# Aquatic ecosystem shifts in response to early human land-use changes in two low-elevation lakes in northwestern Europe


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**ABSTRACT – Growing problems related to eutrophication of (freshwater) aquatic systems, e.g. loss of biodiversity, availability of clean water and problems with its recreational and food services, highlight the necessity for management and conservation of such systems. For this, adequate understanding of the causes and consequences of the shifts in nutrient availability is required, as well as proper reference baselines. Therefore, this study aimed to reconstruct pre-human impact baselines for two low-elevation lakes in northwestern Europe, Hijkermeer and Llangorse Lake, with the use of trophic state transfer functions based on diatoms. Also, the ecosystem's response to these changes was analysed and an attempt was made to delineate natural variability from human impact. Over ca. 3400 yrs the inferred trophic state of Hijkermeer shifted from oligotrophic (12 µg TP/L) to mesotrophic (32 µg TP/L), coinciding with continuously increasing anthropogenic activity in the catchment. The reconstructed trophic state of the Llangorse Lake increased from a eutrophic (54 µg TP/L) to hypereutrophic (168 µg TP/L) state between ca. 5000 and 2500 cal. yr BP and subsequently the trophic state returned again to former levels. This appeared to be related to a simultaneous temporary increase in agriculture as indicated by the pollen record. A remarkable observation was that the relation between the trophic state and diversity seemed to be unimodally distributed and the ecosystem of Llangorse Lake appeared to show a recovery of diversity following the phase of increased nutrient availability and anthropogenic activity. This showcases the resilience of the ecosystem and could be used as a model for (on-going) management and conservation of the present eutrophication problems.**

*Key words: Eutrophication; Palaeolimnology; Diatoms; Transfer functions; Pollen; Diversity; Ecosystem resilience*

# Introduction

Increasing anthropogenic pressure on aquatic systems through enhanced nutrient input from agriculture and sewage, especially phosphorus (P) and nitrogen (N), is causing major local and global environmental problems with respect to water quality (Elser et al. 2007; Conley et al. 2009). This human induced eutrophication causes numerous shifts in ecosystem structure (Davidson and Jeppesen 2013) and generally leads to excessive growth of bloom-forming (noxious) algae (Paerl and Huisman 2008; Burford et al. 2012), which subsequently results in development of hypoxia, light limitation, and loss of biodiversity (Davidson and Jeppesen 2013). These changes impact the quality and availability of clean water, which threatens the recreational and food services the ecosystem supplies, leading to costly mitigation measures (Davidson and Jeppesen 2013).

For adequate management and conservation aiming at restoration of the freshwater ecosystems, it is of great significance to define both the natural pre-disturbed nutrient status, or baseline conditions, and the subsequent ecosystem thresholds triggered by past shifts in nutrients (Withers et al. 2014). This information, combined with data from mesocosm experiments can contribute to the refining of current models that assess the effectiveness of water-quality mitigation (Trolle et al. 2014).

In absence of long-term monitoring data, the biotic proxy data from sedimentary archives can be used as a tool to reconstruct environmental changes back in time (e.g. Batterbee 1999; Cremer et al. 2009; Kirilova et al. 2010). Most ecological baseline research focuses on the period since the industrialisation (Bennion and Appleby 1999; Cremer et al. 2009), i.e. the last ca. 200 years, during which mechanisation took place and use of (artificial) fertilizers in agriculture intensified (Smol 2008). However, anthropogenic activity has potentially impacted aquatic systems years prior (Messerli et al. 2000; Edwards and Whittington 2001), beginning with deforestation. The clearance of forests that is associated with (early) agriculture leads to erosion and less uptake of nutrients by the soil, enhancing nutrient leaching into the aquatic environments (Edwards and Whittington 2001; Dearing et al. 2006).

Even though it is difficult to accurately define the first human impact, it is feasible to use vegetation reconstructions based on pollen preserved in lake sediments to determine the

onset of agriculture and its intensification: identified through a decrease in arboreal pollen and an increase in crops (e.g. *Secale spp.,* rye), together with associated ruderal weeds (e.g. *Centaurea cyanus,* cornflower) (Behre 1981). Archaeological evidence in the catchment of the lake can be also used to support the pollen record (Bakker 2003).

On naturally oligotrophic systems in particular, deforestation and associated erosion is likely to have a subtle but noticeable impact on past trophic conditions in lakes, which largely affects the ecosystem. As diatoms are known to be highly sensitive to water chemical composition, they are often used as proxies for changes in water quality (Bradshaw et al. 2005; Davidson & Jeppesen, 2013; Smol & Stroemer 2010). Available autecological data provides both a qualitative (Vos and de Wolf 1993; Van Dam et al. 1994) and quantitative relation (Bennion et al. 1996; Nodine and Gaiser 2014) between modern diatom assemblages and environmental variables, which can be used to infer past shifts in these environmental parameters based on the diatom assemblages present in a sediment core (Van Dam et al. 1994). In order to quantitatively infer past total phosphorus (TP) concentrations from modern TP concentrations, mathematical transfer functions have been generated for different environmental regions, using a training set of modern surface-sediment diatom samples and contemporary TP concentrations from a large number of lakes (Nodine and Gaiser 2014). Although there is a strong relationship between the diatom assemblage and TP, Juggins and Anderson (2013) state that the transfer functions have to be handled with caution, largely because the model cannot fully reflect the ecological complexity: secondary environmental variables such as alkalinity and water depth can also influence the diatom assemblage. Mostly these transfer functions are applied to infer TP concentrations during the last centuries, however, Bradshaw et al. (2005) demonstrated that they can also be used to reconstruct the past millennia, while discussing the additional pitfalls such as increased potential of taphonomic problems and missing analogues. Spatial (Jeppesen et al. 2000) and temporal (Das et al. 2008) studies highlight the unimodal relation between TP and diversity, where increasing TP concentrations stimulate primary production and initially leads to higher biodiversity. In case of further increase in TP leading to highly eutrophic conditions certain blooming species are favoured causing a subsequent decline in biodiversity. However, linking early agriculture practice over longer timeframes to shifts in water quality and associated ecosystem disturbances has not been analysed extensively. Especially understanding

ecosystem recovery in areas where human activity showed a temporary increase is of great significance for restoration purposes.

Therefore, this study aims to (1) define the timing and reconstruct the water quality of pre-, maximum and post-disturbance water bodies, (2) attempt to separate the imprint of anthropogenic activity from natural variability, so that natural baselines can be identified and (3) relate the shifts in biodiversity to this increasing (and/or decreasing) human impact.

In order to address these aims, two low-elevation lakes in northwestern Europe, Llangorse Lake (Wales, UK) and Hijkermeer (The Netherlands), will be studied: shifts in their water quality and biodiversity during the last ca. 5000 years will be reconstructed with the use of diatoms. Furthermore, the reconstructions will be compared to the land-use history from available and new pollen data. Both lakes, currently differing in trophic state and physical parameters such as depth, size and drainage area, are located in areas where archaeological and pollen data indicate the presence of early human settlements. Ecological theory (Scheffer et al. 2001) and recent observations (Cremer et al. 2009) predict that increased anthropogenic pressure will result in enhanced nutrient availability, which can have major implications for the ecosystem state. Scheffer et al. (2001) state that water clarity does not decrease gradually with enhanced nutrient input, but the lake shifts abruptly from a clear to a turbid state when a certain nutrient threshold is passed. The associated ecosystem perturbation triggers positive feedback mechanisms as it includes the loss of submerged macrophytes, which are major players in controlling the ecosystem in a lake with naturally clear waters and thereby maintains its nutrient level and with that transparency. Fish are on the other hand suggested to maintain a turbid state. This phenomenon is called hysteresis: the occurrence of different stable states in an ecosystem, in which the transition between the states follows differing pathways. In the case of eutrophied lakes, often a lower nutrient level is required for the restoration of the original clear-water state than were present when the shift from a clear to a turbid state occurred. The amount of disturbance a system can handle without shifting to another state or the capability of the ecosystem to return to the pre-disturbed stable state is related to the resilience of the ecosystem and is largely dependent on its structure (Elmqvist et al. 2003). For example, high biodiversity can enhance the resilience when ecological functions are maintained by several species, so that small extinctions do not necessarily lead to drastic shifts in ecosystem functioning (Walker 1995).

Since the anthropogenic pressure differs between the two lake systems of the present study and changes over time, the associated ecosystem response and the natural recovery rates after a maximum in landscape disturbance will be investigated.

## Study area

Hijkermeer (52°53'23"N 6°29'31"E, 14 m.a.s.l) is a pingo-remnant located near the town of Beilen on the Drenthe Plateau in The Netherlands (Fig. 1). The Drenthe Plateau is well known for the megalith tomb constructions, or 'Hunebedden', built by farmers of the Funnel Beaker Culture in the Neolithic around 5000 years BP (Bakker 2003). The lake is small and shallow, with a diameter of 200m and a maximum depth of 1.6m; river inlet and outlets are absent, minimizing the catchment area. A late-glacial chironomid, pollen and diatom study of Hijkermeer has already been provided by Heiri et al. (2007), indicating that the lake was oligo- to mesotrophic during this time-frame (14000-10700 cal. yr BP).

Llangorse Lake (51°55'40.2"N 3°15'10.9"W, 150m m.a.s.l.) is a Lateglacial basin located in the Brecon Beacons in Wales, UK (Fig. 1). The lake consists of two basins and is mainly fed by the river Afon Llynfi, entering in the south and draining in the north, giving the lake a large catchment size. The area surrounding the lake has a long history of anthropogenic activity, indicated by the presence of megalith tombs (Cummings et al. 2002), an old roman road (Chambers 1999) and a 10$^{th}$ century artificial island (crannog), built in the northwest of the lake (Campbell and Lane 1989). Moreover, medieval literature already suggested the presence of algal blooms occurring within the lake (Griffiths 1939). Water chemistry data for the period between 1995-1996 indicates that the lake was alkaline, 2331-2560 µeq/L, at that time, the pH ranged from 7.88 to 8.08 and the TP from 69.6 to 149.7 µg/L, indicative of nutrient-rich conditions and large seasonal differences (Duigan et al. 1999). The TP concentration is currently enhanced by anthropogenic activity, but additionally by the release of the internal phosphorus load stored in the sediment, underlining the need for conservation and management measures (Bennion and Appleby 1999).

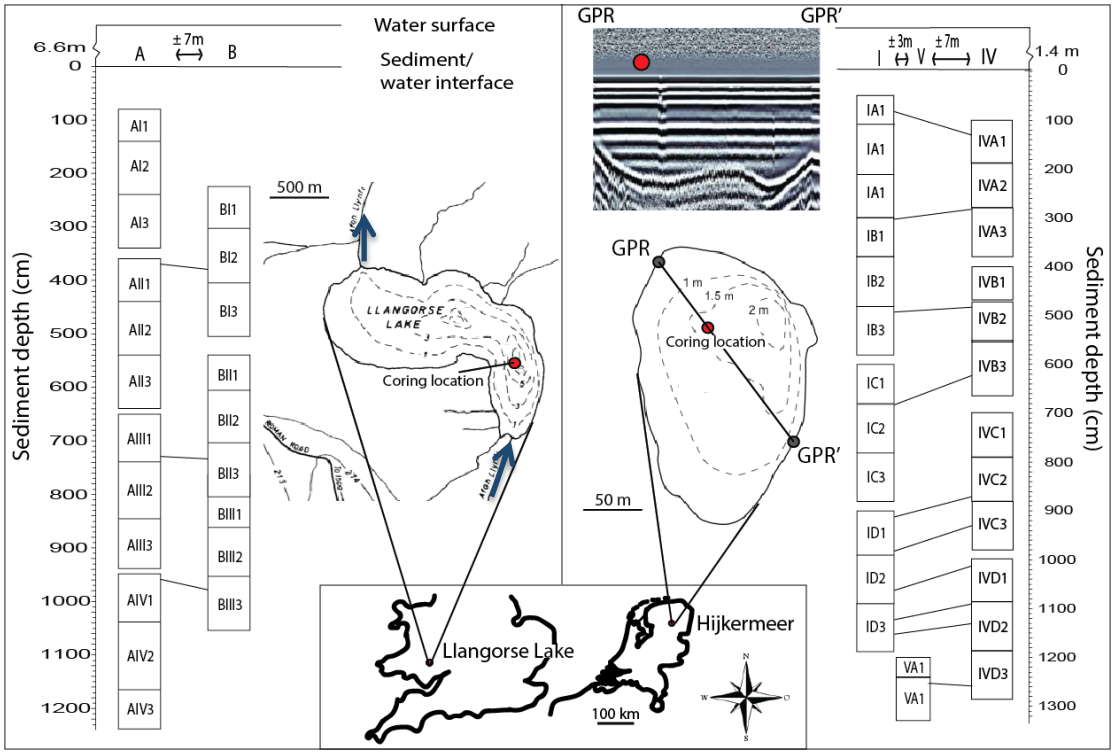


**Figure 1.** Topographic setting of Llangorse Lake and Hijkermeer, including bathymetry based on Jones et al. (1985) and Heiri et al. (2007) respectively, an overview of the retrieved cores in both lakes and the basin structure of Hijkermeer based on GPR measurements.

# Material and methods

## Sediment coring

### Hijkermeer

Sediment cores were collected in spring 2013 at 1.4m water-depth, using a piston corer (UWITEC, Mondsee, Austria) deployed from a floating platform. The coring site was selected based on bathymetry data provided by Heiri et al. (2007) and additional ground-penetrating radar (GPR) surveys to locate the thickest sediment infill and centre of the basin (Fig. 1). Two parallel sediment cores were collected, with a maximum sediment depth of 13.5 meters, comprising 3 core segments of ca. 3 meters each (Fig. 1). These 3-meter core segments were partitioned into ~1 meter sections in the field.

**Llangorse Lake**

Sediment cores were collected in summer 2014 at 7m water-depth, using the same setup as in Hijkermeer. Since the lake has two sub-basins, the centre of each basin was cored; the present study focuses on the sediment cores collected in the southern basin. Two parallel sediment cores were retrieved, with a maximum depth of 12 meters, comprising 3-4 core segments of 3 meters length each (Fig. 1). These 3-meter core segments were partitioned into ~1 meter sections in the field.

## Sedimentological analysis

Cores were transported horizontally and after they were split, the sediments were described and photographed. X-ray fluorescence scans with an Avaatech XRF core scanner were performed on the Hijkermeer cores at the Netherlands institute for Marine Research (NIOZ) to determine major elemental ratios. The sediment surfaces of the split cores were cleaned and covered with a thin (4µm) Ultralene film to avoid contamination from the measurement prism. Measurements were performed at on 1-cm resolution with 10 sec. count time at 10 and 30 kV for light and heavy elements, respectively (Hennekam and De Lange 2012). High-resolution Loss-on-ignition (LOI) was performed on 99 samples representing the entire sequence from Llangorse Lake, according to standard techniques defined by Heiri et al. (2001).

## Age dating and chronology

In the Hijkermeer sequence, a total of fourteen samples containing a sufficient amount of identified terrestrial plant remains were dated by use of Accelerator Mass Spectrometry (AMS) radiocarbon dating (Table 1). The chronology of the sedimentary record of Llangorse Lake is based on seven AMS radiocarbon dates measured on bulk sediment, as well as one lead-210 dating (Table 2), measured on a sediment core retrieved in Llangorse Lake by Jones et al. (1985) that could be correlated to the new core by means of its Loss-on-ignition profile (Fig. 3). The radiocarbon ages were calibrated using IntCal13 curve selection within CALIB 7.0 (Stuiver and Reimer 2013). The average of the smallest and largest intercept was used with a 1-sigma probability. An increase in lead at ca. 100 cm in the Hijkermeer sequence (XRF elemental ratios, fig. 6) is indicative of the onset of air pollution in the Netherlands at ca. 1880 AD (Fig. 6) (Cremer et al. 2010) and was added as an age control point. Regarding the

spreading of the radiocarbon dates, the reconstructed age-depth model for Hijkermeer was separated into two sections: the radiocarbon dates in the lower part of the sequence were interpolated using a fourth order polynomial regression and the upper part of the sequence with a second order polynomial regression. The radiocarbon dates of the Llangorse Lake sequence were interpolated using a fifth order polynomial regression.

## Pollen analysis

A total of 73 samples of the Hijkermeer sequence were processed for pollen analysis following Faegri and Iversen (1989), with increased resolution in the oldest sediments. Sodium pyrophosphate was used to deflocculate clays and a mixture of 9:1 acetic anhydride and sulphuric acid was added for acetolysis. Subsequently the samples were boiled in 10% KOH and finally floatated over sodium polytungstate (s.g.= ~2.1 g $cm^3$) in order to separate organic materials from minerals. Glycerol was added to the processed samples in order to make pollen slides. In samples with sufficient pollen concentration a minimum of 300 palynomorphs was counted, of which at least 200 tree pollen, at 400x magnification under an Olympus CX41 microscope. A pollen diagram was created using TILIA 1.7.16 (Grimm 2011), whereby the pollen percentage sum was based on the regional taxa, e.g. trees/shrubs, upland herbs and cereals. Taxa such as heaths, grasses, aquatics, ferns and mosses were considered to be local and therefore excluded from the pollen sum. Pollen zones were defined following Janssen and Törnqvist (1991).

## Diatom analysis

Subsampling for diatom analysis was focused on sections in the time interval corresponding to the period between 5000 years ago and present, with increased resolution in parts of interest for the study. A total of 17 samples for Hijkermeer and a total of 19 samples for Llangorse Lake were freeze dried and a known weight was processed using potassium permanganate ($KMnO_4$) and 30% HCl to remove the organic material and carbonates, respectively. Slides were prepared using the evaporation tray method of Batterbee (1973). Permanent slides for diatom analysis were prepared using Naphrax® as mounting medium.

In most samples, a minimum of 300 valves were counted at 1500x magnification using Olympus BX51 microscope, fitted with inference phase contrast. A few Hijkermeer samples

contained very low valve concentrations and were therefore counted up to 100-150 valves. Identification and taxonomy was primarily based on Krammer and Lange-Bertalot (1986; 1988; 1991a; 1991b). The stratigraphically constrained sum of squares cluster analysis of the CONISS program (Grimm 1987) provided by TILIA 1.7.16 (Grimm 2011) was used to determine diatom zonation; species with less then 2% abundances were excluded from the calculation.

Water quality was estimated using two methods: A semi-quantitative method and a quantitative method. The former was based on the ecological preference list of Van Dam et al. (1994), which includes the ecological preference of diatoms in brackish and freshwater Dutch lakes comprising 948 taxa (this method will be further referred to as TS-VD). With regards to the quantitative method, total phosphorus was estimated using statistical prediction models based on the Combined TP-dataset comprising data on 345 lakes, which is available on the EDDI website (http://craticula.ncl.ac.uk/Eddi/jsp/)(Batterbee et al. 2000)(this method will be further referred to as diatom inferred-trophic state: DI-TP). For this, WA-PLS (Ter Braak and Juggins 1993) regression was applied to the database, which combines weighted averaging (WA) with partial least squares (PLS) to improve the fit between the biological data and the training set by considering the residual correlations in the biological data (Birks et al. 2003). The performance of the inferred model was assessed by use of bootstrapping, a computer intensive cross-validation procedure that simulates an independent test set from the training set to mimic sampling variation in the training set (Birks et al. 2003). The similarity between a fossil sample and each modern training set sample was validated with the $\chi^2$ distance coefficient of the modern analogue technique (MAT) by comparing the percentile of the distribution of the training set with each sample of the fossil data. Samples exceeding the $10^{th}$ percentile of training set dissimilarity values were regarded as relatively poor analogues and were considered with extra caution. The percentage of fossil species represented in the modern dataset was calculated separately as well. All the analyses were performed using the software C2 version 1.7.4 (Juggins 2007).

Diversity was analysed using a basic rarefaction index (Birks and Line 1991) in order to account for sampling size. More complex diversity indices such as Shannon's or Simpson's diversity index were not suitable, as they also consider the relative frequencies or

representation of the different taxa, which is largely influenced by selective preservation of the diatom frustules.

# Results

## Sedimentological analysis

### Hijkermeer

The Hijkermeer sediment cores consist of a dark brown gyttja (organic mud) with mossy intervals, a few thin (0.5-1 cm) sandy layers and intervals with rootlets/organic material (Fig. 4). The density of these rootlets/sandy layers is especially high around an inferred hiatus at a depth of ca. 1000 cm (Fig. 2 & 4). Both cores show a similar pattern in the major elemental ratios, indicating that they provide a reliable overview of the lake (Fig. 6).

### Llangorse Lake

The lower part of the sediment cores at Llangorse Lake consist of organic mud, which towards the top rapidly shifts to red-brown silty clay at a depth of ca. 390cm (Fig. 5), represented by a major drop in the LOI-curve (Fig. 7).

## Age dating and chronology

### Hijkermeer

Table 1 and figure 2 show the age assessment and age-depth model for Hijkermeer. The interpolation of the oldest datapoints, between 1031 cm and 963 cm, presented a realistic reflection of the ages as the trendline kept within the range of the radiocarbon dates' errorbars. Following this there is an hiatus at ca. 1000 cm (3040 cal. yr BP), after which the radiocarbon dates indicate similar ages of ca. 1000 cal. yr BP up to a depth of ca. 650cm. Hard water effect is unlikely to affect the ages, as macro remains were used for obtaining the radiocarbon dates. No datable material was found above this depth, but combined with the relative data based on an increase in lead, the upper part could be interpolated using a second order polynomial.

**Llangorse Lake**

Table 2 and figure 3 show the age assessment and age-depth model for Llangorse Lake, interpolated using a fifth order polynomial. The LOI curve provided by Jones et al. (1985) and of this study were added to the figure, in order to highlight the strong resemblance between both cores. The two uppermost samples dated by Jones et al. (1985) were disregarded in this paper, as they were most likely contaminated by carbon that may be considered too old. At a depth of ca. 730cm in the core of Jones et al. (1985) relatively high concentrations of carbonates were found of ca. 19% dry weight, which would increase the likelihood of radiocarbon dates that are too old due to the hard water effect, but no radiocarbon dates have been obtained for that specific horizon. Since bulk sediment was used for dating and there is no difference in analysed fraction, no further information is available regarding the reliability of the data points.

**Table 1.** (Radiocarbon) dates from the Hijkermeer sediment core

| Composite depth (cm) | Lab. No. | δ13C (‰) | 14C Age (BP) ±SD | Calibrated age range (1σ)(cal. BP) | Analysed fraction |
|---|---|---|---|---|---|
| **0** | | | | -64 | Core top |
| **100** | | | | 90 | Increase lead - start air pollution |
| **670.5-671.5** | Poz-62543 | -35.4 | 1128±42 | 967-1070 | Leaf indet. |
| **763.5-674.5** | Poz-70595 | | 980±50 | 798-935 | Leaves of *Erica cf. tetralix*, *Calluna* and indet. |
| **790-791.5** | Poz-62544 | -36.3 | 873±29 | 733-892 | *Eleocharis uniglumis/palustris*; twigs indet. |
| **793.5-794.5** | Poz-70596 | | 940±35 | 798-916 | Leaves of *Erica cf. tetralix*, *Calluna* (on twig) and indet.; fruit of *Eleocharis uniglumis/palustris* |
| **864.5-865.5** | Poz-70597 | | 1240±60 | 1085-1262 | Leaf indet |
| **916-917.5** | Poz-62547 | -31.4 | 1190±24 | 1072-1174 | Leaf indet.; twigs; charcoal fragm. |
| **962.5-963.5** | Poz-70598 | | 1055±30 | 931-975 | Seeds of *Betula sp*. and *Erica cf. tetralix*; twig of Ericaceae; leaf indet. |
| **1030.5-1031.5** | Poz-62548 | -29.4 | 3168±34 | 3364-3444 | Leaves indet.; fruit *Carex sp*. |
| **1121.5-1122.5** | Poz-62549 | -44.2 | 3617±51 | 3852-3983 | Seed of *Betula pendula* seed; charcoal fragm. |
| **1180-1181.5** | Poz-70599 | | 4120±50 | 4534-4809 | Seeds of *Betula sp*. and *Erica cf. tetralix*; Leaves of *Erica cf. tetralix*, *Calluna* (on twig) and indet.; flower buds of cf. *Calluna* and indet.; fruit of *Carex obtrubae/vulpine*; *Chenopodium cf. glaucum/rubru* |
| **1211.5-1212.5** | Poz-62550 | -33.9 | 4476±35 | 5043-5279 | Charcoal fragm.; wood fragm; flower bud of cf. *Trifolium* |
| **1231.5-1232.5** | Poz-70603 | | 4680±40 | 5323-5337 | Seeds of *Betula sp*.; leaves of *Erica cf. tetralix*, *Calluna* (on twig) and indet.; Flower buds of cf. *Calluna*; Fruit of *Carex sp*. |
| **1257.5-1258.5** | Poz-62551 | -39.8 | 6113±44 | 6907-7125 | Seed of *Betula pendula*; leaf indet. |
| **1288.5-1289.5** | Poz-70604 | | 7700±80 | 8415-8548 | Seeds and wings of *Betula sp*.; catkin of *Populus* |

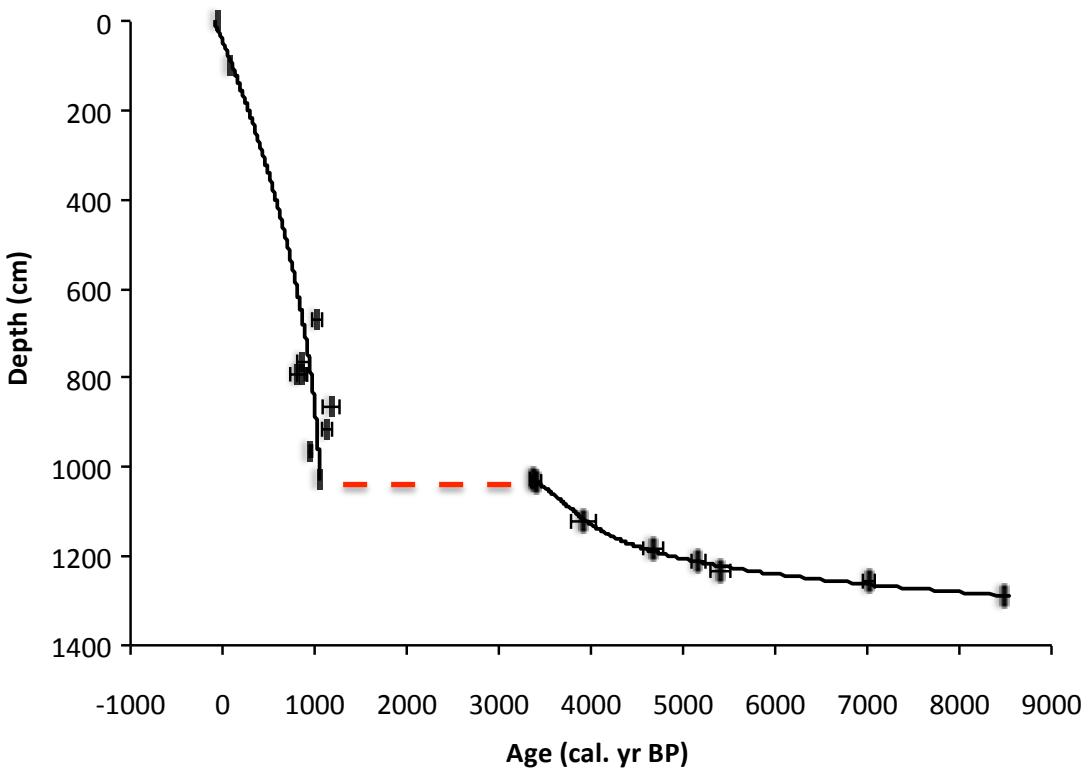


**Figure 2.** Radiocarbon results of the Hijkermeer sediment core and modelled age-depth relationship, the marks represent the average and range between the smallest and largest intercept with a 1-sigma probability.

**Table 2.** (Radiocarbon) dates from the Llangorse Lake sediment core (Jones et al. 1985)

| Jones et al. 1985 (A) | Composite depth present study (cm) | Lab. No. | 14C Age (BP) ±SD | Calibrated age range (1σ)(cal. BP) | Analysed fraction |
|---|---|---|---|---|---|
| **0** | 716 | Core top | | -64 | |
| **65** | 764 | | | 97-123 | Pb-210 |
| **406-416** | 1040-1049 | SRR-2378 | 1980±80 | 1825-2037 | Transition |
| **451-461** | 1080-1088 | SRR-2379 | 3080±80 | 3180-3379 | Brown/black organic mud |
| **527-537** | 1148-1158 | SRR-2380 | 3240±70 | 3392-3558 | Brown/black organic mud |
| **604-614** | 1120-1230 | SRR-2381 | 4380±80 | 4849-5212 | Brown/black organic mud |
| **677-687** | 1290-1300 | SRR-2382 | 4140±80 | 4575-4820 | Brown/black organic mud |
| **759-769** | 1372-1382 | SRR-2383 | 8150±90 | 9004-9253 | Brown/black organic mud |
| **797-805** | 1410-1418 | SRR-2384 | 8720±80 | 9552-9883 | Brown/black organic mud |

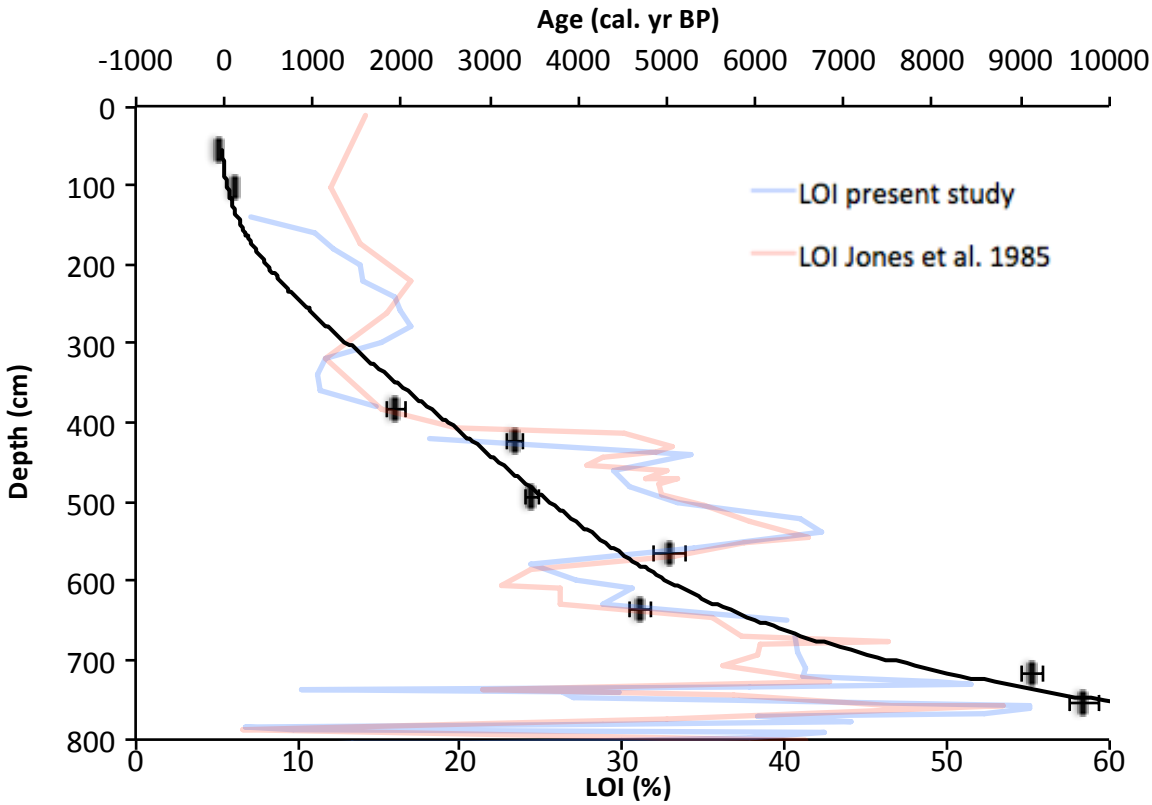


**Figure 3.** Radiocarbon results of the Llangorse Lake sediment core and modelled age-depth relationship, the marks represent the average and range between the smallest and largest intercept with a 1-sigma probability. The LOI curve provided by Jones et al. (1985) (red) and that of the present study (blue) is also included.

## Pollen analysis

The summary pollen diagram of Hijkermeer indicates a general decrease in arboreal pollen and an increase in Cereals and Herbs. A first increase in Cereals occurred during the hiatus at a depth of ca. 1000 cm and a second at a depth of ca. 700 cm (ca. 900 cal. yr BP) coinciding with a sharp increase in aquatic plants and a decline in *Sphagnum*. A more elaborate discussion on the pollen stratigraphy and zones based on biostratigraphy will be provided in a separate paper specifically devoted to this topic. Herein, the age-model presented in this paper will also be correlated to the biostratigraphical zones, because despite the hiatus the pollen record indicates natural succession. Moreover, since all data is analysed on the same

core, comparison between the pollen and diatom analysis as well as the reconstructed water quality is still possible.

In contrast to Hijkermeer, the summary pollen diagram of Llangorse lake, provided by Chambers (1999), does not indicate gradual changes in the vegetation, starting with a sharp decrease in non-arboreal pollen (NAP) at a depth of ca. 600cm (after correlation to the depths of the sediment core studied in this paper, see chronology. Cereals temporarily increase between 425cm and 250cm, corresponding to ca. 3000 to 1000 cal. yr BP.

## Diatom analysis

### Hijkermeer

A total of 60 species were identified within 25 genera, dominated by *Fragilaria spp.* Lyngbye, *Tabellaria flocculosa* (Roth) Knudson and various benthic species including *Achnanthidium minitissimum* (Kützing) Czarnecki (Fig. 4). Two major zones were defined, subdivided into seven subzones (Hijkermeer Diatom Zone; HDZ). The second component of the model to reconstruct TP performed well, indicated by an $R^2$ of 0.80 with a root mean square error (RMSE) of 0.25 $\log_{10}$ TP units and a cross-validated RMSE of prediction (RMSEP) of 0.33 $\log_{10}$ TP units. However, only sample 11 and 12 were below the 10$^{th}$ percentile of training set dissimilarity values and samples 2, 5, 6, 9 and 13-16 even exceeded the 20$^{th}$ percentile. In most of the samples, at least 70% of the fossil species were represented in the training set and in some even more than 90% (Fig. 6).
Overall, there was a generally increasing trend in TSVD (1.3 to 3.5) and DI-TP (12 to 32 µg/L) and the diversity appears to follow shifts in TSVD and DI-TP (Fig. 6).

The lowermost zone, HDZ 2d (1071-1050 cm; ca. 3650-3530 cal. yr BP), is dominated by *Aulacoseira alpigena* (Grunow) Krammer, *Oxyneis binalis* (Ehrenberg) Round and O. binalis var. *elliptica* Flower and is characterised by a TSVD of 1.3 and a DI-TP of 12 µg/L. However, the reconstruction errors were large and only ca. 30% of the total amount of counted species in the sample is represented in the DI-TP calculation, principally because *O. binalis* and *A. alpigena* were not present in the modern training set used for the calibration.

After the hiatus, HDZ 2b/c (1050-910 cm; ca. 3530-1020 cal. yr BP), *Fragilaria spp.* and epiphytic diatoms, mainly from the genera *Eunotia* Ehrenberg, *Cavinula* Mann and Stickle in Round, Crawford & Mann and *Gomphonema* Ehrenberg became more abundant, followed by an increase in *Adlafia* Moser, Lange-Bertalot and Metzeltin*, Nitzschia* Hassall and *Encyonema* Kützing. Within these zones the TSVD and DI-TP peak, with the latter reaching as high as 210 µg/L. However, this sample contained low diatom valve concentrations and therefore only 100 specimens were counted.

The most prominent ecological shift in the sequence occurs in HDZ 2a (910-840 cm; ca. 1020-990 cal. yr BP), when the planktonic species *Aulacoseira subarctica* (Müller) Haworth and *Asterionella formosa* Hassall peak at ca. 1000 cal. yr BP with 70% and 10% respectively. DI-TP values and the TSVD decrease, as well as the inferred diversity.

Within HDZ 1a/b/c (840-55 cm; ca. 990-20 cal. yr BP), the facultative planktonic species (*Fragilaria spp.* and *T. flocculosa*) and the benthic genera (*Nitzschia, Navicula* Bory de Saint-Vincent*, Psammothidium* Bukhtiyarova and Round and *Achnanthidium)* alternate in dominance, with a gradual transition towards assemblages dominated by *Fragilaria spp*. and *T. flocculosa* in the most recent part of the record. The TSVD and DI-TP remain more or less constant, at ca. 3.6 and ca. 30 µg/L respectively.

**Llangorse Lake**

A total of 66 species were identified within 30 genera. Diatom assemblages are dominated by *Fragilaria spp.* and several planktonic species including *Stephanodiscus rotula* (Kützing) Hendey and *Aulacoseira granulata* (Ehrenberg) Simonsen (Fig. 5). Ecosystem shifts are mainly driven by the planktonic species and *Fragilaria spp*. is abundant throughout the record. Two major zones were defined, which were subdivided into six subzones (Llangorse Lake Diatom Zone; LDZ). The model performance values are the same as for Hijkermeer and only samples 3, 4, 6, 11, 12 and 19 were below the 10$^{th}$ percentile of training set dissimilarity values. Between 50% and 94 % of the fossil species were represented in the training set (Fig. 7). A temporary increase can be observed in the TSVD and DI-TP and the diversity follows an inverse pattern in relation to the water quality (Fig. 7).

The oldest part of the record, LDZ 2c (620-560 cm; ca. 5380-4420 cal. yr BP), is characterized by a relative decrease in the planktonic species *S. rotula* and *Cyclotella ocellata* Pantocsek, coinciding with a relative increase in *Fragilaria spp*. and *Cavinula scutelloides* (W. Smith) Lange-Bertalot. Diversity decreases within this zone and TSVD and DI-TP show values of 4.4 and 54 µg/L respectively.

Within LDZ2b (560-510 cm; ca. 4420-3800 cal. yr BP), the benthic species *C. scutteloides* reaches maximum values of ca. 18%, coinciding with a gradual increase in TSVD and DI-TP.

LDZ 2a/1b/c (510-260 cm; ca. 3800-800 cal. yr BP) contain high abundances of planktonic species, in consecutive order: *A. granulata* increases at ca. 340cm, followed by *Cyclotella bodanica* var. *affinis* (Grunow in Van Heurck) Cleve-Euler, *Stephanodiscus* cf. *minutulus/parvus*, *Cyclotella meneghiniana* Kützing, *S. rotula* and *Cyclostephanos dubius* (Fricke) Round. Short-term decline in the relative abundance of the planktonic species and increase in the relative proportions of the facultative planktonic group occurs at ca. 390 cm, coinciding with a decrease in organic matter from ca. 35% to 20%, as indicated by the LOI curve. The diversity and DI-TP fluctuate considerably; with relatively high (180 µg/L) and low (40 µg/L) values both present in the interval. The TSVD indicates high values of ca. 5, except for a short decline to a value of 4.3 that relates to the decrease organic matter at ca. 390 cm.

The uppermost zone of the sequence, LDZ 1a (160-90 cm; ca. 800-50 cal. yr BP), is dominated by *Fragilaria spp..* Nutrient levels return almost back to baseline levels (TSVD=4.4; DI-TP=65 µg/L) and diversity similarly increases to the levels similar to those at the base of the core.

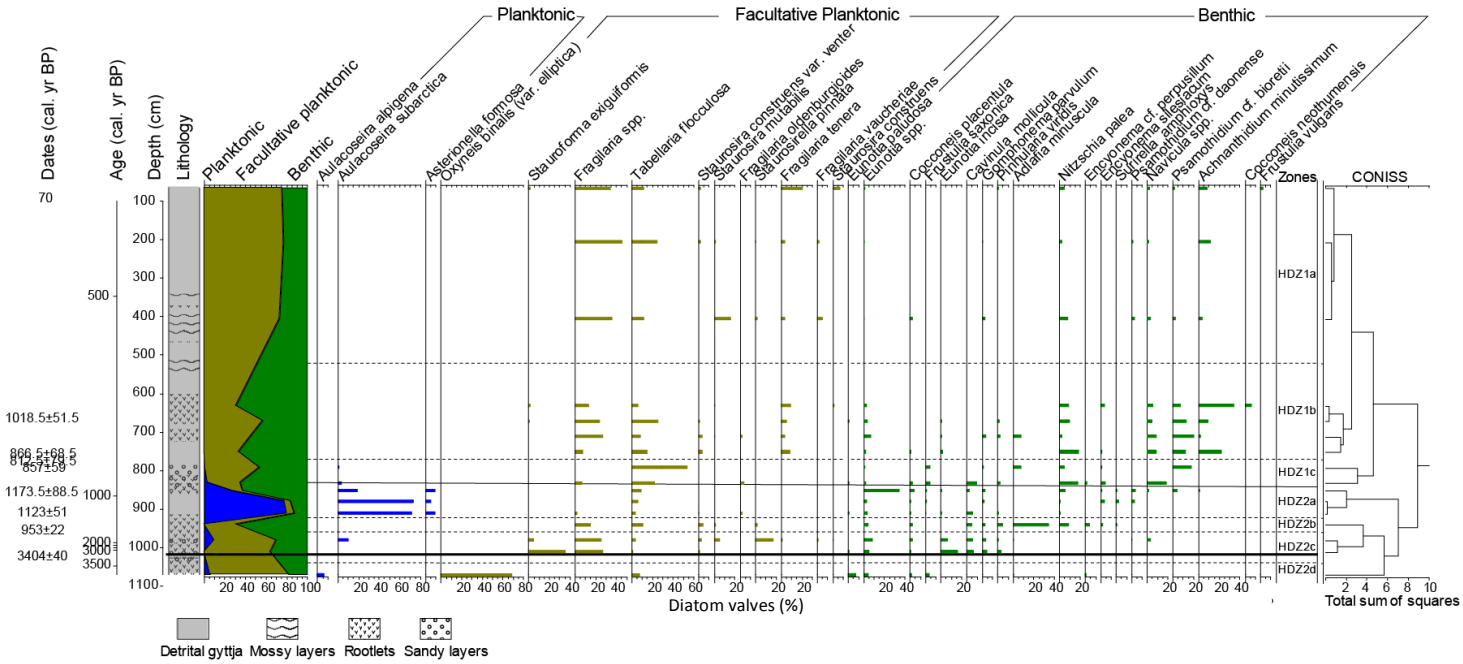


**Figure 4.** Diatom stratigraphy of Hijkermeer, including the lithology. Values are given as percentage of total diatoms counted. Only selected species, with >2% abundance are presented and diatom zonation was based on the CONISS program.

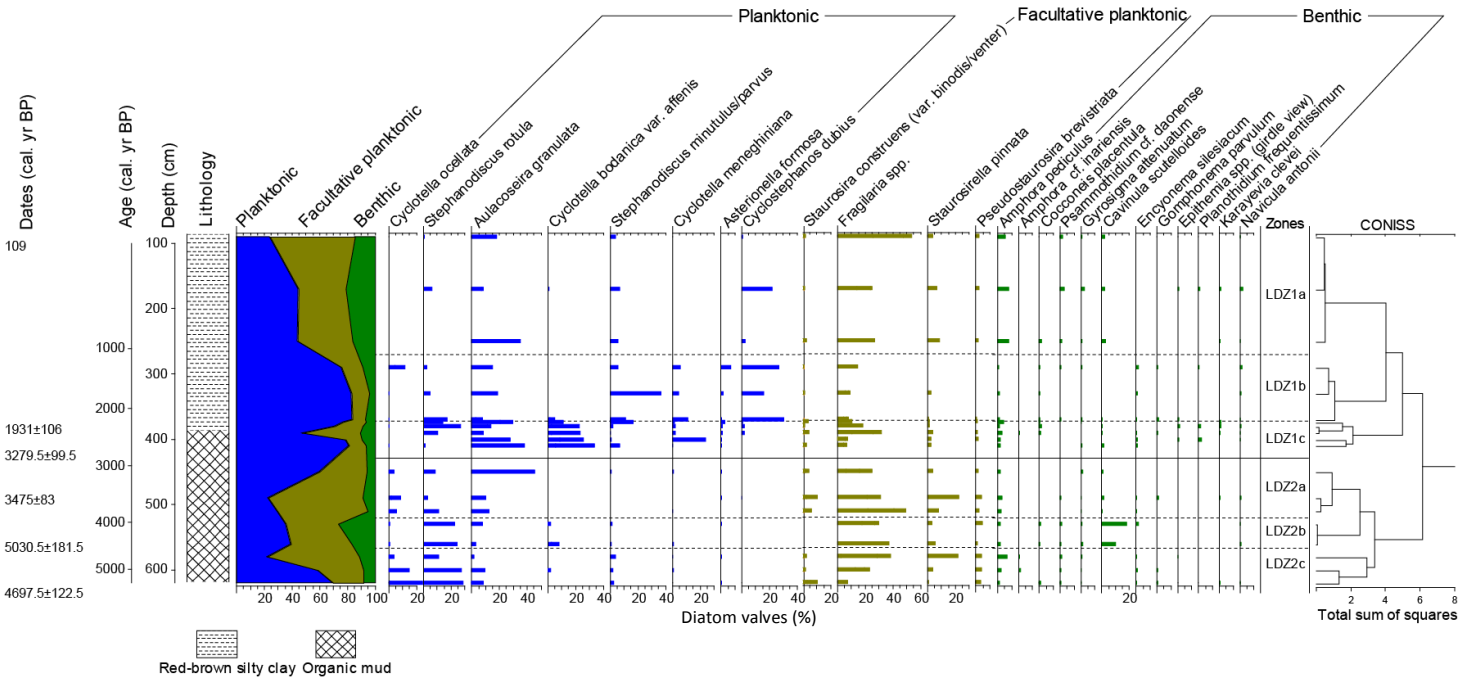


**Figure 5.** Diatom stratigraphy of Llangorse Lake, including the lithology. Values are given as percentage of total diatoms counted. Only selected species, with >2% abundance are presented and diatom zonation was based on the CONISS program.

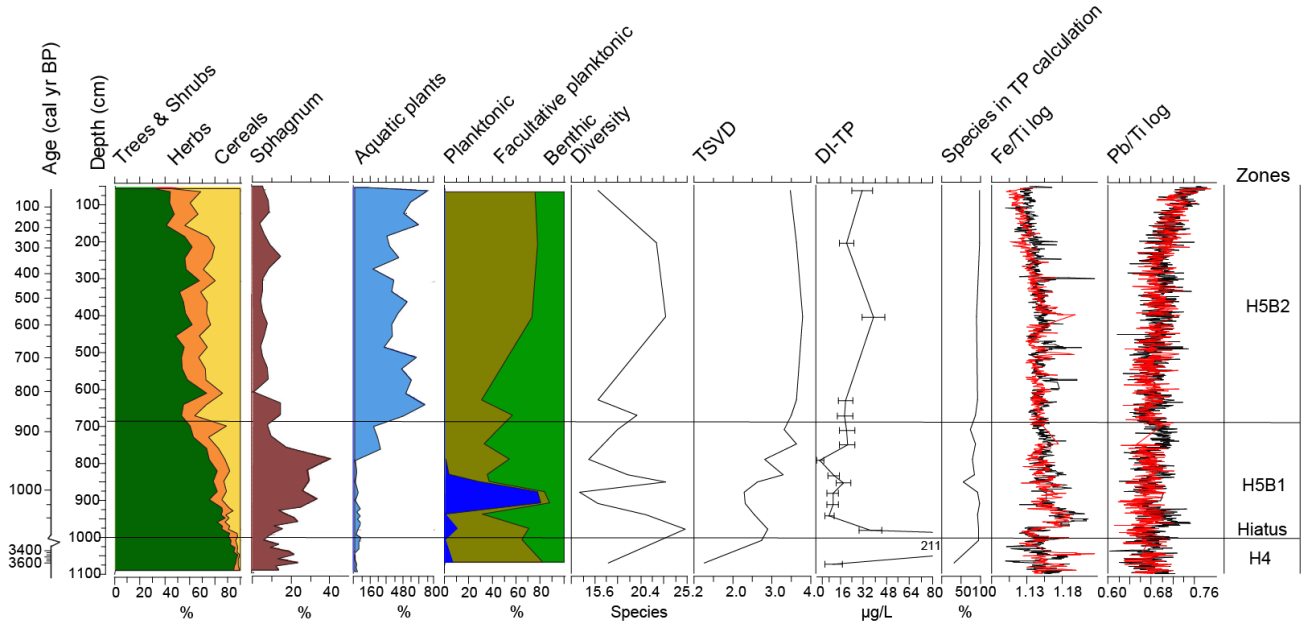


**Figure 6.** Overview of multiple proxies used in this study for the sediment record of Hijkermeer: summary pollen stratigraphy together with Sphagnum and Aquatic plants, summary diatom stratigraphy, rarefaction diversity, TSVD, DI-TP and iron and lead reconstructions. Zones are defined as pollen zones, highlighting major Holocene climate and landscape transitions (H4= Subboreal; H5 is Subatlantic).

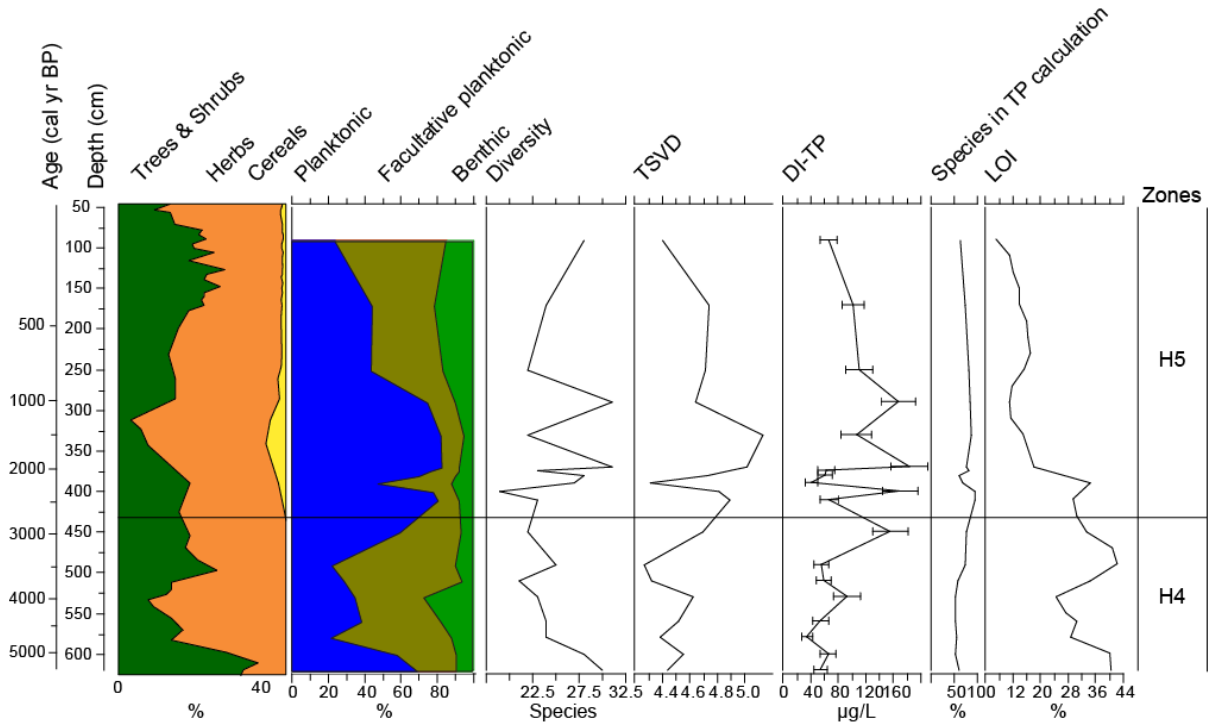


**Figure 7.** Overview of multiple proxies used in this study for the sediment record of Llangorse Lake: summary pollen stratigraphy (Jones et al. 1985), summary diatom stratigraphy, rarefaction diversity, TSVD, DI-TP and LOI reconstructions. Zones are defined on a northwestern European Holocene climate transition at ca. 2800 cal. yr BP (H4= Subboreal; H5 is Subatlantic).

# Discussion

## Hijkermeer

The lack of planktonic species in most of the Hijkermeer samples suggests that the lake has been shallow throughout the sequence, which is confirmed by intervals with rootlets in several parts of the core (Fig. 4). The most notable feature in the record is the hiatus at a depth of ca. 1000 cm from 3400 to 1050 cal. yr BP and most of the shifts in the diatom assemblages appear to be related to it. Unfortunately, in most samples the fossil diatom assemblages do not show clear similarities to the modern training set, but since the TSVD generally followed a similar pattern to the DI-TP, the data will not be disregarded.

### Subboreal (1071-1031 cm; 3650-3400 cal. yr BP)

The low TSVD and DI-TP at a depth of 1071 cm, as well as high abundances of *O. binalis* and *A. alpigena* indicate shallow, turbulent conditions in Hijkermeer. *Oxyneis binalis* is a typical acidobiontic species, occurring in lakes and peatbogs (Flower 1989; Salomaa and Alhonen 1983), while *A. alpigena* is described as blooming species in meso- to eutrophic conditions (Bradbury 1997) and considered as a low pollution tolerant species (Bere and Tundisi 2011) . Combined, the species indicate a decrease in lake water pH that is related to reduced terrigenous inputs and climate-driven pH dynamics (Wilson et al. 2012).

Overall, the diatom data reflects primarily climate forcing and little to almost no anthropogenic influence in the lake during a period that coincides with the Early/Middle Iron Age, when human habitation increased together with cattle grazing. The low diversity corresponds to the oligotrophic circumstances (Davidson and Jeppesen 2013).

### Hiatus (ca. 1000cm)

The interpolated age-model of Hijkermeer shows that the sediment core contains an hiatus at ca. 1000cm depth, for which the most likely explanation would be lowering of the lake level, resulting in partial or complete drying of the lake. Such a scenario would result in limited sedimentation and will make the top layer of the sediment more susceptible to erosional processes (Covich and Stuiver 1974). This hypothesis is supported by the presence of reed and rootlets in the sedimentology at the depth of the hiatus, suggesting that the reed belts surrounding the lake expanded towards the middle of the lake. Alternative

explanations for the hiatus include excessive bioturbation, considering the shallowness of the lake. However, since the XRF elemental ratios of the two parallel sediment cores are well correlated, it is very unlikely that such mechanisms could have caused the hiatus.

The potential mechanism for the lake level lowering, a likely cause for the hiatus, depends on its regional extent and timing. The hiatus spans parts of two pollen stratigraphic zones in the Holocene: the Subboreal and the Subatlantic. Unpublished proxy data from other pingo lakes in The Netherlands, Uddelermeer and Esmeer, also indicate lake level lowering (S. Engels Univ. of Amsterdam, Pers. Comm.), suggesting an event of regional importance. The regression of the North Sea at the end of the Subboreal (Behre 2007) could have caused lowering of the groundwater table resulting in low lake levels. However, as Hijkermeer is situated 14 meters above mean sea level, it is not likely that it was affected by the regression. Moreover, increased precipitation corresponding to the Subboreal-Subatlantic transition at ca. 2800 yr BP would suggest a rise in lake level (Van Geel et al. 1996). Many peatbogs in the Netherlands drained during this transition, due to oversaturation resulting from the increased precipitation, but this is not a likely explanation in the case of a remnant pingo lake (Van Geel et al. 2014). It could have been a shift in the seasonal distribution of precipitation, where a series of dry summers can cause the lake to dry out, oxidizing the top of the organic sediment (Covich and Stuiver 1974). In depth research and comparison between more pingo lakes across the region is required to draw a final conclusion on this matter.

Since the first increase in Cereals in the pollen record occurs within the time frame of the hiatus, the timing of the first imprint of agricultural activity and its effect on the water quality cannot be defined exactly, although post-hiatus cereal percentages are still low (<5%).

**Subatlantic (1000-0cm; 1050 ~ cal. yr BP to present)**

At a depth of ca. 1000cm the interpolated age model shows that sediment started to accumulate again in medieval times (ca. 1050 cal. yr BP), indicating an increase in moisture availability. However, the dominance of epiphytic diatoms at >40% (*Eunotia, Cavinula, Gomphonema*) and *Fragilaria spp.* followed by increased abundances of benthic and epiphytic species from the genera *Adlafia, Nitzschia, Encyonema* still indicate low moisture availability (Van Dam et al. 1994). This suggests that the initial phase after the lake reformed

was characterized by shallow conditions, potentially very variable. This is supported by increased DI-TP, driven by species belonging to the same genera. This increase in trophic state during shallow lake levels may be related to increased allochtonous input and increased nutrient availability due to sediment re-suspension. Following the peak in nutrients, the Fe/Ti ratio (Fig. 6) shows a temporary increase, indicative of changes in the redox state (Rothwell and Rack 2006), which can be related to input of seepage water that is generally characterized by high iron levels (Hofman et al. 2007). The pollen diagram indicates that *Sphagnum* becomes more abundant during this period as well, which could be an explanation for the similar radiocarbon ages between a depth of 963 and 671 cm. Possibly, a floating peat layer was formed on the lake that still allowed for sedimentation to occur from terrestrial input, while also causing organic debris to fall from the bottom and sides of the floating mat that eventually settles on the bottom of the lake as well (Kratz and DeWitt 1986; Swan and Gill 1970). This could result in a mix between various carbon sources and ages that may be deemed too old. Moreover, the pollen record indicates natural succession within this period, suggesting that continuous sedimentation did occur.

The peak of *A. subarctica* and *A. formosa* between 1030 and 990 yr BP suggest a temporarily enhanced inflow of water at the start of the Medieval period. *Aulacoseira subarctica* usually appears in response to moderate increases in nutrients, but is disadvantaged by further enrichment (Gibson et al. 2003). However, the peak coincides with lower TSVD and DI-TP values, most likely due to dilution of nutrients by the increase in water.

Following the planktonic event, the decline in *Sphagnum* together with an increase in Cereals can be interpreted as active removal of peat by humans in the littoral zone of the lake. Furthermore, it also coincides with increased TSVD and DI-TP values, which can be related to the increase in agricultural activities. Increase of aquatic plants in the pollen record after the *Sphagnum* decline indicates enhanced light availability (Hough and Fornwall 1988), as also supported by the age model indicating continuous sedimentation in that period. The diatom record appears to be constant in the uppermost part of the sequence, dominated by facultative planktonic species, indicative of mesotrophic conditions, which is supported by the TSVD and DI-TP values. The increase in facultative planktonics coincides with an increase in diversity, but values decline again towards the youngest sample, corresponding to an

increase in *Fragilaria spp*.. The nearby presence of humans is highlighted by the gradually increasing presence Cereal pollen.

## Llangorse Lake

Unlike for Hijkermeer, fluctuations in planktonic species are the main drivers of shifts in diatom assemblages for Llangorse Lake, which is indicative of higher lake levels. A clear increasing and decreasing pattern can be correlated between the relative abundance of planktonic species, Cereals and the trophic state of the lake, most likely related to anthropogenic activity. The pollen record reveals an offset between the deforestation at the base of the sequence and the onset of agriculture practice. Even though Llangorse Lake contained relatively less poor analogues than Hijkermeer, the use of the DI-TP model is still questionable, especially due to the low percentage of fossil species present in the modern training set. However, just like at Hijkermeer the two methods for reconstructing water quality followed a similar pattern and the shifts in diatom assemblages coincide with the shifts in water quality, which indicates a certain relation.

**Subboreal (620-430 cm; 5200-2700 cal. yr BP)**

The base of this interval corresponds to the Neolithic period and is characterised by relatively high abundances in trees and shrubs (40%). Abundant *S. rotula* and *C. ocellata* indicate that the lake was meso- to eutrophic (Van Dam et al. 1994) during that time. A sharp increase in relative abundance of facultative planktonic species (*Fragilaria spp.*) compared to the aforementioned planktonic species at ca. 600cm (ca. 5000 cal. yr BP) implies a shallower, more turbulent water column. This event coincides with a major decline in arboreal pollen, suggesting forest clearings. Jones et al. (1985) linked this deforestation to accelerated sedimentation rates, supporting the relation between human activity and the shift in the diatom assemblages. Remains of megalithic tombs present in the Brecon Beacons built by farmers in the Neolithic are evidence of the pre-historic farming activities in the area (Cummings et al. 2002).

A further decrease in lake level is indicated by high abundance of *C. scutelloides*, a benthic species that thrives in sandy environments (Jewson et al. 2006). Between ca. 475 and 425 cm (around 3000 cal. yr BP), the TSVD and DI-TP increase from meso- to eutrophic to (hyper)eutrophic conditions (ca. 160 µg TP/L), coinciding with a large decrease in diversity,

which apparently indicates that the species' diversity is inversely related to the trophic state of the lake.

A major increase of *A. granulata* corresponds to a large increase in TSVD and DI-TP (Kilham et al. 1986; Van Dam et al. 1994). The increased availability of nutrients can be related to a further increase in sedimentation, enhancing nutrient leaching and leading to more turbulent waters, which results in re-suspension of nutrients from the sediment.

**Subatlantic (430-0 cm; 2800~ cal. yr BP)**

During the Subatlantic, high abundances of eutrophic *A. granulata* and *C. bodanica* relate to the high values of the TSVD and DI-TP, indicating high nutrient availability and increased primary productivity (Kilham et al. 1986; Van Dam et al. 1994). A relative decrease in planktonic species and an increase in *Fragilaria spp.* at a depth of ca. 390 cm (ca. 2025 cal. yr BP) coincide with an abrupt change in sediment stratigraphy from organic lake mud to silty clay, which presumably reflects anthropogenically-forced enhanced soil input. A shift to smaller planktonic species, including *S.* cf. *minutulus*/*parvus*, *C. meneghiniana* and *C. dubius*, can be related to decreased light availability, e.g low water transparency, as small-sized species with low sinking velocities have a competitive advantage in remaining a sufficient amount of time in the euphotic zone (Winder et al. 2009). The low water clarity possibly results from high productivity due to further increase in nutrients and decrease in lake level, which enhances turbulence. This enhanced nutrient availability is represented by eu- to hypereutrophic conditions according to the TSVD and the DI-TP of ca. 153 µg/L. In this time interval a major climate deterioration occurred: the ca. 2800 BP event that is characterised by a shift to wetter and colder conditions and resulted in widespread settlement abandonment and major long-term changes in land use (Van Geel et al. 1996). Even though Dark (2006) describes that often upland settlements were not abandoned and even flourished during this period, Wales is mentioned as an exception to the rule. This is in direct contrast with the results found in this study, where there appears to be an increase in cultivation. It is evident that the eutrophication corresponds to the increase in Cereals (including Rye), which can be related to major human pressure in the catchment. This is supported by archaeological evidence on the southwestern slopes and interfluves of the catchment, drained by the Afon Llynfi that enters the south of the lake, where the sediment

core was collected: a large Iron Age encampment and a Roman Road that links the Roman forts of *Y Gaer* and *Isca* (Jones et al. 1985; Chambers 1999). Moreover, the peak in Cereals and the water quality reconstructions can be related to the campaign of Frontinus ca. 1875 BP (ca. AD 75), during which the native Silures were subjugated by Roman forces (Jones et al. 1985; Cuomo 2000). The diversity shows major fluctuations during this period of increased anthropogenic activity, corresponding to the turbulent conditions.

Following the Roman Period, Cereals decline and increased arboreal pollen suggest woodland regeneration, and critically, resulting again in lower reconstructed nutrient availability, as indicated by the relative increase in facultative planktonic and benthic species. This points to a decline in human influence on the lake, corresponding to the medieval depression. On the contrary, during the Medieval Period (ca. 1000 AD) the aforementioned crannog was built in the northwestern part of the lake and the Pre-Norman estate encompassed the entire northern part of the lake (Campbell and Lane 1989), which would imply an increase in anthropogenic pressure. A possible explanation for this discrepancy in timing could be the lack of radiocarbon ages for that interval, as no samples were dated between a depth of 100 and 400 cm, resulting in high uncertainties within the age model. It could very well be that this decline in nutrient levels corresponds to the mid-Medieval economic crisis (1290 – 1350 AD), related to the Great Famine and the Black Death, after which the agriculture never truly recovered and many agricultural lands were converted to pastures (Kershaw 1973; Yeloff and Van Geel 2007). Rapidly after anthropogenic activity appears to decrease and the water quality of the lake improves, the diversity increases again as well, highlighting the resilience of the ecosystem.

## (Early) human impact on water quality and diversity

When comparing the two lakes, the diatom and pollen data of Llangorse Lake reveal a higher intensity of human activity, with relatively large fluctuations in Cereals and related response in the diatoms. However, also at Hijkermeer nutrient availability increases along the gradient of increased human agricultural activities as indicated by increase in NAP, despite the hiatus. A major factor contributing to the difference between the two lakes could be the relatively minor anthropogenic activity around Hijkermeer, as the low abundances of cereals in the pollen record suggest, but it can also reflect differences in the lakes' physical parameters. As

mentioned in the study area, Hijkermeer has no inlets or outlets, giving it a small drainage area, whereas Llangorse Lake has a larger catchment and the sediment core was collected close to a river inlet. Therefore, the anthropogenic impact of a far larger area can be expected to affect Llangorse Lake. Also, differences in soil properties can cause such a discrepancy: erosion related to deforestation will have a larger impact on lake systems when the soil is enriched in nutrients: information on the subsurface characters is required in order to support this theory.

Noteworthy is the relation of diversity to water quality, clearly expressed in both lakes. In Hijkermeer the diversity increased with the shift from oligotrophic to mesotrophic conditions and in Llangorse lake the diversity was highest in the periods of eutrophic conditions, as opposed to the period with hypereutrophic conditions. This suggests that diversity is highest in meso- to eutrophic conditions. Many spatial and temporal studies on the relation between diversity and trophic state found this unimodal distribution as well (Jeppesen et al. 2000; Rusak et al. 2004; Das et al. 2008). Few species can cope with very low nutrient availability, whereas very high nutrient availability also increases competition and production, resulting in low light availability and hypoxia due to the decomposition of organic matter (Interlandi & Kilham 2001; Tilman 1982). Together with an increase in grazing pressure, this causes species with better competitive adaptation to expand and dominate. Apparently, water quality is of great influence on diversity, but other factors also play an important role in determining it, even though they are often connected. Nutrient availability (bottom-up control) also controls zooplankton and fish, and with that, grazing pressure on phytoplankton (top-down control)(Jeppesen et al. 2000). This could either shadow or overestimate the impact of the trophic state. Furthermore, sedimentation not only increases nutrient availability, but it also causes turbulence, which appears to have major impact on the species diversity in Llangorse Lake. Other parameters, such as lake level and area, largely driven by climatic changes, seem to contribute largely to changes in diversity in Hijkermeer. Feuchtmayr et al. (2009) show that warming also has a direct effect on the lake water chemistry, increasing among others phosphorus concentration and conductivity, which can significantly affect the aquatic ecosystem. Considering the recent climate warming, it unfortunately remains difficult to use this information when interpreting the results of this study.

The most remarkable result of this study is the quick recovery of the diversity after the decrease in human impact and the corresponding eutrophication in the sediment record of Llangorse Lake. Here, the resilience of the ecosystem is clearly reflected: returning to the pre-disturbed stable state following a shift to an undesirable alternative stable state related to a maximum of human impact (Scheffer et al. 2001; Elmqvist et al. 2003). This implies that proper management of the lake suffering from eutrophication can result in recovering of the ecosystem and is crucial for on-going management and conservation activities, especially relating to the present eutrophication problems in Llangorse Lake (Bennion and Appleby 1999). However, when taking a closer look at the species assemblages, it has to be mentioned that the ecosystem does not recover to pre-human influence conditions but rather to pre-roman conditions, considering that the species that dominated during the Neolithic do not return.

## Conclusions and future implications

Early human impact on water quality can be traced back to as early as 5000 years BP with the use of a qualitative and a quantitative reconstruction based on diatoms. Both methods applied in this study followed a similar pattern, despite the high amount of poor analogues within the DI-TP transfer function. It appears that the onset and increase in agriculture, as indicated by the appearance of Cereals in the pollen record, lead to an increase in nutrient availability in both lakes and a subsequent decrease in Cereals in Llangorse Lake coincided with a decrease in nutrients. Our data support the view that diversity is unimodally related to water quality with the highest diversity occurring in meso- to eutrophic conditions in the studied lakes and Llangorse Lake showcased the ecosystem resilience, as a return to the baseline trophic state levels also lead to increase in diversity. This can be used as a model for the (on-going) management and conservation of the present eutrophication problems, specifically at Llangorse Lake. However, caution has to be taken with regards to the relation between diversity and DI-TP, since shifts in diatom assemblages can also relate to increased turbulence, which is not necessarily related to an increase in TP and could also affect the diversity. Including other biotic proxies, such as aquatic plants and chironomids, can contribute to a more complete indication of the lake's diversity and an investigation of

different responses of the different taxa. Chironomids can also be used to infer local climate conditions, which would provide a better understanding of the relative impact of climate conditions on the ecosystem shifts.

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