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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?**

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46

47 **Abstract**

48 Palaeobotany and palynology are the main direct sources of evidence for studying
49 vegetation diversity dynamics through geological time. However, plant fossil diversity is

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

63

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

65

66 1 Introduction

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

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

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

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

96 **2 What is biodiversity?**

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

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

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

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

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

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

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

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

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

148 3 Taxonomic problems

149 3.1 Macrofossil taxonomy

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

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

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

168 Exactly how a fossil-taxon is defined is a subjective matter and is not covered by the
169 regulations in the *International Code of Nomenclature* (Turland et al. 2018), but then this is
170 no different from neobotany. Because of the constraints of the fossil record (e.g. the inability
171 to test hypotheses relating to reproductive isolation or molecular phylogenetics) fossil-taxa
172 have to be defined largely on morphological and/or anatomical criteria (Bateman and Hilton
173 2009). As with neobotanical systematics (Williams and Ebach 2020, p. 354), however,
174 distributional discontinuities can be helpful guides as to the best morphological and/or
175 anatomical criteria for circumscribing natural taxa of fossils; for instance, it makes little sense
176 to regard fronds of Carboniferous and Triassic ferns with morphologically similar pinnae as
177 conspecific or even cogenetic. However, since most diversity studies at the rank of species or
178 genus tend not to be making comparisons over such long time-scales, this is probably not a
179 significant problem here.

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

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

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

210 The situation is further complicated in that the same plant preserved in different ways
211 (e.g. petrifications and compressions) will be recorded as different fossil-taxa (Galtier 1986;

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

218 3.2 *Palynotaxa*

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

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

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

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

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

268 3.3 *Taxonomic rank*

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

275 Local- and landscape-scale plant macrofossil diversity studies tend to be based on
276 normalised inventories of fossil-species or possibly fossil-genera (Section 3.1). However,
277 species are currently impractical when dealing with diversity changes at regional- or global-
278 scales, and over longer time-scales, as the datasets become too large to collate and check
279 objectively by any individual scientist or team. Even where a large amount of species data
280 has been historically accumulated, such as for the Pennsylvanian Subsystem (see comments
281 by Pfefferkorn et al. 2017), there have been few attempts to collate them coherently and
282 critically. Where such collations have been attempted (e.g. Niklas et al. 1980; Lidgard and
283 Crane 1990), methodological and sampling issues occurred (see comments by Niklas and
284 Tiffney 2010; Cascales-Miñana et al. 2013). Moreover, these early collations were not

285 published and so cannot be subjected to subsequent critical taxonomic re-assessment, making
286 the robustness of the resulting analyses difficult to judge.

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

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

305 But how closely do family dynamics mirror diversity dynamics at lower taxonomic
306 ranks? Analyses on modern-day tropical forests suggest that family and species diversity
307 patterns are broadly similar (e.g. Enquist et al. 2002; Jantz et al. 2014) especially if the data
308 are log transformed to reduce the effect of dominant families (La Torre et al. 2007); see also
309 comments by Giesecke et al. (2019) and Reitalu et al. (2019) on Holocene data from Europe.

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

317 **4 Representativeness of data**

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

332 4.1 *Macrofloral data*

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

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

357 2018). Detailed, three-dimensional sampling such as in underground coal mines along
358 directional and transversal galleries and in coal extraction chambers in particular can provide
359 valuable data (e.g. Gastaldo 1985; DiMichele and Nelson 1989; Popa 1998, 2011, 2014;
360 DiMichele et al. 2007, 2017; Barbacka et al. 2016).

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

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

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

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

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

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

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

413 4.2 *Palynological data*

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

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

432 these species occur in a wide range of plant communities. It can also be impossible to identify
433 their pollen to species level other than in cultivated cereals (Pardoe 2001; Sjögren et al.
434 2015), although phytoliths can be of help here (see below). Most other herbs tend to be under
435 represented in pollen spectra (Leroy and Roiron 1996) as the pollen are dispersed by other
436 vectors and so are not so abundantly produced; they also often have a lower preservation
437 potential. There have been relatively few studies of the representation of herbs in pollen
438 assemblages (Pardoe 2001; Bunting et al. 2016) but the presence of so called “indicator taxa”
439 in pollen samples can give strong evidence that such plants were growing locally (Pardoe
440 1996, 2001, 2006). Data can also be supplemented by evidence from in situ pollen from
441 flowers (e.g. Herendeen et al. 1994) and in exceptional cases from fossils of pollinating
442 animals (e.g. Grímsson et al. 2017).

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

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

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

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

470 4.3 *Pollen and macrofossil data compared*

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

481 Because palynological samples may contain palynomorphs from different habitats, it can be
482 difficult to determine the local-scale vegetation patterns within individual habitats; it may
483 also help explain why palynospectra tend to be more diverse than the macrofloras found in
484 the same bed (e.g. Dimitrova et al. 2005). However, as our understanding of the natural
485 affinities of many palynotaxa is improving, palynology is providing increasingly refined
486 evidence of landscape-scale vegetation diversities (Section 5.2).

487 It is evident that one data source is not better than the other for diversity studies: rather,
488 that palaeobotany and palynology are complementary, and are best investigated in tandem
489 (Birks 2000; Kustatscher et al. 2010; Reitalu et al. 2014; Costamagna et al. 2018).

490 **5 Diversity studies**

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

494 *5.1 Local-scale diversity*

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

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

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

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

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

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

544 Coal deposits often yield well-preserved palynomorphs, which have been extensively
545 used for biostratigraphical studies revealing evidence of the temporal changes in vegetation
546 (e.g. Smith and Butterworth 1967). If intercalated fine-siliciclastic (shaley) coal-bearing
547 samples are also included, palynological assemblages can be particularly species rich. As
548 with the macrofloras, regional to exotic palynomorphs derived from extra-basinal vegetation
549 (Fig. 9) may also be present, which can be ideal for palynological correlation purposes (e.g.
550 Stolle 2007, 2010), but can confuse local-scale micro-macro diversity analyses and the
551 interpretation of vegetational distribution patterns (e.g. Dimitrova et al. 2005). Palynology
552 has also been used to investigate the ecological development of the swamps (e.g. Smith 1962,
553 1968; Habib and Groth 1967; Jasper et al. 2010; Johnston et al. 2017; Eble et al. 2019) and to

554 look at plant diversity at the rank of genus and higher (e.g. Dimitrova and Cleal 2007;
555 Libertín et al. 2009b; Thomas and Dimitrova 2017), but direct translation of the resulting
556 palynological spectra into plant species diversity is difficult.

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

565 5.2 *Landscape-scale diversity*

566 Studies on adpression fossil diversities across depositional basins (e.g. Cleal 2005, 2007,
567 2008a; Goswami and Singh 2013; Huang et al. 2016; Opluštil et al. 2017; Goswami et al.
568 2018; Roopnarine et al. 2018; Saxena et al. 2020) tend to be based on plant remains from a
569 narrow band of habitats. For instance, adpressions from the Pennsylvanian swamps of
570 Euramerica appear to have been dominated by remains of the vegetation growing on clastic
571 substrates such as flood-plains, levees and sand banks, whereas the peat-substrate vegetation,
572 which in fact dominated these swamps, is often poorly represented (Cleal et al. 2012); the
573 peat-substrate vegetation is, in contrast, better represented in the coal ball floras and
574 palynospectra. This is not a problem if the main aim is to document extrinsic effects such as
575 climate or landscape changes, particularly if the sampled habitats are tightly constrained
576 ecologically, but care must be taken not to over-generalise the results in terms of overall
577 vegetation patterns.

578 One of the best sources of detailed data on Palaeozoic landscape-scale diversity are the
579 ash deposits in the Czech Radnice Coal (mentioned in Section 5.1), which have been
580 recorded from numerous localities in both historical collections and several recent
581 excavations. These have allowed lateral variation in the swamp vegetation at one
582 stratigraphical level to be investigated; for instance, studies at the Štílec and Ovčín localities,
583 about 20 km apart, yielded two contrasting assemblages, representing different stages of
584 vegetation succession (Opluštil et al. 2007, 2009a,b, 2014; Libertín et al. 2009a). A similar
585 situation is present in the earliest Permian Wuda ash bed that occurs over an area of more
586 than 60 km², enabling distinct assemblages to be recognised both vertically and laterally
587 (Wang et al. 2012; Opluštil et al. 2020).

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

599 Palynology can provide a more representative picture of landscape-scale diversity as the
600 sediment will contain the pollen from plants growing across the area (Weng et al. 2006). This
601 has proved particularly useful in Quaternary studies where the botanical affinities of the
602 various pollen types are well known (Section 4.2). For instance, palynology has been used to

603 map distribution changes across Europe during the Holocene by Huntley and Birks (1983),
604 and there have been numerous species-specific studies (Hicks 2001; Brewer et al. 2002;
605 Giesecke and Bennett 2004; van der Knaap 2004; Latałowa and van der Knaap 2006; Tinner
606 and Lotter 2006; Giesecke et al. 2007; Pidek et al. 2010; Poska and Pidek 2010). Reitalu et al.
607 (2019) have demonstrated in their study of modern pollen and plant richness across northern
608 Europe that the highest correlations were for trees and shrubs and of wind-pollinated taxa,
609 suggesting that these are the best measures of broad-scale plant richness over several
610 thousands of kilometres.

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

618 5.3 *Regional-scale and global-scale diversities (Evolutionary floras)*

619 Studies on global-scale faunal diversity (e.g. Sepkoski 1978, 1979, 1984, 1988; Bambach
620 1977; Powell and Kowalewski 2002) have shown a progressive increase in species diversity
621 through the Phanerozoic due to an increase in the spatial density of organisms, especially in
622 shallow marine environments (Holland and Sclafani 2015). Similar global and regional
623 studies at the species rank have been attempted in palaeobotany (e.g. Knoll et al. 1979; Niklas
624 et al. 1980) but were hindered by the lack of suitable, taxonomically robust data sets (Section
625 3.3); also by the failure to take into account geographical (especially latitudinal) variations in
626 taxonomic diversity, as has been shown to be an issue with marine invertebrate diversity
627 dynamics (Close et al. 2020). Analogous palaeobotanical studies would, moreover, be

628 unlikely to answer the same sorts of questions of changes in community structure that were
629 being investigated in the faunal record (Section 4).

630 Analyses within narrow taxonomic (e.g. Cleal 2008b,c) or stratigraphical (e.g. Cleal et al.
631 2010; Barbacka et al. 2014) limits have been attempted at the regional-scale, which make it
632 practical for the taxonomic robustness of the data to be critically assessed. However, most
633 larger-scale studies have tended to be based at supra-generic ranks, usually family. For
634 instance, global Phanerozoic plant diversity dynamics were interpreted using Evolutionary
635 Floras (Fig. 10), identified from a factor analysis of a plant family dataset (Cleal and
636 Cascales-Miñana 2014), and these have been used to describe the broad trajectory of
637 vegetation history (Cleal and Thomas 2019; Cleal 2019). More recently, a similar study on
638 pre-Carboniferous floras at the rank of genus is revealing further details of the early phases of
639 plant terrestrialisation (Capel et al., this volume).

640 There are a number of problems with such large-scale plant diversity studies. The
641 taxonomic robustness of the data used is often uncertain, although for plants this is partly
642 avoided by using family-rank data sets (Section 3.3). More difficult is the robustness of the
643 stratigraphical correlations between widely separated floras. Most fossil floras occur in
644 predominantly terrestrial sequences that lack absolute dating or independent
645 biostratigraphical control (e.g. by marine faunas). In local-scale and landscape-scale studies
646 this is less of a problem as lithostratigraphical correlations are often sufficient to provide a
647 temporal framework for comparisons, but these are inadequate for regional-scale and global-
648 scale studies. The palaeobotanical and palynological evidence is itself sometimes used to
649 provide the correlations, but when this is used as the temporal context for the vegetation
650 changes, the arguments become circular. A classic example is the Panchet Formation in India,
651 which is often quoted as justifying the persistence of glossopterids into the Triassic Period,

652 but for which there is in fact no evidence that it is Triassic other than some debatable facies
653 changes and the floras themselves (Saxena et al. 2018).

654 **6 Why study plant diversity in deep time?**

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

674 Palynological research has revealed anthropogenic effects on Holocene plant diversity
675 (Giesecke et al. 2012, 2019). For example, Filipova-Marinova et al. (2014) described an

676 8,000-year long record of vegetation change at Varna Lake (Bulgaria) and showed how the
677 vegetation was strongly influenced by human activity, both through woodland clearance and
678 the establishment of agriculture.

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

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

695 In the Palaeozoic, most attention has been directed to the effect of the Late Palaeozoic
696 Ice Age on plant diversity: did the observed Pennsylvanian – Cisuralian diversity changes in
697 the tropical vegetation cause climate change (e.g. Cleal and Thomas 1999, 2005), or did the
698 climate change cause the vegetation changes (e.g. Pfefferkorn et al. 2008, 2017), or were the
699 two interlocked through feedback loops (Cleal et al. 2010)? Other links that have also been
700 explored are between the diversification of the first woody forests in Late Devonian times

701 and a significant change in ocean water chemistry that caused major reduction in marine
702 faunal diversity (Algeo and Scheckler 1998); and between the very early development of
703 plant diversity during Ordovician times and global cooling and glaciation (Servais et al.
704 2019).

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

721 Identifying vegetation diversity patterns at all scales from the plant fossil record is
722 clearly not easy; whatever the sampling protocol and analytical methods used, the fact will
723 remain that the observed diversity patterns are of the fossils rather than purely of the original
724 vegetation. Nevertheless, the fossil record is the only direct evidence we have of how
725 vegetation has changed through time. By bringing together data from the palaeobotanical and

726 palynological records and interpreting it within the context of the taphonomic filter through
727 which the fossils have passed (Fig. 11) will allow us to understand better how plant-life has
728 responded to changes in climate, landscape and continental configurations, and to the
729 dramatic ecological crises often referred to as mass extinctions.

730 **7 Conclusions**

731 A deeper appreciation of the history of vegetation dynamics can inform present-day
732 landscape management and predictions of future biodiversity and climate. For example, the
733 plant fossil record can provide evidence of the speed at which plants can track climate change
734 and this may prove valuable to predict the response of today's plant vegetation to global
735 warming. It can also provide empirical data to help support and improve models of the
736 dynamic interactions of modern-day vegetation, atmosphere and climate. Evidence from the
737 fossil record clearly has the potential for making a significant contribution to understanding
738 the world today, and emphasises the importance of close co-operation between
739 palaeoecologists and ecologists (Reitalu et al. 2014). Provided that the context of the data is
740 properly understood, including the taxonomy of the fossils (not just the taxonomic names
741 used but what the fossil-taxa mean), the taphonomic processes that caused the fossil to be
742 preserved, and the detailed temporal (stratigraphical) correlations, an underlying signal of
743 vegetation diversity remains waiting to be discovered.

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1687 ultrastructure of *Selaginellites leonardii* and diversity of Selaginellalean spores. *Geo.Alp* 7,
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- 1689

1690 Figure captions

1691 Fig. 1. Variation in productivity of different organs of a plant as illustrated by the pollen,
1692 flowers, leaves, shoots, stem and roots of a hypothetical modern-day angiosperm tree.

1693 Redrawn and adapted from Hughes (1976, fig. 3.6) and Cleal and Thomas (2019, fig. 10.4).

1694 Fig. 2. Three types of diversity that can be recognised in the plant fossil record, using the
1695 Middle Pennsylvanian (c. 310 Ma) swamp vegetation of Variscan Euramerica, based on Cleal
1696 et al. (2012).

1697 Fig. 3. Partial reconstruction of the Late Devonian seed plant *Elkinsia* based on associated
1698 fronds, ovulate structures and anatomically preserved stems. Drawn from by Annette
1699 Townsend (based on Serbet and Rothwell 1992).

1700 Fig. 4. Examples of the differences in the fossil-genera represented by Carboniferous
1701 arborescent lycopsids and sphenopsids. Adapted from Cleal and Thomas (2019).

1702 Fig. 5. Spores of fern *Weichselia reticulata* (Stokes and Webb) Fontaine showing different
1703 maturation stages; Escucha Formation (Albian), Escucha, northern Teruel Province, Spain. A,
1704 General view of a soral cluster up to 2 mm in diameter showing tightly packed peltate
1705 indusia. B, Tightly-packed spores grouped inside a receptaculum. C, Inaperturate, discoidal
1706 spores with smooth exine and lacking trilete mark. D, Packed spores showing different
1707 ontogenetic stages. D, E, Fully-developed tetragonal spores with well-rounded corners and
1708 clear trilete scar. Original unpublished material from the study in Diez et al (2005) with
1709 permission of the authors.

1710 Fig. 6. T⁰ fossil or submerged forests of arborescent lycopsids in the Carboniferous of the
1711 UK. A, Fossil trees rooted in a coal seam being exposed at Brymbo, north Wales (Appleton et
1712 al. 2010). B, Excavated trees in the Victoria Park, Glasgow (Thomas and Seyfullah 2015).

1713 Fig. 7. Comparison of palynological and macrofloral spectra obtained from roof-shales
1714 overlying four Moscovian-age coal seams in South Wales, UK, between the Daren Ddu Seam
1715 at the base and the Llantwit No. 1 Seam at the top. Palynomorphs not represented are extra-
1716 basinal, mainly pollen (e.g. conifers). Macrofossils not represented are indeterminate
1717 remains. Redrawn from Dimitrova et al. (2005, fig. 4).

1718 Fig. 8. Palaeozoic wetland vegetation preserved in the lower unit of the early Moscovian
1719 Whetstone Horizon (Bělka tuff), Ovčín, Central Bohemia, Czech Republic. A, Remains of
1720 cordaites and arborescent lycopsids plotted out on an exposed area of the tuff divided into 1
1721 m² quadrats; the small number against each specimen represents the height above the base of
1722 the tuff that the fossil occurred. B, Reconstruction of forest based on the type of plots shown
1723 in Fig. 7A. From Opluštil et al. (2014), reproduced with permission from Bulletin of
1724 Geosciences.

1725 Fig. 9. Range of basinal and extra-basinal vegetation represented in Moscovian (late
1726 Carboniferous) palynospectra from the Sydney Coalfield, Cape Breton, Canada (Dimitrova et
1727 al. 2011).

1728 Fig. 10. The Evolutionary Floras model of vegetation evolution based on a factor analysis of
1729 global plant-family distribution through the Phanerozoic (Cleal and Cascales-Miñana 2014).

1730 Fig. 11. Factors that affect how we interpret past vegetation diversity from the macrofloral
1731 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		<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>Lepidostrobophyllum</i>	<i>Calamostachys</i>	<i>Bowmanites</i>	<i>Cyathocarpus*</i>	<i>Trigonocarpus</i>	<i>Cardiocarpus</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



Pollen
Quantity available for burial: 10^7
Time of availability: 2 weeks / year
Durability: Durable

Flower
Quantity available for burial: 10^7
Time of availability: 1 week / year
Durability: Ephemeral

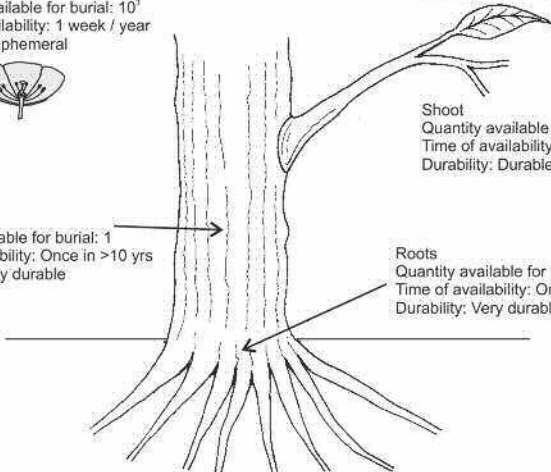


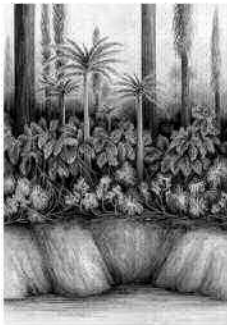
Leaf
Quantity available for burial: 10^6
Time of availability: 4 weeks / year
Durability: Durable

Shoot
Quantity available for burial: 10^3
Time of availability: 2 weeks / year
Durability: Durable

Woody trunk
Quantity available for burial: 1
Time of availability: Once in >10 yrs
Durability: Very durable

Roots
Quantity available for burial: 1
Time of availability: Once in > 10 years
Durability: Very durable

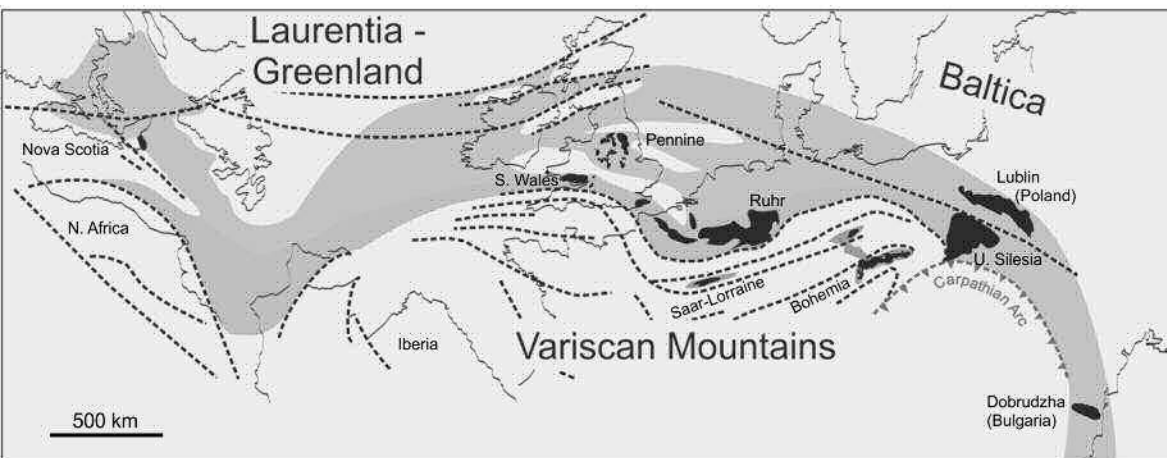




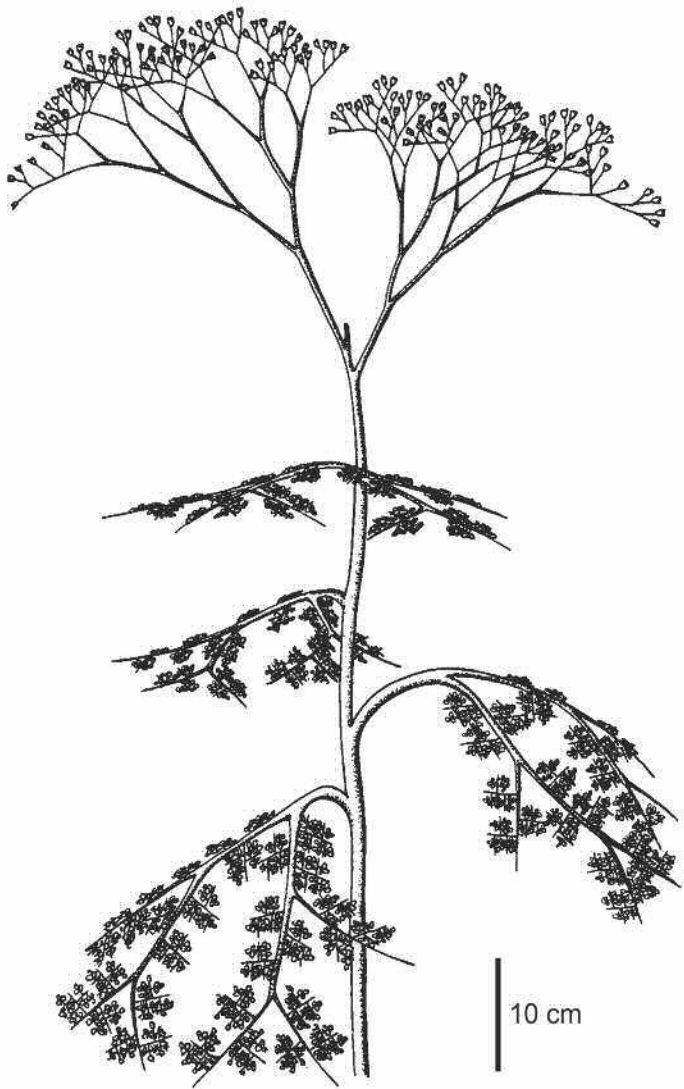
Local-scale diversity ($< 10^3 \text{ km}^2$)
 $\equiv \alpha$ diversity

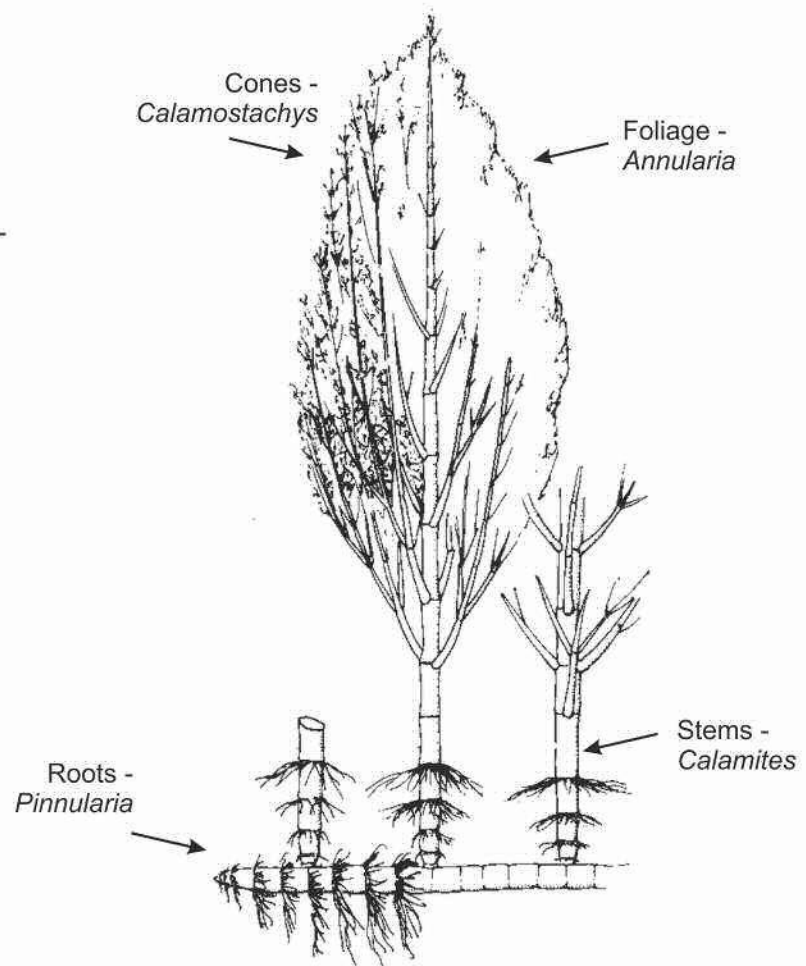
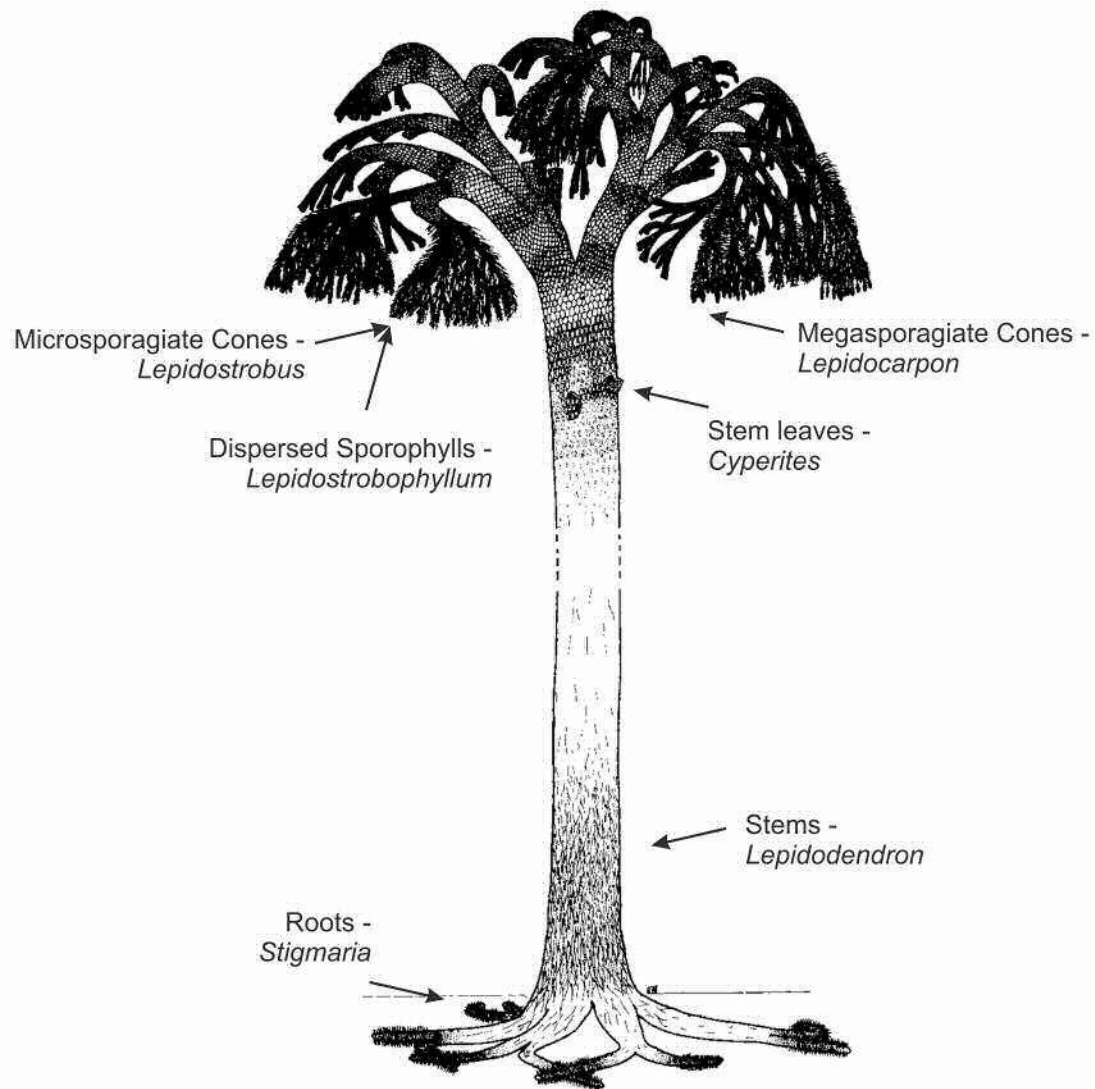


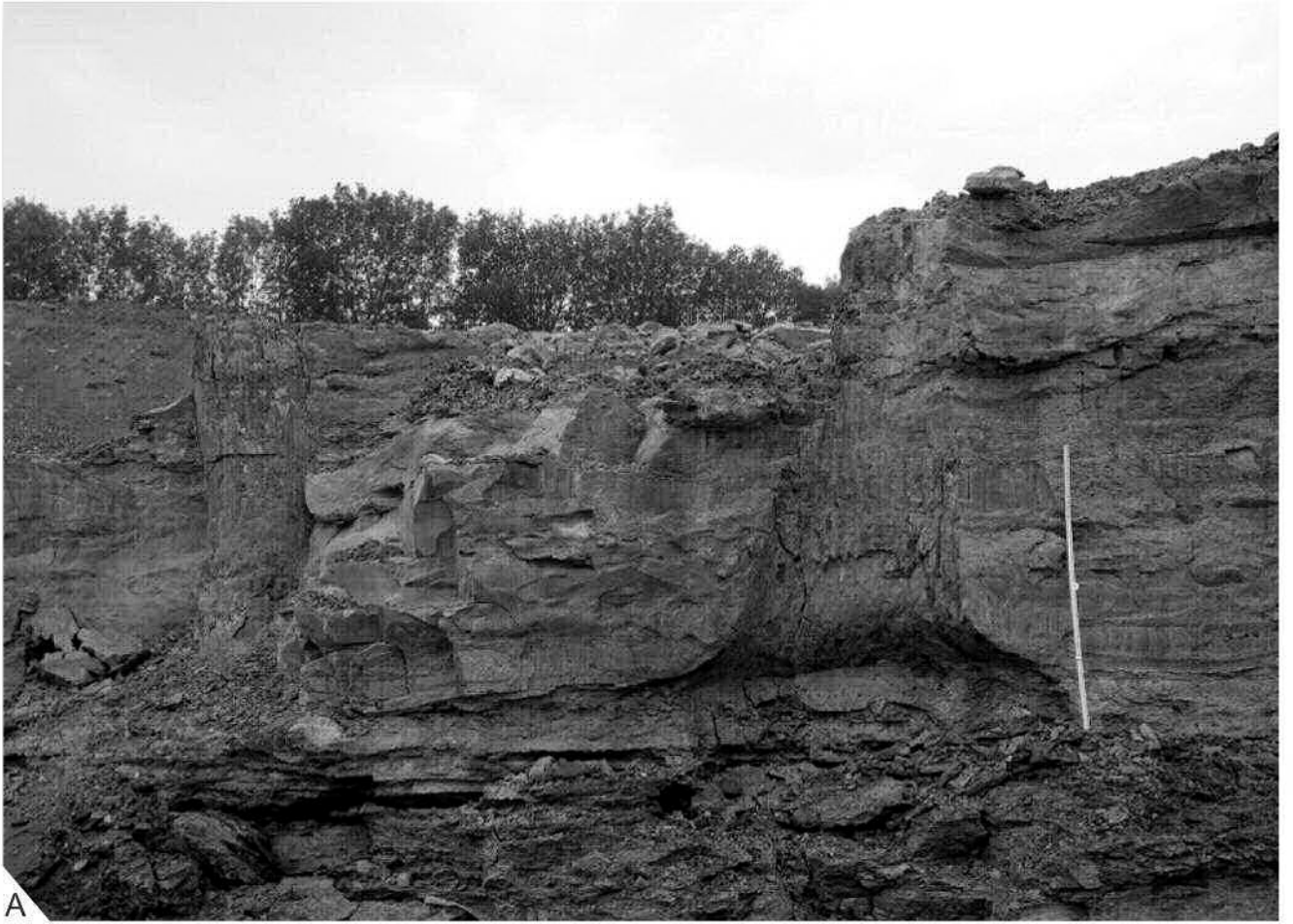
Landscape-scale diversity ($10^3 - 10^5 \text{ km}^2$)
 $\equiv \gamma$ diversity



Regional-scale diversity ($< 10^5 \text{ km}^2$) $\equiv \epsilon$ diversity







A



B

