

Palynological richness and evenness: insights from the taxa accumulation curve

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Abstract Palynology provides the opportunity to make inferences on changes in diversity of terrestrial vegetation over long time scales. The often coarse taxonomic level achievable in pollen analysis, differences in pollen production and dispersal, and the lack of pollen source boundaries hamper the application of diversity indices to palynology. Palynological richness, the number of pollen types at a constant pollen count, is the most robust and widely used diversity indicator for pollen data. However, this index is also influenced by the abundance distribution of pollen types in sediments. In particular, where the index is calculated by rarefaction analysis, information on taxonomic richness at low abundance may be lost. Here we explore information that can be extracted from the accumulation of taxa over consecutive samples. The log-transformed taxa accumulation curve can be broken up into linear sections with different slope and intersect parameters, describing the accumulation of new taxa within the

section. The breaking points may indicate changes in the species pool or in the abundance of high versus low pollen producers. Testing this concept on three pollen diagrams from different landscapes, we find that the break points in the taxa accumulation curves provide convenient zones for identifying changes in richness and evenness. The linear regressions over consecutive samples can be used to inter- and extrapolate to low or extremely high pollen counts, indicating evenness and richness in taxonomic composition within these zones. An evenness indicator, based on the rank-order-abundance is used to assist in the evaluation of the results and the interpretation of the fossil records. Two central European pollen diagrams show major changes in the taxa accumulation curves for the Lateglacial period and the time of human induced land-use changes, while they do not indicate strong changes in the species pool with the onset of the Holocene. In contrast, a central Swedish pollen diagram shows comparatively little change, but high richness during the early Holocene forest establishment. Evenness and palynological richness are related for most periods in the three diagrams, however, sections before forest establishment and after forest clearance show high evenness, which is not necessarily accompanied by high palynological richness, encouraging efforts to separate the two.

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Introduction

Finding the causes for biodiversity patterns in space is a long standing goal in ecology and it has been recognized that processes working through time play an important role

(e.g. Rosenzweig 1995; McGlone 1996; White et al. 2010). Concern about the consequences of global warming for species diversity (e.g. Thomas et al. 2004) has stimulated new research on time dependent processes on large spatial scales (Normand et al. 2011). Numerical techniques and simulations employed in these analyses are powerful tools to explore hypotheses, although they can usually only test the outcome of the proposed scenario against present day patterns. It is therefore important to develop reconstructions of changes in diversity through time, in order to be able to test hypotheses and scenarios of past developments more directly. Pollen, preserved in lake and peat sediments, provides an important opportunity to evaluate past changes in floristic diversity in a landscape. However, palynological information differs from vegetation surveys in three aspects, hampering the application of indexes and ecological theory.

Taxonomy

The major obstacle, hindering comparisons of pollen-derived diversity indicators with floristic ones, is the coarser level of taxonomic identification achievable in pollen analysis. Improved morphological descriptions (e.g. Punt et al. 1976–2009; Beug 2004) and image recognition (Holt et al. 2011) are reducing the gap between pollen taxonomical differentiation and plant taxonomy, but it will probably remain impossible to close it completely. In relatively species-poor floras, a large proportion of the flora may be assigned to distinct pollen types or conversion models may be derived, relating the number of pollen types per sample to floristic richness (Odgaard 1994). For tropical forests with a high diversity of plant families, the assessment of richness at a family level may yield sufficient information to evaluate past changes (Jantz et al. 2013).

The taxonomical detail of identification varies between authors and depends on the pollen preservation, which may vary between samples. This hampers comparisons between sites, and analyses of surface sample data produced by more than one investigator. Assessing pollen type richness on a site basis, however, the identification of pollen types to parent species or genus is not strictly necessary, as long as the level of identification throughout the core is consistent. Here photo documentation using a digital camera is a great improvement, in particular in tropical palynology.

Productivity and dispersal

Differences between taxa in the amounts of pollen production and dispersal by wind or insects distorts the relationship between pollen proportions in sediments and abundance of plants in the surroundings of the study site. This effect may distort the diversity indexes, which

generally contain abundance information. Exchanging a high pollen producer for a low producer in the vegetation, for example *Betula* for *Tilia*, leads to changes in the proportion of all pollen types in a sample, while the diversity index would not change for the vegetation. This problem affects pollen analytical results in general and research efforts have been addressing it for a long time, devising factors (Davis 1963) and models (Prentice 1985; Sugita 1994) to adjust for differences in pollen production and dispersal. These approaches can be applied to reduce the production/deposition bias for the analyses of vegetation change through time (e.g. Nielsen et al. 2012; Reitalu et al. 2013). The different pollen production and dispersal of plants also affects the probability of detection of rare pollen types. Pollen types from taxa with a high pollen production may flood a sample, thereby reducing the probability of encountering pollen types occurring with a lower abundance (see for example Odgaard 1999; Weng et al. 2006).

Absolute abundance and lack of catchment boundaries

Where the interest of an investigation is on the upland vegetation and the investigated site receives most of the pollen by aerial transport, there is no natural limit to the area for which the results will be representative. There is an equal probability of encountering a pollen grain from a rare plant growing beside the study site or from an abundant occurrence of that plant many kilometres away. While it may be possible to define an area for which the information from a pollen diagram is relevant (Sugita 1994), or from within which a certain proportion of a pollen type may originate (Sugita 1993), it will remain impossible to determine whether a single pollen grain has come from within metres or hundreds of kilometres of the study site. The probability of encountering a pollen grain from a distant source increases with decreasing pollen production of the local vegetation. Samples from vegetation types with low pollen production like tundra therefore contain a higher proportion of pollen from distant sources. In these samples, there is also an increased probability of detecting pollen from rare plants (Peros and Gajewski 2008). Thus, changing from a low to high pollen producing environment, such as from an arctic steppe to boreal forest during the Lateglacial in central and northern Europe, represents an extreme case of exchanging a low for a high pollen producer. Where pollen accumulation rates are available, it is possible to calculate the number of pollen types deposited per area of lake sediment surface per year (Van der Knaap 2009). Such estimates provide important insights in situations where woody vegetation with a high pollen production invades a treeless vegetation (Van der Knaap 2009), but are rarely achievable, as they require ideal site conditions and good chronology.

Palynological richness

Palynological richness, the number of pollen types per sample at a standard count sum (Birks and Line 1992), is the most widely accepted diversity index for pollen data. The comparison to a standard count sum is necessary, as the probability of encountering a new pollen type depends on the size of the pollen count (Rull 1987; Weng et al. 2006). Where a standard sum was not maintained during pollen counting, this number is readily obtained through interpolation, using rarefaction (Birks and Line 1992). Thus palynological richness is a simple index with many advantages. Compared to diversity indexes containing abundance information, it is not directly affected by the pollen production/dispersal bias. However, this bias does influence palynological richness through the detection probability. Here pollen counts may be adjusted for the production/dispersal bias and rarefaction applied to the adjusted counts.

It seems that adjusting pollen counts for the production/dispersal bias will solve major problems in reconstructions of past vegetation diversity. However, these techniques require estimates of relative pollen productivity (e.g. Broström et al. 2008; Matthias et al. 2012), which are time-consuming to obtain, affected by large uncertainties and may differ in space and time. It is therefore worthwhile to further explore which aspects of diversity related information can be extracted from pollen data directly. This paper aims to contribute to the growing understanding of palynological diversity measures by exploring concepts and indexes for three datasets from central and northern Europe.

Methods

Datasets

For the purpose of illustration and exploration we have used three pollen diagrams from different landscapes on a north–south gradient. Lobsigensee is a small lake with a diameter of approximately 200 m, situated in an area formerly dominated by *Fagus* forest but today an intensively used agricultural landscape, 12 km northwest of Bern, Switzerland. The site was investigated by several sediment cores, of which the central core (LQ-90) is used here. Its long Lateglacial record and the presence of a Neolithic settlement at its shore result in a diagram with strong changes in vegetation structure and openness through time. Detailed descriptions of all pollen analytical results can be found in Ammann (1989).

Tegeler See, 750 km NNE of Lobsigensee, is situated in Berlin, Germany. The area around this large lake (exceeding

1 km²) is predominantly forested, intercalated with urban areas, while agriculture is generally absent within 5 km of the lake. The pollen diagram comes from a bay with a diameter of 200 m, situated at the north-western shore of the lake, where the vegetation is *Pinus* dominated mixed oak forest on sandy substrates (Brande 1996).

Holtjärnen is situated a further 850 km to the north, in Sweden. This small lake measuring 100 m across is surrounded by boreal forest, dominated by *Picea* and *Pinus*. Agricultural activity is limited in the area, with the nearest fields situated 1.5 km from the lake. Deglaciation occurred only in the early Holocene, when the lake was formed, and the pollen diagram documents the vegetation history starting within a few hundred years after the first plants became established (Giesecke 2005).

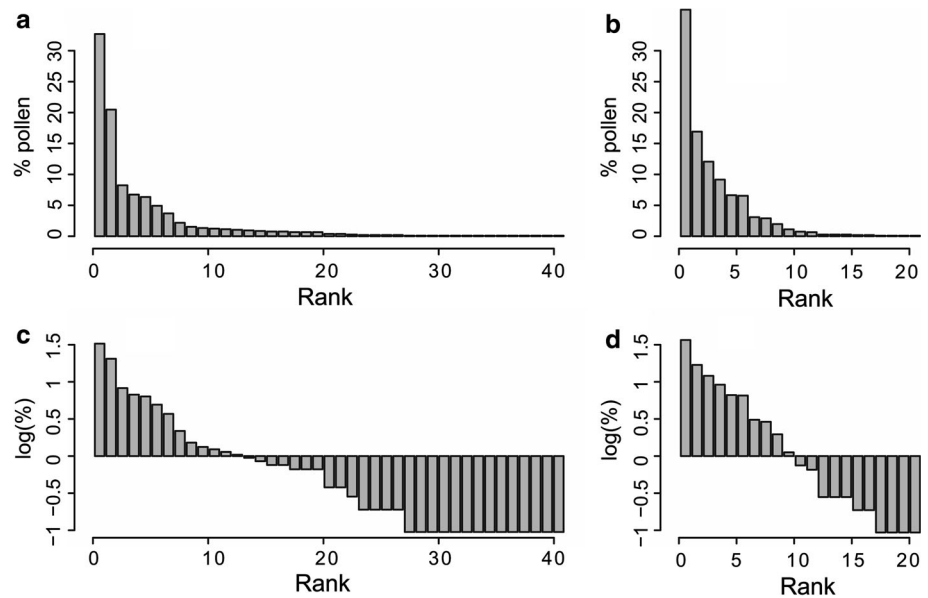
All pollen counts were limited to types produced by terrestrial flowering plants and the pollen taxonomy was adjusted to a similar level of differentiation across the three datasets. The resulting counts per sample are in the order of 1,000 pollen grains per sample, resulting in total numbers of identified pollen of 201,000, 323,000 and 138,000 per pollen diagram for Lobsigensee, Tegeler See and Holtjärnen respectively.

All calculations and computations were carried out using the R platform (R Development Core Team 2011) and the Vegan package (Oksanen et al. 2011). Scripts developed for all analyses can be obtained from the corresponding author.

Evenness

The high pollen production and dispersal of wind pollinated plants results in the dominance of their pollen types, while pollen from insect pollinated species will be rare even if the plants are common in the vegetation, leading to a skewed abundance distribution of pollen types (Fig. 1). It is thus improbable that all pollen types in a sample from diverse vegetation will be detected, while the evenness or equitability of pollen types in that sample may be more easily assessed. It would seem that there is an abundance of evenness indices available from which one can choose (Smith and Wilson 1996; Tuomisto 2012), but most include the number of taxa as a parameter. The number of taxa per sample is highly dependent on the pollen count (Rull 1987) and many of the rare taxa are only encountered once. The abundance of single occurrences would be automatically assigned to the inverse of the pollen count, while their true abundance in the sample would most likely be different. The importance of rare taxa in pollen samples is illustrated by two samples from Lobsigensee (Fig. 1). In the more diverse sample, two thirds of the encountered taxa had an abundance of less than 1 % and one-third were only encountered once.

Fig. 1 Rank-order abundance of pollen counts for two samples from Lobsigensee, with interpolated ages of **a** 1,670 and **b** 7,580 years cal. BP. Plots **c** and **d** display the same samples with the pollen proportions log-transformed. The declining trend is now linear and the slope indicative of sample evenness



The slope of the rank-order versus log abundance gradient (Fig. 1) is an intuitive and visual measure of evenness, proposed by Nee et al. (1992). However, this measure is also influenced by variations in the pollen sum through the detection probability of rare taxa. This influence can be excluded, applying percentage thresholds for the inclusion of taxa. Here a threshold of 1 % is used, so that the index is only calculated based on the abundance distribution of taxa that exceed 1 % in a particular sample. Smith and Wilson (1996) developed this index further by inverting the relationship, standardizing and transforming the index. Without standardization and scaling, the inverted slope of the log abundance versus rank-order approaches 0 for systems dominated by a single taxon, and infinity for complete evenness. As pollen samples are generally dominated by few taxa, the untransformed index may be suitable for pollen data and it is used here.

Richness

Palynological richness (Birks and Line 1992) is calculated using rarefaction to 500 pollen grains, as this is just below the minimum count for any sample in the three sequences. The index is compared to evenness, as calculated above, using a linear regression model. Palynological richness is highly dependent on evenness (Odgaard 2001) and the residuals between the regression model and palynological richness are displayed to highlight the differences. Rarefaction analysis is an interpolation to a lower count size and thus results in a loss of information (Birks and Line 1992). Palynologists often spend much time and effort to identify rare types, which are often important for the reconstruction of the past environment or human activity. Thus in

particular at the low abundance end, confidence in these identifications is high. However, the appearance and disappearance of a particular rare pollen type may not indicate the appearance or disappearance of the parent plant in the surrounding vegetation. In particular where successive samples are at most a few hundred years apart, it may be safe to assume that the plant also occurred in the area at times represented by later samples not containing the pollen type. This concept is little used in Quaternary palynology, but it is readily applied to studies of older sediments, where it is known as the range-through method (e.g. Jaramillo et al. 2010). Here the concept is applied as the accumulation of taxa over three consecutive samples as a running window from the bottom to the top of the sequence. Where the pollen counts are generally high and do not vary too much, the influence of variable count size should be minor and was therefore ignored. While this technique yields smooth changes in palynological richness through time, it has to be kept in mind that this process is deliberately smearing information and thus hiding possible abrupt changes.

The taxa accumulation curve

Accumulating the number of pollen types as well as the pollen sum over consecutive samples takes account of differences in count size and thus makes it possible to use the full pollen taxonomic differentiation per sample. This taxa accumulation curve is influenced by various processes. Assuming a stable regional species pool and no change in vegetation structure, the addition of new taxa over consecutive samples mainly represents a sampling effect that works in two ways: the probability of finding rare pollen

types increases with the number of pollen grains examined. Secondly, local abundances may change through time, and chance events may lead to an increased deposition of pollen types from less abundant species at different points in time. Considering these two effects, it may be assumed that all regionally produced pollen types would eventually be encountered with increasing samples and the taxa accumulation curve would form an asymptote. Although conceptually plausible, such an asymptotic trend has not yet been demonstrated (Weng et al. 2006), while the curves are found to follow power functions (Giesecke et al. 2012). The rate at which new taxa accumulate over consecutive samples is influenced by the evenness of pollen types in the sediment. At high evenness, a large proportion of the pollen type richness is encountered in a small sample and consecutive samples only slowly add new taxa. Conversely, for samples with the same number of pollen types and low evenness few types are encountered in the first sample, while subsequent samples will frequently contain new pollen types.

A change in vegetation structure or in the regional species pool will affect the taxa accumulation curve. For example the postglacial immigration and population expansion or deforestation and agricultural land-use will add new pollen types in addition to the sampling effect described above. In addition a shift in the abundance of high and low pollen producers will result in a shift in the evenness of pollen types and thus change the rate of taxa accumulation over consecutive samples. Such changes in the taxa accumulation curve are best investigated in log-transformation where the trends of the curve become linear. In this transformation the different rates of accumulation of new taxa appear as linear segments with different slopes and intercepts (Giesecke et al. 2012). This characteristic of the taxa accumulation curve is used here with the aim of extracting information on changes in richness and evenness over larger sections of the pollen diagram. To achieve this, the log-transformed taxa accumulation curve is broken up into linear segments (Fig. 2), with the constraint that a segment must contain at least five samples. Linear regression models are applied to an increasing number of samples from the bottom of the sequence to determine where the curve deviates from the linear trend, using a threshold of $R^2 = 0.9$. From this initial division the point with the highest coefficient of determination for a linear regression model is selected and the section cut after this sample. Samples included in this linear section are removed from the dataset and the process is started anew.

As described above, the slope and intercept of these linear segments contain information on evenness and richness of samples within the segment. The values themselves are not easy to interpret and the regression model was therefore used to determine the number of pollen types per pollen count of

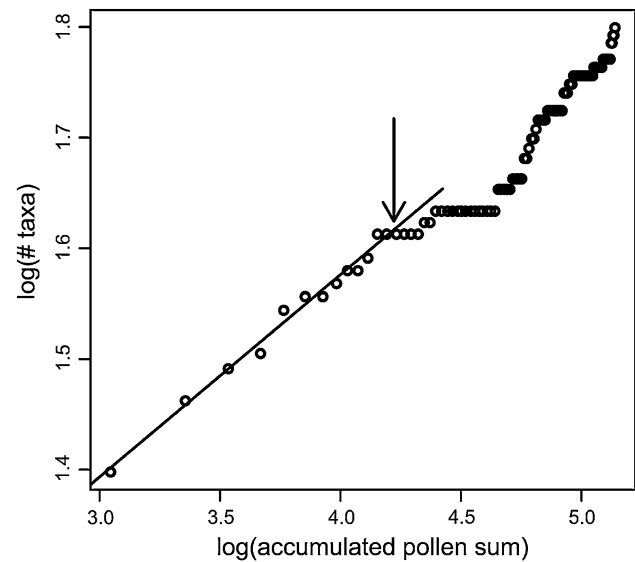


Fig. 2 Taxa accumulation curve for Holtjärnen. The *arrow* marks a breaking point in the curve, where samples start to deviate from the linear trend of the lowermost samples

100 and 10,000 grains. Samples from diverse and even sections have linear regressions with a gentler slope and a high y-intercept resulting in relatively high numbers of pollen types for counts of 100 and 10,000, while samples from diverse but uneven sections have steep slopes leading to low taxon numbers for a count of 100 and high numbers for counts of 10,000.

Results

Evenness as described by the slope of rank-order-abundance including all taxa is highly correlated with palynological richness to high pollen counts. This close relationship can be deduced from the examples in Fig. 1 indicating that the slope is influenced by the abundance of the most common taxa as well as by the number of types at low abundance. For Lobsigensee and Tegeler See, the good correlation holds when raising the threshold for the inclusion of taxa to 1 % on the calculation of evenness (Fig. 3). At this threshold the evenness hardly explains 5 % of the variance in palynological richness at $E(T_{500})$ for the Holtjärnen data, while the relationship is still significant. Regressions using different thresholds for the calculation of evenness and pollen sums in rarefaction analysis yielded residuals with interesting patterns through time, indicating that not all aspects of palynological richness can be explained by changes in evenness. The residuals of the regressions between sample based evenness, with a threshold of 1 % for taxon inclusion and in palynological richness at $E(T_{500})$, are displayed in the b panels of the

Fig. 3 Comparison between sample evenness as the inverse slope of the rank-order abundance of taxa exceeding 1 % in the sample and palynological richness as rarefaction to a pollen sum of 500 grains ($E(T_{500})$)

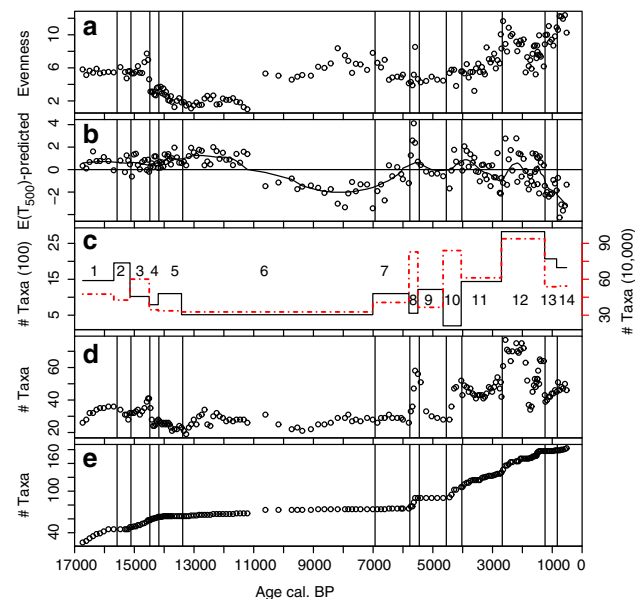
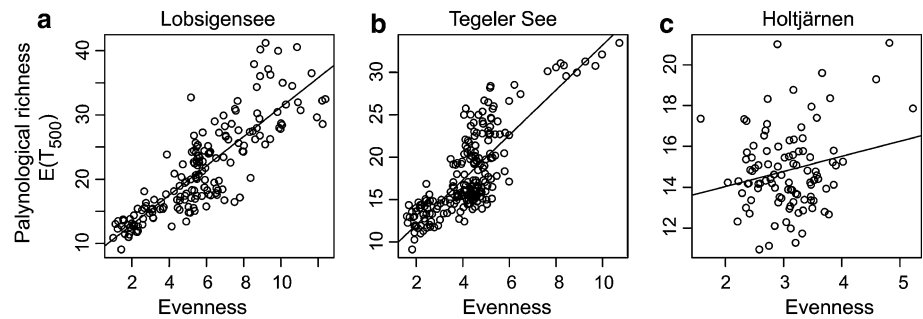


Fig. 4 Lobsigensee evenness and richness indicators. **a** Sample evenness as the inverse slope of the rank-order abundance of taxa exceeding 1 % in the sample; **b** Difference between palynological richness $E(T_{500})$ and predicted palynological richness from the linear regression model (Fig. 3) with evenness (**a**) as a predictor; **c** Estimated pollen type richness at a count of 100 grains (*solid line*) and 10,000 grains (*broken line*) from the taxa accumulation curve over successive sections. Breaking points in the taxa accumulation are used for zonation, identified by increasing numbers; **d** Number of pollen types in three consecutive samples as a running three-term-taxa-accumulation from the base to the top of the diagram; **e** Taxa accumulation curve

composite diagrams depicting evenness and richness indexes.

The richness and evenness parameters for the three sites reveal contrasting histories, emphasizing the effects of Lateglacial climate change and forest establishment as well as human land-use on diversity and evenness. Points of changing slopes in the taxa accumulation curve provide convenient divisions for all results, showing that this procedure detects important changes in the diversity and evenness of the underlying system. While these breaking points are purely derived from information on accumulative presence, they yield zones that often correspond to

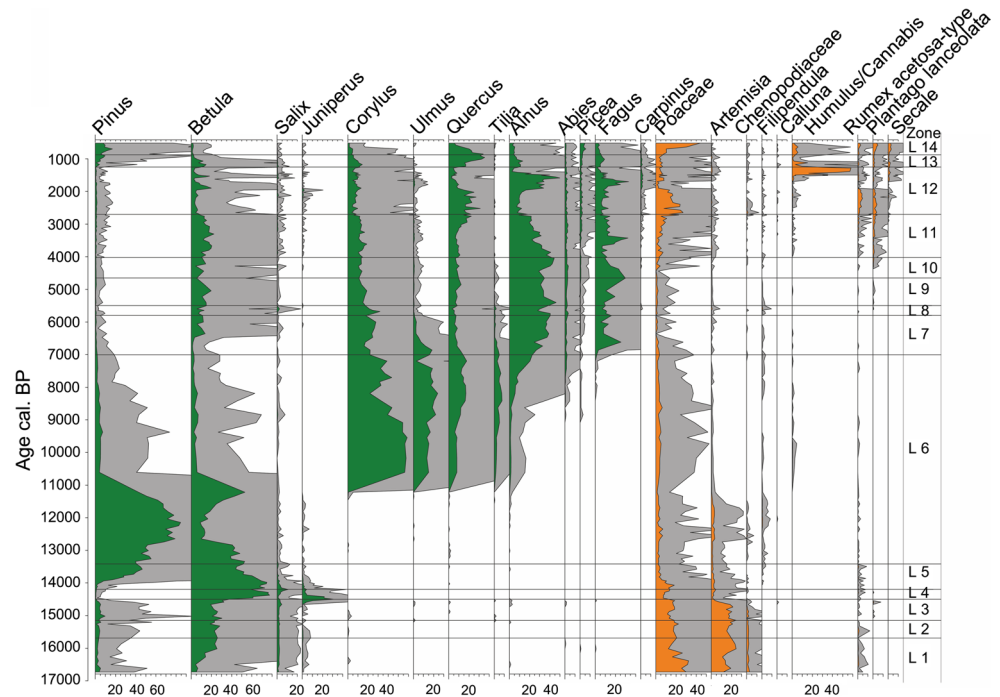
important changes in vegetation composition. However, these zones do not necessarily capture major changes in vegetation composition and may therefore not serve the same purpose as pollen zones determined by clustering or sequence splitting techniques (Gordon and Birks 1972).

The number of pollen types in counts of 10,000 grains represents the overall taxonomic richness of a particular section, which in many cases represents an inter—rather than an extrapolation, as the sections exceed accumulated pollen counts of 10,000 grains. In situations where the segment contains few samples that differ in their taxonomic composition (Fig. 4c, sections 8 and 10), the extrapolations may be biased. Extrapolations to counts of 100 grains represent the intercept of the regression models for the log-transformed taxa accumulation curve. In conjunction with the numbers for counts of 10,000 they indicate the rate of the accumulation of new taxa. For example a high number for 100 with a low for 10,000 indicates a low rate of accumulation and therefore low taxonomic differences between samples, which indicates an overall even distribution of pollen types within a section. The rate of taxa accumulation is represented by the slope parameter of the regression models for the different zones (ESM).

Lobsigensee

The oldest samples from Lobsigensee come from a treeless environment (Fig. 5) where local pollen production was low and long distance transported pollen grains contributed to the palynological richness. Pollen type evenness per sample is high (Fig. 3a), while the gain of new types over consecutive samples is relatively low, leading to a gentle slope in the taxa accumulation curve and low estimates for counts at 10,000 grains (Fig. 4, L1-2). The reduction in the number of pollen types in three consecutive samples (L2) may be explained by an increase in local pollen production, especially with higher pollen producers like *Betula nana*. The peak in *Juniperus* pollen (Fig. 5) marks a break in the slope of the taxa accumulation curve (L3/L4) and also characterizes the expansion of shrubby vegetation with the warming at the onset of the Bølling, leading to a peak in evenness and richness, followed by a sudden drop with the

Fig. 5 Lobsigensee percentage pollen diagram showing selected taxa. Zones correspond to the breaking points in the taxa accumulation curve (Fig. 4c)



expansion of tree birch (L4). The expansion of *Pinus* around 13,800 years ago led to an even stronger dominance of high pollen producers (L5). The Holocene warming did not lead to a change in the slope of the taxa accumulation curve, so that Zone L6 covers the Younger Dryas as well as the early Holocene. The change in forest composition from dominance of *Pinus* to a mix of *Corylus*, *Ulmus* and *Quercus* between 11,000 and 10,000 years ago is visible as a change in evenness. This replacement of one high pollen producer by two others had little effect on the representation of pollen from herbaceous taxa. Moreover, the denser canopy of the broadleaved trees may even have reduced the habitat for herbaceous taxa. In this long section, the palynological richness for a count of 10,000 represents an interpolation, and with 33 taxa it marks the lowest richness of the entire sequence. The end of this period is marked by the expansion of *Fagus* around 7,000 years ago. *Plantago lanceolata* and other pollen types, indicating human land-use, start to appear and the taxa accumulation curve indicates a higher richness of pollen types at low counts (L7) even though the overall sample evenness did not change. The following zone (L8) marks a period when a Neolithic settlement of the Cortaillod culture was in use at the shore of the lake and charred *Triticum* grains indicate local farming. Particularly high palynological richness in two consecutive samples leads to a steep taxa accumulation curve extrapolating one of the highest richness for a count of 10,000. This phase was relatively short and samples quickly drop back to ones containing fewer taxa, while many of the pollen types indicating human impact remain

present, leading to high between-sample evenness (L9). For L10, the taxa accumulation over three samples shows a steep increase over consecutive samples. The low and high extrapolations from the taxa accumulation curve are a result of the successive addition of new taxa rather than indicating low evenness and high richness. This increase leads to a lasting high richness, and high evenness (L11), starting around 4,000 years ago, with the early Bronze Age. Probably further deforestation at the beginning of the Iron Age (L12) explains the final increase in sample evenness and richness. During this period, the flora around Lobsigensee may have been the most diverse in this interglacial. Towards the top of the sequence samples are characterized by high evenness but lower palynological richness.

Tegeler See

The richness and evenness indicators for Tegeler See show a more gradual development (Fig. 6), compared to Lobsigensee. The diagram does not reach back to a time of treeless vegetation (Fig. 7). The oldest samples date to the Allerød, when *Pinus* and *Betula* covered the area around Tegeler See. This explains the low evenness of these samples (T1), as well as the steep taxa accumulation. Also for this site, the beginning of the Holocene does not cause a sudden change in pollen types or richness and the first 2,000 years of the Holocene fall onto the taxa accumulation curve from the Lateglacial. However, the *Juniperus* peak during the Younger Dryas in T2 is accompanied by a

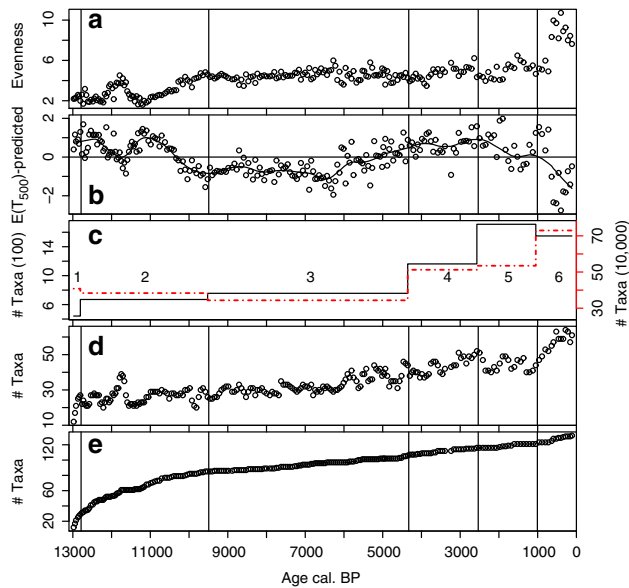


Fig. 6 Tegeler See evenness and richness indicators, for details see explanations in Fig. 4

greater richness of rare types. The T2/T3 boundary occurs right after the expansion of *Alnus* together with the decline in *Corylus*, and this increase in equitability of abundant pollen types is reflected by the rise in the number of pollen types in a sum of 100 grains. The large number of samples for T2 and T3 result in an interpolated value for the count at 10,000, showing that the number of rare types is higher for the Lateglacial and early Holocene compared to the mid Holocene. While regional human land-use is indicated by the continued occurrence of *Plantago lanceolata* from

5,800 years ago, the taxa accumulation curve is not broken until around 4,400 years ago. Archaeological finds near the coring site date to various periods during the Bronze Age. The number of pollen types occurring in adjacent samples increases towards the top of the zone (T4), probably caused by increased human activity so that here also, pollen type richness seems to be linked to human activity near the sampling site. The number of types within three consecutive samples and evenness drops with the onset of the next zone (T5), probably caused by trees and shrubs rapidly reclaiming cleared areas. Other pollen diagrams from the region and the abundance of archaeological finds indicate that human activity during the Bronze Age was more pronounced compared to the following Iron Age, which is in agreement with the richness and evenness curves. The slope of the taxa accumulation curve is lowest in T5, indicating the frequent occurrence of rare types and an altogether lower richness at counts beyond 10,000 grains compared to T4. The youngest samples (T6) are characterized by highest evenness with a strong trend in newly appearing taxa, which influences the slope in the taxa accumulation curve. The high evenness of the youngest samples, however, is not matched by high richness resulting in the highest deviation of the two entities.

Holtjärnen

The area around Holtjärnen only became available for plant growth during the early Holocene, and thus at least partly open vegetation is indicated by the high richness of the oldest samples (Figs. 8, 9, H1). Rare types disappear after the expansion of *Alnus* (H2), which is particularly visible in

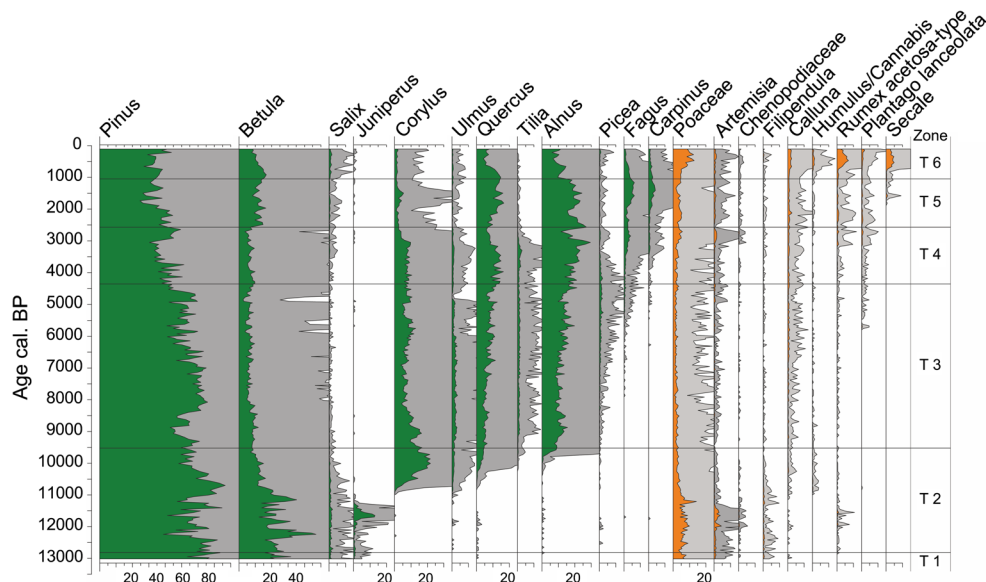


Fig. 7 Tegeler See percentage pollen diagram showing selected taxa. Zones correspond to the breaking points in the taxa accumulation curve (Fig. 6c)

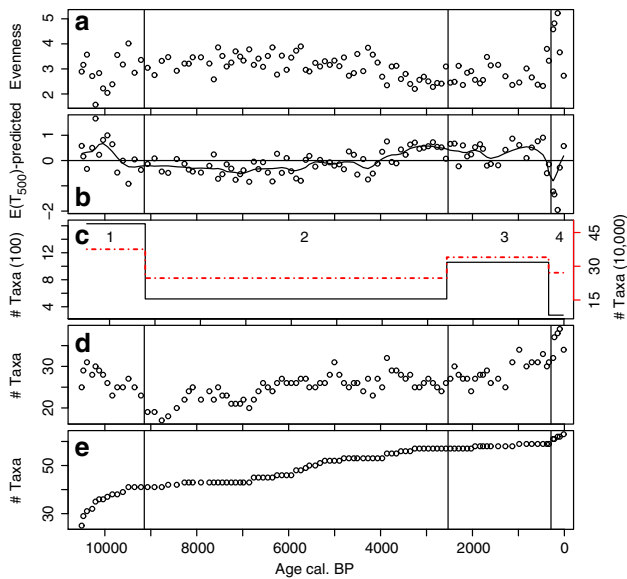


Fig. 8 Holtjärnen evenness and richness indicators, for details see explanations in Fig. 4

the number of taxa in three consecutive samples. Evenness decreases with the decline in thermophilous trees after 4,000 years ago, while the expansion of *Picea* marks a change in the accumulation of new taxa. Pollen types indicating human activity occur from the middle of H2, and increase in abundance in H4. Partial deforestation and increased farming leads to higher frequency of herbaceous taxa, while pollen grains from thermophilous trees disappear in H4.

The overall richness of pollen types changes little throughout the Holocene and the taxa encountered in counts of 10,000 grains demonstrate this. However, the probability of encountering rare types changes particularly

during the early Holocene and is highest around 10,000 years ago and lowest between 8,500 and 9,000 years ago. Samples with the highest evenness are comparably low in palynological richness at a pollen sum of 500 grains, as at the other sites. Between-sample differences, however, are still high resulting in a high slope of the taxa accumulation curve for section H4.

Discussion

The indices

The taxa accumulation curve provides an opportunity to compare pollen type richness at pollen counts that are usually not achieved during standard counts and allows considering the full list of identified types. Palynological richness assessed through rarefaction is a reduction to a common count size and information may be lost, while the use of the taxa accumulation curve provides a means of extrapolation. Moreover, differences in the pollen sum of individual samples should not have an influence. The full spectrum of identifications can also be used in comparisons when combining the samples into bins (Giesecke et al. 2012). However, bins may combine periods with different vegetation structures. Here the breaking points in the taxa accumulation curve provide the means to detect changes in the appearance of new taxa, which may be used to divide pollen analytical results with a focus on palynological richness. The breaking points depend on how much deviation from the log-transformed linear relationship is allowed. Raising the threshold to $R^2 = 0.95$, restricting deviations from a perfect linear relationship, results in only two more zones for Lobsigensee and six more for Tegeler

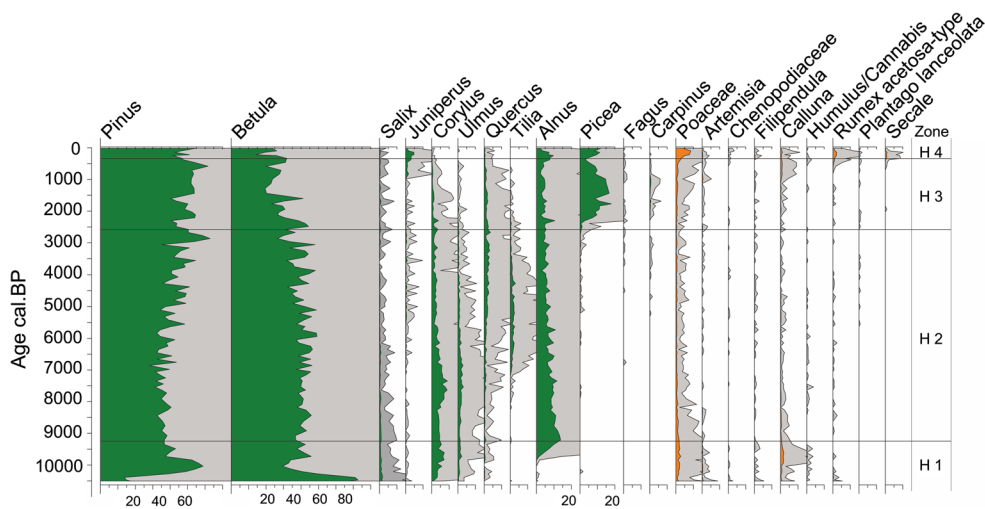


Fig. 9 Holtjärnen percentage pollen diagram showing selected taxa. Zones correspond to the breaking points in the taxa accumulation curve (Fig. 8c)

See. In both cases the additional zones add detail to the Lateglacial and human land-use induced changes. For Lobsigensee, the additional divisions do not separate the long stable section encompassing the Younger Dryas and early Holocene, while for Tegeler See an additional split is set at the beginning of the Holocene, also removing the division after the rise of *Alnus*. The diagram from Hotjärnen is comparatively species poor and lacking strong changes, so that a tighter threshold results here in changes that may be created by chance.

Slope and intercept parameters of the regression models for the log-transformed taxa accumulation curve yield insights into diversity and evenness over consecutive samples. The change of these parameters was visualized by the taxonomic richness at a low and high pollen count, but other forms of visualization are possible. These slope and intercept parameters are susceptible to the successive appearance of new pollen types, as may be expected in connection with the immigration and population expansion of taxa. The effect however, was not pronounced at the beginning of the Holocene, but rather in connection with rapid change in human land-use. This successive appearance of new pollen types is well captured by the taxa accumulation over three samples, highlighting the occurrence of rare types. Even though this upwards propagation of occurrence information creates the impression of smooth trends, abrupt changes in diversity can still be discerned.

Most European trees have a high pollen production, while herbaceous vegetation with low pollen productivity makes up the highest proportion of plant diversity. Thus it is no surprise, that in European landscapes with a high proportion of forest cover, palynological richness is correlated with the size of open landscape around the site (Meltsov et al. 2013). The reduction in forest cover also reduces the dominance of a few pollen types from high pollen producers and therefore also balances the abundance distribution of the different pollen types. The pollen diagrams from Lobsigensee and Tegeler See reflect changing proportions of forest cover through time, and this may explain the good correlation between palynological richness and evenness. Although the slope of the rank-order abundance is an evenness indicator that can be easily visualized, it is directly influenced by the number of taxa included. Colombaroli and Tinner (2013) use the probability of interspecific encounter (Hurlbert 1971) as an evenness indicator in a similar study including Lobsigensee and further sites towards the south. This indicator seems to perform well describing the Lateglacial changes in evenness of Lobsigensee, while it appears less sensitive in depicting the effect of forest clearance. The index was further employed to account for the effect of evenness on palynological richness (Colombaroli and Tinner 2013). This adjusted palynological richness may be useful

in situations such as the Lateglacial to Holocene transition where evenness does affect palynological richness at Lobsigensee. However, the analyses presented here indicate that the relationship between evenness and richness is more complex.

Pollen taxonomic considerations have important implications in all indexes which are highly influenced by presence/absence of pollen types. Where within one sequence different hierarchical levels are used to denote different certainties in identification, for example *Plantago media*, *P. major/media*, *Plantago* undiff., they should be combined at the higher taxonomic level for this type of analysis.

Palaeoecological implications

It is surprising to see that the onset of the Holocene did not result in a break in the taxa accumulation curve for the two southern sites (see also Colombaroli and Tinner 2013). At Kråkenes in western Norway, Birks and Birks (2008) have documented a rapid turnover of taxa at the onset of the Holocene, which they interpret as primary succession, comparable to floristic turnover on recently deglaciated modern glacier forelands. At Lobsigensee and Tegeler See, *Pinus* dominated woodlands developed during the Lateglacial. Although these woods opened during the Younger Dryas cold spell, both lakes remained within the continuous distribution area of *Pinus* woodlands (Theuerkauf and Josten 2012). Thus the species were in place at the onset of the Holocene warming and responded with changing abundances, quickly building up dense forests, hampering the population expansion of newcomers. On the richer soils and with the higher precipitation regime around Lobsigensee, the *Pinus* dominated forest was replaced by a mixed forest within 1,000 years after the onset of the Holocene and this change is pronounced in the evenness index. In contrast, on the nutrient poor sandy soils around Tegeler See, *Pinus* maintained its dominance throughout the Holocene, which may explain the only gradual increase in the abundance of other tree taxa and thus the gradual rise in evenness. Here the expansion of *Alnus* causes a break in the taxon accumulation curve (T2/T3), but this only leads to a small adjustment of the slope and intercept of the regression. Ignoring this adjustment, both pollen diagrams from Lobsigensee and Tegeler See follow a linear trend in log taxa accumulation from the establishment of *Pinus* dominated forest during the Lateglacial until human land use increased the number of pollen types encountered over consecutive samples. Before the human determined phases, the number of different pollen types encountered at a sum of 10,000 is with 33 and 34 almost the same for Lobsigensee and Tegeler See respectively. At Holtjärnen that number for a comparable period is only 25, indicating a lower floristic diversity. The highest richness of pollen types with a count of 10,000 was obtained

for Lobsigensee for the time from the Iron Age to the medieval period and the last millennium for Tegeler See, respectively. These numbers are double and almost triple the numbers for the early Holocene, which could lead to an interpretation that many of those parent plants were only introduced to the region by early farmers. However, the Lobsigensee pollen diagram shows that a large number of pollen types also occur in samples dating to the time of the establishment of woodland at the beginning of the Bølling warming. This period marks a time of strong compositional and structural changes in the vegetation cover, from an arctic steppe over shrubland to woodland vegetation. This succession is comparable to that documented by Birks and Birks (2008) for the onset of the Holocene warming in western Norway. The large number of pollen taxa for this period may be partly attributed to the turnover of the floristic composition, and a number of cold-adapted species may have become locally extinct. However, the pollen types of many herbaceous taxa, which are part of the present central European flora, first appeared in Lateglacial deposits (Giesecke et al. 2012) and then became so rare that they virtually disappeared from pollen diagrams until human land-use increased their habitat (apophytes).

Conclusion

The taxa accumulation curve enables the full use of pollen taxonomical differentiation and provides extrapolation of palynological richness to higher pollen counts. Changes in the trend of the accumulation of new taxa over consecutive samples indicate changes in richness and evenness of the underlying system and these breaking points provide a useful zonation for pollen analytical results where the focus is on palynological richness. Extrapolations from the taxa accumulation curve assume that the vegetation surrounding the sampling site was stable over this period. The successive addition of new taxa to the system, as may occur through increasing human land-use, affects the taxa accumulation curve and such effects need to be evaluated using additional indexes. The upwards propagation of presence over a limited number of samples was found to be a useful index also including the full extent of taxonomic information. Evenness of the distribution of pollen types in the sample is another useful parameter that may be computed using the rank-order-abundance.

The application of these indexes to three pollen diagrams has shown that the onset of the Holocene did not result in strong changes in taxonomic composition. Over a period encompassing the Younger Dryas and the early Holocene, both diagrams from Lobsigensee and Tegeler See follow an even taxon accumulation curve suggesting a stable regional species pool. Landscapes with the highest floristic diversity

are those created by human land-use, unrivalled by natural processes. However, while palynological richness peaked during the last millennium at Tegeler See, it was lower for that period at Lobsigensee. Samples from the last millennium at Lobsigensee have among the highest sample evenness, but lower richness considering all rare types. This makes a good example of the value of separating palynological richness and evenness.

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