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Palynological investigations reveal Eemian interglacial vegetation dynamics at Spiezberg, Bernese Alps, Switzerland

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ABSTRACT

Interglacial pollen records are valuable archives of past vegetation dynamics and provide important information about vegetation responses to different-than-today climates. Interglacial pollen archives pre-dating the Last Glacial Maximum (LGM) are scarce on the Swiss Plateau in contrast to the many available Late Glacial and Holocene records. This is mainly due to the rapidly changing palaeo-environmental conditions throughout the Quaternary and the low preservation potential of material suitable for palynological investigations. The Spiezberg site offers a palynological record situated most proximal to the Alps in Switzerland. Previous investigations tentatively assigned this record to the Eemian interglacial (MIS 5e). We have conducted additional pollen analytical investigations to increase the quantity of pollen information. Besides biostratigraphic interpretations, we use numerical methods such as distance analysis (distantia) and ordination techniques (PCA) to evaluate the similarities and differences between the Spiezberg record and its geographically and chronostratigraphically closest physically dated (U/Th, luminescence) analogues from the Eemian (MIS 5e) and Meikirch 3 (MIS 7a) interglacials. Our palynological investigations reveal the predominance of closed temperate forests with abundant fir (*Abies*) and spruce (*Picea*) as well as evergreen broad-leaved taxa (e.g. *Hedera*). The attribution to the Eemian interglacial relies on the observation of very rare beech (*Fagus*) occurrences, a phase with prominent yew (*Taxus*) and the unimportance of hornbeam (*Carpinus*), all of which are typical Eemian features on the Swiss Plateau. An Eemian age is supported by the numerical comparison with the Beerenmösli (MIS 5e) and Meikirch 3 (MIS 7a) reference records. Furthermore, the *Picea, Taxus* and *Fagus* dynamics observed on the Swiss Plateau during the Eemian are in excellent agreement with vegetational patterns observed elsewhere in Central Europe. Surprisingly, *Carpinus* was almost absent on the Swiss Plateau during the Eemian, whereas it was a major component of the forest at other European sites with a similar elevation as Spiezberg. We explain this by environmental conditions and the strong competition with *Abies alba*. In particular, considering the European Eemian vegetation history and the results of our reconstructions from the Swiss Plateau, we find that *Abies alba* was a highly competitive tree under natural warmer-than-today conditions. This finding provides further evidence that *Abies alba* may benefit from future climate warming.
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1. Introduction

The Swiss Plateau is enclosed by the Alps to the south-east, the Jura Mountains to the west and north-west and Lake Constance and the Rhine river to the east and north-east. At least 15 glacial advances as well as fluvial and lacustrine systems transformed the topography of the Swiss Plateau during the course of the Quaternary, leading to divers and rapidly changing palaeo-geographic settings (Schwenk et al., in review; Graf, 2009; Dürst Stucki et al., 2010; Preusser et al., 2011). The Quaternary chronological framework of the Swiss Plateau is mainly based on absolute dates of

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glacial or fluvial sediments (Ivy-Ochs et al., 2008; Akçar et al., 2014; Gaar et al., 2019; Knudsen et al., 2020). Another way to structure the Quaternary stratigraphy is by exploring glacial and interglacial evidence from fossil pollen assemblages, which differ from interglacial to interglacial (Welten, 1982; Schlüchter et al., 1987; Wegmüller, 1992; Preusser et al., 2005), but are highly similar in regard to the different glacials.

The preservation potential of natural archives suited for palynology is quite low and tends to decrease with age. Therefore, studies on interglacial pollen records prior to the Last Glacial Maximum (LGM), i.e. older than c. 20 thousand years (ka), are scarce (Welten, 1982, 1988; Schlüchter et al., 1987; Wegmüller, 1992), whereas many Holocene and Late Glacial pollen records have been reported from the Swiss Plateau in the past years (Ammann and Tobolski, 1983; Lotter, 1999; Ammann et al., 2014; Rey et al., 2017, 2019). Additionally, even less research has been conducted to complement pollen records predating the LGM with absolute dating (Gondiswil: Wegmüller, 1992; Meikirch: Welten, 1982; Preusser et al., 2005; Thalgut: Preusser and Schlüchter, 2004; Niederwenigen: Welten, 1988; Anselmetti et al., 2010). An important aspect, which is vital to ecology, but affects biostratigraphy, is that fossil pollen assemblages reflect local to sub-regional vegetation dynamics that vary along geographical gradients (Felde et al., 2020), e.g. latitude (Drescher-Schneider, 2000) and altitude (Müller, 2000). This allows reconstructing ecological gradients in space and time, but complicates the biostratigraphic interpretation, in particular for older archives. Therefore, a refinement of interglacial pollen biostratigraphies is a crucial step, which requires an improvement of the spatial resolution of the palynological information.

The Spiezberg sediments contain an interglacial pollen record that is most proximal to the Swiss Alps (Fig. 1). Because of the inner-alpine position of Spiezberg, this site offers a record of ecological conditions for an elevation that is similar to the records on the Swiss Plateau, but for a location embedded in an Alpine environment. Zwahlen et al. (in press) investigated several samples from a drill core (RB 1-05) from Spiezberg and found interglacial pollen assemblages, based on which they tentatively inferred an Eemian age (c. 130–115 ka), corresponding to Marine Isotope Stage (MIS) 5e (Turon, 1984). Here we aim at (i) improving the quantity of pollen data from the Spiezberg site, (ii) numerically assessing the similarities and dissimilarities of the Spiezberg pollen assemblage with its chronostratigraphically and geographically closest analogues of the Eemian (Beerenmösli of the Gondiswil site: Wegmüller, 1992) and of MIS 7a (Meikirch: Welten, 1982; Preusser et al., 2005) and (iii) characterizing potential ecological gradients driving these similarities and dissimilarities.

2. Material and methods

2.1. Study area

The Spiezberg record is situated in the Aare Valley at the northern margin of the Alps at the transition to the Swiss Plateau (Fig. 1a and b). The Spiezberg ('mountain of Spiez') is a ridge on the southern side of Lake Thun, about 30 km south of Bern, Switzerland. The bedrock in the region is made up of Mesozoic limestones of the Penninic thrust nappes. These limestones form the E-W-striking Spiezberg, which was glacially carved to an elevation of 686 m a.s.l., and which currently hosts unconsolidated Quaternary sediments including moraines and lacustrine deposits on its lateral flanks (Fig. 1c and d; Zwahlen et al., in press). The current climate at the Spiezberg is temperate with 1241 mm precipitation per year and an annual mean temperature of 8.6 °C. January and July mean temperatures are −0.7 °C and 18.0 °C, respectively (period 1981–2010; Rnorm and Tnorm grid data sets of MeteoSwiss). Precipitation increases and temperatures decrease on a steep gradient towards the higher elevations of the Alpine topography immediately south of the study site (Fig. 1b).

The drill site RB 1-05 (592 m a.s.l.; 46.69430°N, 7.67078°E) is located on a moraine that hems the Spiezberg on its northern flank, 34 m above Lake Thun (Fig. 1d). The core was drilled in 2005 using a rotational technique and had a total length of 2450 cm. It was first investigated by Zwahlen et al. (in press), who described several m-thick organic-rich palaeolake deposits at 1030–1600 cm depth, that were deposited between two glacigenic diamictites. Zwahlen et al. (in press) analysed 13 samples palynologically from within the organic-rich deposits, and they dated two pieces of fossil wood to >58 ka and c. 46 ka using radiocarbon dating. Their criteria for an age assignment to the Eemian were given by the autochthonous sediment formations (gyttja), the high arboreal pollen content (AP >90%), the presence of evergreen broad-leaved trees, shrubs and lianas (e.g. *Ilex*, *Buxus*, *Hedera*), the abundance of pollen of temperate taxa, and the presence of *Fagus* pollen at very low abundances (<2%). The latter observation is considered as key evidence for distinguishing the Eemian in Europe from other interglacials (Tzedakis et al., 2001; Magri et al., 2006). This palynological pattern was also used as correlation criterion for other sites on the Swiss Plateau (Welten, 1982, 1988).

2.2. Sedimentological analysis of drill core RB 1-05

After the analyses of Zwahlen et al. (in press), the Institute of Plant Sciences, University of Bern, stored the section of RB 1-05 that contains the organic-rich palaeolake deposits (1000–1800 cm depth) in its archive. Desiccation processes during storage resulted in the fragmentation of most parts of this section. The lithological description of the core (0–2450 cm; Fig. 2) is based on own observations of the stored material, the drilling protocol of the Geotechnical Institute from 2005 (available at the geoportal of the Canton of Bern) as well as on Zwahlen et al. (in press). We logged the stored core segment at a scale of 1:10, determined grain sizes and identified the lithofacies following Krüger and Kjaer (1999).

2.3. Palynological analysis

We collected 76 samples of 1 cm^3 (2 cm^3 in case of elevated silt content) for palynological analysis between 1040 cm and 1705 cm depth at intervals of 10 cm. The sampling interval was increased to 2 cm between 1230 cm and 1274 cm depth, where the core is mostly not fragmented. *Lycopodium* tablets were added to each sample before chemical and physical treatment in order to assess pollen concentrations (Stockmarr, 1971). The chemical treatment followed standard lab procedures (Moore et al., 1991), which include HCl, KOH, HF (the latter step was repeated due to the high silt content), acetolysis as well as sieving to remove material >500 μm. The samples were then stained with fuchsin and admixed with glycerine for slide preparation and storage. Pollen grains were identified under a transmitted light microscope. We used the palynological keys by Moore et al. (1991) and Beug (2004), the palynological atlas of Reille (1992) and the reference collection of the Institute of Plant Sciences, University of Bern, for pollen identification. A total terrestrial pollen sum of >200, 100–200 and 50–100 grains was reached in 16, 10 and 4 samples, respectively. In the data shown in this paper, we do not consider the 46 samples in which we were not able to reach a total number of 50 pollen grains, which is considered as the minimum for robust environmental reconstructions (Heiri and Lotter, 2001). This results in pollen data for a total of 43 samples, which includes new data from 30 samples

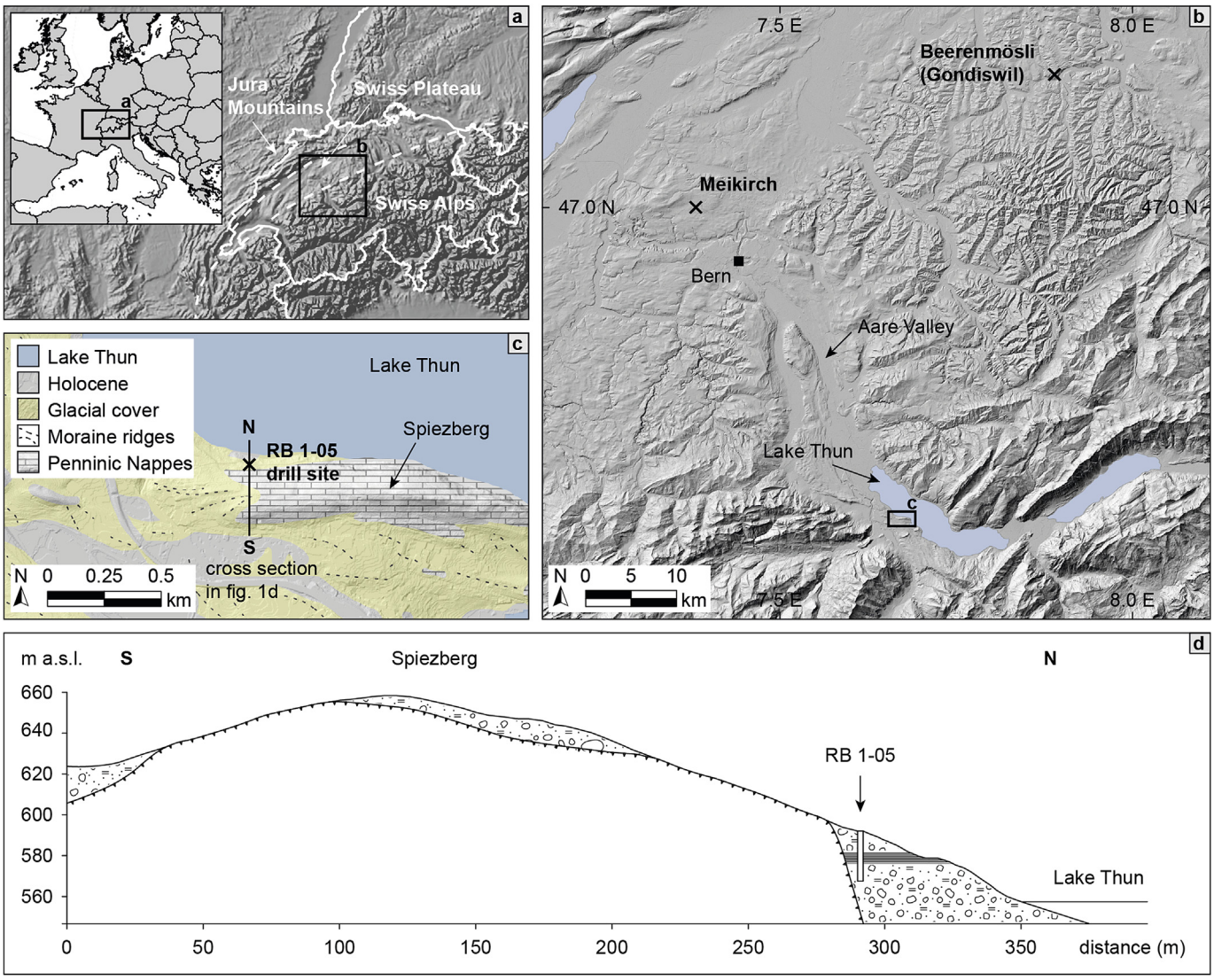

Fig. 1. Overview of the study area and drill site. **a.** Topographic map of Switzerland showing the Swiss Alps and the Jura Mountains enclosing the Swiss Plateau. The dashed white lines illustrate the boundaries between these litho-tectonic units. **b.** Elevation model (SwissAlti3D, ©swisstopo) of the Swiss Plateau and the northern margin of the Swiss Alps showing the sites Gondiswil comprising the Beerenmösli record (Eemian; Wegmüller, 1992) and Meikirch (MIS 7; Welten, 1982; Preusser et al., 2005). The Spiezberg site is located in the Aare Valley on the southern margin of Lake Thun. **c.** Geological situation of the Spiezberg (GeoCover and SwissAlti3D, ©swisstopo) showing the limestone bedrock units of the Penninic Nappes overlain by Quaternary moraines and slack water deposits. Dashed black lines = moraine ridges; solid black line = position of the profile in Fig. 1d; RB 1-05 = position of the drilling. **d.** Vertically exaggerated cross section through the Spiezberg (after Zwahlen et al., in press) with the location of the drill site RB 1-05. (For interpretation of the colour code in the legend of figure 1c, the reader is referred to the Web version of this article.)

reported in this article and the palynological information from 13 additional samples that were presented by Zwahlen et al. (in press). Pollen percentages are calculated based on the terrestrial pollen sum (= 100%) consisting of pollen grains from trees, shrubs and herbs. *Alnus glutinosa*, a species which can be locally dominant in wetlands such as alder carrs, was excluded from the terrestrial pollen sum. This exclusion allowed a numerical comparison of the Spiezberg pollen data with the reference record Beerenmösli (Wegmüller, 1992), where *Alnus glutinosa* is also excluded from the terrestrial pollen sum.

2.4. Reference records: data acquisition and processing

We use two numerically dated pollen records as references for the biostratigraphic correlation, Beerenmösli from the Gondiswil site (Eemian) and Meikirch (MIS 7). Both sites are located on the Swiss Plateau in close vicinity of Spiezberg (Fig. 1b) and are hence most suitable for comparison purposes. The Gondiswil site (Wegmüller, 1992) is situated about 50 km NNE of Spiezberg, where the modern climate is characterized by 1307 mm annual precipitation and an annual mean temperature of 8.0 °C. January and July mean temperatures are −0.7 °C and 17.2 °C, respectively (period 1981–2010; Rnorm and Tnorm grid data sets of MeteoSwiss). Among the three Gondiswil pollen records, Beerenmösli (649 m a.s.l., 47.12319°N, 7.87583°E) is the only one that is numerically dated (U/Th 115.7 ± 4.8 ka), making it the only continuous Eemian palynological record on the Swiss Plateau. The original pollen counts of Beerenmösli are unavailable, but the data is accessible as printed pollen percentage diagram in Wegmüller (1992). For the numerical reanalyses we digitized the diagram using the Plot Digitizer software (version 2.6.8). The digitation precision depends on the image resolution of the scanned diagram as well as on the scale at which the pollen percentage curves are drawn, i.e. linear or logarithmic. Whereas one pixel constantly accounts for 0.5% on

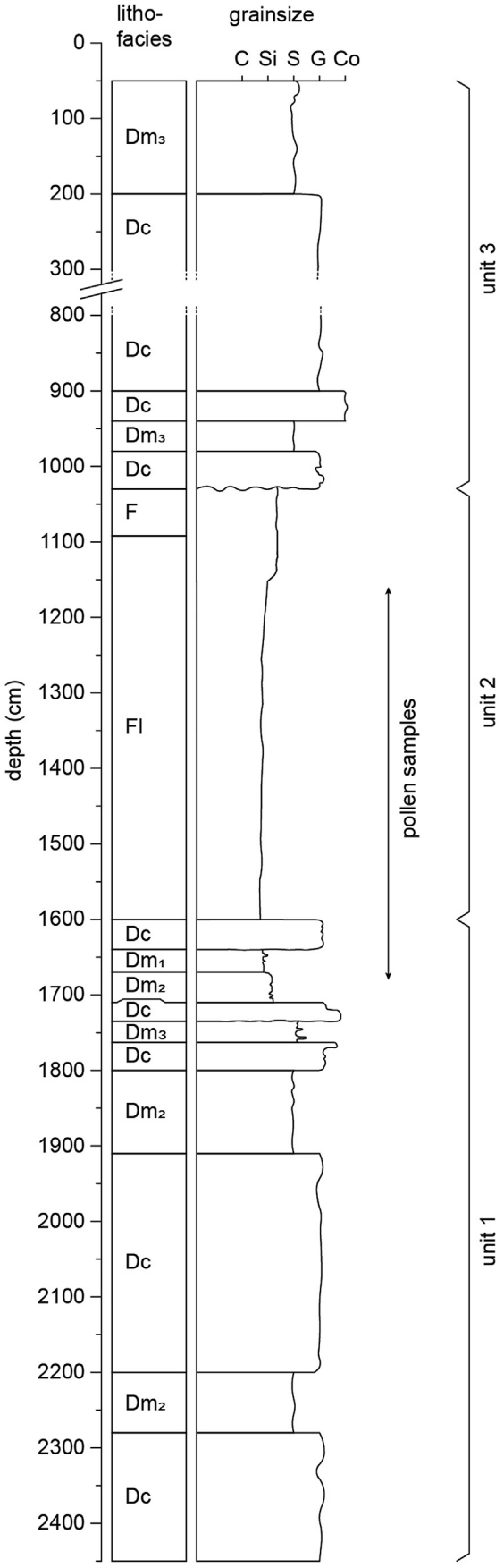

Fig. 2. Lithofacies and grain size of the drill core RB 1-05, Spiezberg. The sedimentary sequence consists of glacial diamicts at the bottom (unit 1), a coarsening upward sequence of partially laminated, organic-rich clayey to sandy silts with plant remains and shell fragments (unit 2) and glacial diamicts on top (unit 3). The depth range of the pollen samples (this study and Zwahlen et al., in press) covers most of unit 2 including the organic-rich gyttja as well as the fine-grained section of unit 1. Grain size abbreviations are C = Clay, Si = Silt, S = Sand, G = Gravel, Co = Cobbles. Lithofacies classification follows Krüger and Kjaer (1999) with F = Fines (predominantly silt and clay); Fl = Laminated fines; Dc = clast-supported diamict; Dm = matrix-supported diamict, indexes: 1 = clast poor, 2 = moderate, 3 = clast rich.

linear scales, the ratio of percentage per pixel increases exponentially with higher percentages on logarithmic scales. We therefore infer a digitation precision of 0.5% for taxa drawn on linear scales, but we are not able of determining an uncertainty for taxa that are drawn on a logarithmic scale in the original diagram (i.e. *Alnus glutinosa*-type, Cyperaceae, *Dryopteris*-type, *Selaginella selaginoides* and *Sphagnum*). Consequently, we did not include any of the latter taxa in the statistical analyses.

Meikirch (Welten, 1982), the second reference site, is located about 40 km NW of Spiezberg. Today's climate at the site (620 m a.s.l., 47.00261°N, 7.37144°E) is characterized by 1104 mm annual precipitation and an annual mean temperature of 8.6 °C. January and July mean temperatures are −0.5 °C and 18.1 °C, respectively (period 1981–2010; Rnorm and Tnorm grid data sets of MeteoSwiss). Among the two available pollen records, profile I is shorter than profile II and contains only the uppermost of the three warm phases of profile II, which were originally proposed to be of Holsteinian and Eemian age, respectively (Welten, 1982). The pollen record of the uppermost warm phase, Meikirch 3, shows relatively high *Fagus* abundances, a pronounced *Carpinus* phase and early *Picea* occurrences, all of which are atypical for Eemian successions on the Swiss Plateau (Welten, 1982; Wegmüller, 1992). In a reinterpretation of the Meikirch record using luminescence dating, Preusser et al. (2005) assigned the warm phases Meikirch 1 to 3 to MIS 7e, 7c and 7a. Although there are some problems to biostratigraphically align the Meikirch record with the MIS 7 record Lac de Bouchet (Reille and Beaulieu, 1995) in France, we follow the chronostratigraphic calibration of the section by Preusser et al. (2005). The pollen record of profile II was subdivided into pollen zones DA1 to DA17a and there is most probably a short sedimentary hiatus between DA9 and DA10 during the transition from a lateglacial *Pinus* and *Betula* phase to an interglacial *Quercus*, *Corylus* and *Ulmus* phase. We decided to work with the pollen data of profile II nonetheless, because the period around the inferred hiatus is lacking (biostratigraphically) in the Spiezberg record (Zwahlen et al., in press) and hence irrelevant for our comparison. The palynological data of profile II of the Meikirch site (Welten, 1982) was extracted from the Alpine Palynological Database (ALPADABA), which is curated by the Institute of Plant Sciences, University of Bern, and a constituent part of NEOTOMA (Williams et al., 2018). Percentages were calculated in the same way as described in section 2.3. for the Spiezberg record, i.e. without considering *Alnus glutinosa*-type pollen in the terrestrial pollen sum. Hence, pollen percentages calculated for this study can slightly differ from those shown in diagram 1a in Welten (1982). The successional trends as well as transient fluctuations of pollen abundances, however, are not influenced by the different calculations. For simplicity, when mentioning the Meikirch record, we will be referring to the palynological data of the uppermost Meikirch warm period of profile II, which corresponds to MIS 7a.

2.5. Numerical methods

2.5.1. Zonation of pollen records

The original zonation of Beerenmösli (Wegmüller, 1992) and

Meikirch (Welten, 1982) is based on optical criteria, which bears the danger of a subjective bias. In order to make the zonation comparable with each other, we numerically determined the local pollen assemblage zones (LPAZ) of all three records (Figs. 3–5). To this extent, we used the optimal partitioning approach with minimum sum-of-squares (Birks and Gordon, 1985) and the broken stick model to determine the number of significant zones (Bennett, 1996). Since both the Beerenmösli and Meikirch records contain cold and/or warm stages that are not recorded at Spiezberg, we did a pre-selection of the LPAZ prior to statistical comparisons between the records. In the case of Beerenmösli, we selected the zones BM-3 to BM-6, i.e. zones 6–10b in Wegmüller's (1992) zonation (Fig. 4), as they are the only zones within the entire sequence containing the temperate and thermophilous taxa that are recorded at Spiezberg. For the same reason we selected zones MK-10 to MK-15 of the Meikirch record, i.e. zones DA10 to DA16 in Welten's (1982) zonation (Fig. 5), which represent the uppermost interglacial (MIS 7a).

2.5.2. Distance analysis

We quantified the total distance (or dissimilarity) based on the Ψ (or PSI) metric (Gordon, 1973; Gordon and Birks, 1974) between the interglacial section of the Spiezberg record (zones SB-2 and SB-3 in Fig. 3; see section 3.2) and the pre-selected sections of the two reference records Beerenmösli and Meikirch. We proceeded through using the R package *distantia* by Benito and Birks (2020) to conduct the following four steps: (i) Calculation of distance matrices between two records. These are based on Euclidean distances between all pairs of samples of the two considered records. (ii) Calculation of the least-cost path through the distance matrices as best possible alignment of the two considered records, using an elastic model (sequence slotting). (iii) Calculation of the total distance along the least-cost path. In this step, straight horizontal or vertical segments of the least-cost path (=blocks) were ignored. As Benito and Birks (2020) already mentioned, blocks can artificially increase the summed distance between two records because the distance to a given sample is counted multiple times. (iv) The final calculation of Ψ, being the summed distance normalized by the sum of internal distances between samples of each record. The normalization ensures the comparability of Ψ values from records of different lengths. In order to assess the significance of the similarity between two records, we compared the original Ψ value against a distribution of Ψ values resulting from 999 restricted permutations. The resulting p-values reflect the proportion of Ψ values that turned out equal or lower than the original Ψ estimate. Note that because the p-values are based on a restricted permutation, they should be interpreted with more caution than classical p-values (Benito and Birks, 2020). The distance matrices as well as the proportional contribution of single taxa to a dissimilarity between the records are shown in Figs. 6 and 7, respectively.

2.5.3. Ordination techniques and significance tests

We used Principal Component Analyses (PCA) conducted with the software Canoco 5.10 (ter Braak and Šmilauer, 2018) to search for similarities between the samples of the three records. Prior to the PCA, the datasets of all three records were harmonized in terms of nomenclature and taxonomic resolution. If a pollen type was only mentioned in some of the three datasets, it was assigned an abundance of 0% in the other ones. If necessary, pollen types were merged to a pollen type of a higher order (e.g. *Ephedra fragilis*-type + *Ephedra distachya*-type = *Ephedra*) in order to ensure consistency in taxonomic resolution. This allowed to generate a spliced dataset comprising all samples of the pre-selected pollen zones of the three records. A Detrended Correspondence Analysis (DCA) conducted over the spliced dataset yielded a gradient length of less than two standard deviations, suggesting that a linear-based method such as PCA is suitable for our purpose (ter Braak and Prentice, 1988). The pollen percentage data was log-transformed prior to the PCA. The results are illustrated by biplots showing species scores (pollen taxa; Fig. 8a) and sample scores of all three records (Fig. 8b) on the first two axes of the PCA. The closer samples plot to each other, the more similar they are in terms of pollen abundances and assemblage. In order to illustrate the stratigraphic position of the samples, which is not considered by the PCA, we grouped samples into polygons according to their LPAZ.

Finally, we used Welch's *t*-test (Welch, 1947) to test whether certain distributions of PCA sample scores, which were determined for individual pollen zones (SB-2, SB-3, BM-4, BM-5) as well as for whole records (Spiezberg, Beerenmösli, Meikirch), are similar at a 1σ significance level. We applied a Bonferroni correction to account for an increase in the probability of type I error, which is expected as a response to multiple testing (Shaffer, 1995).

3. Results and interpretation

3.1. Core lithology and lithofacies at Spiezberg

The combination of our own lithological observations on the Spiezberg material, the description by Zwahlen et al. (in press) and the drilling protocol of the entire core allows us to divide the core into three lithological units (Fig. 2). Unit 1 (2450–1600 cm) is characterized by compacted glacial diamicts where the material is both clast- and matrix-supported. Zwahlen et al. (in press) interpreted this unit as a subglacial till (2450–2280 cm) overlain by moraines of possibly two glacial advances between 2200 and 1710 cm depth. Unit 2 (1600–1030 cm) mainly consists of material in the silt and clay fraction. Zwahlen et al. (in press) described this section as organic-rich with abundant plant remains, shell fragments and 150 cm of silty gyttja (1350–1200 cm). Increasing fine sand concentrations from 1155 cm and the sporadic occurrence of <8 mm-large gravels from 1053 cm onwards indicate a more allochthonous composition of the sediment. We identified horizontal laminations in some segments of the core, i.e. between 1600 and 1400 cm, 1300 and 1223 cm and between 1092 and 1050 cm depths. Between 1150 and 1117 cm depth the laminations are tilted at 40° relative to the vertical coring axis. A sedimentary hiatus at 1030 cm depth marks the top of unit 2. Similar to unit 1, unit 3 is characterized by diamictic material, which suggests a glacial advance (1030–940 cm) and a subsequent subglacial till (940–50 cm) likely of LGM age.

3.2. The Spiezberg palynological record

The Spiezberg palynological record contains three statistically significant local pollen assemblage zones (LPAZ), i.e. SB-1 (1680–1570 cm), SB-2 (1570–1385 cm) and SB-3 (1385–1160 cm) (Fig. 3). SB-1 contains only four pollen samples due to the coarse-grained sediment between 1645 and 1600 cm depth, where no pollen samples were taken. In SB-1, arboreal pollen (AP; trees and shrubs) ranges from 44 to 83% of the terrestrial pollen sum. Most abundant tree and shrub pollen taxa are *Betula*, *Juniperus*, and *Pinus*. Poaceae, *Artemisia* and Chenopodiaceae are the herbaceous pollen taxa with the highest relative abundances. Together these results indicate the occurrence of a tundra steppe, which evolved into an open boreal forest. On the basis of the lithology (allochthonous minerogenic material; Unit 1 in Fig. 2), we interpret the occurrence of pollen from temperate woody taxa (e.g. *Quercus*, *Corylus*) as reworked (Sidler, 1988).

The pollen assemblage in SB-2 is characterized by AP values

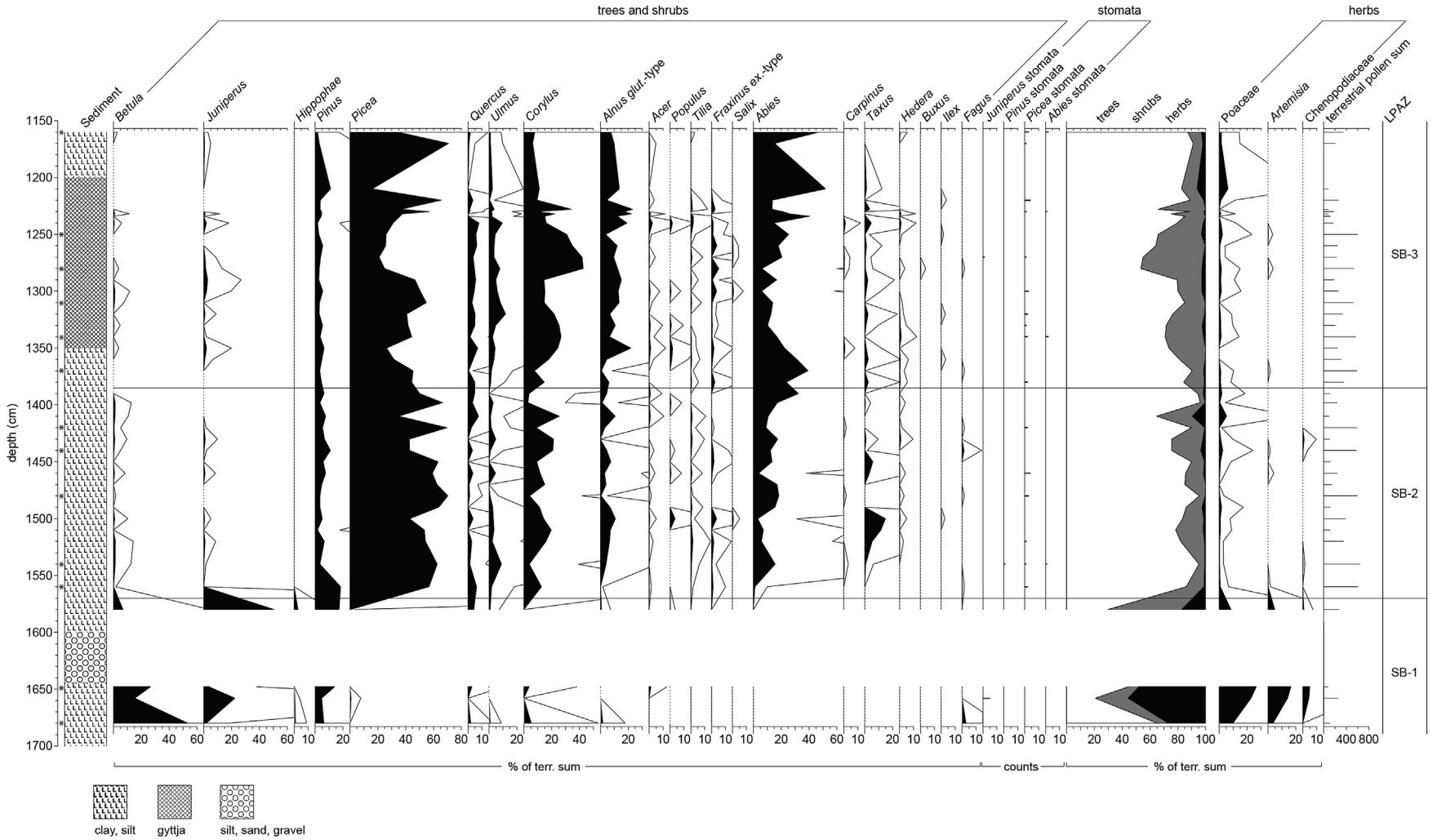

Fig. 3. Pollen percentage diagram (selected taxa) of the Spiezberg record, with black lines as 10x exaggeration. Stomata are shown as counts. The 13 samples presented in Zwahlen et al. (in press) are labelled with asterisks next to the depth column. LPAZ = Local pollen assemblage zones.

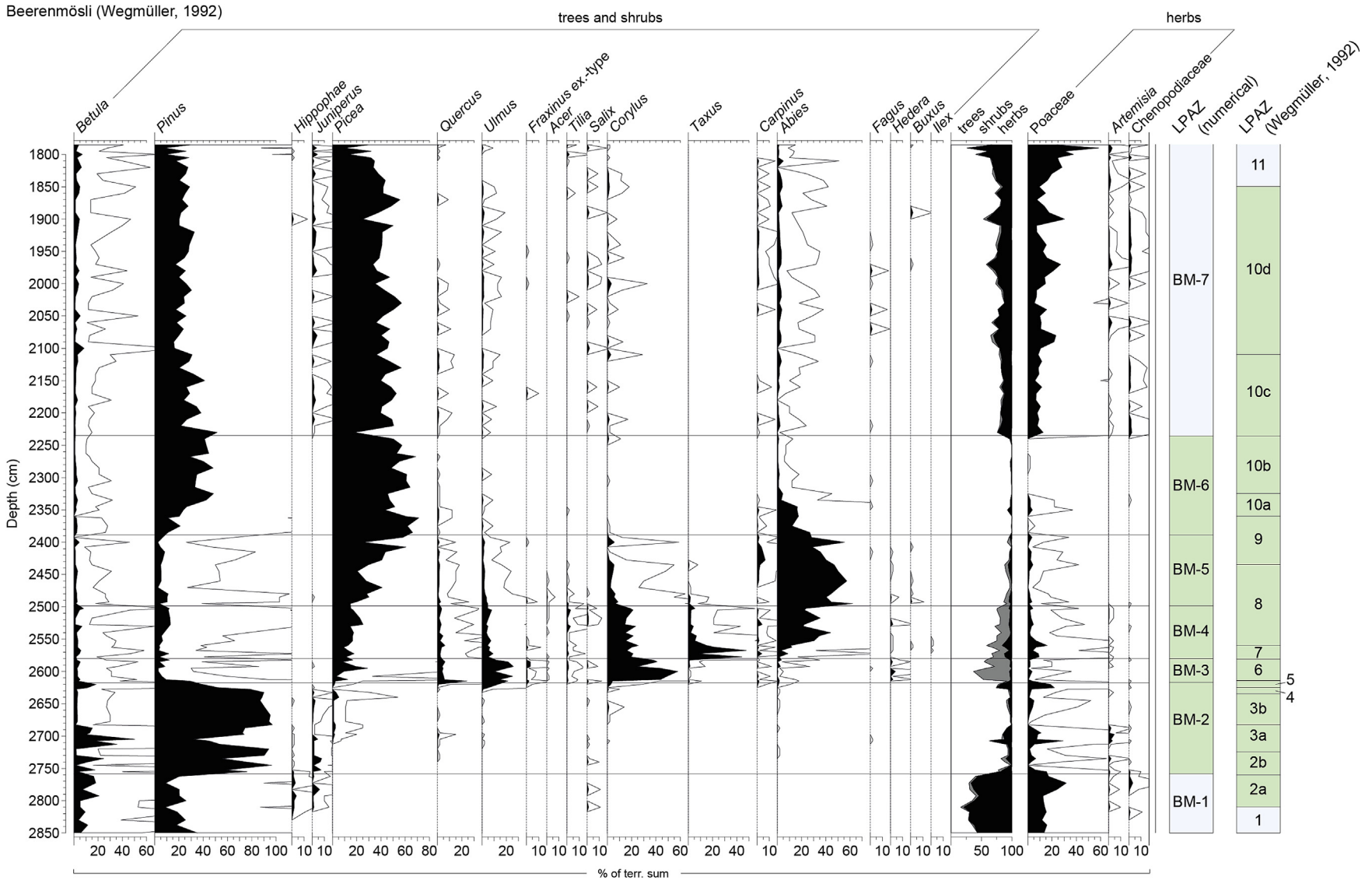

Fig. 4. Pollen percentage diagram (selected taxa) and zonation of the Eemian (MIS 5e; green LPAZ) section of the Beerenmösli record (Wegmüller, 1992), with parts of the preceding and following cold stages (grey LPAZ). LPAZ = local pollen assemblage. Black lines show 10x exaggeration. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

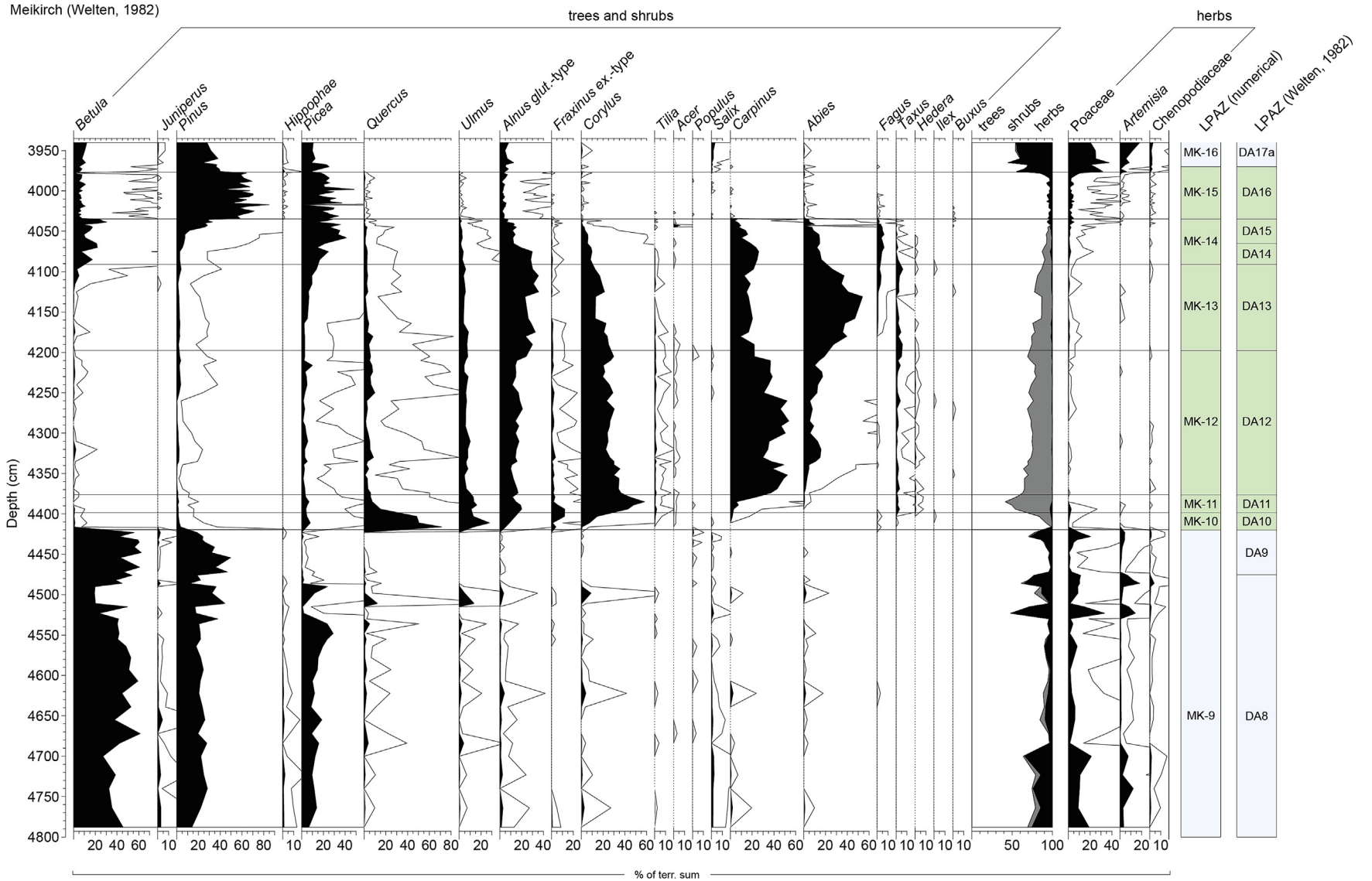

Fig. 5. Pollen percentage diagram (selected taxa) and zonation of the Meikirch 3 interglacial (MIS 7a; green LPAZ) and the late stage of the preceding cold stage (Welten, 1982; Preusser et al., 2005). LPAZ = local pollen assemblage zones. Black lines show 10x exaggeration. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

constantly >90% and mostly >95%. In this assemblage, *Picea* is the most abundant taxon (>40%). *Corylus* and *Abies* abundances show increasing trends upsection throughout SB-2. At around 1400 cm depth, a sharp decline of *Corylus* and an increase in *Abies* pollen is observed, suggesting that the forest became darker. After an initial decrease, *Pinus* pollen is continuously present with a maximum abundance of 11%. *Taxus* shows a marked peak at 1500 cm (14.9%) followed by a less prominent peak at 1450 cm (5.5%) depth. Both peaks are associated with an increasing contribution of *Alnus glutinosa*-type, *Acer* and *Fraxinus excelsior*-type as well as with a decreasing abundance of *Picea* pollen. Temperate *Tilia* follows trends similar to *Fraxinus excelsior*-type, while *Ulmus* together with *Abies* (peak at 1540 cm) precede the other temperate trees. We found *Hedera* pollen from 1520 cm onwards and one single occurrence of *Ilex* pollen at 1500 cm depth. *Carpinus* and *Fagus* pollen never reaches the empirical limit (sensu Watts, 1973) and its abundance remains below 2%, showing that the taxa were either absent or of very minor importance in the vegetation. We interpret SB-2 in the sense that the Swiss Plateau north of Spiezberg was occupied by closed temperate forest vegetation dominated by *Abies* with *Tilia, Acer, Ulmus, Quercus, Fraxinus excelsior* and *Corylus*. Other temperate or oceanic taxa such as *Taxus, Hedera* and probably *Ilex* were present, indicating full interglacial conditions. In contrast, the Alpine topography surrounding Spiezberg in the west, the south and the east, provided ideal conditions for coniferous forests dominated by *Picea*. Using the Holocene as an analogue, we interpret that closed spruce forests were growing above the site (perhaps at altitudes between 1000 and 2000 m a.s.l.). *Picea* probably also grew as individual trees or formed small stands around the lake close to Spiezberg. We base this interpretation on the sporadic occurrence of *Picea* stomata in the samples. Alternatively, the stomata could have been supplied by Alpine rivers from the catchment of the palaeolake.

The compositional change of the pollen assemblage at the beginning of SB-3 is small and only characterized by shifts in taxon abundances rather than by disappearance or appearance of taxa. Similar to SB-2, the most abundant taxon is *Picea*, though less important than in the previous zone. AP is still constantly >90%, usually even >95%, throughout SB-3, but includes more shrubs compared to SB-2. This concerns mainly *Corylus*, which is generally more abundant, whereas *Picea* is less abundant than in the previous zone. More specifically, *Abies* and *Picea* pollen dominate the spectra from the beginning of SB-3 until 1360 cm depth. Further upsection, the abundances of the latter two taxa begin to decrease, followed by an increase in *Corylus*, *Alnus glutinosa*-type and with a slight delay in *Ulmus* pollen, suggesting that light availability increased in the forest. *Corylus* pollen abundances culminate at 1280 cm depth. This gradual change is also accompanied by a shift towards highest percentages of *Fraxinus excelsior*-type. *Quercus*, *Alnus glutinosa*-type and *Ulmus* pollen is generally more abundant than in SB-2. *Pinus* pollen is constantly present with abundances of less than 10% and maximum values towards the end of SB-3, together with a minor increase of non-arboreal pollen (NAP). *Taxus* and *Hedera* pollen is present throughout SB-3, though less important upsection of 1210 cm depth. A similar trend is observed for *Quercus*, *Ulmus*, *Acer*, *Populus*, *Tilia* and *Fraxinus excelsior*-type. Single grains of *Ilex* and *Buxus* were found in this zone. The sample resolution in this topmost part of SB-3 (1240–1160 cm) is lower than in the remaining part of the section. This is due to increasing silt and fine sand content and the resulting low pollen concentrations. As in SB-2, relative abundances of *Carpinus* and *Fagus* pollen never reach 2%.

The pollen record of the older part of SB-3 (until c. 1220 cm depth) suggests that *Abies*, *Tilia, Ulmus, Corylus*, *Fraxinus excelsior, Quercus* and *Alnus glutinosa* were forming closed forests on the Swiss Plateau north of the study site. The higher Alpine elevations were likely covered by *Picea* forests with *Pinus,* though individual trees or stands may have grown around the lake. Drier (summer) conditions might have favoured the expansion of *Corylus* in the course of SB-3. Subsequently, cooling temperatures towards the end of SB-3 became increasingly unfavourable for temperate species such as *Tilia, Ulmus, Corylus*, *Fraxinus excelsior* and *Quercus*. As for SB-2, *Fagus* and *Carpinus* might have been present in the lowlands of the Swiss Plateau, but at the most as little stands. The pattern of pollen abundances displays generally high fluctuations in the diagram, which might be the result of the low terrestrial pollen sum.

3.3. Numerical zonation of the reference pollen records Beerenmösli and Meikirch

Our numerically established zonations of the reference records Beerenmösli (Wegmüller, 1992) and Meikirch (Welten, 1982) differ from the original zonations (Figs. 4 and 5). The Eemian section of the Beerenmösli record was originally divided into 14 pollen zones and subzones (2a to 10d), some of which contain less than 5 samples. Here we present a subdivision into 7 statistically significant zones (BM-1 to BM-7). The original basal subzone (2a) of the Eemian is characterized by arboreal pollen <50%, mostly boreal *Pinus* and *Betula*. We merge this steppic tundra subzone 2a with Wegmüller's (1992) zone 1, forming our new zone BM-1. The following subzones 2b, 3a, 3b, 4, and 5 of Wegmüller (1992) are assembled in our BM-2, that is characterized by a strong dominance of *Pinus* and AP >80%, suggesting the occurrence of boreal forest with some *Betula*. The following zone 6 of Wegmüller (1992) corresponds to BM-3, in which temperate taxa such as *Ulmus*, *Corylus* and *Quercus* expand together with subalpine or boreal *Picea*. Wegmüller's (1992) zone 7 and the lower part of 8 are combined into zone BM-4, which is well confined by a *Taxus* maximum with *Abies*, *Corylus*, *Picea* and *Ulmus*. In the same way, we merge the upper part of Wegmüller's (1992) zone 8 and the lower section of zone 9 into BM-5, in which *Abies* is dominant and temperate trees decline. Towards the end of BM-5 *Picea* becomes co-dominant with *Abies*, suggesting a gradual development from temperate to nemoboreal forests. Declining abundances of *Abies*, the final disappearance of *Corylus* and an increasing contribution of *Pinus* as well as a local maximum of *Picea* mark the transition to BM-6, which corresponds to parts of zone 9, 10a and 10b in Wegmüller (1992). In BM-6, boreal *Picea* and *Pinus* dominate the pollen spectra and temperate *Abies* rapidly decreases, suggesting that nemoboreal forests were replaced by boreal forests, likely in response to further climate cooling. Finally, at 2240 cm depth, a sudden increase of non-arboreal pollen (NAP) from c. 5% to c. 27% and a decline in *Pinus* and *Picea* pollen marks the beginning of zone BM-7 (or zones 10c, 10d and 11 of Wegmüller, 1992). This zone boundary between BM-6 and BM-7 marks the end of the Eemian interglacial. Subsequently the forests opened and steppic tundra expanded (AP <70–90%). *Fagus* never reaches the empirical limit during the entire Eemian both at Beerenmösli and at Spiezberg, but occasionally occurs with a few pollen grains, suggesting that this tree species was either absent or present in very low numbers.

Welten's (1982) zonation of the uppermost Meikirch interglacial and its onset matches very well with our numerical results (Fig. 5). The only difference is that some zones recognized by Welten (1982) are not statistically significant and thus correspond to the rank of subzones (e.g. DA8 and DA9 are merged into MK-9 and DA14 and DA15 into MK-14). Indeed, Welten's (1982) zone boundary between DA9 and DA10 marks the onset of the uppermost Meikirch interglacial. DA8 displays high percentages of AP (mainly *Pinus* and

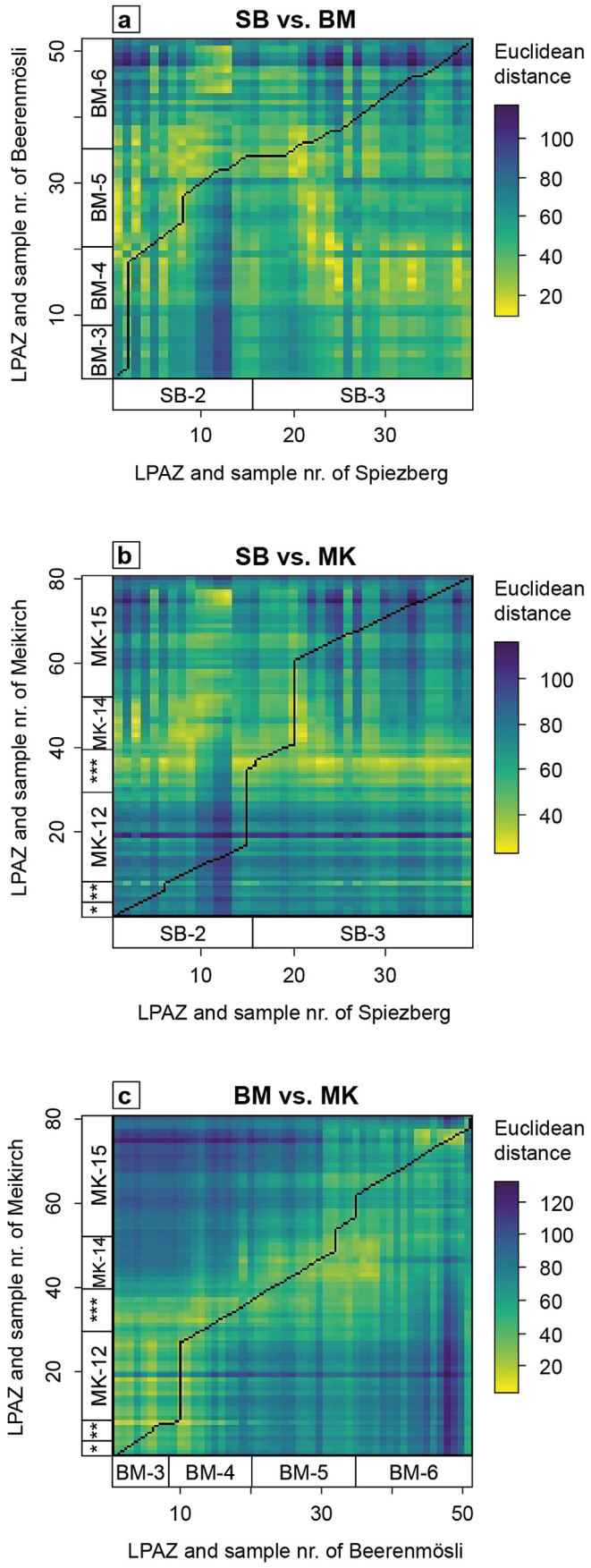

Fig. 6. Distance matrices of pairwise comparisons between pollen records from **a.** Spiezberg (SB) and Beerenmösli (BM), **b.** Spiezberg and Meikirch (MK) and **c.** Beerenmösli and Meikirch. The colour code is according to the Euclidean distances between respective samples. Black lines represent the least-cost path calculated with *distantia* (Benito and Birks, 2020) as best-possible alignment of the records while keeping the stratigraphic order. * = MK-10; ** = MK-11; *** = MK-13.

Betula), while DA9 has a high abundance of NAP (c. 30%; 4430 cm depth). Welten (1982) distinguished these zones from the subsequent interglacial, which is in accordance with the results of our novel numerical zonation. Hence, we follow Welten (1982) and define the beginning of the MIS 7a interglacial with the transition from MK-9 to MK-10.

The Meikirch pollen data (Fig. 5) suggest that during MK-10 and thus at the onset of the uppermost interglacial, temperate forests dominated by *Ulmus* and *Quercus* established, in which *Fraxinus excelsior* and *Corylus* were increasingly admixed. *Carpinus* established in the surrounding forests towards the end of this zone. During MK-11 *Corylus* peaked and became co-dominant. During MK-12 mixed temperate forests dominated by *Carpinus* and *Corylus* established, in which *Abies* became gradually co-dominant. During MK-13 *Abies* abundances reached a peak and *Picea* expanded, although temperate taxa such as *Ulmus, Corylus, Carpinus* and to a smaller extent *Quercus,* remained important. At Meikirch and in contrast to Spiezberg and Beerenmösli, *Fagus* pollen reaches its empirical limit and increases to c. 4%, suggesting an initial population expansion and the establishment of tree stands. The pollen record shows that temperate trees such as *Abies, Ulmus, Quercus* and *Corylus* declined only during MK-14, while boreal *Pinus, Betula* and *Fagus* increased and *Picea* remained abundant, together forming nemoboreal forests. Boreal forests established during MK-15, which in turn were dominated by *Pinus* and *Picea*, when all temperate trees including *Fagus* disappeared. Finally, the expansion of steppic tundra vegetation during MK-16 mark the end of the interglacial.

3.4. Numerical comparison of pollen records

3.4.1. Distance analysis

Distance matrices for each pair of three records were calculated using the R-package *distantia* (Fig. 6; Benito and Birks, 2020). The comparison between the Spiezberg and the Beerenmösli record (Fig. 6a) reveals that zone SB-2 is most similar to zones BM-4, BM-5 and BM-6, whereas the lower part of SB-3 has the highest similarity with BM-5 and the upper part with BM-4, respectively. Similarly, in the comparison between the Spiezberg and the Meikirch record (Fig. 6b), SB-2 has the highest similarity with MK-13, MK-14 and MK-15, whereas SB-3 is most similar to MK-13 and MK-14. This shows that high similarities between pairs of samples do not necessarily follow the stratigraphic order in the comparisons including Spiezberg, which in turn results in an irregular appearance of the distance matrices. In the comparison of the two reference records Beerenmösli and Meikirch (Fig. 6c), however, the similarity does follow the stratigraphic order. Since the least-cost-paths (black lines in Fig. 6) are constrained to the stratigraphic order, they inevitably miss sections with a high similarity in the comparisons including Spiezberg.

The Ψ metric, as a measure for distance (or dissimilarity), has been calculated for all pairs of records (Table 1). Additionally, we calculated p-values to assess the significance of the dissimilarity by comparing it against a distribution of randomized Ψ values (Table 1). The comparison between Spiezberg and the Eemian reference Beerenmösli yielded the lowest dissimilarity ($\Psi = 1.865$; $p = 0.020$). The highest dissimilarity results from the comparison between MIS 7a reference Meikirch and the Spiezberg record ($\Psi = 3.490$; $p = 0.569$). The dissimilarity between Beerenmösli and Meikirch is intermediate ($\Psi = 2.317$; $p = 0.133$) relative to the aforementioned comparisons. Only the dissimilarity between

Table 1
Ψ values resulting from the distance analysis between the pollen records Spiezberg (SB), the Eemian reference Beerenmösli (BM) and MIS 7a reference Meikirch (MK). Ψ increases with increasing dissimilarity between records. p-values result from a restricted permutation, in which the original Ψ value is compared to a set of 999 randomized Ψ values. Only the dissimilarity between SB and BM is significantly lower than the randomized distribution of Ψ values, implying that Spiezberg and Beerenmösli are similar in terms of pollen abundances and assemblage.

	Ψ	p
SB-BM	1.865	0.020[a]
SB-MK	3.490	0.569
BM-MK	2.317	0.133

[a] = significant similarity.

Spiezberg and Beerenmösli is significantly less dissimilar than the randomized distribution of Ψ. Hence, our results support the biostratigraphic assignment of the Spiezberg section to the Eemian as postulated by Zwahlen et al. (in press).

In addition, we calculated the contribution of single taxa to the total dissimilarity between the pollen records. This is done by excluding specific taxa from the analysis with *distantia* (Benito and Birks, 2020) and by calculating the resulting relative change of Ψ (Fig. 7). In this context, the comparison between Spiezberg and Beerenmösli shows that only *Picea* and *Pinus* contribute substantially to the dissimilarity (Fig. 7a). Since both of these taxa are also responsible for most of the dissimilarity between Spiezberg and Meikirch (Fig. 7b) and act neutral in the comparison between the reference sites of both interglacials (Fig. 7c), we interpret this as mainly site-specific rather than a consequence of vegetational differences between the interglacials. All other taxa, but primarily *Abies*, *Corylus* and *Taxus*, contribute to the similarity in the Spiezberg-Beerenmösli comparison, with *Abies* having by far the largest contribution (23.34%) (Fig. 7a). Interestingly, *Carpinus* is the only taxon that contributes to the dissimilarity between Meikirch and both other records (Fig. 7b and c), which is explained by its low abundances at Spiezberg and Beerenmösli.

The main taxa contributing to the dissimilarity between Beerenmösli and Meikirch are next to *Carpinus* and in descending order *Quercus*, *Ulmus* and *Betula*. *Quercus* played a more dominant role during the initial phase of MIS 7a at Meikirch (max. 71.4%; Fig. 5) than during the Eemian at Beerenmösli (max. 24.2%; Fig. 4). After a short expansion at Beerenmösli, *Quercus* was replaced by *Corylus* and only played a minor role thereafter. At Meikirch *Quercus* probably had more time to expand massively until *Corylus* stands became important (MK-10). Such patterns in pollen assemblages are not recorded at Beerenmösli, where *Ulmus* and *Corylus* co-dominate since the onset of the interglacial over the less prominent *Quercus* (BM-3; Fig. 4). Towards the end of MIS 7a, *Betula* abundances increase in MK-14 before the *Pinus* expansion in MK-15 (Fig. 5). This was not the case during the Eemian at Beerenmösli where *Betula* stays low throughout the transition from temperate to boreal vegetation at the end of the interglacial (BM-5 to BM-6; Fig. 4). We consider that this pattern explains the contribution of *Betula* to the dissimilarity between the Beerenmösli and Meikirch records. In summary, the distance analysis with *distantia* allowed us to capture regional differences in the dominant or co-dominant taxa between the sites (*Picea* and *Pinus* dynamics), reflecting the main compositional (*Carpinus*) and successional (*Quercus-Ulmus-Corylus* dynamic) differences between the interglacials.

3.4.2. Ordination

The first two axes of the Principal Component Analysis (PCA) explain 64.9% of the total variance and hence account for a decent overview of the entire dataset (Fig. 8a and b). On PCA axis 1, the most positive species scores are reached in descending order by *Pinus*, *Picea*, *Betula*, *Hippophae*, Poaceae, *Artemisia* and Chenopodiaceae, the most negative species scores by *Corylus*, *Ulmus*, *Quercus*, *Tilia*, *Carpinus*, *Fraxinus excelsior*-type, *Taxus*, *Abies* and *Hedera*, in ascending order. We thus interpret PCA axis 1 as reflecting a climate-driven gradient from boreal pine-spruce-birch forest and grassland vegetation (positive values) to temperate broad-leaved deciduous-fir forests (negative values). On PCA axis 2, the most positive species scores are reached by *Carpinus*, *Betula* and *Fagus*, the most negative by *Picea*, *Abies* and *Juniperus*. Since taxa with similar ecological requirements, e.g. *Fagus* and *Abies* or *Betula* and *Juniperus*, plot on different ends of axis 2, we infer that this axis does not reflect a climate-driven gradient, but rather a combination

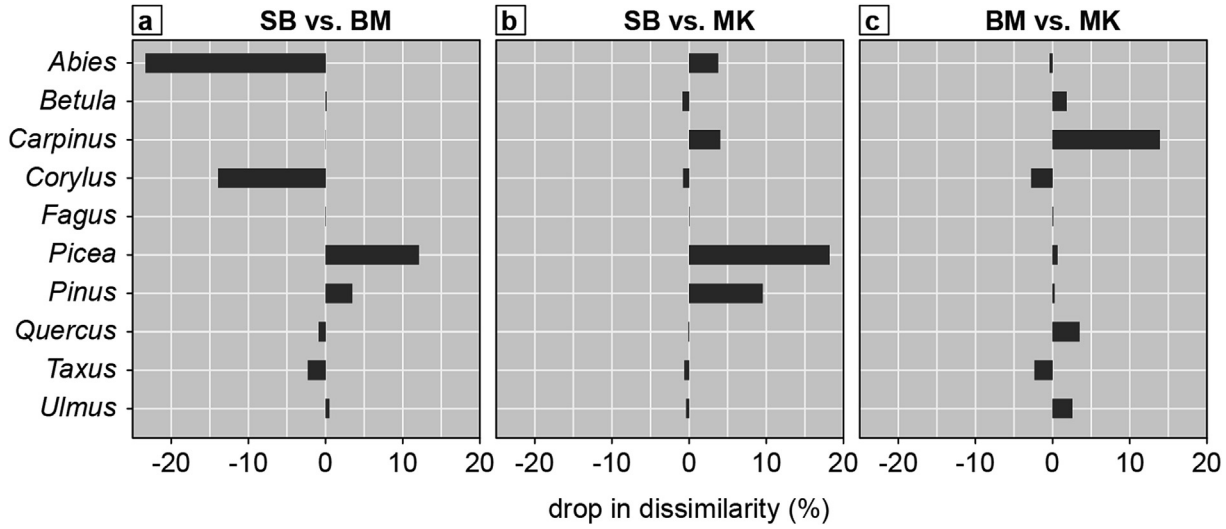

Fig. 7. Drop in dissimilarity (% of Ψ) if a specific taxon is not included in the pairwise comparison between the pollen records at Spiezberg (SB), Beerenmösli (BM) and Meikirch (MK). A positive drop in dissimilarity indicates a contribution of the taxon to dissimilarity. In particular, if the taxon was not included in the analysis, Ψ turned out to be smaller (i.e. more similar) compared to the original value. Vice versa, a negative drop in dissimilarity indicates a contribution of the taxon to similarity. Pollen records included in the comparisons are **a.** SB and BM, **b.** SB and MK and **c.** BM and MK. If SB is included, the most contributing taxa to dissimilarity are *Picea* and *Pinus*. *Carpinus* together with *Quercus*, *Ulmus* and *Betula* are responsible for most of the dissimilarity between the Eemian (BM) and the MIS 7a (MK) references.

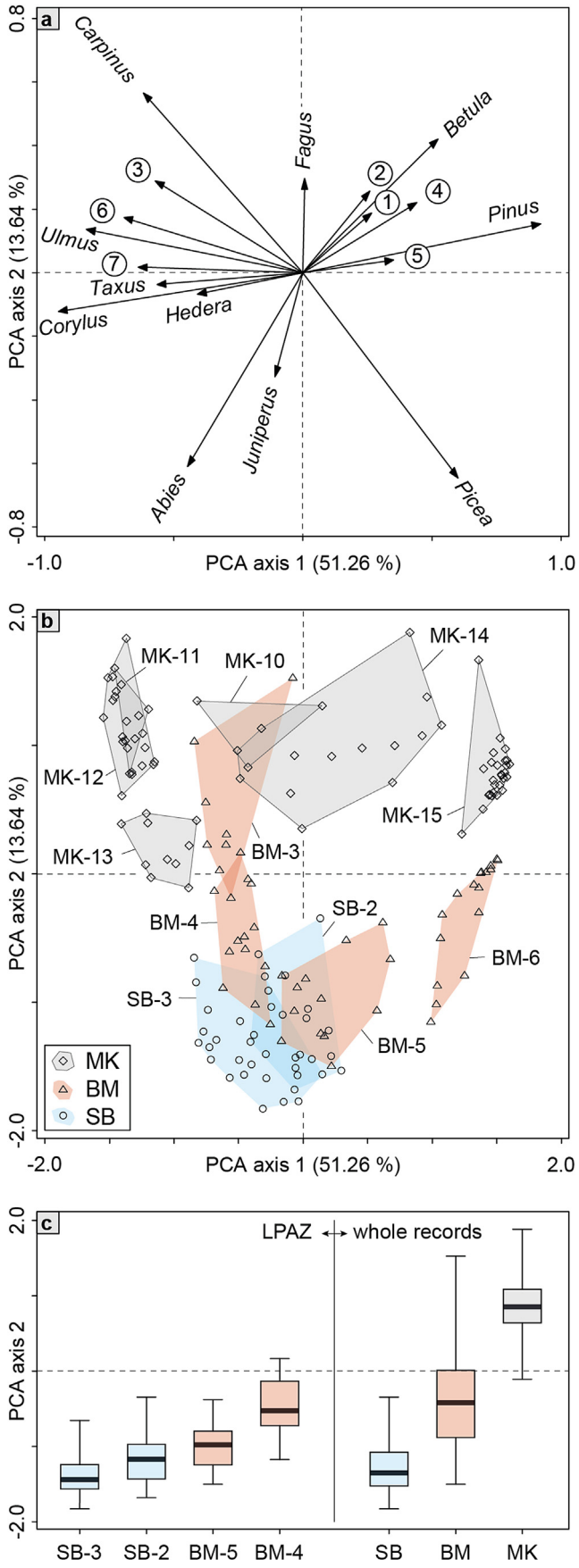

Fig. 8. Results of the PCA including samples of Spiezberg (SB) and the two reference records Beerenmösli (BM, Eemian) and Meikirch (MK, MIS 7a). PCA axis 1 and 2 explain 51.26% and 13.64% of the total variance within the data set. **a.** Scores of selected taxa (top 18). The length of an arrow's vertical (horizontal) component is proportional to its contribution to the total variance of PCA axis 1 (PCA axis 2). 1: *Artemisia*; 2: Chenopodiaceae; 3: *Fraxinus excelsior*-type; 4: *Hippophae*; 5: Poaceae; 6: *Quercus*; 7: *Tilia*. **b.** Sample scores: Samples of each LPAZ are grouped into labelled polygons. The colour code (see legend) is according to the record of the corresponding LPAZ. Proximity of clusters indicates similarity. **c.** Boxplots of sample score distributions along PCA axis 2 for single LPAZ (left) and for whole records (right) of Spiezberg (SB), Beerenmösli (BM) and Meikirch (MK). Significant similarity (Welch's *t*-test) is only given between sample score distributions of SB-2 and BM-5, implying high similarity between pollen abundances and assemblage of the two zones.

of biotic or neutral processes such as competition for light (biotic) or proximity of glacial refugia in the preceding cold stage (neutral).

Samples of all three records are evenly distributed over the positive and negative sectors of PCA axis 1 (Fig. 8b). On PCA axis 2 however, samples of Spiezberg plot exclusively on the negative side, where otherwise only samples from Beerenmösli, but not from Meikirch, occur (with exception of two samples from MK-13). The unbalanced distribution of samples over the two axes is also reflected in the different intra-record variances along both axes (Table 2). Sample score distributions of Meikirch and Beerenmösli show about ten times greater intra-record variance along PCA axis 1 than along axis 2. This suggests that axis 1 drags apart the samples of individual records (intra-record variance) whereas axis 2 drags apart the samples of different records (inter-record variance).

Surprisingly, the intra-record variance of Spiezberg is greater on PCA axis 2 (Table 2), which is opposite to the other two records. As discussed further below, we explain this pattern by the fragmentary nature of the Spiezberg record. The climate gradient covered by the Spiezberg samples is probably spanning only a fraction of a full interglacial, in contrast with the two other, complete interglacial records. In addition, in the case of BM-3, PCA axis 2 seems to drag apart zones from the same record, resulting in a positive position of the BM-3 polygon on this axis. This is reflected in the elevated intra-record variance (0.372; Table 2). As *distantia* (Fig. 7a), the PCA distinguishes *Abies* as a key similarity between Spiezberg and Beerenmösli (e.g. BM-3 compared to BM-4 and BM-5 that resemble most the Spiezberg samples in Fig. 8b).

Our results show that vegetational differences between the records of different interglacials are expressed to a much smaller extent on PCA axis 1 than on axis 2. Consequently, we only considered sample scores of PCA axis 2 when testing for significant similarity (Welch's *t*-test) between Spiezberg and the two reference records. All sample score distributions on PCA axis 2 of either LPAZ or whole records were tested for normal distributions (Shapiro-Wilk-test) prior to applying Welch's *t*-test. For both SB-2 and SB-3 sample score distributions on PCA axis 2, we tested for a possible significant similarity with pollen zones of the other two records. We started with the zone that has the most similar mean value on PCA axis 2, i.e. BM-5 (Fig. 8c). If significantly similar, the test was repeated with the subsequent zone that has the second-most similar mean value on PCA axis 2, i.e. BM-4 (Fig. 8c). Additionally,

Table 2
Intra-record variances of Spiezberg (SB), Beerenmösli (BM) and Meikirch (MK) along PCA axis 1 and axis 2. n = total number of zones included in the PCA. Of all three records, only SB shows a higher intra-record variance explained by PCA axis 2 than by axis 1 as a result of the low number of LPAZ (n = 2), which represents only a fraction of the full interglacial climate gradient.

	Axis 1	Axis 2	n
SB	0.105	0.117	2
BM	0.648	0.372	4
MK	1.606	0.166	5

Table 3
t-statistics of significance test (Welch's t-tests) between sample score distributions along PCA axis 2 of single zones and whole records. SB: Spiezberg, MK: Meikirch, BM: Beerenmösli. Significant similarity is only given between zones SB-2 and BM-5.

	BM-5[a]	BM-4[a]	BM[b]	MK[b]
SB-2 [a]	−1.534[c]	−4.572	–	–
SB-3 [a]	−3.732	–	–	–
SB [b]	–	–	−8.675	−30.304

[a] LPAZ.
[b] whole record.
[c] = significant similarity.

we tested for significant similarity between the sample score distributions on PCA axis 2 of the entire Spiezberg record and the two reference sites. Of the five resulting comparisons listed in Table 3, only the sample score distributions of SB-2 and BM-5 on axis 2 are significantly similar. This again confirms the high similarity between the Spiezberg and the numerically dated Eemian site Beerenmösli.

4. Discussion

4.1. Vegetation history of the Spiezberg record

We infer the occurrence of open birch- and pine-dominated boreal forests for the time recorded at the base of the Spiezberg section (zone SB-1). Such vegetational conditions are typical for late-glacial situations in the study area and have been reconstructed at several sites in Switzerland for the time prior to the onset of the Holocene (Burgäschisee: Rey et al., 2017; Faulenseemoos: Welten, 1944, 1982; Lotter et al., 1996; van der Knaap et al., 2004; Lobsigensee: Ammann and Tobolski, 1983; Ammann, 1989; Moossee: Rey et al., 2019; Murifeld: Welten, 1982; Rotsee: Lotter and Zbinden, 1989; Soppensee: Lotter, 1999), as well as prior to the Eemian (Beerenmösli, Gondiswil-Seilern: Wegmüller, 1992; Thalgut: Welten, 1988; Thungschneit, Dürnten: Welten, 1982; Niederwenigen: Welten, 1988; Anselmetti et al., 2010) and prior to MIS 7a (Meikirch: Welten, 1982; Preusser et al., 2005).

The subsequent vegetational change inferred from shifts in the pollen assemblages at the base of zone SB-2 is remarkably abrupt and may therefore reflect a sedimentary hiatus between zones SB-1 and SB-2. Prior to the expansion of *Abies*, continuous interglacial records of the Holocene, the Eemian and MIS 7a (see references above) from the northern Alps and their forelands usually show evidence for (i) a boreal vegetation phase with closed pine and birch forests and admixed juniper, followed by (ii) a temperate phase with *Quercus*, *Ulmus* and *Corylus* woodlands. Such early interglacial phases are fully, or partly in the case of the latter, missing in the Spiezberg record.

Temperate forests dominated by *Abies* (most likely *Abies alba*; van der Ham et al., 2008), *Ulmus, Tilia, Quercus* and *Corylus* occupied the upper Aare Valley during the time periods of zones SB-2 and SB-3, corresponding to later stages of interglacial vegetation dynamics at other sites in Switzerland during the Eemian (e.g. Welten, 1982; Wegmüller, 1992) and during MIS 7a (Welten, 1982; Preusser et al., 2005). The Alpine topography surrounding Spiezberg in the west, south and east most likely provided cooler and moister conditions, supporting the growth of coniferous forests dominated by *Picea*. The low abundances of herbaceous pollen indicate that these forests of the montane and sub-alpine zones were closed. The presence of thermophilous *Taxus* as well as evergreen broad-leaved *Ilex*, *Hedera* and *Buxus* indicate full interglacial conditions. We exclude the possibility that the Spiezberg data records an interstadial, since evergreen broad-leaved taxa did not occur north of the Alps during such periods (Lang, 1994).

At the top of SB-3, the succession at Spiezberg is capped by glacial sediments. From this point on, continuous interglacial successions from the Swiss Plateau indicate a declining abundance of *Abies* and an increasing frequency of *Pinus* trees – as well as *Betula* in case of the Meikirch site. This suggests the occurrence of closed boreal forests composed of *Pinus* and *Picea* until the re-opening of the vegetation. We conclude that, compared to the other records mentioned above, parts of the interglacial vegetation succession are missing at the beginning and at the end of the Spiezberg record.

4.2. Biostratigraphical comparison of Spiezberg with its closest analogues Beerenmösli and Meikirch

The quantitative and qualitative results unambiguously show that the vegetation history recorded at the Spiezberg site is most comparable with the Eemian record Beerenmösli. Here we identify three key conditions that allow us to attribute the Spiezberg record unambiguously to the Eemian. First, at Spiezberg, it is not sure whether or not *Fagus* was locally present (empirical limit not reached) during the *Abies* phase. But even if *Fagus* trees were growing on the Swiss Plateau, their relative abundance was negligible. Comparable low *Fagus* abundances have been encountered at the Eemian site Beerenmösli (Fig. 4), while at Meikirch, *Fagus* shows a continuous percentage curve reaching c. 4% and therefore must have played a more important role on the Swiss Plateau during MIS 7a (Fig. 5; zones MK-13 and MK-14). The distance analysis does not capture this particular Eemian characteristic of a low *Fagus* abundance as a major difference between the reference sites Beerenmösli and Meikirch (Fig. 7). We explain this by the observation that *Fagus* is only slightly more abundant at Meikirch (max. 6.3%) than at Beerenmösli (max. 1.6%) and at Spiezberg (max. 1.4%). These differences are too low to contribute as much to dissimilarity as e.g. *Carpinus,* whose pollen abundances are markedly different between the interglacials (Figs. 4 and 5). In the ordination however, *Fagus* plays an important role along PCA axis 2 in separating the interglacials from each other (Fig. 8b).

Second, *Abies*-dominated forests with *Picea* and *Corylus* and thermophilous taxa are recorded in both interglacial reference sites (Figs. 4 and 5). However, a phase of such strong *Taxus* expansion as observed at Spiezberg has only been recorded during the Eemian at the Beerenmösli site. This striking difference between the interglacial references Beerenmösli and Meikirch is again not captured by either of the numerical methods used to assess the similarity and dissimilarity between the three pollen records. In the distance analysis with *distantia*, *Taxus* even contributes to the similarity between Beerenmösli and Meikirch (Fig. 7c) and takes a neutral position in the comparison between the Spiezberg and the Meikirch records (Fig. 7b). The reason for this might be the short duration of the *Taxus* phase at Beerenmösli and Spiezberg. This interpretation is justified by the observation that elevated *Taxus* abundances only occur in a few samples (Figs. 3 and 4) so that their contribution to the total dissimilarity appears too low to outplay the else relatively similar *Taxus* abundances during the remaining period of the interglacials. Similarly, *Taxus* is aligned with PCA axis 1 that characterizes a climate control (Fig. 8a) and it does not contribute to the gradient of axis 2, along which the interglacial references are separated.

A third unambiguous diagnostic criterion is related to the relevance of *Carpinus*-dominated forests with abundant *Abies* and *Corylus* on the Swiss Plateau during MIS 7a at Meikirch (zone MK-12) after the decline of *Corylus-Ulmus*-dominated forests (zone MK-11) and prior to the mass expansion of *Abies* (zone MK-13). At Beerenmösli and Spiezberg, any evidence for a *Carpinus*-dominated

forest with *Abies* and *Corylus* is lacking. Instead, *Carpinus* reaches only a small peak of c. 10% at Beerenmösli (BM-5). Furthermore, the timing of the *Carpinus* maximum is different at both reference sites. At Meikirch, it is preceding the *Abies* phase, while at Beerenmösli, it occurs during the *Abies* phase, when *Carpinus* values are minimal at Meikirch. This major compositional and successional difference between the Eemian and MIS 7a vegetation on the Swiss Plateau and the Aare Valley is captured by both numerical comparisons. In the distance analysis with *distantia*, *Carpinus* is responsible for most of the dissimilarity between the reference sites Beerenmösli and Meikirch (Fig. 7c) and contributes to the dissimilarity between Spiezberg and Meikirch. Similarly, *Carpinus* has the most positive score along PCA axis 2 (Fig. 8a). Such important compositional and successional differences cannot be explained by synchronous local effects instead of diachronic vegetation dynamics, given that the sites are located closely to each other (c. 40 km) and only separated by 29 m in altitude.

Along with the three similarities between Spiezberg and Beerenmösli mentioned above (i.e. *Fagus, Taxus* and *Carpinus* dynamics), there is one major dissimilarity. During the entire time interval recorded by the Spiezberg section, *Picea* substantially contributed to the forest composition alongside with *Abies* and *Corylus*, whereas at Beerenmösli, *Picea* was only sub-dominant to *Abies*. This difference appears in the *distantia* results, where *Picea* is responsible for most of the dissimilarity between Spiezberg and Beerenmösli (Fig. 7a). We interpret this dissimilarity as consequence of a geographical gradient separating the two sites. Due to the proximity of Spiezberg to the high elevations of the Alps, it is far more influenced by subalpine vegetation than the Beerenmösli region, which is situated in the hilly landscape on the Swiss Plateau. In this context, the Holocene may serve as an analogue. In particular, at Faulenseemoos (590 m a.s.l.; Welten, 1944, 1988; Lotter et al., 1996; van der Knaap et al., 2004) which is located close to Spiezberg (<5 km SE), *Picea* attained maximum values of c. 20–40% during the Holocene, whereas at Burgäschisee (Rey et al., 2017), a site close to Beerenmösli, *Picea* barely reaches 5%. Similarly, Benito and Birks (2020) found *Picea* to be responsible for most of the dissimilarity between the two Eemian sites Achenhang (Grüger, 1983) and Jammertal (Müller, 2000) in Southern Germany, which are situated in an Alpine and a lowland environment, respectively. We thus infer that the Alps served as refugia for boreal taxa during the Eemian, similar as during the Holocene (after the Holocene Thermal Maximum). Furthermore, because of the locally more humid conditions during the Eemian than today (Scussolini et al., 2019), *Picea* forests may have spread to lower elevations during the Eemian. This would explain the higher *Picea* abundances at Spiezberg compared to the very close Holocene site Faulenseemoos.

4.3. The neighbouring European Eemian context

The Eemian vegetation composition and succession on the Swiss Plateau is comparable with that at Eemian key sites in France (La Grande Pile: Woillard, 1975, 1978; Beaulieu and Reille, 1992b; Les Échets: Beaulieu and Reille, 1984; Ribains: Beaulieu and Reille, 1992a), in Southern Germany (Füramoos: Müller et al., 2003; Samerberg: Grüger, 1979; Jammertal: Müller, 2000), in Northern Germany (Bispingen: Müller, 1974; Field et al., 1994; Gröbern: Litt, 1994; Kühl et al., 2007) and in Austria (Mondsee: Drescher-Schneider and Papesch, 1998). Without exception, the Eemian vegetation succession of Central Europe is characterized by an initial phase of afforestation with *Pinus* and *Betula*, followed by a period when *Quercus*, *Ulmus* and to some extent *Acer* and *Fraxinus* were the most abundant trees before a mass expansion of *Corylus*. Such a succession is equally developed on the Swiss Plateau. Interestingly, *Picea* was already substantially present during the initial Eemian phases on the Swiss Plateau (Wegmüller, 1992). At other European sites close to the Alps, e.g. Samerberg (Grüger, 1979) and Mondsee (Drescher-Schneider and Papesch, 1998), *Picea* shows a similar early and substantial expansion (Ravazzi, 2002), while in France *Picea* only expanded after the temperate *Abies* phase towards the end of the interglacial (Woillard, 1975, 1978; Beaulieu and Reille, 1984, 1992a, 1992b). This possibly reflects the westward spread of *Picea* during the Eemian (Drescher-Schneider, 2000), which has been reconstructed as well for other tree species (Kupryjanowicz et al., 2018). Alternatively, the diverging *Picea* dynamics could be a response to different environmental conditions between these regions (e.g. due to higher precipitations in proximity to the Alps). Indeed, the above-mentioned *Picea* dynamics recorded at Beerenmösli and Spiezberg perfectly reflect the European picture of a vegetation gradient from the Alpine border to the lowland.

On the Swiss Plateau the *Corylus* phase was followed by a period when *Taxus* substantially expanded. This characteristic is observed at most Eemian sites in Western and Central Europe, with the exception of Les Échets. At Les Échets however, the absence of a prominent *Taxus* phase is likely due to a sedimentary hiatus (Beaulieu and Reille, 1984). In contrast to the Swiss Plateau, where *Carpinus* remained only a minor component of the Eemian forest composition in the lowlands (Wegmüller, 1992) and probably never expanded closer to the Alps (Spiezberg), a dominant *Carpinus* phase is recorded in most of the Western and Central European pollen profiles. There are, however, significant regional differences in the pattern of the *Carpinus* expansion during the Eemian. In fact, Müller (2000) proposed elevation thresholds for the formation of a *Carpinus* phase of 560 m a.s.l. in Upper Bavaria and 630 m a.s.l. on the Swiss Plateau farther west. In contrast to Beerenmösli (649 m a.s.l.), which is situated above the local elevation threshold proposed by Müller (2000), Spiezberg (592 m a.s.l.) is located below this threshold and would therefore offer suitable conditions for the development of a *Carpinus* forest. Hence, other factors must have limited the local growth of *Carpinus*. A reason might be the trough-like morphology of the Swiss Plateau, which is enclosed by the Jura Mountains in the NW and the Alps to the SE (Fig. 1a). In addition, large portions of the Swiss Plateau are situated above 630 m a.s.l., which favours the growth of *Abies*. The combination of these two conditions may explain the low abundance of *Carpinus* in the Swiss records, which on a large scale was competitive only at lower altitudes.

The low abundance of *Fagus* on the Swiss Plateau has also been discussed as a main characteristic of the Eemian on a European scale (Drescher-Schneider, 2000; Tzedakis et al., 2001; Magri et al., 2006). A substantial Eemian occurrence of *Fagus* has only been reported from sites in Southern Europe, e.g. in Bulgaria (Bazilova and Djankova, 1976) and in Italy (Follieri et al., 1988; Allen and Huntley, 2009), although *Fagus* was less abundant in the Italian sites. It has been hypothesised that during the Eemian *Carpinus* spread at an early stage and prevented *Fagus* from expanding (Lang, 1994). This might have been a factor at sites farther away from the Alps, where *Carpinus* was a substantial component of the Eemian forests (Beaulieu and Reille, 1984, 1992a, 1992b; Müller, 2000). Such vegetation dynamics, however, did most likely not occur closer to the Alps, where neither *Carpinus* nor *Fagus* played important roles in the forest composition (Grüger, 1979; Wegmüller, 1992; Drescher-Schneider and Papesch, 1998). Therefore, other factors must have limited the spread and the mass expansion of *Fagus* in the northern Alpine forelands during the Eemian. In this context, Tzedakis (1994) discussed drought damage, extermination during the preceding cold stage or pathogen stress as possible reasons.

Based on the results of our ordination, we suggest that *Abies* was the major competitor, which prevented *Fagus* to establish. This relationship between *Abies* and *Fagus* is expressed in the gradient of PCA axis 2 (Fig. 8b), along which both species separate the records into populations that either contain significant *Fagus* pollen abundances, i.e. Meikirch (MIS 7a), or lack *Fagus* constituents, i.e. Beerenmösli and Spiezberg (both Eemian). Similar to the Holocene, when late frost probably caused the late expansion of *Fagus* (Tinner and Lotter, 2001), late frost might have inhibited the expansion of *Fagus* during the Eemian and favoured *Abies*, which is slightly more resistant to frost disturbance. As another explanation, we propose that *Abies* might have been favoured over *Fagus* in Central Europe due to the warmer (Fischer et al., 2018) and probably locally more humid (Scussolini et al., 2019) climatic conditions during the Eemian compared to the Holocene. In Southern Switzerland and Northern Italy, where modern annual mean temperatures are c. 3–4 °C warmer and annual precipitation is c. 300–600 mm higher than on the Swiss Plateau, similar dynamics between the two species occurred during the Holocene (e.g. Tinner et al., 1999; Vescovi et al., 2010). In fact, *Abies alba* massively dominated over *Fagus sylvatica* for millennia, and the latter species could only expand after *Abies alba* started to decline due to fire disturbance for agricultural purposes.

5. Conclusions

Our analytical and numerical investigations of the Spiezberg pollen record are in line with the biostratigraphic correlation with the Eemian of Zwahlen et al. (in press). Despite its fragmentary nature, the Spiezberg section records a considerable part of the Eemian vegetational succession, namely parts of the initial *Picea-Corylus phase*, the interglacial optimum phase with its characteristic *Taxus* peak and parts of the subsequent *Abies* phase. This study underscores the importance of interpreting pollen records in their local geographic context, as illustrated by the unexpectedly missing *Carpinus* phase as well as by the stronger importance of *Picea* at Spiezberg compared to the more distal Eemian sites on the Swiss Plateau, in southern Germany and in France. This is particularly important when comparing sites along altitudinal gradients, along which short distances result in disproportionately strong environmental and vegetational changes. Such steep ecological gradients are present from the Swiss Alps to their forelands, which are also in line with Eemian vegetational patterns described on a Central European scale.

The current distribution of *Abies alba* in Europe is an underestimation of its potential distribution, since it has been narrowed by human impact (Tinner et al., 2013; Ruosch et al., 2016). Under the projected future climate change *Abies alba* is however likely more competitive than widely cultivated or anthropogenically favoured species such as *Picea abies* and *Fagus sylvatica*, which are less adapted to warmer climates (Ellenberg, 2009; Ellenberg and Leuschner, 2010). Holocene sedimentary time series, tree-ring records and dynamic vegetation simulations (e.g. Tinner et al., 2013; Büntgen et al., 2014; Ruosch et al., 2016; Vitasse et al., 2019) also indicate that *Abies alba* might benefit from a warming climate. Based on the seminal studies of Zagwijn (1992, 1996) and our own observations from the Eemian, we use the pre-Holocene interglacial evidence to predict that under future climate warming the potential distribution of *Abies alba* may extend its northern boundary in Central Europe to the Baltic and the North Sea, similar to its spreading during the Eemian.

Author contributions

PS, WT, EG and FS conceptualized the study. PS conducted the sedimentological investigations. PS, JvL and EV conducted the palynological investigations. PS did the numerical investigations, the data visualisation and wrote the draft of the manuscript. DB, EG, FS, GD, MS and WT discussed the results and commented on the manuscript, and GD, WT and FS contributed to the finalization of the text. FS acquired the funding. All authors agree on the science and the style of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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