

Palaeobotanical experiences of plant diversity in deep time. II: How to measure and analyse past plant biodiversity

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1 **Palaeobotanical experiences of plant diversity in deep time. II:**
2 **How to measure and analyse past plant biodiversity**

3

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51 **Abstract**

52 Determining the diversity of past floras helps with interpreting both the history and
53 predicting the future of vegetation change. For global-scale and regional-scale diversity
54 studies especially, secondary data are often used but local-scale studies tend to be based on
55 survey data that require rigorous sampling. The correct sampling strategies depend on the
56 types of fossils being investigated, including their physical size, and whether the aim is to
57 determine taxonomic richness or relative abundance. Describing and comparing diversities
58 can use a range of different metrics, depending on whether binary presence / absence or

59 abundance data are available. Each metric provides a different insight into the diversities and
60 the choice of which to use depends on the research question being investigated. Various
61 numerical approaches are available for identifying spatial and stratigraphical diversity
62 patterns, mainly classificatory techniques (e.g., cluster and parsimony analyses) and
63 ordination (e.g., Detrended Correspondence Analysis, Nonmetric Dimensional Scaling). The
64 choice of technique again depends on the research question, but often it has proved useful to
65 run both types of analysis in tandem. This article is illustrated by past biodiversity case
66 studies from throughout the fossil record, dealing with floras ranging in age from the
67 Devonian to the last few centuries.

68 Keywords: Palaeobotany: Palynology: Taxonomy: Taphonomy: Ordination: Classificatory
69 analysis

70 **1 Introduction**

71 A major agenda-item in palaeobotany and palynology is determining how plant diversity
72 has developed over geological time to produce the vegetation that we see today. This was the
73 subject of a workshop entitled *Tracking changes in plant diversity over the last 400 million*
74 *years*, held in Cardiff in 2014. In a previous paper that arose from this meeting, we looked at
75 exactly what is meant by plant diversity and the extent to which we can investigate it using
76 the plant fossil record (Cleal et al. 2021). This second paper from the meeting will review the
77 background to some of the methods that are used to collect and analyse the diversity data
78 from the plant fossil record. It is not intended as a methodological “cookbook”; relevant
79 guides are published elsewhere (e.g., Magurran 2004; Palmer 2004; Hammer and Harper
80 2006). Rather, it aims to look at some of the methods that have been used, to see how they
81 affect the interpretation of diversity data and to note representative case studies. The
82 numerical techniques that we mention are all available in software packages such as PAST
83 (Hammer et al. 2001), TWINSpan (Hill 1979), MVSP (Kovach 1999) and various R-
84 language routines such as VEGAN (Dixon 2003).

85 **2 Sampling strategies**

86 Even with living vegetation, accurately measuring species diversity can be challenging
87 because of sampling issues (Gotelli and Colwell 2001), but detailed and systematic sampling
88 of plant fossils will indisputably improve the understanding of past vegetation (Hicks et al.
89 2004; DiMichele and Gastaldo 2008). Choosing the appropriate sampling strategy will be
90 influenced by the type of plant fossils being investigated, in particular their size.

91 *2.1 Microfossils and Mesofossils*

92 Microfossils are the smallest plant fossils up to 500 μm in size (e.g., pollen, microspores,
93 phytoliths, micro-charcoal) that are best studied under a high-powered microscope, whilst
94 mesofossils are plant remains 0.5–1.0 mm in size (e.g., megaspores, small seeds, cuticle
95 fragments, fusainised flowers) that can be seen with the naked eye but are usually studied
96 using a low-powered dissecting microscope or a Scanning Electron Microscope (SEM).
97 Quaternary palynologists often include the latter within microfossils (Birks 2007; Mauquoy
98 et al. 2010) but, as they are usually studied using microscopes, they will be referred to here as
99 mesofossils (Wellman et al. 2003; Crepet et al. 2004; Friis et al. 2019).

100 Large samples of microfossils and mesofossils can potentially be obtained from a
101 relatively small amount of material (less than a kg, usually a few g), and so the problem in
102 diversity studies tends to be when to stop counting a particular sample to avoid unproductive
103 work. There have been attempts to analyse numerically the errors in mineral point counts in
104 petrological slides (e.g., Howarth 1998) and a similar approach was used to determine a
105 reasonable sample size for palynological counts (Maher 1972; Dimitrova et al. 2005; Keen et
106 al. 2014). The sample size will be at least partly influenced by the number of taxa present and
107 must be enough to ensure consistency of results (Birks and Birks 1980, p. 165); most
108 Cenozoic palynologists use counts between 300 and 1000 per sample (e.g., Fig. 2), although
109 pre-Cenozoic palynology studies sometimes have to use smaller samples because of limited
110 availability of material.

111 Rarefaction analysis can be used to adjust diversity measurements in different sample
112 sizes (Birks and Line 1992; Wing and Harrington 2001; Seppä and Bennett 2003; Barreda et
113 al. 2012; Matthias et al. 2015; Giesecke et al. 2019). This is where a graph is plotted of how
114 many new taxa are found as progressively more specimens are examined. It is then possible
115 to determine the taxonomic richness in each sample at a pre-determined sample size. It has
116 also been suggested that pollen taxonomic richness should be standardised for a set area and
117 time of sediment accumulation (van der Knaap 2009), but this requires accurate estimates of
118 sediment accumulation, which can be difficult to determine. None of these methods solve the
119 problem of differential pollen productivity and dispersal in different plant groups that can
120 hinder the translation of palynological data into vegetation diversity (Odgaard 1999, 2001,
121 2013; Seppä and Bennett 2003; Weng et al. 2006; Cleal et al. 2021).

122 It can be effective to exclude tree pollen, especially in open situations where long-distance
123 pollen dominates, but this inevitably reduces the pollen sum and requires higher counts to
124 give statistically reliable results. It can, moreover, be difficult to be certain from
125 palynological data whether or not past vegetation was open and that the tree pollen should be
126 excluded (Magri and Parra 2002; Pardoe 2014). The local presence of a particular taxon is
127 often identified by its pollen reaching a threshold percentage (e.g., > 0.5%) but this value
128 may vary between taxa (Lisitsyana et al. 2011). Macrofossil evidence can also be used as an
129 indicator of local presence, especially of trees, since seeds and other remains are heavier than
130 pollen and less easily dispersed.

131 It is also often routine in Quaternary studies to exclude obligate aquatics from the
132 calculation of percentages since (1) they are frequently over-represented, especially in lake

133 sediments, and (2) the aim is often to reconstruct terrestrial (rather than aquatic) vegetation.
134 Samples can also be contaminated by pollen reworked from older sediments, especially in
135 extreme environments with high rates of catchment erosion such as occurred in the late
136 glacial. In many cases however these unusual and often 'older' looking corroded exotic
137 grains can be identified and excluded.

138 Pre-Quaternary studies have usually analysed the entire sample, although Dimitrova et al.
139 (2011) selectively analysed "exotic" pollen and spores from a set of late Carboniferous
140 palynofloras to try and determine patterns of extra-basinal vegetation. By comparing time-
141 equivalent Permian strata and their palynoflora, Stolle (2010, 2011) discovered
142 exotic Gondwana elements and "European" pollen, but in biogeographically atypical regions.
143 The sampling and investigations were based on selected areas with different miospore
144 diversity spectra. Other investigations in lake settings separated well-preserved pollen grains
145 (most likely air-borne just prior to deposition) to obtain the seasonal signal from reworked
146 pollen grains (mostly water-transported) which have been around a longer time before
147 deposition (López-Merino et al. 2016). This approach often required counting more than
148 1500 pollen grains per sample.

149 Inconsistencies in pollen identifications can be partly overcome by using translation tables
150 that transform modern plant species into known distinguishable pollen or spore types – so-
151 called pollen equivalents (Felde et al. 2014; Birks et al. 2016; Giesecke et al. 2019). Other
152 problems include poorly preserved pollen (e.g., *Tsuga* pollen that has been preferentially
153 oxidised in outcrop but is preserved in cored sequence; Brugal et al. 1990; Leroy and Seret
154 1992), large numbers of reworked elements (Hoyle et al. 2018), or gritty samples. Preparation
155 techniques can also cause problems, such as when unusually large pollen (e.g., Palaeozoic
156 medullosalean *Schopfipollenites*) gets lost through sieving (Dimitrova et al. 2010) or where
157 delicate palynomorphs are lost during maceration (Mertens et al. 2012).

158 Where exotic spikes such as *Lycopodium* tablets are used to calculate absolute pollen
159 values, the number of *Lycopodium* tablets added could make a significant difference (Hicks et
160 al. 1999). The statistical confidence with which pollen concentration (per unit of weight or
161 volume) and influx (per unit of time) can be calculated increases with the number of
162 *Lycopodium* spores counted; so, the more tablets that are added to the sample, the more
163 statistically accurate the pollen calculations will be. The number of tablets required depends
164 on the pollen concentration, with the aim of reaching a *Lycopodium* count of more than 100

165 per sample; once 500 *Lycopodium* spores have been counted there are only very small
166 increases in the reliability of the count (Maher 1972).

167 2.2 *Macrofossils*

168 These are the type of hand specimens that dominate most museum collections, including
169 adpressions, casts, moulds and anatomically-preserved petrifications. They may be anything
170 above 2 mm in size, but in practice are typically between 1 cm and 1 m. An assemblage of
171 such fossils is known as a macroflora.

172 Sampling macrofloras in taxonomic diversity studies is usually by an individual-based
173 protocol: specimens are sequentially taken and each new taxon is recorded until a
174 representative sample size is achieved. What constitutes a representative sample size can be
175 estimated using rarefaction analysis (Fig. 1): a graph is plotted of how many new taxa are
176 found as progressively more specimens are examined and a representative sample size has
177 been reached when the graph flattens-off (e.g., Burnham 1994; Cleal et al. 2012; Opluštil et
178 al. 2014).

179 The relative abundance of taxa is determined using a sample-based protocol, where every
180 individual is counted within a particular sample. Sufficiently large samples can avoid some
181 inherent sampling problems; for instance, Davies (1929) recorded every macrofossil found in
182 several tonnes of roof shales above upper Carboniferous coals, resulting in individual
183 macrofloras of up to 30,000 specimens (Thomas, 1986; Cleal 2007; Cleal et al. 2012; King et
184 al. 2012). But such large samples are exceptions and more usually the relative abundance of
185 taxa has to be standardised according to the sample size, using similar approaches to those
186 adopted in plant microfossils (Section 2.1) such as rarefaction analysis (e.g., McElwain et al.
187 2007; Uhl and Lausberg, 2008; Currano et al. 2011; DiMichele et al. 2021). Alternatively,
188 standard-size samples are measured, such as using botanical survey quadrats (Scott, 1978), or
189 pseudo-quadrats created by exposing rectangular areas of bedding plane (Gastaldo et al.
190 2004a) or bringing together specimens until a quadrat-sized area is filled (Iwaniew 1985;
191 Bashforth et al. 2010, 2011). Alternatively, proxy quadrats have been based on “normal size”
192 hand-specimens (Pfefferkorn et al. 1975; Wing and DiMichele 1995; Uhl and Lausberg,
193 2008; Barbacka 2011, 2016; DiMichele et al. 2016, 2021; Cleal et al. 2012; Bashforth and
194 Nelson 2015; DiMichele et al. 2019a,b; Koll and DiMichele 2021) or borehole cores of a set
195 diameter (DiMichele et al. 2000). Various counting strategies have been used, with either all
196 specimens in a quadrat being counted (Dräger 1964; Oshurkova 1967; DiMichele et al. 2007;

197 Stiles et al. 2020), the specimen numbers per quadrat being weighted according to the size of
198 each fragment (Spicer and Hill 1979; Pryor and Gastaldo 2000), or a randomly selected
199 number of specimens per quadrat being counted (Scott 1978, 1979, 1984).

200 Whilst such quadrat and quadrat-like techniques appear to give numerical rigour to the
201 analyses, and have particular benefits with floras dominated by compound foliage that has
202 undergone various levels of fragmentation (Wing and DiMichele 1995), distortions may be
203 introduced according to the technique used (Lambooy and Lesnikowska 1988). For instance,
204 quadrat methods appear to lead to more even species distributions (DiMichele et al. 1991)
205 and quadrat size can have a marked effect on taxonomic richness (Wing and DiMichele
206 1995). Nevertheless, provided there is a consistency in the methods used, quadrats and allied
207 techniques offer one of the best means of comparing relative abundances of fossil taxa
208 between floras.

209 Another method used in botanical habitat work, especially with groundcover of
210 herbaceous plants, is line-intercept survey (Floyd and Anderson 1987; Etchberger and
211 Krausman 1997). A frame bearing regularly-spaced strings that are marked-off at regular
212 intervals (e.g., 20 mm) is placed on the ground and each increment along each string is scored
213 according to the plant species it crosses. A similar approach has been used in palaeobotanical
214 surveys (e.g., Wing et al. 2012).

215 The relative taxonomic abundances and biomass in anatomically-preserved macrofossils
216 can be measured by point counting across the slide at set increments (e.g., Slater et al. 2015)
217 using a microscope with a calibrated stage, where the slide holder can be moved either
218 manually or by motor. Alternatively, the thin section or polished surface can be examined
219 beneath a clear plastic or glass sheet marked with a 1-cm grid, and the plant remains present
220 in each quadrat recorded (e.g., DiMichele and Phillips 1988; Willard 1993; Willard et al.
221 2007).

222 However, because macrofloras usually occur in allochthonous plant beds, they have been
223 subjected to varying levels of sorting, differential preservation and time averaging (Gastaldo
224 1988; Gastaldo et al. 1995; Behrensmeyer et al. 2000; Spicer 2017; Thomas et al. 2019a;
225 Cleal et al. 2021). Consequently, no matter how systematically the macroflora is sampled, it
226 can usually only provide a distorted glimpse of the parent vegetation (Burnham 1993).
227 Choosing the appropriate sampling strategy and size must depend on the research question
228 being investigated (DiMichele and Gastaldo 2008). This can be even more problematic with

229 (older) museum collections where the sampling strategy has not been recorded (e.g., Uhl and
230 Lausberg 2008).

231 2.3 *Megafossils*

232 Megafossils are the largest plant fossils, such as the tree trunks found in in-situ fossil
233 forests (e.g., Becker 1993; DiMichele and Falcon-Lang 2011; Macdonald 2013) or as logjams
234 in fluvial systems (Falcon-Lang and Bashforth 2005; Kędzior and Popa 2013; Gastaldo and
235 Degges 2007). Because of their physical size and weight, such fossils tend to be studied in
236 situ, although there can be exceptions (e.g., Thomas and Seyfullah 2015; Roberts et al. 2016).
237 Where the area of exposure is sufficiently large, local-scale tree density can be measured
238 directly (e.g., Gastaldo 1986a; Hinz et al. 2010; Thomas 2014; Opluštil et al. 2020).
239 Alternatively, it can be measured as trees become progressively exposed by advancing
240 working faces in active quarries and mines (e.g., Gastaldo 1986b; DiMichele and Demaris
241 1987; Mosbrugger et al. 1994; DiMichele et al. 2007; Gastaldo et al. 2004b) or in eroding
242 cliffs (e.g., Francis 1984; Calder et al. 2006; Falcon-Lang 2006; Grey and Finkel 2011).
243 There are also late Quaternary submerged forests exposed in coastal areas by storms
244 (Hayworth 1985, 1986, Nayling et al. 2007, Sherlock 2019; Bailey et al. 2020), along rivers
245 by erosion (Vassio et al. 2008) or in freshwater lakes (Kaiser et al. 2018).

246 Tree density and distribution are measured either through traditional surveying methods
247 (DiMichele et al. 1996a; Thomas 2013; Berry and Marshall 2015) or photogrammetry
248 (Fernández-Lozano and Gutiérrez-Alonso 2017). There is the potential for future use of
249 satellite technology such as Landsat or Sentinel-2 data, although the pixel resolution
250 generally available is too coarse to see individual fossils (e.g., Landsat 32 x 32 m, pan-
251 sharpened to 16x16 m; Sentinel 10 x10 m); aerial photography and high-resolution satellite
252 data such as Google Earth have greater possibilities. Determining taxonomic diversity from
253 fossil forests can be more problematic as the characters necessary for species or genus
254 identification are often not preserved; the groundcover and understory vegetation has also
255 usually been removed by the flooding event that entombed the trunks. In unstable
256 depositional environments it is, moreover, necessary to ensure that the trunks are
257 autochthonous and have not been deposited in an upright position by mudflows or lahars
258 (Fritz 1980).

259 3 Databases

260 Although most local-scale and landscape-scale diversity studies use survey data, regional
261 and global-scale studies require larger samples extracted from secondary datasets. The
262 potential problem with such studies is quality control and this is becoming an increased
263 danger with on-line access to many databases; it has become too easy simply to download
264 and analyse large quantities of data without checking the reliability of the identifications and
265 the provenance of the fossils, and what plant parts and/or preservation states are being
266 recorded. Without detailed checks on the robustness of the records, any diversity analysis
267 using such data is likely to be worthless.

268 3.1 Palynology

269 Late Quaternary vegetation studies have been transformed over the last 30 years through
270 the development of large databases covering broad geographical areas and temporal ranges,
271 such as the European Pollen Database (EPD), the European Modern Pollen Database
272 (EMPD), the Eurasian Modern Pollen Database (EMPD) and the North American Pollen
273 Database (NAPD) (Fyfe et al. 2009; Davis et al. 2013, 2020; Giesecke et al. 2014a; Grimm et
274 al. 2013). These are being incorporated into the Neotoma palaeoecological database
275 (Williams et al. 2018). Although the taxon names are standardised as each new regional
276 database is added to Neotoma, because the records are from disparate sources their reliability
277 and consistency can be difficult to assess; there are also some issues with uneven spatial and
278 temporal coverage. Nevertheless, combined with improved radiocarbon dating and age –
279 depth modelling (e.g., BACON; Blaauw and Christen 2011), these databases are allowing
280 pollen records to be integrated from widely separated areas using a common age scale (e.g.,
281 Grimm et al. 2013; Giesecke et al. 2014b; Blarquez et al. 2014) and so significantly
282 improving the modelling of vegetation dynamics (e.g., Davis et al. 2013; Walsh et al. 2019),
283 which in turn can be compared with climate data (Fig. 3).

284 The most notable attempt to collate pre-Quaternary palynological data was the “Catalog of
285 fossil spores and pollen”, initiated in 1957 by Gerhard Kremp and which continued up until
286 the mid-1980s (Traverse et al. 1970; Riding et al. 2016). The DOS-based “Taxon.exe”
287 database was also a valuable source on older records, but has not been updated lately and
288 seems now to be unavailable. In more recent years, online research via PALYNODATA
289 (<https://paleobotany.ru/palynodata>), a bibliographic database that was continued at least until
290 2006, also based on Gerhard Kremp's initial research, and compiled since 1974 by Palynodata

291 Inc. (J.M. White), has been established. There is also available the CIMP slide collection, an
292 archive of 382 images of holotypes of Palaeozoic miospore species scanned by M. Streel (see
293 more details on the websites of the Laboratory of Palaeobotany, Moscow, Russia). More
294 recently, a collaborative database PalyWeb has been created for Palaeozoic palynological
295 records (Steemans and Breuer 2007) and is an on-going project.

296 3.2 *Macrofloras*

297 The only comprehensive data resource on macrofloral species distributions now available
298 is the Plantae part of the Fossilium Catalogus. Initiated in 1913 by Wilhelmius Jongmans, this
299 has attempted to document every published macrofloral record including remarks on their
300 occurrences, as well as relevant taxonomic and nomenclatural issues (Wagner and van
301 Amerom 1995). The project has continued up to today under the editorships of S. Dijkstra,
302 and then H. van Amerom and J. van der Burgh, and currently (as of 2021) runs to 115
303 volumes (“pars”). Some of the volumes are now available on-line via the Biodiversity
304 Heritage Library and/or Google Books.

305 Some macroflora records have been included in the Paleobiology Database (PBDB; Alroy
306 2003) and this has been used in some palaeobotanical biodiversity studies (e.g., Raymond et
307 al. 2006; Silvestro et al. 2015), but the palaeobotanical coverage remains very patchy in terms
308 of completeness and rigour and consistency of identifications. The Geobiodiversity database
309 (GBDB; Xu et al. 2020) has been available since 2007 and includes detailed accounts of
310 fossil plant occurrences, primarily from within China. Unlike the PBDB, the GBDB records
311 are tied to geological sections, allowing stratigraphy-based diversity comparison to be made
312 within formations and between geological sections. Most recently, a planned Integrative
313 Paleobotany Portal (PBot) aims to provide a means of recording palaeobotanical data but at
314 the time of writing its exact remit and how it relates to the PBDB and GBDB remains
315 unclear.

316 Global compilations of fossil-species appear also to have been attempted by Niklas et al.
317 (1980, 1983, 1985) and used in diversity analyses, but the data were never published. In
318 contrast, Devonian and Carboniferous floristic studies by Mosseichik (2010, 2012, 2014,
319 2019) gave detailed metadata, allowing the records to be verified. Data on global records of
320 fossil-species near the Permian – Triassic boundary are given as supplementary data
321 accompanying Nowak et al. (2019) and are available for download from the journal web site.
322 Global compilations of fossil-genera were published for particular Palaeozoic time-intervals

323 by Raymond (1985), Raymond et al. (1985a,b) and Rowley et al. (1985) and used in floristic
324 analyses. Other diversity analyses of particular taxonomic groups and/or regional areas exist
325 (e.g., Lidgard and Crane 1990; Martinetto and Vassio 2010; Barbacka et al. 2014) although,
326 again, not all of the datasets have been published or updated.

327 The stratigraphical distribution of plant families was documented in Harland (1967 –
328 Fossil Record) and Benton (1993 – Fossil Record 2), and for the gymnosperms by Anderson
329 et al. (2007). These record the first and last occurrences of each known family, with full
330 bibliographic details allowing the evidence to be assessed and verified. The Benton (1993)
331 dataset is now available on-line and, although it has not been updated since the original
332 publications, a modified version of the palaeobotanical part was provided with the on-line
333 version of Cascales-Miñana and Cleal (2014).

334 Data-mining for diversity analyses can be facilitated by using reference managers such as
335 Endnote, Mendeley or Zotero. Endnote is particularly flexible in configuring dedicated fields
336 for recording taxa in references of any type (Popa 2011), while new versions enable detecting
337 taxa directly from attached PDF files associated with reference records. Queries can therefore
338 provide lists of references covering species, genera and families, as well as higher taxa.
339 Online queries directly from dedicated reference managers also enable rapid and robust
340 searches for diversity data; coupling Endnote with portals such as Web of Knowledge / Web
341 of Science can produce rapid records and data conversions.

342 **4 Diversity metrics**

343 There are two aspects to understanding the vegetational taxonomic diversity: the diversity
344 of individual floras and the comparison between floras. Each aspect has its own set of
345 metrics.

346 *4.1 The diversity of a flora*

347 A range of metrics are available to express taxonomic diversity in both palaeobotany and
348 palynology (Magurran 2004; Santini et al. 2017). The following discussion will mainly deal
349 with local-scale diversity, often referred to as α -diversity (Cleal et al. 2021).

350 The taxonomic diversity of a flora consists of its taxonomic richness and its taxonomic
351 evenness (Simpson 1949). Taxonomic richness (the number of taxa present, also termed the
352 standing diversity) is regarded as an important guide to ecological change in modern-day
353 vegetation (Magurran 2004) and has also been used in palaeobotanical studies (summarised

354 by Cleal et al. 2021). The main problem tends to be of sampling: are enough specimens being
355 examined to reveal both rare and the more abundant taxa (see Section 2)?

356 Taxonomic evenness of a flora (whether there are numerous equally abundant taxa, or just
357 a few dominant taxa) is ecologically important as it may affect how the vegetation will
358 respond to environmental change (Magurran 2004). The level of evenness can be judged
359 graphically by plotting a rank abundance distribution curve (or Whittaker Plot), which shows
360 the relative abundance of each taxon ordered sequentially by increasing abundance, plotted
361 against either a logarithmic (Magurran 2004) or linear (Koll and DiMichele 2021; DiMichele
362 et al. 2021) scale. Such plots have been modelled mathematically using probability
363 distributions for ranked data (e.g., broken stick and Zipf-Mandelbrot distributions) to
364 understand how modern-day plant communities become established (Mouillot and Lepretre
365 2000; Magurran 2004) and a similar approach was this was used with palaeobotanical data by
366 McElwain et al. (2009).

367 Various metrics combine taxonomic richness and evenness, referred to as taxonomic
368 heterogeneity indices (Good 1953; Hill 1973a; Shi 1995; Magurran 2004; Colwell and
369 Elsensohn 2014). Simpson's Index is a widely used heterogeneity metric, which ranges from
370 0 to 1 with increasing evenness, and is in essence the probability that any two samples drawn
371 randomly from the flora will belong to the same taxon. This benefits from being conceptually
372 straightforward and so easy to interpret, and has been used in palaeobotany and palynology
373 (e.g., Wing and DiMichele 1995; Uhl and Lausberg, 2008; Pardoe 2021). The main problem
374 is that the Simpson Index can be overly sensitive to the more abundant taxa in a flora, which
375 could be a problem if the rarer species are of interest (Whittaker, 1965). The Simpson Index
376 is sometimes converted to what is called a Diversity Index, either by subtracting its value
377 from 1 (e.g., Whittaker, 1965) or using its reciprocal value (N_2 of Hill, 1973a) and so
378 increases with decreasing evenness; the former has been used in palaeobotany by Pryor and
379 Gastaldo (2000).

380 The Shannon heterogeneity metric not only takes into account the relative numbers of
381 taxa, but also of individuals in the sample, and usually varies from 1.5 to 3.5 with increasing
382 unevenness. However, this was not founded on ecological theory but uses information theory
383 to try and estimate unevenness from the observations (Lande 1996). Although this is not a
384 significant drawback with large samples (Peet 1974), it tends to be rather less sensitive to
385 unevenness than the Simpson Index; it can often overemphasise the effect of the rarest taxa in
386 a flora and so give greater emphasis to taxonomic richness (Nagendra 2002). There have been

387 attempts to overcome this issue (e.g., Pielou's Index which is the Shannon metric divided by
388 the log of the number of taxa; and N_1 of Hill, 1973a, which is the exponential value of the
389 Shannon metric), but there remain fundamental problems with the Shannon index and its
390 derivatives (Lande 1996; Magurran 2004).

391 Both Simpson and Shannon indices are affected by sample size and therefore by sampling
392 effort, and so several non-parametric indices have been developed that only reflect the
393 taxonomic evenness (Magurran 2004; Buzas and Hayek 2005; Chiarucci et al. 2011; Birks et
394 al. 2016; Santini et al. 2017). The simplest are the Berger – Parker Index (the ratio of the
395 number of specimens of the dominant taxon to the total sample size) and the Chao Estimators
396 (which take into account the proportion of singleton and doubleton taxa; Chao 1984, 1987);
397 Chao estimators have been used in palaeobotanical studies by Wing and DiMichele (1995)
398 and Mander et al. (2010).

399 Each of these diversity metrics produce different insights into the taxonomic structure of
400 the assemblage and so in their way are equally valid. However, each of the main metrics has
401 a different mathematical structure and so it is difficult to combine them into a unified scheme.
402 Hill (1973a) therefore proposed a unified system of Hill Numbers based on the main existing
403 metrics but with more compatible mathematical structures: N_0 , which is the taxonomic
404 richness; N_1 , which is the exponential of the Shannon metric; and N_2 , which is the reciprocal
405 of the Simpson heterogeneity metric. Jost (2006) referred to N_1 and N_2 as the "effective
406 number of species" in a community; they represent the number of equally-common species
407 required to give a particular value of an index and so may be regarded as the true level of
408 taxonomic diversity.

409 Whilst it is relatively easily to measure taxonomic evenness in the plant fossil record,
410 interpreting it in terms of vegetation evenness and its ecological impact is less
411 straightforward. Even with living vegetation, taxonomic evenness can be difficult to interpret
412 as the physical size and therefore biomass of each plant will affect its ecological impact (Hill,
413 1973a): a small number of trees will have a much greater effect on a habitat than the same
414 number of herbaceous plants. Furthermore, the ecological impact of biomass varies according
415 to the plant-part: the same biomass of leaves, reproductive structures and woody stems will
416 have significantly different ecological impacts on a habitat. Although some attempts have
417 been made to portion out biomass taxonomically in macrofloras with the aim of improving
418 diversity analyses (Baker and DiMichele 1997; Niklas 2006), in practice it is very difficult, if

419 only because our understanding of the full growth form of most of those fossil plants tends to
420 be incomplete.

421 Interpreting taxonomic evenness in palynofloras is also difficult because of the large
422 variations between plant groups in pollen (and spore) productivity and dispersal (Matthias et
423 al. 2015). Where a large pollen producer (e.g., *Betula*) is replaced by a plant with low pollen
424 production (e.g., *Tilia*), the evenness of the vegetation may not change but the evenness of
425 the resulting pollen sample will be noticeably different. Correction factors (Davis 1963;
426 Andersen 1970) or models of pollen dispersal with relative productivity estimates (Broström
427 et al. 2008; Gaillard et al. 2008) can reduce this problem (Matthias et al. 2015; Felde et al.
428 2016) and have been used in Holocene (Marquer et al. 2014) and Palaeozoic (Willard 1993)
429 studies, but is difficult with extinct groups where the relative or absolute pollen productivities
430 are unknown.

431 4.2 *Comparing the diversities of two floras*

432 Diversity metrics are only really meaningful if they can be compared between different
433 floras. Pair-wise comparisons of taxonomic richness are simple, provided the sample sizes are
434 sufficient to be representative or have been standardised (see Section 2), but this provides
435 only limited insight into the difference between the floras.

436 Usually it is more instructive to compare the taxonomic composition of two floras, for
437 which at least 39 similarity indices are available, each placing different emphasis on the
438 comparison (Shi 1993a,b; Harper 1999). For binary (presence / absence) data, the
439 conceptually simplest is the Jaccard coefficient, which is the ratio of the number of taxa that
440 are shared by two floras to the total number of taxa in the two floras combined, and was
441 regarded by Shi (1993b) as the most robust for palaeoecological studies. Alternatively,
442 DiMichele and Phillips (1988) and McElwain et al. (2007) used the Dice-Sørensen
443 coefficient that gives greater emphasis to co-occurrences of taxa than mismatches. For
444 taxonomic abundance data, several indices are available (reviewed by Hammer and Harper
445 2006) but each tends to give a relatively different emphasis to sample size and so can produce
446 rather different results; for instance, the Euclidean distance can be strongly influenced by
447 large differences between rare taxa, the Bray-Curtis tends to be very sensitive to abundant
448 taxa (e.g., DiMichele et al. 2021) and the squared chord distance gives more weight to the
449 overall composition of the samples (e.g., Pardoe et al. 2010). As with many of these

450 numerical techniques, when interpreting similarity indices, it is essential to understand
451 exactly what the selected index is emphasising.

452 In themselves, these indices provide no measure of statistical significance; could the
453 observed difference be explained merely through chance? If Shannon information metrics
454 have been used to characterise the diversities, there is a t-test available that will provide a
455 probability of significance of the comparison (Hutcheson 1970). With other metrics,
456 bootstrapping can be used where the comparison is repeatedly done on randomly selected
457 subsets of the data, from which a confidence interval can be calculated (Harper 1999).

458 For floras documented using rank abundance plots (Section 4.1), the curves can be
459 compared statistically using the χ^2 test (e.g., Gastaldo et al. 2004a; Willard and Phillips
460 1993). However, this approach assumes data must be counts not percentages, that the
461 categories are independent, and that the sample sizes are sufficiently large. Alternatively, the
462 non-parametric Kolmogorov-Smirnov test that will compare univariate distribution curves
463 and is free of these assumptions (Magurran 2004) as was done by DiMichele et al. (2021).

464 **5 Spatial diversity patterns**

465 Although comparing the diversity of two floras can provide valuable information,
466 comparing floras from different places and habitats can reveal patterns that may be of wider
467 ecological and floristic interest

468 *5.1 Local-scale spatial diversity*

469 Comparing the taxonomic diversities of fossil floras at local scale is usually aimed at
470 identifying the past plant communities in the landscape, but this can be difficult as most fossil
471 floras are fragmented and allochthonous. Nevertheless, by integrating evidence of the relative
472 spatial distribution of the fossils with their sedimentological context, consistent ecogroups of
473 fossil-taxa may be recognisable (Abbink et al 2004; Barbacka 2011; Barbacka et al. 2016;
474 Franz et al. 2019). By relating such ecogroups to the habitat preferences of the component
475 taxa determined from autochthonous floras and / or anatomical details, conceptual models of
476 vegetation communities can be developed. Ecogroups can sometimes be identified in ex-situ
477 spoil tip material (e.g., Procter 1994) or museum collections (e.g., Opluštil et al. 2007;
478 Costamagna et al. 2018; Strullu-Derrien et al. 2021) but the best results are normally obtained
479 from plant beds that can be directly sampled (see Section 2).

480 Spatial patterns in taxonomic diversity can be identified non-metrically by simply
481 tabulating the diversity for each plant bed (e.g., Opluštil et al. 2007, 2009a,b, 2020;
482 DiMichele et al. 2017a; Thomas et al. 2019a) or localities (e.g., Dix 1934; Kerp and Fichter
483 1985). How much of the landscape-scale diversity is accounted for by the differences in
484 local-scale diversity of the individual localities is traditionally referred to as β -diversity. At
485 its simplest, β -diversity can be represented by the Whittaker Index, which is the ratio of the
486 landscape-scale diversity to the average local-scale diversity (Whittaker 1960), but a range of
487 other metrics have since been developed (Koleff et al. 2003). However, diversity patterns
488 across a landscape are best revealed by numerical analysis, particularly ordination (Section
489 5.3.1).

490 5.2 *Floristics*

491 Identifying regional- or global-scale floristic (phytogeographical) patterns in the Cenozoic
492 can be guided by the distribution and ecological tolerances of nearest living relatives (e.g.,
493 the Coexistence Approach of Mosbrugger and Utescher 1997; see also Manchester and
494 Tiffney 2001; Tiffney and Manchester 2001; Liang et al. 2003). A derived approach, widely
495 used in modern ecological modelling, is the identification of Plant Functional Types (PFT)
496 based on traits and physiological capacities of nearest living relatives, and this has been used
497 to reconstruct Cenozoic vegetation patterns (e.g., Utescher & Mosbrugger 2007; François et
498 al. 2011; Popova et al. 2013; Utescher et al. 2017, 2021). However, this becomes increasingly
499 difficult with geologically older floras and floristic patterns have to be determined from
500 intrinsic distributional data obtained directly from the fossil record.

501 Traditionally, floristic patterns were recognised non-metrically, based mainly on the
502 experience of palaeobotanists who had studied a large number of floras (e.g., Gothan 1925,
503 1954; Vakhrameev et al. 1978; Meyen 1987; Mai 1995; Vakhrameev 2006). In essence their
504 approach was to recognise nested sets of floristic units (phytochoria) similar to those used
505 with living floras, in descending order of rank kingdom (or realm), area, province and district
506 (terms anglicised as in Meyen 1987): examples of such studies were by Chaloner and Lacey
507 (1973), Chaloner and Meyen (1973), Meyen (1987), Wnuk (1994), Iannuzzi and Rösler
508 (2000), Mosseichik (2010) and Christiano-de-Souza et al. (2014). As pointed out by
509 Raymond et al. (1985b), however, palaeobotanical phytochoria are conceptually different
510 from those defined on today's vegetation because of the incompleteness of the fossil record.
511 Consequently, Cleal and Thomas (in Cleal 1991, p. 26) suggested that Meyen's (1987) terms
512 for the fossil phytochoria should be modified by adding the prefix "palaeo-". In this modified

513 sense, a palaeokingdom is not just an ancient floristic kingdom, but is a phytochorion defined
514 exclusively on the composition of the fossil floras. These palaeofloristic units should bear
515 some similarity to the floristic structure of the original vegetation, but this relationship is
516 hypothetical and cannot be tested directly. Deciding on the rank of a fossil phytochorion is
517 subjective, but Cleal and Thomas (2019) suggested that, if it is distinguished largely by
518 supra-generic taxa it is a palaeokingdom; if by fossil-genera it is a palaeoarea; if by fossil-
519 species it is a palaeoprovince; and if by just a few fossil-species it is a palaeodistrict.

520 Biomes (or biome formations) are more complex concepts than phytochoria as they are
521 defined by the distribution of the faunas, floras, and various environmental factors such as
522 climate, elevation and substrate conditions (e.g., Whittaker 1962). It has sometimes been
523 possible to recognise modern-day biomes in the Cenozoic record (e.g., Neumann and
524 Bamford 2015). There have also been attempts to recognise biomes in the fossil record (e.g.,
525 Rees and Ziegler 1996; Rees et al. 2000; Rees 2002; DiMichele et al. 2008; Nowak et al.
526 2020), but the fossil record is usually too incomplete for any rigorous delineation of biomes
527 in the sense that they are used with today's biotas.

528 5.3 *Numerical analysis of spatial data*

529 Because of the complexity of the data, most modern palaeofloristic studies tend to use
530 numerical analysis. The data are usually given in a matrix with rows of floras and columns of
531 taxa (either presence / absence or abundances). It is possible simply to calculate a series of
532 similarity coefficients (Section 4.2) between the floras (e.g., Czier 2002, 2016); but the
533 underlying structure of the data is usually shown better using multivariate numerical
534 methods. There are two broad classes of numerical method: ordination that tries to identify
535 linear trends within the data, and classificatory analyses that attempt to identify clusters.
536 Neither is better than the other; they are just providing different insights into the structure of
537 data and Shi (1993b) has recommended that it is often best to use both ordination and
538 classificatory analyses in parallel (e.g., Fig. 4).

539 5.3.1 Ordination

540 Ordination aims to find linear trends within a multivariate dataset and can be a particularly
541 powerful tool for palaeoecological and floristic studies. Several ordination methods are
542 available (Gauch 1982; Shi 1993b, 1995; Davis 2002; Palmer 2004; Hammer and Harper
543 2006). One of the simplest is unconstrained seriation analysis that takes a presence / absence
544 matrix and rearranges the columns and rows so that the presences tend to occur in a broadly

545 diagonal arrangement (Brower and Kile 1988); it is in effect a one-dimensional ordination
546 (Fig. 5). More usually, however, ordination tries to arrange the data in a multidimensional
547 geometric space.

548 One of the first multidimensional ordination methods to be developed was Principal
549 Components Analysis (PCA; Pearson 1901). The original data can be seen as floras plotted in
550 a multidimensional geometrical space where each axis represents a taxon. PCA uses a
551 mathematical procedure (eigenanalysis) to rotate the multidimensional space so the new
552 orthogonal axes (eigenvectors) more efficiently reflect the structure of the data. Rather than
553 each axis representing a single taxon as in the original matrix, each of the eigenvectors now
554 represents several taxa; how much each taxon is represented on an eigenvector is called its
555 loading. It should now be possible to understand the relationships between the floras by how
556 they plot on much fewer axes (the eigenvectors) compared with the original matrix, making
557 the floristic or ecological structure easier to interpret. PCA has been used in plant
558 palaeoecological studies (e.g., Spicer and Hill 1979; Spicer 1981; Birks and Gordon 1985;
559 DiMichele et al. 2002; Barbacka 2014). However, PCA assumes that there is a continuous
560 linear transition in the floras along each eigenvector, which rarely happens in nature (Palmer
561 2004). It is more usual for the floras to show a unimodal distribution, forming clear peaks
562 along the eigenvectors, and will result in a significant curvature in the ordination plots known
563 as the horseshoe-effect (Gauch 1982).

564 Conceptually simpler is Correspondence Analysis (CA) that in its original form uses
565 reciprocal averaging to generate the new geometrical space (Hill 1973b; ter Braak in
566 Jongman et al. 1995; Rees and Ziegler 1999). The sample rows in the data matrix are sorted
567 according to the weighted average of its taxon scores, and then the taxon columns are sorted
568 according to the weighted average of the sample scores. This reciprocal re-scoring and re-
569 sorting of the taxon columns and of the sample rows is repeated until the arrangements of
570 rows and columns stabilise. The resulting taxon and sample scores are then both plotted along
571 what becomes the first axis of the ordination. CA then repeats the re-scoring / re-sorting on
572 the variance not explained by the first axis to establish the second and subsequent, mutually
573 orthogonal axes. As with PCA, most CA studies only use the first few axes, each of which
574 often seems to reflect a significant ecological or floristic gradient. Although this is the
575 conceptually easiest way to calculate and think about CA, the same result can be more
576 efficiently obtained by an eigenanalysis of a matrix of the χ^2 distances between the floras
577 (Greenacre 2010). This is now used in most CA software.

578 CA has the benefit of being relatively free of distributional assumptions: it can deal with
579 binary (presence / absence), abundance and categorical data, does not require data normality
580 or equivalence of variance between samples, and is tolerant of incomplete data (Shi 1995).
581 Unlike PCA, moreover, it assumes that each taxon will show a unimodal rather than linear
582 distribution along the eigenvectors (De'ath 1999), which is what normally occurs in nature.
583 But perhaps of greatest benefit is that CA shows which taxa are responsible for the
584 arrangement of the floras along the eigenvectors, which most other ordination methods do
585 not.

586 Although CA has been used in palaeobotanical studies (Rees et al. 2000, 2002; Coiffard et
587 al. 2008), the ordinations can be difficult to interpret because the technique tends to
588 compresses the data towards either end of each eigenvector and the data are plotted in an
589 arched configuration (albeit less extreme than the horseshoe effect seen in PCA). To
590 overcome this, Hill and Gauch (1980) introduced Detrended Correspondence Analysis
591 (DCA), which flattens-out the CA plot and decompresses the data at the ends of the
592 eigenvectors (e.g., Fig. 6). This detrending has been criticised as it is imposing linear gradient
593 structures on the data that may not be reflecting reality, and the underlying structure may be
594 better shown in un-detrended CA ordinations in higher-dimensional spaces (T. Olszewski,
595 pers. comm. 2021). Furthermore, DCA may distort the ecological distances between the
596 floras along the eigenvectors (Minchin 1987) although their relative rank-order remains the
597 same. The initial arrangement of the data matrix can also affect DCA ordinations (Oxanen
598 and Minchin 1997) but this can be overcome by standardising the arrangement of the rows in
599 the data matrix using unconstrained seriation analysis before running the ordination (Cleal
600 2008b,c). Uneven abundance data can also sometimes cause problems but Burnham (1994)
601 found that this can be mitigated by using log transformations. The many advantages of DCA
602 generally outweigh these drawbacks, and it has been used in many palynological (Caseldine
603 and Pardoe 1994; Pardoe 1996, 2006; Dimitrova et al. 2007, 2011), macrofloral (DiMichele
604 and Phillips 1988, 1996; Burnham 1994; Gemmill and Johnson 1997; DiMichele et al. 1996b;
605 Willard et al. 2007; Barbacka 2011; Looy & Hotton 2014; Saxena et al. 2019; Strullu-Derrien
606 2021), and floristic studies (Thomas 2007; Cleal 2008b,c; Thomas et al. 2019b).

607 Canonical Correspondence Analysis (CCA) is another modification of CA where each
608 flora is assigned one or more known environmental variables. The ordination is then done on
609 axes that are linear combinations of the environmental variables. This approach has been used
610 to relate palynological data to variables such as precipitation or altitude of a site (Gaillard et

611 al., 1994; Hjelle, 1999; Court-Picon, 2004; Finsinger 2007). More recently, CCA has been
612 used to relate clusters of pollen taxa to specific plant communities (Pardoe 1996, 2006,
613 2014).

614 Non-Metric Multidimensional Scaling (NMDS) is an alternative to DCA that uses a matrix
615 of distance indices between the floras rather than of taxon occurrences /abundances in the
616 floras (Kruskal 1964). Firstly, it must be decided how many axes and what distance index are
617 to be used. The floras are then arranged in the geometrical space, either randomly or in a
618 configuration pre-determined using another ordination method (e.g., DCA). The rank-order of
619 the geometrical distances between the floras in this configuration is compared with the rank-
620 order in the original distance matrix, and the level of mismatch is given by a metric referred
621 to as stress. The positions of the data in the geometrical space are then adjusted to try to
622 reduce the mismatch between the rank-orders, and the stress re-calculated. This process is
623 repeated until the stress has been minimised.

624 NMDS is numerically straightforward and will reveal gradations in the data in a low-
625 dimensional space, but will not reveal the detailed structure of the data as well as DCA,
626 especially if the latter is interpreted using more than two dimensions (Ruokolainen and Salo
627 2006). A more significant drawback is that NMDS is based on a matrix of distance indices
628 rather than of taxon occurrences or abundances, and so it does not reveal which taxa are
629 producing the structure resolved by the ordination. It is also not so robust as DCA with noisy
630 data, and the results can vary in different runs and depending on how many dimensions are
631 being used (Shi 1993b). Some of these problems can be resolved (e.g., by making repeated
632 analyses and using the ordination with the lowest stress value). Some authors now use NMDS
633 where DCA may previously have been used in palaeoecological (Willard 1993; DiMichele et
634 al., 1991, 2007, 2017b; Pryor 1996; Bashforth et al. 2011; Barreda et al. 2012; Sala-Pérez et
635 al. 2020) and floristic studies (Cúneo 1996; Barbacka et al. 2014). However, when DCA and
636 NMDS have been compared, they have produced broadly similar ordinations (e.g., DiMichele
637 et al. 1991) and so, given the advantages of DCA (notably that it shows which taxa are
638 exerting the greatest influence on the ordination) it would seem to be preferable.

639 Other ordination methods have occasionally been used with macrofloral studies. Polar
640 Ordination (PO) produces a series of orthogonal eigenvectors from a distance matrix on
641 which the floras can be plotted, and was used by Raymond et al. (1985a,b), Rowley et al.
642 (1985), Raymond (1987) and DiMichele and Phillips (1988). However, defining the PO axes
643 can be subjective (Shi 1993b) and the method has fallen out of fashion in palaeobotany.

644 Principle Coordinates Ordination (PCO) as used by Stiles et al. (2020) is similar to NMDS (it
645 is sometimes referred to as Metric Dimensional Scaling) but uses the absolute values rather
646 than rank-order of the floras in a distance matrix, and suffers from the same drawbacks as
647 NMDS.

648 5.3.2 Classificatory analysis

649 The most widely used classificatory technique, especially in floristic studies, is R-mode
650 cluster analysis, which shows the relationships between floras using a one-dimensional
651 dendrogram (Fig. 6). Various cluster strategies are available (Shi 1993b) but the most
652 commonly used is the Unweighted Pair-Group Method with Arithmetic Mean (UPGMA;
653 Sokal and Michener 1958). Similarity coefficients for all pairs of floras are calculated and the
654 most similar two floras are combined. The mean distance between this pair and all the other
655 floras is then compared, and the most similar flora joins the first pair to form a second cluster.
656 The process is repeated until all of the floras are combined into a single cluster. Particularly
657 for presence / absence data, Shi (1993a,b) recommended Jaccard's similarity coefficient and
658 this was used by Cleal and Shute (1995) with Pennsylvanian-age medullosaleans. Raymond
659 (1987) instead used Dice-Sørensen coefficients to analyse Devonian floras (based on traits
660 rather than strict taxonomy) as these tend to give greater emphasis to co-occurrences of taxa.
661 Various other similarity metrics are available (Shi 1983a,b) but these often have difficulties
662 handling uneven sample sizes (Hammer and Harper 2006). The least sensitive to uneven
663 sample sizes are Raup-Crick Coefficients, which show how often a comparable level of
664 similarity occurs in randomly replicated (by "Monte-Carlo" simulation) samples of the same
665 size (Raup and Crick, 1979; Hohn 2008); these have been used in palaeofloristic studies by
666 Thomas (2007) and Cleal (2008b,c).

667 Although a basic cluster analysis may reveal evidence of phytochoria, it does not show
668 which taxa are characterising the floras. This can partly be revealed by performing a Q-mode
669 analysis (i.e., clustering the taxa against the floras) and plotting the resulting dendrogram at
670 right-angles to the R-mode analysis – a procedure known as two-way clustering. This has
671 been used in a number of palaeozoological studies (e.g., Dominici et al. 2008; Danise and
672 Holland 2017)

673 An alternative classificatory approach is parsimony-based cladistic vicariance
674 biogeography (Humphries and Parenti 1999). Although the results are shown as a cladogram
675 that can superficially resemble a cluster analysis (Fig. 7), the dendrogram is generated in a

676 very different way: rather than looking at the overall similarity between floras, it tries to
677 identify geographical areas with shared taxa. A drawback is that it assumes that a
678 phytochorion develops through the progressive acquisition of taxa, which may not always be
679 the case. On the other hand, the theoretical background to the parsimony algorithm is well
680 established through its use in phylogenetics, and also has the benefit of giving at least some
681 indication of the taxa that are producing the phytochoria. There have been a few attempts to
682 use parsimony in palaeobotanical floristics (Drinnan and Crane 1990; Coiffard et al. 2008)
683 but, where it has been compared with cluster analysis (Hilton and Cleal 2007), the results
684 have not differed significantly.

685 5.3.3 TWINSPAN

686 This is in some ways a hybrid approach, sharing aspects of ordination and classificatory
687 analysis. Hill (1979), who developed the technique, referred to it as “a dichotomized
688 ordination analysis”. It is a DCA-like iterative approach but, instead of using reciprocal re-
689 scoring and re-ordering of the floras and taxa, it successively divides the floras into
690 categories, and then divides the species into categories based on the flora classification.
691 Unlike traditional classificatory techniques, therefore, it is a divisive rather than a clustering
692 algorithm.

693 Several palynological studies have used the method to ordinate vegetation and pollen data
694 (Caseldine 1992; Pardoe, 1996, 2006, 2014; Hjelle 1999; Connor et al. 2004; Connor and
695 Kvavadze 2009). For instance, Caseldine and Pardoe (1994) used it together with DCA to
696 differentiate between groups of surface pollen samples from glacier foreland sequences in
697 southern Norway. These groups were subsequently compared to Holocene pollen data from
698 cores and soil profiles (which were treated as passive samples) to indicate Holocene
699 vegetation and climatic changes. It was also used by Lenz et al. (2006) with high resolution
700 palynological data from Messel, showing a clear succession of middle Eocene plant
701 communities colonizing and invading the area, which had been devastated by the volcanic
702 eruption forming the maar lake.

703 5.3.4 Statistical significance

704 Both ordination and classificatory methods are exploratory approaches aimed at revealing
705 structure within the complex dataset; they do not in themselves provide a statistical measure
706 of significance of any groupings that may be revealed. Cluster analysis results can be tested
707 by bootstrapping where the analysis is repeatedly done on a subset of the data and will show

708 how many replicates are supporting each node on the dendrogram, but this is still not a
709 measure of statistical significance. That significance can be explored using confirmatory or
710 hypothesis-testing methods such as Discriminant Function Analysis, sometimes known as
711 Multivariate Analysis of Variance – MANOVA (e.g., DiMichele and Aronson 1992) but
712 there are problems with this approach with ecological/palaeoecological studies as the data
713 rarely fulfil the necessary underlying distributional assumptions (Anderson and Walsh 2013);
714 preferable are non-parametric comparisons such as PerMANOVA (Anderson 2001; e.g.,
715 Cleal 2008b,c). But it must always be remembered that these methods are only revealing
716 statistical significances – the observed differences and/or similarities could be simply the
717 result of incomplete sampling; they do not show whether the differences are botanically
718 meaningful.

719 **6 Analysing diversity stratigraphically**

720 *6.1 Stratigraphical trends in diversity*

721 Plant biostratigraphy is often regarded merely as a tool for stratigraphical correlation
722 (Cleal 1991, 1999, 2018; Traverse 2007; Opluštil et al. 2021) but it may also be seen as
723 providing evidence of the dynamic changes in plant diversity. Biostratigraphy has much in
724 common with biogeography in that both are seeking patterns in complex distributional data,
725 but there is one fundamental difference: whereas biogeographical data have three-
726 dimensional relationships, biostratigraphical data series are unidirectional as the present
727 cannot influence the past (Dornelas et al. 2013).

728 At its simplest, biostratigraphical data are purely the presence or absence of taxa at
729 different stratigraphical levels, and this may be all that is needed in local-scale diversity
730 studies (Fig. 8). Especially with plant macrofossils, however, individual assemblages are
731 unlikely to be fully representative of landscape-scale vegetation at any one time (Cleal et al.
732 2010). In taxon richness studies, it is normal, therefore, to use range-through data
733 (Boltovskoy 1988): in a stratigraphical sequence of floras A, B, C, if a species is found in A
734 and C but not B, it is still recorded as present in B. The logic is that a particular taxon is
735 unlikely to disappear and then reappear from a landscape at this temporal scale – although we
736 may not see the species in a fossil flora, it was probably still present somewhere in the
737 landscape and was not recorded there because of incomplete collecting, taphonomic factors
738 affecting preservation or local ecological factors. Although this may result in some

739 smoothing of the observed taxonomic diversity curves, it has proved a useful way of
740 investigating broad patterns in landscape-scale vegetation change (DiMichele et al. 1996;
741 Cleal 2005, 2007, 2008a; Gastaldo et al. 2009; Uhl and Cleal 2010; Opluštil et al. 2017;
742 Nowak et al. 2018). The degree to which the range-through method is distorting data can be
743 represented by a Sample Completeness Metric (SCM; Benton 1987), which is simply the
744 ratio of those taxa that are actually observed in a particular fossil assemblage to those taxa
745 that “should” be present (e.g., Cleal et al. 2010; Xing et al. 2016).

746 A related issue is the uncertainty as to the start (First Appearance Datum – FAD) and end
747 (Last Appearance Datum – LAD) of the stratigraphical range of a taxon. If sampling is
748 perfect and taphonomy is having little effect, the FAD and LAD of a taxon’s range should
749 reflect the actual distribution of the taxon, but such criteria are rarely met. This
750 incompleteness in the record will, for instance, explain the “edge-effect” seen in many
751 stratigraphical sequences, where a clear reduction in taxonomic richness occurs towards the
752 top of a stratigraphical sequence (for instance at the top of Fig. 9) or as a hiatus in the record
753 is approached (e.g., Wilf and Johnson 2004). It has little to do with a decline in actual
754 diversity but is simply because of incomplete sampling of the floras near to the stratigraphical
755 break or change. There are numerical methods of assessing the confidence intervals for the
756 FAD and LAD of a taxon (Straus and Sadler 1989; Marshall 1990, 1997) and this was used
757 by Wilf and Johnson (2004) in a study of vegetation responses in Dakota (USA) to the end-
758 Cretaceous biotic crisis.

759 With palynological data, samples are often at a high temporal resolution and so changes in
760 the presence of rare taxa may not be caused by rapid environmental change but is simply a
761 sampling effect. This can be overcome using a taxon-accumulation curve, where the numbers
762 of taxa are summed over consecutive samples and plotted against the accumulated sample
763 count representing sampling effort (Giesecke et al. 2012). These accumulation curves can be
764 described with power functions and deviations from the theoretical relationships may be
765 reflecting past environmental changes such as the onset of human land use (Giesecke et al.
766 2014a). Where the focus of the investigation includes rare pollen types, it may be convenient
767 to combine samples into larger units and even combining pollen diagrams to derive regional
768 taxonomic pools (Giesecke et al. 2012). In the latter case it is crucial to work with pollen
769 diagrams that are harmonized to the same taxonomic rank.

770 Biostratigraphical distributional data are usually represented as range charts (Fig. 8). Early
771 examples of such range charts show the temporal distribution of high-ranked taxa (e.g.,

772 Bronn 1849) but their use with species in palaeobotany was pioneered by Dix (1934) and it is
773 now a fairly standard way of recording stratigraphical distributions of taxa (e.g., Cleal 1978,
774 1984, 2005, 2007, 2008a; Wagner et al. 1983; Willis and Niklas 2004; Bertini 2010). Such
775 charts can be easily used to extract range-through taxonomic diversity data by simply
776 counting how many range bars cross each stratigraphical level. This can then be documented
777 as a graph plotted alongside the stratigraphical column. In principle, the significance of such
778 changes in taxonomic diversity can be determined using standard statistical tests, but in many
779 cases the datasets will fail the required conditions such as normality of distribution and so
780 nonparametric bootstrap tests are usually preferable (Buckland et al. 2005). Also problematic
781 are the uneven sedimentation rates, which make it difficult to use stratigraphical thickness as
782 a time scale against which the diversity changes can be plotted and assessed. Wang et al.
783 (2005) suggested a partial metric to overcome uneven sedimentation rates in different
784 sections, but a simple visual assessment of the stratigraphical trends will usually provide a
785 reasonable indication of any changes in taxonomic diversity through a sequence.

786 It can often be important to determine how the taxonomic balance of fossil floras changes
787 through a sequence. For instance, palynological data are often expressed as a series of parallel
788 diversity curves each representing a particular taxon or groups of interest (Fig. 10; e.g.,
789 Willard et al. 1995; Rull 2000; Schneebeil-Hermann *et al.* 2017). Alternatively, stacked
790 graphs have been used to show the changing diversity of the major plant groups as well as of
791 the flora as a whole (Fig. 8; e.g., Cleal 2005, 2007, 2008a; Opluštil et al. 2017).

792 Biostratigraphical changes are often expressed in terms of biozones. There are several
793 different types of zones (discussed by Cleal 1999 in a palaeobotanical context) but most tend
794 to be assemblage range zones defined by taxa with overlapping stratigraphical ranges and
795 usually delineated by discontinuities in the overall pattern of the stratigraphical ranges.
796 Traditionally these discontinuities would be recognised by visual inspection of range charts,
797 but this can be rather subjective (Gordon and Birks 1972; Bennett 1996). An alternative
798 approach is to calculate the taxonomic similarity coefficients between adjacent floras through
799 a stratigraphical sequence, where discontinuities will be marked by unusually low values;
800 DiMichele and Phillips (1995) used Jaccard coefficients in this way. Discontinuities can also
801 be recognised using constrained cluster analysis of the coefficients (CONISS), which is an R-
802 mode clustering algorithm (usually UPGMA) but with the order of samples kept in their
803 original stratigraphical sequence (Fig. 11; Gordon and Birks 1972; Kovach 1993; Bennett
804 1996; Leroy and Roiron 1996; Leroy et al. 2009; Cleal et al. 2012; Mander et al. 2013).

805 Jaccard and Sørensen-Dice coefficients have been used for presence / absence data (e.g.,
806 Gastaldo et al. 2009a,b), and Euclidean coefficients have been used with abundance data
807 (e.g., Quattrocchio et al. 2013). Raup-Crick coefficients were used by Cleal et al. (2012) and
808 Opluštil et al. (2017), which produced clearly demarcated biozones that largely coincided
809 with the Wagner (1984) non-metric biostratigraphy. The level of taxonomic similarity within
810 the cluster analysis that is used to separate zones is largely subjective, although bootstrapping
811 can provide some evidence of the robustness of the different clusters. Bennett (1996) has also
812 suggested numerical methods for determining how many zones will maximise the
813 explanation of the variance of biostratigraphical data (see also Seppä and Bennett 2003).

814 Another non-parametric way of seeking discontinuities in the plant fossil record,
815 especially if caused by extrinsic factors, is pseudo-cohort analysis (Hoffman and Kitchell
816 1984; Cascales-Miñana and Cleal 2011), a modification of cohort analysis of Raup (1975,
817 1978). This is based on the idea that taxa (like individual organisms) have a mean life
818 expectancy and that the taxa in an assemblage will stochastically become extinct with time
819 (Van Valen 1963). A survivorship curve of all the taxa in a flora plotted through the
820 succeeding stratigraphical interval should form a monotonic curve, as the taxa progressively
821 disappear from the record (Fig. 12). If such curves are plotted for each successive flora, the
822 result should be a series of more-or-less parallel lines; but, if there has been a significant
823 environmental disruption, a marked deflection appears in the lines. Although there may be
824 some questions about the underlying assumptions on which this is based, the technique has
825 proved useful in revealing significant diversity changes both at the level of global extinctions
826 (Cascales-Miñana 2011; Cascales-Miñana and Cleal 2011) and in the study of how specific
827 floras responded to climate and landscape change (Cleal et al. 2012).

828 Ordination has also been applied to identify significant trends in plant biostratigraphical
829 data (Kovach 1993). For instance, DCA has been used to investigate macrofloral evidence of
830 vegetation responses to climate change across the Triassic – Jurassic boundary (McElwain et
831 al. 2007); also, in various Carboniferous (Dimitrova and Cleal 2007), Palaeogene (e.g., Wing
832 and Harrington 2001; Wilf and Johnson 2004; Jaramillo et al. 2010), Neogene (Quattrocchio
833 et al. 2013) and Quaternary (Pidek and Poska 2013; Leroy et al. 2009) palynological studies.
834 As with spatial studies, some authors have now opted to use NMDS rather than DCA for
835 biostratigraphy (e.g., DiMichele and Aronson 1992). Since the data rarely fulfil the
836 underlying assumptions of linear distribution, PCA on its own has not been widely used for
837 plant biostratigraphical studies. An exception has been the use of PCA on transposed datasets

838 (taxa in rows, floras in columns) to try to identify the main palynological assemblages of co-
839 existing taxa rather than groupings of the floras (Festi et al. 2015; López-Merino et al. 2016).

840 Yet another numerical method for recognising biozones is Unitary Associations (Guex
841 1977, 1991). This uses a matrix of taxon occurrences through several stratigraphical
842 sequences and attempts to identify series of assemblage zones that maximise stratigraphical
843 resolution whilst minimising conflicts in the ranges between sections. This has been
844 occasionally applied to palynology (da Silva-Caminha et al. 2010; Kachniasz and da Silva-
845 Caminha 2017) but never with macrofloras. Another numerical method for identifying
846 biozones in palaeozoology is Appearance Event Ordination, which is similar to CA but
847 makes use of both species-associations and stratigraphical data instead of just taxonomic
848 presence – absence data (Alroy 1996) but again has had little application in palynology or
849 palaeobotany.

850 6.2 *Taxonomic origination and extinction*

851 Investigating long-range vegetation diversity dynamics, for instance in the search for
852 responses to mass extinctions or global climatic changes, requires a different approach to
853 traditional biostratigraphy. Because of the large number of floras involved, it is usual to
854 analyse data that have been binned into stratigraphical intervals such as stages or series.
855 However, this binning of the data can distort the detailed pattern of taxonomic originations
856 and extinctions, which can in turn distort diversity patterns; extending species ranges to the
857 boundaries of the stratigraphical units may cause artificially high origination and extinction
858 rates at those boundaries (Raup 1972). In principle, this boundary effect can be minimised by
859 using smaller time intervals, but small time-intervals will provide poorer samples of diversity
860 and thus also, potentially, distort the diversity signal. Varying time intervals represented by
861 each stratigraphical unit will also alter the observed taxonomic diversities in the bins (Raup
862 1972; Raymond and Metz 1995; Cascales-Miñana and Diez 2012). The observed taxonomic
863 diversity can be standardised against the duration of the stratigraphical bin (e.g., Xiong and
864 Wang 2011) but until recently this has been difficult because the available radio-isotopic
865 dating was not accurate enough. However, far better radio-isotopic dating is now available,
866 which can be combined with Milankovitch-cycle sedimentary sequences to provide a
867 temporal accuracy of up to 0.01% or better (Davydov et al. 2010; Waters and Condon 2012;
868 Hoyle et al. 2020). This offers considerable potential for standardising diversity metrics by
869 time.

870 Various metrics have been proposed to deal with data binning and other sampling issues
871 (Hammer and Harper 2006; Cascales-Miñana et al. 2013), but these can themselves distort
872 the extinction and origination metrics (Foote 1994, 2000). A comparative analysis has
873 suggested that no ideal metrics are available for this type of study (Cascales-Miñana et al.
874 2013) but the best results seem to be provided by range-through methods discounting
875 singleton taxa (Van Valen 1984; Gilinsky 1991; Foote 1994, 2000). However, the omission
876 from diversity studies of singleton taxa based on exceptionally preserved floras (e.g., from
877 Rhynie Chert) can significantly distort taxonomic extinction and origination patterns. As with
878 selecting biodiversity metrics, the choice of extinction / origination metrics should be made
879 with an awareness of the strengths and weakness of each, and taking into account the
880 underlying aims of the study.

881 Estimating origination and extinction rates can alternatively use Bayesian methods, which
882 take all fossil occurrences of taxa (including singletons) and uses these to model sampling
883 heterogeneity within the sequence (Silvestro et al. 2014a). Such methods help compensate for
884 uneven sampling and taphonomic distortions, and so are particularly useful when dealing
885 with large-scale but incomplete databases such as the Paleobiology Database (e.g., Silvestro
886 et al. 2014b, 2015).

887 In addition to broad changes in taxonomic richness through geological time, models have
888 been developed that suggest that large-scale groupings of higher-ranked taxa (usually
889 families) can be recognised that form coherent faunal and floral communities, each with its
890 characteristic diversity pattern. The idea was first developed by Sepkoski (1981) who used
891 factor analysis on a database of Phanerozoic marine invertebrate families. Factor analysis is
892 in some ways similar to PCA, but starts with the presumption that there is an underlying set
893 of variables (called latent factors) that can be used to explain the correlations between the
894 observed samples. Determining how many factors to use is often regarded as a contentious
895 issue; in principle, it can be decided beforehand if a specific model is to be tested. However,
896 more normally in an exploratory factor analysis (e.g., Sepkoski 1981) the decision is based on
897 how much of the total variance is being explained (e.g., how many factors will explain, say
898 80 % of the total variance in the data). The designated number factors are then extracted by
899 identifying where there are maximal correlations between the floras. The factors are then
900 rotated to “improve” the ordination. There are various rotation strategies, but the simplest
901 (and arguably the most objective) is VARIMAX that aims to achieve “simple structure”,
902 where a maximum number of floras have high loadings on only one factor, and a maximum

903 number of factors have high loadings for only a few floras (Pedhazur and Schmelkin 1991).
904 The loadings of the floras on each factor (i.e., how much of each flora is represented by the
905 factor) are then adjusted by the amount of the variance unique to that factor.

906 Although factor analysis is conceptually more complex than most other ordination
907 methods, the combination of factor rotation and identifying the variance unique to each factor
908 has proved particularly effective in revealing large-scale floristic and faunal patterns in time
909 and space – emphasising the associations of taxa whose mutual correlations support the floras
910 / faunas, whilst reducing the influence of the other groups of taxa. Using this method,
911 Sepkoski (1981) identified three large-scale Evolutionary Faunas among marine
912 invertebrates, which was subsequently modified by Rojas et al. (2019) into a four-factor
913 model by incorporating spatial data. Cleal and Cascales-Miñana (2014) used the same
914 approach on a global dataset of plant family distribution (modified from Benton 1993, and
915 Anderson et al. 2007) and extracted five Evolutionary Floras, which were named the
916 Eotracheophytic (formerly Rhyniophytic), Eophytic, Palaeophytic, Mesophytic and
917 Cenophytic (the last three being related to concepts originally introduced by Gothan 1912).
918 These Evolutionary Floras have proved useful in describing the broad trajectory of
919 Phanerozoic vegetation history (Cleal and Thomas 2019; Cleal 2021). More recently, a
920 similar analysis has been done on Silurian – Devonian genera and has revealed a more finely-
921 resolved Evolutionary Flora model for the early terrestrial vegetation (Capel et al. 2021).

922 An issue with such studies on long-range diversity trends in the palaeobotanical and
923 palynological records is that they require robust evidence of the relative ages of the fossil
924 floras being studied. As pointed out by Cleal et al. (2021) this can be a problem with
925 terrestrial stratigraphical sequences as the dating is sometimes based on palaeobotanical
926 and/or palynological evidence; there is clearly the potential for circular argument when trying
927 to document vegetation changes against a temporal framework that is itself established on
928 data derived from vegetation changes. It is therefore essential that the stratigraphical
929 relationships of the fossil floras are verified and, where possible, confirmed by independent
930 data such as from radioisotopic dates and/or biostratigraphy of other organismal groups.

931 **7 Conclusions**

932 Modelling past vegetation diversity is not just an abstract, “ivory-tower” exercise; it has
933 real implications for predicting the future response of today’s vegetation to major

934 environmental change, whether that be to fluctuating CO₂ concentrations, climatic
935 parameters, seasonality or plant disease. Improved understanding of fossil diversity will have
936 an impact on how the present and future biodiversity changes are understood and forecasted.
937 But the first step in any such endeavour must be the compilation of robust data on the
938 diversity of plant fossils. This can be based on either data from reliable secondary sources, or
939 data obtained from field surveys provided they are acquired using rigorous sampling
940 strategies and with an understanding of the biases that taphonomy introduces.

941 Fossil diversity can be expressed either as taxonomic richness (how many taxa are
942 present), taxonomic composition (what taxa are present) or taxonomic abundance (how much
943 of each taxon is present). Taxonomic richness is the easiest of these to measure and can
944 provide some evidence of ecological and climatic significance, especially if the richness
945 measures are broken down into taxonomic or ecologically-constrained groups. Taxonomic
946 composition is also relatively easy to determine (provided the palaeobotanist is familiar with
947 the taxonomy of the relevant floras) and has given valuable data for floristic and
948 biostratigraphical diversity studies. Taxonomic abundance is the least easy to determine from
949 the fossil record because of the way that plants fragment, and is often extremely difficult to
950 interpret in terms of the original vegetation. Except for the very few available autochthonous
951 macrofloras, it must be stressed that taxonomic abundance is often more informative of the
952 taphonomy (especially biostratinomy) of the fossil assemblage than of the diversity of the
953 original vegetation.

954 Deciding the analytical approach to use to find patterns in the diversity data can be
955 confusing as there is often no right or wrong method – each will be showing a different and
956 often legitimate insight into the structure of the data, and the choice of approach will depend
957 on what the investigator is trying to show. At a basic level, the choice is between a
958 classificatory approach which tries to find breaks and groupings with the data, and ordination
959 which tries to find linear trends within the data. In most cases, however, both groupings and
960 trends are being sought, and it often makes sense to run both types of analyses in tandem,
961 provided it is kept in mind exactly what type of pattern each analysis is yielding.

962 Numerical analyses of the record will be revealing diversity changes of the fossils and this
963 will only partially reflect the diversity of the original vegetation. There has, for instance, been
964 clear evidence that some plant taxa flourished in habitats only rarely represented in the fossil
965 record and whose ranges are therefore different from those of the plant fossils (e.g., Mamay
966 and Bateman 1991; Zhou 1994; Hamad et al. 2008). Nevertheless, by integrating the data

967 with sedimentological and geochemical evidence, it is possible to start taking the first steps
968 towards developing synecological models for past vegetation at local-, landscape-, regional-
969 and global-scales (Spicer 1989; Krassilov 2003; DiMichele and Gastaldo 2008).

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2017 Captions

2018 Fig. 1. Rarefaction analysis of macrofloras from above the Abergorky and Hafod coal seams
2019 (Pennsylvanian-age, South Wales Coalfield, United Kingdom) giving an indication of the
2020 number of specimens needed to represent the species richness of each flora. N = number of
2021 specimens counted in each flora; dashed line represents 95% confidence intervals of species
2022 richness values. Redrawn from Cleal et al. (2012).

2023 Fig. 2. Example of pollen counting sheet. As the counting proceeds, new arrows are added
2024 from the left to the right representing new transects on the microscope slide and taxon names
2025 are added to the first column left. Each black tick represents an observation. The count is
2026 deemed optimal when it reaches at least 300 terrestrial pollen (excluding unknown, reworked,
2027 aquatics, spores), and when the counting effort does not add significant new taxa. The orange
2028 line has been added to the counting sheet to underline the high number of new taxa at the
2029 beginning of the count, and the absence of new taxa at the end of the count. Drawn by S.
2030 Leroy.

2031 Fig. 3. Distribution of modern pollen samples recorded in the Eurasian Modern Pollen
2032 Database (part of the European Database) across different biomes in (A) geographical space
2033 and (B) climate space. Such databases, illustrating the relationship between modern pollen
2034 assemblages and climatic variables, are invaluable to support studies of past climate, land
2035 cover and land use based on Quaternary pollen records (see Davis et al. 2020).

2036 Fig. 4. Asturian-age palaeofloristic model for Variscan Euramerica based on distribution of
2037 medullosalean and lyginopterdalean species. The analyses, using a combination of Detrended
2038 Correspondence Analysis and cluster analysis (Fig. 6) was described in Cleal (2008b,c).

2039 Fig. 5. Example of unconstrained seriation analysis where the occurrences of species are
2040 arranged in a diagonal across the matrix, indicating the main trend in the variance in the data.
2041 Redrawn from Cleal (2008c).

2042 Fig. 6. Floristic analysis of Medullosales from the upper Asturian (middle Pennsylvanian) of
2043 Variscan Euramerica based on cluster analysis (upper) and Detrended Correspondence
2044 Analysis. From Cleal (2008c).

2045 Fig. 7. Vicariance biogeographical analysis of Carboniferous and Permian anatomically
2046 preserved floras from Euramerica and China, with tree plotted against age, showing strict

2047 consensus of 15 most parsimonious 162 step trees. Number 1 – 6 designate the sequence of
2048 significant floral events as the wetland vegetation evolved. From Hilton and Cleal (2007).

2049 Fig. 8. Part of a range chart showing the distribution of late Bashkirian (early Westphalian)
2050 macrofloras through the sequence in the South Wales Coalfield (United Kingdom). The
2051 range-through species diversity for any stratigraphical level can be determined by counting
2052 across the number of range bars that cross that level; the absolute species diversity is
2053 determined by counting the number of black circles. From Cleal (2007).

2054 Fig. 9. Stacked diversity curve for the Pennsylvanian-age South Wales coalfield (United
2055 Kingdom) showing changing species richness through the succession broken down into the
2056 major plant groups. Redrawn from Cleal (2007).

2057 Fig. 10. A percentage spore-pollen diagram showing changes in the representation of pollen
2058 and spore taxa through a sediment core (AKAD 11-17) collected from the deep-water zone of
2059 the western Black Sea, indicating the vegetation history over the last 20,000 years. Redrawn
2060 from Filipova-Marinova et al. (2021).

2061 Fig. 11. Constrained cluster analysis used to distinguish macrofloral biozones in the
2062 Pennsylvanian – Cisuralian Intra-Sudetic Basin, Czech Republic. Grey intervals correspond
2063 to red-beds. The clustering used the UPGMA algorithm on Raup-Crick Coefficients
2064 representing the taxonomic similarity of each pair of floras. From Opluštil et al. (2017).

2065 Fig. 12. Pseudo-cohort analysis of Pennsylvanian-aged macrofloras of the Ruhr Coalfield
2066 (Germany) showing biostratigraphical events in the floras as a whole, and in the main plant
2067 groups. From Cleal et al. (2012).