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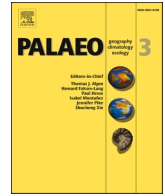
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## New insights into Silurian–Devonian palaeophytogeography

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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.

### 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 heterogeneous (Close et al., 2020; 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., 2022). 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-

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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](#); [Navidi-Izad et al., 2022](#)), albeit recent studies have detected the presence of cryptospores from coeval localities in Laurussia ([Vecoli et al., 2015](#); [Strother et al., 2017](#)). Subsequently, an apparent cosmopolitanism of cryptospores of early land plants during the late Middle and Late Ordovician is observed ([Stemans, 2000](#); [Wellman et al., 2003, 2013, 2022a](#)), 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 periods, 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.

## 2. Data

A new occurrence-based compilation of plant macrofossils was developed from the Silurian–Devonian global-scale dataset of [Capel et al. \(2022\)](#) and primary literature (Data S1, Text 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 (Data S1), tabulated across 48 different geographical units ([Table 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. 1, Table 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,

**Table 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
W-USA	Western USA (Washington, Wyoming)	Laurussia
XNJ	Xinjiang, China	Kazakhstania
YUN	Yunnan, China	NE Gondwana
ZHJ	Zhejiang, China	NE Gondwana

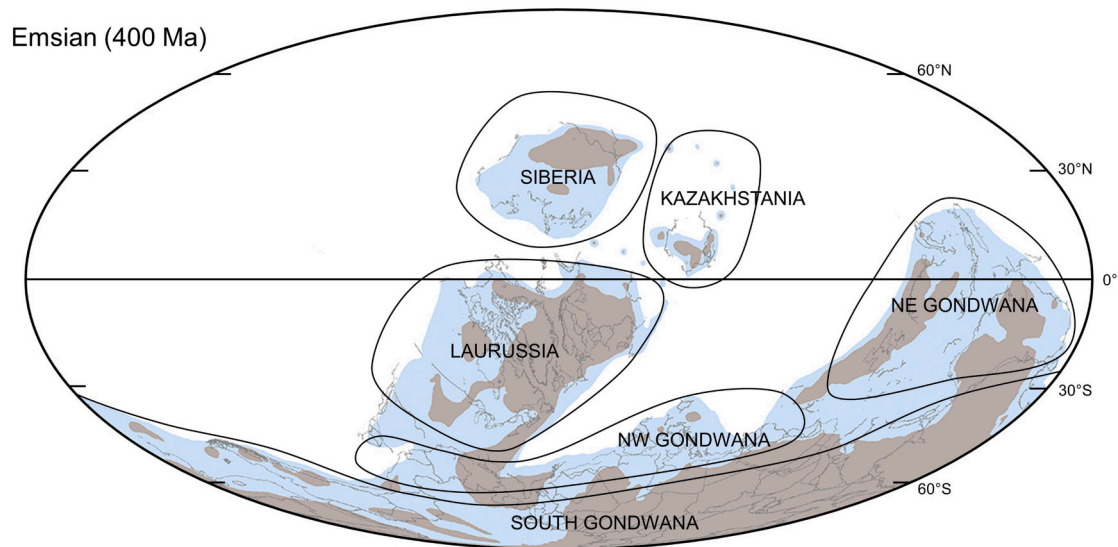


Fig. 1. Palaeogeographical reconstruction for the Early Devonian (Emsian) showing the outlines of each palaeogeographical unit considered in this study. Modified from Scotese et al. (2021).

which demonstrates that taxonomy is 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 Senkevitch (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*.

### 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 (2021) main palaeogeographical regions, i.e., Laurussia, Siberia, Kazakhstania and Gondwana (Fig. 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. 1, Table 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 1, Data 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 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

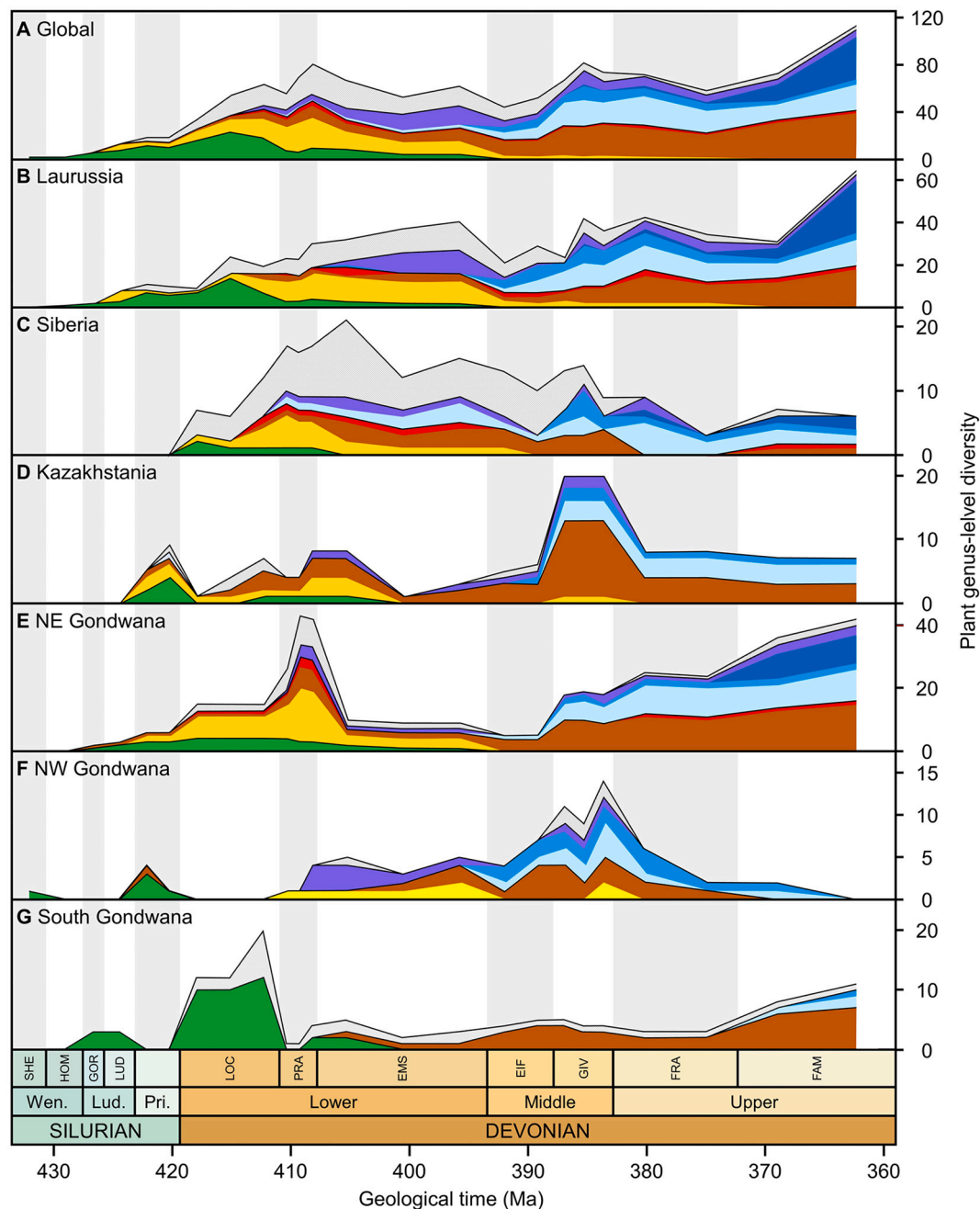
multivariate statistics. More specifically, we used Detrended Correspondence Analyses (DCA; Hill and Gauch, 1980) complemented by additive clustering using the Neighbor-Joining approach (NJ; Saitou and Nei, 1987) to detect past ‘phytochoria’ sensu Meyen (1987). This latter term is meant to refer to geographical 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 palaeokingdoms, 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., 2022).

Hierarchical cluster analyses (hCA) are commonly used to complement DCA to detect the palaeobiogeographical relationships between different areas. Given that our data was found to be gradationally rather than hierarchically structured (as evidenced by our DCAs), a NJ additive cluster analysis was instead performed. This technique is more adequate to retrieve nested structures within this type of data (Vörös and Escarguel, 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 Analysis of Similarities (ANOSIM, 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 (Data 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. List and number of endemic taxa per phytochorion are nonetheless available in Data S4. Taxa under open nomenclature and occurrences where the reliability has been questioned (marked as (?) in Data S1) were also excluded to avoid spurious associations. Multivariate statistics were 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, 2022).



**Fig. 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, Homarian; GOR, Gorstian; LUD, Ludfordian; Wen., Wenlock; Lud., Ludlow; Pri., Pridoli; LOC, Lochkovian; PRA, Pragian; EMS, Emsian; EIF, Eifelian; GIV, Givetian; FRA, Frasnian; FAM, Famennian. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



## 4. Results and discussion

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

Fig. 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. 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. 2C). Diversity recovered in NE Gondwana (South China and Australia) is the second-highest among all palaeogeographical regions after Laurussia (Fig. 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. 2E). The Pragian peak in NE Gondwana appears to contribute significantly to the Pragian peak observed at the global scale (Fig. 2A, E). On the other hand, the poorest region in terms of diversity is NW Gondwana (Fig. 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. 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. 2). For instance, Gondwana is considered the ‘cradle’ of early land plants as evidenced by the first records of trilete spores (Steevens et al., 2009; Gerrienne et al., 2010) and the first unequivocal plant macrofossils (Fig. 2F; Libertin 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. 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), see Capel et al. (2023) for further details. 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. 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. 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. 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. 2G), whereas an important radiation among several groups of euphyllophyte is observed in other regions (Fig. 2B–F), euphyllophytes only appearing in this region in the Famennian (Fig. 2G). Another apparent diachronous event is the spermatophyte radiation occurring earlier and more markedly in Laurussia than in other parts of the world (Fig. 2). In NE Gondwana, spermatophytes only appear in the Famennian, and many regions are still exempt of spermatophytes in the Famennian such as Kazakhstan, NW and South Gondwana (Fig. 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.).

### 4.2. New palaeogeographical patterns of early land plants

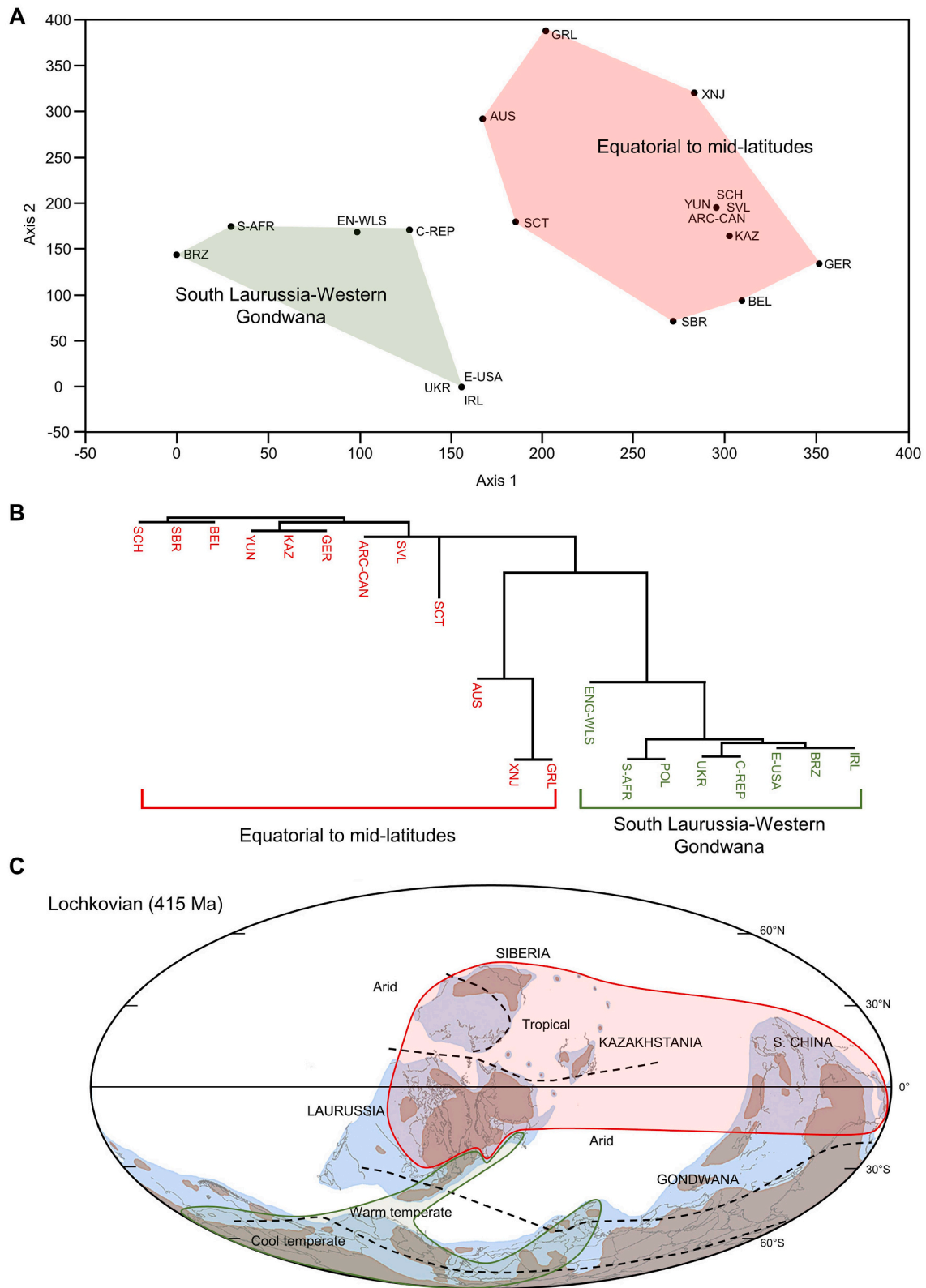
#### 4.2.1. Silurian–Lochkovian palaeophytogeography

DCA and NJ cluster analysis essentially revealed two highly differentiated phytochoria (Fig. 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. 3C). Nevertheless, the NJ cluster analysis exhibit an intermediate cluster constituted of Australia, Xinjiang and Greenland (Fig. 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 to mid-latitudes rather than the South Laurussia–West Gondwana phytochorion (Fig. 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 to mid-latitudes 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 2). These three taxa alone explain >50% of the dissimilarity between the two phytochoria (Table 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 phytochoria 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 endemism, and (3) the number of taxa included in the analyses. Interestingly, Spina and Vecoli (2009) argued that similarities between Gondwanan and Laurussian palynofloras in the Silurian to Lochkovian interval, contrasted with the high degree of bioprovincialism that was defined at the macrofloral level in Raymond et al. (2006), further indicating that their higher number of paleophytogeographical units may indeed originate from a methodological artefact. 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 compared relationships using larger regions (e.g., Baltica or Laurentia). Their analysis likewise 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 delimited due to the lack of data, especially in Gondwana (Fig. 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., 2001a). 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-

### Silurian-Lochkovian



**Fig. 3.** Silurian–Lochkovian palaeophytogeography. (A) DCA scatter plot of geographical units; (B) NJ clustering analysis; (C) extent of each phytochoria transposed onto palaeogeographical maps (Scotese, 2021). Colors: red = Equatorial to mid-latitudes; green = South Laurussia-West Gondwana. Climatic belts (dashed black lines) adapted from Boucot et al. (2013). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 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	
				South Laurussia/ West Gondwana	Equatorial/mid-latitudes
<i>Cooksonia</i>	21.21	23.34	23.34	1.00	0.17
<i>Zosterophyllum</i>	20.23	22.26	45.60	0.13	0.92
<i>Aberlemnia</i>	6.92	7.61	53.21	0.50	0.08
<i>Drepanophycus</i>	5.85	6.44	59.65	0.00	0.33
<i>Salopella</i>	5.72	6.29	65.94	0.13	0.25
<i>Gosslingia</i>	3.38	3.72	69.66	0.13	0.17
<i>Baragwanathia</i>	3.29	3.62	73.28	0.13	0.08
<i>Uskiella</i>	2.94	3.24	76.52	0.25	0.08
<i>Eocooksonia</i>	2.72	3.00	79.51	0.00	0.17
<i>Dutoitia</i>	2.60	2.86	82.37	0.25	0.00

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. 3C).

The Equatorial to mid-latitudes 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 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. 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 (Scotese et al., 2021) 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.

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., 2022b). Wellman et al. (2022b)

further reported that spore diversity in the Lochkovian from Spitzbergen and South Chinese assemblages was low with little endemism, and represented morphologies that are 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).

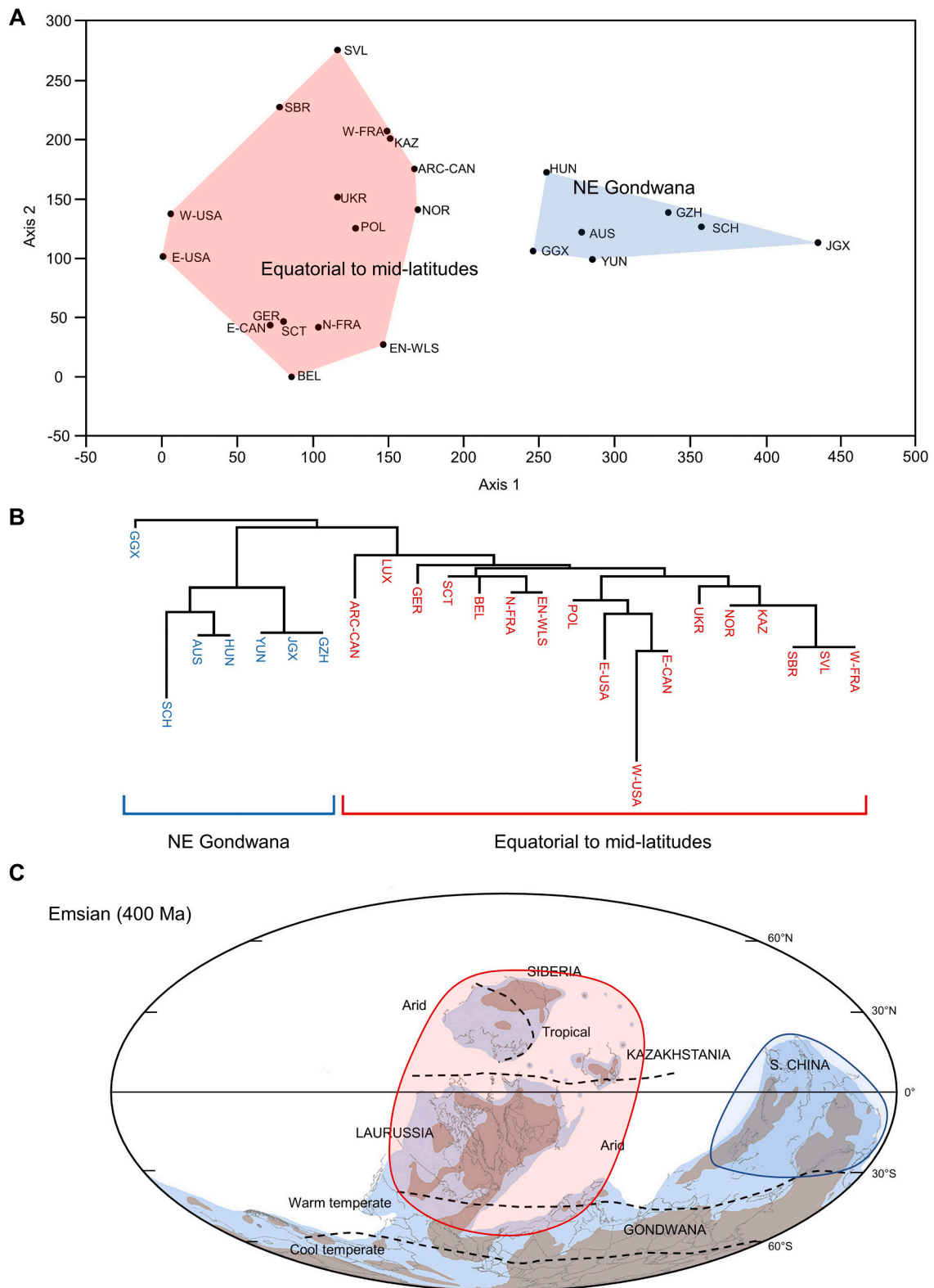
Higher diversity in the higher latitudes has been hypothesized by Wellman et al. (2022b) to be related to: (1) presumed scarcity of continental lands in the tropics (species-area effect); (2) extreme climate in the tropics combined with low oxygen levels; and (3) origination and diversification of land 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. 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).

#### 4.2.2. Pragian–Emsian palaeophytogeography

DCA and NJ cluster analysis show a weakly-differentiated vegetation during this interval (Fig. 4A–B). Nonetheless, accentuated differentiation is observed between South Chinese regions alongside Australia with the rest of geographic units (Fig. 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 palaeogeographical distribution (Fig. 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 *Zosterophyllum* and several South Chinese endemic taxa such as *Pau-thecophyton*, *Demersetheca* and *Yarravia* (recently combined with *Hedeia*), a taxon also shared with Australia (Table 3). The Equatorial to mid-latitudes phytochorion on the other hand, is mostly characterized



### Pragian-Emsian



**Fig. 4.** Pragian–Emsian palaeophytogeography. (A) DCA scatter plot of geographical units; (B) NJ clustering analysis; (C) extent of each phytochoria transposed onto palaeogeographical maps (Scotese, 2021). Colors: red = Equatorial to mid-latitudes; blue = NE Gondwana. Climatic belts (dashed black lines) adapted from Boucou et al. (2013). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 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
<i>Drepanophycus</i>	10.23	12.61	12.61	0.82	0.29
<i>Zosterophyllum</i>	8.05	9.92	22.53	0.59	0.86
<i>Psilophyton</i>	7.74	9.54	32.07	0.65	0.29
<i>Pauthecophyton</i>	5.84	7.20	39.27	0.00	0.43
<i>Adoketophyton</i>	4.48	5.53	44.80	0.00	0.43
<i>Demersatheca</i>	4.48	5.53	50.32	0.00	0.43
<i>Yarravia</i>	3.92	4.84	55.16	0.00	0.43
<i>Guangnania</i>	3.05	3.76	58.92	0.00	0.29
<i>Distichophytum</i>	3.05	3.76	62.67	0.24	0.14
<i>Cooksonia</i>	3.04	3.74	66.42	0.18	0.14
<i>Baragwanathia</i>	2.69	3.32	69.73	0.06	0.29
<i>Gosslingia</i>	2.60	3.21	72.94	0.29	0.00
<i>Uskiella</i>	2.15	2.64	75.58	0.06	0.14
<i>Renalia</i>	2.10	2.59	78.17	0.24	0.00
<i>Leclercqia</i>	1.95	2.40	80.57	0.18	0.00

by the predominance of *Drepanophycus* and *Psilophyton*, but is not as well characterized by endemic taxa as the NE Gondwanan phytochorion (Table 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 2–3). The occurrence of a third South Gondwanan unit in Raymond et al. (1985) results from dating errors of the South African and Antarctic assemblages and accordingly were not re-utilized in the subsequent analysis by Raymond (1987). This unit was characterized by *Haplostigma* and *Palaeostigma* 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 *Palaeostigma* (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., 2001b) 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., 2001b). 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. 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.

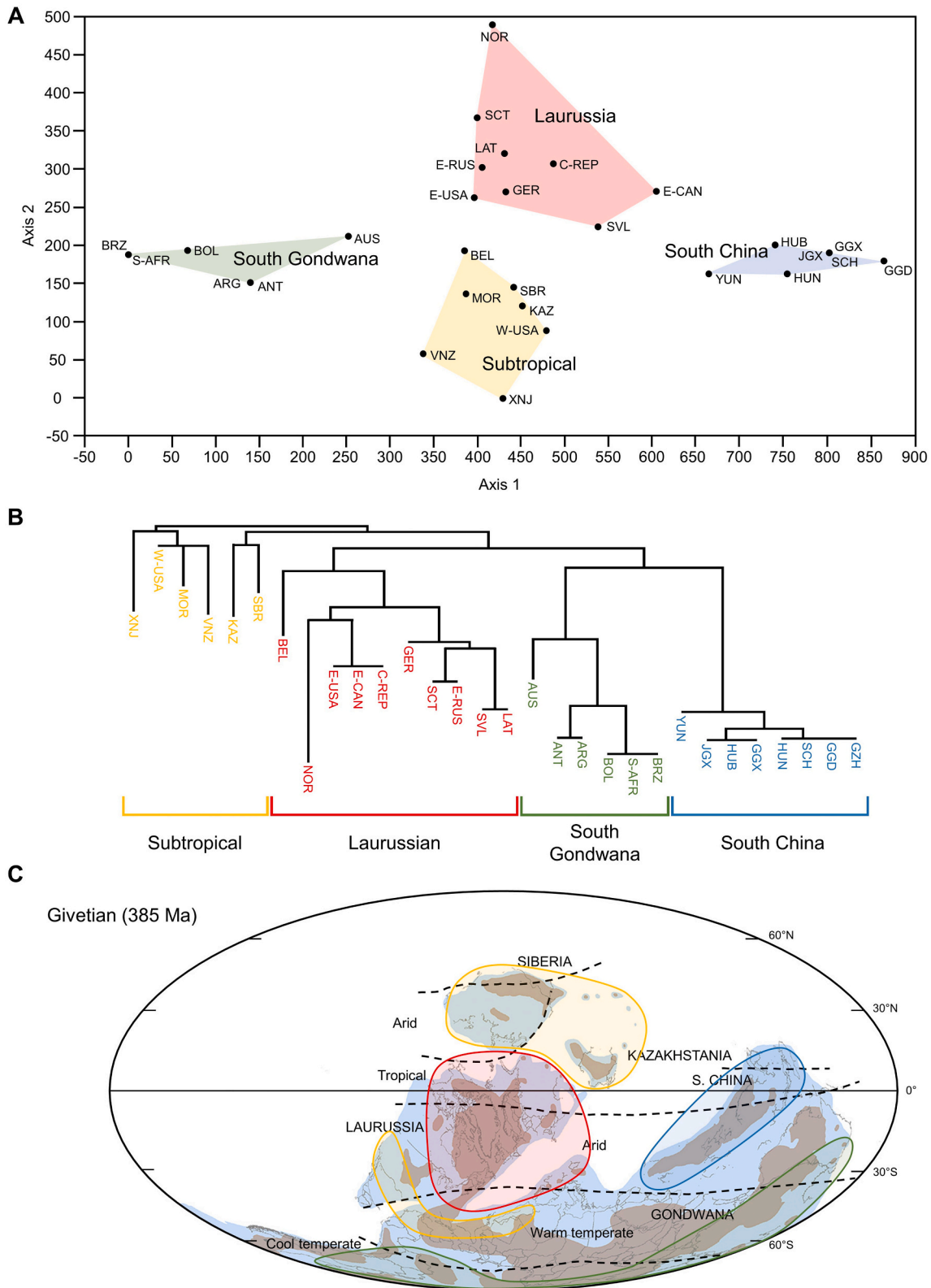
The Pragian–Emsian climate shows apparent marked fluctuations between colder and warmer conditions (Scotese et al., 2021). Nonetheless, palaeotemperature reconstructions from Joachimski et al. (2009) did not recover such important fluctuations, and show temperatures initially elevated in the early Pragian, 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 towards 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).

#### 4.2.3. Middle Devonian palaeophytogeography

The Middle Devonian period is characterized by the highest degree of differentiation of Devonian vegetation (Fig. 5A–B). NJ cluster analysis shows four distinct groups with South Chinese floras appearing highly differentiated from the rest of the assemblages (Fig. 5B). South Gondwanan floras also appear further distinct with longer branch lengths (Fig. 5B). A lesser degree of differentiation is found between the remaining two clusters but appear nonetheless distinct (Fig. 5B). The DCA (Fig. 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. 5B).

These four phytochoria are here referred as: (1) ‘Laurussia’; (2) ‘Subtropical’; (3) ‘South Gondwana’; (4) ‘South China’ and are termed according to their palaeogeographical extent in the Middle Devonian period (Fig. 5C). The Laurussian phytochorion is characterized by the predominance of *Svalbardia*, *Psilophyton* and *Rellimia* (Table 4) whilst the subtropical phytochorion is characterized by the presence of *Leclercqia*

### Middle Devonian



**Fig. 5.** Middle Devonian palaeophytogeography. (A) DCA scatter plot of geographical units; (B) NJ clustering analysis; (C) extent of each phytochoria transposed onto palaeogeographical maps (Scotese, 2021). Colors: red = Laurussia; green = South Gondwana; yellow = Subtropical; blue = South China. Climatic belts (dashed black lines) adapted from Boucot et al. (2013). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 4**

SIMPER results for the Middle Devonian period identifying taxa contributing the most to the observed differences between each phytochorion. 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
? <i>Lepidodendropsis</i>	8.73	9.13	9.13	0.00	0.00	0.00	0.88
<i>Haplostigma</i>	8.19	8.56	17.69	0.00	0.00	1.00	0.00
<i>Leclercqia</i>	7.15	7.48	25.17	0.30	1.00	0.17	0.13
<i>Minarodendron</i>	7.08	7.41	32.57	0.00	0.00	0.00	0.75
<i>Svalbardia</i>	6.19	6.48	39.05	0.70	0.17	0.00	0.00
<i>Psilophyton</i>	4.90	5.12	44.17	0.50	0.17	0.00	0.13
<i>Rellimia</i>	4.77	4.99	49.16	0.50	0.33	0.00	0.00
<i>Artschaliphyton</i>	4.57	4.78	53.94	0.10	0.67	0.33	0.00
<i>Barrandeina</i>	2.93	3.06	57.00	0.30	0.17	0.00	0.00
<i>Palaeostigma</i>	2.91	3.04	60.03	0.00	0.00	0.33	0.00
<i>Thursophyton</i>	2.76	2.88	62.91	0.40	0.00	0.00	0.00
<i>Aneurophyton</i>	2.47	2.58	65.49	0.20	0.50	0.00	0.00
<i>Malanzania</i>	2.34	2.45	67.94	0.00	0.00	0.33	0.00
<i>Pseudosporochnus</i>	2.23	2.33	70.27	0.30	0.17	0.00	0.00
<i>Flabelllofolium</i>	2.19	2.28	72.55	0.10	0.17	0.00	0.13
<i>Anapaulia</i>	1.93	2.02	74.57	0.00	0.33	0.00	0.00
<i>Barsassia</i>	1.86	1.95	76.52	0.00	0.50	0.00	0.00
<i>Serrulacaulis</i>	1.67	1.75	78.27	0.10	0.33	0.00	0.00
<i>Barinophyton</i>	1.41	1.48	79.74	0.20	0.00	0.00	0.00
<i>Lycopodites</i>	1.37	1.44	81.18	0.20	0.17	0.00	0.00

and is most commonly associated with *Artschaliphyton* (= *Haskinsia*) and *Aneurophyton* (Table 4). The South Gondwanan phytochorion corresponds to the occurrence of *Haplostigma* usually associated with *Palaeostigma* and *Malanzania*, these latter taxa all endemic to this phytochorion (Table 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 4).

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 characterized by the presence of *Svalbardia*. *Svalbardia* is sometimes 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; Stein et al., 2012). This habit seems to have initially developed among the pseudosporochnalean cladoxylsids and archaeopteridalean progymnosperms, the dominant elements of the flora found in this phytochorion (Berry and Fairon-Demaret, 2002; Stein et al., 2007, 2020; Meyer-Berthaud et al., 2010). Taxa such as *Psilophyton* and *Svalbardia* (if we consider it similar to *Archaeopteris*) have been interpreted as better adapted to more humid conditions (Wan et al., 2019), although Boucot et al. (2013) reconstructed the climate in most

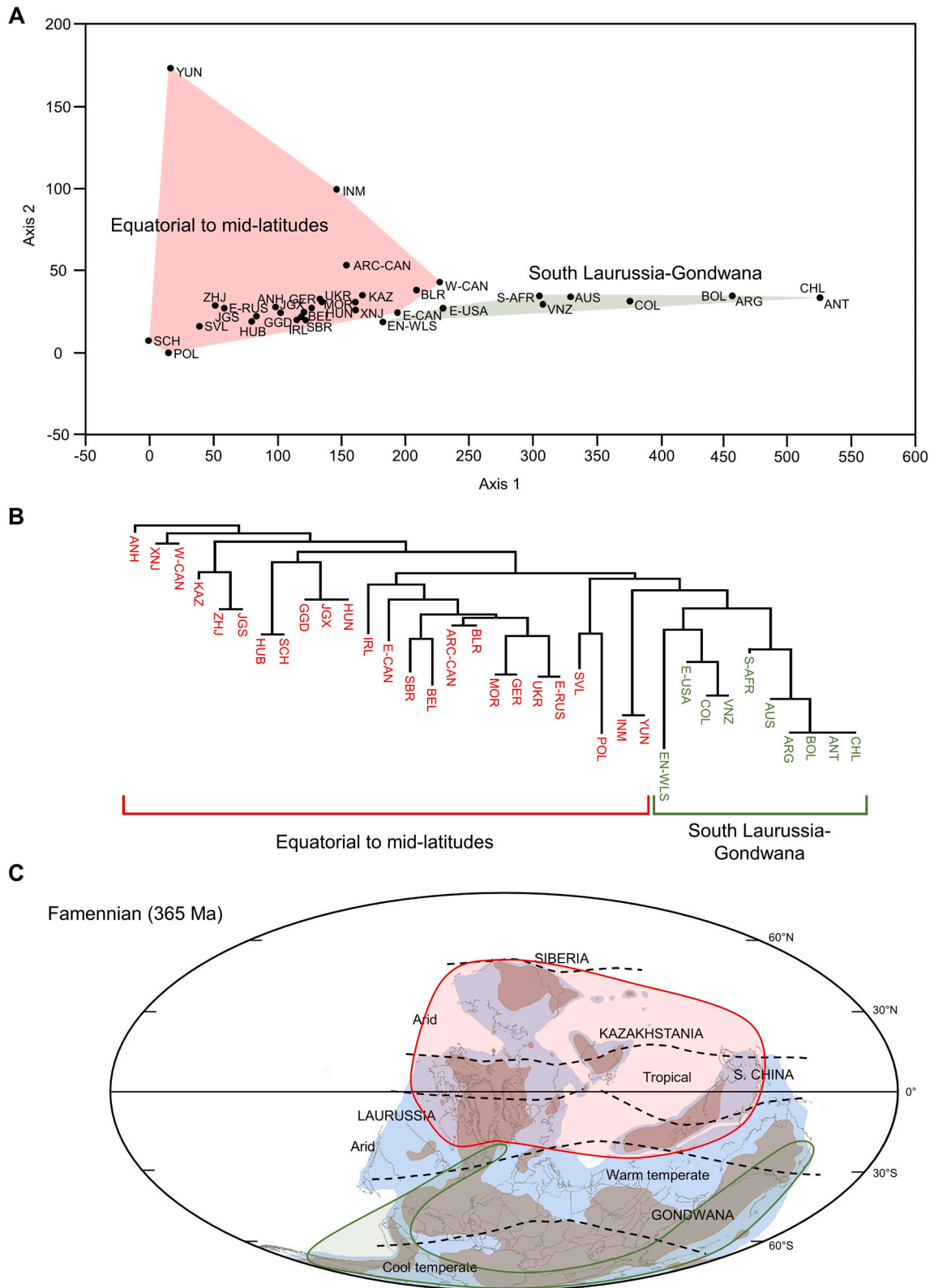
of this area as arid (Fig. 5C). Availability of water may have also been essential for sustaining increasing demand in water for the development of trees (Box, 1996). This phytochorion may therefore represent a vegetation adapted to a tropical-wet environment with occasional dry conditions.

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, carbon isotopic composition of *Leclercqia* and especially *Artschaliphyton* fossils has shown that these plants were 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 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 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 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. 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



### Late Devonian



**Fig. 6.** Late Devonian palaeophytogeography. (A) DCA scatter plot of geographical units; (B) NJ clustering analysis; (C) extent of each phytochoria transposed onto palaeogeographical maps (Scotese, 2021). Colors: red = Equatorial to mid-latitudes; green = South Laurussia-Gondwana. Climatic belts (dashed black lines) adapted from Boucot et al. (2013). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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 appear to have been utterly replaced by this low diversity herbaceous lycophytic flora (Fig. 2G).

The South Chinese phytochorion is totally distinct from other phytochoria with a high proportion of endemic taxa (Fig. 5A–B; Table 4, Data S1). The most biogeographically important taxon is ?*Lepidodendropsis* (Table 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 cladoxylpsid 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. 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 (Joaquimski 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, Matsumura 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.

#### 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. 6A). NJ cluster analysis likewise does not reveal any clearly defined associations but rather a gradual differentiation of vegetation between

geographical units (Fig. 6B). NJ cluster analysis nevertheless identifies a cluster including South Laurussian and Gondwanan assemblages, likewise retrieved in the DCA (Fig. 6A–B). 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 ( $R = 0.46$ ;  $p < 0.01$ ). 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. 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. 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., 2021). 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. 6A–C). The South Laurussia-Gondwana phytochorion similarly to the Middle Devonian South Gondwanan phytochorion is still characterized by the appearance of *Haplostigma* (Table 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 5). This phytochorion is also characterized by the presence of *Colpodexylon* and other taxa from the Middle Devonian South Gondwanan unit (e.g., *Malanzania*). On the other hand, the Equatorial to mid-latitudes phytochorion is represented by nearly all taxa used in the analysis (Table 5). The apparent merging of the South Gondwanan and the southern subtropical flora from the Middle Devonian is probably linked to the 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 5; Matsumura et al., 2015). For instance, late Famennian Gondwanan floras are far more diverse with cosmopolitan taxa such as *Archaeopteris*,

**Table 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
<i>Haplostigma</i>	9.37	10.36	10.36	0.00	0.60
<i>Archaeopteris/Callixylon</i>	8.71	9.63	19.99	0.76	0.40
<i>Leptophloeum</i>	5.95	6.58	26.56	0.44	0.30
<i>Lepidodendropsis</i>	5.38	5.95	32.51	0.44	0.00
<i>Colpodexylon</i>	4.81	5.32	37.83	0.00	0.40
<i>Flabellifolium</i>	4.17	4.61	42.45	0.24	0.30
<i>Sublepidodendron</i>	3.44	3.80	46.24	0.32	0.00
<i>Malanzania</i>	3.30	3.65	49.89	0.00	0.20
<i>Sphenophyllum</i>	2.63	2.91	52.80	0.32	0.00
<i>Barinophyton</i>	2.62	2.90	55.69	0.16	0.20
<i>Tetraxylopteris</i>	2.55	2.82	58.51	0.00	0.30
<i>Hamatophyton</i>	2.50	2.77	61.28	0.24	0.00
<i>Pseudosporogonites</i>	1.89	2.09	63.37	0.04	0.20
<i>Cyclostigma</i>	1.86	2.05	65.42	0.12	0.10
<i>Rhacophyton</i>	1.84	2.03	67.45	0.16	0.10
<i>Svalbardia</i>	1.78	1.97	69.42	0.12	0.10
<i>Archaeocalamites</i>	1.78	1.96	71.39	0.16	0.00
<i>Pietzschia</i>	1.77	1.96	73.34	0.12	0.00
<i>Leclercqia</i>	1.74	1.92	75.27	0.08	0.00
<i>Xenotheca</i>	1.68	1.86	77.12	0.00	0.20
<i>Eviostachya</i>	1.67	1.85	78.97	0.16	0.00
<i>Gilboaphyton</i>	1.61	1.78	80.75	0.04	0.10

*Leptophloeum*, and cladoxyloids, which were not recorded in the Middle Devonian and replaced the poorly diverse herbaceous lycopsid vegetation (Fig. 2G; Anderson et al., 1995; Prestianni and Gess, 2014; Meyer-Berthaud et al., 2021). 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. 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 and Metz (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 Streeel 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).

## 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 floras 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 *Pauthecopyton* 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) Laurussia; (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 cladoxyloids 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.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2023.111393>.

## Declaration of Competing Interest

The authors declare no conflicts of interest.

## Data availability

All data is available in the supplementary material files

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