Using pollen analysis to assess recent changes in floristic diversity, an example from the Swiss Plateau

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Abstract

Assessing the diversity of pollen types in sedimentary deposits is one of the few available proxies for reconstructing past plant diversity. However, several biases complicate pollen based reconstructions. One of the main sources of bias is the overrepresentation of wind-pollinated relative to insect-pollinated plants. Increased abundance of wind-pollinated plants in the catchment changes both the size and the evenness of the total pollen pool, thereby distorting richness estimates based on a constant count sum. Several methods have been proposed to reduce this bias, including separating functional groups (wind-*versus* insect-pollinated), accumulation-based rarefaction, and increasing pollen count sizes. We evaluated these methods using two high-resolution pollen records from the Swiss Plateau, focusing on the effects of historical land-use changes. Our results demonstrate clear biases in standard diversity estimates and show that robust pollen-based diversity reconstructions require high pollen counts. Although, separating wind- and insect-pollinated taxa may provide additional ecological insights, it does not resolve the largest biases and can be potentially misleading. Accumulation-based rarefaction is conceptually and empirically the most robust. However, its practical applicability is limited as it requires precise chronological control, which is often not achievable in pollen records. Using running bins to increase count sizes and rarefaction to a constant sum without separating insect-pollinated taxa may therefore be the simplest way to improve the diversity signal for most pollen diagrams. The pollen records from the Seetal area in Switzerland show a decline in palynological richness that started already at the end of the 19th century. By this time, major landscape reforms had started, leading to a shift from dynamic mixed farming systems to permanent grasslands for dairy farming. This change in land-use is consistent with the decline in palynological richness and an increases in pollen types from nitrophilous plants as well as a decline in wetland taxa. Further intensification occurring later during the 20th century did not cause a further decline of palynological richness. This may reflect the sensitivity of the pollen signal to the initial loss of common insect-pollinated taxa, capturing their initial decline, but not the further reductions of their abundances once they became rare.

1 Introduction

Biodiversity is in steeply declining, threatening the continuity of important ecosystem services that support human wellbeing

35   (MEA, 2005; IPBES, 2019). One of the major causes of this decline is land-use change, particularly related to food-production, as agricultural practices have severely intensified during the last century (Newbold et al., 2015; Raven & Wagner, 2021). In Europe, communities of arable weeds and diverse plant communities of semi-natural grasslands developed over millennia since the introduction of agriculture (Richner et al., 2015; Gigante et al., 2024). These diverse communities were adapted to small-scale agricultural practices and are thought to have impoverished during agricultural development including intensified

40   grazing, improved seed cleaning, increased inputs of artificial fertilizer, pesticide use and the shift from spring to autumn sowing (Storkey et al., 2012; Richner et al., 2015; Gigante et al., 2024). Knowledge of the total loss of floristic diversity in agricultural landscapes and the specific impact of these individual developments is limited due to a scarcity of long-term vegetation surveys, generally not capturing the period before agricultural intensification. Assessing the diversity of subfossil pollen grains provides a unique opportunity for acquiring insights into mechanisms of floristic diversity dynamics at temporal

45   and spatial scales beyond the reach of modern ecological studies (Odgaard, 2001). Although studies have shown that pollen richness correlates positively with plant richness (Meltsov et al., 2011, 2013; Matthias et al., 2015; Felde et al., 2016; Reitalu et al., 2019; Blaus et al., 2020; Connor et al., 2021; Abraham et al., 2022), the relationship is known to be affected by several biases with respect to the representation of individual plant species in the pollen record. The focus of this study is to explore how these biases can be reduced to improve interpretations of changes in past floristic diversity.

50   ### 1.1 Representation biases

The more pollen a plant produces, the higher the chance that its pollen is delivered to a lake or bog, where it is preserved in the sediments and can be subjected to pollen analysis. While some taxa are known to produce much pollen (e.g. *Betula*, *Alnus*, *Pinus*, grasses), others produce very little pollen (e.g. *Viola*) (Birks et al., 2016). Pollination syndrome is the most important underlying explanatory variable of species-specific differences in pollen production. For wind-pollinated plants, the

55   effectiveness of pollination depends greatly the amount of pollen produced, affecting the chance that the pollen reaches a female flower of the same species (Whitehead, 1983). The amount of pollen that a given species produces also varies depending on environmental conditions. For example, individuals at the northern edge producing less pollen than those in the center of a population. Additionally, pollen production is influenced by climate variability, resulting in annual fluctuations (Dahl et al., 2013; Pidek et al., 2010; Nielsen et al., 2010). Pollination syndrome is also effecting pollen dispersal efficiency, which is a

60   second important factor affecting the representation of a plant species in the pollen record. This component is for example affected by characteristics of the pollen grain such as weight and morphology (Tauber, 1965; Bradshaw & Webb, 1985; Sjögren et al., 2008).

65   The representation of plant species in the pollen record is further complicated by limitations to the preservation and identification of the grains themselves. Different pollen types are not equally well preserved (Hevly, 1981). For example, pollen from plants from the Juncaceae family is highly susceptible to degradation and thus rarely recovered from sedimentary records (Birks et al., 2016). The taxonomic resolution that can be obtained for pollen grains is also limiting. The taxonomic detail of identifications depend on the skill of the analyst, preservation state and on the morphological distinctiveness of the

70   grain itself. The maximum taxonomic resolution of pollen counts is bounded by the established microscope techniques and reflected in standard pollen identification keys (Moore et al., 1991; Beug, 2004). As a result, most pollen types are identifiable only to genus level or to a pollen type, which links to a groups of several plant species that produce morphologically similar pollen. Some pollen, such as most members of the Poaceae family, can only be identified to family level (Birks et al., 2016).

75   1.2 Standardization of the sampling effort

The abovementioned biases strongly impact the evenness component of palynological diversity and, consequently, indicators based on relative abundances. Therefore, most studies of pollen diversity have focused on palynological richness. To compare richness between samples in a meaningful way, the sampling effort must be standardized so that observed differences reflect actual differences in the diversity metric used and not differences in the sampling effort. Since the number of pollen types

80   encountered is positively related to the pollen count size, Birks and Line (1992) introduced the use of rarefaction to pollen analysis, so that *the total number of pollen taxa on a constant pollen count sum* can be estimated, hereafter referred to as the *constant count method*. This method has been widely used ever since.

An important but problematic assumption of this method is that the total amount of pollen produced in the absolute pollen source area and, consequently, the flux of pollen is constant. In reality this is hardly ever the case, since pollen influx

85   can vary not only due to changes in rainfall, windiness and tree masting years, but also due to changes in vegetation composition (e.g. when highly productive wind-pollinated trees are replaced by insect-pollinated herbs) (Weng et al., 2006; Van der Knaap, 2009; Birks et al., 2016). Therefore, especially during periods of structural vegetation change, such as the transition from the treeless late-glacial to the tree-dominated Holocene, the *sampled fraction of the total pollen population* differs greatly between samples when counting a constant number of pollen grains. The higher the sampled fraction of the

90   pollen population, the higher the chance of finding rare pollen types, including pollen grains transported from distant regions (Weng et al., 2006). Therefore, the total number of pollen counted may not be the best way to standardize the sampling effort. Instead, a more suitable standardization could aim at a constant proportion of the total pollen population, thus correcting at least in part the distortions caused by overrepresentation of wind-pollinated types.

To overcome this problem of comparing varying pollen populations in time, van der Knaap (2009) suggested an

95   accumulation-based approach to standardize the sampling effort in palynological richness assessments, by estimating *the total number of different pollen taxa deposited on a constant deposition surface per unit time*, hereafter referred to as the *accumulation-based method*. This can be implemented by using rarefaction to a variable sum representing a preset fraction of

the pollen accumulation rate (PAR=grains/cm³/year) of that sample. So, changes in PAR are directly translated into changes in the rarefaction sum, with a smaller sum for lower PAR and vice versa.

100   Another strategy to deal with large variations of the sampling effort caused by changes in abundance of overrepresented taxa is to evaluate palynological richness of wind-pollinated and insect-pollinated taxa separately (Weng et al., 2006; Matthias et al., 2015). Since wind-pollinated species not only produce much more pollen but also disperse the pollen more efficiently than insect-pollinated species, problems caused by representation bias may be reduced by looking at these groups separately.

105   The standard count size (i.e. 300-500 grains) used for pollen-based vegetation reconstructions is often too low to reflect pollen type richness, as most rare pollen types remain undetected (Weng et al., 2006; Weng & Hooghiemstra, 2024). As a strategy to increase sample size, consecutive samples can be binned, at the cost of temporal resolution. Very large bins have been utilized effectively in previous studies investigating postglacial changes in pollen-type richness (Giesecke et al. 2012, 2019).

110   Additional approaches in estimating diversity include the application of correction factors to deal with the distorting effect of representation bias. For example, by detrending the palynological richness curve by the evenness of the pollen assemblage (Colombaroli & Tinner, 2013). It is, however, not clear which effect this has, specifically when probability of interspecific encounter is used as a measure of evenness (Birks et al., 2016). Another strategy consists of adjusting pollen abundances using the REVEALS model (Sugita 2007) by including information on pollen fall speed and relative pollen productivity of the taxa (PPE's) (Matthias et al., 2015, Felde et al., 2016). The disadvantage of this approach is that it is affected by large uncertainties and only applicable to the most common taxa (Giesecke et al. 2014; Matthias et al., 2015). Moreover, comparing predictors of pollen diversity to REVEALS adjusted pollen abundances of surface samples often result in poorer fits compared to the original data (Matthias et al., 2015, Felde et al., 2016).

120   The aim of this paper is to evaluate the effects of using different strategies to reduce the known biases in palynological richness estimates. Three strategies are tested: i) binning of samples; ii) constant count versus accumulation-based; and iii) division of wind- versus insect-pollinated taxa. These strategies are applied to available high-resolution palynological data from Baldeggersee and Hallwilersee, two large lakes located on the Swiss Plateau. These pollen records provide a unique opportunity to compare these strategies due to their high temporal and taxonomic resolution. Moreover, the two records are complementary: the Baldeggersee record provides a detailed account of vegetation development during the last century, whereas the Hallwilersee record extends further back in time, providing a longer historical context. The uncovered trends in palynological richness are interpreted to answer the question: *When, and in which context did floristic diversity start to decline in the Seetal region*?

2 Methods

130 **2.1 Datasets**

Baldeggersee and Hallwilersee are large natural lakes situated on the Swiss Plateau in the Seetal valley. Baldeggersee (47°10'N, 8°17'E) lies at an elevation of 463 m a.s.l. and Hallwilersee (47°28'N, 8°21'E) is

situated at 449 a.s.l (Fig. 1). The distance between the lakes is ca. 3,5 km.
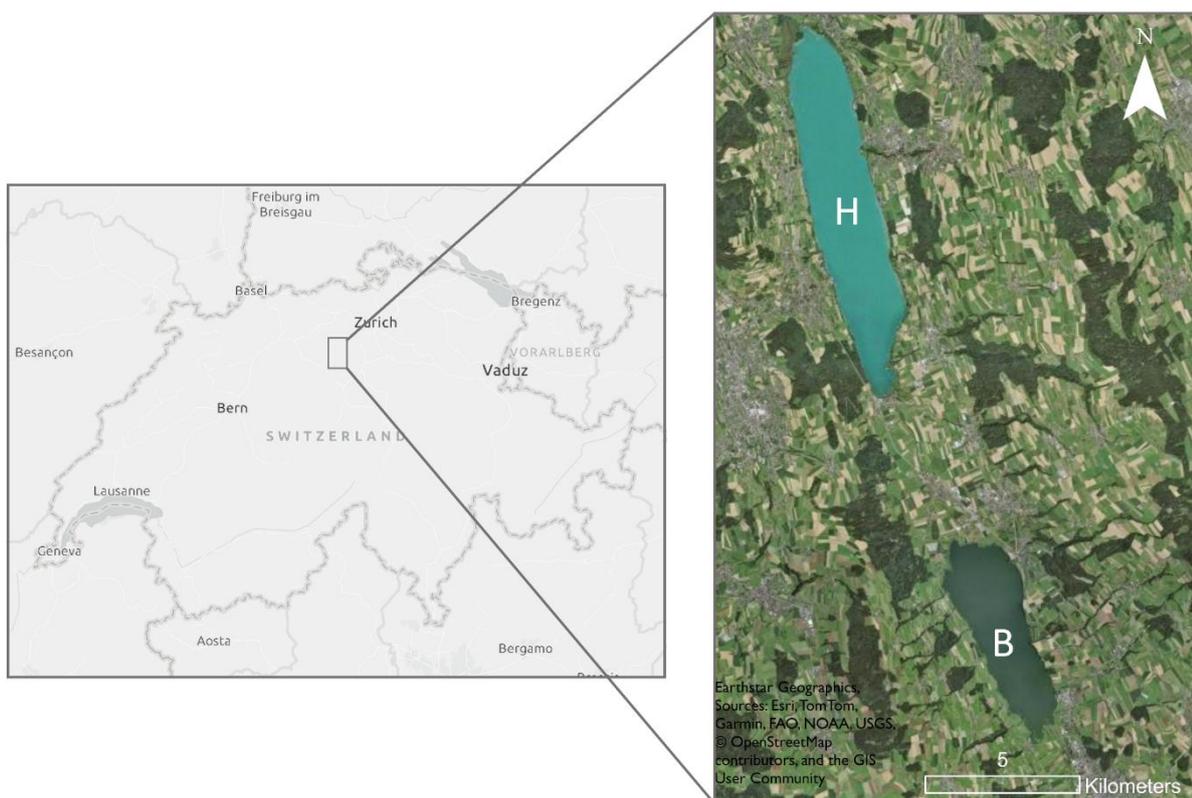
135 **Figure 1.** Baldeggersee (B) and Hallwilersee (H), two large natural lakes located on the Swiss Plateau. Sources: Esri, TomTom, Garmin, FAO, NOAA, USGS, OpenStreetMap contributors, and the GIS User Community | Powered by Esri.

Baldeggersee has a maximum depth of 66 m and a surface area of 5.2 km². The basin is 4.5 km long and 1.5 km wide. Its hydrological catchment area is 73 km², consisting for the largest part of agricultural land (77%), forest (12%) and urban areas (5%) (Wehrli et al., 1997). The lake was cored in 1993 by A.F. Lotter and colleagues with a freeze corer in the deepest part of

140 the basin. The sediments are annually laminated back to 1885, due to seasonal hypolimnetic anoxia caused by eutrophication of the lake (Wehrli et al., 1997). The laminations were sampled by scratching the annual layers with paper cutter blades off a frozen sediment slab of known surface. Further descriptions of the coring and sample preparations are provided in Lotter et al. (1997) and van der Knaap et al. (2000).

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Hallwilersee has a maximum depth of 48 m and a surface area of 9.95 km². The basin is 8.4 km long and 1.5 km wide.

145 Its hydrological catchment area is 128 km². The surrounding area consist mainly of agricultural land, and to a lesser extent of forested and urban areas. A core was taken in 1999 by A.F. Lotter with a gravity corer. Samples were taken with a constant volume (1 ml). Descriptions of the sampling procedures, pollen preparation methods, and interpretations of the main trends in the pollen record, along with their possible causes, are provided by van der Knaap et al. (2023).

The main focus of the studies on Baldeggersee and Hallwilersee was to reconstruct the trophic history of the lakes,

150 for which diatom assemblages and laminations were studied (Wehrli et al., 1997; Lotter and Birks, 1997; Lotter et al., 1997; Lotter, 1998; van der Knaap et al., 2023). While the pollen of both sediment cores were studied in detail, trends have not yet been fully interpreted. The pollen record of Baldeggersee was published in an overview study together with 22 other Swiss sites (van der Knaap et al., 2000). The pollen record of Hallwilersee was published together with the diatom record with some initial interpretations (van der Knaap et al., 2023).

155 The chronology of Baldeggersee is based on the count of individual varves. The more recent layers were very clear, while the undulation an thinness of the varves below the layer corresponding to 1906 AD makes them more difficult to distinguish. Therefore, age assignments of samples older than 1906 have some uncertainty (Lotter et al., 1997). The chronology of Hallwilersee is based on varve counts for the first 20 cm, and on extrapolated sedimentation rates below that (van der Knaap et al., 2023). Therefore the age-model is only considered reliable for the upper 20 cm.

160 **2.2 Separation of pollen functional groups**

Pollen taxa were separated into wind- and insect-pollinated taxa, according to their main pollination syndrome. This separation was suggested by Weng et al. (2006) for two reasons: 1) pollen from wind- and insect-pollinated taxa may be of different origin (regional vs. (extra)-local) and 2) the overrepresentation of -pollinated taxa may have a significant effect on the chance of finding the underrepresented insect-pollinated taxa.

165 Pollen types linked to plant species could be directly assigned to a pollination syndrome based on a search of the species pollination mode in FLORAWEB (https://floraweb.de/), an Internet portal of the German Federal Agency for Nature Conservation (BfN). For pollen taxa identified to a genus level, family level, or a pollen taxon including multiple species, their likely pollination mode was estimated based on a search of at least 5 representative species in that pollen type. In the case of both insect- and wind-pollinated taxa in the pollen type, the taxon was assigned to the wind-pollinated type. Self-pollinating

170 taxa were assigned to the insect-pollinated type. The assignment of pollination mode to the pollen taxa is provided in Table S1.

2.3 Binning

To evaluate the effect of higher sample sizes, pollen assemblages from consecutive depths were binned together with different bin sizes: 5, 10 and 15. A running bin strategy was used so that (in the case of 10 samples, for bin size = 5) bin 1 contains

175 samples 1-5, bin 2 contains samples 2-6 etc. until the last bin, bin 6 which contains samples 6-10. Depending on the focus of

the analysis, the age assigned to the bin can be the youngest age, the oldest age or the average age of all samples in the bin. Using the *youngest age* will give detailed information on the timing of *species gain*. Using the *oldest age* will give detailed information on the timing of *species loss.* Using the average age can be useful to display the trend without focusing specifically on the timing of species loss or gain.

2.4 Analysis of the palynological richness

The objective of the palynological richness analysis is to reconstruct changes in species richness of the surrounding natural upland vegetation. To this end, pollen taxa presumably originating from aquatic plants, cultivated or planted species, distant regions, as well as spore taxa were excluded from the analysis. Table S1 provides the full list of excluded and included taxa.

Palynological richness in the records of Hallwilersee and Baldeggersee was assessed using two different methods: rarefaction to a constant count and accumulation-based rarefaction. Rarefaction analysis to a constant count, generally using the smallest pollen sum among all samples, was performed on the pollen data from both Hallwilersee and Baldeggersee, using the iNEXT package (Hsieh et al., 2016). The confidence intervals of the rarefaction analysis were also calculated with the iNEXT package, obtained by a bootstrap method.

Rarefaction analysis based on accumulation was only performed on the Baldeggersee data, following the methods described by van der Knaap (2009), but instead of using Excel, RAREPOLL and TILIA, all calculations were made in R, using the iNEXT package (Hsieh et al., 2016) for the rarefaction. The used code is available at Zenodo (10.5281/zenodo.19062173). The analyses were performed with different configurations of the datasets, changing the bin size and separating functional groups.

2.5 Correlation table

The absolute pollen deposition may vary not only because of differences in pollen influx into the lake, but also due to in-lake processes such as redeposition, sediment focusing, and increased runoff (Giesecke & Fontana, 2008). Temporal changes in these processes cause pollen accumulation rates to fluctuate or change. Such fluctuations or trends will affect PAR of all pollen taxa causing correlations between the PAR of all taxa where these within-lake processes are more important than the changing flux of individual pollen types. This effect can be assessed in a correlation table and manifest as positive correlations between the accumulation rates of most pollen taxa. To test whether this phenomenon impacts the used data, correlations were tested between PAR of pollen taxa in the Baldeggersee core, using the corrplot package (Wei & Simko, 2024) in R.

2.6 Ellenberg N values for pollen

Reconstructing landscape parameters such as Ellenberg indicator values (Ellenberg 1974, 1979, Ellenberg et al. 1992), can provide more context to a pollen diagram and help illustrate how a landscape changed over time (Gaillard, 1984; Beckman, 2004). Moreover, such reconstructions allow for the extraction of valuable information from infrequently occurring herbaceous pollen types (van der Knaap et al., 2004). Blaus et al. (2020) tested the validity such pollen-based reconstructions by comparing

the obtained values from modern pollen samples to the vegetation-based value and found a significant positive correlation of pollen-based Ellenberg N values to the plant-based values for herbaceous, but not for woody taxa. Ellenberg N is an important indicator of land-use intensification, as nutrient enrichment of the soil allows the land to be used more effectively, increasing crop yields per surface unit. Extensive application of (artificial) fertilizer is thought to be one of the agricultural developments that have the most impact on the floristic composition of the arable lands as well as the surroundings with long-lasting effects (Bobbink et al., 2010; Seabloom et al., 2021), and therefore a relevant parameter to compare to palynological richness estimates.

Pollen Ellenberg N values were assigned to herbaceaous pollen types including a maximum of 3 species occurring in Switzerland north of the Alps, according to INFOFLORA (infoflora.ch), the online National Data and Information Center on the Swiss flora. Ellenberg N values were obtained from FLORAVEG (floraveg.eu; Chytrý, 2024) and assigned to pollen types using the average of the values of the included species (Table S2). Pollen-based Ellenberg N values were then calculated for each sample as the abundance-weighted mean of the Ellenberg N values of the individual pollen types, with insect- and wind-pollinated taxa analyzed separately.

3 Results and interpretations

3.1 Number of pollen types in a constant count

When using the original pollen data and constant count rarefaction for calculating palynological richness, the pollen data from both Baldeggersee and Hallwilersee show a gradual decline during the last century (Fig. A1, top). As the minimum count per sample (used as the rarefaction sum) is higher in Baldeggersee (604) than in Hallwilersee (427), the resulting average palynological richness per sample is also higher (~ 45 pollen types in Baldeggersee, ~40 in Hallwilersee). The decline occurs in both records after ~1910 and is 10 pollen types in Baldeggersee, ~5 in Hallwilersee. Using the same rarefaction sum for both sites (427), the resulting palynological richness curves lie within the uncertainty intervals of each other, indicating that both sites have recorded changes in the vegetation in a similar way (Fig A2). For both sites, the proportion of wind-pollinated taxa correlates strongly with the estimated palynological richness and explains > 60% of the variance in a regression model (Fig. 2). The timing of the marked decline in richness coincides with the increase in wind-pollinated taxa in both records (Fig. B1). This raises the question of whether the trends are a reflection of changes in floristic richness or of changes in the composition of the pollen assemblage.
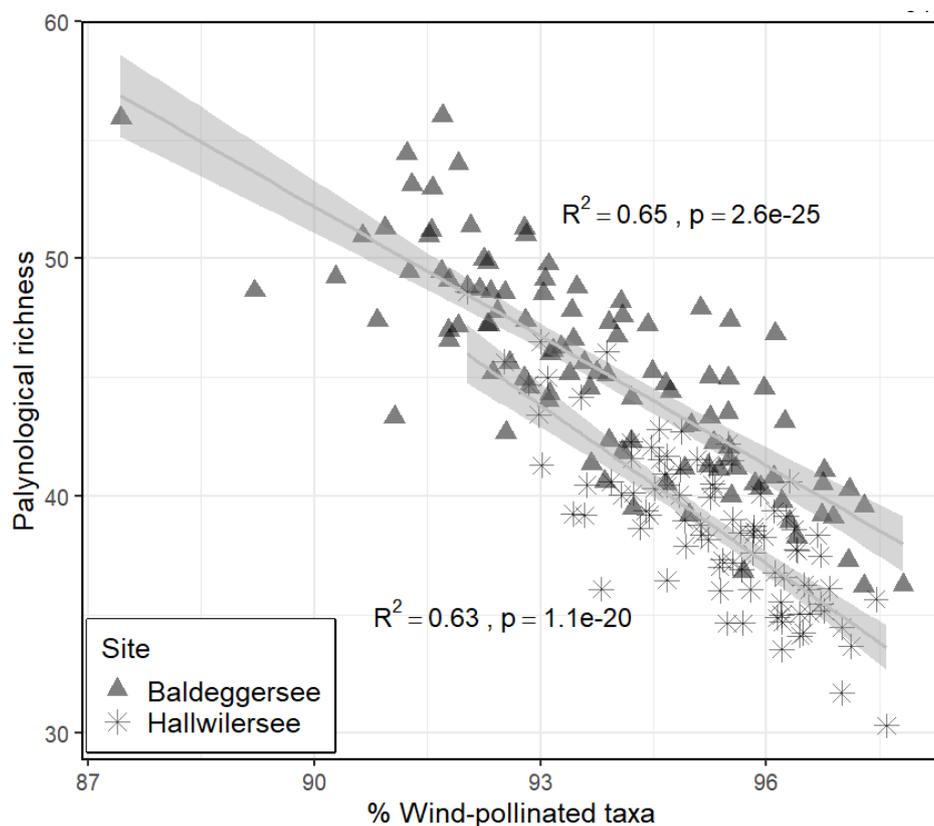
Figure 2. Regression between palynological richness and percentage of wind-pollinated pollen taxa in the pollen assemblages of Hallwilersee and Baldeggersee using rarefaction to a constant count sum (N=427 for Hallwilersee, N=604 for Baldeggersee).

3.2 Increasing the rarefaction sum

Estimating palynological richness separately for wind- and insect-pollinated taxa resulted in two richness curves for each lake (Fig. A1). In both lakes, the richness trends of the wind-pollinated taxa show very little change over time, except for a slight increase of ~2 taxa in Hallwilersee since ~1800 AD. The richness curves of the insect-pollinated taxa also show little change, however, the rarefaction sum is much too low to be able to evaluate changes in richness (12 for Hallwilersee, 17 for Baldeggersee). Insect-pollinated taxa are the rare pollen types in these lakes, comprising less than 3 % of the pollen in both records.

Binning the data results in a strong increase of the average richness of insect-pollinated taxa for Baldeggersee, from ~11 taxa in the unbinned data to ~55 at bin size 15 (Fig. 3, left). This is explained by the sporadic, highly discontinuous occurrence of most insect-pollinated taxa. The binning results in the emergence of clear patterns of change, showing a decrease in richness from 1900-1925 AD followed by an increase. The increase can be dated to ~1945 AD (Fig. C2). A temporary decrease around ~1960 AD is most apparent at bin size 10 though hardly visible at bin size 15, which is likely a result of the lower temporal resolution at the latter bin size. In the wind-pollinated group, the increase of richness with increasing bin size

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is less pronounced (Fig. 3, right). In this group, the richness increases from ~28 in the unbinned data to ~39 at bin size 15.

275   Furthermore, increasing the bin size does not reveal any pattern, except for a slight increase by ~2 taxa in the most recent part of the curve.

Similarly, binning the Hallwilersee data in different bin sizes shows a strong increase in the richness of insect-pollinated taxa with increasing bin size (Fig. C3). A distinct decrease of richness since ~1700 AD and a further decrease during the 20th century emerges in the data from bin size 5 onwards. For the wind-pollinated taxa, binning causes a less pronounced

280   increase in richness, and no specific patterns emerge.

The strength of regression of % wind-pollinated taxa explaining palynological richness decreases with increasing sample size for both Baldeggersee and Hallwilersee (Fig. B2). For Hallwilersee, the regression is not significant from a rarefaction sum of 2256 upwards. For Baldeggersee, the correlation is only non-significant at the highest sample size (N=10539). Comparing the palynological richness trends for the groups of insect- and wind-pollinated taxa with the combined

285   curve, shows that the combined curve is not just the sum of trends in the individual curves. For example, the decline after ~1960 AD in the combined curve (Fig. C1) is not reflected in the separate curves for insect- and wind-pollinated taxa (Fig. 3). Rather, the decline reflects a changing ratio between these groups; the increasing influx of pollen from wind-pollinated taxa in this part of the core causes a further underrepresentation of the insect-pollinated taxa, thereby underestimating palynological richness of the total pollen pool.
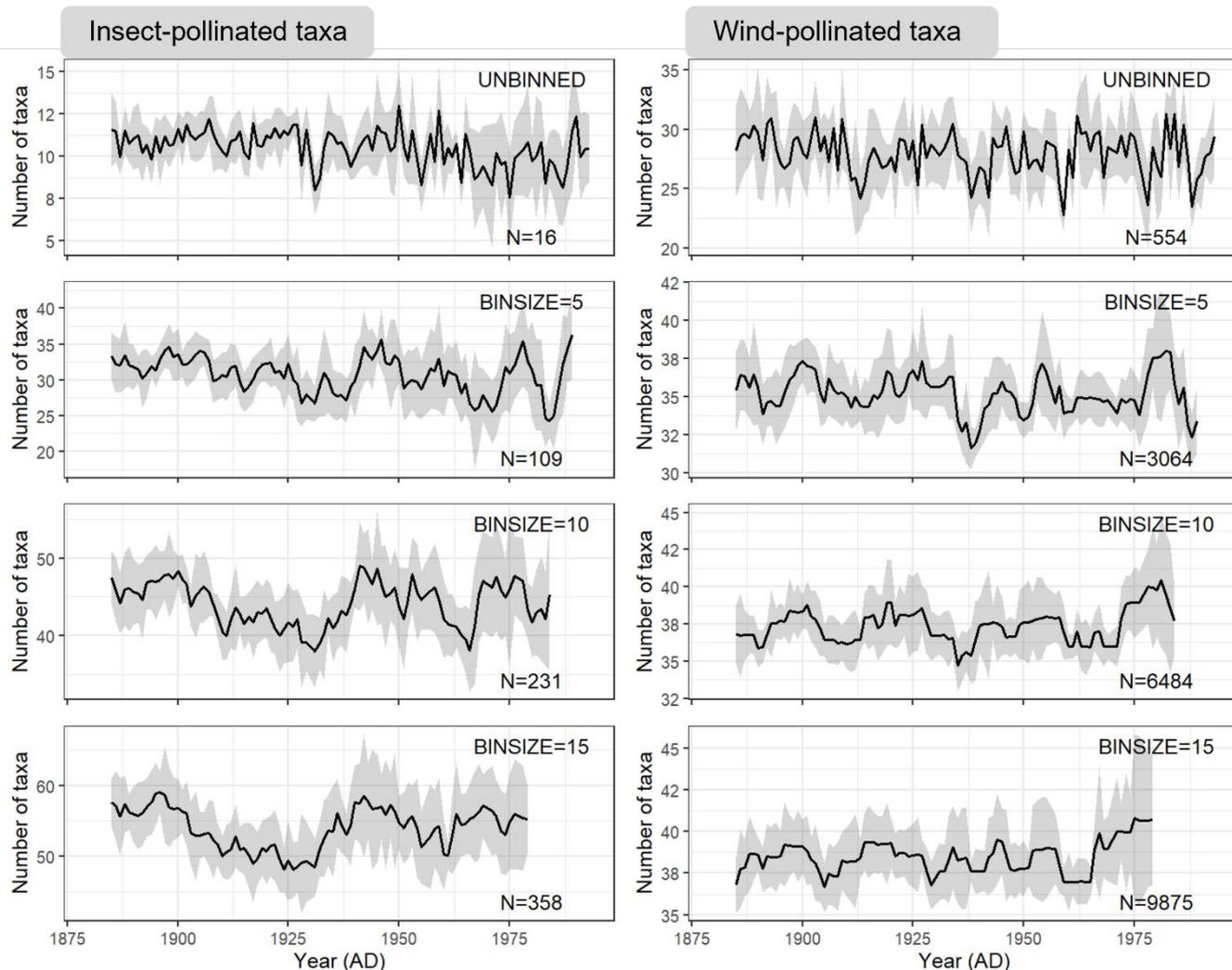
Figure 3. Pollen taxa richness of the pollen assemblages using the constant count method in the Baldeggersee core with increasing bin size of a running bin, with the curve for insect-pollinated taxa on the left and wind-pollinated taxa on the right. The oldest age of the samples in the bin was assigned to each bin, so that the timing of species loss is exact. The rarefaction sum (N) is displayed in the lower right corner of the figures.

3.3 The accumulation-based number of pollen types

To assess whether changes in landscape pollen productivity may have been of significance in the pollen record of Baldeggersee, palynological richness was estimated on the basis of pollen accumulation. This method standardizes sampling effort on pollen accumulation rates (PAR) and assumes that changes in PAR reflect true variations in the influx of pollen types. However, PAR can also be affected by in-lake processes such as sediment focusing or by sampling uncertainties. To assess the combined

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effect of these factors, pairwise correlations of PAR were calculated for the 17 most common pollen taxa in the Baldeggersee core (Fig. D1)

The highest positive correlations were found between *Fraxinus excelsior*/*Alnus glutinosa*-type, *Salix*/*Alnus glutinosa*-type, and *Fraxinus excelsior*/*Salix*. In contrast, *Plantago lanceolata*-type showed negative correlations with these taxa but

305 correlated positively with Cyperaceae, Poaceae, and *Rumex acetosa*-type. These latter three taxa also exhibited slight negative correlations with *Salix*, *Fraxinus excelsior*, and *Alnus glutinosa*-type (except for the Poaceae/*Salix* correlation, which was not significant) and were positively correlated with one another. These correlation patterns align with the long-term compositional trends observed in the pollen record characterized by declining abundances of Poaceae, *Rumex acetosa*-type, and *Plantago lanceolata*-type, and increasing abundances of *Fraxinus excelsior*, *Alnus glutinosa*-type, and *Salix* in the upper portion of the

310 core (van der Knaap et al., 2000). Moreover, the sediment accumulation curve does not show any indications of sediment focusing (Fig. D2). The curve shows two steps of increase in the sediment accumulation rate, which are likely related to increasing biological productivity of the lake due to eutrophication, coinciding with eutrophication steps as identified by the diatom record (Lotter et al., 1997). Therefore, it can be concluded that sediment focusing and sampling uncertainties did not substantially affect the PAR in this record. As such, PAR can be used to standardize sampling effort for palynological richness

315 estimation with some confidence.

Accumulation-based palynological richness shows a clear decline in richness after ~1895 AD of almost 15 taxa (Fig. 4, left). Thereafter, the richness remains constant. Bin size 15 was used in the comparison as it shows the trends most clearly. The wind-pollinated group shows little changes, except for a slight increase of 3-4 taxa after 1980 AD. The insect-pollinated group, however, shows a clear decrease of about 15 taxa after 1895 AD. Comparison of the two methods shows that the curves

320 for wind-pollinated taxa are similar, both in terms of absolute richness as in the absence of a trend. The insect-pollinated curves, however, differ in several aspects. First, the richness in the oldest part is higher in the accumulation-based method, with 70 taxa compared to 58 taxa in the constant count method. The subsequent decline from 1895 AD onwards is captured by both methods and is similar in terms of relative change (21% in the accumulation-based method vs. 19% in the constant count method). The main difference of the two methods is the trend after 1945 AD, with a richness increase in the constant

325 count method by almost 10 taxa, while the curve of the accumulation-based method shows no major change.

The percentage of wind-pollinated taxa in the pollen assemblage also correlates positively to palynological richness estimated with the accumulation-based method at low sampling effort (N= 430-682) (Fig B3), but the regression model loses significance when the bin size is increased. This is also visible by comparison of the combined curve to the individual curves of the insect- versus wind-pollinated taxa (Fig 4, left): the combined curve reflects the sum of the individual curves of the
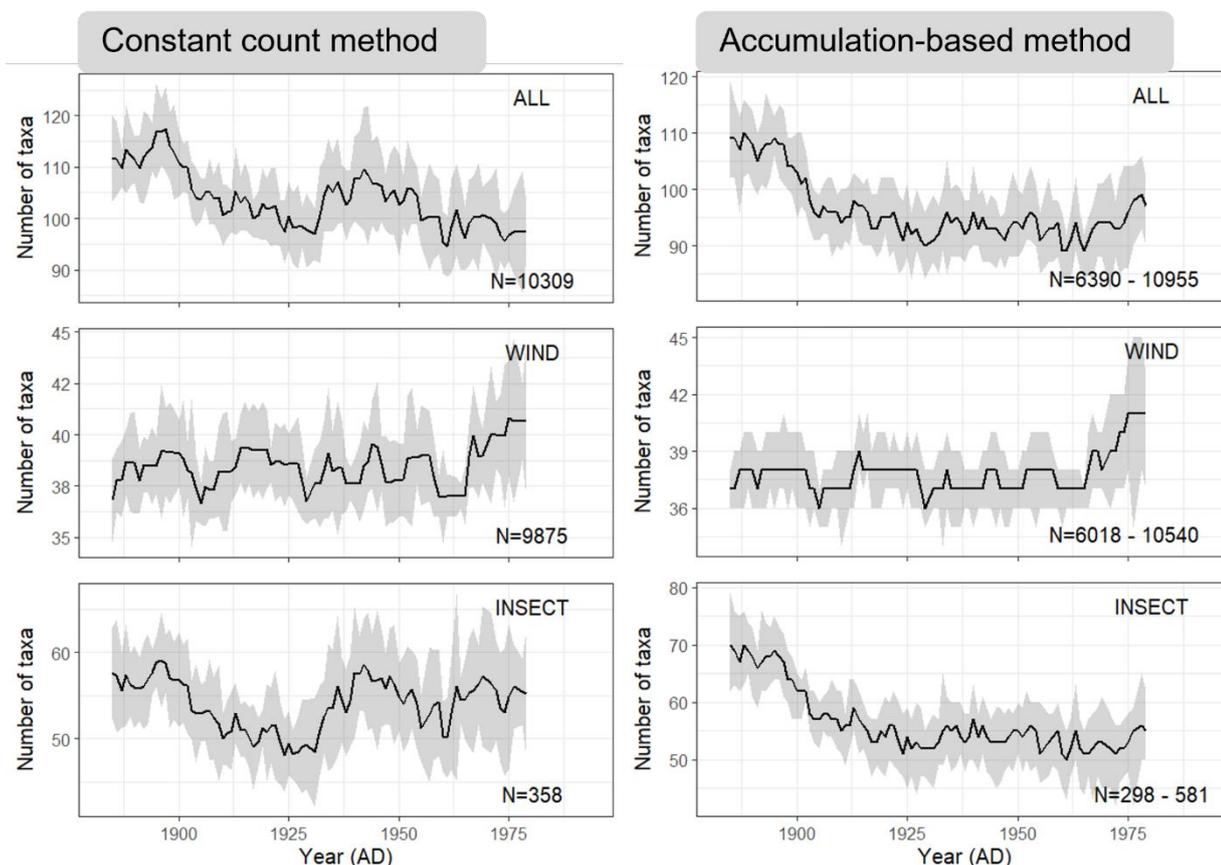
330 separated groups.

Figure 4: Pollen taxa richness of the pollen assemblages in the Baldeggersee core using two different methods: rarefaction to a constant count (left) and rarefaction based on pollen accumulation (right). The data was binned with a bin size of 15. The oldest age of all samples in the bin was assigned to each bin, so that the timing of species loss is exact. The rarefaction sum (N) is displayed in the lower right corner of the figures. The uncertainty envelopes for the accumulation-based method are only a reflection of the uncertainty caused by the rarefaction and do not include the (probably larger) uncertainties in the calculation of the pollen accumulation rates. The uncertainty envelopes of the constant count method reflect only the uncertainty of rarefaction analysis.

3.4 Comparison to Hallwilersee trend

Comparison of the reconstructed palynological richness trend of Baldeggersee with that of Hallwilersee provides additional insights, adding historical context as well as indicating possible spatial heterogeneity of changes in the vegetation. Comparison of the trends revealed that the decline of palynological richness that started at the end of the 19th century, was captured by both records in a very similar manner both quantitatively and temporally (Fig. 5). The Baldeggersee record shows more temporal variation, which can be attributed to the higher temporal resolution of this record compared to Hallwilersee.

3.5 Ellenberg N values

To provide more context to the estimated curves of palynological richness, Ellenberg N values were calculated on the basis of the herbaceous pollen-types. Such reconstructed Ellenberg N values provide an estimation of the soil nutrient status during the

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time of plant growth. As soil nutrient status is strongly linked to agriculture, they thus provide an indication of the degree of agricultural intensification through time. Reconstructed Ellenberg N values for both sites show an increase during the last century for both wind- and insect-pollinated taxa, from ~5-6 to almost 7 (Fig. 6). The Hallwilersee data reveal contrasting

350   trends for the values obtained from the insect-pollinated versus the wind-pollinated taxa in the older part: while the values for the insect-pollinated group are relatively constant until they increase in the last century, the wind-pollinated group shows a decreasing trend from the 15th to the 19th century, before values increase during the last century. In this group, the reconstructed Ellenberg N values in the first time-bin (~1452-1612 AD) are as high as the reconstructed values in the last time-bin (~1919-1998 AD).

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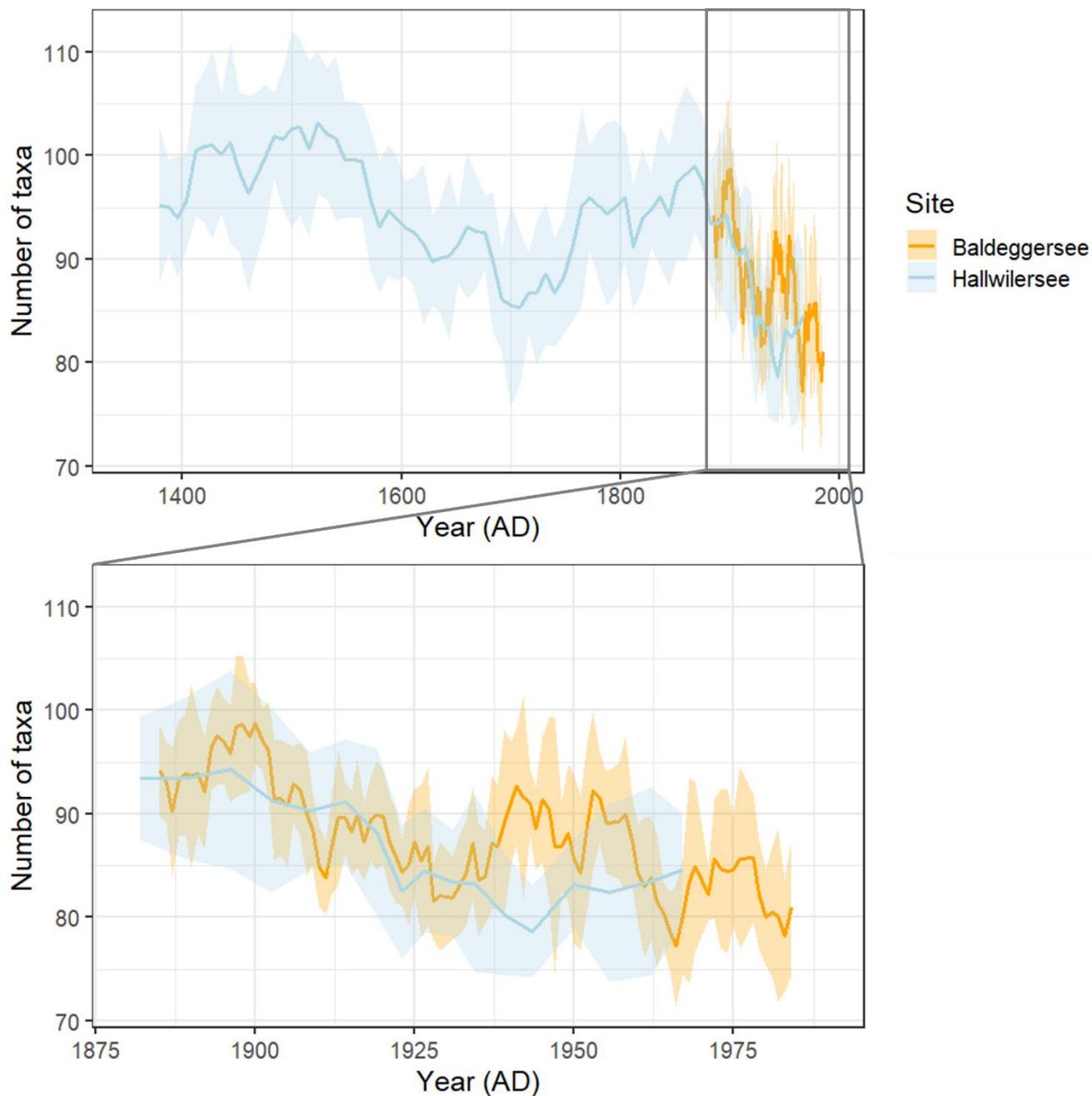
Figure 5. Estimated palynological richness in the cores of Hallwilersee and Baldeggersee. A running bin with the size of 10 was applied to both sites and bins were subsequently rarified to the same pollen sum (N=5807). The oldest age of all samples in the bin was assigned to each bin, so that the timing of species loss is exact. The age-depth model of the Hallwilersee record has a high uncertainty for the samples older than the 20th century.
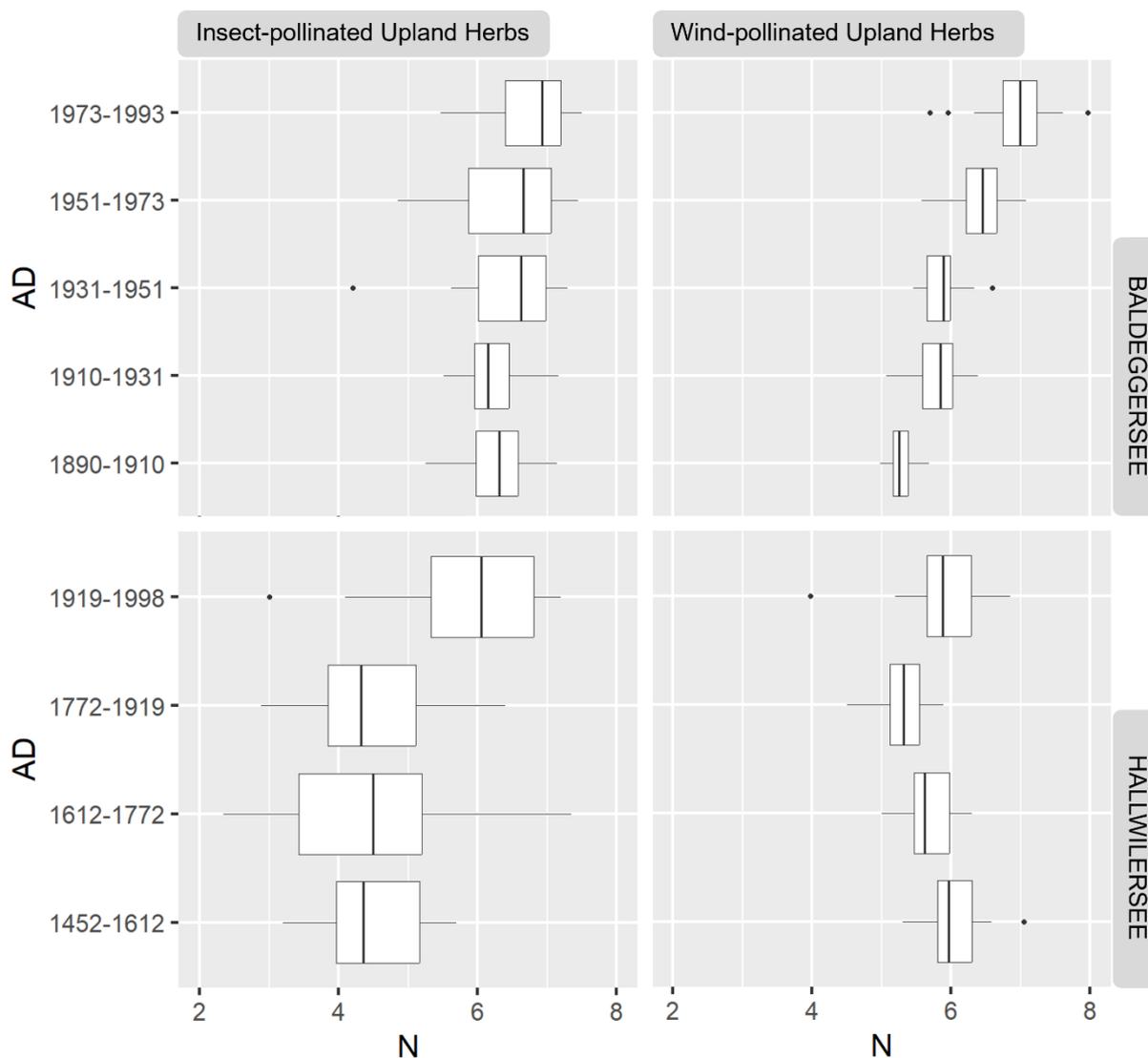
Figure 6. Pollen-based Ellenberg N values for binned samples in the Baldeggersee and Hallwilersee cores. The values where calculated
separately for the wind-pollinated and insect-pollinated upland herbs. The reconstruction of the wind-pollinated group was based on only 11
taxa for Hallwilersee and 12 taxa for Baldeggersee, which were well represented in the pollen record (6941 pollen in Baldeggersee, 3137
pollen in Hallwilersee). The insect-pollinated group was more poorly represented (959 pollen grains in BDS, 390 in HWS) but consisted of
more taxa (40 for Baldeggersee and 22 for Hallwilersee).

4 Discussion

4.1 Methodological considerations

The pollen data from Baldeggersee and Hallwilersee illustrate the strong dependence of palynological richness (constant count)

on the proportion of pollen from wind-pollinated plants (Fig 2). This is due to the high pollen production of wind-pollinated

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plants (Faegri et al., 1989), which changes the influx of pollen originating from the catchment with de- or afforestation. As standard pollen counting is carried out to a more or less constant sum, this effectively changes both the analyzed fraction and the composition of the pollen sample, reducing the likelihood of detecting rare pollen types. This also displays in a rarefaction curve, which saturates more slowly as the percentage of wind-pollinated taxa increases. This study has set out to reduce these effects by testing three different data treatments and their combinations: i) the binning of samples; ii) constant count diversity versus the accumulation-based diversity; and iii) the division of wind- versus insect-pollinated taxa.

4.1.1 Binning

Binning (combining samples) increases the total pollen count similar to increasing the count size of individual samples, making it more likely to detect rare pollen types. Binning had a strong effect across all data treatments, revealing trends that were not evident in the original data. The effect was particularly pronounced for insect-pollinated taxa, which showed a substantial increase in richness when samples were combined (Fig 3, left).

For the data of Baldeggersee and Halwillersee, binning reduced the impact of the proportion of pollen from wind-pollinated plants on richness (Fig. B2). This likely reflects the reduced impact that evenness has at higher sample sizes, an effect also noted by van der Knaap (2009). This effect may be interpreted in the context of the sample rarefaction curve: in assemblages dominated by a few taxa with high pollen productivity, rarefaction curves rise more slowly and reach their asymptote at higher samples sizes. The farther a sample is from the asymptote, the stronger the underestimation of true richness at a given sample size.

A major advantage of binning is that it can be applied after data collection with standard count sizes, rather than increasing the sampling effort per sample in the study design (Keen et al. 2014). In the annually laminated Baldeggersee record, binning additionally smooths abundance fluctuations in tree taxa potentially caused by interannual variability in pollen production (van der Knaap et al., 2010; Nielsen et al. 2010). However, binning samples has the trade-off of reducing the temporal resolution. The use of running bins, rather than fixed bins, minimizes this loss as it allows changes to be more precisely localized. Nonetheless, short-lived changes may be obscured, as binning inevitably smears information across time (Giesecke et al., 2014). This was also visible in the curves for different bin sizes in the datasets examined here: some trends appearing at intermediate bin sizes disappeared again at larger ones. A further effect of binning can occur during periods of rapid vegetation change. Bins that contain samples taken before and after a marked transition contain pollen types from both vegetation types, resulting in a temporary increase in palynological richness, even though the floristic richness of the vegetation never increased at any single moment in time.

4.1.2 Constant count vs. accumulation-based method

The accumulation-based method estimates richness from a fixed proportion of the calculated pollen accumulation rates (van der Knaap, 2009) and thus differs fundamentally from the constant count method. If total pollen accumulation rates would

405 remain constant through time, both methods would yield identical results. In the Baldeggersee record, however, pollen accumulation rates vary substantially over time, leading to different richness trends depending on the method used.

These differences reveal two problems with the constant count method. First, an increase in palynological richness after ~1945 AD, most pronounced in the insect-pollinated group, is present in the constant count method, but not in the accumulation-based method. This likely reflects an artefact of analyzing a larger proportion of the total sample, as pollen accumulation rates were generally lower after 1945 AD, most notably for insect-pollinated taxa (Fig D3). Analyzing a larger

410 fraction of the total sample increases the chance of encountering rare pollen types, including long-distance taxa, thereby overestimating its richness (Weng, 2006). Second, the decrease in richness after ~1960 AD is visible only in the combined curve of the constant count method, and results from an increased influx of wind-pollinated tree pollen that swamps the assemblages. Such a decline is absent in either of the separated functional groups, indicating that it results from a shift in the relative proportions of the groups rather than from a true ecological trend. This illustrates a limitation of the constant count

415 method: the combined richness curve can diverge from the sum of the trends of individual groups due to shifts in their relative proportions. In contrast, the combined curve estimated with the accumulation-based method does reflect the sum of the individual group trends. Despite these differences, both methods clearly document a decline in palynological richness from ~1895 AD, indicating that major ecological changes may be captured regardless of the method.

At low pollen sums (N ~600), richness estimates from the accumulation-based method are still influenced by the

420 proportion of wind-pollinated taxa (Fig. B3), although less strongly than the constant count method (Fig. B2). This indicates that there are additional factors that influence the correlation between % pollen from wind-pollinated plants and richness, besides a different proportion of the sample being analyzed.

Although we consider the accumulation-based method as the superior method for estimating pollen diversity, it has limited practical applicability due to large uncertainties in most cases. Pollen accumulation rate estimates generally have high

425 uncertainties, due to 1) the propagation of age-depth model uncertainties, 2) sample-treatment uncertainties, such as uncertainties of estimated volumes, added exotes, and counts (Maher 1981) and 3) within-lake sediment dynamics, including redeposition, slumping, and differential settling of pollen (Davis & Brubaker, 1973; Davis & Ford, 1982; Giesecke & Fontana 2008; van der Knaap, 2009). In many sediment sequences, these uncertainties may exceed the magnitude of the inferred richness trends.

430 In the Baldeggersee record, uncertainties in accumulation rates were not quantified as each sample was extracted from one annual layer. Also, the correlation table (Fig. D1) does not provide indications that focusing or other lake internal processes had a detectable impact. The observed changes in sedimentation rates coincide with eutrophication steps reconstructed from the diatom record (Lotter et al., 1997), indicating that they are more likely linked to increases in biological production rather than sediment redistribution. Importantly, these changes do not coincide with the periods during which the

435 constant count and accumulation-based methods show divergent richness trends, indicating that the differences between the two methods are not an artefact of depositional processes.

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4.1.3 Separation of insect- vs. wind-pollinated taxa

Comparison of the constant-count and accumulation-based methods shows that separating functional groups resolves the bias of the constant count approach caused by the swamping of pollen assemblages due to increased tree pollen influx after ~1970 AD, but not the bias related to marked shifts in pollen accumulation rates (PAR). The apparent post-1945 increase in richness is in fact further amplified when insect-pollinated taxa are analyzed separately. In this group, PAR show a particularly clear decrease through time (Fig. D3). As a result, a constant pollen count represents an increasingly large fraction of the total pollen pool. Separating functional groups therefore amplified, rather than reduced, this bias. Moreover, without independent information on PAR, it is impossible to determine whether deviations from the constant count richness curve reflect bias correction or instead represent newly introduced or amplified biases. Consequently, the additional information gained from functional-group separation is limited or potentially misleading unless it is combined with the accumulation-based method or information on PAR, as done here.

Apart from the purpose of reducing biases introduced by changes in their relative proportions, separating wind- and insect-pollinated taxa may be ecologically meaningful. Wind- and insect-pollinated taxa are likely to represent vegetation patterns at different spatial scales (Weng et al., 2006). Modern pollen–vegetation comparison studies indicate that richness of insect-pollinated taxa is more closely related to local vegetation richness, whereas richness of wind-pollinated taxa reflects diversity at broader spatial scales (Meltsov et al., 2011; Reitalu et al., 2019).

In this study, separating functional groups reveals that all major richness changes occur within the insect-pollinated group, highlighting the importance of sufficient sampling effort to detect diversity changes beyond shifts in the proportion of wind-pollinated taxa. It must be noted, however, that insect-pollinated taxa are likely to be particularly underrepresented here due to the large size of both lakes.

4.1 Ecological and environmental insights

While the data from Baldeggersee allow comparing different methods, the additional data from Hallwilersee provide a longer time perspective of vegetation development in the area. Due to uncertainty in the age–depth model, the exact extent of the record is uncertain but the oldest sediments were likely deposited during the Late Middle Ages. Four main phases are visible in the floristic richness curve (Fig. 5): 1) high pollen richness during the Late Middle Ages, 2) decline during forest recovery, 3) increase with reopening of the landscape, and 4) steep decline during the 20th century.

The Late Middle Ages are characterized by the highest floristic richness compared to the rest of the sequence. Similarly, peak richness during this time was observed in pollen records from southern Sweden (Lindbladh & Bradshaw, 1995; Berglund et al., 2008; Sköld et al., 2010; Spitzig et al., 2025). This high richness has been linked to extensive, and small-scale, dynamic agricultural activities that occurred in Europe during this time, creating a rich habitat for plant species adapted to disturbed and open environments. This is also reflected in a detailed analysis of pollen records from southern Germany, revealing many sporadically occurring pollen types from members of the Aphanion and Caucalidion plant communities during

470 this time (Rösch, 2014; Rösch 2016). According to Rösch (2014), this indicates that cultivation took place on less fertile, poor and dry soils, on which cereals such as *Secale cereale* and *Avena sativa* were cultivated in extensively managed fields, providing habitats for many characteristic weeds, including plant communities of Aphanion on acidic soils and Caucalidion on base rich soils. Although many of the plant species in these communities are insect-pollinated, and therefore rare in pollen records, sporadic occurrences provide valuable information (Rösch, 2014; Rösch, 2016). In the Hallwilersee record, taxa such as *Centaurea cyanus*, *Orlaya grandiflora*, *Papaver rhoeas*-type, *Scleranthus*, *Melampyrum*, and *Torilis arvensis*, indicate this

475 type of land-use in the Seetal region during the late Middle Ages. Their decline in younger samples reflects a reduction of this land-use type that is also reflected by the current status of these communities on the Swiss national red list as "critically endangered" (Delarze at al., 2016). Interestingly, the average pollen-based Ellenberg N values of the wind-pollinated group are rather high (Fig. 6), with average values in the oldest part of the core similar to the post-industrial average. In contrast, the average for the insect-pollinated group in the oldest part of the core is much lower than the post-industrial average. The high

480 Ellenberg N value of the wind-pollinated group is specifically determined by a high proportion of *Urtica* pollen in the oldest sediments. Both *Urtica dioica* and *Urtica urens* occur in the study region. *Urtica dioica* preferably grows on moisture- and nutrient-rich soils and develops most vigorously in the half-shade (Olson, 1921). This type of habitat would have been abundant in the area due to the practice of silvopasture, which was common in temperate Europe during this time and caused an infield-outfield transfer of nutrients (Rösch, 2014). Alternatively, the grains could originate from *Urtica urens*, which grows in

485 strongly manured, disturbed places such as dung heaps, vegetable gardens, watering points and small fenced fields containing husbandry animals (Weeda et al., 1985). In any case, the high reconstructed Ellenberg N value during this period likely reflects *Urtica* growing vigorously on a few strongly manured patches rather than large-scale fertilization of all fields and pastures in the catchment.

During the phase of forest recovery, palynological richness declines and the pollen record shows an increase in

490 arboreal pollen. Cereal pollen and associated arable weeds decrease clearly, which could reflect a phase of agricultural abandonment. Due to the uncertainty of the age of this period, it is difficult to establish the cause of this decline, but it is clear that with the decline of the cereal cultivation, the associated weeds of the Caucalidion and Aphanion plant communities decline as well. Although possibly a real effect, it must also be considered that the decline in richness during this phase could be explained by forest regrowth alone. The increasing pollen productivity of the area would result in a smaller proportion of the

495 accumulated pollen being analyzed.

In the third phase, reflecting landscape reopening, *Secale* and Cerealia pollen together with some of their associated weeds recover, although *Centaurea cyanus* is less abundant than it had been during the first phase. Poaceae and *Plantago lanceolata* become more frequent, suggesting an increasingly large amount land being used for meadows and/or pastures (van der Knaap, 2023). This interpretation is further supported by the increased occurrence of other taxa associated with fodder

500 production such as *Trifolium pratense*-type and *Onobrychis*. Similarly, this shift and the associated increase in production of fodder plants was also recognized in the pollen record from Egelsee, nearby Bern (Stevanon et al., 2024). After the initial recovery of cereal production, *Secale* and other cereals decrease, while pasture/meadow indicators show an further increase,

suggesting a shift from mixed- towards dairy-based farming systems before the start of the 20th century. This timing is roughly coherent with the drop in cereal prices during the late 19th century, caused by cheap imported grains from the US during increased international trade, so that dairy farming became more profitable and became the main sector of Swiss agriculture (Hofmann, 2020; Stuber & Wunderli, 2021). Moreover, these increased possibilities for long-distance trading shifted farms away from being closed-circuit systems and more and more materials such as marl and lime for enrichment of the soil and seeds where imported from outside the farm areas (Thomson, 1968). Increased enrichment of pastures/meadows in the Seetal area during the 19th century is indicated by a rapid decrease in the abundance of plants growing on poor soils such as *Rumex acetosella* and *Plantago media* as well as a reduction in sporadic occurrences of *Orlaya grandiflora* and *Jasione*. At the same time, taxa associated with higher soil nutrient status such as *Heracleum*, *Mercurialis annua* and *Urtica* show a marked increase. Towards the end of the 19th century, laminations of the Baldeggersee sediments started as a consequence of hypoxia on the bottom of the lake, induced by eutrophication. The start of laminations is thus a sign of further intensification of land-use. Additionally, intensification of land use is also indicated by a decline of wetland taxa such as Cyperaceae and *Thelypteris palustris*, possibly reflecting the reduction of wetland area to create land suitable for agriculture as part of a civil engineering project that started in 1868 (Schneider & Eugster, 2007).

The decline of palynological richness during the last century in the Baldeggersee and Hallwilersee pollen records (Fig. 5) matches findings from resurveyed vegetation plots on the Swiss Plateau in grasslands (Widmer et al., 2025, 2026) and on arable fields (Richner et al., 2017), recording a loss in plant diversity. The most pronounced decline was found for geophytes and species adapted to low nutrient conditions and cool temperatures, whereas increases were found for nutrient-demanding, mowing tolerant species, grasses and neophytes (Richner et al., 2017; Widmer et al., 2025, 2026), with the strongest diversity loss observed at low elevations (Widmer et al., 2025). The Hallwilersee and Baldeggersee pollen records show similar trends but reveal that species adapted to low nutrient conditions already started to decline in the 19th century, before the start of the first vegetation surveys. Moreover, both pollen records show a strong increase in gras pollen towards the 20th century, but percentages decline again from ~1925 onwards. A decline of grass pollen during the last century was also found by Theuerkauf et al. (2015) in a pollen record from northeastern Germany. Here, the decline was interpreted not as a decrease in grassland area but, based on analysis of land-use statistics and pollen accumulation rates, as a reflection of intensified use of the existing meadows. Specifically, earlier and more frequent mowing reduces the amount of plants that reach flowering stage, although changes in species composition could also have an effect (Theuerkauf et al., 2015). The Baldeggersee record supports this interpretation, as NAP pollen accumulation rates decrease during the 20th century, while the landscape openness remained roughly the same or even increased in some areas where orchards where cut down (van der Knaap et al., 2000).

From ~1925 AD onwards, palynological richness in the examined records remains relatively constant. Interestingly, during this period major steps of further land-use intensification are historically recognized (Stuber & Wunderli, 2021), and these also partially reflect in the pollen record as pollen-based Ellenberg N values further increase (Fig. 6). Also, maize is increasingly cultivated from ~1950 onwards (van der Knaap et al., 2000). Moreover, the resurveyed vegetation plots show additional declines during this time (Richner et al., 2017; Widmer et al., 2026). Therefore, it seems unlikely that all loss of the

present floristic diversity already occurred at the beginning of the 20ᵗʰ century. Possibly, this is a reflection of the sensitivity of the pollen record to plant diversity loss, especially when this is mainly a loss of underrepresented insect-pollinated species: the pollen record captures their initial decline, but not the subsequent disappearance, when these taxa have already become

540   rare.

5 Conclusions

The assessment of palynological richness in the pollen record provides a unique opportunity to gain insight into changes in floristic diversity of the landscape beyond the reach of observational surveys. Biases inherent in pollen data can be reduced using a combination of strategies. The most robust results are obtained with a combination of the accumulation-based method

545   and the binning of consecutive samples, so that both the overall sampling effort and the standardization of the sampling effort are improved. However, this is not always feasible as the application of the accumulation-based method requires very precise chronological control and minimal within-lake redepositional processes. The simplest way to improve diversity estimates based on pollen counts is the binning of samples without separation of functional groups. However, in this case, trends must be interpreted with caution as changes in the total size of the pollen pool cause distortions. Specifically, increased influx from

550   tree stands close to the lake as well as reduced pollen productivity of non-arboreal taxa due to land use intensification distorted palynological richness trends using the constant count method in the records assessed in this study.

            The decline in palynological richness in the records from Baldeggersee and Hallwilersee started already at the end of the 20ᵗʰ century, and richness remained relatively constant hereafter, from ~1925 AD onwards. Before, during and after this decline, the pollen record shows signs of agricultural intensification, including increased manuring, a shift from mixed- to

555   dairy-farming and the conversion of wetlands to agricultural fields.
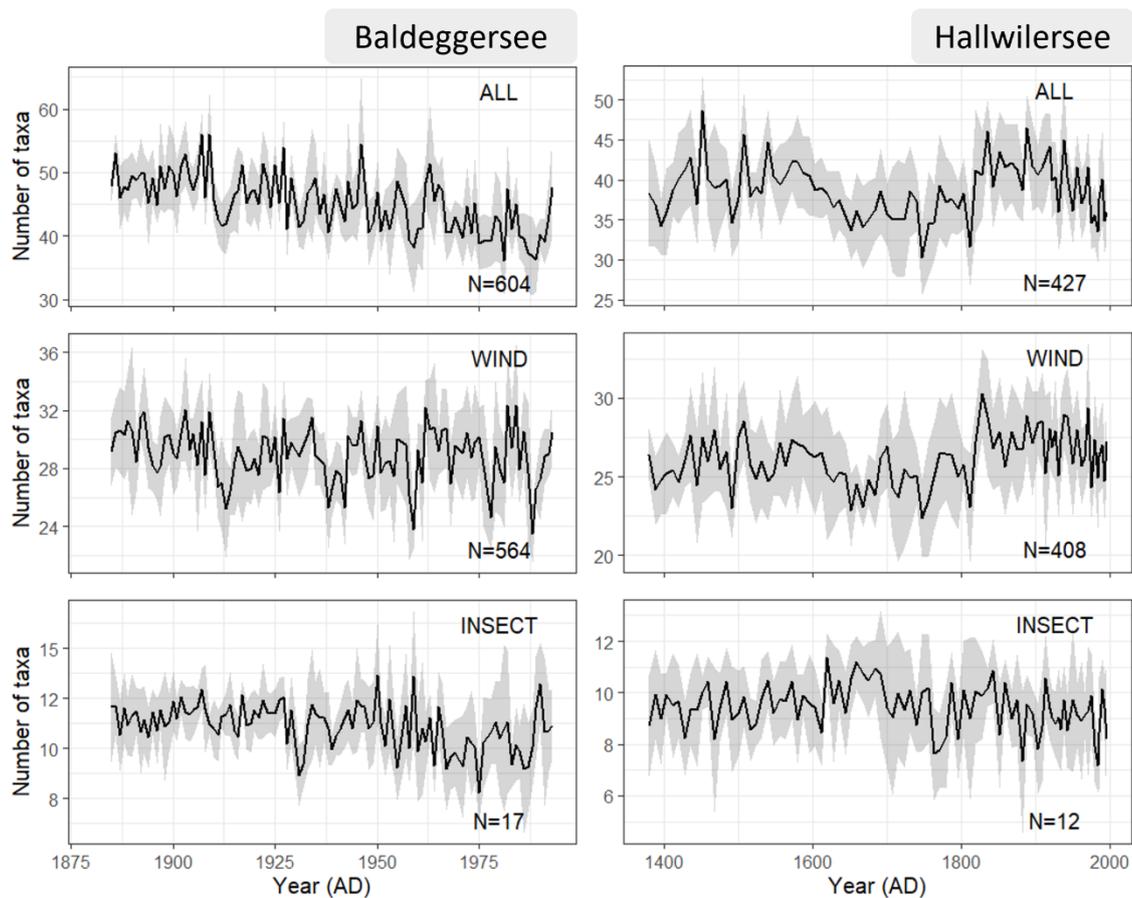
Appendix A

Figure A1. Palynological richness of the pollen assemblages in the cores of Baldeggersee and Hallwilersee before (ALL) and after the separation of pollen functional groups (INSECT, WIND). The rarefaction sum (N) is displayed in the lower right corner of the figures.
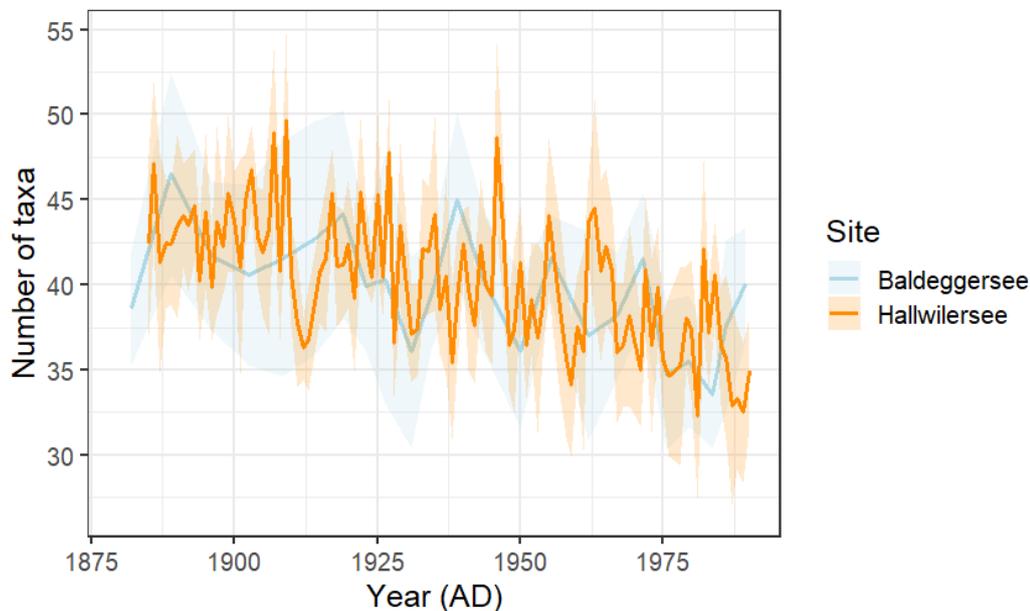
Figure A2. Palynological richness of the pollen assemblages in the cores of Baldeggersee and Hallwilersee on the same rarefaction sum (N=427).
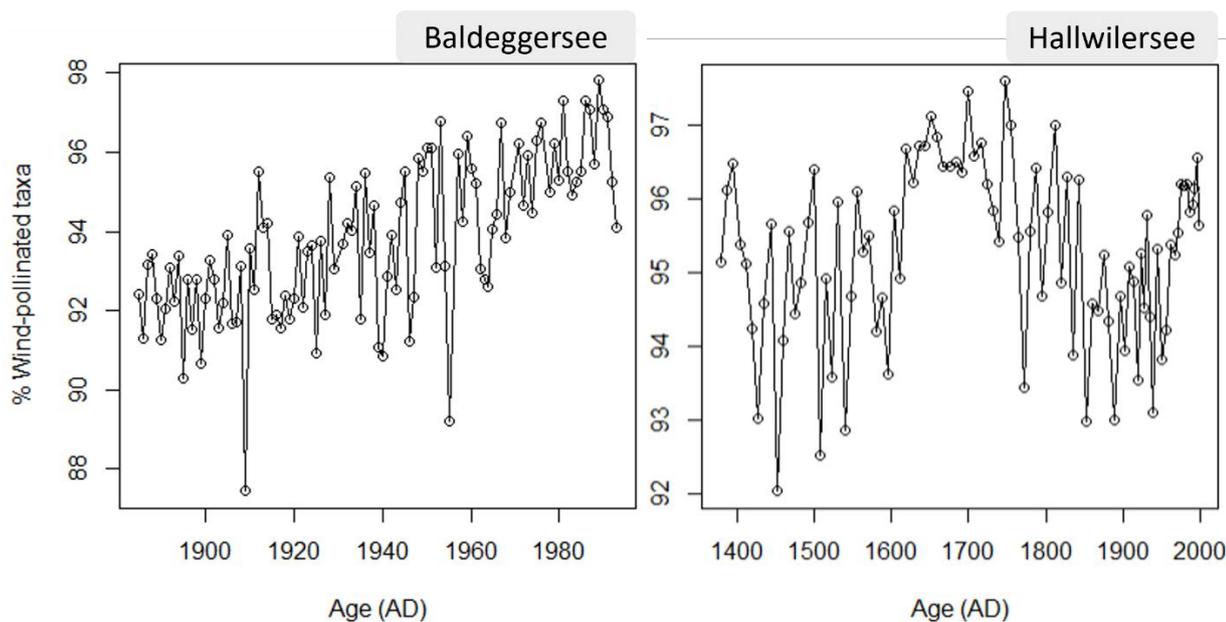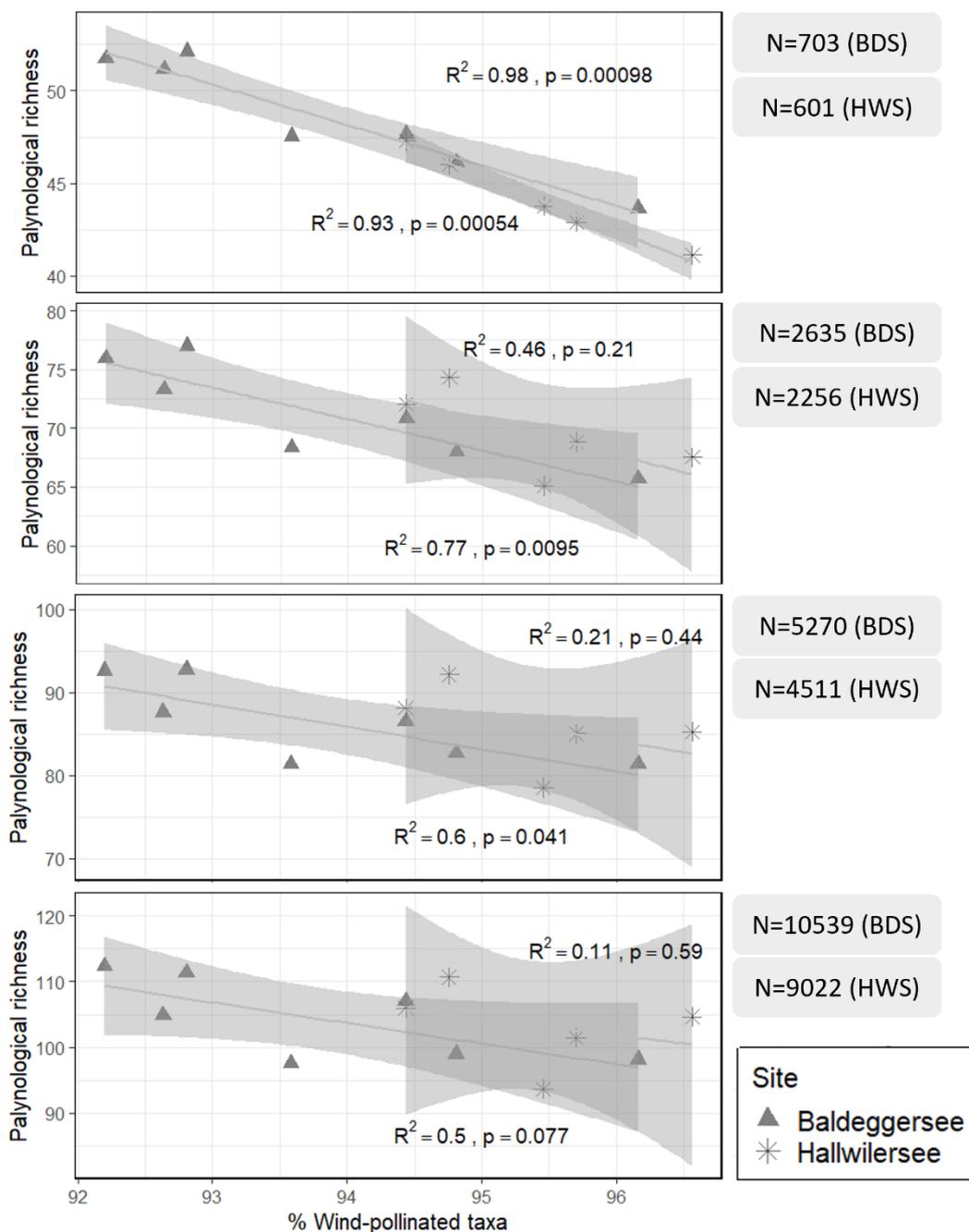
575 **Appendix B**

**Figure B1.** Percentage of wind-pollinated taxa in pollen assemblages of the Baldeggersee and Hallwilersee cores through time.

Figure B2. Regression between the palynological richness and % wind-pollinated pollen taxa in the pollen assemblages of Hallwilersee and Baldeggersee using rarefaction to a constant count with increasing rarefaction sum (N). The pollen data was binned in consecutive bins of 15.
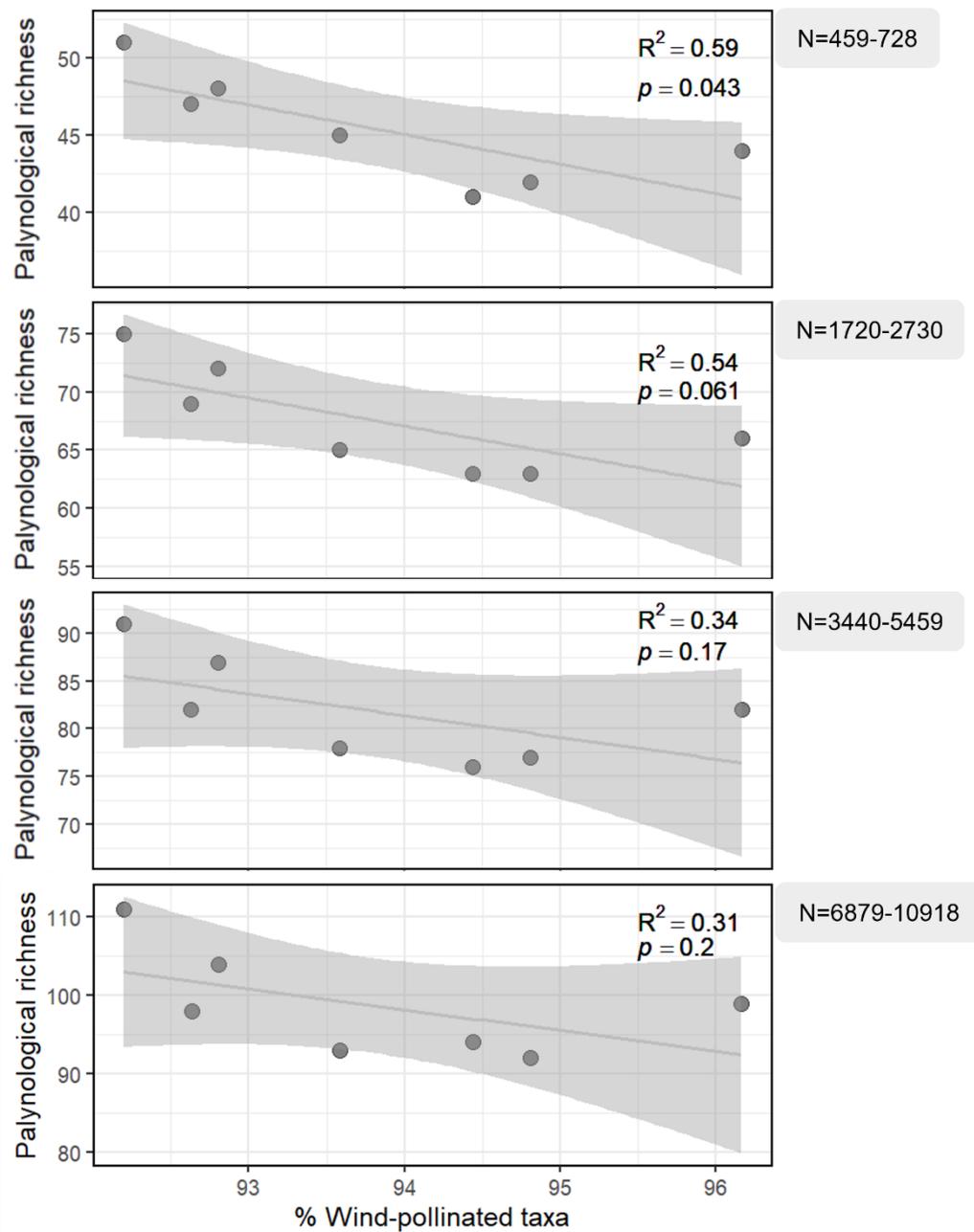
Figure B3. Regression between the palynological richness and % wind-pollinated pollen taxa in the pollen assemblage of Baldeggersee using accumulation-based rarefaction with increasing rarefaction sum (N). The pollen data was binned in consecutive bins of 15.
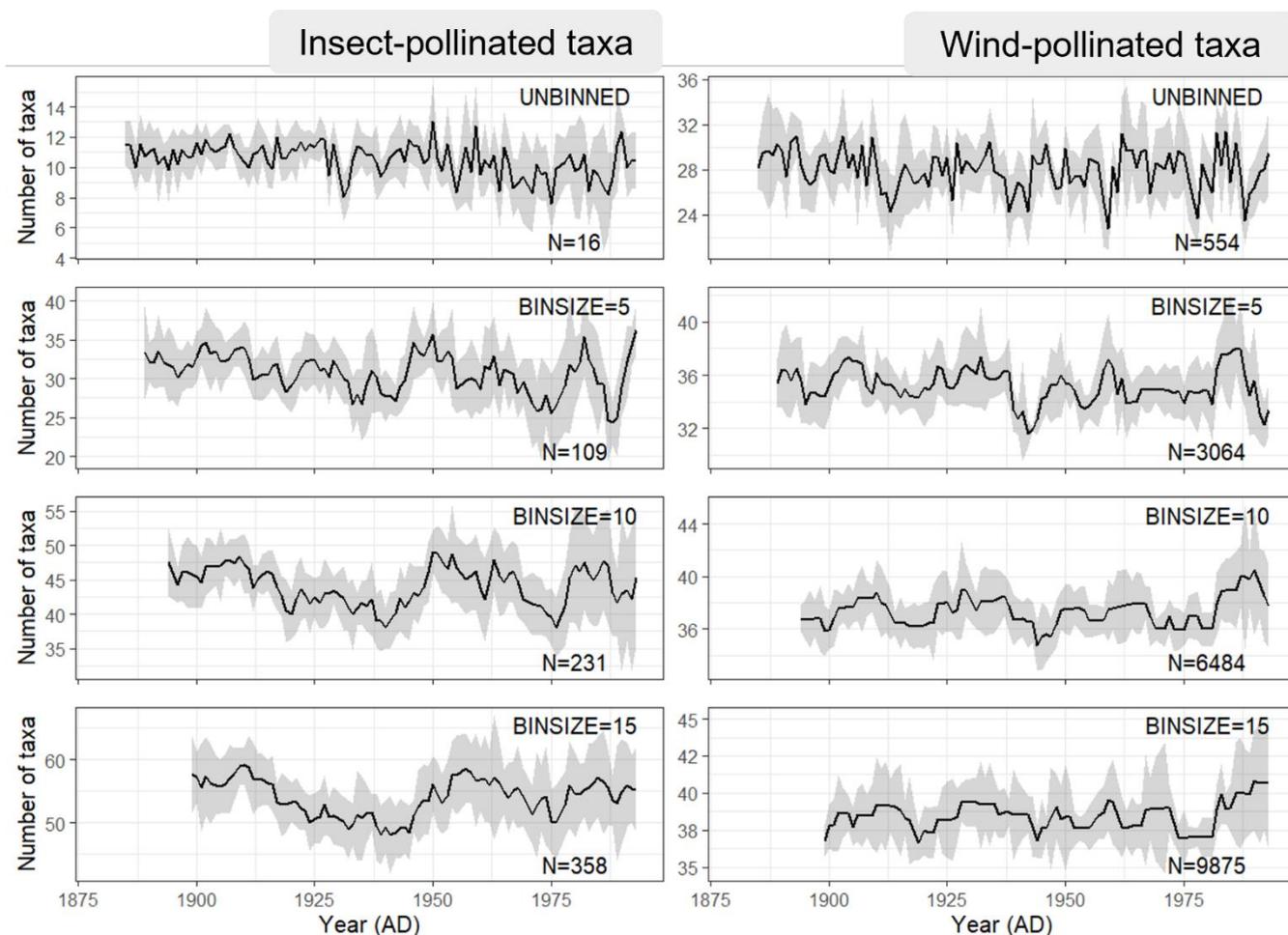
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Appendix C

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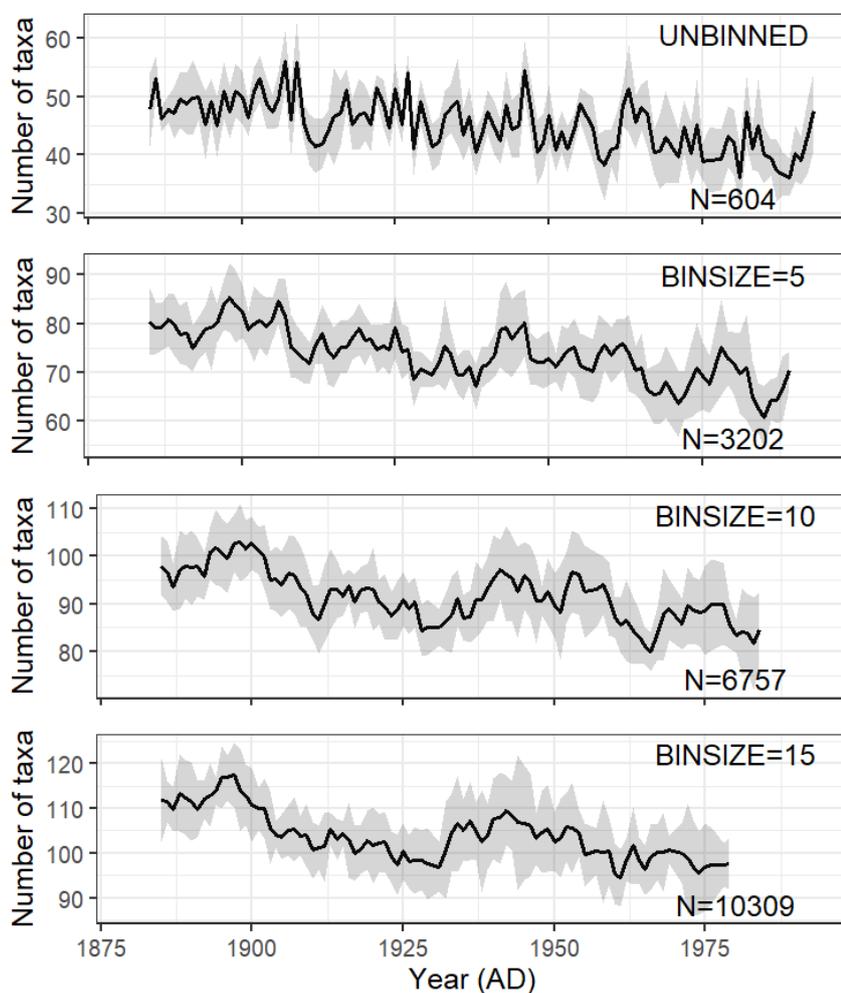
Figure C1. Palynological richness of the pollen assemblages in the Baldeggersee core with increasing bin-size of the running bin. The oldest age of all samples in the bin was assigned to each bin, so that the timing of species loss is exact. The rarefaction sum (N) is displayed in the lower right corner of the figures.

Figure C2. Palynological richness of the pollen assemblages in the Baldeggersee core with increasing bin-size of the running bin. Richness
was estimated separately for the insect-pollinated (left) and wind-pollinated (right) taxa. The youngest age of all samples in the bin was
assigned to each bin, so that the timing of species gain is exact. The rarefaction sum (N) is displayed in the lower right corner of the figures.
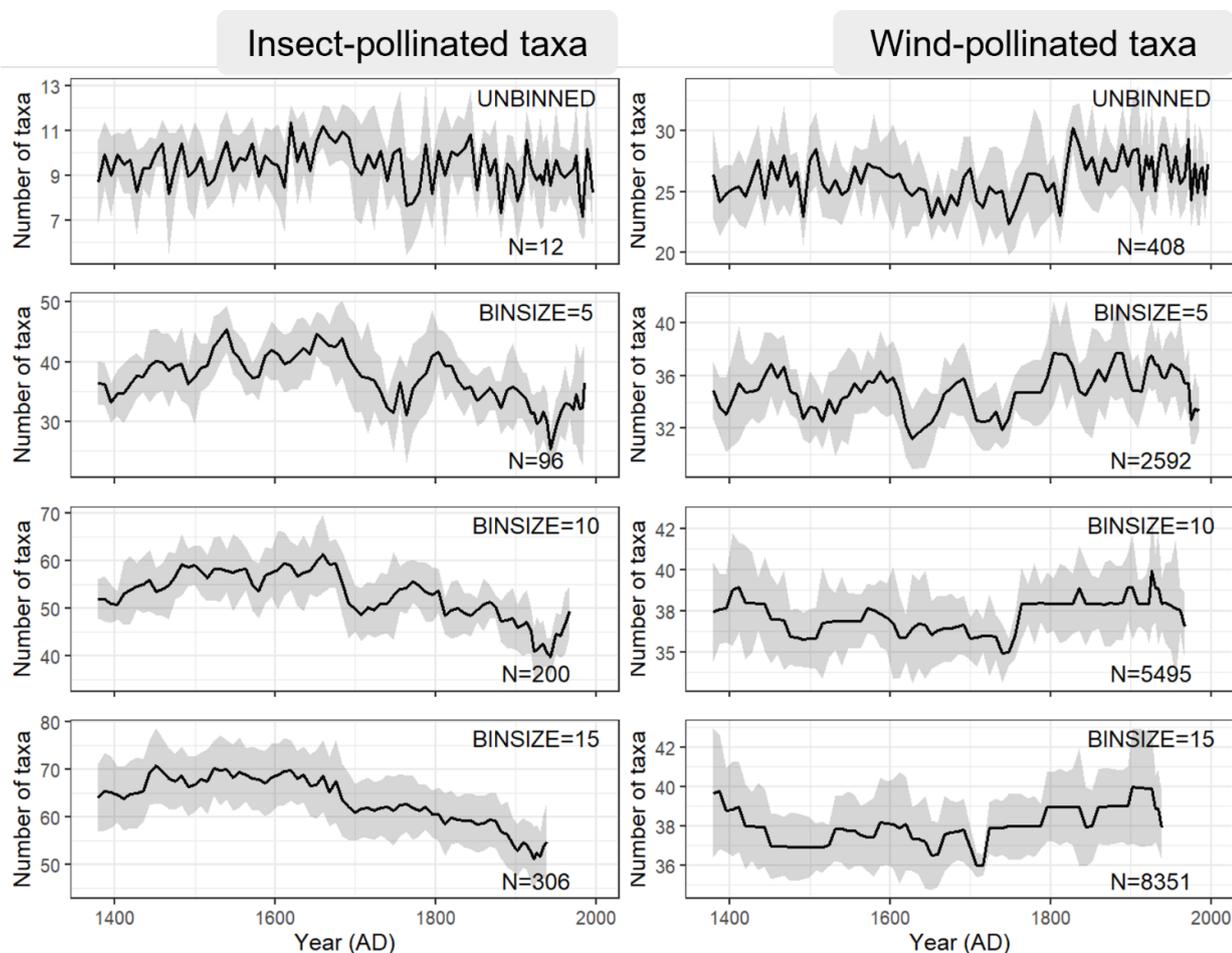
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Figure C3. Palynological richness of the pollen assemblages in the Hallwilersee core with increasing bin-size of the running bin. Richness was estimated separately for the insect-pollinated (left) and wind-pollinated (right) taxa. The youngest age of all samples in the bin was assigned to each bin, so that the timing of species gain is exact. The rarefaction sum (N) is displayed in the lower right corner of the figures.

Appendix D
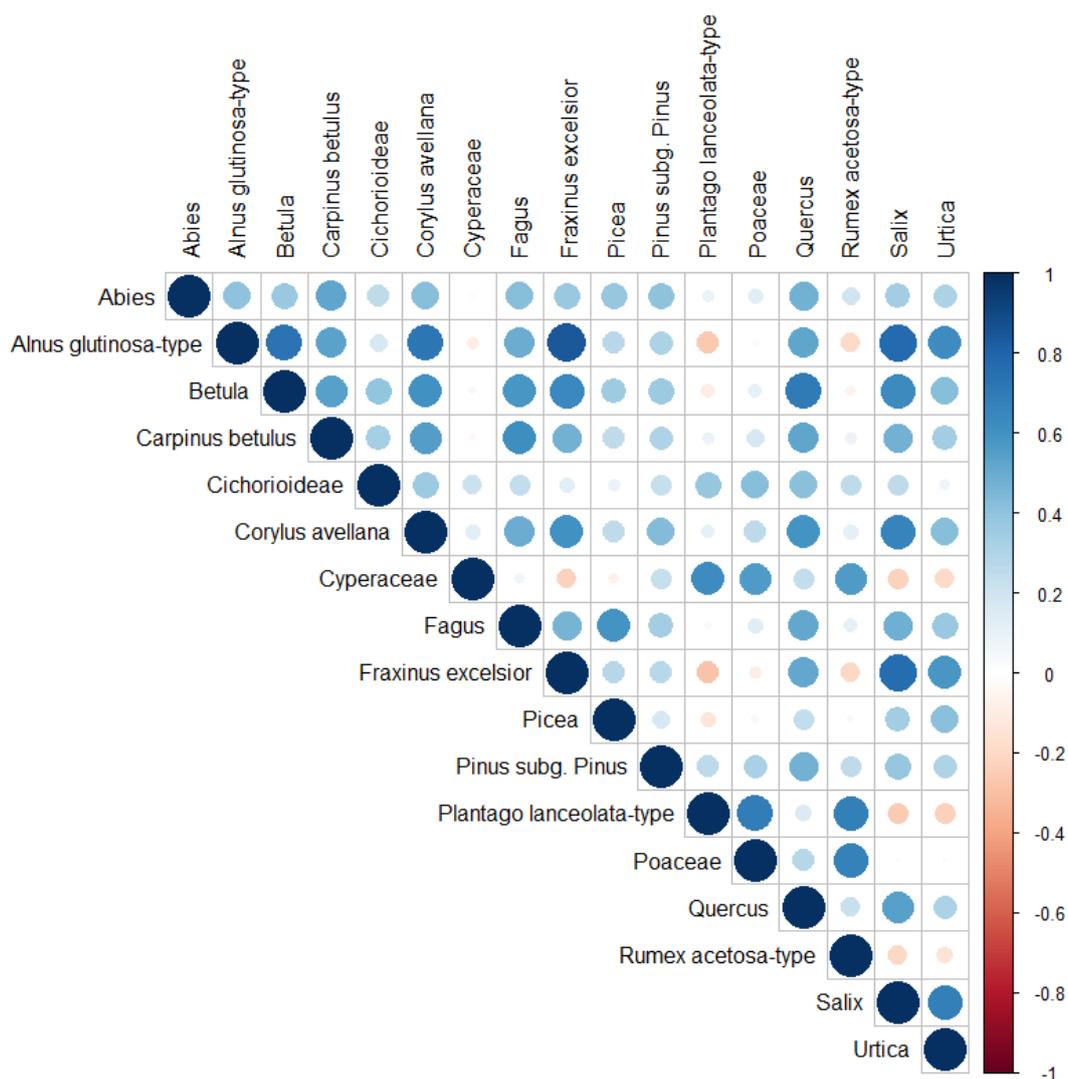
Figure D1. Correlation table for pollen taxa in Baldeggersee. Fields with insignificant (p<0.05) correlations are left blank. The color indicates the nature of the correlation coefficient (strength and direction of the correlation).
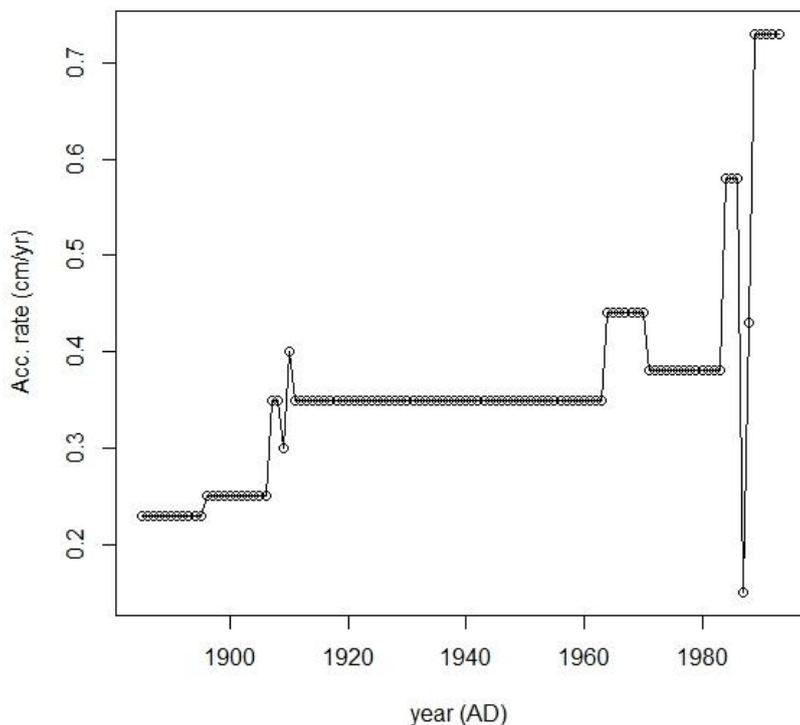
Figure D2. Sediment accumulation rate through time in the Baldeggersee core.
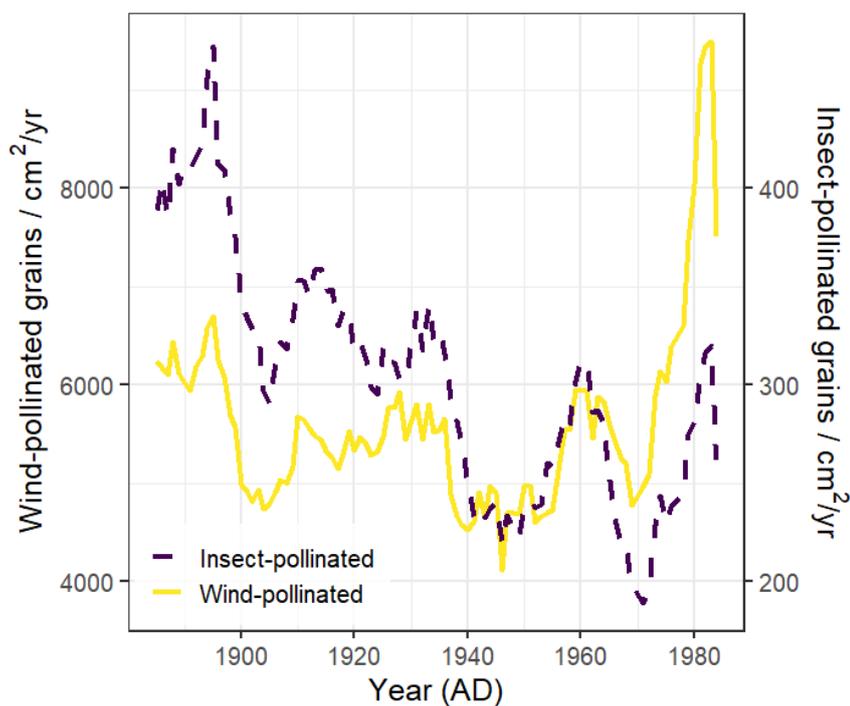

Figure D3: Pollen accumulation rates of wind-pollinated and insect-pollinated taxa in the Baldeggersee core (pollen data binned in running bins of 10). The oldest age of all samples in the bin was assigned to each bin, so that the timing of species loss is exact.

Author contributions

CMH and TG designed the research. CMH analyzed the data and wrote the original draft. TG, WOK and JFNL reviewed and edited the manuscript.

Competing interests

685 The authors declare that they have no conflict of interest.

Code availability

The code used in this study is available online at: https://doi.org/10.5281/zenodo.19062173

Data availability

The data used in this study is available in Neotoma. (Baldeggersee: https://doi.org/10.21233/MSSS-4C43; Hallwilersee

690 https://doi.org/10.21233/BWX7-HQ40)

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