J Paleolimnol (2008) 40:357–368
DOI 10.1007/s10933-007-9166-2

ORIGINAL PAPER

Testing the reliability of pollen-based diversity estimates

Matthew Charles Peros · Konrad Gajewski

Received: 28 August 2007 / Accepted: 18 October 2007 / Published online: 13 November 2007

Abstract Rarefaction analysis is a common tool for estimating pollen richness. Using modern and fossil pollen data from the Canadian Arctic and Greenland, we examine the effects of pollen concentration (grains/cc) and evenness (the distribution of species abundances) on palynological richness. Our results show that pollen richness and concentration have a strong negative correlation at low pollen concentrations. There is a positive correlation between pollen evenness and richness, although the strength of this relationship is difficult to determine. Rarefaction analysis on samples of low concentration or high evenness is likely to lead to pollen richness being less underestimated than on samples of high concentration or low evenness. These findings corroborate theoretical research on these issues.

Keywords Pollen analysis · Rarefaction · Diversity · Pollen concentration · Evenness · Paleoecology · Arctic

M. C. Peros (✉) · K. Gajewski
Laboratory for Paleoclimatology and Climatology,
Department of Geography, University of Ottawa,
60 University Avenue, Ottawa, ON, Canada K1N 6N5
e-mail: mperos@uottawa.ca

Introduction

Fossil pollen data are used to infer past floral diversity based on the premise that at the landscape scale, pollen and plant diversity is roughly correlated (e.g., Moore 1973; Seppä 1998; Weng et al. 2007). Several diversity estimation techniques have been employed in such investigations, including the Simpson (Ritchie 1982; Cwynar 1982) and Shannon indices (Weng et al. 2007). These indices account for both species richness (the number of species) and evenness (the distribution of species abundances) (Legendre and Legendre 1998). However, they do not account for sample size, leading to the possibility that more taxa will be encountered in samples with higher pollen sums (Weng et al. 2006). To address this problem, Birks and Line (1992) introduced to the Quaternary paleoecological community the concept of rarefaction, a technique that permits the estimation of palynological richness using standardized pollen counts. However, despite the now widespread use of rarefaction (e.g., Bennett et al. 1992; Seppä 1998; Berglund et al. 2007), its limitations—which may include potential relationships among pollen concentration, evenness, and richness—are rarely addressed when interpreting paleoecological data (Odgaard 2001; Weng et al. 2006). To permit reliable interpretations of pollen-based richness estimates, it is essential to critically examine how factors such as concentration and evenness influence rarefaction results.

The purpose of this paper is to use modern and fossil pollen data to test two key hypotheses related to the estimation of palynological richness and assess the importance of these factors in understanding diversity in pollen assemblages:

(1) That palynological richness is negatively correlated with pollen concentration (Weng et al. 2006); and
(2) That palynological richness is positively correlated with pollen evenness (Odgaard 2001).

The premise behind hypothesis 1 is that in a sample of low pollen concentration, a larger proportion of the total pollen in the sediment will have to be counted to achieve the same number of grains as a sample with a high concentration (Weng et al. 2006). In this case, where a larger proportion of the total population of pollen grains is counted, more rare taxa would be detected, inflating the richness of the lower concentration sample relative to a high concentration sample. Hypothesis 2 suggests that the presence of a few abundant taxa (e.g., anemophilous and well-dispersed taxa such as *Pinus*) may impede the detection of lower frequency taxa compared to samples where taxon frequencies are more even. Therefore, unevenness in pollen frequencies would lead to palynological richness being greatly underestimated (Odgaard 2001; Weng et al. 2006).

The potential influence of concentration and evenness on palynological richness has been recognized (Seppä 1998; Odgaard 1999), and theoretical models have been used to predict their effects (Weng et al. 2006; see also Smol 1981). However, few studies have striven to test these hypotheses using actual pollen data (but see Räsänen et al. 2004). We do so here, using modern and fossil pollen data from the Canadian Arctic and Greenland. Samples from the Arctic are ideal to study pollen-based diversity problems, since: (1) the floral and palynological diversity is low compared to other regions, suggesting that a larger proportion of pollen taxa can be detected and identified; (2) the lack of trees means that the dispersal of herb and shrub pollen has not been impeded by larger plants, ensuring that they are better represented than in forest environments (Odgaard 1999); (3) pollen concentrations are relatively low, so any concentration effects may be detectable (Gajewski 1995). Furthermore, the study sites we use in this paper are located well north of treeline, making it possible to remove ‘long-distance’ taxa from the pollen sum so that we can focus on plants of the tundra environment (Weng et al. 2006).

Methods

Rarefaction permits an estimation of pollen richness using a standardized pollen count (Birks and Line 1992). This standardization is important since palynological richness depends in part on pollen sum—as the sum increases, more taxa can potentially be detected. The units of rarefaction analysis represent the estimated number of pollen taxa reduced to a certain pollen sum, usually the lowest sum of the group of samples being compared. The estimated number of taxa [$E(T_n)$] is given by:

$$E(T_n) = \sum_{i=1}^{T} 1 - \left[\frac{(N-N_i)!(N-n)!}{(N-N_i-n)!N!}\right]$$

where $E(T_n)$ is the expected palynological richness in a standardized pollen count N_i, T is the palynological richness in the original pollen count, N is the overall pollen sum, and n is the number of grains selected for standardization in the rarefied sample (Birks and Line 1992; Weng et al. 2006). It is important to note that unless all pollen grains are detected and enumerated, rarefied richness will always underestimate the richness of the population.

Evenness (or equitability) represents the degree to which taxon frequencies are similar (Olszewski 2004). Despite the numerous evenness indices available (Legendre and Legendre 1998), it remains an under-utilized parameter in palynological analysis (Odgaard 2001). In one of the few palynological studies where evenness was calculated, Räsänen et al. (2004) utilized a variation of the Shannon diversity index and showed a correlation between pollen evenness and richness within a series of moss polsters. In this paper, we use another index of evenness, Hurlbert’s (1971) probability of interspecific encounter (PIE). This index, which ranges from zero to one, represents the probability that two individual pollen grains, randomly selected (without replacement) will be of different taxa (Hurlbert 1971). Thus, samples dominated by a few taxa (low evenness), will have a PIE value closer to zero compared to samples where the taxa are more evenly distributed. The utility of this metric for palynological data is that it is not biased by sample size or species richness, unlike several other evenness measures (Olszewski 2004). The value of PIE is given by:

$$\Delta_1 = 1 - \sum_{i=1}^{T} \left(\frac{n_i}{N}\right)\left(\frac{n_i - 1}{N - 1}\right)$$

where Δ_1 is the PIE, T is the richness of the sample, n_i is the abundance of the ith taxa, and N is the overall pollen sum.

Rarefaction determinations were computed using PAST (Hammer et al. 2001) and PIE calculations were implemented in Microsoft Excel. In both cases, calculations were undertaken on the same datasets, which comprised all lacustrine samples ($n = 218$) in the 'Arctic' biome of the North American Modern Pollen Database (Whitmore et al. 2005) and on all fossil samples from four lake sediment cores from the central and western Canadian Arctic (core RS36, from Gajewski 1995; JR01 from Zabenskie and Gajewski 2007; KR02 from Peros and Gajewski in press; and SL06, unpublished) (Fig. 1). The modern pollen data were generated by several analysts; Gajewski and Zabenskie counted the pollen in cores RS36 and JR01, respectively, and Peros counted the pollen in cores KR02 and SL06. Fossil pollen counts were derived from 1-cm-thick subsamples roughly evenly spaced along the length of each core.

The total pollen sum of each modern and fossil sample varied, but in this study only those taxa (both pollen and spores) that have their distributions primarily in the Canadian Arctic (Porsild and Cody 1980) were retained for analysis; all tree, unidentified and indeterminable grains were removed before rarefaction and evenness analyses to ensure that only tundra taxa were incorporated into the sum. After removing these grains, only those samples with a pollen sum greater or equal to 100 were retained for analysis. The pollen data were input as counts and underwent a 10-step rarefaction (i.e., the output consisted of pollen sums of 10, 20, 30, etc., grains).

Pollen concentration was determined for 138 of the modern samples and the entire fossil dataset using standard procedures (Faegri and Iversen 1989). Some modern samples lacked the necessary information for calculating concentration and were excluded. The concentration values reflect the summed concentrations of the same Arctic taxa used in the rarefaction and evenness analyses.

Relationships between variables were assessed by examining scatter-plots and by calculating Pearson's

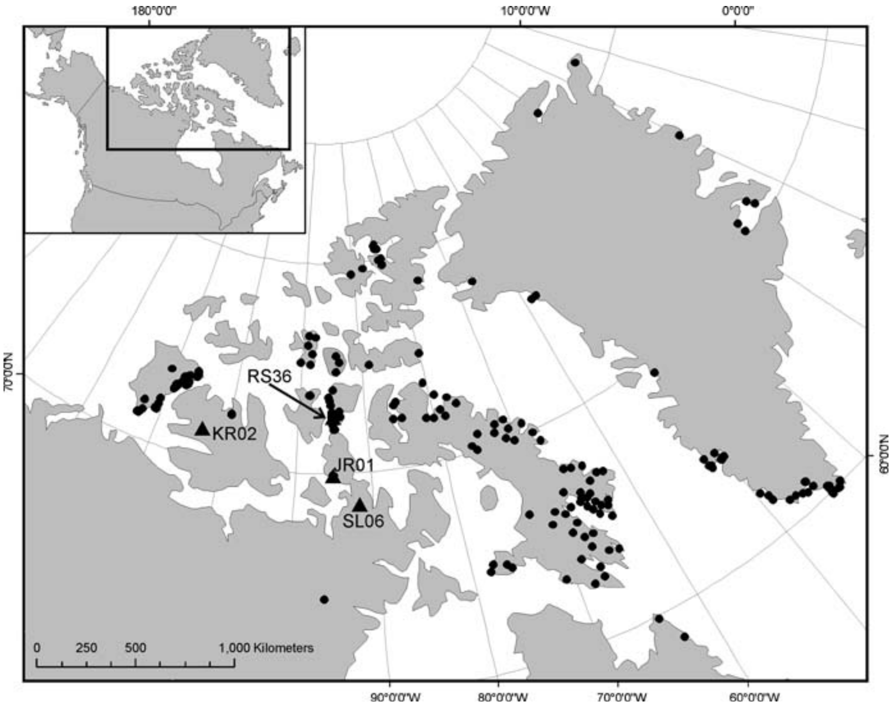

Fig. 1 Map of modern and fossil Arctic pollen sites discussed in this paper, with the exception of Abernethy Forest, Scotland (Birks and Mathewes 1978)

r correlation coefficients for variables with linear relationships. These techniques were implemented in S+ and Microsoft Excel.

Results

Modern pollen data

In total, 198 modern samples had 'Arctic pollen' sums equal to or greater than 100 grains (i.e., this sum did not include tree, unidentifiable, or indeterminable grains). Within these 198 samples, 34 Arctic pollen types were selected for rarefaction analysis. A plot of palynological richness [$E(T_{100})$] versus latitude (Fig. 2a) indicates that pollen richness gradually increases to a maximum at around 72°N, and then decreases slightly at 80°N, the latitude of central Ellesmere Island. Figure 2b, which includes only those sites with an Arctic pollen sum equal to or greater than 300 grains ($n = 51$) shows a similar trend, suggesting that overall patterns of

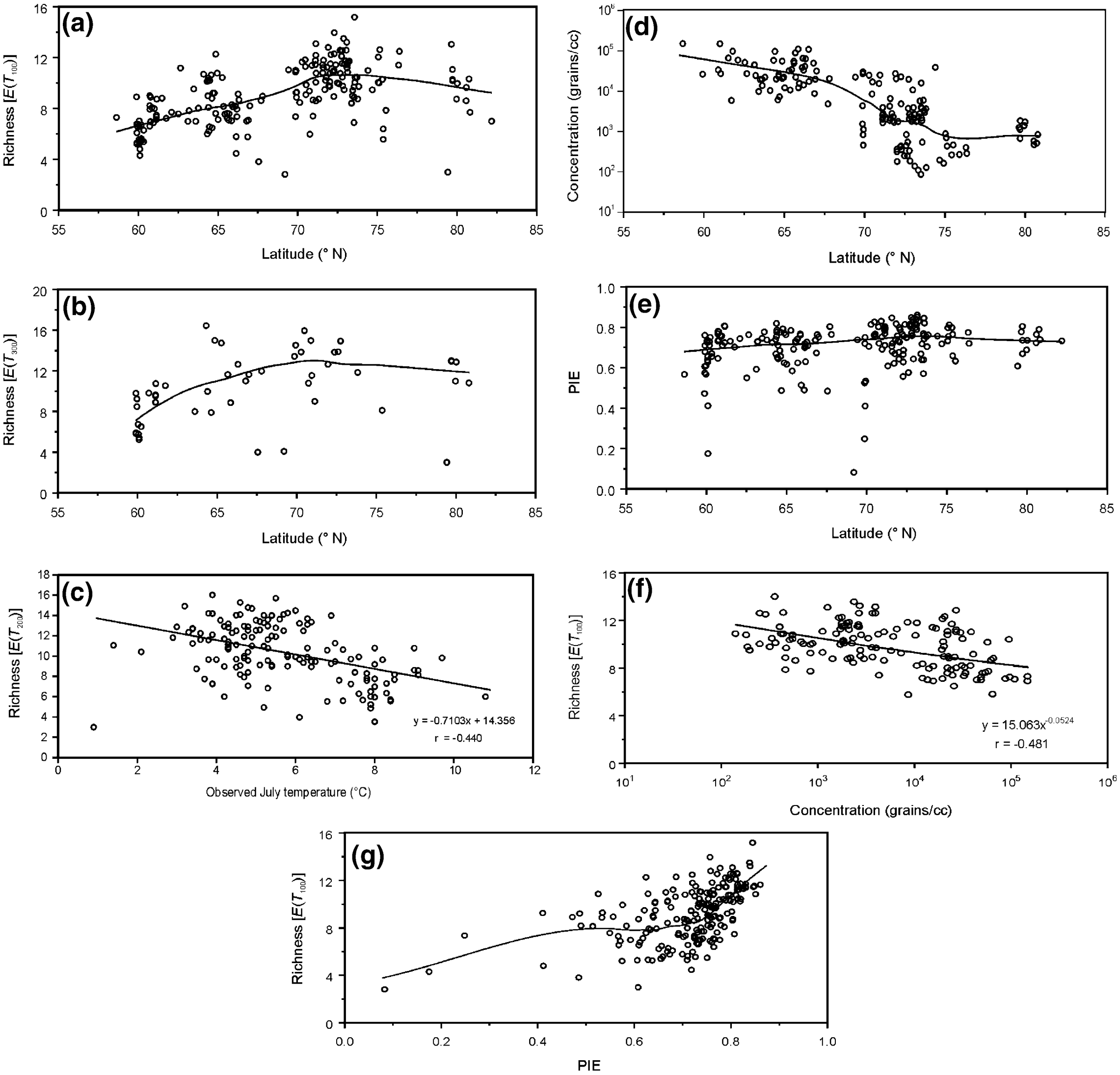

Fig. 2 Scatter-plots of Arctic samples from the North American Modern Pollen Database (Whitmore et al. 2005): (**a**) Estimated pollen richness [$E(T_{100})$] versus latitude; (**b**) Same as (**a**), but with [$E(T_{300})$]; (**c**) Pollen richness [$E(T_{200})$] versus observed July air temperature; (**d**) Pollen concentration versus latitude; (**e**) Probability of interspecific encounter (PIE) versus latitude; (**f**) Pollen concentration versus richness [$E(T_{100})$]; and (**g**) Pollen richness [$E(T_{100})$] versus PIE. A loess smoother was applied to the data

palynological richness are not overly sensitive to the magnitude of the sum for Arctic pollen types.

In general, plant species diversity decreases to the north in the Canadian Arctic, but the actual pattern of vegetation zonation is more complex, with lowest plant diversity in the northwestern islands, and higher diversity in parts of the northeast (Young 1971; Edlund and Alt 1989). For example, the Fosheim Peninsula—where a number of the modern pollen samples were collected—is a 'polar oasis' located on central Ellesmere Island, which supports a Low or Middle Arctic-type of vegetation community (Gajewski 2002). When this vegetation zonation is accounted for, this pattern of increasing and then decreasing pollen richness with latitude is the reverse of regional-scale observations of plant diversity, which tend to show that plant diversity and productivity decrease with increasing latitude (Young 1971). Furthermore, pollen richness [$E(T_{200})$] is negatively correlated with summer temperature (Fig. 2c), a finding again opposite to the clear positive relation seen between plant species richness and July temperature across the Canadian Arctic (Rannie 1986).

Figure 2d shows that pollen concentration decreases with increasing latitude, with the exception of samples from the relatively productive Fosheim Peninsula, a pattern that is in contrast to the palynological richness results shown in Fig. 2a and b. This pattern corresponds with the decrease in the primary production of the regional flora. While variations in sediment accumulation rates may also influence pollen concentration across this latitudinal gradient, the two-orders-of-magnitude decrease in pollen concentration across the Middle- to High Arctic transition suggests that plant primary production is the major factor controlling Arctic pollen concentration.

In contrast to the pattern in concentration, pollen evenness shows only a very weak relation with latitude (Fig. 2e). When concentration and richness are compared (Fig. 2f), a strong relationship is apparent, with higher richness generally being registered in samples of lower concentration. In addition, there is a strong, positive relationship between pollen richness and the probability of interspecific encounter (PIE; Fig. 2g). As richness decreases, however, values of PIE occur over a broader range, indicating that samples of high richness within the modern dataset generally have fairly evenly distributed species frequencies.

Fossil pollen data

Summary diagrams of the five most abundant local and regional pollen types at each site, along with estimated palynological richness, are shown in Fig. 3. Core KR02 comprises 69 samples and 23 taxa (Peros and Gajewski in press); SL06 35 samples and 29 taxa (unpublished data); RS36 18 samples and 32 taxa (Gajewski 1995); and JR01 58 samples and 22 taxa (Zabenskie and Gajewski 2007). Cyperaceae is the most abundant pollen type in each of the four diagrams. Poaceae and *Salix* are also present in moderately high quantities, although herbs such as *Oxyria*, Saxifragaceae, and *Artemisia* are also common. At sites KR02, RS36, and JR01, estimated palynological richness [$E(T_{100})$] is variable but appears to increase over the course of the Holocene. The pollen richness record for core SL06 shows no clear trend over the ~2500 years it represents.

Figure 4 shows the palynological richness of the fossil samples plotted against pollen concentration. Cores KR02 and RS36 show statistically significant negative linear relationships between the two variables (Table 1). Core JR01 shows a similar trend, albeit one that is weaker and is only apparent with the inclusion of the three highest concentration samples. The pattern of the samples from core SL06 is similar to that of JR01, although there appear to be two samples that are potential outliers. When these samples are removed, a statistically significant negative relationship is apparent, as is found in the other three cores (Table 1).

Scatter-plots of pollen richness and PIE-estimated evenness for the fossil samples are shown in Fig. 5. Each of these relationships is positive, linear, and statistically significant at a range of pollen sums (Table 1). These relationships are also stronger than those between pollen richness and concentration, with r values averaging ~0.7 compared to ~0.63 and less in the latter case. Furthermore, there do not appear to be outliers in the plot of samples from core SL06, unlike the previous figure.

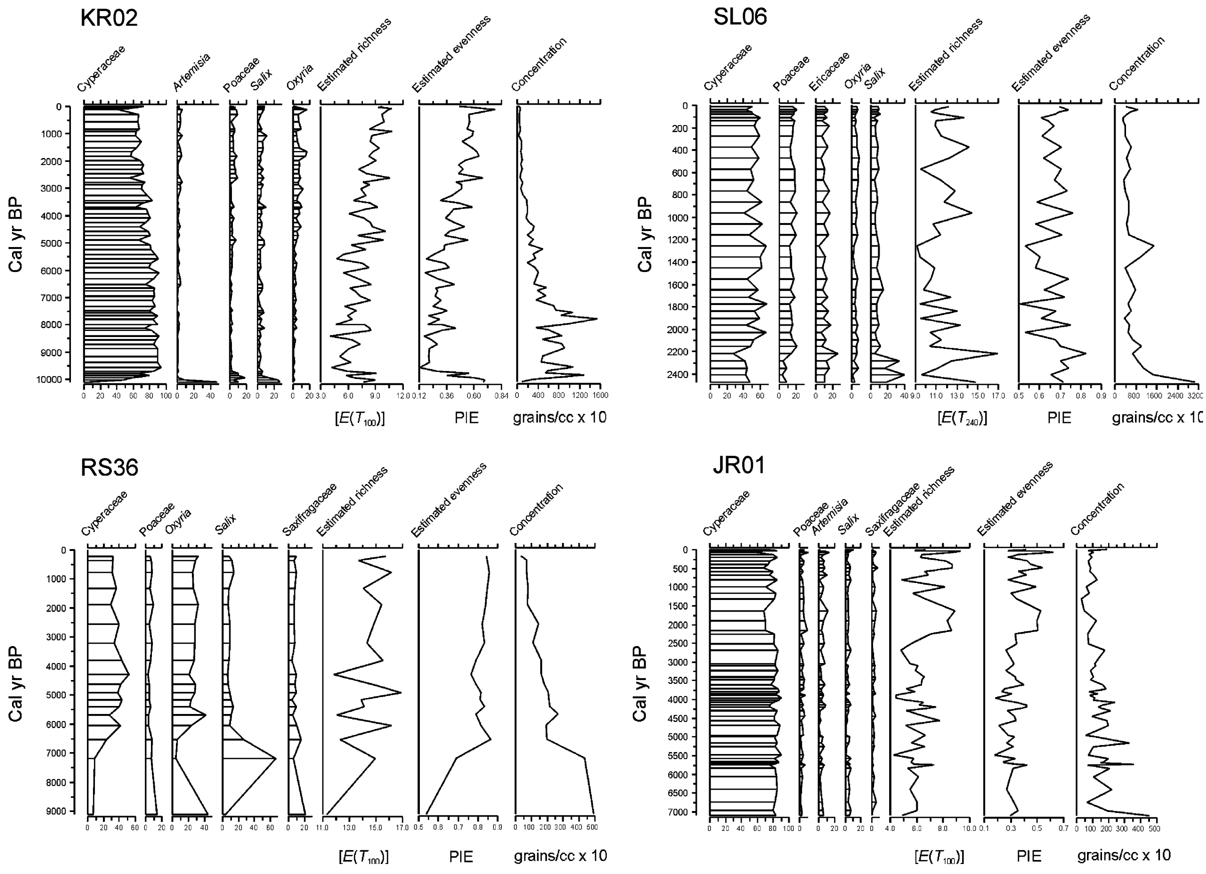

Fig. 3 Summary pollen percentage, rarefaction estimated richness, estimated evenness (PIE; probability of interspecific encounter), and concentration data for four lake-sediment cores from the Canadian Arctic plotted against calibrated years BP (Stuiver et al. 1998). The values of all columns are based on the percentage of the local and regional pollen sum. Note that the sums for the rarefaction results vary

Discussion

The results are consistent with hypotheses 1 and 2: there exists a negative relationship between pollen richness and concentration and a positive relationship between pollen richness and evenness for both modern and fossil pollen data (Odgaard 2001; Weng et al. 2006). Fundamentally, both of these relationships are a function of the degree to which the sample is representative of the population from which it is derived. Usually, only a small fraction of any population is detected and enumerated (Odgaard 2001). Our findings show that under certain circumstances, rarefied richness is highly influenced by both the abundance of grains within, and evenness of, the population.

Pollen concentration

Weng et al. (2006) argue that the effect of concentration may be important when interpreting temporal transitions between biomes (e.g., treeline), where significant differences in concentrations occur. Our results suggest that concentration can be important even within the same biome, and that concentration values that vary by only a few thousand grains are sufficient for this effect to be detectable.

To further elucidate the effect of concentration, we have re-examined data from Abernethy Forest, Scotland (Birks and Mathewes 1978), which was used as a case study in Birks and Line (1992). Pollen richness was estimated using all pollen grains from 49 samples (sample counts range from 96 to 648) that date from

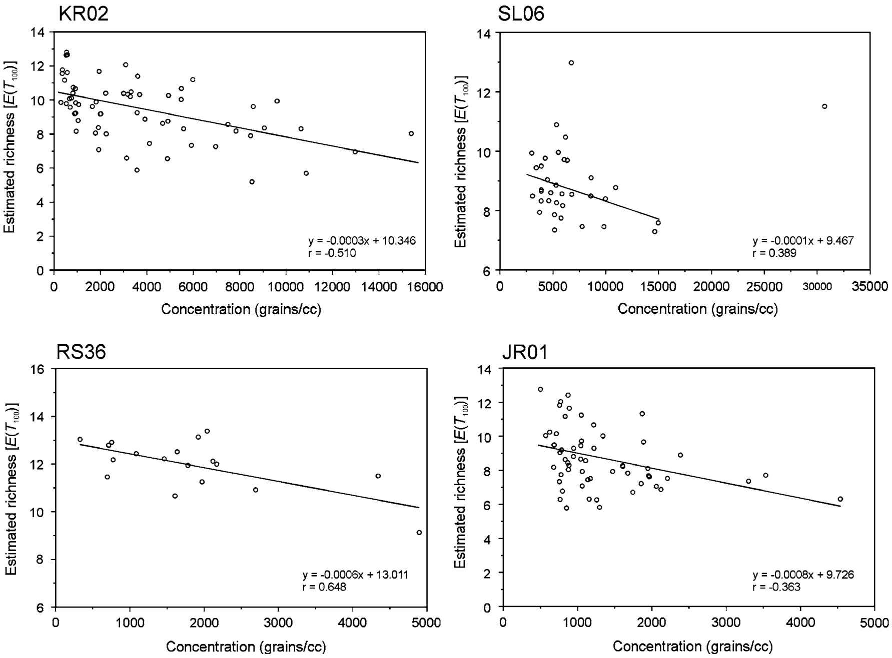

Fig. 4 Scatter-plots of pollen concentration versus estimated pollen richness [$E(T_{100})$] for each site shown in Fig. 3

Table 1 Pearson's *r* correlations between pollen concentration and PIE-derived evenness values compared to pollen richness for various rarefied sample sizes

Core and rarefied sample size		Pollen concentration	Evenness (PIE)	Degrees of freedom
KR02	100	−0.510*	0.704*	62
	150	−0.381*	0.476*	46
	200	−0.479*	0.230	11
SL06	100	−0.392*	0.546*	31
	150	−0.387*	0.518*	31
	200	−0.386*	0.498*	31
	250	−0.382*	0.499*	30
	300	−0.391*	0.290	24
	350	−0.568*	0.452	10
RS36	100	−0.649*	0.712*	16
	150	−0.510*	−0.536*	16
	200	−0.416*	0.431	16
	250	−0.469	0.367	11
JR01	100	−0.360*	0.770*	55
	150	−0.168	0.548*	30
	200	−0.422*	0.709*	15

Values denoted with '*' are significant at $P < 0.05$. The upper count value for each core is the highest rarefied sample size with 10 or more samples at 50 count intervals

5500 to 12300 ^{14}C yr BP (Fig. 6). Palynological richness is highest during the Younger and Older Dryas periods (Fig. 6a), which Birks and Line (1992) interpret as representing a diverse landscape of herb-dominated vegetation types, frequent disturbance, and much bare ground. Based on our results, however, we offer an alternative interpretation: that the high pollen richness of these periods is largely an artifact of their corresponding low pollen concentrations (Fig. 6a). This claim is supported by a strong correlation between estimated pollen richness [$E(T_{90})$] and concentration (Fig. 6b).

Despite this relationship, higher concentration samples may not be sensitive to this concentration

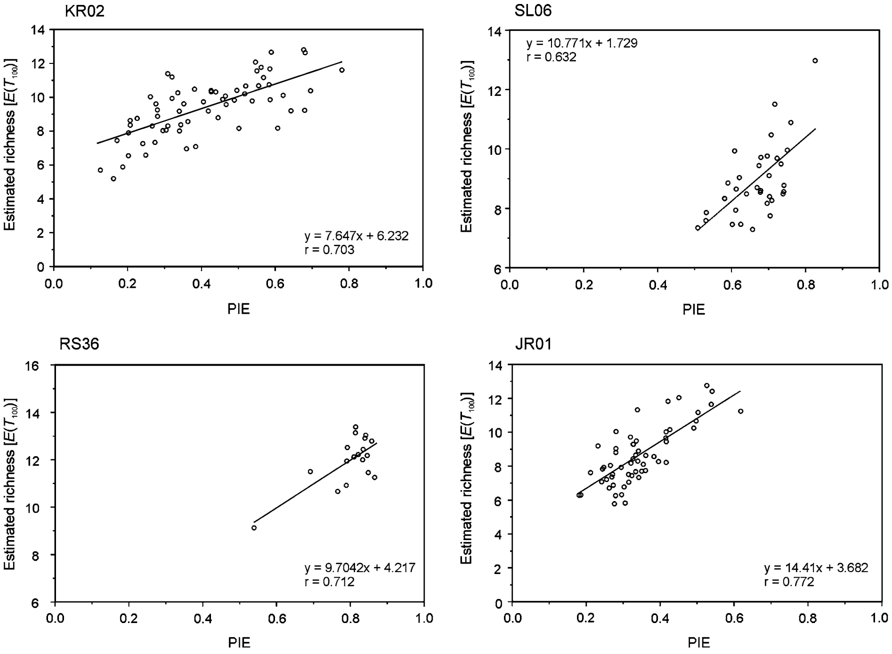

Fig. 5 Scatter-plots of pollen evenness versus estimated pollen richness for each site shown in Fig. 3

effect. In more productive regions, where concentrations may be orders of magnitude higher than in the Middle to High Arctic, the ratio of the sample count to the total pollen content will tend to be low, potentially reducing the impact of concentration on the computation of pollen richness. Fig. 6c and d show the same data from Abernethy Forest, and the modern pollen data from Fig. 2f, re-plotted using linear *x*-axes. In both cases, the ranges of the concentration values far exceed those of the fossil samples shown in Fig. 4. The negative relationship occurs only in samples of low concentration. This pattern suggests that in low concentration samples, richness is disproportionately affected by the abundance of grains in the sample, and that in high concentration samples the effect is much less important. It is critical to be aware of this when interpreting rarefaction data from low productivity regions, such as Arctic or desert biomes, or fossil data where low concentrations occurred in the past.

Pollen evenness

While the evenness results are consistent with hypothesis 2, the strong correlations may be related to a fundamental problem associated with evenness: that the number of different grains that are detected and enumerated are biased by the evenness of the total population—when this latter value is relatively even, the detected richness will be comparable to that of the population; when the population is uneven, the detected richness will be underestimated (Odgaard 1999; Weng et al. 2006). Unfortunately, testing this hypothesis by correlating the detected richness with the detected evenness, as we have done here, cannot completely resolve the issue, because a measurement of population evenness is needed, but we only have an estimate of the potentially biased sample. Furthermore, the apparent strength of the relationship between rarefaction-derived pollen richness and PIE may also be due to the fact that the two values are not completely independent; PIE is in fact calculated as part of the rarefaction process (Olszewski 2004). Nevertheless, scatter-plots of evenness and richness may still be useful to identify those samples that do not fit the general trend (Olszewski personal communication, 2007). In such cases, outliers may actually represent samples that have meaningful richness values, relatively unaffected by either evenness or concentration.

Relating concentration and evenness

Deconvolving the effects of concentration and evenness on sample richness requires a careful

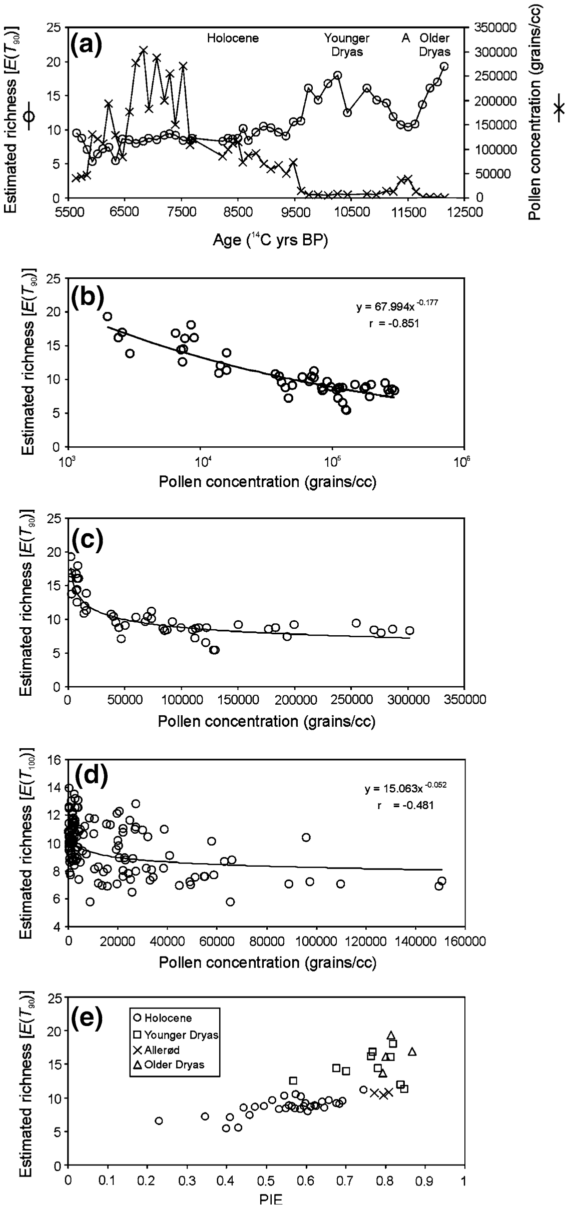

Fig. 6 (**a**) Pollen richness [$E(T_{90})$] and concentration data from Abernethy Forest, Scotland (Birks and Mathewes 1978)—'A' refers to Allerød; (**b**) Estimated richness versus concentration for all 49 samples from frame (**a**); (**c**) Same as (**b**), but with a linear x-axis; (**d**) Same data as Fig. 2f, using a linear x-axis; and (**e**) Plot of evenness (PIE) versus richness for the Abernethy Forest dataset. The symbols correspond to the time period as shown in the legend and frame (**a**)

examination of both sets of data. For example, Fig. 6e shows estimated richness versus PIE for the Abernethy Forest dataset. The samples with the highest estimated richness values, which date to the Younger and Older Dryas periods (the squares and triangles, respectively), also record the most even frequencies. This suggests that the richness of these samples is not as influenced by evenness as the samples of Holocene age (circles), which are relatively uneven (the most abundant pollen type in the late-glacial samples is *Artemisia*, at ~40–60%, but in the Holocene samples it is *Betula* or *Pinus*, at ~70–80%; Birks and Mathewes 1978). In contrast, the high concentrations of the Holocene-age samples suggest that this factor was not as important in influencing their richness values, unlike those of the Younger and Older Dryas periods (Fig. 6a and c). Thus, it seems likely that the richness of the Holocene samples is more greatly underestimated than the richness of samples from the Younger and Older Dryas periods. In other words, the richness of the populations of the various levels may be more uniform than the estimated values indicate for all 49 samples.

Similarly, how should the richness values in Fig. 3 be interpreted? Based solely on the increases in richness seen in cores KR02, RS36, and JR01, it would be tempting to infer that floral richness increased around these sites over the course of the Holocene. However, another interpretation is also plausible: the increase in pollen richness is a function of a long-term decrease in pollen concentration and/or an increase in plant evenness at each of these sites (Figs. 3 and 4). Both these factors may be due to long-term cooling across the western and central Canadian Arctic, a trend that has been inferred from a range of proxies (Fisher et al. 1995; Kaplan and Wolfe 2006) as well as pollen influx values at all three sites (Gajewski 1995; Zabenskie and Gajewski 2007; Peros and Gajewski in press). The long term cooling may have resulted in lower pollen concentrations by impacting primary production (Peros and Gajewski in press), and it may have decreased the abundance of Cyperaceae (dominant in the Low Arctic) in relation to other Arctic herbs. Both these scenarios can explain the increase in detected richness without an increase in floral richness occurring. Thus, in the Canadian Arctic, long-term trends in pollen richness may be an artifact of changes in pollen concentration or evenness rather than the introduction of new species into the area of investigation.

From this, it follows that pollen concentration and evenness may be related. If high pollen

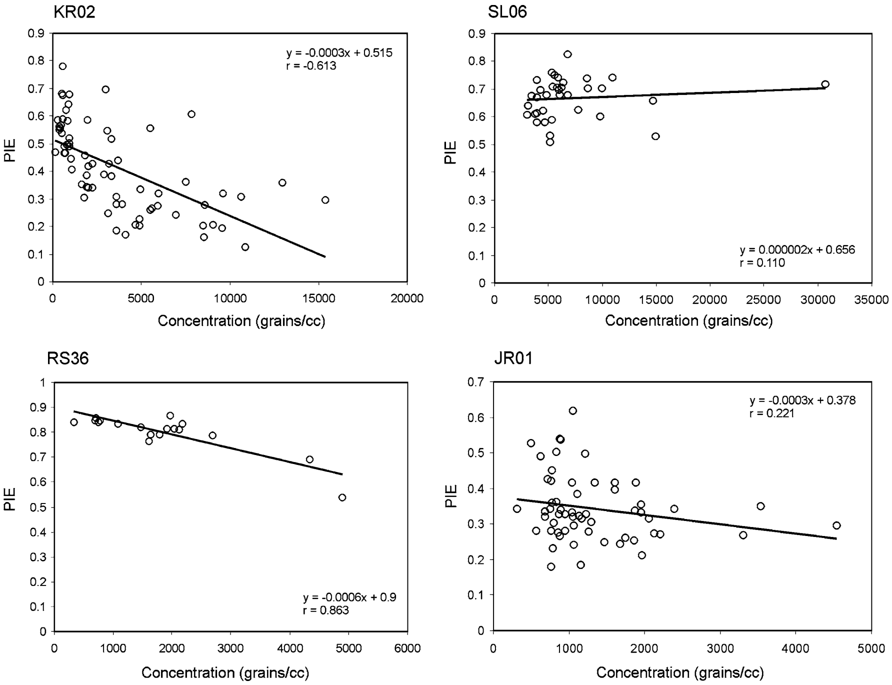

Fig. 7 Scatter-plots of pollen concentration versus estimated pollen evenness for each site shown in Fig. 3

concentrations are caused by the high production of a few plants (in the case of the Arctic, mostly Cyperaceae), this will lead to samples of low evenness, compared to samples of low production, where samples would have more even frequencies (van der Knaap personal communication, 2007). This relationship is apparent in cores KR02, RS36, and JR01 (Fig. 7), whose scatter-plots appear similar to those of Fig. 4, due to the strong correlation between evenness and richness (Fig. 5). Thus, pollen production (and sedimentation rates) determine pollen concentrations, which can influence evenness, and the probability that rare taxa are detected. This explanation of how concentration affects detected pollen richness differs from that of Weng et al. 2006 (discussed above), who suggest that the detection of more rare taxa in low concentration samples is because a greater proportion of the population is enumerated. Clearly, more work is needed to disentangle the complex relationship between concentration, evenness, and richness.

Ultimately, interpretations of pollen richness must be made cautiously and with an understanding of the entire range of factors that can influence rarefaction results (Birks and Line 1992; Weng et al. 2007). Particular attention needs to be given to samples of low concentration, such as those from low productivity areas such as the Arctic. However, the extent to which increasing the pollen sum would offset this problem is unclear. For example, a negative correlation between pollen richness and concentration appears to exist in three cores from southern Baffin Island, cores that have $E(T_n)$ values that range from 196 to 544. The authors note that periods of elevated palynological richness are linked to the expansion of open herb tundra (Fréchette et al. 2006); this relationship may reflect the productivity of these systems rather than their species richness.

Conclusions

Since the pioneering work of Birks and Line (1992), rarefaction analysis has become increasingly common in palynological investigations. However, the linkages between sample diversity, population diversity, and floral diversity are complex. A myriad of issues, including pollen production and dispersal mechanisms (Weng et al. 2007), influx (Smol 1981), sample size (Weng et al. 2006), and the relationship between pollen and plant diversity require careful consideration when interpreting rarefaction-derived pollen richness estimates. In this paper, we tested two important hypotheses relating pollen richness to concentration and evenness (Odgaard 2001; Weng et al. 2006). We show that pollen concentration can be important in the detection of rare taxa and thus influence pollen richness. Sample richness and evenness are positively correlated, but the strength of this relationship is likely inflated. Future investigations of this nature will help facilitate improved estimates of past plant diversity.

Acknowledgements We are grateful to the Canadian Foundation for Climate and Atmospheric Sciences (CFCAS) and the Natural Sciences and Engineering Research Council of Canada (NSERC) for financial support. We thank Tom Olszewski, Pim van der Knaap, André Viau, and an anonymous reviewer for valuable comments. Pollen counts for the Abernethy Forest core were obtained from the European Pollen Database; Hilary Birks kindly provided the associated concentration data. Any errors, misinterpretations, or omissions are ours alone.

References

Bennett KD, Boreham S, Sharp MJ, Switsur VR (1992) Holocene history of environment, vegetation and human settlement on Catta Ness, Lunnasting, Shetland. J Ecol 80:241–273

Berglund BE, Gaillard MJ, Bjorkman L, Persson T (2007) Long-term changes in floristic diversity in southern Sweden: palynological richness, vegetation dynamics and land-use. Veg Hist Archaeobot. doi:10.1007/s00334-007-0094-x

Birks HH, Mathewes RW (1978) Studies in the vegetational history of Scotland. V. Late Devensian and Early Flandrian pollen and macrofossil stratigraphy at Abernethy Forest, Inverness-Shire. New Phytol 80:455–484

Birks HJB, Line JM (1992) The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. Holocene 2:1–10

Cwynar LC (1982) A Late-Quaternary vegetation history from Hanging Lake, Northern Yukon. Ecol Monogr 52:1–24

Edlund SA, Alt BT (1989) Regional congruence of vegetation and summer climate patterns in the Queen Elizabeth Islands, Northwest Territories, Canada. Arctic 42:3–23

Faegri K, Iversen J (1989) Textbook of pollen analysis, 4th edn. John Wiley & Sons, Chichester, p 328

Fisher DA, Koerner RM, Reeh N (1995) Holocene climatic records from Agassiz Ice Cap, Ellesmere Island, NWT, Canada. Holocene 5:19–24

Fréchette B, Wolfe AP, Miller GH, Richard PJH, de Vernal A (2006) Vegetation and climate of the last interglacial on Baffin Island, Arctic Canada. Palaeogeogr Palaeoclimatol Palaeoecol 236:91–106

Gajewski K (1995) Modern and Holocene pollen assemblages from some small arctic lakes on Somerset Island, NWT, Canada. Quaternary Res 44:228–236

Gajewski K (2002) Modern pollen assemblages in lake sediments from the Canadian Arctic. Arct Antarct Alp Res 34:26–32

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4:9

Hurlbert SH (1971) The nonconcept of species diversity: a critique and alternative parameters. Ecology 52:577–586

Kaplan MR, Wolfe AP (2006) Spatial and temporal variability of Holocene temperature in the North Atlantic region. Quaternary Res 65:223–231

Legendre P, Legendre L (1998) Numerical ecology. Elsevier, Amsterdam, p 853

Moore PD (1973) The influence of prehistoric cultures upon the initiation and spread of blanket bog in upland Wales. Nature 241:350–353

Odgaard BV (1999) Fossil pollen as a record of past biodiversity. J Biogeogr 26:7–17

Odgaard BV (2001) Palaeoecological perspectives on pattern and process in plant diversity and distribution adjustments: a comment on recent development. Divers Distrib 7:197–201

Olszewski TD (2004) A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. Oikos 104:377–387

Peros MC, Gajewski K (in press) Holocene climate and vegetation change on Victoria Island, western Canadian Arctic. Quaternary Sci Rev

Porsild AE, Cody WJ (1980) Vascular plants of the Continental Northwest Territories, Canada. National Museum of Canada, Ottawa, p 667

Rannie WF (1986) Summer air temperature and number of vascular species in Arctic Canada. Arctic 39:133–137

Räsänen S, Hicks S, Odgaard BV (2004) Pollen deposition in mosses and in a modified 'Tauber trap' from Hailuoto, Finland: what exactly do the mosses record? Rev Palaeobot Palynol 129:103–116

Ritchie JC (1982) The modern and late-Quaternary vegetation of the Doll Creek Area, north Yukon, Canada. New Phytol 90:563–603

Seppä H (1998) Postglacial trends in palynological richness in the northern Fennoscandian tree-line area and their ecological interpretation. Holocene 8:43–53

Smol JP (1981) Problems associated with the use of "species diversity" in paleolimnological studies. Quaternary Res 15:209–212

Stuiver M, Reimer PJ, Bard E, Beck JW, Burr GS, Hughen K, Kromer B, McCormac G, van der Plicht J, Spurk M (1998) INTCAL98 Radiocarbon Age Calibration, 24000-0 cal BP. Radiocarbon 40:1041–1083

Weng C, Hooghiemstra H, Duivenvoorden JF (2006) Challenges in estimating past plant diversity from fossil pollen data: statistical assessment, problems, and possible solutions. Divers Distrib 12:310–318

Weng C, Hooghiemstra H, Duivenvoorden JF (2007) Response of pollen diversity to the climate-driven altitudinal shift of vegetation in the Colombian Andes. Philos Trans R Soc Lond B Biol Sci 362:253–262

Whitmore J, Gajewski K, Sawada M, Willimas JW, Minckley T, Shuman B, Bartlein PJ, Webb T III, Viau AE, Shafer S, Andersen PM, Brubaker LB (2005) A North American modern pollen database for multi-scale paleoecological and paleoclimatic applications. Quaternary Sci Rev 24:1828–1848

Young SB (1971) Vascular flora of St. Lawrence Island, with special reference to floristic zonation in the Arctic regions. Contrib Gray Herb Harv Univ 201:1–115

Zabenskie SD, Gajewski K (2007) Post-glacial climatic change on Boothia Peninsula, Nunavut, Canada. Quaternary Res 68:261–270