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Palaeontology
The Palaeontological Association
www.palass.org

[Palaeontology, Vol. 66, Part 2, 2023, e12644]

RAPID COMMUNICATION

THE EFFECT OF GEOLOGICAL BIASES ON OUR PERCEPTION OF EARLY LAND PLANT RADIATION

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Typescript received 22 July 2022; accepted in revised form 14 December 2022

Abstract: The Silurian–Devonian plant radiation was a critical development in the evolution of early terrestrial ecosystems. Characterizing 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 biodiversification. 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 rank are significantly correlated with fluctuations of sedimentary rock volume, especially of non-marine fossiliferous deposits. The lack of terrestrial sedimentary deposits before the Emsian (Early Devonian) makes it difficult to obtain an accurate depiction of the pre-Emsian plant diversification in North America. However, complementary analyses reveal that sampling-standardized diversity patterns partially correct 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.

Key words: land plants, Silurian, Devonian, diversity, sampling-standardization, rock record.

THE 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 & Foote 2001; Smith & 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 for sampling (Raup 1976; Peters 2005; Smith 2007); (2) a third unaccounted element (e.g. sea-level), is synchronously driving both variables, frequently referred as the 'common-cause hypothesis' (Peters & Foote 2002; Peters 2005; Butler *et al.* 2011); and (3) sampling proxies and diversity are at least partially redundant, 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 2007; Smith *et al.* 2012), bias effects on the terrestrial record have 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. However, their analysis was based on a distorted and impoverished dataset of what today are referred to as fossil-species (Cleal & 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, and suggested that some changing

doi: 10.1111/pala.12644

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 the evaluation of 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 (*c.* 430–360 Ma) radiation of early land plants. Overall, this time interval is characterized 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 (Niklas *et al.* 1980; Edwards & Davies 1990; Raymond & Metz 1995; Cascales-Miñana 2016; Capel *et al.* 2021, 2022). 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, the pattern shown in the macrofossil record contrasts with those based on the microfossil record and calibrated molecular phylogenetic trees, both suggesting an earlier, and more important, pre-Silurian diversification (Wellman *et al.* 2013, 2022; Morris *et al.* 2018). The cause of this discrepancy remains disputed, with many potential factors having been invoked, such as taphonomic and/or sampling issues, and the dearth of preserved non-marine sediments (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 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 North American records, which offer the best available data for comparing reliable occurrence data with sampling proxies.

DATA AND METHOD

The raw data consist of 421 fossil occurrences of North American plant species, sampled from Ludfordian (upper Silurian) to Famennian (Upper Devonian) 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 S1). Occurrence data were filtered to avoid synonymies, 'artificial' fossil-taxa (*sensu* Cleal & 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, lithological 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 & 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 S2). From this, we calculated the rock volume and outcrop area per time interval (age/stage). Rock volume (polygon area × 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 S2), 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 S2) corresponding to the proportion of non-marine deposits in each case. Outcrop area was inferred from the sediment coverage area (Peters & 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 2010). An optimal quorum value of 0.5 was found using 1000 iterations to generate sampling-standardized 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 generalized-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 (v.3.5.2; R Core Team 2013) using the package epaleo (v.0.8.27; C. Monnet, University of Lille).

RESULTS

Both observed (Figs 1A, S1A) and sampling-standardized (Figs 1B, S1B) plant richness broadly mirror rock volume trend (Fig. 1C). 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. 1D). However, rock volume displays more variability between stages than outcrop area, being extremely limited before the Emsian and closely resembling the diversity pattern (Fig. 1C). Correlations between raw time series are all

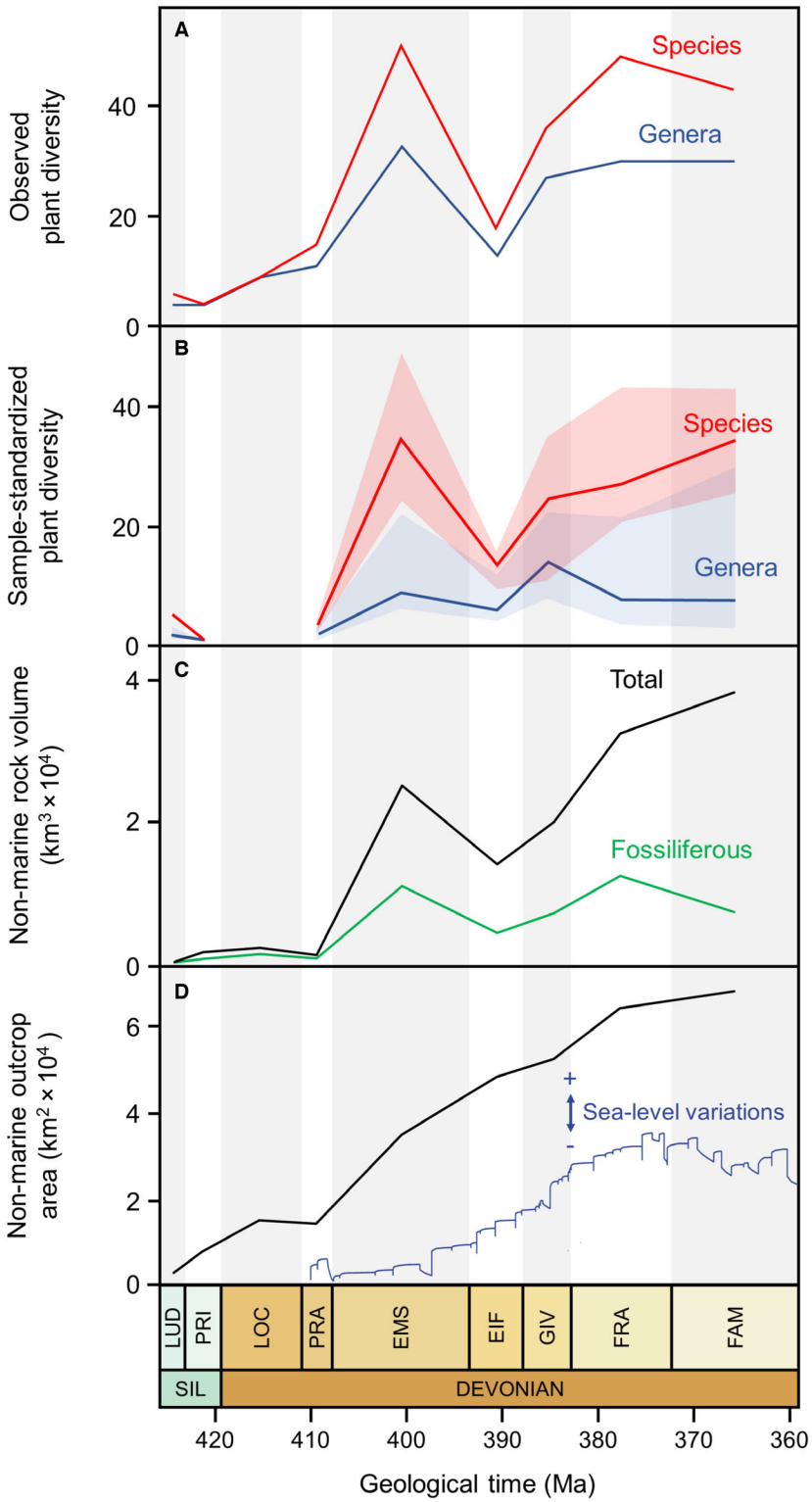

FIG. 1. Silurian–Devonian variations of plant diversity and geological proxies in North America. Diversity patterns based on observed (A) and sampling-standardized (B) values. Coloured shading represents 95% confidence interval (B). C, non-marine rock volume. D, non-marine outcrop area and sea-level fluctuations (extracted from Johnson *et al.* 1985). *Abbreviations*: EIF, Eifelian; EMS, Emsian; FAM, Famennian; FRA, Frasnian; GIV, Givetian; GOR, Gorstian; HOM, Homerian; LOC, Lochkovian; LUD, Ludfordian; PRA, Pragian; PRI, Pridoli; SIL, Silurian.

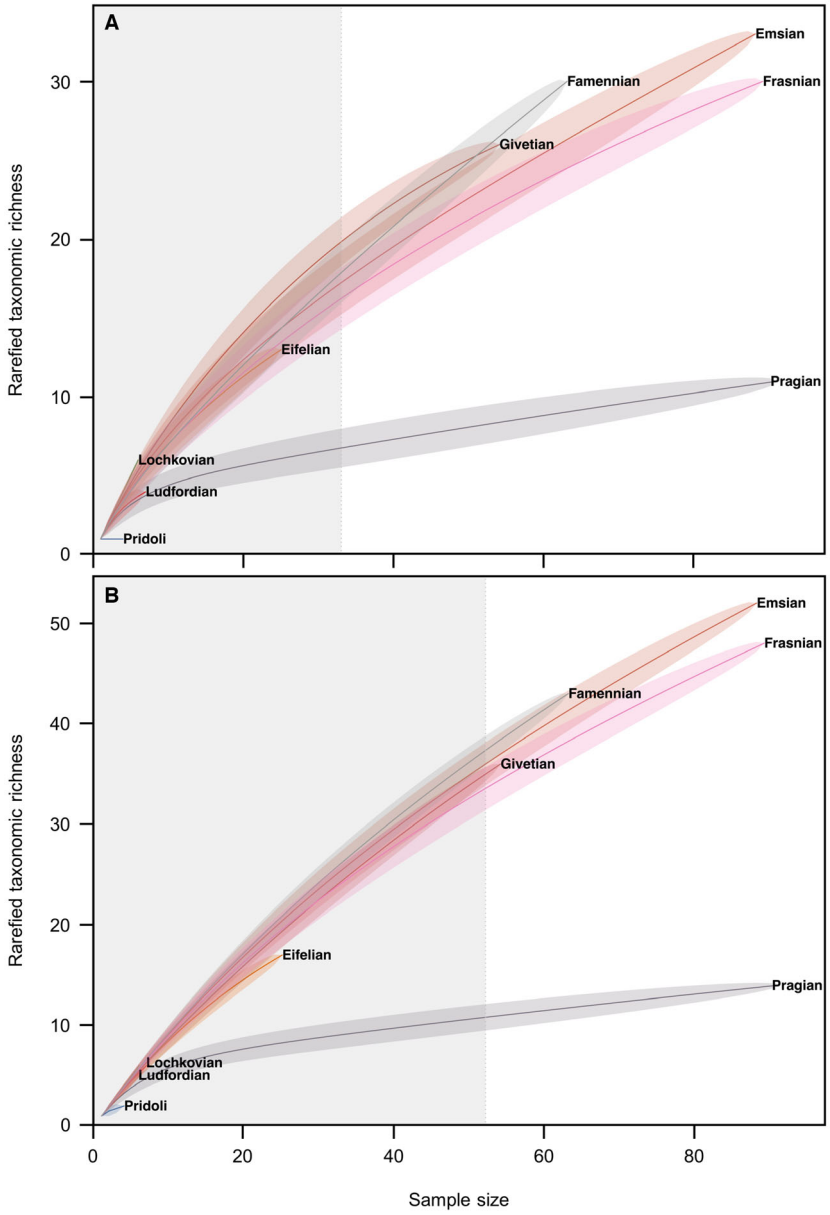

FIG. 2. Genus (A) and species (B) sized-based rarefaction curves per time interval. Coloured shading around each curve shows 95% confidence interval. Grey area represents rarefaction quota. See Data and Method for details.

strong as is often the case for long-term trends in such analyses (Table 1). However, detrended correlations (Table 1) identify only the number of localities and volume of fossiliferous deposits as significant predictors of both species and genera diversity over shorter timescales. Correlation analysis further demonstrates that standardized 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 1). Rarefaction curves (Fig. 2) 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. 1A–C). Complementary analysis based on non-marine records provided similar results, and likewise suggested generic diversity could be less influenced by sampling (Table S3; Fig. S2).

DISCUSSION

A selection of sampling proxies allegedly accounting for both sampling effort and heterogeneity of the rock record

TABLE 1. Correlation analysis between observed and sampling-standardized diversity and considered sampling proxies.

Sampling proxies	Observed diversity								Sampling-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***

Data analysis based on raw and generalized-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**.

were tested to identify biasing factors (Table 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 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.* 2014). This mechanism may arguably justify the absence of correlation once data are detrended (Table 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.* 2014; Table 1). Regardless, decoupling of the relationship between the variables is expected as sampling progresses and it becomes increasingly plausible that already described taxa will be found. Sampling of Devonian plants appears, at first glance, to not have been thoroughly completed (Fig. 2). One exception occurs in the Pragian (Fig. 2) but is uniquely linked to a monographic effect resulting from an exhaustive sampling of plants from the Bathurst Island marine deposits, Arctic Canada (Kotyk 1998; Table S1). Nonetheless, the observed pattern is mostly controlled by plant diversity recovered from non-marine deposits (Figs 1, S1). It may stem from the fact that plants preserved in terrestrial deposits have usually undergone less transport, and are therefore less fragmented and more likely to be identified. However Wall *et al.* (2011) suggested that the original pool of preserved terrestrial biodiversity is so restricted that any new locality discovery still leads to the description of a significant number of new taxa, even when sampling is adequate. Since North America is historically a well-sampled continent for Devonian plants, 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 (Figs 2, S2). 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 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 & 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 epeiric seas during this period (Scotese 2021), making spatial heterogeneity in sampling a non-preponderant factor to explain diversity changes.

Eustatic variation 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. 1D). 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 S1); and (2) impact of endemism 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 & 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 1). Figure 2 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-standardized species diversity remains significantly correlated with this proxy (Table 1). Higher-level taxa with longer longevities may also diminish the effect of short-term variation of the rock record (Smith 2007). Another possibility is that increased preserved rock quantity leads to larger numbers of fragmentary fossils, in turn artificially inflating species count by palaeontologists naming new species based on fragments that cannot be synonymized 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-standardized patterns (Fig. 1B) 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 1). In fact, this pervasive bias remains since 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. 1D). 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. 1B, E), even though global patterns suggest a massive diversification (Capel *et al.* 2022). While a lack of terrestrial deposits can partly explain the scarcity of plant macrofossils (Fig. 1D; Table 1), this factor cannot solely explain this 40 myr gap. Preservation of allochthonous assemblages in marine sediments remains possible and is relatively common (Table S1). This is exemplified by 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 of the total absence of plant fossils (other than putative fragments) during this period (Gensel 2008).

CONCLUSION

Our results overall reveal that when sampling is extensive, observed patterns of early plant diversity still partly reflect the heterogeneity of the rock record, which 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 can coverage-based rarefaction 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.

Acknowledgements. The authors thank Dr Mihai Tomescu (Humboldt State University) and Dr Kelly Matsunaga (University of Kansas) for clarifications on several North American Devonian floras. Authors also thank two anonymous reviewers for helpful suggestions and comments on the manuscript. Research funded by EARTHGREEN project (ANR-20-CE01-0002-01). This is Paleobiology Database official publication number 446.

Author contributions. **Conceptualization** E. Capel (EC), C. Monnet (CM), B. Cascales-Miñana (BC-M); **Data Curation** EC; **Formal Analysis** CM; **Funding Acquisition** T. Servais (TS), BC-M; **Methodology** EC, CM, BC-M; **Writing – Original Draft** EC; **Writing – Review & Editing** EC, CM, C.J. Cleal, J. Xue, TS, BC-M.

Editor. Benjamin Bomfleur

SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.12644):

Appendix S1. Includes Figures S1, S2, and references cited in Table S1.

Figure S1. Observed and sampling-standardized variations of the Silurian–Devonian plant diversity in North America. Diversity data based on non-marine records only.

Figure S2. Genus and species sized-based rarefaction curves per time interval. Diversity data based on non-marine records only.

Table S1. North American Silurian–Devonian plant fossil occurrences considered in this study.

Table S2. North American Silurian–Devonian lithostratigraphic units considered in this study.

Table S3. Correlation analysis between observed and sampling-standardized diversity and considered sampling proxies.

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