

Palaeobotanical experiences of plant diversity in deep time. 1:

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1 **Palaeobotanical experiences of plant diversity in deep time. 1:**

2 **How well can we identify past plant diversity in the fossil record?**

3
4 Christopher J. Cleal^{a§}, Heather S. Pardoe^a, Christopher M. Berry^b, Borja Cascales-Miñana^c,
5 Basil A.S. Davis^d, Jose B. Diez^e, Mariana V. Filipova-Marinova^f, Thomas Giesecke^g, Jason
6 Hilton^h, Dimiter Ivanovⁱ, Evelyn Kustatscher^j, Suzanne A. G. Leroy^k, Jennifer C. McElwain^l,
7 Stanislav Opluštil^m, Mihai Emilian Popaⁿ, Leyla J. Seyfullah^o, Ellen Stolle^p, Barry A.
8 Thomas^q and Dieter Uhl^r

9 ^a Department of Natural Sciences, National Museum Wales, Cardiff CF10 3NP, UK,
10 chris.cleal@museumwales.ac.uk, heather.pardoe@museumwales.ac.uk

11 ^b School of Earth and Ocean Sciences, Cardiff University, Cardiff CF10 3AT, UK,
12 berrycm@cardiff.ac.uk

13 ^c CNRS, Univ. Lille, UMR 8198, Evo-Eco-Paleo, F-59000, Lille, France, [borja.cascales-](mailto:borja.cascales-minana@univ-lille.fr)
14 minana@univ-lille.fr

15 ^d Institute of Earth Surface Dynamics IDYST, University of Lausanne, Bâtiment Géopolis
16 CH-1015, Lausanne, Switzerland, basil.davis@unil.ch

17 ^e Department of Marine Geosciences and Land Management, Universidade de Vigo, 36310
18 Vigo, Spain, jbdiez@uvigo.es

19 ^f Varna Regional Museum of History, 41 Maria Louisa Boulevard, 9000 Varna, Bulgaria

20 ^g Palaeoecology, Department of Physical Geography, University of Utrecht, P.O. Box 80115,
21 3508 TC, Utrecht, The Netherlands, t.giesecke@uu.nl

22 ^h School of Geography, Earth and Environmental Sciences, University of Birmingham,
23 Birmingham, B15 2TT, UK, j.m.hilton@bham.ac.uk

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

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

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

31 ^l School of Biology and Environmental Science, University College Dublin, Ireland,
32 jennifer.mcelwain@gmail.com

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

35 ⁿ Southwest Petroleum University, School of Geosciences and Technology, 8, Xindu Ave.,
36 610500 Xindu, Chengdu, China; University of Bucharest, Faculty of Geology and
37 Geophysics, Department of Geology and Doctoral School of Geology, Laboratory of
38 Palaeontology, 1, N. Bălcescu Ave., 010041, Bucharest, Romania, mihai@mepopa.com

39 ^o Department of Palaeontology, University of Vienna, Althanstraße 14, 1090 Vienna, Austria,
40 leyla.seyfullah@univie.ac.at

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

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

44 ^r Senckenberg Forschungsinstitut und Naturmuseum, 60325 Frankfurt am Main, Germany,
45 dieter.uhl@senckenberg.de

46 [§] Corresponding author

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48

49 **Abstract**

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

65

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

67

68 **1 Introduction**

69 Vegetation has played a central role in the evolution of the Earth's biosphere, atmosphere
70 and landscape (Beerling 2007; Davies and Gibling 2010; Wellman 2010; Willis and
71 McElwain 2013); whilst it is possible to envisage a world having evolved with plants but no
72 animals, a world of animals without plants could not function. The raised public awareness of
73 the important ecosystem services provided by vegetation, including carbon capture to help
74 mitigate climate change, providing the foundations of all terrestrial trophic systems, and the
75 psychological benefits it brings to mankind, has resulted in a global research programme on
76 today's plant diversity and ecology (Antonelli et al. 2020). However, this only provides a
77 snapshot of a continuous ecological and evolutionary play that has taken place through some
78 500 million years of "Deep Time". To appreciate properly the significance of events such as
79 the current biodiversity crisis ("the 6th mass extinction") and to anticipate potential outcomes,
80 it is vital that we understand this history of vegetation evolution.

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

86 This is one of two papers arising from a workshop on past plant diversity entitled
87 *Tracking changes in plant diversity over the last 400 million years*, which brought together
88 specialists on diversity studies in fossil floras ranging in age from Devonian to Quaternary .
89 The aim was to explore the different analytical methodologies and interpretative approaches
90 used to investigate Phanerozoic plant diversity dynamics. The present contribution addresses
91 what exactly we mean by biodiversity and to what extent can we extract biodiversity patterns
92 from the plant fossil record. We will attempt to look at the relevant issues surrounding both

93 plant macrofossils (i.e. fossils that can normally be seen with the naked eye, including
94 compressions / impressions / adpressions, casts / moulds and anatomically preserved fossils –
95 see Cleal and Thomas 2019) and microfossils (pollen, spores and phytoliths). The issues
96 surrounding sampling and analytical methods used will be discussed in our second paper (in
97 preparation).

98 **2 What is biodiversity?**

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

105 Taxonomic diversity in ecological studies consists of two factors: taxonomic richness
106 and taxonomic evenness (Tuomisto 2012). Taxonomic richness (the number of taxa present)
107 might be expected to be relatively easy to measure in both modern-day habitats and the fossil
108 record; Magurran (2004) has suggested that this alone can be a sensitive indicator of
109 ecological change. However, total richness can be difficult to determine if there are rare
110 species present, as these may be missed in surveys. A far more nuanced understanding of the
111 functioning of a flora will be obtained by determining its taxonomic evenness using
112 measurements such as Simpson's Index (e.g. Lande 1996; Veech et al. 2002) but this is only
113 really meaningful if it is reflecting the relative numbers of the organisms present. Variations
114 in the productivity of pollen, foliage and seeds between different plant parts (Fig. 1) mean
115 that taxonomic evenness of fossil-taxa in a fossil flora will bear little or no relationship to the
116 taxonomic evenness of the original vegetation. The situation is particularly complex with

117 foliage, especially in pre-Cenozoic floras where the leaves are often compound structures that
118 fragmented in different ways during abscission, transportation and preservation. Taxonomic
119 evenness of a fossil flora may therefore be strongly influenced by taphonomy and how the
120 plants fragmented post-mortem; although such data may provide some evidence as to relative
121 biomass allocation within the vegetation (e.g. Baker and DiMichele 1997), its value for
122 determining taxonomic evenness is limited.

123 Scale will clearly be critical in any diversity study, whether palaeontological or
124 biological (Bennington et al. 2009). R.H. Whittaker (1960) developed the most frequently
125 used concepts of taxonomic diversity for extant biotas, broadly recognised as α -diversity
126 (diversity in particular habitats) and β -diversity (diversity between habitats within a
127 landscape); these were then integrated to provide a γ -diversity (overall diversity within the
128 landscape). R.H. Whittaker (1977) later extended this scheme to include δ -diversity (diversity
129 between landscapes in a biogeographical province) and ϵ -diversity (overall diversity within
130 that province). However, R.H. Whittaker's (1960) terms were intentionally rather vague and
131 as a consequence have been used by different scientists in different ways (see Swingland
132 2001; Magurran 2004; Hamilton 2005 for reviews).

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

136 (1) Local-scale diversity: the diversity of plant fossils observed in a single locality and
137 which probably reflects plant diversity within c. 1000 m² (c. 30 m x 30 m). In a palynological
138 context, it might more realistically refer to vegetation within up to 1 km². This will broadly
139 equate to the α -diversity of the parent vegetation.

140 (2) Landscape-scale diversity: the diversity of plant fossils observed within a typical
141 depositional basin and which probably reflects plant diversity within up to c. 10^5 km² (c. 300
142 km x 300 km) This will broadly equate to the γ -diversity of the parent vegetation.

143 (3) Regional-scale diversity: the diversity of plant fossils observed within a
144 palaeofloristic province and probably reflects plant diversity within more than 10^5 km². This
145 will broadly equate to the ϵ -diversity of the parent vegetation.

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

150 **3 Taxonomic problems**

151 *3.1 Macrofossil taxonomy*

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

158 With Cenozoic macrofloras (including Quaternary) it is often still possible to work with
159 whole-plant taxa (e.g. Huang et al. 2016) but the situation is more difficult with older floras
160 where palaeobotanists are dealing with extinct groups. Only rarely are completely
161 reconstructed organisms available to work with; even if a whole, articulated plant is
162 preserved (e.g. the early seed plant *Elkinsia* – Fig. 3) anatomical details are never completely
163 preserved. Palaeobotanists working on these stratigraphically older floras therefore use a

164 different taxonomic approach. Although this has changed in detail over the years (Cleal and
165 Thomas 2010), the underlying principle has in effect remained the same since the time of
166 Sternberg (1820) and Brongniart (1822): different parts of the plant are classified and named
167 separately as fossil-taxa (Turland et al. 2018, Art. 1.2). Mostly these are fossil-species and
168 fossil-genera, although in principle they can be of any rank (see Cleal and Shute 2012 for an
169 example of using fossil-families).

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

183 The problem with using fossil-taxa for diversity studies is that a simple summation of the
184 names listed in published taxonomic lists will both significantly overestimate the number of
185 biological species represented, and distort the relative representation of the different plant
186 groups present (Cleal et al. 2012). For instance, in Carboniferous arborescent lycopsids, a
187 single biological species may be represented by up to six separate compression fossil-species,
188 whereas sphenopsids in the same flora may only have four fossil-species (Fig. 4; Table 1). An

189 added complication is that the fossil-taxa of the different plant parts are probably indicative
190 of different taxonomic ranks of the original organism: for instance, *Stigmaria ficoides*
191 (Sternberg) Brongniart is a fossil-species of phylogenetically conservative lycopsid rootstock
192 that effectively cannot be distinguished across many members of the order, whereas the stems
193 and cones have more sophisticated combinations of derived evolutionary characters and so
194 their fossil-species probably correlate better with the biological species of the organisms.

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

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

221 3.2 *Palynotaxa*

222 Palynological studies on Quaternary floras tend to use whole-plant taxa, based on
223 morphological comparisons with pollen that have been extracted from living plants. It is
224 sometimes possible to distinguish pollen from closely related plant species based purely on
225 morphology but often palynological studies tend to focus mainly on differentiating plants at
226 the generic rank. Attempts have been made to use DNA barcoding to improve the taxonomic
227 resolution in Quaternary studies (e.g. Seppä and Bennett 2003); for instance, Petit et al.
228 (2002) demonstrated that the modern genetic diversity of oak is consistent with the pollen
229 evidence in a study of post-glacial oak migration. However, most Quaternary palynological
230 studies remain essentially morphology-based.

231 With older floras, the known relationship between the pollen / spores and their parent
232 plants is less certain and so palynologists have developed separate taxonomic schemes
233 (Chaloner 1999). Some proposed taxonomies are completely artificial with the taxa defined
234 purely on morphological criteria with a non-Linnaean nomenclature, such as used in many
235 oil-company palynological databases and in the Biorecords methodology of Hughes (1963)
236 (see Traverse, 2007 for a review). Other taxonomies use a Linnaean-style nomenclature but
237 with taxa that were still essentially morphological (e.g. Potonié 1956, 1958, 1960) and it is

238 this approach which is most usually widely used today in pre-Neogene studies (e.g. Jasper et
239 al. 2010; Stolle 2007, 2012, 2016; Hochuli et al. 2016).

240 Because the botanical affinities of many pre-Neogene palynotaxa are uncertain, it can be
241 difficult to translate observed palynodiversity trends into floristic trends. Thomas (1987) and
242 Mander and Punyasena (2014) suggested that the situation could be improved by revising the
243 diagnoses of palynotaxa based on evidence from in situ palynomorphs in fructifications, data
244 which is now being increasingly collated (e.g. Balme 1995; Bek 2017). Experience with
245 Palaeogene and Neogene pollen and spores has also shown that a combination of light
246 microscopy and scanning electron microscopy based on individual grains (Ferguson et al.
247 2007), although very time consuming, can help to improve their assignment to a particular
248 plant genus or family, or perhaps even to map it into an established framework represented by
249 one or more phylogenetic trees. (e.g. Grímsson et al. 2011a,b, 2015a,b). Chemical analysis
250 such as using FTIR (Fourier Transform Infra-Red) and fluorescence spectroscopy can also be
251 helpful in determining affinities of particular palynomorphs (e.g. Mitsumoto et al. 2009;
252 Steemans et al. 2010; Urban et al. 2010). This approach has shown that more traditional
253 approaches utilizing only light microscopy tend to underestimate the number of taxa present
254 in a palynoflora (Hofmann and Gregor 2018).

255 An added complication is the variation in morphology of pollen and spores during
256 maturation, as shown for instance in the fern *Weichselia reticulata* (Stokes and Webb)
257 Fontaine (Fig. 5). This is not an issue in most diversity studies on dispersed palynofloras, as
258 plants do not normally release their pollen or spores before they are fully mature. However, if
259 a plant has been subjected to trauma such as a storm, immature pollen and spores may be
260 prematurely released and preserved, and this could inflate the diversity of a palynofloras.
261 Although labour intensive, it is possible to determine whether different morphologies

262 represent different states of maturity or just variability of miospore forms within a species
263 using sporoderm ultrastructure analysis (e.g. Zavialova et al. 2010).

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

271 3.3 *Taxonomic rank*

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

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

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

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

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

308 But how closely do family dynamics mirror diversity dynamics at lower taxonomic
309 ranks? Analyses on modern-day tropical forests suggest that family and species diversity
310 patterns are broadly similar (e.g. Enquist et al. 2002; Jantz et al. 2014) especially if the data
311 are log transformed to reduce the effect of dominant families (La Torre et al. 2007); see also

312 comments by Giesecke et al. (2019) and Reitalu et al. (2019) on Holocene data from Europe.
313 However, this does not take into account the taphonomic filter that fossil floras have been
314 subjected to; many Palaeozoic and Mesozoic plant fossils cannot be assigned to families due
315 to missing, or difficult to deduce, features of reproductive organs or cauline anatomy,
316 suggesting the fossil record of families is incomplete. On the other hand, regional- and
317 global-scale vegetation analyses (e.g. Cascales-Minana et al. 2013) may benefit from using
318 family data because they may help smooth out some of the sampling problems encountered in
319 such large-scale analyses. This is clearly a subject that needs further investigation.

320 **4 Representativeness of data**

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

335 4.1 *Macrofloral data*

336 Autochthonous floras (sometimes misleadingly referred to as “Lagerstätten”) provide the
337 most reliable data on original plant diversity, especially at a local-scale, but these are rare.
338 One of the best documented is the Devonian Rhynie Chert (e.g. Edwards et al. 2018;
339 Garwood et al. 2019; Strullu-Derrien et al. 2019) where an in situ and almost complete
340 terrestrial biota is preserved including relatively small, herbaceous plants. Autochthonous
341 fossil floras with larger, woody plants are much rarer. There are exceptions, such as the
342 Palaeozoic swamp forests that were rapidly covered by volcanic ash (Sections 5.1, 5.2); but
343 more usually, the so-called T⁰ fossil or submerged forests (DiMichele and Falcon-Lang 2011)
344 are only partly autochthonous. They form where an area of forests has been engulfed by a
345 flood of sediment and casts of the stumps have been preserved in situ (e.g. Fig. 6; for other
346 examples see Heyworth and Kidson 1982; Francis 1983; Gastaldo 1985; Pole 2001; Calder et
347 al. 2006; Wagner and Diez 2007; Moir et al. 2010; Stein et al. 2012; Berry and Marshall
348 2015; Thomas and Seyfullah 2015; Falcon-Lang et al. 2016), but most of the herbaceous
349 ground-cover and liana species have been winnowed-out (Thomas 2014). Other types of
350 “fossil forests” consist of petrified logs preserved as log-jams that have been subject to
351 varying degrees of transportation (e.g. Falcon-Lang and Bashforth 2005) and thus also
352 difficult to use for diversity studies.

353 More typically, plant beds occur in fluvio-lacustrine deposits, where disarticulated plant
354 remains have accumulated after varying degrees of transportation either by wind or water
355 (Burnham 1989; Gastaldo et al. 1995, Kędzior and Popa 2013, 2018; Thomas and Cleal
356 2015). This is in marked contrast to many fossil faunal communities, which tend to be much
357 less prone to transportation (Kidwell and Holland 2002). Many attempts at palaeoecological
358 studies on such plant beds have documented in great detail the sedimentological context
359 where the fossils occur (e.g. Scott 1978, 1989; Gomez et al. 2012; Kędzior and Popa 2013,

360 2018). Detailed, three-dimensional sampling such as in underground coal mines along
361 directional and transversal galleries and in coal extraction chambers in particular can provide
362 valuable data (e.g. Gastaldo 1985; DiMichele and Nelson 1989; Popa 1998, 2011, 2014;
363 DiMichele et al. 2007, 2017; Barbacka et al. 2016).

364 However, the plant remains will have been transported over varying distances, making it
365 difficult to translate the observed distribution of the fossils into original plant diversity
366 (Gastaldo 1992). In a few cases, the fossils in such plant beds seem to have been subjected to
367 only limited transport, such as where a river-bank bank has collapsed and the plant remains
368 have become entombed in a crevasse-splay (e.g. Cleal and Thomas 1988; Laveine and Belhis
369 2007). More usually, however, the plant remains are at least partly allochthonous. Actualistic
370 studies suggest they will include only a variable representation of the immediately local
371 vegetation (e.g. Burnham 1989, 1994) mixed with remains derived from riparian vegetation
372 growing some distance upstream (Spicer 1980, 1981; Scheihing and Pfefferkorn 1984;
373 Ferguson 1985; Gastaldo et al. 1987; Gastaldo and Huc 1992).

374 By carefully documenting the co-occurrence of species within individual beds, the
375 composition of individual plant communities can be estimated (e.g. Procter 1994; Bashforth
376 et al. 2010, 2011; Barbacka 2012; Barbacka et al. 2016; Thomas et al. 2020). However,
377 locating those communities in the original vegetation / habitat matrix requires a detailed
378 understanding of the sedimentology of the deposits (DiMichele and Gastaldo 2008; Reitalu et
379 al. 2014) and is at best difficult. Moreover, taphonomic factors may distort the observed
380 diversities. Variations in edaphic conditions can cause variable post-mortem decay of the
381 plant tissue (Gastaldo 1992; Gastaldo and Demko 2011). It has been suggested that
382 differential decay of plant groups may distort the species composition (Scott 1979; Wing and
383 DiMichele 1995) although the effect of this may have been exaggerated (Locatelli et al. 2016;
384 Tomescu et al. 2018). More significant may be differential sorting of the plant remains during

385 transportation: smaller plant fragments will tend to travel further and softer, heavier plant
386 fragments sink more quickly (e.g. Steart et al. 2002). Some element of time-averaging may
387 even occur within a single plant bed depending on depositional rates of the sediment.

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

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

406 Fossil floras can also occur in maar lake deposits (e.g. the Messel World Heritage Site –
407 Collinson et al. 2012). Such lakes are caused by phreatomagmatic explosions resulting from
408 the interaction of erupting magma and water, and can occur almost anywhere within a
409 landscape and thus may be surrounded by a different type of vegetation to that growing

410 adjacent to lakes formed in fluvio-lacustrine settings. For instance, the late Oligocene Norken
411 fluvio-lacustrine deposits contain predominantly remains of riparian and swamp vegetation
412 (Uhl et al. 2018) but these are almost totally absent from the nearby, almost contemporary
413 Enspel maar lake deposits (Köhler and Uhl 2014). Plant remains in such lakes also
414 experience less hydro-mechanical stress due to water transport and so can preserve delicate
415 plant structure such as flowers (e.g. Uhl 2015).

416 4.2 *Palynological data*

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

427 Another problem is the great variation in pollen productivity between different plant
428 species. Current evidence for northern and temperate latitudes suggests that Quaternary
429 palynological data are particularly robust for most trees (with a few notable exceptions such
430 as *Larix*) and wind-pollinated taxa, and provide a good measure of broad-scale plant richness
431 over several thousands of kilometres (Reitalu et al. 2019); this is less so for tropical
432 environments due to the higher number of insect-pollinated plants. Among herbs, the Poaceae
433 are the most abundant wind-pollinated plants, and their pollen can be widely dispersed.
434 However, the source of Poaceae and Cyperaceae pollen can be difficult to elucidate because

435 these species occur in a wide range of plant communities. It can also be impossible to identify
436 their pollen to species level other than in cultivated cereals (Pardoe 2001; Sjögren et al.
437 2015), although phytoliths can be of help here (see below). Most other herbs tend to be under
438 represented in pollen spectra (Leroy and Roiron 1996) as the pollen are dispersed by other
439 vectors and so are not so abundantly produced; they also often have a lower preservation
440 potential. There have been relatively few studies of the representation of herbs in pollen
441 assemblages (Pardoe 2001; Bunting et al. 2016) but the presence of so called “indicator taxa”
442 in pollen samples can give strong evidence that such plants were growing locally (Pardoe
443 1996, 2001, 2006). Data can also be supplemented by evidence from in situ pollen from
444 flowers (e.g. Herendeen et al. 1994) and in exceptional cases from fossils of pollinating
445 animals (e.g. Grímsson et al. 2017).

446 Recent initiatives such as the Pollen Monitoring Programme (PMP) are now helping us
447 gain a greater understanding of the relationship between pollen, vegetation and environmental
448 variables. The PMP has been instrumental in the publication of several decades-long records
449 from across Europe (Hicks et al. 1996; Giesecke et al. 2010). The PMP has addressed a
450 variety of problems including the representation of individual taxa (Hicks et al. 1994; Hicks,
451 2001, Ertl et al 2012; Pidek et al. 2010), the representation of plant communities (van der
452 Knaap et al. 2001; Pidek 2004; Gerasimidis et al. 2006), and the influence of sampling
453 medium on palynological diversity (Pardoe et al. 2010; Litsitsyna et al. 2012).

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

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

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

473 *4.3 Pollen and macrofossil data compared*

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

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

493 **5 Diversity studies**

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

497 *5.1 Local-scale diversity*

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

506 Palynological data tend to be even more problematic for local-scale diversity studies due
507 to variations in how far the palynomorphs have been transported. For instance, pollen of

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

519 Local-scale past plant diversity is best determined in the rare autochthonous fossil floras
520 although even here the data are often incomplete (Section 4.1). Some of the best examples of
521 autochthonous floras preserving forest vegetation including both the trees and herbaceous
522 plants are in Palaeozoic volcanic ash-fall deposits (e.g. Wagner 1989; Rössler and Barthel
523 1998; Wang et al. 2012; Luthardt et al. 2016). Examples studied in great detail are in an ash
524 band in the early Moscovian Radnice Coal in the Czech Republic, where about 0.5 m of
525 volcanic ash engulfed an area of swamp vegetation. The lower part of the deposit contains in
526 situ stumps and the groundcover vegetation, which, because the ash fell almost vertically,
527 was mostly not winnowed out. The upper parts of the ash band, in contrast, includes remains
528 of the upper parts of the trees, together with epiphytes and lianas, brought down by the
529 weight of the ash sometime after the deposit had fallen (Pšenička and Opluštil 2013). A
530 careful survey of the plant remains in different levels of the ash deposit (Fig. 8) not only
531 allowed the reconstruction of the taxonomic composition, spatial distribution and density of

532 vegetation cover, but also revealed evidence of plant to plant interactions and living strategies
533 in extraordinary detail (Opluštil et al. 2007, 2009a,b, 2014; Libertín et al. 2009a).

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

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

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

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

567 5.2 *Landscape-scale diversity*

568 Studies on compression fossil diversities across depositional basins (e.g. Cleal 2005,
569 2007, 2008a; Goswami and Singh 2013; Huang et al. 2016; Opluštil et al. 2017; Goswami et
570 al. 2018; Roopnarine et al. 2018; Saxena et al. 2020) tend to be based on plant remains from a
571 narrow band of habitats. For instance, compressions from the Pennsylvanian swamps of
572 Euramerica appear to have been dominated by remains of the vegetation growing on clastic
573 substrates such as flood-plains, levees and sand banks, whereas the peat-substrate vegetation,
574 which in fact dominated these swamps, is often poorly represented (Cleal et al. 2012); the
575 peat-substrate vegetation is, in contrast, better represented in the coal ball floras and
576 palynospectra. This is not a problem if the main aim is to document extrinsic effects such as
577 climate or landscape changes, particularly if the sampled habitats are tightly constrained
578 ecologically, but care must be taken not to over-generalise the results in terms of overall
579 vegetation patterns.

580 One of the best sources of detailed data on Palaeozoic landscape-scale diversity are the
581 ash deposits in the Czech Radnice Coal (mentioned in Section 5.1), which have been

582 recorded from numerous localities in both historical collections and several recent
583 excavations. These have allowed lateral variation in the swamp vegetation at one
584 stratigraphical level to be investigated; for instance, studies at the Štílec and Ovčín localities,
585 about 20 km apart, yielded two contrasting assemblages, representing different stages of
586 vegetation succession (Opluštil et al. 2007, 2009a,b, 2014; Libertín et al. 2009a). A similar
587 situation is present in the earliest Permian Wuda ash bed that occurs over an area of more
588 than 60 km², enabling distinct assemblages to be recognised both vertically and laterally
589 (Wang et al. 2012).

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

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

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

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

620 5.3 *Regional-scale and global-scale diversities (Evolutionary floras)*

621 Studies on global-scale faunal diversity (e.g. Sepkoski 1978, 1979, 1984, 1988; Bambach
622 1977; Powell and Kowalewski 2002) have shown a progressive increase in species diversity
623 through the Phanerozoic due to an increase in the spatial density of organisms, especially in
624 shallow marine environments (Holland and Sclafani 2015). Similar global and regional
625 studies at the species rank have been attempted in palaeobotany (e.g. Knoll et al. 1979; Niklas
626 et al. 1980) but were hindered by the lack of suitable, taxonomically robust data sets (Section
627 3.3); also by the failure to take into account geographical (especially latitudinal) variations in
628 taxonomic diversity, as has been shown to be an issue with marine invertebrate diversity
629 dynamics (Close et al. 2020). Analogous palaeobotanical studies would, moreover, be
630 unlikely to answer the same sorts of questions of changes in community structure that were
631 being investigated in the faunal record (Section 4).

632 Analyses within narrow taxonomic (e.g. Cleal 2008b,c) or stratigraphical (e.g. Cleal et al.
633 2010; Barbacka et al. 2014) limits have been attempted at the regional-scale, which make it
634 practical for the taxonomic robustness of the data to be critically assessed. However, most
635 larger-scale studies have tended to be based at supra-generic ranks, usually family. For
636 instance, global Phanerozoic plant diversity dynamics were interpreted using Evolutionary
637 Floras (Fig. 10), identified from a factor analysis of a plant family dataset (Cleal and
638 Cascales-Miñana 2014), and these have been used to describe the broad trajectory of
639 vegetation history (Cleal and Thomas 2019; Cleal 2019). More recently, a similar study on
640 pre-Carboniferous floras at the rank of genus is revealing further details of the early phases of
641 plant terrestrialisation (Capel et al., this volume).

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

656 **6 Why study plant diversity in deep time?**

657 Studies of past plant diversity dynamics are particularly important for providing a
658 comparison with models used to describe the response of vegetation to recent climate change
659 (Willis et al. 2010; Reitalu et al. 2014). For instance, the Quaternary record has indicated that
660 glacial-interglacial changes have induced large-scale shifts in plant distributions (Willis and
661 Bhagwat 2009; Giesecke et al. 2017), although there was sometimes a lag between climatic
662 change and vegetation change (Leroy et al. 2011). Some warm-loving and cold-loving
663 deciduous tree species became extinct in Europe during glacial phases (Willis and Niklas
664 2004; Bertini 2010), due not only to climate change, but also to disease, competition and
665 extreme conditions in refugia (Leroy 2007). For those species that survived the glacial
666 phases, refugia such as in southern Europe were essential (Bennett et al. 1991; Leroy and
667 Arpe 2007). In contrast, conifers and some climatically less sensitive angiosperm trees found
668 refugia further north in Europe during glacial phases (crypto-refugia; Willis et al. 2000;
669 Bhagwat and Willis 2008) whereas herbaceous species typical of tundra and steppe
670 vegetation have been forced into upland refugia during the forest dominated phase of the
671 Holocene (Bennett and Provan 2008). It is evident that these refugia have been vital for the
672 shaping of present-day biogeographical patterns and the assemblage of extant communities
673 (Willis and Bhagwat 2009). Refugia have also been used to explain the responses of
674 vegetation to climate changes in Carboniferous tropical swamps (e.g. Falcon-Lang and
675 DiMichele 2010; Looy et al. 2014).

676 Palynological research has revealed anthropogenic effects on Holocene plant diversity
677 (Giesecke et al. 2012, 2019). For example, Filipova-Marinova et al. (2014) described an
678 8,000 year long record of vegetation change at Varna Lake (Bulgaria) and showed how the
679 vegetation was strongly influenced by human activity, both through woodland clearance and
680 the establishment of agriculture.

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

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

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

705 plant diversity during Ordovician times and global cooling and glaciation (Servais et al.
706 2019).

707 Another major theme of research has been the effect of mass extinctions on vegetation
708 (McElwain and Punyasena 2007; Cascales-Miñana et al. 2013). Clearly extensive destruction
709 of vegetation occurred during three of the five classic “mass extinctions” of Sepkoski (1978,
710 1979, 1984): at the boundaries between the Permian – Triassic (e.g. Looy et al. 1999; Hochuli
711 et al. 2016, 2017), Triassic – Jurassic (e.g. McElwain et al 2007; Mander et al. 2013;
712 McElwain 2018) and Cretaceous – Palaeogene (e.g. Vajda and Bercovici 2014). However, a
713 key criterion for recognising a true mass extinction (Raup and Sepkoski 1982) is that it
714 should significantly disrupt the overall trajectory of evolution and this did not occur with
715 plants at most of these biotic crises (McElwain and Punyasena 2007; Cascales-Miñana 2011,
716 2012; Cascales-Miñana and Cleal 2011; Cascales-Miñana and Diez 2012; Cascales-Miñana et
717 al. 2013). Only at the Permian – Triassic boundary does there seem to have been any
718 significant clade disruption (Cascales-Miñana and Cleal 2014; Cascales-Miñana et al. 2016),
719 and even here the pattern of extinction was more complex than with the marine faunas
720 (Hochuli et al. 2016; Nowak et al. 2019). The fossil record seems to suggest that plants were
721 much less vulnerable to biotic crises compared with faunas (Traverse 1988; McElwain and
722 Punyasena 2007; McElwain et al. 2007; Cascales-Miñana et al. 2018).

723 Identifying vegetation diversity patterns at all scales from the plant fossil record is
724 clearly not easy; whatever the sampling protocol and analytical methods used, the fact will
725 remain that the observed diversity patterns are of the fossils rather than purely of the original
726 vegetation. Nevertheless, the fossil record is the only direct evidence we have of how
727 vegetation has changed through time. By bringing together data from the palaeobotanical and
728 palynological records and interpreting it within the context of the taphonomic filter through
729 which the fossils have passed (Fig. 11) will allow us to understand better how plant-life has

730 responded to changes in climate, landscape and continental configurations, and to the
731 dramatic ecological crises often referred to as mass extinctions.

732 **7 Conclusions**

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

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1689 Figure captions

1690 Fig. 1. Variation in productivity of different organs of a plant as illustrated by the pollen,
1691 flowers, leaves, shoots, stem and roots of a hypothetical modern-day angiosperm tree.

1692 Redrawn and adapted from Hughes (1976, fig. 3.6) and Cleal and Thomas (2019, fig. 10.4).

1693 Fig. 2. Three types of diversity that can be recognised in the plant fossil record, using the
1694 Middle Pennsylvanian (c. 310 Ma) swamp vegetation of Variscan Euramerica, based on Cleal
1695 et al. (2012).

1696 Fig. 3. Morphological similarity of late Permian gigantopterid leaves (A, C, *Gigantonoclea*
1697 *hallei* (Halle) Wang) and modern angiosperm leaves (B, *Castanea sativa* Miller; D, *Quercus*
1698 *robur* L.). All scale bars = 10 mm. A, C, Naturhistoriska Riksmuseet (NRM), Stockholm (A,
1699 NRM S128498; C, NRM S128494), B, D, Royal Botanic Gardens Edinburgh herbarium
1700 (RBGE). Adapted from Glasspool et al. (2004).

1701 Fig. 4. Partial reconstruction of the Late Devonian seed plant *Elkinsia* based on associated
1702 fronds, ovulate structures and anatomically preserved stems. Drawn from by Annette
1703 Townsend (based on Serbet and Rothwell 1992).

1704 Fig. 5. Examples of the differences in the fossil-genera represented by Carboniferous
1705 arborescent lycopsids and sphenopsids. Adapted from Cleal and Thomas (2019).

1706 Fig. 6. Spores of fern *Weischelia reticulata* (Stokes and Webb) Fontaine showing different
1707 maturation stages; Escucha Formation (Albian), Escucha, northern Teruel Province, Spain. A,
1708 General view of a soral cluster up to 2 mm in diameter showing tightly packed peltate
1709 indusia. B, Tightly-packed spores grouped inside a receptaculum. C, Inaperturate, discoidal
1710 spores with smooth exine and lacking trilete mark. D, Packed spores showing different
1711 ontogenetic stages. D, E, Fully-developed tetragonal spores with well-rounded corners and

- 1712 clear trilete scar. Original unpublished material from the study in Diez et al (2005) with
1713 permission of the authors.
- 1714 Fig. 7. T⁰ fossil or submerged forests of arborescent lycopsids in the Carboniferous of the
1715 UK. A, Fossil trees rooted in a coal seam being exposed at Brymbo, north Wales (Appleton et
1716 al. 2010). B, Excavated trees in the Victoria Park, Glasgow (Thomas and Seyfullah 2015).
- 1717 Fig. 8. Palaeozoic wetland vegetation preserved in the lower unit of the early Moscovian
1718 Whetstone Horizon (Bělka tuff), Ovčín, Central Bohemia, Czech Republic. A, Remains of
1719 cordaites and arborescent lycopsids plotted out on an exposed area of the tuff divided into 1
1720 m² quadrats; the small number against each specimen represents the height above the base of
1721 the tuff that the fossil occurred. B, Reconstruction of forest based on the type of plots shown
1722 in Fig. 7A. From Opluštil et al. (2014).
- 1723 Fig. 9. Comparison of palynological and macrofloral spectra obtained from roof-shales
1724 overlying four Moscovian-age coal seams in South Wales, UK, between the Daren Ddu Seam
1725 at the base and the Llantwit No. 1 Seam at the top. Redrawn from Dimitrova et al. (2005, fig.
1726 4).
- 1727 Fig. 10. Range of basinal and extra-basinal vegetation represented in Moscovian (late
1728 Carboniferous) palynospectra from the Sydney Coalfield, Cape Breton, Canada (Dimitrova et
1729 al. 2011).
- 1730 Fig. 11. The Evolutionary Floras model of vegetation evolution based on a factor analysis of
1731 global plant-family distribution through the Phanerozoic (Cleal and Cascales-Miñana 2014).
- 1732 Fig. 12. Factors that affect how we interpret past vegetation diversity from the macrofloral
1733 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	Marattialean	Medullosaleans	Cordaites
Stems		<i>Lepidophloios*</i>	<i>Calamites</i>	<i>Sphenophyllum*</i>	<i>Caulopteris</i>	-	<i>Artisia</i>
Foliage		<i>Cyperites</i>	<i>Annularia*</i>			<i>Alethopteris*</i>	<i>Cordaites*</i>
Reproductive structures	Female	<i>Lepidocarpon</i>			<i>Cyathocarpus*</i>	<i>Trigonocarpus</i>	<i>Cardiocarpus</i>
		<i>Lepidostrobophyllum</i>	<i>Calamostachys</i>	<i>Bowmanites</i>			
	Male	<i>Lepidostrobus</i>				<i>Whittleseya</i>	<i>Cordaitanthus</i>
Rooting structures		<i>Stigmara</i>	<i>Pinnularia</i>	-	-	-	-
Total fossil-genera		6	4	2	2	3	4