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

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ABSTRACT

Determining the diversity of past floras helps with interpreting both the history and predicting the future of vegetation change. For global-scale and regional-scale diversity studies especially, secondary data are often used but local-scale studies tend to be based on survey data that require rigorous sampling. The correct sampling strategies depend on the types of fossils being investigated, including their physical size, and whether the aim is to determine taxonomic richness or relative abundance. Describing and comparing diversities can use a range of different metrics, depending on whether binary presence/absence or abundance data are available. Each metric provides a different insight into the diversities and the choice of which to use depends on the research question being investigated. Various numerical approaches are available for identifying spatial and stratigraphical diversity patterns, mainly classificatory techniques (e.g., cluster and parsimony analyses) and ordination (e.g.,

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Detrended Correspondence Analysis, Nonmetric Dimensional Scaling). The 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 studies from throughout the fossil record, dealing with floras ranging in age from the Devonian to the last few centuries.

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 microfossils (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).

Large samples of microfossils and mesofossils can potentially be obtained from a relatively small amount of material (less than a kg, usually a few g), and so the problem in 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 petrological slides (e.g., Howarth, 1998) and a similar approach was used to determine a reasonable sample size for palynological counts (Maher, 1972; Dimitrova et al., 2005; Keen et al., 2014). The sample size will be at least partly influenced by the number of taxa present and must be enough to ensure consistency of results (Birks and Birks, 1980, p. 165); most Cenozoic palynologists use counts between 300 and 1000 per sample (e.g., Fig. 2), although pre-Cenozoic palynology studies sometimes have to use smaller samples because of limited availability of material.

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 al., 2012; Matthias et al., 2015; Giesecke et al., 2019). This is where a graph is plotted of how many new taxa are found as progressively more specimens are examined. It is then possible 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 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 problem of differential pollen productivity and dispersal in different plant groups that can hinder the translation of palynological data into vegetation diversity (Odgaard, 1999, 2001, 2013; Seppä and Bennett, 2003; Weng et al., 2006; Cleal et al., 2021).

It can be effective to exclude tree pollen, especially in open situations where long-distance pollen dominates, but this inevitably reduces the pollen sum and requires higher counts to give statistically reliable results. It can, moreover, be difficult to be certain from palynological data whether or not past vegetation was open and that the tree pollen should be excluded (Magri and Parra, 2002; Pardoe, 2014, 2021). The local presence of a particular taxon is often identified by its pollen reaching a threshold percentage (e.g., > 0.5%) but this value may vary between taxa (Lisitsyna et al., 2011). Macrofossil evidence can also be used as an indicator of local presence, especially of trees, since seeds and other remains are heavier than pollen and less easily dispersed.

It is also often routine in Quaternary studies to exclude obligate aquatics from the calculation of percentages since (1) they are frequently over-represented, especially in lake sediments, and (2) the aim is often to reconstruct terrestrial (rather than aquatic) vegetation. Samples can also be contaminated by pollen reworked from older sediments, especially in extreme environments with high rates of catchment erosion such as occurred in the late glacial. In many cases however these unusual and often ‘older’ looking corroded exotic grains can be identified and excluded.

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 palynofloras to try and determine patterns of extra-basinal vegetation. By comparing time-equivalent Permian strata and their palynoflora, Stolle (2010, 2011) discovered exotic Gondwana elements and “European” pollen, but in biogeographically atypical regions. The sampling and investigations were based on selected areas with different microspore diversity spectra. Other investigations in lake settings separated well-preserved pollen grains (most likely air-borne just prior to deposition) to obtain the seasonal signal from reworked 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 1500 pollen grains per sample.

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

2.2. Macrofossils

These are the type of hand specimens that dominate most museum collections, including adpressions, casts, moulds and anatomically-preserved petrifications. 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; McElwain et al., 2007; Cleal et al., 2012; Opluštil et al., 2014).

The relative abundance of taxa is determined using a sample-based protocol, where every individual is counted within a particular sample. Sufficiently large samples can avoid some inherent sampling problems; for instance, Davies (1929) recorded every macrofossil found in several tonnes of roof shales above upper Carboniferous coals, resulting in individual macrofloras of up to 30,000 specimens (Thomas, 1986; Cleal, 2007; Cleal et al., 2012; King et al., 2011). But such large samples are exceptions and more usually the relative abundance of taxa has to be standardised according to the sample size, using similar approaches to those adopted in plant microfossils (Section 2.1) such as rarefaction analysis (e.g., McElwain et al., 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 pseudo-quadrats created by exposing rectangular areas of bedding plane (Gastaldo et al., 2004a) or bringing together specimens until a quadrat-sized area is filled (Iwaniw, 1985; Bashforth et al., 2010, 2011). Alternatively, proxy quadrats have been based on “normal size” hand-specimens (Pfefferkorn et al., 1975; Wing and DiMichele, 1995; Uhl

and Lausberg, 2008; Barbacka, 2011; Barbacka et al., 2016; DiMichele et al., 2016, 2021; Cleal et al., 2012; Bashforth and Nelson, 2015; DiMichele et al., 2019a, 2019b; Koll and DiMichele, 2021) or borehole cores of a set diameter (DiMichele et al., 2000). Various counting strategies have been used, with either all specimens in a quadrat being counted (Dräger, 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).

Whilst such quadrat and quadrat-like techniques appear to give numerical rigour to the analyses, and have particular benefits with floras dominated by compound foliage that has undergone various levels of fragmentation (Wing and DiMichele, 1995), distortions may be introduced according to the technique used (Lambooy and Lesnikowska, 1988). For instance, quadrat methods appear to lead to more even species distributions (DiMichele et al., 1991) and quadrat size can have a marked effect on taxonomic richness (Wing and DiMichele, 1995). Nevertheless, provided there is a consistency in the methods used, quadrats and allied techniques offer one of the best means of comparing relative abundances of fossil taxa 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; Behrensmeier et al., 2000; Spicer, 1988; 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

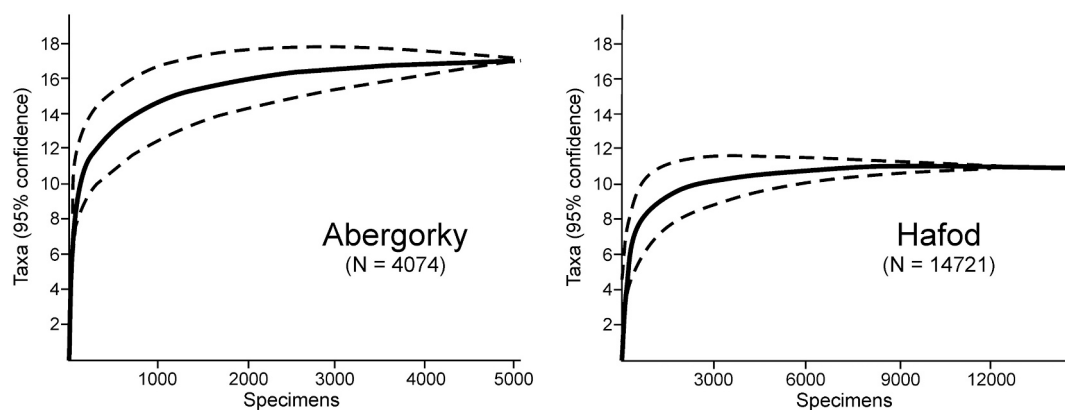


Fig. 1. Rarefaction analysis of macrofloras from above the Abergorky and Hafod coal seams (Pennsylvanian-age, South Wales Coalfield, United Kingdom) giving an indication of the number of specimens needed to represent the species richness of each flora. N = number of specimens counted in each flora; dashed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

Site and sample Name	Counting date	Type of microscope and magnification	Analyst name
Alnus			111
Deciduous Quercus			41
Carpinus betulus			55
Poaceae			38
Asteraceae tubul.			2
Amaranthac.			12
Monoete psilate			3
Parrotia persica			9
Polygonum persicaria			6
Convolvulus			2
Cistus			1
Cerealia			6
Potamogeton			1
Ulmus-Zelkova)		17
Reworked			1
Fagus			4
Pterocarya			1
Cyperaceae			14
Unknown			1
Artemisia			3
Pinus			2
Pteridium aquilinum			1
Juglans			1
Vitis			1
Ilex			1

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. Leroy.

has not been recorded (e.g., Uhl and Lausberg, 2008).

2.3. Megafossils

Megafossils are the largest plant fossils, such as the tree trunks found in in-situ fossil forests (e.g., Becker, 1993; DiMichele and Falcon-Lang, 2011; MacDonald, 2013) or as logjams in fluvial systems (Falcon-Lang and Bashforth, 2005; Kędzior and Popa, 2013; Gastaldo and 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). Where the area of exposure is sufficiently large, local-scale tree density can be measured directly (e.g., Gastaldo, 1986a; Hinz et al., 2010; Thomas, 2013; Opluštil et al., 2020).

Alternatively, it can be measured as trees become progressively exposed by advancing working faces in active quarries and mines (e.g., Gastaldo, 1986b; DiMichele and DeMaris, 1987; Mosbrugger et al., 1994; DiMichele et al., 2007; Gastaldo et al., 2004b) or in eroding cliffs (e.g., Francis, 1984; Calder et al., 2006; Falcon-Lang, 2006; Grey and Finkel, 2011). There are also late Quaternary submerged forests exposed in coastal areas by storms (Hayworth, 1985; Heyworth, 1986; Nayling et al., 2007; Sherlock, 2019; Bailey et al., 2020), along rivers 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 (DiMichele et al., 1996a; Thomas, 2013; Stein et al., 2012) or photogrammetry (Fernández-Lozano and Gutiérrez-Alonso, 2017). There is the potential for future use of satellite

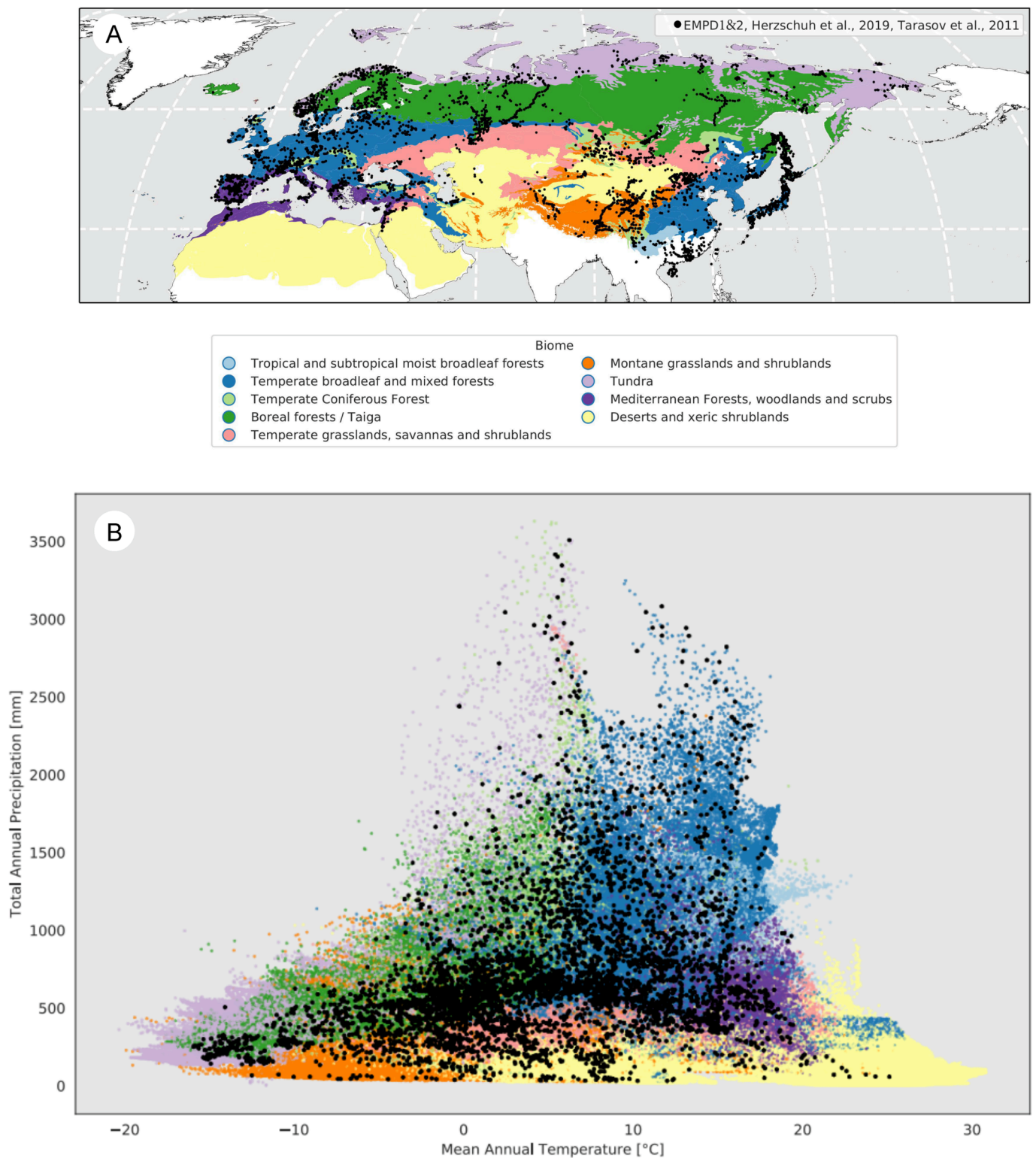


Fig. 3. Distribution of modern pollen samples recorded in the Eurasian Modern Pollen Database (part of the European Pollen Database) across different biomes in (A) geographical space and (B) climate space. Such databases, illustrating the relationship between modern pollen assemblages and climatic variables,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

technology such as Landsat or Sentinel-2 data, although the pixel resolution generally available is too coarse to see individual fossils (e.g., Landsat 32×32 m, pan-sharpened to 16×16 m; Sentinel 10×10 m); aerial photography and high-resolution satellite data such as Google Earth have greater possibilities. Determining taxonomic diversity from

fossil forests can be more problematic as the characters necessary for species or genus 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 depositional environments it is, moreover, necessary to ensure that the trunks are

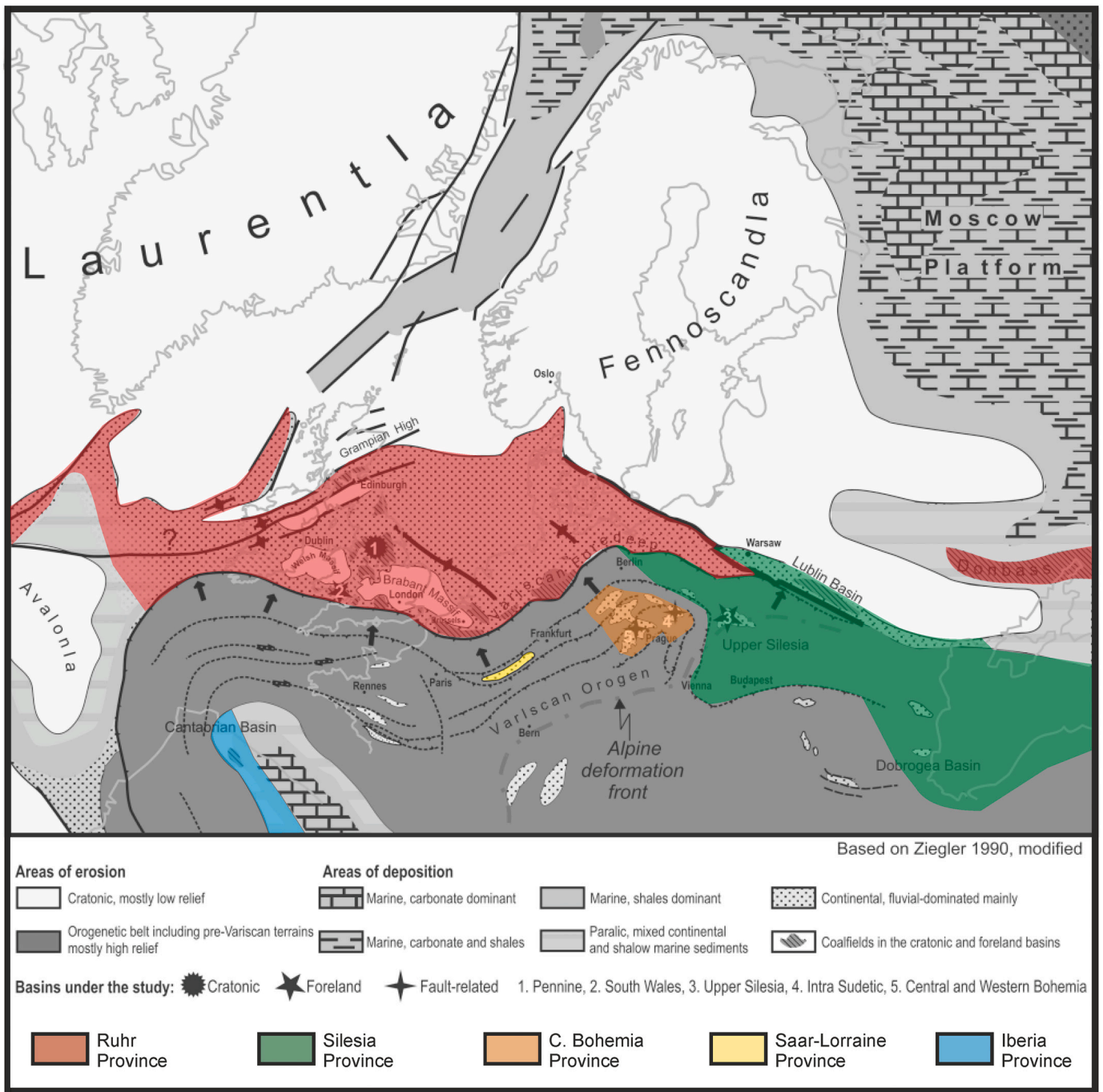


Fig. 4. Asturian-age palaeofloristic model for Variscan Euramerica based on distribution of medulloslean and lyginopterdalean species. The analyses, using a combination of Detrended Correspondence Analysis and cluster analysis (Fig. 6) was described in Cleal (2008b, 2008c).

autochthonous and have not been deposited in an upright position by mudflows or lahars (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., 2014; Grimm et al., 2013). These are being incorporated into the Neotoma palaeoecological database (Williams et al.,

	<i>Neuropteris flexuosa</i>	<i>Alethopteris robusta</i>	<i>Macroneuropteris macrophylla</i>	<i>Alethopteris nevessii</i>	<i>Alethopteris serrii</i>	<i>Laveineopteris dussartii</i>	<i>Alethopteris ambigua</i>	<i>Laveineopteris rarneris</i>	<i>Neuropteris ovata</i>	<i>Macroneuropteris scheuchzeri</i>	<i>Alethopteris pseudograndinioides</i>	<i>Linopteris obliqua</i>	<i>Neuropteris ex gr. obliqua</i>	<i>Alethopteris lonchitica</i>	<i>Callipteridium aramasii</i>	<i>Callipteridium jongmansii</i>	<i>Linopteris elongata</i>	<i>Linopteris palentina</i>	<i>Neuropteris resobae</i>	<i>Linopteris neuropteroides</i>	<i>Margaritopteris coemansii</i>	<i>Alethopteris grandinii</i>	<i>Neuropteris plicata</i>	<i>Neuropteris subauriculata</i>	<i>Odontopteris reichiana</i>	<i>Neuropteris britannica</i>	
Canada	1	1																									
SW Britain	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1												
Pennines				1	1	1	1	1	1	1	1		1														
NW Germany				1	1	1	1	1	1	1	1	1	1														
N Turkey						1	1	1	1	1	1	1	1	1													
Dobrudzha						1	1	1	1	1	1	1	1	1						1							
U Silesia							1	1	1	1	1	1	1	1	1					1							
NW Spain						1	1	1	1	1	1	1	1	1	1	1	1	1	1								
Saar-Lorraine									1												1	1		1	1		
Central Bohemia										1	1	1	1	1	1	1				1			1	1	1	1	
Intra-sudetic															1	1							1				
Zwickau															1					1						1	1

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).

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 of 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 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. Streele (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 (Stemans and Breuer, 2007) and is an ongoing project.

3.2. Macrofloras

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

Some macroflora records have been included in the Paleobiology Database (PBDB; Alroy, 2003) and this has been used in some palaeobotanical biodiversity studies (e.g., Raymond et al., 2006;

Silvestro et al., 2015), but the palaeobotanical coverage remains very patchy in terms of completeness and rigour and consistency of identifications. The Geobiodiversity database (GBDB; Xu et al., 2020) has been available since 2007 and includes detailed accounts of fossil plant occurrences, primarily from within China. Unlike the PBDB, the GBDB records are tied to geological sections, allowing stratigraphy-based diversity comparison to be made within formations and between geological sections. Most recently, a planned Integrative Paleobotany Portal (PBot) aims to provide a means of recording palaeobotanical data but at the time of writing its exact remit and how it relates to the PBDB and GBDB remains 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, 1985b) 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

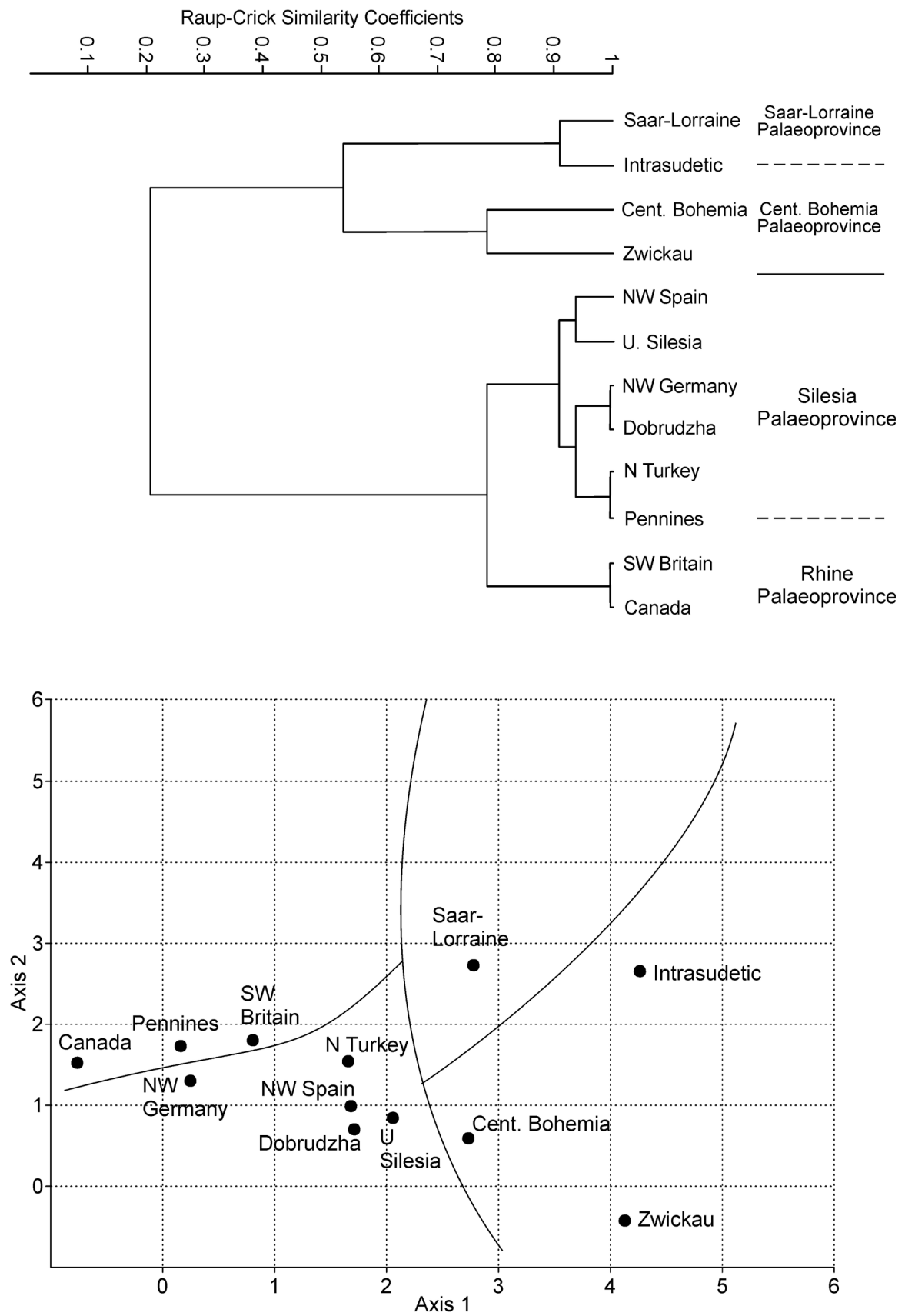


Fig. 6. Floristic analysis of Medullosales from the upper Asturian (middle Pennsylvanian) of Variscan Euramerica based on cluster analysis (upper) and Detrended Correspondence Analysis. From Cleal (2008c).

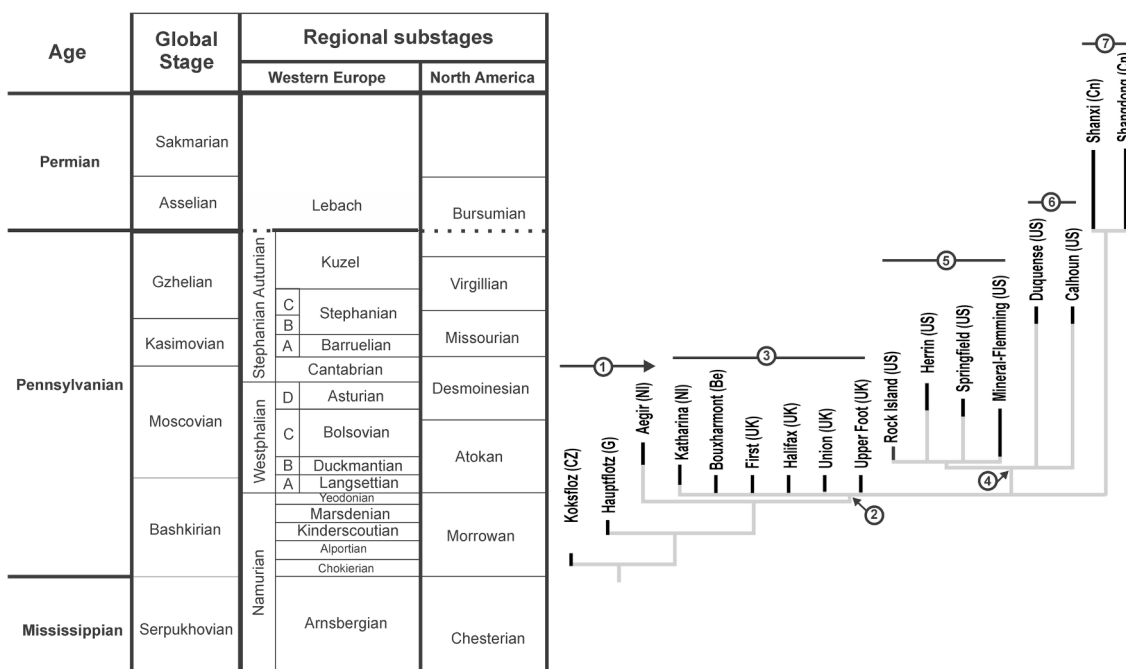


Fig. 7. Vicariance biogeographical analysis of Carboniferous and Permian anatomically preserved floras from Euramerica and China, with tree plotted against age, showing strict consensus of 15 most parsimonious 162 step trees. Number 1–6 designate the sequence of significant floral events as the wetland vegetation evolved. From Hilton and Cleal (2007).

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

Taxonomic evenness of a flora (whether there are numerous equally abundant taxa, or just a few dominant taxa) is ecologically important as it may affect how the vegetation will respond to environmental change (Magurran, 2004). The level of evenness can be judged graphically by plotting a rank abundance distribution curve (or Whittaker Plot), which shows the relative abundance of each taxon ordered sequentially by increasing abundance, plotted 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 distributions for ranked data (e.g., broken stick and Zipf-Mandelbrot distributions) to understand how modern-day plant communities become established (Mouillot and Lepretre, 2000; Magurran, 2004) and a similar approach to this was used with palaeobotanical data by McElwain et al. (2009).

Various metrics combine taxonomic richness and evenness, referred to as taxonomic 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 0 to 1 with increasing evenness, and is in essence the probability that any two samples drawn randomly from the flora will belong to the same taxon. This benefits from being conceptually straightforward and so easy to interpret, and has been used in palaeobotany and palynology (e.g., Wing and DiMichele, 1995; Uhl and Lausberg, 2008; Pardoe, 2021). The main problem is that the Simpson Index can be overly sensitive to the more abundant taxa in a flora, which could be a problem if the rarer species are of interest (Whittaker, 1965). The Simpson Index is sometimes converted to what is called a Diversity Index, either by subtracting its value from 1 (e.g., Whittaker, 1965) or using its reciprocal value (N_2 of Hill, 1973a) and so increases with decreasing evenness; the former has been used in palaeobotany by Pryor and Gastaldo (2000).

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).

Both Simpson and Shannon indices are affected by sample size and therefore by sampling effort, and so several non-parametric indices have been developed that only reflect the taxonomic evenness (Magurran, 2004; Buzas and Hayek, 2005; Chiarucci et al., 2011; Birks et al., 2016; Santini et al., 2017). The simplest are the Berger – Parker Index (the ratio of the number of specimens of the dominant taxon to the total sample size) and the Chao Estimators (which take into account the

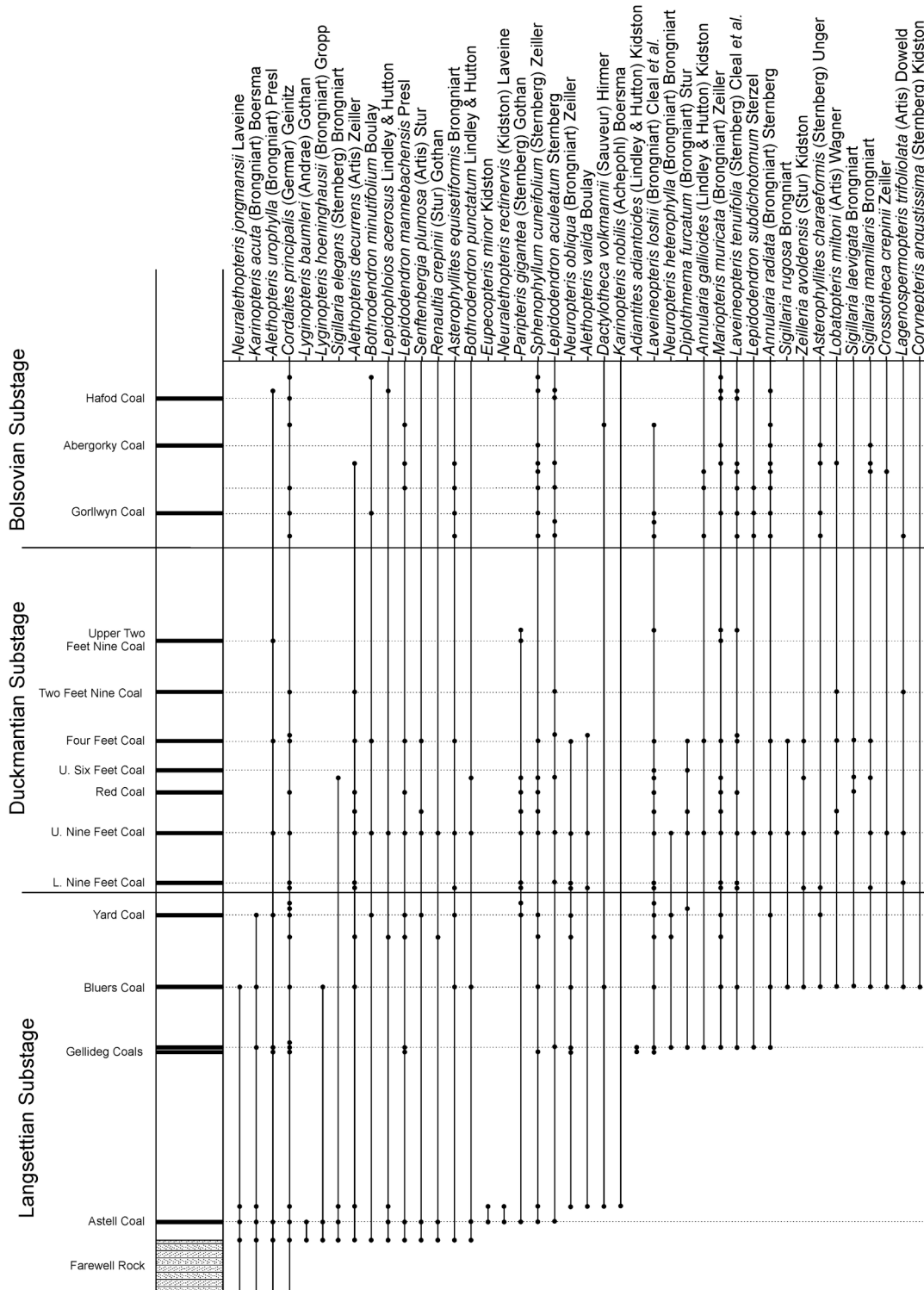


Fig. 8. Part of a range chart showing the distribution of late Bashkirian (early Westphalian) macrofloras through the sequence in the South Wales Coalfield (United Kingdom). The range-through species diversity for any stratigraphical level can be determined by counting across the number of range bars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

proportion of singleton and doubleton taxa; Chao, 1984, 1987); Chao estimators have been used in palaeobotanical studies by Wing and DiMichele (1995) and Mander et al. (2010).

Each of these diversity metrics produce different insights into the taxonomic structure of the assemblage and so in their way are equally valid. However, each of the main metrics has a different mathematical structure and so it is difficult to combine them into a unified scheme. Hill

(1973a) therefore proposed a unified system of Hill Numbers based on the main existing metrics but with more compatible mathematical structures: N_0 , which is the taxonomic richness; N_1 , which is the exponential of the Shannon metric; and N_2 , which is the reciprocal of the Simpson heterogeneity metric. Jost (2006) referred to N_1 and N_2 as the “effective number of species” in a community; they represent the number of equally-common species required to give a particular value of an index and so

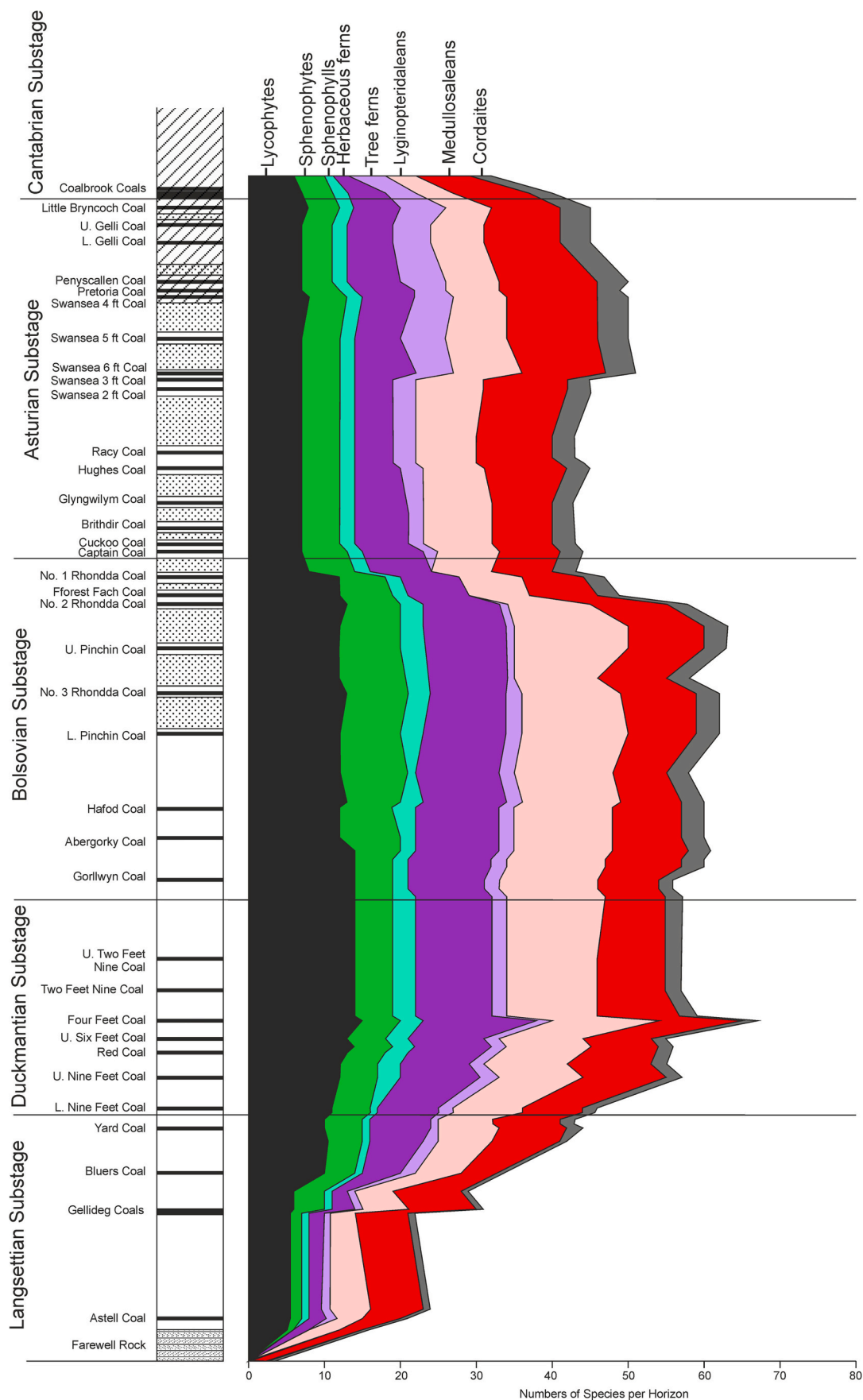


Fig. 9. Stacked diversity curve for the Pennsylvanian-age South Wales coalfield (United Kingdom) showing changing species richness through the succession broken down into the major plant groups. Redrawn from Cleal (2007).

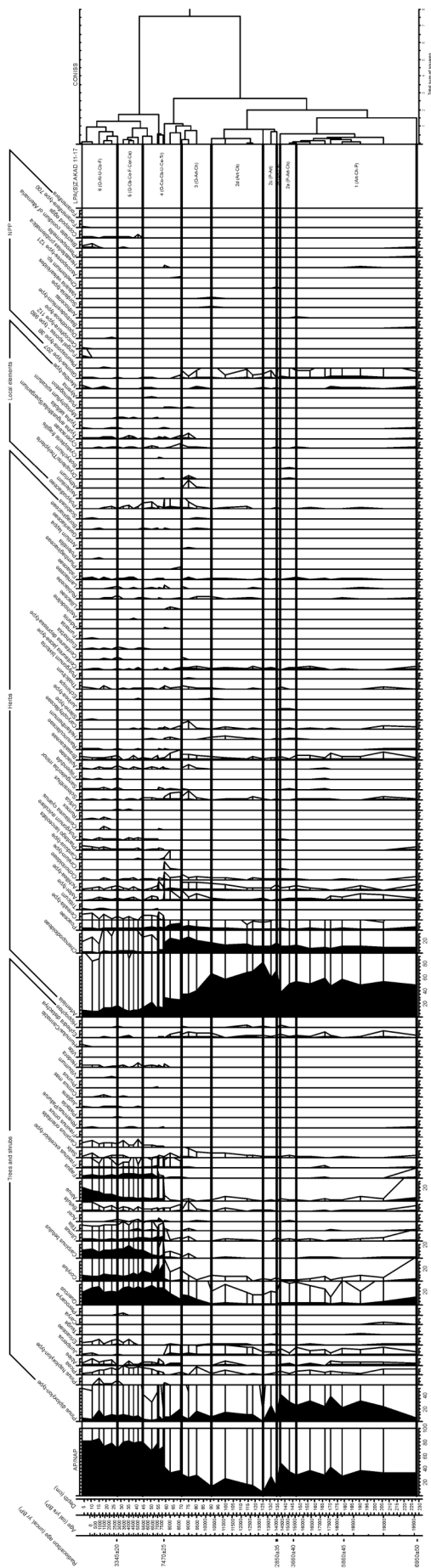


Fig. 10. A percentage spore-pollen diagram showing changes in the representation of pollen and spore taxa through a sediment core (AKAD 11–17) collected from the deep-water zone of the western Black Sea, indicating the vegetation history over the last 20,000 years. Redrawn from Filipova-Marinoва et al.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

may be regarded as the true level of taxonomic diversity.

Whilst it is relatively easily to measure taxonomic evenness in the plant fossil record, interpreting it in terms of vegetation evenness and its ecological impact is less straightforward. Even with living vegetation, taxonomic evenness can be difficult to interpret as the physical size and therefore biomass of each plant will affect its ecological impact (Hill, 1973a): a small number of trees will have a much greater effect on a habitat than the same number of herbaceous plants. Furthermore, the ecological impact of biomass varies according to the plant-part: the same biomass of leaves, reproductive structures and woody stems will have significantly different ecological impacts on a habitat. Although some attempts have been made to portion out biomass taxonomically in macrofloras with the aim of improving 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 to be incomplete.

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

4.2. Comparing the diversities of two floras

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

Usually it is more instructive to compare the taxonomic composition of two floras. At least 39 similarity indices are available for this purpose, each placing different emphasis on the comparison (Shi, 1993a, 1993b; Harper, 1999). For binary (presence/absence) data, the conceptually simplest is the Jaccard coefficient, which is the ratio of the number of taxa that are shared by two floras to the total number of taxa in the two floras combined, and was regarded by Shi (1993b) as the most robust for palaeoecological studies. Alternatively, DiMichele and Phillips (1988) and McElwain et al. (2007) used the Dice-Sørensen coefficient that gives greater emphasis to co-occurrences of taxa than mismatches. For taxonomic abundance data, several indices are available (reviewed by Hammer and Harper, 2006) but each tends to give a relatively different emphasis to sample size and so can produce rather different results; for instance, the Euclidean distance can be strongly influenced by 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 overall composition of the samples (e.g., Pardoe et al., 2010). As with many of these numerical techniques, when interpreting similarity indices, it is essential to understand exactly what the selected index is emphasising.

In themselves, these indices provide no measure of statistical significance; could the observed difference be explained merely through

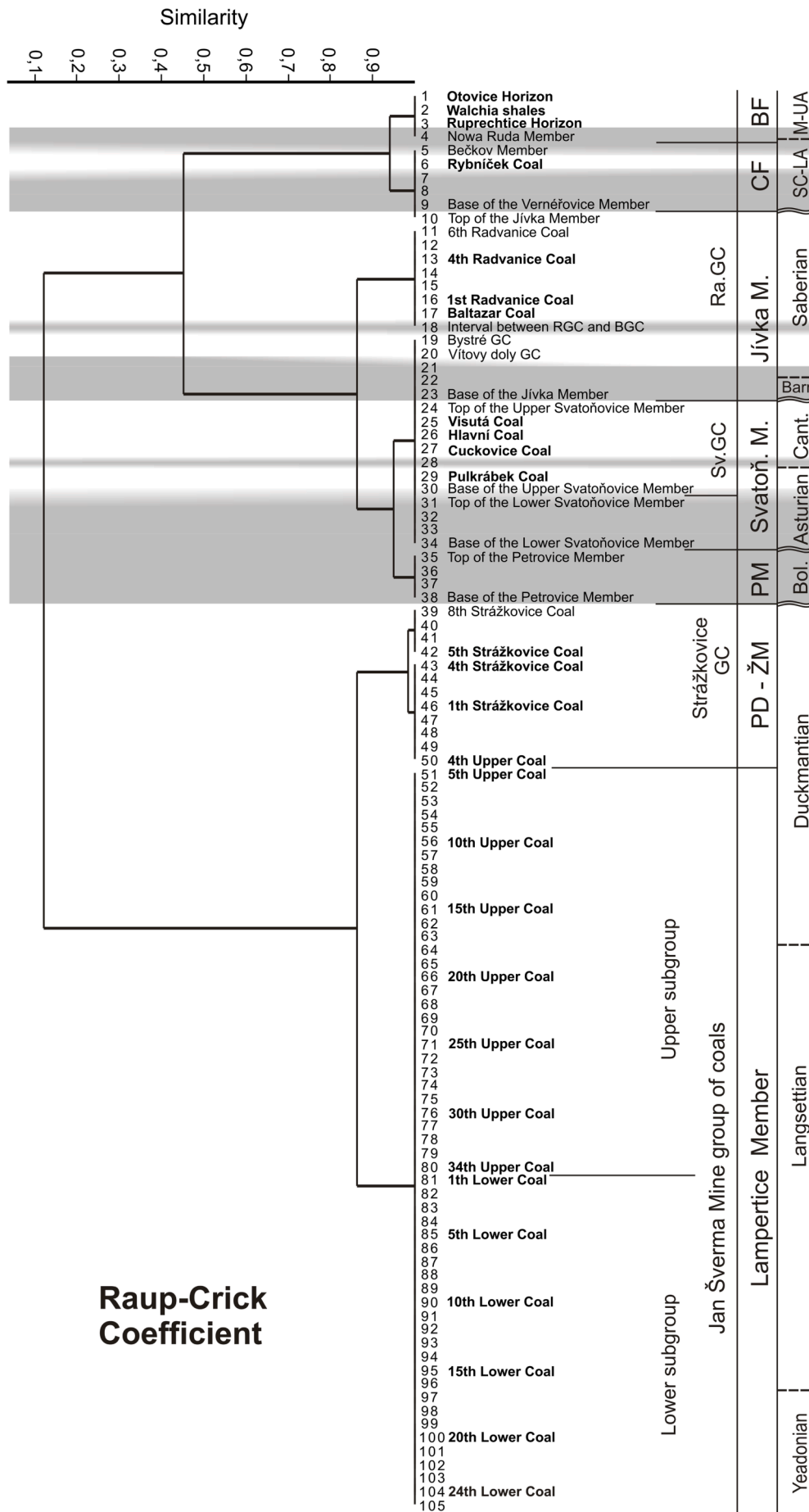


Fig. 11. Constrained cluster analysis used to distinguish macrofloral biozones in the Pennsylvanian – Cisuralian Intra-Sudetic Basin, Czech Republic. Grey intervals correspond to red-beds. The clustering used the UPGMA algorithm on Raup-Crick Coefficients representing the taxonomic similarity of each pair of floras. From Opluštil et al. (2017). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

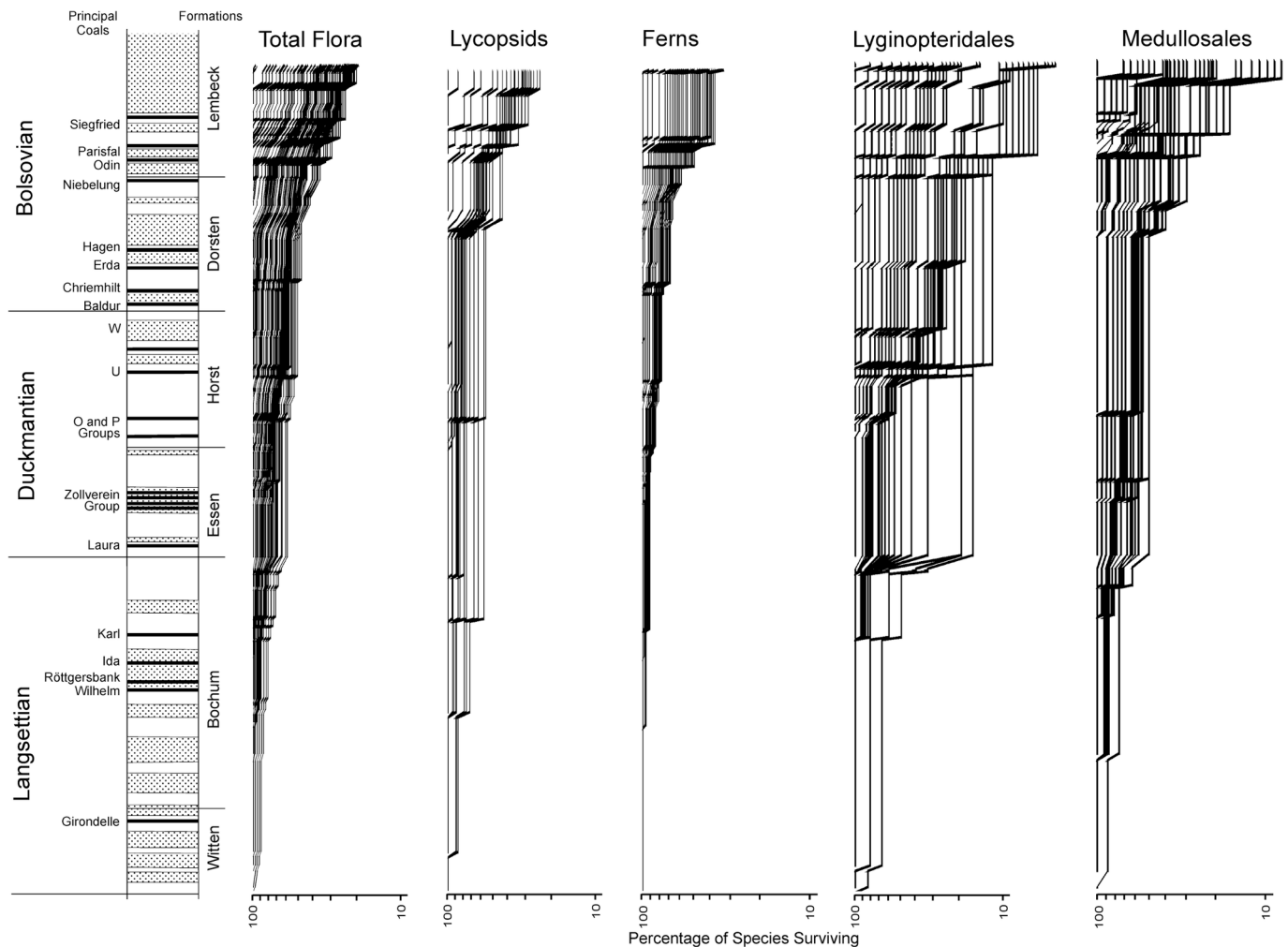


Fig. 12. Pseudo-cohort analysis of Pennsylvanian-aged macrofloras of the Ruhr Coalfield (Germany) showing biostratigraphical events in the floras as a whole, and in the main plant groups. From Cleal et al. (2012).

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 rather than percentages, that the categories are independent, and that the sample sizes are sufficiently large. Alternatively, the non-parametric Kolmogorov-Smirnov test compares univariate distribution curves and is free of these assumptions (Magurran, 2004) as was demonstrated by DiMichele et al. (2021).

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.

5.1. Local-scale spatial diversity

Comparing the taxonomic diversities of fossil floras at local scale is usually aimed at 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 spatial distribution of the fossils with their sedimentological context, consistent ecogroups of 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 taxa determined from autochthonous floras and/or anatomical details, conceptual models of 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; Costamagna et al., 2018; Strullu-Derrien et al., 2021) but the best results are normally

obtained from plant beds that can be directly sampled (see Section 2).

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

5.2. Floristics

Identifying regional- or global-scale floristic (phytogeographical) patterns in the Cenozoic can be guided by the distribution and ecological tolerances of nearest living relatives (e.g., the Coexistence Approach of Mosbrugger and Utescher, 1997; see also Manchester and Tiffney, 2001; Tiffney and Manchester, 2001; Liang et al., 2003). A derived approach, widely used in modern ecological modelling, is the identification of Plant Functional Types (PFT) based on traits and physiological capacities of nearest living relatives, and this has been used to reconstruct Cenozoic vegetation patterns (e.g., Utescher and Mosbrugger, 2007; François et al., 2011; Popova et al., 2019; Utescher et al., 2017, 2021). However, this becomes increasingly difficult with geologically older floras and floristic patterns have to be determined from intrinsic distributional data obtained directly from the fossil record.

Traditionally, floristic patterns were recognised non-metrically, based mainly on the experience of palaeobotanists who had studied a large number of floras (e.g., Gothan, 1915; Gothan, 1954; Vakhrameev et al., 1978; Meyen, 1987; Mai, 1995; Vakhrameev, 2006). In essence their approach was to recognise nested sets of floristic units (phytochoria) similar to those used 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 (1973), Chaloner and Meyen (1973), Meyen (1987), Wnuk (1996), Iannuzzi and Rösler (2000), Mosseichik (2010) and Christiano-de-Souza et al. (2014). As pointed out by Raymond et al. (1985b), however, palaeobotanical phytochoria are conceptually different from those defined on today's vegetation because of the incompleteness of the fossil record. Consequently, Cleal and Thomas (in Cleal, 1991, p. 26) suggested that Meyen's (1987) terms for the fossil phytochoria should be modified by adding the prefix "palaeo-". In this modified sense, a palaeokingdom is not just an ancient floristic kingdom, but is a phytochorion defined exclusively on the composition of the fossil floras. These palaeofloristic units should bear some similarity to the floristic structure of the original vegetation, but this relationship is hypothetical and cannot be tested directly. Deciding on the rank of a fossil phytochorion is subjective, but Cleal and Thomas (2019) suggested that, if it is distinguished largely by supra-generic taxa it is a palaeokingdom; if by fossil-genera it is a palaeoarea; if by fossil-species it is a palaeoprovince; and if by just a few fossil-species it is a palaeodistrict.

Biomes (or biome formations) are more complex concepts than phytochoria as they are defined by the distribution of the faunas, floras, and various environmental factors such as 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 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., 2020), and research is ongoing to combine paleo-traits data from fossil observations (McElwain et al., 2016; Wilson et al., 2017) with terrestrial ecosystem scale models (such as paleo-BGC, White et al., 2020) to determine the biogeographical limits of palaeo-traits in deep time, or at least to assign a well-studied

fossil floral locality to a palaeo-biome (White et al., 2020).

5.3. Numerical analysis of spatial data

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

5.3.1. Ordination

Ordination aims to find linear trends within a multivariate dataset and can be a particularly powerful tool for palaeoecological and floristic studies. Several ordination methods are available (Gauch, 1982; Shi, 1993b, 1995; Davis, 2002; Palmer, 2004; Hammer and Harper, 2006). One of the simplest is unconstrained seriation analysis that takes a presence/absence 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 multi-dimensional geometric space.

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

Conceptually simpler is Correspondence Analysis (CA) that in its original form uses reciprocal averaging to generate the new geometrical space (Hill, 1973b; ter Braak in 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 according to the weighted average of the sample scores. This reciprocal re-scoring and re-sorting of the taxon columns and of the sample rows is repeated until the arrangements of rows and columns stabilise. The resulting taxon and sample scores are then both plotted along what becomes the first axis of the ordination. CA then repeats the re-scoring/re-sorting on the variance not explained by the first axis to establish the second and subsequent, mutually orthogonal axes. As with PCA, most CA studies only use the first few axes, each of which often seems to reflect a significant ecological or floristic gradient. Although this is the 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 (Greenacre, 2010). This is now used in most CA software.

CA has the benefit of being relatively free of distributional assumptions: it can deal with 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). Unlike PCA, moreover, it assumes that each taxon will show a unimodal rather than linear 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 arrangement of the floras along the eigenvectors, which most other ordination methods do not.

Although CA has been used in palaeobotanical studies (Rees et al., 2000, 2002; Coiffard et al., 2008), the ordinations can be difficult to interpret because the technique tends to compress the data towards either end of each eigenvector and the data are plotted in an arched configuration (albeit less extreme than the horseshoe effect seen in PCA). To overcome this, Hill and Gauch (1980) introduced Detrended Correspondence Analysis (DCA), which flattens-out the CA plot and decompresses the data at the ends of the eigenvectors (e.g., Fig. 6). This detrending has been criticised as it is imposing linear gradient structures on the data that may not be reflecting reality, and the underlying structure may be better shown in un-detrended CA ordinations in higher-dimensional spaces (T. Olszewski, pers. comm. 2021). Furthermore, DCA may distort the ecological distances between the floras along the eigenvectors (Minchin, 1987) although their relative rank-order remains the same. The initial arrangement of the data matrix can also affect DCA ordinations (Oxanen and Minchin, 1997) but this can be overcome by standardising the arrangement of the rows in the data matrix using unconstrained seriation analysis before running the ordination (Cleal, 2008b, 2008c). Uneven abundance data can also sometimes cause problems but Burnham (1994) found that this can be mitigated by using log transformations. The many advantages of DCA generally outweigh these drawbacks, and it has been used in many palynological (Caseldine and Pardoe, 1994; Pardoe, 1996, 2006; Dimitrova and Cleal, 2007; Dimitrova et al., 2011), macrofloral (DiMichele and Phillips, 1988, 1996; Burnham, 1994; Gemmill and Johnson, 1997; DiMichele et al., 1996b; McElwain et al., 2007; Wing et al., 2005; Willard et al., 2007; Barbacka, 2011; Looy and Hotton, 2014; Saxena et al., 2019; Strullu-Derrien et al., 2021), and floristic studies (Thomas, 2007; Cleal, 2008b, 2008c; Thomas et al., 2019b).

Canonical Correspondence Analysis (CCA) is another modification of CA where each flora is assigned one or more known environmental variables. The ordination is then done on axes that are linear combinations of the environmental variables. This approach has been used to relate palynological data to variables such as precipitation or altitude of a site (Gaillard et al., 1994; Hjelle, 1999; Court-Picon et al., 2006; Finsinger et al., 2007). More recently, CCA has been used to relate clusters of pollen taxa to specific plant communities (Pardoe, 1996, 2006, 2014).

Non-Metric Multidimensional Scaling (NMDS) is an alternative to DCA that uses a matrix of distance indices between the floras rather than of taxon occurrences/abundances in the 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 configuration pre-determined using another ordination method (e.g., DCA). The rank-order of the geometrical distances between the floras in this configuration is compared with the rank-order in the original distance matrix, and the level of mismatch is given by a metric referred to as stress. The positions of the data in the geometrical space are then adjusted to try to reduce the mismatch between the rank-orders, and the stress re-calculated. This process is repeated until the stress has been minimised.

NMDS is numerically straightforward and will reveal gradations in the data in a low-dimensional space, but will not reveal the detailed structure of the data as well as DCA, especially if the latter is interpreted using more than two dimensions (Ruokolainen and Salo, 2006). A more significant drawback is that NMDS is based on a matrix of distance

indices rather than of taxon occurrences or abundances, and so it does not reveal which taxa are producing the structure resolved by the ordination. It is also not so robust as DCA with noisy data, and the results can vary in different runs and depending on how many dimensions are being used (Shi, 1993b). Some of these problems can be resolved (e.g., by making repeated analyses and using the ordination with the lowest stress value). Some authors now use NMDS where DCA may previously have been used in palaeoecological (Willard, 1993; DiMichele et al., 1991, 2007, 2017b; Pryor, 1996; Bashforth et al., 2011; Barreda et al., 2012; Sala-Pérez et al., 2020) and floristic studies (Cúneo, 1996; Barbacka et al., 2014). However, when DCA and 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 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, 1985b), 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. 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.

5.3.2. Classificatory analysis

The most widely used classificatory technique, especially in floristic studies, is R-mode cluster analysis, which shows the relationships between floras using a one-dimensional dendrogram (Fig. 6). Various cluster strategies are available (Shi, 1993b) but the most commonly used is the Unweighted Pair-Group Method with Arithmetic Mean (UPGMA; Sokal and Michener, 1958). Similarity coefficients for all pairs of floras are calculated and the most similar two floras are combined. The mean distance between this pair and all the other floras is then compared, and the most similar flora joins the first pair to form a second cluster. The process is repeated until all of the floras are combined into a single cluster. Particularly for presence/absence data, Shi (1993a, 1993b) recommended Jaccard's similarity coefficient and this was used by Cleal and Shute (1995) with Pennsylvanian-age medullosaleans. Raymond (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. Various other similarity metrics are available (Shi, 1993a; Shi, 1993b) but these often have difficulties 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 similarity occurs in randomly replicated (by "Monte-Carlo" simulation) samples of the same size (Raup and Crick, 1979; Hohn, 2018); these have been used in palaeofloristic studies by Thomas (2007) and Cleal (2008b, 2008c).

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 very different way: rather than looking at the overall similarity between floras, it tries to identify geographical areas with shared taxa. A drawback is that it assumes that a phytochorion develops through the progressive acquisition of taxa, which may not always be the case. On the other hand, the

theoretical background to the parsimony algorithm is well established through its use in phylogenetics, and also has the benefit of giving at least some indication of the taxa that are producing the phytochoria. There have been a few attempts to use parsimony in palaeobotanical floristics (Drinnan and Crane, 1990; Coiffard et al., 2008) but, where it has been compared with cluster analysis (Hilton and Cleal, 2007), the results have not differed significantly.

5.3.3. TWINSPLAN

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 re-scoring 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.

Several palynological studies have used the method to ordinate vegetation and pollen data (Caseldine and Pardoe, 1994; Pardoe, 1996, 2006, 2014; Hjelle, 1999; Connor et al., 2004; Connor and Kvavadze, 2009). For instance, Caseldine and Pardoe (1994) used it together with DCA to differentiate between groups of surface pollen samples from glacier foreland sequences in southern Norway. These groups were subsequently compared to Holocene pollen data from cores and soil profiles (which were treated as passive samples) to indicate Holocene vegetation and climatic changes. It was also used by Lenz et al. (2007) with high resolution palynological data from Messel, showing a clear succession of middle Eocene plant communities colonizing and invading the area, which had been devastated by the volcanic eruption forming the maar lake.

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

6. Analysing diversity stratigraphically

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 three-dimensional relationships, biostratigraphical data series are unidirectional as the present cannot influence the past (Dornelas et al., 2013).

At its simplest, biostratigraphical data are purely the presence or

absence of taxa at 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 unlikely to be fully representative of landscape-scale vegetation at any one time (Cleal et al., 2012). In taxon richness studies, it is normal, therefore, to use range-through data (Boltovskoy, 1988): in a stratigraphical sequence of floras A, B, C, if a species is found in A and C but not B, it is still recorded as present in B. The logic is that a particular taxon is unlikely to disappear and then reappear from a landscape at this temporal scale – although we may not see the species in a fossil flora, it was probably still present somewhere in the landscape and was not recorded there because of incomplete collecting, taphonomic factors 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., 1996a; Cleal, 2005, 2007, 2008a; Gastaldo et al., 2009a; Uhl and Cleal, 2010; Opluštil et al., 2017; Nowak et al., 2019). 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).

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

With palynological data, samples are often at a high temporal resolution and so changes in the presence of rare taxa may not be caused by rapid environmental change but is simply a sampling effect. This can be overcome using a taxon-accumulation curve, where the numbers of taxa are summed over consecutive samples and plotted against the accumulated sample count representing sampling effort (Giesecke et al., 2012). These accumulation curves can be described with power functions and deviations from the theoretical relationships may be reflecting past environmental changes such as the onset of human land use (Giesecke et al., 2014a). Where the focus of the investigation includes rare pollen types, it may be convenient to combine samples into larger units and even combining pollen diagrams to derive regional taxonomic pools (Giesecke et al., 2012). In the latter case it is crucial to work with pollen 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., Bronn, 1849) but their use with species in palaeobotany was pioneered by Dix (1934) and it is now a fairly standard way of recording stratigraphical distributions of taxa (e.g., Cleal, 1978, 1984, 2005, 2007, 2008a; Wagner et al., 1983; Willis and Niklas, 2004; Bertini, 2010). Such charts can be easily used to extract range-through taxonomic diversity data by simply 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 changes in taxonomic diversity can be determined using standard statistical tests, but in many cases the datasets will fail the required conditions such as normality of distribution and so nonparametric bootstrap tests are usually preferable (Buckland

et al., 2005). Also problematic are the uneven sedimentation rates, which make it difficult to use stratigraphical thickness as a time scale against which the diversity changes can be plotted and assessed. Wang et al. (2005) suggested a partial metric to overcome uneven sedimentation rates in different sections, but a simple visual assessment of the stratigraphical trends will usually provide a 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., Wing and DiMichele, 1995; Rull, 2000; Schneebeil-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).

Biostratigraphical changes are often expressed in terms of biozones. There are several different types of zones (discussed by Cleal, 1999 in a palaeobotanical context) but most tend to be assemblage range zones defined by taxa with overlapping stratigraphical ranges and usually delineated by discontinuities in the overall pattern of the stratigraphical ranges. Traditionally these discontinuities would be recognised by visual inspection of range charts, but this can be rather subjective (Gordon and Birks, 1972; Bennett, 1996). An alternative approach is to calculate the taxonomic similarity coefficients between adjacent floras through a stratigraphical sequence, where discontinuities will be marked by unusually low values; DiMichele and Phillips (1995) used Jaccard coefficients in this way. Discontinuities can also be recognised using constrained cluster analysis of the coefficients (CONISS), which is an R-mode clustering algorithm (usually UPGMA) but with the order of samples kept in their original stratigraphical sequence (Fig. 11; Gordon and Birks, 1972; Kovach, 1993; Bennett, 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, 2009b), 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 suggested numerical methods for determining how many zones will maximise the explanation of the variance of biostratigraphical data (see also Seppä and Bennett, 2003).

Another non-parametric way of seeking discontinuities in the plant fossil record, especially if caused by extrinsic factors, is pseudo-cohort analysis (Hoffman and Kitchell, 1984; Cascales-Miñana and Cleal, 2011), a modification of cohort analysis of Raup (1975, 1978). This is based on the idea that taxa (like individual organisms) have a mean life expectancy and that the taxa in an assemblage will stochastically become extinct with time (Van Valen, 1973). A survivorship curve of all the taxa in a flora plotted through the succeeding stratigraphical interval should form a monotonic curve, as the taxa progressively disappear from the record (Fig. 12). If such curves are plotted for each successive flora, the result should be a series of more-or-less parallel lines; but, if there has been a significant environmental disruption, a marked deflection appears in the lines. Although there may be some questions about the underlying assumptions on which this is based, the technique has proved useful in revealing significant diversity changes both at the level of global extinctions (Cascales-Miñana, 2011; Cascales-Miñana and Cleal, 2011) and in the study of how specific floras responded to climate and landscape change (Cleal et al., 2012).

Ordination has also been applied to identify significant trends in plant biostratigraphical data (Kovach, 1993). For instance, DCA has been used to investigate macrofloral evidence of vegetation responses to climate change across the Triassic – Jurassic boundary (McElwain et al.,

2007); also, in various Carboniferous (Dimitrova and Cleal, 2007), Palaeogene (e.g., Wing and Harrington, 2001; Wilf and Johnson, 2004; Jaramillo et al., 2010), Neogene (Quattrocchio et al., 2013) and Quaternary (Pidek and Poska, 2013; Leroy et al., 2009) palynological studies. As with spatial studies, some authors have now opted to use NMDS rather than DCA for biostratigraphy (e.g., DiMichele and Aronson, 1992). Since the data rarely fulfil the underlying assumptions of linear distribution, PCA on its own has not been widely used for plant biostratigraphical studies. An exception has been the use of PCA on transposed datasets (taxa in rows, floras in columns) to try to identify the main palynological assemblages of co-existing 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, 1977, 1991). This uses a matrix of taxon occurrences through several stratigraphical sequences and attempts to identify series of assemblage zones that maximise stratigraphical resolution whilst minimising conflicts in the ranges between sections. This has been occasionally applied to palynology (da Silva-Caminha et al., 2010; Kachniasz and da Silva-Caminha, 2017) but never with macrofloras. Another numerical method for identifying biozones in palaeozoology is Appearance Event Ordination, which is similar to CA but makes use of both species-associations and stratigraphical data instead of just taxonomic presence – absence data (Alroy, 1994) but again has had little application in palynology or palaeobotany.

6.2. Taxonomic origination and extinction

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

Various metrics have been proposed to deal with data binning and other sampling issues (Hammer and Harper, 2006; Cascales-Miñana et al., 2013), but these can themselves distort 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., 2010, 2013) but the best results seem to be provided by range-through methods discounting 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 Rhynie Chert) can significantly distort taxonomic extinction and origination patterns. As with selecting biodiversity metrics, the choice of extinction/origination metrics should be made with an awareness of the strengths and weakness of each, and taking into account the 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).

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

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

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

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.

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

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

Numerical analyses of the fossil record will reveal 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; Krasilov, 2003; DiMichele and Gastaldo, 2008).

Declaration of Competing Interest

All of the authors of this paper confirm that there are no conflicts of interest.

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