

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

39	ABBREVIATIONS
40	APSA absolute pollen-source area
41	CoCA co-correspondence analysis
42	PIE probability of interspecific encounter
43	PPE pollen-productivity estimate
44	RPSA relevant pollen-source area

45

46 1. Introduction

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

51 Many Quaternary palynologists have studied changes in pollen-assemblage diversity (hereafter
52 called pollen diversity) using various diversity measures such as Shannon's information index
53 (entropy) (e.g. Moore, 1973; Küttel, 1984), Simpson's index (e.g. Cwynar, 1982; Morley, 1982;
54 Ritchie, 1982), or Williams (1964) α -index (Birks, 1973a; Morley, 1982), and changes in pollen
55 richness through time from pollen-stratigraphical data using rarefaction analysis (Heck et al., 1975;
56 Simberloff, 1978; Tipper, 1979; Birks and Line, 1992) (see Table 1 for selected examples of such
57 rarefaction-based studies). There are, however, very few studies that explore how modern pollen
58 richness or diversity relates to contemporary floristic richness or landscape diversity (see Birks,
59 1973a; Flenley, 2005; Weng et al., 2006; Odgaard, 2008; Meltsov et al., 2011; 2013; Goring et al.,
60 2013; Jantz et al., 2014; Felde, 2015; Felde et al., 2015; Matthias et al., 2015).

61 In contrast to other studies on pollen-floristic richness that find a positive relationship
62 between pollen and floristic richness, Goring et al. (2013) report a slightly negative modelled
63 relationship between smoothed pollen richness and smoothed floristic richness in the Pacific
64 Northwest of North America. Their model shows a weak but statistically significant ($p < 0.001$)
65 negative relationship, suggesting that higher pollen richness is associated with lower regional plant
66 richness. They write that "We believe this study is the first to empirically test the relationship
67 between plant and pollen richness and fails to find a significant relationship" and conclude that "The
68 fundamental inability to relate pollen richness to plant richness in this analysis does not invalidate
69 other studies that show robust changes in pollen richness over time, but it calls into question
70 whether these changes reflect underlying changes in plant richness, or some other change in plant
71 composition or structure" and they suggest that "the lack of a meaningful statistical relationship
72 between measures of plant and pollen richness ... calls into question the use of fossil pollen

73 assemblages as a measure of species richness over time”. These findings contrast with results of
74 other studies where statistically significant positive relationships between pollen and floristic
75 richness have been found at a range of spatial scales (Birks, 1973a; Flenley, 2005; Odgaard, 2008;
76 Meltsov et al., 2011; Felde, 2015; Felde et al., 2015).

77 In the last 10–15 years there have been major developments within modern ecology and
78 biogeography in the clarification and understanding of the theoretical basis of different estimators of
79 taxon richness, evenness, and diversity (e.g. Olszewski, 2004; Jost, 2006, 2007, 2010a, 2010b, 2014;
80 Jost et al., 2011; Gotelli and Ellison, 2013; Chao et al., 2014a, 2014b; Chiu and Chao, 2014), in the
81 assessment of the strengths and weaknesses of the multitude of evenness and diversity measures
82 (e.g. Smith and Wilson, 1996; Ricotta, 2003; Jurasinski et al., 2009; Tuomisto, 2010a, 2010b, 2012;
83 Anderson et al., 2011), and in the increasing adoption and use of Hill’s (1973) unified notation of
84 diversity indices and related evenness measures (e.g. Jost, 2006, 2007, 2009, 2010a, 2014; Hoffman
85 and Hoffman, 2008; Chao et al., 2010, 2012, 2014a, 2014b; Colwell, 2010; Ellison, 2010; Jost et al.,
86 2011; Gotelli and Ellison, 2013; Chiu and Chao, 2014; Chiu et al., 2014; Koch and Jurasinski, 2015).
87 Few of these developments have, as yet, been adopted in Quaternary palynological research or
88 literature, in contrast to Deep-time palaeoecology (e.g. Olszewski, 2004, 2010).

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

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

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

105 2. Definitions and terminology

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

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

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

115 *Translation table* – a table that lists all the known plant taxa for a region and their equivalent pollen
116 or spore types and permits the translation or transformation of a plant taxon to its appropriate
117 pollen or spore type (pollen equivalents) (Bennett, 1995-2007; Felde et al., 2012, 2014a, 2015; Felde
118 2015).

119 *Diversity index* – a measure that attempts to combine species (taxon) richness and species (taxon)
120 relative abundances (evenness) (heterogeneity index: Peet, 1974; Pielou, 1975). Colwell (2010) and
121 Tuomisto (2010a, 2010b, 2010c, 2011) favour measures of “true diversity” (cf. Gorelick, 2011;
122 Boenigk et al., 2015) which treat, as Hill (1973) proposed, species (taxon) richness (Hill N_0) and the
123 ‘numbers equivalents’ of Shannon’s (Hill N_1) and Simpson’s (Hill N_2) indices as points along a single
124 mathematical continuum (e.g. Jost, 2006, 2010a; Colwell, 2010; Ellison, 2010; Gotelli and Ellison,
125 2013). ‘Numbers equivalents’ is a term used by economists (Adelman, 1969) whereas ecologists most
126 commonly use ‘effective number of species (taxa)’.

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

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

141 *Evenness* – the distribution of individual types of pollen grains or spores within a pollen assemblage
142 or the variability in taxon abundances in a vegetation sample. Evenness, according to Tuomisto
143 (2012) should only be used when evenness is assessed as diversity/richness. Other terms (e.g.
144 ‘equitability’) should be used for measures that estimate other features in the variability of taxon
145 abundance (Tuomisto, 2012).

146 **3. Data needs**

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

151 *3.1. Modern pollen data*

152 All modern (and fossil) pollen data should be of consistent high quality, be at the lowest
153 possible taxonomic level, have a consistent and defined nomenclature, be from the same
154 sedimentary environment (e.g. small lakes), be sampled using consistent field methods, prepared
155 using identical laboratory procedures, and counted using consistent analytical protocols. Thanks to
156 improved microscopy and the ever-increasing quantity and quality of modern pollen reference
157 material and of critical pollen floras, keys, and monographs (e.g. Punt et al., 1976–2009; Fægri et al.,
158 1989; Beug, 2004), the pollen and spore taxonomic level (e.g. Peglar, 1993; Odgaard, 1994; van der
159 Knaap and van Leeuwen, 1994; Felde et al., 2012, 2014a, 2015) is steadily improving. Many data sets
160 are not, however, of such high standards, having been analysed 20–30 years ago or to a lower
161 taxonomic resolution. This is a major limitation in using data from large pollen databases to study
162 pollen richness because such data are not usually internally consistent due to inevitable between-
163 analyst differences in field, laboratory, and analytical procedures, site selection criteria, and pollen
164 and spore taxonomic resolution and nomenclature. Goring et al. (2013) who used such a database
165 emphasise that “records in large databases contain a mixture of taxonomic levels that must,
166 ultimately, be resolved to the lowest taxonomic equivalent. Effectively this coarsened taxonomic
167 resolution can significantly affect the ecological interpretations of pollen data”.

168 3.2 Modern floristic and vegetation data

169 Obtaining modern floristic and vegetation data at the appropriate spatial scale for comparison
170 with modern pollen data is a challenge in all studies of modern pollen–plant relationships (e.g.
171 Andersen, 1970; Birks, 1973a, 1973b; Hjelle, 1998, 1999; Broström et al., 2004, 2005, 2008; Bunting
172 et al., 2005, 2013; Gaillard et al., 2008; Bunting and Hjelle, 2010; Hjelle and Sugita, 2012; Matthias et
173 al., 2012, 2015; Matthias and Giesecke, 2014; Hjelle et al., 2015; Li et al., 2015). As *all* the flora and
174 vegetation in the absolute pollen-source area (APSA) (*sensu* Sugita, 1993) for the site from which
175 pollen data have been obtained cannot usually be realistically surveyed, the aim should be to obtain
176 representative samples of the flora and vegetation within the relevant pollen-source area (RPSA)
177 (*sensu* Sugita, 1994). If the modern pollen data reflect local pollen deposition (*sensu* Janssen, 1966,
178 1973, 1981) and are derived from moss polsters (e.g. Birks, 1973a, 1973b; Hjelle, 1998, 1999) or
179 surface soils (e.g. Wright et al., 1967), vegetation data from a 2 × 2 m or a 10 × 10 m plot within
180 which the surface pollen sample(s) was(were) collected are appropriate. An alternative approach is
181 to sample the surrounding vegetation in a series of concentric rings for different radii around the
182 pollen sampling site (e.g. Broström et al., 2004, 2008; Bunting et al., 2005, Li et al., 2015).

183 If the modern pollen data are derived from surface sediments from the deepest part of small-
184 or medium-sized lakes (diameters ca 150–500 m, area ca 10–50 ha) and thus primarily reflect
185 regional pollen deposition (*sensu* Janssen, 1966, 1973, 1981) (e.g. Odgaard, 2008; Meltsov et al.,
186 2011, 2013; Matthias et al., 2012, 2015; Felde et al., 2014a, 2015; Matthias and Giesecke, 2014), the
187 extent and positioning of vegetation samples can be designed in light of results from model
188 simulations of pollen deposition in basins of different sizes within a forested landscape and of the
189 RPSA at the regional scale (Sugita, 1994, 2007, 2013; Davis, 2000). These simulations suggest that for
190 a lake 500 m in diameter within a forested landscape, the likely RPSA may be within a 500–2000 m
191 radius from the lake edge. Empirical studies (e.g. Nielsen and Odgaard, 2004; Nielsen and Sugita,
192 2005; Gaillard et al., 2008; Soepboer et al., 2007; Poska et al., 2011; Hjelle and Sugita, 2012; Sugita,
193 2013), generally support these model estimates with empirical estimates between 400 and 1500 m.
194 Variables such as vegetation structure and composition, disturbance, and the mosaic nature and
195 openness of the vegetation in the lake catchment can influence the RPSA (Hellman et al., 2009a,
196 2009b; Mazier et al., 2012; Matthias and Giesecke, 2014). The RPSA for lakes in treeless arctic or
197 alpine landscapes will be considerably larger than for lakes in forested landscapes. One of the
198 assumptions of Sugita’s (1993, 1994, 2007, 2013) simulation model is “no pollen inputs from water
199 inlets or surface run-off are considered”. Given the strong evidence for water-borne pollen being a
200 major part of the pollen input into small- and medium-sized lakes, at least in north-west Europe (e.g.

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

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

224 Goring et al. (2013) adopt a different approach to obtaining plant-richness data which they use
225 to assess modern pollen–plant richness relationships in the Pacific Northwest. Instead of collecting
226 site-specific floristic or vegetational data, they obtain plant-richness data from a database of plant
227 communities in British Columbia (Canada) containing 48,706 vegetation plots sampled with a
228 standard 400 m² plot design (except in alpine, grassland, or wetland habitats) and from a regional
229 vascular plant richness database for British Columbia based on plots and herbarium records
230 aggregated into 50 × 50 km grid cells. Because these vegetational and richness data are not directly
231 matched to the 167 modern pollen sites, Goring et al. (2013) use spatial smoothing models to
232 estimate plant richness using the 50 × 50 km grid cell data and the 400 m² plot data reduced to
233 14,529 plots (33,067 plots were removed because they had “low site quality flags”). After taxonomic
234 harmonisation, these smoothed floristic richness estimates from British Columbia were compared

235 with smoothed richness of the modern pollen data from the 167 sites in British Columbia and also
236 extrapolated for the 397 pollen sites in Washington, Oregon, Montana, and Idaho (USA). They also
237 used modern pollen richness to predict plant richness using spatial modelling and smoothing
238 techniques.

239 Decisions about whether to use databases to obtain plant richness data (e.g. Goring et al.,
240 2013) or whether to collect site-specific vegetational and floristic data (e.g. Odgaard, 2008; Meltsov
241 et al., 2011, 2013; Felde et al., 2014a, 2015) are critical in exploring modern pollen–plant richness
242 relationships. For field surveys, decisions on the size, extent, and location of sampling plots
243 immediately arise. Collecting modern detailed vegetation data is time-consuming; surveying the flora
244 and vegetation of the catchment of a small lake usually requires at least one field day. Using
245 ‘secondary’ richness data from broad-scale vegetation or biodiversity databases clearly avoids time-
246 consuming fieldwork and the need for plant determinations. However, estimating plant richness
247 from such sources with different spatial resolutions, field recorders, data qualities and quantities,
248 and data sources and consistency rather than collecting site-specific field data in a consistent way
249 may contribute to Goring et al.’s (2013) failure “to obtain clear and meaningful relationships
250 between measures of plant richness and pollen richness at any spatial scale and at any taxonomic
251 level”.

252 3.3 Pollen–plant translation tables

253 Because of the inherent limitations of current pollen and spore morphology, it is not (and
254 probably never will be) possible to identify every plant species from its pollen or spores. It is
255 therefore essential to be able to translate or transform plant species in modern vegetation into
256 known distinguishable pollen or spore types, so-called pollen equivalents (*sensu* Goring et al., 2013).
257 Felde et al. (2012) and Felde (2015) present such translation tables for the presumed native and non-
258 native flora of Norway (see also Bennett (1995–2007) for a comparable translation table for the
259 British and Irish flora). As different pollen analysts, even those working in the same laboratory (e.g.
260 Jackson et al., 2014), and different pollen-morphological monographs and keys sometimes differ in
261 their morphological categories, Felde et al. (2012) and Felde (2015) provide translation tables (with
262 synonyms) for the four most commonly used pollen-morphological texts (see Felde et al., 2014a).
263 Some plant taxa (e.g. *Oxyria digyna*, *Rumex conglomeratus*, *Athyrium distentifolium*, *Dryopteris filix-*
264 *mas*, *D. carthusiana*) may produce two or more morphologically different pollen or spore types
265 (Birks, 1973b). In such cases it is necessary to merge such morphological types into one general
266 pollen or spore taxon (e.g. *Dryopteris*-type including spores of *D. filix-mas*, *D. carthusiana*, and
267 *Athyrium distentifolium*, etc. – see Birks, 1973b) and to merge the corresponding plant species in the

268 vegetation into one corresponding plant taxon (Birks, 1973a, 1973b; Felde et al., 2014a, 2015).
269 Inevitably all such translations and the creation of pollen equivalents result in the loss of taxonomic
270 information and a decrease in taxonomic resolution (see Table 2) (Odgaard, 1994, 1999, 2007, 2013).
271 Outside tropical areas, the ratio of plant species in the vegetation to identifiable pollen and spore
272 taxa (pollen equivalents) is generally between 1.5 and 2.4 (Table 2), due to ecologically important
273 species-rich families (e.g. Cyperaceae, Poaceae) producing only a few consistently identifiable pollen
274 types, or families that either produce pollen that is rarely preserved (e.g. Juncaceae) or produce
275 almost no pollen (e.g. Violaceae). The high ratio of 25.8 for Goring et al. (2013) (Table 2) suggests
276 that using a translation table for the entire North American Modern Pollen Database (Whitmore et
277 al., 2005) may result in a serious lack of taxonomic resolution in the modern floristic data from British
278 Columbia when translated into identifiable pollen and spore types. It is also very unusual to have
279 more identified pollen types (78) than potentially identifiable pollen equivalents (67) in the
280 vegetation, as in Goring et al. (2013) (Table 2). They suggest that “one issue driving the lack of
281 relationship between the richness measures may be the lack of taxonomic resolution in the pollen
282 data set”. Whilst that is almost certainly the case, it is important to emphasise that the achieved
283 taxonomic resolutions in the pollen data and the associated translation tables determine the
284 taxonomic resolution of the modern floristic data when the plant species are translated into
285 identifiable pollen equivalents. Using a translation table for British Columbia plant species and pollen
286 types rather than for the entire North America may improve the taxonomic resolution in the Goring
287 et al. (2013) study. Moreover, Goring et al. (2013) note that 21% (363 species) of the species in their
288 modern vegetation data have no equivalent pollen taxon, highlighting the need for basic pollen-
289 morphological studies in their study area. ‘Taxonomic smoothing’ (*sensu* Mander, 2011; Goring et al.,
290 2013; Mander and Punyasena, 2014) plagues all Deep-time and Quaternary pollen analysis (e.g. Birks,
291 1973a, 1973b; Odgaard, 1994, 1999, 2007, 2013), not only pollen–plant richness studies. Plant
292 macrofossils can help to improve the taxonomic precision attainable from Quaternary plant
293 assemblages (e.g. Birks HH, 1980, 2001, 2013; Birks and Birks, 2000; Birks HJB, 2014), but no fossil
294 plant assemblage, microfossil or macrofossil or both, can ever have the taxonomic precision or
295 comprehensiveness of modern vegetation assemblages (Mander and Punyasena, 2014).

296 3.4 Co-variation between modern pollen and vegetation

297 Before considering modern pollen–plant-richness patterns, it is important to quantify the
298 degree of co-variation between modern pollen assemblages and vegetation composition and
299 between modern pollen assemblages and pollen equivalents in the vegetation composition. Co-
300 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

333 assumptions are not met by pollen data, these indices are not appropriate for pollen–plant richness
334 studies.

335 The most robust estimate of richness is the expected number of taxa ($E(S_n)$) found in samples
336 of equal size (n) as estimated by rarefaction analysis (Sanders, 1968; Hurlbert, 1971; Heck et al.,
337 1975; Simberloff, 1978; Birks and Line, 1992; Gotelli and Graves, 1996; Gotelli and Ellison, 2013). A
338 rarefaction estimate is the expected number of taxa in a sub-sample of n individuals selected at
339 random without replacement from an assemblage containing S taxa and N individuals (Hurlbert,
340 1971). This is, in reality, what a palynologist achieves when counting to a pre-determined *standard*
341 number of pollen grains (e.g. 500) in a sediment sample. Such estimates permit standardisation of
342 count-size and hence comparisons of richness between samples (Malmgren and Sagaroodi, 1985).
343 Rarefaction analysis was introduced into Quaternary palynology by Birks and Line (1992). It has been
344 widely used (see Table 1) to estimate palynological richness for fossil pollen counts of different
345 original sizes when scaled to a common size ('base-sum' or 'individual index' *sensu* Smith and Grassle
346 (1977)) by considering the relative frequencies of individuals within categories (e.g. pollen or spore
347 types). Rarefaction analysis can be used whenever individual objects (e.g. pollen grains) at one
348 hierarchical level are classified into groups (e.g. pollen morphological types) at a higher level
349 (Simberloff, 1978, 1979). Rarefaction does not assume any particular hierarchical distribution in
350 contrast to log-series or log-normal distributions (Simberloff, 1979; Gotelli and Graves, 1996; Gotelli
351 and Ellison, 2013). However, when used to compare S between samples or sites, the counts should
352 be derived from the same underlying distribution.

353 Rarefaction analysis makes various biological assumptions (Simberloff, 1978, 1979; Tipper,
354 1979; Gotelli and Colwell, 2011; Gotelli and Ellison, 2013) that are discussed in a palynological
355 context by Birks and Line (1992). The most critical are (1) the observed pollen count in each sample is
356 a statistically adequate and representative sample of the underlying pollen assemblage in that
357 sample and that this assemblage is a statistically representative sample of the total pollen input
358 (pollen population) to the site under investigation (Odgaard, 1999, 2001, 2007, 2013) and (2) the
359 pollen spectra being compared have been consistently sampled and analysed to comparable
360 taxonomic detail (Raup, 1975; Simberloff, 1979) and are from similar depositional environments
361 (Tipper, 1979). These assumptions are basic to all quantitative pollen analyses (Birks and Birks, 1980;
362 Birks and Gordon, 1985; Birks HJB, 2013) and are not unique to rarefaction analysis of palynological
363 data. Rarefaction can in theory result in loss of information (Magurran, 2004, 2011) because prior to
364 rarefaction the number of taxa and their counts are known for each sample, whereas after
365 rarefaction we only know $E(S_n)$. However, given a sample of size N with S taxa and modern computing
366 power it is possible to draw at random without replacement a large number (e.g. 1000) of

367 subsamples of base-sum n from the entire sample of size N (Simberloff, 1970, 1972; Gotelli and
 368 Graves, 1996; Gotelli and Ellison, 2013) and to use the mean or median of these subsamples as an
 369 estimate of $E(S_n)$. The counts for the individual taxa in the 1000 random subsamples are estimates of
 370 the taxon frequencies for sample size n with $E(S_n)$ pollen and spore types (Gotelli and Graves, 1996;
 371 Gotelli and Ellison, 2013). These randomly selected subsamples, all rarefied to the same base-sum
 372 can then be used to estimate diversity and evenness and their associated variances or inter-quartile
 373 ranges for the sample that is being rarefied (see Sections 4.2 and 4.3).

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

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

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

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

393 *4.2 Evenness estimation*

394 As all ecology textbooks state, diversity (see Sections 2 and 4.3) is a complex function made up
 395 of taxon richness and taxon evenness (abundances) (e.g. Ludwig and Reynolds, 1988; Magurran,
 396 2004; Gotelli and Ellison, 2013). Focusing on taxon richness ignores differences in the abundance of

397 taxa, although the shape of a rarefaction curve depends on the commonness versus the rareness of
 398 taxa (Gotelli and Ellison, 2013). Jost (2010a) explores in detail the relation between evenness and
 399 diversity and concludes that “contrary to common belief, decomposition of diversity into
 400 independent richness and evenness components is mathematically impossible. However, *richness*
 401 can be decomposed into independent diversity and evenness or inequality components”. Evenness
 402 and richness are intimately related – the shape of the rarefaction curve is affected by the relative
 403 abundances of the taxa; almost all evenness measures are affected by the number of taxa in the
 404 assemblage; and the minimum value that evenness can obtain for a given data set depends on
 405 richness (Jost, 2010a; Tuomisto, 2012; Gotelli and Ellison, 2013). Tuomisto (2012) proposes that

$$406 \quad \text{Diversity} = \text{Richness} \times \text{Evenness} \quad (1)$$

407 and so

$$408 \quad \text{Evenness} = \text{Diversity} / \text{Richness} \quad (2)$$

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

$$413 \quad \text{Richness} = \text{Diversity} \times \text{Unevenness} \quad (3)$$

414 where

$$415 \quad \text{Unevenness} = \text{Richness} / \text{Diversity}$$

$$416 \quad = 1 / \text{Evenness} \quad (4) \text{ (Tuomisto, 2012)}$$

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

427 (2012) also proposes that the term 'evenness' should only be used to refer to equations (2) or (4) and
428 that other terms be used for equitability measures that estimate other properties of assemblage data
429 sets.

430 Since Odgaard (1999, 2001, 2007, 2008, 2013) highlighted the role of palynological evenness (=
431 equitability) in influencing estimated values of palynological richness, palynologists have used several
432 'evenness' measures or other measures to quantify palynological 'evenness' in modern (e.g. Räsänen
433 et al., 2004; Odgaard, 2008, 2013; Peros and Gajewski, 2008; Meltsov et al., 2013) and fossil (e.g. van
434 der Knaap, 2009; Mortensen et al., 2011; Fredh et al., 2012, 2013; Giesecke et al., 2012, 2014;
435 Ammann et al., 2013; Colombaroli and Tinner, 2013; Colombaroli et al., 2013; Marquer et al., 2014;
436 Schwörrer et al. 2015) pollen assemblages. 'Evenness' measures have also been used with plant
437 macrofossil assemblages (Blarquez et al., 2013). Just as the concepts of evenness, richness, and
438 diversity are confused in ecology, palynologists have shown confusion in what they have used as an
439 'evenness' measure. Peros and Gajewski (2008) introduced into Quaternary palynology Hurlbert's
440 (1971) probability of interspecific encounter (PIE). This ranges from 0 to 1 and represents the
441 probability that two individual pollen grains, randomly selected (without replacement) will be of
442 different taxa. Those samples dominated by few taxa will have a PIE value close to 0 compared to
443 samples where there is a greater variety of taxa. It is not biased by sample size (Bulinski, 2007) or
444 taxon richness, unlike several other 'evenness' measures (Olszewski, 2004; Peros and Gajewski, 2008)
445 and it is easily derived from Simpson's (1949) diversity measure (Hill's (1973) N_2 is the inverse of
446 Simpson's measure when an adjustment is made for small sample sizes). PIE was first developed to
447 estimate linguistic diversity (Greenberg, 1956). PIE has, however, been used as an 'evenness'
448 measure by Peros and Gajewski (2008), van der Knaap (2009), Ammann et al. (2013), Blarquez et al.
449 (2013), Colombaroli and Tinner (2013), Colombaroli et al. (2013) and Schwörrer et al. (2015). It has
450 also been used as the basis for calculating "an evenness-detrended palynological richness" in which
451 palynological richness (estimated by rarefaction) is regressed on palynological 'evenness' (estimated
452 as PIE). The residuals (richness - 'evenness') are plotted as an "evenness-detrended palynological
453 richness" (Colombaroli and Tinner, 2013; Schwörrer et al. 2015). A critical question is whether
454 Hurlbert's (1971) PIE should be used as a diversity measure as Greenberg (1956) and Gotelli and
455 Ellison (2013) present it or as an 'evenness' measure as Olszewski (2004) and Peros and Gajewski
456 (2008) present it? Hurlbert (1971) introduced PIE (and a corrected version of rarefaction estimation)
457 *not* as a diversity *or* an 'evenness' measure but as a 'species composition parameter' with a
458 straightforward biological interpretation as an alternative to the diversity-index approach which
459 Hurlbert (1971) dubbed "the nonconcept of species diversity". Gotelli and Ellison (2013) list three
460 advantages of using PIE as a simple *diversity* measure: (1) it has easily interpretable units of

461 probability and corresponds intuitively to a diversity measure based on encountering novel taxa
 462 while sampling, (2) it is insensitive to sample size unlike taxon richness, as a rarefaction curve of PIE is
 463 a straight line, and (3) PIE measures the slope of a rarefaction curve measured at its base (Olszewski,
 464 2004). Smith and Wilson (1996) do not consider PIE as an ‘evenness’ index in their comprehensive
 465 “consumer’s guides to evenness” and related indices. It is thus unclear what “evenness-detrended
 466 palynological richness” (Colombaroli and Tinner, 2013; Schwörrer et al. 2015) is actually estimating,
 467 especially in light of Jost’s (2010a) demonstration that richness and evenness are not numerically
 468 independent.

469 Other than PIE, ‘evenness’ (equitability) measures commonly used by palynologists include (1)
 470 Pielou’s (1975; 1977) J' which expresses the Shannon diversity (entropy) measure H' relative to the
 471 maximum value that H' can obtain when all the taxa in the sample are perfectly even with one
 472 individual grain per taxon (e.g. Räsänen et al., 2004; Odgaard, 2007; Mortensen et al., 2011; Fredh et
 473 al., 2012, 2013; Keen et al., 2014; Marquer et al., 2014); (2) $E_{1/D}$ which is the complement of
 474 Simpson’s (1949) index of dominance divided by S (Meltsov et al., 2011; Odgaard, 2013; Reitalu et al.,
 475 2015) and is independent of species richness and theoretically ranges from almost zero (when one
 476 taxon is very dominant) to 1 (at maximum evenness); and (3) a modified version of Smith and
 477 Wilson’s (1996) E_Q measure (Nee et al., 1992) which is $-2/\pi \arctan$ of the slope of the scaled rank of
 478 abundance in relation to log abundance fitted by least-squares regression (Giesecke et al., 2012). E_Q
 479 and $E_{1/D}$ have been shown by Smith and Wilson (1996) to have excellent performances in their
 480 comparative tests, whereas J' is poor in relation to these in not being independent of taxon richness.
 481 Odgaard (2008 and unpublished), Giesecke et al. (2012), and Matthias et al. (2015) have rarefied
 482 pollen assemblages to a low base-sum of 10–30 grains. In this rarefaction, numerically abundant taxa
 483 will dominate in such a small rarefied sample and the probability of including less abundant taxa is
 484 low. The $E(S_n)$ in this case is strongly correlated to Hill’s N_2 (Matthias et al., 2015), so $E(S_n)$ to a low
 485 base-sum may be estimating diversity of very abundant taxa (e.g. N_2) rather than their evenness.

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

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

490 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
 491 argues that a meaningful evenness measure should be independent of taxon richness and proposes
 492 N_2 / N_1 as an appropriate measure (Sheldon, 1969). Alatalo (1981) modified this to be $(N_2 - 1) / (N_1$

493 – 1) so as “to give a better approach to intuitive evenness” (= index $F_{2,1}$ in Smith and Wilson (1996)).
 494 Hill (1973) commented that “the difference $N1 - N2$ may be more characteristic of the community
 495 than is the evenness $N2 / N1$... Fairly obviously, however, evenness should be regarded as secondary
 496 and in routine analysis the original diversity number $N2$ and $N1$, or $N2$ and $N0$ are to be preferred”.
 497 The computer program Canoco 5 (ter Braak and Šmilauer, 2012) gives as basic statistics of a
 498 compositional data-table not only sample mean, median, variance, total occurrences, and relative
 499 counts of species within samples but also sample values of $N1$, $N2$, $N2 / N1$, H' , and $H' / \log(N0)$ (a
 500 Shannon entropy-related measure of compositional ‘evenness’), and the logarithm of the number of
 501 occurrences (the maximum achievable value of H' for a given number of occurrences) and has a
 502 similar relation to H' as the number of taxa ($N0$) has to $N1$. Felde et al. (2015) show with modern
 503 pollen assemblages that values of Hurlbert’s (1971) PIE measure are highly correlated to Hill’s (1973)
 504 $N1$ and $N2$, whereas PIE has lower but statistically significant correlations with evenness measures
 505 $N1 / N2$, $N2 - 1 / N1 - 1$, $N1 / N0$, $N1 - 1 / N0 - 1$, and $N1 - N2$. In that study, PIE behaves most
 506 closely to Hill’s $N1$ and $N2$ diversity measures.

507 Hill’s (1973) $N2 / N1$ index and Alatalo’s (1981) modified Hill ratio are generally unaffected by
 508 richness (Smith and Wilson, 1996) but they fail Smith and Wilson’s (1996) requirement 2, namely that
 509 they must decrease when the abundance of the least abundant taxon in an assemblage is marginally
 510 reduced. Index $E_{1/D}$ (Smith and Wilson, 1996; Odgaard, 2013) is equivalent to the ratio of Hill
 511 numbers $N2 / N0$ and it performs well in Smith and Wilson’s (1996) tests.

512 Ludwig and Reynolds (1988) present other evenness measures based on Hill numbers such as
 513 $\log_e(N1) / \log_e(N0)$ (= Pielou’s (1975; 1977) J'), $N1 / N0$, and $(N1 - 1) / (N0 - 1)$ (Heip, 1974). All these
 514 involve $N0$ and are thus not totally independent of the number of taxa in the assemblage unless $N0$
 515 (total number of taxa) is standardised first for all the samples being considered by rarefaction
 516 analysis and $N1$ (and $N2$) is estimated from a set of rarefied samples derived from repeated
 517 resampling without replacement to a standard base-sum (Sections 4.1 and 4.3). Gotelli and Ellison
 518 (2013) comment that “sample size effects are important for all the other Hill numbers [excluding $N0$],
 519 although their effect diminishes as q [the exponent in a Hill number] is increased”. Their example
 520 (see Fig. 13.7 and Tables 13.1 and 13.2 in Gotelli and Ellison (2013)) shows that the effects of sample
 521 size quickly diminish with sample size and the effective numbers of taxa ($N1$, $N2$, $N3$) are stable with
 522 a sample size of 75–100 individuals.

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

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

531 *4.3 Diversity estimation*

532 It is widely known that there is a bewildering plethora of diversity measures (e.g. McIntosh,
533 1967; Peet, 1974, 1975; Pielou, 1975, 1977; Routledge, 1979; Washington, 1984; Ghent, 1991;
534 Magurran, 2004; Maurer and McGill, 2011; Legendre and Legendre, 2012) that try to combine
535 taxonomic richness and taxon abundances (‘evenness’) into a single index (see Section 2). As Ludwig
536 and Reynolds (1988) emphasise, the biggest obstacle in using many such diversity measures is
537 interpreting what this single summary statistic might mean biologically. A given value may, in one
538 case, result from various combinations of richness and ‘evenness’ and thus the same value of a
539 diversity index may result from an assemblage with low richness and high ‘evenness’ or from a
540 different assemblage with high richness and low ‘evenness’. In addition we have the uncertainty
541 about what ‘evenness’ actually comprises, as discussed above (see Section 4.2). The units of many
542 diversity measures differ greatly, making comparisons very difficult and making interpretation
543 virtually impossible (Ludwig and Reynolds, 1988).

544 The idea of a family of diversity measures was formalised in ecology by Hill (1973) although
545 MacArthur (1965) had first proposed Hill numbers as diversity measures. So-called Hill numbers or
546 numbers equivalents originated in economics (Adelman, 1969; Ellison, 2010) and physics (Jost, 2006).
547 They have recently undergone a major resurgence of interest amongst ecologists (e.g. Jost, 2006,
548 2007, 2010a, 2010b, 2014; Colwell, 2010; Tuomisto, 2010a, 2010b; Chao et al., 2012; 2014a, 2014b;
549 Gotelli and Ellison, 2013; Chiu and Chao, 2014; Skácelová and Lepš, 2014; Koch and Jurasinski, 2015)
550 and evolutionary biologists and phylogeneticists (e.g. Jost, 2008; Chao et al., 2010; Chiu and Chao,
551 2014; Chiu et al., 2014). Colwell (2010) describes Hill numbers as measures of “true diversity” which
552 treat taxon richness and the numbers equivalents of the Shannon and the Simpson diversity
553 measures (entropies *sensu* Jost, 2006) as points along a single mathematical continuum (Hill, 1973).
554 They are one of several diversity-index families (Tóthmérész, 1995) and one of the most useful for
555 ordering assemblages or communities of all sizes in terms of their diversity.

556 Hill’s (1973) diversity measures (Box 2) are in units of taxa and are called ‘effective number of
557 taxa’ of the assemblage according to the selected diversity measure. Most remarkably, irrespective

558 of which diversity measure one starts with (e.g. taxon richness, Shannon entropy, the exponential of
559 Shannon entropy, Simpson concentration, inverse Simpson, Gini-Simpson index, Renyi entropy, and
560 many others), a simple algorithm for the effective number of taxa always yields the same formula
561 (Jost, 2006, 2014). The algorithm calculates the diversity measure for D equally-common taxa (each
562 taxon therefore has a frequency of $1 / D$), sets the resulting expression equal to the actual value of
563 the diversity measure, and solves that equation for D . This value of D is the effective number of taxa
564 or “true diversity” (Boenigk et al., 2015). The effective number of taxa is a measure of the degree to
565 which proportional abundances are distributed among the taxa (Gotelli and Ellison, 2013) (see
566 Section 2). N_0 is the number of taxa in a sample regardless of their abundances, N_1 (the exponential
567 of the widely used Shannon diversity or entropy measure) estimates the number of abundant taxa in
568 an assemblage as it weights each taxon exactly by its relative abundance, and N_2 (the reciprocal of
569 Simpson’s diversity or concentration measure) estimates the number of very abundant taxa in an
570 assemblage (Box 2). It pays most attention to the most abundant taxa as it involves the sum of the
571 squares of the species abundances. Uncommon taxa hardly contribute to N_2 . In other words, the
572 effective number of taxa is a measure of the number of taxa in an assemblage when each taxon is
573 unweighted (N_0) or weighted by its abundance (N_1) or its squared abundance (N_2). As Gotelli and
574 Ellison (2013) conclude, “Hill numbers provide a useful family of diversity indices that consistently
575 incorporate relative abundances while at the same time express diversity in units of effective number
576 of species”. One important property of Hill’s (1973) effective number of taxa is the so-called
577 ‘doubling property’ that ensures the ratios of effective numbers of taxa behave as one would expect
578 intuitively. Thus if one assemblage is twice as diverse as another, the ratio of their effective number
579 of taxa is always 2, regardless of the index on which this ratio is based. This is very different from the
580 behaviour of the ratio of other diversity indices based not on effective numbers of taxa but on the
581 taxa (Jost, 2014). Jost (2006, 2014) recommends the term “effective number of species [taxa]” or
582 “numbers equivalents” because the term ‘diversity’ means so many different things to different
583 biologists. Jost (2014) “hopes that someday biologists can all agree that the word ‘diversity’ should
584 properly be applied only to quantities like qD [where the exponent q is a non-negative integer that
585 defines the particular Hill number and D is the diversity index] which have the mathematical
586 properties we intuitively expect of a diversity” (see Box 2).

587 Despite Hill numbers being introduced (Hill, 1973) as a unifying notation for diversity measures
588 in ecology and discussed in several different areas of ecology and palaeoecology (e.g. Peet, 1974;
589 Daget, 1980; van Dam and ter Braak, 1981; van Dam, 1982; ter Braak, 1983; Birks and Line, 1992),
590 they remained barely used until Jost (2006, 2007, 2010a) re-introduced Hill numbers in the context of
591 diversity, evenness, and partitioning diversity. In a Forum of ‘Partitioning Diversity’ all the

592 contributing authors agreed that using “numbers equivalents instead of the classical diversity indices
593 (or entropies) such as the H' [Shannon index] should be used in any diversity partitioning ... Even if
594 interest is only on describing the diversity of a single assemblage, the numbers equivalent, not the
595 entropy, should be the diversity measure of choice” (Ellison, 2010). Hill’s N_2 has been widely used as
596 a diversity measure in palaeolimnology, probably not because of its mathematical properties or
597 ecological elegance but because it was (until Canoco 5; ter Braak and Šmilauer, 2012) the only
598 diversity measure calculated in the widely-used CANOCO program (versions 2 to 4.5). The neglect of
599 Hill numbers by ecologists until Jost (2006) is surprising in light of Routledge’s (1979) early review on
600 “Diversity indices: which ones are admissible?” in which he concludes that “ N_2 is the best, single
601 measure of diversity, and that the only other index worth considering is N_1 ”.

602 Gotelli and Ellison (2013) discuss two caveats in the use of Hill numbers. First, no diversity
603 measure can completely separate taxon richness from taxon evenness (Jost, 2010a) (see Section 4.2).
604 Second, Hill numbers can be influenced by sampling effects, for example N_0 is influenced by the
605 number of individuals in the count but this can be standardised by rarefaction analysis solved
606 analytically (e.g. Heck et al., 1975) or by repeated random subsampling without replacement (Gotelli
607 and Ellison, 2013) (see Sections 4.1 and 4.2). Sample sizes can also influence values of N_1 and N_2 but
608 their impacts decrease as the exponent q in the general formula for calculating a Hill number
609 increases (Soetaert and Heip, 1990). As q increases, the diversity measure places ever increasing
610 weight on the most abundant taxa in the assemblage. With $q = 5$, the Hill number rapidly converges
611 to the inverse of the relative abundance of the most common taxon.

612 One potential solution to the possible effects of sample size on N_1 and N_2 is to estimate not
613 only N_0 but also N_1 and N_2 from a rarefied sample (or many randomised subsamples without
614 replacement) of the original assemblage (Soetaert and Heip, 1990; Rühland et al., 2014; Felde et al.,
615 2015) (see Sections 4.1 and 4.2) and to do this for all the assemblages of interest, using the same
616 appropriate base-sum, thereby providing estimates of N_0 , N_1 , and N_2 , and their associated variances
617 for each assemblage independent of count size (see also Kindt et al., 2006; Chao et al., 2014a, 2014b;
618 Colwell and Elsensohn, 2014).

619 Pollen analysts have rarely used diversity measures and have concentrated on estimates of
620 palynological richness (Birks and Line, 1992). Diversity measures that have been used include
621 Shannon’s entropy (e.g. Moore, 1973; Küttel, 1984) and Simpson’s index (e.g. Cwynar, 1982; Morley,
622 1982; Ritchie, 1982). These measures can be easily converted into Hill (1973) numbers for ease of
623 comparison and interpretation. Hurlbert’s (1971) PIE (see Section 4.2) has also been used but as a
624 measure of ‘evenness’ rather than of diversity (e.g. Peros and Gajewski, 2008; van der Knaap, 2009;

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

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

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

649 *4.4 Statistical modelling techniques*

650 Quantifying and evaluating the numerical relationship between pollen richness and plant
651 richness (both $N0$) and between pollen diversity ($N1$, $N2$), plant diversity ($N1$, $N2$), pollen evenness
652 ($N2 / N1$, $N2 - 1 / N1 - 1$, etc.), and plant evenness ($N2 / N1$, $N2 - 1 / N1 - 1$, $N1 - N2$, etc.) when the
653 floristic data have been translated into pollen equivalents involves statistical regression models
654 within the general framework of generalised linear models (GLMs) with a Poisson (e.g. Goring et al.,
655 2013) or normal error function. The same regression approach can be used for evaluating
656 relationships between pollen richness and landscape structure (Meltsov et al., 2013). For an

657 introduction to statistical modelling using GLM and model selection, see Birks (2012b). More detailed
658 accounts of GLM modelling include Crawley (1993, 2005, 2007), Faraway (2005, 2006), and Fox and
659 Weisberg (2011). As in all statistical modelling, the simplest statistically significant model should be
660 the one favoured (Birks, 2012b). There are various criteria for jointly assessing model simplicity and
661 statistical significance such as the Akaike Information Criterion and the related Bayes (Schwarz)
662 Information Criterion where model fit, complexity, and sample size are all considered (see Burnham
663 and Anderson, 2002; Anderson, 2008; Hastie et al., 2009; Murtaugh, 2009; Gotelli and Ellison, 2013
664 for details).

665 **5. Problems in assessing modern pollen–plant relationships**

666 *5.1 Introduction*

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

685 *5.2 Biases in pollen-assembly records of richness*

686 Odgaard (1999, 2001, 2007, 2008, 2013) has emphasised that there are three major biases in
687 interpreting changes in pollen richness from fossil assemblages as reflections of past floristic

688 richness. These biases also relate to assessing modern pollen–plant richness relationships. The biases
689 are taxonomic precision, sample size, and pollen representation (Odgaard, 1999, 2001, 2007, 2013).

690 5.2.1 Taxonomic precision

691 Pollen and pteridophyte spores can often only be identified to a group of species (e.g.
692 *Ranunculus acris*-type), to genus level (e.g. *Quercus*), or even only to family level (e.g. Poaceae). This
693 restricted taxonomic precision results inevitably in a non-linear relationship between plant richness
694 and pollen richness (Odgaard, 1994, 2007, 2013). The number of pollen and spore taxa in an
695 assemblage—modern or fossil—is clearly not a *direct* reflection of plant richness in the vegetation
696 that produced the pollen assemblage (see Table 2). With a very low number of plant species in the
697 vegetation (e.g. middle boreal forest, heathland, arctic tundra) the ratio between plant and pollen
698 richness may be close to 1:1 or 1.5:1. In vegetation with more taxa (e.g. temperate deciduous forests,
699 grasslands) the ratio may be 2:1 or 3:1, or even higher (Odgaard, 2013). Odgaard (1994) shows that
700 the modern relationship between plant and pollen richness is almost identical in three different
701 vegetation types in western Denmark. He used this modern relationship to transform pollen richness
702 (NO based on rarefaction) into estimates of past floristic richness (Odgaard, 2013). It is not known
703 whether the relationships between plant and pollen richness that Odgaard (1994) established hold
704 for other vegetation types elsewhere. Preliminary studies in Norway (Felde, 2015) and Scotland
705 (Birks, unpublished data) suggest broadly similar and robust relationships between plant richness and
706 pollen richness. In this case pollen types can be thought of taxa ‘higher’ (broader) than plant species.

707 In a very different context, namely conservation biogeography and contemporary biodiversity
708 assessment, Mazaris et al. (2010) have shown that one can predict the number of plant species
709 surprisingly well from the richness of a few common genera, families, or orders. Many biodiversity
710 assessments today are based on genus or ‘higher’ taxa (e.g. Williams and Gaston, 1994; Andersen,
711 1995; Pearman and Weber, 2007). These and other studies illustrate the robust nature of species–
712 ‘higher’ taxon relationships.

713 An alternative approach to the problem of bias due to taxonomic precision is to construct
714 pollen–plant translation tables where plant species in the flora of interest (e.g. Norway) are grouped
715 into the relevant pollen or spore morphological taxa, given our present knowledge of the pollen and
716 spore morphology of the flora in the area of interest (Bennett, 1995-2007; Felde et al., 2012, 2014a,
717 2015; Felde, 2015). There is clearly a loss of information in such translations as families such as
718 Poaceae or Cyperaceae that contain many plant species produce only a small number (ca. 6) of
719 distinctive pollen morphological types. This bias due to taxonomic imprecision will only be reduced
720 by improved pollen morphology and microscopy (e.g. Andersen, 1979; Odgaard, 1994; Beug, 2004;

721 Lacourse and May, 2012) and by alternative approaches to pollen identification and/or counting (e.g.
 722 Birks and Peglar, 1980; Lindbladh et al., 2002; Heintzmann and Ficz, 2006; Huang et al., 2009;
 723 MacLeod et al., 2010; Barton et al., 2011; Holt et al., 2011; May and Lacourse, 2012; Punyasena et al.,
 724 2012; Sivaguru et al., 2012; Johnsrud et al., 2013; Mander et al., 2013, 2014; Holt and Bennett, 2014;
 725 Jan et al., 2015).

726 *5.2.2 Pollen-sample and underlying pollen-population magnitudes*

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

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

$$744 \log_e (N1) / \log_e (N0)$$

745 It is possible that pollen richness and evenness are inherently correlated in the Räsänen et al. (2004)
 746 study because the evenness measure used is not independent of observed richness and hence count
 747 size as $N0$ forms the denominator. As discussed above (Section 4.3), it is important to use evenness
 748 measures that are independent of the number of taxa (and hence count size). $N0$ should be
 749 standardised for all the assemblages being considered and $N1$, $N2$, and derived evenness measures
 750 based on Hill numbers (see above) should be based on a rarefied sample (e.g. Rühland et al., 2014) or
 751 an ensemble of randomly drawn rarefied samples for fair comparisons of richness, diversity, and
 752 evenness, and their associated variances (Chao et al., 2014; Felde et al., 2015).

753 An important assumption of rarefaction analysis (Birks and Line, 1992; Gotelli and Colwell,
754 2011; Gotelli and Ellison, 2013) is that the size of the underlying pollen population (all the pollen
755 produced in the APSA) from which the pollen assemblage or sample is derived from is constant in
756 space or time. This is probably rarely the case (Odgaard, 2007, 2013), for example between treeless
757 late-glacial, tree-dominated mid-Holocene, and herb- and heath-dominated late-Holocene pollen
758 assemblages. If the underlying pollen population size varies whilst the sample size is kept constant
759 (by rarefaction), the sampled fraction of the vast (and unknown) underlying pollen population varies
760 and pollen richness may change as a result of this effect (Odgaard, 2007, 2013). Odgaard (1999) and
761 van der Knaap (2009) (see also Connor et al., 2012; Ammann et al., 2013; Colombaroli and Tinner,
762 2013; Colombaroli et al., 2013) present some solutions to reduce the dependence of pollen richness
763 on the sample-to-population ratio by using 'quasi-absolute' (Odgaard, 1999) or 'absolute' (van der
764 Knaap, 2009) pollen-accumulation rates (flux density) to estimate the pollen richness that would
765 have been recorded if the same fraction of the underlying pollen population (pollen production from
766 the APSA) had been sampled. This problem of the changing size of the underlying pollen population is
767 most acute in situations where vegetation and its resulting pollen population has changed markedly
768 over time (e.g. in the late-glacial (van der Knaap, 2009; Ammann et al., 2013)) but it can also occur in
769 modern assemblages from different vegetation types (e.g. tundra, boreal forest) which have very
770 different modern pollen productivities (Ritchie and Lichti-Federovich, 1967; Birks, 1973a).

771 5.2.3 Pollen-representation bias

772 Giesecke et al. (2014) argue that pollen richness estimated from rarefaction analysis is a simple
773 measure with many advantages. As discussed above, it is influenced by the detection probability of
774 rare pollen types. Pollen types from plant taxa with a high pollen production and wide dispersal
775 commonly dominate a pollen assemblage, thereby reducing the probability of detecting pollen types
776 with a poorer representation and/or a low abundance in the RPSA or APSA (Odgaard, 1999, 2007,
777 2013; Weng et al., 2006). Pollen counts can, however, be transformed using general purpose pollen-
778 representation values (e.g. Andersen, 1970, 1978) or more detailed pollen-productivity estimates
779 (e.g. Broström et al., 2008; Gaillard et al., 2008; Poska et al., 2011; Hjelle and Sugita, 2012; Mazier et
780 al., 2012; Hjelle et al., 2015; Mehl et al., 2015) in conjunction with the REVEALS model (Sugita, 2007)
781 to reduce the inherent representation bias in pollen assemblages. The transformed counts can then
782 be used in rarefaction to estimate N_0 and subsequently N_1 , N_2 , and related evenness measures
783 (Felde et al., 2015; Matthias et al., 2015). It is important to note, however, that recent work on
784 deriving PPEs in different geographical areas or ecological landscapes (e.g. Abraham and Kozakova,
785 2012; Abraham et al., 2014; Baker et al., 2015; Niemeyer et al., 2015), at different historical times
786 (e.g. Theuerkauf et al., 2015), or based on different pollen dispersal models (e.g. Theuerkauf et al.

787 2012; Sjögren et al., 2015) is highlighting important differences in such estimates and the problems in
788 deriving robust PPEs. Moreover, reducing pollen-representation bias will only really be achievable for
789 the most abundant pollen taxa as obtaining reliable and robust representation values and PPEs is
790 very difficult and extremely time consuming. Such values for the rare pollen taxa would have a high
791 uncertainty and variance (Parsons and Prentice, 1981).

792 Alternative approaches to minimising pollen-representation bias and thus estimating taxon
793 abundances over space and time involve Bayesian hierarchical modelling (Paciorek and McLachlan,
794 2009). These approaches have considerable promise because of their explicit spatio-temporal
795 representation, quantification at the scale of trees and vegetation rather than pollen, and
796 characterisation of the many uncertainties in estimating past plant abundances (Paciorek and
797 McLachlan, 2009).

798 *5.3 Richness, evenness, and diversity concepts*

799 An inherent problem in any assessment of pollen–plant richness, evenness, or diversity
800 relationships is that the three concepts are very closely linked (Jost, 2010a), with diversity consisting
801 of components of richness and of evenness. If based on Hill numbers and estimated from rarefied
802 samples to minimise bias due to count size (Felde et al., 2015), richness, evenness, and diversity are
803 numerical summary statistics (*sensu* Birks HJB, 2013) of pollen assemblages, or “assemblage
804 composition parameters” (Hurlbert, 1971). Following Hill (1973), plots of N_0 richness, N_1 and N_2
805 diversity, and N_1 / N_0 , N_2 / N_1 , and $N_2 - 1 / N_1 - 1$ evenness (all with their associated variances) for
806 pollen assemblages in space or time can provide useful summaries of certain aspects of complex
807 multivariate pollen-assemblage data (e.g. Felde, 2015; Felde et al., 2015). They are “mere numbers
808 and should be distinguished from the theories which they support” (Hill, 1973).

809 **6. Other approaches to studying pollen-assemblage richness patterns**

810 Giesecke et al. (2012, 2014) experimented with the sample-based slope of the rank-order
811 abundance as well as between-sample taxon abundance using fossil data from sites in different parts
812 of Europe as a means of assessing equitability in pollen assemblages. Although Giesecke et al. (2012,
813 2014) used these curves to detect patterns of pollen richness and equitability through time, the same
814 approach can be applied to modern pollen data to assess palynological equitability visually and not
815 based on Hill numbers or other diversity or equitability measures. When plotting log-transformed
816 pollen percentages (proportions) of a sample against rank-order, the slope of the plot is an intuitive
817 and graphical measure of palynological equitability (Nee et al., 1992). This slope is influenced by
818 variations in the pollen count-size through changes in the probability of finding rare pollen taxa with

819 different count sizes (Rull, 1987; Weng et al., 2006). Giesecke et al. (2012, 2014) minimised this
820 count-size dependency by setting thresholds for taxon inclusion (>1% (Giesecke et al., 2014) or >0.3%
821 (Giesecke et al., 2012)) in a particular pollen assemblage. However, the value of the threshold
822 determines the aspect of the abundance distribution of pollen types in the sample being
823 investigated. When using a low threshold, the relationship in a pollen sample is driven by the number
824 of taxa or richness, whereas a higher threshold evaluates the equitability of the abundant taxa which
825 is close to what many diversity measures estimate.

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

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

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

852 they should be used more widely to summarise compositional properties of pollen-assemblage data
853 in time and space.

854 **7. Future challenges and research opportunities**

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

861 *7.1 Interpretation of past pollen-assemblage richness*

862 Recent studies have shown that modern pollen-assemblage richness does reflect, in part,
863 contemporary floristic richness at both the local site and regional landscape scales. Odgaard (2007,
864 2013) comments in discussing fossil pollen assemblages and past pollen richness that “rarefaction
865 estimates are often inappropriately interpreted as an index of past species richness” and he
866 concludes that “rarefaction estimates of pollen species are ... a complex reflection of many processes
867 such as pollen production, evenness, pollen dispersal, landscape pollen productivity, and possible
868 floristic richness. Although more work is needed to resolve these complexities, pollen productivity
869 seems a much more important control of palynological richness than does floristic richness”. In the
870 same vein, Goring et al. (2013) question whether temporal changes in pollen richness reflect
871 underlying changes in plant richness or some other change in plant composition or structure.

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

880 We now know that with high-quality pollen data and appropriate vegetation data and by
881 reducing the taxonomic and, if possible, the pollen representation (\equiv evenness) biases inherent in
882 pollen assemblages (Odgaard 1999, 2001, 2007, 2013), there are statistically significant relationships

883 between pollen and plant richness (e.g. Felde et al., 2015). Meltsov et al. (2013) studied pollen and
884 plant richness around nine lakes in southern Estonia along a land-cover gradient from semi-open to
885 closed forest. They estimated landscape structure within eight radii (250–2000 m) around each lake
886 on the basis of landscape openness and three summary statistics of landscape richness, evenness,
887 and diversity. They show that pollen richness has a statistically significant positive relationship with
888 landscape structure within radii greater than 1000 m. They conclude that within one floristic or
889 climatic region “pollen richness gives reliable estimates about the variation in floristic richness and
890 landscape structure; however, caution must be taken when comparing pollen-inferred vegetation
891 diversities from different regions or when interpreting fossil pollen records from times with highly
892 different vegetation associations”. This Estonian study is, as far as we know, the first study where
893 modern pollen richness is considered specifically in relation to landscape structure. A second study in
894 Germany by Matthias et al. (2015) confirms some of the trends in the Estonian study and shows that
895 palynological richness to a rarefaction base-sum of 10 as an index of pollen diversity (highly
896 correlated to $N1$ and $N2$) strongly reflects landscape diversity. The results of Meltsov et al. (2013),
897 Felde et al. (2015), and Matthias et al. (2015) raise several questions: is the observed relationship
898 between modern pollen richness and floristic richness at the regional scale (Felde et al., 2015) a
899 reflection of a direct pollen–vegetation richness link; or alternatively, is it a result of a landscape
900 mosaic-vegetation richness link *and* a vegetation-pollen richness link? A third hypothesis is that it is a
901 result of complex and poorly understood interactions between landscape and vegetation dynamics,
902 structure, and diversity, and hence pollen richness. Ecologists are increasingly recognising the
903 importance of landscape structure and heterogeneity (‘geodiversity’) in influencing floristic and
904 vegetation richness over a range of spatial scales (e.g. Burnett et al., 1998; Nichols et al., 1998;
905 Carranza et al., 2007; Rocchini et al., 2010; Gray, 2013; Stein et al., 2014; Hjort et al., 2012, 2015).

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

910 *7.2 Estimating taxon richness from plant macrofossil assemblages*

911 There is renewed interest in Quaternary plant macrofossils and an increase in the quantity and
912 quality of studies based on plant macrofossils (e.g. Birks HH, 2001, 2013; Birks HJB and Birks HH,
913 2008; Jackson, 2012; Birks HH and Birks HJB, 2013; Birks HJB, 2014; Jackson et al., 2014). Quaternary
914 macrofossil assemblages have, however, rarely been used to estimate taxon richness (Blarquez et al.,
915 2010, 2013; Leys et al., 2014) in contrast to Deep-time palaeobiological studies involving animal or

916 plant macrofossils (e.g. Foote and Miller, 2007; McElwain and Punyasena, 2007; McElwain et al.,
917 2007, 2009; Mander et al., 2010; Patzkowsky and Holland, 2012) or Quaternary palaeozoological
918 studies (e.g. Lyman, 2008; Hadly and Barnosky, 2009; Blois et al., 2010; Macken and Reed, 2014). It is
919 clearly not a simple task to estimate an ecologically useful richness measure from plant macrofossil
920 data as there are even more potential sources of bias to be considered and accounted for, including
921 taxonomic problems, the mixed nature of macrofossil data, count-size, productivity, dispersability,
922 deposition, and preservation (Jackson, 2012; Birks, 2014) than with pollen data. This is an area where
923 more work is clearly needed (e.g. Blarquez et al., 2013).

924 7.3 Pollen richness at different ecological or spatial scales

925 Whittaker (1977) proposes that plant richness or diversity can be studied as inventory diversity
926 at the community (alpha diversity), landscape (gamma diversity), and regional (epsilon diversity)
927 scales (see also Whittaker et al., 2001; Willis and Whittaker, 2002; Jurasinski et al., 2009; Tuomisto,
928 2010a, 2010b; Anderson et al., 2011) along with changes or turnover (differentiation diversity)
929 between communities (beta diversity) and between landscapes (delta diversity) (Odgaard 2007,
930 2013) (see Table 3). Contemporary ecologists (e.g. Ellison, 2010) and Deep-time palaeobiologists (e.g.
931 Sepkoski, 1988) have simplified Whittaker's (1977) five components to three (Whittaker, 1972) –
932 alpha, beta, and gamma. Alpha is local richness or diversity and is estimated or measured within a
933 defined place such as a vegetation quadrat, a forest plot, or a single stream. Gamma is regional
934 richness or diversity and it is the total diversity estimated or measured for a group of localities in an
935 area, such as all quadrats in a study, all forest stands, or all streams in a catchment. Beta diversity
936 links alpha and gamma, or local and regional, richnesses and diversities and is “the extent of
937 differentiation of communities along habitat gradients” (Whittaker, 1972; Ellison, 2010; Beck et al.,
938 2013). Alpha and gamma richness or diversity can be estimated or measured directly either as
939 numbers of species (richness) or as numbers of species weighted by their relative abundances in the
940 sample (diversity). Beta diversity, in contrast, is a quantity derived from alpha and gamma richnesses
941 or diversities (Ellison 2010). Odgaard (2007, 2013) suggests that pollen data may reflect the alpha,
942 gamma, and epsilon scales (*sensu* Whittaker, 1977) or the alpha and gamma scales (*sensu* Whittaker,
943 1972) depending on site size, location, and other features whereas plant macrofossil data are more
944 local and primarily reflect the alpha scale.

945 The estimation of beta diversity is discussed in Section 7.4 but here we outline possible future
946 challenges in reconstructing and assessing past richness patterns at the gamma (landscape) and
947 alpha (local) scales. Odgaard (2007, 2013) summarises the very detailed study of 13 pollen sequences
948 from a 15 ha bog in south Wales by Smith and Cloutman (1988) in terms of the changing richness of

949 inferred vegetation types (based on pollen assemblages) through the Holocene and the progressive
950 homogenisation and impoverishment of landscape diversity as blanket bog expanded in the
951 landscape in the last 3000 years. This reconstruction is at the landscape (gamma diversity) scale. It is
952 possible to shift to the local site scale (alpha diversity) and to study richness changes through time
953 within the landscape scale, along the lines of the unique study of 11 very small upland pollen sites in
954 Scotland by Hanley et al. (2008). The local changes in pollen richness were then related statistically to
955 changes in land management, livestock grazing pressures driven by economic change, and land
956 abandonment. By careful study design, rigorous site selection, and detailed pollen analyses, it would
957 be possible to detect changes in richness in time and, to some extent, in space (Birks, 2012c) and
958 hence to improve the application of palaeoecology in conservation and land management (Davies et
959 al., 2014).

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

972 *7.4 Diversity partitioning and estimating beta diversity*

973 The basic idea of diversity partitioning or decomposition is that the total estimated diversity of
974 a study area can be partitioned into the diversity inherent in its constituent parts (inventory diversity)
975 plus the diversity due to the differences between these constituent parts (differentiation diversity)
976 (Olszewski, 2010). Diversity partitioning is increasingly being used in ecology (e.g. Legendre et al.,
977 2005, 2009; Głowacki et al., 2011), biogeography (e.g. Qian et al., 2005), conservation biology (e.g.
978 Jost et al., 2010), and Deep-time palaeoecology (e.g. Patzkowsky and Holland, 2007; Mander et al.,
979 2010), as a tool for directly addressing how the structure of higher-level systems reflect interactions
980 between lower-level units in response to environmental and evolutionary changes.

981 As outlined above (Section 7.3) ecologists tend to work with three components of diversity
982 (Table 3) – alpha (an inventory diversity), beta (a differentiation diversity), and gamma (an inventory
983 diversity). Whilst alpha and gamma diversities can be measured (or at least estimated) as a result of
984 surveys or inventories (Jurasinski et al., 2009), beta diversity is a derived quantity and there is no
985 consensus about how to derive this quantity from alpha and gamma diversities and how to interpret
986 beta diversity (Ellison, 2010). Whittaker (1960) proposes that gamma diversity is the product of alpha
987 and beta diversity (multiplicative model) and thus beta diversity can be estimated by dividing gamma
988 by alpha. Lande (1996) (see also Veech et al., 2002) suggests that an additive model of diversity
989 (alpha + beta = gamma) provides a more natural means of estimating beta diversity as an additive
990 concept (Ellison, 2010; Legendre, 2014). Jost (2007) and Jost et al. (2010) propose that by using Hill
991 numbers, Whittaker’s multiplicative concept (alpha × beta = gamma) is true for all indices. In this
992 case, Jost’s (2007) “true beta diversity” is the effective number of distinct communities or
993 assemblage types (see Felde et al., 2015 for examples). Jost (2007) also shows that Shannon’s
994 entropy is the only standard diversity measure that can be decomposed into meaningful alpha, beta,
995 and gamma components when assemblage weights are unequal. Jost’s (2007) proposals have
996 naturally led to considerable discussion, resulting in a Forum in *Ecology* (Ellison, 2010) with
997 contributions by Baselga (2010), Jost (2010b), Ricotta (2010), Veech and Crist (2010a, 2010b), and
998 Wilsey (2010). Little consensus emerged about how to partition diversity, as all the approaches
999 discussed make demands on the underlying sampling and make simplifying assumptions about the
1000 real world (Ellison, 2010). Ellison (2010) concludes “a real breakthrough would require a method to
1001 measure beta diversity independently of either alpha or gamma diversities” and “there is much yet
1002 to be done to identify and characterise patterns of biological diversity”. Tuomisto (2010a, 2010b,
1003 2010c, 2011) proposes that “true beta diversity” is obtained when the effective number of species in
1004 a data set (“true gamma diversity”) is multiplicatively partitioned into the effective number of species
1005 per compositionally distinct virtual sampling unit (“true alpha diversity” α_d) and the effective number
1006 of such compositional units ($\beta_{md} = \gamma / \alpha_d$) (Tuomisto, 2010a, 2010c, 2011). Partitioning “true gamma
1007 diversity” multiplicatively rather than additively into alpha and beta components permits a unified
1008 treatment not only of alpha and gamma diversities but also beta diversity as “a count of an effective
1009 number of types of entities (Routledge 1977, 1979, Jost 2006, 2007)” (Colwell, 2010). Diversity
1010 partitioning and beta diversity remain remarkably contentious issues in ecology (e.g. Pélissier and
1011 Couteron, 2007; de Bello et al., 2010; Marcon et al., 2012; Baselga and Leprier, 2015) despite the
1012 recent advances by Jost (2007, 2010b), the comprehensive reviews by Tuomisto (2010a, 2010b) and
1013 Jurasinski et al. (2009), and the subsequent commentaries by Jurasinski and Koch (2011), Tuomisto
1014 (2011), and Moreno and Rodríguez (2010, 2011).

1015 An important attempt to try to resolve the debates about diversity partitioning (Chao et al.,
1016 2012) clarifies the terms “independence” and “statistical independence”. Multiplicative beta diversity
1017 depends on the number of assemblages whereas additive beta diversity depends on alpha
1018 (equivalently of gamma) diversity. They propose transformations to remove these dependencies and
1019 demonstrate that the transformed multiplicative beta and additive beta diversities both lead to the
1020 same classes of measures which are always in the range of 0–1. They can thus be used to compare
1021 relative similarity or differentiation among assemblages or community types across one or more
1022 regions (Chao et al., 2012).

1023 Rarefaction analysis is another potentially useful approach to estimating beta diversity (e.g.
1024 Olszewski, 2004, 2010; Crist and Veech, 2006). Olszewski (2010) suggests that the divergence
1025 between sample-based (groups of samples or stratigraphic sequences – Gotelli and Colwell, 2001,
1026 2011; Scarponi and Kowalewski, 2007; Chiarucci et al., 2008; Gotelli and Ellison, 2013) and individual-
1027 based (single assemblage or sequence) rarefaction curves of a composite collection (gamma
1028 diversity) incorporating all the samples (alpha diversity) contributing to a specific hierarchical level
1029 reflects the degree of non-random compositional difference within the smaller scale units (beta
1030 diversity) (Scarponi and Kowalewski, 2007). When considering diversity *sensu stricto* based on taxon
1031 relative abundances, Olszewski (2010) proposes that Shannon’s entropy (Jost, 2006) can be
1032 partitioned additively with beta entropy equalling gamma entropy (based on a composite sample)
1033 minus entropy equalling alpha diversity of the constituent samples. As entropy (Jost, 2006) can be
1034 readily converted to effective richness of number of species (the number of taxa that would result in
1035 the same entropy value if they were all equally abundant) (Jost, 2006, 2007), effective richness is
1036 derived from Shannon’s entropy partitions multiplicatively and beta diversity is the number of
1037 compositionally distinct smaller units that contribute to the total gamma diversity at the higher level
1038 (see also Jost, 2007; Jost et al., 2010; Tuomisto, 2010a; Chao et al., 2012; Felde et al, 2015).

1039 A recent study by Blarquez et al. (2014) applied diversity partitioning to Quaternary
1040 palynological data. They selected 205 pollen sequences from 12 ecoregions, each with similar
1041 environment, species composition, and ecological processes today, within the North American boreal
1042 forest–taiga regions. They used Shannon’s entropies and following Jost (2007, 2010) they partitioned
1043 diversity into independent alpha, beta, and gamma components. They used the alpha Shannon
1044 entropy and for each ecoregion calculated the mean entropy per site for 1000 year time-windows.
1045 The Shannon entropy was converted to its numbers equivalent to derive “true alpha diversity” (Jost,
1046 2007). Shannon’s entropy was used because it is the only measure that satisfies Lande’s (1996)
1047 condition that alpha diversity is less than or equal to gamma diversity when assemblage weights are
1048 unequal. Gamma diversity was estimated by pooling the alpha entropies at all sites and for each

1049 time-window and converting this to its numbers equivalent. In the framework of numbers
1050 equivalents, beta diversity could then be estimated by Whittaker's (1972) multiplicative rule and
1051 calculated as the gamma component divided by the alpha component (Blarquez et al., 2014). They
1052 further investigated beta diversity by decomposing it into two components – nestedness and
1053 turnover (Baselga, 2010; Baselga and Orme, 2012; Legendre, 2014). Nestedness (= richness
1054 difference: Legendre, 2014) represents non-random loss of taxa, namely within a given region sites
1055 with fewer taxa are the subset of sites with more taxa. Turnover (= replacement: Legendre, 2014)
1056 represents the replacement of taxa as result of temporal or spatial sorting (Blarquez et al., 2014).

1057 Pollen diversity of the North American boreal forest–taiga regions underwent substantial
1058 changes in response to major climatic shifts in the late-glacial and early Holocene. The nestedness
1059 component within beta diversity probably reflected plant migration as it generally peaked before the
1060 turnover component. Turnover may result from various factors including spatial and temporal sorting
1061 of assemblages in response to changing environmental conditions and habitat conditions (Blarquez et
1062 al., 2014). Pollen diversity was generally maximal in the late-glacial and early Holocene and
1063 progressively decreased during the Holocene (cf. Birks and Line, 1992).

1064 Diversity partitioning has been more widely used in Deep-time palaeoecology (e.g. Layou,
1065 2007; Patzkowsky and Holland, 2007; Heim, 2009; Holland, 2010; Mander et al., 2010; Olszewski,
1066 2010; Vavrek and Larsson, 2010; Hautmann, 2014). Partitioning of diversity using richness is difficult
1067 due to the sensitivity of richness to sample size (e.g. Scarponi and Kowalewski, 2007).

1068 Just as variation partitioning in canonical ordination and multiple regression (Borcard et al.,
1069 1992; Legendre, 2008; Legendre and Legendre, 2012) has become a standard data-analytical tool in
1070 ecology and palaeoecology (e.g. Legendre and Birks, 2012; Simpson and Hall, 2012), hierarchical
1071 diversity partitioning has the potential to infer ecological processes from palaeoecological data when
1072 the data are collected using a sampling strategy that balances sample size and distribution among
1073 possible categories. The study on the effects of the Richmondian invasion on the structure of
1074 invertebrate fossil assemblages in the Cincinnati Arch during the late Ordovician by Patzkowsky and
1075 Holland (2007) (see also Olszewski, 2010) is an elegant example of how diversity partitioning at
1076 multiple hierarchical levels in Deep-time palaeoecology can be used creatively to address current
1077 issues in ecology. It also illustrates how palaeoecology can contribute to understanding ecological
1078 processes acting over long time intervals, namely broad-scale invasions by taxa. It exemplifies Flessa
1079 and Jackson's (2005) review of exploiting "the geological record of ecological dynamics" to
1080 understand the biotic effects of future environmental change. Patzkowsky and Holland (2007)
1081 partitioned data from different depositional sequences into three levels of inventory diversity (*sensu*

1082 Magurran, 2004; Jurasinski et al., 2009 – see Table 3)—(1) collection diversity estimated as the
1083 average Shannon entropy of all collections in each sequence (α_c), (2) habitat diversity (α_h) estimated
1084 as the average Shannon entropy of habitats (shallow and deep) within each sequence ($\alpha_h = \alpha_e + \beta_w$),
1085 and (3) stratigraphic sequences (i.e. landscape) diversity (α_s) estimated as the total Shannon entropy
1086 of each sequence ($\alpha_s = \alpha_c + \beta_w + \beta_b$) separated by two levels of differentiation diversity (Table 3)—one
1087 for between-collections–within-habitats (β_w) and one for between-habitats–within-sequences (β_b).
1088 By the end of the Richmondian invasion, richness had increased by almost 40%, mainly as a result of
1089 increases within habitats (α_h) with a smaller contribution from among-collections–within-habitats
1090 (β_w) (Olszewski, 2010). The main ecological interpretation is that assemblages in local patches (i.e.
1091 sampled by individual collections) accommodated new species without substantially changing their
1092 diversity but that they became more distinct from one another within habitats (Olszewski, 2010).
1093 Legendre (2014) discusses further approaches to partitioning beta diversity into replacement
1094 (turnover) and richness-difference (nestedness) components.

1095 Related to beta diversity (*sensu* Whittaker, 1972) is assemblage compositional turnover along
1096 gradients in space or time (Jurasinski et al., 2009; Tuomisto, 2010a, 2010b). Tuomisto (2010c)
1097 emphasises that as turnover does not quantify the effective number of taxa, it is not a true diversity
1098 and should be specifically called what it is quantifying, in this case compositional turnover.
1099 Detrended canonical correspondence analysis (ter Braak, 1986; Birks, 2007) with the ordination
1100 constrained by sample age or depth as the sole predictor variable provides a comparative summary
1101 of compositional turnover within and between stratigraphical sequences (e.g. Smol et al., 2005; Birks
1102 and Birks, 2008; Feurdean et al., 2012; Colombaroli and Tinner, 2013, Colombaroli et al., 2013; Leys
1103 et al., 2014). Other multivariate ordination approaches are also useful in displaying and quantifying
1104 aspects of alpha and beta diversity, and assemblage composition and differentiation (e.g. ter Braak,
1105 1983; Legendre et al., 2005; Anderson et al., 2006, 2011; Heegaard et al., 2006; Legendre, 2008;
1106 Legendre and Legendre, 2012; Legendre and De Cáceres, 2013; Nieto-Lugilde et al., 2015). The use of
1107 compositional (dis)similarity or distance measures to assess differences in taxon composition as a
1108 means of estimating beta diversity is reviewed by Jost et al. (2011). Jurasinski et al. (2009) discuss
1109 other facets of beta diversity and approaches to estimating it, including variation in taxon richness,
1110 sum-of-squares or dispersion of a taxon matrix, the slope of distance-decay relationships or ‘halving
1111 distances’, and the slope of taxon-area curves.

1112 *7.5 Pollen pools, dark richness, and hidden richness*

1113 Ecologists and biogeographers have long used the concept of the species pool in considering
1114 contemporary and historical determinants of diversity at a range of spatial scales (e.g. Pärtel et al.,

1115 1996; Zobel, 1992, 1997; Zobel et al., 2011; Carstensen et al., 2013; Lososová et al., 2015; Zobel,
1116 2015). Pärtel et al. (1996) distinguished two types of species pool – the regional or potential pool
1117 consisting of those species that occur in a specified geographical area and that can be expected on
1118 the basis of their ecological requirements to occur in a particular vegetation type; and the actual or
1119 realised species pool defined as the species that actually are present in the vegetation type of
1120 interest.

1121 Quaternary pollen analysts implicitly or explicitly use the concept of a potential species pool,
1122 namely those plants that may contribute pollen to a particular site. A pollen pool can be defined as
1123 consisting of plant taxa that produce morphologically distinctive pollen or spores in a specified
1124 geographical area, such as a lake catchment, a vegetation-landform unit (Felde et al., 2014b), an
1125 entire country (e.g. Birks, 1973b; Bennett, 1995-2007; Felde et al., 2012), or an entire continent
1126 (Whitmore et al., 2005). This potential pollen pool is important not only in limiting the underlying
1127 flora to be considered in pollen identifications (e.g. Birks, 1973b, Hansen and Cushing, 1973; Lacourse
1128 and May, 2012) but also in the creation of plant–pollen translation tables and delimitation of pollen
1129 equivalents that are essential in assessing pollen–plant richness relationships. Although there is a
1130 finite probability of finding a pollen grain of any taxon in the world (Cushing, 1963), about 40–70% of
1131 the potential pollen pool for an area the size of Norway can be found in regional-scale pollen
1132 assemblages (Table 2). Up to 85% of the pool may be found in local-scale pollen assemblages (Table
1133 2). The 15–60% of the pollen pool that is rarely, if ever, found consists mainly of low-growing
1134 entomophilous plants with very low pollen production, very poor pollen dispersal, and/or very poor
1135 pollen preservation (e.g. *Geranium*, *Oxalis*, *Viola*, *Linum*, *Calystegia*, *Primula*, *Malva*, *Euphorbia*,
1136 *Orchidaceae*, *Juncus*, *Luzula*). Just as there is so-called dark diversity in ecology (Pärtel et al., 2011;
1137 Pärtel, 2014; Riiback et al., 2015) and biogeography (Ronk et al., 2015), namely species in the
1138 potential species pool that can potentially inhabit particular ecological conditions or geographical
1139 areas but are absent from a particular habitat, vegetation type, or area, there is ‘dark richness’ in
1140 pollen analysis. This consists of pollen and spore types in the potential pollen pool whose parent
1141 plants could occur in the past vegetation that produced a particular pollen assemblage but are
1142 absent from the assemblage. Pärtel (2014) has recently distinguished in modern biotic assemblages
1143 an additional type of absent taxa, so-called hidden diversity consisting of taxa that are absent from a
1144 given survey such as plants in a dormant state or are so rare as to be overlooked in traditional field
1145 sampling. They can be detected by, for example, modern environmental-DNA techniques applied to
1146 soil samples (e.g. Valenti et al., 2008; Epp et al., 2012; Yoccoz et al., 2012). In the case of pollen
1147 assemblages, the distinction between dark richness and hidden richness of pollen types is very fuzzy
1148 as taxa such as *Geranium* and *Juncus* are generally “palynologically silent taxa” (Ritchie, 1987) but

1149 very occasionally their pollen is found. Strictly hidden richness in pollen assemblages refers to taxa
1150 that produce no pollen or produce pollen that is not preserved (e.g. *Najas*, *Zostera*, *Vallisneria*,
1151 *Ceratophyllum*).

1152 A problem largely unique to pollen assemblages is false richness or false presences (Birks,
1153 2014), namely pollen dispersed over far distances (extra-regional pollen; *sensu* Janssen, 1966, 1973,
1154 1981) from areas well outside the RPSA of a site (e.g. *Ephedra* pollen in late-glacial assemblages from
1155 western Scotland (Birks, 1973b)). Modern pollen assemblages from Svalbard (Birks et al., 2004)
1156 contain 48 pollen and spore taxa. Twelve of these represent plants that do not grow on Svalbard
1157 today. This extra-regional pollen must have been carried by wind as long-distance transport. Such
1158 false presences are thus a source of bias in modern pollen assemblages from arctic, alpine, and other
1159 treeless environments. False presences can also be a serious problem in interpreting last glacial or
1160 late-glacial pollen assemblages because such assemblages often contain not only long-distance extra-
1161 regional pollen (e.g. *Pinus*, *Ephedra*) but also secondarily redeposited pollen such as *Quercus*, *Alnus*,
1162 *Ulmus*, and *Tilia* (e.g. Andersen, 1961; Cushing, 1963, Birks, 1973b).

1163 Table 4 summarises the various types of richness that arise when considering pollen-
1164 assemblage richness.

1165 Dark diversity of plants and dark richness of pollen equivalents cannot be directly measured,
1166 but their relative size can be approximately inferred. One simple approach (cf. Lewis et al., 2015) for
1167 dark richness of pollen is to list those pollen and spore types present and their likely plant
1168 equivalents, and consider the ecological indicator values of these plant equivalents for
1169 environmental variables such as light, moisture, soil reaction, and soil fertility (nitrogen) (e.g.
1170 Ellenberg et al., 1991; Hill et al., 2004) to derive approximate environmental scores for the past flora
1171 and vegetation within the RPSA for the observed pollen assemblage. If we assume that these
1172 environmental scores are representative of the past flora and vegetation, it is possible to use Hill et
1173 al. (2004) or Ellenberg et al. (1991) in conjunction with plant distributional data and ecological
1174 knowledge of the study areas to list all the likely plants and their pollen equivalents not found in the
1175 fossil pollen assemblage. The total number of such pollen equivalents is the 'dark richness' (plus
1176 'hidden diversity'). For Holocene pollen assemblages from western and southern Norway, the dark
1177 pollen richness is about 30–35% of the potential pollen pool for these areas (Birks, unpublished
1178 data). For late-glacial pollen assemblages from the Isle of Skye (north-west Scotland) (Birks, 1973b),
1179 the dark pollen richness is higher (Birks, unpublished data), about 50–60% of the potential pollen
1180 pool defined on the basis of the present-day vascular plant flora and vegetation of the Isle of Skye
1181 and neighbouring islands (Birks, 1973b; Murray and Birks, 2005). There are many possible reasons for

1182 the different relative sizes of the dark pollen richness in the late-glacial and the Holocene, such as
1183 different proportions of anemophilous and entomophilous and tall-growing and low-growing plants
1184 in the potential pollen pools, different taphonomies, different proportions of local, regional, and
1185 extra-regional pollen (*sensu* Janssen, 1966, 1973, 1981), plant migration and local extinctions over
1186 time, and the difficulties of defining realistic pollen pools for no-analogue late-glacial floras,
1187 vegetation, and landscapes. There is the need for more sophisticated assessments of dark pollen
1188 richness to help to provide a more realistic and complete view of past vegetation and ecosystems.
1189 For modern vegetation, Pärtel et al. (2013) attempt to link realised local diversity and inferred dark
1190 diversity within the general species-pool concept to derive a simple community completeness index
1191 based on the log-ratio of observed richness to dark diversity. Developing and interpreting such an
1192 index based on pollen-assemblage richness and dark richness is a challenge for future study,
1193 especially to detect which taxa are absent from past assemblages and to infer possible reasons for
1194 their absences.

1195 *7.6 Functional and phylogenetic diversity*

1196 Functional diversity (FD) is an important component of biodiversity that considers the range of
1197 functions that organisms perform in communities and ecosystems (Purvis and Hector, 2000; Hooper
1198 et al., 2002; Petchey and Gaston, 2002, 2006; Pakeman, 2011; Mace et al., 2014). It not only serves as
1199 a descriptor of an assemblage or community but it also is an indicator of ecosystem function. It is the
1200 extent of functional differences among species in a community (Tilman, 2001; Petchey and Gaston,
1201 2002) and is thought to be an important determinant of ecosystem processes and functioning. As FD
1202 is the diversity of species traits in a community or ecosystem, it captures information about
1203 functional traits that may be missing in measures of taxonomic richness or diversity. There has been,
1204 just as with the estimation of taxonomic diversity, a proliferation of measures to estimate the
1205 different components of FD, namely functional richness, functional evenness, and functional
1206 divergence (e.g. Petchley et al. 2004; Mason et al., 2005; Walker et al., 2008; Poos et al., 2009;
1207 Schleuter et al., 2010; Casanoves et al., 2011). Estimating FD often requires analysis of several
1208 different types of variables (continuous, ordinal, nominal, multi-choice nominal, circular, fuzzy, etc.).
1209 Pavoine et al. (2009) extend Gower's (1971) coefficient of similarity for mixed data to include new
1210 data types. Not surprisingly, Hill numbers have now been generalised to consider not only taxonomic
1211 diversity but also phylogenetic and functional diversity, thereby providing a unified framework for
1212 measuring several aspects of biodiversity (Chao et al., 2010, 2014a, 2014b; Gotelli and Chao, 2013;
1213 Chiu and Chao, 2014). FD (differences among taxon traits) and phylogenetic diversity (based on taxon
1214 evolutionary history) (Chao et al., 2010, 2014a, 2014b; Chiu and Chao, 2014) have now been

1215 integrated into a single framework of attribute diversity based on Hill numbers of taxonomic entities,
1216 functional entities, and /or phylogenetic entities, with each entity weighted by its relative abundance
1217 (Chiu and Chao, 2014). FD has rapidly become an important part of community and ecosystem
1218 studies as it attempts to quantify aspects of diversity that may influence community assembly and
1219 function. FD is also being studied in Deep-time palaeobiology (e.g. Miller et al., 2014). The relation
1220 between FD and taxonomic richness and diversity is complex as it appears to be context-dependent
1221 (Cadotte et al., 2011).

1222 To date, very few Quaternary palynologists have considered functional or phylogenetic
1223 diversity. Collins et al. (2013) and Davis et al. (2015) explore temporal and spatial patterns in plant
1224 functional type diversity during the Holocene using palynological data from across Europe. Other
1225 attempts at linking functional traits with pollen data include Gachet et al. (2003), Barboni et al.
1226 (2004), Lacourse (2009), and Kuneš et al. (2011) or with testate amoeba assemblages (Fournier et al.
1227 2015). Goring et al. (2013) propose utilising functional trait or phylogenetic information “to unite [...]”
1228 plant and pollen taxa, such that the richness values from pollen are not evaluated on their own, but
1229 in a multivariate form that provides information about the structure of the pollen assemblage in an
1230 evolutionary or functional manner. This information may be integrated in measures of functional
1231 richness (Mason *et al.* 2005) but the choice of functional characters may strongly affect our ability to
1232 detect a relationship”. Goring et al. (2013) suggest that this approach of using both taxa and traits
1233 and taking account of phylogenetic constraints will result in “a greater integration of
1234 palaeoecological data and analysis into macroecological research”. Clearly such an approach requires
1235 not only high quality pollen and spore data but also reliable phylogenetic (Velland et al., 2011) and
1236 functional trait (Weiher, 2011) information for all the taxa concerned. As with pollen-richness
1237 estimation, problems of pollen taxonomic precision and ‘smoothing’ (*sensu* Mander, 2011), pollen-
1238 representation bias, and sampling considerations will also arise in considering functional diversity of
1239 modern pollen-assemblages in relation to contemporary vegetation. Thus the exploration of
1240 functional and phylogenetic diversity of modern and fossil pollen assemblages is a very considerable
1241 challenge.

1242 This challenge has recently been faced by Reitalu et al. (2015) who have explored temporal
1243 patterns in taxonomic richness and evenness, functional diversity, and phylogenetic diversity, all
1244 based on late-glacial and Holocene pollen data from 20 sites in Estonia and Latvia. They show that
1245 shifts in the functional and phylogenetic diversity of the pollen data are closely related to climate
1246 change and suggest that trait differences play an important role in long-term biotic responses to
1247 climate change. Human impact in the last 2000 years has had a negative influence on functional and
1248 phylogenetic diversity in the pollen assemblages due to the decline of plant taxa with certain traits

1249 leading to functional convergence and the expansion of some taxa from particular phylogenetic
1250 lineages. Clearly there is a need for further such studies that simultaneously explore taxonomic,
1251 functional, and phylogenetic diversity of modern and fossil pollen assemblages.

1252 **8. Conclusions**

1253 In answer to the question posed in the title of this review, recent detailed studies (e.g.
1254 Odgaard, 2008; Meltsov et al., 2011; Felde, 2015; Felde et al., 2015) and earlier less detailed studies
1255 (e.g. Birks, 1973a; Flenley, 2005) demonstrate that pollen-assemblage richness does reflect floristic
1256 richness. However, this relationship is not a simple or exact 1:1 relationship. Pollen richness is also a
1257 function of landscape structure, openness, and diversity within the APSA or RPSA (Meltsov et al.,
1258 2013; Matthias et al., 2015), as proposed and discussed by Birks and Line (1992), of the pollination
1259 syndromes in the flora within the APSA (Meltsov et al., 2011), and of dispersal and other taphonomic
1260 processes (Birks and Line, 1992).

1261 Pollen richness, evenness, and diversity—expressed as Hill (1973) numbers—are estimates of
1262 particular numerical characteristics of modern and fossil pollen assemblages (Birks HJB, 2013) or
1263 “species composition parameters” (Hurlbert, 1971). Like all such estimates or summary statistics
1264 derived from complex multivariate data, the estimates may be biased in various ways. In the case of
1265 estimates of pollen richness, they are biased by factors such as count size, taxonomic precision, the
1266 underlying pollen sample:underlying pollen population ratio, and pollen representation (productivity
1267 and dispersal) (Odgaard, 1999, 2001, 2007, 2008, 2013). Several approaches reviewed above
1268 (Sections 4.1 and 5.2) have been developed to minimise these biases but the biases cannot be fully
1269 eliminated as they are inherent in all pollen-assemblage data.

1270 As discussed above, assessing the relationship between modern pollen and floristic richness
1271 requires high quality and consistent palynological data and site-specific floristic/vegetational data.
1272 The findings of Goring et al. (2013) of a slightly negative modelled relationship between “smoothed
1273 pollen richness” and “smoothed floristic richness” in the Pacific Northwest and thus that higher
1274 pollen richness occurs with lower floristic richness may be a result of the absence of site-specific
1275 floristic or richness data collected at a spatial scale appropriate for comparison with regional-scale
1276 pollen deposition in lakes in their study area.

1277 The recent developments in the clarification of the concepts of richness, evenness, and
1278 diversity, in the unification of measures to estimate them, and in the distinction between concepts
1279 and the measures used to estimate them has greatly simplified diversity research. Hill (1973)

1280 numbers provide a conceptually simple and mathematically rigorous basis for estimating richness,
1281 evenness, and diversity.

1282 Estimates as Hill numbers of pollen richness, evenness, and diversity can be calculated for
1283 fossil pollen-assemblage data collected in comparable taxonomic and analytical detail as the modern
1284 pollen-assemblage data and from sites of similar size and morphometry to the lakes at which the
1285 modern assemblages were studied. These estimates and their variances can be plotted
1286 stratigraphically to provide profiles of richness, diversity, and evenness through time (e.g. Felde,
1287 2015). Estimates of richness, diversity, and evenness for assemblages from several sites can be
1288 compared if all the data sets, possibly after transformations using pollen-representation values, are
1289 rarefied to the same base-sum for estimating not only N_0 but also N_1 and N_2 and their ratios as
1290 evenness measures (e.g. Felde et al., 2015).

1291 Flenley (2003) in his future-looking “Some prospects for lake sediment analysis in the 21st
1292 century” identifies six possible developments based on his own research interests and experiences.
1293 One is “palyno-richness and palyno-diversity” (see also Flenley, 2005). With the recent developments
1294 reviewed here, we think that changes in pollen richness, evenness, and diversity through time can be
1295 estimated and compared in space to explore their patterns in time and space. Potential drivers of
1296 past changes can then be explored using the types of approaches of, for example, Hanley et al.
1297 (2008), Lacourse (2009), and Reitalu et al. (2013), thereby helping to close “the gap between plant
1298 ecology and Quaternary palaeoecology” (Reitalu et al., 2014).

1299 As in all studies on the representation of flora and vegetation in Quaternary fossil assemblages
1300 (Jackson, 2012) (and in almost any palaeoecological study), there are always several known knowns,
1301 some known unknowns and unknown knowns, and probably an embarrassingly large number of
1302 unknown unknowns. In the context of pollen–floristic richness relationships, what are these four
1303 combinations of knowns and unknowns? An obvious example of a known known or more or less solid
1304 fact, observation, or inference, is that *Pinus* trees produce more pollen and disperse their pollen
1305 farther than *Tilia* trees do. Critical known unknowns concern sources of error, uncertainty, and bias
1306 in pollen data. Attempts are being continually made to minimise and estimate them, but we do not
1307 usually know enough about them and their interactions in nature to make realistic estimates of these
1308 uncertainties. Unknown knowns are things we may know so well that we are no longer explicitly
1309 aware that we know them (Jackson, 2012). What is an unknown known and what is a known known
1310 is partly determined by education, research school, awareness of the older literature, and hence age
1311 of the scientist concerned. For example, the rich literature on pollen production, dispersal,
1312 deposition, and taphonomy from the 1960s–1980s, often published in books or symposium

1313 proceedings (e.g. Birks and West, 1973) is increasingly ignored in the literature of the 2010s. Much of
 1314 the older literature, not always written in English and often published as ‘local’ monographs is not
 1315 currently available in an electronic format and represents an important ‘loss of information’ (see also
 1316 Blois, 2012). This is sadly prevalent in much of the recent literature on quantitative pollen–plant
 1317 relationships and vegetation and landscape reconstructions. The fourth combination, unknown
 1318 unknowns, represents our ignorance at the present time but thanks to creative and critical scientific
 1319 research, unknown unknowns can become known knowns or known unknowns. Studies on pollen–
 1320 plant richness relationships build on several well-founded known knowns, strive to reduce the known
 1321 unknowns, and try to convert some unknown unknowns into known knowns or known unknowns.
 1322 Given the vast old and ever-expanding relevant new literature on diversity, functional diversity,
 1323 phylogenetic diversity, functional traits, pollen representation, and handling uncertainties in
 1324 reconstructions, we all have to work to reduce important information loss and hence the unknown
 1325 knowns and to consider in more critical detail the known unknowns.

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1335

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2474 **Table 1**

2475 Selected examples of studies where pollen richness has been estimated from fossil pollen assemblages using rarefaction
2476 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	<i>Ulmus</i> 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

2477 LG = Late-glacial; LGM = Last glacial maximum

2478

2479 **Table 2**

2480 Effects of translation of terrestrial plant species recorded in modern vegetation to potentially identifiable terrestrial pollen
 2481 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)

2482 * includes pollen samples from Washington, Oregon, Idaho, and Montana, as well as British Columbia where the floristic or
 2483 vegetational data are derived from

2484

2485 **Table 3**

2486 Different categories of inventory and differentiation diversity in relation to ecological scale of investigation (after Whittaker,
 2487 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	-

2488

2489 **Table 4**

2490 Different types of palynological richness relevant to pollen assemblages (after Birks and Line, 1992; Birks, 2014; Pärtel,
 2491 2014)

Type	Sources	Example
False richness (false presences)	Extra-regional pollen	<i>Pinus</i> pollen in high-Arctic areas
Hidden richness	No pollen produced or preserved	<i>Najas</i> , <i>Vallisneria</i> , <i>Elodea</i> , <i>Ceratophyllum</i> , <i>Zostera</i>
Dark richness	Generally palynologically 'silent' taxa	<i>Viola</i> , <i>Geranium</i> , <i>Oxalis</i> , <i>Malva</i>
Observed richness	Pollen counts standardised to a constant count-size. Includes false richness (false presences)	Hill N_0 ; $E(S_n)$ from rarefaction

2492

2493

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

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

2494

Box 2. Hill numbers

The general formula for a Hill number is

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

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.

2495

2496

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