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

2 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

- 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
- 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 guides are published elsewhere (e.g., Magurran 2004; Palmer 2004; Hammer and Harper 79 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

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.

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 Ouaternary palynologists often include the latter within macrofossils (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 work. There have been attempts to analyse numerically the errors in mineral point counts in 103 104 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 sizes (Birks and Line 1992; Wing and Harrington 2001; Seppä and Bennett 2003; Barreda et 112 113 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 also been suggested that pollen taxonomic richness should be standardised for a set area and 116 117 time of sediment accumulation (van der Knaap 2009), but this requires accurate estimates of sediment accumulation, which can be difficult to determine. None of these methods solve the 118 119 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. (2011) selectively analysed "exotic" pollen and spores from a set of late Carboniferous 139 palynofloras to try and determine patterns of extra-basinal vegetation. By comparing time-140 equivalent Permian strata and their palynoflora, Stolle (2010, 2011) discovered 141 142 exotic Gondwana elements and "European" pollen, but in biogeographically atypical regions. The sampling and investigations were based on selected areas with different miospore 143 144 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 deposition (López-Merino et al. 2016). This approach often required counting more than 147 148 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).

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

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

167 2.2 Macrofossils

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

Sampling macrofloras in taxonomic diversity studies is usually by an individual-based protocol: specimens are sequentially taken and each new taxon is recorded until a representative sample size is achieved. What constitutes a representative sample size can be estimated using rarefaction analysis (Fig. 1): a graph is plotted of how many new taxa are found as progressively more specimens are examined and a representative sample size has been reached when the graph flattens-off (e.g., Burnham 1994; Cleal et al. 2012; Opluštil et 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, standard-size samples are measured, such as using botanical survey quadrats (Scott, 1978), or 188 189 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;

Stiles et al. 2020), the specimen numbers per quadrat being weighted according to the size of
each fragment (Spicer and Hill 1979; Pryor and Gastaldo 2000), or a randomly selected
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.

Another method used in botanical habitat work, especially with groundcover of herbaceous plants, is line-intercept survey (Floyd and Anderson 1987; Etchberger and Krausman 1997). A frame bearing regularly-spaced strings that are marked-off at regular intervals (e.g., 20 mm) is placed on the ground and each increment along each string is scored

according to the plant species it crosses. A similar approach has been used in palaeobotanical
surveys (e.g., Wing et al. 2012).

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

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

(older) museum collections where the sampling strategy has not been recorded (e.g., Uhl andLausberg 2008).

231 2.3 Megafossils

Megafossils are the largest plant fossils, such as the tree trunks found in in-situ fossil 232 233 forests (e.g., Becker 1993; DiMichele and Falcon-Lang 2011; Macdonald 2013) or as logiams 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 situ, although there can be exceptions (e.g., Thomas and Seyfullah 2015; Roberts et al. 2016). 236 237 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 (Hayworth 1985, 1986, Nayling et al. 2007, Sherlock 2019; Bailey et al. 2020), along rivers 244 245 by erosion (Vassio et al. 2008) or in freshwater lakes (Kaiser et al. 2018). Tree density and distribution are measured either through traditional surveying methods 246 247 (DiMichele et al. 1996a; Thomas 2013; Berry and Marshall 2015) or photogrammetry (Fernández-Lozano and Gutiérrez-Alonso 2017). There is the potential for future use of 248 249 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

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

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 potential problem with such studies is quality control and this is becoming an increased 262 263 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, such as the European Pollen Database (EPD), the European Modern Pollen Database 271 272 (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).

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

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Inc. (J.M. White), has been established. There is also available the CIMP slide collection, an archive of 382 images of holotypes of Palaeozoic miospore species scanned by M. Streel (see more details on the websites of the Laboratory of Palaeobotany, Moscow, Russia). More recently, a collaborative database PalyWeb has been created for Palaeozoic palynological 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 is the Plantae part of the Fossilium Catalogus. Initiated in 1913 by Wilhelmius Jongmans, this 298 299 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 Heritage Library and/or Google Books. 304

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.

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

326 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).

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 for recording taxa in references of any type (Popa 2011), while new versions enable detecting 336 337 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. 338 339 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

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.

346 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

by Cleal et al. 2021). The main problem tends to be of sampling: are enough specimens beingexamined 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 et al. 2021) scale. Such plots have been modelled mathematically using probability 362 363 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 Elsensohn 2014). Simpson's Index is a widely used heterogeneity metric, which ranges from 369 370 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 (N₂ of Hill, 1973a) and so 378 increases with decreasing evenness; the former has been used in palaeobotany by Pryor and Gastaldo (2000). 379

The Shannon heterogeneity metric not only takes into account the relative numbers of taxa, but also of individuals in the sample, and usually varies from 1.5 to 3.5 with increasing unevenness. However, this was not founded on ecological theory but uses information theory to try and estimate unevenness from the observations (Lande 1996). Although this is not a significant drawback with large samples (Peet 1974), it tends to be rather less sensitive to unevenness than the Simpson Index; it can often overemphasise the effect of the rarest taxa in a flora and so give greater emphasis to taxonomic richness (Nagendra 2002). There have been attempts to overcome this issue (e.g., Pielou's Index which is the Shannon metric divided by the log of the number of taxa; and N_1 of Hill, 1973a, which is the exponential value of the Shannon metric), but there remain fundamental problems with the Shannon index and its 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 metrics but with more compatible mathematical structures: N₀, which is the taxonomic 403 404 richness; N₁, which is the exponential of the Shannon metric; and N₂, which is the reciprocal of the Simpson heterogeneity metric. Jost (2006) referred to N1 and N2 as the "effective 405 406 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

only because our understanding of the full growth form of most of those fossil plants tends tobe incomplete.

421 Interpreting taxonomic evenness in palynofloras is also difficult because of the large variations between plant groups in pollen (and spore) productivity and dispersal (Matthias et 422 423 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 taxa (e.g., DiMichele et al. 2021) and the squared chord distance gives more weight to the 448 449 overall composition of the samples (e.g., Pardoe et al. 2010). As with many of these

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

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

464 **5** Spatial diversity patterns

Although comparing the diversity of two floras can provide valuable information,
comparing floras from different places and habitats can reveal patterns that may be of wider
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 floras are fragmented and allochthonous. Nevertheless, by integrating evidence of the relative 471 472 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; Franz et al. 2019). By relating such ecogroups to the habitat preferences of the component 474 taxa determined from autochthonous floras and / or anatomical details, conceptual models of 475 476 vegetation communities can be developed. Ecogroups can sometimes be identified in ex-situ spoil tip material (e.g., Procter 1994) or museum collections (e.g., Opluštil et al. 2007; 477 478 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; DiMichele et al. 2017a; Thomas et al. 2019a) or localities (e.g., Dix 1934; Kerp and Fichter 482 1985). How much of the landscape-scale diversity is accounted for by the differences in 483 484 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; Francois 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 (terms anglicised as in Meyen 1987): examples of such studies were by Chaloner and Lacey 506 507 (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

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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 possible to recognise modern-day biomes in the Cenozoic record (e.g., Neumann and 523 524 Bamford 2015). There have also been attempts to recognise biomes in the fossil record (e.g., Rees and Ziegler 1996; Rees et al. 2000; Rees 2002; DiMichele et al. 2008; Nowak et al. 525 526 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 diagonal arrangement (Brower and Kile 1988); it is in effect a one-dimensional ordination
(Fig. 5). More usually, however, ordination tries to arrange the data in a multidimensional
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 as the horseshoe-effect (Gauch 1982). 563

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 according to the weighted average of its taxon scores, and then the taxon columns are sorted 567 568 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 efficiently obtained by an eigenanalysis of a matrix of the χ^2 distances between the floras 576 (Greenacre 2010). This is now used in most CA software. 577

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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 or equivalence of variance between samples, and is tolerant of incomplete data (Shi 1995). 580 Unlike PCA, moreover, it assumes that each taxon will show a unimodal rather than linear 581 582 distribution along the eigenvectors (De'ath 1999), which is what normally occurs in nature. But perhaps of greatest benefit is that CA shows which taxa are responsible for the 583 584 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 al., 1994; Hjelle, 1999; Court-Picon, 2004; Finsinger 2007). More recently, CCA has been
used to relate clusters of pollen taxa to specific plant communities (Pardoe 1996, 2006,
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 to be used. The floras are then arranged in the geometrical space, either randomly or in a 617 618 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 et al. 1991) and so, given the advantages of DCA (notably that it shows which taxa are 637 638 exerting the greatest influence on the ordination) it would seem to be preferable.

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

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Principle Coordinates Ordination (PCO) as used by Stiles et al. (2020) is similar to NMDS (it
is sometimes referred to as Metric Dimensional Scaling) but uses the absolute values rather
than rank-order of the floras in a distance matrix, and suffers from the same drawbacks as
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 for presence / absence data, Shi (1993a,b) recommended Jaccard's similarity coefficient and 657 658 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 rather than strict taxonomy) as these tend to give greater emphasis to co-occurrences of taxa. 660 Various other similarity metrics are available (Shi 1983a,b) but these often have difficulties 661 662 handling uneven sample sizes (Hammer and Harper 2006). The least sensitive to uneven sample sizes are Raup-Crick Coefficients, which show how often a comparable level of 663 664 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 Thomas (2007) and Cleal (2008b,c). 666

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

An alternative classificatory approach is parsimony-based cladistic vicariance
biogeography (Humphries and Parenti 1999). Although the results are shown as a cladogram
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

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

Both ordination and classificatory methods are exploratory approaches aimed at revealing structure within the complex dataset; they do not in themselves provide a statistical measure of significance of any groupings that may be revealed. Cluster analysis results can be tested 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); preferable are non-parametric comparisons such as PerMANOVA (Anderson 2001; e.g., 714 715 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

Plant biostratigraphy is often regarded merely as a tool for stratigraphical correlation
(Cleal 1991, 1999, 2018; Traverse 2007; Opluštil et al. 2021) but it may also be seen as
providing evidence of the dynamic changes in plant diversity. Biostratigraphy has much in
common with biogeography in that both are seeking patterns in complex distributional data,
but there is one fundamental difference: whereas biogeographical data have threedimensional relationships, biostratigraphical data series are unidirectional as the present
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 studies (Fig. 8). Especially with plant macrofossils, however, individual assemblages are 730 731 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

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

Biostratigraphical distributional data are usually represented as range charts (Fig. 8). Early
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 as a graph plotted alongside the stratigraphical column. In principle, the significance of such 777 778 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.

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

Jaccard and Sørensen-Dice coefficients have been used for presence / absence data (e.g.,
Gastaldo et al. 2009a,b), and Euclidean coefficients have been used with abundance data
(e.g., Quattrocchio et al. 2013). Raup-Crick coefficients were used by Cleal et al. (2012) and
Opluštil et al. (2017), which produced clearly demarcated biozones that largely coincided
with the Wagner (1984) non-metric biostratigraphy. The level of taxonomic similarity within

the cluster analysis that is used to separate zones is largely subjective, although bootstrapping
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 28.

(taxa in rows, floras in columns) to try to identify the main palynological assemblages of coexisting taxa rather than groupings of the floras (Festi et al. 2015; López-Merino et al. 2016).
Yet another numerical method for recognising biozones is Unitary Associations (Guex

841 1977, 1991). This uses a matrix of taxon occurrences through several stratigraphical sequences and attempts to identify series of assemblage zones that maximise stratigraphical 842 843 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 biozones in palaeozoology is Appearance Event Ordination, which is similar to CA but 846 847 makes use of both species-associations and stratigraphical data instead of just taxonomic presence – absence data (Alroy 1996) but again has had little application in palynology or 848 849 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 diversity can be standardised against the duration of the stratigraphical bin (e.g., Xiong and 863 Wang 2011) but until recently this has been difficult because the available radio-isotopic 864 865 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 suggested that no ideal metrics are available for this type of study (Cascales-Miñana et al. 873 874 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 from diversity studies of singleton taxa based on exceptionally preserved floras (e.g., from 876 877 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.

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

number of factors have high loadings for only a few floras (Pedhauzur and Schmelkin 1991).
The loadings of the floras on each factor (i.e., how much of each flora is represented by the
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

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

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

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

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

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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).

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

Fig. 4. Asturian-age palaeofloristic model for Variscan Euramerica based on distribution of
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

arranged in a diagonal across the matrix, indicating the main trend in the variance in the data.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 Correspondence2044 Analysis. From Cleal (2008c).

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

69.

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).

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).

Fig. 10. A percentage spore-pollen diagram showing changes in the representation of pollen

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).
- 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).