data analysis based on Spearman’s rank correlation coefficient (ρ). *Significant value ($p < 0.05$). **Very significant value ($p < 0.01$).

a plateau in the Middle to Late Devonian. This pattern has remained the accepted paradigm over subsequent decades (see e.g., Hilton et al., 2003; Gutak et al., 2011; Xue et al., 2015a). However, these models were based on plant fossil compilations using the data then available, which included relatively small numbers of taxa, and where the age estimations were often inaccurate. In addition, the early studies were not global in scope as they were mainly restricted to the western Europe and North America fossil records (Raymond and Metz, 1995).

The numerous taxonomic description and revisions in the recent past, coupled with an increased interest in assemblages in Gondwana (e.g., Prestianni et al., 2012; Moisan et al., 2011; Meyer-Berthaud et al., 2003, 2016c; Berry et al., 2000; Berry and Gensel, 2019) and South China (see Xue et al., 2018 for a review), have now provided us with a

much-improved dataset on which to re-investigate early land plant diversification. A re-evaluation of global Silurian–Mississippian macrofossil plant diversity by Cascales-Miñana et al. (2016), using similar diversity metrics to the ones employed in this study, demonstrated that the observed pattern is in fact more nuanced than previously thought, with apparent diversity peaks being manifest in the Pragian and Givetian, as well as a noticeable depletion event in the Eifelian.

Although our results (Fig. 6) are qualitatively similar, there are differences because of the use of a finer stratigraphical resolution, which provides better temporal constraints of diversity fluctuations. For instance, results show a late Emsian peak of total diversity (Fig. 6), instead of a general reduction of diversity throughout the Emsian as a whole (Cascales-Miñana, 2016, fig. 1). Previous lycopsid and

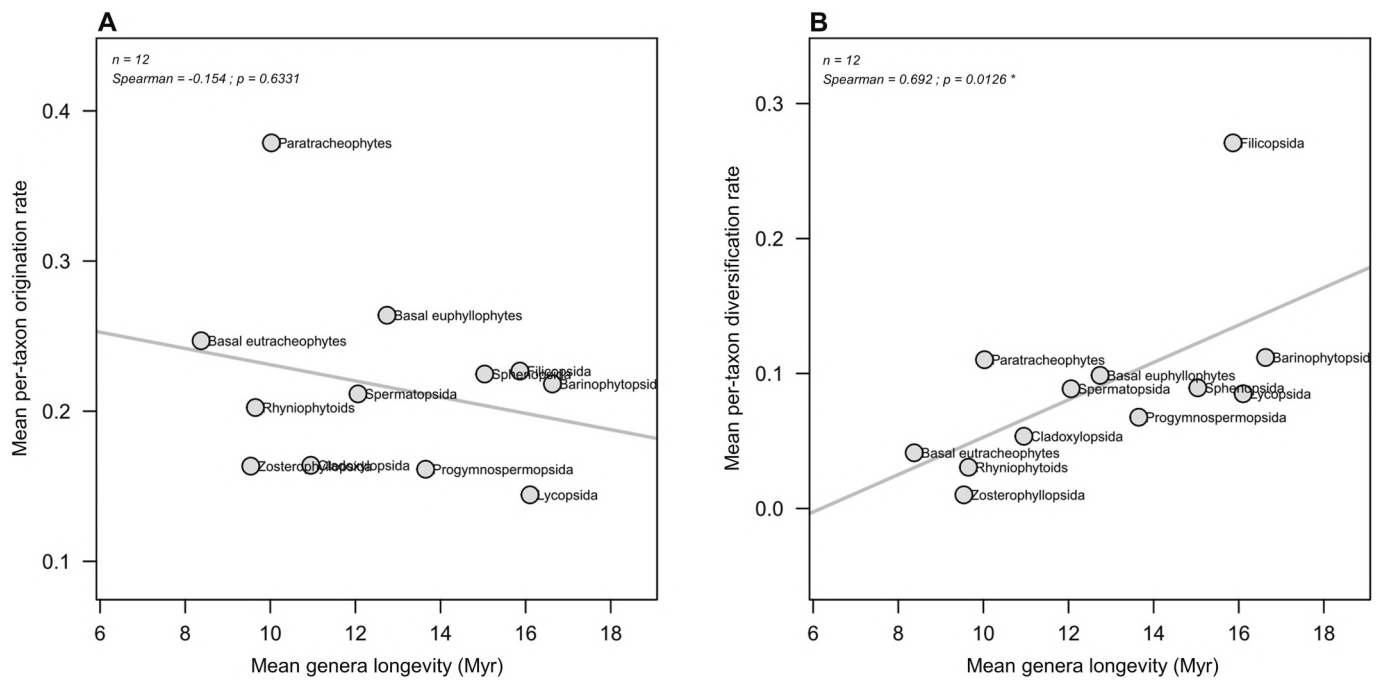


Fig. 13. Comparison between mean per-taxon origination (A) and diversification (B) rates and mean genera longevity of main tracheophyte groups. Data analysis based on Spearman's rank correlation coefficient (ρ). *Significant value ($p < 0.05$).

euphyllophyte diversity patterns (Cascales-Miñana, 2016, fig. 3) present an almost continuous growth from their appearance to the Mississippian, without any noticeable peaks really standing out. Our results have shown that the steady growth in apparent diversity is punctuated by pronounced peaks, discernible in both the overall diversity (Fig. 6) and the diversity in the two main monophyletic clades (Fig. 7A, D).

There have also been several global studies of Silurian–Devonian palynological diversity to complement the work on the macrofossil record (Chaloner, 1967; Knoll et al., 1984; Cascales-Miñana, 2016). Because of their high preservation potential, and high rates of production and dispersal (Wellman and Gray, 2000; Wellman et al., 2013), the spore record could be regarded as a more reliable indicator of past plant diversity, being less affected by preservation and geological biases than macrofloras. Indeed, spores are vastly more abundant and preserved in more sediment types than early plant macrofossils. This is especially so in the early Ordovician–Silurian history of land plants where macrofossils are exceptionally rare (Wellman et al., 2003, 2013; Salamon et al., 2018; Servais et al., 2019, fig. 2). However, multiple factors tend to inflate spore taxic diversity and the biological affinities of many of the dispersed spore taxa are unknown. It also distorts the relative representation of the different plant groups. Furthermore, several spore-taxa have been recovered from the same sporangium and, conversely, the same spore taxa can be found in sporangia of different plant species, genera or even clades (e.g., Allen, 1980; Gensel, 1980; Edwards and Richardson, 1996; Bek, 2017). Interpretation of vegetational changes using spores therefore requires caution (Cleal et al., 2021; Cascales-Miñana et al., 2022, tables 2–3). Global spore diversity continuously increases through the Devonian, but with no identifiable peaks (Knoll et al., 1984; Cascales-Miñana, 2016). On a more regional scale, palynological diversities have been shown to have similar trajectories to that seen in the macrofossil record, such as in South China (Xiong et al., 2013; Shen et al., 2020), indicating that both records have been subject to similar underlying controls and biases. However, it seems that the real strength of palynology in diversity studies will be at a landscape or local scale, where many of these distorting effects are less pronounced (Cleal et al., 2021).

In recent years, there has been increased interest in the regional variation in Silurian–Devonian vegetation diversity patterns. If sampling

is homogeneous, regional patterns might be expected to reflect global diversity fluctuations over time (Alroy, 2003). For instance, Cascales-Miñana and Meyer-Berthaud (2015) showed there to be remarkable similarities in the diversity patterns of Zosterophylloids from different palaeogeographical regions. In other cases, however, regional variations in diversity patterns have been identified. In Laurussia (North America, Europe, the Russian platform) the evidence suggests a continuous increase from the late Silurian to the Emsian, followed by an overall decrease from the Eifelian to the middle Famennian, and then another increase in the late Famennian (Raymond and Metz, 1995). More recent work on eastern Euramerica (USA, Canada, northern Europe, western Russia; Lu et al., 2021) suggested a period of diversification in the Early to Middle Devonian, followed by two noticeable peaks in the Givetian and the Famennian, separated by a strong Frasnian trough. Overall, these results are broadly like the pattern observed here (Fig. 6). In contrast, in Siberia (Gutak et al., 2011) and northern Russia (Orlova et al., 2016), significant peaks in vegetation diversity have been reported in the Frasnian and early Famennian, whereas in South China diversity peaks occurred in the Pragian, Givetian and Famennian (Wang et al., 2010; Xiong et al., 2013; Xue et al., 2018). These differences may be partly reflecting sampling and geological biases inherent in such studies. Alternatively, however, it may be reflecting the provincialism that has been previously suggested to have existed with Devonian floras (Raymond et al., 1985, 2006; Raymond, 1987; Edwards, 1990; Edwards and Berry, 1991; Hao and Xue, 2013).

5.2. Sampling bias and geological constraints on the early plant fossil record

A significant correlation has been found between the number of fossil plant-bearing localities and raw diversity counts, and so predicted and observed diversity patterns display striking similarities (Fig. 15A–B). However, while at first glance, Silurian–Devonian plant diversity patterns could appear essentially the result of sampling bias, the number of localities may co-vary with abundance and diversity, and so diversity may not be just a response to heterogeneous sampling or lack of fossiliferous localities. This is particularly true for the earliest record of plant macrofossils in the Silurian, as plants were not as widespread as they

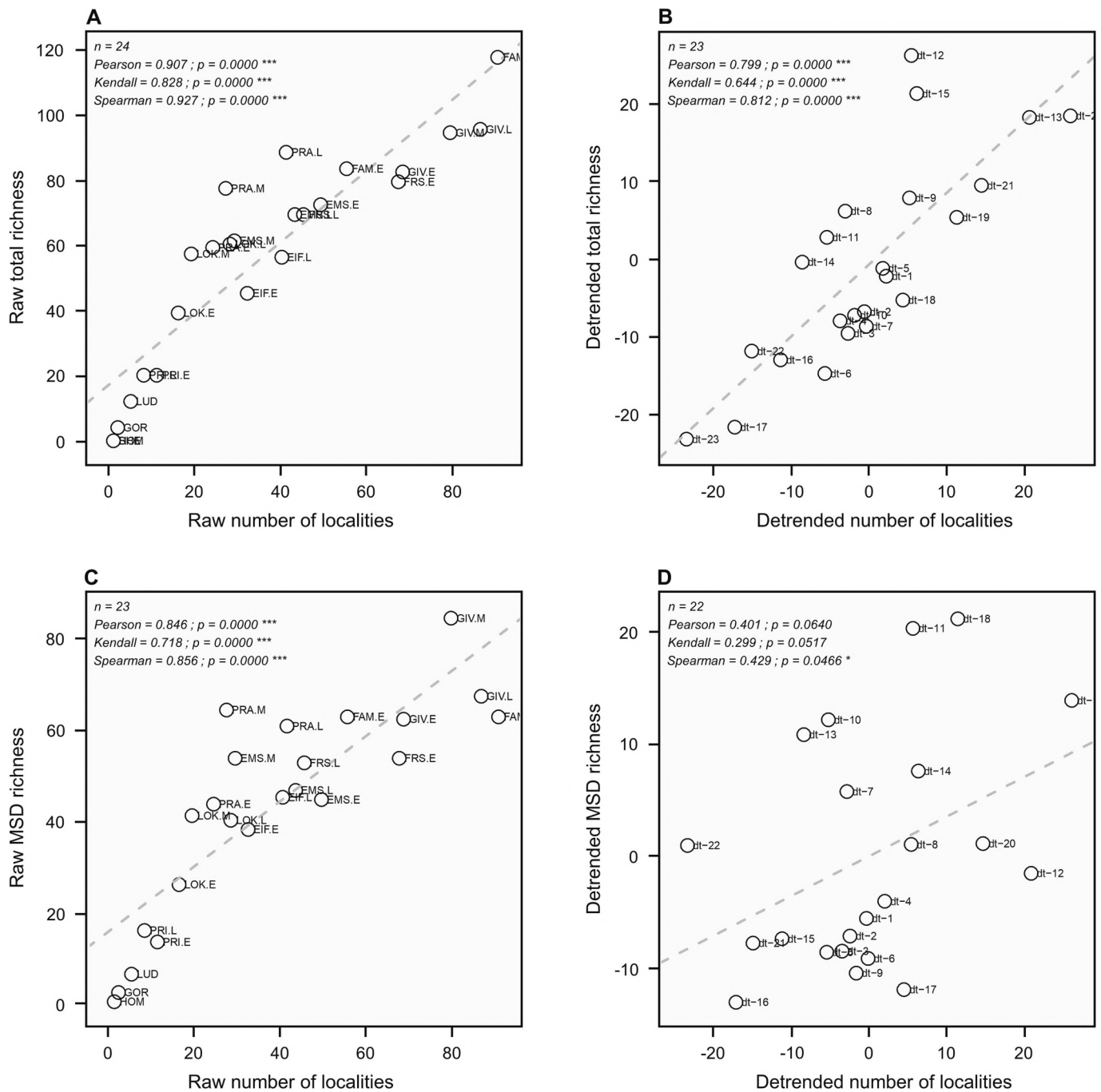


Fig. 14. Comparison between total (A–B) and mean-standing (C–D; MSD) diversity of tracheophyte genera and the number of sampled localities per time unit. Data analysis performed on raw (A, C) and detrended (B, D) data through generalized-differencing (GD). Correlations based on Pearson's, Kendall's, and Spearman's correlation coefficients. *Significant value ($p < 0.05$). ***Highly significant value ($p < 0.001$).

were later in the Devonian; the low number of localities in fact probably reflects actual low plant abundance and diversity of the vegetation, implying a redundancy effect. In our view, although impacted by sampling bias (Fig. 15C–D), the concomitant increase of diversity and number of localities between the middle Silurian and the middle Early Devonian (Fig. 6) probably also reflects the progressive colonisation of the land by plants (Le Hir et al., 2011; Davies et al., 2021; Gensel et al., 2020). In fact, the higher-than-expected diversities at the Lochkovian and Pragian suggest more of a diversification signal than a sampling driven pattern (Fig. 15C–D). Furthermore, the observed diversity peaks in the Pragian and the Givetian (Figs. 6 and 15B) are also probably a true diversification, as is the observed depletion in diversity at the Eifelian.

These findings corroborate the first estimations of sampling biases on early land plant diversity in Cascales-Miñana and Meyer-Berthaud (2014, 2015) using the zosterophylloids fossil record.

So far, sampling biases in the palaeobotanical record have been scarcely evaluated (Cleal et al., 2021; Pardoe et al., 2021). With Lloyd's (2012) method, the difficulty resides in properly assessing which proxy may be used to standardise the amount of diversity found within each time unit. For instance, many studies have used outcrop or exposure area as a proxy to capture the amount of rock accessible for sampling to correct for sampling biases (e.g., Crampton et al., 2003; Smith and McGowan, 2007; Smith et al., 2012). However, more than one type of sampling bias can affect a raw diversity curve and the effects of those

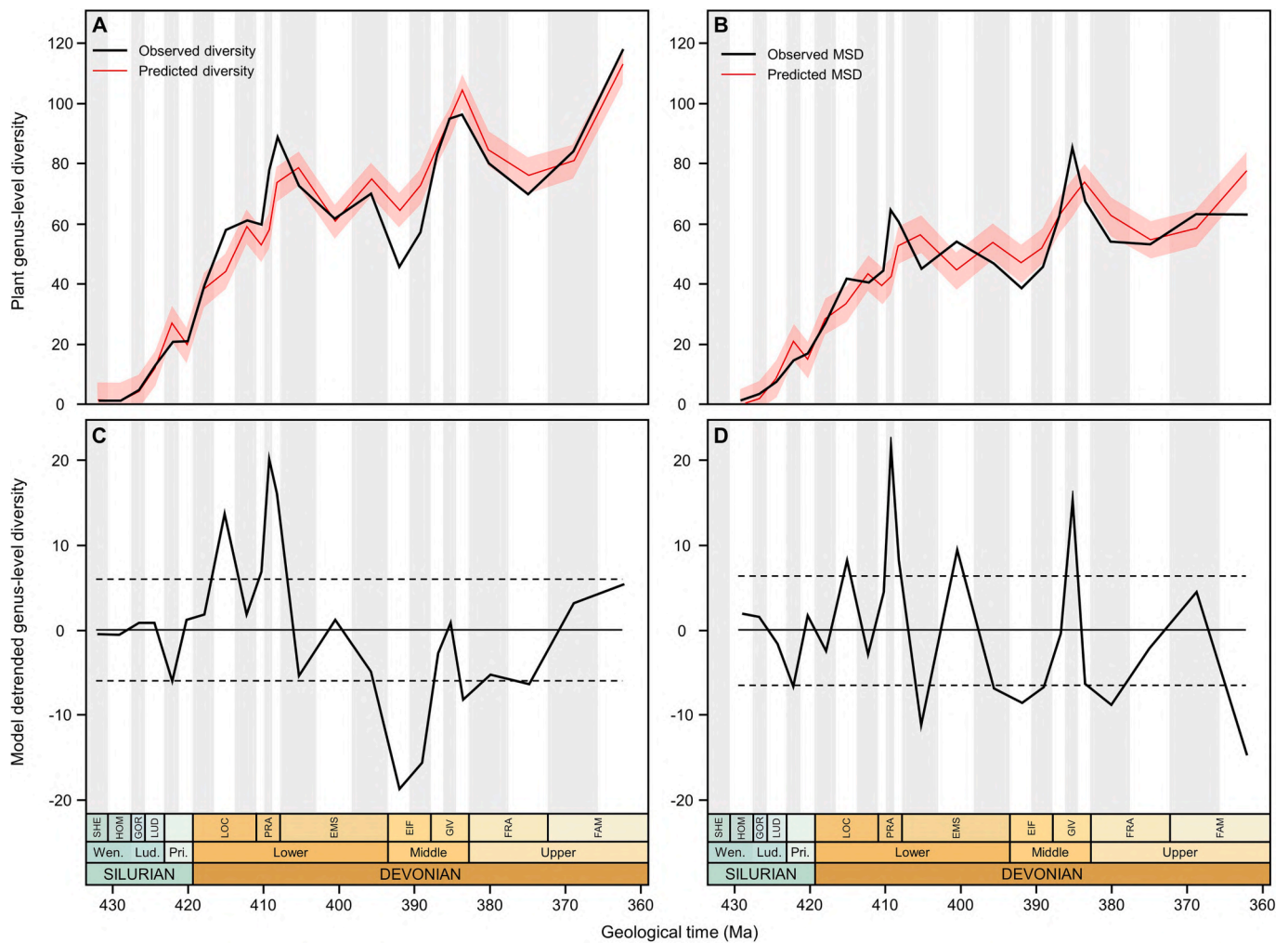


Fig. 15. Comparison between observed and predicted patterns of total (A) and mean-standing (B; MSD) diversity of plant genera. Sampling-corrected (residual) patterns of total (C) and MSD (D) diversity of plant genera. Dashed lines represent the 95% confidence interval of the proxy-biased model. Statistical significance is assumed when diversity values exceed such interval. See [Lloyd \(2012\)](#) for details. Abbreviations, same as in [Fig. 6](#).

biases may be widely different between clades ([Benton et al., 2013](#)). The availability of such proxies is also often lacking (e.g., for palaeobotanical studies, there are no global compilations of outcrop area or rock volume or terrestrial sedimentary deposits). The choice of locality counts as a proxy, as used here, is based on the following logic: as more localities are discovered, more effort is put into sampling, which enhances collection levels, and hence, observed diversity. However, if sampling effort is homogenous and extensive, locality counts may themselves be controlled by other larger biases linked to the quality and amount of fossiliferous sedimentary rocks available from different ages ([Smith and McGowan, 2011](#); [Dunhill et al., 2014a, 2014b](#); [Walker et al., 2017b](#)).

It has been suggested that marine diversity patterns through time have been controlled by tectonics and changing sea-level – the so-called ‘common-cause’ (CC) hypothesis ([Peters, 2005](#); [Smith and McGowan, 2011](#); [Smith and Benson, 2013](#); [Zaffos et al., 2017](#); [Close et al., 2018](#)). Analogous cycles of transgression and regressions may also have affected the diversity observed in the plant fossil record, which is naturally skewed towards lowland rather than upland vegetation: uplands are generally erosional, and not depositional environments ([Thomas and Cleal, 2017](#); [Cleal and Cascales-Miñana, 2019](#)), and there are no unequivocal examples of preserved *in situ* upland vegetation until the Carboniferous, and are in fact generally rare throughout the Phanerozoic ([Falcon-Lang, 2003](#); [Boyce and Lee, 2017](#)).

Recently, [Kocsis and Scotese \(2020\)](#) estimated the amount of continental flooding over the course of the Phanerozoic to provide a proxy for

the extent of terrestrial lowland areas available for vegetation. If the CC hypothesis can equally be applied to plants, then we should observe a negative correlation with the amount of continental flooding. Such a correlation is apparent in the late Silurian, Early Devonian and Late Devonian, but not during the Middle Devonian ([Fig. 16A–B](#)). This might suggest that during the Early Devonian, the increase in available paralic habitats during regressive phases may have been helping drive the diversification of the early terrestrial vegetation but, by the Middle Devonian, plants had evolved adaptive strategies to take advantage of most of those habitats and so diversification declined. The Givetian plant diversification, coinciding with an overall increase in transgressive flooding, is less easy to explain, unless habitat fragmentation in the lowlands was raising selection pressure that raised diversification. Although other biases such as sampling effort may be affecting diversity in the macrofloral record over relatively short stratigraphical intervals such as stages, CC-like effects were probably more influential for explaining the diversity dynamics over longer time scales ([Smith and McGowan, 2011](#)).

“Molecular clock” data suggest that tracheophytes appeared in the early Silurian or perhaps, even the Late Ordovician ([Morris et al., 2018b](#)). Several hypotheses have been invoked to explain the lack of tracheophyte microfossils before the middle Silurian and their paucity in the upper Silurian (e.g., [Gensel, 2008](#); [Decombeix et al., 2019](#)). For instance, plants may not have been growing in environments that would allow them to be effectively transported into appropriate depositional

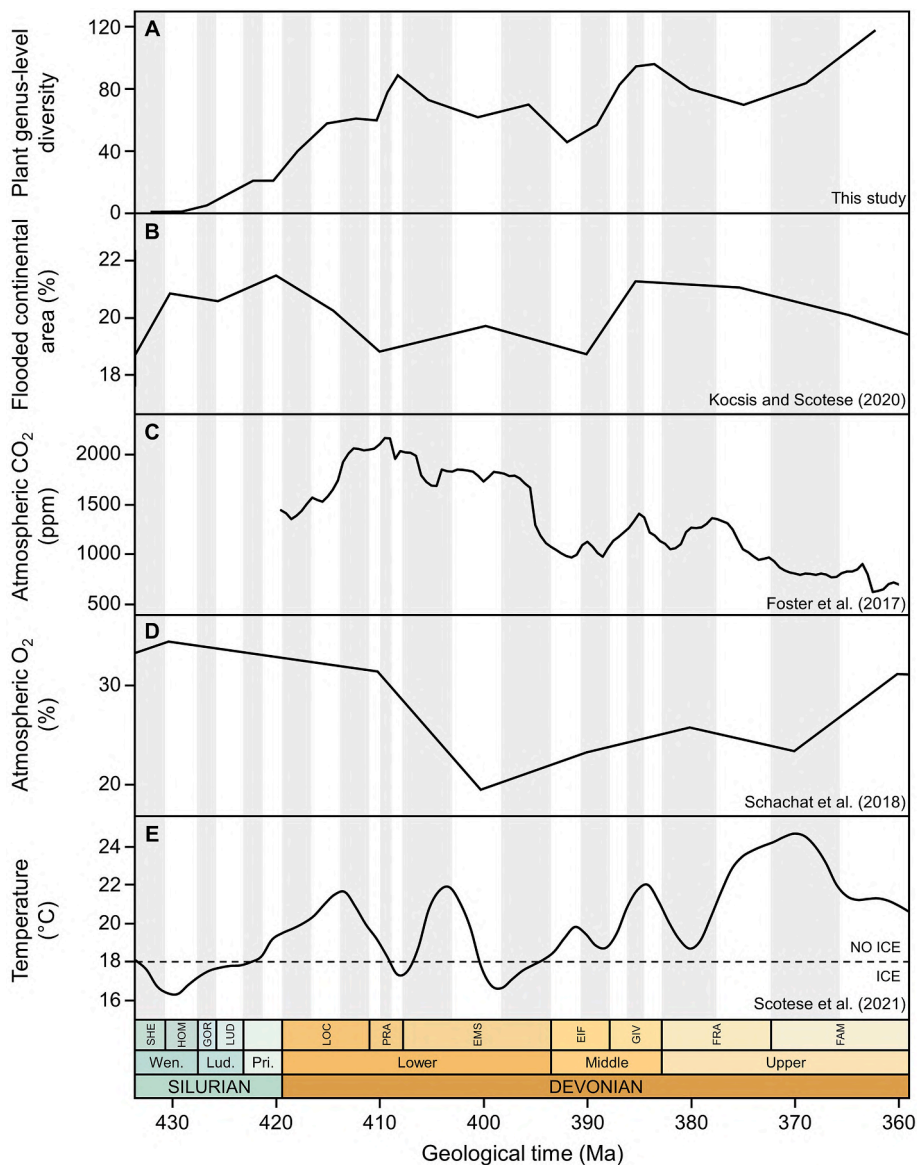


Fig. 16. Comparison between total diversity pattern of tracheophyte genera (A) and fluctuations of different abiotic factors (B–E) during the Silurian-Devonian time interval. (B) Flooded continental area. (C) Atmospheric CO₂ levels. (D) Atmospheric O₂ levels. (E) Global average temperature. Abbreviations, same as in Fig. 6.

basins (Wellman, 2004). The lack of degradation-resistant tissues in early land plants except for spores has also been suggested as a major factor (Strother et al., 1996; Kenrick et al., 2012). Servais et al. (2019) pointed out that there is a progressive change in the fossil record of plants through the Late Ordovician and Silurian from isolated cryptospores, to isolated sporangia, to sporangia borne on increasingly long axes. This suggests that only the spore-bearing organs of these early plants were initially being subaerially exposed but that this exposure was being progressively increased to facilitate improved spore dispersal. Since only these spore-bearing structures would have adaptive features to survive drying in subaerial conditions, these will be the only parts of the very early plants that would survive fossilisation. It was only in the late Silurian and Early Devonian that plants became adapted to a fully (or mostly) subaerial life and therefore had a reasonably high preservation potential.

Another commonly invoked reason for the poor pre-Devonian macroflora record is the apparent lack of terrestrial deposits (e.g., Kenrick and Crane, 1997a, 1997b; Kenrick et al., 2012; Morris et al., 2018b). Whilst Devonian plant macrofossils are mainly found in lowland terrestrial deposits (e.g., Edwards and Richardson, 2004; Kennedy et al.,

2012), Silurian plant macrofossils are all allochthonous remains found in marine sediments (Raymond et al., 2006; Wellman et al., 2013). The extensive continental flooding that evidently took place during the Silurian (Fig. 16B) may, therefore, also help explain the paucity of Silurian plant macrofossils (Kenrick et al., 2012).

Another significant factor that may affect measures of plant fossil diversity is post-depositional erosion of terrestrial sedimentary deposits (Smith, 2007; Smith et al., 2012), which may have particularly affected the types of strata in which macrofloras typically occur. Knoll et al. (1979) already showed that the extent of terrestrial outcrop area through time is strongly correlated with the amount of plant fossil-taxa described from North America, and Cascales-Miñana et al. (2013) found similar correlations at a global scale using the total sedimentary rock record. Another example is in South China, where the lack of terrestrial Emsian–Eifelian deposits, linked to a regional transgression, may explain the near absence of plant fossils of this age here (Hao and Xue, 2013; Xiong et al., 2013; Xue et al., 2018).

5.3. Biosphere dynamics and early land plant diversification

The impact of the development of terrestrial vegetation on atmospheric CO₂ concentrations, and consequently on climate, has been extensively discussed (e.g., Berner, 1997, 2005; Algeo et al., 1995, 2001; Algeo and Scheckler, 1998; Berner and Kothavala, 2001; Beerling, 2007; Strother et al., 2010; Lenton et al., 2012; Ibarra et al., 2019; Dahl and Arens, 2020; Chen et al., 2021). Increasing carbon sequestration due to the evolution of larger plants and enhanced silicate weathering rates caused by plant roots have been invoked as the main reasons for falling CO₂ levels and a cooling climate during the Devonian (Berner, 1997; Simon et al., 2007; Algeo and Scheckler, 2010; Le Hir et al., 2011; Foster et al., 2017; Brugger et al., 2019; Fig. 16C). Furthermore, the observed taxonomic diversification of the macrofloras indicates that plants were becoming adapted to growing in a wider range of habitats, thereby increasing vegetation cover. This increase in vegetation cover may also have reduced the planet's albedo and so increased global temperatures, especially during the Late Devonian (Le Hir et al., 2011), although the effects of this may have been overestimated (Brugger et al., 2019).

Carbon sequestration due to the general increase in plant biomass during the Devonian might be expected to produce higher levels of atmospheric O₂ (Strother et al., 2010; Lenton et al., 2012; Elrick et al., 2022). The GEOCARBSULF model (Berner, 2006, 2009; Royer et al., 2014) has predicted remarkably high atmospheric O₂ levels already in the Silurian (Schachat et al., 2018; Fig. 16D) and this could have been linked to increased phytoplankton primary production, and/or an earlier terrestrialization of plants suggested by the microfossil record (Strother et al., 2010; Lenton et al., 2012; Servais et al., 2019). However, O₂ levels in fact reportedly fell during the Devonian (Fig. 16D) and appears to have been unaffected by the expansion of plant diversity at this time.

Global temperatures have been a major influence on Phanerozoic global diversity trajectories in both marine faunas (Erwin, 2009; Mayhew et al., 2008, 2012) and terrestrial floras (e.g., DiMichele et al., 2001; McElwain et al., 2007; Heimhofer et al., 2018; Slater et al., 2019). The palaeobotanical record suggests that there were major floral turnovers during global warming and cooling events, with significant selective adaptations or extinctions of clades when migration was unable to mitigate the effects of ecological pressures (Knoll and Niklas, 1987). Overall, however, the evidence of climate having affected early land plant diversification is equivocal. Although the late Silurian and Devonian was mostly a warm time in Earth history (Scotese, 2021; Scotese et al., 2021) with global temperatures between 2–10°C warmer than today (Fig. 16E), we observe little correlation between the dynamics of global temperature and of plant taxonomic diversity (Fig. 16A, E; see also Jones and Eichenseer, 2021 for further discussion).

Rhyniophytoids are more commonly found in the higher latitudes in the upper Silurian–Lochkovian and may have been better suited to seasonal temperate climates (Edwards et al., 2001; Gerrienne et al., 2001; Gess and Prestianni, 2021). Moreover, Edwards and Richardson (2004) hypothesized that their life cycle was well-adapted to a seasonally arid tropical to subtropical climate such as found in southern Laurussia during those times. Zosterophylloids, on the other hand, were preferentially located in palaeotropical to palaeoequatorial regions, indicating that they may have favoured warmer and wetter conditions (Edwards and Richardson, 2004; Raymond et al., 2006; Cascales-Miñana and Meyer-Berthaud, 2015), although what adaptive features favoured those conditions are still unknown (Pšenička et al., 2021). The climate progressively warmed from the late Silurian until the Pragian (Fig. 16D), possibly acting as a catalyst to the progressive demise of the basal-most tracheophytes, while favouring other groups (e.g., zosterophylloids). The colder climate beginning in the middle Emsian through the Middle Devonian may have reciprocally precipitated the zosterophylloid decline shown in Fig. 7C (Cascales-Miñana and Meyer-Berthaud, 2015).

During the late Emsian–Eifelian, lycopsids continuously diversified,

whilst other clades such as the zosterophylloids and euphyllophytes (mainly basal euphyllophytes) were declining, particularly in the Eifelian (Fig. 7C, D). There is increasing evidence that lycopsids were the dominant (Fig. 7B) plant group inhabiting the highest palaeolatitudes in the Middle Devonian and may have been better adapted to cooler temperate climates (Moisan et al., 2011; Matsumura et al., 2015), whilst coeval assemblages from the palaeotropical regions were taxonomically more diverse. The colder conditions of the late Early to Middle Devonian may have favoured lycopsid diversification over euphyllophytes and zosterophylloids.

The diversification of vegetation in the Late Devonian was accompanied by generally warmer conditions (Scotese et al., 2021, Fig. 16E), with *Archaeopteris* trees growing both within the palaeoantarctic circle and in palaeoequatorial regions (Anderson et al., 1995; Gess and Whitfield, 2020). There is some evidence of glaciation in the latest Famennian in high to mid-palaeolatitude Laurussia and Gondwana (e.g., diamictites and dropstones – see Kaiser et al., 2016; Marshall et al., 2020), but there is no evidence of a corresponding decline in plant diversity in any of the major clades.

High pCO₂ levels have been implicated in the absence of megaphyllous leaves before the middle Pragian (e.g., *Eophyllophyton*; Fig. 3F) as they would have quickly overheated, restricting photosynthetic efficiency. However, as atmospheric CO₂ levels decreased throughout the Devonian, leaf stomatal density would also have increased, allowing higher transpiration rates to cool the photosynthetic surfaces (Beerling et al., 2001; Xue et al., 2015a). Megaphylls also require an efficient hydraulic system to adjust to their higher water demands and this will have acted as a selective pressure towards more complex tissues such as secondary xylem (Osborne et al., 2004a, 2004b). Megaphylls would have been an important asset in the competition for light and space (Beerling and Fleming, 2007; Osborne et al., 2004b) and would have contributed to the observed euphyllophyte radiation in the Middle to Late Devonian (Figs. 7D, 10J–L). The lycopsids, in contrast, were also prominent components of Middle Devonian and later Palaeophytic vegetation (Figs. 7B, 10D–F), but did not develop megaphyllous leaves and achieved tree-sized statures using different strategies than euphyllophytes (Meyer-Berthaud and Decombeix, 2009).

5.4. Timing and evolution of early floras

Increasing complexity and the development of key innovations in land plants have been generally assumed to be one of the main drivers of the taxonomic diversification in Silurian–Devonian vegetation (e.g., Prestianni et al., 2012, and references therein). Niklas et al. (1983) has previously shown that the earliest plant taxa (e.g., zosterophylloids, lycopsids) had longer longevities and lower diversification rates than taxa that appeared subsequently (e.g., monilophytes, spermatophytes). However, we have found no clear pattern emerging, although more primitive plant groups such as basal eutracheophytes, rhyniophytoids and zosterophylloids seem to have had lower longevities and diversification rates than euphyllophyte groups and lycopsids (Fig. 13B).

Based on Foote's (2000b) approach (Fig. 12), extinction rates were shown to be slightly more significant than origination rates in explaining diversity changes in early vegetation. This suggests that extrinsic factors may be more influential than evolutionary innovations and ecological opportunities in explaining the diversity fluctuations in these floras. However, the difference is not very significant, and it is likely that there was more than one controlling factor. The kinetic model of Sepkoski (1978, 1979, 1984) predicts that evolutionary rates are diversity dependent: origination rates should decrease, and extinction rates increase with time, due to for instance ecological saturation and increased competition (Knoll et al., 1984). While, origination rates clearly decrease with time, extinction rates are relatively constant despite the two extinction peaks in the end-Pragian and end-Givetian (Fig. 9B).

Overall diversity trajectories of tracheophytes in the Devonian can be mainly explained by the diversity fluctuations observed in the two most

prominent clades, the lycophytes and euphyllophytes (Fig. 7A, D). However, major fluctuations in total diversity in the Devonian are never due to the diversity variations of only one clade. For instance, the Pragian and Givetian peaks and the Famennian maximum were each caused by in the diversification of at least two clades (Figs. 6–7). This supports a diversification pattern linked to major clade reorganisations, with the two major reductions in diversity corresponding to the starts of the Early Eophytic and Late Eophytic Floras of Cleal and Cascales-Miñana (2014, 2021; see also Capel et al., 2021).

The initial diversification of plants, between the middle Silurian and the Early Devonian (Pragian), is related to high origination rates (Fig. 9A) particularly among the lycophytes (Fig. 10A). However, as shown by Fig. 15, most of this initial pattern cannot be distinguished from sampling bias, especially during the Silurian. Interestingly, although zosterophylloids and lycopsids appear during the same epoch (Kotyk et al., 2002; Tims, 1980), they do not diversify significantly until the Lochkovian and Pragian, respectively (Figs. 7B–C, 10D, G), where significant peaks are observed (Fig. 15). In the Lochkovian, plant diversification was further triggered by the development of the Eotracheophytic Flora mostly dominated by basal eutracheophyte groups such as rhyniophytoids and taxa of unknown affinities (Capel et al., 2021). The subsequent replacement of the rhyniophytic by lycophytic vegetation in the Early Devonian is probably linked to the progressively better adaptation of lycophytes to the terrestrial environment with for example, some improvement in plant hydraulics rendering them more competitive against the rhyniophytic plants (Cascales-Miñana et al., 2019b; Decombeix et al., 2019). Consequently, plant diversity reached its first maximum in the middle to late Pragian with the domination of zosterophylls, together with other groups such as lycopsids and basal euphyllophytes (Figs. 6, 7B, D).

The Emsian and Eifelian represent the time of transition between the Early and Late Eophytic Flora reflected by the change from a zosterophylloids- to a lycopsid-dominated vegetation. Cascales-Miñana and Meyer-Berthaud (2014, 2015) suggested that the zosterophylloids decline after the Pragian may have been the result of competition with lycopsids and the earliest euphyllophytes; the evidence presented here suggests that the euphyllophytes may have been the more significant competitors. External, but unknown factors may also have played a part in the diversity decline. The lower diversity appears linked more to persistently low origination rates throughout the Emsian–Eifelian time interval rather than increased extinction rates (Fig. 7A–B). Moreover, sampling biases seem to have less impact than expected on the apparent dynamics of plant macrofossils through the Early-Middle Devonian boundary from which significant excursions are observed (Fig. 15). This would support the Cascales-Miñana's (2016) interpretation of the Eifelian depletion as the result of the overlapping of the different dynamics in three different clades (zosterophylloids, lycopsids, and euphyllophytes).

The Middle Devonian witnessed the appearance of the first forested landscapes as euphyllophyte (pseudosporochnalean cladoxyloids and aneurophytes) and lycopsid plants increased in size and height (Meyer-Berthaud and Decombeix, 2009; Xue et al., 2018; Stein et al., 2012; Stein et al., 2020). In the Givetian, the congruent diversification of both the lycopsid and the euphyllophyte (progymnosperms and monilophytes) clades is of particular interest (Figs. 7B, E, 8D). The occurrence of convergent evolution both in terms of changes in reproduction (e.g., heterospory; Bateman and DiMichele, 1994) but also in the development of the tree-habit (Senkevitch et al., 1993; Berry and Marshall, 2015; Crepet and Niklas, 2019; Berry, 2019), tends to suggest that these two clades were competing for the same resources of light and nutrients.

The Frasnian represents another transition period with the decline in diversity of progymnosperms, cladoxyloids and lycopsids (Figs. 7A, 8C–D). However, in the Famennian, another pulse of diversity is observed in both the lycopsids and euphyllophytes, the latter mainly deriving from the spermatophyte radiation (Figs. 7B, D, 8F). Prestianni and Gerrienne (2010) suggested that spermatophytes initially developed

in upland marginal to extra-basinal habitats, but in the Late Devonian they took advantage of a progressive freeing of the *Archaeopteris* forest habitats in the lowlands, and so started to enter more regularly into the macrofossil record (Decombeix et al., 2011); this seems to be corroborated by the observed decline of progymnosperm diversity preceding the spermatophyte radiation (Fig. 8D, F). Indeed, spermatophytes do not appear to have diversified at the expense of lycopsids as they were both diversifying at this time (Figs. 7B, 8F). These changes in vegetation recorded in the Upper Devonian macrofloral record correspond to the change from Late Eophytic to Palaeophytic floras of Capel et al., 2021.

6. Conclusions

- i. Here, we have supplied an in-depth characterization of the Silurian–Devonian pattern of vascular plant macrofossils. Results have shown key diversification events linked to the development and demise of different plant groups such as, in a first order, lycophytes, and euphyllophytes, and in a second order, lycopsids, zosterophylloids, as well as monilophytes and lignophytes. Results have further revealed common patterns to be caused by major ecological changes occurring during the terrestrialization process. For instance, we see pronounced peaks, discernible in both the overall diversity and the diversity in the two main monophyletic clades, i.e., lycophytes and euphyllophytes, which punctuate the early plant diversity pattern. Likewise, we have identified major origination–extinction pulses that resulted in the main floral transitions over time, such as the change to a forested landscape during the Middle Devonian.
- ii. For the first time, the large-scale impact has been evaluated of sampling bias in our conception of the early radiation and diversification of vascular plants. Results have shown a highly significant correlation between the apparent diversity and the number of sampling sites through time, which suggests a strong sampling bias on the early land plant fossil record. However, we find a non-homogeneous sampling effect that suggests major gain and losses of diversity should reflect a true biological signal. Results have further shown that other factors, such as the amount of continental flooding could be influencing the observed patterns. Evidence seems to suggest that the increase of paralic habitats during regressive phases could have contributed to the early diversification of vegetation.
- iii. Moreover, a comparison of abiotic factors with the observed diversity patterns does not show significant correlations, further stressing the importance of intrinsic factors on land plant diversification. Although climate change may have affected the dynamics of individual clades, especially among the lycophytes, its impact on vegetation diversity in this hothouse climate is unclear. Similarly, the role of decreasing atmospheric CO₂ levels in the evolution and radiation of euphyllophytes still requires further investigation. O₂ levels seem to have been unaffected by the expansion of terrestrial vegetation.
- iv. Finally, taxonomic turnover rates appear not to be related to a different reproduction strategy of each plant group, as previously suggested. The main fluctuations in Devonian plant diversity were always triggered by variations in more than one clade and/or plant group. Our results suggest that extrinsic factors may have been more influential than the appearance of evolutionary innovations in explaining the diversity patterns, and emphasize that the timeline of the early diversification of vascular plants is reflected in the Evolutionary Floras model.

7. Future perspectives and research directions

This study highlights the sampling impact on major trends of plant diversity during the Silurian–Devonian time interval. However, little is known about such impacts on particular plant groups and/or

paleogeographical regions, which is challenging. In fact, recent works (e.g., Wellman et al., 2022) suggest that floral diversity is impacted by palaeocontinental configuration, and intimately linked to the spatial distribution of collecting areas, which requires further investigations. This is especially relevant in order to infer how climate might have affected various plant clades and their likely climatic tolerances, which are to this day not yet well-circumscribed.

The changing nature of the rock record does have a major effect on sampling and the apparent plant diversity seen in the microfossils. Future efforts should be focused on discerning how geological signal drives our understanding of plant diversification, especially among early land plants. This is a major gap in this discipline, especially if we consider that a global stratigraphic database is unavailable. This absence of a reliable estimation of terrestrial sedimentary outcrop area or rock volume hinders a full analysis of the potential effect of sampling bias on the diversity signal of early land plants. We believe that new integrative studies will further clarify the sampling issues and illuminate the interactions between early plants and abiotic factors, and that this will shed new light on the early history of how vegetation became adapted to subaerial life and laid the foundations for the terrestrial world as we see it today.

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Disclosure statement

The authors reported no potential conflict of interest.

Declaration of Competing Interest

None.

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