Does pollen-assemblage richness reflect floristic richness? A review of recent developments and future challenges

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ABSTRACT

Current interest and debate on pollen-assemblage richness as a proxy for past plant richness have prompted us to review recent developments in assessing whether modern pollen-assemblage richness reflects contemporary floristic richness. We present basic definitions and outline key terminology. We outline four basic needs in assessing pollen–plant richness relationships – modern pollen data, modern vegetation data, pollen–plant translation tables, and quantification of the co-variation between modern pollen and vegetation compositional data. We discuss three key estimates and one numerical tool – richness estimation, evenness estimation, diversity estimation, and statistical modelling. We consider the inherent problems and biases in assessing pollen–plant richness relationships – taxonomic precision, pollen-sample:pollen-population ratios, pollen-representation bias, and underlying concepts of evenness and diversity. We summarise alternative approaches to studying pollen–plant richness relationships. We show that almost all studies which have compared modern pollen richness with contemporary site-specific plant richness reveal good relationships between palynological richness and plant richness. We outline future challenges and research opportunities – interpreting past pollen-richness patterns, estimating richness from macrofossils, studying pollen richness at different scales, partitioning diversity and estimating beta diversity, estimating false, hidden, and dark richness, and considering past functional and phylogenetic diversity from pollen data. We conclude with an assessment of the current state-of-knowledge about whether pollen richness reflects floristic richness and explore what is known and unknown in our understanding of pollen–plant richness relationships.

6 *Keywords*: alpha, beta, and gamma diversity; dark diversity and richness; equitability; Hill numbers; pollen equivalents; vegetation sampling

ABBREVIATIONS

APSA	absolute pollen-source area
CoCA	co-correspondence analysis
PIE	probability of interspecific encounter
PPE	pollen-productivity estimate
RPSA	relevant pollen-source area

1. Introduction

Does pollen-assemblage richness reflect floristic richness? Anyone who has counted modern pollen spectra or Quaternary (Q-time; Jackson, 2001) fossil pollen assemblages from, for example, the northern boreal forests, temperate deciduous forests, the Mediterranean region, or the tropics would answer yes, of course it does and might think that this is a trivial or uninteresting question.

Many Quaternary palynologists have studied changes in pollen-assemblage diversity (hereafter called pollen diversity) using various diversity measures such as Shannon's information index (entropy) (e.g. Moore, 1973; Küttel, 1984), Simpson's index (e.g. Cwynar, 1982; Morley, 1982; Ritchie, 1982), or Williams (1964) α-index (Birks, 1973a; Morley, 1982), and changes in pollen richness through time from pollen-stratigraphical data using rarefaction analysis (Heck et al., 1975; Simberloff, 1978; Tipper, 1979; Birks and Line, 1992) (see Table 1 for selected examples of such rarefaction-based studies). There are, however, very few studies that explore how modern pollen richness or diversity relates to contemporary floristic richness or landscape diversity (see Birks, 1973a; Flenley, 2005; Weng et al., 2006; Odgaard, 2008; Meltsov et al., 2011; 2013; Goring et al., 2013; Jantz et al., 2014; Felde, 2015; Felde et al., 2015; Matthias et al., 2015).

In contrast to other studies on pollen-floristic richness that find a positive relationship between pollen and floristic richness, Goring et al. (2013) report a slightly negative modelled relationship between smoothed pollen richness and smoothed floristic richness in the Pacific Northwest of North America. Their model shows a weak but statistically significant (p <0.001) negative relationship, suggesting that higher pollen richness is associated with lower regional plant richness. They write that "We believe this study is the first to empirically test the relationship between plant and pollen richness and fails to find a significant relationship" and conclude that "The fundamental inability to relate pollen richness to plant richness in this analysis does not invalidate other studies that show robust changes in pollen richness over time, but it calls into question whether these changes reflect underlying changes in plant richness, or some other change in plant composition or structure" and they suggest that "the lack of a meaningful statistical relationship between measures of plant and pollen richness … calls into question the use of fossil pollen assemblages as a measure of species richness over time". These findings contrast with results of other studies where statistically significant positive relationships between pollen and floristic richness have been found at a range of spatial scales (Birks, 1973a; Flenley, 2005; Odgaard, 2008; Meltsov et al., 2011; Felde, 2015; Felde et al., 2015).

In the last 10–15 years there have been major developments within modern ecology and biogeography in the clarification and understanding of the theoretical basis of different estimators of taxon richness, evenness, and diversity (e.g. Olszewski, 2004; Jost, 2006, 2007, 2010a, 2010b, 2014; Jost et al., 2011; Gotelli and Ellison, 2013; Chao et al., 2014a, 2014b; Chiu and Chao, 2014), in the assessment of the strengths and weaknesses of the multitude of evenness and diversity measures (e.g. Smith and Wilson, 1996; Ricotta, 2003; Jurasinski et al., 2009; Tuomisto, 2010a, 2010b, 2012; Anderson et al., 2011), and in the increasing adoption and use of Hill's (1973) unified notation of diversity indices and related evenness measures (e.g. Jost, 2006, 2007, 2009, 2010a, 2014; Hoffman and Hoffman, 2008; Chao et al., 2010, 2012, 2014a, 2014b; Colwell, 2010; Ellison, 2010; Jost et al., 2011; Gotelli and Ellison, 2013; Chiu and Chao, 2014; Chiu et al., 2014; Koch and Juransinski, 2015). Few of these developments have, as yet, been adopted in Quaternary palynological research or literature, in contrast to Deep-time palaeoecology (e.g. Olszewski, 2004, 2010).

Given the increased interest in documenting and understanding patterns of richness over a wide range of spatial and temporal scales being shown by palynologists and other palaeoecologists working in both Q-time and Deep-time (*sensu* Jackson, 2001) (see Box 1 for a selection of publications), and the important developments in how to estimate diversity and richness being made by ecologists and theoretical biologists (e.g. Hill, 1973; Jost, 2006; Dornelas et al., 2012; Gotelli and Ellison, 2013; Chao et al., 2014a, 2014b; Chiu and Chao, 2014; McGill et al., 2015), it is timely to review what data and numerical tools are needed to test whether there are statistically significant relationships between pollen and floristic richness and diversity today, as well as to outline recent developments within ecology in estimating diversity and richness that are relevant to Quaternary palynologists.

We review what data and what summarisation statistics and numerical tools are needed to study modern pollen—plant richness relationships. We discuss the inherent problems in such data and associated estimators. We outline some alternative approaches in studying such relationships and in detecting richness and diversity patterns in time using fossil pollen. We conclude with a discussion of future challenges and potential research opportunities and some general comments.

As a background to our review, we present definitions of the main terms we use.

2. Definitions and terminology

Pollen richness (density) (≡ palynological richness, pollen-assemblage richness) – the number of terrestrial pollen and spore types present in a modern or fossil pollen assemblage or count (Birks and Line, 1992).

Plant richness (≡ floristic richness, vegetation richness) – the number of terrestrial vascular plant taxa (usually species or their pollen equivalents) in a specified area (McIntosh, 1967). As Gaston (1996) comments about richness in general, its meaning is generally understood and there is no need to derive complex indices to express richness. It is simply one potentially useful measure of biodiversity.

Pollen equivalents – the pollen or spore type(s) produced by a particular plant taxon (family, genus, species) (Birks, 1973a; Odgaard, 1994; Goring et al., 2013).

Translation table – a table that lists all the known plant taxa for a region and their equivalent pollen or spore types and permits the translation or transformation of a plant taxon to its appropriate pollen or spore type (pollen equivalents) (Bennett, 1995-2007; Felde et al., 2012, 2014a, 2015; Felde 2015).

Diversity index – a measure that attempts to combine species (taxon) richness and species (taxon) relative abundances (evenness) (heterogeneity index: Peet, 1974; Pielou, 1975). Colwell (2010) and Tuomisto (2010a, 2010b, 2010c, 2011) favour measures of "true diversity" (cf. Gorelick, 2011; Boenigk et al., 2015) which treat, as Hill (1973) proposed, species (taxon) richness (Hill $N0$) and the 'numbers equivalents' of Shannon's (Hill $N1$) and Simpson's (Hill $N2$) indices as points along a single mathematical continuum (e.g. Jost, 2006, 2010a; Colwell, 2010; Ellison, 2010; Gotelli and Ellison, 2013). 'Numbers equivalents' is a term used by economists (Adelman, 1969) whereas ecologists most commonly use 'effective number of species (taxa)'.

Hill numbers – a family of diversity indices that overcome the problems of many of the most commonly used diversity indices. Hill numbers (1973) (see Box 2 for their general formula) preserve the doubling property, they quantify diversity in units of modified species (taxon) counts, and they are equivalent to algebraic transformations of most other diversity indices. They were first proposed as diversity measures by MacArthur (1965) and Hill (1973). They were discussed in a palynological context by Birks and Line (1992) but they have been barely used in palaeoecology for about 40 years (but see van Dam and ter Braak, 1981; van Dam, 1982; ter Braak, 1983). They were reintroduced to palaeoecology by Birks (2012a) and to ecology and expanded by Jost (2006, 2007, 2010a, 2014), Chao et al. (2012, 2014a, 2014b), and Chiu and Chao (2014)

Effective number of species (taxa) (≡ numbers equivalents, "true diversity" *sensu* Boenigk et al., 2015) – the basic unit of Hill (1973) numbers; the equivalent number of equally abundant species (taxa). If the observed species (taxa) richness in a sample is 12 but the effective number of species (taxa) is 6, the diversity is equivalent to that of a hypothetical assemblage with 6 equally abundant species (taxa) (Gotelli and Ellison, 2013, Boenigk et al., 2015).

Evenness – the distribution of individual types of pollen grains or spores within a pollen assemblage or the variability in taxon abundances in a vegetation sample. Evenness, according to Tuomisto (2012) should only be used when evenness is assessed as diversity/richness. Other terms (e.g. 'equitability') should be used for measures that estimate other features in the variability of taxon abundance (Tuomisto, 2012).

3. Data needs

There are four essential needs prior to studying modern pollen–plant richness relationships. Two are high quality pollen and floristic data, one is a tool to translate plant taxa into pollen or spore taxa (pollen equivalents), and one is a means of quantifying the degree of correspondence between modern pollen assemblages and contemporary vegetation composition in the study area.

3.1. Modern pollen data

All modern (and fossil) pollen data should be of consistent high quality, be at the lowest possible taxonomic level, have a consistent and defined nomenclature, be from the same sedimentary environment (e.g. small lakes), be sampled using consistent field methods, prepared using identical laboratory procedures, and counted using consistent analytical protocols. Thanks to improved microscopy and the ever-increasing quantity and quality of modern pollen reference material and of critical pollen floras, keys, and monographs (e.g. Punt et al., 1976-2009; Fægri et al., 1989; Beug, 2004), the pollen and spore taxonomic level (e.g. Peglar, 1993; Odgaard, 1994; van der Knaap and van Leeuwen, 1994; Felde et al., 2012, 2014a, 2015) is steadily improving. Many data sets are not, however, of such high standards, having been analysed 20–30 years ago or to a lower taxonomic resolution. This is a major limitation in using data from large pollen databases to study pollen richness because such data are not usually internally consistent due to inevitable between-analyst differences in field, laboratory, and analytical procedures, site selection criteria, and pollen and spore taxonomic resolution and nomenclature. Goring et al. (2013) who used such a database emphasise that "records in large databases contain a mixture of taxonomic levels that must, ultimately, be resolved to the lowest taxonomic equivalent. Effectively this coarsened taxonomic resolution can significantly affect the ecological interpretations of pollen data".

3.2 Modern floristic and vegetation data

Obtaining modern floristic and vegetation data at the appropriate spatial scale for comparison with modern pollen data is a challenge in all studies of modern pollen–plant relationships (e.g. Andersen, 1970; Birks, 1973a, 1973b; Hjelle, 1998, 1999; Broström et al., 2004, 2005, 2008; Bunting et al., 2005, 2013; Gaillard et al., 2008; Bunting and Hjelle, 2010; Hjelle and Sugita, 2012; Matthias et al., 2012, 2015; Matthias and Giesecke, 2014; Hjelle et al., 2015; Li et al., 2015). As *all* the flora and vegetation in the absolute pollen-source area (APSA) (*sensu* Sugita, 1993) for the site from which pollen data have been obtained cannot usually be realistically surveyed, the aim should be to obtain representative samples of the flora and vegetation within the relevant pollen-source area (RPSA) (*sensu* Sugita, 1994). If the modern pollen data reflect local pollen deposition (*sensu* Janssen, 1966, 1973, 1981) and are derived from moss polsters (e.g. Birks, 1973a, 1973b; Hjelle, 1998, 1999) or surface soils (e.g. Wright et al., 1967), vegetation data from a 2 × 2 m or a 10 × 10 m plot within which the surface pollen sample(s) was(were) collected are appropriate. An alternative approach is to sample the surrounding vegetation in a series of concentric rings for different radii around the pollen sampling site (e.g. Broström et al., 2004, 2008; Bunting et al., 2005, Li et al., 2015).

If the modern pollen data are derived from surface sediments from the deepest part of small- or medium-sized lakes (diameters ca 150–500 m, area ca 10–50 ha) and thus primarily reflect regional pollen deposition (*sensu* Janssen, 1966, 1973, 1981) (e.g. Odgaard, 2008; Meltsov et al., 2011, 2013; Matthias et al., 2012, 2015; Felde et al., 2014a, 2015; Matthias and Giesecke, 2014), the extent and positioning of vegetation samples can be designed in light of results from model simulations of pollen deposition in basins of different sizes within a forested landscape and of the RPSA at the regional scale (Sugita, 1994, 2007, 2013; Davis, 2000). These simulations suggest that for a lake 500 m in diameter within a forested landscape, the likely RPSA may be within a 500–2000 m radius from the lake edge. Empirical studies (e.g. Nielsen and Odgaard, 2004; Nielsen and Sugita, 2005; Gaillard et al., 2008; Soepboer et al., 2007; Poska et al., 2011; Hjelle and Sugita, 2012; Sugita, 2013), generally support these model estimates with empirical estimates between 400 and 1500 m. Variables such as vegetation structure and composition, disturbance, and the mosaic nature and openness of the vegetation in the lake catchment can influence the RPSA (Hellman et al., 2009a, 2009b; Mazier et al., 2012; Matthias and Giesecke, 2014). The RPSA for lakes in treeless arctic or alpine landscapes will be considerably larger than for lakes in forested landscapes. One of the assumptions of Sugita's (1993, 1994, 2007, 2013) simulation model is "no pollen inputs from water inlets or surface run-off are considered". Given the strong evidence for water-borne pollen being a major part of the pollen input into small- and medium-sized lakes, at least in north-west Europe (e.g.

Peck, 1973; Bonny, 1976, 1980; Jackson, 1994) it is possible that the RPSA in some regions may be smaller than the estimates from Sugita's (1994, 2007, 2013) model that is based entirely on aerial pollen dispersal.

Meltsov et al. (2011) in their detailed study of pollen richness in relation to floristic richness in southern Estonia surveyed vegetation within a 250 m radius around their nine study lakes. Felde et al. (2014a, 2015) compiled plant species lists and associated estimated frequency values for a 500 m radius from the edge of their 52 study lakes in southern Norway. Odgaard (2008, unpublished) collected vegetation data along eight transects running 2000 m from the edge of 16 lakes in Denmark (see also Nielsen, 2004; Nielsen and Odgaard, 2005). Parsons et al. (1980) and Prentice et al. (1987) used forest-inventory data from survey plots within 5, 10, 16, 20, 25, 50, and 100 km radii from each lake in their work in Finland and southern Sweden. In their study on pollen-accumulation rates in relation to tree abundance, Matthias and Giesecke (2014) used forest-inventory data from a 15 km radius of 18 lakes in north-east Germany using concentric rings of increasing radii from 25 m close to a lake and a 1 km radius at a distance of 5 km. Clearly vegetational sampling for lakes that record regional pollen deposition (*sensu* Janssen, 1966, 1973, 1981) is inevitably a compromise. The probability of pollen coming from a particular plant population within the RPSA or APSA decreases with increasing distance from the lake (Davis, 2000). If the vegetation within the lake's catchment is relatively homogenous spatially, a 250–500 m sampling radius may be an adequate compromise between intensive studies of a few lakes and less extensive studies of many lakes. Each species in the vegetation should be given an estimated simple abundance or frequency value to allow numerical comparisons between the vegetation composition and the modern pollen-assemblage data by, for example, co-correspondence analysis (ter Braak and Schaffers, 2004; Felde et al., 2014a). This type of analysis is a useful preliminary before studying pollen–plant richness relationships (see Section 3.4).

Goring et al. (2013) adopt a different approach to obtaining plant-richness data which they use to assess modern pollen–plant richness relationships in the Pacific Northwest. Instead of collecting site-specific floristic or vegetational data, they obtain plant-richness data from a database of plant communities in British Columbia (Canada) containing 48,706 vegetation plots sampled with a standard 400 m^2 plot design (except in alpine, grassland, or wetland habitats) and from a regional vascular plant richness database for British Columbia based on plots and herbarium records aggregated into 50 $\times$ 50 km grid cells. Because these vegetational and richness data are not directly matched to the 167 modern pollen sites, Goring et al. (2013) use spatial smoothing models to estimate plant richness using the 50 $\times$ 50 km grid cell data and the 400 m^2 plot data reduced to 14,529 plots (33,067 plots were removed because they had "low site quality flags"). After taxonomic harmonisation, these smoothed floristic richness estimates from British Columbia were compared with smoothed richness of the modern pollen data from the 167 sites in British Columbia and also extrapolated for the 397 pollen sites in Washington, Oregon, Montana, and Idaho (USA). They also used modern pollen richness to predict plant richness using spatial modelling and smoothing techniques.

Decisions about whether to use databases to obtain plant richness data (e.g. Goring et al., 2013) or whether to collect site-specific vegetational and floristic data (e.g. Odgaard, 2008; Meltsov et al., 2011, 2013; Felde et al., 2014a, 2015) are critical in exploring modern pollen–plant richness relationships. For field surveys, decisions on the size, extent, and location of sampling plots immediately arise. Collecting modern detailed vegetation data is time-consuming; surveying the flora and vegetation of the catchment of a small lake usually requires at least one field day. Using 'secondary' richness data from broad-scale vegetation or biodiversity databases clearly avoids time-consuming fieldwork and the need for plant determinations. However, estimating plant richness from such sources with different spatial resolutions, field recorders, data qualities and quantities, and data sources and consistency rather than collecting site-specific field data in a consistent way may contribute to Goring et al.'s (2013) failure "to obtain clear and meaningful relationships between measures of plant richness and pollen richness at any spatial scale and at any taxonomic level".

3.3 Pollen–plant translation tables

Because of the inherent limitations of current pollen and spore morphology, it is not (and probably never will be) possible to identify every plant species from its pollen or spores. It is therefore essential to be able to translate or transform plant species in modern vegetation into known distinguishable pollen or spore types, so-called pollen equivalents (*sensu* Goring et al., 2013). Felde et al. (2012) and Felde (2015) present such translation tables for the presumed native and non-native flora of Norway (see also Bennett (1995-2007) for a comparable translation table for the British and Irish flora). As different pollen analysts, even those working in the same laboratory (e.g. Jackson et al., 2014), and different pollen-morphological monographs and keys sometimes differ in their morphological categories, Felde et al. (2012) and Felde (2015) provide translation tables (with synonyms) for the four most commonly used pollen-morphological texts (see Felde et al., 2014a). Some plant taxa (e.g. *Oxyria digyna, Rumex conglomeratus, Athyrium distentifolium, Dryopteris filix-mas, D. carthusiana*) may produce two or more morphologically different pollen or spore types (Birks, 1973b). In such cases it is necessary to merge such morphological types into one general pollen or spore taxon (e.g. *Dryopteris*-type including spores of *D. filix-mas*, *D. carthusiana*, and *Athyrium distentifolium*, etc. – see Birks, 1973b) and to merge the corresponding plant species in the vegetation into one corresponding plant taxon (Birks, 1973a, 1973b; Felde et al., 2014a, 2015). Inevitably all such translations and the creation of pollen equivalents result in the loss of taxonomic information and a decrease in taxonomic resolution (see Table 2) (Odgaard, 1994, 1999, 2007, 2013). Outside tropical areas, the ratio of plant species in the vegetation to identifiable pollen and spore taxa (pollen equivalents) is generally between 1.5 and 2.4 (Table 2), due to ecologically important species-rich families (e.g. Cyperaceae, Poaceae) producing only a few consistently identifiable pollen types, or families that either produce pollen that is rarely preserved (e.g. Juncaceae) or produce almost no pollen (e.g. Violaceae). The high ratio of 25.8 for Goring et al. (2013) (Table 2) suggests that using a translation table for the entire North American Modern Pollen Database (Whitmore et al., 2005) may result in a serious lack of taxonomic resolution in the modern floristic data from British Columbia when translated into identifiable pollen and spore types. It is also very unusual to have more identified pollen types (78) than potentially identifiable pollen equivalents (67) in the vegetation, as in Goring et al. (2013) (Table 2). They suggest that "one issue driving the lack of relationship between the richness measures may be the lack of taxonomic resolution in the pollen data set". Whilst that is almost certainly the case, it is important to emphasise that the achieved taxonomic resolutions in the pollen data and the associated translation tables determine the taxonomic resolution of the modern floristic data when the plant species are translated into identifiable pollen equivalents. Using a translation table for British Columbia plant species and pollen types rather than for the entire North America may improve the taxonomic resolution in the Goring et al. (2013) study. Moreover, Goring et al. (2013) note that 21% (363 species) of the species in their modern vegetation data have no equivalent pollen taxon, highlighting the need for basic pollen-morphological studies in their study area. 'Taxonomic smoothing' (*sensu* Mander, 2011; Goring et al., 2013; Mander and Punyasena, 2014) plagues all Deep-time and Quaternary pollen analysis (e.g. Birks, 1973a, 1973b; Odgaard, 1994, 1999, 2007, 2013), not only pollen–plant richness studies. Plant macrofossils can help to improve the taxonomic precision attainable from Quaternary plant assemblages (e.g. Birks HH, 1980, 2001, 2013; Birks and Birks, 2000; Birks HJB, 2014), but no fossil plant assemblage, microfossil or macrofossil or both, can ever have the taxonomic precision or comprehensiveness of modern vegetation assemblages (Mander and Punyasena, 2014).

3.4 Co-variation between modern pollen and vegetation

Before considering modern pollen–plant-richness patterns, it is important to quantify the degree of co-variation between modern pollen assemblages and vegetation composition and between modern pollen assemblages and pollen equivalents in the vegetation composition. Co-correspondence analysis (Co-CA) (ter Braak and Schaffers, 2004; Schaffers et al., 2008; Müller et al.,

2011) allows the direct comparison of two different multivariate compositional assemblage data sets derived from identical sampling sites (Felde et al., 2014a, 2015). Co-CA attempts to identify the underlying pattern that is common in both data sets by maximising the weighted covariance between the weighted averaged taxon scores of one data set with the weighted averaged taxon scores of the other data set (ter Braak and Schaffers, 2004). It can be used in both an asymmetric predictive mode and a symmetric descriptive mode. Only the symmetric mode is appropriate with modern pollen and vegetation data because the two data sets are not totally independent as the pollen assemblages are derived from the regional vegetation (Felde et al., 2015). Symmetric Co-CA is closely related to the more general approach of co-inertia analysis (Dolédec and Chessel, 1994; Dray et al., 2003) which could also be used to assess co-variation between modern pollen assemblages and modern vegetation data.

Felde et al. (2014a, 2015) show the value of using CoCA to quantify co-variation between modern pollen assemblages and vegetation and/or their pollen equivalents before exploring richness relationships along an elevational gradient in southern Norway. There is strong co-variation until near the tree-line and in the low-alpine zone. This decreased co-variation at high elevation is presumably because of far-distance transport of pollen from lower elevations and the increasing number of palynological 'blind-spots' (*sensu* Davis 1963) or 'silent areas' (*sensu* Birks 1973a, 1973b) in alpine vegetation that is dominated by low-growing herbs and graminoids which are barely registered in the pollen assemblages.

4. Data analytical needs

We discuss three essential numerical estimates and one basic statistical tool in the analysis of modern pollen and plant data for establishing whether richness of modern pollen assemblages reflects floristic richness of contemporary vegetation.

4.1 Richness estimation

The most unambiguous measure of taxon richness is S, the total number of pollen and spore taxa in a pollen assemblage or plant species (or pollen equivalents) in a vegetation (floristic) sample (see Section 2 and Gaston, 1996). However, as S depends on the sample size (pollen count size and the vegetation area surveyed, and thus the time spent collecting the two data sets), S is of limited value as a comparative richness index (Rull, 1987; Ludwig and Reynolds, 1988). Richness indices have been proposed that estimate richness independently of sample size (e.g. Peet, 1974; Ludwig and Reynolds, 1988) but such indices generally make crippling assumptions about the functional relationship between S and N, where N is the total number of pollen grains counted. As these assumptions are not met by pollen data, these indices are not appropriate for pollen–plant richness studies.

The most robust estimate of richness is the expected number of taxa ($E(S_n)$) found in samples of equal size (n) as estimated by rarefaction analysis (Sanders, 1968; Hurlbert, 1971; Heck et al., 1975; Simberloff, 1978; Birks and Line, 1992; Gotelli and Graves, 1996; Gotelli and Ellison, 2013). A rarefaction estimate is the expected number of taxa in a sub-sample of n individuals selected at random without replacement from an assemblage containing S taxa and N individuals (Hurlbert, 1971). This is, in reality, what a palynologist achieves when counting to a pre-determined *standard* number of pollen grains (e.g. 500) in a sediment sample. Such estimates permit standardisation of count-size and hence comparisons of richness between samples (Malmgren and Sigaroodi, 1985). Rarefaction analysis was introduced into Quaternary palynology by Birks and Line (1992). It has been widely used (see Table 1) to estimate palynological richness for fossil pollen counts of different original sizes when scaled to a common size ('base-sum' or 'individual index' *sensu* Smith and Grassle (1977)) by considering the relative frequencies of individuals within categories (e.g. pollen or spore types). Rarefaction analysis can be used whenever individual objects (e.g. pollen grains) at one hierarchical level are classified into groups (e.g. pollen morphological types) at a higher level (Simberloff, 1978, 1979). Rarefaction does not assume any particular hierarchical distribution in contrast to log-series or log-normal distributions (Simberloff, 1979; Gotelli and Graves, 1996; Gotelli and Ellison, 2013). However, when used to compare S between samples or sites, the counts should be derived from the same underlying distribution.

Rarefaction analysis makes various biological assumptions (Simberloff, 1978, 1979; Tipper, 1979; Gotelli and Colwell, 2011; Gotelli and Ellison, 2013) that are discussed in a palynological context by Birks and Line (1992). The most critical are (1) the observed pollen count in each sample is a statistically adequate and representative sample of the underlying pollen assemblage in that sample and that this assemblage is a statistically representative sample of the total pollen input (pollen population) to the site under investigation (Odgaard, 1999, 2001, 2007, 2013) and (2) the pollen spectra being compared have been consistently sampled and analysed to comparable taxonomic detail (Raup, 1975; Simberloff, 1979) and are from similar depositional environments (Tipper, 1979). These assumptions are basic to all quantitative pollen analyses (Birks and Birks, 1980; Birks and Gordon, 1985; Birks HJB, 2013) and are not unique to rarefaction analysis of palynological data. Rarefaction can in theory result in loss of information (Magurran, 2004, 2011) because prior to rarefaction the number of taxa and their counts are known for each sample, whereas after rarefaction we only know $E(S_n)$. However, given a sample of size N with S taxa and modern computing power it is possible to draw at random without replacement a large number (e.g. 1000) of subsamples of base-sum *n* from the entire sample of size *N* (Simberloff, 1970, 1972; Gotelli and Graves, 1996; Gotelli and Ellison, 2013) and to use the mean or median of these subsamples as an estimate of $E(S_n)$. The counts for the individual taxa in the 1000 random subsamples are estimates of the taxon frequencies for sample size *n* with $E(S_n)$ pollen and spore types (Gotelli and Graves, 1996; Gotelli and Ellison, 2013). These randomly selected subsamples, all rarefied to the same base-sum can then be used to estimate diversity and evenness and their associated variances or inter-quartile ranges for the sample that is being rarefied (see Sections 4.2 and 4.3).

Gotelli and Ellison (2013) suggest that taxon richness should be termed taxon density, the number of taxa per sample unit (James and Warmer, 1982) (e.g. estimated number of pollen taxa per base-sum, number of plant species present in a particular total area). Taxon density depends on two components (Gotelli and Ellison, 2013)

$$\frac{taxa}{sample} = \frac{individuals}{sample} \times \frac{taxa}{individuals}$$

Two assemblages may differ in the value of taxa/sample because of differences in the number of taxa/individuals (which is quantified by the rarefaction curve with base-sums from 1 to *N*) or differences in the number of individuals/sample. Variation in the number of individuals/sample may result from differences in sampling effort (how many grains were counted or what proportion of the underlying population was sampled) (Odgaard, 2007, 2013) or detection probability (e.g. pollination type) (Meltsov et al., 2011, 2013; Giesecke et al. 2014) or other biological factors. Rarefaction is a straightforward means of controlling for differences in the number of individuals per sample and their effect of taxon richness (Gotelli and Ellison, 2013). Gotelli and Colwell (2011) discuss in detail the distinction between taxon richness and taxon density and conclude that "whenever sampling is involved, species density is a slippery concept that is often misused and misunderstood". We do not encourage the use of the term taxon density in a palynological context to avoid confusion with the term flux density (Birks and Gordon, 1985; Thompson, 1980), the appropriate term for pollen influx or pollen-accumulation rates (Thompson, 1980).

We return to the assumptions of rarefaction analysis in Section 5 when we discuss problems in assessing modern pollen–plant-richness relationships.

4.2 Evenness estimation

As all ecology textbooks state, diversity (see Sections 2 and 4.3) is a complex function made up of taxon richness and taxon evenness (abundances) (e.g. Ludwig and Reynolds, 1988; Magurran, 2004; Gotelli and Ellison, 2013). Focusing on taxon richness ignores differences in the abundance of taxa, although the shape of a rarefaction curve depends on the commonness versus the rareness of taxa (Gotelli and Ellison, 2013). Jost (2010a) explores in detail the relation between evenness and diversity and concludes that “contrary to common belief, decomposition of diversity into independent richness and evenness components is mathematically impossible. However, *richness* can be decomposed into independent diversity and evenness or inequality components”. Evenness and richness are intimately related – the shape of the rarefaction curve is affected by the relative abundances of the taxa; almost all evenness measures are affected by the number of taxa in the assemblage; and the minimum value that evenness can obtain for a given data set depends on richness (Jost, 2010a; Tuomisto, 2012; Gotelli and Ellison, 2013). Tuomisto (2012) proposes that

$$\text{Diversity} = \text{Richness} \times \text{Evenness} \qquad (1)$$

and so

$$\text{Evenness} = \text{Diversity} / \text{Richness} \qquad (2)$$

As Jost (2010a) shows, richness and evenness are not numerically independent of each other, whereas diversity and evenness are numerically independent because one does not constrain the range of values that can be taken by the other in any way (Tuomisto, 2012). Therefore Jost (2010a) proposes that richness rather than diversity can be partitioned as

$$\text{Richness} = \text{Diversity} \times \text{Unevenness} \qquad (3)$$

where

$$\text{Unevenness} = \text{Richness} / \text{Diversity}$$

$$= 1 / \text{Evenness} \qquad (4)$$ (Tuomisto, 2012)

Despite the simplicity of these four equations (Tuomisto, 2012) and the general (but not unanimous) agreement on how to estimate and express richness (Gotelli and Colwell, 2011), there is considerable disagreement on how to estimate and express diversity with its vast plethora of different diversity indices (e.g. Peet, 1974; Pielou, 1975; Routledge, 1979; Magurran, 2011). This has resulted in many different definitions and measures of evenness and equitability (e.g. Sheldon, 1969; Heip, 1974; Alatalo, 1981; Routledge, 1983; Molinari, 1989; Camargo, 1993, 1995; Bulla, 1994; Smith and Wilson, 1996; Hill, 1997; Ricotta, 2004; Gosselin, 2006; Tuomisto, 2012). Tuomisto (2012) proposes that because there is a logical and universally accepted definition of diversity (Hill, 1973) as Hill numbers or numbers equivalents (Ellison, 2010; Jost, 2006), a logical approach to defining evenness (or unevenness) is to use equations (2) or (4), respectively (Tuomisto, 2012). Tuomisto

(2012) also proposes that the term 'evenness' should only be used to refer to equations (2) or (4) and that other terms be used for equitability measures that estimate other properties of assemblage data sets.

Since Odgaard (1999, 2001, 2007, 2008, 2013) highlighted the role of palynological evenness (= equitability) in influencing estimated values of palynological richness, palynologists have used several 'evenness' measures or other measures to quantify palynological 'evenness' in modern (e.g. Räsänen et al., 2004; Odgaard, 2008, 2013; Peros and Gajewski, 2008; Meltsov et al., 2013) and fossil (e.g. van der Knaap, 2009; Mortensen et al., 2011; Fredh et al., 2012, 2013; Giesecke et al., 2012, 2014; Ammann et al., 2013; Colombaroli and Tinner, 2013; Colombaroli et al., 2013; Marquer et al., 2014; Schwörrer et al. 2015) pollen assemblages. 'Evenness' measures have also been used with plant macrofossil assemblages (Blarquez et al., 2013). Just as the concepts of evenness, richness, and diversity are confused in ecology, palynologists have shown confusion in what they have used as an 'evenness' measure. Peros and Gajewski (2008) introduced into Quaternary palynology Hurlbert's (1971) probability of interspecific encounter (PIE). This ranges from 0 to 1 and represents the probability that two individual pollen grains, randomly selected (without replacement) will be of different taxa. Those samples dominated by few taxa will have a PIE value close to 0 compared to samples where there is a greater variety of taxa. It is not biased by sample size (Bulinski, 2007) or taxon richness, unlike several other 'evenness' measures (Olszewski, 2004; Peros and Gajewski, 2008) and it is easily derived from Simpson's (1949) diversity measure (Hill's (1973) N2 is the inverse of Simpson's measure when an adjustment is made for small sample sizes). PIE was first developed to estimate linguistic diversity (Greenberg, 1956). PIE has, however, been used as an 'evenness' measure by Peros and Gajewski (2008), van der Knaap (2009), Ammann et al. (2013), Blarquez et al. (2013), Colombaroli and Tinner (2013), Colombaroli et al. (2013) and Schwörrer et al. (2015). It has also been used as the basis for calculating "an evenness-detrended palynological richness" in which palynological richness (estimated by rarefaction) is regressed on palynological 'evenness' (estimated as PIE). The residuals (richness – 'evenness') are plotted as an "evenness-detrended palynological richness" (Colombaroli and Tinner, 2013; Schwörrer et al. 2015). A critical question is whether Hurlbert's (1971) PIE should be used as a diversity measure as Greenberg (1956) and Gotelli and Ellison (2013) present it or as an 'evenness' measure as Olszewski (2004) and Peros and Gajewski (2008) present it? Hurlbert (1971) introduced PIE (and a corrected version of rarefaction estimation) *not* as a diversity *or* an 'evenness' measure but as a 'species composition parameter' with a straightforward biological interpretation as an alternative to the diversity-index approach which Hurlbert (1971) dubbed "the nonconcept of species diversity". Gotelli and Ellison (2013) list three advantages of using PIE as a simple *diversity* measure: (1) it has easily interpretable units of probability and corresponds intuitively to a diversity measure based on encountering novel taxa while sampling, (2) it is insensitive to sample size unlike taxon richness, as a rarefaction curve of PIE is a straight line, and (3) PIE measures the slope of a rarefaction curve measured at its base (Olszewski, 2004). Smith and Wilson (1996) do not consider PIE as an 'evenness' index in their comprehensive "consumer's guides to evenness" and related indices. It is thus unclear what "evenness-detrended palynological richness" (Colombaroli and Tinner, 2013; Schwörrer et al. 2015) is actually estimating, especially in light of Jost's (2010a) demonstration that richness and evenness are not numerically independent.

Other than PIE, 'evenness' (equitability) measures commonly used by palynologists include (1) Pielou's (1975; 1977) J' which expresses the Shannon diversity (entropy) measure H' relative to the maximum value that H' can obtain when all the taxa in the sample are perfectly even with one individual grain per taxon (e.g. Räsänen et al., 2004; Odgaard, 2007; Mortensen et al., 2011; Fredh et al., 2012, 2013; Keen et al., 2014; Marquer et al., 2014); (2) $E_{1/D}$ which is the complement of Simpson's (1949) index of dominance divided by S (Meltsov et al., 2011; Odgaard, 2013; Reitalu et al., 2015) and is independent of species richness and theoretically ranges from almost zero (when one taxon is very dominant) to 1 (at maximum evenness); and (3) a modified version of Smith and Wilson's (1996) E_Q measure (Nee et al., 1992) which is $-2/\pi$ arctan of the slope of the scaled rank of abundance in relation to log abundance fitted by least-squares regression (Giesecke et al., 2012). E_Q and $E_{1/D}$ have been shown by Smith and Wilson (1996) to have excellent performances in their comparative tests, whereas J' is poor in relation to these in not being independent of taxon richness. Odgaard (2008 and unpublished), Giesecke et al. (2012), and Matthias et al. (2015) have rarefied pollen assemblages to a low base-sum of 10–30 grains. In this rarefaction, numerically abundant taxa will dominate in such a small rarefied sample and the probability of including less abundant taxa is low. The $E(S_n)$ in this case is strongly correlated to Hill's $N2$ (Matthias et al., 2015), so $E(S_n)$ to a low base-sum may be estimating diversity of very abundant taxa (e.g. $N2$) rather than their evenness.

Hill's (1973) diversity numbers (Box 2) are all expressed in the same units of effective number of taxa, the equivalent number of equally abundant taxa, but differ in their sensitivity to rare taxa (Ricotta, 2004). Hill (1973) proposes that evenness be estimated by a double continuum ratio of Hill numbers

$$E_{\alpha,\beta} = N_\alpha / N_\beta$$

where E is evenness, N is a Hill number, and α and β are the orders of N and $\alpha \neq \beta$. Hill (1973) also argues that a meaningful evenness measure should be independent of taxon richness and proposes $N2$ / $N1$ as an appropriate measure (Sheldon, 1969). Alatalo (1981) modified this to be ($N2$ – 1) / ($N1$

– 1) so as "to give a better approach to intuitive evenness" (= index $F_{2,1}$ in Smith and Wilson (1996)). Hill (1973) commented that "the difference *N*1 – *N*2 may be more characteristic of the community than is the evenness *N*2 / *N*1 … Fairly obviously, however, evenness should be regarded as secondary and in routine analysis the original diversity number *N*2 and *N*1, or *N*2 and *N*0 are to be preferred". The computer program Canoco 5 (ter Braak and Šmilauer, 2012) gives as basic statistics of a compositional data-table not only sample mean, median, variance, total occurrences, and relative counts of species within samples but also sample values of *N*1, *N*2, *N*2 / *N*1, *H*′, and *H*′ / log(*N*0) (a Shannon entropy-related measure of compositional 'evenness'), and the logarithm of the number of occurrences (the maximum achievable value of *H*′ for a given number of occurrences) and has a similar relation to *H*′ as the number of taxa (*N*0) has to *N*1. Felde et al. (2015) show with modern pollen assemblages that values of Hurlbert's (1971) PIE measure are highly correlated to Hill's (1973) *N*1 and *N*2, whereas PIE has lower but statistically significant correlations with evenness measures *N*1 / *N*2, *N*2 – 1 / *N*1 – 1, *N*1 / *N*0, *N*1 – 1 / *N*0 – 1, and *N*1 – *N*2. In that study, PIE behaves most closely to Hill's *N*1 and *N*2 diversity measures.

Hill's (1973) *N*2 / *N*1 index and Alatalo's (1981) modified Hill ratio are generally unaffected by richness (Smith and Wilson, 1996) but they fail Smith and Wilson's (1996) requirement 2, namely that they must decrease when the abundance of the least abundant taxon in an assemblage is marginally reduced. Index $E_{1/D}$ (Smith and Wilson, 1996; Odgaard, 2013) is equivalent to the ratio of Hill numbers *N*2 / *N*0 and it performs well in Smith and Wilson's (1996) tests.

Ludwig and Reynolds (1988) present other evenness measures based on Hill numbers such as $\log_e$ (*N*1) / $\log_e$ (*N*0) (= Pielou's (1975; 1977) *J*′), *N*1 / *N*0, and (*N*1 – 1) / (*N*0 – 1) (Heip, 1974). All these involve *N*0 and are thus not totally independent of the number of taxa in the assemblage unless *N*0 (total number of taxa) is standardised first for all the samples being considered by rarefaction analysis and *N*1 (and *N*2) is estimated from a set of rarefied samples derived from repeated resampling without replacement to a standard base-sum (Sections 4.1 and 4.3). Gotelli and Ellison (2013) comment that "sample size effects are important for all the other Hill numbers [excluding *N*0], although their effect diminishes as *q* [the exponent in a Hill number] is increased". Their example (see Fig. 13.7 and Tables 13.1 and 13.2 in Gotelli and Ellison (2013)) shows that the effects of sample size quickly diminish with sample size and the effective numbers of taxa (*N*1, *N*2, *N*3) are stable with a sample size of 75–100 individuals.

Alatalo (1981) conclude that "there is no single way to measure evenness" and the comprehensive reviews by Smith and Wilson (1996) and Tuomisto (2012) show in detail how true Alatalo's (1981) early conclusion is.

Because of the complexity of estimating evenness and of the underlying concepts of evenness and equitability, we suggest that numerically and conceptually simple estimates of evenness based on Hill numbers should only be used to characterise some basic numerical properties of "species composition parameters" (*sensu* Hurlbert, 1971) of a pollen assemblage, modern or fossil (e.g. Felde et al., 2015).

4.3 Diversity estimation

It is widely known that there is a bewildering plethora of diversity measures (e.g. McIntosh, 1967; Peet, 1974, 1975; Pielou, 1975, 1977; Routledge, 1979; Washington, 1984; Ghent, 1991; Magurran, 2004; Maurer and McGill, 2011; Legendre and Legendre, 2012) that try to combine taxonomic richness and taxon abundances ('evenness') into a single index (see Section 2). As Ludwig and Reynolds (1988) emphasise, the biggest obstacle in using many such diversity measures is interpreting what this single summary statistic might mean biologically. A given value may, in one case, result from various combinations of richness and 'evenness' and thus the same value of a diversity index may result from an assemblage with low richness and high 'evenness' or from a different assemblage with high richness and low 'evenness'. In addition we have the uncertainty about what 'evenness' actually comprises, as discussed above (see Section 4.2). The units of many diversity measures differ greatly, making comparisons very difficult and making interpretation virtually impossible (Ludwig and Reynolds, 1988).

The idea of a family of diversity measures was formalised in ecology by Hill (1973) although MacArthur (1965) had first proposed Hill numbers as diversity measures. So-called Hill numbers or numbers equivalents originated in economics (Adelman, 1969; Ellison, 2010) and physics (Jost, 2006). They have recently undergone a major resurgence of interest amongst ecologists (e.g. Jost, 2006, 2007, 2010a, 2010b, 2014; Colwell, 2010; Tuomisto, 2010a, 2010b; Chao et al., 2012; 2014a, 2014b; Gotelli and Ellison, 2013; Chiu and Chao, 2014; Skácelová and Lepš, 2014; Koch and Jurasinski, 2015) and evolutionary biologists and phylogeneticists (e.g. Jost, 2008; Chao et al., 2010; Chiu and Chao, 2014; Chiu et al., 2014). Colwell (2010) describes Hill numbers as measures of "true diversity" which treat taxon richness and the numbers equivalents of the Shannon and the Simpson diversity measures (entropies *sensu* Jost, 2006) as points along a single mathematical continuum (Hill, 1973). They are one of several diversity-index families (Tóthmérész, 1995) and one of the most useful for ordering assemblages or communities of all sizes in terms of their diversity.

Hill's (1973) diversity measures (Box 2) are in units of taxa and are called 'effective number of taxa' of the assemblage according to the selected diversity measure. Most remarkably, irrespective of which diversity measure one starts with (e.g. taxon richness, Shannon entropy, the exponential of Shannon entropy, Simpson concentration, inverse Simpson, Gini-Simpson index, Renyi entropy, and many others), a simple algorithm for the effective number of taxa always yields the same formula (Jost, 2006, 2014). The algorithm calculates the diversity measure for *D* equally-common taxa (each taxon therefore has a frequency of 1 / *D*), sets the resulting expression equal to the actual value of the diversity measure, and solves that equation for *D*. This value of *D* is the effective number of taxa or "true diversity" (Boenigk et al., 2015). The effective number of taxa is a measure of the degree to which proportional abundances are distributed among the taxa (Gotelli and Ellison, 2013) (see Section 2). *N*0 is the number of taxa in a sample regardless of their abundances, *N*1 (the exponential of the widely used Shannon diversity or entropy measure) estimates the number of abundant taxa in an assemblage as it weights each taxon exactly by its relative abundance, and *N*2 (the reciprocal of Simpson's diversity or concentration measure) estimates the number of very abundant taxa in an assemblage (Box 2). It pays most attention to the most abundant taxa as it involves the sum of the squares of the species abundances. Uncommon taxa hardly contribute to *N*2. In other words, the effective number of taxa is a measure of the number of taxa in an assemblage when each taxon is unweighted (*N*0) or weighted by its abundance (*N*1) or its squared abundance (*N*2). As Gotelli and Ellison (2013) conclude, "Hill numbers provide a useful family of diversity indices that consistently incorporate relative abundances while at the same time express diversity in units of effective number of species". One important property of Hill's (1973) effective number of taxa is the so-called 'doubling property' that ensures the ratios of effective numbers of taxa behave as one would expect intuitively. Thus if one assemblage is twice as diverse as another, the ratio of their effective number of taxa is always 2, regardless of the index on which this ratio is based. This is very different from the behaviour of the ratio of other diversity indices based not on effective numbers of taxa but on the taxa (Jost, 2014). Jost (2006, 2014) recommends the term "effective number of species [taxa]" or "numbers equivalents" because the term 'diversity' means so many different things to different biologists. Jost (2014) "hopes that someday biologists can all agree that the word 'diversity' should properly be applied only to quantities like ${}^{q}D$ [where the exponent *q* is a non-negative integer that defines the particular Hill number and *D* is the diversity index] which have the mathematical properties we intuitively expect of a diversity" (see Box 2).

Despite Hill numbers being introduced (Hill, 1973) as a unifying notation for diversity measures in ecology and discussed in several different areas of ecology and palaeoecology (e.g. Peet, 1974; Daget, 1980; van Dam and ter Braak, 1981; van Dam, 1982; ter Braak, 1983; Birks and Line, 1992), they remained barely used until Jost (2006, 2007, 2010a) re-introduced Hill numbers in the context of diversity, evenness, and partitioning diversity. In a Forum of 'Partitioning Diversity' all the contributing authors agreed that using "numbers equivalents instead of the classical diversity indices (or entropies) such as the *H*′ [Shannon index] should be used in any diversity partitioning … Even if interest is only on describing the diversity of a single assemblage, the numbers equivalent, not the entropy, should be the diversity measure of choice" (Ellison, 2010). Hill's *N*2 has been widely used as a diversity measure in palaeolimnology, probably not because of its mathematical properties or ecological elegance but because it was (until Canoco 5; ter Braak and Šmilauer, 2012) the only diversity measure calculated in the widely-used CANOCO program (versions 2 to 4.5). The neglect of Hill numbers by ecologists until Jost (2006) is surprising in light of Routledge's (1979) early review on "Diversity indices: which ones are admissible?" in which he concludes that "*N*2 is the best, single measure of diversity, and that the only other index worth considering is *N*1".

Gotelli and Ellison (2013) discuss two caveats in the use of Hill numbers. First, no diversity measure can completely separate taxon richness from taxon evenness (Jost, 2010a) (see Section 4.2). Second, Hill numbers can be influenced by sampling effects, for example *N*0 is influenced by the number of individuals in the count but this can be standardised by rarefaction analysis solved analytically (e.g. Heck et al., 1975) or by repeated random subsampling without replacement (Gotelli and Ellison, 2013) (see Sections 4.1 and 4.2). Sample sizes can also influence values of *N*1 and *N*2 but their impacts decrease as the exponent q in the general formula for calculating a Hill number increases (Soetaert and Heip, 1990). As q increases, the diversity measure places ever increasing weight on the most abundant taxa in the assemblage. With $q = 5$, the Hill number rapidly converges to the inverse of the relative abundance of the most common taxon.

One potential solution to the possible effects of sample size on *N*1 and *N*2 is to estimate not only *N*0 but also *N*1 and *N*2 from a rarefied sample (or many randomised subsamples without replacement) of the original assemblage (Soetaert and Heip, 1990; Rühland et al., 2014; Felde et al., 2015) (see Sections 4.1 and 4.2) and to do this for all the assemblages of interest, using the same appropriate base-sum, thereby providing estimates of *N*0, *N*1, and *N*2, and their associated variances for each assemblage independent of count size (see also Kindt et al., 2006; Chao et al., 2014a, 2014b; Colwell and Elsensohn, 2014).

Pollen analysts have rarely used diversity measures and have concentrated on estimates of palynological richness (Birks and Line, 1992). Diversity measures that have been used include Shannon's entropy (e.g. Moore, 1973; Küttel, 1984) and Simpson's index (e.g. Cwynar, 1982; Morley, 1982; Ritchie, 1982). These measures can be easily converted into Hill (1973) numbers for ease of comparison and interpretation. Hurlbert's (1971) PIE (see Section 4.2) has also been used but as a measure of 'evenness' rather than of diversity (e.g. Peros and Gajewski, 2008; van der Knaap, 2009;

Colombaroli and Tinner, 2013; Colombaroli et al., 2013; Schwörrer et al., 2015). Meltsov et al. (2013) used Simpson's diversity index (λ; $N2 = 1 - \lambda$) and its related evenness measure ($E_{1/D} = N2 / N0$) to quantify landscape diversity within eight radii (250–2500 m) around their study lakes in southern Estonia in order to investigate the role of landscape structure and mosaic and floristic richness in influencing palynological richness.

The relation between Hill numbers and Hurlbert's (1971) PIE measure has been clarified (Dauby and Hardy, 2012). Chao et al. (2014a, 2014b) show that these two classes of infinity orders are mathematically equivalent and thus they contain the same information about diversity. Given a reference assemblage, rarefaction and extrapolation formulae (Colwell et al., 2012) for taxon richness provide estimates of Hurlbert's PIE measure. The approach of Chao et al. (2014a, 2014b) thus unifies Hill numbers and Hurlbert's (1971) measures as tools for quantifying taxon richness and diversity.

Jost (2014) recommends that when measuring diversity, the trio of diversity of order zero ($N0$, taxon richness), diversity of order one ($N1$, exponential of Shannon entropy), and diversity of order two ($N2$, reciprocal of the Simpson index) gives more information about the assemblages than any single measure. It makes good sense to present all three so that the degree of dominance in the assemblages can be seen by looking at the changes from $N0$ to $N1$, and from $N1$ to $N2$. Hill's (1973) approach of using a continuous range of diversities (0, 0.5, 1, 1.5, 2) and graphing the results gives a clear visualisation of the degree of dominance in the assemblage. This is useful when comparing a small number of samples. $N0$, $N1$, and $N2$ or $N0$ and $N2/N1$ are more informative when considering a full pollen sequence. Diversity of order one ($N1$) should be used when estimating independent alpha and beta diversities of multiple assemblages (Jost, 2007, 2010b, 2014). Alpha and beta diversity and diversity partitioning are discussed below under Future challenges and research opportunities (Section 7).

4.4 Statistical modelling techniques

Quantifying and evaluating the numerical relationship between pollen richness and plant richness (both $N0$) and between pollen diversity ($N1$, $N2$), plant diversity ($N1$, $N2$), pollen evenness ($N2 / N1$, $N2 - 1 / N1 - 1$, etc.), and plant evenness ($N2 / N1$, $N2 - 1 / N1 - 1$, $N1 - N2$, etc.) when the floristic data have been translated into pollen equivalents involves statistical regression models within the general framework of generalised linear models (GLMs) with a Poisson (e.g. Goring et al., 2013) or normal error function. The same regression approach can be used for evaluating relationships between pollen richness and landscape structure (Meltsov et al., 2013). For an introduction to statistical modelling using GLM and model selection, see Birks (2012b). More detailed accounts of GLM modelling include Crawley (1993, 2005, 2007), Faraway (2005, 2006), and Fox and Weisberg (2011). As in all statistical modelling, the simplest statistically significant model should be the one favoured (Birks, 2012b). There are various criteria for jointly assessing model simplicity and statistical significance such as the Akaike Information Criterion and the related Bayes (Schwarz) Information Criterion where model fit, complexity, and sample size are all considered (see Burnham and Anderson, 2002; Anderson, 2008; Hastie et al., 2009; Murtaugh, 2009; Gotelli and Ellison, 2013 for details).

5. Problems in assessing modern pollen–plant relationships

5.1 Introduction

As in all Q-time and Deep-time palaeoecology, varying data quality creates problems in comparing and synthesising data sets, for example in assessing pollen–plant richness relationships, taxon-richness changes through time, and diversity patterns in space. The highest quality pollen data are required in evaluating pollen–plant richness relationships in terms of consistent site selection, careful and consistent field sampling, consistent laboratory and analytical procedures, and pollen taxonomic precision. How to obtain appropriate richness data for modern vegetation is not fully resolved (see Section 3.2). The studies that have compared modern pollen richness with contemporary plant richness have all used very different approaches to acquiring modern plant richness values, some based on field vegetation surveys (e.g. Birks, 1973a; Odgaard, 2008; Meltsov et al., 2011, 2013; Felde et al., 2014a, 2015), others based entirely on regional databases (e.g. Goring et al., 2013). A similarly wide range of vegetational sampling approaches has also been used in collecting vegetation data for estimating pollen-representation values (‘R-values’) or pollen-productivity estimates (PPEs) (e.g. Davis, 1963; Andersen, 1970; Parsons et al., 1980; Prentice and Parsons, 1983; Prentice et al., 1987; Broström et al., 2004, 2005, 2008; Räsänen et al., 2007; Gaillard et al., 2008; Bunting and Hjelle, 2010; Matthias et al., 2012; Bunting et al., 2013; Matthias and Giesecke, 2014). Sampling and surveying modern vegetation in appropriate and robust ways are keys in assessing quantitative relationships between pollen and modern floristic richness, vegetation composition, or plant abundances.

5.2 Biases in pollen-assemblage records of richness

Odgaard (1999, 2001, 2007, 2008, 2013) has emphasised that there are three major biases in interpreting changes in pollen richness from fossil assemblages as reflections of past floristic richness. These biases also relate to assessing modern pollen–plant richness relationships. The biases are taxonomic precision, sample size, and pollen representation (Odgaard, 1999, 2001, 2007, 2013).

5.2.1 Taxonomic precision

Pollen and pteridophyte spores can often only be identified to a group of species (e.g. *Ranunculus acris*-type), to genus level (e.g. *Quercus*), or even only to family level (e.g. Poaceae). This restricted taxonomic precision results inevitably in a non-linear relationship between plant richness and pollen richness (Odgaard, 1994, 2007, 2013). The number of pollen and spore taxa in an assemblage—modern or fossil—is clearly not a *direct* reflection of plant richness in the vegetation that produced the pollen assemblage (see Table 2). With a very low number of plant species in the vegetation (e.g. middle boreal forest, heathland, arctic tundra) the ratio between plant and pollen richness may be close to 1:1 or 1.5:1. In vegetation with more taxa (e.g. temperate deciduous forests, grasslands) the ratio may be 2:1 or 3:1, or even higher (Odgaard, 2013). Odgaard (1994) shows that the modern relationship between plant and pollen richness is almost identical in three different vegetation types in western Denmark. He used this modern relationship to transform pollen richness ($N0$ based on rarefaction) into estimates of past floristic richness (Odgaard, 2013). It is not known whether the relationships between plant and pollen richness that Odgaard (1994) established hold for other vegetation types elsewhere. Preliminary studies in Norway (Felde, 2015) and Scotland (Birks, unpublished data) suggest broadly similar and robust relationships between plant richness and pollen richness. In this case pollen types can be thought of taxa 'higher' (broader) than plant species.

In a very different context, namely conservation biogeography and contemporary biodiversity assessment, Mazaris et al. (2010) have shown that one can predict the number of plant species surprisingly well from the richness of a few common genera, families, or orders. Many biodiversity assessments today are based on genus or 'higher' taxa (e.g. Williams and Gaston, 1994; Andersen, 1995; Pearman and Weber, 2007). These and other studies illustrate the robust nature of species–'higher' taxon relationships.

An alternative approach to the problem of bias due to taxonomic precision is to construct pollen–plant translation tables where plant species in the flora of interest (e.g. Norway) are grouped into the relevant pollen or spore morphological taxa, given our present knowledge of the pollen and spore morphology of the flora in the area of interest (Bennett, 1995-2007; Felde et al., 2012, 2014a, 2015; Felde, 2015). There is clearly a loss of information in such translations as families such as Poaceae or Cyperaceae that contain many plant species produce only a small number (ca. 6) of distinctive pollen morphological types. This bias due to taxonomic imprecision will only be reduced by improved pollen morphology and microscopy (e.g. Andersen, 1979; Odgaard, 1994; Beug, 2004;

Lacourse and May, 2012) and by alternative approaches to pollen identification and/or counting (e.g. Birks and Peglar, 1980; Lindbladh et al., 2002; Heintzmann and Ficz, 2006; Huang et al., 2009; MacLeod et al., 2010; Barton et al., 2011; Holt et al., 2011; May and Lacourse, 2012; Punyasena et al., 2012; Sivaguru et al., 2012; Johnsrud et al., 2013; Mander et al., 2013, 2014; Holt and Bennett, 2014; Jan et al., 2015).

5.2.2 Pollen-sample and underlying pollen-population magnitudes

As the pollen richness of an assemblage—modern or fossil—is determined by the pollen-count size (Rull, 1987), all comparisons of pollen richness between assemblages must be based on richness estimated from samples of identical size. Rarefaction analysis (Tipper, 1979; Birks and Line, 1992) provides pollen-richness estimates for all assemblages as if they were all based on counts of identical size. Rarefaction does not allow extrapolation to numbers of taxa in a larger sample (but see Gotelli and Colwell, 2011; Colwell et al., 2012; 2004; Chao et al., 2014), only interpolation to a count size or base-sum smaller than the largest count size in the data set of interest (Birks and Line, 1992; Odgaard, 2013).

Odgaard (1999, 2007, 2013) emphasises that pollen-richness estimates are strongly biased by the ‘evenness’ of the sampled pollen assemblage and by a varying underlying pollen population size. The high pollen production and wide dispersal of many wind-pollinated plants results in the dominance of these pollen types in pollen assemblages, whereas pollen from entomophilous species may be rare or even absent, despite the plants being frequent in the vegetation. This representation bias, a combination of differential pollen productivity and differential pollen dispersal, leads to a skewed abundance distribution with high unevenness (or low evenness) of pollen types (Giesecke et al., 2014). Räsänen et al. (2004) show that rarefaction estimates of pollen richness correlate strongly with evenness based on Pielou’s (1975) J’ which, in terms of Hill numbers is

$$\log_e (N1) / \log_e (N0)$$

It is possible that pollen richness and evenness are inherently correlated in the Räsänen et al. (2004) study because the evenness measure used is not independent of observed richness and hence count size as *N*0 forms the denominator. As discussed above (Section 4.3), it is important to use evenness measures that are independent of the number of taxa (and hence count size). *N*0 should be standardised for all the assemblages being considered and *N*1, *N*2, and derived evenness measures based on Hill numbers (see above) should be based on a rarefied sample (e.g. Rühland et al., 2014) or an ensemble of randomly drawn rarefied samples for fair comparisons of richness, diversity, and evenness, and their associated variances (Chao et al., 2014; Felde et al., 2015).

An important assumption of rarefaction analysis (Birks and Line, 1992; Gotelli and Colwell, 2011; Gotelli and Ellison, 2013) is that the size of the underlying pollen population (all the pollen produced in the APSA) from which the pollen assemblage or sample is derived from is constant in space or time. This is probably rarely the case (Odgaard, 2007, 2013), for example between treeless late-glacial, tree-dominated mid-Holocene, and herb- and heath-dominated late-Holocene pollen assemblages. If the underlying pollen population size varies whilst the sample size is kept constant (by rarefaction), the sampled fraction of the vast (and unknown) underlying pollen population varies and pollen richness may change as a result of this effect (Odgaard, 2007, 2013). Odgaard (1999) and van der Knaap (2009) (see also Connor et al., 2012; Ammann et al., 2013; Colombaroli and Tinner, 2013; Colombaroli et al., 2013) present some solutions to reduce the dependence of pollen richness on the sample-to-population ratio by using 'quasi-absolute' (Odgaard, 1999) or 'absolute' (van der Knaap, 2009) pollen-accumulation rates (flux density) to estimate the pollen richness that would have been recorded if the same fraction of the underlying pollen population (pollen production from the APSA) had been sampled. This problem of the changing size of the underlying pollen population is most acute in situations where vegetation and its resulting pollen population has changed markedly over time (e.g. in the late-glacial (van der Knaap, 2009; Ammann et al., 2013)) but it can also occur in modern assemblages from different vegetation types (e.g. tundra, boreal forest) which have very different modern pollen productivities (Ritchie and Lichti-Federovich, 1967; Birks, 1973a).

5.2.3 Pollen-representation bias

Giesecke et al. (2014) argue that pollen richness estimated from rarefaction analysis is a simple measure with many advantages. As discussed above, it is influenced by the detection probability of rare pollen types. Pollen types from plant taxa with a high pollen production and wide dispersal commonly dominate a pollen assemblage, thereby reducing the probability of detecting pollen types with a poorer representation and/or a low abundance in the RPSA or APSA (Odgaard, 1999, 2007, 2013; Weng et al., 2006). Pollen counts can, however, be transformed using general purpose pollen-representation values (e.g. Andersen, 1970, 1978) or more detailed pollen-productivity estimates (e.g. Broström et al., 2008; Gaillard et al., 2008; Poska et al., 2011; Hjelle and Sugita, 2012; Mazier et al., 2012; Hjelle et al., 2015; Mehl et al., 2015) in conjunction with the REVEALS model (Sugita, 2007) to reduce the inherent representation bias in pollen assemblages. The transformed counts can then be used in rarefaction to estimate $N0$ and subsequently $N1$, $N2$, and related evenness measures (Felde et al., 2015; Matthias et al., 2015). It is important to note, however, that recent work on deriving PPEs in different geographical areas or ecological landscapes (e.g. Abraham and Kozakova, 2012; Abraham et al., 2014; Baker et al., 2015; Niemeyer et al., 2015), at different historical times (e.g. Theuerkauf et al., 2015), or based on different pollen dispersal models (e.g. Theuerkauf et al.

2012; Sjögren et al., 2015) is highlighting important differences in such estimates and the problems in deriving robust PPEs. Moreover, reducing pollen-representation bias will only really be achievable for the most abundant pollen taxa as obtaining reliable and robust representation values and PPEs is very difficult and extremely time consuming. Such values for the rare pollen taxa would have a high uncertainty and variance (Parsons and Prentice, 1981).

Alternative approaches to minimising pollen-representation bias and thus estimating taxon abundances over space and time involve Bayesian hierarchical modelling (Paciorek and McLachlan, 2009). These approaches have considerable promise because of their explicit spatio-temporal representation, quantification at the scale of trees and vegetation rather than pollen, and characterisation of the many uncertainties in estimating past plant abundances (Paciorek and McLachlan, 2009).

5.3 Richness, evenness, and diversity concepts

An inherent problem in any assessment of pollen–plant richness, evenness, or diversity relationships is that the three concepts are very closely linked (Jost, 2010a), with diversity consisting of components of richness and of evenness. If based on Hill numbers and estimated from rarefied samples to minimise bias due to count size (Felde et al., 2015), richness, evenness, and diversity are numerical summary statistics (*sensu* Birks HJB, 2013) of pollen assemblages, or "assemblage composition parameters" (Hurlbert, 1971). Following Hill (1973), plots of $N0$ richness, $N1$ and $N2$ diversity, and $N1$ / $N0$, $N2$ / $N1$, and $N2 - 1$ / $N1 - 1$ evenness (all with their associated variances) for pollen assemblages in space or time can provide useful summaries of certain aspects of complex multivariate pollen-assemblage data (e.g. Felde, 2015; Felde et al., 2015). They are "mere numbers and should be distinguished from the theories which they support" (Hill, 1973).

6. Other approaches to studying pollen-assemblage richness patterns

Giesecke et al. (2012, 2014) experimented with the sample-based slope of the rank-order abundance as well as between-sample taxon abundance using fossil data from sites in different parts of Europe as a means of assessing equitability in pollen assemblages. Although Giesecke et al. (2012, 2014) used these curves to detect patterns of pollen richness and equitability through time, the same approach can be applied to modern pollen data to assess palynological equitability visually and not based on Hill numbers or other diversity or equitability measures. When plotting log-transformed pollen percentages (proportions) of a sample against rank-order, the slope of the plot is an intuitive and graphical measure of palynological equitability (Nee et al., 1992). This slope is influenced by variations in the pollen count-size through changes in the probability of finding rare pollen taxa with different count sizes (Rull, 1987; Weng et al., 2006). Giesecke et al. (2012, 2014) minimised this count-size dependency by setting thresholds for taxon inclusion (>1% (Giesecke et al., 2014) or >0.3% (Giesecke et al., 2012)) in a particular pollen assemblage. However, the value of the threshold determines the aspect of the abundance distribution of pollen types in the sample being investigated. When using a low threshold, the relationship in a pollen sample is driven by the number of taxa or richness, whereas a higher threshold evaluates the equitability of the abundant taxa which is close to what many diversity measures estimate.

The accumulation of taxa over a consecutive series of modern samples (e.g. latitudinally within a broad vegetation type such as Setesdal in southern Norway (Felde et al., 2014a, 2015)) following Giesecke et al. (2012) permits plots of log-transformed taxon accumulation versus log-transformed accumulated numbers of grains counts for different vegetation types today. Such plots can help identify patterns of pollen richness and equitability between vegetation types due, for example, to shifts in the relative abundance of high and low pollen producers or changes in the evenness and diversity of the landscape mosaic (Giesecke et al., 2014). The same approach can be applied to an entire modern pollen data set and break-points in the taxon-accumulation curve identified by piece-wise regression (Toms and Lesperance, 2003; Heegaard et al., 2006; Engels and Cwynar, 2011). The geographical location of these break-points along the transect of sites or along the first ordination axis (principal components analysis, (detrended) correspondence analysis, principal curves - Felde et al., 2014b) of the modern pollen data can then be compared with changes in the modern vegetation data, possibly also summarised as a major ordination axis.

Taxon-accumulation curves can also be used to illustrate and quantify turnover (beta diversity) within modern assemblages from different vegetation or habitat types or geographical areas (e.g. Ricotta et al., 2002; Magurran, 2004; Kindt and Coe, 2005; Kindt, 2014; Terlizzi et al., 2014) and to compare richness, evenness, and diversity properties of different assemblages (e.g. Gotelli and Colwell, 2001; Ugland et al., 2003; Colwell et al., 2004; Magurran, 2004, 2011; Kindt et al., 2006; McGill, 2011).

In the context of fossil pollen assemblages, Giesecke et al. (2012) emphasise that taxon-accumulation curves showing the pollen taxa–pollen count relationship for a pollen-stratigraphical sequence are, in effect, illustrating taxon–time relationships. Such taxon–time curves have been shown to be valuable in ecological and Deep-time studies (e.g. McKinney and Frederick, 1999; Adler and Lauenroth, 2003; White et al., 2006). They may also be useful in Q-time studies (e.g. Giesecke et al., 2014) where their strength lies in using the many rare taxa and potentially in characterising changes in landscape patterns. They are simple to construct (Oksanen et al., 2013; Kindt, 2014) and they should be used more widely to summarise compositional properties of pollen-assemblage data in time and space.

7. Future challenges and research opportunities

In this Section we outline six future challenges and potential research opportunities in studying pollen-assemblage richness patterns in space and time. These concern the interpretation of past pollen-assemblage richness changes; estimation of taxon richness from plant macrofossils; studying pollen richness at different ecological or spatial scales; partitioning diversity and estimating beta diversity; the concepts of the species pool, pollen pool, hidden diversity, dark diversity, and dark richness; and functional and phylogenetic diversity.

7.1 Interpretation of past pollen-assemblage richness

Recent studies have shown that modern pollen-assemblage richness does reflect, in part, contemporary floristic richness at both the local site and regional landscape scales. Odgaard (2007, 2013) comments in discussing fossil pollen assemblages and past pollen richness that “rarefaction estimates are often inappropriately interpreted as an index of past species richness” and he concludes that “rarefaction estimates of pollen species are … a complex reflection of many processes such as pollen production, evenness, pollen dispersal, landscape pollen productivity, and possible floristic richness. Although more work is needed to resolve these complexities, pollen productivity seems a much more important control of palynological richness than does floristic richness”. In the same vein, Goring et al. (2013) question whether temporal changes in pollen richness reflect underlying changes in plant richness or some other change in plant composition or structure.

When Birks and Line (1992) introduced rarefaction analysis to estimate pollen richness from late-Quaternary pollen-stratigraphical sequences, they suggested that “although factors such as local site characteristics and pollen production, dispersal, and input may influence temporal changes in richness, changes in palynological richness are interpreted as reflecting the changing floristic richness of the vegetation types in the pollen-source area of a lake and the changing mosaic structure of the landscape through time”. They emphasised that the “combination of a changing mosaic structure of the landscape through time and the floristic richness of the constituent vegetational types within the landscape” are the main drivers of the changing patterns of pollen richness through time.

We now know that with high-quality pollen data and appropriate vegetation data and by reducing the taxonomic and, if possible, the pollen representation (≡ evenness) biases inherent in pollen assemblages (Odgaard 1999, 2001, 2007, 2013), there are statistically significant relationships between pollen and plant richness (e.g. Felde et al., 2015). Meltsov et al. (2013) studied pollen and plant richness around nine lakes in southern Estonia along a land-cover gradient from semi-open to closed forest. They estimated landscape structure within eight radii (250–2000 m) around each lake on the basis of landscape openness and three summary statistics of landscape richness, evenness, and diversity. They show that pollen richness has a statistically significant positive relationship with landscape structure within radii greater than 1000 m. They conclude that within one floristic or climatic region "pollen richness gives reliable estimates about the variation in floristic richness and landscape structure; however, caution must be taken when comparing pollen-inferred vegetation diversities from different regions or when interpreting fossil pollen records from times with highly different vegetation associations". This Estonian study is, as far as we know, the first study where modern pollen richness is considered specifically in relation to landscape structure. A second study in Germany by Matthias et al. (2015) confirms some of the trends in the Estonian study and shows that palynological richness to a rarefaction base-sum of 10 as an index of pollen diversity (highly correlated to *N*1 and *N*2) strongly reflects landscape diversity. The results of Meltsov et al. (2013), Felde et al. (2015), and Matthias et al. (2015) raise several questions: is the observed relationship between modern pollen richness and floristic richness at the regional scale (Felde et al., 2015) a reflection of a direct pollen–vegetation richness link; or alternatively, is it a result of a landscape mosaic-vegetation richness link *and* a vegetation-pollen richness link? A third hypothesis is that it is a result of complex and poorly understood interactions between landscape and vegetation dynamics, structure, and diversity, and hence pollen richness. Ecologists are increasingly recognising the importance of landscape structure and heterogeneity ('geodiversity') in influencing floristic and vegetation richness over a range of spatial scales (e.g. Burnett et al., 1998; Nichols et al., 1998; Carranza et al., 2007; Rocchini et al., 2010; Gray, 2013; Stein et al., 2014; Hjort et al., 2012, 2015).

There is thus a clear need for many more such studies that take advantage of new quantitative approaches to estimate landscape structure and heterogeneity and habitat fragmentation (see Box 3 for a selection of relevant publications) as a basis for comparing modern pollen richness, floristic richness, and landscape features.

7.2 Estimating taxon richness from plant macrofossil assemblages

There is renewed interest in Quaternary plant macrofossils and an increase in the quantity and quality of studies based on plant macrofossils (e.g. Birks HH, 2001, 2013; Birks HJB and Birks HH, 2008; Jackson, 2012; Birks HH and Birks HJB, 2013; Birks HJB, 2014; Jackson et al., 2014). Quaternary macrofossil assemblages have, however, rarely been used to estimate taxon richness (Blarquez et al., 2010, 2013; Leys et al., 2014) in contrast to Deep-time palaeobiological studies involving animal or plant macrofossils (e.g. Foote and Miller, 2007; McElwain and Punyasena, 2007; McElwain et al., 2007, 2009; Mander et al., 2010; Patzkowsky and Holland, 2012) or Quaternary palaeozoological studies (e.g. Lyman, 2008; Hadly and Barnosky, 2009; Blois et al., 2010; Macken and Reed, 2014). It is clearly not a simple task to estimate an ecologically useful richness measure from plant macrofossil data as there are even more potential sources of bias to be considered and accounted for, including taxonomic problems, the mixed nature of macrofossil data, count-size, productivity, dispersability, deposition, and preservation (Jackson, 2012; Birks, 2014) than with pollen data. This is an area where more work is clearly needed (e.g. Blarquez et al., 2013).

7.3 Pollen richness at different ecological or spatial scales

Whittaker (1977) proposes that plant richness or diversity can be studied as inventory diversity at the community (alpha diversity), landscape (gamma diversity), and regional (epsilon diversity) scales (see also Whittaker et al., 2001; Willis and Whittaker, 2002; Jurasinski et al., 2009; Tuomisto, 2010a, 2010b; Anderson et al., 2011) along with changes or turnover (differentiation diversity) between communities (beta diversity) and between landscapes (delta diversity) (Odgaard 2007, 2013) (see Table 3). Contemporary ecologists (e.g. Ellison, 2010) and Deep-time palaeobiologists (e.g. Sepkoski, 1988) have simplified Whittaker's (1977) five components to three (Whittaker, 1972) – alpha, beta, and gamma. Alpha is local richness or diversity and is estimated or measured within a defined place such as a vegetation quadrat, a forest plot, or a single stream. Gamma is regional richness or diversity and it is the total diversity estimated or measured for a group of localities in an area, such as all quadrats in a study, all forest stands, or all streams in a catchment. Beta diversity links alpha and gamma, or local and regional, richnesses and diversities and is "the extent of differentiation of communities along habitat gradients" (Whittaker, 1972; Ellison, 2010; Beck et al., 2013). Alpha and gamma richness or diversity can be estimated or measured directly either as numbers of species (richness) or as numbers of species weighted by their relative abundances in the sample (diversity). Beta diversity, in contrast, is a quantity derived from alpha and gamma richnesses or diversities (Ellison 2010). Odgaard (2007, 2013) suggests that pollen data may reflect the alpha, gamma, and epsilon scales (*sensu* Whittaker, 1977) or the alpha and gamma scales (*sensu* Whittaker, 1972) depending on site size, location, and other features whereas plant macrofossil data are more local and primarily reflect the alpha scale.

The estimation of beta diversity is discussed in Section 7.4 but here we outline possible future challenges in reconstructing and assessing past richness patterns at the gamma (landscape) and alpha (local) scales. Odgaard (2007, 2013) summarises the very detailed study of 13 pollen sequences from a 15 ha bog in south Wales by Smith and Cloutman (1988) in terms of the changing richness of inferred vegetation types (based on pollen assemblages) through the Holocene and the progressive homogenisation and impoverishment of landscape diversity as blanket bog expanded in the landscape in the last 3000 years. This reconstruction is at the landscape (gamma diversity) scale. It is possible to shift to the local site scale (alpha diversity) and to study richness changes through time within the landscape scale, along the lines of the unique study of 11 very small upland pollen sites in Scotland by Hanley et al. (2008). The local changes in pollen richness were then related statistically to changes in land management, livestock grazing pressures driven by economic change, and land abandonment. By careful study design, rigorous site selection, and detailed pollen analyses, it would be possible to detect changes in richness in time and, to some extent, in space (Birks, 2012c) and hence to improve the application of palaeoecology in conservation and land management (Davies et al., 2014).

Issues about ecological and spatial scales in palaeoecology and modern ecology (e.g. Whittaker et al., 2001; Willis and Whittaker, 2002; Birks, 2012c; Barton et al., 2013; Seddon et al., 2014) continue to create conceptual, methodological, and communication barriers between ecologists and palaeoecologists (Varela et al., 2015). Bennington et al. (2009) comment "The greatest barrier to communicating and collaborating with neoecologists is not that data collected from extant ecosystems are necessarily different or more complete than paleoecological data but, rather, that these two data sets commonly represent or are collected at different scales. If such differences of scale can be understood and quantified, then they can be reconciled and even exploited." Questions of scale are critical in the interpretation of richness and diversity patterns in both ecology and palaeoecology (Odgaard 2007, 2013; Jackson, 2012; Birks, 2012c, 2014; Jackson et al., 2014) and appropriate definitions of scales of study need careful thought and further development if neoecologists and palaeoecologists are to communicate and collaborate effectively.

7.4 Diversity partitioning and estimating beta diversity

The basic idea of diversity partitioning or decomposition is that the total estimated diversity of a study area can be partitioned into the diversity inherent in its constituent parts (inventory diversity) plus the diversity due to the differences between these constituent parts (differentiation diversity) (Olszewski, 2010). Diversity partitioning is increasingly being used in ecology (e.g. Legendre et al., 2005, 2009; Głowacki et al., 2011), biogeography (e.g. Qian et al., 2005), conservation biology (e.g. Jost et al., 2010), and Deep-time palaeoecology (e.g. Patzkowsky and Holland, 2007; Mander et al., 2010), as a tool for directly addressing how the structure of higher-level systems reflect interactions between lower-level units in response to environmental and evolutionary changes.

As outlined above (Section 7.3) ecologists tend to work with three components of diversity (Table 3) – alpha (an inventory diversity), beta (a differentiation diversity), and gamma (an inventory diversity). Whilst alpha and gamma diversities can be measured (or at least estimated) as a result of surveys or inventories (Jurasinski et al., 2009), beta diversity is a derived quantity and there is no consensus about how to derive this quantity from alpha and gamma diversities and how to interpret beta diversity (Ellison, 2010). Whittaker (1960) proposes that gamma diversity is the product of alpha and beta diversity (multiplicative model) and thus beta diversity can be estimated by dividing gamma by alpha. Lande (1996) (see also Veech et al., 2002) suggests that an additive model of diversity (alpha + beta = gamma) provides a more natural means of estimating beta diversity as an additive concept (Ellison, 2010; Legendre, 2014). Jost (2007) and Jost et al. (2010) propose that by using Hill numbers, Whittaker's multiplicative concept (alpha × beta = gamma) is true for all indices. In this case, Jost's (2007) "true beta diversity" is the effective number of distinct communities or assemblage types (see Felde et al., 2015 for examples). Jost (2007) also shows that Shannon's entropy is the only standard diversity measure that can be decomposed into meaningful alpha, beta, and gamma components when assemblage weights are unequal. Jost's (2007) proposals have naturally led to considerable discussion, resulting in a Forum in *Ecology* (Ellison, 2010) with contributions by Baselga (2010), Jost (2010b), Ricotta (2010), Veech and Crist (2010a, 2010b), and Wilsey (2010). Little consensus emerged about how to partition diversity, as all the approaches discussed make demands on the underlying sampling and make simplifying assumptions about the real world (Ellison, 2010). Ellison (2010) concludes "a real breakthrough would require a method to measure beta diversity independently of either alpha or gamma diversities" and "there is much yet to be done to identify and characterise patterns of biological diversity". Tuomisto (2010a, 2010b, 2010c, 2011) proposes that "true beta diversity" is obtained when the effective number of species in a data set ("true gamma diversity") is multiplicatively partitioned into the effective number of species per compositionally distinct virtual sampling unit ("true alpha diversity" α_d) and the effective number of such compositional units ($\beta_{md} = \gamma / \alpha_d$) (Tuomisto, 2010a, 2010c, 2011). Partitioning "true gamma diversity" multiplicatively rather than additively into alpha and beta components permits a unified treatment not only of alpha and gamma diversities but also beta diversity as "a count of an effective number of types of entities (Routledge 1977, 1979, Jost 2006, 2007)" (Colwell, 2010). Diversity partitioning and beta diversity remain remarkably contentious issues in ecology (e.g. Pélissier and Couteron, 2007; de Bello et al., 2010; Marcon et al., 2012; Baselga and Leprier, 2015) despite the recent advances by Jost (2007, 2010b), the comprehensive reviews by Tuomisto (2010a, 2010b) and Jurasinski et al. (2009), and the subsequent commentaries by Juransinki and Koch (2011), Tuomisto (2011), and Moreno and Rodríguez (2010, 2011).

An important attempt to try to resolve the debates about diversity partitioning (Chao et al., 2012) clarifies the terms “independence” and “statistical independence”. Multiplicative beta diversity depends on the number of assemblages whereas additive beta diversity depends on alpha (equivalently of gamma) diversity. They propose transformations to remove these dependencies and demonstrate that the transformed multiplicative beta and additive beta diversities both lead to the same classes of measures which are always in the range of 0–1. They can thus be used to compare relative similarity or differentiation among assemblages or community types across one or more regions (Chao et al., 2012).

Rarefaction analysis is another potentially useful approach to estimating beta diversity (e.g. Olszewski, 2004, 2010; Crist and Veech, 2006). Olszewski (2010) suggests that the divergence between sample-based (groups of samples or stratigraphic sequences – Gotelli and Colwell, 2001, 2011; Scarponi and Kowalewski, 2007; Chiarucci et al., 2008; Gotelli and Ellison, 2013) and individual-based (single assemblage or sequence) rarefaction curves of a composite collection (gamma diversity) incorporating all the samples (alpha diversity) contributing to a specific hierarchical level reflects the degree of non-random compositional difference within the smaller scale units (beta diversity) (Scarponi and Kowalewski, 2007). When considering diversity *sensu stricto* based on taxon relative abundances, Olszewski (2010) proposes that Shannon’s entropy (Jost, 2006) can be partitioned additively with beta entropy equalling gamma entropy (based on a composite sample) minus entropy equalling alpha diversity of the constituent samples. As entropy (Jost, 2006) can be readily converted to effective richness of number of species (the number of taxa that would result in the same entropy value if they were all equally abundant) (Jost, 2006, 2007), effective richness is derived from Shannon’s entropy partitions multiplicatively and beta diversity is the number of compositionally distinct smaller units that contribute to the total gamma diversity at the higher level (see also Jost, 2007; Jost et al., 2010; Tuomisto, 2010a; Chao et al., 2012; Felde et al, 2015).

A recent study by Blarquez et al. (2014) applied diversity partitioning to Quaternary palynological data. They selected 205 pollen sequences from 12 ecoregions, each with similar environment, species composition, and ecological processes today, within the North American boreal forest–taiga regions. They used Shannon’s entropies and following Jost (2007, 2010) they partitioned diversity into independent alpha, beta, and gamma components. They used the alpha Shannon entropy and for each ecoregion calculated the mean entropy per site for 1000 year time-windows. The Shannon entropy was converted to its numbers equivalent to derive “true alpha diversity” (Jost, 2007). Shannon’s entropy was used because it is the only measure that satisfies Lande’s (1996) condition that alpha diversity is less than or equal to gamma diversity when assemblage weights are unequal. Gamma diversity was estimated by pooling the alpha entropies at all sites and for each time-window and converting this to its numbers equivalent. In the framework of numbers equivalents, beta diversity could then be estimated by Whittaker's (1972) multiplicative rule and calculated as the gamma component divided by the alpha component (Blarquez et al., 2014). They further investigated beta diversity by decomposing it into two components – nestedness and turnover (Baselga, 2010; Baselga and Orme, 2012; Legendre, 2014). Nestedness (= richness difference: Legendre, 2014) represents non-random loss of taxa, namely within a given region sites with fewer taxa are the subset of sites with more taxa. Turnover (= replacement: Legendre, 2014) represents the replacement of taxa as result of temporal or spatial sorting (Blarquez et al., 2014).

Pollen diversity of the North American boreal forest–taiga regions underwent substantial changes in response to major climatic shifts in the late-glacial and early Holocene. The nestedness component within beta diversity probably reflected plant migration as it generally peaked before the turnover component. Turnover may result from various factors including spatial and temporal sorting of assemblages in response to changing environmental conditions and habitat conditions (Blarquez et al., 2014). Pollen diversity was generally maximal in the late-glacial and early Holocene and progressively decreased during the Holocene (cf. Birks and Line, 1992).

Diversity partitioning has been more widely used in Deep-time palaeoecology (e.g. Layou, 2007; Patzkowsky and Holland, 2007; Heim, 2009; Holland, 2010; Mander et al., 2010; Olszewski, 2010; Vavrek and Larsson, 2010; Hautmann, 2014). Partitioning of diversity using richness is difficult due to the sensitivity of richness to sample size (e.g. Scarponi and Kowalewski, 2007).

Just as variation partitioning in canonical ordination and multiple regression (Borcard et al., 1992; Legendre, 2008; Legendre and Legendre, 2012) has become a standard data-analytical tool in ecology and palaeoecology (e.g. Legendre and Birks, 2012; Simpson and Hall, 2012), hierarchical diversity partitioning has the potential to infer ecological processes from palaeoecological data when the data are collected using a sampling strategy that balances sample size and distribution among possible categories. The study on the effects of the Richmondian invasion on the structure of invertebrate fossil assemblages in the Cincinnati Arch during the late Ordovician by Patzkowsky and Holland (2007) (see also Olszewski, 2010) is an elegant example of how diversity partitioning at multiple hierarchical levels in Deep-time palaeoecology can be used creatively to address current issues in ecology. It also illustrates how palaeoecology can contribute to understanding ecological processes acting over long time intervals, namely broad-scale invasions by taxa. It exemplifies Flessa and Jackson's (2005) review of exploiting "the geological record of ecological dynamics" to understand the biotic effects of future environmental change. Patzkowsky and Holland (2007) partitioned data from different depositional sequences into three levels of inventory diversity (*sensu*

Magurran, 2004; Jurasinski et al., 2009 – see Table 3)—(1) collection diversity estimated as the average Shannon entropy of all collections in each sequence (α_c), (2) habitat diversity (α_h) estimated as the average Shannon entropy of habitats (shallow and deep) within each sequence ($\alpha_h = \alpha_e + \beta_w$), and (3) stratigraphic sequences (i.e. landscape) diversity (α_s) estimated as the total Shannon entropy of each sequence ($\alpha_s = \alpha_c + \beta_w + \beta_b$) separated by two levels of differentiation diversity (Table 3)—one for between-collections–within-habitats (β_w) and one for between-habitats–within-sequences (β_b). By the end of the Richmondian invasion, richness had increased by almost 40%, mainly as a result of increases within habitats (α_h) with a smaller contribution from among-collections–within-habitats (β_w) (Olszewski, 2010). The main ecological interpretation is that assemblages in local patches (i.e. sampled by individual collections) accommodated new species without substantially changing their diversity but that they became more distinct from one another within habitats (Olszewski, 2010). Legendre (2014) discusses further approaches to partitioning beta diversity into replacement (turnover) and richness-difference (nestedness) components.

Related to beta diversity (*sensu* Whittaker, 1972) is assemblage compositional turnover along gradients in space or time (Jurasinski et al., 2009; Tuomisto, 2010a, 2010b). Tuomisto (2010c) emphasises that as turnover does not quantify the effective number of taxa, it is not a true diversity and should be specifically called what it is quantifying, in this case compositional turnover. Detrended canonical correspondence analysis (ter Braak, 1986; Birks, 2007) with the ordination constrained by sample age or depth as the sole predictor variable provides a comparative summary of compositional turnover within and between stratigraphical sequences (e.g. Smol et al., 2005; Birks and Birks, 2008; Feurdean et al., 2012; Colombaroli and Tinner, 2013, Colombaroli et al., 2013; Leys et al., 2014). Other multivariate ordination approaches are also useful in displaying and quantifying aspects of alpha and beta diversity, and assemblage composition and differentiation (e.g. ter Braak, 1983; Legendre et al., 2005; Anderson et al., 2006, 2011; Heegaard et al., 2006; Legendre, 2008; Legendre and Legendre, 2012; Legendre and De Cáceres, 2013; Nieto-Lugilde et al., 2015). The use of compositional (dis)similarity or distance measures to assess differences in taxon composition as a means of estimating beta diversity is reviewed by Jost et al. (2011). Jurasinski et al. (2009) discuss other facets of beta diversity and approaches to estimating it, including variation in taxon richness, sum-of-squares or dispersion of a taxon matrix, the slope of distance-decay relationships or ‘halving distances’, and the slope of taxon-area curves.

7.5 Pollen pools, dark richness, and hidden richness

Ecologists and biogeographers have long used the concept of the species pool in considering contemporary and historical determinants of diversity at a range of spatial scales (e.g. Pärtel et al., 1996; Zobel, 1992, 1997; Zobel et al., 2011; Carstensen et al., 2013; Lososová et al., 2015; Zobel, 2015). Pärtel et al. (1996) distinguished two types of species pool – the regional or potential pool consisting of those species that occur in a specified geographical area and that can be expected on the basis of their ecological requirements to occur in a particular vegetation type; and the actual or realised species pool defined as the species that actually are present in the vegetation type of interest.

Quaternary pollen analysts implicitly or explicitly use the concept of a potential species pool, namely those plants that may contribute pollen to a particular site. A pollen pool can be defined as consisting of plant taxa that produce morphologically distinctive pollen or spores in a specified geographical area, such as a lake catchment, a vegetation-landform unit (Felde et al., 2014b), an entire country (e.g. Birks, 1973b; Bennett, 1995-2007; Felde et al., 2012), or an entire continent (Whitmore et al., 2005). This potential pollen pool is important not only in limiting the underlying flora to be considered in pollen identifications (e.g. Birks, 1973b, Hansen and Cushing, 1973; Lacourse and May, 2012) but also in the creation of plant–pollen translation tables and delimitation of pollen equivalents that are essential in assessing pollen–plant richness relationships. Although there is a finite probability of finding a pollen grain of any taxon in the world (Cushing, 1963), about 40–70% of the potential pollen pool for an area the size of Norway can be found in regional-scale pollen assemblages (Table 2). Up to 85% of the pool may be found in local-scale pollen assemblages (Table 2). The 15–60% of the pollen pool that is rarely, if ever, found consists mainly of low-growing entomophilous plants with very low pollen production, very poor pollen dispersal, and/or very poor pollen preservation (e.g. *Geranium, Oxalis, Viola, Linum, Calystegia, Primula, Malva, Euphorbia,* Orchidaceae, *Juncus, Luzula*). Just as there is so-called dark diversity in ecology (Pärtel et al., 2011; Pärtel, 2014; Riiback et al., 2015) and biogeography (Ronk et al., 2015), namely species in the potential species pool that can potentially inhabit particular ecological conditions or geographical areas but are absent from a particular habitat, vegetation type, or area, there is ‘dark richness’ in pollen analysis. This consists of pollen and spore types in the potential pollen pool whose parent plants could occur in the past vegetation that produced a particular pollen assemblage but are absent from the assemblage. Pärtel (2014) has recently distinguished in modern biotic assemblages an additional type of absent taxa, so-called hidden diversity consisting of taxa that are absent from a given survey such as plants in a dormant state or are so rare as to be overlooked in traditional field sampling. They can be detected by, for example, modern environmental-DNA techniques applied to soil samples (e.g. Valenti et al., 2008; Epp et al., 2012; Yoccoz et al., 2012). In the case of pollen assemblages, the distinction between dark richness and hidden richness of pollen types is very fuzzy as taxa such as *Geranium* and *Juncus* are generally “palynologically silent taxa” (Ritchie, 1987) but very occasionally their pollen is found. Strictly hidden richness in pollen assemblages refers to taxa that produce no pollen or produce pollen that is not preserved (e.g. *Najas*, *Zostera, Vallisneria, Ceratophyllum*).

A problem largely unique to pollen assemblages is false richness or false presences (Birks, 2014), namely pollen dispersed over far distances (extra-regional pollen; *sensu* Janssen, 1966, 1973, 1981) from areas well outside the RPSA of a site (e.g. *Ephedra* pollen in late-glacial assemblages from western Scotland (Birks, 1973b)). Modern pollen assemblages from Svalbard (Birks et al., 2004) contain 48 pollen and spore taxa. Twelve of these represent plants that do not grow on Svalbard today. This extra-regional pollen must have been carried by wind as long-distance transport. Such false presences are thus a source of bias in modern pollen assemblages from arctic, alpine, and other treeless environments. False presences can also be a serious problem in interpreting last glacial or late-glacial pollen assemblages because such assemblages often contain not only long-distance extra-regional pollen (e.g. *Pinus, Ephedra*) but also secondarily redeposited pollen such as *Quercus, Alnus, Ulmus*, and *Tilia* (e.g. Andersen, 1961; Cushing, 1963, Birks, 1973b).

Table 4 summarises the various types of richness that arise when considering pollen-assemblage richness.

Dark diversity of plants and dark richness of pollen equivalents cannot be directly measured, but their relative size can be approximately inferred. One simple approach (cf. Lewis et al., 2015) for dark richness of pollen is to list those pollen and spore types present and their likely plant equivalents, and consider the ecological indicator values of these plant equivalents for environmental variables such as light, moisture, soil reaction, and soil fertility (nitrogen) (e.g. Ellenberg et al., 1991; Hill et al., 2004) to derive approximate environmental scores for the past flora and vegetation within the RPSA for the observed pollen assemblage. If we assume that these environmental scores are representative of the past flora and vegetation, it is possible to use Hill et al. (2004) or Ellenberg et al. (1991) in conjunction with plant distributional data and ecological knowledge of the study areas to list all the likely plants and their pollen equivalents not found in the fossil pollen assemblage. The total number of such pollen equivalents is the ‘dark richness’ (plus ‘hidden diversity’). For Holocene pollen assemblages from western and southern Norway, the dark pollen richness is about 30–35% of the potential pollen pool for these areas (Birks, unpublished data). For late-glacial pollen assemblages from the Isle of Skye (north-west Scotland) (Birks, 1973b), the dark pollen richness is higher (Birks, unpublished data), about 50–60% of the potential pollen pool defined on the basis of the present-day vascular plant flora and vegetation of the Isle of Skye and neighbouring islands (Birks, 1973b; Murray and Birks, 2005). There are many possible reasons for the different relative sizes of the dark pollen richness in the late-glacial and the Holocene, such as different proportions of anemophilous and entomophilous and tall-growing and low-growing plants in the potential pollen pools, different taphonomies, different proportions of local, regional, and extra-regional pollen (*sensu* Janssen, 1966, 1973, 1981), plant migration and local extinctions over time, and the difficulties of defining realistic pollen pools for no-analogue late-glacial floras, vegetation, and landscapes. There is the need for more sophisticated assessments of dark pollen richness to help to provide a more realistic and complete view of past vegetation and ecosystems. For modern vegetation, Pärtel et al. (2013) attempt to link realised local diversity and inferred dark diversity within the general species-pool concept to derive a simple community completeness index based on the log-ratio of observed richness to dark diversity. Developing and interpreting such an index based on pollen-assemblage richness and dark richness is a challenge for future study, especially to detect which taxa are absent from past assemblages and to infer possible reasons for their absences.

7.6 Functional and phylogenetic diversity

Functional diversity (FD) is an important component of biodiversity that considers the range of functions that organisms perform in communities and ecosystems (Purvis and Hector, 2000; Hooper et al., 2002; Petchey and Gaston, 2002, 2006; Pakeman, 2011; Mace et al., 2014). It not only serves as a descriptor of an assemblage or community but it also is an indicator of ecosystem function. It is the extent of functional differences among species in a community (Tilman, 2001; Petchey and Gaston, 2002) and is thought to be an important determinant of ecosystem processes and functioning. As FD is the diversity of species traits in a community or ecosystem, it captures information about functional traits that may be missing in measures of taxonomic richness or diversity. There has been, just as with the estimation of taxonomic diversity, a proliferation of measures to estimate the different components of FD, namely functional richness, functional evenness, and functional divergence (e.g. Petchley et al. 2004; Mason et al., 2005; Walker et al., 2008; Poos et al., 2009; Schleuter et al., 2010; Casanoves et al., 2011). Estimating FD often requires analysis of several different types of variables (continuous, ordinal, nominal, multi-choice nominal, circular, fuzzy, etc.). Pavoine et al. (2009) extend Gower's (1971) coefficient of similarity for mixed data to include new data types. Not surprisingly, Hill numbers have now been generalised to consider not only taxonomic diversity but also phylogenetic and functional diversity, thereby providing a unified framework for measuring several aspects of biodiversity (Chao et al., 2010, 2014a, 2014b; Gotelli and Chao, 2013; Chiu and Chao, 2014). FD (differences among taxon traits) and phylogenetic diversity (based on taxon evolutionary history) (Chao et al., 2010, 2014a, 2014b; Chiu and Chao, 2014) have now been integrated into a single framework of attribute diversity based on Hill numbers of taxonomic entities, functional entities, and /or phylogenetic entities, with each entity weighted by its relative abundance (Chiu and Chao, 2014). FD has rapidly become an important part of community and ecosystem studies as it attempts to quantify aspects of diversity that may influence community assembly and function. FD is also being studied in Deep-time palaeobiology (e.g. Miller et al., 2014). The relation between FD and taxonomic richness and diversity is complex as it appears to be context-dependent (Cadotte et al., 2011).

To date, very few Quaternary palynologists have considered functional or phylogenetic diversity. Collins et al. (2013) and Davis et al. (2015) explore temporal and spatial patterns in plant functional type diversity during the Holocene using palynological data from across Europe. Other attempts at linking functional traits with pollen data include Gachet et al. (2003), Barboni et al. (2004), Lacourse (2009), and Kuneš et al. (2011) or with testate amoeba assemblages (Fournier et al. 2015). Goring et al. (2013) propose utilising functional trait or phylogenetic information “to unite […] plant and pollen taxa, such that the richness values from pollen are not evaluated on their own, but in a multivariate form that provides information about the structure of the pollen assemblage in an evolutionary or functional manner. This information may be integrated in measures of functional richness (Mason *et al.* 2005) but the choice of functional characters may strongly affect our ability to detect a relationship”. Goring et al. (2013) suggest that this approach of using both taxa and traits and taking account of phylogenetic constraints will result in “a greater integration of palaeoecological data and analysis into macroecological research”. Clearly such an approach requires not only high quality pollen and spore data but also reliable phylogenetic (Velland et al., 2011) and functional trait (Weihar, 2011) information for all the taxa concerned. As with pollen-richness estimation, problems of pollen taxonomic precision and ‘smoothing’ (*sensu* Mander, 2011), pollen-representation bias, and sampling considerations will also arise in considering functional diversity of modern pollen-assemblages in relation to contemporary vegetation. Thus the exploration of functional and phylogenetic diversity of modern and fossil pollen assemblages is a very considerable challenge.

This challenge has recently been faced by Reitalu et al. (2015) who have explored temporal patterns in taxonomic richness and evenness, functional diversity, and phylogenetic diversity, all based on late-glacial and Holocene pollen data from 20 sites in Estonia and Latvia. They show that shifts in the functional and phylogenetic diversity of the pollen data are closely related to climate change and suggest that trait differences play an important role in long-term biotic responses to climate change. Human impact in the last 2000 years has had a negative influence on functional and phylogenetic diversity in the pollen assembalges due to the decline of plant taxa with certain traits leading to functional convergence and the expansion of some taxa from particular phylogenetic lineages. Clearly there is a need for further such studies that simultaneously explore taxonomic, functional, and phylogenetic diversity of modern and fossil pollen assemblages.

8. Conclusions

In answer to the question posed in the title of this review, recent detailed studies (e.g. Odgaard, 2008; Meltsov et al., 2011; Felde, 2015; Felde et al., 2015) and earlier less detailed studies (e.g. Birks, 1973a; Flenley, 2005) demonstrate that pollen-assemblage richness does reflect floristic richness. However, this relationship is not a simple or exact 1:1 relationship. Pollen richness is also a function of landscape structure, openness, and diversity within the APSA or RPSA (Meltsov et al., 2013; Matthias et al., 2015), as proposed and discussed by Birks and Line (1992), of the pollination syndromes in the flora within the APSA (Meltsov et al., 2011), and of dispersal and other taphonomic processes (Birks and Line, 1992).

Pollen richness, evenness, and diversity—expressed as Hill (1973) numbers—are estimates of particular numerical characteristics of modern and fossil pollen assemblages (Birks HJB, 2013) or “species composition parameters” (Hurlbert, 1971). Like all such estimates or summary statistics derived from complex multivariate data, the estimates may be biased in various ways. In the case of estimates of pollen richness, they are biased by factors such as count size, taxonomic precision, the underlying pollen sample:underlying pollen population ratio, and pollen representation (productivity and dispersal) (Odgaard, 1999, 2001, 2007, 2008, 2013). Several approaches reviewed above (Sections 4.1 and 5.2) have been developed to minimise these biases but the biases cannot be fully eliminated as they are inherent in all pollen-assemblage data.

As discussed above, assessing the relationship between modern pollen and floristic richness requires high quality and consistent palynological data and site-specific floristic/vegetational data. The findings of Goring et al. (2013) of a slightly negative modelled relationship between “smoothed pollen richness” and “smoothed floristic richness” in the Pacific Northwest and thus that higher pollen richness occurs with lower floristic richness may be a result of the absence of site-specific floristic or richness data collected at a spatial scale appropriate for comparison with regional-scale pollen deposition in lakes in their study area.

The recent developments in the clarification of the concepts of richness, evenness, and diversity, in the unification of measures to estimate them, and in the distinction between concepts and the measures used to estimate them has greatly simplified diversity research. Hill (1973) numbers provide a conceptually simple and mathematically rigorous basis for estimating richness, evenness, and diversity.

Estimates as Hill numbers of pollen richness, evenness, and diversity can be calculated for fossil pollen-assemblage data collected in comparable taxonomic and analytical detail as the modern pollen-assemblage data and from sites of similar size and morphometry to the lakes at which the modern assemblages were studied. These estimates and their variances can be plotted stratigraphically to provide profiles of richness, diversity, and evenness through time (e.g. Felde, 2015). Estimates of richness, diversity, and evenness for assemblages from several sites can be compared if all the data sets, possibly after transformations using pollen-representation values, are rarefied to the same base-sum for estimating not only $N0$ but also $N1$ and $N2$ and their ratios as evenness measures (e.g. Felde et al., 2015).

Flenley (2003) in his future-looking "Some prospects for lake sediment analysis in the 21st century" identifies six possible developments based on his own research interests and experiences. One is "palyno-richness and palyno-diversity" (see also Flenley, 2005). With the recent developments reviewed here, we think that changes in pollen richness, evenness, and diversity through time can be estimated and compared in space to explore their patterns in time and space. Potential drivers of past changes can then be explored using the types of approaches of, for example, Hanley et al. (2008), Lacourse (2009), and Reitalu et al. (2013), thereby helping to close "the gap between plant ecology and Quaternary palaeoecology" (Reitalu et al., 2014).

As in all studies on the representation of flora and vegetation in Quaternary fossil assemblages (Jackson, 2012) (and in almost any palaeoecological study), there are always several known knowns, some known unknowns and unknown knowns, and probably an embarrassingly large number of unknown unknowns. In the context of pollen–floristic richness relationships, what are these four combinations of knowns and unknowns? An obvious example of a known known or more or less solid fact, observation, or inference, is that *Pinus* trees produce more pollen and disperse their pollen farther than *Tilia* trees do. Critical known unknowns concern sources of error, uncertainty, and bias in pollen data. Attempts are being continually made to minimise and estimate them, but we do not usually know enough about them and their interactions in nature to make realistic estimates of these uncertainties. Unknown knowns are things we may know so well that we are no longer explicitly aware that we know them (Jackson, 2012). What is an unknown known and what is a known known is partly determined by education, research school, awareness of the older literature, and hence age of the scientist concerned. For example, the rich literature on pollen production, dispersal, deposition, and taphonomy from the 1960s–1980s, often published in books or symposium proceedings (e.g. Birks and West, 1973) is increasingly ignored in the literature of the 2010s. Much of the older literature, not always written in English and often published as 'local' monographs is not currently available in an electronic format and represents an important 'loss of information' (see also Blois, 2012). This is sadly prevalent in much of the recent literature on quantitative pollen–plant relationships and vegetation and landscape reconstructions. The fourth combination, unknown unknowns, represents our ignorance at the present time but thanks to creative and critical scientific research, unknown unknowns can become known knowns or known unknowns. Studies on pollen–plant richness relationships build on several well-founded known knowns, strive to reduce the known unknowns, and try to convert some unknown unknowns into known knowns or known unknowns. Given the vast old and ever-expanding relevant new literature on diversity, functional diversity, phylogenetic diversity, functional traits, pollen representation, and handling uncertainties in reconstructions, we all have to work to reduce important information loss and hence the unknown knowns and to consider in more critical detail the known unknowns.

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Table 1

Selected examples of studies where pollen richness has been estimated from fossil pollen assemblages using rarefaction analysis. The study country, time span, and in general research topic are given.

Publication	Country	Time span	Research topic
Berglund et al. (1991)	Sweden	Holocene	Cultural landscape
Bennett et al. (1992)	Scotland	Holocene	Vegetation history
Birks and Line (1992)	UK	LG, Holocene	Methodological development and vegetation history
Grönlund and Asikainen (1992a)	Finland	Holocene	Land-use changes
Grönlund and Asikainen (1992b)	Finland	Holocene	Cultural landscape
Grönlund et al. (1992)	Finland	Holocene	Land-use history
Andersen and Rasmussen (1993)	Denmark	Mid Holocene	*Ulmus* decline
Fossitt (1994)	Ireland	LG, Holocene	Vegetation history
Odgaard (1994)	Denmark	Holocene	Intermediate disturbance hypothesis testing
Ammann (1995)	Switzerland	Holocene	Alpine history
Andersen (1992-93)	Denmark	Holocene	Vegetation history
Bunting (1995)	Scotland	Holocene	General history
Lindbladh and Bradshaw (1995)	Sweden	Mid to late Holocene	Cultural landscape
Bunting (1996)	Scotland	Holocene	Heathland development
Fossitt (1996)	Scotland	Holocene	Vegetation history
Lagerås (1996)	Sweden	Holocene	Cultural landscape
Birks et al. (1988)	UK, Sweden	Holocene	Cultural landscape
Lindbladh and Bradshaw (1998)	Sweden	Holocene	Forest history
Seppä (1998)	Norway, Finland	Holocene	Vegetational dynamics
Odgaard (1999)	Denmark	Holocene	Methodological development
Veski et al. (2005)	Estonia	Holocene	Cultural landscape
Willis et al. (2007)	Hungary	Late Pliocene	Water-energy dynamics
Berglund et al. (2008a)	Sweden	LG, Holocene	Vegetation history, cultural landscape
Berglund et al. (2008b)	Sweden	Holocene	Vegetation history, cultural landscape
Birks and Birks (2008)	Norway	LG, early Holocene	Revegetation, responses to climate
Hanley et al. (2008)	Scotland	Late Holocene	Land-use and farming history
van der Knaap (2009)	Switzerland	LG	Methodological development
Saarse et al. (2009)	Estonia	LG, early Holocene	Vegetation history
Carcaillet et al. (2010)	Canada	Holocene	Fire history
Valsecchi et al. (2010)	Switzerland	Late Holocene	Cultural landscape, conservation
Willis et al. (2010)	Norway	LG, early Holocene	Responses to climate
Morales-Molino et al. (2011)	Spain	LG	Vegetation history, fire dynamics
Connor et al. (2012)	Azores	Holocene	Invasions, vegetation history
Fredh et al. (2012)	Sweden	Late Holocene	Cultural landscape
Giesecke et al. (2012)	Sweden, Germany	LG, Holocene	Methodological development, migration impacts
Ammann et al. (2013)	Switzerland	LG	Revegetation dynamics
Bjune et al. (2013)	Norway	Late Holocene	Forest dynamics
Clear et al. (2013)	Finland	Mid to late Holocene	Fire history
Colombaroli and Tinner (2013)	Switzerland	Mid to late Holocene	Human impact
Colombaroli et al. (2013)	Switzerland	Mid to late Holocene	Human impact
Feurdean et al. (2013)	Romania	Holocene	Land use
Fredh et al. (2013)	Sweden	Late Holocene	Cultural landscape
Giesecke et al. (2014)	Sweden, Germany, Switzerland	Holocene	Methodological development
Keen et al. (2014)	Bolivia, Peru, Ecuador, Ghana	LGM, Holocene	Methodological development
Ledger et al. (2014)	Greenland	Late Holocene	Human impact and landscape history
Majecka (2014)	Poland	Eemian	Vegetation history

Morales-Molino and García-Antón (2014)	Spain	LG, Holocene	Vegetation history, fire dynamics
Whitney et al. (2014)	Bolivia	40 k	Responses to climate
Burrough and Willis (2015)	Zambia	Mid to late Holocene	Vegetation resilience
Clear et al. (2015)	Finland	Holocene	Forest history and dynamics
Felde (2015)	Norway	Holocene	Vegetation history, methodological developments
Mehl et al. (2015)	Norway	Holocene	Vegetation history, cultural landscape
Reitalu et al. (2015)	Estonia	LG, Holocene	Methodological development, functional and phylogenetic diversity
Schwörrer et al. (2015)	Switzerland	Mid Holocene	Forest dynamics and human impact
Stivrins et al. (2015)	Latvia	Late Holocene	Human impact
Åkesson et al. (2015)	Sweden	Holocene	Vegetation history

LG = Late-glacial; LGM = Last glacial maximum

Table 2

Effects of translation of terrestrial plant species recorded in modern vegetation to potentially identifiable terrestrial pollen and spore types ('pollen equivalents') in relation to the actual number of pollen and spore types found

Area	No. plant species recorded	No. potentially identifiable pollen/spore types ('pollen equivalents')	Ratio of plant species to identifiable pollen/spore types	No. identified pollen/spore types found	Ratio of identified to identifiable pollen/spore types	Reference
Estonia	307	127	2.4	52	0.41	Meltsov et al. (2011)
S Norway	406	180	2.3	125	0.69	Felde et al. (2014a, 2015)
Scotland	164	97	1.7	83	0.86	Birks (1973a, 1973b)
British Columbia	1729	67	25.8	78*	1.16*	Goring et al. (2013)
Denmark (woodland)	82	44	1.9	-	-	Odgaard (1994)
Denmark (oak scrub)	93	42	2.2	-	-	Odgaard (1994)
Denmark (heathland)	110	58	1.9	-	-	Odgaard (1994)
Denmark (weed vegetation)	35	24	1.5	-	-	Odgaard (1994)

* includes pollen samples from Washington, Oregon, Idaho, and Montana, as well as British Columbia where the floristic or vegetational data are derived from

Table 3

Different categories of inventory and differentiation diversity in relation to ecological scale of investigation (after Whittaker, 1972; Magurran, 2004)

	Inventory diversity	**Differentiation diversity**
Within sample	Point diversity	-
Between samples within habitat or sediment core	-	Pattern diversity
Within community, habitat, or sediment core	Alpha diversity	-
Between communities, habitats, or sediment cores within landscape	-	Beta diversity
Within landscape	Gamma diversity	-
Between landscapes	-	Delta diversity
Within biogeographical region, province, or biome	Epsilon diversity	-

Table 4

Different types of palynological richness relevant to pollen assemblages (after Birks and Line, 1992; Birks, 2014; Pärtel, 2014)

Type	**Sources**	**Example**
False richness (false presences)	Extra-regional pollen	*Pinus* pollen in high-Arctic areas
Hidden richness	No pollen produced or preserved	*Najas, Vallisneria, Elodea, Ceratophyllum, Zostera*
Dark richness	Generally palynologically 'silent' taxa	*Viola, Geranium, Oxalis, Malva*
Observed richness	Pollen counts standardised to a constant count-size. Includes false richness (false presences)	Hill *N*0; $E(S_n)$ from rarefaction

Box 1. Publications by palynologists and other palaeoecologists working on richness patterns in both Q-time and Deep-time (*sensu* Jackson, 2001)

Sepkoski, 1988
Odgaard, 1994, 2007, 2008, 2013
Flenley, 2005
Jaramillo et al., 2006, 2010
Huntley and Kowalewski, 2007
McElwain and Punyasena, 2007
McElwain et al., 2007, 2009
Scarponi and Kowalewski, 2007
Willis et al., 2007, 2010
Mayhew et al., 2008
Yashura and Cronin, 2008
Yasuhara et al., 2008, 2009, 2012a, 2012b, 2014
Hadly and Barnosky, 2009
Blois et al., 2010
Hoorn et al., 2010
Mander et al., 2010
Terry, 2010
Benton et al., 2011
Hannisdal and Peters, 2011
Smith and McGowan, 2011
Willis and MacDonald, 2011
Giesecke et al., 2012, 2014
Rull, 2012
Colombaroli et al., 2013
Colombaroli and Tinner, 2013
Fritz et al., 2013
Sniderman et al., 2013
Kocsis et al., 2014
Lazarus et al., 2014
Macken and Reed, 2014
Seddon et al., 2014
Vázquez-Riveira and Currie, 2015
Boenigk et al., 2015
Darroch and Wagner, 2015
De Blasio et al., 2015
Hunt et al., 2015
McGill et al., 2015
Nieto-Lugilde et al., 2015
Noetinger, 2015
Nürnberg and Aberhan, 2015
Reitalu et al., 2015
Schwörrer et al., 2015

Box 2. Hill numbers

The general formula for a Hill number is

$$^{q}D = \left(\sum_{i=1}^{S} p_i^q \right)^{1/(1-q)}$$

where p_i is the relative frequency of each taxon ($p_i = n_i / N$ for i = 1 to S) in the assemblage,
n_i is the count for taxon i,
N is the total count-size,
S is the total number of taxa in the assemblage, and
q is a non-negative integer that defines a particular Hill number.

Changing q gives a family of diversity indices. If $q = 0$, the Hill number is $N0$; if $q = 1$, the Hill number is $N1$. However, with $q = 1$ the general equation above cannot be solved directly as $1/(1 - q)$ is undefined but in the limit it approaches the exponential of the familiar Shannon entropy or diversity measure. Each species is weighted by its relative frequency; if $q = 2$, the Hill number is $N2$ (equivalent to the inverse of Simpson's index of concentration) and common and abundant species receive greater weight than less abundant species (Gotelli and Ellison, 2013) with rare species making almost no contribution to the summation.

Box 3. Publications on quantitative procedures to estimate landscape structure and heterogeneity and habitat fragmentation at the spatial scale of pollen-source areas

Palmer, 1988, 1992
Forman, 1995
Gustafson, 1998
Longley et al., 2001
Turner et al., 2001
Steiner and Köhler, 2003
Wagner and Fortin, 2005
Wiens and Moss, 2005
Dufour et al., 2006
Carranza et al., 2007
Cushman et al., 2008
Shao and Wu, 2008
Uuemaa et al., 2008
Jones and Vaughan, 2010
Rocchini et al. 2010
Hjort and Luoto, 2012
Hjort et al., 2012
Ewers et al., 2013
Wang et al., 2014