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

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

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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

3.

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.

4.

1   Introduction

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

2   Sampling strategies

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

2.1   *Microfossils and Mesofossils*

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

5.

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 petrifactions. 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 (Iwaniw 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 (Drägert 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 (Lamboy 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).

3   Databases

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

3.1   Palynology

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

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

by Raymond (1985), Raymond et al. (1985a,b) and Rowley et al. (1985) and used in floristic

analyses. Other diversity analyses of particular taxonomic groups and/or regional areas exist

(e.g., Lidgard and Crane 1990; Martinetto and Vassio 2010; Barbacka et al. 2014) although,

again, not all of the datasets have been published or updated.

The stratigraphical distribution of plant families was documented in Harland (1967 –

Fossil Record) and Benton (1993 – Fossil Record 2), and for the gymnosperms by Anderson

et al. (2007). These record the first and last occurrences of each known family, with full

bibliographic details allowing the evidence to be assessed and verified. The Benton (1993)

dataset is now available on-line and, although it has not been updated since the original

publications, a modified version of the palaeobotanical part was provided with the on-line

version of Cascales-Miñana and Cleal (2014).

Data-mining for diversity analyses can be facilitated by using reference managers such as

Endnote, Mendeley or Zotero. Endnote is particularly flexible in configuring dedicated fields

for recording taxa in references of any type (Popa 2011), while new versions enable detecting

taxa directly from attached PDF files associated with reference records. Queries can therefore

provide lists of references covering species, genera and families, as well as higher taxa.

Online queries directly from dedicated reference managers also enable rapid and robust

searches for diversity data; coupling Endnote with portals such as Web of Knowledge / Web

of Science can produce rapid records and data conversions.

4   Diversity metrics

There are two aspects to understanding the vegetational taxonomic diversity: the diversity

of individual floras and the comparison between floras. Each aspect has its own set of

metrics.

4.1   The diversity of a flora

A range of metrics are available to express taxonomic diversity in both palaeobotany and

palynology (Magurran 2004; Santini et al. 2017). The following discussion will mainly deal

with local-scale diversity, often referred to as α-diversity (Cleal et al. 2021).

The taxonomic diversity of a flora consists of its taxonomic richness and its taxonomic

evenness (Simpson 1949). Taxonomic richness (the number of taxa present, also termed the

standing diversity) is regarded as an important guide to ecological change in modern-day

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 (Maguran 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.

22.

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; Schneebeli-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 (Pedhauzur 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 CO_2 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

32.

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 air 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).