University of Birmingham
Research at Birmingham

Palaeobotanical experiences of plant diversity in deep time. 1:

Cleal, Christopher; Pardoe, Heather; Berry, Christopher; Cascales-Miñana, Borja; Davis, Basil; Diez, Jose; Martina, Filipova-Marinova; Hiesecke, Thomas; Hilton, Jason; Ivanov, Dimiter; Susanne, Leroy; MacElwain, Jennifer; Opluštil, Stanislav; Popa, Mihai; Seyfullah, Leyla; Stolle, Ellen ; Thomas, Barry ; Uhl, Dieter

DOI:
10.1016/j.palaeo.2021.110481

License:
Creative Commons: Attribution-NonCommercial-NoDerivs (CC BY-NC-ND)

Document Version
Peer reviewed version

Citation for published version (Harvard):
Cleal, C, Pardoe, H, Berry, C, Cascales-Miñana, B, Davis, B, Diez, J, Martina, F-M, Hiesecke, T, Hilton, J, Ivanov, D, Susanne, L, MacElwain, J, Opluštil, S, Popa, M, Seyfullah, L, Stolle, E, Thomas, B & Uhl, D 2021, 'Palaeobotanical experiences of plant diversity in deep time. 1: How well can we identify past plant diversity in the fossil record?', *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 576, 110481. https://doi.org/10.1016/j.palaeo.2021.110481

Link to publication on Research at Birmingham portal

General rights
Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

•Users may freely distribute the URL that is used to identify this publication.
•Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
•User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
•Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy
While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

Download date: 19. Apr. 2024

Palaeobotanical experiences of plant diversity in deep time. 1: How well can we identify past plant diversity in the fossil record?

Christopher J. Cleal[a§], Heather S. Pardoe[a], Christopher M. Berry[b], Borja Cascales-Miñana[c], Basil A.S. Davis[d], Jose B. Diez[e], Mariana V. Filipova-Marinova[f], Thomas Giesecke[g], Jason Hilton[h], Dimiter Ivanov[i], Evelyn Kustatscher[j], Suzanne A. G. Leroy[k], Jennifer C. McElwain[l], Stanislav Opluštil[m], Mihai Emilian Popa[n], Leyla J. Seyfullah[o], Ellen Stolle[p], Barry A. Thomas[q] and Dieter Uhl[r]

[a] Department of Natural Sciences, National Museum Wales, Cardiff CF10 3NP, UK, chris.cleal@museumwales.ac.uk, heather.pardoe@museumwales.ac.uk
[b] School of Earth and Ocean Sciences, Cardiff University, Cardiff CF10 3AT, UK, berrycm@cardiff.ac.uk
[c] CNRS, Univ. Lille, UMR 8198, Evo-Eco-Paleo, F-59000, Lille, France, borja.cascales-minana@univ-lille.fr
[d] Institute of Earth Surface Dynamics IDYST, University of Lausanne, Bâtiment Géopolis CH-1015, Lausanne, Switzerland, basil.davis@unil.ch
[e] Department of Marine Geosciences and Land Management, Universidade de Vigo, 36310 Vigo, Spain, jbdiez@uvigo.es
[f] Varna Regional Museum of History, 41 Maria Louisa Boulevard, 9000 Varna, Bulgaria
[g] Palaeoecology, Department of Physical Geography, University of Utrecht, P.O. Box 80115, 3508 TC, Utrecht, The Netherlands, t.giesecke@uu.nl
[h] School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, B15 2TT, UK, j.m.hilton@bham.ac.uk

[i] Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Acad. G. Bonchev Street, 23, 1113 Sofia, Bulgaria, dimiter@gbg.bg

[j] Museum of Nature South Tyrol, Bindergasse/Via Bottai 1, Bozen / Bolzano, 39100, Italy, evelyn.kustatscher@naturmuseum.it

[k] Aix Marseille Univ, CNRS, Minist Culture, LAMPEA, UMR 7269, 5 rue du Château de l'Horloge, 13094, Aix-en-Provence, France, leroy@mmsh.univ-aix.fr; School of Environmental Sciences, University of Liverpool, L69 3GP Liverpool, UK

[l] School of Biology and Environmental Science, University College Dublin, Ireland, jennifer.mcelwain@gmail.com

[m] Institute of Geology and Palaeontology, Charles University, Albertov 6, 128 43 Prague 2, Czech Republic, stanislav.oplustil@natur.cuni.cz

[n] Southwest Petroleum University, School of Geosciences and Technology, 8, Xindu Ave., 610500 Xindu, Chengdu, China; University of Bucharest, Faculty of Geology and Geophysics, Department of Geology and Doctoral School of Geology, Laboratory of Palaeontology, 1, N. Bălcescu Ave., 010041, Bucharest, Romania, mihai@mepopa.com

[o] Department of Palaeontology, University of Vienna, Althanstraße 14, 1090 Vienna, Austria, leyla.seyfullah@univie.ac.at

[p] *EP Research, 59320 Ennigerloh-Westkirchen, Germany, e.stolle.research@mail.de

[q] Institute of Biological, Environmental and Rural Sciences, University of Aberystwyth, Aberystwyth SY23 1NL, UK, bat@aber.ac.uk

[r] Senckenberg Forschungsinstitut und Naturmuseum, 60325 Frankfurt am Main, Germany, dieter.uhl@senckenberg.de

[§] Corresponding author

Abstract

Palaeobotany and palynology are the main direct sources of evidence for studying vegetation diversity dynamics through geological time. However, plant fossil diversity is affected by various factors other than vegetation diversity, which need to be taken into account in such studies. The use of fossil-taxa will potentially inflate perceived plant diversities, requiring taxonomic lists to be normalised. Autochthonous floras provide the most direct evidence of vegetation diversity but these are rare; most plant beds are allochthonous with plant remains that have been subjected to varying levels of fragmentation, transportation and time averaging. Local-scale vegetation diversity is especially difficult to determine from the fossil record, even with rigorous sampling protocols and detailed sedimentological analysis. Landscape-scale and regional-scale vegetation diversities are more reliably determined but usually at the rank of family. Macrofossil and palynological data tend to reveal evidence of different aspects of plant diversity, and the best results are obtained if the two diversity signals are integrated. Despite the inherent difficulties, the plant fossil record provides clear evidence of the dynamic history of vegetation through geological times, including the effects of major processes such as climate changes and mass extinctions.

Keywords: Palaeobotany, Palynology, Biodiversity, Taxonomy, Taphonomy, Vegetation

1 Introduction

Vegetation has played a central role in the evolution of the Earth's biosphere, atmosphere and landscape (Beerling 2007; Davies and Gibling 2010; Wellman 2010; Willis and McElwain 2013); whilst it is possible to envisage a world having evolved with plants but no animals, a world of animals without plants could not function. The raised public awareness of the important ecosystem services provided by vegetation, including carbon capture to help mitigate climate change, providing the foundations of all terrestrial trophic systems, and the psychological benefits it brings to mankind, has resulted in a global research programme on today's plant diversity and ecology (Antonelli et al. 2020). However, this only provides a snapshot of a continuous ecological and evolutionary play that has taken place through some 500 million years of "Deep Time". To appreciate properly the significance of events such as the current biodiversity crisis ("the 6th mass extinction") and to anticipate potential outcomes, it is vital that we understand this history of vegetation evolution.

Research into vegetation history started over two centuries ago (for summary see Andrews 1980) but with the primary focus on plant phylogeny (Taylor et al. 2009; Cleal and Thomas 2019). In recent years, interest in the study of plant fossil diversity has grown (as summarised by Wing and DiMichele 1992; Willis and McElwain 2013) but investigating it remains challenging (Wing and DiMichele 1995).

This is one of two papers arising from a workshop on past plant diversity entitled *Tracking changes in plant diversity over the last 400 million years*, which brought together specialists on diversity studies in fossil floras ranging in age from Devonian to Quaternary . The aim was to explore the different analytical methodologies and interpretative approaches used to investigate Phanerozoic plant diversity dynamics. The present contribution addresses what exactly we mean by biodiversity and to what extent can we extract biodiversity patterns from the plant fossil record. We will attempt to look at the relevant issues surrounding both plant macrofossils (i.e. fossils that can normally be seen with the naked eye, including compressions / impressions / adpressions, casts / moulds and anatomically preserved fossils – see Cleal and Thomas 2019) and microfossils (pollen, spores and phytoliths). The issues surrounding sampling and analytical methods used will be discussed in our second paper (in preparation).

2 What is biodiversity?

In biology, biodiversity is sometimes used to refer to functional diversity (the range of traits in an assemblage) or phylogenetic diversity (the evolutionary breadth of an assemblage) (Dornelas et al. 2012; Vellend et al. 2011, 2017). Palaeobotanists also sometimes investigate trait diversity, such as the use of leaf physiognomy for estimating past climatic temperatures (Wolfe 1993; Glasspool et al 2004). But diversity analyses of the plant fossil record tend to be overwhelmingly of taxonomic diversity, and it is on this that we will focus here.

Taxonomic diversity in ecological studies consists of two factors: taxonomic richness and taxonomic evenness (Tuomisto 2012). Taxonomic richness (the number of taxa present) might be expected to be relatively easy to measure in both modern-day habitats and the fossil record; Magurran (2004) has suggested that this alone can be a sensitive indicator of ecological change. However, total richness can be difficult to determine if there are rare species present, as these may be missed in surveys. A far more nuanced understanding of the functioning of a flora will be obtained by determining its taxonomic evenness using measurements such as Simpson's Index (e.g. Lande 1996; Veech et al. 2002) but this is only really meaningful if it is reflecting the relative numbers of the organisms present. Variations in the productivity of pollen, foliage and seeds between different plant parts (Fig. 1) mean that taxonomic evenness of fossil-taxa in a fossil flora will bear little or no relationship to the taxonomic evenness of the original vegetation. The situation is particularly complex with foliage, especially in pre-Cenozoic floras where the leaves are often compound structures that fragmented in different ways during abscission, transportation and preservation. Taxonomic evenness of a fossil flora may therefore be strongly influenced by taphonomy and how the plants fragmented post-mortem; although such data may provide some evidence as to relative biomass allocation within the vegetation (e.g. Baker and DiMichele 1997), its value for determining taxonomic evenness is limited.

Scale will clearly be critical in any diversity study, whether palaeontological or biological (Bennington et al. 2009). R.H. Whittaker (1960) developed the most frequently used concepts of taxonomic diversity for extant biotas, broadly recognised as α-diversity (diversity in particular habitats) and β-diversity (diversity between habitats within a landscape); these were then integrated to provide a γ-diversity (overall diversity within the landscape). R.H. Whittaker (1977) later extended this scheme to include δ-diversity (diversity between landscapes in a biogeographical province) and ε-diversity (overall diversity within that province). However, R.H. Whittaker's (1960) terms were intentionally rather vague and as a consequence have been used by different scientists in different ways (see Swingland 2001; Magurran 2004; Hamilton 2005 for reviews).

In an attempt to introduce taxonomic diversity concepts that more realistically reflect the plant fossil record, Cleal et al. (2012) adopted a more flexible approach similar to those used by R.J. Whittaker et al. (2001); see also Birks et al. (2016a,b) (Fig. 2):

(1) Local-scale diversity: the diversity of plant fossils observed in a single locality and which probably reflects plant diversity within c. 1000 m^2 (c. 30 m x 30 m). In a palynological context, it might more realistically refer to vegetation within up to 1 km^2. This will broadly equate to the α-diversity of the parent vegetation.

(2) Landscape-scale diversity: the diversity of plant fossils observed within a typical depositional basin and which probably reflects plant diversity within up to c. 10^5 km^2 (c. 300 km x 300 km) This will broadly equate to the γ-diversity of the parent vegetation.

(3) Regional-scale diversity: the diversity of plant fossils observed within a palaeofloristic province and probably reflects plant diversity within more than 10^5 km^2. This will broadly equate to the ε-diversity of the parent vegetation.

It is important to remember that the diversities observed in the fossil record (both macrofloral and palynological) represent the diversities of the fossils, and only partially reflect the diversities of the parent vegetation (Gastaldo 1992; Birks et al. 2016). Some of the resulting issues will be discussed later in this paper (Section 4).

3 Taxonomic problems

3.1 Macrofossil taxonomy

The concept of biodiversity is inevitably tied to taxonomy (Khuroo et al. 2007). In neobotany this is relatively straightforward as the taxonomy is based on whole-organism taxa in which their lifecycles and development can be observed. There will always be disagreements among botanists as to whether a particular genus of plants contains one or more species, or a group of species belong to one or more genera, but at least botanists have whole organisms against which to test their taxonomies.

With Cenozoic macrofloras (including Quaternary) it is often still possible to work with whole-plant taxa (e.g. Huang et al. 2016) but the situation is more difficult with older floras where palaeobotanists are dealing with extinct groups. Only rarely are completely reconstructed organisms available to work with; even if a whole, articulated plant is preserved (e.g. the early seed plant *Elkinsia* – Fig. 3) anatomical details are never completely preserved. Palaeobotanists working on these stratigraphically older floras therefore use a different taxonomic approach. Although this has changed in detail over the years (Cleal and Thomas 2010), the underlying principle has in effect remained the same since the time of Sternberg (1820) and Brongniart (1822): different parts of the plant are classified and named separately as fossil-taxa (Turland et al. 2018, Art. 1.2). Mostly these are fossil-species and fossil-genera, although in principle they can be of any rank (see Cleal and Shute 2012 for an example of using fossil-families).

Exactly how a fossil-taxon is defined is a subjective matter and is not covered by the regulations in the *International Code of Nomenclature* (Turland et al. 2018), but this is no different from neobotany. Because of the constraints of the fossil record (e.g. the inability to test hypotheses relating to reproductive isolation or molecular phylogenetics) fossil-taxa have to be defined purely on morphological and/or anatomical criteria. Bateman and Hilton (2009, p. 1256) recommended that each fossil-taxon "…must consistently possess at least one morphological feature that it shares with no other [taxon]" (their autapospecies concept) and should not take into account geographical or stratigraphical criteria. Whether this latter point is always supportable is perhaps a moot point: for instance, is it helpful to place leaves of Permian gigantopterids and of Cenozoic angiosperms in the same fossil-genus simply because they have the same, diagnostic characters (Fig. 3)? However, since most diversity studies at the rank of species or genus tend not to be making comparisons over such long time-scales, this is probably not a significant problem here.

The problem with using fossil-taxa for diversity studies is that a simple summation of the names listed in published taxonomic lists will both significantly overestimate the number of biological species represented, and distort the relative representation of the different plant groups present (Cleal et al. 2012). For instance, in Carboniferous arborescent lycopsids, a single biological species may be represented by up to six separate compression fossil-species, whereas sphenopsids in the same flora may only have four fossil-species (Fig. 4; Table 1). An added complication is that the fossil-taxa of the different plant parts are probably indicative of different taxonomic ranks of the original organism: for instance, *Stigmaria ficoides* (Sternberg) Brongniart is a fossil-species of phylogenetically conservative lycopsid rootstock that effectively cannot be distinguished across many members of the order, whereas the stems and cones have more sophisticated combinations of derived evolutionary characters and so their fossil-species probably correlate better with the biological species of the organisms.

One solution would be only to study whole reconstructed plants (DiMichele and Gastaldo 2008). This is feasible when dealing with higher-ranked taxa such as families (e.g. Anderson et al. 2007) but at the present time there are too few reconstructions to provide meaningful diversity data at the rank of species or genus. A solution is to normalise the dataset by identifying, for each plant group, the plant part whose fossil-taxonomy is most likely to reflect the original, whole-organism taxonomy (e.g. Hilton and Cleal 2007; Cleal et al. 2012). For instance, the study of the late Carboniferous tropical swamps focussed mainly on foliage taxa, except with the arborescent lycophytes for which the outer periderm layer ("bark") of their trunks was used (Table 1; Cleal 2005, 2007, 2008a). Leaf morphotypes have also been successfully used in this way with Cretaceous and Palaeogene angiosperms (e.g. Johnson 2002). Although these vegetative fossil-taxa may not provide the best evidence of phylogenetic relationships (reproductive structures would probably be better for this – e.g. Meyen 1984), they are probably providing a robust reflection of the plant species diversity (Cleal et al. 2012). This will inevitably be imperfect; for instance, cuticle studies of Carboniferous *Cordaites* and *Selaginella* foliage have shown that diversities will be significantly underestimated if the identifications are based purely on morphological data (e.g. Thomas 2005; Šimůnek 2007). There is no easy solution to this issue and simply has to be accepted in such diversity studies.

The situation is further complicated in that the same plant preserved in different ways (e.g. petrifactions and compressions) will be recorded as different fossil-taxa (Galtier 1986; Bateman and DiMichele 1992; Bateman et al. 1992; Bateman and Hilton 2009; Thomas and Cleal 2020). It is critical, therefore, to ensure that assessments of diversity do not duplicate fossil-taxa in the same assemblage or locality that are preserved in different ways; for instance, if an assemblage should include lycopsid cones as both compressions and permineralisations, the taxonomic list should be normalized so that diversity is not artificially inflated by "double counting".

3.2 Palynotaxa

Palynological studies on Quaternary floras tend to use whole-plant taxa, based on morphological comparisons with pollen that have been extracted from living plants. It is sometimes possible to distinguish pollen from closely related plant species based purely on morphology but often palynological studies tend to focus mainly on differentiating plants at the generic rank. Attempts have been made to use DNA barcoding to improve the taxonomic resolution in Quaternary studies (e.g. Seppä and Bennett 2003); for instance, Petit et al. (2002) demonstrated that the modern genetic diversity of oak is consistent with the pollen evidence in a study of post-glacial oak migration. However, most Quaternary palynological studies remain essentially morphology-based.

With older floras, the known relationship between the pollen / spores and their parent plants is less certain and so palynologists have developed separate taxonomic schemes (Chaloner 1999). Some proposed taxonomies are completely artificial with the taxa defined purely on morphological criteria with a non-Linnaean nomenclature, such as used in many oil-company palynological databases and in the Biorecords methodology of Hughes (1963) (see Traverse, 2007 for a review). Other taxonomies use a Linnaean-style nomenclature but with taxa that were still essentially morphological (e.g. Potonié 1956, 1958, 1960) and it is this approach which is most usually widely used today in pre-Neogene studies (e.g. Jasper et al. 2010; Stolle 2007, 2012, 2016; Hochuli et al. 2016).

Because the botanical affinities of many pre-Neogene palynotaxa are uncertain, it can be difficult to translate observed palynodiversity trends into floristic trends. Thomas (1987) and Mander and Punyasena (2014) suggested that the situation could be improved by revising the diagnoses of palynotaxa based on evidence from in situ palynomorphs in fructifications, data which is now being increasingly collated (e.g. Balme 1995; Bek 2017). Experience with Palaeogene and Neogene pollen and spores has also shown that a combination of light microscopy and scanning electron microscopy based on individual grains (Ferguson et al. 2007), although very time consuming, can help to improve their assignment to a particular plant genus or family, or perhaps even to map it into an established framework represented by one or more phylogenetic trees. (e.g. Grímsson et al. 2011a,b, 2015a,b). Chemical analysis such as using FTIR (Fourier Transform Intra-Red) and fluorescence spectroscopy can also be helpful in determining affinities of particular palynormophs (e.g. Mitsumoto et al. 2009; Steemans et al. 2010; Urban et al. 2010). This approach has shown that more traditional approaches utilizing only light microscopy tend to underestimate the number of taxa present in a palynoflora (Hofmann and Gregor 2018).

An added complication is the variation in morphology of pollen and spores during maturation, as shown for instance in the fern *Weichselia reticulata* (Stokes and Webb) Fontaine (Fig. 5). This is not an issue in most diversity studies on dispersed palynofloras, as plants do not normally release their pollen or spores before they are fully mature. However, if a plant has been subjected to trauma such as a storm, immature pollen and spores may be prematurely released and preserved, and this could inflate the diversity of a palynofloras. Although labour intensive, it is possible to determine whether different morphologies represent different states of maturity or just variability of miospore forms within a species using sporoderm ultrastructure analysis (e.g. Zavialova et al. 2010).

Because of the problems of classifying stratigraphically older palynotaxa a number of purely morphological suprageneric classifications have been developed (see Traverse 2007 for a review). Especially in Palaeozoic palynofloras, a nested hierarchy of morphological groups (anteturma, turma, subturma, etc.) developed by Potonié (1934) is still widely used, and provides a useful framework for descriptive studies. However, as these groups are strictly morphological, they rarely relate to botanical suprageneric groups and so are of limited use in diversity studies.

3.3 Taxonomic rank

Because of the problem of relating pollen and spores to particular plant species, using palynology for species diversity studies can be difficult (Mander and Punyasena 2014); even in the Quaternary where the relationship between pollen and parent plants is better-known, most palynological diversity studies tend to be at the rank of genus or even family (Giesecke et al. 2014). Such studies have nevertheless provided valuable evidence of vegetation dynamics especially at the landscape-scale (Section 5.2).

Local- and landscape-scale plant macrofossil diversity studies tend to be based on normalised inventories of fossil-species or possibly fossil-genera (Section 3.1). However, species are currently impractical when dealing with diversity changes at regional- or global-scales, and over longer time-scales, as the datasets become too large to collate and check objectively by any individual scientist or team. Even where a large amount of species data has been historically accumulated, such as for the Pennsylvanian Subsystem (see comments by Pfefferkorn et al. 2017), there have been few attempts to collate them coherently and critically. Where such collations have been attempted (e.g. Niklas et al. 1980; Lidgard and Crane 1990), methodological and sampling issues occurred (see comments by Niklas and

Tiffney 2010; Cascales-Miñana et al. 2013). Moreover, these early collations were not published and so cannot be subjected to subsequent critical taxonomic re-assessment, making the robustness of the resulting analyses difficult to judge.

The situation may potentially improve with the development of large-scale computer databases of fossil occurrences, such as those for Cenozoic angiosperms (Xing et al. 2016; Williams et al. 2018). Palaeobotanical data have also been included in the Paleobiology Database (Alroy 2003) although its coverage for plant fossils remains uneven, and is far below that in other groups such as fossil vertebrates. Various numerical approaches have been investigated that aim to overcome the issues of incomplete sampling of such databases (e.g. Silvestro et al. 2015; Beri et al. 2020) but the intractable problem remains of verifying the taxonomic robustness of the data; if the data cannot be trusted, how can the results of any analysis? This is an area where palaeobotany needs to improve in order to catch up with other fossil groups and make sustained impact in analytical methodologies.

In the absence of usable databases, the solution adopted in many regional- and global-scale macrofloral diversity studies is to analyse changes at the rank of family. Family is the lowest rank of fossil-taxa based almost exclusively on whole organisms and so potentially the dynamics of the fossil-families should be comparable with those of the original parent families. A number of global collations of plant fossil-family distributions through geological time are available (e.g. Harland 1967; Benton 1993; Collinson 1996; Anderson et al. 2007) and they include the evidence on which the records were based and so can be subjected to later critical assessment and potential revision (Cascales-Miñana and Cleal 2014).

But how closely do family dynamics mirror diversity dynamics at lower taxonomic ranks? Analyses on modern-day tropical forests suggest that family and species diversity patterns are broadly similar (e.g. Enquist et al. 2002; Jantz et al. 2014) especially if the data are log transformed to reduce the effect of dominant families (La Torre et al. 2007); see also comments by Giesecke et al. (2019) and Reitalu et al. (2019) on Holocene data from Europe. However, this does not take into account the taphonomic filter that fossil floras have been subjected to; many Palaeozoic and Mesozoic plant fossils cannot be assigned to families due to missing, or difficult to deduce, features of reproductive organs or cauline anatomy, suggesting the fossil record of families is incomplete. On the other hand, regional- and global-scale vegetation analyses (e.g. Cascales-Minana et al. 2013) may benefit from using family data because they may help smooth out some of the sampling problems encountered in such large-scale analyses. This is clearly a subject that needs further investigation.

4 Representativeness of data

There have been many studies looking at the effects of representativeness on diversity studies in the macrofossil record, such as the effects of sampling and taphonomy, but mainly dealing with faunas, notably marine invertebrates (e.g. Kowalewski et al. 2006). However, the issues surrounding such faunal studies are fundamentally different from those facing palaeobotanists and palynologists, as most palaeozoologists have the luxury of dealing with the remains of whole organisms (or at least their hard-parts, such as shells or exoskeletons); even vertebrate palaeozoologists tend to deal with whole-organism taxa. Palaeobotanists and palynologists, in contrast, deal almost exclusively with allochthonous and fragmentary remains; there are exceptions, as we will discuss, but these tend to be rare and scattered, and difficult to use in diversity studies. This means that diversity studies on the plant fossil record are addressing quite different questions to those being usually asked by palaeozoologists: palaeobotanists and palynologists tend to be looking at broad composition of vegetation either in terms of taxa or biomass rather than looking at changing community structure in terms of individual organisms (e.g. Bambach 1977).

4.1 Macrofloral data

Autochthonous floras (sometimes misleadingly referred to as “Lagerstätten”) provide the most reliable data on original plant diversity, especially at a local-scale, but these are rare. One of the best documented is the Devonian Rhynie Chert (e.g. Edwards et al. 2018; Garwood et al. 2019; Strullu-Derrien et al. 2019) where an in situ and almost complete terrestrial biota is preserved including relatively small, herbaceous plants. Autochthonous fossil floras with larger, woody plants are much rarer. There are exceptions, such as the Palaeozoic swamp forests that were rapidly covered by volcanic ash (Sections 5.1, 5.2); but more usually, the so-called T^0 fossil or submerged forests (DiMichele and Falcon-Lang 2011) are only partly autochthonous. They form where an area of forests has been engulfed by a flood of sediment and casts of the stumps have been preserved in situ (e.g. Fig. 6; for other examples see Heyworth and Kidson 1982; Francis 1983; Gastaldo 1985; Pole 2001; Calder et al. 2006; Wagner and Diez 2007; Moir et al. 2010; Stein et al. 2012; Berry and Marshall 2015; Thomas and Seyfullah 2015; Falcon-Lang et al. 2016), but most of the herbaceous ground-cover and liana species have been winnowed-out (Thomas 2014). Other types of “fossil forests” consist of petrified logs preserved as log-jams that have been subject to varying degrees of transportation (e.g. Falcon-Lang and Bashforth 2005) and thus also difficult to use for diversity studies.

More typically, plant beds occur in fluvio-lacustrine deposits, where disarticulated plant remains have accumulated after varying degrees of transportation either by wind or water (Burnham 1989; Gastaldo et al. 1995, Kędzior and Popa 2013, 2018; Thomas and Cleal 2015). This is in marked contrast to many fossil faunal communities, which tend to be much less prone to transportation (Kidwell and Holland 2002). Many attempts at palaeoecological studies on such plant beds have documented in great detail the sedimentological context where the fossils occur (e.g. Scott 1978, 1989; Gomez et al. 2012; Kędzior and Popa 2013, 2018). Detailed, three-dimensional sampling such as in underground coal mines along directional and transversal galleries and in coal extraction chambers in particular can provide valuable data (e.g. Gastaldo 1985; DiMichele and Nelson 1989; Popa 1998, 2011, 2014; DiMichele et al. 2007, 2017; Barbacka et al. 2016).

However, the plant remains will have been transported over varying distances, making it difficult to translate the observed distribution of the fossils into original plant diversity (Gastaldo 1992). In a few cases, the fossils in such plant beds seem to have been subjected to only limited transport, such as where a river-bank bank has collapsed and the plant remains have become entombed in a crevasse-splay (e.g. Cleal and Thomas 1988; Laveine and Belhis 2007). More usually, however, the plant remains are at least partly allochthonous. Actualistic studies suggest they will include only a variable representation of the immediately local vegetation (e.g. Burnham 1989, 1994) mixed with remains derived from riparian vegetation growing some distance upstream (Spicer 1980, 1981; Scheihing and Pfefferkorn 1984; Ferguson 1985; Gastaldo et al. 1987; Gastaldo and Huc 1992).

By carefully documenting the co-occurrence of species within individual beds, the composition of individual plant communities can be estimated (e.g. Procter 1994; Bashforth et al. 2010, 2011; Barbacka 2012; Barbacka et al. 2016; Thomas et al. 2020). However, locating those communities in the original vegetation / habitat matrix requires a detailed understanding of the sedimentology of the deposits (DiMichele and Gastaldo 2008; Reitalu et al. 2014) and is at best difficult. Moreover, taphonomic factors may distort the observed diversities. Variations in edaphic conditions can cause variable post-mortem decay of the plant tissue (Gastaldo 1992; Gastaldo and Demko 2011). It has been suggested that differential decay of plant groups may distort the species composition (Scott 1979; Wing and DiMichele 1995) although the effect of this may have been exaggerated (Locatelli et al. 2016; Tomescu et al. 2018). More significant may be differential sorting of the plant remains during transportation: smaller plant fragments will tend to travel further and softer, heavier plant fragments sink more quickly (e.g. Steart et al. 2002). Some element of time-averaging may even occur within a single plant bed depending on depositional rates of the sediment.

Plant remains preserved in shallow marine deposits are usually fragmentary and not concentrated into distinct plant beds, although there can be exceptions caused by storm surges (e.g. Kustatscher et al. 2010). Fossil floras preserved in marine deposits can include the remains of coastal vegetation such as mangroves (e.g. Collinson 1993). During late Permian times, climatic conditions were unfavourable for plant growth in continental Europe and so vegetation tended to be concentrated in coastal areas; remains of this vegetation has been found in shallow marine deposits, preserved particularly during transgression phases (Kustatscher et al. 2017).

Some plant macrofossils preserved in marine strata have been interpreted as plant remains washed down from hinterland vegetation (e.g. Rothwell et al. 1996; Rice et al. 1996; Cleal and Rees 2003) and are notably different from what is seen in fluvio-lacustrine plant beds. “Exotic”, extra-basinal plant remains have also sometimes been reported from fluvio-lacustrine plant beds (e.g. Cleal and Thomas 2004; Uhl 2006; Opluštil et al. 2007). Generally, however, plants growing in places away from rivers or lakes are poorly represented as macrofossils. For instance, grasses, which are obviously major components of terrestrial vegetation today, have a very poor macrofossil record and much of what we know of their evolution is based on palynology (Section 4.2) or dispersed phytoliths derived from their leaves (e.g. Piperno and Pearsall 1998; Strömberg 2004, 2011).

Fossil floras can also occur in maar lake deposits (e.g. the Messel World Heritage Site – Collinson et al. 2012). Such lakes are caused by phreatomagmatic explosions resulting from the interaction of erupting magma and water, and can occur almost anywhere within a landscape and thus may be surrounded by a different type of vegetation to that growing adjacent to lakes formed in fluvio-lacustrine settings. For instance, the late Oligocene Norken fluvio-lacustrine deposits contain predominantly remains of riparian and swamp vegetation (Uhl et al. 2018) but these are almost totally absent from the nearby, almost contemporary Enspel maar lake deposits (Köhler and Uhl 2014). Plant remains in such lakes also experience less hydro-mechanical stress due to water transport and so can preserve delicate plant structure such as flowers (e.g. Uhl 2015).

4.2 Palynological data

Palynology has been widely used for Quaternary landscape-scale diversity studies (Giesecke et al. 2014); but translating the data into vegetation patterns can be problematic because of significant variation in pollen productivity from year to year (Andersen 1970; Sugita 1993; Hicks 1985; Barnekow et al. 2007; Pidek et al. 2010; Giesecke et al. 2014). However, this is partly mitigated by most sediment samples representing several years; for example, in the Lake Sapanca sequence (N-W Turkey) sub-annual samples taken at a 5 mm resolution revealed no seasonality in the palynology signal, probably due to bioturbation of the lake sediment (Leroy et al. 2009). On the other hand, in the alternating black and white sediment layers of the Dead Sea (López-Merino et al. 2016), the seasonality of the pollen production was used to determine if the lamina couplets were varves or a laminated sediment.

Another problem is the great variation in pollen productivity between different plant species. Current evidence for northern and temperate latitudes suggests that Quaternary palynological data are particularly robust for most trees (with a few notable exceptions such as *Larix*) and wind-pollinated taxa, and provide a good measure of broad-scale plant richness over several thousands of kilometres (Reitalu et al. 2019); this is less so for tropical environments due to the higher number of insect-pollinated plants. Among herbs, the Poaceae are the most abundant wind-pollinated plants, and their pollen can be widely dispersed. However, the source of Poaceae and Cyperaceae pollen can be difficult to elucidate because these species occur in a wide range of plant communities. It can also be impossible to identify their pollen to species level other than in cultivated cereals (Pardoe 2001; Sjögren et al. 2015), although phytoliths can be of help here (see below). Most other herbs tend to be under represented in pollen spectra (Leroy and Roiron 1996) as the pollen are dispersed by other vectors and so are not so abundantly produced; they also often have a lower preservation potential. There have been relatively few studies of the representation of herbs in pollen assemblages (Pardoe 2001; Bunting et al. 2016) but the presence of so called "indicator taxa" in pollen samples can give strong evidence that such plants were growing locally (Pardoe 1996, 2001, 2006). Data can also be supplemented by evidence from in situ pollen from flowers (e.g. Herendeen et al. 1994) and in exceptional cases from fossils of pollinating animals (e.g. Grímsson et al. 2017).

Recent initiatives such as the Pollen Monitoring Programme (PMP) are now helping us gain a greater understanding of the relationship between pollen, vegetation and environmental variables. The PMP has been instrumental in the publication of several decades-long records from across Europe (Hicks et al. 1996; Giesecke et al. 2010). The PMP has addressed a variety of problems including the representation of individual taxa (Hicks et al. 1994; Hicks, 2001, Ertl et al 2012; Pidek et al. 2010), the representation of plant communities (van der Knaap et al. 2001; Pidek 2004; Gerasimidis et al. 2006), and the influence of sampling medium on palynological diversity (Pardoe et al. 2010; Litsitsyna et al. 2012).

Although not strictly palynological, phytoliths are another type of plant microfossils that provide valuable evidence of terrestrial vegetation (Strömberg et al. 2018). There can be taphonomic issues due to silica dissolution (Cabanes and Shahack-Gross 2015) but they are nevertheless essential indicators of grass diversity in Cenozoic vegetation, which are usually poorly represented as pollen and macrofossils (Piperno and Pearsall 1998; Piperno 2002;

Strömberg 2004, 2011; Rashid et al. 2019). There are also records of pre-Cenozoic phytoliths (e.g. Carter 1999) but their affinities remain uncertain.

In principle, palynodata can be corrected using R-coefficients (sensu Davis 1963) representing the ratio between the observed pollen abundances and the abundance of plants in the parent vegetation. R-coefficients can be estimated for Quaternary data based on actualistic comparisons between surface pollen data and field vegetation surveys (although even here problems may occur because of some of the mathematical assumption involved – Parsons and Prentice 1981). Such an approach is more difficult with tests on the robustness of pre-Quaternary palynodata as often no independent measure of vegetation composition can be used to calculate the R-coefficients. Nevertheless, it has been attempted with the late Carboniferous swamps where available autochthonous macrofloras allow the coefficients to be estimated (Willard 1993; Opluštil et al. 2009). Palynofacies signals can also help in determining the robustness of palynological data by indicating the depositional and palaeoenvironmental situation of the studied strata (e.g. Stolle et al. 2012, pl. 1, fig. 2).

4.3 Pollen and macrofossil data compared

When diversity data from the macrofloral and palynological records are compared (e.g. Leroy and Roiron 1996; Dimitrova et al. 2005; Birks and Bjune 2010; Xiong et al. 2013; Bjune 2014; Looy et al. 2014; DiMichele et al. 2018) rather different signals are often revealed both in the plant groups represented and the relative proportions of those plant groups (Fig. 7). The macrofloral record is regarded as giving a more detailed picture of plant species richness, especially at a local-scale (Birks and Birks 1980). However, this tends to represent only a fairly narrow band of habitats, and the much smaller sample sizes usually available compared with palynology will often be insufficient to capture diversity patterns. Palynology, in contrast, will give a better understanding of vegetation patterns across a wider range of habitats and at a landscape-scale (Dimitrova et al. 2010; Costamagna et al. 2018).

Because palynological samples may contain palynomorphs from different habitats, it can be difficult to determine the local-scale vegetation patterns within individual habitats; it may also help explain why palynospectra tend to be more diverse than the macrofloras found in the same bed (e.g. Dimitrova et al. 2005). However, as our understanding of the natural affinities of many palynotaxa is improving, palynology is proving increasingly refined evidence of landscape-scale vegetation diversities (Section 5.2). It is evident that one data source is not better than the other for diversity studies: rather, that palaeobotany and palynology are complementary, and are best investigated in tandem (Birks 2000; Kustatscher et al. 2010; Reitalu et al. 2014; Costamagna et al. 2018).

5 Diversity studies

It is beyond the scope of this paper to review all examples of palaeobotanical and palynological diversity studies; the following discussion aims merely to illustrate some of the types of analyses that have been attempted.

5.1 Local-scale diversity

Most allochthonous fossil macrofloras tend to reflect local-scale plant diversity (Cleal et al. 2012). However, the complexity of the sedimentary systems in which they usually occur (Section 3.1) means that the diversity of each individual bed needs to be analysed separately as each flush of sediment is likely to have remains from a different set of plant communities. Even if the plant beds are rigorously sampled (e.g. Scott 1978, 1979), a detailed understanding of the sedimentology is required before it is possible to unscramble the local-scale plant diversity patterns from the mosaic of habitats represented in most allochthonous plant bed (Kędzior and Popa 2013, 2018).

Palynological data tend to be even more problematic for local-scale diversity studies due to variations in how far the palynomorphs have been transported. For instance, pollen of modern-day *Picea* has been found in the Canadian Arctic, 3000 km from its source (Campbell et al. 1999); in the Palaeozoic, conifer pollen appears to have been blown in from a considerable distance (e.g. Bless et al. 1977); some pollen in Carboniferous tropical palynofloras even appear to have originated from high-latitude, Gondwana vegetation (Dimitrova et al. 2011). Even long-distance water transportation of pollen has been reported; for example, Holocene *Podocarpus* pollen that have been found in Nile delta deposits may have been transported > 2,000 km along the river from their source in the Ethiopian Highlands (Leroy 1992). Although such exotics will normally be rare in palynofloras, they represent the end-members of a gradational spectrum of palynomorph abundances reflecting differences in transportation distances, making it difficult to extract local-scale diversity patterns, especially in fluvial and delta settings (Weng et al. 2006).

Local-scale past plant diversity is best determined in the rare autochthonous fossil floras although even here the data are often incomplete (Section 4.1). Some of the best examples of autochthonous floras preserving forest vegetation including both the trees and herbaceous plants are in Palaeozoic volcanic ash-fall deposits (e.g. Wagner 1989; Rössler and Barthel 1998; Wang et al. 2012; Luthardt et al. 2016). Examples studied in great detail are in an ash band in the early Moscovian Radnice Coal in the Czech Republic, where about 0.5 m of volcanic ash engulfed an area of swamp vegetation. The lower part of the deposit contains in situ stumps and the groundcover vegetation, which, because the ash fell almost vertically, was mostly not winnowed out. The upper parts of the ash band, in contrast, includes remains of the upper parts of the trees, together with epiphytes and lianas, brought down by the weight of the ash sometime after the deposit had fallen (Pšenička and Opluštil 2013). A careful survey of the plant remains in different levels of the ash deposit (Fig. 8) not only allowed the reconstruction of the taxonomic composition, spatial distribution and density of vegetation cover, but also revealed evidence of plant to plant interactions and living strategies in extraordinary detail (Opluštil et al. 2007, 2009a,b, 2014; Libertín et al. 2009a).

Many coals (but not all – Glasspool 2003) are the remains of parautochthonous peat and so, as with modern-day peat deposits (e.g. Mauquoy et al. 2010), have the potential to reveal local-scale plant diversity. When the peat has changed into coal through compaction and diagenesis, however, the plant remains become homogenised and so difficult to identify. Notable exceptions are when the peat has been subjected to early mineralisation that preserves the anatomy of the plant remains in often exquisite detail. Sometimes most or all the peat deposit has been mineralised (e.g. Galtier 2008; Slater et al. 2015) but more commonly the mineralisation is localised, such as in the coal balls (mainly calcitic nodules) found in some Palaeozoic coal seams. There have been several local-scale diversity studies on coal balls (e.g. DiMichele and Phillips 1988; DiMichele et al. 1991; Willard 1993; Baker and DiMichele 1997; DiMichele et al. 2002; Willard et al. 2007), which produced evidence of biomass allocation within the peat, which in turn gave some localised evidence of species diversity.

Coal deposits often yield well-preserved palynomorphs, which have been extensively used for biostratigraphical studies revealing evidence of the temporal changes in vegetation (e.g. Smith and Butterworth 1967). If intercalated fine-siliciclastic (shaley) coal-bearing samples are also included, palynological assemblages can be particularly species rich. As with the macrofloras, regional to exotic extra-basinal palynomorphs may also be present (Fig. 9), which can be ideal for palynological correlation purposes (e.g. Stolle 2007, 2010), but can confuse local-scale species richness analyses. Palynology has also been used to investigate the ecological development of the swamps (e.g. Smith 1962, 1968; Habib and Groth 1967; Jasper et al. 2010; Johnston et al. 2017; Eble et al. 2019) and to look at plant diversity at the rank of genus and higher (e.g. Dimitrova and Cleal 2007; Libertín et al. 2009b; Thomas and

Dimitrova 2017), but direct translation of the resulting palynological spectra into plant species diversity is difficult.

Another distinctive parautochthonous source of plant remains is amber, mainly of Cretaceous to Neogene age. Amber can be produced by both conifer (Sadowski et al. 2017) and angiosperm trees (Rust et al. 2010), and can result in exquisite preservation, especially of delicate structures such as flowers (Poinar 2002; Gandolfo et al. 2018), fern sori (Sadowski et al. 2019) and even microscopic algae (Schmidt et al. 2006). Some of these deposits have been studied since the middle 19th century, but amber can be a very selective fossil trap (e.g. Solórzano Kraemer et al. 2018) and so our understanding of the plant diversity of these forests is still incomplete.

5.2 Landscape-scale diversity

Studies on compression fossil diversities across depositional basins (e.g. Cleal 2005, 2007, 2008a; Goswami and Singh 2013; Huang et al. 2016; Opluštil et al. 2017; Goswami et al. 2018; Roopnarine et al. 2018; Saxena et al. 2020) tend to be based on plant remains from a narrow band of habitats. For instance, compressions from the Pennsylvanian swamps of Euramerica appear to have been dominated by remains of the vegetation growing on clastic substrates such as flood-plains, levees and sand banks, whereas the peat-substrate vegetation, which in fact dominated these swamps, is often poorly represented (Cleal et al. 2012); the peat-substrate vegetation is, in contrast, better represented in the coal ball floras and palynospectra. This is not a problem if the main aim is to document extrinsic effects such as climate or landscape changes, particularly if the sampled habitats are tightly constrained ecologically, but care must be taken not to over-generalise the results in terms of overall vegetation patterns.

One of the best sources of detailed data on Palaeozoic landscape-scale diversity are the ash deposits in the Czech Radnice Coal (mentioned in Section 5.1), which have been recorded from numerous localities in both historical collections and several recent excavations. These have allowed lateral variation in the swamp vegetation at one stratigraphical level to be investigated; for instance, studies at the Štilec and Ovčín localities, about 20 km apart, yielded two contrasting assemblages, representing different stages of vegetation succession (Opluštil et al. 2007, 2009a,b, 2014; Libertín et al. 2009a). A similar situation is present in the earliest Permian Wuda ash bed that occurs over an area of more than 60 km^2, enabling distinct assemblages to be recognised both vertically and laterally (Wang et al. 2012).

Floras with anatomically preserved petrifactions and permineralisations are more difficult to use for landscape-scale diversity studies. Most such floras tend to be isolated localities reflecting the exceptional conditions that caused the preservation, and so usually only reflect local-scale diversity. The most notable exceptions are the Pennsylvanian-age coal balls floras that occur extensively across the Late Palaeozoic tropical belt but, although they have been the subject of a number of taxonomic collations (e.g. Phillips 1980; Galtier 1997), no detailed landscape-scale diversity studies have been attempted. In palaeozoological studies, such preservational “hot-spots” have proved a problem by suggesting abnormally high diversities at particular stratigraphical levels, often referred to as the “Lagerstätte effect” (e.g. Benton 1995; Butler et al. 2013), but evidence of this distorting effect on plant fossil diversities is less clear (see comments by Cascales-Miñana and Gerrienne 2017).

Palynology can provide a more representative picture of landscape-scale diversity as the sediment will contain the pollen from plants growing across the area (Weng et al. 2006). This has proved particularly useful in Quaternary studies where the botanical affinities of the various pollen types are well known (Section 4.2). For instance, palynology has been used to map distribution changes across Europe during the Holocene by Huntley and Birks (1983), and there have been numerous species-specific studies (Hicks 2001; Brewer et al. 2002;

Giesecke and Bennett 2004; van der Knaap 2004; Latałowa and van der Knaap 2006; Tinner and Lotter 2006; Giesecke et al. 2007; Pidek et al. 2010; Poska and Pidek 2010). Reitalu et al. (2019) have demonstrated in their study of modern pollen and plant richness across northern Europe that the highest correlations were for trees and shrubs and of wind-pollinated taxa, suggesting that these are the best measures of broad-scale plant richness over several thousands of kilometres.

Improvements in our knowledge of the general affinities of many pre-Neogene palynotaxa (Section 3.2) now allow palynology to identify broad patterns of landscape-scale plant diversity (Abbink et al. 2004; Dimitrova et al. 2005, 2010; Dimitrova and Cleal 2007; Kustatscher et al. 2010; Beri et al. 2018; Franz et al. 2019). However, remaining uncertainties about variations in palynomorph productivity and dispersal between species, and the morphological variation of palynomorphs within plant species, make it difficult to use some taxa for detailed landscape-scale plant diversity studies (Section 4.2).

5.3 Regional-scale and global-scale diversities (Evolutionary floras)

Studies on global-scale faunal diversity (e.g. Sepkoski 1978, 1979, 1984, 1988; Bambach 1977; Powell and Kowalewski 2002) have shown a progressive increase in species doveraity through the Phanerozoic due to an increase in the spatial density of organisms, especially in shallow marine environments (Holland and Sclafani 2015). Similar global and regional studies at the species rank have been attempted in palaeobotany (e.g. Knoll et al. 1979; Niklas et al. 1980) but were hindered by the lack of suitable, taxonomically robust data sets (Section 3.3); also by the failure to take into account geographical (especially latitudinal) variations in taxonomic diversity, as has been shown to be an issue with marine invertebrate diversity dynamics (Close et al. 2020). Analogous palaeobotanical studies would, moreover, be unlikely to answer the same sorts of questions of changes in community structure that were being investigated in the faunal record (Section 4).

Analyses within narrow taxonomic (e.g. Cleal 2008b,c) or stratigraphical (e.g. Cleal et al. 2010; Barbacka et al. 2014) limits have been attempted at the regional-scale, which make it practical for the taxonomic robustness of the data to be critically assessed. However, most larger-scale studies have tended to be based at supra-generic ranks, usually family. For instance, global Phanerozoic plant diversity dynamics were interpreted using Evolutionary Floras (Fig. 10), identified from a factor analysis of a plant family dataset (Cleal and Cascales-Miñana 2014), and these have been used to describe the broad trajectory of vegetation history (Cleal and Thomas 2019; Cleal 2019). More recently, a similar study on pre-Carboniferous floras at the rank of genus is revealing further details of the early phases of plant terrestrialisation (Capel et al., this volume).

There are a number of problems with such large-scale plant diversity studies. The taxonomic robustness of the data used is often uncertain, although for plants this is partly avoided by using family-rank data sets (Section 3.3). More difficult is the robustness of the stratigraphical correlations between widely separated floras. Most fossil floras occur in predominantly terrestrial sequences that lack absolute dating or independent biostratigraphical control (e.g. by marine faunas). In local-scale and landscape-scale studies this is less of a problem as lithostratigraphical correlations are often sufficient to provide a temporal framework for comparisons, but these are inadequate for regional-scale and global-scale studies. The palaeobotanical and palynological evidence is itself sometimes used to provide the correlations, but when this is used as the temporal context for the vegetation changes, the arguments become circular. A classic example is the Panchet Formation in India, which is often quoted as justifying the persistence of glossopterids into the Triassic Period, but for which there is in fact no evidence that it is Triassic other than some debatable facies changes and the floras themselves (Saxena et al. 2018).

6 Why study plant diversity in deep time?

Studies of past plant diversity dynamics are particularly important for providing a comparison with models used to describe the response of vegetation to recent climate change (Willis et al. 2010; Reitalu et al. 2014). For instance, the Quaternary record has indicated that glacial-interglacial changes have induced large-scale shifts in plant distributions (Willis and Bhagwat 2009; Giesecke et al. 2017), although there was sometimes a lag between climatic change and vegetation change (Leroy et al. 2011). Some warm-loving and cold-loving deciduous tree species became extinct in Europe during glacial phases (Willis and Niklas 2004; Bertini 2010), due not only to climate change, but also to disease, competition and extreme conditions in refugia (Leroy 2007). For those species that survived the glacial phases, refugia such as in southern Europe were essential (Bennett et al. 1991; Leroy and Arpe 2007). In contrast, conifers and some climatically less sensitive angiosperm trees found refugia further north in Europe during glacial phases (crypto-refugia; Willis et al. 2000; Bhagwat and Willis 2008) whereas herbaceous species typical of tundra and steppe vegetation have been forced into upland refugia during the forest dominated phase of the Holocene (Bennett and Provan 2008). It is evident that these refugia have been vital for the shaping of present-day biogeographical patterns and the assemblage of extant communities (Willis and Bhagwat 2009). Refugia have also been used to explain the responses of vegetation to climate changes in Carboniferous tropical swamps (e.g. Falcon-Lang and DiMichele 2010; Looy et al. 2014).

Palynological research has revealed anthropogenic effects on Holocene plant diversity (Giesecke et al. 2012, 2019). For example, Filipova-Marinova et al. (2014) described an 8,000 year long record of vegetation change at Varna Lake (Bulgaria) and showed how the vegetation was strongly influenced by human activity, both through woodland clearance and the establishment of agriculture.

Rull (2011, 2013) has explored the drivers of neotropical diversity since early Neogene times, and concluded that it is the result of complex ecological and evolutionary trends initiated by tectonic events and palaeogeographical reorganisations, and was maintained by Pleistocene climatic changes. The palynological record during the Palaeocene – Eocene Thermal Maximum indicated an increase in diversity in tropical (Jaramillo et al. 2010) and polar vegetation (Willard et al. 2019), whereas in temperate latitudes the effects were less marked (e.g. Wing et al. 2003) except sometimes for a change to more fire-prone vegetation (Collinson et al. 2009).

Further back in geological time, the analyses are more difficult because we are looking at plants that are only distantly related to modern-day vegetation, but the comparisons can nevertheless be insightful. Many Mesozoic studies have focussed on how vegetation recovered from the Permian – Triassic and Triassic – Jurassic biotic crises (e.g. Grauvogel-Stamm and Ash 2005; Yu et al. 2015). For instance, Hochuli et al. (2016) showed the complex pattern of recovery of the post-extinction, Early Triassic vegetation. Various other floral changes were recorded at the Triassic – Jurassic boundary in Greenland (McElwain et al. 2007) and at the Hettangian-Sinemurian boundary in the South Carpathians (Popa 2000).

In the Palaeozoic, most attention has been directed to the effect of the Late Palaeozoic Ice Age on plant diversity: did the observed Pennsylvanian – Cisuralian diversity changes in the tropical vegetation cause climate change (e.g. Cleal and Thomas 1999, 2005), or did the climate change cause the vegetation changes (e.g. Pfefferkorn et al. 2008, 2017), or were the two interlocked through feedback loops (Cleal et al. 2010)? Other links that have also been explored are between the diversification of the first woody forests in Late Devonian times and a significant change in ocean water chemistry that caused major reduction in marine faunal diversity (Algeo and Scheckler 1998); and between the very early development of plant diversity during Ordovician times and global cooling and glaciation (Servais et al. 2019).

Another major theme of research has been the effect of mass extinctions on vegetation (McElwain and Punyasena 2007; Cascales-Miñana et al. 2013). Clearly extensive destruction of vegetation occurred during three of the five classic "mass extinctions" of Sepkoski (1978, 1979, 1984): at the boundaries between the Permian – Triassic (e.g. Looy et al. 1999; Hochuli et al. 2016, 2017), Triassic – Jurassic (e.g. McElwain et al 2007; Mander et al. 2013; McElwain 2018) and Cretaceous – Palaeogene (e.g. Vajda and Bercovici 2014). However, a key criterion for recognising a true mass extinction (Raup and Sepkoski 1982) is that it should significantly disrupt the overall trajectory of evolution and this did not occur with plants at most of these biotic crises (McElwain and Punyasena 2007; Cascales-Miñana 2011, 2012; Cascales-Miñana and Cleal 2011; Cascales-Miñana and Diez 2012; Cascales-Miñana et al. 2013). Only at the Permian – Triassic boundary does there seem to have been any significant clade disruption (Cascales-Miñana and Cleal 2014; Cascales-Miñana et al. 2016), and even here the pattern of extinction was more complex than with the marine faunas (Hochuli et al. 2016; Nowak et al. 2019). The fossil record seems to suggest that plants were much less vulnerable to biotic crises compared with faunas (Traverse 1988; McElwain and Punyasena 2007; McElwain et al. 2007; Cascales-Miñana et al. 2018).

Identifying vegetation diversity patterns at all scales from the plant fossil record is clearly not easy; whatever the sampling protocol and analytical methods used, the fact will remain that the observed diversity patterns are of the fossils rather than purely of the original vegetation. Nevertheless, the fossil record is the only direct evidence we have of how vegetation has changed through time. By bringing together data from the palaeobotanical and palynological records and interpreting it within the context of the taphonomic filter through which the fossils have passed (Fig. 11) will allow us to understand better how plant-life has responded to changes in climate, landscape and continental configurations, and to the dramatic ecological crises often referred to as mass extinctions.

7 Conclusions

A deeper appreciation of the history of vegetation dynamics can inform present-day landscape management and predictions of future biodiversity and climate. For example, the plant fossil record can provide evidence of the speed at which plants can track climate change and this may prove valuable to predict the response of today's plant vegetation to global warming. It can also provide empirical data to help support and improve models of the dynamic interactions of modern-day vegetation, atmosphere and climate. Evidence from the fossil record clearly has the potential for making a significant contribution to understanding the world today, and emphasises the importance of close co-operation between palaeoecologists and ecologists. Provided that the context of the data is properly understood, including the taxonomy of the fossils (not just the taxonomic names used but what the fossil-taxa mean), the taphonomic processes that caused the fossil to be preserved, and the detailed temporal (stratigraphical) correlations, an underlying signal of vegetation diversity remains waiting to be discovered.

Acknowledgements

The authors are grateful to the European Science Foundation for supporting the Exploratory Workshop entitled *Tracking changes in plant diversity over the last 400 million years*, held in 2014 at National Museum Wales, Cardiff, UK. Ian Glasspool is thanked for providing the images used in Fig. 3. This is a contribution to National Museum Wales Research Project NS25 *Plant diversity through 450 million years of Earth history.*

8 References

Abbink, O.A., van Konijnenburg-van Cittert, J.H.A., Visscher, H., 2004. A sporomorph ecogroup model for the Northwest European Jurassic-Lower Cretaceous: concepts and framework. Netherlands Journal of Geosciences 83, 17–31.

Algeo, T.J., Scheckler, S.E., 1998. Terrestrial-marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 353, 113–130.

Alroy, J., 2003. Global databases will yield reliable measures of global biodiversity. Paleobiology 29, 26–29.

Andersen, S.T., 1970. The relative pollen productivity and pollen representation of north European trees, and correction factors for tree pollen spectra. Danmarks Geologiske Undersögelse, Raekke 2, 1–99.

Anderson, J.M., Anderson, H.M., Cleal, C.J., 2007. Brief history of the gymnosperms: classification, biodiversity, phytogeography and ecology. Strelitzia 20, 1–279.

Andrews, H.N., 1980. The fossil hunters. In search of ancient plants. Cornell University Press, Ithaca and London.

Antonelli, A., Fry, C., Smith, R.J., Simmonds, M.S.J., Kersey, P.J., Pritchard, H.W., Abbo, M.S., Acedo, C., Adams, J., Ainsworth, A.M., Allkin, B., Annecke, W., Bachman, S.P., Bacon, K., Bárrios, S., Barstow, C., Battison, A., Bell, E., Bensusan, K., Bidartondo, M.I., Blackhall-Miles, R.J., Borrell, J.S., Brearley, F.Q., Breman, E., Brewer, R.F.A., Brodie, J., Cámara-Leret, R., Campostrini Forzza, R., Cannon, P., Carine, M., Carretero, J., Cavagnaro, T.R., Cazar, M.-E., Chapman, T., Cheek, M., Clubbe, C., Cockel, C., Collemare, J., Cooper, A., Copeland, A.I., Corcoran, M., Couch, C., Cowell, C., Crous, P., da Silva, M., Dalle, G., Das, D., David, J.C., Davies, L., Davies, N., De Canha, M.N., de Lirio, E.J., Demissew, S., Diazgranados, M., Dickie, J., Dines, T., Douglas, B., Dröge, G., Dulloo, M.E., Fang, R., Farlow, A., Farrar, K., Fay, M.F., Felix, J., Forest, F., Forrest, L.L., Fulcher, T., Gafforov, Y., Gardiner, L.M., Gâteblé, G., Gaya, E., Geslin, B., Gonçalves, S.C., Gore, C.J.N., Govaerts, R., Gowda, B., Grace, O.M., Grall, A., Haelewaters, D., Halley, J.M., Hamilton, M.A., Hazra, A., Heller, T., Hollingsworth, P.M., Holstein, N., Howes, M.-J.R., Hughes, M., Hunter, D., Hutchinson, N., Hyde, K., Iganci, J., Jones, M., Kelly, L.J., Kirk, P., Koch, H., Krisai-Greilhuber, I., Lall, N., Langat, M.K., Leaman, D.J., Leão, T.C., Lee, M.A., Leitch, I.J., Leon, C., Lettice, E., Lewis, G.P., Li, L., Lindon, H., Liu, J.S., Liu, U., Llewellyn, T., Looney, B., Lovett, J.C., Łuczaj, Ł., Lulekal, E., Maggassouba, S., Malécot, V., Martin, C., Masera, O.R., Mattana, E., Maxted, N., Mba, C., McGinn, K.J., Metheringham, C., Miles, S., Miller, J., Milliken, W., Moat, J., Moore, P.G.P., Morim, M.P., Mueller, G.M., Muminjanov, H., Negrão, R., Nic Lughadha, E., Nicolson, N., Niskanen, T., Nono Womdim, R., Noorani, A., Obreza, M., O'Donnell, K., O'Hanlon, R., Onana, J.-M., Ondo, I., Padulosi, S., Paton, A., Pearce, T., Pérez Escobar, O.A., Pieroni, A., Pironon, S., Prescott, T.A.K., Qi, Y.D., Qin, H., Quave, C.L., Rajaovelona, L., Razanajatovo, H., Reich, P.B., Rianawati, E., Rich, T.C.G., Richards, S.L., Rivers, M.C., Ross, A., Rumsey, F., Ryan, M., Ryan, P., Sagala, S., Sanchez, M.D., Sharrock, S., Shrestha, K.K., Sim, J., Sirakaya, A., Sjöman, H., Smidt, E.C., Smith, D., Smith, P., Smith, S.R., Sofo, A., Spence, N., Stanworth, A., Stara, K., Stevenson, P.C., Stroh, P., Suz, L.M., Tambam, B.B., Tatsis, E.C., Taylor, I., Thiers, B., Thormann, I., Trivedi, C., Twilley, D., Twyford, A.D., Ulian, T., Utteridge, T.,Vaglica, V., Vásquez-Londoño, C., Victor, J., Viruel, J., Walker, B.E., Walker, K., Walsh, A., Way, M., Wilbraham, J., Wilkin, P., Wilkinson, T., Williams, C., Winterton, D., Wong, K.M., Woodfield-Pascoe, N., Woodman, J., Wyatt, L., Wynberg, R., Zhang, B.G., 2020. State of the world's plants and fungi 2020. Royal Botanic Gardens, Kew. DOI: https://doi.org/10.34885/172

Appleton, P., Malpas, J., Thomas, B.A., Cleal, C.J., 2011. The Brymbo fossil forest. Geology Today 27, 107–113.

Baker, R.A., DiMichele, W.A., 1997. Biomass allocation in Late Pennsylvanian coal-swamp plants. Palaios 12, 127–132.

Balme, B.E., 1995. Fossil in situ spores and pollen grains: an annotated catalogue. Review of Palaeobotany and Palynology 87, 81–323.

Bambach, R.K., 1977. Species richness in marine benthic habitats through the Phanerozoic. Paleobiology 3, 152–167.

Barbacka, M., 2012. Biodiversity and reconstruction of Early Jurassic flora from the Mecsek Mountains (southern Hungary). Acta Palaeobotanica 51, 127–179.

Barbacka, M., Bodor, E., Jarzynka, A., Kustatscher, E., Pacyna, G., Popa, M.E., Scanu, G.G., Thévenard, F., Ziaja, J., 2014. European Jurassic floras: statistics and palaeoenvironmental proxies. Acta Palaeobotanica 54, 173–195.

Barbacka, M., Popa, M.E., Mitka, J., Bodor, E., Püspöki, Z., McIntosh, R.W., 2016. A quantitative approach for identifying plant ecogroups in the Romanian Early Jurassic terrestrial vegetation. Palaeogeography, Palaeoclimatology, Palaeoecology 446, 44–54.

Barnekow, L., Loader, N.J., Hicks, S., Froyd, C.A., Goslar, T., 2007. Strong correlation between summer temperature and pollen accumulation rates for *Pinus sylvestris*, *Picea abies* and *Betula* spp. in a high-resolution record from northern Sweden Journal of Quaternary Science 22, 653–658.

Bashforth, A.R., Falcon-Lang, H.J., Gibling, M.R., 2010. Vegetation heterogeneity on a Late Pennsylvanian braided-river plain draining the Variscan Mountains, La Magdalena Coalfield, northwestern Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 292, 367–390.

Bashforth, A.R., Drábková, J., Opluštil, S., Gibling, M.R., Falcon-Lang, H.J., 2011. Landscape gradients and patchiness in riparian vegetation on a Middle Pennsylvanian braided-river plain prone to flood disturbance (Nýřany Member, Central and Western Bohemian Basin, Czech Republic). Review of Palaeobotany and Palynology 163, 153–189.

Bateman, R.M., DiMichele, W.A., 1992. The rhizomorphic lycopsids: A case-study in paleobotanical classification. Sytematic Botany 21, 535–552.

Bateman, R.M., Hilton, J., 2009. Palaeobotanical systematics for the phylogenetic age: applying organ–species, form–species and phylogenetic species concepts in a framework of reconstructed fossil and extant whole–plants. Taxon 58, 1254–1280.

Bateman, R.M., DiMichele, W.A., Willard, D.A., 1992. Experimental cladistics-analysis of anatomically preserved arborescent lycopsids from the Carboniferous of Euramerica – An essay on palaeobotanical phylogenies. Annals of the Missouri Botanical Garden 79, 500–559.

Beerling, D., 2007. The emerald planet: how plants changed Earth's history. Oxford University Press, Oxford.

Bek, J., 2017. Paleozoic in situ spores and pollen. Lycopsida. Palaeontographica Abteilung B 296, 1–111.

Bennett, K.D., Provan, J., 2008. What do we mean by refugia? Quaternary Science Reviews 27, 2449–2455.

Bennett, K.D., Tzedakis, P.C., Willis, K.J., Quaternary refugia of north European trees. Journal of Biogeography 18, 103–115.

Bennington, J.B., Dimichele, W.A., Badgley, C., Bambach, R.K., Barrett, P.M., Behrensmeyer, A.K., Bobe, R., Burnham, R.J., Daeschler, E.B., Dam, J.V., Eronen, J.T., et al., 2009. Critical issues of scale in paleoecology. Palaios 24, 1–4.

Benton, M.J. (Ed.), 1993. The Fossil Record 2. Chapman and Hall, London.

Benton, M.J., 1995. Diversification and extinction in the history of life. Science 268, 52–58.

Beri, A., Martínez-Blanco, X., Tejera, L., Piñeyro, A., Souza, P.A., 2018. Palynodiversity patterns and paleoclimatic changes in the late Paleozoic in Brazil and Uruguay. Boletín Geológico y Minero 129, 599–614.

Beri, Á., Martínez-Blanco, X., Varela, L., di Pasquo, M., de Souza, P.A., 2020. Sampling biases and Paleozoic sporomorphs diversity dynamics in Western Gondwana strata. Journal of South American Earth Sciences 98, doi.org/10.1016/j.jsames.2019.102457.

Berry, C.M., Marshall, J.E., 2015. Lycopsid forests in the early Late Devonian paleoequatorial zone of Svalbard. Geology 43, 1043–1046.

Bertini, A., 2010. Pliocene to Pleistocene palynoflora and vegetation in Italy: state of the art. Quaternary International 225, 5–24.

Bhagwat, S.A., Willis, K.J., 2008. Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? Journal of Biogeography 35, 465–482.

Birks, H.H., Birks, H.J.B., 2000. Future uses of pollen analysis must include plant macrofossils. Journal of Biogeography 27, 31–35.

Birks, H.H., Bjune, A.E., 2010. Can we detect a west-Norwegian treeline from modern samples of plant remains and pollen? Results from the DOORMAT project. Vegetation History and Archaeobotany 19, 325–340.

Birks, H.J.B., Birks, H.H., 1980. Quaternary Palaeoecology. Edward Arnold, London.

Birks, H.J.B., Felde, V.A., Seddon, A.W., 2016a. Biodiversity trends within the Holocene. The Holocene 26, 994–1001.

Birks, H.J.B., Felde, V.A., Bjune, A.E., Grytnes, J.A., Seppä, H., Giesecke, T., 2016b. Does pollen-assemblage richness reflect floristic richness? A review of recent developments and future challenges. Review of Palaeobotany and Palynology 228, 1–25.

Birks, H.J.B., Line, J.M., 1992. The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. The Holocene 2, 1–10.

Bjune, A.E., 2014. After 8 years of annual pollen trapping across the treeline in western Norway: are the data still anomalous? Vegetation History and Archaeobotany 23, 299–308.

Bless, M.J.M., Loboziak, S., Streel, M., 1977. An upper Westphalian C ‘hinterland’ microflora from the Haaksbergen-1 Borehole (Netherlands). Mededelingen Rijks Geologische Dienst 28, 135–147.

Brewer, S. Cheddadi, R., de Beaulieu, J.L., Reille, M., 2002. The spread of deciduous *Quercus* throughout Europe since the last glacial period. Forest Ecology and Management 156, 27–48.

Brongniart, A., 1822. Sur la classification et la distribution des végétaux fossiles en général, et sur ceux des terrains de sédiment supérieur en particulier. Introduction, Chapitre I. Mémoires du Muséum d’Histoire Naturelle 8, 203–240.

Bunting, M.J., Grant, M.J., Waller, M.P., 2016. Pollen signals of ground flora in managed woodlands. Review of Palaeobotany and Palynology 224, 121–133.

Burnham, R.J., 1989. Relationships between standing vegetation and leaf litter in a paratropical forest: implications for paleobotany. Review of Palaeobotany and Palynology 58, 5–32.

Burnham, R.J., 1994. Paleoecological and floristic heterogeneity in the plant-fossil record: an analysis based on the Eocene of Washington. U.S. Geological Survey Bulletin 2085, B1–B35.

Butler, R.J., Benson, R.B., Barrett, P.M., 2013. Pterosaur diversity: untangling the influence of sampling biases, Lagerstätten, and genuine biodiversity signals. Palaeogeography, Palaeoclimatology, Palaeoecology 372, 78–87.

Cabanes, D., Shahack-Gross, R., 2015. Understanding fossil phytolith preservation: The role of partial dissolution in paleoecology and archaeology. PLoS ONE 10(5), e0125532

Calder, J.H., Gibling, M.R., Scott, A.C., Davies, S.J., Hebert, B.L., Greb, S.F., DiMichele, W.A., 2006. A fossil lycopsid forest succession in the classic Joggins section of Nova Scotia: paleoecology of a disturbance-prone Pennsylvanian wetland, in: Greb, S.F., DiMichele, W.A. (Eds), Wetlands through time. Geological Society of America Special Paper 399, pp. 169–195.

Campbell, I.D., McDonald, K., Flannigan, M.D., Kringayark, J., 1999. Long-distance transport of pollen into the Arctic. Nature 399, 29–30.

Carter, J.A., 1999. Late Devonian, Permian and Triassic phytoliths from Antarctica. Micropaleontology 45, 56–61.

Cascales-Miñana, B., 2011. New insights into the reading of Paleozoic plant fossil record discontinuities. Historical Biology 23, 115–130.

Cascales-Miñana, B., 2012. Disentangling temporal patterns in our perception of the fossil history of gymnosperms. Historical Biology 24, 143–159.

Cascales-Miñana, B., Cleal, C.J., 2011. Plant fossil record and survival analysis. Lethaia 45, 71–82.

Cascales-Miñana, B., Cleal, C.J., 2014. The plant fossil record reflects just two great extinction events. Terra Nova 26, 195–200.

Cascales-Miñana, B., Gerrienne, P., 2017. *Teruelia diezii* gen. et sp. nov.: an early polysporangiophyte from the Lower Devonian of the Iberian Peninsula. Palaeontology 60, 199–212.

Cascales-Miñana, B., Cleal, C. J., Diez, J.B., 2013. What is the best way to measure extinction? A reflection from the palaeobotanical record. Earth-Science Reviews 124, 126–147.

Cascales-Miñana, B., Diez, J.B., Gerrienne, P., Cleal, C.J., 2016. A palaeobotanical perspective on the great end-Permian biotic crisis. Historical Biology 28, 1066–1074.

Cascales-Miñana, B., Servais, T., Cleal, C.J., Gerrienne, P., Anderson, J., 2018. Plants—the great survivors! Geology Today 34, 224–229.

Cascales-Miñana, B., Diez, J.B., 2012. The effect of singletons and interval length on interpreting diversity trends from the palaeobotanical record. Palaeontologia Electronica 15 (1), 6A.

Chaloner, W.G., 1999. Taxonomic and nomenclatural alternatives, in: Jones, T.P., Rowe, N.P. (Eds.), Fossil plants and spores. Modern techniques. Geological Society, London, pp 179–183.

Cleal, C.J., 2005. The Westphalian macrofloral record from the cratonic central Pennines Basin, UK. Zeitschrift der Deutschen Gesellschaft für Geowissenschaften 156, 387–410.

Cleal, C.J., 2007. The Westphalian-Stephanian macrofloral record from the South Wales Coalfield. Geological Magazine 144, 465–486.

Cleal, C.J., 2008a. Westphalian-Stephanian macrofloras of the southern Pennines Basin, UK. Studia Geologica Polonica 129, 25–41.

Cleal, C.J., 2008b. Palaeofloristics of Middle Pennsylvanian lyginopteridaleans in Variscan Euramerica. Palaeogeography, Palaeoclimatology, Palaeoecology 261, 1–14.

Cleal, C.J., 2008c. Palaeofloristics of Middle Pennsylvanian medullosaleans in Variscan Euramerica. Palaeogeography, Palaeoclimatology, Palaeoecology 268, 164–180.

Cleal, C.J., 2019 (in press). Paleozoic plants. In Encyclopaedia of Earth sciences. Elsevier, Amsterdam.

Cleal, C.J., Cascales-Miñana, B., 2014. Composition and dynamics of the great Phanerozoic Evolutionary Floras. Lethaia 47, 469–484.

Cleal, C.J., Rees, P.M., 2003. The Middle Jurassic flora from Stonesfield, Oxfordshire, UK. Palaeontology 46, 739–801.

Cleal, C.J., Shute, C.H., 2012. The systematic and palaeoecological value of foliage anatomy in Late Palaeozoic medullosalean seed-plants. Journal of Systematic Palaeontology 10, 765–800.

Cleal, C.J., Thomas, B.A., 1988. The Westphalian fossil floras from the Cattybrook Claypit, Avon (Great Britain). Geobios 21, 409–433.

Cleal, C.J., Thomas, B.A., 1999. Tectonics, tropical forest destruction and global warming in the Late Palaeozoic. Acta Palaeobotanica, Supplement 2, 17–19.

Cleal, C.J., Thomas, B.A., 2004. Late Carboniferous palaeobotany of the upper Bideford Formation, north Devon: a coastal setting for a Coal Measures flora. Proceedings of the Geologists' Association 115, 267–281.

Cleal, C.J., Thomas, B.A., 2005. Palaeozoic tropical rainforests and their effect on global climates: is the past the key to the present? Geobiology 3, 13–31.

Cleal, C.J., Thomas, B.A., 2010. Botanical nomenclature and plant fossils. Taxon 59, 261–268.

Cleal, C.J., Thomas, B.A., 2019. Introduction to plant fossils. Second edition. Cambridge University Press, Cambridge.

Cleal, C.J., Opluštil, S., Thomas, B.A., Tenchov, Y., 2010. Late Moscovian terrestrial biotas and palaeoenvironments of Variscan Euramerica. Netherlands Journal of Geosciences 88, 181–278.

Cleal, C.J., Uhl, D., Cascales-Miñana, B., Thomas, B.A., Bashforth, A.R., King, S.C., Zodrow, E.L., 2012. Plant biodiversity changes in Carboniferous tropical wetlands. Earth-Science Reviews 114, 124–155.

Close, R.A., Benson, R.B.J., Saupe, E.E., Clapham, M.E., Butler, R.J., 2020. The spatial structure of Phanerozoic marine animal diversity. Science 368, 420-424.

Collinson, M.E., 1993. Taphonomy and fruiting biology of recent and fossil *Nypa*. Special Papers in Palaeontology 49, 165–180.

Collinson, M.E., 1996. "What use are fossil ferns?" - 20 years on: with a review of the fossil history of extant pteridophyte families and genera, in: Camus, M.G., Johns, R.J. (Eds.), Pteridology in perspective. Royal Botanic Gardens, Kew, pp. 349–394.

Collinson, M.E., Manchester, S.R., Wilde, V., 2012. Fossil fruits and seeds of the Middle Eocene Messel biota, Germany. Abhandlungen der Senckenberg Gesellschaft für Naturforschung 570, 251 pp.

Collinson, M.E., Steart, D.C., Harrington, G.J., Hooker, J.J., Scott, A.C., Allen, L.O., Glasspool, I.J., Gibbons, S.J., 2009. Palynological evidence of vegetation dynamics in response to palaeoenvironmental change across the onset of the Paleocene-Eocene Thermal Maximum at Cobham, Southern England. Grana 48, 38–66.

Costamagna, L.G., Kustatscher, E., Scanu, G.G., Del Rio, M., Pittau, P., van Konijnenburg-van Cittert, J.H., 2018. A palaeoenvironmental reconstruction of the Middle Jurassic of Sardinia (Italy) based on integrated palaeobotanical, palynological and lithofacies data assessment. Palaeobiodiversity and Palaeoenvironments 98, 111–138.

Davies, N.S., Gibling, M.R., 2010. Cambrian to Devonian evolution of alluvial systems: the sedimentological impact of the earliest land plants. Earth-Science Reviews 98, 171–200.

Davis, M.B., 1963. On the theory of pollen analysis. American Journal of Science 261, 897–912.

Diez, J.B., Sender, L.M., Villanueva-Amadoz, U., Ferrer, J., Rubio, C., 2005. New data regarding *Weichselia reticulata*: Soral clusters and the spore developmental process. Review of Palaeobotany and Palynology 135, 99–107

DiMichele, W.A., Falcon-Lang, H.J., 2011. Pennsylvanian 'fossil forests' in growth position (T^0 assemblages): origin, taphonomic bias and palaeoecological insights. Journal of the Geological Society, London 168, 585–605.

DiMichele, W.A., Gastaldo, R.A., 2008. Plant paleoecology in deep time. Annals of the Missouri Botanical Garden 95, 144–198.

DiMichele, W.A., Nelson, W.J., 1989. Small-scale spatial heterogeneity in Pennsylvanian-age vegetation from the roof shale of the Springfield Coal (Illinois Basin). Palaios 4, 276–280.

DiMichele, W.A., Phillips, T.L., 1988. Paleoecology of the Middle Pennsylvanian-age Herrin coal swamp (Illinois) near a contemporaneous river system, the Walshville paleochannel. Review of Palaeobotany and Palynology 56, 151–176.

DiMichele, W.A., Philips, T.L., McBrinn, G.E., 1991. Quantitative analysis and paleoecology of the Secor coal and roof shale floras (Middle Pennsylvanian, Oklahoma). Palaios 6, 390–409.

DiMichele, W.A., Phillips, T.L., Nelson, W.J., 2002. Place vs. time and vegetational persistence: a comparison of four tropical mires from the Illinois Basin during the height of the Pennsylvanian Ice Age. International Journal of Coal Geology 50, 43–72.

DiMichele, W.A., Falcon-Lang, H.J., Nelson, W.J., Elrick, S.D., Ames, P.R., 2007. Ecological gradients within a Pennsylvanian mire forest. Geology 35, 415–418.

DiMichele, W.A., Elrick, S.D., Nelson, W.J., 2017. Vegetational zonation in a swamp forest, Middle Pennsylvanian, Illinois Basin, USA, indicates niche differentiation in a wetland plant community. Palaeogeography, Palaeoclimatology, Palaeoecology 487, 71–92.

DiMichele, W.A., Hook, R.W., Kerp, H., Hotton, C.L., Looy, C.V., Chaney, D.S., 2018. Lower Permian Flora of the Sanzenbacher Ranch, Clay County, Texas, in: Krins, M., Harper, C.J., Cúneo, R., Rothwell, G.E. (eds.), Transformative paleobotany: papers to commemorate the life and legacy of Thomas N. Taylor. Elsevier, Amsterdam, pp. 95–126.

Dimitrova, T.K., Cleal, C.J., 2007. Palynological evidence for late Westphalian–early Stephanian vegetation change in the Dobrudzha Coalfield, NE Bulgaria. Geological Magazine 144, 513–524.

Dimitrova, T.K., Cleal, C.J., Thomas, B.A., 2005. Palynology of late Westphalian – early Stephanian coal-bearing deposits in the eastern South Wales Coalfield. Geological Magazine 142, 809–821.

Dimitrova, T.K., Cleal, C.J., Thomas, B.A., 2011. Palynological evidence for Pennsylvanian extra-basinal vegetation in Atlantic Canada. Journal of the Geological Society 168, 559–569.

Dimitrova, T.K., Zodrow, E.L., Cleal, C.J., Thomas, B.A., 2010. Palynological evidence for Pennsylvanian (Late Carboniferous) vegetation change in the Sydney Coalfield, eastern Canada. Geological Journal 45, 388–396.

Dornelas, M., Magurran, A.E., Buckland, S.T., Chao, A., Chazdon, R.L., Colwell, R.K., Curtis, T., Gaston, K.J., Gotelli, N.J., Kosnik, M.A., McGill, B., 2012. Quantifying temporal change in biodiversity: challenges and opportunities. Proceedings of the Royal Society B: Biological Sciences 280, 20121931

Eble, C.F., Greb, S.F., Williams, D.A., Hower, J.C., O'Keefe, J.M., 2019. Palynology, organic petrology and geochemistry of the Bell coal bed in Western Kentucky, Eastern Interior (Illinois) Basin, USA. International Journal of Coal Geology 213, 103264.

Edwards, D., Kenrick, P., Dolan, L., 2018, History and contemporary significance of the Rhynie cherts-our earliest preserved terrestrial ecosystem. Philosophical Transactions of the Royal Society of London. Series B 373(1739), 20160489.

Enquist, B.J., Haskell, J.P., Tiffney, B.H., 2002. General patterns of taxonomic and biomass partitioning in extant and fossil plant communities. Nature 419, 610–613.

Ertl, C., Pessi, A.M., Huusko, A., Hicks, S., Kubin, E., Heino, S., 2012, Assessing the proportion of "extra-local" pollen by means of modern aerobiological and phenological records — An example from Scots pine (*Pinus sylvestris* L.) in northern Finland. Review of Palaeobotany and Palynology 185, 1–12.

Falcon-Lang, H.J., Bashforth, A.R., 2005. Morphology, anatomy, and upland ecology of large cordaitalean trees from the Middle Pennsylvanian of Newfoundland. Review of Palaeobotany and Palynology 135, 223–243.

Falcon-Lang, H.J. and DiMichele, W.A., 2010. What happened to the coal forests during Pennsylvanian glacial phases? Palaios 25, 611–617.

Falcon-Lang, H.J., Kurzawe, F., Lucas, S.G., 2016. A Late Pennsylvanian coniferopsid forest in growth position, near Socorro, New Mexico, USA: tree systematics and palaeoclimatic significance. Review of Palaeobotany and Palynology 225, 67–83.

Ferguson, D.K., 1985. The origin of leaf assemblages – new light on an old problem. Review of Palaeobotany and Palynology 46, 117–188.

Ferguson, D.K., 2005. Plant taphonomy: ruminations on the past, the present, and the future. Palaios 20, 418–428.

Ferguson, D.K., Zetter, R., Paudayal, K.N., 2007. The need for SEM in palaeopalynology. Comptes Rendus Palévol 6, 423–430.

Filipova-Marinova, M.V., Kvavadze, E.V., Connor, S.E., Sjögren, P., 2010. Estimating absolute pollen productivity for some European Tertiary-relict taxa. Vegetation History and Archaeobotany 19, 351–364.

Francis, J.E., 1983. The dominant conifer of the Jurassic Purbeck formation, England. Palaeontology 26, 277–294.

Franz, M., Kustatscher, E., Heunisch, C., Niegel, S., Röhling, H.G., 2019. The Schilfsandstein and its flora; arguments for a humid mid-Carnian episode? Journal of the Geological Society 176, 133–148.

Galtier, J., 1986. Taxonomic problems due to preservation: comparing compression and permineralised taxa, in: Spicer, R.A., Thomas, B.A (Eds.), Systematic and taxonomic approaches in palaeobotany. Oxford University Press, Oxford (Systematics Association, Special Volume 31), pp. 1–16.

Galtier, J., 1997. Coal-ball floras of the Namurian-Westphalian of Europe. Review of Palaeobotany and Palynology 95, 51–72.

Galtier, J., 2008. A new look at the permineralized flora of Grand-Croix (Late Pennsylvanian, Saint-Etienne basin, France). Review of Palaeobotany and Palynology 152, 129–140.

Gandolfo, M.A., Nixon, K.C., Crepet, W.L., Grimaldi, D.A., 2018. A late Cretaceous fagalean inflorescence preserved in amber from New Jersey. American Journal of Botany 105, 1424–1435.

Garwood, R.J., Oliver, H., Spencer, A.R.T., 2019. An introduction to the Rhynie chert. Geological Magazine 157, 47–64.

Gastaldo, R.A., 1985. Implications on the paleoecology of autochthonous lycopods in clastic sedimentary environments of the Early Pennsylvanian of Alabama. Palaeogeography, Palaeoclimatology, Palaeoecology 53, 191–212.

Gastaldo, R.A. 1992. Taphonomic considerations for plant evolutionary investigations. The Palaeobotanist 41, 211–223.

Gastaldo, R.A., Demko, T.M., 2011. The relationship between continental landscape evolution and the plant-fossil record: long term hydrologic controls on preservation, in: Allison, P.A., Bottjer, D.J. (Eds.), Taphonomy. Process and bias through time. Springer Netherlands, pp. 249-285.

Gastaldo, R.A., Douglass, D.P., McCarroll, S.M., 1987. Origin, characteristics, and provenance of plant macrodetritus in a Holocene crevasse splay mobile delta, Alabama. Palaios 2, 229–240.

Gastaldo, R.A., Huc, A.-Y., 1992. Sediment facies, depositional environments, and distribution of phytoclasts in the Recent Mahakam River Delta, Kalimantan, Indonesia. Palaios 7, 574–590.

Gastaldo, R.A., Pfefferkorn, H.W., DiMichele, W.A., 1995. Taphonomic and sedimentologic characterization of roof-shale floras. Memoirs of the Geological Society of America 185, 341–352.

Gerasimidis, A., Panajiotidis, S., Hicks, S., Athanasiadis, N., 2006. An eight-year record of pollen deposition in the Pieria mountains (N. Greece) and its significance for interpreting fossil pollen assemblages. Review of Palaeobotany and Palynology 141, 231–243.

Giesecke, T., Ammann, B., Brande, A., 2014. Palynological richness and evenness: insights from the taxa accumulation curve. Vegetation History and Archaeobotany 23, 217–228.

Giesecke, T., Bennett, K.D., 2004. The Holocene spread of *Picea abies* (L.) Karst. in Fennoscandia and adjacent areas. Journal of Biogeography 31, 1–26.

Giesecke, T., Hickler, T., Kunkel, T., Sykes, M.T., Bradshaw R.H.W., 2007. Towards an understanding of the Holocene distribution of *Fagus sylvatica* L. Journal of Biogeography 34, 118–131.

Giesecke, T., Fontana, S.L., van der Knaap, W.O., Pardoe, H.S., Pidek, I.A., 2010. From early pollen trapping experiments to the pollen monitoring programme. Vegetation History and Archaeobotany 19, 247–258.

Giesecke, T., Wolters, S., Jahns, S., Brande, A., 2012. Exploring Holocene changes in palynological richness in Northern Europe – did postglacial immigration matter? PLos One 7 e51624. Doi:10.1371/journal.pone.0051624.

Giesecke, T., Davis, B., Brewer, S. Finsinger, W., Wolters, S., Blaauw, M., de Beaulieu, J.-L., Binney, H., Fyfe, R.M., Gaillard, M.-J., Gil-Romera, G., van der Knaap, W.O., Kuneš, P., Kühl, N., van Leeuwen, J.F.N., Leydet, M., Lotter, A.F., Ortu, E., Semmler, M., Bradshaw, R.H.W., 2014. Towards mapping the late Quaternary vegetation change of Europe. Vegetation History and Archaeobotany 23, 75–86.

Giesecke, T., Wolters, S., van Leeuwen, J.F., van der Knaap, P.W., Leydet, M., Brewer, S., 2019. Postglacial change of the floristic diversity gradient in Europe. Nature Communications 10(1), 1–7.

Glasspool, I.J., 2003. Hypautochthonous–allochthonous coal deposition in the Permian, South African, Witbank Basin No. 2 seam; a combined approach using sedimentology, coal petrology and palaeontology. International Journal of Coal Geology 53, 81–135.

Glasspool, I.J., Hilton, J., Collinson, M.E., Wang, S.J., 2004. Foliar physiognomy in Cathaysian gigantopterids and the potential to track Palaeozoic climates using an extinct plant group. Palaeogeography, Palaeoclimatology, Palaeoecology 205, 69–110.

Gomez, B., Gillot, T., Daviero-Gomez, V., Coiffard, C., Spagna, P., Yans, J., 2012. Mesofossil plant remains from the Barremian of Hautrage (Mons Basin, Belgium), with taphonomy, paleoecology, and paleoenvironment insights, in: Godefroit, P. (Ed.), Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems. Indiana University Press, Bloomington, pp. 97–112.

Goswami, S., Singh, K.J., 2013. Floral biodiversity and geology of the Talcher Basin, Orissa, India during the Permian–Triassic interval. Geological Journal 48, 39–56.

Goswami, S., Saxena, A., Singh, K.J., Chandra, S., Cleal, C.J., 2018. An appraisal of the Permian palaeobiodiversity and geology of the Ib-River Basin, eastern coastal area, India. Journal of Asian Earth Sciences 157, 283–301.

Grauvogel-Stamm, L., Ash, S.R., 2005. Recovery of the Triassic land flora from the end-Permian life crisis. Comptes Rendus Palevol 4, 593–608.

Grímsson, F., Zetter, R., 2011a. Combined LM and SEM study of the Middle Miocene (Sarmatian) palynoflora from the Lavanttal Basin, Austria: Part II. Pinophyta (Cupressaceae, Pinaceae and Sciadopityaceae). Grana 50, 262–310.

Grímsson, F., Zetter, R., Baal C., 2011b. Combined LM and SEM study of the Middle Miocene (Sarmatian) palynoflora from the Lavanttal Basin, Austria: Part I. Bryophyta, Lycopodiophyta, Pteridophyta, Ginkgophyta, and Gnetophyta. Grana 50, 102–28.

Grímsson, F., Grimm, G.W., Meller, B., Bouchal, J.M., Zetter, R., 2015a. Combined LM and SEM study of the middle Miocene (Sarmatian) palynoflora from the Lavanttal Basin, Austria: Part IV. Magnoliophyta 2 – Fagales to Rosales. Grana 55, 101–63.

Grímsson, F., Meller, B., Bouchal, J.M., Zetter, R., 2015b. Combined LM and SEM study of the middle Miocene (Sarmatian) palynoflora from the Lavanttal Basin, Austria: part III. Magnoliophyta 1 –Magnoliales to Fabales. Grana 54, 85–128.

Grímsson, F., Zetter, R., Labandeira, C.C., Engel, M.S., Wappler, T., 2017. Taxonomic description of *in situ* bee pollen from the middle Eocene of Germany. Grana 56: 37–70.

Habib, D., Groth, P.K., 1967. Paleoecology of migrating Carboniferous peat environments. Palaeogeography, Palaeoclimatology, Palaeoecology 3, 185–195.

Hamilton, A.J., 2005. Species diversity or biodiversity? Journal of Environmental Management 75, 89–92.

Harland, W.B. (Ed.), 1967. The Fossil Record: a symposium with documentation. Geological Society, London.

Herendeen, P.S., Crepet, W.L., Nixon, K.C., 1994. Fossil flowers and pollen of Lauraceae from the Upper Cretaceous of New Jersey. Plant Systematics and Evolution 189, 29–40.

Heyworth, A., Kidson, C., 1982. Sea-level changes in southwest England and Wales. Proceedings of the Geologists' Association 93, 91–111.

Hicks, S., 1985. Modern pollen deposition records from Kuusamo, Finland I. Seasonal and annual variation. Grana 24,167–184.

Hicks, S., 2001. The use of annual arboreal pollen deposition values for delimiting tree-lines in the landscape and exploring models of pollen dispersal. Review of Palaeobotany and Palynology 117, 1–29.

Hicks, S., Ammann, B., Latałowa, M., Pardoe, H., Tinsley, H., 1996. European Pollen Monitoring Programme: Project Description and Guidelines. Oulu University Press, Oulu.

Hicks, S., Helander, M., Heino, S., 1994. Birch pollen production, transport and deposition for the period 1984-1993 at Kevo, Finland. Aerobiologia 10, 183–191.

Hilton, J., Cleal, C.J., 2007. The relationship between Euramerican and Cathaysian tropical floras in the Late Palaeozoic: palaeobiogeographical and palaeogeographical implications. Earth–Science Reviews 85, 85–116.

Hochuli, P.A., Sanson-Barrera, A., Schneebeli-Hermann, E., Bucher, H., 2016. Severest crisis overlooked—Worst disruption of terrestrial environments postdates the Permian–Triassic mass extinction. Nature Scientific Reports, 6:28372 | DOI: 10.1038/srep28372.

Hochuli, P.A., Schneebeli-Hermann, E., Mangerud, G., Bucher, H. 2017. Evidence for atmospheric pollution across the Permian-Triassic transition. Geology 45, 1123–1126.

Hofmann, C.-C., Gregor, H.J., 2018. Scanning electron microscope investigations of pollen from an atypical mid-Eocene coal facies in Stolzenbach mine (PreußenElektra) near Borken (Kassel, Lower Hesse, Germany). Review of Palaeobotany and Palynology 252, 41–63.

Holland, S.M., Sclafani, J.A., 2015. Phanerozoic diversity and neutral theory. Paleobiology 41, 369–376.

Huang, Y., Jia, L., Wang, Q., Mosbrugger, V., Utescher, T., Su, T., Zhou, Z., 2016. Cenozoic plant diversity of Yunnan: a review. Plant Diversity 38, 271–282.

Hughes, N.F., 1963. The assignment of species of fossils to genera. Taxon 12, 336–337.

Hughes, N.F., 1976. Palaeobiology of angiosperms. Cambridge University Press, Cambidge.

Huntley, B., Birks, H.J.B., 1983. An Atlas of Past and Present Pollen Maps for Europe: 0-13000 Years Ago. Cambridge University Press, Cambridge.

Jantz, N., Homeier, J., Behling, H., 2014. Representativeness of tree diversity in the modern pollen rain of Andean montane forests. Journal of Vegetation Science 25, 481–490.

Jaramillo, C., Ochoa, D., Contreras, L., Pagani, M., Carvajal-Ortiz, H., Pratt, L.M., Krishnan, S., Cardona, A., Romero, M., Quiroz, L., Rodriguez, G., et al. 2010. Effects of rapid global warming at the Paleocene-Eocene boundary on neotropical vegetation. Science 330, 957–961.

Jasper, K., Hartkopf-Fröder, C., Flajs, G., Littke, R., 2010. Palaeoecological evolution of Duckmantian wetlands in the Ruhr Basin (western Germany): A palynological and coal petrographical analysis. Review of Palaeobotany and Palynology 162, 123–145.

Johnson, K.R., 2002. The megaflora of the Hell Creek and lower Fort Union formations in the western Dakotas: Vegetational response to climate change, the Cretaceous-Tertiary boundary event, and rapid marine transgression, in: Hartman, J.H., Johnson, K.R., Nichols, D.J. (Eds.), The Hell Creek Formation and the Cretaceous-Tertiary boundary in the northern Great Plains: An integrated continental record of the end of the Cretaceous. Geological Society of America, Special Papers 361, 329–391.

Johnston, M.N., Eble, C.F., O'Keefe, J.M., Freeman, R.L., Hower, J.C., 2017. Petrology and palynology of the Middle Pennsylvanian Leatherwood coal bed, Eastern Kentucky: Indications for depositional environments. International Journal of Coal Geology 181, 23–38.

Kędzior, A., Popa, M.E., 2013. Sedimentology of the Early Jurassic terrestrial Steierdorf Formation in Anina, Colonia Cehă Quarry, South Carpathians, Romania. Acta Geologica Polonica 63, 175–199.

Kędzior, A., Popa, M.E., 2018. An Early Jurassic braided river system from Mehadia, South Carpathians, Romania. Geological Quarterly 62, 415–432.

Khuroo, A.A., Dar, G.H., Khan, Z.S., Malik, A.H., 2007. Exploring an inherent interface between taxonomy and biodiversity: current problems and future challenges. Journal for Nature Conservation 15, 256–261.

Kidwell, S.M., Holland, S.M., 2002. The quality of the fossil record: implications for evolutionary analyses. Annual Review of Ecology and Systematics 33, 561–88.

Knoll, A.H., Niklas, K.J., Tiffney, B.H., 1979. Phanerozoic land-plant diversity in North America. Science 206, 1400–1402.

Köhler, J., Uhl, D., 2014. Die Blatt- und Karpoflora der oberoligozänen Fossillagerstätte Enspel (Westerwald, Rheinland-Pfalz, W-Deutschland). Mainzer naturwissenschaftliches Archiv, Beihefte 35, 1–87.

Kowalewski, M., Kiessling, W., Aberhan, M., Fürsich, F.T., Scarponi, D., Wood, S.L.B., Hoffmeister, A.P., 2006. Ecological, taxonomic, and taphonomic components of the post-Paleozoic increase in sample-level species diversity of marine benthos. Paleobiology 32, 533–561.

Kustatscher, E., van Konijnenburg-van Cittert, J.H.A., Roghi, G., 2010. Macrofloras and palynomorphs as possible proxies for palaeoclimatic and palaeoecological studies: A case study from the Pelsonian (Middle Triassic) of Kühwiesenkopf/Monte Prà della Vacca (Olang Dolomites, N-Italy). Palaeogeography, Palaeoclimatology, Palaeoecology 290, 71–80.

Kustatscher, E., Bernardi, M., Petti, F.M., Franz, M., van Konijnenburg-van Cittert, J.H.A., Kerp, H., 2017. Sea-level changes in the Lopingian (late Permian) of the north-western Tethys and their effects on the terrestrial palaeoenvironments, biota and fossil preservation. Global and Planetary Change 148, 166–180.

Lande, R., 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76, 5–13.

Latałowa, M., van der Knaap, W.O., 2006. Late Quaternary expansion of Norway spruce *Picea abies* (L.) Karst. in Europe according to pollen data. Quaternary Science Reviews 25, 2780–2805.

La Torre, M.D.L.Á., Herrando-Pérez, S., Young, K.R., 2007. Diversity and structural patterns for tropical montane and premontane forests of central Peru, with an assessment of the use of higher-taxon surrogacy. Biodiversity and Conservation 16, 2965–2988.

Laveine, J.P., Belhis, A., 2007. Frond architecture of the seed-fern *Macroneuropteris scheuchzeri*, based on Pennsylvanian specimens from the Northern France coal field. Palaeontographica, Abteilung B 277, 1–41.

Leroy, S.A.G., 1992. Palynological evidence of *Azolla nilotica* Dec. in recent Holocene of eastern Nile Delta, and its environment. Vegetation History and Archaeobotany 1, 43-52.

Leroy, S.A.G., Arpe, K., 2007. Glacial refugia for summer-green trees in Europe and south-west Asia as proposed by ECHAM3 time-slice atmospheric model simulations. Journal of Biogeography 34, 2115–2128.

Leroy, S.A.G., Arpe, K., Mikolajewicz, U., 2011. Vegetation context and climatic limits of the early Pleistocene hominin dispersal in Europe. Quaternary Science Reviews 30, 1448–1463.

Leroy, S.A.G., Boyraz, S., Gürbüz, A., 2009. High-resolution palynological analysis in Lake Sapanca as a tool to detect earthquakes on the North Anatolian Fault. Quaternary Science Reviews 28, 2616–2632.

Leroy, S.A.G., Roiron, P., 1996. Final Pliocene macro and micro floras of Bernasso (Escandorgue, France). Review of Palaeobotany and Palynology 94, 295–328.

Libertín, M., Opluštil, S., Pšenièka, J., Bek, J., Sýkarová, I., Daškova, J., 2009a. Middle Pennsylvanian pioneer plant assemblage buried in situ by volcanic ash-fall, central Bohemia, Czech Republic. Review of Palaeobotany and Palynology 155, 204–233.

Libertín, M., Dašková, J., Opluštil, S., Bek, J., Edress, N., 2009b. A palaeoecological model for a vegetated early Westphalian intramontane valley (Intra-Sudetic Basin, Czech Republic). Review of Palaeobotany and Palynology 155, 175–203.

Lidgard, S., Crane, P.R., 1990. Angiosperm diversification and Cretaceous floristic trends: a comparison of palynofloras and leaf macrofloras. Paleobiology 16, 77–93.

Litsitsyna, O.V, Hicks, S. Huusko, A., 2012. Do moss samples, pollen traps and modern lake sediments all collect pollen in the same way? Vegetation History and Archaeobotany 21, 187–199.

Locatelli, E.R., Krajewski, L., Chochinov, A.V., Laflamme, M., 2016. Taphonomic variance between marattialean ferns and medullosan seed ferns in the Carboniferous Mazon Creek Lagerstätte, Illinois, USA. Palaios 31, 97–110.

Looy, C.V., Brugman, W.A., Dilcher, D.L., Visscher, H., 1999. The delayed resurgence of equatorial forests after the Permian–Triassic ecologic crisis. Proceedings of the National Academy of Sciences 96, 13857–13862.

Looy, C.V., Stevenson, R.A., van Hoof, T.B., Mander, L., 2014. Evidence for coal forest refugia in the seasonally dry Pennsylvanian tropical lowlands of the Illinois Basin, USA. PeerJ 2, p.e630.

López-Merino, L., Leroy, S.A.G., Eshel, A., Epshtein, V., Belmaker, R., Bookman, R., 2016. Using palynology to re-assess the Dead Sea laminated sediments - indeed varves? Quaternary Science Reviews 140, 49–66.

Luthardt, L., Rößler, R., Schneider, J.W., 2016. Palaeoclimatic and site-specific conditions in the early Permian fossil forest of Chemnitz — Sedimentological, geochemical and palaeobotanical evidence. Palaeogeography, Palaeoclimatology, Palaeoecology 441, 627–652.

McElwain, J.C., 2018. Paleobotany and global change: Important lessons for species to biomes from vegetation responses to past global change. Annual Review of Plant Biology 69, 761–787.

McElwain, J.C., Punyasena, S.W., 2007. Mass extinction events and the plant fossil record. Trends in Ecology and Evolution 22, 548–557.

McElwain, J.C., Popa, M.E., Hesselbo, S.P., Haworth, D.M., Surlyk, F., 2007. Macroecological responses of terrestrial vegetation to climatic and atmospheric change across the Triassic/Jurassic boundary in East Greenland. Paleobiology 33, 547–573.

Magurran, A.E., 2004. Measuring biological diversity. Wiley-Blackwell, Oxford.

Mander, L., Punyasena, S.W., 2014. On the taxonomic resolution of pollen and spore records of Earth's vegetation. International Journal of Plant Sciences 175, 931–945.

Mander, L., Kürschner, W.M., McElwain, J.C., 2013. Palynostratigraphy and vegetation history of the Triassic–Jurassic transition in East Greenland. Journal of the Geological Society 170, 37–46.

Mauquoy, D., Hughes, P.D.M., Van Geel, B., 2010. A protocol for plant macrofossil analysis of peat deposits. Mires and Peat 7, 1–5.

Meyen, S.V., 1984. Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record. Botanical Review 50, 1–111.

Mitsumoto, K., Yabusaki, K., Aoyagi, H., 2009. Classification of pollen species using autofluorescence image analysis. Journal of Bioscience and Bioengineering 107, 90–94.

Moir, A., Leroy, S.A.G., Brown, D., Collins, P., 2010. Dendrochronological evidence for a lower water table on peatland around 3200-3000 BC from sub-fossil pine in northern Scotland. The Holocene 20, 931–942.

Niklas, K.J., Tiffney, B.H., 2010. The quantification of plant biodiversity through time. Philosophical Transactions of the Royal Society of London, Series B 345, 35–44.

Niklas, K.J., Tiffney, B.H., Knoll, A.H., 1980. Apparent changes in the diversity of fossil plants. Evolutionary Biology 12, 1–89.

Nowak, H., Schneebeli-Hermann, E., Kustatscher, E., 2019. A non-extinction event for plants during the end-Permian mass extinction. Nature Communications, doi.org/10.1038/s41467-018-07945-w.

Opluštil, S., Pšenička, J., Libertín, M., Šimůnek, Z., 2007. Vegetation patterns of Westphalian and lower Stephanian mire assemblages preserved in tuff beds of the continental basins of Czech Republic. Review of Palaeobotany and Palynology 143, 107–154.

Opluštil, S., Pšenička, J., Libertín, M., Bashforth, A., Šimůnek, Z., 2009a. A Middle Pennsylvanian (Bolsovian) peat-forming forest preserved in situ in volcanic ash of the Whetstone Horizon in the Radnice Basin, Czech Republic. Review of Palaeobotany and Palynology 155, 234–274.

Opluštil, S., Pšenička, J., Libertín, M., Bek, J., Dašková, J., Šimůnek, Z., Drábková, J., 2009b. Composition and structure of an *in situ* Middle Pennsylvanian peat-forming plant assemblage in volcanic ash, Radnice Basin (Czech Republic). Palaios 24, 726–746.

Opluštil, S., Pšenička, J., Bek, J., Wang. J., Feng, Z., Libertín, M., Šimůnek, Z., Bureš, J., Drábková, J., 2014. T^0 peat-forming plant assemblage preserved in growth position by volcanic ash-fall: A case study from the Middle Pennsylvanian of the Czech Republic. Bulletin of Geosciences 89, 773–818.

Opluštil, S., Šimůnek, Z., Pšenička, J., Bek, J., Libertín, M., 2017. A 25 million year macrofloral record (Carboniferous–Permian) in the Czech part of the Intra-Sudetic Basin; biostratigraphy, plant diversity and vegetation patterns. Review of Palaeobotany and Palynology 244, 241–307.

Pan, Y.-L., Hill, S.C., Pinnick, R.G., House, J.M., Flagan, R.C., Chang, R.K., 2011. Dual-excitation-wavelength fluorescence spectra and elastic scattering for differentiation of single airborne pollen and fungal. Atmospheric Environment 14, 1555–1563.

Pardoe, H.S., 1996. Micro-scale patterns of modern pollen deposition within three alpine plant communities. New Phytologist 132, 327–341.

Pardoe, H.S., 2001. The representation of taxa in surface pollen spectra on alpine and sub-alpine glacier forelands in southern Norway. Review of Palaeobotany and Palynology 117, 63–78.

Pardoe, H.S., 2006. Surface pollen deposition on glacier forelands in southern Norway I: local patterns of representation and source area at Storbreen, Jotunheimen. The Holocene 16, 1149–1161.

Pardoe, H.S., Giesecke, T., van der Knaap, W.O., Svitavská-Svobodová, H., Kvavadze, E.V., Panajiotidis, S., Gerasimidis, A., Pidek, I.A., Zimny, M., Świeta-Musznicka, J., Latalowa, M., Noryskiewicz, A.M., Bozilova, E., Tonkov, S., Filipova-Marinova, M.V., van Leeuwen, J.F.N., Kalniņa, L., 2010. Comparing pollen spectra from modified Tauber traps and moss samples: examples from a selection of woodlands across Europe. Vegetation history and Archaeobotany 19, 271–283.

Parsons, R.W., Prentice, I.C., 1981. Statistical approaches to R-values and the pollen—vegetation relationship. Review of Palaeobotany and Palynology 32, 127–152.

Petit, R.J., Brewer, S., Bordacs, S., et al., 2002. Identification of refugia and post-glacial colonisation routes of European white oaks based on chloroplast DNA and fossil pollen evidence. Forest Ecology and Management 156, 49–74.

Pfefferkorn, H.W., Gastaldo, R.A., DiMichele, W.A., Phillips, T.L., 2008. Pennsylvanian tropical floras from the United States as a record of changing climate, in: Fielding, C.R., Frank, T.D., Isbell, J.L. (Eds.), Resolving the Late Paleozoic Ice Age in Time and Space. Geological Society of America Special Paper 441, 305–316.

Pfefferkorn, H.W., Gastaldo, R.A., DiMichele, W.A., 2017. Impact of an icehouse climate interval on tropical vegetation and plant evolution. Stratigraphy 14, 365–376.

Phillips, T.L., 1980. Stratigraphic and geographic occurrences of permineralized coal-swamp plants–Upper Carboniferous and Europe, in: Dilcher, D.L., Taylor, T.N. (Eds.), Biostratigraphy of fossil plants. Hutchinson & Ross, Stroundsburg, PA, pp. 25–92.

Pidek, I.A., 2004. Preliminary results of pollen trapping in the region of the Roztocze National Park (SE Poland). Annales of the University M. Curie-Sklodowska, Sect. B 49, 143–159.

Pidek, I.A., Svitavská-Svobodová, H., van der Knaap, W.O., Noryśkiewicz, A.M., Filbrandt-Czaja, A., Noryśkiewicz, B., Latałowa, M., Zimny, M., Święta-Musznicka, J., Bozilova, E., Tonkov, S., Filipova-Marinova, M., Poska, A., Giesecke, T., Gikov, A., 2010. Variation in annual pollen accumulation rates of *Fagus* along a N–S transect in Europe based on pollen traps. Vegetation history and Archaeobotany 19, 259–270.

Piperno, D.R., 2002. Phytoliths, in: Mulholl, S.C, Rapp, G. (eds.) Tracking environmental change using lake sediments. Springer, Dordrecht, pp. 235–251.

Piperno, D.R., Pearsall, D.M., 1998. The silica bodies of tropical American grasses: morphology, taxonomy, and implications for grass systematics and fossil phytolith identification. Smithsonian Institution, Washington DC (Contributions to Botany 85).

Poinar, G., jr, 2002. Fossil palm flowers in Dominican and Baltic amber. Botanical Journal of the Linnean Society 139, 361–367.

Pole, M., 2001. Repeated flood events and fossil forests at Curio Bay (Middle Jurassic), New Zealand. Sedimentary Geology 144, 223–242.

Popa, M.E., 1998. The Liassic continental flora of Romania: Systematics, stratigraphy and paleoecology. Acta Botanica Horti Bucurestensis 1997–1998, 177–184.

Popa, M.E., 2000. Aspects of Romanian Early Jurassic palaeobotany and palynology. Part III. Phytostratigraphy of the Getic Nappe. Acta Palaeontologica Romaniae 2, 377–386.

Popa, M.E., 2011. Field and laboratory techniques in plant compressions: an integrated approach. Acta Palaeontologica Romaniae 7, 279–283.

Popa, M.E., 2014. Early Jurassic bennettitalean reproductive structures of Romania. Palaeobiodiversity and Palaeoenvironments 94, 327–362.

Poska, A., Pidek, I.A., 2010. Pollen dispersal and deposition characteristics of *Abies alba*, *Fagus sylvatica* and *Pinus sylvestris*, Roztocze region (SE Poland). Vegetation History and Archaeobotany 19, 91–101.

Potonié, R., 1934. Zur Morphologie der fossilen Pollen und Sporen. Arbeiten aus dem Institut für Paläobotanik und Petrographie Brennsteine 4, 5–24

Potonié, R., 1956. Synopsis der Gattungen der Sporae dispersae, Teil 1: *Sporites*. Geologisches Jahrbuch 23, 1–103.

Potonié, R., 1958. Synopsis der Gattungen der Sporae dispersae. II. Teil: *Sporites* (Nachträge), *Saccites*, *Aletes, Praecolpates, Polyplicates, Monocolpates*. Geologisches Jahrbuch 31, 1–114.

Potonié, R., 1960. Synopsis der Gattungen der Sporae dispersae: III. Teil: Nachträge *Sporites*, Fortsetzung *Pollenites* mit Generalregister zu Teil I-II. Geologisches Jahrbuch 39, 1–189.

Powell, M.G., Kowalewski, M., 2002. Increase in evenness and sampled alpha diversity through the Phanerozoic: comparison of early Paleozoic and Cenozoic marine fossil assemblages. Geology 30, 31–334.

Procter, C.J., 1994. Carboniferous fossil plant assemblages and palaeoecology at the Writhlington Nature Reserve. Proceedings of the Geologists' Association 105, 277–286.

Pšenička, J., Opluštil, S., 2013. The epifytic plants in the fossil record and its example from in situ tuff from Pennsylvanian of Radnice Basin (Czech Republic). Bulletin of Geosciences 88, 401–416.

Rashid, I., Mir, S.H., Zurro, D., Dar, R.A., Reshi, Z.A., 2019. Phytoliths as proxies of the past. Earth-Science Reviews 194, 234–250.

Raup, D.M., Sepkoski, J.J., 1982. Mass extinctions in the marine fossil record. Science 215**,** 1501–1503.

Reitalu, T., Bjune, A.E., Blaus, A., Giesecke, T. Helm, T., Matthias, I., Peglar, S.M., Salonen, J.S., Seppä, H., Väli, V., Birks, H.J.B., 2019. Patterns of modern pollen and plant richness across northern Europe. Journal of Ecology 107, 1662–1677.

Reitalu, T., Kuneš, P., Giesecke, T., 2014. Closing the gap between plant ecology and Quaternary palaeoecology. Journal of Vegetation Science 25, 1188–1194.

Rice, J., Rothwell, G.W., Mapes, G., Mapes, R.H., 1996. *Suavitas imbricata* gen. et sp. nov., an anatomically preserved seed analogue of putative lycophyte affinities from Upper Pennsylvanian marine deposits. American Journal of Botany 83, 1083–1090.

Roopnarine, P.D., Angielczyk, K.D., Weik, A., Dineen, A., 2018. Ecological persistence, incumbency and reorganization in the Karoo Basin during the Permian-Triassic transition. Earth-Science Reviews 189, 244–263.

Rößler, R., Barthel, M., 1998. Rotliegend taphocoenoses preservation favoured by rhyolithic explosive volcanism. Freiberger Forschungshefte, Paläontologie, Stratigraphie, Fazies C 474(6), 59–101.

Rothwell, G.W., Mapes, G., Mapes, R.H., 1996. Anatomically preserved vojnovskyalean seed plants in Upper Pennsylvanian (Stephanian) marine shales of North America. Journal of Paleontology 70, 1067-1079.

Rull, V., 2011. Neotropical biodiversity: timing and potential drivers. Trends in Ecology and Evolution 26, 508–513.

Rull, V., 2013. Some problems in the study of the origin of neotropical biodiversity using palaeoecological and molecular phylogenetic evidence. Systematics and Biodiversity 11, 415–423.

Rust, J., Singh, H., Rana, R.S., McCann, T., Singh, L., Anderson, K., Sarkar, N., Nascimbene, P.C., Stebner, F., Thomas, J.C., et al., 2010. Biogeographic and evolutionary implications of a diverse paleobiotain amber from the early Eocene of India. Proceedings of the National Academy of Sciences 107, 18360–18365.

Sadowski E.-M., Schmidt A.R., Seyfullah L.J., Kunzmann L., 2017. Conifers of the ‘Baltic amber forest’ and their palaeoecological significance. Stapfia 106, 1–73.

Sadowski, E.M., Seyfullah, L.J., Regalado, L., Skadell, L.E., Gehler, A., Gröhn, C., Hoffeins, C., Hoffeins, H.W., Neumann, C., Schneider, H., Schmidt, A.R., 2019. How diverse were ferns in the Baltic amber forest? Journal of Systematics and Evolution 57, 305–328.

Saxena, A., Singh, K.J., Cleal, C.J., Chandra, S., Goswami, S., Shabbar, H., 2018. Development of the Glossopteris flora and its end Permian demise in the Tatapani–Ramkola Coalfield, Son–Mahanadi Basin, India. Geological Journal 54, 2472–2494.

Saxena, A., Murthy, S., Singh, K.J., 2020. Floral diversity and environment during the early Permian: a case study from Jarangdih Colliery, East Bokaro Coalfield, Damodar Basin, India. Palaeobiodiversity and Palaeoenvironments 100, 33–50.

Scheihing, M.H., Pfefferkorn, H.W., 1984. The taphonomy of land plants in the Orinoco Delta: a model for the incorporation of plant parts in clastic sediments of Late Carboniferous age of Euramerica. Review of Palaeobotany and Palynology 41, 205–240.

Schmidt, A.R., Ragazzi, E., Coppellotti, O., Roghi, G., 2006. A microworld in Triassic amber – Amber as old as the first dinosaurs captured the diversity of microbial life 220 million years ago. Nature 444, 835–836.

Scott, A.C., 1978. Sedimentological and ecological control of Westphalian B plant assemblages from West Yorkshire. Proceedings of the Yorkshire Geological Society 41, 461–508.

Scott, A.C., 1979. The ecology of Coal Measure floras from northern Britain. Proceedings of the Geologists' Association 90, 97–116.

Sepkoski, J.J., jr, 1978. A kinetic-model of phanerozoic taxonomic diversity I. Analysis of marine orders. Paleobiology 4, 223–251.

Sepkoski, J.J., jr 1979. A kinetic-model of phanerozoic taxonomic diversity II. Early phanerozoic families and multiple equilibria. Paleobiology 5, 222–251.

Sepkoski, J.J., jr, 1984. A kinetic-model of phanerozoic taxonomic diversity III. Post-Paleozoic families and mass extinctions. Paleobiology 10, 246–267.

Sepkoski, J.J., jr, 1988. Alpha, beta, or gamma: where does all the diversity go? Paleobiology 14, 221–234.

Seppä, H., Bennett, K.D., 2003. Quaternary pollen analysis: recent progress in palaeoecology and palaeoclimatology. Progress in Physical Geography 27, 548–579.

Serbet, R., Rothwell, G.W., 1992. Characterizing the most primitive seed ferns. I. A reconstruction of *Elkinsia polymorpha*. International Journal of Plant Sciences 153, 602–621.

Servais, T., Cascales-Miñana, B., Cleal, C.J., Gerrienne, P., Harper, D.A., Neumann, M., 2019. Revisiting the Great Ordovician Diversification of land plants: Recent data and perspectives. Palaeogeography, Palaeoclimatology, Palaeoecology 534, 13 pp.

Silvestro, D., Cascales-Miñana, B., Bacon, C.D., Antonelli, A., 2015. Revisiting the origin and diversification of vascular plants through a comprehensive Bayesian analysis of the fossil record. New Phytologist 207, 425–436.

Šimůnek, Z., 2007. New classification of the genus *Cordaites* from the Carboniferous and Permian of the Bohemian Massif, based on cuticle micromorphology. Sborník Národního Muzea v Praze, Serie B, Přírodní Vìdy 62, 97–210.

Sjögren, P., van der Knaap, W.O., van Leeuwen, J.F.N., 2015. Pollen dispersal properties of Poaceae and Cyperaceae: first estimates of their absolute pollen productivities. Review of Palaeobotany and Palynology 216, 123–131.

Slater, B.J., McLoughlin, S., Hilton, J., 2015. A high-latitude Gondwanan lagerstätte: the Permian permineralised peat biota of the Prince Charles Mountains, Antarctica. Gondwana Research 27, 1446–1473.

Smith, A.H.V., 1962. The palaeoecology of Carboniferous peats based on the microspores and petrography of bituminous coals. Proceedings of the Yorkshire Geological Society 33, 423–474.

Smith, A.H.V., 1968. Seam profiles and seam characters, in: Murchison, D.G., Westoll, T.S. (Eds.), Coal and coalbearing strata. Oliver and Boyd, Edinburgh, pp. 31–40.

Smith, A.H.V., Butterworth, M.A., 1967. Miospores in the coal seams of the Carboniferous of Great Britain. Palaeontological Association, (Special Papers in Palaeontology 1).

Solórzano Kraemer, M.M., Delclòs, X., Clapham, M., Arillo A., Peris, D., Jäger, P., Stebner, F., Peñalver E., 2018. Arthropods in modern resins reveal if amber accurately recorded forest arthropod communities. Proceedings of the National Academy of Sciences 115, 6739–6744.

Spicer, R.A., 1980. The importance of depositional sorting to the biostratigraphy of plant megafossils, in: Dilcher, D.L., Taylor, T.N. (Eds.), Biostratigraphy of fossil plants. Dowden, Hutchinson and Ross, Stroudsburg PA, pp. 171–183.

Spicer, R.A., 1981. The sorting and deposition of allochthonous plant material in a modern environment at Silwood Lake, Silwood Park, Berkshire, England. Professional Papers of the U.S. Geological Survey 1143, 1–77.

Steart, D.C., Boon, P.I., Greenwood, D.R., Diamond, N.T., 2002. Transport of leaf litter in upland streams of *Eucalyptus* and *Nothofagus* forests in south-eastern Australia. Archiv für Hydrobiologie 156, 43–61.

Steemans P., Lepot, K., Marshall, C.P., le Herissé, A., Javaux, E.J., 2010. FTIR characterisation of the chemical composition of Silurian miospores (cryptospores and trilete spores) from Gotland, Sweden. Review of Palaeobotany and Palynology 162, 577–590.

Stein, W.E., Berry, C.M., Hernick, L.V., Mannolini, F., 2012. Surprisingly complex community discovered in the mid-Devonian fossil forest at Gilboa. Nature 483, 78.

Sternberg, K.M. von, 1820. Versuch einer geognostisch–botanischen Darstellung der Flora der Vorwelt, Vol. I. 1. F. Fleischer, Leipzig

Stolle, E., 2007. Regional Permian palynological correlations: Southeast Turkey – Northern Iraq. Comunicações Geológicas 94, 125–143.

Stolle, E., 2010. Recognition of southern Gondwanan palynomorphs at Gondwana's northern margin – and biostratigraphic correlation of Permian strata from SE Turkey and Australia, in: Shen, S.-Z., Henderson, C.M., Somerville, I.D. (Eds.), Lopingian (Late Permian) stratigraphy of the world, major events and environmental change. Geological Journal 45, 336–349.

Stolle, E., 2011. Pollen-dominated European palynological assemblages from the Permian of NW Turkey (Asia Minor) palaeogeographical context and microfloral affinities. Geological Quarterly 55, 181–186.

Stolle, E., 2012. Co-occurrence of *Sinuspores sinuatus* (Artüz) Ravn, 1986 with established palynological markers indicating younger strata: AK-1X well section (Pennsylvanian, Zonguldak Basin, NW Turkey) and the correlation to the stratigraphic system. Geologia Croatica 65, 375–385.

Stolle, E., 2016. Çakraz Formation, Çamdağ area, NW Turkey: early/mid-Permian age, Rotliegend (Germany) and Southern Alps (Italy) equivalent—a stratigraphic re-assessment via palynological long-distance correlation. Geological Journal 51, 223–235.

Stolle, E., Yalçın, M.N., Kozlu, H. 2012. Palynofacies and bulk organic geochemistry of Permian clastics in the eastern Taurids: Implications for hydrocarbon potential, in: Yalçın, M.N., Çorbacıoğlu, H., Aksu, Ö., Bozdoğan, N. (Eds.), Paleozoic of northern Gondwana and its petroleum potential. Turkish Association of Petroleum Geologists, Ankara (Special Publication 6), pp. 119–122.

Strömberg, C.A., 2004. Using phytolith assemblages to reconstruct the origin and spread of grass-dominated habitats in the great plains of North America during the late Eocene to early Miocene. Palaeogeography, Palaeoclimatology, Palaeoecology 207, 239–275.

Strömberg, C.A., 2011. Evolution of grasses and grassland ecosystems. Annual Review of Earth and Planetary Sciences 39, 517–544.

Strömberg, C.A., Dunn, R.E., Crifò, C., Harris, E.B., 2018. Phytoliths in paleoecology: analytical considerations, current use, and future directions, in: Croft, D.A., Su, D., Simpson, S.W. (Eds.), Methods in paleoecology. Springer, Cham, pp. 235–287.

Strullu-Derrien, C., Kenrick, P., Knoll, A.H., 2019. The Rhynie chert. Current Biology 29, 1218–1223.

Sugita, S.A., 1993. Model of pollen source area for an entire lake surface. Quaternary Research 39, 239–244.

Swingland, I.R., 2001. Biodiversity, definition of, in: Levin, S.A. (Ed.), Encyclopedia of biodiversity. Volume 1. Academic Press, San Diego, pp. 377–391.

Taylor, T.N., Taylor, E.L., Kings, M., 2009. Paleobiology. The biology and evolution of fossil plants. [Second Edition]. Academic Press, Burlington.

Thomas, B.A., 1987. The use of in-situ spores for defining species of dispersed spores. Review of Palaeobotany and Palynology 51, 227–233.

Thomas, B.A., 2005. A reinvestigation of *Selaginella* species from the Asturian (Westphalian D) of the Zwickau coalfield, Germany and their assignment to the new sub genus *Hexaphyllum*. Zeitschrift der Deutschen Gesellschaft für Geowissenschaften 156, 403–418.

Thomas, B.A., 2014. In situ stems: preservation states and growth habits of the Pennsylvanian (Carboniferous) calamitaleans based upon new studies of *Calamites* Sternberg, 1820 in the Duckmantian at Brymbo, North Wales, UK. Palaeontology 57, 21–36.

Thomas, B.A., Cleal, C.J., 2015. Cyclones and the formation of plant beds in late Carboniferous tropical swamps. Palaeobiodiversity and Palaeoenvironments 95, 531–536.

Thomas, B.A., Seyfullah, L.J., 2015. *Stigmaria* Brongniart: a new specimen from Duckmantian (Lower Pennsylvanian) Brymbo (Wrexham, North Wales) together with a review of known casts and how they were preserved. Geological Magazine 152, 858–870.

Thomas, B.A., Cleal, C.J., 2020. The nomenclature of fossil-taxa representing different preservational states: *Lepidodendron* as a case-study. Taxon, doi.org/10.1002/tax.12291.

Thomas, B.A., Dimitrova, T.K., 2017. Ecological changes in Pennsylvanian (Asturian and early Cantabrian) coal floras inferred from lycophyte microspore abundances. Earth Science Reviews 171, 646–662.

Thomas, B.A., Appleton, P., Cleal, C.J., Seyfullah, L.J., 2020. The distribution of plant fossils and their palaeoecology in Duckmantian (Bashkirian, Lower Pennsylvanian) strata at Brymbo, North Wales, UK. Geological Journal 55, 3179–3207.

Tinner, W., Lotter, A.F., 2006. Holocene expansions of *Fagus sylvatica* and *Abies alba* in Central Europe: where are we after eight decades of debate? Quaternary Science Reviews 25, 526–549.

Tomescu, A.M., Bomfleur, B., Bippus, A.C., Savoretti, A., 2018. Why are bryophytes so rare in the fossil record? A spotlight on taphonomy and fossil preservation, in: Krings, M., Harper, C.J., Cuneo, N.R., Rothwell, G.W. (Eds.), Transformative paleobotany. Elsevier, Amsterdam, pp. 375–416.

Traverse, A., 1988. Plant evolution dances to a different beat. Plant and animal evolutionary mechanisms compared. Historical Biology 1, 227–301.

Traverse, A., 2007. Paleopalynology (2nd edition). Springer, Dordrecht.

Tuomisto, H., 2012. An updated consumer’s guide to evenness and related indices. Oikos 121, 1203–1218.

Uhl, D., 2006. Some considerations on the taphonomy of conifer remains from the Late Permian of Europe. Neues Jahrbuch für Geologie & Paläontologie, Monatshefte 08/2006, 483–502.

Uhl, D. 2015. Preliminary note on fossil flowers and inflorescences from the Late Oligocene of Enspel (Westerwald, W-Germany). Palaeobiodiversity and Palaeoenvironments 95, 47–53.

Uhl, D., Cleal, C.J., 2010. Late Carboniferous vegetation change in lowland and intramontane basins. International Journal of Coal Geology 83, 318–328.

Uhl, D., Krüger, P.S., Wuttke, M., 2018. Epidermal anatomy of *Glyptostrobus europaeus* (Brongn.) Unger from the late Oligocene of the Westerwald (Rhineland-Palatinate, W-Germany). Fossil Imprint 74, 334–340.

Urban, M.A., Nelson, D.M., Jiménez-Moreno, G., Châteauneuf, J.J., Pearson, A., Hu, F.S., 2010. Isotopic evidence of C_4 grasses in southwestern Europe during the Early Oligocene–Middle Miocene. Geology 38, 1091–1094.

Vajda, V., Bercovici, A., 2014. The global vegetation pattern across the Cretaceous–Paleogene mass extinction interval: A template for other extinction events. Global and Planetary Change 122, 29–49.

van der Knaap, W.O., van Leeuwen, J.F., Finsinger, W., Gobet, E., Pini, R., Schweizer, A., Valsecchi, V., Ammann, B., 2005. Migration and population expansion of *Abies*, *Fagus*, *Picea*, and *Quercus* since 15000 years in and across the Alps, based on pollen-percentage threshold values. Quaternary Science Reviews 24, 645–680.

Vellend, M., Cornwell, W.K., Magnuson-Ford, K., Mooers, A.Ø., 2011. Measuring phylogenetic biodiversity, in: McGill, B.J., Magurran, A. (eds.), Biological diversity: frontiers in measurement and assessment. Oxford University Press, Oxford, pp. 194–207.

Vellend, M., Baeten, L., Becker-Scarpitta, A., Boucher-Lalonde, V., McCune, J.L., Messier, J., Myers-Smith, I.H., Sax, D.F., 2017. Plant biodiversity change across scales during the Anthropocene. Annual Review of Plant Biology 68, 563–586.

Wagner, R.H., 1989. A late Stephanian forest swamp with *Sporangiostrobus* fossilized by volcanic ash fall in the Puertollano Basin, central Spain. International Journal of Coal Geology 12, 523–552.

Wagner, R.H., Diez, J.B., 2007. Verdeña (Spain): Life and death of a Carboniferous forest community. Compte Rendu Palevol 6, 495–504

Wang Deming, Qin Min, Liu Le, Liu Lu, Zhou Yi, Zhang Yingying, Huang Pu, Xue Jinzhuang, Zhang Shuhui, Meng Meicen, 2019. The most extensive Devonian fossil forest with small lycopsid trees bearing the earliest stigmarian roots. Current Biology 29, 2604–2615.

Wang Jun, Pfefferkorn, H.W., Zhang Yi, Feng Zhou, 2012. Permian vegetational Pompeii from Inner Mongolia and its implications for landscape paleoecology and paleobiogeography of Cathaysia. Proceedings of the National Academy of Sciences 109, 4927–4932.

Wellman, C.H., 2010. The invasion of the land by plants: when and where? New Phytologist 188, 306–309.

Weng, C., Hooghiemstra, H., Duivenvoorden, J.F., 2006. Challenges in estimating past plant diversity from fossil pollen data: statistical assessment, problems, and possible solutions. Diversity and distributions 12, 310–318.

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30, 279–338.

Whittaker, R.H., 1977. Evolution of species diversity in land communities. Evolutionary Biology 10, 1–67.

Whittaker, R.J., Willis, K.J., Field, R., 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography 28, 453–470.

Willard, D.A., 1993. Vegetational patterns in the Springfield coal (Middle Pennsylvanian, Illinois Basin): comparison of miospore and coal-ball records. Geological Society of America, Special Paper 286, 139–152.

Willard, D.A., Donders, T.H., Reichgelt, T., Greenwood, D.R., Sangiorgi, F., Peterse, F., Nierop, K.G., Frieling, J., Schouten, S., Sluijs, A., 2019. Arctic vegetation, temperature, and hydrology during Early Eocene transient global warming events. Global and Planetary Change 178, 139–152.

Willard, D.A., Phillips, T.L., Lesnikowska, A.D., DiMichele, W.A., 2007. Paleoecology of the Late Pennsylvanian-age Calhoun coal bed and implications for long-term dynamics of wetland ecosystems. International Journal of Coal Geology 69, 21–54.

Williams, J.W., Grimm, E.C., Blois, J.L., Charles, D.F., Davis, E.B., Goring, S.J., Graham, R.W., Smith, A.J., Anderson, M., Arroyo-Cabrales, J., Ashworth, A.C., 2018. The Neotoma Paleoecology Database, a multiproxy, international, community-curated data resource. Quaternary Research 89, 156–177.

Willis, K.J., Bennett, K.D., Bhagwat, S.A., Birks, H.J.B., 2010. Perspective 4°C and beyond: What did this mean for biodiversity in the past? Systematics and Biodiversity 8, 3–9.

Willis, K.J., Bhagwat, S.L., 2009. Biodiversity and climate change. Science 326, 806–807.

Willis, K.J., McElwain, J., 2013. The evolution of plants (2nd edition). Oxford University Press, Oxford.

Willis, K.J., Niklas, K.J., 2004. The role of Quaternary environmental change in plant macroevolution: the exception or the rule? Philosophical Transactions of the Royal Society B Biological Series 359, 159–72.

Willis, K.J., Rudner, E., Sümegi, P., 2000. The full-glacial forests of central and southeastern Europe. Quaternary Research 53, 203–213.

Wing, S.L., DiMichele, W.A., 1992. Ecological characterization of fossil plants, in: Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.-D., Wing, S.L. (Eds.) Terrestrial ecosystems through time. University of Chicago Press, Chicago, pp. 139–180.

Wing, S.L., DiMichele, W.A., 1995. Conflict between local and global changes in plant diversity through geological time. Palaios 10, 551–564.

Wing, S.L., Harrington, G.J., Bowen, G.J., Koch, P.L., 2003. Floral change during the initial Eocene thermal maximum in the Powder River Basin, Wyoming, in: Wing, S.L., Gingerich, P.D., Schmitz, B., Thomas, E. (Eds.), Causes and Consequences of Globally Warm Climates in the Early Paleogene. Geological Society of America, Boulder, Colorado, (Special Paper 369), pp. 425-440.

Wolfe, J.A., 1993. A method of obtaining climatic parameters from leaf assemblages. U.S. Geological Survey Bulletin 2040, 1–71.

Xing, Y., Gandolfo, M.A., Onstein, R.E., Cantrill, D.J., Jacobs, B.F., Jordan, G.J., Lee, D.E., Popova, S., Srivastava, R., Su, T., Vikulin, S.V., 2016. Testing the biases in the rich Cenozoic angiosperm macrofossil record. International Journal of Plant Sciences 177, 371–388.

Xiong C., Wang D., Wang Q., Benton, M.J., Xue J., Meng M., Zhao Q., Zhang, J., 2013. Diversity dynamics of Silurian–Early Carboniferous land plants in South China. PLoS One 8(9), p.e75706.

Yu, J., Broutin, J., Chen, Z.Q., Shi, X., Li, H., Chu, D., Huang, Q., 2015. Vegetation changeover across the Permian–Triassic Boundary in Southwest China: extinction, survival, recovery and palaeoclimate: a critical review. Earth-Science Reviews 149, 203–224.

Zavialova, N., Kustatscher, E., van Konijnenburg-van Cittert, J.H.A., 2010. Spore ultrastructure of *Selaginellites leonardii* and diversity of Selaginellalean spores. Geo.Alp 7, 1–17.

Figure captions

Fig. 1. Variation in productivity of different organs of a plant as illustrated by the pollen, flowers, leaves, shoots, stem and roots of a hypothetical modern-day angiosperm tree. Redrawn and adapted from Hughes (1976, fig. 3.6) and Cleal and Thomas (2019, fig. 10.4).

Fig. 2. Three types of diversity that can be recognised in the plant fossil record, using the Middle Pennsylvanian (c. 310 Ma) swamp vegetation of Variscan Euramerica, based on Cleal et al. (2012).

Fig. 3. Morphological similarity of late Permian gigantopterid leaves (A, C, *Gigantonoclea hallei* (Halle) Wang) and modern angiosperm leaves (B, *Castanea sativa* Miller; D, *Quercus robur* L.). All scale bars = 10 mm. A, C, Naturhistoriska Riksmuseet (NRM), Stockholm (A, NRM S128498; C, NRM S128494), B, D, Royal Botanic Gardens Edinburgh herbarium (RBGE). Adapted from Glasspool et al. (2004).

Fig. 4. Partial reconstruction of the Late Devonian seed plant *Elkinsia* based on associated fronds, ovulate structures and anatomically preserved stems. Drawn from by Annette Townsend (based on Serbet and Rothwell 1992).

Fig. 5. Examples of the differences in the fossil-genera represented by Carboniferous arborescent lycopsids and sphenopsids. Adapted from Cleal and Thomas (2019).

Fig. 6. Spores of fern *Weischelia reticulata* (Stokes and Webb) Fontaine showing different maturation stages; Escucha Formation (Albian), Escucha, northern Teruel Province, Spain. A, General view of a soral cluster up to 2 mm in diameter showing tightly packed peltate indusia. B, Tightly-packed spores grouped inside a receptaculum. C, Inaperturate, discoidal spores with smooth exine and lacking trilete mark. D, Packed spores showing different ontogenetic stages. D, E, Fully-developed tetragonal spores with well-rounded corners and

clear trilete scar. Original unpublished material from the study in Diez et al (2005) with permission of the authors.

Fig. 7. T^0 fossil or submerged forests of arborescent lycopsids in the Carboniferous of the UK. A, Fossil trees rooted in a coal seam being exposed at Brymbo, north Wales (Appleton et al. 2010). B, Excavated trees in the Victoria Park, Glasgow (Thomas and Seyfullah 2015).

Fig. 8. Palaeozoic wetland vegetation preserved in the lower unit of the early Moscovian Whetstone Horizon (Bělka tuff), Ovčin, Central Bohemia, Czech Republic. A, Remains of cordaites and arborescent lycopsids plotted out on an exposed area of the tuff divided into 1 m^2 quadrats; the small number against each specimen represents the height above the base of the tuff that the fossil occurred. B, Reconstruction of forest based on the type of plots shown in Fig. 7A. From Opluštil et al. (2014).

Fig. 9. Comparison of palynological and macrofloral spectra obtained from roof-shales overlying four Moscovian-age coal seams in South Wales, UK, between the Daren Ddu Seam at the base and the Llantwit No. 1 Seam at the top. Redrawn from Dimitrova et al. (2005, fig. 4).

Fig. 10. Range of basinal and extra-basinal vegetation represented in Moscovian (late Carboniferous) palynospectra from the Sydney Coalfield, Cape Breton, Canada (Dimitrova et al. 2011).

Fig. 11. The Evolutionary Floras model of vegetation evolution based on a factor analysis of global plant-family distribution through the Phanerozoic (Cleal and Cascales-Miñana 2014).

Fig. 12. Factors that affect how we interpret past vegetation diversity from the macrofloral and palynological records, demonstrating the importance of integrating the two sets of data.

Table 1. Fossil-genera assigned to different parts of six representative plants from the main groups in the late Carboniferous tropical coal swamps. The fossil-genera selected to represent each plant group in taxonomic diversity studies (e.g. Cleal et al. 2012) designated by an asterisk (*). This does not include the pollen/spores produced by these plants.

		Lycospids	Calamites	Sphenophylls	Marattialeans	Medullosaleans	Cordaites
Stems		*Lepidophloios**	*Calamites*	*Sphenophyllum**	*Caulopteris*	-	*Artisia*
Foliage		*Cyperites*	*Annularia**		*Cyathocarpus**	*Alethopteris**	*Cordaites**
Reproductive structures	Female	*Lepidocarpon* *Lepidostrobophyllum*	*Calamostachys*	*Bowmanites*		*Trigonocarpus*	*Cardiocarpus*
	Male	*Lepidostrobus*				*Whittleseya*	*Cordaitanthus*
Rooting structures		*Stigmaria*	*Pinnularia*	-	-	-	-
Total fossil-genera		6	4	2	2	3	4