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The great Silurian-Devonian terrestrial revolution: diversity and early evolution of land plants

La grande révolution terrestre du Silurien-Dévonien : diversité et évolution des premières plantes terrestres

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Chapter I: Introduction

Modern land plants (embryophytes) are highly diverse with over 370,000 species currently recorded, among which, *ca.* 80% are flowering plants (angiosperms), resulting from their extraordinary radiation beginning in the Early Cretaceous (*ca.* 135 Ma) (Friis et al., 2010; Christenhusz and Byng, 2016). Nonetheless, phylogenetic studies based on extant plants suggest that numerous lineages appeared and diversified far earlier, in the Early Paleozoic (500–360 Ma) (Gerrienne et al., 2016; Morris et al., 2018a). History being written by the victors, lineages still extant today only allow to capture a fraction of plant's evolutionary history (Quental and Marshall, 2010). However, a glimpse of the hidden history of plant evolution and diversification is accessible to us via the plant fossil record. The Silurian–Devonian period (*ca.* 440–360 Ma) in particular attracted scrutiny among paleobotanists by the unparalleled explosion in terms of morphological disparity and diversity among plants, coinciding with their progressive conquest of the continental surfaces also known as the 'terrestrialization' process (Vecoli et al., 2010; Kenrick et al., 2012).

Terrestrialization of plants is generally assumed to have had profound consequences on key biogeochemical cycles such as carbon, through increased weathering rates, and carbon storage and burial, leading to changes in atmospheric O_2 and CO_2 levels (Algeo et al., 1995; Algeo and Scheckler, 1998, 2010; Strother et al., 2010; Kenrick et al., 2012; Lenton et al., 2016). This process also paved the way for animal colonization of continents, with plant's role as primary producers on continents, thus creating the modern terrestrial intricate ecosystems that we know of today (Schear and Selden, 2001; Labandeira, 2013; Buatois et al., 2022). Even though crown group Embryophyta may have originated in the Cambrian (*ca.* 500 Ma) and effects of plant terrestrialization may have begun earlier (Lenton et al., 2012; Wellman and Strother, 2015; Morris et al., 2018a; Servais et al., 2019), it is only during the late Silurian–Devonian period that vascular plants (tracheophytes) appeared and substantially diversified (Gray, 1993; Bateman et al., 1998; Steemans et al., 2009; Prestianni and Gerrienne, 2010). By the Middle Devonian, all extant lineages of vascular plants were already represented in the macrofossil record (Fig. I.1). This lineage diversification is concomitant with an increase in morphological and functional complexity in both vegetative and fertile organs with the development of key evolutionary innovation (e.g., leaves, wood, seeds) (Fig. I.1; Steemans et al., 2012; Gensel et al., 2020; Leslie et al., 2021). A large increase in plant size during these times has transformed terrestrial settings consisting of scarce diminutive vegetation of bryophytic or tracheophytic plants (e.g.,

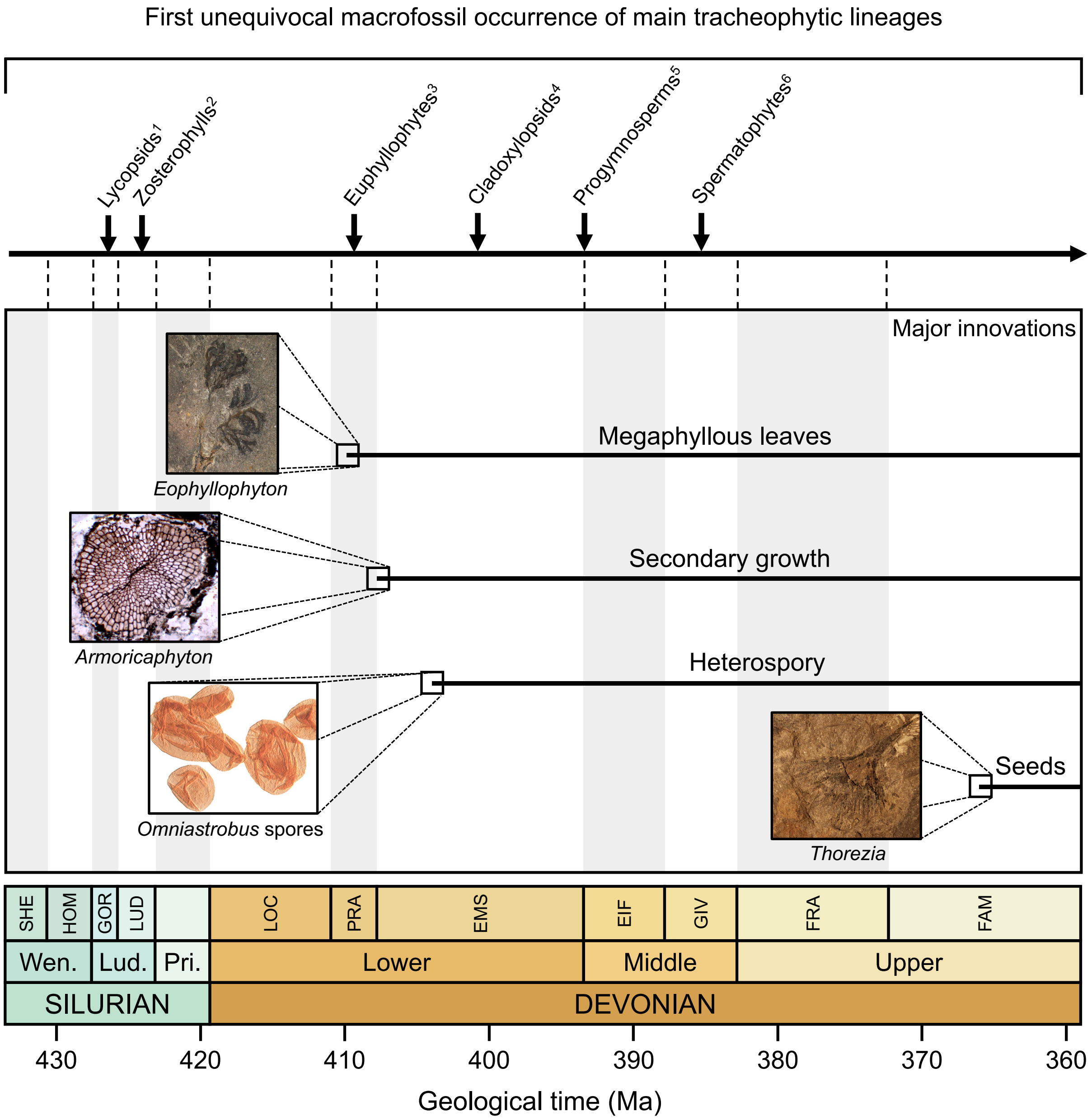

Figure I.1: Stratigraphic ranges of major innovations in the tracheophyte clade and earliest occurrence of main tracheophytic plant lineages in the macrofossil record. Each taxon illustrated represents the first or a coeval occurrence of associated innovations. Illustrations of taxa extracted from: *Eophyllophyton* (Capel et al., 2022a, fig. 3F); *Armoricaphyton* (Gerrienne and Gensel, 2016, pl. I, 4); *Omniastrobus* (Bonacorsi et al., 2020, fig. 1G); *Thorezia* (Capel et al., 2022a, fig. 5F). References: 1. Rickards (2000), 2. Kotyk et al. (2002), 3. Hao (1988), 4. Durieux et al. (2021), 5. Schweitzer (1999), 6. Gerrienne et al. (2004). *Basal euphyllophytes (former Trimerophytopsida). Relative lengths of time units based on Cohen et al. (2013; updated). Abbreviations: SHE, Sheinwoodian; HOM, Homerian; GOR, Gorstian; LUD, Ludfordian; Wen., Wenlock; Lud., Ludlow; Pri., Pridoli; LOC, Lochkovian; PRA, Pragian; EMS, Emsian; EIF, Eifelian; GIV, Givetian; FRA, Frasnian; FAM, Famennian.

Cooksonia, a few centimeters in height) into extensive forests with modern-size trees such as *Archaeopteris* up to 40 meters tall (Meyer-Berthaud, 2000; Gerrienne et al., 2006; Xue et al., 2018).

To unravel the timing and magnitude of this stepwise adaptive radiation, paleobotanists have sought to quantify diversity through time to discern the causes and mechanisms contributing to this pivotal moment in Earth's history. Nonetheless, the tempo and mode of this diversification remains controversial: early works (i.e., Niklas et al., 1980, 1985; Knoll et al., 1984) have emphasized on a global protracted increase of macrofossil taxonomic diversity during the Silurian–Devonian period. On the other hand, recent compilations documented more disparities in this pattern (i.e., Cascales-Miñana, 2016). These discrepancies lead to question the dynamics of diversification, whether they were mostly intrinsic (Knoll et al., 1984), such as shown in the kinetic model of Sepkoski (1978, 1979, 1984) or if they were affected and/or controlled by external factors (e.g., paleogeography, climate) (Cascales-Miñana and Meyer-Berthaud, 2015; Wellman et al., 2022a). Does the pattern obtained represent a congruent diversification and extinction of several plant lineages such as shown in the 'Evolutionary floras' model (Cleal and Cascales-Miñana, 2014) or the result of independent dynamics within each plant clade (Niklas et al., 1983)? These queries have suffered from the lack of up-to-date appropriate macrofossil-based diversity datasets with sufficient resolution.

However, it is now well-established that raw diversity patterns are inherently flawed and distorted by a wide array of biases, which may lead to spurious conclusions regarding diversity dynamics and their interpretation (Smith, 2007a; Smith and McGowan, 2011). Even though these biases have been extensively studied in other (mostly animal) groups, these biases have only been seldom identified in the plant fossil record and especially the earliest plant fossil record (Knoll et al., 1979; Wall et al., 2011). Characterization of biasing agents is especially relevant in light of the controversy over the microfossil record of spores implying a more substantial and earlier radiation than what the macrofossil record suggests (e.g., Kenrick et al., 2012; Wellman et al., 2013). This infers the question of whether the macrofossil plant record is actually adequate to describe early land plant diversification and if biological signals can be reliably extracted through its quantification. Several regional-level studies (Gutak et al., 2011; Xiong et al., 2013; Xue et al., 2018) have revealed paleogeographic heterogeneities in early land plant diversity patterns: do these represent real disparities or are they merely the product of sampling issues and/or geological incompleteness (Cascales-Miñana and Meyer-Berthaud, 2015)? The lack of proxies to test the impact of these biasing factors on diversity patterns have hampered the concrete identification of such biases for plants and if they can be corrected accordingly.

Throughout the rest of this introductory chapter, we will focus on the challenges and obstacles linked to quantifying fossil plant biodiversity through time, as well as providing an overview of previous attempts at characterizing early land plant diversity and the discrepancies and questions that emerged from it. Lastly, biases allegedly distorting our view of early land plant diversification are reviewed, and the possible ways to correct them are also presented.

I.1. Characterizing fossil plant diversity: the microfossil vs. the macrofossil record

Past plant biodiversity can be reconstructed from the microfossil record of spores, pollen, cuticles, and other microscopic fragments, and through the meso- to macrofossil record, consisting in fossils observable at the naked eye (Pardoe et al., 2021). The microfossil record, especially of spores and pollen, has the advantage of being abundant and commonly found in terrestrial- to marine sedimentary rocks (Heusser, 1978; Gray, 1985). They are produced in great quantities by their respective parent plants and concurrently possess a high preservation potential due to their sporopollenin walls, highly resistant to biodegradation, making them extremely useful tools for high-resolution biostratigraphy of continental sedimentary deposits (Steemans, 1989; Wellman and Gray, 2000; Wellman et al., 2013; Pardoe et al., 2021). Macrofossils on the other hand, despite being far scarcer, are more informative to identify the biological affinities of the parent plant with a higher amount of characters possibly being preserved (Thornill et al., 2012). This aspect is essential to reconstruct phylogenies and the evolutionary history of plants (Kenrick and Crane, 1997a, 1997b).

The abundance and continuity in the microfossil record are a considerable asset compared to the macrofossil record to quantify past biodiversity (Gray, 1985). Consequently, studies have often relied on the microfossil record for their ability to provide a high-resolution reconstruction and representation of vegetational changes (e.g., Jaramillo et al., 2006, 2010; Slater et al., 2019). This approach is extremely powerful and effective when the parent plant of spores and pollen can be reliably inferred as it is often the case for recent fossil floras e.g., in the Quaternary (Birks et al., 2016). However, as we attempt to reconstruct diversity of increasingly ancient time periods, taxonomic resolution progressively reduces, as these relationships become gradually more putative (Mander et al., 2014). It becomes particularly problematic for earliest land plants as the biological affinities of most spores morphospecies are unknown, which renders almost impossible (thus far) an accurate representation of vegetational changes through time during the Silurian–Devonian period). In addition, it is also well known that spore morphologies are often simpler and similar morphologies have been documented to be produced by different parent plants. Therefore, microfossil diversity does not necessarily equate to parent plant diversity and potentially represent a significant bias (see Cascales-Miñana et al., 2022, for further discussion). Understanding the mechanisms leading to diversity changes can only be achieved through identification of the plant groups represented. In this way, using the macrofossil record to reconstruct earliest plant diversity is a commendable approach despite the inherent problems that it engenders linked to the record’s patchiness and incompleteness.

I.2. Plant macrofossil diversity: what are we actually measuring?

Macrofossil plant diversity is measured using fossil-taxa described from individual or a combination of fossil vegetative organs (e.g., leaves, stems, bark) and/or reproductive organs (e.g., sporangia, cones) (Cascales-Miñana et al., 2013; Cleal et al., 2012; Cleal et al., 2021; Pardoe et al., 2021). Historically, since plants are rarely preserved in their entirety and since oftentimes plants are represented by very fragmented pieces, palaeobotanical nomenclature has developed into giving different taxonomic names for each separate plant organ, which may or may not belong to the same parent plant (Cleal and Thomas, 2010). Moreover, plant fossils preserved under different modes of preservation may be named differently despite belonging to the same parent plant taxon e.g., *Archaeopteris* for adpression fossils of foliage and fertile remains and *Callixylon* for anatomically-preserved stems and roots (Galtier, 1986; Tanrattana et al., 2017; Thomas and Cleal, 2020). Adpressions *sensu* Shute and Cleal (1988) i.e., a plant compressed leaving an imprint in the matrix (impression), where the original organic matter is at least partially preserved, constitute the bulk of the plant fossil record. However, a non-negligible and arguably equally important part of the plant fossil record consists in structures preserved in three dimensions displaying external morphology such as casts and molds, or permineralizations with the original anatomy of the plant preserved (Taylor et al., 2009). This idiosyncrasy of paleobotanical nomenclature constitutes another hurdle in measuring past plant diversity as it can artificially augment it. Moreover, the number of fossil-taxa for an individual plant depends on the number of organs produced by the original plant (Cleal et al., 2012). Therefore, when compiling plant diversity, it is important to remember that what is really represented is the number of fossil-taxa and not the number of whole plants.

To counter these taxonomic issues, a first alternative is using families as taxonomic unit to quantify taxonomic richness as it represents the level closest from a whole plant concept, but a certain degree of resolution is lost and the diversification and extinctions signals are blurred (Cascales-Miñana et al., 2013; Cleal et al., 2021). On the other hand, species level is generally thought of not being adequate to represent diversity due to synonyms, endemisms, and considering certain species are sometime based on very fragmentary pieces (Knoll et al., 1984; Cascales-Miñana, 2016). For early land plants, the genus level is usually regarded as the lowest taxonomic level useful for biodiversity studies that most paleobotanists will agree on (Knoll et al., 1984).

In addition to taxonomic issues, preservation topics are also prevalent. Upland vegetation is rarely preserved given that these represent erosional and not depositional environments (Cleal et al., 2012). Plant fossils are often found in former wet environments such as lakes, river deltas, and coastal settings, associated with high sedimentation rates (Gastaldo and Demko, 2011). Preservation is facilitated in the presence of anoxic-dysoxic conditions mostly present towards more stagnant waters such as swamps, lake bottoms or former meanders (Greenwood, 1991). This means that we oftentimes have to deal with plant diversity that is almost exclusively originating from humid environments not necessarily representative of all vegetation, although full conquest of terrestrial (especially dryer) settings is usually thought to not have occurred before the end of the Devonian (Wing and DiMichele, 1995; Gastaldo and Demko, 2011; Le Hir et al., 2011).

I.3. Reconstructing plant diversity in deep time: a historical perspective

Interest in quantifying biodiversity through time arose quite early in the history of paleontology with firstly Phillips (1860) producing the first Phanerozoic animal diversity curve based on the British fossil record, despite remaining descriptive and not rigorously quantified. The modern approach of measuring diversity through geological time i.e., quantification of the number of taxa in a defined time unit, and more specifically, stratigraphic intervals, did not come until Newell (1952, 1967). It is however with the 'Quantitative Revolution' (Sepkoski, 2005), notoriously initiated by Stephen Gould, Thomas Schopf, David Raup and Jack Sepkoski in the 1970s, that quantitative paleontology truly emerged. The establishment of the first global Phanerozoic animal diversity curve in Sepkoski (1981), using large compendia of stratigraphic ranges of marine invertebrate taxa radically transformed the field. The recognition of the infamous "Big Five" mass extinctions formally characterized in Raup and Sepkoski (1982) had a profound impact in paleontology - and also to a certain extent popular culture - and has undeniably oriented research towards the study of these large-scale events. This ensued in the following decades to a plethora of studies seeking to quantify diversity fluctuation through time in various clades.

In the wake of this 'Quantitative Revolution', a similar interest in characterizing plant diversity over the Phanerozoic arose with works of Andrew H. Knoll, Karl J. Niklas and Bruce H. Tiffney in the late 1970s and 1980s (Knoll et al., 1979; Niklas et al., 1980; 1983, Niklas, 1988) revealing entirely different dynamics to those of marine organisms. Nevertheless, despite this initial enthusiasm, plants have since spawned less interest notwithstanding their evident importance given their role as e.g., primary producers, niche construction, biogeochemical cycles, and thereby affected the evolutionary history of marine and terrestrial animal groups (Algeo et al., 2001; Shear and Selden, 2001; Clack, 2007; Bault et al., 2022a). A renewed interest in recent years has revived the debate over the specificities of Phanerozoic plant diversity dynamics. First of all, mass extinctions revealed in the marine fossil record often do not correspond to mass extinctions in the floral record (Fig. I.2), with only two extinction events retrieved by Cascales-Miñana and Cleal (2014) in the end–Carboniferous and in the middle–late Permian, the latter one even being contentious (Nowak et al., 2019). Secondly, the overarching trajectory of plant dynamics was quite distinct from the marine animal dynamics as shown in the "Evolutionary faunas" model of Sepkoski (1981) *vs*. the "Evolutionary floras" model by Cleal and Cascales-Miñana (2014) (Fig. I.2). In this model, the Silurian-Devonian period appeared especially critical in land plant diversification with the emergence of three different successive Evolutionary floras termed Rhyniophytic, Eophytic and Paleophytic (Fig. I.2).

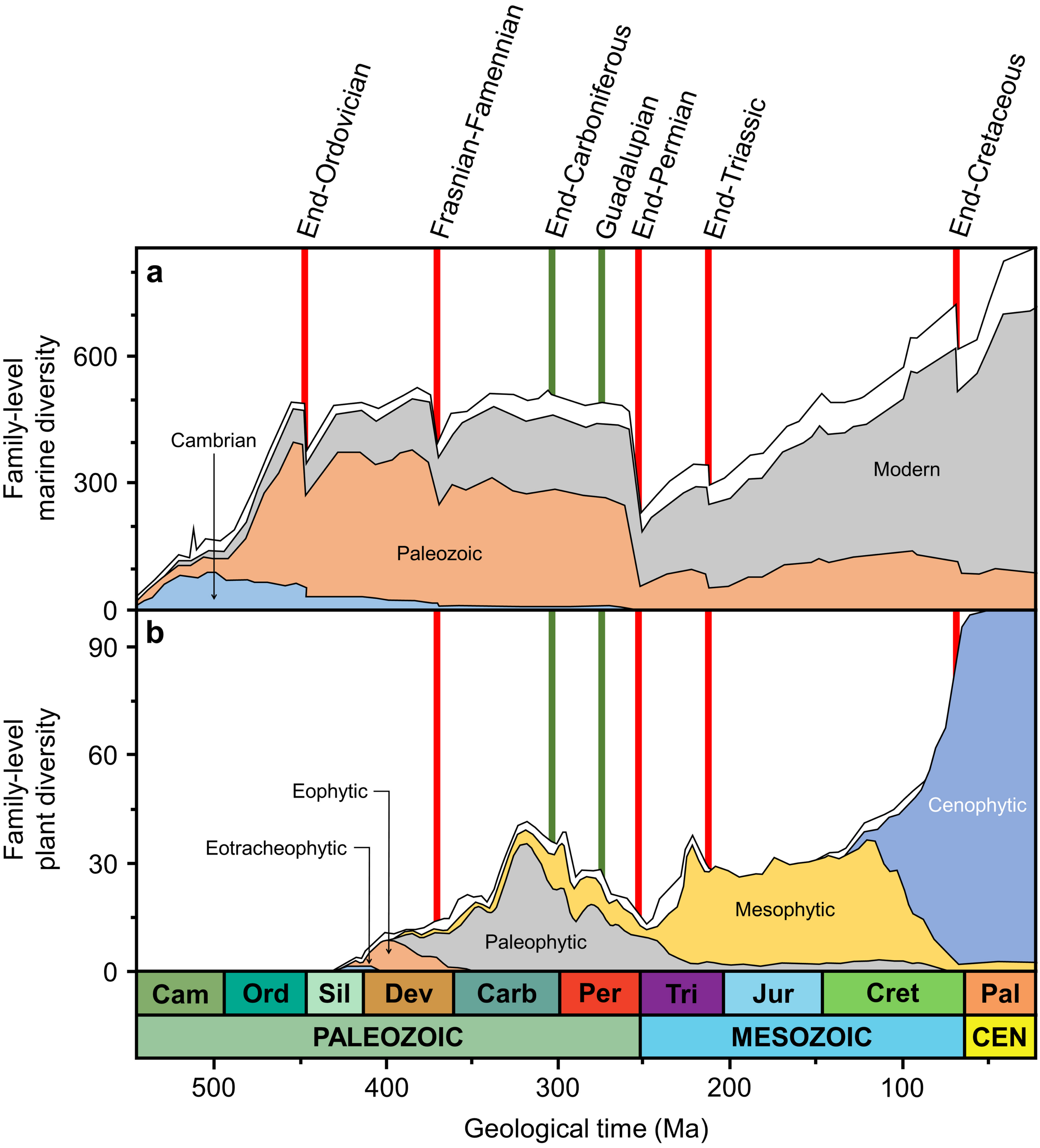

Figure I.2: Comparison of the Evolutionary faunas and evolutionary floras models. Vertical red lines indicate the 'Big Five' marine mass extinctions; vertical green lines the plant biotic crises. (a. redrawn from Sepkoski (1981); b. redrawn from Cleal and Cascales-Miñana, 2014). Extracted from Cascales-Miñana et al. (2018).

This major turnover in Paleozoic vegetation noticed in the plant macrofossil record is one of the reasons why paleobotanists have historically preferentially focused on this time period to quantify plant diversity (Knoll et al., 1984; Niklas et al., 1985; Boulter et al., 1988; Edwards and Davies, 1990, Raymond and Metz, 1995). These early works were initially based on particularly restricted datasets (Edwards and Davies, 1990), as Devonian floras had not been as intensively studied compared to, e.g., Carboniferous floras, studied since the beginning of the industrial revolution and the exploitation of coal mines (Cleal et al., 2012). Main attempts to reproduce a global early land plant macrofossil diversity curve are here summarized (Fig. I.3). These different studies have compiled diversity using unequal time frames and time bins lengths (e.g., stage or substage level) making comparison sometimes arduous. Nevertheless, a clear observation is that global-scale diversity continues to inflate since the 1980s as

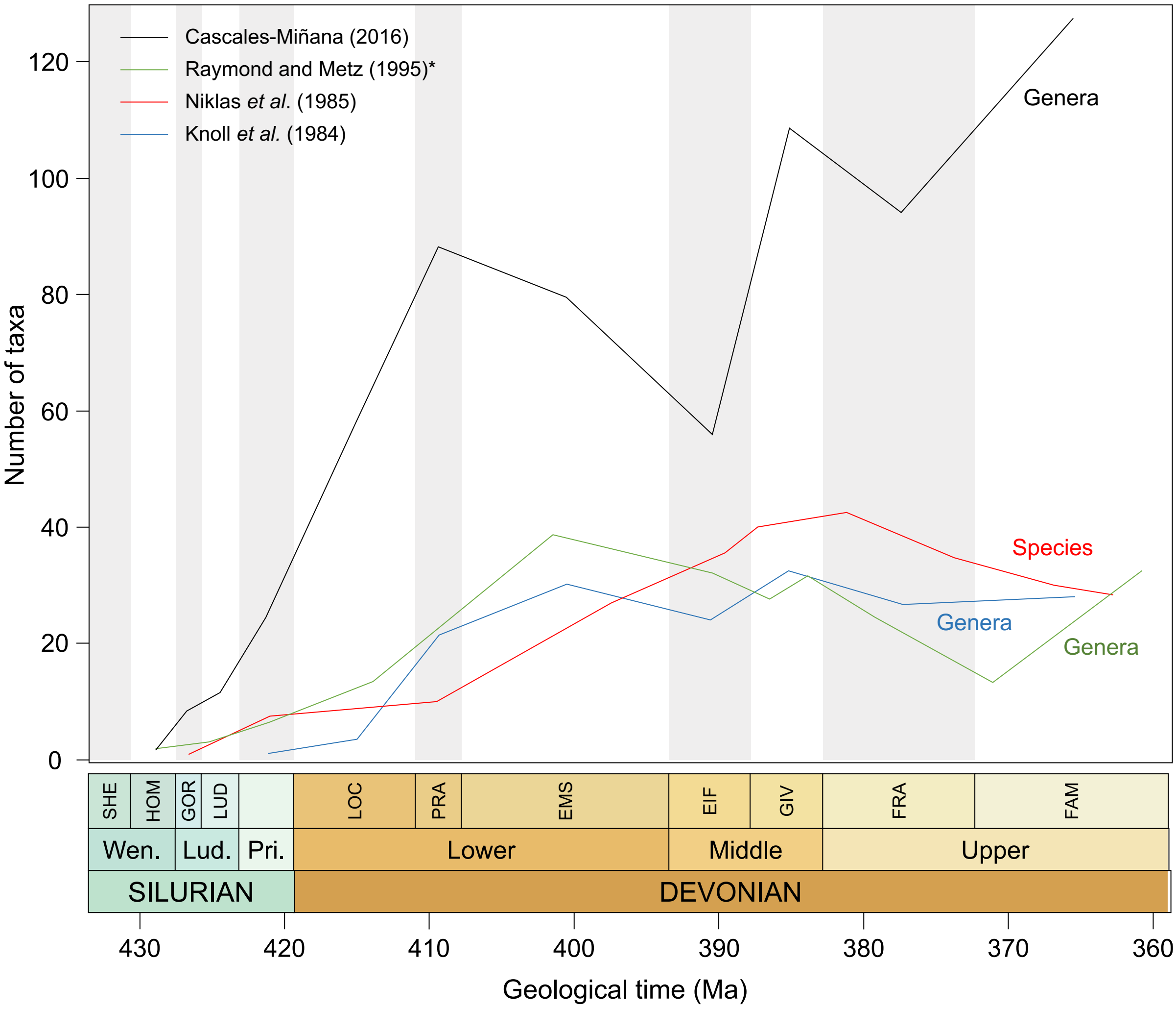

Figure I.3: Comparison between previous global Silurian–Devonian tracheophyte diversity curves. *Based on the Laurussian fossil record only. Relative lengths of time units based on Cohen et al. (2013; updated). Abbreviations same as in Fig. I.1.

more research is accomplished and sampling progresses (Fig. I.3). Consequently, the shape of the diversity curve has drastically changed over the years (Fig. I.3). Earliest studies initially showed an increase of diversity during the Silurian–Early Devonian period and then stasis or slight decrease during the Middle–Late Devonian, whilst recent compilations rather present an almost continuous rise of diversity interrupted by occasional drops.

I.4. Biases affecting reconstructed diversity

Concurrently to the success of the first diversity curves, several paleontologists such as David M. Raup began to question the reality of these patterns extracted from face-value diversity (i.e., based on the range of first and last occurrence of taxa). Raup (1972, 1976) identified a series of potential biases, mostly linked to the varying availability of fossils and effort put into describing them, that may distort diversity reconstructions, although their impact could not yet be well-assessed due to the lack of precise enough data on biasing factors. However, in a turn of event, D.M. Raup in a joint paper together with J.J. Sepkoski (Sepkoski et al., 1981), argued that a real underlying signal could be extracted from the range-based approach despite biases, and that this curve is adequate to describe diversity trajectories of Phanerozoic marine life. Critics of the 'Sepkoski curve' were then revived in the early 2000s as more adequate proxies, representative of biases allegedly corrupting the original biological, were found to correlate with diversity measures (i.e., Alroy, 2000; Alroy et al., 2001; Peters and Foote 2001, 2002; Smith 2001, 2007a, 2007b; Crampton et al. 2003; Peters 2005, Smith and McGowan 2005, 2007). These works have almost exclusively focused on the marine record, and it is only recently that such biases have begun to be identified in the terrestrial fossil record of animals, while the characterization of these biases on the paleobotanical record is still in its infancy (Smith and McGowan, 2007; Wall et al., 2009; 2011; Butler et al. 2011; Mannion et al., 2011; Fröbisch, 2008; 2013; Cascales-Miñana et al., 2013; Dunhill et al., 2014; Close et al., 2017, 2019). Beyond the taxonomic issues inherent to the paleobotanical record complicating the measure of past plant diversity studies previously mentioned, a series of biases have been qualitatively identified in the plant fossil record (Fig. I.4).

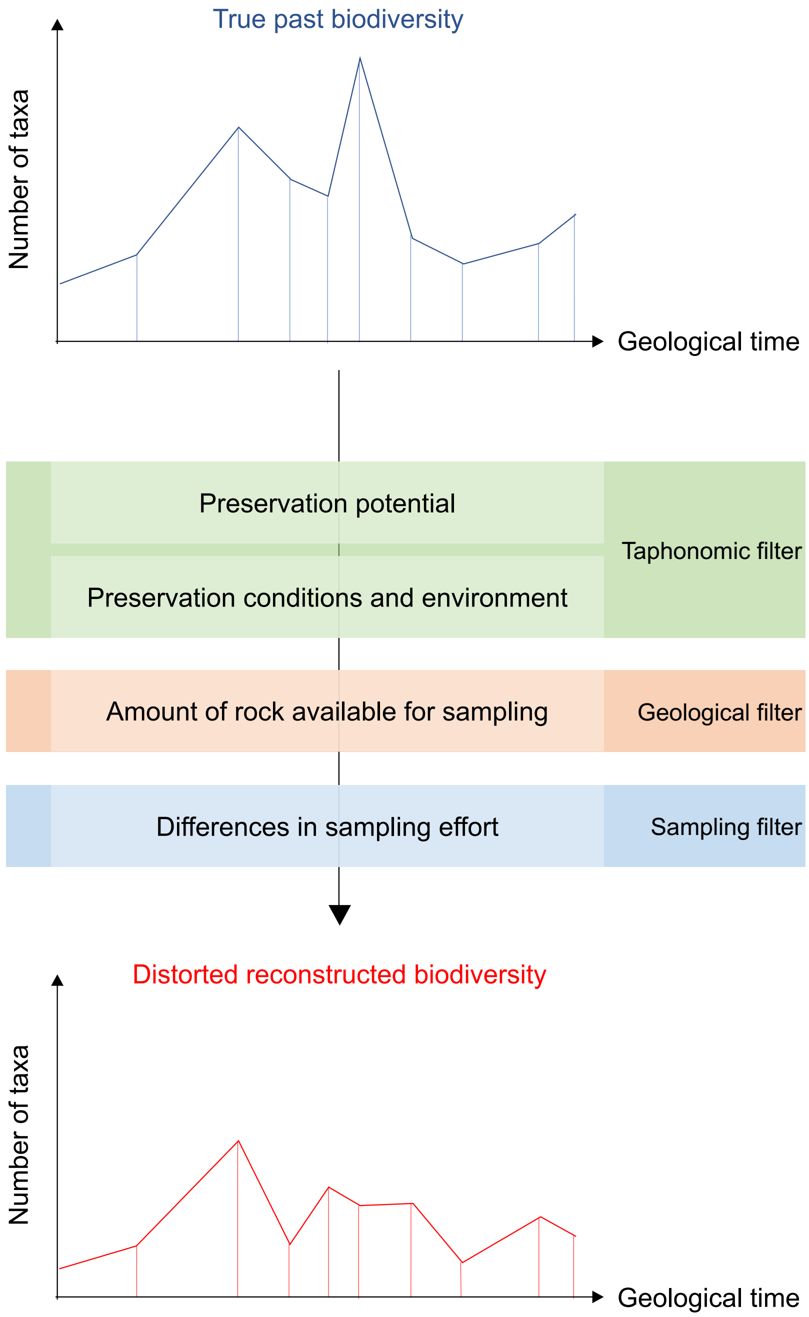

Figure I.4: Schematic flow chart showing the main biasing agents that distort our view of past biodiversity. Modified from Smith and McGowan (2011).

I.4.1. Taphonomic biases

The preservation potential of organisms highly depends on their original composition and structure of tissues through their resistance to biodegradation (Briggs, 1995,1999). Moreover, fossilization also relies on the suitability of the environment of deposition post-mortem and the diagenetic processes that follows (Fig. I.4). This entire process leads to only a tiny fraction of original living organisms being preserved in the rock record. For diversity studies, as long as the preservation potential of plants remains consistent throughout the aimed studied time interval, this factor does not lead to large-scale biases (Smith and McGowan, 2011). However, during the Silurian–Devonian period, new plant organs and tissues are developed (Fig. I.1), known to each have an intrinsic preservation potential (Gastaldo, 1988, Spicer, 1989, 1991). For instance, the production of increasingly heavily-lignified tissues such as wood, considered to be more resistant to degradation processes (Greenwood, 1991; Mustoe, 2017), may have changed the preservation potential of plants in their early history. This taphonomic bias is difficult to account for but has been previously invoked to explain the lack of plant macrofossils before the middle Silurian, when spores, more resistant to taphonomic processes, are commonly found (Strother et al., 1996; Steemans et al., 2009; Kenrick et al., 2012). In the same way, bryophytes, resolved to have appeared earlier than tracheophytes, are especially rare in the fossil record, which has been attributed to a lower preservation potential (Gray, 1985; Edwards et al., 1998; Wellman, 2010; Puttick et al., 2018; Morris et al., 2018a). Nevertheless, recent reinvestigations of bryophyte taphonomy in Tomescu et al. (2018) have rather supported the existence of a ‘human’ bias in which paleobotanists are not trained to recognize these small-sized organisms. This bias could potentially equally affect earliest tracheophytic plants, closer in architecture and size to bryophytes.

Occasionally, tissues or features usually recalcitrant to taphonomic processes may be preserved with a high degree of fidelity in what is termed *Lagerstätten* (Locatelli, 2014). The occurrence of *Lagerstätten* have been documented to affect diversity reconstructions, as it can drastically increase observed diversity in time intervals where they occur (Raup, 1972). Nevertheless, this bias seems to impact more strenuously certain animal clades rather than plants, especially if their fossil record is extremely patchy and the taxonomic identification heavily relies on complete specimens and soft-body preservations (Butler et al., 2009; 2013; Brocklehurst et al., 2012; Dean et al., 2016; Flannery Sutherland et al., 2019; de Celis, 2021). Besides, only two plant *Lagerstätten* are recorded in the Silurian–Devonian period, most famously the Rhynie chert which should not fundamentally alter diversity measures (Morris et al., 2018b; Garwood et al. 2020).

I.4.2. Geological biases

Raup (1972) highly suspected that recovered fossil diversity is affected or controlled by geological incompleteness. Typically, this effect is recognized when measures reflecting the sedimentary rock record (e.g., outcrop area, rock volume) follow the same trajectories as diversity through time (Smith and McGowan, 2007; Smith et al., 2012). The pioneering work of Knoll et al. (1979), firstly outlined the relationship tying the paleobotanical and geological record, recovering a substantial correlation between plant diversity measures and terrestrial rock volume in North America. Based on the premise that most plant fossils are collected from continental deposits, an insufficient terrestrial rock record could theoretically lead to less plant diversity being recovered. The lack of non-marine sedimentary deposits prior to the Devonian period may also explain the 40 Myr gap between the micro- and macrofossil record, but has never been quantitatively assessed (Kenrick and Crane 1997a, 1997b; Kenrick et al., 2012; Morris et al., 2018a). Few studies following Knoll et al. (1979) have further characterized this bias on plant fossil diversity reconstructions. Wall et al. (2011) studied this impact on the Phanerozoic terrestrial fossil record and detected a relationship with outcrop area of terrestrial deposits. Likewise, Cascales-Miñana et al. (2013), recovered a significant correlation between vascular plant diversity and total volume of sedimentary rock over geological time. However, all these studies have relied on outdated rock volume and outcrop area estimations with extremely poor resolution (series or period level). The impact of the heterogeneity of the geological record on short-term plant diversity variations (e.g., at stage level) remains scanty.

I.4.3. Sampling biases

Differences in sampling effort is a major concern in quantitative paleontology given that stratigraphic intervals have not being evenly sampled (Fig. I.3). This has been highlighted over the years as one of the most important biases affecting reconstructed diversity in deep time (Fig. I.3, Raup, 1972, 1976; Alroy, 2000, 2010a, 2000b; Smith and McGowan, 2011). Intensively sampled time intervals with true low biological richness may appear richer at face-value diversity than a poorly sampled but in reality, truly diverse intervals. Moreover, sampling effort may be geographically heterogenous in addition to being temporally heterogeneous (Close et al., 2019, 2020a, 2000b). For societal and historical reasons, paleontological research has been concentrated in North America and (Western) Europe which skews our perspective towards that of those regions, and ‘global’ diversity curves may not truly reflect global diversity (Raja et al., 2022). Silurian–Devonian paleobotany is no exception even though this bias tends to diminish with the full-scale description of Chinese floras (Hao and Xue, 2013; Xue et al., 2018) and furthermore with recent works beginning to fill the gap in former Gondwana (e.g., Prestianni et al., 2012a; Meyer-Berthaud et al., 2021; Gess and Prestianni, 2021), considered by many as the cradle of early land plants (Gerrienne et al., 2010, 2016; Decombeix et al., 2019; Meyer-Berthaud et al., 2021).

I.5. Sampling-corrected approaches

Following the increasing evidence that large-scale biases may distort raw diversity patterns, different techniques have been developed to tentatively mitigate or remove biasing signals. Paleontologists have firstly attempted to overcome sampling gaps in the fossil record using the range-through method (i.e., based on stratigraphic ranges of taxa) such as in Sepkoski (1981). Other measures of diversity were subsequently developed, initially to address the issue of unequal length of stratigraphic time intervals as there are more opportunities to sample in longer time intervals, artificially increasing diversity (Cooper et al., 2004). The aim was to reduce or remove the weight of single-interval taxa, more likely to be the result of sampling biases, e.g., *Lagerstätten*, and of larger time bins (Van Valen, 1984; Foote, 2000a, 2000b). This problem was also recently addressed through the development of the uniform time bin approach to remove the effect of time discretization (i.e., segmentation into biozones) (Gibert and Escarguel, 2017).

However, most other methods have focused on correcting for sampling and geological biases. The residual diversity method alternatively called the residual approach, developed by Smith and McGowan (2007) and refined by Lloyd (2012), retrieves residual diversity after subtraction of diversity predicted from a model, itself based on a proxy that theoretically represent sampling signals. This method has been previously used on early land plants focusing on the zosterophyll record (Cascales-Miñana and Meyer-Berthaud, 2014, 2015). Nonetheless, the most praised method currently is coverage-based rarefaction, also commonly known as shareholder quorum subsampling (SQS) developed by John Alroy (Alroy et al., 2008; Alroy, 2010a, 2010b, 2013). This method differs from a classical size-based rarefaction in which diversity is calculated through down-sampling to an arbitrary sample size, whereas SQS down-samples until it reaches a 'quorum' level, representing a certain sum proportion of these taxa relative occurrence frequency (Bault et al., 2021). This technique has been demonstrated to be the most accurate way to remove the effect of uneven sampling (Close et al., 2018). Nonetheless, this approach requires occurrence-based data, vastly more time consuming to compile than the classical stratigraphic range data.

The emergence of the Paleobiology Database (PBDB) recording occurrences of fossil taxa through a worldwide collaborative work has made possible the 'Alroy' Phanerozoic marine diversity curve (Alroy et al., 2008; Alroy, 2010a). While arguably much effort has been put into filling the PBDB for selected groups of terrestrial and marine animals, the PBDB record of plant fossils, and especially of Silurian–Devonian plants, remains largely incomplete, not taxonomically up to date, with many occurences being imprecisely dated. Additionally, a large percentage consists of only North American and Western European records, hindering the possibility to retrieve a truly global curve (Raja et al., 2022). This is one of the reasons why coverage-based rarefaction has almost never been utilized to correct plant taxonomic richness measures. To implement both classical methods and new occurrence-based analyses, new up to date datasets are required to extract the most accurate diversity patterns.

I.6. Objectives and thesis structure

The aim of this thesis is to characterize early temporal and spatial dynamics of terrestrial macroflora from the appearance of land plants (i.e. embryophytes) to the development of well-established forests (i.e. Silurian to Late Devonian, ~430–360 Ma), to substantially improve our understanding of tempo and mode of early land plant diversification and to identify its drivers. Sampling and geological biases on the early plant macrofossil record have thus far only mostly been evaluated qualitatively but not quantitatively. These biasing agents will be further explored, and through the application of sampling-standardized methods, attempt to obtain the most accurate depiction of early land plant radiation. This thesis is organized as follows:

Chapter II (Capel et al., 2021) is focused on the dynamics of early land plants at the global scale. The 'Evolutionary Flora' model was revisited using a newly compiled genus-level diversity dataset, focusing on the Silurian–earliest Carboniferous period to provide a more detailed picture of turnover in early vegetation and underpin the underlying structure explaining the observed raw diversity pattern.

Chapter III addresses the issue of sampling and geological biases on the macrofossil record. Firstly, in Capel et al. (2022a), global dynamics are further characterized for tracheophytes as a whole, and within major clades, through a series of diversity metrics and evolutionary rates. Sampling-corrected patterns were obtained via the residual diversity method to determine to what extent the observed fluctuations are artifactual. The role of intrinsic and external factors on plant dynamics were also assessed. The recovered pattern was also confronted to a series of abiotic factors potentially influencing biological signals. Secondly, Chapter III expands on the issue of sampling and geological issues by testing the hypothesis of the non-marine rock record controlling the observed diversity pattern. Focusing on North America, a new occurrence-based dataset was compiled, and various sampling and geological proxies extracted from the Macrostrat database were correlated to diversity measures. Finally, the efficiency of coverage-based rarefaction (SQS) to recover biases-free plant diversity patterns was also investigated.

Chapter IV focuses on spatial heterogeneities in early vegetation diversification. Diachronicity in land plant radiation was firstly investigated through a regional dissection of the global diversity curve. The spatial differentiation of the vegetation was then additionally characterized through the identification of phytochoria across the Silurian–Devonian period. Their paleogeographic distribution and degree of differentiation was then subjected to discussion regarding the impact of climate and geographic barriers on early land plant distribution and dispersion.

The above-mentioned chapters in this thesis outlined the necessity of obtaining accurate and reliable data for reconstructing past biodiversity dynamics. Finally, Chapter V (Capel et al., 2022b) provides a revision of an historical Early Devonian plant fossil assemblage from northern France that was achieved to obtain refined age constraints and taxonomic identifications, destined for future analyses. The paleogeographical implications of this assemblage were also discussed.

Chapter II: Silurian–Devonian evolutionary floras

This chapter is a slightly modified version of an article published in *Palaeogeography, Palaeoclimatology, Palaeoecology* called “**A factor analysis approach to modelling the early diversification of terrestrial vegetation**” (https://doi.org/10.1016/j.palaeo.2020.110170). The published version of this article can be found in appendix 1.

A factor analysis approach to modelling the early diversification of terrestrial vegetation

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Abstract

Data from a new comprehensive macrofossil-based compilation of early plant genera are analyzed via a Q-mode factor analysis. This compilation ranges from the Silurian to the earliest Carboniferous and illustrates the key vegetation changes that took place during the configuration of early terrestrial ecosystems. Results reveal that four factors can be used to explain more than 90% of the variance in the data. These factors are interpreted as the major phases of the early land plant evolution: a first Eotracheophytic flora (Silurian–Lochkovian) dominated by basal eutracheophytes and rhyniophytoids, an early Eophytic Flora (Early Devonian) dominated by zosterophylls, a transitional late Eophytic Flora (Middle Devonian–earliest Carboniferous) dominated by lycopsids and cladoxylopsids, and finally, the earliest phase of the Palaeophytic Flora (Late Devonian–earliest Carboniferous) dominated by the first seed plants. These floras present different but complementary diversity patterns, which help us to understand the overall trajectory of changes in plant diversity. Results further show how the maximum peaks of diversity appear linked to the rise of each new flora but, interestingly, these diversifications are not associated with any exponential declines of the previously dominant one. This new four-phase diversification model reflects the early steps of Earth's greening.

Keywords: Devonian, Early land plants, Factor analysis, Plant macrofossil, Plant radiation, Terrestrialization

II.1. Introduction

The terrestrialization of plants (embryophytes; Janvier, 2010; Gerrienne et al., 2016; Servais et al., 2019) during Ordovician–Devonian times altered early land ecosystems, instigating the development of soils, and causing major $p\mathrm{CO}_2$ fluctuations and changes in geochemical cycles (Algeo and Scheckler, 1998; Beerling, 2007; Kenrick et al., 2012; Morris et al., 2015; Xue et al., 2015a, 2016; Qie et al., 2019). These changes were triggered by key diversification events among plants linked to the appearance of evolutionary innovations, such as vascular tissues, leaves, seeds and secondary growth (i.e., wood), which together culminated in the establishing of the earliest forests (Decombeix et al., 2011; Kenrick et al., 2012; Xue et al., 2015a, 2016, 2018; Cascales-Miñana et al., 2019a; Wang et al., 2019; Stein et al., 2020). Since the 1980s, various researchers have focused their attention on documenting the diversity pattern of this early vegetation (e.g., Banks, 1980; Knoll et al., 1984; Edwards and Davies, 1990; Raymond and Metz, 1995; Meyer-Berthaud et al., 2010; Stein et al., 2012; Cascales-Miñana 2016; Xue et al., 2016; Wang et al., 2019). This pattern, essential to understand the development of the early land biosphere, is characterized by a series of key diversity fluctuations. Such fluctuations range from the Ordovician–Silurian appearance of small plants, such as rhyniophytoids (many of them putative vascular plants, i.e., tracheophytes; Steemans et al., 2012; Gerrienne et al., 2016; Salamon et al., 2018), the earliest zosterophylls and lycopsids (Gensel and Berry, 2001; Kotyk et al., 2002), to the Early Devonian (Pragian) explosion of early leafy plants (i.e., euphyllophytes; Tomescu, 2009; Hao and Xue, 2013; Bickner and Tomescu, 2019), followed by the rise of the first forests and early seed plants in the Middle and Late Devonian, respectively (Decombeix et al., 2011; Xue et al. 2015a, 2016; Stein et al., 2020). However, since many evolutionary innovations occurred during this time, the documentation of the early dynamics of plant diversity remains controversial.

The global trajectory of Phanerozoic vegetation history can be interpreted as a series of major evolutionary phases; the so-called Evolutionary Floras (see Cleal and Cascales-Miñana, 2014, and references therein for details). This model, which confirmed the major floral subdivisions previously suggested by Gothan (1912); (see also Niklas et al., 1983, 1985; Edwards and Selden, 1992; Gray, 1993), is homologous to the famous Sepkoski's (1981) Evolutionary Faunas (Cascales- Miñana et al., 2018, fig. 1). Importantly, the Cleal and Cascales-Miñana’s (2014) Evolutionary Floras reveal that Silurian–Devonian land plant diversification is expressed as at least three different great floras, termed Eotracheophytic, Eophytic and Palaeophytic (Servais et al., 2019, fig. 1B). This suggests that, beyond the known problems of sampling and geological bias that of course obscure raw diversity patterns, there is an underlying structure in the observed diversity data of early floras, which deserves further investigation. This is the aim of the present paper.

II.2. Data

This study is based on a new, comprehensive macrofossil-based compilation of Silurian–lowermost Carboniferous (Tournaisian) fossil-genera. Raw data were collected from a variety of sources. Initially, we used review papers that listed plant fossil diversity for specific time intervals, such as Wellman et al. (2013) for the Silurian, or a specific geographic location, such as Xiong et al. (2013), or more recently Xue et al. (2018), for South China. Special mention should be made of the exquisite monographic study of the Early Devonian fossil record undertaken by Barrett (2016). Subsequently, plant fossil data were extracted from the Paleobiology Database via Fossilworks (http://fossilworks.org/) which were cross-checked against the primary references and, when possible, more recent literature. Lastly, numerous taxa were added from the primary literature, particularly recently described genera such as *Lilingostrobus*, *Rinistachya*, *Kossoviella*, *Guangdedendron*, *Qianshouia* or *Keraphyton* (Gerrienne et al., 2018; Prestianni and Gess, 2018; Orlova et al., 2019; Wang et al., 2019; Huang et al., 2020; Champreux et al., 2020).

To assess the maximum genus-level diversity, three types of data were considered. First, well-defined genera were listed that contained well-defined species (e.g., *Cooksonia pertoni*), and certain species in open nomenclature (e.g., *Cooksonia* cf. *pertoni*). Secondly, genera recorded with a ‘cf.’ were listed to bring together all species resembling such genera (e.g., cf. *Cooksonia hemisphaerica*). Lastly, genera recorded with an ‘aff.’ were listed to include taxa that have an affinity to that genus but whose assignment is still ambiguous (e.g., aff. *Zosterophyllum*). Overall, “artificial” genera (e.g., *Taeniocrada*) or synonyms of other taxa already listed were omitted. Likewise, some entries were also filtered to

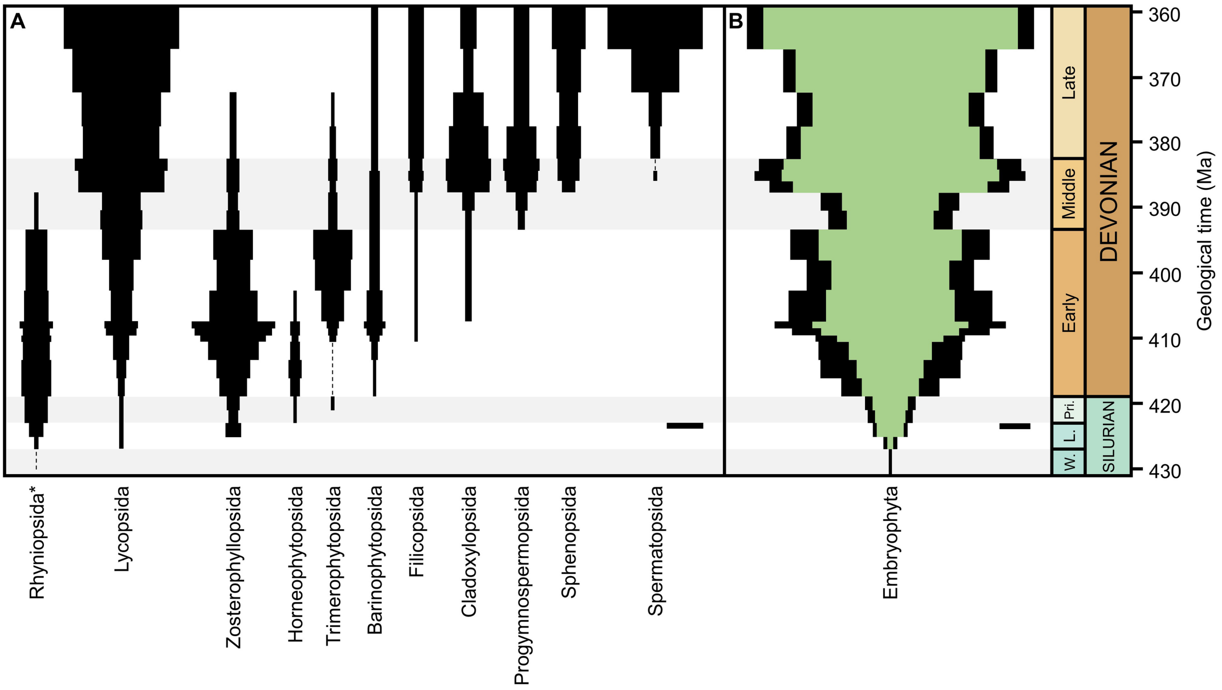

Figure II.1: Spindle diagrams showing the main diversity variations within plant classes (A) and the total shape of plant diversity (B) of the Silurian–Devonian time interval. Green colour highlights the total diversity pattern from well-established classes only (B). The width of each diagram indicates the number of fossil genera. The spindle diagrams undoubtedly can contain errors especially due to taxa with controversial affinities. Relative lengths of time units based on Cohen et al. (2013; updated). Abbreviations: W., Wenlock; L., Ludlow; Pri., Pridoli. *Note that Rhyniopsida includes herein current paratracheophytes and rhyniophytoids only. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

minimize an overlap of fossil-taxa for different plant parts (e.g., *Callixylon*/*Archaeopteris* or *Calamophyton*/*Duisbergia*; Meyer-Berthaud et al., 2000; Giesen and Berry, 2013) or different phases of life cycle (e.g., gametophytes). In total, more than 500 plant macrofossil genera were included, which provides a robust view of the major changes that took place during land plant diversification (Fig. II.1).

The raw dataset was codified at stage and sub-stage level according to the literature and following the International Chronostratigraphic Chart 2019 (Cohen et al., 2013, updated). Twenty-five time units with an average resolution of 3.4 Myr were used. Each entry included the name and systematic affinity of the genus, its first and last stratigraphic occurrences, and the sampled localities on which the data were based. Raw data are available in Tables II.S1-II.S2. See also Text II.S1 for full referencing.

II.3. Methods

II.3.1. Factor analysis

We ran a CABFAC version of the Q-mode factor analysis on a data matrix containing the number of plant macrofossil genera occurring in each stratigraphic interval, grouped according to suprageneric taxonomic categories as defined below. The analysis was made using the PAST software package version 2.17 (Hammer et al., 2001). This method, widely used to analyse many different fossil-based datasets (e. g., Bottjer and Jablonski, 1988; Erwin, 1990; Sallan and Coates, 2010; Figueirido et al., 2012; Cleal and Cascales-Miñana, 2014), recognises different factors (orthogonal eigenvectors), each of which has associated eigenvalues (factor loadings) for each stratigraphical interval and the percentage of the total variance explained by that factor. Each factor also has a factor score for each plant group, which reflects the importance of that group on the factor. Following standard procedures, factor results were then rotated with a procedure known as Kaiser's (1958) Varimax rotation. The purpose of the rotation is to enhance the discrimination of the variables into the resulting factors, which will therefore represent more accurately the distinct associations of plant groups by reducing the influence of plant groups that are not typically correlated with this association on raw data. Each factor ultimately represents a proportion of the total genus-level diversity curve of each suprageneric group (Sepkoski, 1981; Cleal and Cascales-Miñana, 2014). From this, we extracted the patterns of association among the main early plant groups that explain the whole diversity pattern of Silurian–Devonian fossil floras.

II.3.2. Assignment of taxa to categories

To implement the factor analysis, taxa must be assigned to categories. As in previous models (e.g., Sepkoski, 1981), taxa were firstly grouped in taxonomic classes (Fig. II.1A). Subsequently, taxa whose class attribution was controversial or undetermined (~25% of the dataset) were assigned to groups based on evolutionary and/or morphological criteria. The Rhyniopsida required special attention. Taxa traditionally assigned to this class currently cover many different plant lineages, including paratracheophytes (i.e., former Rhyniaceae; Gerrienne et al., 2006) and basal eutracheophytes (e.g., *Cooksonia*; Kenrick and Crane, 1997a; Crane et al., 2004; Gerrienne et al., 2016). The group also includes rhyniophyte-like plants or rhyniophytoids (e.g., *Uskiella* or *Electorotheca*; Morris et al., 2018), i.e., plants similar to tracheophytes but lacking evidence of vascular tissue, or plants of unknown affinities (Steemans et al., 2012). Other categories used for data analysis include cryptophytes (i.e., basal embryophytes; Morris et al., 2018), protracheophytes (i.e., *Aglaophyton*/*Teruelia*; Kenrick and Crane, 1997a; Cascales-Miñana and Gerrienne, 2017; Cascales-Miñana et al., 2019a) and stenokoleales (Momont et al., 2016a; Toledo et al., 2018). *Incertae sedis* taxa (~16% of dataset) were grouped into two categories given that many of these plants presented euphyllophyte affinities. Basal euphyllophytes (i.e., formerly trimerophytes; Tomescu, 2009; Gensel, 2018) were treated like a single group. In total, 18 categories integrating the whole taxonomic and morphological diversity of early land plants were used for the data analysis (see Table II.1).

Table II.1: List of Silurian-Devonian plant groups considered in this study.

1.	Barinophytopsida	7.	Filicopsida	13.	Protracheophyta
2.	Basal euphyllophytes	8.	Horneophytopsida	14.	Rhyniophytoids
3.	Basal eutracheophytes	9.	Incertae sedis	15.	Spermatopsida
4.	Cladoxylopsida	10.	Lycopsida	16.	Sphenopsida
5.	Cryptophyta	11.	Paratracheophyta	17.	Stenokoleales
6.	Euphyllophyta inc. sed.	12.	Progymnospermopsida	18.	Zosterophyllopsida

II.4. Results

Fig. II.1A shows the distribution of genus-level diversity among the main classes of Silurian – Devonian land plants. From this, we see that each class seems to have its own pattern of diversity change, although some similarities are noteworthy. For instance, major Early Devonian groups such as rhyniopsids and zosterophyllopsids show a diversification in the mid-Early Devonian followed by a significant depletion at Early–Middle Devonian boundary. We also see a second diversification in the Middle Devonian among the lycopsids, cladoxylopsids and progymnosperms (Fig. II.1A). A Late Devonian diversification of seed plants coinciding with a sustained increase of lycopsids is also noted (Fig. II.1A). In the Silurian–Devonian fossil record, many taxa are class-level *incertae sedis* so Fig. II.1A does not include all plant diversity. However, this seems to be not so critical given that the general pattern of diversification and decay of the well-defined classes captures most of the total pattern of plant taxonomic diversity (Fig. II.1B). This pattern is characterized by a gradual increase from the Ludlow, a

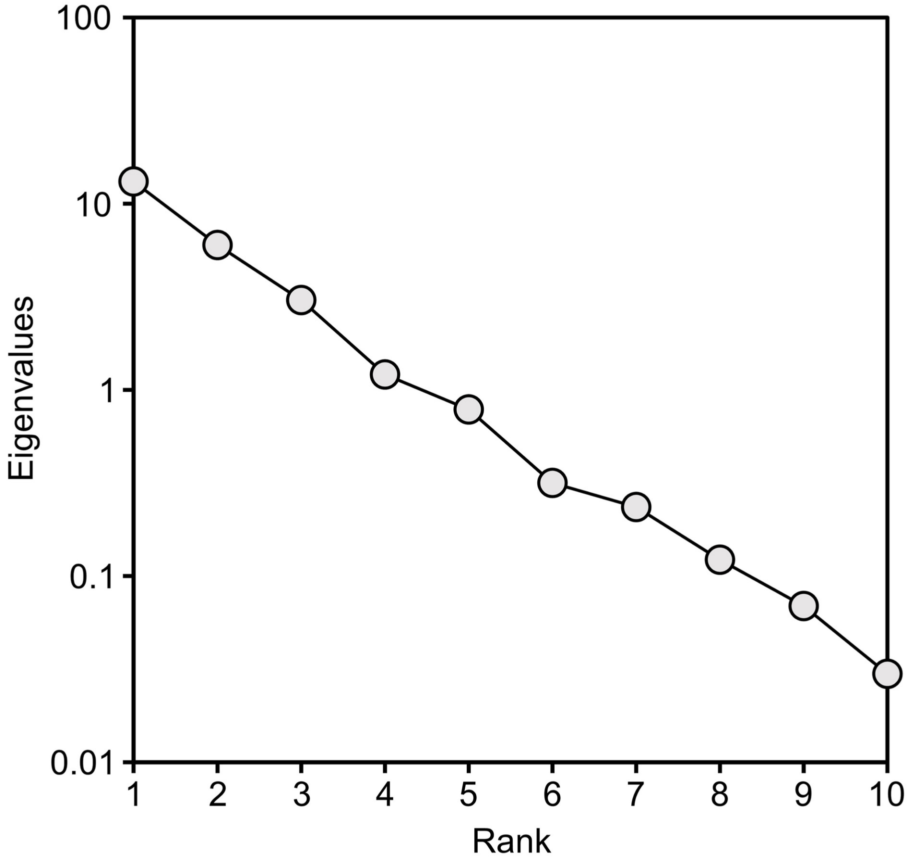

Figure II.2: Scree graph showing eigenvalues from a Q-mode factor analysis of plant genera plotted logarithmically against their ranks. See Methods for details.

great diversification in the mid-Early Devonian, a sudden decrease in the Early–Middle Devonian transition, an important pulse of diversification in the late Middle Devonian, a moderate reduction of diversity in the earliest Late Devonian, and finally, a pronounced and sustained increase towards the

Table II.2: Variance proportion explained by the first ten eigenvectors from a Q-mode factor analysis run through the macrofossil diversity of plant genera from the mid-Silurian to the lowermost Carboniferous. See Methods for details.

Eigenvector	% Variance
1	52.69
2	23.96
3	12.13
4	4.83
5	3.14
6	1.27
7	0.94
8	0.49
9	0.28
10	0.12

Carboniferous (Fig. II.1B).

Sepkoski (1981) chose a solution of three factors that explained c. 91% of the variance of marine faunal diversity. This was based on a "scree test" (see Sepkoski, 1981, fig. 2 for details), where the eigenvalues represented by each successive factor are plotted logarithmically. If there is an abrupt break in the slope of the resulting line, this is used to indicate the number of factors that should be recognised. We applied a similar approach with our data (Fig. II.2), but no break in the slope was observed. A similar result was obtained by Cleal and Cascales-Miñana (2014), who therefore used instead the Kaiser Rule, in which the number of factors is decided based on how many are needed to account for 90% of the total variance of data. In the present study, using this guideline, the first four generated factors were used as the basis of the model to explain the Silurian–Devonian plant diversity patterns (see Table II.2). The robustness of the model is supported by the fact that each factor is taxonomically and stratigraphically

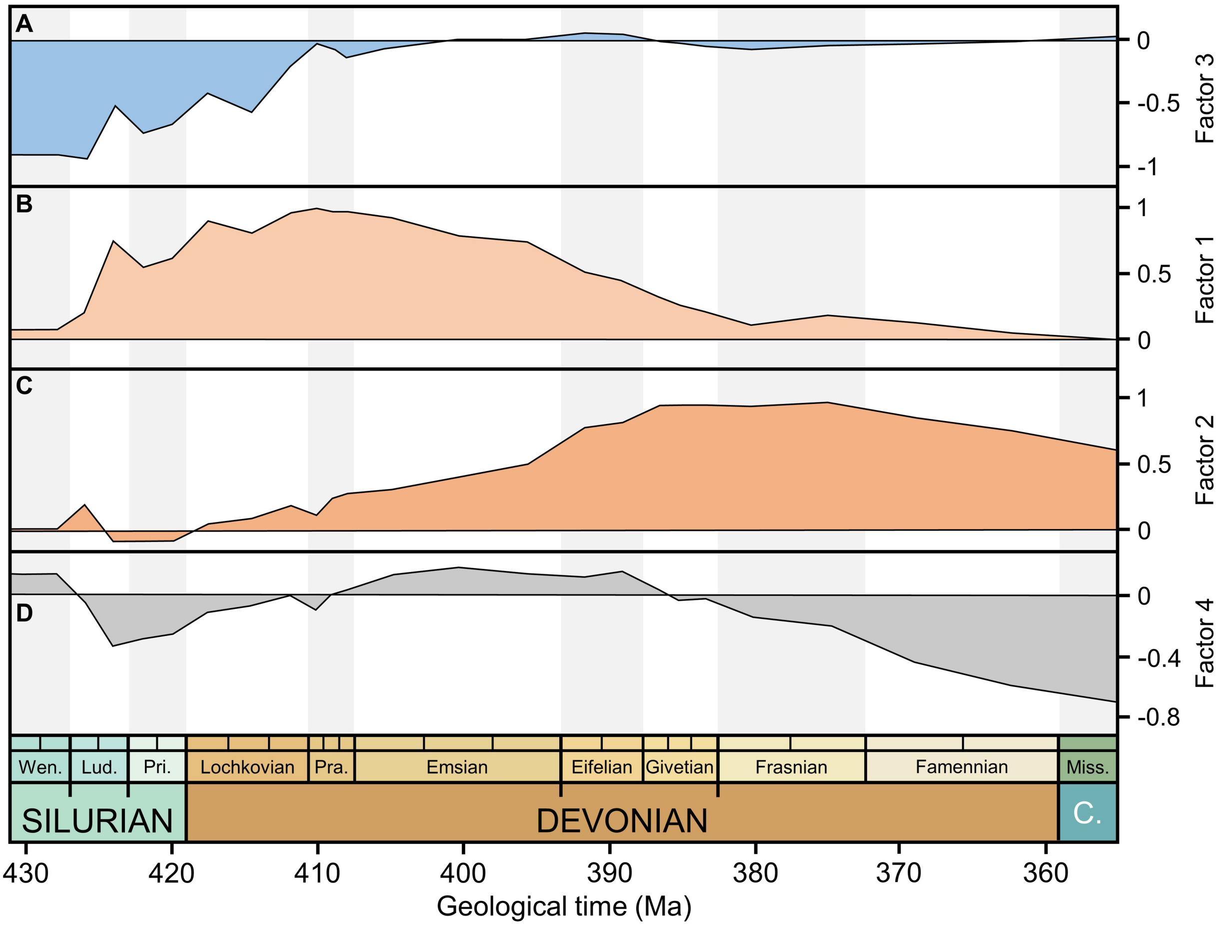

Figure II.3: Loadings of successive time intervals on rotated factors from a four-factor Q-mode analysis of plant genera plotted against absolute time. Factors represented in stratigraphical order. Relative lengths of used time units based on Cohen et al. (2013; updated). See Methods for details. Abbreviations: Wen., Wenlock; Lud., Ludlow; Pri., Pridoli; Pra., Pragian; Miss., Mississippian; C., Carboniferous.

coherent, with clear temporal trends (compare comments by Flessa and Imbrie, 1975 on a faunal model), and thus seems to be reflecting the overall trajectory of Silurian–Devonian vegetation history (see below). The factor analysis was implemented twice, with and without *Incertae sedis* taxa, and these produced indistinguishable results.

These four rotated factors are interpreted as reflecting the major evolutionary phases of the diversification of early terrestrial floras. The floral composition of each factor is summarized in Table II.3. Fig. II.3 illustrates the loadings of each factor for the successive time intervals, from which the genus-level diversities represented by each factor/flora have been calculated. This was done for each stratigraphical interval by squaring each of its four loading values and multiplying them by the total diversity for that interval (Fig. II.4). The resulting four-factor model of early land plant diversification (Figs. II.3-II.4) may be summarized (in stratigraphic order) as follows.

Table II.3. Scores of the main plant groups on the four rotated factors. The floral composition is given in four groups: scores ≥ 2 (factors 1-2) or -2 (factors 3-4); scores ≥ 1 (factors 1-2) or -1 (factors 3-4); scores ≥ 0.5 (factors 1-2) or -0.5 (factors 3-4); scores ≥ 0.2 (factors 1-2) or -0.2 (factors 3-4).

Factor 1	Factor 2	Factor 3	Factor 4
Zosterophyllopsida (3.08)	Lycopsida (3.40)	Basal eutracheophytes (-4.07)	Spermatopsida (-3.17)
Rhyniophytoids (1.77)	Cladoxylopsida (1.30)		
Basal euphyllophytes (0.56)	Progymnospermopsida (0.98) Sphenopsida (0.65) Filicopsida (0.50)	Rhyniophytoids (-0.80)	Lycopsida (-0.74)
Horneophytopsida (0.43) Barinophytopsida (0.42) Lycopsida (0.21) Paratracheophyta (0.20)	Spermatopsida (0.48) Basal euphyllophytes (0.44) Barinophytopsida (0.34)	Lycopsida (-0.33)	Sphenopsida (-0.48) Filicopsida (-0.34)

II.4.1. Factor 3 (Silurian-earliest Devonian)

This factor is dominated by basal eutracheophytes and rhyniophytoids, with other minor elements including basal lycopsids (Table II.3). This factor represents the Eotracheophytic flora (the Rhyniophytic flora *sensu* Cleal and Cascales-Miñana, 2014), and is compared to the previously described “Rhyniophytic Phase” of plant evolution (Edwards and Selden, 1992) and Gray’s (1993) “Eotracheophytic Flora”. The Eotracheophytic flora reflects the initial pulse of plant diversity and the main growth of taxonomic richness from the mid-Silurian to the earliest Devonian, which reached its maximum during the mid-Lochkovian (Fig. II.4).

II.4.2. Factor 1 (Early Devonian)

This factor is dominated by zosterophyllopsids and rhyniophytoids, with other minor elements including horneophytopsids and paratracheophytes (Table II.3). Interestingly, this factor also sees the early phase of the development of euphyllophyte plants. This factor represents the early phases of Cleal and Cascales-Miñana's (2014) Eophytic flora. This flora reaches its maximum diversity peak at the end-Pragian and represents the main component of Early Devonian plant diversity. After reaching a second peak at the end of the early Devonian, this early Eophytic Flora undergoes a progressive decline until the Frasnian–Famennian boundary (Fig. II.4).

II.4.3. Factor 2 (Middle Devonian-earliest Carboniferous)

This factor is dominated by lycopsids and cladoxylopsids, together with a diverse range of other groups (Table II.3). Significantly, the progymnosperms, sphenopsids and filicopsids appear in this flora. This factor corresponds to a late phase of the Eophytic flora. After an initial diversification towards the end-Early Devonian, this flora shows an explosive diversification during the Middle Devonian with a maximum diversity peak at the Givetian. These late Eophytic floras slowly decline during the Late Devonian (Fig. II.4). An overall diversity peak in the late Famennian is also observed (Fig. II.4).

II.4.4. Factor 4 (Late Devonian-earliest Carboniferous)

This factor is clearly dominated by spermatopsids (Table II.3), mainly early seed ferns such as Calamopityales and Lyginopteridales (Wang and Liu, 2015), together with several groups including lycopsids and filicopsids (Table II.3). This factor corresponds to the earliest phase of Cleal and Cascales-Miñana's (2014) Palaeophytic flora. This flora started an exponential diversification from the

Frasnian/Famennian boundary (Fig. II.4) and rapidly became dominant during the Carboniferous (Servais et al., 2019, fig. 1B).

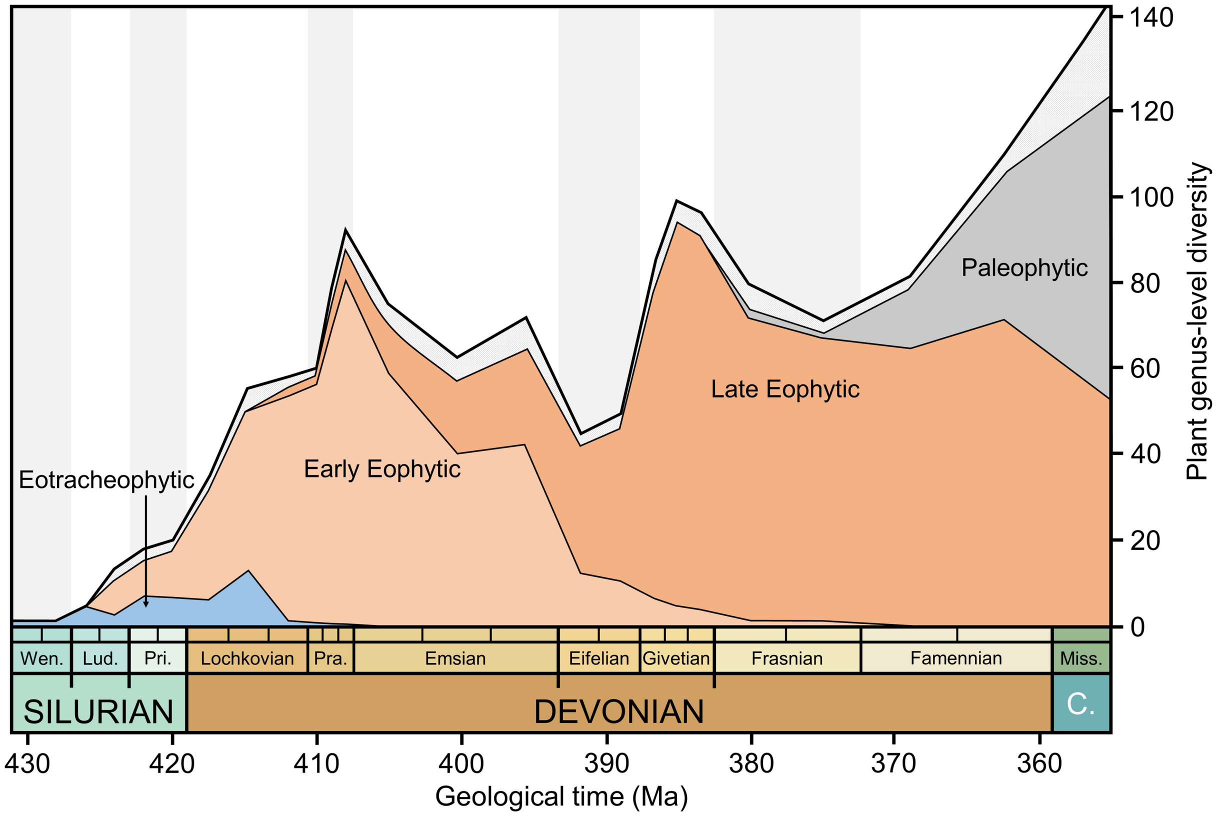

Figure II.4: Representation of changing genus-level diversities within each of the evolutionary floras indicated by the four-factor model described in this paper. The highlighted uppermost curve shows the total pattern of the plant genus-level diversity through time. The stippled area immediately below represents the residual diversity not explained by the model. Relative lengths of time units based on Cohen et al. (2013; updated). See Methods for details. Abbreviations: Wen., Wenlock; Lud., Ludlow; Pri., Pridoli; Pra., Pragian; Miss., Mississippian; C., Carboniferous.

II.5. Discussion

Total diversity patterns of early land plants based on taxon counts are inevitably flawed due to inherent taphonomic and sampling biases introduced by the fossil record. For instance, the volume of terrestrial rock exposed is an acknowledged bias (see Kenrick et al., 2012). There are also facies biases, notably because the plant fossil record is almost entirely from lowland nearshore deposits, which largely excludes remains of plants from extra-basinal habitats (similar to the situation in Carboniferous floras – Thomas and Cleal, 2017). A particular concern is the effect of sampling on taxon counts: for example, there are very few non-marine strata available for collecting in the Silurian (e.g., Kenrick et al., 2012;

Hao and Xue, 2013; Wellman et al., 2013). Nevertheless, our results have clearly revealed changing patterns, affecting distinct plant groups and intervals, which are more suggestive of a biological signal than of geological bias. This can be observed for instance in the Eotracheophytic-Eophytic turnover, where although total diversity is consistently increasing, Eotracheophytic diversity is progressively diminishing (Fig. II.4). The Silurian–Devonian plant fossil record shows the highest known diversity and disparity of plant groups. This is simply because all known plant groups except flowering plants, both living and fossil, are represented (Gerrienne et al., 2016, fig. 2; Cascales-Miñana et al., 2019a, fig. 3). Nevertheless, despite these great variations in form, the factor analysis has revealed a rather simple diversity pattern of floral changes. This pattern shows a clear succession of "major evolutionary steps", growing in complexity from simple, small, leafless herbaceous plants to highly developed woody seed-plants, including the tree habit. Without doubt, this diversification allowed plant life to colonize different and new terrestrial environments, to create an emerging greening of Earth's surface. This scenario is quite logical and is evident for instance from the growing size of Devonian plants (Xue et al., 2018, fig. 16). However, beyond statistically supporting this collective view, the factor analysis provides an objective way of measuring the "weight" of change between early floras and their composition. For instance, from this, we can see how the dominance of the late Eophytic flora, which included the earliest forest plants, occurred very rapidly before the end of the Middle Devonian.

Like in the Sepkoski (1981) model, one of most important aspects in the history of these early Evolutionary Floras is that their rise and subsequent decline seem to be closely related to the total pattern of apparent plant diversity. The changes in total taxonomic richness per time interval is shown in Fig. II.4 by the uppermost bold curve. The stippled field below this curve represents the residual diversity not explained by the four-factor solution of the model. This residual part is overall quite uniform and small, only becoming slightly larger from the end of the Devonian (probably as a response to greater "noise" in the factors with the lowest eigenvalues). The small size of this residual diversity suggests that the first four selected factors, and the Evolutionary Floras represented by them, provide a robust framework to explain the overall diversity pattern, as well as providing a first-order description of the composition changes of each flora during the Devonian.

The scaling of the four-factor model to total generic diversity suggests that each of the major evolutionary floras is associated with a specific phase of plant diversification (Fig. II.4). From this, we see that after an initial and continuous Silurian–Lower Devonian diversification in the Eotracheophytic flora, followed by an early diversification of the Eophytic flora, several ascending diversity trends can be observed. The first, at the end-Pragian, was a result of the rise and developing dominance of the early Eophytic flora. The second one, in the Givetian, was clearly related to an "explosive" expansion of the late Eophytic flora. The last significant increase of diversity occurs in the late Famennian and is linked to the initial diversification of the Palaeophytic flora. So, it seems that each of the four floras had its own independent but complementary pattern of generic diversity, which combined to produce the total dynamics of Silurian–Devonian plant diversity. The pattern of growth and decline of the early evolutionary floras suggests ecological displacement as the main cause of each turnover, but there is no equilibrium phase or exponential decline as is observed in the marine Evolutionary Faunas model.

Evolutionary innovations and the consequential diversification of various plant groups have been postulated to be the cause of turnover between different floras. This is partially supported here, especially for the Early Devonian Eotracheophytic-Eophytic transition. The changing pattern of these first floras, consisting of basal eutracheophytes, rhyniophytopsids and zosterophylls (Table II.3), can be comfortably related to the improvements in the water-conducting system of land plants (Kenrick and Crane, 1997a; Kenrick et al., 2012; Gensel, 2018). Overall, it is hypothesized that the rise of each of these floras was probably linked to key evolutionary developments such as in the growth in complexity (i.e., optimization) of the architecture of vascular system (Strullu-Derrien et al., 2013; Decombeix et al., 2019). At this time, land plants were undertaking a massive adaptive radiation and almost every anatomical-physiological aspect was rapidly evolving. This scenario would support the idea of an initial colonization of the earliest terrestrial environments linked to improvements in hydraulic efficiency (Wilson, 2013, 2016; Cascales-Miñana et al., 2019b; Decombeix et al., 2019).

In contrast, the extremely high morphological disparity observed in the Middle–Late Devonian Evolutionary Floras do not support a diversification pattern that was always driven by the appearance and/or improvements of key evolutionary innovations. For instance, this can be observed from the

Famennian, where the increase of plant diversity was a response to the dynamics of more than one great flora (Fig. II.4). Thus, the appearance of the late Eophytic flora, which involved the worldwide colonization of lowland areas by the archaeopteridalean progymnosperms and pseudosporochnales (Cladoxylopsida), saw the development of the earliest forested landscapes (Meyer-Berthaud et al., 1999; Stein et al., 2007; Meyer-Berthaud and Decombeix, 2007; Decombeix et al., 2011); while the earliest phase of the Palaeophytic flora, which represents a transitional stage characterized by open vegetation ecosystems, included the first seed plants, notably non-arborescent pteridosperms, colonizing disturbed habitats (Mintz et al., 2010; Prestianni and Gerrienne, 2010; Decombeix et al., 2011).

During the last decades, significant discoveries of Devonian plants have been made in South China (see e.g., Hao and Xue, 2013; Xue et al., 2018, and references therein). After analysing the Silurian–Devonian taxonomic diversity of this record, Xiong et al. (2013) observed several major fluctuations of genus-level plant diversity, one at the Pragian, another from the mid-Givetian to mid-Frasnian, and a last one in the late Famennian. These fluctuations are similar to the results reported herein (Fig. II.4), and suggest a common worldwide pattern of plant diversification. Xue et al. (2018) also performed a similar study to Xiong et al. (2013), but using a more conservative approach by retaining well-defined taxa only. Significantly, the proportions of major plant groups over time in the South China Block shown by Xue et al. (2018, fig. 9) approximately reflect the dominant elements of the Evolutionary Floras, e.g., the transition from a zosterophyllopsid-dominated flora to a lycopsid-dominated flora (Table II.3); this provides further support for a global pattern of subsequent diversification phases of early vegetation. In contrast, although diversity studies on South China plant fossils suggest a Givetian crisis similar in magnitude to the Frasnian–Famennian marine crisis (Xiong et al., 2013), we see no global crisis in the vegetation of the Middle Devonian (Fig. II.1B). Rather, our model shows a sustained increase in plant taxonomic and morphological diversity at this time (Fig. II.1A), triggered by the late Eophytic diversification (Fig. II.4). Likewise, our model suggests that the reduction in plant diversity at the beginning of the Late Devonian (Fig. II.4) is linked to the start of the Eophytic-Palaeophytic transition that resulted in more complex forested ecosystems.

II.6. Conclusions

Results have shown that the largest part of the variation dynamics in generic richness within the main Silurian–Devonian plant groups can be explained through a four-phase diversification model. This model is based on (1) a first Eotracheophytic flora that dominates the Silurian fossil record but decays suddenly after the Lochkovian, (2) an early Eophytic Flora that dominates the Early Devonian showing a continuous increase until the Pragian, (3) a late Eophytic Flora that dominates from the Middle Devonian to the Carboniferous, and lastly, (4) a sustained increase of a Palaeophytic flora from the Frasnian/Famennian boundary. Each evolutionary flora appears to be associated with distinct phases of diversification of early terrestrial ecosystems. The Eotracheophytic flora is associated with the earliest radiation of vascular plants, while the Eophytic floras are associated with the expansion of zosterophyllopsids and of lycopsids, respectively, and the appearance of cladoxylopsids and progymnosperms, i.e., the earliest trees. Likewise, the Palaeophytic flora is linked to the earliest diversification of seed plants. Finally, the results show that the expansion of each new flora triggers the progressive decline of the previously dominant flora, which suggests ecological displacement. In this sense, the pattern of succession of the early Evolutionary floras reflects the transition from environments covered by herbaceous plants to an early forested planet.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2020.110170. or upon request.

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Chapter III: Biases and temporal dynamics in early plant diversity reconstructions

This chapter consists in two separate articles. Firstly, a lightly modified version of an article published in *Earth-Science Reviews* named “ **The Silurian-Devonian terrestrial revolution: Diversity patterns and sampling bias of the vascular plant macrofossil record**” found available online at https://doi.org/10.1016/j.earscirev.2022.104085. The published version of this paper can also be found in appendix 2. The second article is an original manuscript of a rapid communication sent to the journal *Palaeontology* called “**The effect of geological biases on our perception of early land plant radiation**” and preliminarily accepted with minor revisions upon peer-reviews.

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.

Keywords: Early vascular plants; Earth landscape; Palaeodiversity; Radiation; Plant macrofossils; Tracheophytes; Sampling bias.

III.1.1. 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. III.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; Libertin et al., 2018; Gensel et al., 2020; Gensel, 2021), which were replaced in the Devonian by floras characterized by an "explosion" in morphological disparity (Fig. III.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

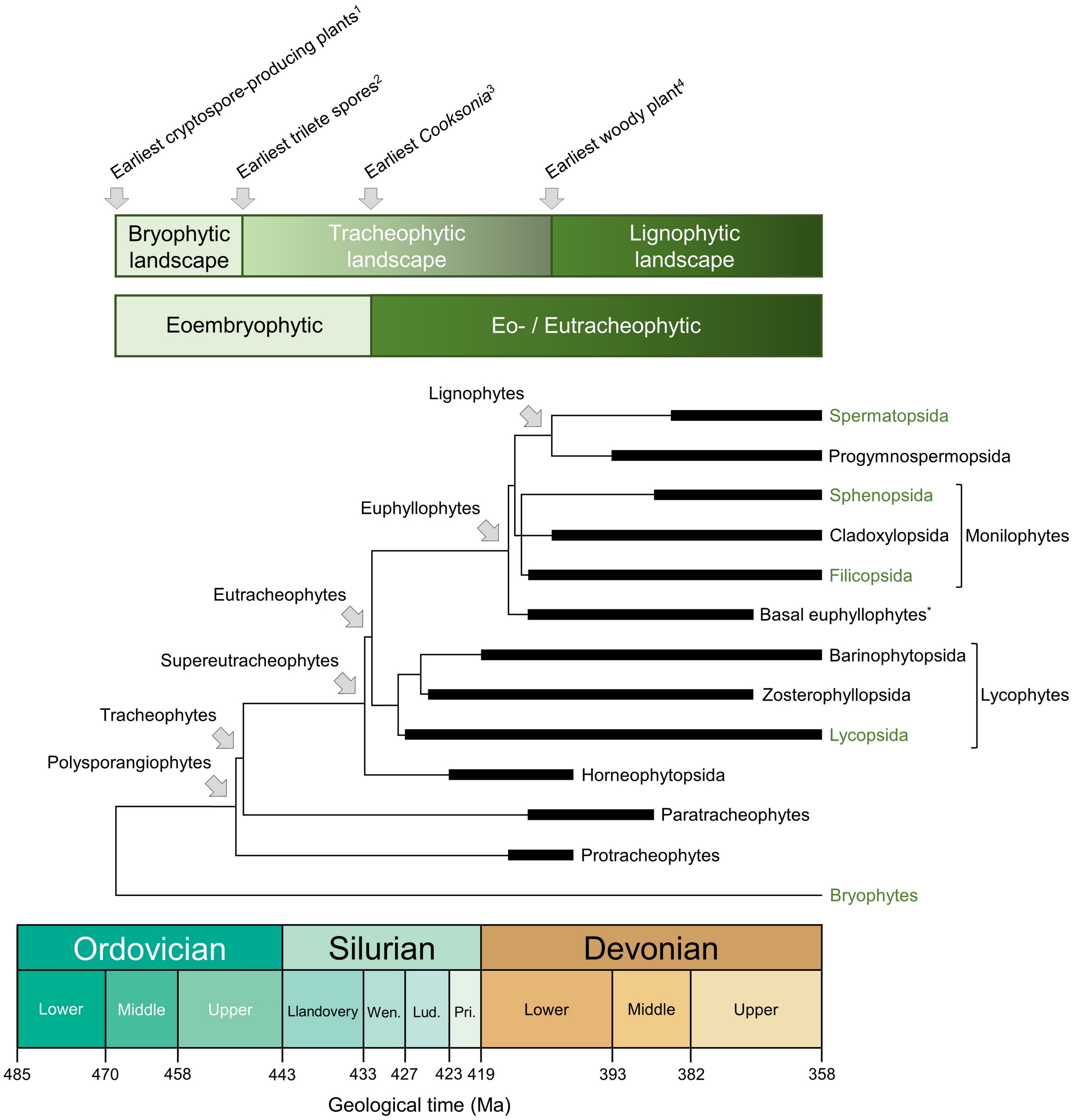

Figure III.1: Early evolutionary framework of embryophytes. Bryophytic, tracheophytic and lignophytic landscapes *sensu* Strother et al. (2010). Eoembryophytic and Eutracheophytic steps of plant evolution *sensu* Gray (1993). Data from Gerrienne et al. (2016, and references therein). Modified from Servais 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 Trimerophytopsida.

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, zosterophyllopsids 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. III.1). In the Middle and Late Devonian, arborescent forms developed in multiple clades, including cladoxylopsids (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. III.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., 2019b; Crepet and Niklas, 2019; Bonacorsi et al., 2020; Niklas and Crepet, 2020). The influence of plant terrestrialization on the physical environment including atmospheric CO_2 and O_2 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; 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.

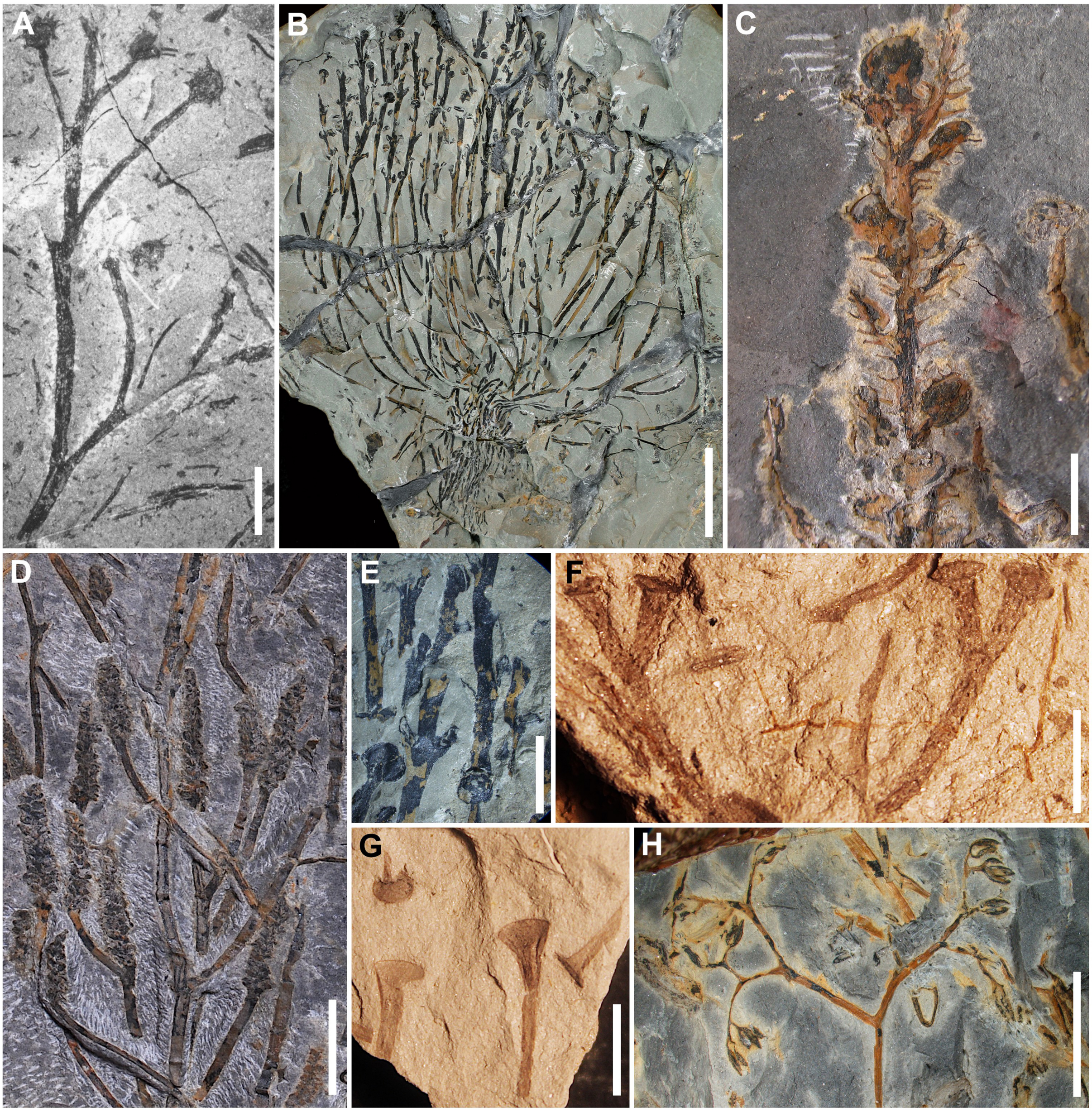

Figure III.2: Morphological diversity of Silurian–Devonian floras (I). (A) *Eocooksonia sphaerica* (Senkevitsch) Doweld (Basal eutracheophytes). Axis showing pseudomonopodial branching and terminal sporangia. Specimen PKUB14902, upper Silurian (Pridoli) Wutubulake Formation of Xinjiang, China (Xue et 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) *Pauthecophyton gracile* Xue et al. (Basal euphyllophytes). 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.

III.1.2. 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, 1997b; 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. III.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, 1997b), which also include non-vascular fossil plants such as the eophytes (Edwards et al., 2022) and

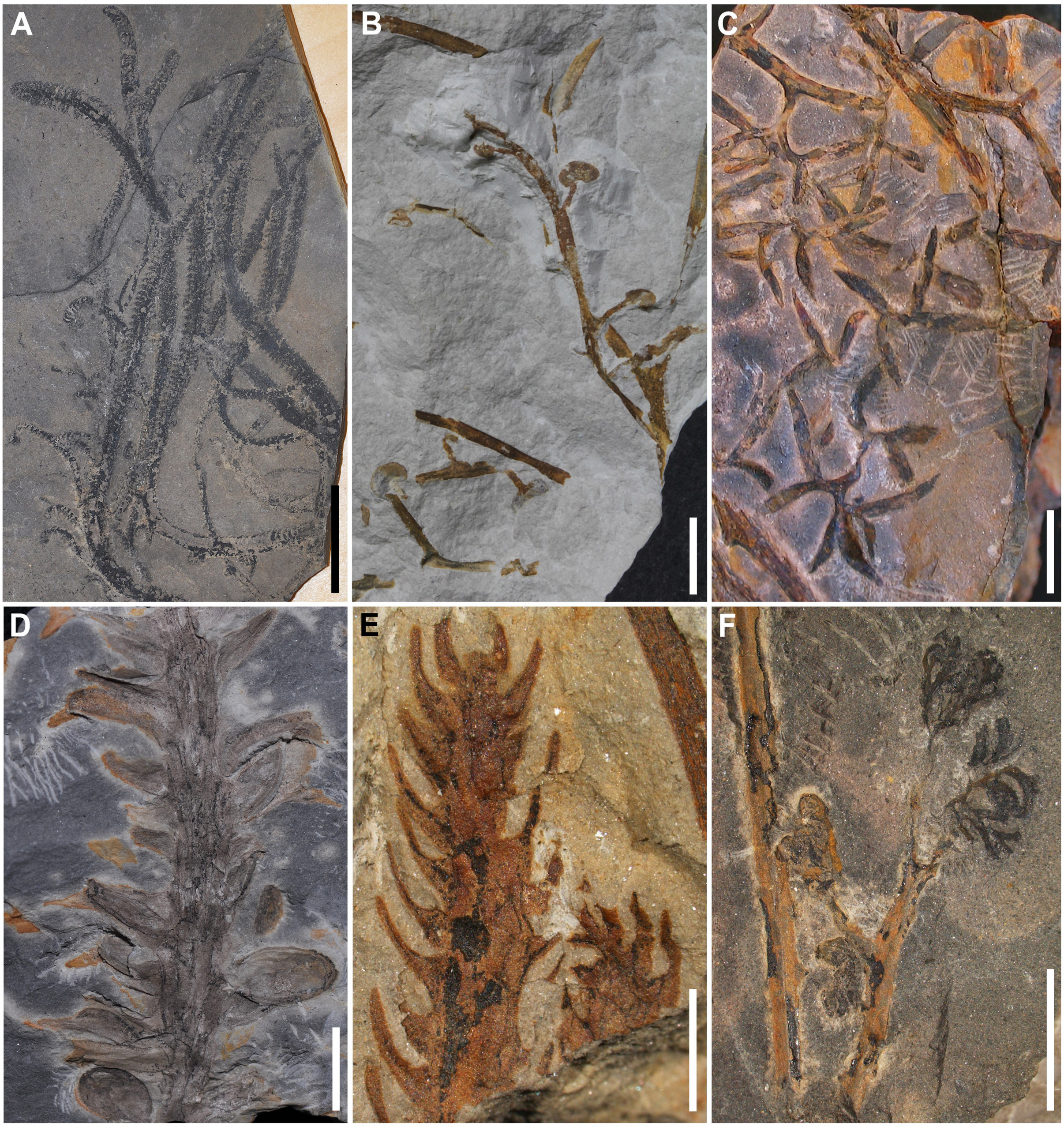

Figure III.3: Morphological diversity of Silurian–Devonian floras (II). (A) *Bathurstia denticulata* Hueber (Zosterophyllopsida). Fertile axes with terminal spikes. Specimen US704-8326, Lower Devonian (Pragian) Bathurst Island Formation of Nunavut, Canada (Kotyk and Basinger, 2000, fig. 3). Scale bar = 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. (Barinophytopsida). 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.

the protracheophytes, the latter being represented by *Aglaophyton*/*Teruelia* (Edwards, 1986; Cascales-Miñana and Gerrienne, 2017; Fig. III.1). Kenrick and Crane's (1997b) analysis included the Horneophytopsida within the protracheophytes, although subsequent investigations have suggested the presence of irregular wall thickenings in *Horneophyton*, resolving Horneophytopsida as a sister clade to the eutracheophytes (i.e., true vascular plants; Cascales-Miñana et al., 2019a; Fig. III.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., 2019b; Decombeix et al., 2019; Fig. III.1).

The two main lineages of eutracheophytes living today, lycophytes and euphyllophytes, are considered monophyletic (Kenrick and Crane, 1997a; Qiu et al., 2006; Crepet and Niklas, 2018, 2019). Lycopsida and Zosterophyllopsida are the two main classes usually recognized in the Lycophytina *sensu* Kenrick and Crane (1997b), while the sister-group relationship of these two groups has been questioned by other analyses (Hao and Xue, 2013; Fig. III.2). Lycopsids 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. III.3–III.4). Zosterophyllopsids in contrast are leafless and bear reniform sporangia (Banks, 1968; Hueber, 1972; Cascales-Miñana and Meyer-Berthaud, 2014;

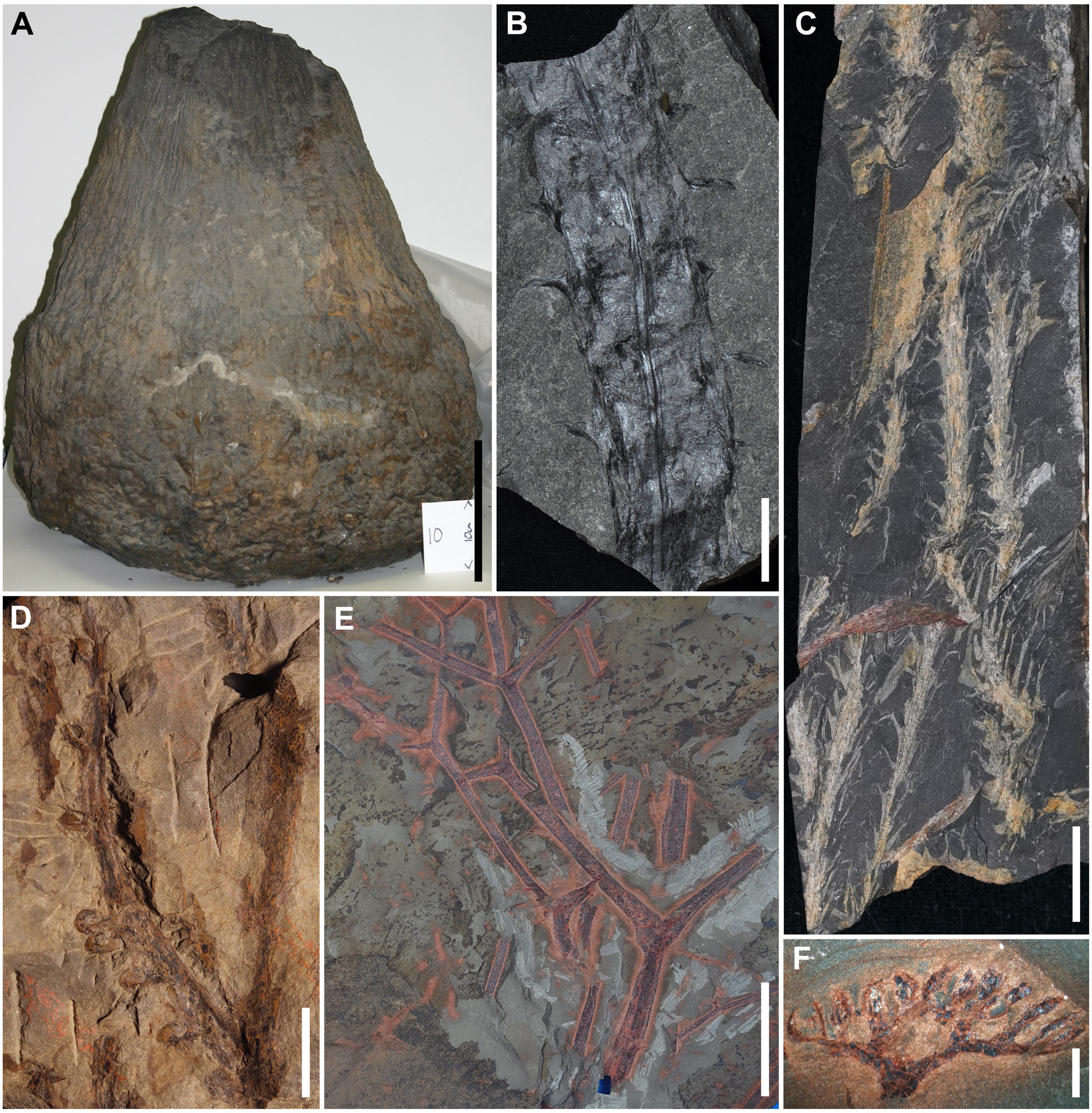

Figure III.4: Morphological diversity of Silurian–Devonian floras (III). (A) *Eospermatopteris* (Cladoxylopsida) cast. Photo by Chris Berry, courtesy of William E. Stein. Scale bar = 20 cm. (B) *Drepanophycus qujingensis* Li et Edwards (Lycopsida). Leafy axis. Specimen PKUB18299, Lower Devonian (Pragian–Emsian) 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, 1996a, 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.

Fig. III.2). Barinophytopsids 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 (1997b) found them paraphyletic to other lycophytes and excluded taxa lacking circinate vernation 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. III1–III2).

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, 1997b; 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. III.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. III.1, III.4, III.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., 2016b;

Decombeix et al., 2019). Progymnosperms (Aneurophytales, Archaeopteridales, Protopityales 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. III.1, III.4). The

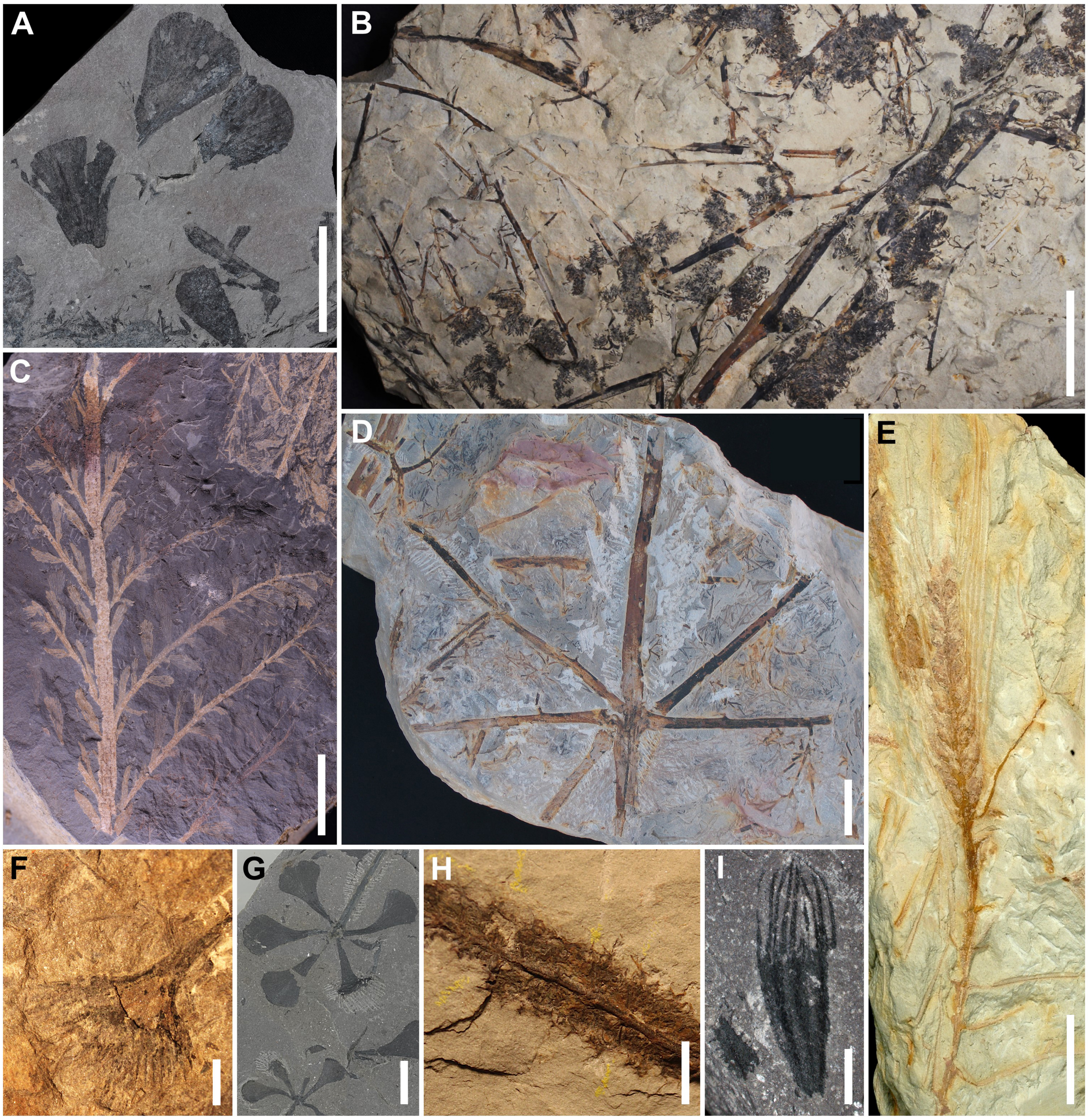

Figure III.5: Morphological diversity of Silurian–Devonian floras (IV). *Xihuphyllum megalofolium* (Wu) Chen emend. Huang et al. (Sphenopsida). Detached leaves. Specimen PKUB13606a, Upper Devonian (Famennian) Wutong Formation of Zhejiang, China (Huang et al., fig. 6A). Scale bar = 50 mm. (B) *Rhacophyton 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* (Goeppert) 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 vezerensis* 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.

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 Hilu, 2009; Toledo et al., 2018; Fig. III.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. III.5) but some do not show any cupules (e.g., *Guazia*; 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 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, zosterophyllopsids, as well as monilophytes and lignophytes (Fig. III.1). Regarding the considered groups, we tested major class-level categories, which include barinophytopsids, filicopsids, cladoxylopsids, progymnosperms, sphenopsids and spermatopsids (Fig. III.1).

III.1.3. Materials and methods

III.1.3.1. Data compilation

The analysis described here uses both diversity and sampling data. Diversity data came from the Capel et al. (2021, table II.S1) plant macrofossil-based compilation, with slight modifications (Table III.S1). The employed dataset consists of the first and last appearance datum (FADs–LADs) 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, endemicity 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 III.S1). Importantly, while some taxa have a highly detailed temporal assignation (e.g., Gutak et al., 2011), others present a less precise resolution (e.g., Prestianni et al., 2012). Hence, in an attemto 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 III.S1, Text III.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., 2017). 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 III.S2. Raw diversity and sampling data are also available on request.

III.1.3.2 Processing methods

III.1.3.2.1. 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:

$$N_{\mathrm{tot}} = N_{\mathrm{FL}} + N_{\mathrm{bL}} + N_{\mathrm{Ft}} + N_{\mathrm{bt}} \qquad (1)$$

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):

$$N_{\mathrm{b}} = N_{\mathrm{bL}} + N_{\mathrm{bt}} \qquad (2)$$

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):

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

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):

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

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

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:

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

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

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 λ + μ.

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 totaldiversity 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.

III.1.3.2.2. 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.

III.1.4. Results

III.1.4.1. Taxonomic diversity estimates

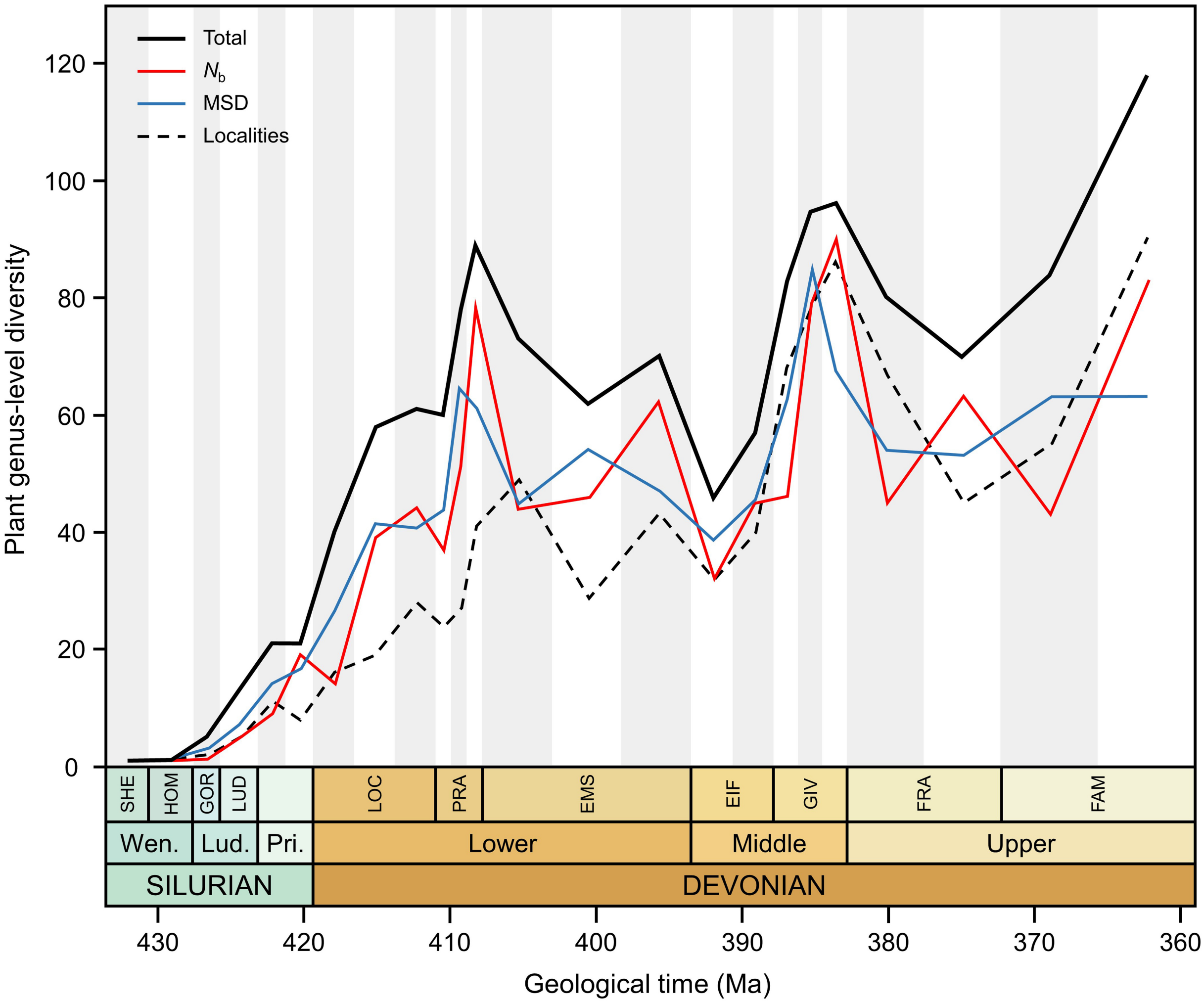

Figure III.6: Silurian–Devonian diversity patterns of tracheophytes. Bold, red and blue lines show total, boundary-crossing (N_b) and mean-standing (MSD) diversity of plant genera per time unit, respectively. Dashed line shows the sampled localities per time unit. Alternation of white and grey boxes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

Large-scale diversity patterns of Silurian–Devonian tracheophytes, including dynamics of major taxonomic groups, are shown in Figs. III.6–III.8. From this, we see that the total diversity of tracheophytes increases steadily from the Ludlow (late Silurian) to the Lochkovian (earliest Devonian) (Fig. III.6), caused mainly by increases in the lycophytes (Fig. III.7A), notably basal lycopsids (Fig. III.7B) and zosterophyllopsids (Fig. III.7C). Thereafter, taxonomic diversity reached a brief plateau

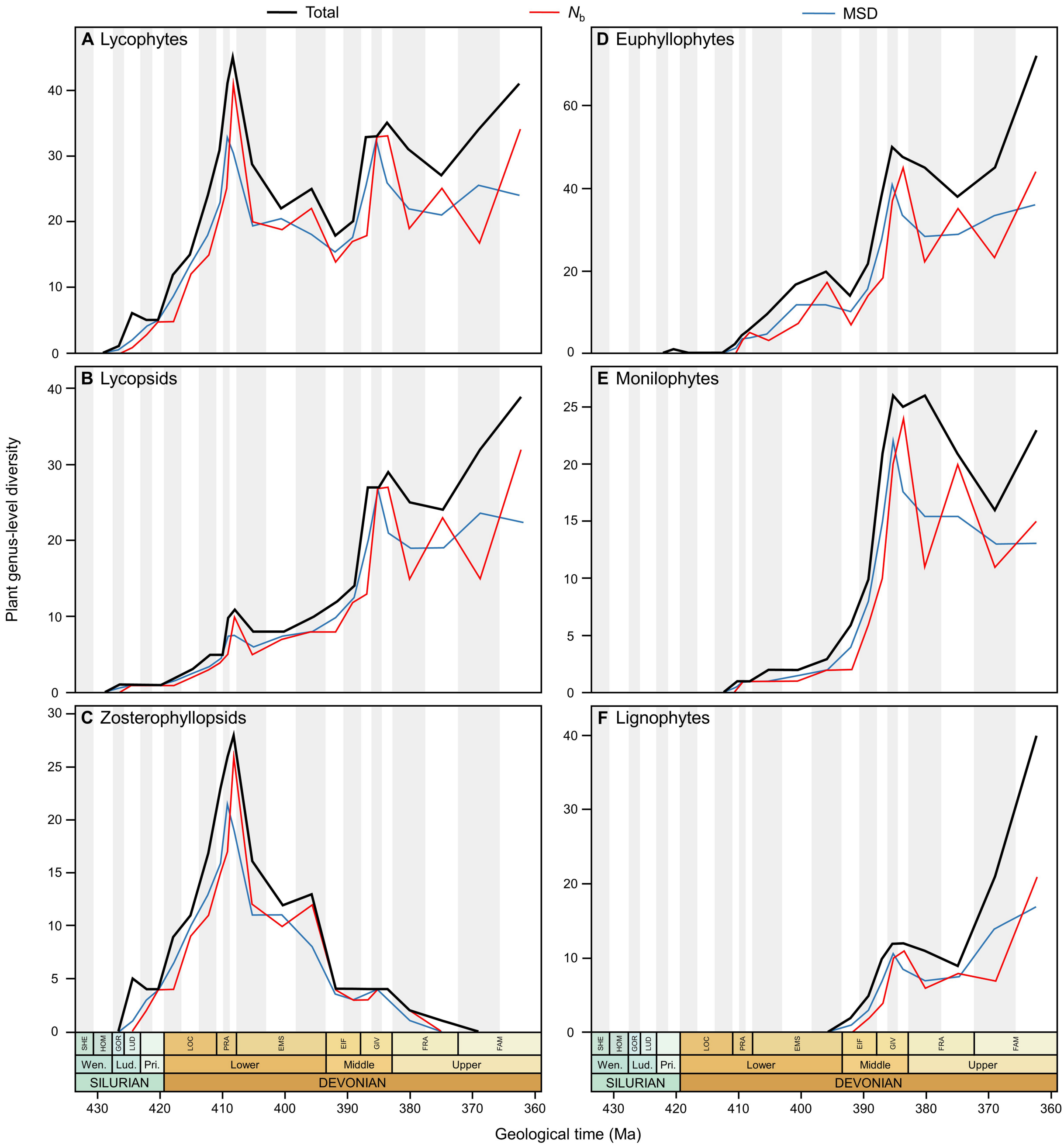

Figure III.7: Silurian–Devonian diversity patterns of main tracheophyte clades. Bold, red and blue lines show total, boundary-crossing (N_b) and mean-standing (MSD) diversity of plant genera per time unit, respectively. (A) Lycophytes; (B) Lycopsids; (C) Zosterophyllopsids; (D) Euphyllophytes; (E) Monilophytes;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

during the Lochkovian (Fig. III.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 zosterophyllopsid and barinophytopsid diversities (Figs. III.7C, III.8A), and to a lesser extent, a minor lycopsid diversity peak (Fig. III.7B). Subsequently, tracheophyte diversity

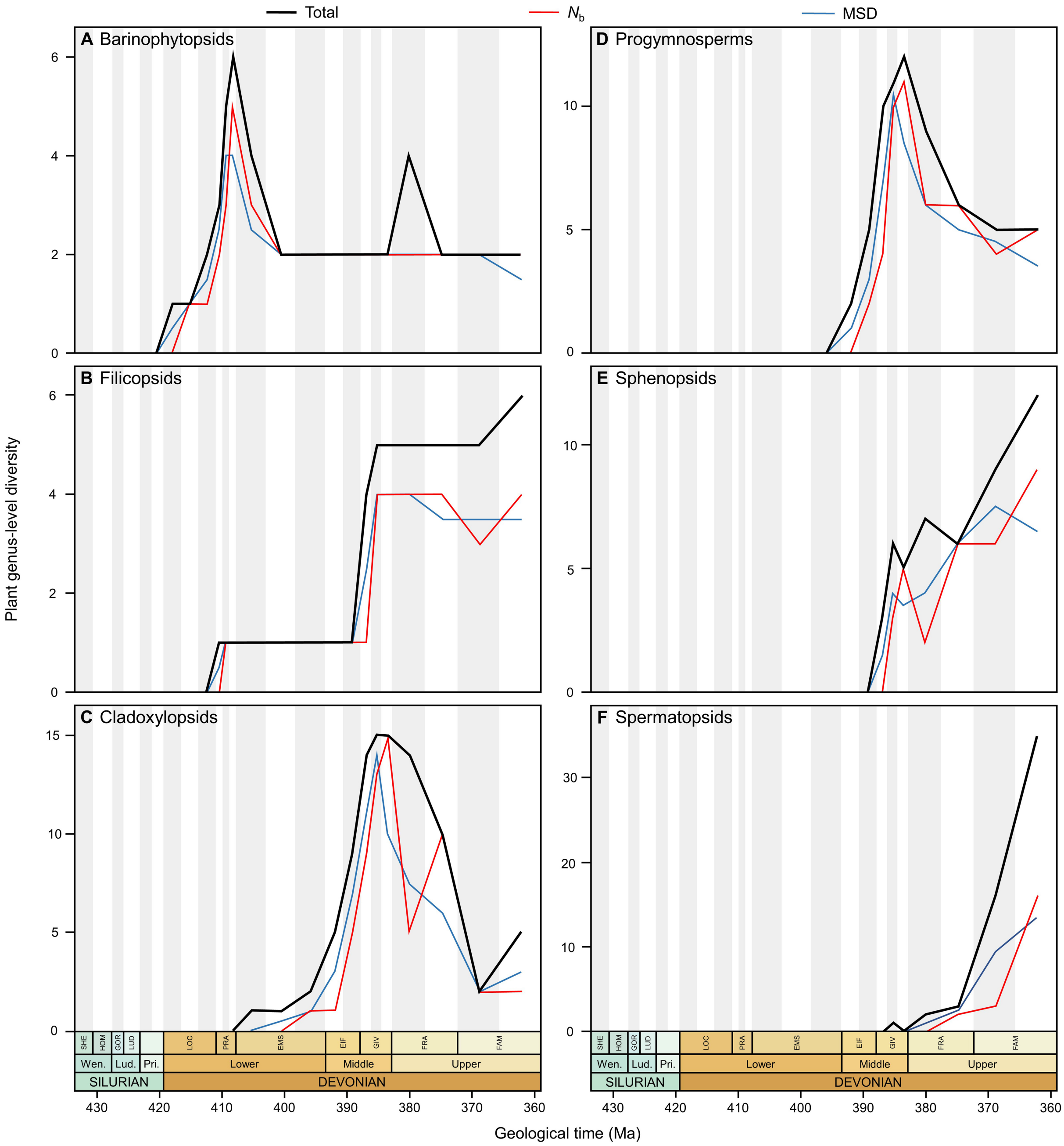

Figure III.8: Silurian–Devonian diversity patterns of main tracheophyte groups. Bold, red and blue lines show total, boundary-crossing (N_b) and mean-standing (MSD) diversity of plant genera per time unit, respectively. (A) Barinophytopsids; (B) Filicopsids; (C) Cladoxylopsids; (D) Progymnosperms; (E)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

begins to decline in the Emsian, followed by a minor increment towards the end of the Early Devonian (Fig. III.6) caused by lycopsids and basal euphyllophytes (Fig. III.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. III.6). This is principally due to a strong decline in zosterophyllopsids (Fig. III.7C). Interestingly, the Eifelian diversity of tracheophytes reaches levels not seen since Lochkovian times (Fig. III.6). After that, a second diversity peak is observed during the Givetian (late Middle Devonian) (Fig. III.6), triggered by an important pulse of both lycophyte (Fig. III.7A) and euphyllophyte diversity (Fig. III.7D). More specifically, the Givetian diversification involves lycopsids (Fig. III.7B), and almost all major groups of monilophytes (Fig. III.7E), such as filicopsids (Fig. III.8B) and especially cladoxylopsids (Fig. III.8C), as well as lignophytes, notably progymnosperms (Fig. III.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. III.8C–D). Tracheophyte diversity steadily increases again throughout the Famennian (latest Devonian), where the highest values are observed (Fig. III.6), triggered mainly by a diversification of lycophytes (Fig. III.7A), euphyllophytes (Fig. III.7D) and lignophytes (Fig. III.7F). It is further sustained by the diversity increase of sphenopsids (Fig. III.8E), and spermatopsids (Fig. III.8F), and results in an overall exponential increase in diversity.

The N_b and MSD metrics follow the same trends as total diversity (Fig. III.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. III.6), which shows some discrepancies from the observed MSD changes (Fig. III.6); indeed, the MSD pattern does not capture a late Frasnian diversity peak recorded in boundary-crossing fluctuations (Fig. III.6). This discrepancy is also seen in the diversity curves for each of the major clades (Fig. III.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. III.7), and in each different plant group (Fig. III.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. III.6 (Fig. III.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).

III.1.4.2. Origination, extinction, and turnover rates

Fig. III.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. III.9A). After that, an important origination pulse occurs at the base of the Givetian (Middle Devonian) (Fig. III.9A). In contrast, the extinction pattern shows highest values at the end-Pragian and the end-Givetian (Fig. III.9B). There are no major differences observed between per-taxon and per-capita rate measures for

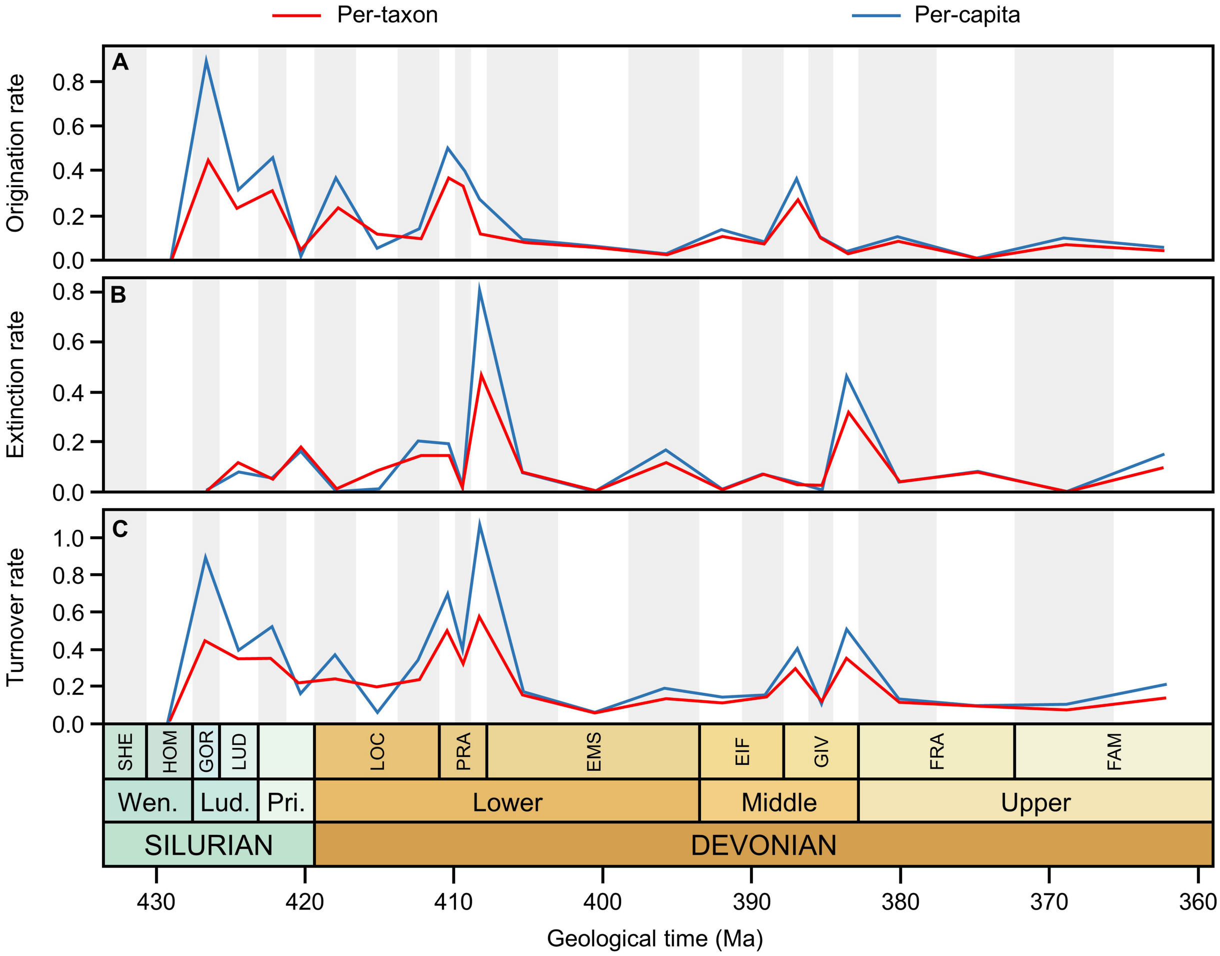

Figure III.9: Silurian–Devonian macroevolutionary patterns of tracheophytes. Red and blue lines show per-taxon and per-capita origination (A), extinction (B) and turnover (C) rates of plant genera, respectively. Abbreviations, same as in Fig. III.6.

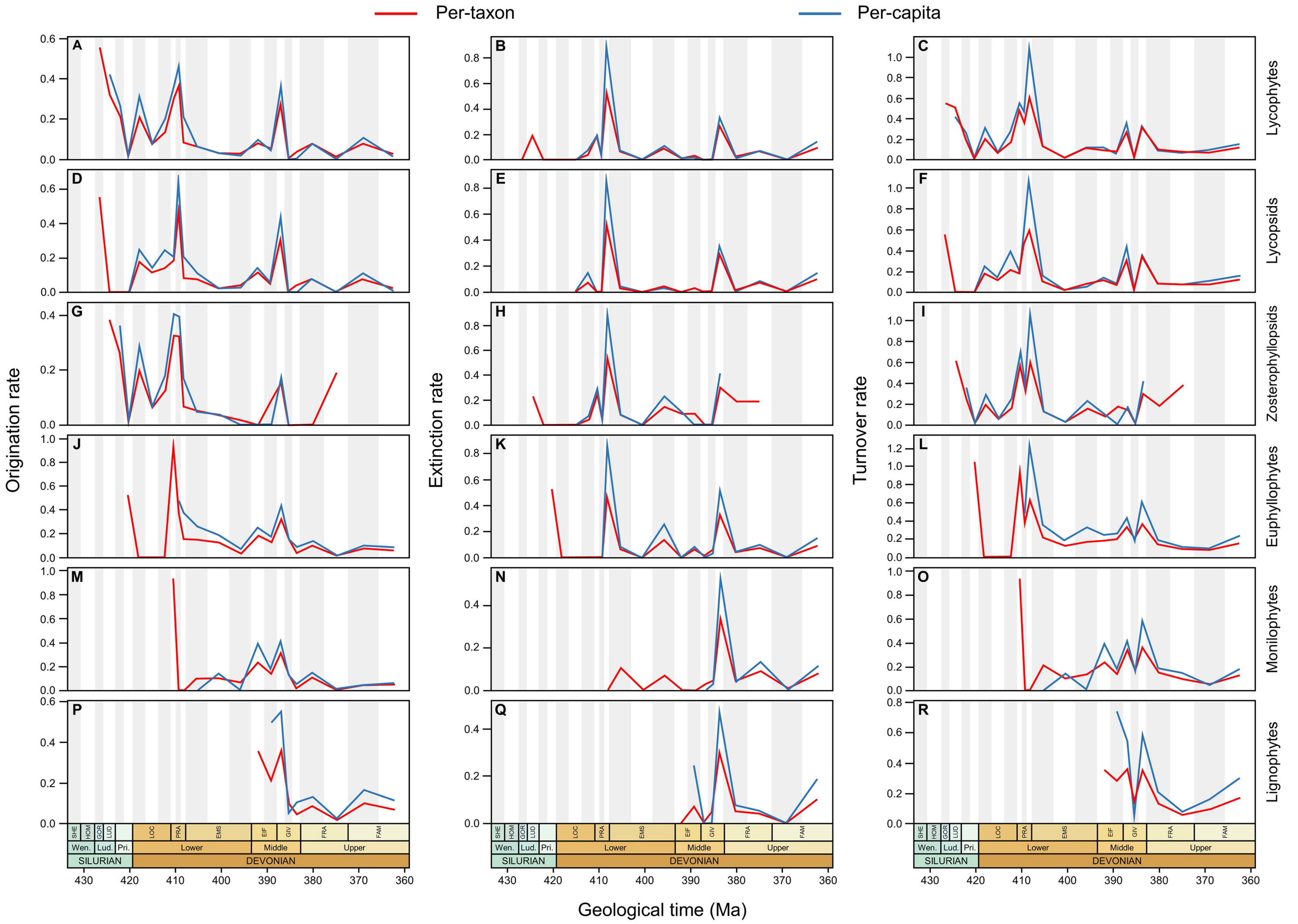

Figure III.10: Silurian–Devonian macroevolutionary patterns of main tracheophyte clades. Red and blue lines show per-taxon and per-capita origination (left column), extinction (central column) and turnover (right column) rates of plant genera, respectively. (A–C) Lycophytes; (D–F) Lycopsids; (G–I) Zosterophyllopsids;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

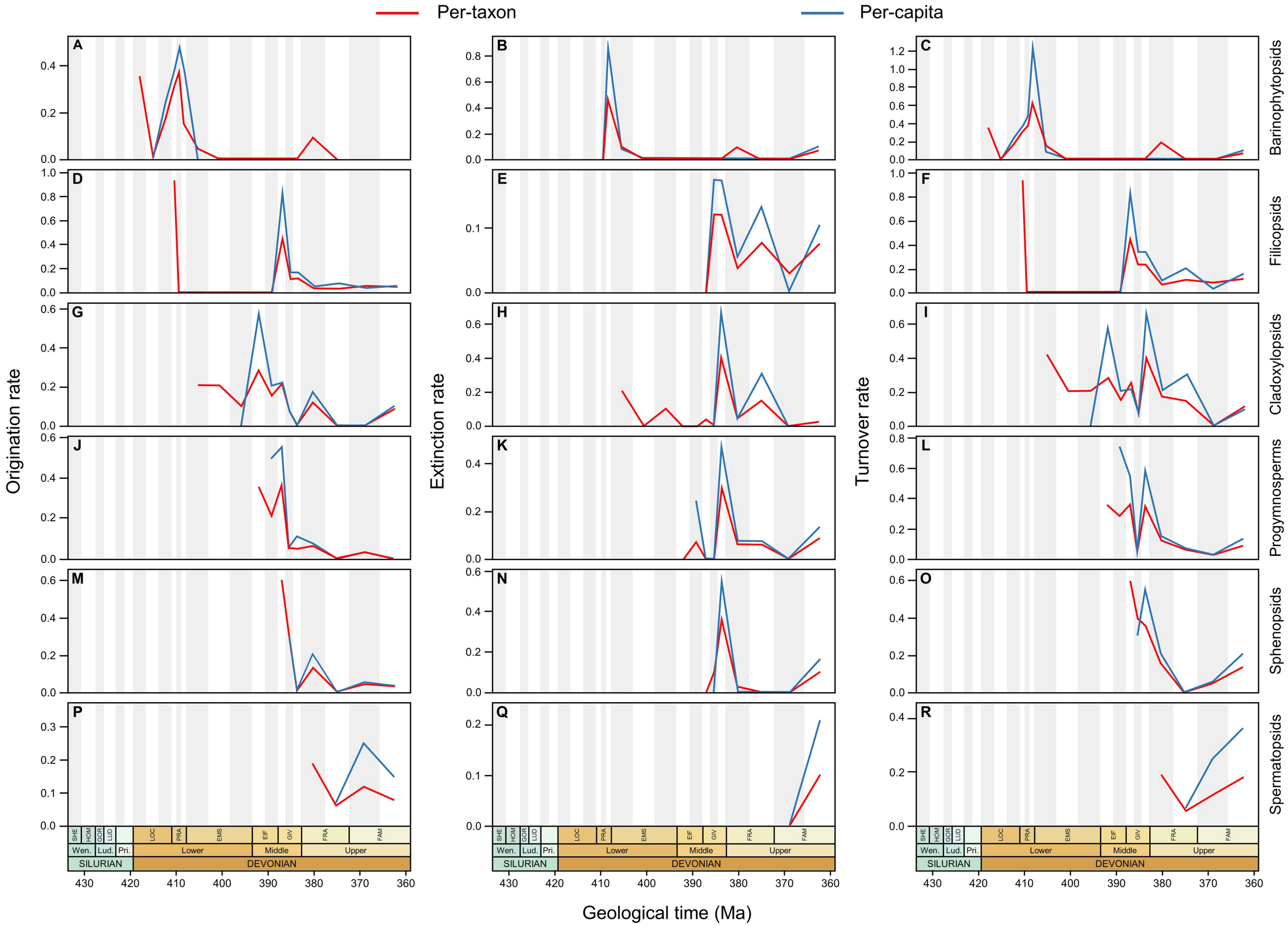

Figure III.11: Silurian–Devonian macroevolutionary patterns of main tracheophyte groups. Red and blue lines show per-taxon and per-capita origination (left column), extinction (central column) and turnover (right column) rates of plant genera, respectively. (A–C) Barinophytopsids; (D–F) Filicopsids;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

originations or extinctions (Fig. III.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. III.9C). After that, highest turnover pulses are observed in the Pragian and the Givetian (Fig. III.9C), indicating an important amount of change in floristic composition during these intervals.

Within clades and groups (Figs. III.10–III.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. III.10A–B), including lycopsids (Fig. III.10D–E), zosterophyllopsids (Fig. III.10G–H), and barinophytopsids (Fig. III.11A–B), as well as from basal euphyllophytes (Fig. III.10J–K). Likewise, Middle Devonian (Givetian) origination-extinction peaks are shared by all tested clades, including monilophytes (Fig. III.10M–N), filicopsids (Fig. III.11D–E), cladoxylopsids (Fig. III.11H) and sphenopsids (Fig. III.11M–N), as well as lignophytes (Fig. III.10P–Q), such as progymnosperms (Fig. III.11J–K). Results further show an isolated origination increment driven by Middle Devonian (Eifelian) cladoxylopsids (Fig. III.11G). Moreover, the turnover rate shows two major pulses: one in the Pragian mainly concerning lycophytes (Figs. III.10C, III.10F, III.10I, III.11C), and a second one in the Givetian involving euphyllophytes (Figs. III.10–11L, III.10–11O, III.10R, III.11F, III.11I). Finally, evolutionary patterns of spermatopsids show a clear diversification towards the end of the Devonian (Fig. III.11P–R).

Fig. III.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, 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

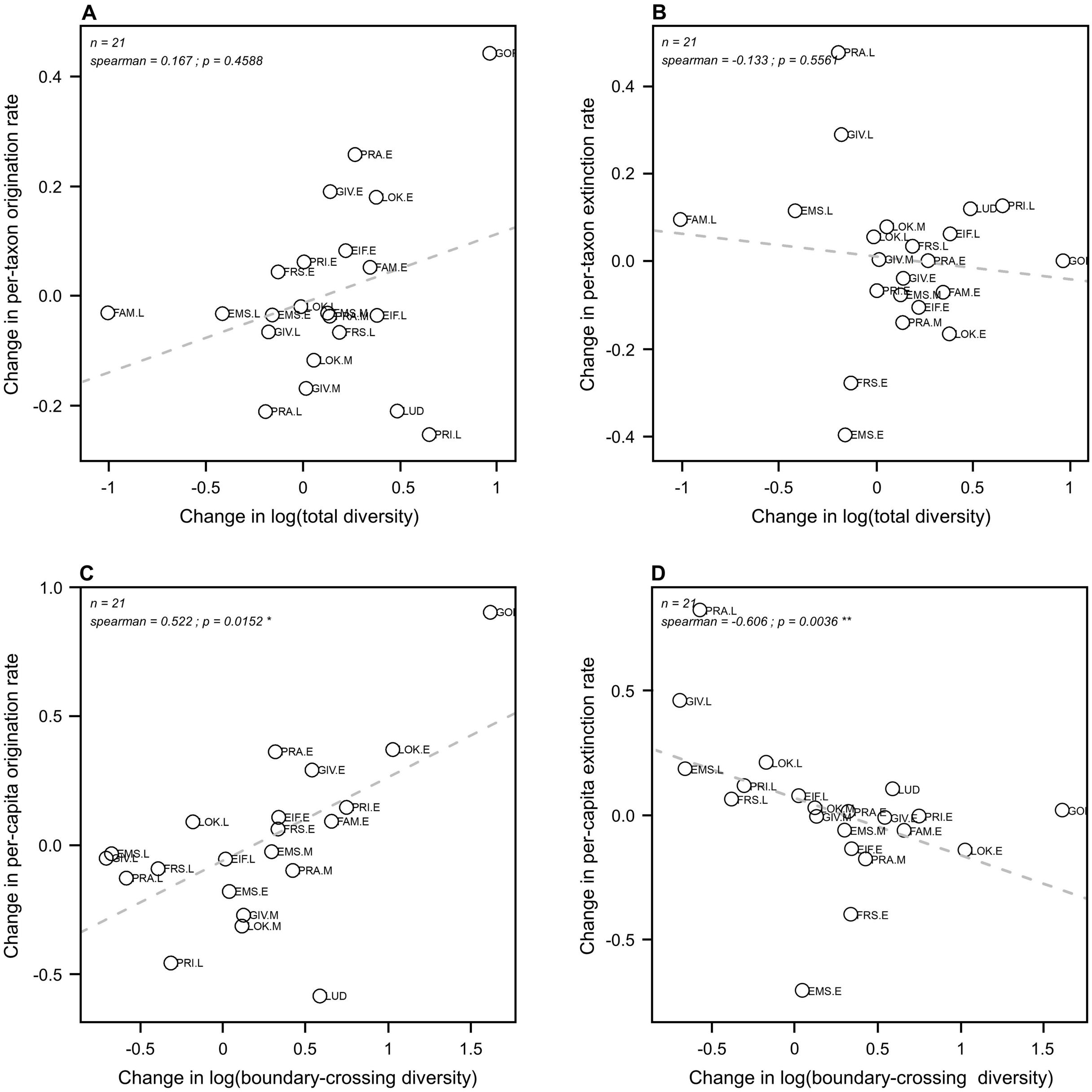

Figure III.12: Comparison between change in total (A–B) and boundary-crossing (C–D) diversity and change in per-taxon and per-capita origination-extinction rates of tracheophyte genera, respectively. Data analysis based on Spearman's rank correlation coefficient (*rho*). *Significant value (p < 0.05).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

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. III.12A–B). But importantly, results show significant correlation values in both cases from standing metrics (Fig. III.12C–D). Results further show stronger correlation levels between changes in extinction values and changes in diversity (*rho* = -0.60, p < 0.01; Fig. III.12D), which suggests that for Silurian–Devonian floras, variations in

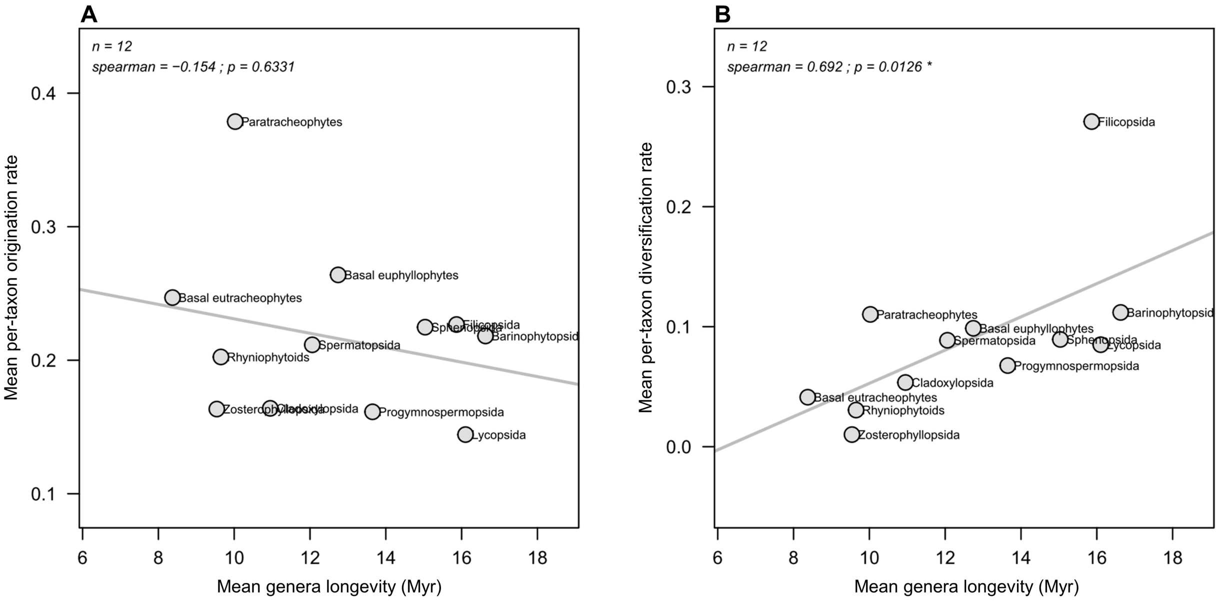

Figure III.13: Comparison between mean per-taxon origination (A) and diversification (B) rates and mean genera longevity of main tracheophyte groups. Data analysis based on Spearman's rank correlation coefficient (*rho*). *Significant value ($p < 0.05$).

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 that overall patterns of increasing origination rates and decreasing observed longevities between major 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. III.13A), probably due to the high volatility observed both within and among groups (Fig. III.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. III.10–III.11). Complementary analysis based on summed origination and diversification rate values provided identical results (Fig. III.S3).

III.1.4.3. 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. III.6 plots the number of sampled localities per time unit and confirms that high diversity values tend to be associated with high sampling

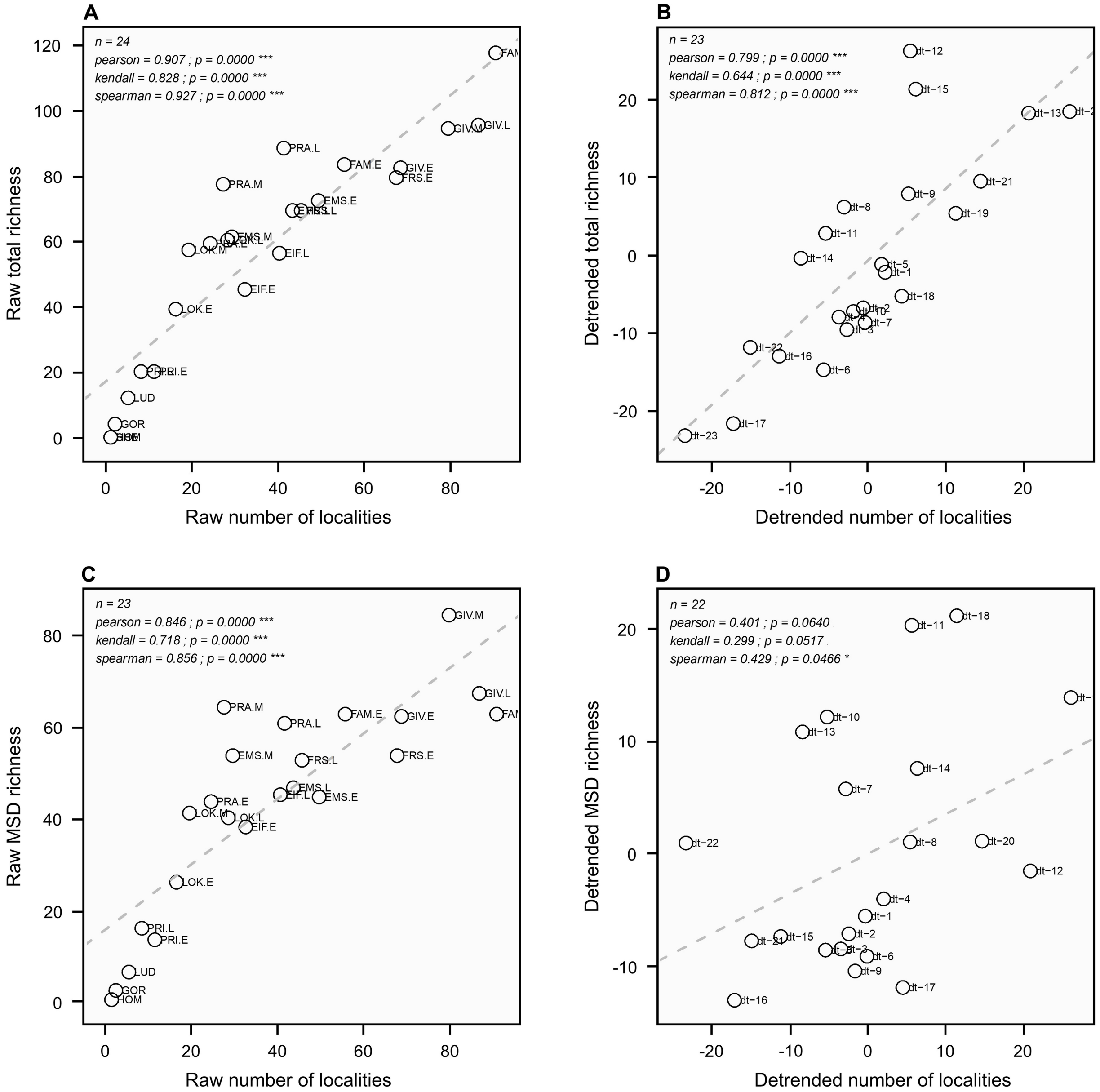

Figure III.14: Comparison between total (A–B) and mean-standing (C–D; MSD) diversity of tracheophyte genera and the number of sampled localities per time unit. Data analysis performed on raw (A, C) and detrended (B, D) data through generalized-differencing (GD). Correlations based on Pearson's, Kendall's,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

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 III.S2, Text III.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. III.14A–B). However, MSD is only significantly correlated with site numbers when raw MSD data are used (Fig. III.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.

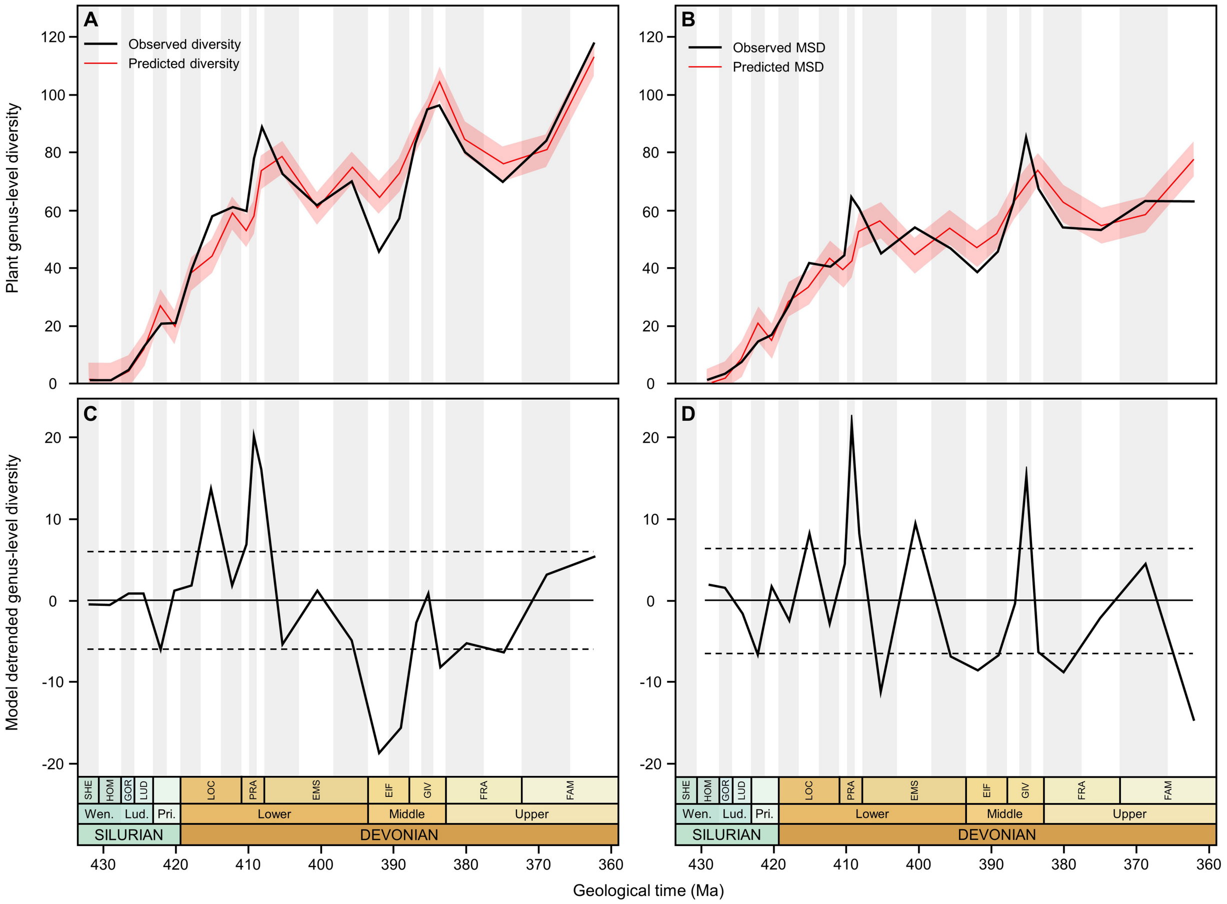

Figure III.15: Comparison between observed and predicted patterns of total (A) and mean-standing (B; MSD) diversity of plant genera. Sampling-corrected (residual) patterns of total (C) and MSD (D) diversity of plant genera. Dashed lines represent the 95% confidence interval of the proxy-biased model.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

Fig. III.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. III.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. III.15C–D. These sampling-corrected data mainly fall within the 95% confidence interval suggesting that the trends are mainly being driven by sampling (Fig. III.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. III.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. III.15D).

III.1.5. Discussion

III.1.5.1. Apparent patterns of early land 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 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 (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. III.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. III.6), instead of a general reduction of diversity throughout the Emsian as a whole (Cascales-Miñana, 2016, fig. 1). Previous lycopsid and 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. III.6) and the diversity in the two main monophyletic clades (Fig. III.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 Zosterophyllopsida 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. III.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, 1990a; Edwards and Berry, 1991; Hao and Xue, 2013).

III.1.5.2. 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. III.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 heterogenous 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 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. III.15C–D), the concomitant increase of diversity and number of localities between the middle Silurian and the middle Early Devonian (Fig. III.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. III.15C–D). Furthermore, the observed diversity peaks in the Pragian and the Givetian (Figs. III.6 and III.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 zosterophyllopsid 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 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., 2017).

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. III.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

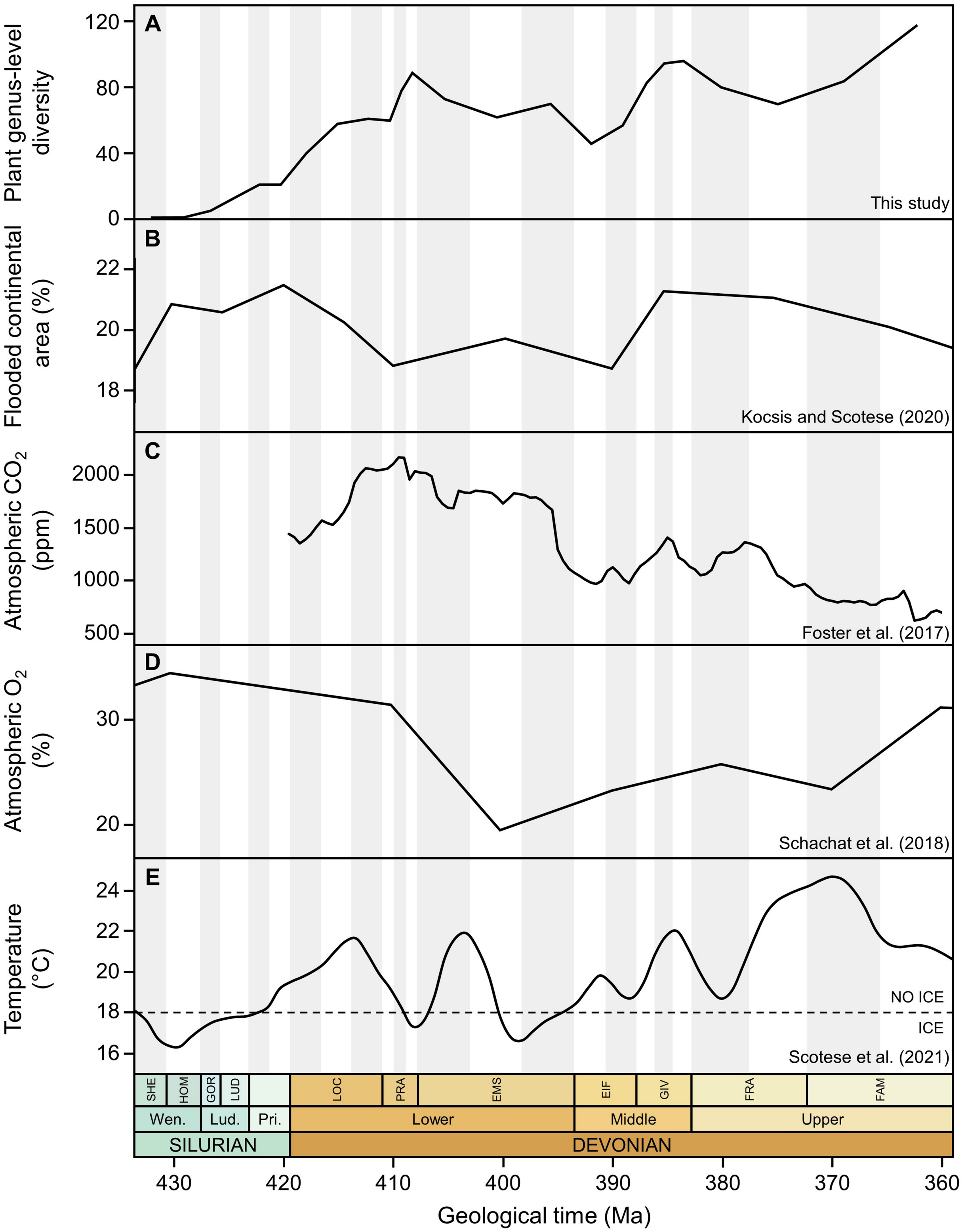

Figure III.16: Comparison between total diversity pattern of tracheophyte genera (A) and fluctuations of different abiotic factors (B–E) during the Silurian-Devonian time interval. (B) Flooded continental area. (C) Atmospheric CO_2 levels. (D) Atmospheric O_2 levels. (E) Global average temperature. Abbreviations, same as in Fig. III.6.

tracheophyte macrofossils 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 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. III.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, 2007a; 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).

III.1.5.3. Biosphere dynamics and early land plant diversification

The impact of the development of terrestrial vegetation on atmospheric CO_2 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 CO_2 levels and a cooling climate during the Devonian (Berner, 1997; Simon et al., 2007; Algeo and Schecker, 2010; Le Hir et al., 2011; Foster et al., 2017; Brugger et al., 2019; Fig. III.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 O_2 (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 O_2 levels already in the Silurian (Schachat et al., 2018; Fig. III.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., 2016; Servais et al., 2019). However, O_2 levels in fact reportedly fell during the Devonian (Fig. III.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. III.16E), we observe little correlation between the dynamics of global temperature and of plant taxonomic diversity (Fig. III.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., 2001a; 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. Zosterophyllopsids, 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. III.16D), possibly acting as a catalyst to the progressive demise of the basal-most tracheophytes, while favouring other groups (e.g., zosterophyllopsids). The colder climate beginning in the middle Emsian through the Middle Devonian may have reciprocally precipitated the zosterophyllopsid decline shown in Fig. III.7C (Cascales-Miñana and Meyer-Berthaud, 2015).

During the late Emsian-Eifelian, lycopsids continuously diversified, whilst other clades such as the zosterophyllopsids and euphyllophytes (mainly basal euphyllophytes) were declining, particularly in the Eifelian (Fig. III.7C, D). There is increasing evidence that lycopsids were the dominant (Fig. III.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 zosterophyllopsids.

The diversification of vegetation in the Late Devonian was accompanied by generally warmer conditions (Scotese et al., 2021, Fig. III.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 $p\text{CO}_2$ levels have been implicated in the absence of megaphyllous leaves before the middle Pragian (e.g., *Eophyllophyton*; Fig. III.3F) as they would have quickly overheated, restricting photosynthetic efficiency. However, as atmospheric CO_2 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 would 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. III.7D, III.10J–L). The lycopsids, in contrast, were also prominent components of Middle Devonian and later Palaeophytic vegetation (Figs. III.7B, III.10D–F), but did not develop megaphyllous leaves and achieved tree-sized statures using different strategies than euphyllophytes (Meyer-Berthaud and Decombeix, 2009).

III.1.5.4. 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., zosterophyllopsids, 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 zosterophyllopsids seem to have had lower longevities and diversification rates than euphyllophyte groups and lycopsids (Fig. III.13B).

Based on Foote's (2000b) approach (Fig. III.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. III.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. III.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. III.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. III.9A) particularly among the lycophytes (Fig. III.10A). However, as shown by Fig. III.15, most of this initial pattern cannot be distinguished from sampling bias, especially during the Silurian. Interestingly, although zosterophyllopsids 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. III.7B–C, III.10D, G), where significant peaks are observed

(Fig. III.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. III.6, III.7B, D).

The Emsian and Eifelian represent the time of transition between the Early and Late Eophytic Flora reflected by the change from a zosterophyllopsid- to a lycopsid-dominated vegetation. Cascales-Miñana and Meyer-Berthaud (2014, 2015) suggested that the zosterophyllopsid 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. III.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. III.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 (zosterophyllopsids, lycopsids, and euphyllophytes).

The Middle Devonian witnessed the appearance of the first forested landscapes as euphyllophyte (pseudosporochnalean cladoxylopsids 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. III.7B, E, III.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 (Senkevitsch 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, cladoxylopsids and lycopsids (Figs. III.7A, III.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. III.7B, D, III.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. III.8D, F). Indeed, spermatophytes do not appear to have diversified at the expense of lycopsids as they were both diversifying at this time (Figs. III.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; see also Cleal and Cascales-Miñana, 2021).

III.1.6. 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, zosterophyllopsids, 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 CO_2 levels in the evolution and radiation of euphyllophytes still requires further investigation. O_2 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.

III.1.7. 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., 2022a) 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 macrofossils. 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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The effect of geological biases on our perception of early land plant radiation

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Abstract

The Silurian–Devonian plant radiation was a critical development in the evolution of early terrestrial ecosystems. Characterising the diversity dynamics of this radiation has been a focus of numerous studies. However, little is known about the impact of geological bias on our perception of this event. Here, we use a new, comprehensive compilation of plant occurrences from North America, together with a Macrostrat lithological dataset, to elucidate the relationships between the palaeobotanical and geological records of early land plants. Results show that observed, raw diversity patterns at both species and genus ranks are significantly correlated with fluctuations of sedimentary rock volume, especially of non-marine fossiliferous deposits. For instance, the lack of sedimentary deposits before the Emsian (Early Devonian) makes it difficult to obtain an accurate depiction of the pre-Emsian plant diversification. However, complementary analyses reveal that sampling-standardised diversity patterns partially corrects the raw trajectories, especially at the genus-level if enough preserved non-marine sediments are available for sampling. Our findings highlight that geological incompleteness remains a fundamental bias for describing early plant diversification. This indicates that, even when sampling is extensive, observed diversity patterns potentially reflect the heterogeneity of the rock record, which blurs our understanding of the early history of land vegetation.

Keywords: land plants, Silurian, Devonian, diversity, sampling-standardisation, rock record

III.2.1. Introduction

Reliability of palaeontological diversity curves has been called into question due to the potential impact of a wide array of sampling, geological and taphonomic biases (e.g., Benton et al., 2011, 2013). This was based on the observation that diversity measures and various sampling proxies often co-vary across multiple marine and terrestrial groups (Peters and Foote 2001; Smith and McGowan, 2007, 2011; Smith et al., 2012). There are three main explanations: (1) the 'bias model', where fossil biodiversity is directly controlled by the rock record accessible to sampling (Raup, 1976; Peters, 2005; Smith, 2007a); (2) a third unaccounted element (e.g., sea-level), is synchronously driving both variables, frequently referred as the 'common-cause hypothesis' (Peters and Foote 2002; Peters, 2005; Butler et al., 2011); and (3) sampling proxies and diversity are at least partially redundant with each other, which can occur especially where the fossil record is patchy (Benton et al., 2011; Dunhill et al., 2018). Quantifying the impact of these biases is central for palaeodiversity studies. However, while major evidence has been documented from the marine realm (Smith, 2007a; Smith and McGowan, 2012), bias effects on the terrestrial record has not been so well investigated (Wall et al., 2011), especially for the early land plants.

In 1979, Knoll et al. suggested that, for a given time interval, there is a strong correlation between the outcrop area of non-marine deposits and the observed plant species diversity in North America. Unfortunately, their analysis was based on a distorted and impoverished dataset of what today are referred to as fossil-species (Cleal and Thomas, 2021), the diversity of which may bear little resemblance to the diversity of biological plant species (Cleal et al., 2021). Nevertheless, the results of Knoll et al. (1979) showed the importance of taking into account factors such as outcrop area when investigating diversity changes in the palaeobotanical record. Cascales-Miñana et al. (2013) further investigated this issue by testing the relationship between the volume of sedimentary rock and observed palaeobotanical diversity worldwide, which suggested that some changing patterns of diversity could be more apparent than real. However, these results were constrained by using period/system-level geological data that do not allow evaluating specific episodes of diversification.

Herein, for the first time, we integrate plant fossil and geological data at a finer temporal resolution to explore the Silurian–Devonian (~430–360 Ma) radiation of early land plants. Overall, this time interval is characterised by an explosive diversification in the palaeobotanical record during the Early Devonian followed by a series of increasing diversity fluctuations that capture the early transition from herbaceous to forested land ecosystems (Cascales-Miñana, 2016; Capel et al., 2021, 2022a). Nevertheless, the lack of detailed evidence about how geological biases influence our interpretation of the dynamics of early plant diversity calls into question the detailed timing and magnitude of this radiation. Indeed, this pattern contrasts with the microfossil record suggesting an earlier, and more important, pre-Silurian diversification (Wellman et al., 2013, 2022a). The cause of this discrepancy remains disputed, although other factors have been put forward such as taphonomic and/or sampling issues, the dearth of preserved non-marine sediments has been previously invoked (Kenrick et al., 2012; Decombeix et al., 2019). We attempt to correct this situation by discerning whether the observed radiation in the palaeobotanical record reflects to a true biological signal, or if it is mainly a product of the heterogeneity of the rock record. Like Knoll et al. (1979), we have focused on the North America records, which offer the best available data for comparing reliable occurrence data with sampling proxies.

III.2.2 Data and methods

The raw data consist of 421 fossil occurrences of North American plant species sampled from Ludfordian (late Silurian) to Famennian (Late Devonian)-aged lithostratigraphic units from the Paleobiology Database (PBDB, https://paleobiodb.org/), completed and revised with data extracted from primary literature. Locality, formation, age and depositional environment data were retrieved for each occurrence (Table III.S3 in the Supplemental Material[1]). Occurrence data were filtered to avoid synonymies, 'artificial' fossil-taxa (*sensu* Cleal and Thomas, 2021) and fossil-taxa known to belong to the same biological taxon (e.g., stems and foliage of the same plant but assigned to different fossil-taxa). Moreover, lithologic data belonging to 143 non-marine rock units covering the target time interval were extracted from Macrostrat (https://macrostrat.org/). The marine Macrostrat units re-interpreted as terrestrial in Davies and Gibling (2010) were also added.

For each rock unit, the range duration, environment of deposition, fossiliferous (macrofossil) character, as well as the maximum thickness and surface of deposits were listed (Table III.S4). From this, we calculated the rock volume and outcrop area per time interval (age/stage). Rock volume (polygon area x maximum thickness) was obtained from the volumes of each rock unit ranging into the target stage. In the case of a given rock unit covering more than one stage (Table III.S4), we applied a correction factor corresponding to the proportion of each time interval represented in the target interval. A further correction was added in mixed rock units (Table III.S4) corresponding to the proportion of non-marine deposits in each case. Outcrop area was inferred from the sediment coverage area (Peters and Heim, 2010), which represents the sum of column areas containing non-marine rocks.

Plant richness variation through time was estimated via the range-through approach and coverage-based rarefaction analysis (Alroy, 2010b). An optimal quorum value of 0.5 was found using 1000 iterations to generate sampling-standardised diversity curves. We operated a ‘maximum’ approach, where dated occurrences spanning two time-units were counted in both. Size-based rarefaction curves were further produced to evaluate sampling levels between time units. To this, we set a resampling quota representing maximum observed within-stage diversity (Marcot et al., 2016), which indicated the time intervals with insufficient sampling coverage. Diversity analyses were conducted from both total records and only non-marine occurrences.

Correlation between diversity metrics and sampling/geological measures was tested using Spearman’s rank coefficients (r_s). Correlation analysis was run from both raw and generalised-differenced (detrended) data to avoid false positives due to autocorrelation. Detrended data were obtained using Graeme Lloyd’s gen.diff function. *P*-values lower than 0.05 were considered as significant. Data analysis was performed from R environment (version 3.5.2) using the package ‘epaleo’ (version 0.8.27; Monnet C., University of Lille).

III.2.3. Results

Both observed (Fig. III.17A, Fig. S4A) and sampling-standardised (Fig. III.17B, Fig. S4B) plant richness broadly mirrors rock volume trend (Fig. III.17C). For instance, the major Early Devonian

(Emsian) diversity pulse and the subsequent fluctuation pattern follows the main variations of non-marine rock volume. Both eustatic sea-level and non-marine outcrop area also increase throughout the Devonian (Fig. III.17D). However, rock volume displays more variability between stages than outcrop area, being extremely limited before the Emsian and closely resembling diversity pattern (Fig. III.17C). Correlations between raw time series are all strong as is often the case for long-term trends in such analyses (Table III.1). However, detrended correlations (Table III.1) solely identifies the number of localities and volume of fossiliferous deposits as a significant predictor of both species and genera diversity over shorter timescales. Correlation analysis further demonstrates that standardised diversity does not exhibit significant covariations with any measures of sampling effort (e.g., fossil localities) and that the amount of fossiliferous rock volume remains the best diversity predictor (Table III.1). Rarefaction curves (Fig. III.18) suggest incomplete sampling before the Pragian and the presence of a Middle Devonian (Eifelian) gap. Importantly, the Eifelian depletion of plant diversity is reflected in the pattern of rock volume, which further supports the impact of geological signal on observed diversity (Fig. III.17A–C). Complementary analysis based on non-marine records provided similar results, and likewise suggested generic diversity could be less influenced by sampling (Table III.S5, Fig. III.S5).

TABLE III.1. CORRELATION ANALYSIS BETWEEN OBSERVED AND SAMPLE-STANDARIZED DIVERSITY AND CONSIDERED SAMPLING PROXIES.

Sampling proxies	Observed diversity								Sample-standardized diversity							
	Genera				Species				Genera				Species			
	Raw		Detrended		Raw		Detrended		Raw		Detrended		Raw		Detrended	
	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p
Plant-bearing formations	0.83	**0.008****	0.24	0.570	0.82	**0.006****	0.36	0.385	0.77	**0.025***	-0.07	0.879	0.77	0.025	-	-
Plant-bearing localities	0.70	**0.037***	0.86	**0.007****	0.73	**0.025***	0.93	**0.001****	0.52	0.183	-	-	0.43	0.289	-	-
Non-marine outcrop area	0.81	**0.009****	-0.12	0.778	0.78	**0.013***	-0.12	0.779	0.71	**0.047***	0.60	0.148	0.79	**0.021***	0.04	0.939
Non-marine rock volume	0.88	**0.002****	0.48	0.233	0.85	**0.003****	0.67	0.070	0.71	**0.047***	-0.07	0.879	0.88	**0.004****	0.64	0.119
Non-marine fossiliferous rock volume	0.95	**0.000*****	0.79	**0.021***	0.95	**0.000*****	0.83	**0.010****	0.76	**0.028***	0.46	0.294	0.83	**0.010****	0.82	**0.023***

Note: Data analysis based on raw and generalised-differenced (detrended) data. In each case, Spearman's rank coefficients (r_s) with their corresponding probability values (p) are shown. Significant ($^{*}p < 0.05$), highly significant ($^{**}p < 0.01$), and very highly significant ($^{***}p < 0.001$) correlations appear in bold.

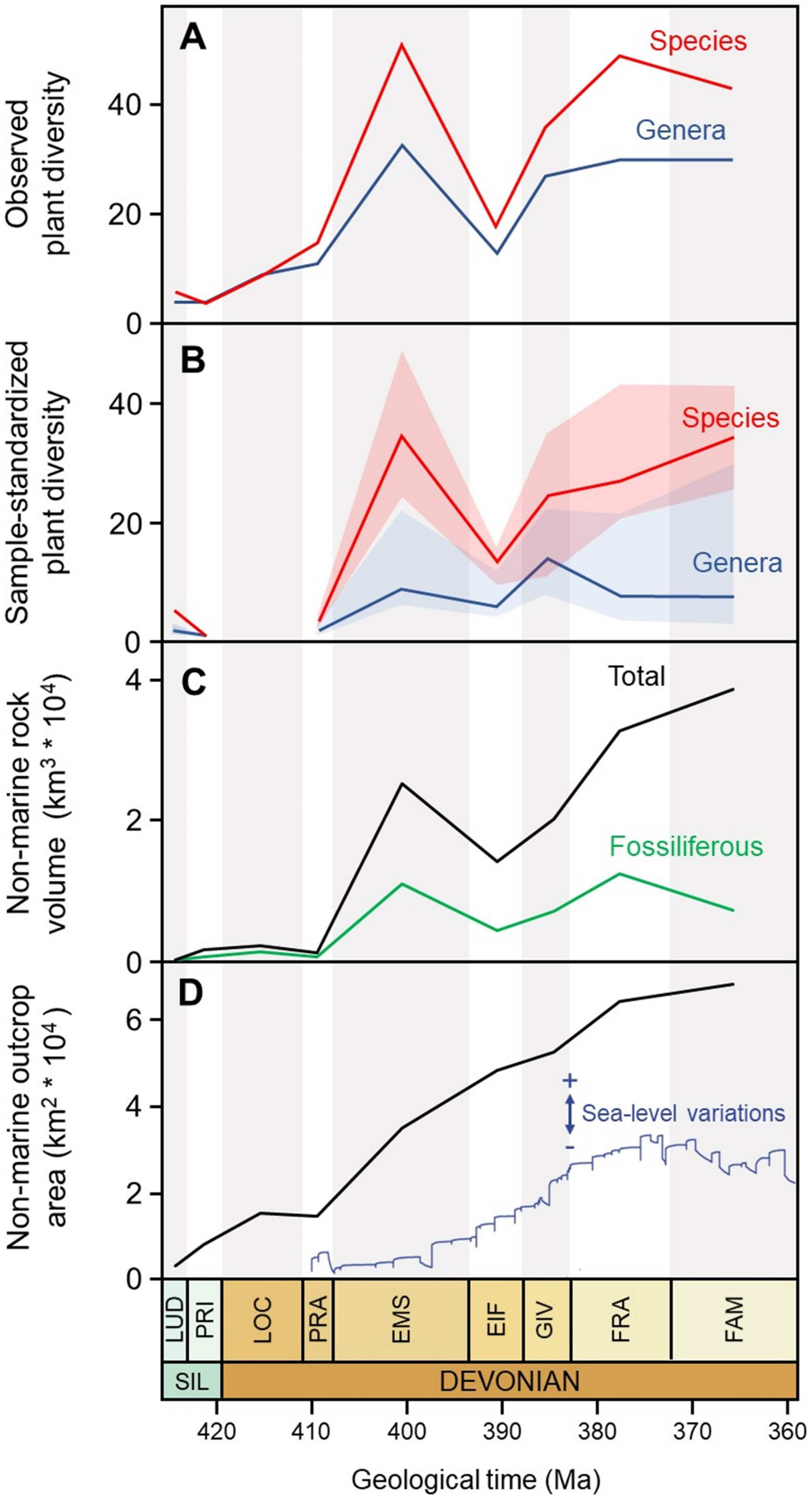

Figure III.17. Silurian–Devonian variations of plant diversity and geological proxies in North America. Diversity patterns based on observed (A) and sampling-standardised (B) values. Lighter areas represent 95% confidence interval (B). (C) Non-marine outcrop area and sea-level fluctuations (extracted from Johnson *et al.* 1985). (D) Non-marine rock volume. Abbreviations: SIL, Silurian; SHE, Sheinwoodian; HOM, Homerian; GOR, Gorstian; LUD, Ludfordian; Wen., Wenlock; Lud., Ludlow; Pri., Pridoli; LOC, Lochkovian; PRA, Pragian; EMS, Emsian; EIF, Eifelian; GIV, Givetian; FRA, Frasnian; FAM, Famennian.

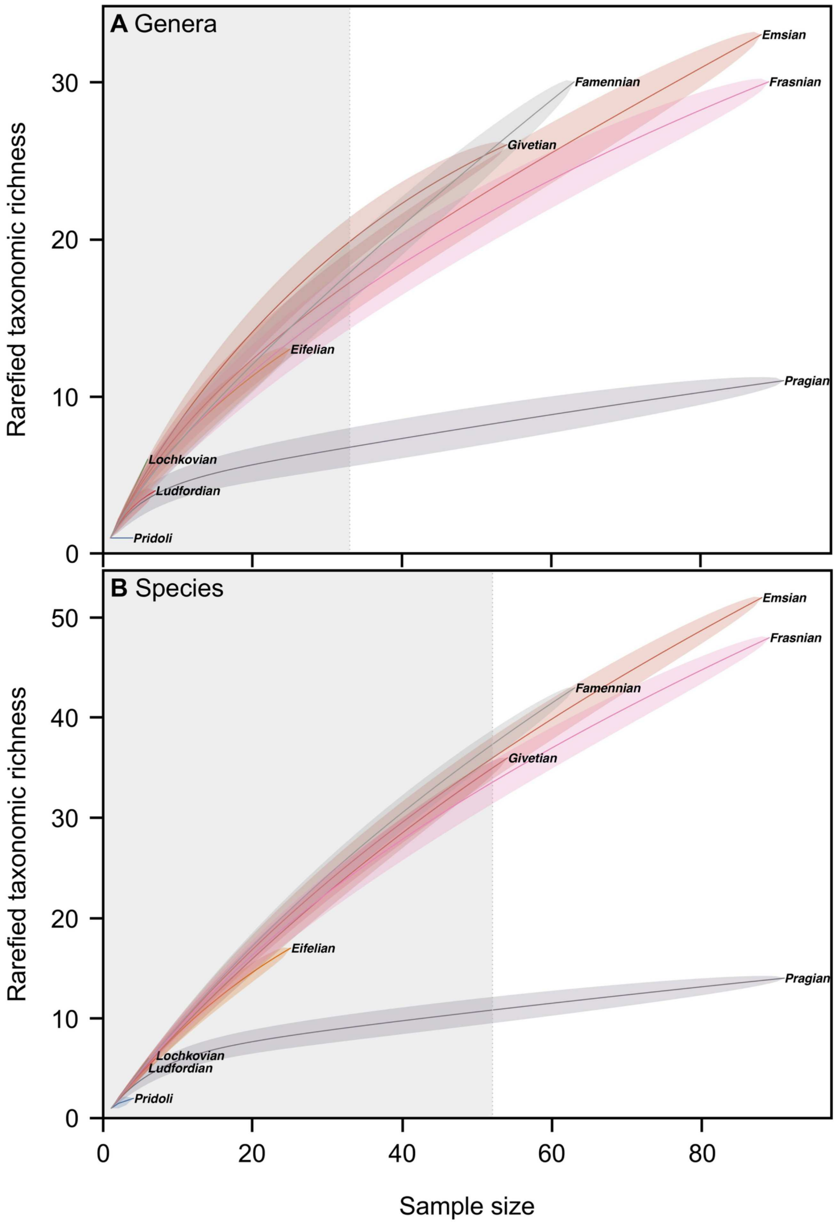

Figure III.18: Genera (A) and species (B) sized-based rarefaction curves per time interval. Colour area around each curve shows 95% confidence interval. Grey area represents rarefaction quota. See Methods for details.

III.3.3. Discussion

A selection of sampling proxies allegedly accounting for both sampling effort and heterogeneity of the rock record, were tested to identify biasing factors (Table III.1). Firstly, formation counts failed to capture variations in thickness and aerial exposure known to greatly influence the amount of rocks to sample (Dunhill et al., 2018), perhaps partly explaining the lack of meaningful correlation in this instance with diversity (Table III.1). Likewise, outcrop area has faced recent criticisms linked to its failure to reflect actual exposure area, hence, not representing accurately the potential to recover fossils

(Dunhill et al., 2014a). This mechanism may arguably justify the absence of correlation once data are detrended (Table III.1).

Enhanced effort in discovering new localities yielding plant fossils logically results in a higher number of described taxa. Nonetheless, correlations may also emerge since the richest fossiliferous units attract palaeontologists, making the directionality of the relationship difficult to disentangle (Dunhill et al., 2014a; Table III.1). Regardless, decoupling of the relationship is expected between both variables as sampling progresses as it becomes increasingly plausible to find already described taxa. Sampling of Devonian plants appears, at first glance, to not have been thoroughly completed (Fig. III.18). One exception occurs in the Pragian but is uniquely linked to a monographic effect (Fig. III.18). However, Wall et al., (2011) suggested that the original pool of preserved terrestrial biodiversity is so restricted that any new discoveries of localities still leads to the description of a significant number of new taxa, even when sampling is adequate. Since North America is a historically well-sampled continent for Devonian plants, so sampling may have been itself limited by the geographical and geological context (i.e., Devonian exposure of continental rocks), explaining the shape of rarefaction curves (Fig. III.18, III.S5). This effect would certainly be reflected in a correlation with non-marine rock volume or outcrop area, as more material leads to more specimens being collected and described, resulting in higher recorded diversity. Non-marine fossiliferous rock volume presents the strongest correlation with observed diversity, more than rock volume as a whole (Table III.1). Contrary to total non-marine rock volume, the use of macro-fossiliferous rock units removes, at least partially, the impact of taphonomic/ diagenetic processes precluding macrofossils to be preserved initially, whilst including all potential plant-bearing units, to mitigate redundancy (Peters and Heim, 2010). These lines of evidence imply that plant diversity trajectories are genuinely biased by the quantity of fossiliferous non-marine rocks through time.

Beyond the bias of the number of terrestrial deposits, there is also the influence of their spatial distribution. As shown by Close et al. (2017), apparent diversity fluctuations can be linked to changes in the spatial extent of sampling. However, a subcontinental scale study such as this one, mitigates the impact of this factor as vegetation differences across regions are less important than at the global scale.

Additionally, data for each stage consistently come from the same regions: the Appalachians, the Arctic Archipelago and scattered records from the western part of the continent mostly covered by epireic seas during this period (Scotese, 2021), making spatial heterogeneity in sampling a non-preponderant factor to explain diversity changes.

Eustatic variations in sea-level is often invoked to explain covariation between rock volume or outcrop area and diversity, although its existence in the terrestrial realm remains equivocal (Peters, 2005, Benton et al., 2013). Under the 'common cause' principle, sea-level rise reduces terrestrial sedimentary accommodation space, and concurrently diminishes habitable area for plants, lowering preserved biodiversity. Devonian sea-level rise is concomitant with the shift towards increased non-marine outcrop area, volume, and diversity, and so is incompatible with this scenario (Fig. III.17D). An alternative mechanism is that during high stands, plant diversity can increase through greater habitat fragmentation, whilst the potential of preservation in shallow marine environments increases (Butler et al., 2011). This latter hypothesis can likewise be rejected since: (1) no significant trend was identified in the dataset towards an increase of taxa preserved in non-marine sediments throughout the Devonian (Table III.S3); and (2) impact of endemisms is probably strongly overprinted by the scarcity of non-marine deposits (Wall et al., 2011). Preserved rock volume depends on the original accommodation space resulting from interactions between tectonic events and subsequent erosion (Davies and McMahon, 2021), and not solely sea-level fluctuations, possibly explaining the apparent lack of relationship.

Interestingly, observed genus-level diversity is more decoupled from the non-marine rock record than species diversity (Table III.1). Fig. III.18 shows that sampling is even less complete at the species level, indicating that the amount of fossiliferous rock volume available for sampling is even less adequate to retrieve accurate species counts. This may at least partly explain why sampling-standardised species diversity remains significantly correlated with this proxy (Table III.1). Higher-level taxa with longer longevities may also diminish the effect of short-term variation of the rock record (Smith, 2007a). Another possibility is that increased preserved rock quantity leads to larger amounts of fragmentary fossils, in turn artificially inflating species count by palaeontologists naming new species based on fragments that cannot be synonymised with similar taxa (Benton et al., 2013). Plant fossil nomenclature makes plant diversity studies particularly sensitive to the latter as different organs of the same plant may be classified as separate species or genera (Cleal et al., 2021).

Sampling-standardised patterns (Fig. III.17B) seem to, at least, partially correct uneven sampling along with intensity, although a marginally significant correlation remains at the species-level with non-marine fossiliferous rock volume, indicating that sampling coverage is related to geological completeness (Wall et al., 2009; Table III.1). A more pervasive bias remains, in that this continental-scale study does not offer a representative sample of past biodiversity, as < 0.5% of original habitable area is preserved, and as some stages are severely underrepresented in non-marine facies (Wall et al., 2009; Close et al., 2017; Fig. III.17D). A striking example occurs before the Emsian where low observed and subsampled plant diversity can be directly linked to the lack of non-marine units (Fig. III.17B, E), even though global patterns suggest a massive diversification (Capel et al., 2022a). While lack of terrestrial deposits can partly explain the scarcity of plant macrofossils (Fig. III.17D, Table III.1), this factor cannot solely explain this 40 myr gap. Preservation of allochthonous assemblages in marine sediments remains possible and is relatively common (Table III.S3). This is exemplified in the fact that plant macrofossils in the Silurian are exclusively found in marine sediments (Wellman et al., 2013). Difference in preservation potential between early land plant and spores may provide a better explanation to the total absence of plant fossils (other than putative fragments) during this period (Gensel et al., 2008).

Our results overall reveal that when sampling is extensive, observed patterns of early plant diversity still partly reflect the heterogeneity of the rock record, and this tends to obscure our understanding of the Silurian–Devonian terrestrialization. In fact, the scarcity of non-marine sediments, not controlled by sea-level changes but rather by the continental tectonic context, seems to constrain the amount of diversity retrievable. Furthermore, taphonomic biases, especially in the Ordovician and early Silurian periods, may also have had a part to play but few studies have focused on this aspect. It appears that only once a certain number of terrestrial deposits is accessible for sampling that coverage-based rarefaction can begin to estimate true past biodiversity more accurately. Lack of terrestrial sediments, especially before the Emsian in North America prevents such a scenario. Thus, the observed sudden 'explosion' of global plant diversity shown from the latest Silurian–Early Devonian macrofossil record is probably strongly controlled by major facies change in well-sampled areas (e.g., Western Europe, China), which remains a biasing factor at least throughout the rest of the Devonian.

Supporting information to this manuscript can be found in appendix 3.

Author contributions. **Conceptualization** E. Capel, C. Monnet, B. Cascales-Miñana; **Data Curation** E. Capel; **Formal Analysis** C. Monnet; **Funding Acquisition** T. Servais, B. Cascales-Miñana; **Investigation** E. Capel, C. Monnet, C.J. Cleal, J. Xue, B. Cascales-Miñana; **Methodology** E. Capel, C. Monnet, B. Cascales-Miñana; **Project Administration** E. Capel, B. Cascales-Miñana; **Resources/Software** C. Monnet, **Supervision** E. Capel, B. Cascales-Miñana; **Validation** E. Capel, C. Monnet, B. Cascales-Miñana; **Visualization** E. Capel, B. Cascales-Miñana; **Writing – Original Draft** E. Capel; **Writing – Review & Editing** E. Capel, C. Monnet, C.J. Cleal, J. Xue, T. Servais, B. Cascales-Miñana.

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Chapter IV: Spatial dynamics in early land plant radiation

This chapter consists of a single article entitled “**New insights into Silurian-Devonian palaeophytogeography**” submitted to the journal *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* and currently undergoing peer review.

New insights into Silurian–Devonian palaeophytogeography

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Abstract

The Silurian–Devonian plant radiation was an event triggered by the progressive colonization of subaerial habitats. Nevertheless, it is still unclear whether this radiation was globally uniform or whether alternative diversification scenarios emerged depending on the geographical context. Here, we report on early land plant diversity patterns across different previously defined palaeogeographical units (i.e., Laurussia, Siberia, Kazakhstania, NE, NW and South Gondwana). Results reveal apparent diachronous events of diversification and extinction partly resulting from uneven sampling effort, especially in Gondwana. Global diversity patterns are most similar to the Laurussian curve suggesting that the observed global dynamics are mostly controlled by the historically best-sampled continents. Nevertheless, changes in floral composition through time become less prone to sampling biases, and reveal geographical disparities that indicate a non-random distribution of the Silurian–Devonian vegetation. Consequently, we further performed a set of multivariate analyses to revisit the palaeophytogeographical signal through four time-intervals (i.e., Silurian–Lochkovian, Pragian–Emsian, Middle and Late Devonian), which revealed that spatial differentiation of vegetation was mainly controlled by climatic conditions and to a lesser extent geographical barriers. Most importantly, we find the maximum provincialism during cooler periods such as during the Silurian–Lochkovian and Middle Devonian, whilst warmer periods (Pragian–Emsian and Late Devonian) coincided with increased cosmopolitanism among early land plants.

Keywords: Devonian, palaeophytogeography, phytochoria, plant macrofossils, Silurian

IV.1. Introduction

Recent advances in the study of early land plant macrofossils have revealed a diversity pattern shaped by the overlapping dynamics of multiple floras (Capel et al., 2021). However, this was based on global-scale diversity compilations that may homogenize geographical disparities at a regional to continental scale. This raises the question of whether diversity patterns are, as a whole and in individual groups, synchronous between different study areas. The same questions have arisen for the understanding of the global Phanerozoic marine diversity curves (e.g., McGowan and Smith, 2008) or the Mesozoic tetrapod record, both marine and terrestrial (e.g., Benson et al., 2010; Close et al., 2017). There is now a growing body of analyses that imply that the global diversity patterns in the fossil record are not really global, but regionally heterogenous (Close et al., 2020a; Flannery-Sutherland et al., 2022).

The few studies that previously focused on reconstructing regional early land plant diversity trends (Raymond and Metz, 1995; Xiong et al., 2013; Cascales-Miñana and Meyer-Berthaud, 2015; Xue et al., 2018) provided contrasting results regarding the relative timing of land plant radiation. Such patterns are potentially affected by sampling and geological biases that hindered obtaining a representative sample of original past biodiversity (Capel et al., 2022a). Importantly, while an analysis of the global diversity curve is a first step in identifying the impact of climatic and/or geographical barriers on dispersion and diversification of early land plants (e.g., Cascales-Miñana and Meyer-Berthaud, 2015; Xue et al., 2018), many questions still remain regarding the spatial distribution of vegetation and its degree of differentiation during the terrestrialization process (Gerrienne et al., 2016; Servais et al., 2019).

Most previous work on Silurian–Devonian palaeophytogeography was done over 30 years ago (Raymond et al., 1985; Raymond, 1987; Edwards, 1990a; Edwards and Berry, 1991), and so requires re-evaluation. Many of these earlier studies used non-numerical approaches (e.g., Petrosyan, 1967; Edwards, 1973; Gensel, 1986; Edwards, 1990a; Edwards and Berry, 1991), at least partly because of the limited number of fossil occurrences that were then available. However, there are now substantial new datasets especially from previously under-sampled areas (e.g., Gondwana and the South China block) that make it more feasible to use multivariate analyses (e.g., Pardoe et al., 2021) to assess the phytogeographical relationships. In addition, most of these earlier studies looked at the Silurian–Early Devonian fossil record, whilst Middle and Late Devonian palaeophytogeography were only partially evaluated, despite this being a time-interval that was arguably just as critical in early plant evolution, for instance seeing the development of the first-forested ecosystems (Stein et al., 2012, 2020; Berry and Marshall, 2015; Capel et al., 2021).

Earliest evidence from cryptospores indicates a possible Gondwanan origin of earliest land plants, because the oldest land-plant derived spores were found during the earlier parts of the Ordovician from this large palaeocontinent (Rubinstein et al., 2010; Servais et al., 2019; Benachour et al., 2022). Subsequently an apparent cosmopolitanism of cryptospores of early land plants during the late Middle and Late Ordovician is observed (Steemans, 2000; Wellman et al., 2003, 2013, 2022b), although this cannot be corroborated from the poor macrofossil record. A certain level of provincialism has then been suggested for the following late Silurian and Early Devonian, but there were significant differences in the methods used in the various studies to recognise the palaeobiogeographical provinces (e.g., Raymond et al., 1985, 2006; Edwards and Berry, 1991). See Edwards and Berry (1991) and Wnuk (1996) for a comprehensive overview of previous attempts and the inconsistencies that ensued for defining palaeophytogeographical units, and their outlines. As with the marine faunas, provincialism is assumed to have decreased through the Devonian Period, and Late Devonian floras are generally assumed to be rather cosmopolitan (Edwards, 1973; Gensel, 1986; Edwards and Berry, 1991; Wnuk, 1996; Streel et al., 2000; Raymond and Metz, 2004).

Here, we attempt to clarify discrepancies between previous studies and to obtain an updated framework for the spatial differentiation of Silurian–Devonian vegetation. Firstly, we evaluate plant diversity changes through time within different palaeogeographical regions to detect spatial disparities in diversification patterns. Secondly, using a combination of multivariate statistical analyses, phytochorial (i.e., paleophytogeographical) units are re-defined, and the spatial distribution of vegetation is discussed. We further assess the influence of factors such as geographical and climatic barriers on the dispersion and diversification of early land plants.

IV.2. Data

A new occurrence-based compilation of plant macrofossils was developed from the Silurian–Devonian global-scale dataset of Capel et al. (2022a) and primary literature (Table IV.S1, Text IV.S1). Plant richness was slightly modified by inclusion of recently described taxa, such as *Teyoua* (Huang et al., 2022) or *Taungurungia* (McSweeney et al. 2022a). In total, the raw data consists of nearly 900 fossil occurrences belonging to 410 plant genera (Table IV.S1), tabulated across 48 different geographical units (Table IV.1). Each geographical unit corresponds to one or more plant fossil-bearing localities often grouped at the regional (e.g., Svalbard) or at national-level (e.g., Morocco). Previous studies demonstrated that grouping closely situated localities is preferable, as assemblages of identical age, only separated by a short distance, may be very distinct in terms of composition due to non-spatial factors (e.g., local habitat conditions, preservation and/or facies), appearing consequently as 'mismatched' in palaeogeographical analyses (e.g., Raymond et al., 1985). Grouping of fossil localities was also carried out by taking into account palaeogeography. For instance, Siberia was a separate palaeocontinent during the Silurian–Devonian time interval (Scotese, 2021), and its assemblages should therefore be differentiated from those of European Russian assemblages which was presumably part of Laurussia at this time (Fig. IV.1, Table IV.1). Plant occurrences were compiled at stage and sub-stage level. Sub-stages are informal subdivisions of approximately equal duration corresponding to temporal divisions that have been widely used in the literature for dating plant fossils. Absolute ages are according to the International Chronostratigraphic Chart 2022 (https://stratigraphy.org/ICSchart/ChronostratChart2022-02.pdf).

Data compilation was achieved at the genus-level as the vast majority of plant species in the Silurian–Devonian only occur once, making the available amount of data even less useful for reconstructing palaeogeographical relationships. Furthermore, taxa identified at the species-level may be more subject to 'regional taxonomic bias' where a newly discovered plant-fossil may be described as a new species linked to different regional practices or lack of communication due to language barriers (Raymond, 1987). This bias is somewhat mitigated at the genus-level, although it is not exempt from it. Raymond

(1987) and Raymond et al. (2006) addressed this potential issue and used plant traits rather than taxonomic (genus) names, but the results were almost identical, which demonstrates that taxonomy is

Table IV.1: Geographical units considered in this study with their corresponding palaeogeographical unit.

Abbreviation	Geographical unit	Palaeogeographical unit
ANH	Anhui, China	NE Gondwana
ANT	Antarctica	South Gondwana
ARC-CAN	Arctic Canada (Nunavut, Alaska)	Laurussia
ARG	Argentina	South Gondwana
AUS	Australia	NE Gondwana
BEL	Belgium	Laurussia
BLR	Belarus	Laurussia
BOL	Bolivia	South Gondwana
BRZ	Brazil	South Gondwana
C-REP	Czech Republic	NW Gondwana
CHL	Chile	South Gondwana
COL	Colombia	NW Gondwana
E-CAN	Eastern Canada (Quebec, Ontario, New Brunswick)	Laurussia
E-RUS	European Russia (West of Urals mountains)	Laurussia
E-USA	Eastern USA (Maine, New York, Pennsylvania, Virginia, W. Virginia, Kentucky, Ohio, Indiana)	Laurussia
EN-WLS	England/Wales	Laurussia
GER	Germany	Laurussia
GGD	Guangdong, China	NE Gondwana
GGX	Guangxi, China	NE Gondwana
GRL	Greenland	Laurussia
GZH	Guizhou, China	NE Gondwana
HUB	Hubei, China	NE Gondwana
HUN	Hunan, China	NE Gondwana
INM	Inner Mongolia, China	NE Gondwana
IRL	Ireland	Laurussia
JGS	Jiangsu, China	NE Gondwana
JGX	Jiangxi, China	NE Gondwana
KAZ	Kazakhstan	Kazakhstania
LAT	Latvia	Laurussia
LUX	Luxembourg	Laurussia
MOR	Morocco	NW Gondwana
N-FRA	Northern France	Laurussia
NOR	Continental Norway	Laurussia
POL	Poland	Laurussia
S-AFR	South Africa	South Gondwana
SBR	Siberia, Russia	Siberia
SCH	Sichuan, China	NE Gondwana
SCT	Scotland	Laurussia
SVL	Svalbard, Norway (Spitzbergen, Bear Island)	Laurussia
UKR	Ukraine	Laurussia
VNZ	Venezuela	NW Gondwana
VTM	Vietnam	NE Gondwana
W-CAN	Western Canada (Alberta)	Laurussia
W-FRA	Western France	NW Gondwana

Table IV.1: Continued.

Abbreviation	Geographical unit	Palaeogeographical unit
W-USA	Western USA (Washington, Wyoming)	Laurussia
XNJ	Xinjiang, China	Kazakhstania
YUN	Yunnan, China	NE Gondwana
ZHJ	Zheijiang, China	NE Gondwana

appropriate in such palaeogeographical analyses. In addition, since the 1980s, communication between researchers across the world has greatly improved and this bias has tended to decrease over time; for example, *Junggaria spinosa* from Xinjiang, China in Dou et al. (1983) has been found by Cai et al. (1993) to be identical to *Eocooksonia* (*Cooksonella*) *sphaerica* from Kazakhstan described in Senkevitsch (1976). This remains an important issue, especially with floras described from the former-USSR, mainly Russia and Kazakhstan, although recent studies reviewing previously described floras have allowed more confident identifications, despite that some reports are often not illustrated or thoroughly described (i.e., Gutak et al., 2011). Other problems arise notably from plant fossil taxonomy, where different parts of the plant are assigned to different fossil-taxa: for instance, the records of *Archaeopteris* foliage and *Callixylon* stems have been combined. We have also excluded 'artificial-fossil genera' *sensu* Cleal and Thomas (2021), such as e.g., *Hostinella*, *Psilophytites* or *Dawsonites*.

IV.3. Methods

Firstly, we plotted the sampled in-bin diversity patterns of Silurian–Devonian plant genera at both a global scale, and at regional scales based on Scotese's (2021) main palaeogeographical regions, i.e., Laurussia, Siberia, Kazakhstania and Gondwana (Fig. IV.1). The former Gondwanan continent, being presumably spread from the South Pole to the Equator and therefore reflecting a wide variety of climates and landscapes, was divided into several areas: northwest (NW), northeast (NE) and South Gondwana (Fig. IV.1, Table IV.1). A dataset of global genus-level diversity was compiled based on the age-range of each occurrence and sub-datasets were created for each palaeogeographical unit (Table IV.1, Table IV.S2). In each dataset, biological affinity of genera was added based on Capel et al. (2021). Genus-level diversity for major clades (i.e., lycopsids, zosterophylls, monilophytes, progymnosperms and spermatophytes), and for each palaeogeographical unit was calculated to illustrate changes in vegetation

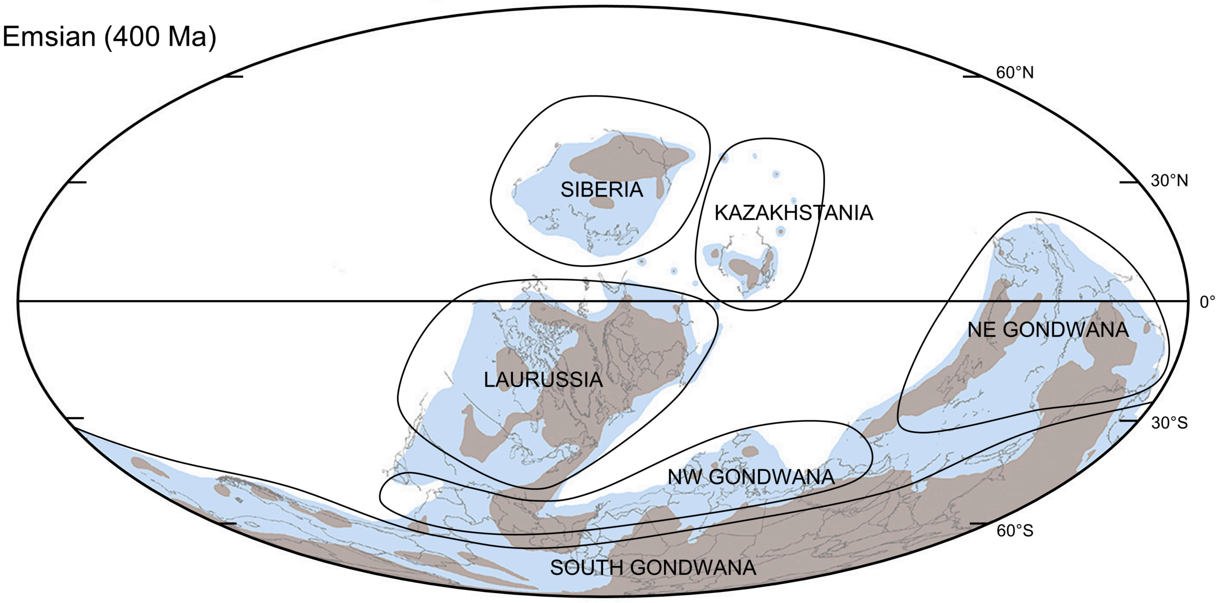

Figure IV.1: Palaeogeographical reconstruction for the Early Devonian (Emsian) showing the outlines of each palaeogeographical unit considered in this study. Modified from Scotese (2021).

composition through time. Taxa under open nomenclature (e.g., cf. *Sawdonia*) and associated occurrences were here included to obtain a more accurate representation of vegetational changes, since a more conservative approach may exclude a significant number of taxa and occurrences for which the higher-level classification is known (e.g., cf. *Sawdonia* spp. presumably having affinities with zosterophylls despite needing generic reassessment).

Secondly, palaeobiogeographical signals were identified via multivariate statistics. More specifically, we used a Detrended Correspondence Analyses (DCA; Hill and Gauch, 1980) complemented by additive clustering using the Neighbour-Joining approach (NJ; Saitou and Nei, 1987) to detect past “phytochoria” *sensu* Meyen (1987). This latter term is meant to refer to geographical areas defined by a uniform vegetation composition. Different ranks for fossil phytochoria based on their degree of similarities have been established (i.e., kingdom to district) by e.g., Meyen (1987). Previous works on the Silurian–Devonian period have often referred to their recovered phytochorial units as “palaeophytogeographical units” (e.g., Raymond, 1987, Raymond et al. 1985, 2006) without presuming their hierarchical level. Since phytochoria’s hierarchical system is a concept adapted for extant vegetation classification, Cleal (1991) proposed to refer to these fossil phytochoria as palaeokindoms, palaeoareas, palaeoprovince and palaeodistrict, respectively defined by supra-generic taxa, fossil genera, fossil species, and lastly by a few fossil-species (Cleal and Thomas, 2019, Pardoe et al., 2021).

However, the lack of hierarchical structure in our data (see below), precludes further classification within such a hierarchical scheme. DCA is an ordination technique often used to detect biogeographical signals (see Pardoe et al., 2021 and references therein). Correspondence analysis (CA) positions both samples (geographical units) and variables (taxa) in the same space maintaining correspondence between both (see e.g., Hammer and Harper, 2008 for details). DCA is conceptually similar but avoids the occurrence of arch and Pinocchio effects that may occur with a simple CA (Cleal, 2008; Hammer and Harper, 2008; Bault et al., 2022b).

Hierarchical cluster analyses (hCA) are commonly used to complement DCA to detect the palaeobiogeographical relationships between different areas. However, this approach can be problematic with data that are essentially gradational rather than hierarchical in structure (as is revealed for our data by the DCA) and Vörös et al. (2020) argued that NJ additive cluster analysis is better suited to such work (Vörös et al., 2020). Simpson's similarity index was used for NJ cluster analyses as it is recommended when there are large differences in sample size (Simpson, 1943; Uhl and Lausberg, 2008). Once phytochoria were established based on DCA and NJ cluster analyses, an ANOSIM test (10.000 permutations) was then performed to assess the degree of differentiation between them and if these differences are statistically significant (Clarke, 1993). Finally, a Similarity Percentage Analysis (SIMPER; Clarke, 1993) based on the Bray-Curtis index revealed the relative contribution of each taxon to the dissimilarity between defined phytochoria and their occurrence frequency in each phytochorion.

These analyses required the elaboration of matrices composed of incidence (presence/absence) data for each studied time interval (Table IV.S3). Taxa known to only occur in one geographic unit (endemics) were excluded from analyses, as they do not provide useful information to reconstruct spatial relationships. Taxa under open nomenclature and occurrences where the reliability has been questioned (marked as (?) in Table IV.S1) were also excluded to avoid spurious associations. Multivariate statistics was performed using PAST software (Hammer et al., 2001), v. 3.26. Each analysis was carried out for the Silurian–Lochkovian, Pragian–Emsian, Middle Devonian and Late Devonian time intervals, independently. These temporal divisions were adopted because they (1) broadly represent the subdivisions previously used in the literature (Raymond et al., 1985; Raymond, 1987; Raymond et al.,

2006) and (2) reflect the major floral changes observed in the macrofossil record (Capel et al., 2021, 2022a).

IV.4. Results and discussion

IV.4.1. Palaeogeographical differences in Silurian–Devonian plant diversity

Fig. IV.2 shows diversity trajectories of plant diversity at the global-scale and from each of the selected palaeogeographical units. Diversity fluctuations in Laurussia are strikingly similar to the ones observed at the global-scale, despite few differences, most notably the occurrence of an Emsian rather than a Pragian peak (Fig. IV.2A–B). The diversity pattern recorded in Siberia on the other hand, is highly dissimilar with diversity values higher in the Early Devonian than in the Middle–Late Devonian period (Fig. IV.2C). Diversity recovered in NE Gondwana (South China and Australia) is the second-highest among all palaeogeographical regions after Laurussia (Fig. IV.2E). Nevertheless, the pattern observed contrasts with that of Laurussia with a recognisable peak occurring in the Pragian, followed by a major decline in the Emsian–Eifelian period, until diversification resumes during the Givetian and overall increases during the Late Devonian (Fig. IV.2E). The Pragian peak in NE Gondwana appears to contribute significantly to the Pragian peak observed at the global scale (Fig. IV.2A, E) On the other hand, the poorest region in terms of diversity is NW Gondwana (Fig. IV.2F). South Gondwana presents the most distinct pattern of all palaeogeographical regions with very low diversity across most of the Silurian–Devonian period with, counterintuitively, the highest diversity being recorded in the Lochkovian (Fig. IV.2G).

These extensive inconsistencies in diversity fluctuations through time between the different palaeogeographical regions are not necessarily suggesting a different early land plant diversification scenario according to the palaeogeographical region. The global curve is itself an addition of diversities coming from very unevenly sampled regions (Fig. IV.2). For instance, Gondwana is considered the ‘cradle’ of early land plants as evidenced by the first cryptospores (Wellman et al., 2013) and trilete spores (Steemans et al., 2009; Gerrienne et al., 2010) and the first unequivocal plant macrofossils (Fig.

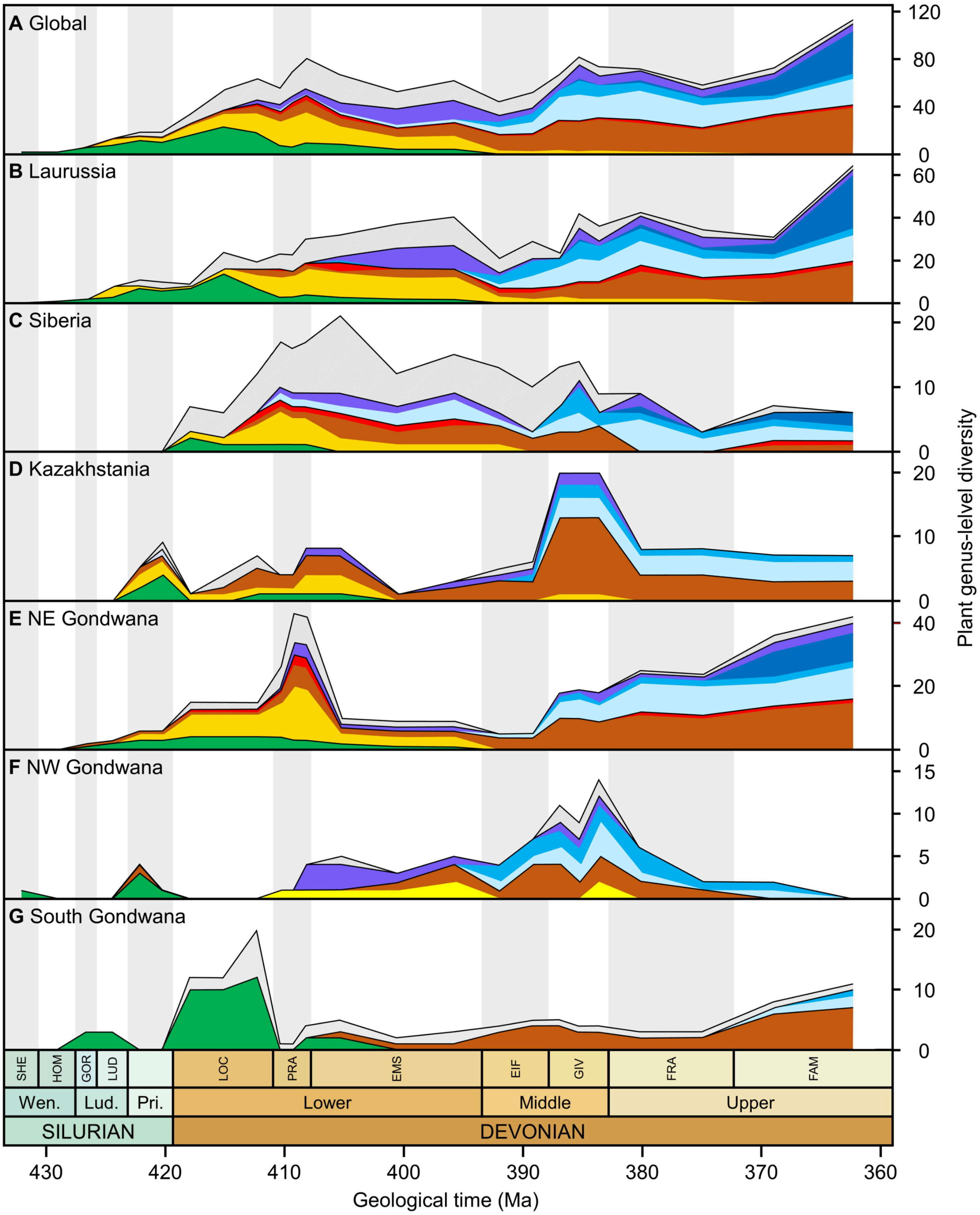

Figure IV.2: Sampled-in-bin diversity patterns of Silurian–Devonian plant macrofossil genera per phytogeographical unit. (A) Global; (B) Laurussia; (C) Siberia; (D) Kazakhstania; (E) NE Gondwana; (F) NW Gondwana; (G) Southern Gondwana. Colors: green = basal eutracheophytes and rhyniophytoids; yellow = zosterophylls; brown = lycopsids; red = other lycophytes; light blue = monilophytes; blue = progymnosperms; dark blue = spermatophytes; purple = other euphyllophytes; hashed grey = *Incertae sedis* taxa. Abbreviations: SHE, Sheinwoodian; HOM, Homerian; GOR, Gorstian; LUD, Ludfordian; Wen., Wenlock; Lud., Ludlow; Pri., Pridoli; LOC, Lochkovian; PRA, Pragian; EMS, Emsian; EIF, Eifelian; GIV, Givetian; FRA, Frasnian; FAM, Famennian.

IV.2F; Libertín et al., 2018) being recorded there, but Gondwana only accounts for a small proportion of global diversity in comparison with its size, although Chinese and Australian floras are now arguably better sampled. Even well-sampled regions such as Laurussia (Fig. IV.2B) are also showing a non-representative sample of past biodiversity linked to geological factors (i.e., amount of non-marine sedimentary rocks available for sampling). This factor has also been invoked to explain the apparent decreases of diversity in South China (Hao and Xue, 2013) and Siberia (Gutak et al. 2011). Lastly, the high proportion of *Incertae sedis* taxa in Siberia (Fig. IV.2D) also illustrates the necessity to revise previously described Russian floras (Benton et al., 2017; Edwards and Li, 2018).

Although face-value diversity may be biased, it is likely that all plant groups are equally affected by these biases, making it reasonable to extract evidence of vegetation changes from the fossil diversity trends. On one hand, several changes in vegetation appear more or less coeval such as the diversification of lycopsids, progymnosperms and monilophytes (Fig. IV.2). On the other hand, while all palaeogeographical units experience a massive radiation of zosterophylls during the Early Devonian, zosterophylls are absent in South Gondwana (Fig. IV.2G). Likewise, the flora in the Middle Devonian until the early Late Devonian is characterized by an impoverished lycopsid-dominated flora with an apparent absence of euphyllophytes (Fig. IV.2G), whereas an important radiation among several groups of euphyllophyte is observed in other regions (Fig. IV.2B–F), euphyllophytes only appearing in this region in the Famennian (Fig. IV.2G). Another apparent diachronous event is the spermatophyte radiation occurring earlier and more markedly in Laurussia than in other parts of the world (Fig. IV.2). In NE Gondwana, spermatophytes only appear in the Famennian, and many regions are still exempt of spermatophytes in the Famennian such as Kazakhstania, NW and South Gondwana (Fig. IV.2D, F–G) indicating an initially spatially-restricted spermatophyte radiation event. Nevertheless, this may also at least partly result from a sampling bias as spermatophytes have been recently found in the high latitudes of Gondwana in the late Famennian (Cyrille Prestianni, pers. comm.).

IV.4.2. New palaeogeographical patterns of early land plants

IV.4.2.1. Silurian–Lochkovian palaeophytogeography

DCA and NJ cluster analysis essentially revealed two highly differentiated phytochoria (Fig. IV.3A–B). These phytochoria are termed (1) 'Equatorial to mid-latitudes' as geographic units constituting this phytochorion are mostly located in the palaeotropics and (2) 'South Laurussia-West Gondwana' in reference to the corresponding unit found in Raymond et al. (2006) (Fig. IV.3C). Nevertheless, the NJ cluster analysis exhibit an intermediate cluster constituted of Australia, Xinjiang and Greenland (Fig. IV.3B). This apparent cluster has no biogeographical meaning and is caused by the shared occurrence of *Salopella* (Data S1, S3). The DCA on the other hand shows Australia, Xinjiang and Greenland more closely related to other regions of the Equatorial-low latitudes rather than the South Laurussia-West Gondwana phytochorion (Fig. IV.3A). This division into two phytochoria is additionally supported by the ANOSIM test with a high R value indicating statistically significant differences in composition between phytochoria ($R = 0.67$, $p < 0.01$). SIMPER analyses reveal that the equatorial-low latitude unit is characterized by the occurrence of *Zosterophyllum* whilst the other is mostly defined by the occurrence of *Cooksonia* and to a lesser extent *Aberlemnia*, a closely related taxon (Table IV.2). These three taxa alone explain more than 50% of the dissimilarity between the two phytochoria (Table IV.2).

The most recent palaeophytogeographical analysis using macrofossil taxa for this time interval was by Raymond et al. (2006). Our results differ significantly from their analysis although some common signals can be seen. Raymond et al. (2006) identified four units or 'phytochoria': their South Laurussian-Northwest Gondwanan unit essentially corresponds to our Southern Laurussian-Western Gondwanan phytochorion. On the other hand, the North Laurussian, Northeast Gondwanan and the Kazakhstanian unit are here captured as a single phytochorion. These three latter phytogeographic units found in Raymond et al. (2006) are all composed of two localities separated from each other by a very short distance with a near identical taxonomic composition. Therefore, it appears that the discrepancies with Raymond et al. (2006) are mainly linked to a (1) slightly different methodological approach, (2) the choice of lumping closely related localities into one regional unit, which affects the level of endemicity, and (3) the number of taxa included in the analyses. Wellman et al. (2013), using spores instead of macrofossils, adopted a similar strategy to the present study by avoiding the use of single localities and

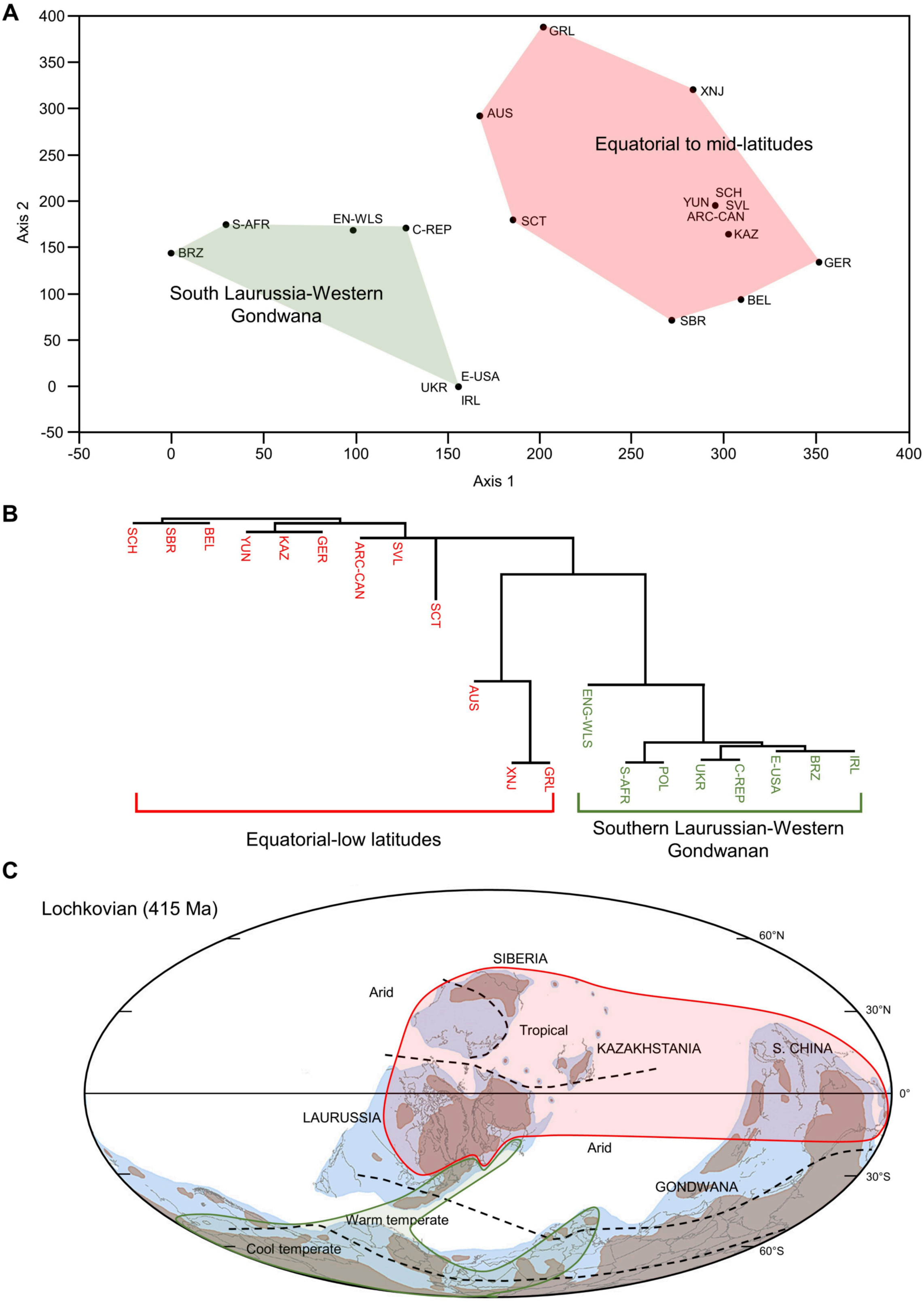

Figure IV.3: Silurian–Lochkovian palaeophytogeography. (A) DCA scatter plot of geographical units; (B) NJ clustering analysis; (C) extent of each phytochoria transposed onto palaeogeographic maps (Scotese, 2021). Colors: red = Equatorial-low latitudes; green = South Laurussia-West Gondwana. Climatic belts (dashed black lines) adapted from Boucot et al. (2013).

Table IV.2: SIMPER results for the Silurian–Lochkovian time interval identifying taxa contributing the most to the observed differences between each phytochoria. First column represents taxa contributing to 80% of the overall average dissimilarity (OAD) ranked in order of decreasing contribution to OAD. Second column shows the percentage of the dissimilarity that each taxon contributes to the OAD. Third column represents the cumulative percentage of dissimilarity. Last columns represent the mean frequency of taxa per phytochorion.

Taxon	Dissimilarity	Contribution (%)	Cumulative (%)	Frequency	
				Southern Laurussian/ Western Gondwanan	Equatorial/low latitudes
Cooksonia	21.21	23.34	23.34	1.00	0.17
Zosterophyllum	20.23	22.26	45.60	0.13	0.92
Aberlemnia	6.92	7.61	53.21	0.50	0.08
Drepanophycus	5.85	6.44	59.65	0.00	0.33
Salopella	5.72	6.29	65.94	0.13	0.25
Gosslingia	3.38	3.72	69.66	0.13	0.17
Baragwanathia	3.29	3.62	73.28	0.13	0.08
Uskiella	2.94	3.24	76.52	0.25	0.08
Eocooksonia	2.72	3.00	79.51	0.00	0.17
Dutoitia	2.60	2.86	82.37	0.25	0.00

compared relationships using larger regions (e.g., Baltica or Laurentia). Interestingly, their analysis showed that during the Pridoli, a Gondwanan and South Laurussian region clustered together, and Laurentia, South China and Baltica formed a second cluster (Wellman et al., 2013, fig. 29.10a,b), which broadly corresponds to our two phytochoria (Fig. 3C).

The outlines of the Western Gondwana-Southern Laurussia phytochorion are not clearly delimitated due to the lack of data, especially in Gondwana (Fig. IV.3C). Nevertheless, it is possible that it was even more extended, given that *Cooksonia* was possibly reported in the Pridoli of Libya (Daber, 1971; Wellman et al., 2013) and that rhyniophytoids were also excavated in the Ludlow series of Bolivia (Edwards et al., 2001b). Since most Laurussian localities containing *Cooksonia* are of late Silurian age, apart from the Anglo-Welsh basin where it occurs until the Middle Lochkovian, we can infer that the extent of the Western Gondwanan-Southern Laurussian phytochorion was gradually reduced until it was completely replaced by the flora composing the equatorial to mid-latitudes phytochorion by the end of the Lochkovian in Laurussia. For instance, the first Belgian and German assemblages are presumably at their oldest late Lochkovian in age (Schweitzer, 1983; Gerrienne, 1993; Gossmann et al., 2021), and are more closely resembling Pragian floras from England with taxa such as *Zosterophyllum*, *Drepanophycus* and *Gosslingia* than Anglo-Welsh middle Lochkovian assemblages (Edwards and Richardson, 2004). The outlines of these two phytochoria in this part of Laurussia are here not therefore perfectly defined because localities are not exactly coeval (Fig. IV.3C).

The equatorial to mid-latitude phytochorion is generally constituted of plants of a higher degree of complexity such as zosterophylls and lycopsids whilst the Western Gondwanan-Southern Laurussian is highly dominated by rhyniophytoids and other basal eutracheophytes (Tims, 1980; Kotyk et al., 2002;

Edwards and Richardson, 2004; Table IV.2). This replacement of rhyniophytoids by a zosterophyll-dominated flora is clearly seen occurring earlier in the Silurian in NE Gondwana and other equatorial palaeocontinents such as Kazakhstania, whereas Laurussian and especially South Gondwanan assemblages are still dominated by rhyniophytoids in the Lochkovian (Fig. IV.2). One interpretation could be that the zosterophyll-dominated Early Eophytic Flora (Capel et al., 2021) originally developed and replaced the Eotracheophytic flora quite early in the Silurian in equatorial to tropical regions. On the other hand, the rhyniophytoid-dominated Eotracheophytic Flora (Capel et al., 2021) persisted in the mid-to high latitudes in the Lochkovian, with Laurussia and Gondwana acting as refugia.

Climatic barriers appear to be the most prominent factor to explain the geographical distribution of both these phytochoria whilst geographical barriers appear to only be a minor component. The adaptation of zosterophylls and rhyniophytoids to warmer and colder climates respectively has been hypothesized in several studies (e.g., Edwards and Richardson, 2004; Raymond et al., 2006), although the features favouring these adaptations remain unclear. Regardless of the cause of these better adaptations, however, the warming climate during the late Silurian and Lochkovian seems to have triggered the expansion of the Early Eophytic Flora and caused the disappearance of the Eotracheophytic Flora from Laurussia at the end-Lochkovian (Scotese et al., 2021).

During this time, floras where zosterophylls occur (e.g., Australia, Svalbard and Arctic Canada) initially tend to be comparatively less diverse than coeval floras containing *Cooksonia* and other rhyniophytoids (e.g., Anglo-Welsh basin, South Africa and Brazil) (Gerrienne et al., 2001; Kotyk et al., 2002; Edwards and Richardson, 2004; Morris and Edwards, 2014; McSweeney et al., 2020; Gess and Prestianni, 2021). This is also reflected in the microfossil record where equatorial assemblages (Svalbard, South China) appear far less diverse than higher latitude assemblages (Wellman et al., 2022a). Wellman et al. (2022a) further reported that spore diversity in the Lochkovian from Spitzbergen and South Chinese assemblages was low with little endemism, and represented morphologies usually associated with zosterophylls. However, a fairly diverse Lochkovian macrofossil zosterophyll flora from Sichuan and Yunnan was recovered, accompanied by a high degree of endemism (e.g., Hao et al., 2007; Xue, 2009; Hao et al., 2010; Edwards et al., 2016). The discrepancy between macrofossil and microfossil endemism levels in South China may be linked to similarities in spore morphology among different zosterophyll taxa (Cascales-Miñana et al., 2022).

Higher diversity in the higher latitudes has been hypothesized by Wellman et al. (2022a) to be related to: (1) presumed scarcity of continental lands in the tropics (species-area effect); (2) extreme climate in the tropics combined with low oxygen levels; and (3) origination and diversification of land plants on Gondwana before a migration towards the lower latitudes. However, given the evidence presented above, our interpretation is that the dominant elements (i.e., zosterophylls) of the Early Eophytic flora may have firstly evolved in the tropical regions leading to an early replacement of the Eotracheophytic Flora. Perhaps, the appearance of the zosterophyll-like plants may have originally profoundly disrupted rhyniophytoid-dominated ecosystems through increased competition and consequently reduced diversity of rhyniophytoids, explaining original low diversity, but once a new equilibrium was reached, diversity increased again rapidly with zosterophylls as the dominant group (e.g., Laurussia, Fig. IV.2B). This explanation is corroborated by the dynamics observed in the Evolutionary Flora model, where the transition between floras is associated with an initial decrease of diversity. Once the Early Eophytic phase takes place, rhyniophytoids become minority elements of that flora and progressively disappear (Capel et al., 2021).

IV.4.2.2. Pragian–Emsian palaeophytogeography

DCA and NJ cluster analysis show a weakly-differentiated vegetation during this interval (Fig. IV.4A–B). Nonetheless, accentuated differentiation is observed between South Chinese regions alongside Australia with the rest of geographic units (Fig. IV.4A–B). Two phytochoria units can therefore be distinguished and are termed: (1) 'Equatorial to mid-latitudes' and (2) 'NE Gondwana' phytochorion based on their palaeogeographic distribution (Fig. IV.4C). This differentiation is corroborated by the ANOSIM test ($R = 0.44$; $p < 0.01$) despite a relatively low R-value indicating a higher degree of similarity between phytochoria compared to the Silurian–Lochkovian period. SIMPER analysis shows that the NE Gondwanan phytochorion is mostly characterized by the presence of

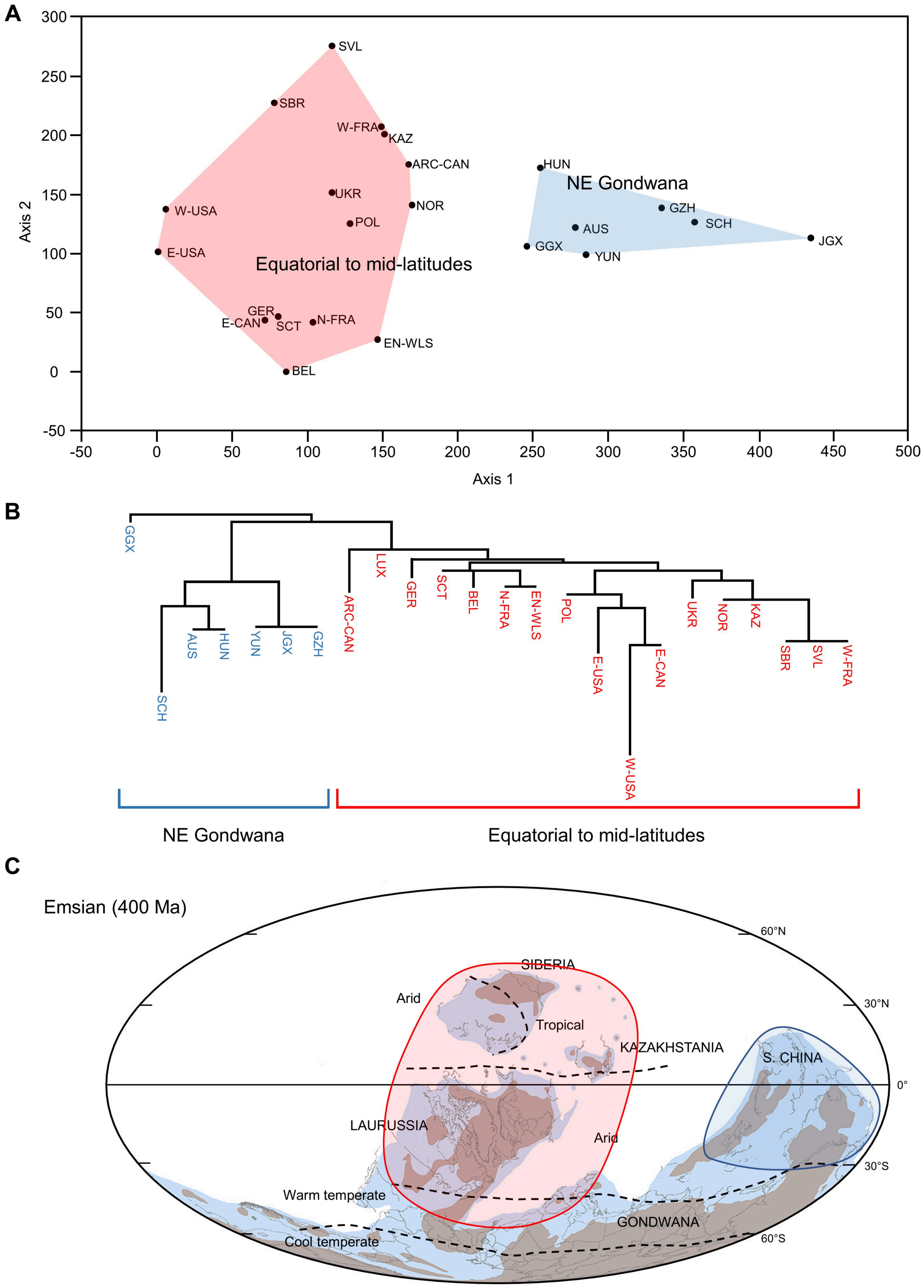

Figure IV.4: Pragian–Emsian palaeophytogeography. (A) DCA scatter plot of geographical units; (B) NJ clustering analysis; (C) extent of each phytochoria transposed onto palaeogeographic maps (Scotese, 2021). Colors: red = Equatorial-low latitudes; green = South Laurussia-West Gondwana. Climatic belts (dashed black lines) adapted from Boucot et al. (2013).

Table IV.3: SIMPER results for the Pragian–Emsian time interval identifying taxa contributing the most to the observed differences between each phytochoria. First column represents taxa contributing to 80% of the overall average dissimilarity (OAD) ranked in order of decreasing contribution to OAD. Second column shows the percentage of the dissimilarity that each taxon contributes to the OAD. Third column represents the cumulative percentage of dissimilarity. Last columns represent the mean frequency of taxa per phytochorion.

Taxon	Dissimilarity	Contribution (%)	Cumulative (%)	Frequency	
				Equatorial/ mid-latitudes	North-eastern Gondwana
Drepanophycus	10.23	12.61	12.61	0.82	0.29
Zosterophyllum	8.05	9.92	22.53	0.59	0.86
Psilophyton	7.74	9.54	32.07	0.65	0.29
Pauthecophyton	5.84	7.20	39.27	0.00	0.43
Adoketophyton	4.48	5.53	44.80	0.00	0.43
Demersatheca	4.48	5.53	50.32	0.00	0.43
Yarravia	3.92	4.84	55.16	0.00	0.43
Guangnania	3.05	3.76	58.92	0.00	0.29
Distichophytum	3.05	3.76	62.67	0.24	0.14
Cooksonia	3.04	3.74	66.42	0.18	0.14
Baragwanathia	2.69	3.32	69.73	0.06	0.29
Gosslingia	2.60	3.21	72.94	0.29	0.00
Uskiella	2.15	2.64	75.58	0.06	0.14
Renalia	2.10	2.59	78.17	0.24	0.00
Leclercqia	1.95	2.40	80.57	0.18	0.00

Zosterophyllum and several South Chinese endemic taxa such as *Pauthecophyton*, *Demersetheca* and *Yarravia* (recently combined with *Hedeia*), a taxon also shared with Australia (Table IV.3). The equatorial to mid-latitudes phytochorion on the other hand, is mostly characterized by the predominance of *Drepanophycus* and *Psilophyton*, but is not as well characterized by endemic taxa as the NE Gondwanan phytochorion (Table IV.3).

Raymond et al. (1985) covered the same time interval and identified three main biogeographic entities which were named ‘equatorial-low latitudes’, ‘South Gondwana’, and ‘Australia’. The ‘Equatorial–low latitudes’ unit corresponds to our ‘Equatorial to mid-latitudes’ phytochorion except for the South Chinese assemblages which were clustered into this unit by Raymond et al. (1985). More recent descriptions of the South Chinese floras demonstrated a greater similarity with Australian floras leading to Hao and Gensel (1998) suggesting a Northeastern Gondwanan province, similarly to Hao and Xue (2013). The recent reviews of Lower Devonian Australian floras by McSweeney et al. (2021, 2022b) further reinforced the ties between South China and Australian assemblages. The analysis made by Raymond (1987) using plant traits instead of taxonomic names recovered the same major units as Raymond et al. (1985) except for a province covering Kazakhstan and the Sahara (Algeria). This latter assemblage (Lemoigne, 1967) needs revision and was therefore not included in our analysis. Moreover, this unit was characterized by the occurrence of *Cooksonia* but our analysis shows that *Cooksonia* is not a strongly biogeographical meaningful taxon in the Pragian–Emsian, contrary to the Silurian–Lochkovian period (Tables IV.2–IV.3). The occurrence of a third South Gondwanan unit in Raymond et al. (1985) results from dating errors of the South African and Antarctican assemblages and accordingly were not re-utilized in the subsequent analysis by Raymond (1987). This unit was characterized by *Haplostigma* and *Paleostigma* from assemblages now known to be Middle Devonian in age. Nevertheless, *Haplostigma* was reportedly found in the Emsian of Argentina although it is most frequently found in Middle to Late Devonian assemblages, similarly to *Paleostigma* (Matsumura et al., 2015 and references therein).

Only one reliable assemblage from South Gondwana (Argentina) of Pragian–Emsian age has been described (Edwards et al., 2001a) but this could not be included in our analysis as it did not share any taxa with other Pragian–Emsian assemblages. These plants were originally thought to be Lochkovian in age as they displayed a similar grade of organisation with plants from Lochkovian English and Brazilian localities (Edwards et al., 2001a). However, these plants were subsequently re-assessed as late Pragian to early Emsian (Edwards et al., 2009). Southernmost Gondwanan assemblages seem to have retained characteristics of the Silurian–Lochkovian West Gondwana-South Laurussia phytochorion and by extension, the Eotracheophytic Flora (Fig. IV.2G; Capel et al., 2021). It appears that the early phase of the Eophytic Flora never reached the southernmost latitudes. However, description of new floras in Southern Gondwana are required to confirm this assumption. On the other hand, Peri-Gondwanan and assemblages on the northern margin of Gondwana such as the one recorded in France (Armorica) are clearly closer in composition to other Laurussian localities compared to the Argentinian assemblage (Gerrienne et al., 1999; Ducassou et al., 2009; Gerrienne et al., 2010). Gerrienne et al. (1999) nevertheless argued that despite the similarities with other Laurussian assemblages, Morocco might represent a separate phytogeographical sub-unit.

The Pragian–Emsian climate shows apparent marked fluctuations between colder and warmer conditions (Scotese et al., 2021). Nonetheless, palaeotemperature reconstructions from Joachimski et al. (2009) did not recover such important fluctuations and shows temperatures initially elevated in the early Pragian and then progressively decreasing during the rest of the studied interval except in the early Emsian, similarly to Scotese et al. (2021)’s study. Lack of data from high latitudes does not allow a clear assessment of climate’s impact on vegetation composition and dispersal. Nevertheless, the fact that vegetation shows a certain degree of uniformity points toward a warm climate. The only differentiation seems to be linked to the geographical remoteness of South China and Australia from other floras, indicating that the main barrier for dispersal was not climatic in this case. The endemism in South China observed for both macrofossil and microfossils are more marked than in Australia probably reflecting a higher degree of isolation (Xue et al., 2018).

IV.4.2.3. Middle Devonian palaeophytogeography

The Middle Devonian period is characterized by the highest degree of differentiation of Devonian vegetation (Fig IV.5A–B). NJ cluster analysis shows four distinct groups with South Chinese floras appearing highly differentiated from the rest of the assemblages (Fig. IV.5B). South Gondwanan floras also appear further distinct with longer branch lengths (Fig. IV.5B). A lesser degree of differentiation is found between the remaining two clusters but appear nonetheless distinct (Fig. IV.5B). The DCA (Fig. IV.5A) strongly corroborates this distinction into four different phytochoria which is additionally supported by a very high R value (R= 0.77; $p < 0.01$) using the ANOSIM test (Fig. IV.5B).

These four phytochoria are here referred as: (1) 'Laurussia'; (2) 'Subtropical'; (3) 'South Gondwana'; (4) 'South China' phytochoria and are termed according to their palaeogeographical extent in the Middle Devonian period (Fig. IV.5C). The Laurussian phytochorion is characterized by the predominance of *Svalbardia*, *Psilophyton* and *Rellimia* (Table IV.4) whilst the subtropical phytochorion is characterized by the presence of *Leclercqia* and is most commonly associated with *Artschaliphyton* (=*Haskinsia*) and *Aneurophyton* (Table IV.4). The South Gondwanan phytochorion corresponds to the occurrence of *Haplostigma* usually associated with *Paleostigma*, *Malanzania* and *Praeramunculus,* these latter taxa all endemic to this phytochorion (Table IV.4). The South Chinese province is mostly characterized by the occurrence of *Lepidodendropsis* and *Minarodendron* whilst only sharing a handful of taxa with other phytochoria (Table IV.4).

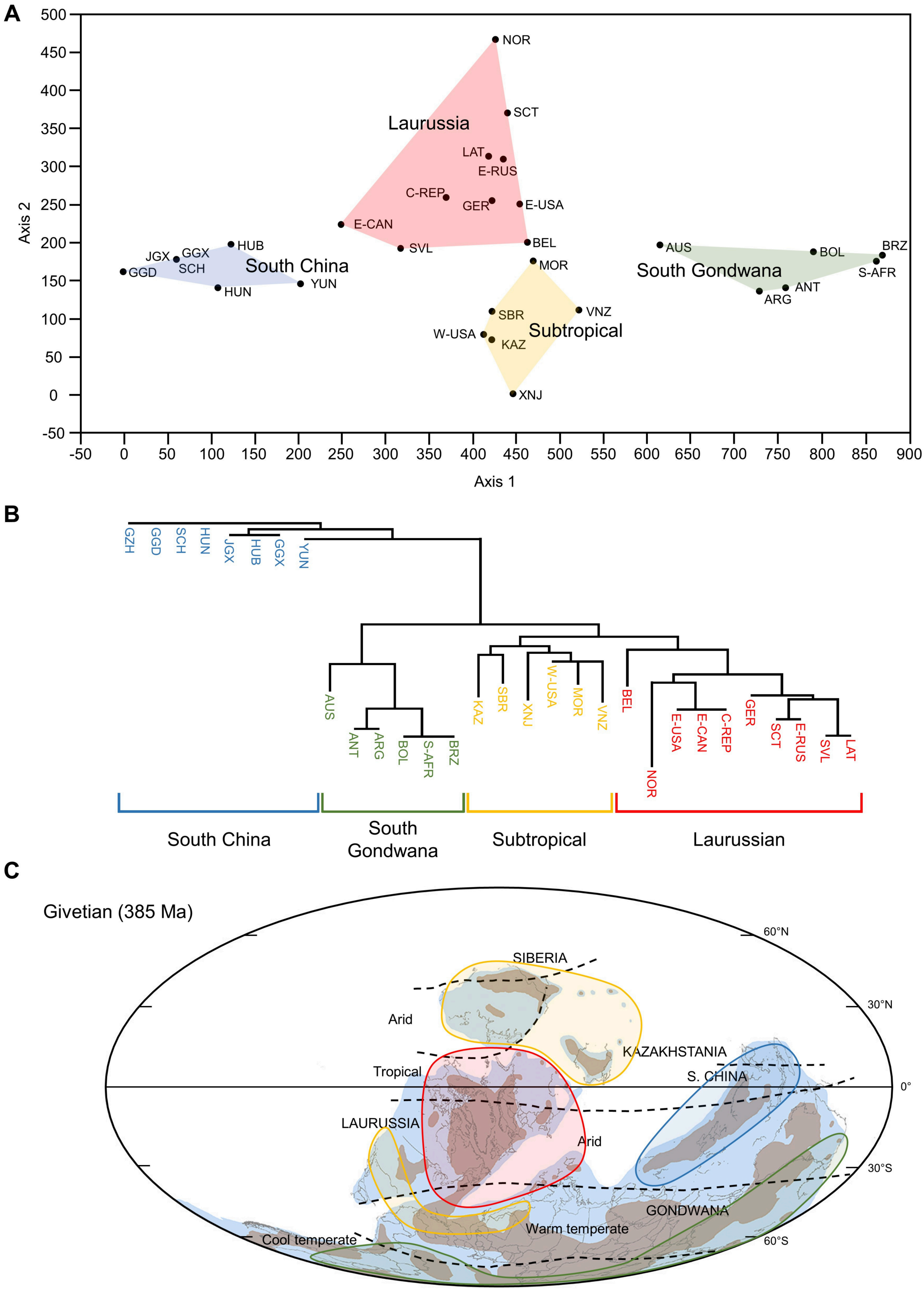

Figure IV.5: Middle Devonian palaeophytogeography. (A) DCA scatter plot of geographical units; (B) NJ clustering analysis; (C) extent of each phytochoria transposed onto palaeogeographic maps (Scotese, 2021). Colors: red = Equatorial-low latitudes; green = South Laurussia-West Gondwana. Climatic belts (dashed black lines) adapted from Boucot et al. (2013).

The only other palaeophytogeographical study using numerical analyses covering this period was Raymond and Metz (2004) but this only focused on a short period of time (mid- to late Givetian), thereby excluding many assemblages from the analysis and making comparison with our study problematic. Nonetheless, Raymond and Metz (2004) also found four different provinces. A Spitzbergen-Canada unit dominated by *Svalbardia* similarly to our Laurussian phytochorion. Another (Europe-Appalachian Basin) was dominated among others by *Rellimia* and *Artschaliphyton* could be also an equivalent to our Laurussian phytochorion. A third one (Kazakhstan-China) unit dominated by *Leclercqia*, *Barrandeina* an *Karagandella* similarly to our subtropical phytochorion. However, *Barrandeina* and *Karagandella* records from China have since been synonymized into a new taxon (Wang and Berry, 2006). A Siberia-Mongolia unit was also recognized but is not found in our analyses. Lastly, a South Gondwanan unit is inferred. Even though there are some discrepancies, the increased degree of differentiation of Middle Devonian floras are found in both studies and some common patterns can be retrieved.

The Laurussian phytochorion is strongly associated by the presence of *Svalbardia*. *Svalbardia* is sometime regarded as a synonym of *Archaeopteris*, but most authors have retained the distinction due to *Svalbardia* having ultimate branches and individual leaves borne spirally on the axis, and more slender leaves, even though fertile structures are similar (Chaloner, 1972). This phytochorion is where there is extensive evidence for the origination of the first forested ecosystem (Berry and Marshall, 2015,

Table IV.4: SIMPER results for the Middle Devonian period identifying taxa contributing the most to the observed differences between each phytochoria. First column represents taxa contributing to 80% of the overall average dissimilarity (OAD) ranked in order of decreasing contribution to OAD. Second column shows the percentage of the dissimilarity that each taxon contributes to the OAD. Third column represents the cumulative percentage of dissimilarity. Last columns represent the mean frequency of taxa per phytochorion.

Taxon	Dissimilarity	Contribution (%)	Cumulative (%)	Frequency			
				Laurussia	Subtropical	South Gondwana	South China
Lepidodendropsis	8.55	8.94	8.94	0.00	0.00	0.00	0.88
Haplostigma	7.72	8.07	17.01	0.00	0.00	1.00	0.00
Leclercqia	7.06	7.38	24.39	0.30	1.00	0.17	0.13
Minarodendron	6.94	7.26	31.65	0.00	0.00	0.00	0.75
Svalbardia	6.09	6.37	38.02	0.70	0.17	0.00	0.00
Psilophyton	4.82	5.04	43.05	0.50	0.17	0.00	0.13
Rellimia	4.70	4.92	47.97	0.50	0.33	0.00	0.00
Artschaliphyton	4.38	4.58	52.55	0.10	0.67	0.33	0.00
Barrandeina	2.89	3.02	55.57	0.30	0.17	0.00	0.00
Thursophyton	2.72	2.84	58.41	0.40	0.00	0.00	0.00
Palaeostigma	2.62	2.74	61.15	0.00	0.00	0.33	0.00
Aneurophyton	2.45	2.56	63.71	0.20	0.50	0.00	0.00
Pseudosporochnus	2.20	2.30	66.01	0.30	0.17	0.00	0.00
Flabellofolium	2.16	2.25	68.26	0.10	0.17	0.00	0.13
Malanzania	2.16	2.25	70.51	0.00	0.00	0.33	0.00
Praeramunculus	2.16	2.25	72.77	0.00	0.00	0.33	0.00
Anapaulia	1.91	2.00	74.76	0.00	0.33	0.00	0.00
Barsassia	1.85	1.93	76.70	0.00	0.50	0.00	0.00
Serrulacaulis	1.66	1.74	78.43	0.10	0.33	0.00	0.00
Barinophyton	1.39	1.46	79.89	0.20	0.00	0.00	0.00
Lycopodites	1.36	1.43	81.31	0.20	0.17	0.00	0.00

Stein et al., 2012). Taxa such as *Psilophyton* and *Svalbardia* (if we consider it similar to *Archaeopteri*s) have been interpreted as better adapted more humid conditions (Wan et al., 2019), although Boucot et al. (2013) reconstructed the climate in most of this area as arid (Fig. IV.5C). Availability of water may have also been essential for sustaining increasing demand in water for the development of trees (Box, 1996). This phytochorion may therefore represent a vegetation adapted to a tropical-wet environment with occasional dry conditions.

The subtropical phytochorion manifests itself by the occurrence of *Leclercqia* and its association with *Artschaliphyton* and *Aneurophyton. Leclercqia* and *Artschaliphyton* (*=Haskinsia*) are both herbaceous lycophytic plants while *Aneurophyton* is a small-sized aneurophytalean progymnosperm (Strullu-Derrien and Gerrienne, 2008). The fact that the flora is characterized by small shrubby and herbaceous plants tends to suggest a more arid growing environment. In fact, *Leclercqia* was hypothesized by Meyer-Berthaud et al. (2003) to show adaptation to dry environments with its small stature and rigid dissected leaves. In addition, *Leclerqia* and especially *Artschaliphyton* have been shown using isotopic data to be better adapted to drier-environments corroborated by morphological features for minimizing water-loss such as partially enclosed sporangia and overlapping leaves (Meyer-Berthaud et al., 2003; Wan et al., 2019). Furthermore, this phytochorion occurs in both hemispheres and its occurrence corresponds broadly with subtropical palaeolatitudes characterized by higher aridity. It is important to note that this phytochorion is the closest in terms of vegetation composition to the Laurussian flora and might therefore just represent a variation of the Laurussian flora adapted to a drier climate.

The South Gondwanan phytochorion is very distinct from the rest of previously described phytochoria (Table IV.4). The existence of a South Gondwanan unit, alternatively called Gondwanan realm by Edwards (1990b) has long been speculated (Edwards, 1990b; Wnuk, 1996; Raymond and Metz, 2004). It is characterized by the genus *Haplostigma* (Table IV.4), an herbaceous lycopsid fossil-genus for stems without leaves and fertile structures (Moisan et al., 2011). This phytochorion shares very few taxa with other regions of the world, mainly *Artschaliphyton* (Table IV.4). However, the Australian flora shares several taxa usually associated with other phytochoria such as *Leclercqia*, *Astralocaulis* and *Tetraxylopteris* (Data S1, S3) and appears closer on the NJ and DCA with other assemblages from other phytochoria (Fig. IV.5A–B). These records occurred at lower latitudes than the record of *Haplostigma* found in New South Wales (McLoughlin and Long, 1994) and it is therefore possible that only Southern Australia is included in the South Gondwana phytochorion. Interestingly, the probable remnants of the Eotracheophytic flora occurring in the Silurian–Lochkovian and possibly in the highest latitudes of Gondwana during the Pragian–Emsian, finally appears to have been utterly replaced by this low diversity herbaceous lycophytic flora (Fig. IV.2G).

The South Chinese phytochorion is totally distinct from other phytochoria with a high proportion of endemic taxa (Fig. IV.5A–B; Table IV.4, Data S1). The most biogeographically important taxon is ?*Lepidodendropsis* (Table IV.4). Even though this lycopod genus is not actually *Lepidodendropsis*, it was kept for this analysis, as it is an important Middle Devonian South Chinese taxon (Xue et al., 2018). South Chinese floras are dominated by a lycopsid and cladoxylopsid vegetation, but there is notable absence of both aneurophytalean – archeopteridalean progymnosperms (Xue et al., 2018). Although being located in the tropical regions and sharing an apparent similar climate to Laurussia (Fig. IV.5C), the vegetation appears highly different. Plants are also smaller than those occurring in coeval floras from the USA (Gilboa) with only small tree-like lycopods (Stein et al., 2007; Meyer-Berthaud and Decombeix, 2012; Xue et al 2018).

A colder climate is recorded during the Middle Devonian (Joachimski et al., 2009; Scotese et al., 2021) compared to the Early Devonian and may have therefore contributed to this increased differentiation of vegetation by tightening the latitudinal temperature gradient. The colder climate may have also hindered the possible dispersal of tropical Laurussian taxa towards South China through Gondwana and vice versa explaining the high endemism recorded among South Chinese floras. The distinct vegetation in South Gondwana also appears to be a product of the colder climatic conditions. Indeed, Matsumara et al. (2015) argued that these smaller and possibly fast-growing herbaceous lycopsids in South Gondwana were well adapted to cold conditions and the alternation of long periods of darkness and light.

IV.4.2.4. Late Devonian palaeophytogeography

The Late Devonian is characterized by a relatively homogenous vegetation with DCA mainly showing differentiation along axis 1 (Fig. IV.6A). NJ cluster analysis likewise does not reveal any clearly defined associations but rather a gradual differentiation of vegetation between geographical units (Fig. IV.6B). NJ cluster analysis nevertheless identifies a cluster including South Laurussian and Gondwanan assemblages (Fig. IV.6B). This cluster can be also retrieved in the DCA despite some overlapping between the two groups for Eastern USA, Western Canadian and Anglo-Welsh assemblages (Fig. IV.6A). The ANOSIM test also indicates that vegetation is far more homogenous than during the Middle Devonian with a lower R value of dissimilarity between the two defined cluster ($R = 0.43$; $p < 0.01$). South Chinese provinces still appear closely related although their degree of differentiation from other floras is far less significant than during the Middle Devonian and appear even related to remote locations such as Western Canada and Kazakhstan (Fig. IV.6A–B). However, the only record from the Yunnan province and the recently described assemblage from Inner Mongolia appear significantly different in the DCA (Fig. IV.6A). This is mainly due to the occurrence of *Leclercqia* (Data S1). Nevertheless, *Leclercqia* occurrences in both provinces are poorly dated and may be Middle Devonian in age (Xu et al., 2020; Bai et al., 2021a). More precise age and additional data from other localities from these regions would be necessary to further attest their distinctiveness.

Two palaeophytogeographical units were therefore identified: the (1) ‘Equatorial to mid-latitudes’ and the (2) ‘South Laurussia-Gondwana’ phytochoria (Fig. IV.6A–C). The South Laurussia-Gondwana phytochorion similarly to the Middle Devonian South Gondwanan phytochorion is still characterized by the appearance of *Haplostigma* (Table IV.5). However, assemblages found in this phytochorion frequently share taxa also more reminiscent of the equatorial to mid-latitudes phytochorion such as *Archaeopteris* and *Leptophloeum* (Table IV.6). This phytochorion is also characterized by the presence of *Colpodexylon* and other taxa from the Middle Devonian South Gondwanan unit (e.g., *Praeramunculus* and *Malanzania*). On the other hand, the equatorial to mid-latitudes phytochorion is represented by nearly all taxa used in the analysis (Table IV.6). The apparent merging of the South Gondwanan and the southern subtropical flora from the Middle Devonian is probably linked to the

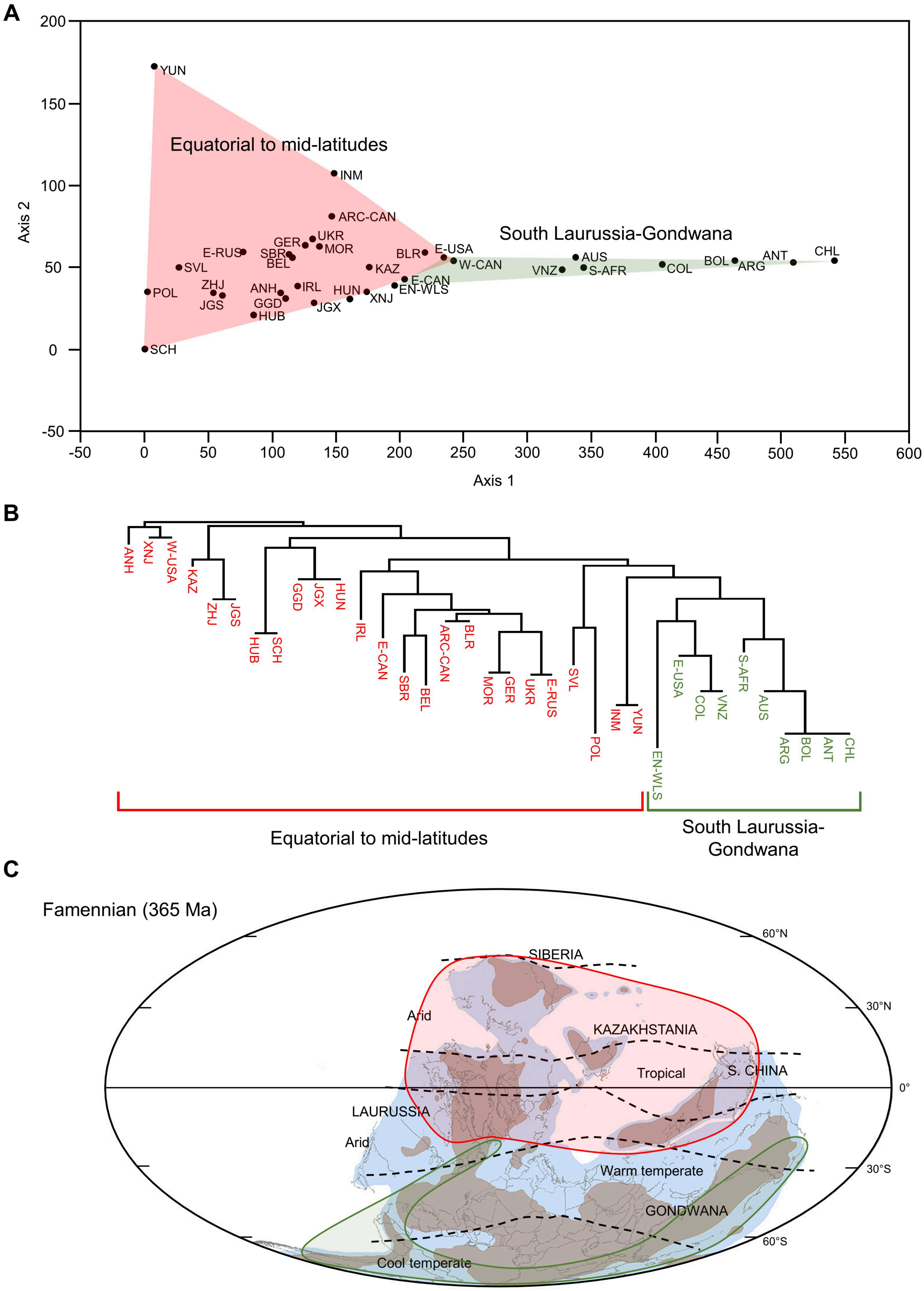

Figure IV.6: Late Devonian palaeophytogeography. (A) DCA scatter plot of geographical units; (B) NJ clustering analysis; (C) extent of each phytochoria transposed onto palaeogeographic maps (Scotese, 2021). Colors: red = Equatorial-low latitudes; green = South Laurussia-West Gondwana. Climatic belts (dashed black lines) adapted from Boucot et al. (2013).

Table IV.5: SIMPER results for the Late Devonian period identifying taxa contributing the most to the observed differences between each phytochoria. First column represents taxa contributing to 80% of the overall average dissimilarity (OAD) ranked in order of decreasing contribution to OAD. Second column shows the percentage of the dissimilarity that each taxon contributes to the OAD. Third column represents the cumulative percentage of dissimilarity. Last columns represent the mean frequency of taxa per phytochorion.

Taxon	Dissimilarity	Contribution (%)	Cumulative (%)	Frequency	
				Equatorial/ mid-latitudes	South Laurussia/ Gondwana
Haplostigma	9.00	9.92	9.92	0.00	0.60
Archaeopteris/*Callixylon*	8.50	9.36	19.28	0.76	0.40
Leptophloeum	5.80	6.39	25.66	0.44	0.30
Lepidodendropsis	5.26	5.80	31.46	0.44	0.00
Colpodexylon	4.71	5.19	36.65	0.00	0.40
Flabellofolium	4.05	4.46	41.11	0.24	0.30
Sublepidodendron	3.37	3.71	44.82	0.32	0.00
Malanzania	3.04	3.35	48.17	0.00	0.20
Barinophyton	2.59	2.85	51.02	0.16	0.20
Sphenophyllum	2.59	2.85	53.87	0.32	0.00
Tetraxylopteris	2.55	2.81	56.68	0.00	0.30
Hamatophyton	2.46	2.71	59.38	0.24	0.00
Praeramunculus	2.34	2.58	61.96	0.00	0.20
Pseudosporogonites	1.89	2.08	64.04	0.04	0.20
Cyclostigma	1.82	2.01	66.05	0.12	0.10
Rhacophyton	1.81	2.00	68.04	0.16	0.10
Svalbardia	1.75	1.93	69.97	0.12	0.10
Archaeocalamites	1.74	1.91	71.88	0.16	0.00
Pietzschia	1.72	1.90	73.78	0.12	0.00
Leclercqia	1.68	1.86	75.64	0.08	0.00
Xenotheca	1.68	1.85	77.49	0.00	0.20
Eviostachya	1.64	1.81	79.30	0.16	0.00
Gilboaphyton	1.60	1.76	81.05	0.04	0.10

migration of taxa from the mid-latitudes towards the pole. For instance, *Colpodexylon* found in Eastern USA, Colombia and Venezuela during the Givetian-early Frasnian is found in South Africa during the Famennian. *Haplostigma* also seems to become less present although many of the Famennian occurrences represents poorly dated occurrences (Table IV.5; Matsumara et al., 2015). For instance, late Famennian Gondwanan floras are far more diverse with cosmopolitan taxa such as *Archaeopteris*, *Leptophloeum*, and cladoxylopsids, which were not recorded in the Middle Devonian and replaced the poorly diverse herbaceous lycopsid vegetation (Fig. IV.2G; Anderson et al., 1995; Prestianni and Gess, 2014; Meyer-Berthaud et al., 2022). This pattern of increasing uniformity is also seen with the South Chinese provinces which are now well-nested within the equatorial to mid-latitudes phytochorion (Fig. IV.6A–B). The introduction of many different cosmopolitan taxa, most notably *Archaeopteris*, has drastically changed the degree of endemism in South China compared to the Middle Devonian. Large arborescent forms are now found both among lycopsids (*Sublepidodendron*, *Lepidodendropsis*) and archeopteridalean progymnosperms in contrast to the mostly herbaceous vegetation during the Middle Devonian (Xue et al., 2018).

Raymond et al. (2004) attempted to determine phytochoria during the late and latest Famennian (Strunian). Nevertheless, similarly to our analysis, they struggled to demonstrate any significant degree of differentiation among floras. Evidence of a homogenization from both the macroflora in this study and miospores in Streel et al. (2000) indicates a weaker latitudinal gradient during the Late Devonian, and especially the Famennian. The increased cosmopolitanism in the Late Devonian can be clearly linked with the unusually warm climate during this period with global temperatures reaching +10°C compared to modern day levels at the Frasnian/Famennian boundary and remaining more than +7°C above present during the Famennian (Scotese et al., 2021).

IV.5. Conclusions

Global Silurian–Devonian land plant diversity patterns were herein analysed in different palaeogeographical units with the aim of characterizing early land plant radiation. Unsurprisingly, Laurussian diversity patterns are the most similar to the global record whilst other regions are clearly under-sampled (e.g., Gondwana) and/or profoundly affected by geological incompleteness (e.g., South China) making them difficult to interpret. Nevertheless, vegetation change through time is less affected by sampling issues and several diachronous events are here recognized such as the zosterophyll or spermatophyte radiation. Moreover, spatial differentiation of Silurian–Devonian was characterized as follows:

(a) Two phytochoria were recovered for the Silurian–Lochkovian period: an ‘equatorial to mid-latitudes’ unit defined by the presence of *Zosterophyllum*, and a ‘South Laurussia-West Gondwana’ phytochorion dominated by rhyniophytoids such as *Cooksonia* and *Aberlemnia*. This division into two biogeographical units can be correlated with climatic conditions, with zosterophylls apparently favouring warm to hot conditions and rhyniophytoids proliferating in mid- to high latitudes.

(b) In the Pragian–Emsian, two phytochoria are also defined: a ‘Northeast Gondwana’ unit differentiated from an ‘equatorial to mid-latitudes’ unit by the presence of taxa such as *Pauthecophyton* or *Yarravia*. Climatic conditions do not appear to control the observed pattern but rather geographical barriers, notably the relative isolation of South China and Australia. However, lack of data prevents a conclusive presence of a third unit in South Gondwana which may include the remains of a rhyniophytic grade flora surviving under colder conditions.

(c) During the Middle Devonian, vegetation is highly differentiated with four distinct phytochoria recognized: (1) Laurussian; (2) Subtropical; (3) South Gondwana; (4) South China. The Laurussian phytochorion is characterized by, among others, *Svalbardia*, and appears to represent a flora adapted to wetter conditions and includes evidence of the first trees and forests. The subtropical phytochorion appears related to drier conditions defined by the presence of *Leclercqia* and *Artschaliphyton.* South Chinese floras are characterized by a high degree of endemism and are composed of herbaceous lycophytes and cladoxylopsids but lacked progymnosperms that otherwise thrived in other tropical regions such as Laurussia. The South Gondwanan phytochorion is characterized by a low-diversity of endemic herbaceous lycophytes, possibly well-adapted to colder conditions.

(d) During the Late Devonian, the vegetation is globally quite homogenous with only an Equatorial to mid-latitudes phytochorion and a South Laurussian-Gondwanan phytochorion recovered, despite not being highly differentiated. The very warm climate during this period is probably the main factor leading to this reduction in latitudinal differentiation compared to the Middle Devonian.

This first re-assessment of Silurian-Devonian paleophytogeography, using classical methods to recover diversity patterns and phytochoria, suggests a significant role of climate into dispersion and diversification of early land plants, that merits further evaluation. Innovative methods requiring higher geographical resolution occurrence-based datasets could more precisely locate centres of originations and diversification. Likewise, using both empirical (plant fossils) and modelled diversity to characterize the former latitudinal diversity gradient and its evolution through time, may shed further light on climate change impact over early land plant evolution.

Supporting information is available upon request from the corresponding author.

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Chapter V: A review of a Lower Devonian plant assemblage

This chapter is a slightly modified version of an article published (in press) in *Botany Letters* entitled "**Revisiting the Rebreuve plant assemblage from the Lower Devonian of Artois, northern France**" The published version of this article can be found online at: https://doi.org/10.1080/23818107.2022.2101516. This article was also popularized in the French publication *Sciences et Avenir*: https://www.sciencesetavenir.fr/archeo-paleo/paleontologie/la-deuxieme-plus-ancienne-flore-de-france-montre-que-le-nord-de-la-france-etait-separe-du-reste-du-pays-par-un-grand-ocean_166255.

Revisiting the Rebreuve plant assemblage from the Lower Devonian of Artois, northern France

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Abstract

French Lower Devonian floras are rare, especially compared to certain other Western European countries. In this study, we reassess an assemblage collected in the 1930s in the Rebreuve quarry (Pas-de-Calais, northern France). We describe new features in several taxa and update taxonomic names from original descriptions. For instance, re-examination of vegetative remains previously described as *Psilophyton princeps*, led to the discovery of fertile structures allowing us to refer these specimens to *Sawdonia*. In total, this flora consists of 10 taxa, including up to four different *Psilophyton* species, such as *P. parvulum*. Other taxa include *Danziella artesiana, Drepanophycus* cf. *spinaeformis, Sporogonites exuberans* and some specimens of *Taeniocrada* and *Sciadophyton*, revealing a diverse Lower Devonian plant assemblage. The Rebreuve assemblage represents a typical Emsian flora from Laurussia and bears striking resemblance with coeval Belgian assemblages. Previous palynological investigations, in addition to the similarities with well-dated Belgian floras, suggest an early Emsian age for this assemblage. The paleogeographical implications of findings are discussed.

Keywords: Lower Devonian; France; Plant fossils; Rebreuve; *Sawdonia*; *Psilophyton*; *Drepanophycus*

V.1. Introduction

Western Europe has historically been a major source of Lower Devonian plant fossils (see e.g., Gerrienne, 1983, 1993; Schweitzer, 1983; Edwards and Richardson, 2004; Morris and Edwards, 2014; Gossmann et al., 2021). Lower Devonian outcrops in northern France (Artois region) are far less extensive, compared to the nearby Belgian Ardennes and German Rhenish region. Plant fossils have only been recovered from a handful of localities (Bertrand, 1913; Corsin, 1933; Degouy, 1973; Leclercq, 1975). Lower Devonian plants were first discovered in the Artois region by Gosselet and Dollé (1910) at a quarry in Matringhem (Fig. V.1A-B). Plant fossils were subsequently reported by Corsin (1933) at a quarry in Rebreuve (Fig. V.1C), 30 km ESE of Matringhem. However, this short note only included a brief account of the findings. The Rebreuve assemblage was then formally described by Danzé-Corsin (1956b), revealing a richer assemblage than previously thought. Twelve taxa were identified, including two new species: *Zosterophyllum artesianum* and *Yarravia minor*. More recently, reinvestigation of *Z. artesianum* was undertaken by Edwards (2006) leading to the erection of a new genus for this plant: *Danziella artesiana*, classed as an *incertae sedis* taxon with zosterophyll affinities. Edwards (2006) emphasized, as well as other authors (e.g., Hao and Gensel, 1995; Hao and Xue, 2013; Gess and Prestianni, 2021; McSweeney et al., 2021), the necessity of reinvestigating the entire fossil content of this assemblage, as several taxa appeared dubiously identified.

Furthermore, the age of these localities in the Artois region is still not properly constrained. They were originally dated as Taunusien (~Pragian), mainly based on a correlation with other localities possessing a similar floral composition. However, this age is questionable. Further studies indicate younger ages using spore and ostracoderm biostratigraphy (Degouy, 1973; Leclercq, 1975; Blieck and Janvier, 1989), leading Edwards (2006) to conservatively refer to these localities as Pragian–Emsian.

The aim of this paper is to provide a taxonomic revision of the Rebreuve assemblage described by Danzé-Corsin (1956b), based on specimens collected by Corsin (1933), housed within the paleontological collections of the University of Lille (France). The age of the flora is also reexamined using previous palynological studies and lithostratigraphic correlations. Finally, the composition of this flora and its paleophytogeographic implications are discussed.

V.2. Geological setting and stratigraphy

Rebreuve is situated in the Artois region of the Pas-de- Calais department, France (Fig. V.1A–B). In this area, the Devonian basement is uncomformably overlain by Cretaceous/Paleogene sediments. During the Cenozoic, Devonian sediments were uplifted because of structural inversion of Paleozoic normal faults, caused by the reactivation of the Midi thrust (Delattre, 1969; Minguely et al., 2010). It is along this series of faults, generally oriented NW-SE, that Devonian rocks locally outcrop (Fig. V.1B). However, Devonian rocks are also exposed due to erosion caused by several rivers in the immediate vicinity of the faults (Fig. V.1C).

The Devonian outcrops in Rebreuve are situated in the Brette River valley between the Pernes and Marqueffles fault lines (Fig. V.1B–C). No natural exposure occurs in this area, and stratigraphy of the layers could only be characterized based on the outcrops unveiled by active quarrying operations (Loc. 1, Fig. V.1C). The Grès de Rebreuve Formation consists of white sandstones intermittently separated by red schists and mudstones (Delattre, 1969). Plants were found at various levels within the sandstones in either white, grey or orange mudstone lenses, each more or less micaceous and sandy (Corsin, 1933; Danzé-Corsin, 1956b; Edwards 2006). Most of these lenses were sterile and only a few yielded plant remains (Corsin, 1933). Unfortunately, the quarry is no longer active, and has since been flooded, making the outcrops inaccessible for additional sampling. Corsin (1933) and Danzé-Corsin (1956b) argued that the plant remains had not been transported over long distances (autochthonous or parautochtonous assemblage), as some specimens are well-preserved and sometimes nearly complete (e.g., *Danziella artesiana*). Delattre (1969) interpreted the facies as coastal or lagoonal, similar to the other Lower Devonian outcrops of the region.

The La Comté-Beugin massif represents the closest Devonian outcrops to Rebreuve, occurring along the Pernes fault line, and further south along the Lawe river banks about 3 km west of Rebreuve (Loc.

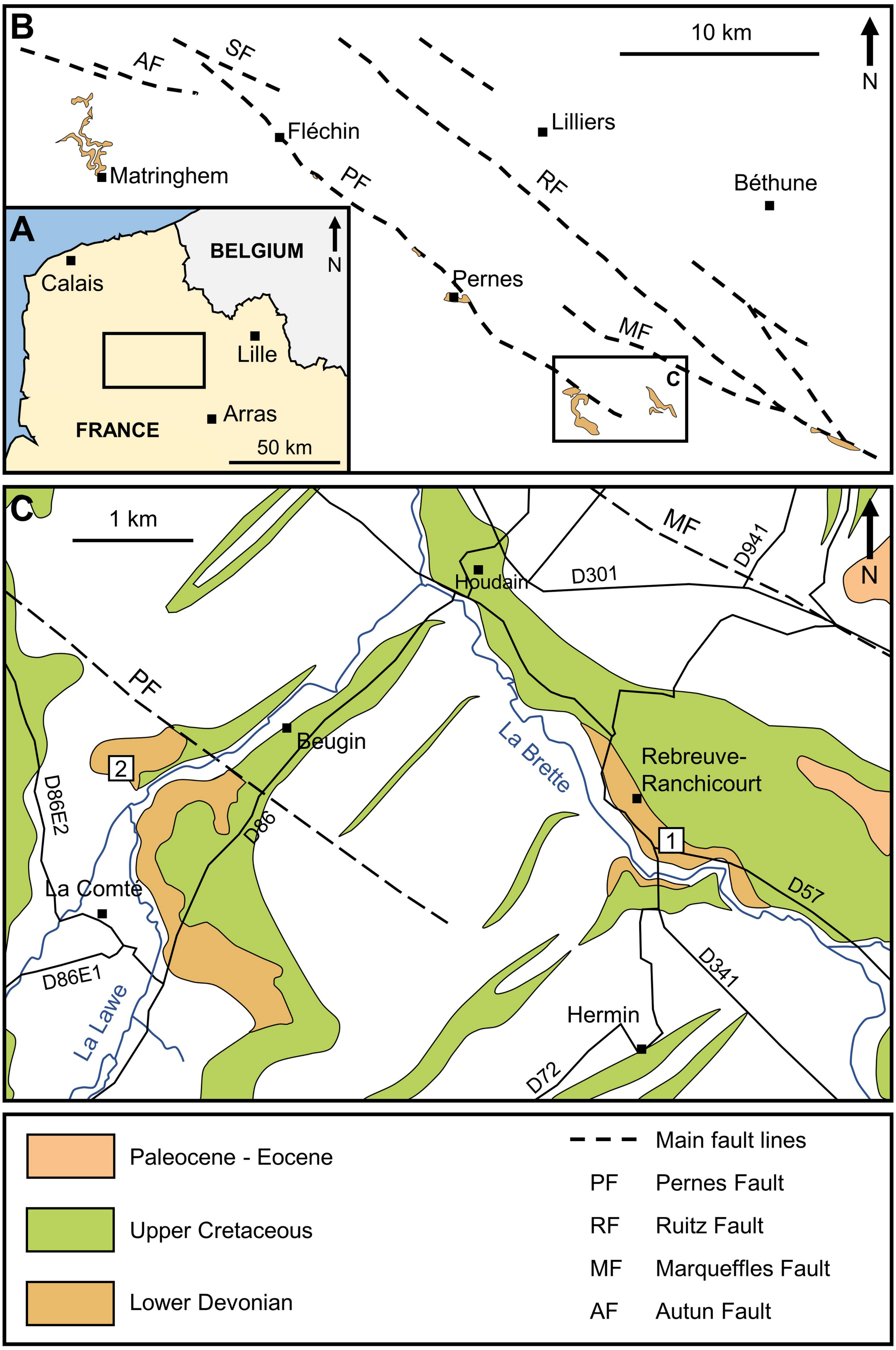

Figure V.1: Geography of the study area. a. Map of northern France showing the location of the study area. b. Map of the studied area highlighting the main fault lines and Devonian outcrops (Redrawn from Minguely et al., 2010). c. Geological map of Rebreuve- La Comté-Beugin redrawn based on scanned maps of northern France at 1/50,000 scale (https://infoterre.brgm.fr/), also including the location of plant fossil localities: 1. Rebreuve quarry, 2. Bois d'Épenin quarry.

2, Fig. V.1B–C). In this area, spores were found in grey to green fine-grained shales, in the Bois d'Épenin quarry (Degouy, 1973; Loc. 2, Fig. V.1C), associated with "*Psilophyton*" fragments, without any further description nor illustrations of the macroflora. These specimens could not be located within the collections of the University of Lille. Spores were identified by M. Streel (Liège) in Degouy (1973) and the locality was originally dated as late Pragian. However, our taxonomic revision of the assemblage instead suggests an early Emsian age (Fig. V.2). Contrary to the La Comté-Beugin and Matringhem areas, a detailed study of the Rebreuve Devonian outcrops has not been undertaken, and no previous attempts have been made to date these rocks. Our own attempts to recover palynomorphs were all unsuccessful.

The Devonian basement being covered by Cretaceous sediments, the dip and direction of Devonian sediment layers around Rebreuve are mostly unknown and quite complex near this fault system. It is therefore difficult to directly extrapolate an age for the Rebreuve assemblage based on La Comté-Beugin

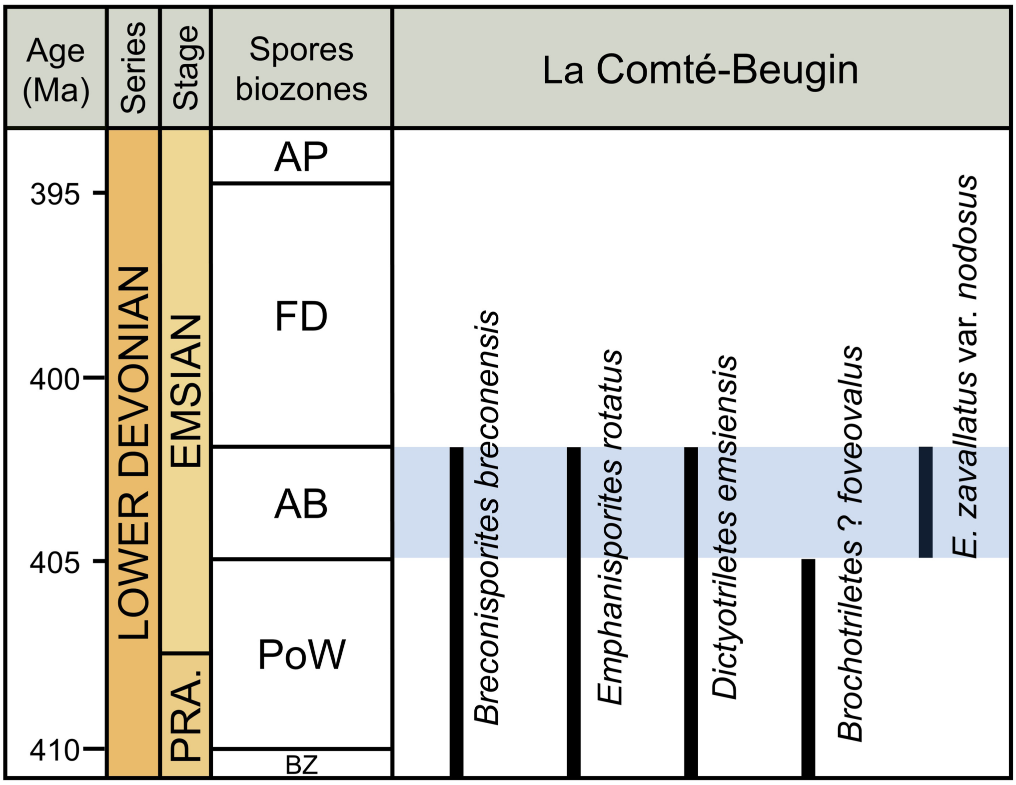

Figure V.2: Stratigraphic ranges of several key spore taxa described in La Comté-Beugin. Blue boxes represent the assigned temporal interval of each locality. Absolute ages according to the International Chronostratigraphic Chart (v2020/12). Miospore biozones according to Steemans (1989) adapted from the Geological Time Scale (Gradstein et al., 2020): BZ, *breconensis–zavallatus*; PoW, *polygonalis–wetteldorfensis*; AB, *annulatus–bellatulus*; FD, *foveolatus–dubia*; AP, *apiculatus–proteus*. Abbreviations: PRA., Pragian.

outcrops. Nevertheless, the “Grès de Rebreuve” Formation has been interpreted to be an analog to the other sandstone formations of the region, based on their similar lithofacies (Delattre, 1969; Blieck et al., 1988). Since an (early) Emsian age has been recovered both in La Comté-Beugin (Fig. V.2) and Matringhem-Vincly (Leclercq, 1975) using spore biostratigraphy, a similar age can be assumed in Rebreuve. Without any biostratigraphic tools to directly date Rebreuve rocks, this age remains equivocal, but the association of plants described in this paper seems to corroborate this estimation (see discussion).

V.3. Materials and methods

The Rebreuve assemblage consists of about 100 specimens collected by P. Corsin and P. Bertrand in 1933 during a thorough sampling in the Rebreuve quarry (Loc. 1, Fig. V.1C). Fossils are preserved as adpressions and impressions. Unfortunately, a few specimens illustrated in Danzé-Corsin (1956b) could not be reinvestigated as they could not be located within the collections. Although P. Danzé-Corsin already undertook some *dégagement* on certain specimens, additional *dégagement* was performed using triangular steel needles to reveal further details (Fairon- Demaret et al., 1999). Macrophotography was achieved using a CANON EOS 700D and a macro lens. Studied plant fossils are housed in the paleontological collections of the University of Lille, France.

V.4. Plant descriptions

***Incertae sedis* Bryophyta**

1. *Sporogonites exuberans*

1956b *Sporogonites exuberans* Halle, Danzé-Corsin, pl. III, figs. 9–9a.

Material. This plant is represented by a single specimen (part and counterpart) numbered USTL 3709A and USTL 3709B (Fig. V.3A).

Description. This specimen consists of an undivided slender axis bearing a single terminal sporangium (Fig. V.3A). The stem is 8 mm long and its maximum width reaches 0.25 mm. The stem is not connected to any other structure and appears truncated at its base. The shape of the sporangium is ellipsoidal with an acutely pointed apex and is 4.5 mm long, and 1.7 mm wide at its maximum. The distal part of the stem progressively widens. The lower half of the sporangium is marked by at least four longitudinal ridges alternating with grooves. The base of the sporangium is 2.4 mm long and separated from the 1.8 mm long apical area by a 0.3 mm median ridge.

Interpretation. Elongated sporangia borne terminally on a slender and smooth undivided axis are singular to the genus *Sporogonites*, firstly described by Halle (1916) based on specimens from Röragen, Norway. The type species *S. exuberans* discovered in Norway was subsequently found in the Pragian and Emsian of Wales (Croft and Lang, 1942) and Belgium (Lang, 1937; Stockmans, 1940; Andrews, 1958; Gerrienne, 1993). Other species include *S. chapmanii* from Australia (Lang and Cookson, 1930) and *S. yunnanense* from China (Hsü, 1966). However, *Sporogonites* was subsequently discovered in older (late Silurian–Lochkovian) strata in Brazil (Gerrienne et al., 2001; Gonez, 2012), Vietnam (Gonez, 2012) and South Africa (Gess and Prestianni, 2021).

A wide array of sporangial morphologies was documented among all currently recognized species (Bharadwaj, 1981). One of the most distinctive features of this Rebreuve specimen is the sporangium's acutely pointed apex (Fig. V.3A), whereas most species possess a rounded to bluntly pointed apex. This feature is uniquely known to occur in one early Emsian locality from Belgium, in the Carrière du Bois de Bescaille in Estinnes-au-Mont (Stockmans, 1940). The distinct nature of these specimens already led Lang (1937) to refer to them as *S. exuberans* f. *belgica*. Stockmans (1940) illustrated a few of these specimens (Planche IV, figures 6, 8), without distinguishing them from other *S. exuberans* occurrences in Belgium. However, Bharadwaj (1981) went further than Lang (1937) and created a new species (*S. belgica*) to accommodate them, characterized by "oval capsules with acutely conical tips and the apical

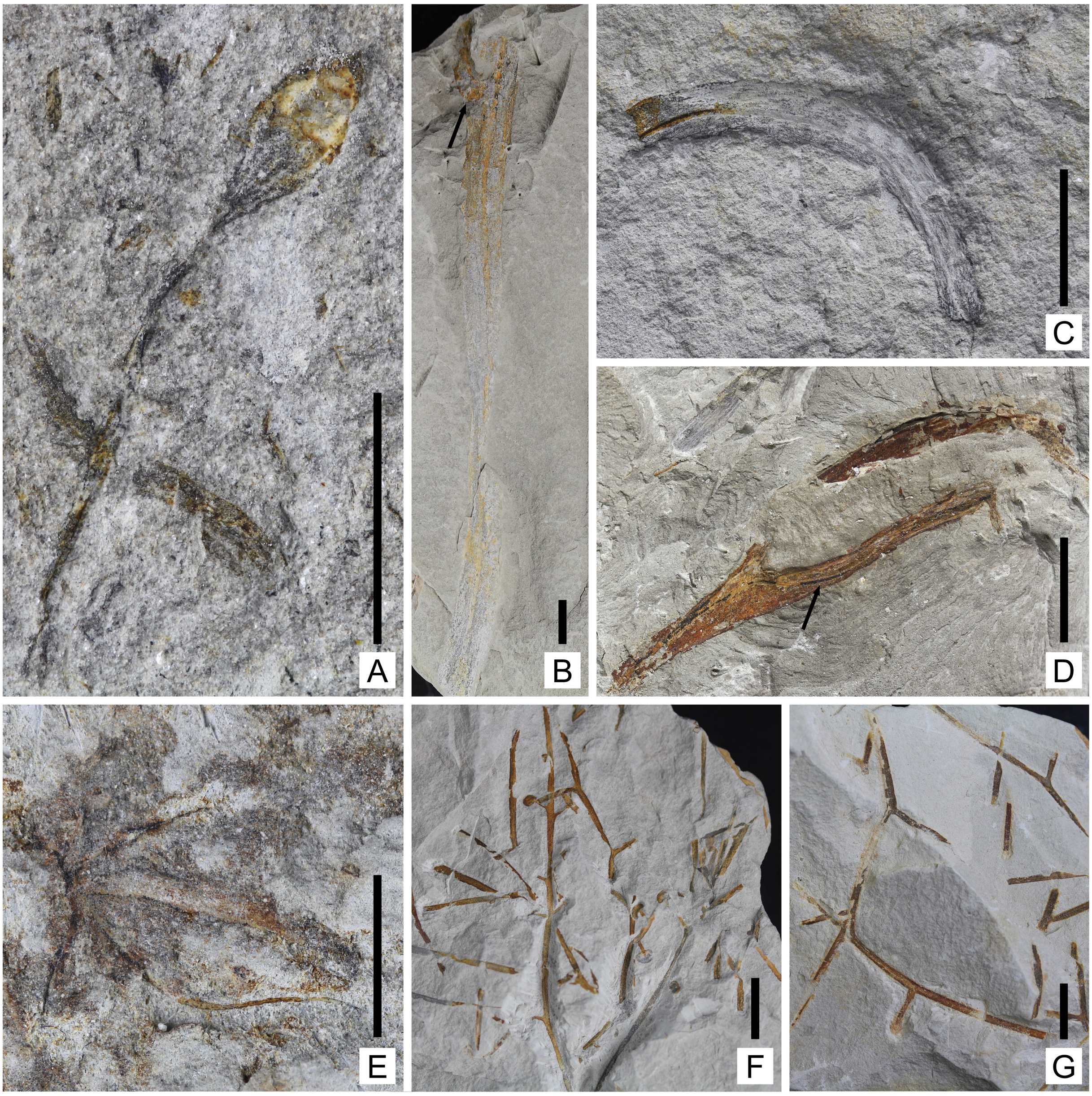

Figure V.3: Plant fossils from the Rebreuve assemblage, France (I). A, *Sporogonites exuberans*, axis bearing a single terminal sporangium, USTL3709B. B, *Taeniocrada* sp., general view of specimen USTL 3643; note the location of an anisotomous dichotomy at arrow. C, *Taeniocrada* sp., axis showing a central vascular strand and vascular strand trace, USTL3674B. D, *Taeniocrada* sp, specimen displaying an isotomous dichotomy; note the meandering vascular strand at arrow, USTL 3818. E, *Sciadophyton* sp., general view of specimen USTL 3686. F, *Danziella artesiana*, general view of lectotype showing axes bearing sporangia on short stalks, USTL 3595A. G, *Danziella artesiana*, specimen showing sterile axes, isotomously branched at a wide angle, USTL 3610A. Scale bars: A, E = 5 mm; B–D, F–G = 10 mm.

and basal part separated by a median, wide band". This emendation of the genus and species was subsequently ignored in the literature. Gerrienne (1993) in his inventory of Belgian Early Devonian plants still classed all Belgian specimens as belonging to *S. exuberans*. We thereby refer to this specimen as *S. exuberans*, whilst acknowledging its distinctiveness from the type specimens from Norway.

Reinvestigation of the genus would be required to further discriminate if it is a distinct species or whether the morphotype falls within the range of intraspecific variability of *S. exuberans*.

Rhyniopsida

2. *Taeniocrada* sp.

1933 *Taeniocrada* sp. White, Corsin

1933 *Taeniocrada decheniana* Kräusel and Weyland, Corsin

1956b *Taeniocrada decheniana* Kräusel and Weyland, Danzé-Corsin, pl. II, figs. 7–8.

Material. Several fragments are found scattered in numerous samples. Description is here based on best preserved specimens: USTL 3643 (Fig. V.3B), USTL 3669, USTL 3674B (Fig. V.3C), USTL 3699A and USTL 3818 (Fig. V.3D).

Description. This plant consists of smooth naked axes measuring between 2.5 and 11.6 mm wide. The longest axis measured is 14.8 cm long (Fig. V.3B). A conspicuous vascular strand or vascular strand impression, less than 1.2 mm wide, can be observed on all specimens (Fig. V.3B–D). The width of the vascular strand is more or less proportional to the width of the stem. This vascular strand is usually found at the center of the axis (Fig. V.3C) but it can also be seen meandering on several specimens (Fig. V.3D at arrow). Branching is rare, although anisotomous (Fig. V.3B at arrow) and isotomous (Fig. V.3D) branching are recorded on separate specimens. No fertile axes were identified.

Interpretation. Naked axes showing a meandering vascular strand are typical of *Stockmansella langii* (basionym *Taeniocrada langii*) bearing lateral sporangia, and the fossil-genus *Taeniocrada* formerly solely based on sterile axes (Fairon-Demaret, 1985, 1986). *Taeniocrada*-like axes are commonly found in Lower Devonian strata (e.g. Kräusel and Weyland, 1930; Stockmans, 1940; Kennedy et al., 2012; Cascales-Miñana et al., 2015). Among well-defined Lower Devonian *Taeniocrada* species, *T.*

decheniana is characterized by very frequent bifurcations and circinate tips. *T. dubia* is on the other hand exhibits small oblong punctae on the surface of axes. None of those features are recorded in the Rebreuve specimens. Vegetative axes herein described bear the most resemblance with those of *S. langii* and other vegetative axes defined as *Taeniocrada* sp. in Stockmans (1940, pl.VI, fig. 1b, pl. X, fig. 5). However, the lack of fertile structures precludes assignation of these specimens to either *Stockmansella* or any other species of *Taeniocrada* where fertile remains have been found (Taylor, 1986). In addition, the lack of preserved anatomy of water-conducting cells is problematic as such axes may belong to a zosterophyll or a rhyniophyte. Considering all of this, we leave those specimens as *Taeniocrada* sp.

Gametophyte *Incertae sedis*

3. *Sciadophyton* sp.

1956b *Sciadophyton* cf. *laxum* (Dawson) Steinmann, Danzé-Corsin, pl. II, figs. 10–10a.

Material. Several poorly preserved specimens can be observed along a single bedding plane on one sample numbered USTL 3686. The best-preserved specimen is illustrated and provides a basis for description (Fig. V.3E).

Description. Four slender axes departing radially from an elongated center 2 mm in length and 0.5 mm wide. Axes between 3.2 and 10 mm long with a maximum width of 0.3 mm. The specimen is incompletely preserved so the actual number of axes radiating from the center is unknown.

Interpretation. Axes expanding radially from a center in a rosette-like configuration is characteristic of the genus *Sciadophyton* (Remy et al., 1980a, 1980b, 1992, 1993). This taxon is often found in other European Lower Devonian localities (i.e. Stockmans, 1940; Croft and Lang, 1942; Remy et al., 1992). Similar structures have already been interpreted as gametophytes of different taxa in different lineages such as *Zosterophylum rhenanum, Stockmansella langii* (Schweitzer, 1983) or *Huvenia kluei* (Hass and

Remy, 1991). Due to the specimen's incompleteness and until the affinities of *Sciadophyton* are clarified, it is wiser to refer to this specimen as *Sciadophyton* sp.

Lycophytes – Zosterophyllopsida

4. *Danziella artesiana*

See Edwards (2006) for complete description and discussion of these specimens.

Material. About 20 specimens have been identified in the collections. The lectotype numbered USTL 3595A (Fig. V.3F), as well as sterile axes USTL 3610A, Fig. V.3G), are here illustrated.

Description and interpretation. This plant consists of smooth leafless axes with bivalved sporangia borne laterally on long straight stalks (Fig. V.3F–G). It was originally described as a new species (*Zosterophyllum artesianum*) in Danzé-Corsin (1956b). However, Edwards (2006) excluded this taxon from *Zosterophyllum* due to its lack of compact spike and the fact that sporangia in *Zosterophyllum* are upright and inserted on short stalks. Its placement within the zosterophyll clade remains equivocal due to its simplicity in organization and lack of preserved anatomy. Nevertheless, Edwards (2006) hypothesized that *Danziella* may be a representative of a stem-lineage of the Zosterophyllopsida.

Remarks. Edwards (2006) described this new taxon as coming from the Rebreuve locality although she also illustrated two specimens reportedly coming from Matringhem. However, Danzé-Corsin (1956a) did not mention or illustrate any specimens, whether fertile or sterile, similar to *Danziella* in Matringhem, indicating that they were not originally recorded there. Upon reinspection, it is clear that all specimens of *Danziella* come from Rebreuve as they are preserved in a finer-grained lighter color matrix characteristic of other samples from Rebreuve. This mistake stems from a mixing of specimens over the years in the collections. *D. artesiana* should therefore be excluded from the Matringhem assemblage.

5. *Sawdonia* sp.

1933 *Psilophyton princeps* Dawson, Corsin.

1956b *Psilophyton princeps* Dawson, Danzé-Corsin, pl. II, figs. 1–3.

Material. 14 specimens were identified in the collections. Description is based on specimen numbered USTL 3547, USTL 3638A, USTL 3639, USTL 3649 (Fig. V.4A), USTL 3645 (Fig. V.4B), USTL 3631 (Fig. V.4C, G), USTL 3644–1 (Fig. V.4D, F), USTL 3644–2 (Fig. V.4D, H), USTL 3548 (Fig. V.4E) and USTL 3650A.

Description. Spiny axes up to 12 cm long on largest samples (Fig. V.4A). Axes diameter between 2.2 – (4) – 7.4 mm ($n = 20$). Branching is planar and mostly anisotomous (Fig. V.4A-B), although isotomous (Fig. V.4C) and pseudomonopodial (Fig. V.4D) branching also occurs. Shortly after its divergence from the main axis, the lateral branch recurves upward, growing in parallel to the main axis. Interval between two dichotomies varies from 1.2 to 3.5 cm (Fig. V.4A at arrow, Fig. V.4C–D), although most specimens do not show more than one branch departing from the main axis. One subaxillary bud close to the branching point (3.4 mm wide, 2.7 mm high) is also observed (Fig. V.4D–E at white arrows). All axes are covered with spines and/or spine scars. Spine scars form oval to circular depressions in the matrix (Fig. V.4E). Spines are locally helically arranged on the stem surface and up to 5 spine scars are observed in each gyre (spines on the visible side of axis) suggesting at least 10 spines per helix (Fig. V.4E). Up to four parallel helices are shown (Fig. V.4E). Each helix is inclined at a 35–50° angle. Vertical distance between each helix is around 1 mm. Spine scars are separated from each other by a distance of 0.20 to 0.65 mm. Spines have a stout appearance and a deltoid shape, with a triangular base, sometime slightly decurrent, tapering into an acute or apiculate tip (Fig. V.4F). The tip may sometime be abaxially recurved (Fig. V.4F). Spines are 0.5 – (1.2) – 2.2 mm wide at base ($n = 30$) and are between 0.5 – (1.2) – 1.9 mm long ($n = 30$).

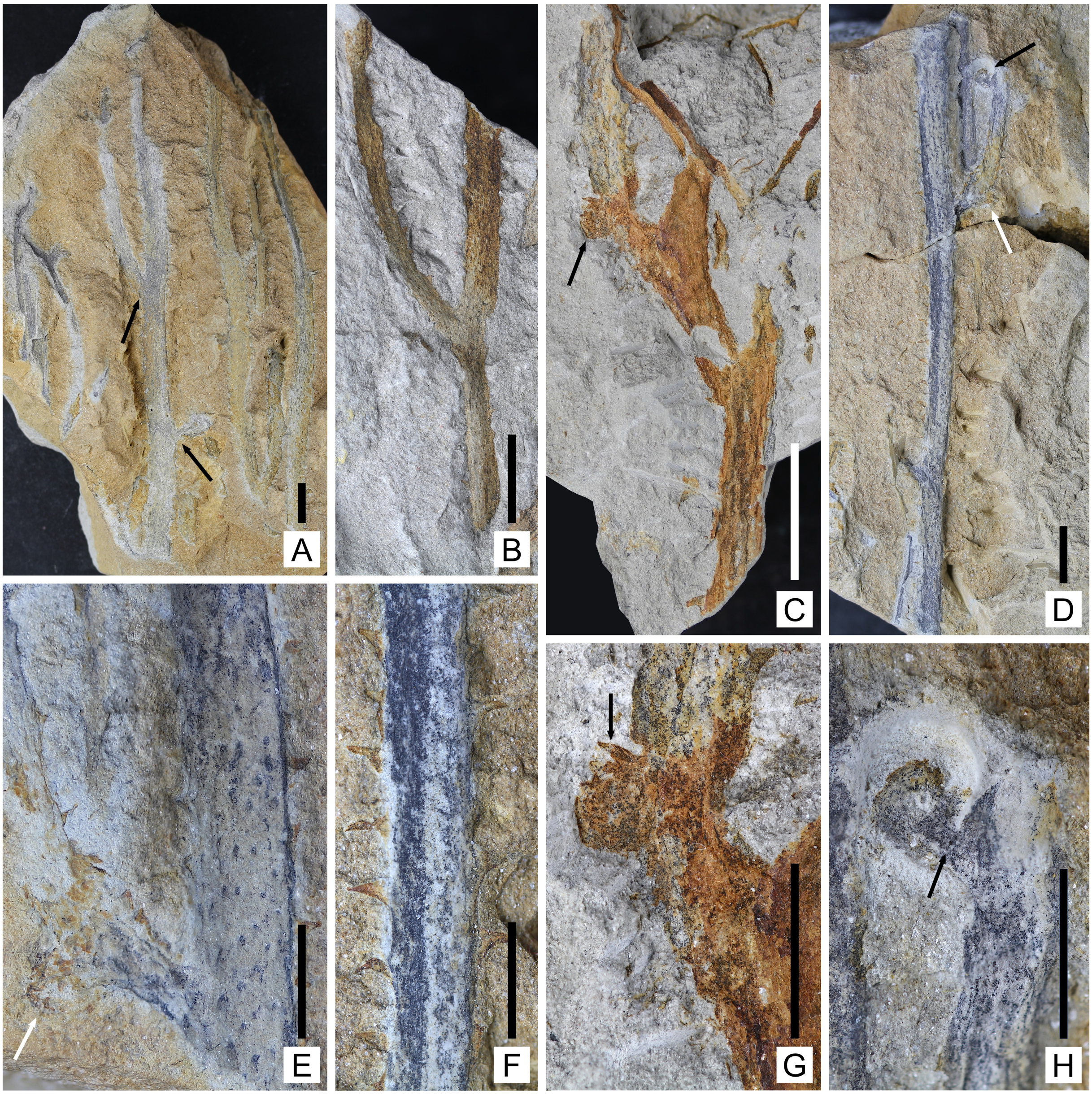

Figure V.4: *Sawdonia* sp. from the Rebreuve assemblage, France. A, Vegetative axes with anisotomous type of branching; note two successive dichotomies at arrows, USTL 3649. B, Anisotomously branching sterile axis, USTL 3645. C, General view of a fertile specimen displaying two consecutive isotomous dichotomies; note the position of sporangium-like structure at arrow, USTL 3631. D, General view of a fertile specimen displaying a pseudomonopodial type of branching; white arrow points to the location of a subaxillary bud; black arrow shows the location of sporangium-like structure, USTL 3644–1 and USTL 3644–2. E, Counterpart of specimen illustrated in Figure 4D showing the helical arrangement of spine scars; arrow show the counterpart of the subaxillary bud, USTL 3548. F, Detailed view of specimen illustrated in Figure 4D displaying diversity of spine morphologies encountered on a single axis, USTL 3644–1. G, Detailed view of specimen illustrated in Figure 4C with sporangium-like structure seen in adaxial view. Arrow shows the location of spines on the abaxial valve, USTL 3631. H, Detailed view of specimen illustrated in Figure 4D with sporangium-like structure seen in abaxial view. Arrow shows the stalk connecting the axis with sporangium, USTL 3644–2. Scale bars: A–D = 10 mm; E–H = 5 mm.

Two sporangia-like structures were identified on two separate potential fertile axes (Fig. V.4C–D at black arrows). They are borne laterally on stalks on either side of the fertile axis (Fig. V.4G–H). Sporangia-like structures are rounded to oval and are 2.4–3 mm long and 2.1–2.5 mm wide. Spines are visible on the upper margin (Fig. V.4G at arrow) and are smaller than spines on axes (0.3–0.7 mm). In both cases, sporangia-like structures are folded around the axis and bent downward into the matrix hindering the possibility to potentially simultaneously observe both valves. One specimen shows sporangium-like structure in abaxial view, with a distinct structure interpreted as a stalk, curved upward at a 50° angle (Fig. V.4H at arrow). The stalk is 2.6 mm long and 0.8 mm wide (Fig. V.4H). On the other specimen (Fig. V.4G), the sporangium-like structure is seen in adaxial view but only the abaxial valve can be recognized, probably covering the smaller adaxial valve.

Interpretation. Danzé-Corsin (1956b) assigned these vegetative specimens to *Psilophyton princeps* Dawson based on Halle (1916)'s definition of what was originally described as *Psilophyton princeps* var. *ornatum* in Dawson (1871), now called *Sawdonia ornata* (Hueber, 1971). The *dégagement* of two likely sporangia contributes to a better comprehension of this plant. These sporangia-like structures lack an ostensible dehiscence margin and could also be easily mistaken for a bud (Gensel and Berry, 2016). Nevertheless, certain features such as dehiscence margin, stalk and spines on sporangium are often poorly preserved (Gensel and Berry 2016, figs. 3–4). In addition, the amount of remaining organic matter preserved here probably prevents simultaneous observation of all features (Fig. V.4H–G). Certain features indicate that these structure are more likely sporangia than buds: (1) buds tend to be larger than sporangia e.g. the subaxillary bud in Fig. V.4D–E, (2) buds grow in the same plane as the subtending axis unlike sporangia which are often found folded around the axis (Gensel and Berry 2016, figs. 9d–f), a characteristic clearly seen in Fig. V.4H, (3) spines on buds (Fig. V.4D–E) are not as developed as on structures interpreted as sporangia (Fig. V.4H), and (4) a well-defined stalk can be observed in Fig. V.4G. The lack of dehiscence margin may also be explained by the structures representing immature sporangia (Gensel and Berry, 2016).

Axes with lateral sporangia both bearing emergences are characteristic of several Lower Devonian taxa with zosterophyll affinities such as *Faironella* (Gerrienne, 1996a), *Odonax* and *Sawdonia* (see Jensen and Gensel, 2013, table 1). *Odonax* differs from our specimens by having small scaly denticulate emergences and compact bilateral strobili of sporangia (Gerrienne, 1996b). *Faironella* is distinct from our specimens by possessing, among other features (see Gerrienne, 1996a), mostly dichotomous and K-branching with oval sporangia and cuneiform in its adaxial part. Here, the branching pattern, emergences morphology, the presence of rounded lateral sporangia bearing spines on the abaxial valve, subtended by a short stalk, can allow us to confidently compare this taxon to *Sawdonia*. The diagnosis of this taxon was recently emended by Gensel and Berry (2016) and subsequently by Berry and Gensel (2019) mainly linked to the fact that sporangia consisted of unequal valves whereas they were previously thought to be equal. We cannot clearly see both valves on our specimens but the fact that the abaxial valve is the only visible one indicates that valves are indeed unequal.

Rebreuve specimens, when compared with other species of *Sawdonia* share common features of currently both well-defined species from the Lower Devonian (Gensel and Berry, 2016; Berry and Gensel, 2019, table 1). On the other hand, the late Middle Devonian species *S. hippotheca*, differs more markedly in terms of branching, emergence type and sporangial morphology (Berry and Gensel, 2019). Spines on our specimens resembles more those of *S. deblondii*, despite their stouter appearance. Helical arrangement of spines has not been previously documented in *Sawdonia*, but reexamination of transfers of *S. ornata* from the type locality confirmed this feature to locally occur in this species. Branching is more prevalent here than in *S. deblondii*, but branching pattern has characteristics of both species: *S. deblondii* (iso- to anisodichotomous and K-branching) and *S. ornata* (pseudomonopodial). In terms of sporangial morphology and size, the sporangia of Rebreuve specimens are more reminiscent of *S. ornata* than *S. deblondii*. The only exception is that the stalk in Rebreuve specimens is longer than in *S. ornata* and occurring within the size range of *S. deblondii*. The Rebreuve specimens do not fit exactly in either species and therefore might potentially represent a new species. Without further information on valve morphology and sporangium arrangement on axis, we refer to these specimens as *Sawdonia* sp.

Lycophytes - Lycopsida

6. *Drepanophycus* cf. *spinaeformis*

1933 *Arthrostigma gracile* Dawson (= *Drepanophycus* Göppert), Corsin.

1956b *Drepanophycus spinaeformis* Göppert, Danzé-Corsin, pl. II, figs. 5–6.

Material. About 15 specimens are recognized in the assemblage. Description is based on specimens numbered USTL 3625 (Fig. V.5A), USTL 3619 (Fig. V.5B), USTL 3626A (Fig. V.5C), USTL 3620 (Fig. V.5D), USTL 3621 (Fig. V.5E) and USTL 3527B (Fig. V.5F).

Description. This plant consists of fragmented vegetative axes measuring up to 15 cm long (Fig. V.5A). Axes range from 0.7 to 2.2 cm in width. The largest specimen clearly shows the trace of a central vascular strand reaching 2.3 mm in diameter (Fig. V.5B at arrow). Isotomous branching is observed, dividing at a wide angle (Fig. V.5C). Each lateral then recurves and grows in parallel to each other in the same direction as the parent axis (Fig. V.5C). One specimen displays H-type branching, the daughter axis growing in the same plane and parallel to the parent axis (Fig. V.5D). Specimens have a smooth irregular surface with a ribboned-like aspect. Microphylls are not preserved. However, leaf bases are noticeable on the axes surface, appearing as small round to oval depressions (Fig. V.5E at arrows). The distance between leaf bases ranges from 6.2 to 9.6 mm. No discernable arrangement of microphylls can be distinguished on stems. One lateral bud bearing six visible microphylls less than 1 mm long is observed (Fig. V.5F at arrow). No fertile axes were found.

Interpretation. Danzé-Corsin (1956b) correctly assigned this plant to *Drepanophycus spinaeformis* based on the singular morphology, size and aspect of *Drepanophycus* vegetative axes described in Kräusel and Weyland (1930) and Stockmans (1940). *Drepanophycus* is a widespread cosmopolitan taxon most commonly found in Emsian strata albeit not exclusively (see e.g., Banks and Grierson, 1968). Here, we report previously undescribed features that further corroborate the assignation of these specimens to *D. spinaeformis*. Firstly, the occurrence of H-branching patterns (Fig. V.5C) is also well

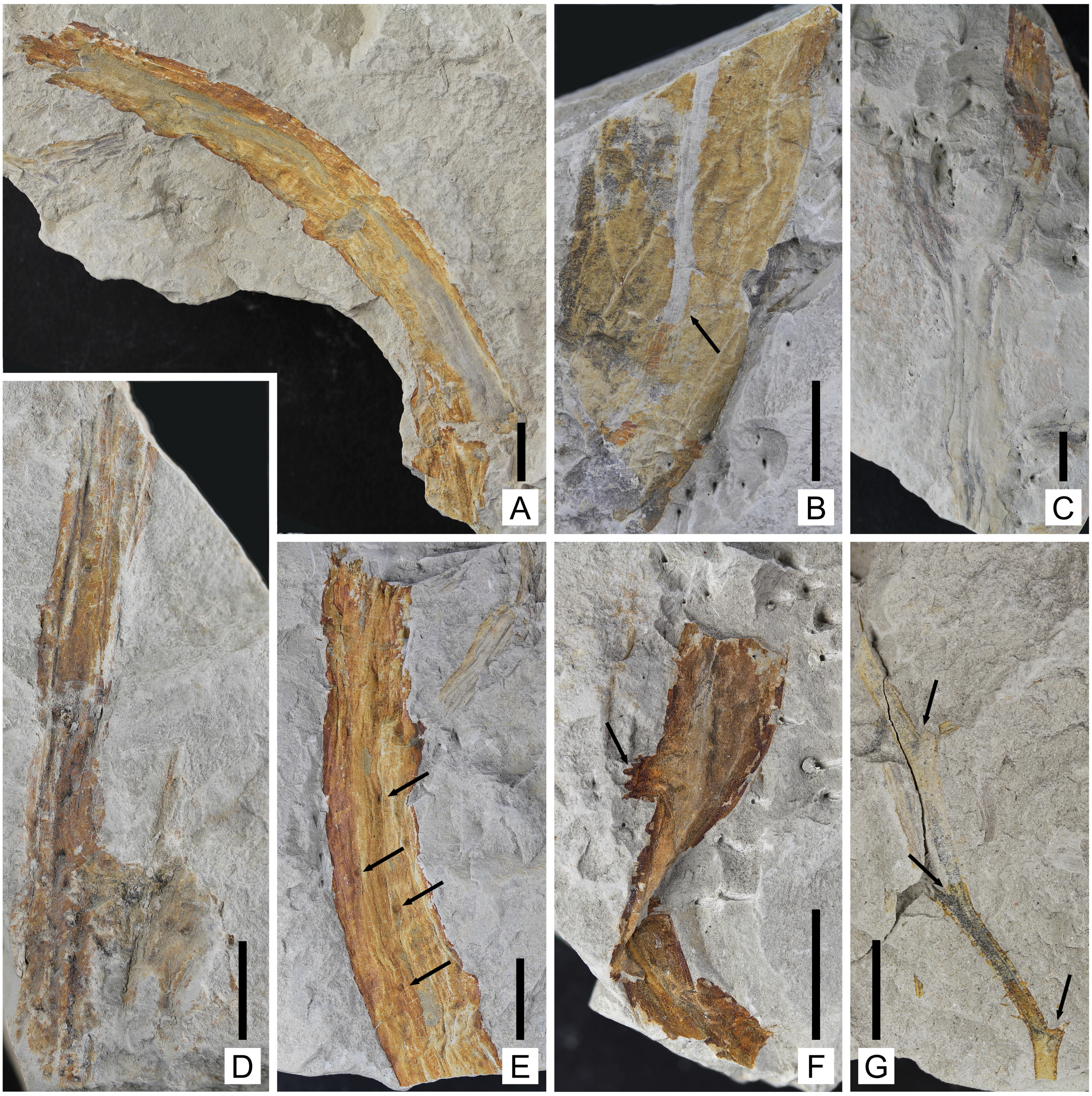

Figure V.5: Plant fossils from the Rebreuve assemblage, France (II). A, *Drepanophycus* cf. *spinaeformis*, general view of a large vegetative specimen, USTL 3625. B, *Drepanophycus* cf. *spinaeformis*, specimen showing the trace of a vascular strand in the center of the axis, USTL 3619. C, *Drepanophycus* cf. *spinaeformis*, impression of an axis dividing isotomously, USTL 3626A. D, *Drepanophycus* cf. *spinaeformis*, specimen displaying H-type of branching, USTL 3620. E, *Drepanophycus* cf. *spinaeformis*, well-preserved vegetative axis bearing round to oval depressions interpreted as leave scars at arrows, USTL 3621. F, *Drepanophycus* cf. *spinaeformis*, specimen bearing one lateral bud showing several small microphylls at arrow, USTL 3527B. G, "*Psilophyton*" *burnotense*, spiny axis showing three successive anisotomous dichotomies at arrows; USTL 3685. Scale bars = 10 mm.

documented in *D. spinaeformis* (Croft and Lang, 1942; Banks and Grierson, 1968; Rayner, 1984). Lateral buds are also a known feature to occur in *D. spinaeformis* and the specimen from Rebreuve (Fig. V.5F) bears strong similarities with buds from specimens from the type locality (Li et al., 2000, figs.

22–23). *D. qujingensis* differs from our specimens by the absence of K- and H-branching (Li and Edwards, 1995), whilst they differ from *Sengelia radicans* (another Drepanophycales) by not exclusively possessing the K-branching pattern (Matsunaga and Tomescu, 2017). *D. gaspianus* is characterized by a pronounced rhomboidal pattern on axes representing the zone of attachment of leaves, a feature not found on our specimens (Fairon-Demaret, 1977). The absence of preserved microphylls and fertile parts precludes a firm assignation of these specimens to *D. spinaeformis*. These features are known to be better preserved (or even uniquely found) on aerial stems rather than on rhizomes. We therefore interpret the Rebreuve specimens as perhaps rhizomes of *D. spinaeformis* considering their smooth surface bearing leaf bases (Fig. V.5E), similar to rhizomes from the type locality (Li et al., 2000).

Euphyllophytina

7. *"Psilophyton" burnotense*

1956b *Psilophyton* sp. Dawson, Danzé-Corsin, pl. II, fig. 4.

Material. A single specimen was identified in the collections USTL 3685 (Fig. V.5G).

Description. Truncated spiny axis. Main axis 2 mm wide and 5.2 cm long. Three successive anisotomous dichotomies, distant from each other by 1.7–1.8 cm, are observed (Fig. V.5G at arrows). Distichous arrangement of branches occurring alternately on either side of the main axis. Lateral axes narrower than main axis (1 mm wide). One lateral after first dichotomy tapers rapidly giving the impression of an aborted branch (Fig. V.5G at arrow). Spines slender, less than 1 mm long and less than 0.5 mm wide at their base. Spines are triangular at base then subulate. A thickened margin is noticeable on all the length of the main axis and laterals. No fertile parts were found in connection to the sterile axis.

Interpretation. Danzé-Corsin (1956b) recognized this specimen as different from *Psilophyton princeps* (*Sawdonia* sp. in this study), acknowledging similarities with *Psilophyton goldschmidtii*, without formally designating it as belonging to this species. This specimen could be assignable to the form-genus *Psilophytites*, which circumscribes vegetative axes bearing undivided spines (Høeg, 1952). Nevertheless, the presence of a thickened margin allows us to compare this axis with other taxa that possesses this feature. Currently, anisodichotomously branched vegetative axes bearing slender pointed emergences and presenting a thickened margin is characteristic of either *Psilophyton burnotense* (syn. *P. goldschmidtii*), a basal euphyllophyte, or *Margophyton goldschmidtii*, a zosterophyll (Gerrienne, 1991). The history of these taxa is rather complex (see Schweitzer, 1989 for details). Such axes were first described in Belgium under the name *Lepidodendron burnotense* in Gilkinet (1875). Other vegetative specimens with similar morphology were subsequently found in Röragen, Norway for which Halle (1916) created the species *Psilophyton goldschmidtii.* This name was later reutilized by Stockmans (1940) for describing his Belgian specimens, likewise uniquely vegetative. Nevertheless, the epithet *burnotense* in Gilkinet (1875) had priority, so newly found German specimens were consequently named *Psilophyton burnotense* (Kräusel and Weyland, 1948).

However, the discovery of identical axes to *P. burnotense* in the Emsian of Siberia bearing lateral sporangia, thereby indicating zosterophyll affinities, blurred our understanding of this taxon (Zakharova, 1981). Zakharova (1981) synonymized European specimens of *P. goldschmidtii, P. burnotense* and the Siberian specimens under a new combination: *Margophyton goldschmidtii.* Nevertheless, Schweitzer (1989) demonstrated that European specimens of *Psilophyton burnotense* did possess terminal sporangia, therefore belonging to a distinct lineage to *Margophyton*. The Rebreuve specimen is identical to the *P. goldschmidtii* described in Stockmans (1940). Specimens found in Belgium were later conservatively renamed "*Psilophyton*" *burnotense* by Gerrienne (1983, 1993). In Gerrienne (1993)'s opinion, the lack of fertile structures in Belgian specimens could not lead to the definitive assignation to *Psilophyton*, these axes could equally belong to *Margophyton*. We follow the same approach here by being conservative regarding its assignation to *Psilophyton*.

8. cf. *Psilophyton forbesii*

1956b *Dawsonites arcuatus* Halle, Danzé-Corsin, pl. III, figs. 7–7a.

Material. Only one specimen was recovered (part and counterpart) numbered USTL 3705 and USTL 3706 (Fig. V.6A). It consists of a faint impression with very little original organic matter preserved.

Description. It consists of two pairs of fusiform sporangia subtended by short stalks measuring 4.8 mm long in total, and 0.6 mm in width (Fig. V.6A). Since no axes were found connected to the stalks, the length of each individual stalk is unknown. Stalk and sporangia surface devoid of emergences. The two pairs of sporangia are pendant and a sinistral torsion of the sporangia pair can be distinguished. Each individual sporangium is 4.1 mm long and between 0.5 and 1 mm wide. No dehiscence line could be detected on any of the sporangia.

Interpretation. Pairs of fusiform sporangia twisted around each other are characteristic of several basal euphyllophyte taxa such as *Psilophyton, Pertica* and *Trimerophyton* (Gerrienne, 1997, table 2). However, pairs of sporangia in *Pertica* and *Trimerophyton* are erect and not pendulous, like our specimen (Fig. V.6A). This specimen was originally described as *Dawsonites arcuatus* in Danzé-Corsin (1956b). *Dawsonites* is a genus intended to circumscribe fertile axes resembling to those of *Psilophyton* or other basal euphyllophytes that are not connected or associated with sterile axes. *Dawsonites arcuatus* has since been renamed *Psilophyton arcuatum* for German material by Schweitzer (1980) and later for Norwegian specimens (Schweitzer and Heumann, 1993) because there was enough material to assign it to *Psilophyton*. This taxon was subsequently synonymized by Gerrienne (1997) with *P. forbesii* that likewise occurs in the USA (Andrews et al., 1968), Canada (Gensel, 1979) and Belgium (Gerrienne, 1997). Among all *Psilophyton* species currently described, sporangia correspond the most in terms of size and shape with *P. forbesii* and especially with the ones described in Gerrienne (1997) that are slightly thinner than other occurrences. However, the lack of associated fertile or sterile axes does not allow us to categorically assign this specimen to *Psilophyton* despite the obvious similarities with *P. forbesii*.

9. *Psilophyton parvulum*

1956b *Hostimella* sp. Barrande, Danzé-Corsin, pl. II, fig. 9.

1956b *Dawsonites* cf. *minor* Stockmans, Danzé-Corsin, pl. II, fig. 9.

1956b *Dawsonites* cf. *minor* Stockmans, Danzé-Corsin, pl. III, figs. 5–6.

Material. Many fragments were found isolated in several samples or found in dense tufts, mixed with axes belonging to *Danziella artesiana* (Fig. V.6B). The description is based on USTL 3609-1-2 (Fig. V.6B, E), USTL 3616–1 (Fig. V.6C, F) and USTL 3814 (Fig. V.6D).

Description. Fragmented sterile and fertile axes up to 3.5 cm long (Fig. V.6B–C). Axes are less than 1.4 mm wide and the surface is striated longitudinally. Branching may be pseudomonopodial, anisotomous (Fig. V.6C) or isotomous (Fig. V.6D). Pairs of fusiform sporangia were found attached to fertile axes morphologically similar to vegetative axes in two samples (Fig. V.6B–C at black arrows), and are therefore inferred as belonging to the same plant. Pairs are subtended by short stalks (0.2 mm wide) resulting from an isotomous dichotomy (Fig. V.6E–F). Sporangia measure between 1.3 and 1.5 mm long and between 0.3 and 0.5 mm wide. Sporangia are erect (borne in the continuation of the direction of the axis) and twisted in a sinistral direction. No dehiscence line is observed on specimens. The tips of the sporangia can be acute (Fig. V.6E) or blunt (Fig. V.6F).

Interpretation. Dichotomous axes bearing distally pairs of fusiform sporangia twisted around each other, also points to the genus *Psilophyton* (Gerrienne, 1997). *Psilophyton* species with surface of axes devoid of emergences and striated, is characteristic of both *P. forbesii* and *P. parvulum* (Gerrienne, 1995, fig. 2). The main differences between the two species is the size: *P. parvulum* being much smaller in terms

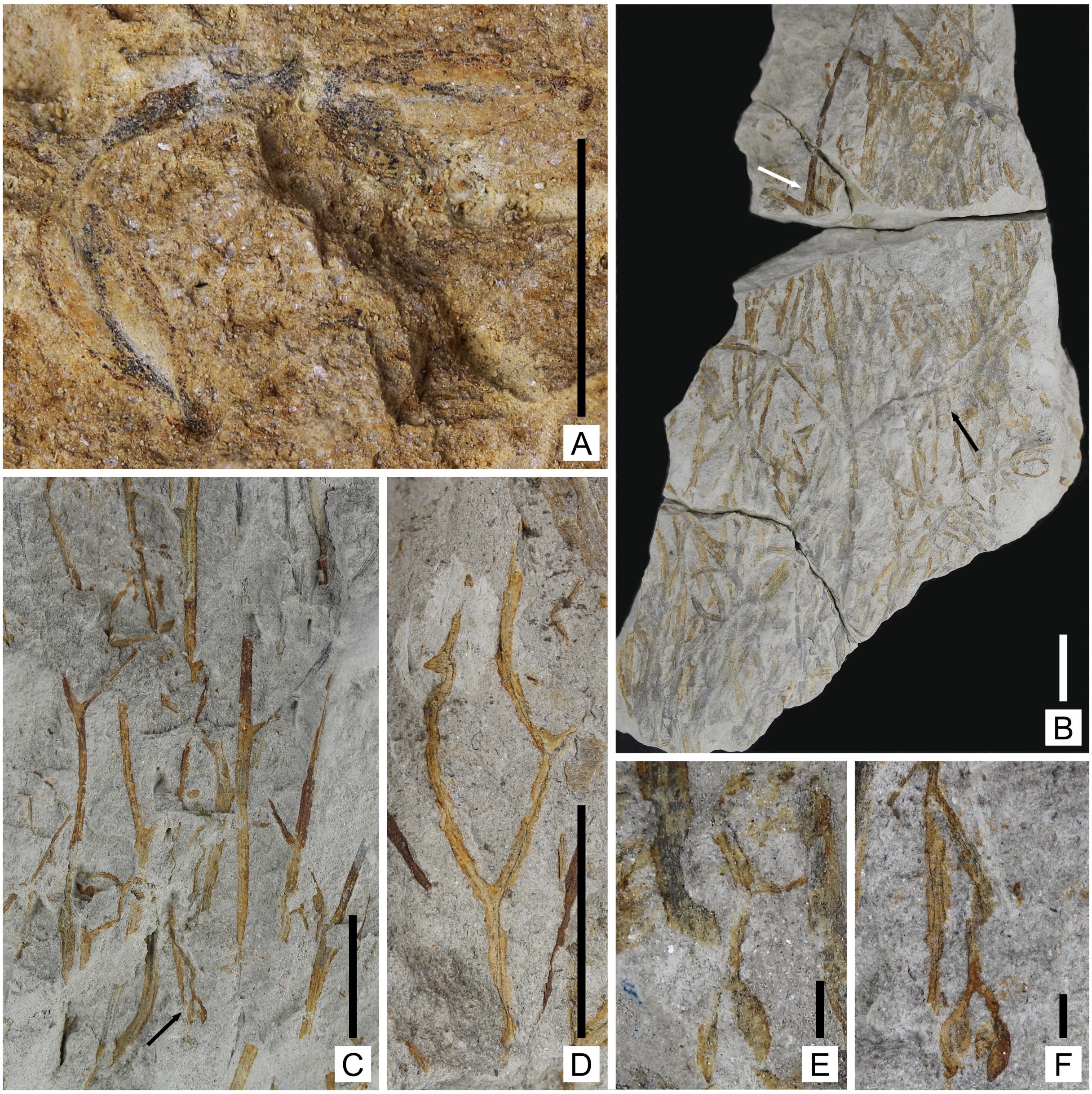

Figure V.6: Plant fossils from the Rebreuve assemblage, France (III). A, cf. *Psilophyton forbesii*, general view of specimen USTL 3706 bearing two pairs of fusiform sporangia connected by a short stalk. B, General view of axes of *Psilophyton parvulum* and *Danziella artesiana*. Arrow points to the location of a fertile axis of *P. parvulum* shown in Figure 6E. White arrow shows the location of an identifiable *Danziella* axis; USTL 3609–1 and USTL 3609–2. C, *Psilophyton parvulum*, general view of various vegetative striated axes displaying pseudomonopodial and anisotomous branching. Black arrow indicates location of a fertile axis shown in Figure 6F; USTL 3616–1. D, *Psilophyton parvulum* vegetative striated axis displaying two successive isotomous dichotomies, USTL 3814. E, *Psilophyton parvulum*, detailed view of truncated fertile axis bearing terminally a pair of sporangia, USTL 3609–1 and 3609–2. F, *Psilophyton parvulum*, detailed view of truncated fertile axis bearing terminally two pairs of twisted sporangia; USTL 3616–1. Scale bars: A = 5 mm; B–D = 10 mm; E–F = 1 mm.

of axes diameter and sporangia than *P. forbesii*. *P. dapsile* is also one of the smallest species of *Psilophyton* but it differs from our specimens by only possessing an isotomous branching pattern, and additionally, the size-range of its sporangia does not overlap with our specimens (Kasper et al., 1974; Gerrienne, 1995, fig. 2). The specimens herein described conform in all aspects with *P. parvulum* (branching pattern, sterile and fertile axes size and morphology) and can therefore confidently be identified as this taxon. Danzé-Corsin (1956b) originally described this species as two separate taxa albeit highly suspecting the connection between the *Hostimella* sp. axes (now sterile axes of *P. parvulum*) and *Dawsonite*s cf. *minor* (now fertile axes of *P. parvulum*). Careful reexamination of the material clearly showed the similarity of fertile and sterile axes and allows us to consider them as belonging to the same entity. Axes of *Danziella artesiana* and *P. parvulum* are of equivalent size and can be easily confused, especially when found mixed in dense mats (Fig. V.6B). Nevertheless, axes of *Danziella* can be distinguished with their wider dichotomizing angle and their unstriated smoother axes surface (Fig. V.3F–G). Here, a specimen (Fig. V.6B) interpreted as presumed sterile axes of *D. artesiana* in Edwards (2006, pl. III, fig. 1), is actually mostly constituted of axes of *P. parvulum*.

10. cf. *Psilophyton* sp.

Material. One specimen is recorded with both part USTL 3670 (Figure V.7A) and counterpart USTL 3742 (Fig. V.7B) preserved.

Description. Isotomously dichotomizing naked axis (Fig. V.7A–B). Intervals between dichotomies shorten distally as well as width of branches. The main axis is 3.1 mm wide, first-order branches are 1.9–2 mm wide and second-order branches 1.5–1.7 mm wide. Ultimate branchlets slightly tapper, recurve, before ending in an acute tip. Ultimate vegetative branchlets are 4 mm long and are 0.6–0.7 mm wide at their base. One pair of sporangia has been uncovered (Fig. V.7B, at arrow), although it is not directly connected to the vegetative specimen. The only entirely visible sporangium is 3.9 mm long and 1 mm wide. Sporangia are elongated and slightly fusiform, ending in a blunt tip.

Interpretation. This specimen was not described nor figured in Danzé-Corsin (1956b). Tapering isotomously dividing sterile axes ending in slightly recurved terminal branchlets is typical of several basal euphyllophyte taxa such as *Psilophyton* and *Pertica* (Kasper and Andrews, 1972; Gensel, 1979). This type of axis is different from *Psilophyton parvulum* (Fig. V.6B–F) present in this assemblage by its apparent smooth surface and larger size. *P. krauselii* and *P. dapsile* do not correspond with this vegetative specimen given that their axes diameter is smaller than 3 mm (Obrhel, 1959; Kasper et al., 1974; Andrews et al., 1977). *P. microspinosum* and *P. charientos* have emergences and ultimate branchlets divide at a wider angle (Kasper et al., 1974; Gensel, 1979). This specimen also presents similarities with *P. szaferi*, but lacks enations, a typical trait of this species (Zdebska, 1986). *Pertica* is a closely related taxon, which also bears similar axes ending in recurved ultimate branchlets (Kasper and Andrews, 1972, fig. 6–7), so an assignation of the vegetative specimen to *Psilophyton* cannot be asserted with confidence.

On the other hand, sporangia uncovered present striking similarities in size and shape to sporangia described as cf. *P. forbesii* in the assemblage (Fig. V.6A). Nevertheless, there is no unequivocal connection between the axis and sporangia, and axes of *P. forbesii* are usually clearly striated although distal branches may apparently sometimes lack this feature (Gerrienne, 1997 and references therein). Sporangia of *Pertica* occur as dense clusters and are elliptical, not fusiform, which, if we believe there is connection, precludes an assignation to *Pertica*. Without a direct connection with sporangia and the lack of distinctive features on the vegetative specimen, we refer to this specimen as a possible *Psilophyton*.

V.5. Excluded taxa from the Rebreuve assemblage

Yarravia is a genus of probably either rhyniophyte or trimerophyte affinities of the late Silurian and early Devonian of Australia, China and South Africa (McSweeney et al., 2021; Gess and Prestianni, 2021). Danzé-Corsin (1956b, pl. III, fig. 10–10a) created a new species based on a single specimen from Rebreuve. She described it as a spherical synangium subtended by a short stalk on a smooth axis, with perhaps 4 or 5 sporangia united at their base but separated in their most distal parts. P. Danzé-Corsin

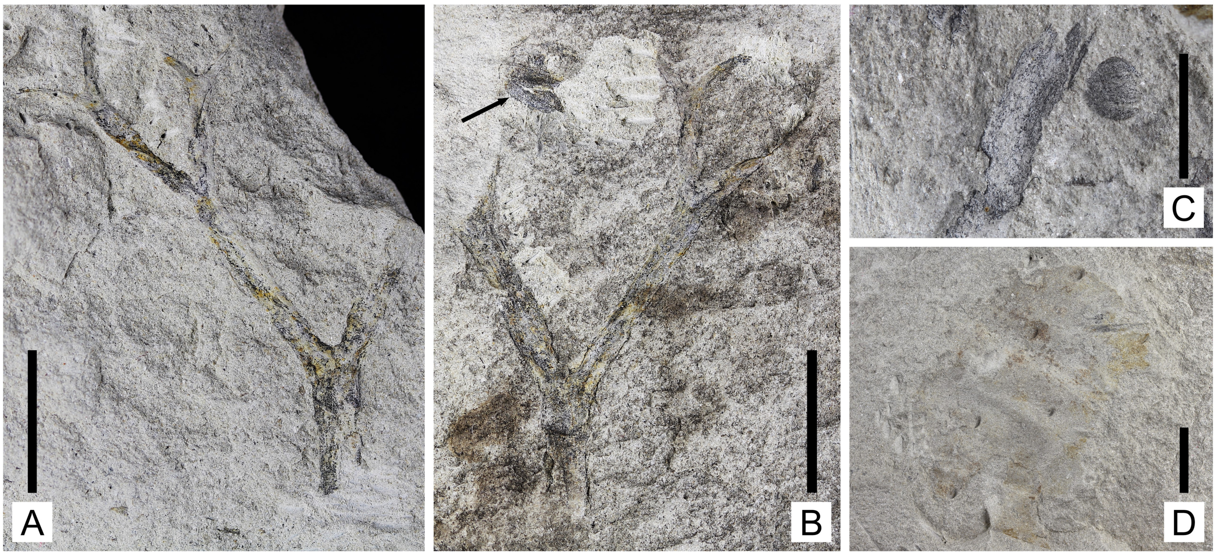

Figure V.7: Plant fossils from the Rebreuve assemblage, France (IV). A, cf. *Psilophyton* sp., vegetative axis displaying three successive isotomous dichotomies terminating in tapering recurved ultimate appendages, USTL 3670. B, cf. *Psilophyton* sp., counterpart of specimen USTL 3670 shown in Figure 7A; isolated pair of sporangia at arrow, USTL 3742. C, *Psilophyton*-like stem initially described as *Yarravia minor* n. sp. in Danzé-Corsin (1956b); USTL 3829. D, Unknown structure interpreted as *Cyclostigma* sp. in Danzé-Corsin (1956b), USTL 3670. Scale bars: A–B, D = 10 mm; C = 5 mm.

compared this specimen with *Y. subsfaerica* and *Y. oblonga* but distinguished it by its much smaller size, hence calling this plant *Y. minor*. However, *Yarravia*'s fructifications are borne terminally (McSweeney et al., 2021). This plant's apparent "fructification" is borne laterally, even though contrary to Danzé-Corsin (1956b)'s observations, a stalk connecting sporangia and stem is not visible here (Fig. V.7c). Upon reexamination, this specimen appears to represent a folded *Psilophyton*-like stem and should therefore be excluded from *Yarravia*.

Danzé-Corsin (1956b, pl. II, fig. 11–11a) also described one specimen consisting of a 4 cm wide and 2 cm long smooth impression, with several oval-shaped holes in the matrix, separated from each other by 10– 15 mm (Fig. V.7D). She interpreted these marks as leafscars and compared this fossil to the aspect of a *Cyclostigma* bark impression (Chaloner, 1968; Doweld, 2017). In addition to the fact that *Cyclostigma* is an exclusively Late Devonian-early Carboniferous lycopod tree, this specimen simply does not conform to the diagnosis of *Cyclostigma* (Chaloner, 1968), and the nature of this fossil remains enigmatic.

V.6. Discussion

The Rebreuve assemblage represents a moderately well-preserved, and taxonomically diverse Lower Devonian flora. Taxonomic description of numerous early Devonian plants since the 1950s made possible a better understanding of the plants recorded in this assemblage. Table V.1 lists the original taxonomic composition of the flora recorded by Danzé-Corsin (1956b) and our revised list based on this study. This reinvestigation led to the discovery of likely fertile remains of *Sawdonia* not originally described in Danzé-Corsin (1956b). This discovery is a key finding as the diagnosis of *Sawdonia* has recently been emended (Gensel and Berry, 2016; Berry and Gensel, 2019). It resulted in many formerly described *Sawdonia* species being excluded from the genus due to inconsistencies with the diagnosis in terms of sporangial morphology or emergence type (Gensel and Berry, 2016). The Rebreuve assemblage therefore represents a new occurrence of *Sawdonia* (Berry and Gensel, 2019, table 1), the second known occurrence of *Psilophyton parvulum* (Gerrienne, 1995) and the single known record of *Danziella artesiana* (Edwards, 2006). All major taxonomic groups present in the Lower Devonian are represented here (Bryophyta, Rhyniopsida, Zosterophyllopsida, Lycopsida and Euphyllophytina). Zosterophylls (*Danziella artesiana* and *Sawdonia* sp.) are the most abundant components representing a little less than 50% of the entire fossil flora. Basal euphyllophytes are less common but are fairly diverse with potentially up to four different species of *Psilophyton* featured in the flora (Table V.1).

Table V.1. List of Rebreuve plant fossil taxa.

Danzé-Corsin (1956b)	This study
Sporogonites exuberans	*Sporogonites exuberans*
Taeniocrada decheniana	*Taeniocrada* sp.
Sciadophyton cf. *laxum*	*Sciadophyton* sp.
Zosterophyllum artesianum	*Danziella artesiana*
Psilophyton princeps	*Sawdonia* sp.
Drepanophycus spinaeformis	*Drepanophycus* cf. *spinaeformis*
Psilophyton sp.	*'Psilophyton' burnotense*
Dawsonites arcuatus	cf. *Psilophyton forbesii*
Hostinella sp. *Dawsonites* cf. *minor*	*Psilophyton parvulum*
-	cf. *Psilophyton* sp.
Yarravia minor	-
Cyclostigma sp.	-

The association of plants found in Rebreuve is common in Emsian Western European and North American assemblages, see e.g. Germany (Schweitzer, 1983), Scotland (Rayner, 1983, 1984), Norway (Halle, 1916; Schweitzer and Heumann, 1993) and Eastern Canada (Kennedy et al., 2012; Gensel and Berry, 2016). More specifically, this flora bears a striking resemblance to Belgian assemblages and especially those found in the early Emsian (AB biozone of Steemans, 1989) Grès de Wépion Formation such as Marchin or Thuin (Gerrienne, 1993 and references therein). The age of these Belgian localities is similar to the age found in La Comté-Beugin (Fig. V.2) and an early Emsian age for Rebreuve plants can be reliably inferred. This assemblage therefore probably represents the second oldest French flora (Strullu-Derrien et al., 2010). Other French early Devonian floras are rare and exclusively found (other than in the Artois region), in the Armorican massif (Ducassou et al., 2009; Strullu- Derrien et al., 2010; Gerrienne et al., 2011). The preservation state of most Armorican plants makes comparison with this flora rather difficult. Nevertheless, Lower Devonian Armorican assemblages do not share any common taxa with Rebreuve other than the cosmopolitan taxon *Psilophyton*. The similarities between Rebreuve and other Western European and North American Emsian floras is compatible with the reconstructed position of Lower Devonian paleocontinents, being all located on Laurussia, whereas Armorica was located on the peri-Gondwanan margin (Scotese, 2014).

Recent attempts to quantify early land plant diversity through time (e.g. Capel et al., 2021, 2022a) requires reliably identified and well-dated plant fossil occurrences. It is also essential for reconstructing accurate paleophytogeographical relationships (Raymond et al., 1985, 2006; Wellman et al., 2013). For instance, in this case, the exclusion of *Yarravia* from the assemblage has profound consequences for Lower Devonian paleophytogeography, as this taxon is otherwise uniquely found in Gondwanan assemblages (McSweeney et al., 2021). Synthetic works that compile and revise already described plant fossils collected over the past century are critically important (e.g. Gerrienne, 1993; Edwards and Richardson, 2004) and this study contributes toward this objective. Considering this, in addition to the Rebreuve assemblage, the Matringhem flora (Danzé-Corsin, 1956a), located 30 km west of Rebreuve is also in need of revision and will be redescribed in a future study.

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General conclusions

This thesis aims at using a wide array of quantitative methods to assess both temporal and spatial dynamics of early (Silurian–Devonian) terrestrial macrofloras and identify potential drivers of diversity.

After the introductory Chapter I, the Chapter II demonstrates that the 'Evolutionary Floras' model, used to describe global Phanerozoic vegetation history at the family rank, was equally adequate to reveal more detailed underlying dynamics in Silurian−Devonian vegetation. The replication of a Q-mode factor analysis at the genus level and substage resolution, led to better temporal constraints of each evolutionary flora. The Eotracheophytic flora, strongly dominated by basal eutracheophytes and rhyniophytoids, thrived between the middle Silurian and the Lochkovian (Early Devonian). The succeeding Eophytic flora (*sensu* Cleal and Cascales-Miñana, 2014) prevailing in the Devonian is here found to be actually composed of two distinct phases: an early phase dominated by zosterophylls in the Early Devonian, and a late phase linked to the diversification of lycopsids, cladoxylopsids and progymnosperms. Lastly, the rise of the Palaeophytic flora in the latest Devonian is strongly related to the spermatophyte radiation. The rise of a new evolutionary flora appears to provoke the decline of the preceding flora, suggesting major ecological shifts, caused by the rapid growing complexity of vascular plants and ecosystems during this critical period.

Chapter III firstly expands on characterizing global total and within clades diversity dynamics. The apparent pattern is shown to represent an overall increase punctuated by peaks and throughs, regardless of the metrics used. The main dynamics are linked to congruent events of diversification and extinction, especially within the two main plant clades: lycophytes and euphyllophytes, corroborating the dynamics captured in the 'Evolutionary Floras' model. No apparent diversity-dependence of evolutionary rates are recovered, suggesting that early land plant radiation does not follow the kinetic model of diversification, contradicting anterior findings (Knoll et al., 1984). Statistical analyses also do not support intrinsic dynamics linked to different innate reproductive strategies contrary to Niklas et al. (1983), and external causes were resolved to be slightly more preponderant to explain diversity variations. However, abiotic factors such as atmospheric CO_2 and O_2 levels, temperatures, potentially explaining the observed pattern are not convincingly identified.

Thereafter, Chapter III focuses on sampling and geological biases potentially affecting both global and regional scales of the observed diversity patterns. Firstly, sampling-corrected patterns using the residual diversity method are obtained for total global plant diversity. Although sections of the pattern seem to reflect sampling effort, some signals appear more real than apparent, such as the Pragian and Givetian peaks and the diversity depletion event in the Eifelian. Nonetheless, a smaller-scale study focusing on North America is achieved to further assess the impact of geological incompleteness. Using geological proxies extracted from the Macrostrat database and a newly-compiled occurrence-based dataset, we show that the raw plant diversity pattern was driven by non-marine rock fossiliferous rock volume. This correlation is shown not to result of a third-controlling factor such as eustatic sea-level changes under a 'common-cause hypothesis'. The near complete lack of non-marine sedimentary rocks in North America prior to the Emsian prevents obtaining a sufficient sample of past biodiversity to recover accurate diversity patterns. In consequence, the most efficient sampling-standardizing techniques only appears to partially correct temporal sample size heterogeneity. The scarcity of continental deposits displaying the earliest evolutionary history of land plants can be reliably considered a significant contributing factor to explain the 40 Myr gap between the first micro- and macrofossil records.

Chapter 4 specifically focuses on the spatial diversity dynamics of early floras. The paleogeographical dissection of global diversity first revealed that our view of early land plant radiation remains highly tributary of the Laurussian fossil record. Secondly, the diversification of each plant clade was found to be mostly synchronous across paleoregions, except for zosterophylls and spermatophytes. Increasing evidence suggests that the cradle of zosterophylls was located in the equatorial to tropical regions, and that their dispersion and diversification may be partly linked to concomitant increasing temperatures. The predominance of rhyniophytoids in the highest latitudes in the Early Devonian and their subsequent replacement by a poorly diverse lycophytic vegetation, imply specialized adaptations of these plants to colder regions. These paleogeographical discrepancies therefore suggests a spatial dimension to evolutionary floras, possibly climatologically constrained. In fact, the identification of phytochoria using classical multivariate statistical analyses unveil a spatial differentiation and distribution more climatologically- than geographically-induced. Moreover, a higher degree of differentiation is recovered during cooler periods (i.e., Silurian–earliest Devonian, Middle Devonian), whilst an increased cosmopolitan distribution of vegetation was detected during warmer time intervals (i.e., late Early Devonian and Late Devonian), further indicating a climatic control over plant dispersion.

In Chapter V, the re-description of the Lower Devonian Rebreuve fossil flora from northern France, originally described in Corsin (1933) and Danzé-Corsin (1956b), was undertaken and revealed a fairly diverse assemblage consisting of 10 different taxa. The most notable findings include the second known occurrence of *Psilophyton parvulum* and the discovery of fertile specimens of *Sawdonia*. Re-investigation of the sole specimen attributed previously to *Yarravia minor* led to its exclusion from the genus due to lack of any diagnosable features, confirming that this taxon is, thus far, only found in former Gondwanan regions. The re-evaluation of the palynological investigations and lithostratigraphic correlations permits to provide a more precise age (early Emsian), possibly making it the second-oldest French flora, despite the lack of other biostratigraphically-useful fossils to confirm this inference. This assemblage is typical of other coeval Laurussian assemblages and is especially reminiscent of floras from the nearby Belgian Ardennes. This work epitomized the need of revising historical assemblages, and their necessity for future diversity analyses that require taxonomically up to date and precisely dated fossil occurrences.

Perspectives

Modern diversity studies now heavily rely on exhaustive occurrence-based datasets to compute sampling-standardized diversity (e.g., Lazarus et al., 2014; Tennant et al., 2016; Carvalho et al., 2021). In Chapter III, occurrence data are only recovered for the North American continent, but sample size in certain intervals is not suitable to adequately apply sampling-standardizing techniques, owing to deep-seated geological biases. It is still uncertain whether a worldwide occurrence database would contain sufficient data to get a representative sample of past biodiversity, and if we can reliably extract biological signals through sampling-standardization. Regardless, compiling this type of database would unlock the use of a new set of tools to apply the most recent and rigorous methods to study either diversity or biogeography (Close et al., 2019, 2020a, 2020b; Jones et al., 2021).

This thesis employes in Chapter III two different approaches to obtain sampling-corrected patterns: the residual diversity method (Lloyd, 2012) and sampling-standardization (Alroy, 2010a, 2010b). Another approach relies on phylogenetic trees to fill the gaps caused by geological and sampling biases, represented by ghost lineages (Bell and Lloyd, 2015). This is a promising approach given the severity of these biases identified in Chapter III. However, this technique requires up-to date phylogenies made with a substantial number of taxa, which is not yet available for early land plants.

Chapter IV reveals an important spatial component into early land plant radiation. Similarly to Wellman et al. (2022a), we hypothesize that the latitudinal diversity gradient in the earliest history of vascular plants may have been dramatically different to the current pole to equator increment in diversity. The latitudinal diversity gradient is one of the most fundamental and prevailing patterns in biogeography (Willig et al., 2003; Hillebrand, 2004). Characterization of the former latitudinal diversity gradient through fossil and modelled data (Zacaï et al., 2021) should be further explored to better understand the role of climate over early land plant radiation. Newly developed approaches (Escarguel and Legendre, 2006; Gibert et al., 2022) could also be applied to shed light on the possible spatial diachronicity in the onset of each evolutionary flora identified in Chapter II, in order to find their centers of origination and characterize their pattern of dispersion through time.

Lastly, the re-evaluation of the Lower Devonian assemblage from northern France (Chapter V), yields new, sometimes rare, occurrences of plant fossil-taxa. These revisions of previously studied floras are crucial as any description or re-description of taxa improves our comprehension of early land plant evolution. Recent re-investigations of historical collections of Emsian plants (i.e., Bickner and Tomescu, 2019; Toledo et al., 2021; Durieux et al., 2021) have demonstrated the paramount importance of anatomically-preserved specimens to reconstruct the evolutionary history of early land plants (Nibbelink and Tomescu, 2021). Preliminary re-examination of plant fossils of similar age than the Rebreuve assemblage (Emsian), collected in Matringhem (30 km west of Rebreuve) over a century ago and described in Danzé-Corsin (1956a), have revealed the presence of anatomically-preserved axes, that likewise merit further investigations.

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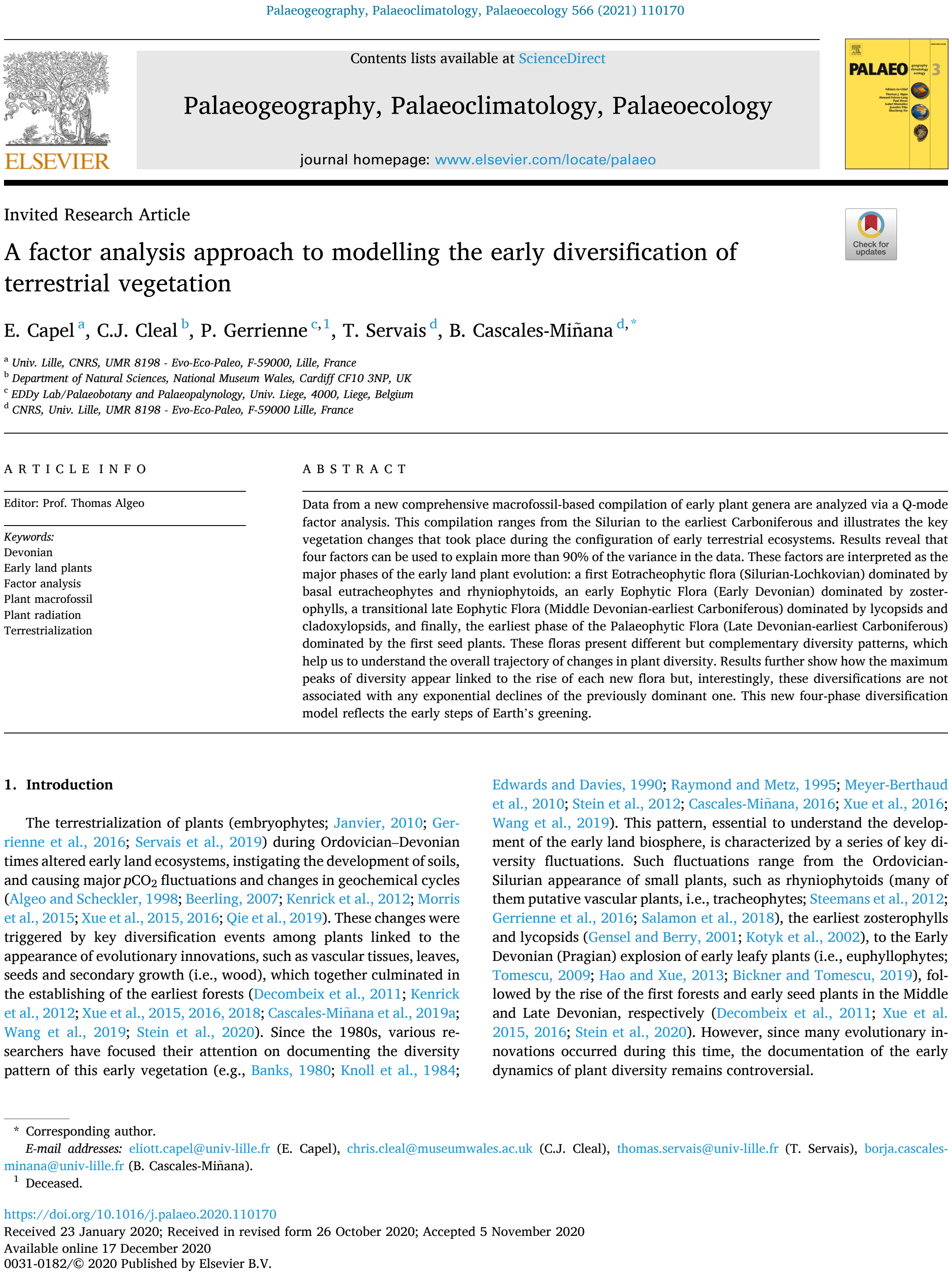
Appendices

Appendix 1



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Invited Research Article

A factor analysis approach to modelling the early diversification of terrestrial vegetation

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ABSTRACT

Data from a new comprehensive macrofossil-based compilation of early plant genera are analyzed via a Q-mode factor analysis. This compilation ranges from the Silurian to the earliest Carboniferous and illustrates the key vegetation changes that took place during the configuration of early terrestrial ecosystems. Results reveal that four factors can be used to explain more than 90% of the variance in the data. These factors are interpreted as the major phases of the early land plant evolution: a first Eotracheophytic flora (Silurian-Lochkovian) dominated by basal eutracheophytes and rhyniophytoids, an early Eophytic Flora (Early Devonian) dominated by zosterophylls, a transitional late Eophytic Flora (Middle Devonian-earliest Carboniferous) dominated by lycopsids and cladoxylopsids, and finally, the earliest phase of the Palaeophytic Flora (Late Devonian-earliest Carboniferous) dominated by the first seed plants. These floras present different but complementary diversity patterns, which help us to understand the overall trajectory of changes in plant diversity. Results further show how the maximum peaks of diversity appear linked to the rise of each new flora but, interestingly, these diversifications are not associated with any exponential declines of the previously dominant one. This new four-phase diversification model reflects the early steps of Earth's greening.

1. Introduction

The terrestrialization of plants (embryophytes; Janvier, 2010; Gerrienne et al., 2016; Servais et al., 2019) during Ordovician–Devonian times altered early land ecosystems, instigating the development of soils, and causing major $p\mathrm{CO_2}$ fluctuations and changes in geochemical cycles (Algeo and Scheckler, 1998; Beerling, 2007; Kenrick et al., 2012; Morris et al., 2015; Xue et al., 2015, 2016; Qie et al., 2019). These changes were triggered by key diversification events among plants linked to the appearance of evolutionary innovations, such as vascular tissues, leaves, seeds and secondary growth (i.e., wood), which together culminated in the establishing of the earliest forests (Decombeix et al., 2011; Kenrick et al., 2012; Xue et al., 2015, 2016, 2018; Cascales-Miñana et al., 2019a; Wang et al., 2019; Stein et al., 2020). Since the 1980s, various researchers have focused their attention on documenting the diversity pattern of this early vegetation (e.g., Banks, 1980; Knoll et al., 1984; Edwards and Davies, 1990; Raymond and Metz, 1995; Meyer-Berthaud et al., 2010; Stein et al., 2012; Cascales-Miñana, 2016; Xue et al., 2016; Wang et al., 2019). This pattern, essential to understand the development of the early land biosphere, is characterized by a series of key diversity fluctuations. Such fluctuations range from the Ordovician-Silurian appearance of small plants, such as rhyniophytoids (many of them putative vascular plants, i.e., tracheophytes; Steemans et al., 2012; Gerrienne et al., 2016; Salamon et al., 2018), the earliest zosterophylls and lycopsids (Gensel and Berry, 2001; Kotyk et al., 2002), to the Early Devonian (Pragian) explosion of early leafy plants (i.e., euphyllophytes; Tomescu, 2009; Hao and Xue, 2013; Bickner and Tomescu, 2019), followed by the rise of the first forests and early seed plants in the Middle and Late Devonian, respectively (Decombeix et al., 2011; Xue et al. 2015, 2016; Stein et al., 2020). However, since many evolutionary innovations occurred during this time, the documentation of the early dynamics of plant diversity remains controversial.

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The global trajectory of Phanerozoic vegetation history can be interpreted as a series of major evolutionary phases; the so-called Evolutionary Floras (see Cleal and Cascales-Miñana, 2014, and references therein for details). This model, which confirmed the major floral subdivisions previously suggested by Gothan (1912); (see also Niklas et al., 1983, 1985; Edwards and Selden, 1992; Gray, 1993), is homologous to the famous Sepkoski's (1981) Evolutionary Faunas (Cascales-Miñana et al., 2018, fig. 1). Importantly, the Cleal and Cascales-Miñana's (2014) Evolutionary Floras reveal that Silurian-Devonian land plant diversification is expressed as at least three different great floras, termed Eotracheophytic, Eophytic and Palaeophytic (Servais et al., 2019, fig. 1B). This suggests that, beyond the known problems of sampling and geological bias that of course obscure raw diversity patterns, there is an underlying structure in the observed diversity data of early floras, which deserves further investigation. This is the aim of the present paper.

2. Data

This study is based on a new, comprehensive macrofossil-based compilation of Silurian-lowermost Carboniferous (Tournaisian) fossil-genera. Raw data were collected from a variety of sources. Initially, we used review papers that listed plant fossil diversity for specific time intervals, such as Wellman et al. (2013) for the Silurian, or a specific geographic location, such as Xiong et al. (2013), or more recently Xue et al. (2018), for South China. Special mention should be made of the exquisite monographic study of the Early Devonian fossil record undertaken by Barrett (2016). Subsequently, plant fossil data were extracted from the Paleobiology Database via Fossilworks (http://fossilworks.org/) which were cross-checked against the primary references and, when possible, more recent literature. Lastly, numerous taxa were added from the primary literature, particularly recently described genera such as *Lilingostrobus*, *Rinistachya*, *Kossoviella*, *Guangdedendron*, *Qianshouia* or *Keraphyton* (Gerrienne et al., 2018; Prestianni and Gess, 2018; Orlova et al., 2019; Wang et al., 2019; Huang et al., 2020; Champreux et al., 2020).

To assess the maximum genus-level diversity, three types of data were considered. First, well-defined genera were listed that contained well-defined species (e.g., *Cooksonia pertoni*), and certain species in open nomenclature (e.g., *Cooksonia* cf. *pertoni*). Secondly, genera recorded with a 'cf.' were listed to bring together all species resembling such genera (e.g., cf. *Cooksonia hemisphaerica*). Lastly, genera recorded with an 'aff.' were listed to include taxa that have an affinity to that genus but whose assignment is still ambiguous (e.g., aff. *Zosterophyllum*). Overall, "artificial" genera (e.g., *Taeniocrada*) or synonyms of other taxa already listed were omitted. Likewise, some entries were also filtered to minimize an overlap of fossil-taxa for different plant parts (e.g., *Callixylon/Archaeopteris* or *Calamophyton/Duisbergia*; Meyer-Berthaud et al., 2000; Giesen and Berry, 2013) or different phases of life cycle (e.g., gametophytes). In total, more than 500 plant macrofossil genera were included, which provides a robust view of the major changes that took place during land plant diversification (Fig. 1).

The raw dataset was codified at stage and sub-stage level according to the literature and following the International Chronostratigraphic Chart 2019 (Cohen et al., 2013, updated). Twenty-five time units with an average resolution of 3.4 Myr were used. Each entry included the name and systematic affinity of the genus, its first and last stratigraphic occurrences, and the sampled localities on which the data were based. Raw data are available in Tables S1-S2. See also Text S1 for full referencing.

3. Methods

3.1. Factor analysis

We ran a CABFAC version of the Q-mode factor analysis on a data matrix containing the number of plant macrofossil genera occurring in each stratigraphic interval, grouped according to suprageneric

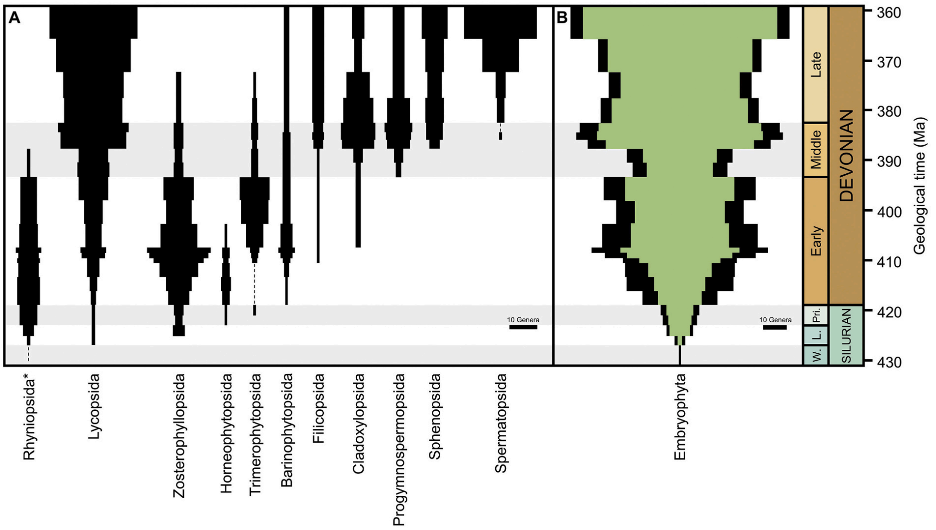

Fig. 1. Spindle diagrams showing the main diversity variations within plant classes (A) and the total shape of plant diversity (B) of the Silurian-Devonian time interval. Green colour highlights the total diversity pattern from well-established classes only (B). The width of each diagram indicates the number of fossil genera. The spindle diagrams undoubtedly can contain errors especially due to taxa with controversial affinities. Relative lengths of time units based on Cohen et al. (2013; updated). Abbreviations: W., Wenlock; L., Ludlow; Pri., Pridoli. *Note that Rhyniopsida includes herein current paratracheophytes and rhyniophytoids only. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

taxonomic categories as defined below. The analysis was made using the PAST software package version 2.17 (Hammer et al., 2001). This method, widely used to analyse many different fossil-based datasets (e. g., Bottjer and Jablonski, 1988; Erwin, 1990; Sallan and Coates, 2010; Figueirido et al., 2012; Cleal and Cascales-Miñana, 2014), recognises different factors (orthogonal eigenvectors), each of which has associated eigenvalues (factor loadings) for each stratigraphical interval and the percentage of the total variance explained by that factor. Each factor also has a factor score for each plant group, which reflects the importance of that group on the factor. Following standard procedures, factor results were then rotated with a procedure known as Kaiser's (1958) Varimax rotation. The purpose of the rotation is to enhance the discrimination of the variables into the resulting factors, which will therefore represent more accurately the distinct associations of plant groups by reducing the influence of plant groups that are not typically correlated with this association on raw data. Each factor ultimately represents a proportion of the total genus-level diversity curve of each suprageneric group (Sepkoski, 1981; Cleal and Cascales-Miñana, 2014). From this, we extracted the patterns of association among the main early plant groups that explain the whole diversity pattern of Silurian-Devonian fossil floras.

3.2. *Assignment of taxa to categories*

To implement the factor analysis, taxa must be assigned to categories. As in previous models (e.g., Sepkoski, 1981), taxa were firstly grouped in taxonomic classes (Fig. 1A). Subsequently, taxa whose class attribution was controversial or undetermined (~25% of the dataset) were assigned to groups based on evolutionary and/or morphological criteria. The Rhyniopsida required special attention. Taxa traditionally assigned to this class currently cover many different plant lineages, including paratracheophytes (i.e., former Rhyniaceae; Gerrienne et al., 2006) and basal eutracheophytes (e.g., *Cooksonia*; Kenrick and Crane, 1997; Crane et al., 2004; Gerrienne et al., 2016). The group also includes rhyniophyte-like plants or rhyniophytoids (e.g., *Uskiella* or *Electorotheca*; Morris et al., 2018), i.e., plants similar to tracheophytes but lacking evidence of vascular tissue, or plants of unknown affinities (Steemans et al., 2012). Other categories used for data analysis include cryptophytes (i.e., basal embryophytes; Morris et al., 2018), protracheophytes (i.e., *Aglaophyton/Teruelia*; Kenrick and Crane, 1997; Cascales-Miñana and Gerrienne, 2017; Cascales-Miñana et al., 2019a) and stenokoleales (Momont et al., 2016; Toledo et al. 2018). ***Incertae sedis*** taxa (~16% of dataset) were grouped into two categories given that many of these plants presented euphyllophyte affinities. Basal euphyllophytes (i.e., formerly trimerophytes; Tomescu, 2009; Gensel, 2018) were treated like a single group. In total, 18 categories integrating the whole taxonomic and morphological diversity of early land plants were used for the data analysis (see Table 1).

4. Results

Fig. 1A shows the distribution of genus-level diversity among the main classes of Silurian – Devonian land plants. From this, we see that each class seems to have its own pattern of diversity change, although some similarities are noteworthy. For instance, major Early Devonian groups such as rhyniopsids and zosterophyllopsids show a diversification in the mid-Early Devonian followed by a significant depletion at the Early-Middle Devonian boundary. We also see a second diversification in the Middle Devonian among the lycopsids, cladoxylopsids and progymnosperms (Fig. 1A). A Late Devonian diversification of seed plants coinciding with a sustained increase of lycopsids is also noted (Fig. 1A). In the Silurian-Devonian fossil record, many taxa are class-level *incertae sedis* so Fig. 1A does not include all plant diversity. However, this seems to be not so critical given that the general pattern of diversification and decay of the well-defined classes captures most of the total pattern of plant taxonomic diversity (Fig. 1B). This pattern is characterized by a gradual increase from the Ludlow, a great diversification in the mid-Early Devonian, a sudden decrease in the Early-Middle Devonian transition, an important pulse of diversification in the late Middle Devonian, a moderate reduction of diversity in the earliest Late Devonian, and finally, a pronounced and sustained increase towards the Carboniferous (Fig. 1B).

Sepkoski (1981) chose a solution of three factors that explained c. 91% of the variance of marine faunal diversity. This was based on a "scree test" (see Sepkoski, 1981, fig. 2 for details), where the eigenvalues represented by each successive factor are plotted logarithmically. If there is an abrupt break in the slope of the resulting line, this is used to indicate the number of factors that should be recognised. We applied a similar approach with our data (Fig. 2), but no break in the slope was observed. A similar result was obtained by Cleal and Cascales-Miñana (2014), who therefore used instead the Kaiser Rule, in which the number of factors is decided based on how many are needed to account for 90% of the total variance of data. In the present study, using this guideline, the first four generated factors were used as the basis of the model to explain the Silurian-Devonian plant diversity patterns (see Table 2). The robustness of the model is supported by the fact that each factor is taxonomically and stratigraphically coherent, with clear temporal trends (compare comments by Flessa and Imbrie, 1975 on a faunal model), and thus seems to be reflecting the overall trajectory of Silurian-Devonian vegetation history (see below). The factor analysis was implemented twice, with and without *Incertae sedis* taxa, and these produced indistinguishable results.

These four rotated factors are interpreted as reflecting the major evolutionary phases of the diversification of early terrestrial floras. The floral composition of each factor is summarized in Table 3. Fig. 3 illustrates the loadings of each factor for the successive time intervals, from which the genus-level diversities represented by each factor/flora have been calculated. This was done for each stratigraphical interval by

Table 1
List of Silurian-Devonian plant groups considered in this study.

1. Barinophytopsida
2. Basal euphyllophytes
3. Basal eutracheophytes
4. Cladoxylopsida
5. Cryptophyta
6. Euphyllophyta inc. sed.
7. Filicopsida
8. Horneophytopsida
9. *Incertae sedis*
10. Lycopsida
11. Paratracheophyta
12. Progymnospermopsida
13. Protracheophyta
14. Rhyniophytoids
15. Spermatopsida
16. Sphenopsida
17. Stenokoleales
18. Zosterophyllopsida

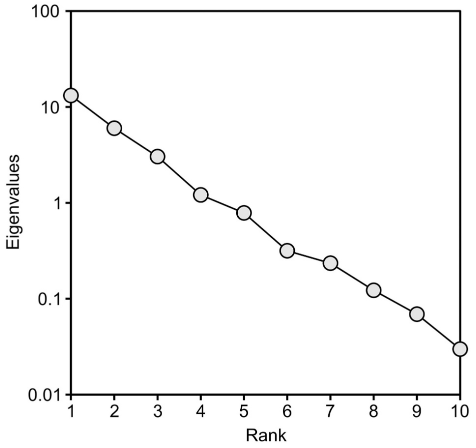

Fig. 2. Scree graph showing eigenvalues from a Q-mode factor analysis of plant genera plotted logarithmically against their ranks. See Methods for details.

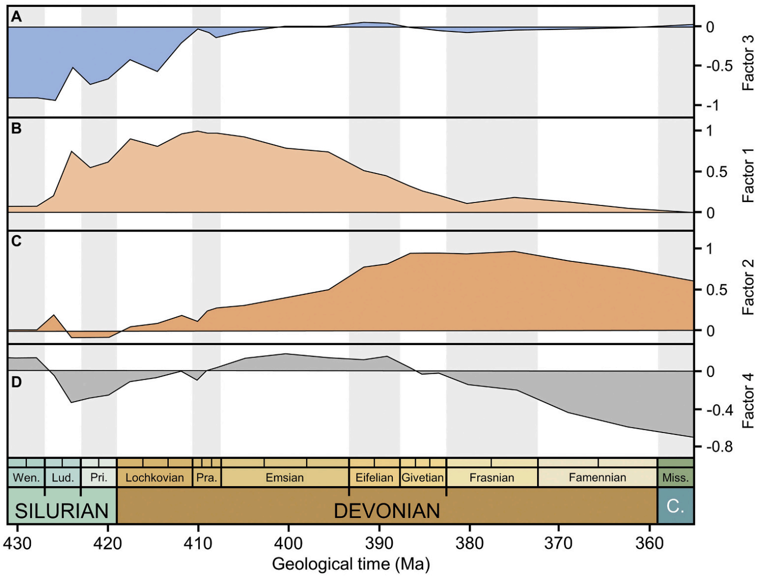

Fig. 3. Loadings of successive time intervals on rotated factors from a four-factor Q-mode analysis of plant genera plotted against absolute time. Factors represented in stratigraphical order. Relative lengths of used time units based on Cohen et al. (2013; updated). See Methods for details. Abbreviations: Wen., Wenlock; Lud., Ludlow; Pri., Pridoli; Pra., Pragian; Miss., Mississippian; C., Carboniferous.

Table 2
Variance proportion explained by the first ten eigenvectors from a Q-mode factor analysis run through the macrofossil diversity of plant genera from the mid-Silurian to the lowermost Carboniferous. See Methods for details.

Eigenvector	% Variance
1	52.69
2	23.96
3	12.13
4	4.83
5	3.14
6	1.27
7	0.94
8	0.49
9	0.28
10	0.12

squaring each of its four loading values and multiplying them by the total diversity for that interval (Fig. 4). The resulting four-factor model of early land plant diversification (Figs. 3-4) may be summarized (in stratigraphic order) as follows.

4.1.1. *Factor 3 (Silurian-earliest Devonian)*

This factor is dominated by basal eutracheophytes and rhyniophytoids, with other minor elements including basal lycopsids (Table 3). This factor represents the Eotracheophytic flora (the Rhyniophytic flora sensu Cleal and Cascales-Miñana, 2014), and is compared to the previously described “Rhyniophytic Phase” of plant evolution (Edwards and Selden, 1992) and Gray’s (1993) “Eotracheophytic Flora”. The Eotracheophytic flora reflects the initial pulse of plant diversity and the main growth of taxonomic richness from the mid-Silurian to the earliest Devonian, which reached its maximum during the mid-Lochkovian (Fig. 4).

Table 3
Scores of the main plant groups on the four rotated factors. The floral composition is given in four groups: scores ≥2 (factors 1–2) or − 2 (factors 3–4); scores ≥1 (factors 1–2) or − 1 (factors 3–4); scores ≥0.5 (factors 1–2) or − 0.5 (factors 3–4); scores ≥0.2 (factors 1–2) or − 0.2 (factors 3–4).

Factor 1	Factor 2	Factor 3	Factor 4
Zosterophyllopsida (3.08)	Lycopsida (3.40)	Basal eutracheophytes (−4.07)	Spermatopsida (−3.17)
Rhyniophytoids (1.77)	Cladoxylopsida (1.30)		
Basal euphyllophytes (0.56)	Progymnospermopsida (0.98) Sphenopsida (0.65) Filicopsida (0.50)	Rhyniophytoids (−0.80)	Lycopsida (−0.74)
Horneophytopsida (0.43) Barinophytopsida (0.42) Lycopsida (0.21) Paratracheophyta (0.20)	Spermatopsida (0.48) Basal euphyllophytes (0.44) Barinophytopsida (0.34)	Lycopsida (−0.33)	Sphenopsida (−0.48) Filicopsida (−0.34)

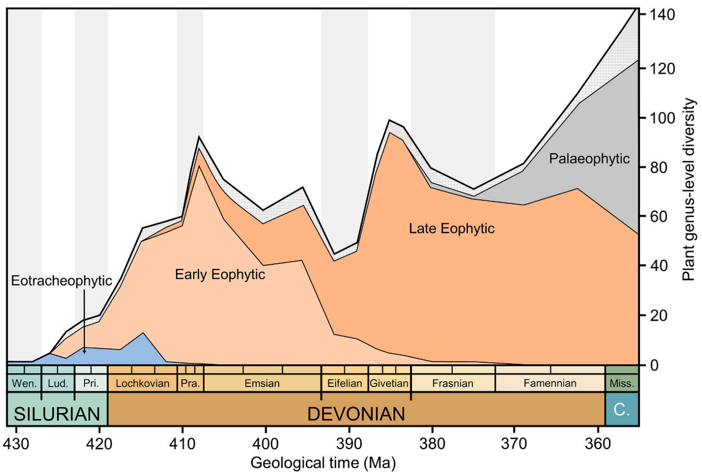

Fig. 4. Representation of changing genus-level diversities within each of the evolutionary floras indicated by the four-factor model described in this paper. The highlighted uppermost curve shows the total pattern of the plant genus-level diversity through time. The stippled area immediately below represents the residual diversity not explained by the model. Relative lengths of time units based on Cohen et al. (2013; updated). See Methods for details. Abbreviations: Wen., Wenlock; Lud., Ludlow; Pri., Pridoli; Pra., Pragian; Miss., Mississippian; C., Carboniferous.

4.1.2. *Factor 1 (Early Devonian)*

This factor is dominated by zosterophyllopsids and rhyniophytoids, with other minor elements including horneophytopsids and paratracheophytes (Table 3). Interestingly, this factor also sees the early phase of the development of euphyllophyte plants. This factor represents the early phases of Cleal and Cascales-Miñana's (2014) Eophytic flora. This flora reaches its maximum diversity peak at the end-Pragian and represents the main component of Early Devonian plant diversity. After reaching a second peak at the end of the early Devonian, this early Eophytic Flora undergoes a progressive decline until the Frasnian-Famennian boundary (Fig. 4).

4.1.3. *Factor 2 (Middle Devonian-earliest Carboniferous)*

This factor is dominated by lycopsids and cladoxylopsids, together with a diverse range of other groups (Table 3). Significantly, the progymnosperms, sphenopsids and filicopsids appear in this flora. This factor corresponds to a late phase of the Eophytic flora. After an initial diversification towards the end-Early Devonian, this flora shows an explosive diversification during the Middle Devonian with a maximum diversity peak at the Givetian. These late Eophytic floras slowly decline during the Late Devonian (Fig. 4). An overall diversity peak in the late Famennian is also observed (Fig. 4).

4.1.4. *Factor 4 (Late Devonian-earliest Carboniferous)*

This factor is clearly dominated by spermatopsids (Table 3), mainly early seed ferns such as Calamopityales and Lyginopteridales (Wang and Liu, 2015), together with several groups including lycopsids and filicopsids (Table 3). This factor corresponds to the earliest phase of Cleal and Cascales-Miñana's (2014) Palaeophytic flora. This flora started an exponential diversification from the Frasnian/Famennian boundary (Fig. 4) and rapidly became dominant during the Carboniferous (Servais et al., 2019, fig. 1B).

5. Discussion

Total diversity patterns of early land plants based on taxon counts are inevitably flawed due to inherent taphonomic and sampling biases introduced by the fossil record. For instance, the volume of terrestrial rock exposed is an acknowledged bias (see Kenrick et al., 2012). There are also facies biases, notably because the plant fossil record is almost entirely from lowland nearshore deposits, which largely excludes remains of plants from extra-basinal habitats (similar to the situation in Carboniferous floras – Thomas and Cleal, 2017). A particular concern is the effect of sampling on taxon counts: for example, there are very few non-marine strata available for collecting in the Silurian (e.g., Kenrick et al., 2012; Hao and Xue, 2013; Wellman et al., 2013). Nevertheless, our results have clearly revealed changing patterns, affecting distinct plant groups and intervals, which are more suggestive of a biological signal than of geological bias. This can be observed for instance in the Eotracheophytic-Eophytic turnover, where although total diversity is consistently increasing, Eotracheophytic diversity is progressively diminishing (Fig. 4).

The Silurian-Devonian plant fossil record shows the highest known diversity and disparity of plant groups. This is simply because all known plant groups except flowering plants, both living and fossil, are represented (Gerrienne et al., 2016, fig. 2; Cascales-Miñana et al., 2019a, fig. 3). Nevertheless, despite these great variations in form, the factor analysis has revealed a rather simple diversity pattern of floral changes. This pattern shows a clear succession of "major evolutionary steps", growing in complexity from simple, small, leafless herbaceous plants to highly developed woody seed-plants, including the tree habit. Without doubt, this diversification allowed plant life to colonize different and new terrestrial environments, to create an emerging greening of Earth's surface. This scenario is quite logical and is evident for instance from the growing size of Devonian plants (Xue et al., 2018, fig. 16). However, beyond statistically supporting this collective view, the factor analysis provides an objective way of measuring the "weight" of change between early floras and their composition. For instance, from this, we can see how the dominance of the late Eophytic flora, which included the earliest forest plants, occurred very rapidly before the end of the Middle Devonian.

Like in the Sepkoski (1981) model, one of most important aspects in the history of these early Evolutionary Floras is that their rise and subsequent decline seem to be closely related to the total pattern of apparent plant diversity. The changes in total taxonomic richness per time interval is shown in Fig. 4 by the uppermost bold curve. The stippled field below this curve represents the residual diversity not explained by the four-factor solution of the model. This residual part is overall quite uniform and small, only becoming slightly larger from the end of the Devonian (probably as a response to greater "noise" in the factors with the lowest eigenvalues). The small size of this residual diversity suggests that the first four selected factors, and the Evolutionary

Floras represented by them, provide a robust framework to explain the overall diversity pattern, as well as providing a first-order description of the composition changes of each flora during the Devonian.

The scaling of the four-factor model to total generic diversity suggests that each of the major evolutionary floras is associated with a specific phase of plant diversification (Fig. 4). From this, we see that after an initial and continuous Silurian-Lower Devonian diversification in the Eotracheophytic flora, followed by an early diversification of the Eophytic flora, several ascending diversity trends can be observed. The first, at the end-Pragian, was a result of the rise and developing dominance of the early Eophytic flora. The second one, in the Givetian, was clearly related to an “explosive” expansion of the late Eophytic flora. The last significant increase of diversity occurs in the late Famennian and is linked to the initial diversification of the Palaeophytic flora. So, it seems that each of the four floras had its own independent but complementary pattern of generic diversity, which combined to produce the total dynamics of Silurian-Devonian plant diversity. The pattern of growth and decline of the early evolutionary floras suggests ecological displacement as the main cause of each turnover, but there is no equilibrium phase or exponential decline as is observed in the marine Evolutionary Faunas model.

Evolutionary innovations and the consequential diversification of various plant groups have been postulated to be the cause of turnover between different floras. This is partially supported here, especially for the Early Devonian Eotracheophytic-Eophytic transition. The changing pattern of these first floras, consisting of basal eutracheophytes, rhyniophytopsids and zosterophylls (Table 3), can be comfortably related to the improvements in the water-conducting system of land plants (Kenrick and Crane, 1997; Kenrick et al., 2012; Gensel, 2018). Overall, it is hypothesized that the rise of each of these floras was probably linked to key evolutionary developments such as in the growth in complexity (i.e., optimization) of the architecture of vascular system (Strullu-Derrien et al., 2013; Decombeix et al., 2019). At this time, land plants were undertaking a massive adaptive radiation and almost every anatomical-physiological aspect was rapidly evolving. This scenario would support the idea of an initial colonization of the earliest terrestrial environments linked to improvements in hydraulic efficiency (Wilson, 2013, 2016; Cascales-Miñana et al., 2019b; Decombeix et al., 2019).

In contrast, the extremely high morphological disparity observed in the Middle-Late Devonian Evolutionary Floras do not support a diversification pattern that was always driven by the appearance and/or improvements of key evolutionary innovations. For instance, this can be observed from the Famennian, where the increase of plant diversity was a response to the dynamics of more than one great flora (Fig. 4). Thus, the appearance of the late Eophytic flora, which involved the worldwide colonization of lowland areas by the archaeopteridalean progymnosperms and pseudosporochnales (Cladoxylopsida), saw the development of the earliest forested landscapes (Meyer-Berthaud et al., 1999; Stein et al., 2007; Meyer-Berthaud and Decombeix, 2007; Decombeix et al., 2011); while the earliest phase of the Palaeophytic flora, which represents a transitional stage characterized by open vegetation ecosystems, included the first seed plants, notably non-arborescent pteridosperms, colonizing disturbed habitats (Mintz et al., 2010; Prestianni and Gerrienne, 2010; Decombeix et al., 2011).

During the last decades, significant discoveries of Devonian plants have been made in South China (see e.g., Hao and Xue, 2013; Xue et al., 2018, and references therein). After analysing the Silurian-Devonian taxonomic diversity of this record, Xiong et al. (2013) observed several major fluctuations of genus-level plant diversity, one at the Pragian, another from the mid-Givetian to mid-Frasnian, and a last one in the late Famennian. These fluctuations are similar to the results reported herein (Fig. 4), and suggest a common worldwide pattern of plant diversification. Xue et al. (2018) also performed a similar study to Xiong et al. (2013), but using a more conservative approach by retaining well-defined taxa only. Significantly, the proportions of major plant groups over time in the South China Block shown by Xue et al. (2018, fig. 9) approximately reflect the dominant elements of the Evolutionary Floras, e.g., the transition from a zosterophyllopsid-dominated flora to a lycopsid-dominated flora (Table 3); this provides further support for a global pattern of subsequent diversification phases of early vegetation. In contrast, although diversity studies on South China plant fossils suggest a Givetian crisis similar in magnitude to the Frasnian-Famennian marine crisis (Xiong et al., 2013), we see no global crisis in the vegetation of the Middle Devonian (Fig. 1B). Rather, our model shows a sustained increase in plant taxonomic and morphological diversity at this time (Figs. 1A), triggered by the late Eophytic diversification (Fig. 4). Likewise, our model suggests that the reduction in plant diversity at the beginning of the Late Devonian (Fig. 4) is linked to the start of the Eophytic-Palaeophytic transition that resulted in more complex forested ecosystems.

6. Conclusions

Results have shown that the largest part of the variation dynamics in generic richness within the main Silurian-Devonian plant groups can be explained through a four-phase diversification model. This model is based on (1) a first Eotracheophytic flora that dominates the Silurian fossil record but decays suddenly after the Lochkovian, (2) an early Eophytic Flora that dominates the Early Devonian showing a continuous increase until the Pragian, (3) a late Eophytic Flora that dominates from the Middle Devonian to the Carboniferous, and lastly, (4) a sustained increase of a Palaeophytic flora from the Frasnian/Famennian boundary. Each evolutionary flora appears to be associated with distinct phases of diversification of early terrestrial ecosystems. The Eotracheophytic flora is associated with the earliest radiation of vascular plants, while the Eophytic floras are associated with the expansion of zosterophyllopsids and of lycopsids, respectively, and the appearance of cladoxylopsids and progymnosperms, i.e., the earliest trees. Likewise, the Palaeophytic flora is linked to the earliest diversification of seed plants. Finally, the results show that the expansion of each new flora triggers the progressive decline of the previously dominant flora, which suggests ecological displacement. In this sense, the pattern of succession of the early Evolutionary floras reflects the transition from environments covered by herbaceous plants to an early forested planet.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2020.110170.

Declaration of Competing Interest

The authors declare no conflicts of interest.

Acknowledgments

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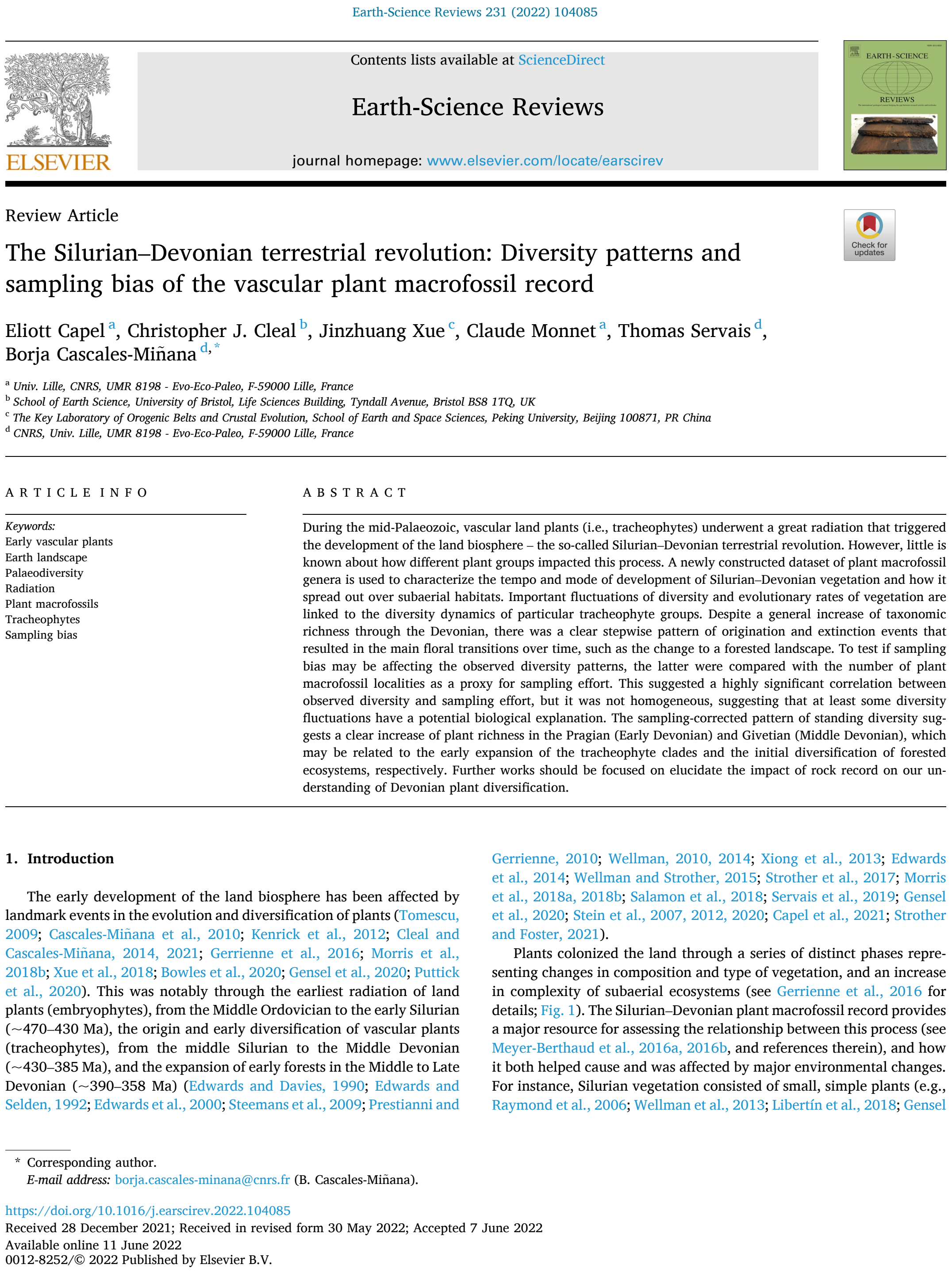
Appendix 2



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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, zosterophyllopsids 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 cladoxylopsids (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 CO$_2$ and O$_2$ 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;

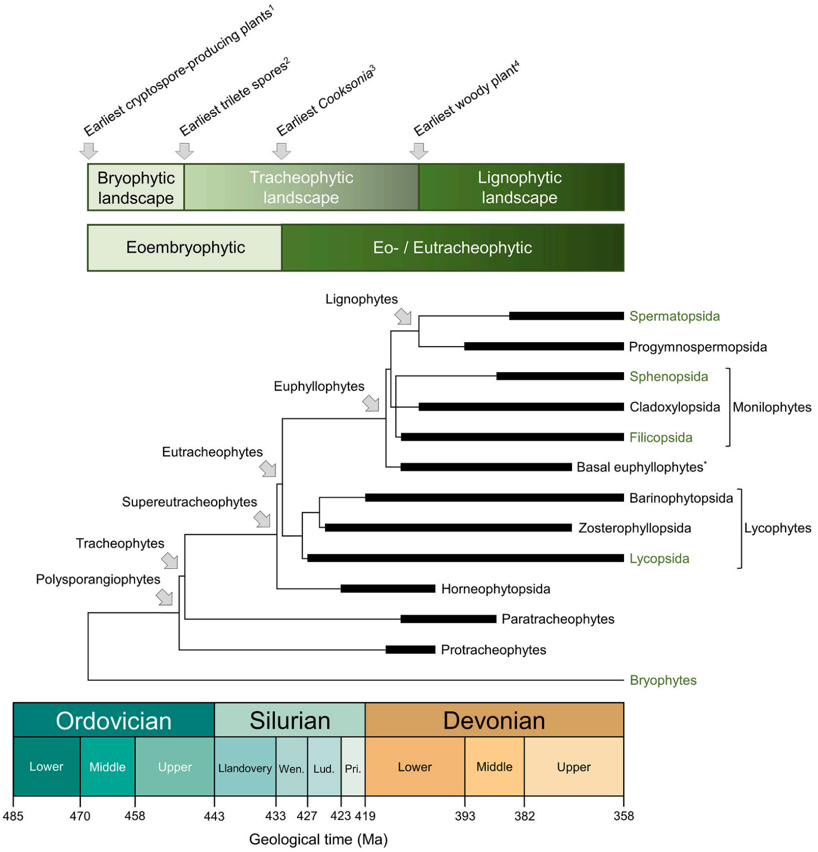


Fig. 1. Early evolutionary framework of embryophytes. Bryophytic, tracheophytic and lignophytic landscapes *sensu* Strother et al. (2010). Eoembryophytic and Eutracheophytic steps of plant evolution *sensu* Gray (1993). Data from Gerrienne et al. (2016, and references therein). Modified from Servais 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 Trimerophytopsida.

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 Horneophytopsida within the protracheophytes, although subsequent investigations have suggested the presence of irregular wall thickenings in *Horneophyton*, resolving Horneophytopsida 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). Lycopsida 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). Lycopsids 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). Barinophytopsids 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 vernation 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, Protopityales, 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 Hilu, 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., *Guazia*; 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

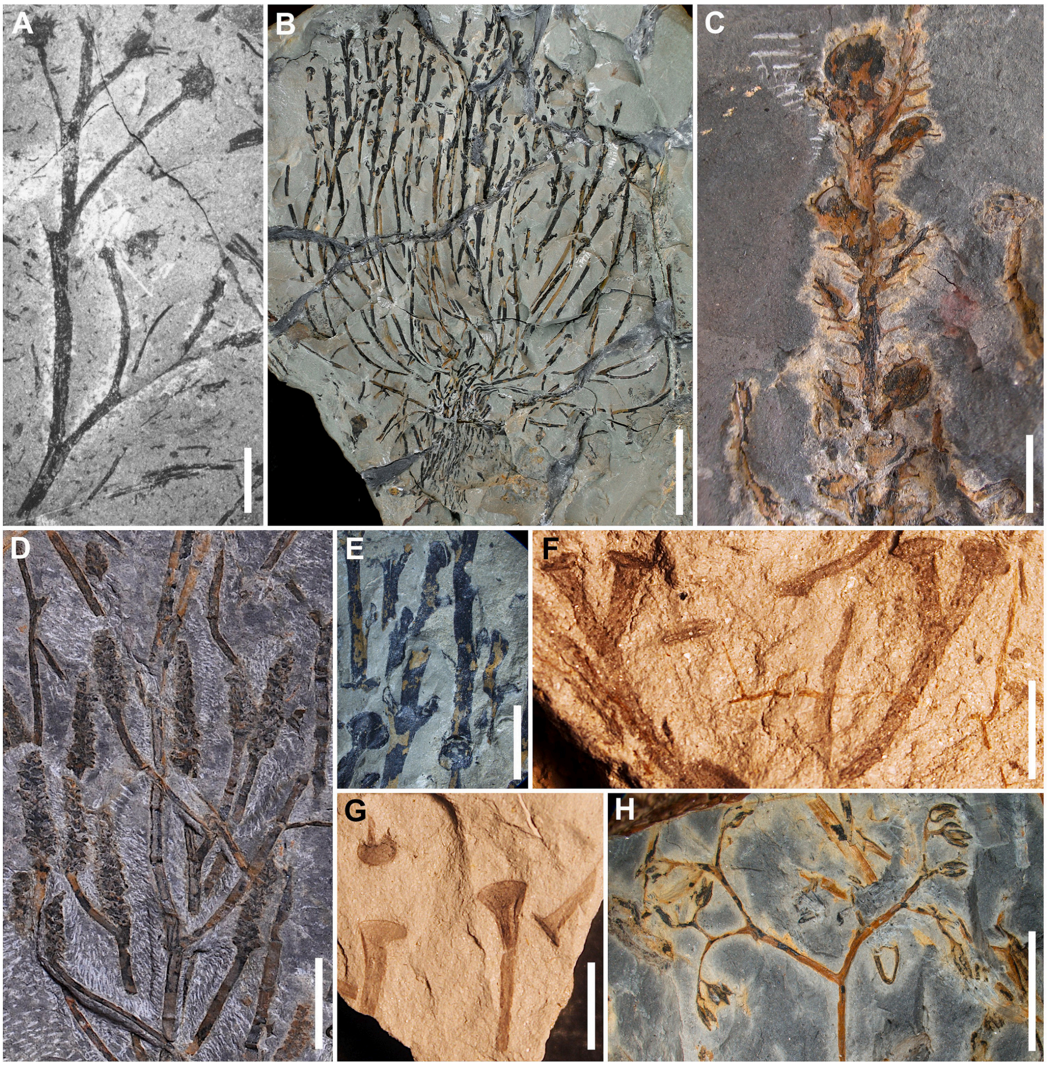


Fig. 2. Morphological diversity of Silurian–Devonian floras (I). (A) *Eocooksonia sphaerica* (Senkevitsch) Doweld (Basal eutracheophytes). Axis showing pseudo-monopodial branching and terminal sporangia. Specimen PKUB14902, upper Silurian (Pridoli) Wutubulake Formation of Xinjiang, China (Xue et al., 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) *Pauthecophyton gracile* Xue et al. (Basal euphyllophytes). 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.

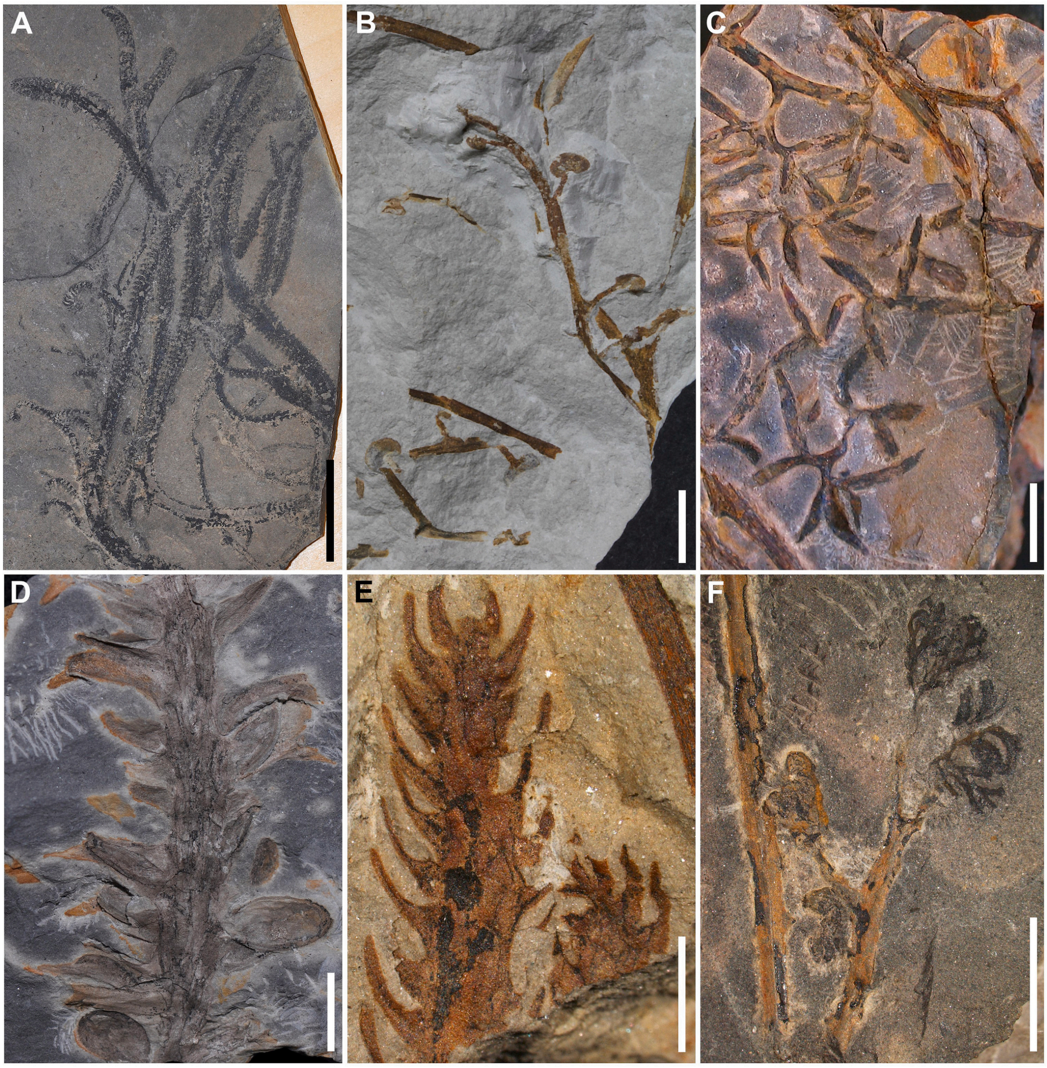


Fig. 3. Morphological diversity of Silurian–Devonian floras (II). (A) *Bathurstia denticulata* Hueber (Zosterophyllopsida). Fertile axes with terminal spikes. Specimen US704-8326, Lower Devonian (Pragian) Bathurst Island Formation of Nunavut, Canada (Kotyk and Basinger, 2000, fig. 3). Scale bar = 3 cm. (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. (Barinophytopsida). 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.

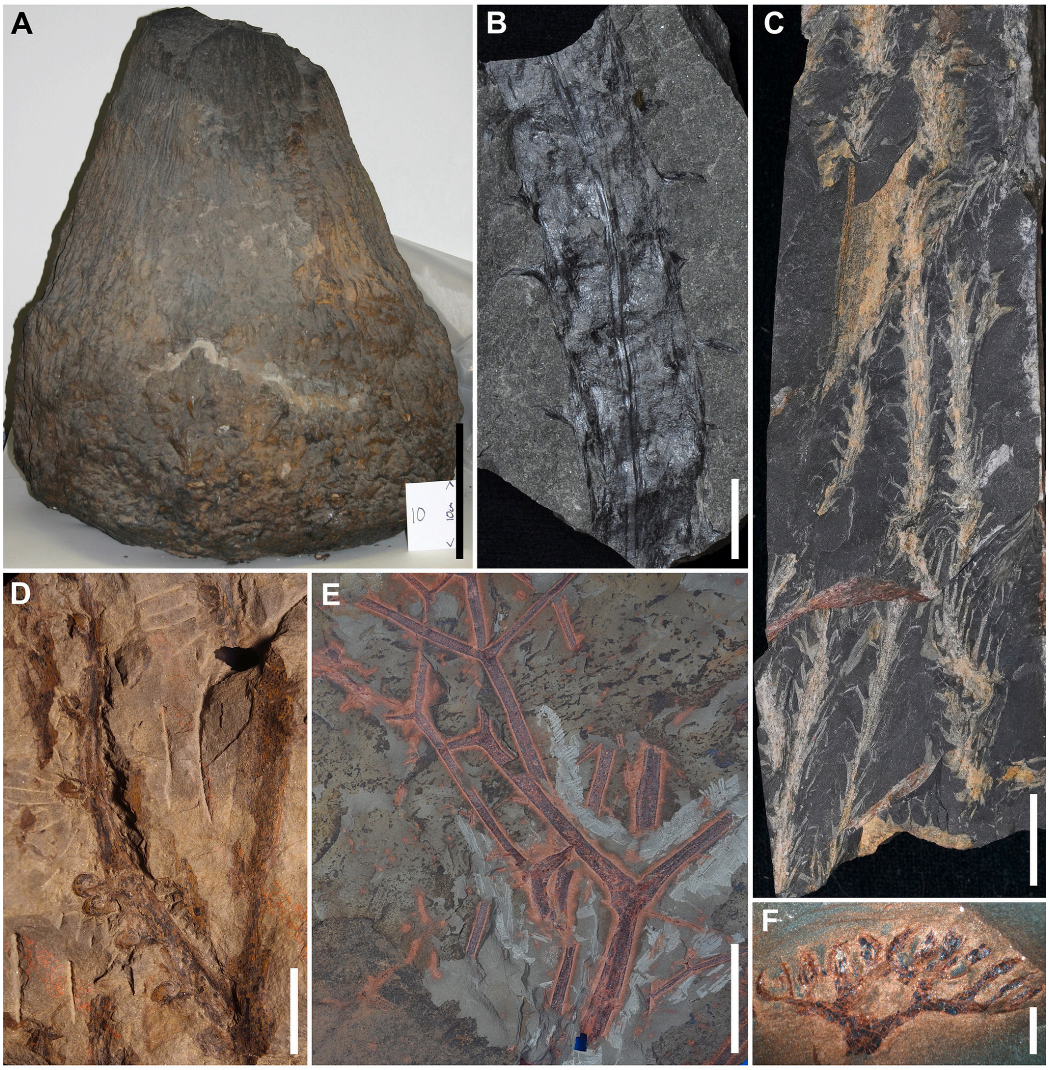


Fig. 4. Morphological diversity of Silurian–Devonian floras (III). (A) *Eospermatopteris* (Cladoxylopsida) cast. Photo by Chris Berry, courtesy of William E. Stein. Scale bar = 20 cm. (B) *Drepanophycus qujingensis* Li et Edwards (Lycopsida). Leafy axis. Specimen PKUB18299, Lower Devonian (Pragian–Emsian) 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, zosterophyllopsids, as well as monilophytes and lignophytes (Fig. 1). Regarding the considered groups, we tested major class-level categories, which include barinophytopsids, filicopsids, cladoxylopsids, progymnosperms, sphenopsids and spermatopsids (Fig. 1).

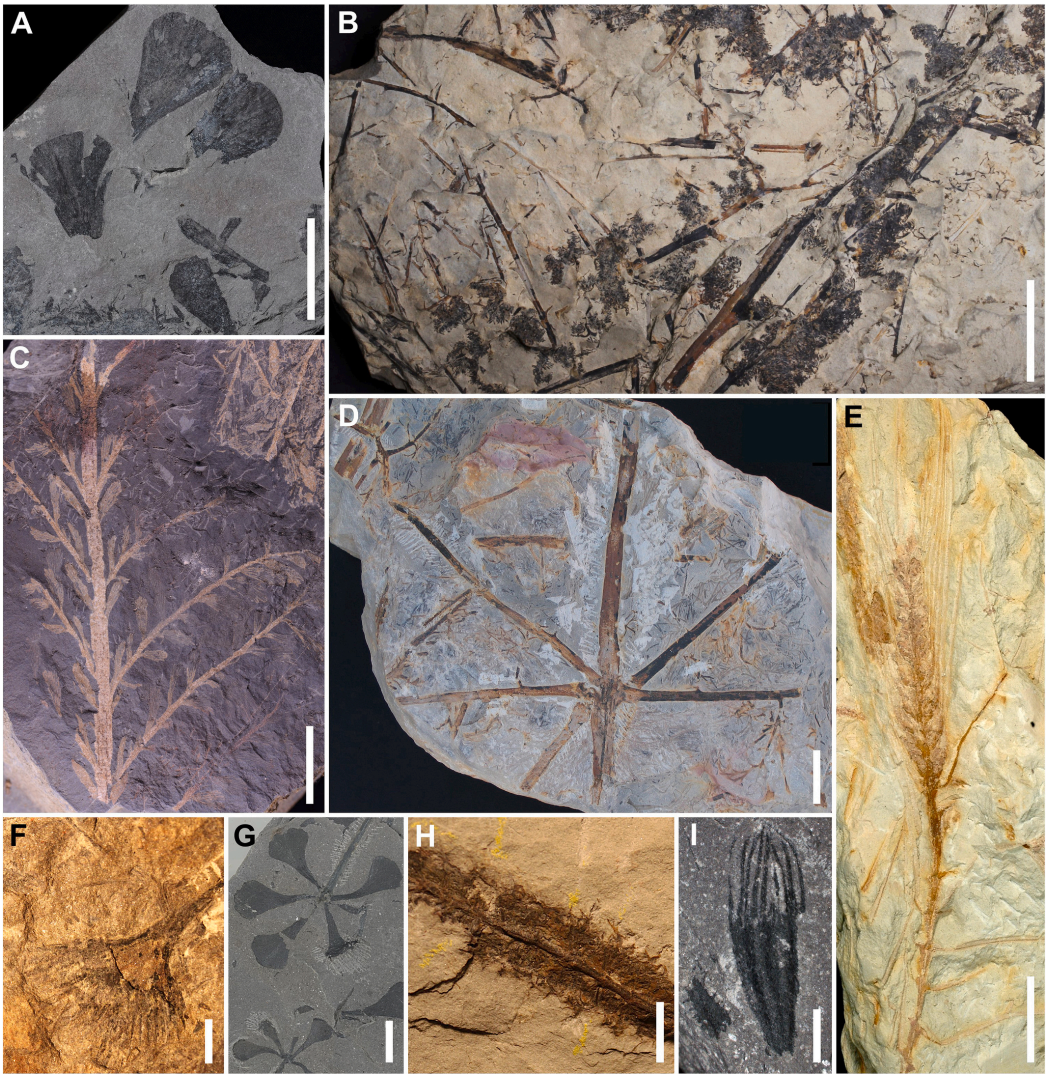


Fig. 5. Morphological diversity of Silurian–Devonian floras (IV). *Xihuphyllum megalofolium* (Wu) Chen emend. Huang et al. (Sphenopsida). Detached leaves. Specimen PKUB13606a, Upper Devonian (Famennian) Wutong Formation of Zhejiang, China (Huang et al., 2017, fig. 6A). Scale bar = 50 mm. (B) *Rhacophyton 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* (Goeppert) 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 vezerensis* 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, endemicity 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 assignation (e.g., Gutak et al., 2011), others present a less precise resolution (e.g., Prestianni et al., 2012). Hence, in an attemto 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:

$$N_{\text{tot}} = N_{\text{FL}} + N_{\text{bL}} + N_{\text{Ft}} + N_{\text{bt}} \tag{1}$$

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):

$$N_{\text{b}} = N_{\text{bL}} + N_{\text{bt}} \tag{2}$$

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):

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

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):

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

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

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:

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

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

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 zosterophyllopsids (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 zosterophyllopsid and barinophytopsid 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 euphyllophytes (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 zosterophyllopsids (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 euphyllophyte diversity (Fig. 7D). More specifically, the Givetian diversification involves lycopsids (Fig. 7B), and almost all major groups of monilophytes (Fig. 7E), such as filicopsids

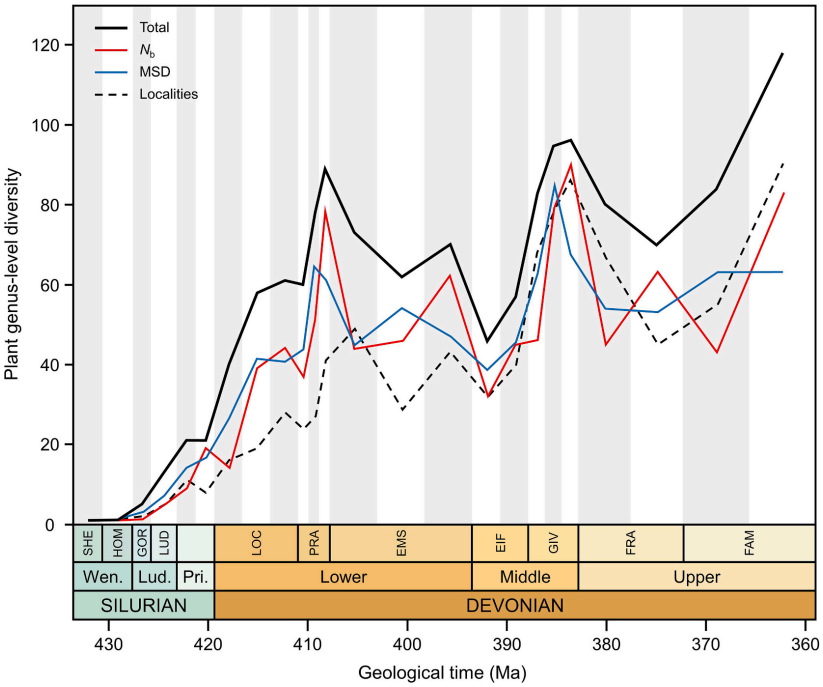


Fig. 6. Silurian–Devonian diversity patterns of tracheophytes. Bold, red and blue lines show total, boundary-crossing (N_b) and mean-standing (MSD) diversity of plant genera per time unit, respectively. Dashed line shows the sampled localities per time unit. Alternation of white and grey boxes represent the different used time units (stage to sub-stage level). Abbreviations: SHE, Sheinwoodian; HOM, Homerian; GOR, Gorstian; LUD, Ludfordian; Wen., Wenlock; Lud., Ludlow; 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), zosterophyllopsids (Fig. 10G–H), and barinophytopsids (Fig. 11A–B), as

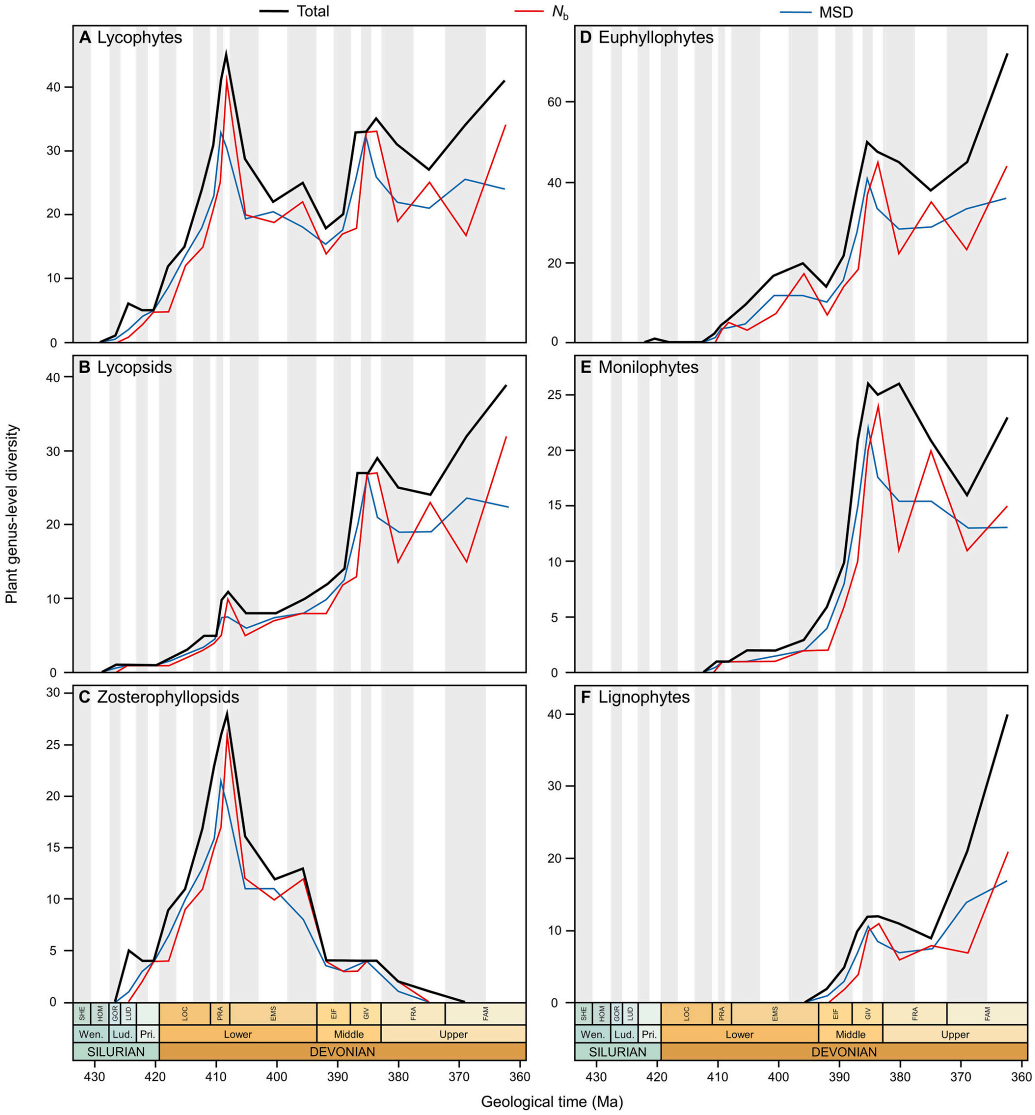


Fig. 7. Silurian–Devonian diversity patterns of main tracheophyte clades. Bold, red and blue lines show total, boundary-crossing (N_b) and mean-standing (MSD) diversity of plant genera per time unit, respectively. (A) Lycophytes; (B) Lycopsids; (C) Zosterophyllopsids; (D) Euphyllophytes; (E) Monilophytes;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

well as from basal euphyllophytes (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), cladoxylopsids (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) cladoxylopsids (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 euphyllophytes (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,

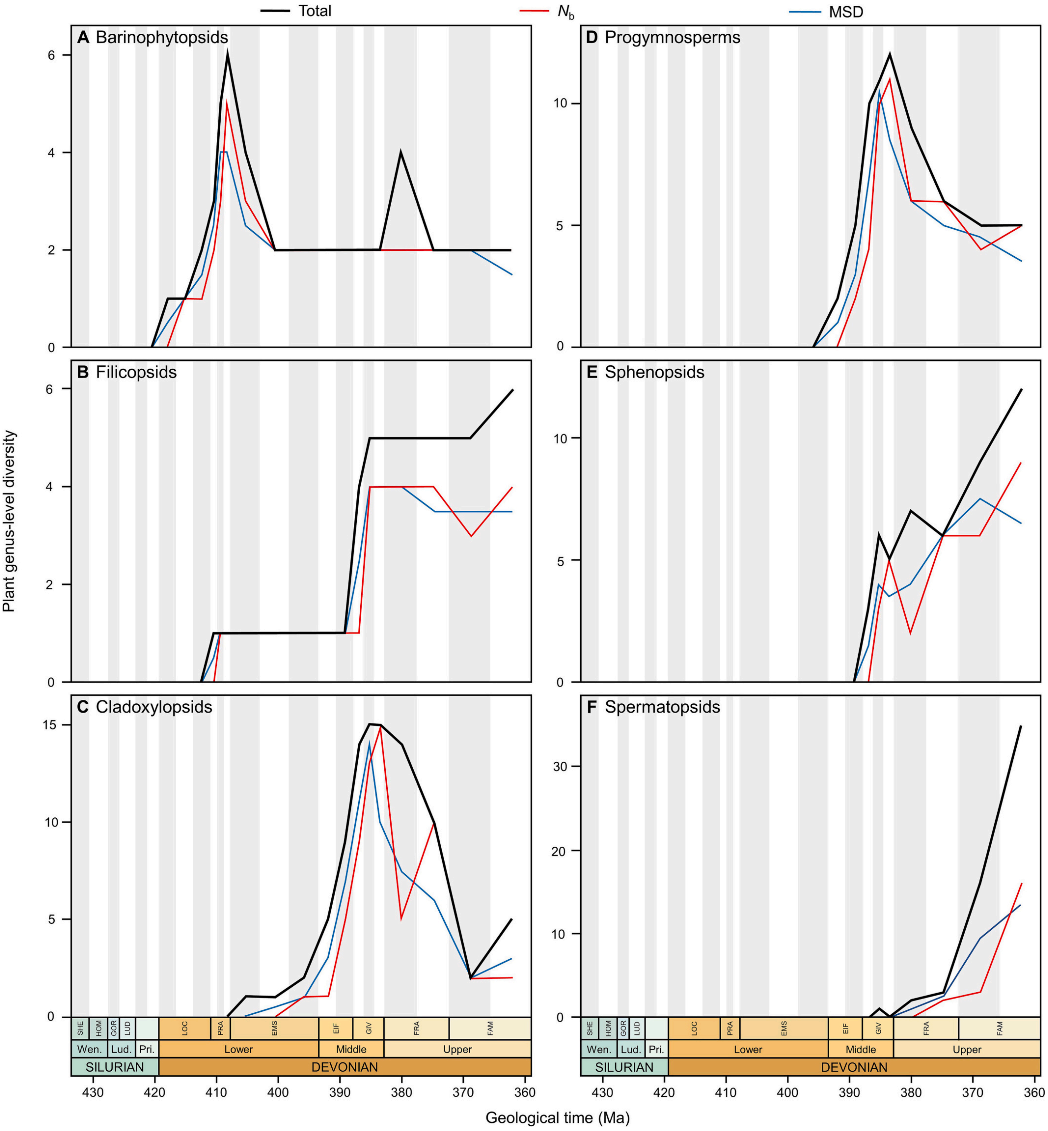


Fig. 8. Silurian–Devonian diversity patterns of main tracheophyte groups. Bold, red and blue lines show total, boundary-crossing (N_b) and mean-standing (MSD) diversity of plant genera per time unit, respectively. (A) Barinophytopsids; (B) Filicopsids; (C) Cladoxylopsids; (D) Progymnosperms; (E) Sphenopsids;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

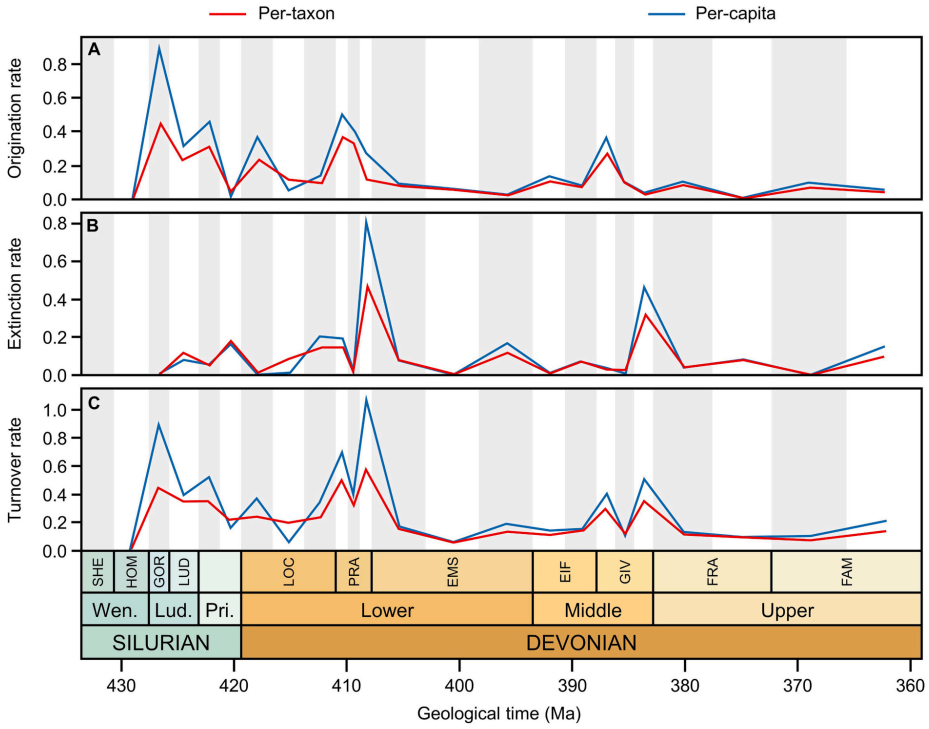


Fig. 9. Silurian–Devonian macroevolutionary patterns of tracheophytes. Red and blue lines show per-taxon and per-capita origination (A), extinction (B) and turnover (C) rates of plant genera, respectively. Abbreviations, same as in Fig. 6.

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

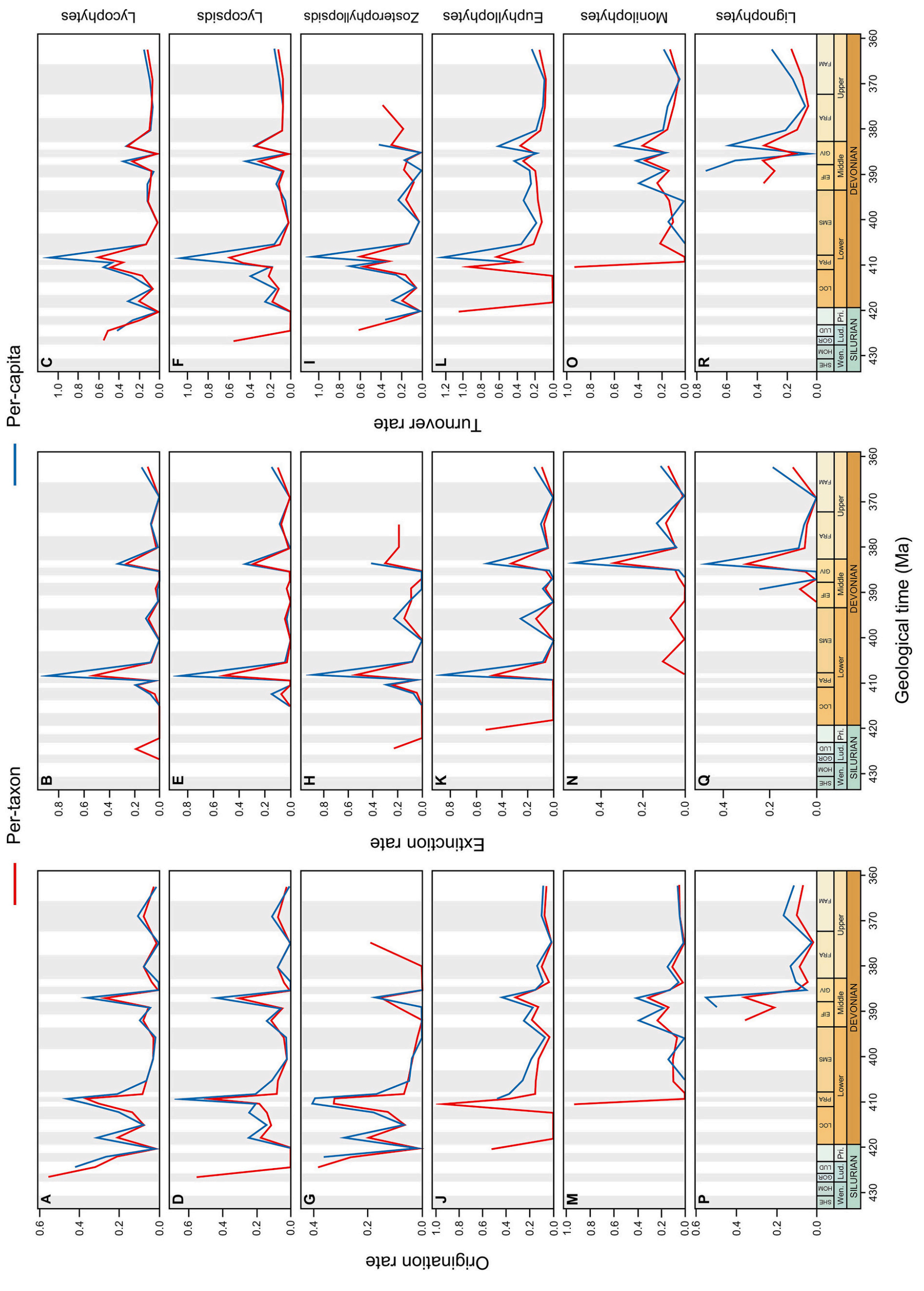


Fig. 10. Silurian–Devonian macroevolutionary patterns of main tracheophyte clades. Red and blue lines show per-taxon and per-capita origination (left column), extinction (central column) and turnover (right column) rates of plant genera, respectively. (A–C) Lycophytes; (D–F) Lycopsids; (G–I) Zosterophyllopsids;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

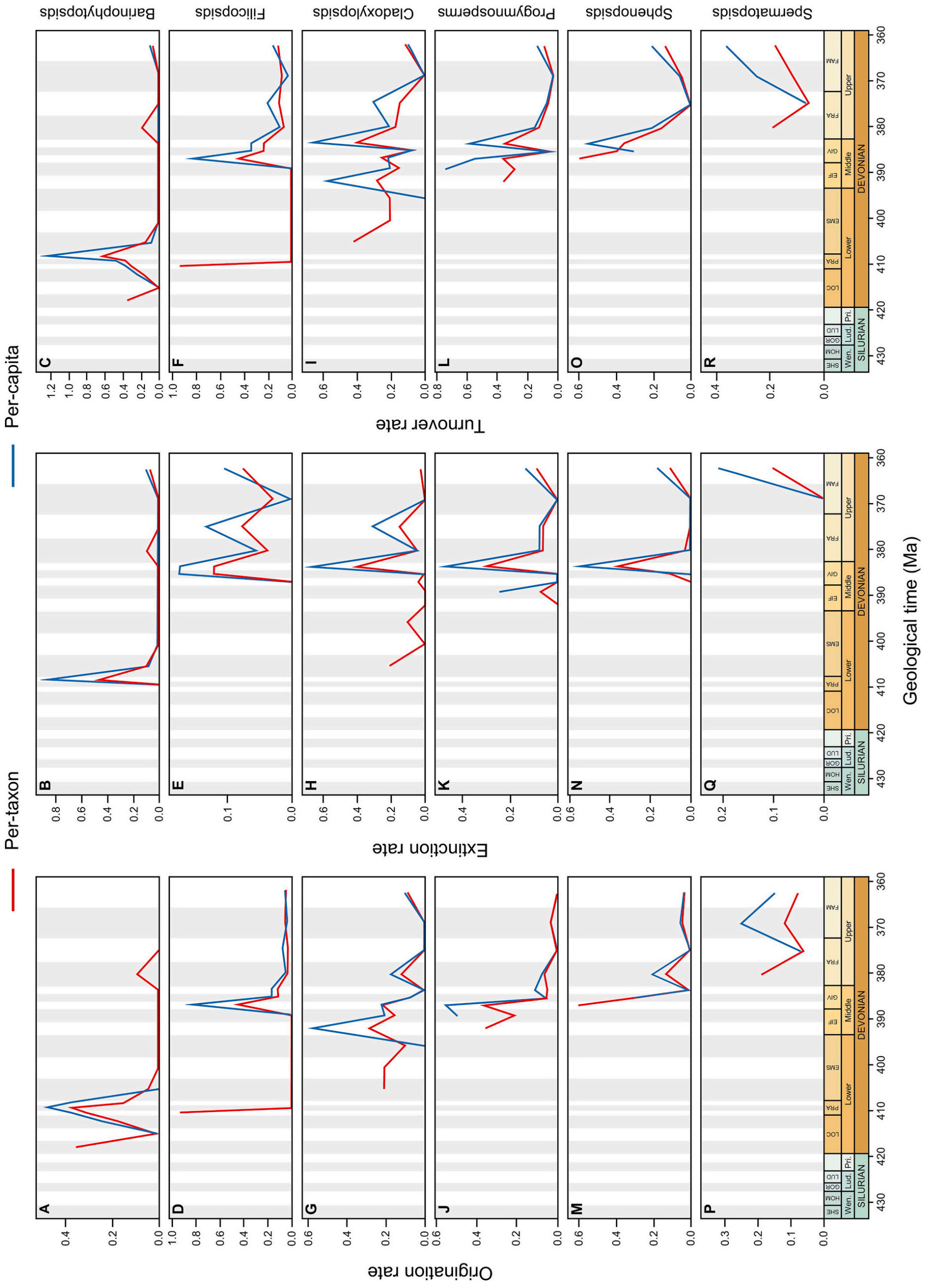


Fig. 11. Silurian–Devonian macroevolutionary patterns of main tracheophyte groups. Red and blue lines show per-taxon and per-capita origination (left column), extinction (central column) and turnover (right column) rates of plant genera, respectively. (A–C) Barinophytopsids; (D–F) Filicopsids; (G–I)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

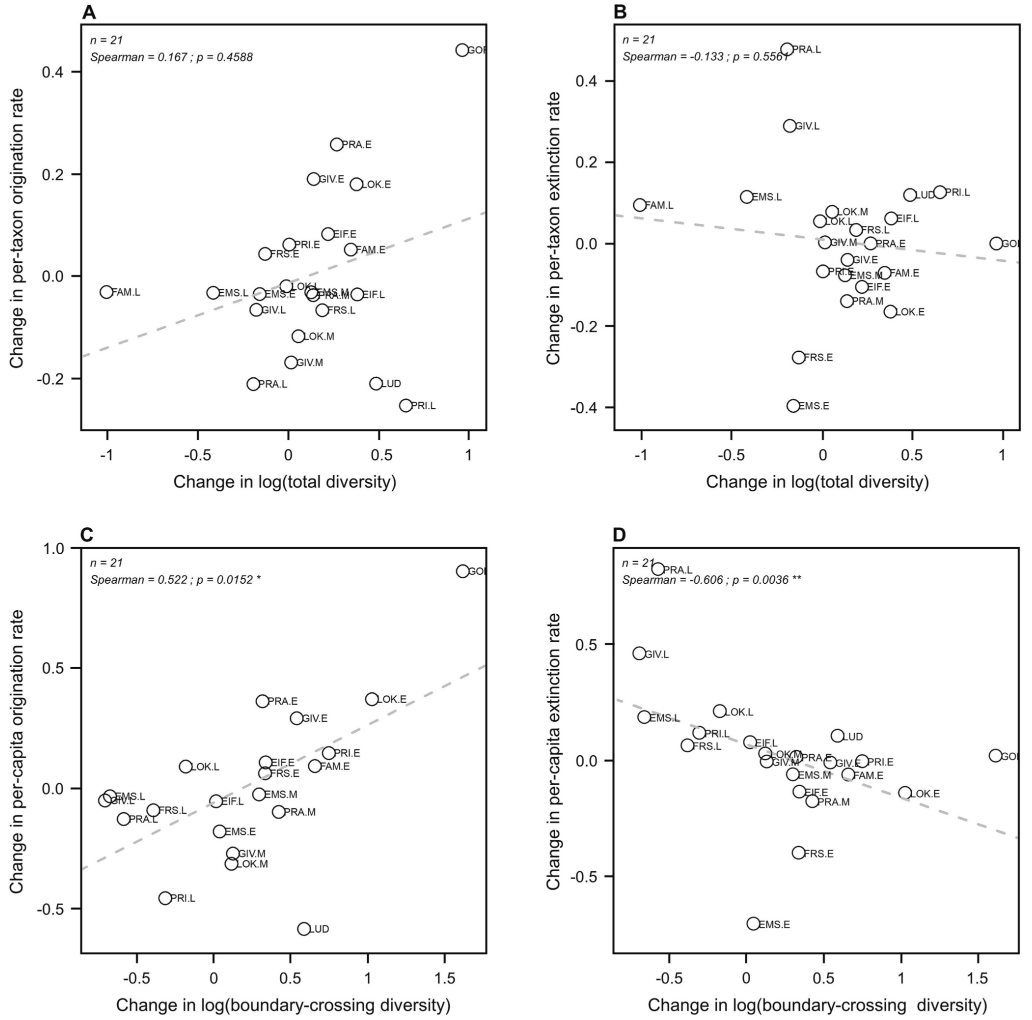


Fig. 12. Comparison between change in total (A–B) and boundary-crossing (C–D) diversity and change in per-taxon and per-capita origination-extinction rates of tracheophyte genera, respectively. Data analysis based on Spearman's rank correlation coefficient (*rho*). *Significant value ($p < 0.05$). **Very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

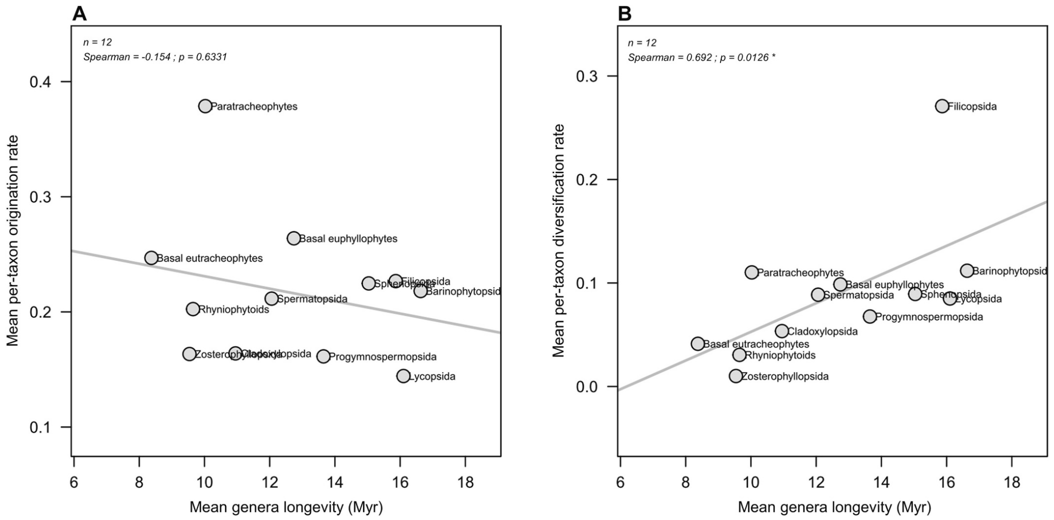


Fig. 13. Comparison between mean per-taxon origination (A) and diversification (B) rates and mean genera longevity of main tracheophyte groups. Data analysis based on Spearman's rank correlation coefficient (*rho*). *Significant value ($p < 0.05$).

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 Zosterophyllopsida 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 heterogenous 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

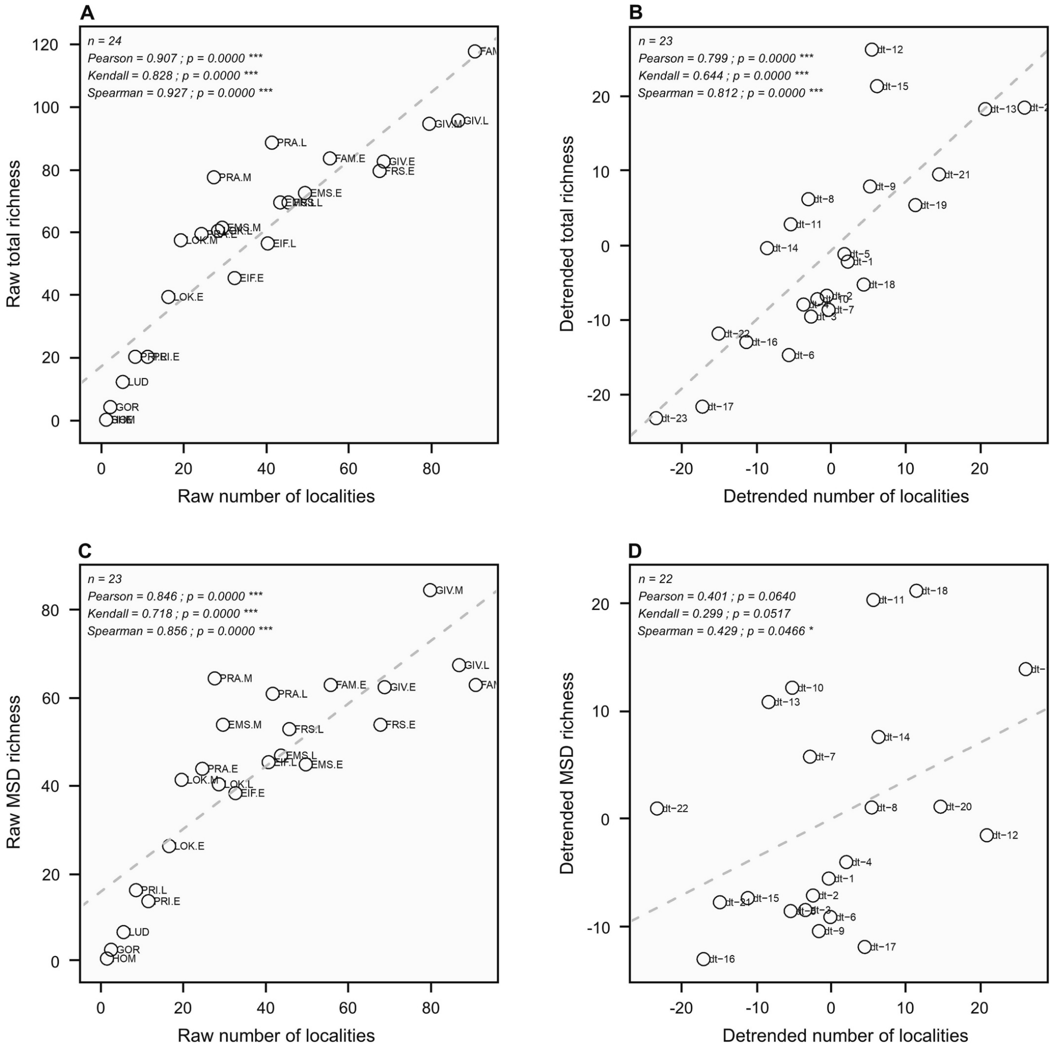


Fig. 14. Comparison between total (A–B) and mean-standing (C–D; MSD) diversity of tracheophyte genera and the number of sampled localities per time unit. Data analysis performed on raw (A, C) and detrended (B, D) data through generalized-differencing (GD). Correlations based on Pearson's, Kendall's, 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 zosterophyllopsid 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

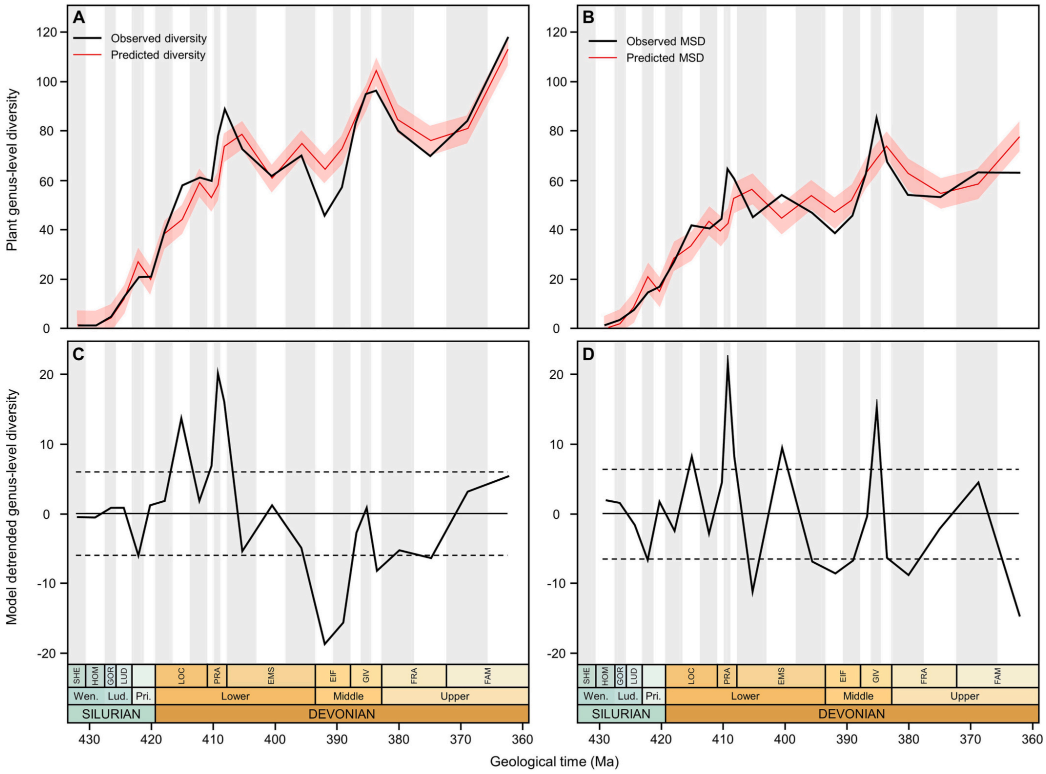


Fig. 15. Comparison between observed and predicted patterns of total (A) and mean-standing (B; MSD) diversity of plant genera. Sampling-corrected (residual) patterns of total (C) and MSD (D) diversity of plant genera. Dashed lines represent the 95% confidence interval of the proxy-biased model. Statistical 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 macrofossils 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

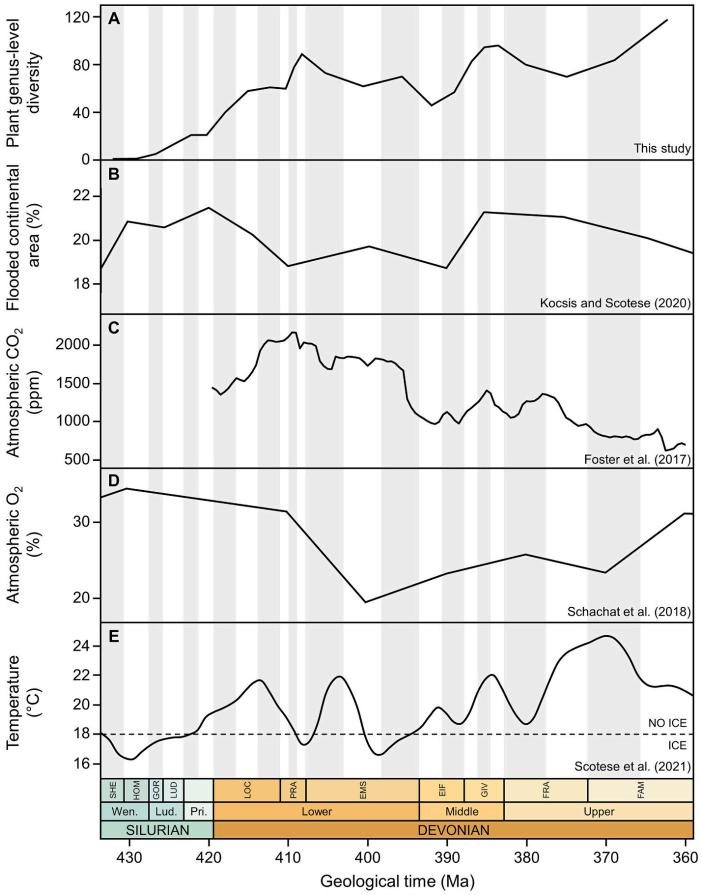


Fig. 16. Comparison between total diversity pattern of tracheophyte genera (A) and fluctuations of different abiotic factors (B–E) during the Silurian-Devonian time interval. (B) Flooded continental area. (C) Atmospheric CO$_2$ levels. (D) Atmospheric O$_2$ levels. (E) Global average temperature. Abbreviations, 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 CO_2 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 CO_2 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 O_2 (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 O_2 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, O_2 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. Zosterophyllopsids, 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., zosterophyllopsids). The colder climate beginning in the middle Emsian through the Middle Devonian may have reciprocally precipitated the zosterophyllopsid 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 zosterophyllopsids 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 zosterophyllopsids.

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.

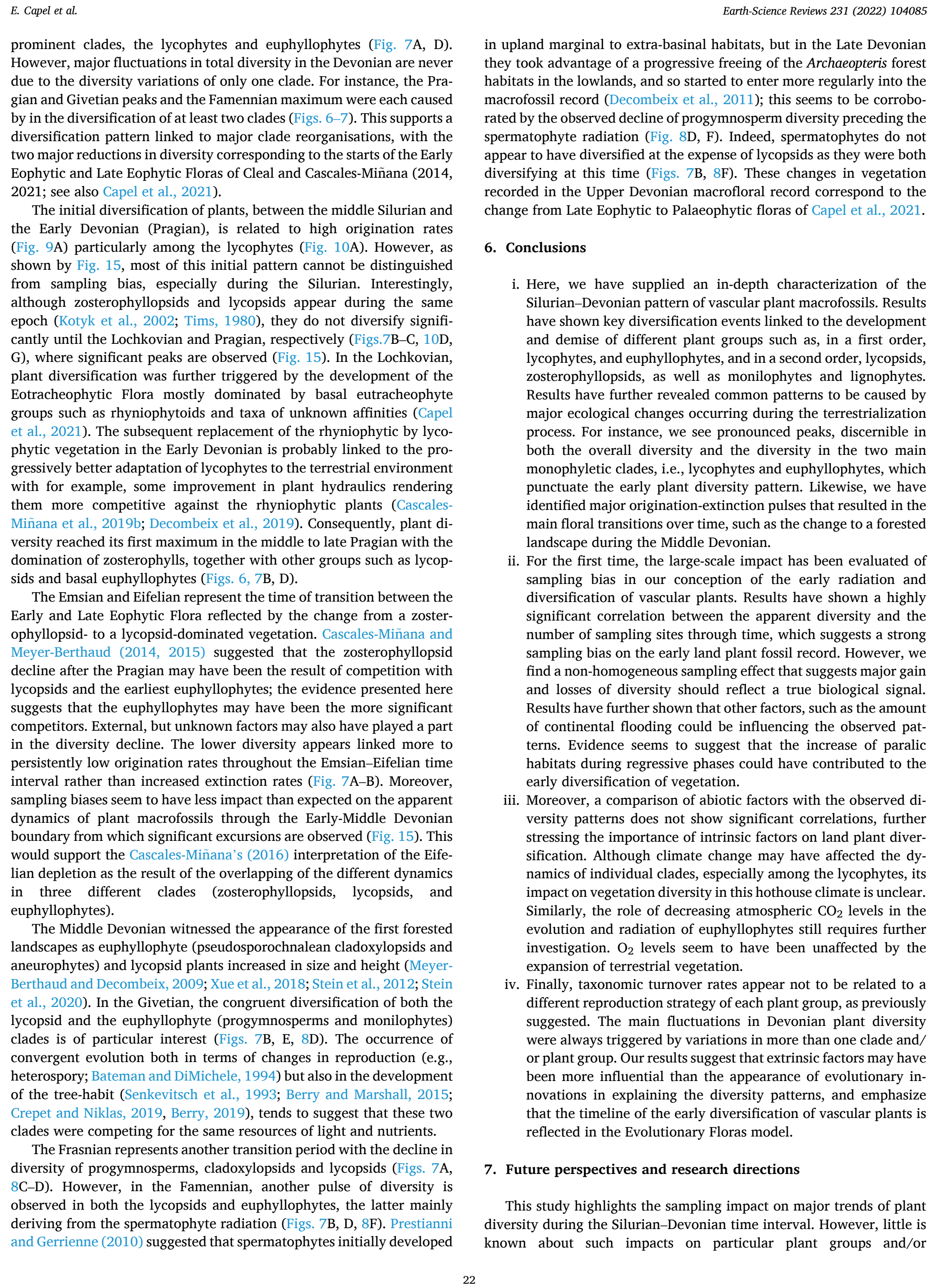
High pCO_2 levels have been implicated in the absence of megaphyllous leaves before the middle Pragian (e.g., *Eophyllophyton*; Fig. 3F) as they would have quickly overheated, restricting photosynthetic efficiency. However, as atmospheric CO_2 levels decreased throughout the Devonian, leaf stomatal density 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., zosterophyllopsids, 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 zosterophyllopsids 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 zosterophyllopsids 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 zosterophyllopsid- to a lycopsid-dominated vegetation. Cascales-Miñana and Meyer-Berthaud (2014, 2015) suggested that the zosterophyllopsid 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 (zosterophyllopsids, lycopsids, and euphyllophytes).

The Middle Devonian witnessed the appearance of the first forested landscapes as euphyllophyte (pseudosporochnalean cladoxylopsids 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 (Senkevitsch 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, cladoxylopsids 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, zosterophyllopsids, 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 CO_2 levels in the evolution and radiation of euphyllophytes still requires further investigation. O_2 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 macrofossils. 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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Appendix 3: Supporting information and figures from Chapter III "Biases and temporally dynamics in early plant diversity reconstructions".

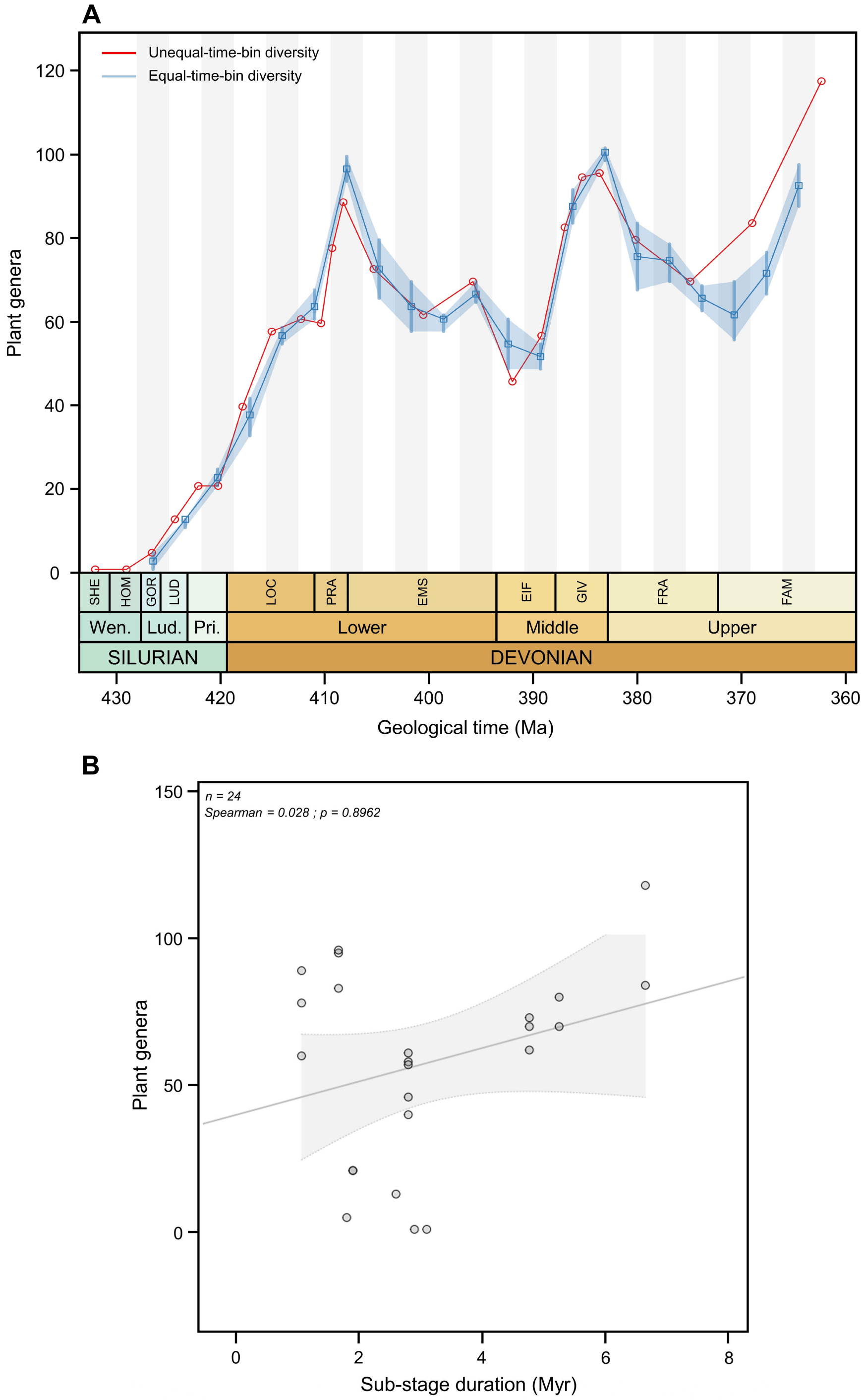

Figure III.S1: Comparison between the total diversity pattern using unequal time bins and the continuous-time average curve of plant diversity (A). Vertical solid lines show the 95% confidence interval of the reconstructed taxonomic richness. Abbreviations: SHE, Sheinwoodian; HOM, Homerian; GOR, Gorstian; LUD, Ludfordian; Wen., Wenlock; Lud., Ludlow; Pri., Pridoli; LOC, Lochkovian; PRA, Pragian; EMS, Emsian; EIF, Eifelian; GIV, Givetian; FRA, Frasnian; FAM, Famennian. (B) Relationship among plant richness and interval lenghts used in this study. Data analysis based on Spearman's rank correlation coefficient (*rho*).

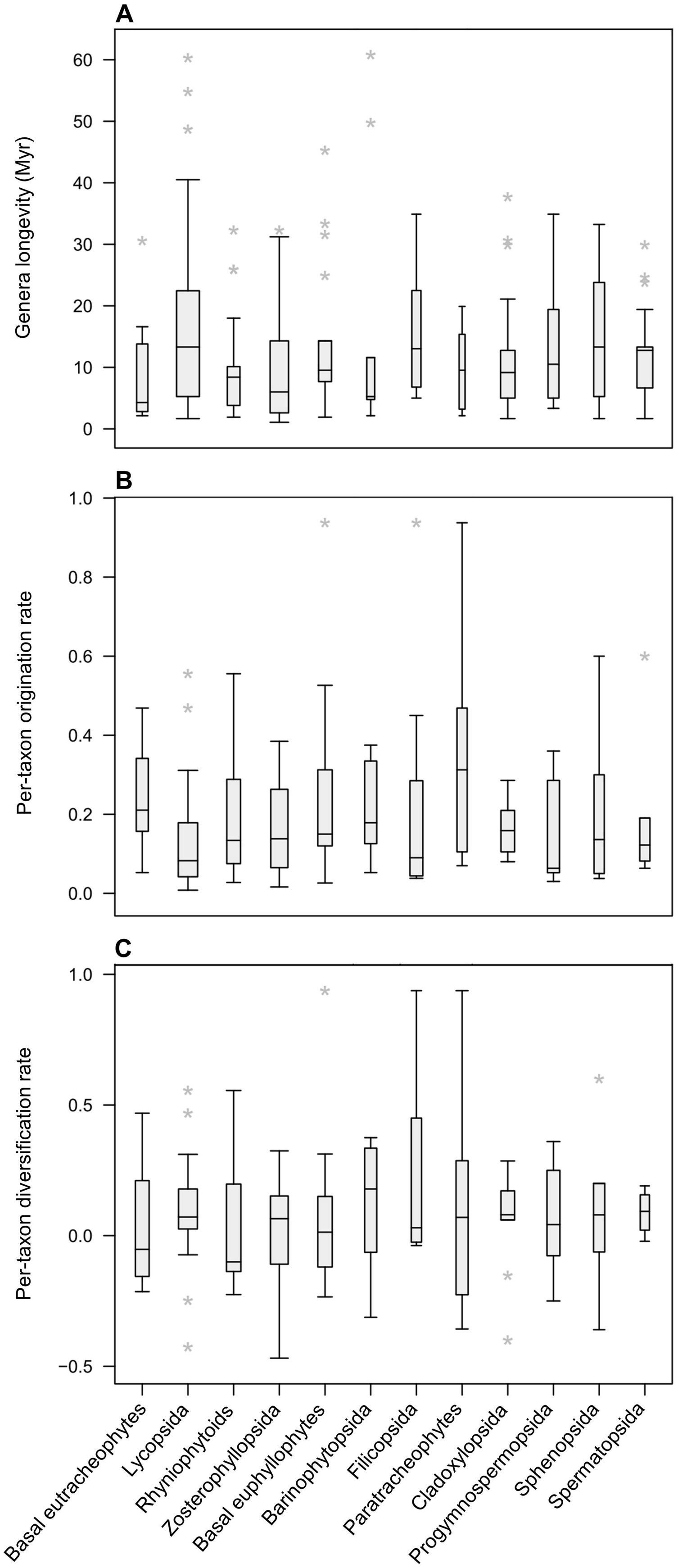

Figure III.S2: Variability of observed genera longevity, origination, and diversification values between main plant groups.

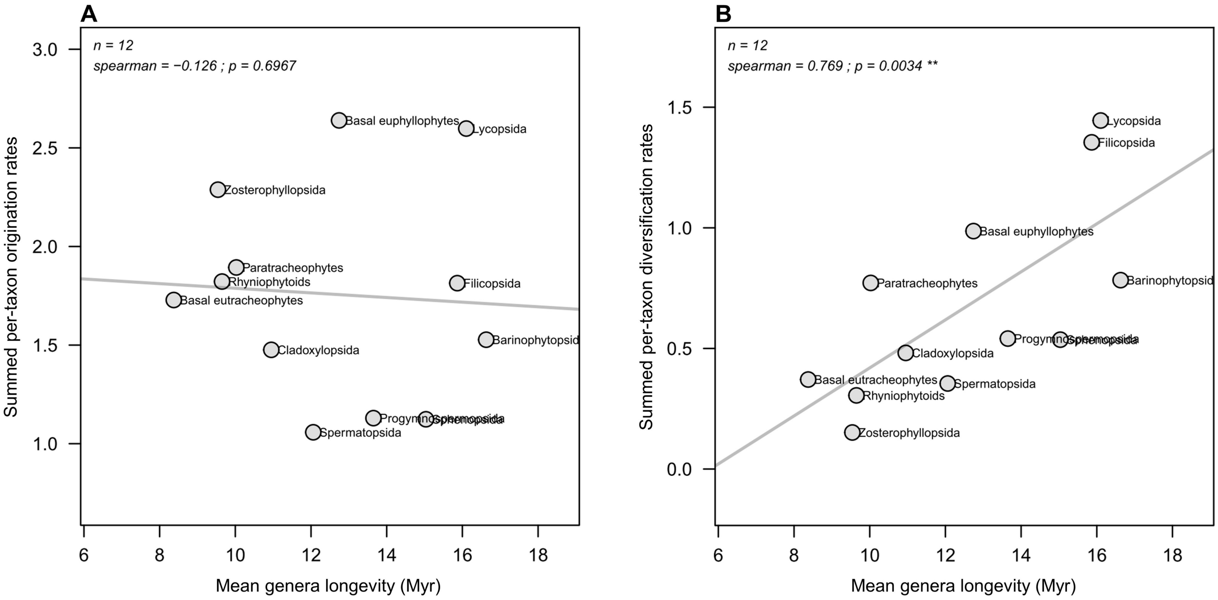

Figure III.S3: Comparison between summed per-taxon origination (A) and diversification (B) rates and mean genera longevity of main tracheophyte groups. Data analysis based on Spearman's rank correlation coefficient (*rho*). **Significant at the 0.01 level

Table III.S3. North American Silurian–Devonian plant fossil occurrences considered in this study.

Table III.S3: NORTH AMERICAN SILURIAN–DEVONIAN PLANT FOSSIL OCCURRENCES CONSIDERED IN THIS STUDY.

N°	Genus	Species	Locality	Formation	Range	Environment	References
1	*Actinoxylon*	*Actinoxylon banksii*	Cairo quarry, Greene County, New York, USA	Kiskatom	Givetian	Non-marine	Matten, 1968
2	*Adelocladoxis*	*Adelocladoxis praecox*	South shore, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Durieux et al., 2021
3	*Amphidoxodendron*	*Amphidoxodendron dichotomum*	Riverside Quarry, Gilboa Schoharie County, New York, USA	Moscow	Givetian	Non-marine	Grierson and Banks, 1963
4	*Amphidoxodendron*	*Amphidoxodendron dichotomum*	Loc 2, West Saugerties, Ulster County, New York USA	Kiskatom	Givetian	Non-marine	Grierson and Banks, 1963
5	cf. *Aneurophyton*	*Aneurophyton* sp.	SW Ellesmere island, NWT Canada	Strathcona Fiord	Eifelian	Non-marine	Scheckler et al., 1990
6	*Aneurophyton*	*Aneurophyton germanicum*	Pond Eddy, Sullivan County, New York, USA	Delaware River Flags	Frasnian	Non-marine	Serlin and Banks, 1978
7	aff. *Aneurophyton*	*Aneurophyton olnense*	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
8	*Arachnoxylon*	*Arachnoxylon minor*	Radford, Montgomery County, Virginia, USA	Millboro Shale	Eifelian	Marine	Stein et al., 1983
9	*Arachnoxylon*	*Arachnoxylon kopfi*	Ravine, Canandaigua Lake, New York, USA	Tully Pyrite	Givetian	Marine	Read, 1938
10	*Archaeopteris*	*Archaeopteris halliana*	Perry, Washington County, Maine, USA	Perry	Frasnian–Famennian	Non-marine	Smith and White, 1905
11	*Archaeopteris*	*Archaeopteris rogersi*	Perry, Washington County, Maine, USA	Perry	Frasnian–Famennian	Non-marine	Smith and White, 1905
12	*Archaeopteris*	*Archaeopteris macilenta*	Ghost river, Rockies, Alberta, Canada	Yahatinda	Frasnian	Non-marine	Scheckler, 1978
13	*Archaeopteris*	*Archaeopteris* sp.	Ghost river, Rockies, Alberta, Canada	Yahatinda	Frasnian	Non-marine	Scheckler, 1978
14	*Archaeopteris*	*Archaeopteris obtusa*	Bird Fiord, Ellesmere island, NWT Canada	Nordstrand Point	Frasnian	Non-marine	Scheckler et al., 1990
15	*Archaeopteris*	*Archaeopteris macilenta*	Bird Fiord, Ellesmere island, NWT Canada	Nordstrand Point	Frasnian	Non-marine	Scheckler et al., 1990
16	*Archaeopteris*	*Archaeopteris obtusa*	Goose Fiord, Ellesmere island, NWT Canada	Fram	Frasnian	Non-marine	Andrews et al., 1965
17	*Archaeopteris*	*Archaeopteris obtusa*	SW Ellesmere island, NWT Canada	Hell Gate	Frasnian	Non-marine	Scheckler et al., 1990
18	*Archaeopteris*	*Archaeopteris halliana*	Escuminac B, Scaumenac Bay, Quebec, Canada	Escuminac	Frasnian	Marine	Gensel and Barnett-Lawrence, 1996
19	*Archaeopteris*	*Archaeopteris obtusa*	Escuminac B, Scaumenac Bay, Quebec, Canada	Escuminac	Frasnian	Marine	Gensel and Barnett-Lawrence, 1996
20	*Archaeopteris*	*Archaeopteris latifolia*	Loc 1, Ohiopyle, Fayette County, Pennsylvania, USA	Foreknobs	Frasnian	Non-marine	Arnold, 1939
21	*Archaeopteris*	*Archaeopteris macilenta*	Loc 1, Ohiopyle, Fayette County, Pennsylvania, USA	Foreknobs	Frasnian	Non-marine	Arnold, 1939
22	*Archaeopteris*	*Archaeopteris* sp.	Loc 6, Horseshoe Curve, Blair County, Pennsylvania, USA	Lower Pocono	Frasnian	Non-marine	Arnold, 1939
23	*Archaeopteris*	*Archaeopteris halliana*	Loc 8, Meshoppen, Wyoming County, Pennsylvania, USA	Foreknobs	Frasnian	Non-marine	Arnold, 1939
24	*Archaeopteris*	*Archaeopteris halliana*	Loc 9, Factoryville, Wyoming County, Pennsylvania, USA	Foreknobs	Frasnian	Non-marine	Arnold, 1939
25	*Archaeopteris*	*Archaeopteris macilenta*	Loc 9, Factoryville, Wyoming County, Pennsylvania, USA	Foreknobs	Frasnian	Non-marine	Arnold, 1939
26	*Archaeopteris*	*Archaeopteris minor*	Loc 9, Factoryville, Wyoming County, Pennsylvania, USA	Foreknobs	Frasnian	Non-marine	Arnold, 1939
27	*Archaeopteris*	*Archaeopteris macilenta*	Steenberg quarry, Schoharie County, New York, USA	Oneonta	Frasnian	Non-marine	Carluccio et al., 1966
28	*Archaeopteris*	*Archaeopteris* sp.	Mountain quarry, Greene County, New York, USA	Oneonta	Frasnian	Non-marine	Carluccio et al., 1966
29	*Archaeopteris*	*Archaeopteris macilenta*	Cannonsville dam-Stilesville quarry, Delaware County, New York, USA	Walton	Frasnian	Non-marine	Beck, 1971
30	*Archaeopteris*	*Archaeopteris sphenophyllifolia*	Cannonsville dam-Stilesville quarry, Delaware County, New York, USA	Walton	Frasnian	Non-marine	Carluccio et al., 1966

Table III.S3: CONTINUED.

N°	Genus	Species	Locality	Formation	Range	Environment	References
31	*Archaeopteris*	*Archaeopteris obtusa*	Cannonsville dam-Stilesville quarry, Delaware County, New York, USA	Walton	Frasnian	Non-marine	Carluccio et al., 1966
32	*Archaeopteris*	*Archaeopteris hibernica*	Cannonsville dam-Stilesville quarry, Delaware County, New York, USA	Walton	Frasnian	Non-marine	Carluccio et al., 1966
33	*Archaeopteris*	cf. *Archaeopteris macilenta*	Bluestone Quarry, Delaware County, New York, USA	Walton	Frasnian	Non-marine	Beck, 1960
34	*Archaeopteris*	*Archaeopteris sphenophyllifolia*	Hawks Nest, Orange County, New York, USA	Delaware River Flags	Frasnian	Non-marine	Arnold, 1939
35	*Archaeopteris*	*Archaeopteris halliana*	Loc 10, Sexton's Quarry, Chemung County, New York, USA	Foreknobs	Frasnian	Non-marine	Arnold, 1939
36	*Archaeopteris*	*Archaeopteris macilenta*	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
37	*Archaeopteris*	*Archaeopteris halliana*	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
38	*Archaeopteris*	*Archaeopteris obtusa*	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
39	*Archaeopteris*	*Archaeopteris sphenophyllifolia*	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
40	*Archaeopteris*	*Archaeopteris hibernica*	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
41	*Archaeopteris*	*Archaeopteris macilenta*	Valley Head, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Phillips et al., 1972
42	*Archaeopteris*	*Archaeopteris halliana*	Valley Head, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Phillips et al., 1972
43	*Archaeopteris*	*Archaeopteris hibernica*	Valley Head, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
44	*Archaeopteris*	*Archaeopteris latifolia*	Loc 5, Cambell Hollow, McKean County, Pennsylvania, USA	Oswayo sandstone	Famennian	Marine	Arnold, 1939
45	*Archaeopteris*	*Archaeopteris latifolia*	Loc 4, Bush Hill, McKean County, Pennsylvania, USA	Cuba silt shale	Famennian	Marine	Arnold, 1939
46	*Archaeopteris*	*Archaeopteris halliana*	Loc 7, Coxton Narrows, Luzerne County, Pennsylvania, USA	Chery Ridge Red Shale	Famennian	Undet.	Arnold, 1939
47	*Archaeopteris*	*Archaeopteris* sp.	Loc 2, Canfield Quarry, Silvara Bradford County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Beck, 1971
48	*Archaeopteris*	*Archaeopteris macilenta*	Red Hill, Clinton County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Cressler, 2006
49	*Archaeopteris*	*Archaeopteris hibernica*	Red Hill, Clinton County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Cressler, 2006
50	*Archaeopteris*	*Archaeopteris obtusa*	Red Hill, Clinton County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Cressler, 2006
51	*Archaeopteris*	*Archaeopteris halliana*	Red Hill, Clinton County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Cressler, 2006
52	*Archaeopteris*	*Archaeopteris hibernica*	Trout run, Lycoming County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Broussard et al., 2018
53	*Archaeopteris*	*Archaeopteris macilenta*	Trout run, Lycoming County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Broussard et al., 2018
54	*Archaeopteris*	*Archaeopteris* sp.	Loc 3, Rock City, Cattaraugus County, New York, USA	Cattaraugus	Famennian	Non-marine	Arnold, 1939
55	*Archaeosigillaria*	*Archaeosigillaria* sp.	Loc 36, Portland Point Quarry, Tompkins County, New York, USA	Geneseo Shale	Givetian	Marine	Grierson and Banks, 1963
56	*Archaeosigillaria*	*Archaeosigillaria vanuxemi*	Loc 37, Moonshine Falls, Cayuga County, New York, USA	Ludlowville	Givetian	Marine	Grierson and Banks, 1963
57	cf. *Archaeosigillaria*	*Archaeosigillaria vanuxemi*	Loc 33, Rose Hill, Onondaga County, New York, USA	Ludlowville	Givetian	Marine	Grierson and Banks, 1963
58	*Archaeosigillaria*	*Archaeosigillaria* sp.	Loc 31, DeRuyter, Madison County, New York, USA	Tully Limestone	Givetian	Marine	Grierson and Banks, 1963
59	*Archaeosigillaria*	*Archaeosigillaria vanuxemi*	Loc 27, New Berlin, Chenango County, New York, USA	Moscow	Givetian	Non-marine	Grierson and Banks, 1963
60	*Archaeosigillaria*	*Archaeosigillaria primaeva*	Springbrook, Erie, County, New, York, USA	Rhinestreet shale	Frasnian	Marine	Arnold, 1939

Table III.S3: CONTINUED.

N°	Genus	Species	Locality	Formation	Range	Environment	References
61	cf. *Archaeosigillaria*	*Archaeosigillaria vanuxemi*	Loc 38a, Cornell University, Tompkins County, New York, USA	Ithaca	Frasnian	Marine	Grierson and Banks, 1963
62	*Archaeosigillaria*	*Archaeosigillaria vanuxemi*	Loc 34, Allen's Quarry, Tioga County, New York, USA	Foreknobs	Frasnian	Non-marine	Grierson and Banks, 1963
63	cf. *Archaeosigillaria*	*Archaeosigillaria* sp.	Loc 30, South Oxford, Chenango County, New York, USA	Oneonta	Frasnian	Non-marine	Grierson and Banks, 1963
64	*Archaeosperma*	*Archaeosperma arnoldii*	Loc 4, Bush Hill, McKean County, Pennsylvania, USA	Cuba silt shale	Famennian	Marine	Pettitt and Beck, 1968
65	*Artschaliphyton*	*Artschaliphyton colophyllum*	Brown mountain, Schoharie County, New York, USA	Panther Mountain	Givetian	Marine	Bonamo et al., 1988
66	*Artschaliphyton*	*Artschaliphyton colophyllum*	Loc 16, Jefferson Schoharie County, New York, USA	Moscow	Givetian	Non-marine	Grierson and Banks, 1963
67	*Artschaliphyton*	*Artschaliphyton colophyllum*	Loc 15, Summit route 10, Schoharie County, New York, USA	Moscow	Givetian	Non-marine	Grierson and Banks, 1963
68	*Artschaliphyton*	*Artschaliphyton colophyllum*	Loc 14, Richmondville, Schoharie County, New York, USA	Panther Mountain	Givetian	Marine	Grierson and Banks, 1963
69	*Artschaliphyton*	*Artschaliphyton colophyllum*	Loc 13, Schoharie Reservoir, Schoharie County, New York, USA	Moscow	Givetian	Non-marine	Grierson and Banks, 1963
70	*Artschaliphyton*	*Artschaliphyton colophyllum*	Walton Farm, Durham Greene County, New York, USA	Kiskatom	Givetian	Non-marine	Grierson and Banks, 1963
71	*Artschaliphyton*	*Artschaliphyton colophyllum*	Durham Falls, Greene County, New York, USA	Kiskatom	Givetian	Non-marine	Grierson and Banks, 1963
72	*Artschaliphyton*	*Artschaliphyton colophyllum*	Loc 32, Skaneateles Lake, New York, USA	Ludlowville	Givetian	Marine	Grierson and Banks, 1963
73	*Artschaliphyton*	*Artschaliphyton colophyllum*	Loc 28, Madison Reservoir, Madison County, New York, USA	Skaneateles	Givetian	Marine	Grierson and Banks, 1963
74	*Artschaliphyton*	*Artschaliphyton colophyllum*	Loc 1, West Hurley, Ulster County, New York, USA	Kiskatom	Givetian	Non-marine	Grierson and Banks, 1963
75	*Artschaliphyton*	*Artschaliphyton colophyllum*	Loc 6, Mountain Crest Quarry, Greene County, New York, USA	Oneonta	Frasnian	Non-marine	Grierson and Banks, 1963
76	cf. *Astralocaulis*	*Astralocaulis* sp.	Winslow Farm, Presque Isle, Maine, USA	Mapleton	Givetian	Undet.	Kasper et al., 1988
77	*Astralocaulis*	*Astralocaulis mummii*	Ravine, Canandaigua Lake, New York, USA	Tully Pyrite	Givetian	Marine	Read, 1938
78	*Baragwanathia*	*Baragwanathia abitibiensis*	GSC Loc 6437, Abitibi River, Ontario, Canada	Sextant	Emsian	Non-marine	Hueber, 1983
79	*Baragwanathia*	*Baragwanathia abitibiensis*	GSC Loc 6438, Abitibi River, Ontario, Canada	Sextant	Emsian	Non-marine	Hueber, 1983
80	*Baragwanathia*	*Baragwanathia abitibiensis*	GSC Loc 6439, Abitibi River, Ontario, Canada	Sextant	Emsian	Non-marine	Hueber, 1983
81	*Baragwanathia*	*Baragwanathia abitibiensis*	GSC Loc 6440, Abitibi River, Ontario, Canada	Sextant	Emsian	Non-marine	Hueber, 1983
82	*Baragwanathia*	*Baragwanathia abitibiensis*	GSC Loc 6441, Abitibi River, Ontario, Canada	Sextant	Emsian	Non-marine	Hueber, 1983
83	*Barinophyton*	*Barinophyton richardsoni*	Perry, Washington County, Maine, USA	Perry	Frasnian–Famennian	Non-marine	Smith and White, 1905
84	*Barinophyton*	*Barinophyton* sp.	Bird Fiord, Ellesmere island, NWT Canada	Nordstrand Point	Frasnian	Non-marine	Scheckler et al., 1990
85	*Barinophyton*	*Barinophyton citrulliforme*	SW Ellesmere island, NWT Canada	Hell Gate	Frasnian	Non-marine	Scheckler et al., 1990
86	cf. *Barinophyton*	*Barinophyton* sp.	Escuminac A, Scaumenac Bay, Quebec, Canada	Escuminac	Frasnian	Marine	Gensel and Barnett-Lawrence, 1996
87	*Barinophyton*	*Barinophyton sibericum*	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
88	*Barinophyton*	*Barinophyton citrulliforme*	Burtville, Potter County, Pennsylvania USA	Catskill	Famennian	Non-marine	Brauer, 1980
89	*Barinophyton*	cf. *Barinophyton obscurum*	Burtville, Potter County, Pennsylvania USA	Catskill	Famennian	Non-marine	Brauer, 1980
90	*Barinophyton*	*Barinophyton obscurum*	Red Hill, Clinton County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Cressler, 2006

Table III.S3: CONTINUED.

N°	Genus	Species	Locality	Formation	Range	Environment	References
91	*Barinophyton*	*Barinophyton sibericum*	Red Hill, Clinton County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Cressler, 2006
92	*Barinophyton*	*Barinophyton citrulliforme*	Loc 3, Rock City, Cattaraugus County, New York, USA	Cattaraugus	Famennian	Non-marine	Arnold, 1939
93	*Barrandeina*	*Barrandeina aroostookensis*?	Winslow Farm, Presque Isle, Maine, USA	Mapleton	Givetian	Undet.	Schopf, 1964
94	cf. *Bathurstia*	*Bathurstia* sp.	Loc US600, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Ludfordian	Marine	Kotyk et al., 2002
95	cf. *Bathurstia*	*Bathurstia* sp.	Loc US384, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Ludfordian	Marine	Kotyk et al., 2002
96	*Bathurstia*	*Bathurstia denticulata*	Loc US620, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
97	*Bathurstia*	*Bathurstia denticulata*	Loc US625, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
98	*Bathurstia*	*Bathurstia denticulata*	Loc US633, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
99	*Bathurstia*	*Bathurstia denticulata*	Loc US636, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
100	*Bathurstia*	*Bathurstia denticulata*	Loc US637, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
101	*Bathurstia*	*Bathurstia denticulata*	Loc US640, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
102	*Bathurstia*	*Bathurstia denticulata*	Loc US641, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
103	*Bathurstia*	*Bathurstia denticulata*	Loc US642, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
104	*Bathurstia*	*Bathurstia denticulata*	Loc US644, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
105	*Bathurstia*	*Bathurstia denticulata*	Loc US645, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
106	*Bathurstia*	*Bathurstia denticulata*	Loc US646, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
107	*Bathurstia*	*Bathurstia denticulata*	Loc US604, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
108	*Bathurstia*	*Bathurstia denticulata*	Loc US607, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
109	*Bathurstia*	*Bathurstia denticulata*	Loc US609, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
110	*Bathurstia*	*Bathurstia denticulata*	Loc US617, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
111	*Bathurstia*	*Bathurstia denticulata*	Loc US685, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
112	*Bathurstia*	*Bathurstia denticulata*	Loc 8370, Young Inlet, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk and Basinger, 2000
113	cf. *Bathurstia*	*Bathurstia* sp.	Seal Rock, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Hotton et al., 2001
114	cf. *Bathurstia*	*Bathurstia* sp.	Loc R, Campbellton, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Hotton et al., 2001
115	*Bisporangiostrobus*	*Bisporangiostrobus harrisii*	Union City, Erie County, Pennsylvania, USA	Venango	Famennian	Marine	Chitaley and McGregor, 1988
116	*Bitelaria*	*Bitelaria dubjanski*	Loc D, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Johnson and Gensel, 1992
117	*Cairoa*	*Cairoa lamanekii*	Cairo quarry, Greene County, New York, USA	Kiskatom	Givetian	Non-marine	Matten, 1973
118	*Calamophyton*	*Calamophyton forbesii*	Winslow Farm, Presque Isle, Maine, USA	Mapleton	Givetian	Undet.	Schopf, 1964
119	cf. *Calamophyton*	*Calamophyton* sp.	Winslow Farm, Presque Isle, Maine, USA	Mapleton	Givetian	Undet.	Kasper et al., 1988
120	*Calamophyton*	*Calamophyton bicephalum*	Ashokan Reservoir, Ulster County, New York, USA	Ashokan	Givetian	Non-marine	Bonamo and Banks, 1966
121	*Callixylon*	*Callixylon petryi*	Loc 1, Taughannock Gorge, Tompkins County, New York, USA	Sherbure Sandstone	Givetian	Non-marine	Beck, 1953

Table III.S3: CONTINUED.

N°	Genus	Species	Locality	Formation	Range	Environment	References
122	*Callixylon*?	*Callixylon* sp.	Perry, Washington County, Maine, USA	Perry	Frasnian–Famennian	Non-marine	Kräusel and Weyland, 1941
123	*Callixylon*	*Callixylon erianum*	Cattaraugus Creek, Erie County, New York, USA	Gowanda shale	Frasnian–Famennian	Marine	Arnold, 1935
124	*Callixylon*	*Callixylon newberryi*	Paxton quarry, Alpina County, Michigan, USA	Antrim shale	Frasnian–Famennian	Marine	Arnold, 1934
125	*Callixylon*	*Callixylon zalessky*	Ghost river, Rockies, Alberta, Canada	Yahatinda	Frasnian	Non-marine	Scheckler, 1978
126	*Callixylon*	cf. *Callixylon zalessky*	Ghost river, Rockies, Alberta, Canada	Yahatinda	Frasnian	Non-marine	Scheckler, 1978
127	*Callixylon*	*Callixylon* sp.	Ghost river, Rockies, Alberta, Canada	Yahatinda	Frasnian	Non-marine	Scheckler, 1978
128	*Callixylon*	*Callixylon trifilievi*	Pan American Imperial A 1 Cairn 2-11, Alberta, Canada	Wood bend eq	Frasnian	Undet.	Campbell, 1963
129	*Callixylon*	*Callixylon* sp.	Bird Fiord, Ellesmere island, NWT Canada	Nordstrand Point	Frasnian	Non-marine	Scheckler et al., 1990
130	*Callixylon*	*Callixylon* sp.	SW Ellesmere island, NWT Canada	Upper Hecla Bay	Frasnian	Non-marine	Scheckler et al., 1990
131	*Callixylon*	*Callixylon* sp.	SW Ellesmere island, NWT Canada	Hell Gate	Frasnian	Non-marine	Scheckler et al., 1990
132	*Callixylon*	*Callixylon* sp.	Brush Mountain, Montgomery County, Virginia, USA	Foreknobs	Frasnian	Non-marine	Skog, 1983
133	*Callixylon*	*Callixylon petryi*	Steenberg quarry, Schoharie County, New York, USA	Oneonta	Frasnian	Non-marine	Carluccio et al., 1966
134	*Callixylon*	cf. *Callixylon zalesskyi*	Steenberg quarry, Schoharie County, New York, USA	Oneonta	Frasnian	Non-marine	Carluccio et al., 1966
135	*Callixylon*	*Callixylon zalesskyi*	Tri-County Asphalt quarry, Greene County, New York, USA	Oneonta	Frasnian	Non-marine	Scheckler, 1978
136	*Callixylon*	*Callixylon* sp.	Bristol Center, Ontario County, New York, USA	Genundewa Limestone	Frasnian	Marine	Arnold, 1930
137	*Callixylon*	*Callixylon petryi*	Loc 3, Wilder Run Creek, New York, USA	Genundewa Limestone	Frasnian	Marine	Beck, 1953
138	*Callixylon*	*Callixylon* sp.	Cannonsville dam-Stilesville quarry, Delaware County, New York, USA	Walton	Frasnian	Non-marine	Carluccio et al., 1966
139	*Callixylon*	*Callixylon zalesskyi*	Bluestone quarry, Delaware County, New York, USA	Walton	Frasnian	Non-marine	Beck, 1960
140	*Callixylon*	*Callixylon newberryi*	Henryville, Clarke County, Indiana, USA	Blackiston	Famennian	Marine	Stubblefield and Taylor, 1985
141	*Callixylon*	*Callixylon clevelandensis*	Intersection of I-71 and West 130th Street, Cleveland, Ohio, USA	Ohio Shale	Famennian	Marine	Chitaley, 1992
142	*Callixylon*	*Callixylon beckii*	Rocky river, Cleveland, Ohio, USA	Ohio Shale	Famennian	Marine	Chitaley and Cai, 2001
143	*Callixylon*	*Callixylon huronensis*	Kettle Point, Ontario, Canada	Huron Shale	Famennian	Marine	Chitaley and Cai, 2001
144	*Callixylon*	*Callixylon* sp.	Rawley Springs, Rockingham County, Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
145	*Callixylon*	*Callixylon erianum*	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
146	*Callixylon*	*Callixylon* sp.	Durbin, Pocahontas County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
147	*Callixylon*	*Callixylon* sp.	Valley Head, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Phillips et al., 1972
148	*Callixylon*	*Callixylon* sp.	Loc 5, Cambell Hollow, McKean County, Pennsylvania, USA	Oswayo sandstone	Famennian	Marine	Arnold 1939
149	*Callixylon*	*Callixylon* sp.	Loc 4, Bush Hill, McKean County, Pennsylvania, USA	Cuba silt shale	Famennian	Marine	Arnold 1939
150	*Chaleuria*	*Chaleuria cirrosa*	Loc A, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Andrews et al., 1974
151	cf. *Cladoxylon*	*Cladoxylon* sp.	Winslow Farm, Presque Isle, Maine, USA	Mapleton	Givetian	Undet.	Kasper et al., 1988

Table III.S3: CONTINUED.

N°	Genus	Species	Locality	Formation	Range	Environment	References
152	*Clevelandodendron*	*Clevelandodendron ohioensis*	Intersection of I-71 and West 130th Street, Cleveland, Ohio, USA	Ohio Shale	Famennian	Marine	Chital.,ey and Pigg 1996
153	cf. *Colpodexylon*	*Colpodexylon* sp.	Loc 40, Hubbard Quarry, Seneca County, New York, USA	Geneseo Shale	Givetian	Marine	Grierson and Banks, 1963
154	*Colpodexylon*	*Colpodexylon trifurcatum*	Loc 3, Mount Peter, Orange County, New York, USA	Bellvale Sandstone	Givetian	Non-marine	Banks, 1944
155	cf. *Colpodexylon*	*Colpodexylon deatsii*	Steenberg quarry, South mountain, Schoharie County, New York, USA	Oneonta	Frasnian	Non-marine	Grierson and Banks, 1963
156	*Colpodexylon*	*Colpodexylon deatsii*	Steenberg quarry, South mountain, Schoharie County, New York, USA	Oneonta	Frasnian	Non-marine	Grierson and Banks, 1963
157	*Colpodexylon*	*Colpodexylon deatsii*	Loc 6, Mountain Crest quarry, Greene County, New York, USA	Oneonta	Frasnian	Non-marine	Grierson and Banks, 1963
158	*Colpodexylon*	*Colpodexylon* sp.	Loc 44, Dansville, Livingston County, New York, USA	Rhinestreet shale	Frasnian	Marine	Grierson and Banks, 1963
159	*Colpodexylon*	*Colpodexylon* sp.	Loc 29, West Hill, Chenango County, New York, USA	Oneonta	Frasnian	Non-marine	Grierson and Banks, 1963
160	cf. *Colpodexylon*	*Colpodexylon* sp.	Loc 26, Sidney, Delaware County, New York, USA	Oneonta	Frasnian	Non-marine	Grierson and Banks, 1963
161	*Colpodexylon*	*Colpodexylon* sp.	Loc 21, Lake Delaware, Delaware County, New York, USA	Walton	Frasnian	Non-marine	Grierson and Banks, 1963
162	*Colpodexylon*	*Colpodexylon* sp.	Davidson quarry, Davenport, Delaware County, New York, USA	Oneonta	Frasnian	Non-marine	Grierson and Banks, 1963
163	*Colpodexylon*	*Colpodexylon* sp.	Loc 20, Barryville, Sullivan County, New York, USA	Walton	Frasnian	Non-marine	Grierson and Banks, 1963
164	*Colpodexylon*	*Colpodexylon trifurcatum*	Pond Eddy, Sullivan County, New York, USA	Delaware River Flags	Frasnian	Non-marine	Banks, 1944
165	*Colpodexylon*	*Colpodexylon deatsii*	Pond Eddy, Sullivan County, New York, USA	Delaware River Flags	Frasnian	Non-marine	Banks, 1944
166	*Colpodexylon*	*Colpodexylon* sp.	Hawks Nest, Orange County, New York, USA	Delaware River Flags	Frasnian	Non-marine	Grierson and Banks, 1963
167	*Condrusia*	*Condrusia*sp.	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
168	*Cooksonia*	*Cooksonia* sp.	Loc 1, Ridgemount quarry, Fort Erie, Ontario, Canada	Williamsville	Pridoli stage	Marine	Edwards et al., 2004
169	*Cooksonia*?	*Cooksonia* sp.	Loc 1, Ridgemount quarry, Fort Erie, Ontario, Canada	Williamsville	Pridoli stage	Marine	Edwards et al., 2004
170	*Cooksonia*	cf. *Cooksonia hemisphaerica*	Loc 2a, Spinnerville, Herkimer County, New York, USA	Flidders Green	Pridoli stage	Marine	Edwards et al., 2004
171	*Cooksonia*	*Cooksonia*sp.	Loc 2b, Cedarville, Herkimer County, New York, USA	Flidders Green	Pridoli stage	Marine	Edwards et al., 2004
172	*Cooksonia*	*Cooksonia*sp.	Loc US616, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
173	*Crenaticaulis*	*Crenaticaulis verruculosus*	Seal Rock, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Banks and Davies, 1969
174	*Crossia*	*Crossia virginiana*	Radford Route, Montgomery County, Virginia, USA	Millboro Shale	Eifelian	Marine	Beck and Stein, 1993
175	cf. *Cyclostigma*	*Cyclostigma kiltorkense*	Perry, Washington County, Maine, USA	Perry	Frasnian–Famennian	Non-marine	Kräusel and Weyland, 1941
176	*Cyclostigma*	*Cyclostigma antrimense*	Paxton quarry, Alpina County, Michigan, USA	Antrim shale	Frasnian–Famennian	Marine	Doweld, 2017
177	*Distichophytum*	*Distichophytum* sp.	Loc US600, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Ludfordian	Marine	Kotyk et al., 2002
178	*Distichophytum*	*Distichophytum ovatum*	Loc US622, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
179	*Distichophytum*	*Distichophytum ovatum*	Loc US636, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
180	*Distichophytum*	*Distichophytum ovatum*	Loc US642, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
181	*Distichophytum*	*Distichophytum ovatum*	Loc US664, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998

Table III.S3: CONTINUED.

N°	Genus	Species	Locality	Formation	Range	Environment	References
182	*Distichophytum*	*Distichophytum ovatum*	Loc US605, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
183	*Distichophytum*	*Distichophytum ovatum*	Loc US607, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
184	*Distichophytum*	*Distichophytum ovatum*	Loc US608, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
185	*Distichophytum*	*Distichophytum ovatum*	Loc US609, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
186	*Distichophytum*	*Distichophytum ovatum*	Loc US617, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
187	*Distichophytum*	*Distichophytum ovatum*	Loc US618, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
188	*Distichophytum*	*Distichophytum ovatum*	Loc US619, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
189	*Distichophytum*	*Distichophytum ovatum*	Loc US685, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
190	*Distichophytum*	*Distichophytum ovatum*	Beartooth Butte, Park County, Wyoming, USA	Beartooth Butte	Emsian	Non-marine	Tanner, 1983
191	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc US628, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
192	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc US633, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
193	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc US636, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
194	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc US637, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
195	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc US645, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
196	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc US664, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
197	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc US604, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
198	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc US605, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
199	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc US606, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
200	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc US607, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
201	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc US608, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
202	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc US610, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
203	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc US612, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
204	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc US617, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
205	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc US683, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
206	*Drepanophycus*	cf. *Drepanophycus spinaeformis*	Loc 8370, Young Inlet, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Hueber, 1972
207	cf. *Drepanophycus*	*Drepanophycus* sp.	Lapatrie, Quebec Canada	Compton	Emsian	Marine	Hueber et al., 1990
208	*Drepanophycus*	*Drepanophycus* sp.	Loc C-3, Noyes Island, SE Alaska, USA	Karheen	Emsian	Marine	Churkin et al., 1969
209	*Drepanophycus*	*Drepanophycus gaspianus*	GSC Loc 6440, Abitibi River, Ontario, Canada	Sextant	Emsian	Non-marine	Hueber, 1983
210	*Drepanophycus*	*Drepanophycus spinaeformis*	Seal Rock, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Stubblefield and Banks, 1978
211	*Drepanophycus*	*Drepanophycus gaspianus*	Loc F, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Grierson and Hueber, 1968
212	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc F, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Grierson and Hueber, 1968

Table III.S3: CONTINUED.

N°	Genus	Species	Locality	Formation	Range	Environment	References
213	*Drepanophycus*	*Drepanophycus* sp.	Loc A, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Andrews et al., 1974
214	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc R, Campbellton, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Grierson and Hueber, 1968
215	*Drepanophycus*	*Drepanophycus gaspianus*	Loc L, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Grierson and Hueber, 1968
216	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc L, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Grierson and Hueber, 1968
217	*Drepanophycus*	*Drepanophycus spinaeformis*	Loc K, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Li et al., 2001
218	*Drepanophycus*	*Drepanophycus* sp.	Loc 4, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Andrews et al., 1977
219	*Drepanophycus*	*Drepanophycus spinaeformis*	La Poile-Cinq Cerf, SW Newfoundland, Canada	Billiards Brook	Emsian–Eifelian	Undet.	Dorf and Cooper, 1943
220	*Drepanophycus*	*Drepanophycus spinaeformis*	Brown mountain, Schoharie County, New York, USA	Panther Mountain	Givetian	Marine	Stubblefield and Banks, 1978
221	*Drepanophycus*	*Drepanophycus spinaeformis*	Cairo quarry, Greene County, New York, USA	Kiskatom	Givetian	Non-marine	Stubblefield and Banks, 1978
222	*Drepanophycus*	*Drepanophycus spinosus*	Loc 41, Fayette quarry, Seneca County, New York, USA	Skaneateles	Givetian	Marine	Grierson and Banks, 1963
223	*Drepanophycus*	*Drepanophycus spinaeformis*	Route 23A, Greene County, New York, USA	Oneonta	Frasnian	Non-marine	Banks and Grierson, 1968
224	*Drepanophycus*	*Drepanophycus spinaeformis*	Tri-County Asphalt quarry, Greene County, New York, USA	Oneonta	Frasnian	Non-marine	Banks and Grierson, 1968
225	*Duodimidia*	*Duodimidia pfefferkornii*	Red Hill, Clinton County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Cressler et al., 2010
226	*Eddianna*	*Eddianna gaspiana*	South shore, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Pfeiler and Tomescu, 2018
227	*Eddya*	*Eddya sullivanensis*	Pond Eddy, Sullivan County, New York, USA	Delaware River Flags	Frasnian	Non-marine	Beck, 1967
228	*Elkinsia*	*Elkinsia polymorpha*	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Rothwell et al., 1989
229	*Ellesmeris*	*Ellesmeris sphenopteroides*	Bird Fiord, Ellesmere island, NWT Canada	Nordstrand Point	Frasnian	Non-marine	Hill et al., 1997
230	*Eospermatopteris*	*Eospermatopteris eriana*	Riverside quarry, Schoharie County, New York, USA	Moscow	Givetian	Non-marine	Stein et al., 2012
231	*Eospermatopteris*	*Eospermatopteris eriana*	Manorkill Falls, Schoharie County, New York, USA	Moscow	Givetian	Non-marine	Boyer, 1995
232	*Eospermatopteris*	*Eospermatopteris eriana*	Steenberg quarry, Schoharie County, New York, USA	Oneonta	Frasnian	Non-marine	Stein et al., 2007
233	cf. *Eviostachya*	*Eviostachya* sp.	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
234	*Flabellofolium*	*Flabellofolium brownianum*	Perry, Washington County, Maine, USA	Perry	Frasnian–Famennian	Non-marine	Smith and White, 1905
235	*Flabellofolium*	*Flabellofolium* sp.	Escuminac B, Scaumenac Bay, Quebec, Canada	Escuminac	Frasnian	Marine	Gensel and Barnett-Lawrence, 1996
236	*Flemingites*	*Flemingites gallowayi*	Loc 5, Cambell Hollow, McKean County, Pennsylvania, USA	Oswayo sandstone	Famennian	Marine	Arnold, 1933
237	*Forania*	*Forania plegiospinosa*	Loc A, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Jensen and Gensel, 2013
238	*Forania*	*Forania plegiospinosa*	Loc G, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Jensen and Gensel, 2013
239	*Forania*	*Forania plegiospinosa*	Loc H, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Jensen and Gensel, 2013
240	*Franhueberia*	*Franhueberia gerriennei*	South shore, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Hoffman and Tomescu, 2013
241	*Gilboaphyton*	*Gilboaphyton goldringiae*	Riverside quarry, Schoharie County, New York, USA	Moscow	Givetian	Non-marine	Fairon-Demaret and Banks, 1978
242	*Gilboaphyton*	*Gilboaphyton griersonii*	Loc 10, Honk Falls, Ulster County, New York, USA	Moscow eq	Givetian	Non-marine	Grierson and Banks, 1963

Table III.S3: CONTINUED.

N°	Genus	Species	Locality	Formation	Range	Environment	References
243	*Gillespia*	*Gillespia randolphensis*	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Erwin and Rothwell, 1989
244	*Gillespiea*	*Gillespiea randolphensis*	Red Hill, Clinton County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Cressler, 2006
245	*Gmujij*	*Gmujij tetraxylopteroides*	South shore, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Pfeiler and Tomescu, 2021
246	cf. *Gosslingia*	*Gosslingia*sp.	Cottonwood Canyon, Big Horn County, Wyoming, USA	Beartooth Butte	Lochkovian–Pragian	Non-marine	Noetinger et al., 2021
247	*Hierogramma*	*Hierogramma* sp.	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
248	*Huvenia*	*Huvenia* sp.	Seal Rock, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Hotton et al., 2001
249	*Ibyka*	*Ibyka amphikoma*	Riverside quarry, Schoharie County, New York, USA	Moscow	Givetian	Non-marine	Skog and Banks, 1973
250	*Iridopteris*	*Iridopteris eriensis*	Radford Route, Montgomery County, Virginia, USA	Millboro Shale	Eifelian	Marine	Stein, 1982b
251	*Iridopteris*	*Iridopteris eriensis*	Spring Creek, Erie County, New York, USA	Tully Pyrite	Givetian	Marine	Arnold, 1940
252	*Jowingera*	*Jowingera triloba*	South shore, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Bickner and Tomescu, 2019
253	*Kaulangiophyton*	*Kaulangiophyton akantha*	Loc 1, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Gensel et al., 1969
254	*Kenrickia*	*Kenrickia bivena*	South shore, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Toledo et al., 2021
255	cf. *Leclercqia*	*Leclercqia*sp.	Cottonwood Canyon, Big Horn County, Wyoming, USA	Beartooth Butte	Lochkovian–Pragian	Non-marine	Noetinger et al., 2021
256	*Leclercqia*	*Leclercqia complexa*	Beartooth Butte, Park County, Wyoming, USA	Beartooth Butte	Emsian	Non-marine	Tanner, 1983
257	*Leclercqia*	*Leclercqia complexa*	Loc Q, Altholville, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Gensel and Albright, 2006
258	*Leclercqia*	*Leclercqia complexa*	Loc F, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Gensel and Albright, 2006
259	*Leclercqia*	*Leclercqia andrewsii*	Loc B, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Gensel and Kasper, 2005
260	*Leclercqia*	*Leclercqia andrewsii*	Loc 7, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Kasper and Forbes, 1979
261	*Leclercqia*	*Leclercqia scolopendra*	Northwest Lime, Whatcom County, Washington, USA	Chilliwack	Givetian	Marine	Benca et al., 2014
262	*Leclercqia*	*Leclercqia complexa*	Northwest Lime, Whatcom County, Washington, USA	Chilliwack	Givetian	Marine	Benca et al., 2014
263	*Leclercqia*	*Leclercqia complexa*	Brown mountain, Schoharie County, New York, USA	Panther Mountain	Givetian	Marine	Banks et al., 1972
264	cf. *Lepidodendropsis*	*Lepidodendropsis* sp.	Red Hill, Clinton County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Cressler and Pfefferkorn, 2005
265	cf. *Lepidosigillaria*	*Lepidosigillaria* sp.	Tri-County Asphalt quarry, Greene County, New York, USA	Oneonta	Frasnian	Non-marine	Grierson and Banks, 1963
266	cf. *Lepidosigillaria*	*Lepidosigillaria whitei*	Amsdel Creek, Erie County, New York, USA	Middlesex shale	Frasnian	Marine	Grierson and Banks, 1963
267	*Lepidosigillaria*	*Lepidosigillaria whitei*	Loc 43, Grimes Gully, Ontario County, New York, USA	Hatch Shale	Frasnian	Marine	White, 1907
268	*Lepidosigillaria*	*Lepidosigillaria* sp.	Loc 38b, Cornell University, Tompkins County, New York, USA	Ithaca	Frasnian	Marine	Grierson and Banks, 1963
269	cf. *Lepidosigillaria*	*Lepidosigillaria whitei*	Loc 35, Hungerford, Tompkins County, New York, USA	Enfield	Frasnian	Non-marine	Grierson and Banks, 1963
270	cf. *Lepidosigillaria*	*Lepidosigillaria* sp.	Loc 23, Callicoon, Sullivan County, New York, USA	Walton	Frasnian	Non-marine	Grierson and Banks, 1963
271	*Leptocentroxyla*	*Leptocentroxyla tetrarcha*	South shore, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Bickner and Tomescu, 2019

Table III.S3: CONTINUED.

N°	Genus	Species	Locality	Formation	Range	Environment	References
272	*Leptophloeum*	*Leptophloeum rhombicum*	Perry, Washington County, Maine, USA	Perry	Frasnian–Famennian	Non-marine	Smith and White, 1905
273	*Leptophloeum*	*Leptophloeum rhombicum*	Goose Fiord, Ellesmere island, NWT Canada	Fram	Frasnian	Non-marine	Andrews et al., 1965
274	*Leptophloeum*	*Leptophloeum rhombicum*	Jura Creek, Exshaw Front Ranges, Alberta, Canada	Palliser	Famennian	Marine	Pratt and van Heerde, 2017
275	*Loganophyton*	*Loganophyton dawsoni*	Loc A, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Kräusel and Weyland, 1961
276	*Macivera*	*Macivera gracilis*	Loc US385, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Ludfordian	Marine	Kotyk et al., 2002
277	*Melvillipteris*	*Melvillipteris quadriseriata*	Baldwin River, Melville Island, NWT Canada	Parry Islands	Famennian	Non-marine	Xue and Basinger, 2016
278	*Omniastrobus*	*Omniastrobus dawsonii*	Loc F, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Bonacorsi et al., 2021
279	*Oocampsa*	*Oocampsa catheta*	Loc B, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Andrews et al., 1975
280	*Oricilla*	*Oricilla bilinearis*	Loc E, Restigouche River, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Gensel, 1982b
281	*Otzinachsonia*	*Otzinachsonia beerboweri*	Red Hill, Clinton County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Cressler and Pfefferkorn, 2005
282	cf. *Pertica*	*Pertica* sp.	Cottonwood Canyon, Big Horn County, Wyoming, USA	Beartooth Butte	Lochkovian–Pragian	Non-marine	Noetinger et al., 2021
283	cf. *Pertica*	*Pertica* sp.	Seal Rock, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Doran et al., 1978
284	*Pertica*	*Pertica varia*	Seal Rock, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Granoff et al., 1976
285	*Pertica*	*Pertica dalhousii*	Loc A, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Doran et al., 1978
286	*Pertica*	*Pertica quadrifaria*	Loc 2, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Kasper and Andrews, 1972
287	*Pertica*	*Pertica quadrifaria*	Loc 7, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Kasper and Andrews, 1972
288	*Phytokneme*	*Phytokneme rhodona*	Knifley quadrangle, Adair County, Kentucky, USA	Chattanooga	Frasnian–Famennian	Marine	Andrews et al., 1971
289	*Prolepidodendron*	*Prolepidodendron breviinternodium*	Loc 5, Cambell Hollow, McKean County, Pennsylvania, USA	Oswayo sandstone	Famennian	Marine	Arnold, 1939
290	*Prosseria*	*Prosseria grandis*	Kimble Gully, Yates County, New York, USA	West River Shale	Frasnian	Marine	Read, 1953
291	*Proteokalon*	*Proteokalon petryi*	Tri-County Asphalt quarry, Greene County, New York, USA	Oneonta	Frasnian	Non-marine	Scheckler and Banks, 1971
292	cf. *Protobarinophyton*	*Protobarinophyton* sp.	Escuminac A, Scaumenac Bay, Quebec, Canada	Escuminac	Frasnian	Marine	Gensel and Barnett-Lawrence, 1996
293	*Protobarinophyton*	*Protobarinophyton pennsylvanicum*	Burtville, Potter County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Brauer, 1981
294	*Protolepidodendron*	*Protolepidodendron* sp.	Riverside quarry, Schoharie County, New York, USA	Moscow	Givetian	Non-marine	Skog and Banks, 1973
295	*Protolepidodendron*	*Protolepidodendron gilboense*	Riverside quarry, Schoharie County, New York, USA	Moscow	Givetian	Non-marine	Grierson and Banks, 1963
296	*Pseudobornia*	*Pseudobornia ursina*	Loc Be 661, NE Alaska, USA	Undet.	Frasnian–Famennian	Undet.	Mamay, 1962
297	*Pseudobornia*	*Pseudobornia ursina*	Loc Rr 635, NE Alaska, USA	Undet.	Frasnian–Famennian	Undet.	Mamay, 1962
298	cf. *Pseudosporochnus*	*Pseudosporochnus* sp.	SW Ellesmere island, NWT Canada	Strathcona Fiord	Eifelian	Non-marine	Scheckler et al., 1990
299	*Pseudosporochnus*	*Pseudosporochnus hueberi*	Cairo quarry, Greene County, New York, USA	Kiskatom	Givetian	Non-marine	Stein and Hueber, 1989
300	*Pseudosporochnus*	*Pseudosporochnus hueberi*	East Cave Mountain, Greene County, New York, USA	Oneonta	Frasnian	Non-marine	Stein and Hueber, 1989

Table III.S3: CONTINUED.

N°	Genus	Species	Locality	Formation	Range	Environment	References
301	*Pseudosporochnus*	*Pseudosporochnus hueberi*	Tri-County Asphalt quarry, Greene County, New York, USA	Oneonta	Frasnian	Non-marine	Stein and Hueber, 1989
302	*Pseudosporogonites*	*Pseudosporogonites bertrandii*	Red Hill, Clinton County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Cressler et al., 2010
303	*Psilophyton*	*Psilophyton dawsonii*	GSC Loc 6439, Abitibi River, Ontario, Canada	Sextant	Emsian	Non-marine	Banks et al., 1975
304	*Psilophyton*	*Psilophyton dawsonii*	GSC Loc 6441, Abitibi River, Ontario, Canada	Sextant	Emsian	Non-marine	Banks et al., 1975
305	*Psilophyton*	*Psilophyton forbesii*	Seal Rock, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Gensel, 1979
306	*Psilophyton*	*Psilophyton dawsonii*	South shore, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Banks, 1981
307	*Psilophyton*	*Psilophyton crenulatum*	Loc Q, Altholville, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Doran, 1980
308	*Psilophyton*	*Psilophyton charientos*	Loc B, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Gensel, 1979
309	*Psilophyton*	*Psilophyton* sp.	Loc A, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Jensen and Gensel, 2013
310	*Psilophyton*	*Psilophyton coniculum*	Loc L, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Trant and Gensel, 1985
311	*Psilophyton*	*Psilophyton princeps*	Loc K, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Dawson, 1882
312	*Psilophyton*	*Psilophyton dapsile*	Loc 1, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Kasper et al., 1974
313	*Psilophyton*	*Psilophyton forbesii*	Loc 3, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Kasper et al., 1974
314	*Psilophyton*	*Psilophyton forbesii*	Loc 5, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Kasper et al., 1974
315	*Psilophyton*	*Psilophyton microspinosum*	Loc 6, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Kasper et al., 1974
316	*Psilophyton*	*Psilophyton microspinosum*	Loc 3, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Kasper et al., 1974
317	*Psilophyton*	*Psilophyton* sp.	Loc 1, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Andrews et al., 1977
318	cf. *Psilophyton*	*Psilophyton dapsile*	St Froid/Eagle Lakes 1, Maine, USA	Fish River Lake	Emsian–Eifelian	Non-marine	Kasper and Forbes, 1983
319	*Reimannia*	*Reimannia aldenense*	Spring Creek, Erie County, New York, USA	Ludlowville	Givetian	Marine	Stein, 1982a
320	cf. *Rellimia*	*Rellimia* sp.	SW Ellesmere island, NWT Canada	Strathcona Fiord	Eifelian	Non-marine	Scheckler et al., 1990
321	cf. *Rellimia*	*Rellimia* sp.	SW Ellesmere island, NWT Canada	Lower Hecla Bay	Eifelian	Non-marine	Scheckler et al., 1990
322	*Rellimia*	*Rellimia thomsonii*	Brown mountain, Schoharie County, New York, USA	Panther Mountain	Givetian	Marine	Dannenhoffer and Bonamo, 1989
323	*Renalia*	*Renalia dorfii*	Beartooth Butte, Park County, Wyoming, USA	Beartooth Butte	Emsian	Non-marine	Tanner, 1983
324	*Renalia*	*Renalia hueberi*	Seal Rock, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Hotton et al., 2001
325	*Renalia*	*Renalia hueberi*	Fort Peninsule, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Marine	Gensel, 1976
326	cf. *Rhacophyton*	*Rhacophyton* sp.	Winslow Farm, Presque Isle, Maine USA	Mapleton	Givetian	Undet.	Kasper et al., 1988
327	*Rhacophyton*	*Rhacophyton incertum*	Perry, Washington County, Maine, USA	Perry	Frasnian–Famennian	Non-marine	Kräusel and Weyland, 1941
328	*Rhacophyton*	*Rhacophyton* sp.	Rawley Springs, Rockingham County, Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
329	*Rhacophyton*	*Rhacophyton ceratangium*	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986

Table III.S3: CONTINUED.

N°	Genus	Species	Locality	Formation	Range	Environment	References
330	*Rhacophyton*	*Rhacophyton ceratangium*	Valley Head, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Cornet et al., 1976
331	*Rhacophyton*	*Rhacophyton ceratangium*	Red Hill, Clinton County, Pennsylvania, USA	Catskill	Famennian	Non-marine	Cressler, 2006
332	*Rhymokalon*	*Rhymokalon trichium*	Tri-County Asphalt quarry, Greene County, New York, USA	Oneonta	Frasnian	Non-marine	Scheckler, 1975
333	*Rotoxylon*	*Rotoxylon dawsonii*	Canandaigua Lake, Ontario County, New York, USA	Genundewa Limestone	Frasnian	Marine	Cordi and Stein, 2005
334	cf. *Sawdonia*	*Sawdonia* sp.	Loc 8370, Young Inlet, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Hueber, 1972
335	cf. *Sawdonia*	*Sawdonia* sp.	Loc 8376, Young Inlet, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Hueber, 1972
336	cf. *Sawdonia*	*Sawdonia* sp.	Ste Cecile, Quebec, Canada	Compton	Emsian	Marine	Hueber et al., 1990
337	cf. *Sawdonia*	*Sawdonia* sp.	GSC Loc 6437, Abitibi River, Ontario, Canada	Sextant	Emsian	Non-marine	Hueber, 1983
338	cf. *Sawdonia*	*Sawdonia* sp.	Beartooth Butte, Park County, Wyoming, USA	Beartooth Butte	Emsian	Non-marine	Tanner, 1983
339	*Sawdonia*	*Sawdonia ornata*	Seal Rock, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Gensel and Berry, 2016
340	*Sawdonia*	*Sawdonia ornata*	Loc F, Dalhousie Junction, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Gensel and Albright, 2006
341	*Sawdonia*	*Sawdonia acanthotheca*	Loc M, Peuplier Point, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Gensel et al., 1975
342	cf. *Sawdonia*	*Sawdonia* sp.	Loc 1, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Dorf and Rankin, 1962
343	cf. *Sawdonia*	*Sawdonia* sp.	Loc 2, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Dorf and Rankin, 1962
344	cf. *Sawdonia*	*Sawdonia* sp.	Loc 3, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Dorf and Rankin, 1962
345	cf. *Sawdonia*	*Sawdonia* sp.	Loc 4, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Dorf and Rankin, 1962
346	cf. *Sawdonia*	*Sawdonia* sp.	Winslow Farm, Presque Isle, Maine USA	Mapleton	Givetian	Undet.	Schopf, 1964
347	cf. *Sawdonia*	*Sawdonia* sp.	Steenberg quarry, Schoharie County, New York, USA	Oneonta	Frasnian	Non-marine	Hueber and Grierson, 1961
348	*Sengelia*	*Sengelia radicans*	Cottonwood Canyon, Big Horn County, Wyoming, USA	Beartooth Butte	Lochkovian–Pragian	Non-marine	Noetinger et al., 2021
349	*Sengelia*	*Sengelia radicans*	Beartooth Butte, Park County, Wyoming, USA	Beartooth Butte	Emsian	Non-marine	Tanner, 1983
350	*Serrulacaulis*	*Serrulacaulis furcatus*	Steenberg quarry, Schoharie County, New York, USA	Oneonta	Frasnian	Non-marine	Hueber and Banks, 1979
351	*Smeadia*	*Smeadia clevelandensis*	Intersection of I-71 and West 130th Street, Cleveland, Ohio, USA	Ohio Shale	Famennian	Marine	Chitaley and Cheng, 2004
352	*Sphenophyllum*	*Sphenophyllum subtenerrimmum*	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
353	*Sphenopteris*	*Sphenopteris* sp.	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
354	*Spinocespitosus*	*Spinocespitosus parallelus*	Falke quarry, Greene County, New York, USA	Oneonta	Frasnian	Non-marine	Besier, 1981
355	*Stenokoleos*	*Stenokoleos holmesii*	Cairo quarry, Greene County, New York, USA	Kiskatom	Givetian	Non-marine	Matten, 1992
356	*Stenokoleos*	*Stenokoleos* sp.	Cairo quarry, Greene County, New York, USA	Kiskatom	Givetian	Non-marine	Matten, 1975
357	*Stenokoleos*	*Stenokoleos bifidus*	Steenberg quarry, Schoharie County, New York, USA	Oneonta	Frasnian	Non-marine	Matten and Banks, 1969
358	*Stenoloboxyla*	*Stenoloboxyla ambigua*	South shore, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Bickner and Tomescu, 2019

Table III.S3: CONTINUED.

N°	Genus	Species	Locality	Formation	Range	Environment	References
359	*Stockmansella*	*Stockmansella* sp.	Seal Rock, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Hotton et al., 2001
360	*Svalbardia*	*Svalbardia fissilis*	Bird Fiord, Ellesmere island, NWT Canada	Nordstrand Point	Frasnian	Non-marine	Scheckler et al., 1990
361	*Svalbardia*	*Svalbardia fissilis*	Goose Fiord, Ellesmere island, NWT Canada	Fram	Frasnian	Non-marine	Andrews et al., 1965
362	*Svalbardia*	*Svalbardia fissilis*	SW Ellesmere island, NWT Canada	Upper Hecla Bay	Frasnian	Non-marine	Scheckler et al., 1990
363	*Svalbardia*	*Svalbardia fissilis*	SW Ellesmere island, NWT Canada	Hell Gate	Frasnian	Non-marine	Scheckler et al., 1990
364	*Svalbardia*	*Svalbardia banksii*	Pond Eddy, Sullivan County, New York, USA	Delaware River Flags	Frasnian	Non-marine	Matten, 1981
365	*Tainioxyla*	*Tainioxyla quebecana*	South shore, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Bickner and Tomescu, 2019
366	*Tetraxylopteris*	*Tetraxylopteris schmidtii*	Tri-County Asphalt quarry, Greene County, New York, USA	Oneonta	Frasnian	Non-marine	Bonamo and Banks, 1967
367	*Tetraxylopteris*	*Tetraxylopteris schmidtii*	Davidson quarry, Delaware County, New York, USA	Oneonta	Frasnian	Non-marine	Beck, 1957
368	*Tetraxylopteris*	*Tetraxylopteris schmidtii*	Hawks Nest, Orange County, New York, USA	Delaware River Flags	Frasnian	Non-marine	Beck, 1957
369	*Thursophyton*	*Thursophyton* sp.	Loc 1, Trout Brook, Maine, USA	Trout Valley	Emsian–Eifelian	Non-marine	Andrews et al., 1977
370	*Triloboxylon*	*Triloboxylon arnoldii*	Cairo quarry, Greene County, New York, USA	Kiskatom	Givetian	Non-marine	Matten, 1974
371	*Triloboxylon*	*Triloboxylon arnoldii*	Spring Creek, Erie County, New York, USA	Ludlowville	Givetian	Marine	Matten, 1974
372	*Triloboxylon*	*Triloboxylon ashlandicum*	Tri-County Asphalt quarry, Greene County, New York, USA	Oneonta	Frasnian	Non-marine	Matten and Banks, 1966
373	cf. *Trimerophyton*	*Trimerophyton* sp.	Cottonwood Canyon, Big Horn County, Wyoming, USA	Beartooth Butte	Lochkovian–Pragian	Non-marine	Noetinger et al., 2021
374	*Trimerophyton*	*Trimerophyton robustius*	Seal Rock, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Kräusel and Weyland, 1961
375	*Xenocladia*	*Xenocladia medullosina*	Spring Creek, Erie County, New York, USA	Tully Pyrite	Givetian	Marine	Arnold, 1940
376	*Xenocladia*	*Xenocladia medullosina*	Springbrook, Erie County, New York, USA	Ludlowville	Givetian	Marine	Arnold, 1952
377	*Xenotheca*	*Xenotheca* sp.	Elkins, Randolph County, West Virginia, USA	Hampshire	Famennian	Non-marine	Scheckler, 1986
378	*Zosterophyllum*	*Zosterophyllum* sp.	Loc US384, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Ludfordian	Marine	Kotyk et al., 2002
379	aff. *Zosterophyllum*	*Zosterophyllum* sp. A	Loc US688, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Ludfordian	Marine	Kotyk et al., 2002
380	aff. *Zosterophyllum*	*Zosterophyllum* sp. B	Loc US383, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Ludfordian	Marine	Kotyk et al., 2002
381	cf. *Zosterophyllum*	*Zosterophyllum* sp.	Cottonwood Canyon, Big Horn County, Wyoming, USA	Beartooth Butte	Lochkovian–Pragian	Non-marine	Noetinger et al., 2021
382	*Zosterophyllum*	*Zosterophyllum arcticum*	Loc US628, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
383	*Zosterophyllum*	*Zosterophyllum arcticum*	Loc US633, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
384	*Zosterophyllum*	*Zosterophyllum arcticum*	Loc US636, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
385	*Zosterophyllum*	*Zosterophyllum arcticum*	Loc US664, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
386	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US628, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
387	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US631, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
388	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US632, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998

Table III.S3: CONTINUED.

N°	Genus	Species	Locality	Formation	Range	Environment	References
389	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US636, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
390	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US637, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
391	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US643, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
392	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US645, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
393	*Zosterophyllum*	*Zosterophyllum* sp.	Loc US642, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
394	*Zosterophyllum*	*Zosterophyllum* sp.	Loc US643, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
395	*Zosterophyllum*	*Zosterophyllum* sp.	Loc US644, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
396	*Zosterophyllum*	*Zosterophyllum* sp.	Loc US649, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
397	*Zosterophyllum*	*Zosterophyllum* sp.	Loc US664, Cheyne River, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
398	*Zosterophyllum*	*Zosterophyllum arcticum*	Loc US608, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
399	*Zosterophyllum*	*Zosterophyllum arcticum*	Loc US617, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
400	*Zosterophyllum*	*Zosterophyllum arcticum*	Loc US618, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
401	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US604, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
402	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US605, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
403	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US606, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
404	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US607, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
405	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US609, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
406	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US610, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
407	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US615, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
408	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US616, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
409	*Zosterophyllum*	*Zosterophyllum reflexum*	Loc US617, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
410	*Zosterophyllum*	*Zosterophyllum* sp.	Loc US616, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
411	*Zosterophyllum*	*Zosterophyllum* sp.	Loc US617, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
412	*Zosterophyllum*	*Zosterophyllum* sp.	Loc US614, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
413	*Zosterophyllum*	*Zosterophyllum* sp.	Loc US605, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
414	*Zosterophyllum*	*Zosterophyllum* sp.	Loc US606, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
415	*Zosterophyllum*	*Zosterophyllum* sp.	Loc US607, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
416	*Zosterophyllum*	*Zosterophyllum* sp.	Loc US609, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
417	*Zosterophyllum*	*Zosterophyllum* sp.	Loc US617, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
418	*Zosterophyllum*	*Zosterophyllum* sp.	Loc US616, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Bathurst Island	Pragian	Marine	Kotyk, 1998
419	cf. *Zosterophyllum*	*Zosterophyllum* sp.	Beartooth Butte, Park County, Wyoming, USA	Beartooth Butte	Emsian	Non-marine	Tanner, 1983

Table III.S3: CONTINUED.

N°	Genus	Species	Locality	Formation	Range	Environment	References
420	*Zosterophyllum*	*Zosterophyllum* sp.	Seal Rock, Gaspé Bay, Quebec, Canada	Battery Point	Emsian	Non-marine	Hotton et al., 2001
421	*Zosterophyllum*	*Zosterophyllum divaricatum*	Loc M, Peuplier Point, New Brunswick, Canada	Campbellton	Emsian	Non-marine	Gensel, 1982a

Note: For each entry, the temporal range, the sampled localities/formations, and the environment of deposition is provided.

Table III.S4. North American Silurian–Devonian lithostratigraphic units considered in this study.

Table III.S4: North American Silurian–Devonian lithostratigraphic units considered in this study

N°	Unit	Range	Environment	Fossiliferous	Thickness (m)	Surface (km^2)
1	Unit 10499 - Trout Valley Fm.	Emsian	Non-marine	Yes	500	15253
2	Unit 1065 - Price Fm.	Famennian–Tournaisian	Non-marine	No	182	3176
3	Unit 1130 - Price Fm.	Famennian–Tournaisian	Mixed	Yes	375	2729
4	Unit 1286 - Hampshire Fm.	Famennian	Non-marine	No	200	8320
5	Unit 1394 - Hampshire Fm.	Famennian	Non-marine	No	200	5425
6	Unit 1405 - Hampshire Fm.	Famennian	Non-marine	No	610	5738
7	Unit 1510 - Hampshire Fm.	Frasnian–Famennian	Mixed	Yes	670	3578
8	Unit 1541 - Bay Fm.	Eifelian–Givetian	Non-marine	No	430	14464
9	Unit 15806 - Darby Fm.	Frasnian–Famennian	Mixed	No	60	17355
10	Unit 15928 - Darby Fm.	Frasnian–Famennian	Mixed	No	60	40996
11	Unit 16027 - Beartooth Butte Fm.	Lochkovian–Emsian	Mixed	Yes	45	15866
12	Unit 1681 - Hampshire Fm.	Famennian	Non-marine	Yes	500	9995
13	Unit 18739 - Lake Branch	Emsian–Eifelian	Mixed	No	1219	33211
14	Unit 18740 - York River	Emsian	Mixed	No	4267	33211
15	Unit 18772 - Pools Cove	Frasnian	Non-marine	No	1524	8329
16	Unit 18779 - Terrenceville	Frasnian	Non-marine	No	305	10699
17	Unit 18794 - Bay Du Nord	Lochkovian–Eifelian	Mixed	Yes	4572	22862
18	Unit 18879 - McAdam Lake	Emsian–Givetian	Non-marine	No	340	16826
19	Unit 18904 - Knoydart	Lochkovian–Pragian	Non-marine	Yes	305	11656
20	Unit 18906 - Bloomsburg Fm.	Pridoli	Mixed	Yes	122	11655
21	Unit 18919 - Knoydart	Lochkovian–Pragian	Non-marine	No	305	8712
22	Unit 18928 - Horton Gp.	Famennian–Tournaisian	Non-marine	Yes	274	8712
23	Unit 18955 - Unnamed	Pragian	Non-marine	No	300	9598
24	Unit 18961 - Perry	Frasnian–Famennian	Non-marine	Yes	1200	9598
25	Unit 19071 - Battery Point	Emsian–Eifelian	Non-marine	Yes	2134	21872
26	Unit 19072 - York Lake	Emsian	Non-marine	Yes	1524	21872
27	Unit 19100 - Malbaie	Eifelian	Non-marine	Yes	610	5649
28	Unit 19101 - Battery Point	Emsian–Eifelian	Mixed	Yes	2134	5649
29	Unit 19102 - York River	Emsian	Mixed	Yes	610	5649

Table III.S4: CONTINUED.

N°	Unit	Range	Environment	Fossiliferous	Thickness (m)	Surface (km^2)
30	Unit 19119 - Memramcook	Famennian–Tournaisian	Non-marine	Yes	457	14905
31	Unit 19162 - Pirate Cove	Emsian	Non-marine	Yes	213	17315
32	Unit 19163 - Unnamed	Emsian	Mixed	No	1524	17315
33	Unit 19166 - Escuminac	Frasnian	Non-marine	Yes	122	17315
34	Unit 19167 - Fleurant	Frasnian	Non-marine	No	15	17315
35	Unit 1958 - Hampshire Fm.	Famennian	Non-marine	No	1067	4248
36	Unit 1960 - Foreknobs Fm.	Famennian	Mixed	Yes	690	4248
37	Unit 1987 - Bloomsburg Fm.	Ludfordian	Mixed	No	18	4248
38	Unit 22697 - Bloomsburg Fm.	Ludlow–Pridoli	Mixed	No	122	3479
39	Unit 22701 - Long Run	Frasnian	Non-marine	Yes	303	11981
40	Unit 22832 - York River	Emsian	Non-marine	No	1524	21872
41	Unit 34142 - Earn	Lochkovian–Givetian	Non-marine	No	50	28297
42	Unit 34143 - Earn	Frasnian–Tournaisian	Non-marine	No	200	28297
43	Unit 34763 - Parry Islands Fm.	Frasnian–Famennian	Non-marine	No	5700	25554
44	Unit 34804 - Peel Sound	Pridoli	Mixed	No	450	41091
45	Unit 34805 - Peel Sound	Lochkovian	Mixed	No	300	41091
46	Unit 34819 - Somerset Fm.	Ludfordian	Mixed	Yes	280	13332
47	Unit 34820 - Peel Sound	Pridoli	Mixed	Yes	920	13332
48	Unit 34821 - Peel Sound	Lochkovian	Mixed	No	120	13332
49	Unit 34908 - Strathcona Fiord Fm.	Eifelian	Non-marine	No	200	11711
50	Unit 34909 - Hecla Bay Fm.	Givetian	Non-marine	No	50	11711
51	Unit 34940 - Strathcona Fiord Fm.	Emsian–Eifelian	Mixed	No	520	17004
52	Unit 34941 - Hecla Bay Fm.	Eifelian–Givetian	Non-marine	No	240	17004
53	Unit 34961 - Parry Islands Fm.	Frasnian–Famennian	Non-marine	No	300	20574
54	Unit 35002 - Blackley Fm.	Eifelian	Mixed	No	700	42913
55	Unit 35003 - Cape De Bray Fm.	Eifelian–Givetian	Mixed	No	900	42913
56	Unit 35032 - Cape De Bray Fm.	Eifelian	Mixed	No	910	48117
57	Unit 35033 - Weatherall Fm.	Eifelian–Givetian	Mixed	Yes	1440	48117
58	Unit 35043 - Hecla Bay Fm.	Givetian	Non-marine	No	800	57212

Table III.S4: CONTINUED.

N°	Unit	Range	Environment	Fossiliferous	Thickness (m)	Surface (km^2)
59	Unit 35044 - Beverley Inlet Fm.	Frasnian	Non-marine	No	500	57212
60	Unit 35045 - Burnett Point Mbr.	Frasnian–Famennian	Non-marine	No	300	57212
61	Unit 35046 - Cape Fortune Mbr.	Famennian	Non-marine	No	200	57212
62	Unit 35047 - Consett Head Mbr.	Famennian	Non-marine	No	150	57212
63	Unit 35093 - Hecla Bay Fm.	Eifelian–Givetian	Non-marine	No	1000	45507
64	Unit 35094 - Beverley Inlet Fm.	Frasnian	Non-marine	Yes	650	45507
65	Unit 35095 - Burnett Point Mbr.	Frasnian–Famennian	Non-marine	No	450	45507
66	Unit 35117 - Hecla Bay Fm.	Eifelian–Givetian	Non-marine	No	900	30642
67	Unit 35118 - Beverley Inlet Fm.	Frasnian	Non-marine	No	450	30642
68	Unit 35119 - Parry Islands Fm.	Frasnian–Famennian	Non-marine	No	200	30642
69	Unit 35127 - Disappointment Bay Fm.	Emsian	Mixed	No	200	29140
70	Unit 35130 - Hecla Bay Fm.	Eifelian–Givetian	Non-marine	No	600	29140
71	Unit 35131 - Parry Islands Fm.	Famennian	Non-marine	No	370	29140
72	Unit 35144 - Prince Alfred Fm.	Pragian	Non-marine	No	10	13699
73	Unit 35145 - Disappointment Bay Fm.	Emsian	Mixed	Yes	200	13699
74	Unit 35148 - Hecla Bay Fm.	Givetian	Non-marine	No	300	13699
75	Unit 35165 - Snowblind Bay Fm.	Lochkovian	Mixed	Yes	450	10561
76	Unit 35166 - Prince Alfred Fm.	Pragian	Non-marine	No	20	10561
77	Unit 35167 - Disappointment Bay Fm.	Emsian–Eifelian	Mixed	Yes	200	10561
78	Unit 35171 - Hecla Bay Fm.	Givetian	Non-marine	No	300	10561
79	Unit 35181 - Prince Alfred Fm.	Pragian	Non-marine	No	20	23131
80	Unit 35184 - Strathcona Fiord Fm.	Eifelian	Non-marine	No	90	23131
81	Unit 35185 - Hecla Bay Fm.	Givetian	Non-marine	No	300	23131
82	Unit 35186 - Fram Fm.	Frasnian	Mixed	No	300	23131
83	Unit 35187- Hell Gate Fm.	Frasnian	Mixed	No	200	23131
84	Unit 35188 - Nordstrand Point Fm.	Frasnian	Non-marine	No	490	23131
85	Unit 35189 - Parry Islands Fm.	Frasnian–Famennian	Non-marine	No	660	23131
86	Unit 35466 - Strathcona Fiord Fm.	Eifelian	Mixed	Yes	200	14464
87	Unit 35467 - Hecla Bay Fm.	Eifelian–Givetian	Non-marine	Yes	430	14464

Table III.S4: CONTINUED.

N°	Unit	Range	Environment	Fossiliferous	Thickness (m)	Surface (km^2)
88	Unit 35468 - Fram Fm.	Frasnian	Non-marine	Yes	1130	14464
89	Unit 35469 - Hell Gate Fm.	Frasnian	Mixed	Yes	640	14464
90	Unit 35470 - Nordstrand Point Fm.	Frasnian	Non-marine	Yes	670	14464
91	Unit 35494 - Strathcona Fiord Fm.	Emsian–Eifelian	Non-marine	No	1100	10821
92	Unit 35495 - Hecla Bay Fm.	Eifelian–Givetian	Non-marine	No	640	10821
93	Unit 35495 - Hecla Fm.	Eifelian–Givetian	Non-marine	No	640	10821
94	Unit 35496 - Fram Fm.	Frasnian	Non-marine	Yes	1480	10821
95	Unit 35550 - Strathcona Fiord Fm.	Emsian–Eifelian	Non-marine	No	710	7032
96	Unit 35551 - Hecla Bay Fm.	Eifelian–Givetian	Non-marine	No	590	7032
97	Unit 36157 - Sextant Fm.	Emsian	Non-marine	Yes	45	45210
98	Unit 36545 - Clam Bank Fm.	Ludlow–Pridoli	Mixed	Yes	500	4942
99	Unit 37297 - Gilwood Fm.	Givetian	Non-marine	No	10	78237
100	Unit 37759 - Yahatinda Fm.	Frasnian	Mixed	Yes	10	5091
101	Unit 38191 - Imperial Fm.	Frasnian–Famennian	Non-marine	No	200	30825
102	Unit 38240 - Imperial Fm.	Frasnian–Tournaisian	Non-marine	No	1000	28002
103	Unit 38523 - Keg River Fm.	Eifelian	Mixed	No	40	36967
104	Unit 5284 - Conglomerate Mbr. (Kanayut Conglomerate)	Frasnian–Tournaisian	Non-marine	No	700	19714
105	Unit 5285 - Lower Shale Mbr. (Kanayut Conglomerate)	Famennian	Mixed	No	1160	19714
106	Unit 5288 - Wacke Mbr. (Hunt Fork Shale)	Famennian	Non-marine	No	700	19714
107	Unit 5289 - Shale Mbr. (Hunt Fork Shale)	Frasnian–Famennian	Non-marine	No	700	19714
108	Unit 5428 - Hampshire Fm.	Famennian	Non-marine	No	427	5804
109	Unit 7559 - Hampshire Fm.	Famennian	Non-marine	No	620	5979
110	Unit 7613 - Bloomsburg Fm.	Ludfordian	Mixed	Yes	60	4416
111	Unit 7705 - Hampshire Fm.	Famennian	Non-marine	No	670	17251
112	Unit 7707 - Bradford Gp	Frasnian–Famennian	Non-marine	No	150	17251
113	Unit 7807 - Hampshire Fm.	Famennian	Non-marine	No	545	12044
114	Unit 7811 - Duncannon Mbr. (Catskill Fm.)	Famennian	Non-marine	No	914	12044
115	Unit 7812 - Sherman Creek Mbr. (Catskill Fm.)	Frasnian–Famennian	Non-marine	No	485	12044
116	Unit 7934 - Duncannon Mbr. (Catskill Fm.)	Famennian	Non-marine	No	914	9633

Table III.S4: CONTINUED.

N°	Unit	Range	Environment	Fossiliferous	Thickness (m)	Surface (km^2)
117	Unit 7935 - Clarks Ferry Mbr. (Catskill Fm.)	Famennian	Non-marine	No	69	9633
118	Unit 7936 - Sherman Creek Mbr. (Catskill Fm.)	Frasnian–Famennian	Non-marine	No	1128	9633
119	Unit 8106 - Huntley Mountain Fm.	Famennian–Tournaisian	Non-marine	No	175	20502
120	Unit 8108 - Duncannon Mbr. (Catskill Fm.)	Famennian	Non-marine	Yes	180	20502
121	Unit 8109 - Sherman Creek Mbr. (Catskill Fm.)	Frasnian–Famennian	Non-marine	Yes	366	20502
122	Unit 8177 - Duncannon Mbr. (Catskill Fm.)	Famennian	Non-marine	Yes	302	11981
123	Unit 8178 - Poplar Gap Mbr. (Catskill Fm.)	Famennian	Non-marine	Yes	515	11981
124	Unit 8179 - Packerton Mbr. (Catskill Fm.)	Frasnian–Famennian	Non-marine	Yes	91	11981
125	Unit 8180 - Long Run/Walcksville Mbrs. (Catskill Fm.)	Frasnian	Non-marine	Yes	303	11981
126	Unit 8181 - Towamensing Mbr. (Catskill Fm.)	Frasnian	Non-marine	Yes	303	11981
127	Unit 8183 - Mahantango Fm.	Givetian	Mixed	No	606	11981
128	Unit 8224 - Duncannon Mbr. (Catskill Fm.)	Famennian	Non-marine	Yes	467	11732
129	Unit 8225 - Clarks Ferry Mbr. (Catskill Fm.)	Famennian	Non-marine	No	313	11732
130	Unit 8226 - Sherman Creek Mbr. (Catskill Fm.)	Frasnian–Famennian	Non-marine	No	1168	11732
131	Unit 8347 - Skunnemunk Conglomerate	Givetian–Frasnian	Non-marine	No	914	4577
132	Unit 8348 - Bellvale Sandstone	Givetian	Non-marine	Yes	610	4577
133	Unit 8364 - Conewango Gp.	Famennian	Mixed	Yes	213	18733
134	Unit 8366 - Conneaut Gp.	Famennian	Mixed	Yes	214	18733
135	Unit 8420 - Conewango Gp.	Famennian	Mixed	No	150	26811
136	Unit 8421 - Conneaut Gp.	Famennian	Mixed	Yes	200	26811
137	Unit 8515 - Walton Fm.	Frasnian	Non-marine	Yes	300	10773
138	Unit 8516 - Oneonta Fm.	Frasnian	Non-marine	Yes	400	10773
139	Unit 8521 - Moscow Fm.	Givetian	Mixed	Yes	150	10773
140	Unit 8564 - Manorkill Fm.	Givetian–Frasnian	Non-marine	Yes	76	6315
142	Unit 8567 - Mahantango Fm.	Givetian	Mixed	No	1000	6315
143	Unit 35034 - Hecla Bay Fm.	Frasnian	Non-marine	Yes	1000	48117

Note: Raw data extracted from Macrostrat (https://macrostrat.org). Compiled information includes the temporal range, associated environment represented, as well as the maximum thickness and surface. The fossiliferous (macrofossil) character of included units is also indicated.

Table III.S5. Correlation analysis between observed and sampling-standardised diversity and considered sampling proxies.

Table III.S5: CORRELATION ANALYSIS BETWEEN OBSERVED AND SAMPLE-STANDARDISED DIVERSITY AND CONSIDERED SAMPLING PROXIES.

Sampling proxies	Observed diversity								Sample-standardized diversity							
	Genera				Species				Genera				Species			
	Raw		Detrended		Raw		Detrended		Raw		Detrended		Raw		Detrended	
	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*
Plant-bearing formations	0.95	**0.001*****	0.43	0.397	0.95	**0.001*****	0.54	0.266	0.46	0.434	-	-	0.46	0.434	-	-
Plant-bearing localities	0.93	**0.003****	0.77	0.072	0.93	**0.003****	0.89	**0.019***	0.60	0.285	-	-	0.30	0.624	-	-
Non-marine outcrop area	0.60	0.159	-	-	0.60	0.159	-	-	-0.20	0.747	-	-	-0.10	0.873	-	-
Non-marine rock volume	0.85	**0.016***	0.94	**0.005****	0.85	**0.016***	1.00	**0.000*****	0.00	1.000	-	-	0.60	0.285	-	-
Non-marine fossiliferous rock volume	0.96	**0.001*****	0.71	0.111	0.95	**0.001*****	0.77	0.072	0.30	0.624	-	-	0.60	0.285	-	-

Note: Data analysis based on raw and generalised-differenced (detrended) data. Diversity data based on non-marine records only. In each case, Spearman's rank coefficients (r_s) with their corresponding probability values (*p*) are shown. Significant ($^{*}p < 0.05$), highly significant ($^{**}p < 0.01$), and very highly significant ($^{***}p < 0.001$) correlations appear in bold.

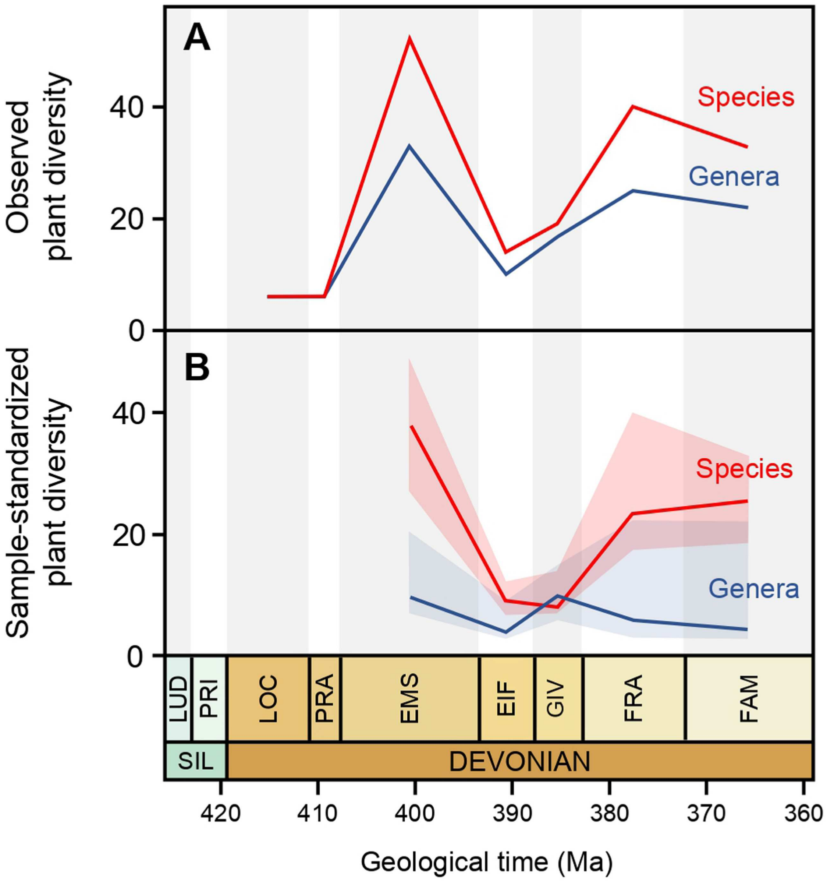

Figure III.S4: Observed (A) and sampling-standardised (B) variations of the Silurian–Devonian plant diversity in North America. Diversity data based on non-marine records only. Lighter areas represent 95% confidence interval (B). Abbreviations: SIL, Silurian; SHE, Sheinwoodian; HOM, Homerian; GOR, Gorstian; LUD, Ludfordian; Wen., Wenlock; Lud., Ludlow; Pri., Pridoli; LOC, Lochkovian; PRA, Pragian; EMS, Emsian; EIF, Eifelian; GIV, Givetian; FRA, Frasnian; FAM, Famennian.

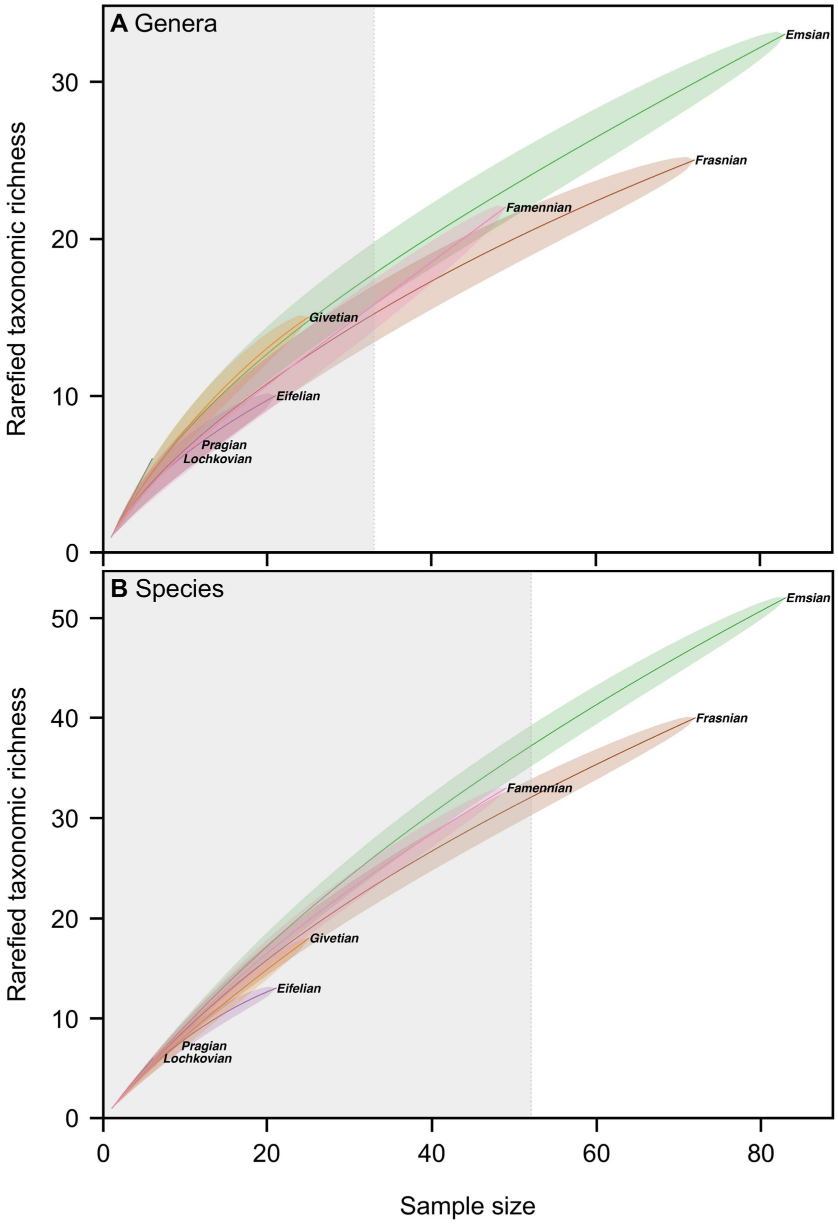

Fig. III.S5. Genera (A) and species (B) sized-based rarefaction curves per time interval. Diversity data based on non-marine records only. Colour area around each curve shows 95% confidence interval. Grey area represents rarefaction quota. See Methods for details.

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Abstract

Plants underwent an extensive Silurian–Devonian diversification during their progressive colonization of terrestrial surfaces (440-360 Ma). Nonetheless, the tempo and mode of this radiation remains controversial, and drivers of diversity have yet to be clearly identified. This thesis, through a series of newly-compiled datasets of plant macrofossils, and via a wide array of quantitative methods, characterizes temporal and spatial dynamics. It further evaluates the biases that may alter our perception of this landmark event. Firstly, a four-factor model was found adequate to describe the underlying structure of early vegetation dynamics. The pattern suggests ecological shifts during transitions phases, further corroborated through an in-depth characterization of global plant diversity patterns. Nevertheless, the general pattern of Silurian–Devonian plant diversity was found to heavily depend on sampling effort, although several signals of diversification and extinction seemed to be dissociated from it, implying real underlying biological signals. A subsequent continental-scale study further demonstrated that, in addition to sampling heterogeneity, geological incompleteness remained an important element in driving apparent early land plant diversity patterns. This bias is not easily corrected even with the most advanced sampling-standardization methods. Furthermore, paleogeographical discrepancies were assessed to uncover a possible spatial component into early land plant radiation. This led to the discovery of a climatologically-driven plant distribution and dispersion, further enhanced during colder periods. Lastly, this thesis includes a review of an Early Devonian plant fossil assemblage from northern France, providing taxonomically up to date and well-dated occurrences to integrate in future studies.

Keywords – early land plants, Devonian, Silurian, palaeodiversity, sampling bias, geological bias, Palaeophytogeography

Résumé

Les plantes ont connu une période de diversification intense pendant le Silurien-Dévonien, correspondant à la colonisation progressive des milieux terrestres (440-360 Ma). Néanmoins, le tempo et le mode de cette radiation restent controversés, et les facteurs contrôlant la diversité n'ont pas encore été clairement identifiés. Cette thèse, à travers plusieurs jeux de données de macrofossiles de plantes et via un large éventail de méthodes quantitatives, a permis de caractériser leurs dynamiques spatiales et temporelles. Ce travail évalue également les biais qui peuvent altérer notre perception de cette radiation. Tout d'abord, un modèle à quatre facteurs s'est avéré adéquat pour décrire la structure sous-jacente de la dynamique de diversification des premières plantes. Le modèle suggère des basculements écologiques pendant les phases de transition, corroboré à travers une caractérisation approfondie des patrons globaux de diversité végétale. Cependant, les fluctuations de diversité durant le Silurien-Dévonien dépendent fortement de l'effort d’échantillonnage, bien que plusieurs signaux de diversification et d'extinction semblent en être dissociés. Une étude subséquente à l’échelle continentale a démontré que les lacunes géologiques demeuraient également un élément important expliquant l’allure des patrons apparents de diversité des premières plantes terrestres. Ce biais est difficilement corrigeable même en ayant recours aux méthodes de normalisation de l’échantillonnage les plus avancées. Les divergences paléogéographiques ont ensuite été évaluées afin de mettre en évidence une éventuelle composante spatiale dans la radiation des premières plantes terrestres. Cette analyse a permis de mettre en evidence l’influence du climat sur la distribution et la dispersion de la végétation, notamment lors des périodes les plus froides. Enfin, cette thèse comprend une révision d'un assemblage de plantes fossiles du Dévonien inférieur du nord de la France, fournissant des occurrences taxonomiquement à jour et bien datées qui pourront être intégrées dans des études ultérieures.

Mots clés – plantes terrestres, Dévonien, Silurien, paléodiversité, biais d’échantillonnage, biais géologiques, Paléophytogéographie