Response to Editor

Dear Prof. Combourieu-Nebout,

first of all we would like to thank you for handling our manuscript. We appreciate your very helpful comments and suggestions on the manuscript. We went through them carefully and reconsidered the suggestions by the two reviewers.

Attached we send you our detailed responses to the comments and the revised manuscript (marked-up version). We believe that we did our best to respond to all comments so that the quality of our manuscript improved.

We hope that our corrections and adjustments will meet your requirements.

Kind regards,

Fabian Rey & Co-authors

“1 – Title: I agree that the title do not fit with the paper as the deglaciation is develop in a special paragraph in the paper but the terms used of "impact on deglaciation" in the title or of "climate-driven deglaciation" in paragraph 5.1 title are not adequate here in my opinion. So I suggest to change the title in “Climate impact on vegetation dynamics since the Last Glacial Maximum at Moossee” or if you want to conserve the term of deglaciation “Climate impact on vegetation dynamics during the last deglaciation and Holocene” and to change as well the title of the 5.1 paragraph Or you choose to focus only on the deglaciation and your discussion has to be extended more on this period and restricted on the Holocene.”

We thank the Editor for this suggestion. Since Referee #2 raised the same point, we changed the title as followed: ‘Climate impacts on vegetation and fire dynamics since the last deglaciation at Moossee’. We also adjusted the title of the first chapter in the discussion: ‘Vegetation and fire dynamics from the last deglaciation to the Mid Holocene’.

“2- Concerning the references, I agree also with Rev. 2 that the important papers published on Les Echets and La Grande-Pile, even if they have not the same resolution as your record, have to be cited at least in the introduction to set the study framework in a width area and highlight the importance of your new work to respond to questions on the climate/environment interaction. You may add one sentence with these references to show the importance of high resolution studies in this area and not only cite paper or synthesis or modelling and regional papers on Switzerland. So please find a way to evoque the old series.”

We included the two sites from Western Europe in the introduction as requested. The limitation of these sites is that they are undated for the period of interest and have very low temporal resolution, so that their value in this context is very limited. Bergsee (Southern Germany) and the sites in Northern Italy were already part of the submitted manuscript. Hence, with the present references we include major parts of the peri-alpine forelands.

“3- Paleo diversity data needs to be shown if such record is informative for the discussion on climate influence and vegetation but not only that you want to show here all your data. Please remove it if not or justify more why you want to present it here.”

We strongly believe that the results are important since DE-PRI fits well with DCA axis 1 and Poaceae %, implying that our palaeodiversity estimations go in line with openness, which is of paramount importance for understanding biodiversity dynamics over the past 19,000 years. In the lower part, the openness is climate induced, in the upper part human induced openness is leading to a higher diversity. We state this in the results part and it is part of the discussion as well (second paragraph in the first chapter and second paragraph in the second chapter). We added new sentences in the discussion to emphasize this issue.

"4- Concerning the interpretation of Sporormiella, I will be very interested to see the influx of Sporormiella and the extension of your discussion regarding the interpretation in occurrence/absence of the curves of this NPP? Did you have other coprophilous NPP that reinforced you interpretation? Please discuss more on that point as it is strange that the coprophilous are present only during the deglaciation. I see that when you present the curve in the Fig 4. Data of Nielsen show the presence of Megafauna are very general. Did you have informations about what happened near your site? And what about the other nearby sites? In the nearby site of Burgäschisee, Sporormiella is not so represented. why? and what about the Holocene, it is impossible to see anything in your diagram but you say they are sporadic. Does it means that there is no indications of livestock in the studied area in the recent periods? So it means that you have only farming. And what about the nearby sites? Did I understand in the good way? Perhaps this part of the discussion has to be more developed."

The trends of the *Sporormiella* percentages and influx values are indeed very similar. We now also include the percentages and influx values of *Cercophora* in Fig. 4, which support our previous interpretations. The data of Nielsen (2013) and Cupillard et al. (2015) is a compilation of the whole region (Western Swiss Plateau, Jura Mountains) and are the most detailed available in Switzerland. However, we also mark with the grey horizontal bar the time window of local reindeer hunter camps at Moossee in Fig. 4. Hence, we have local and regional archaeological and zooarchaeological evidence of Pleistocene herbivores which all support our interpretation. Under "Study Site" (second paragraph), we describe the local archaeology and specifically the spectacular local hunter camps. We repeat this in the discussion (third paragraph) and even more, we show the position of the local hunter camps in Fig. 1b (points C and D). Nielsen (2018) is so detailed that in his publication, the hunting grounds around Moossee are recognized as very rich due to high numbers of animals found (important seasonal migration routes close by). It is unknown if the numbers of herbivores were lower at Burgäschisee, however the lower the percentages of *Sporormiella* may imply that they were lower. This would mean that we have a prominent local *Sporormiella* signal at Moossee. However, this comparison of numbers remains to some degree speculative and more research is definitely needed. We never wrote, that coprophilous fungi spores are only present in the Oldest Dryas. We also find them later on but only punctually with the onset of local agricultural activities. However, the values are always rather low in previously studied lowland sites (see e.g. Hillbrand et al., 2014; Rey et al., 2017) and the reasons for this are not clear yet. One possible explanation could be that dung was removed and re-used as fertilizer on the crop fields, as archaeologically proven for the Metal Ages. If this is the case, coprophilous fungi would not grow. This is very different in the remote Alps, where usually high numbers of coprophilous spores are found (e.g. Schwörer et al., 2015; Dietre et al., 2019). A very interesting topic indeed, but unfortunately beyond the scope of what we would like to discuss in the present paper but to be elaborated in the future.

"5- in Fig. 4 you only show july temperature from modellers? have you test some climate quantifications on your data? it will be usefull to see really what hapenned around your site."

The July temperatures shown in Figs. 4 and 5 is a compilation of an independent proxy-based temperature reconstruction based on chironomids. These are non-biting midges that among many proxies are known to deliver best July temperature estimates. This data set has been previously published in Finsinger et al. (2019). We carefully describe this in the figure captions and also in the text (third paragraph of the first chapter in the discussion). This compilation is state of the art and most importantly independent from pollen or model simulations. Climatically it covers Central Europe and Northern Italy. Independent chironomid analysis from the same site would even be more suitable. Here, more studies are certainly needed. We cannot use our pollen data set as a proxy for climate changes and interpret major vegetation re-organizations a response of climate change. This would be highly circular and we thus basically avoid it.

"6- In Fig.1, do not use white for the numbering of the sites and the countries limits, please change that, it is unreadable.

In Fig. 3, perhaps it will be more readable if you cut your complete diagram in two parts in portrait one below the other with a remind of the depth, ages, lithology, pollen zones and synthetic trees/shrub/herb diagram. Please do that and you can be able to enlarge the two parts of the diagram that result in a more readable figure."

We thank the Editor for these suggestions. We changed the numbering of the sites in the revised map using semi-transparent boxes below the white numbers (Fig. 1a). In Fig. 1b the numbering was included in the circles. Furthermore, we highlighted the present study site and the coring location with a different colour. After these changes, we do believe that the readability has increased. We could not use red colour (which would be about as prominent as white) due to the green backgrounds (red-green colour blindness).

For the review process we had to include the figures in a rather low resolution. Additionally, the page margins of the template used for the Climate of the Past discussion papers are quite wide. This makes the figures smaller. The readability for both Figs. 1 (map) and 3 (pollen diagram) will be better with the higher resolution and more narrow page margins. To address your concern we printed out Fig. 3 in reduced size 15x9 cm and the pollen diagram is still very readable. We also consulted colleagues from other labs and they think it is are very readable. We considered to split the pollen diagram (Fig. 3) but we prefer not to do so. We already show a limited number of pollen taxa and in this case it is standard across many publications from different research groups/ teams not to split pollen diagrams (e.g. de Beaulieu and Reille, 1992; Tinner et al., 1999; Rösch et al., 2014; Azuara et al., 2015; Rey et al., 2017; Feeser et al., 2016; Dendievel et al., 2019).

Response to Referee #1

We thank the reviewer for the very positive feedback and the minor suggestions. We considered all comments and suggestions carefully. Below, we reply to all comments of the reviewer.

“Line 31: I prefer not splitting infinitives, so suggest ‘to modify irreversibly’.”

We changed this as suggested in the text.

“Line 74: Change “with predominantly sandstones between” to ‘with predominantly sandstone in between’. Change “north” to ‘north’ and “South” to ‘south’”

We accepted all corrections and changed them accordingly.

“Line 76: Change “West” to ‘west’ and “East” to ‘east’”

We corrected these two points as suggested.

“Line 90: Hyphenate “lake shore villages” (‘lake-shore villages’)”

We changed this as suggested.

“Line 94: ‘centre’ rather than “center””

We changed ‘center’ (American English) to ‘centre’ (British English) as the reviewer prefers BE.

“Line 96: Change “in town” to ‘in the town’”

We added ‘the’ as suggested.

“Line 97: ‘centre’ rather than “center””

Again AE vs. BE. We changed it to ‘centre’ as suggested (see above)

“Line 103: Change “an UWITEC” to ‘a UWITEC’”

We corrected this accordingly.

“Line 127: Change “assess” to ‘estimate’”

We exchanged this in the text.

“Line 146: Change “data was” to ‘data were’”

We corrected this mistake.

“Line 150: Also Birks et al. (2015) Rev Pal Pal for a review.”

We added this additional reference in the text.

“Lines 154-159: I have reservations about PRI/PIE and using the residuals + PRI. See Birks et al. (2016).”

We thank the reviewer for this critical remark. We are aware that the use of the different biodiversity estimates in palaeoecology is intensely debated. The procedure we followed has been regularly implemented (see Colombaroli and Tinner, 2013; Schwörer et al., 2015; Rey et al., 2019a). We also show that PRI and DE-PRI generally indicate similar trends when PIE is high and we give explanations why PRI and DE-PRI in some cases may differ (see lines 297-303). Parts of the presented biodiversity estimations have been previously published (see Rey et al., 2019a) and to be able to compare the complete data set, we would like to keep the estimates as they are. Furthermore, DE-PRI goes well in line with DCA axis 1 and Poaceae %, which means that all curve are connected to openness. This is certainly an interesting result and worth to show in the present manuscript.

“Line 165: Personally, I would have used DCCA with depth as the constraining variable (Birks 2007, VHA) as pollen data are time-ordered. DCA does not take account of the depth. It does not make much difference but DCCA is for the purist.”

We thank the reviewer for this remark. We indeed calculated several options through and decided to show the results for the DCA which is more widespread and generally better known than DCCA.

“Line 224: Change “releasing” to ‘leading to’”

We exchanged this as suggested.

“Line 228: Change “released” to ‘resulted in’”

We changed this accordingly.

“Line 241: Change “reestablishment” to ‘re-establishment’”

We changed this in the text.

“Line 273: Change “land use phases” to ‘land-use phases’”

We hyphenated this in the text.

“Line 284: Change “favoring” to ‘favouring’”

Once more AE vs. BE. We changed it to ‘favouring’ as suggested.

“Line 286: Change “land use phases” to ‘land-use phases’”

We changed this accordingly (see above).

“Line 332: Prefer ‘to form quickly’ rather than “to quickly form””

We changed this to the reviewer’s preference.

“Line 333: Add a comma after “First” (‘First, arboreal …)”

We added a comma in the text.

“Line 349: Delete “first””

We deleted the word “first” as suggested.

“Line 350: Change “dwarf birch thickets” to ‘dwarf-birch thickets’”

We hyphenated this in the text.

“Line 357: Change “North” to ‘north’”

We corrected this in the text.

“Line 359: Change “wide-spread” to ‘widespread’”

We changed this accordingly.

“Line 370: Add ‘and’ before “Rangifer””

We added the word “and” in the text.

“Line 376: Change “Betula pendula” to ‘B. pendula’”

We changed this as suggested by the reviewer.

“Line 378: Add ‘the’ before “tree””

We inserted the word “the” in the text.

“Line 416: Change “favored” to ‘favoured’”

We changed this as suggested.

“Line 429: Change “land use history” to ‘land-use history’”

We changed this accordingly.

“Line 431: Add ‘the’ before “first””

We inserted the word “the” in the sentence.

“Line 432: Change “falls” to ‘fall’”

We corrected this in the text.

“Line 438: Change “land use” to ‘land-use’”

We changed this as suggested.

“Line 443: Change “land use phases” to ‘land-use phases’”

As above: we changed this in the text.

“Line 445: Change “land use phases” to ‘land-use phases’”

Again: we changed this in the text.

“Line 453: Change “favorable” to ‘favourable’”

Again AE vs. BE. We used “favourable” as suggested by the reviewer.

“Line 459: Add ‘the’ before “driving””

We added the word “the” in the text.

“Line 466: Change “reestablish” to ‘re-establish’”

We changed this in the text.

“Line 469: Change “drought resistant” to ‘drought-resistant’”

We changed this as suggested.

“Line 480: Do you have Betula humilis?”

We thank the reviewer for this question. In fact, *Betula humilis* regularly occurred in Switzerland in the past (like *Betula nana*). However, since we do not have the plant macrofossils from the species and the pollen cannot be distinguished from *Betula nana* (unlike tree Betula such as *Betula pubescens* and *Betula pendula*), we deleted “*Betula humilis*” in the text.

“Line 515: Change “identification” to ‘identifications’”

We changed this accordingly.

“Line 910: Change “neolithic” to ‘Neolithic’”

We corrected this mistake.

Response to Referee #2

We thank the reviewer for the positive comments and the few critical points. We are glad that the reviewer was impressed by the labor we invested for the pollen analysis and the chronology. We went through all the comments and the replies are attached below.

"1. Title : the ms does not really investigate the impact of climate on deglaciation, except in the first paragraph of the discussion where extent and retreat of ice sheet is briefly discussed in reference to radiocarbon age from lacustrine record north and south of the Alps. Therefore, this seems to be a little off the main topic of the paper. I would advise to change the title to reflect the focus on vegetation and fire (that does not appear in the title's current form)."

We thank the reviewer for this suggestion. We set the adjusted title as followed: 'Climate impacts on vegetation and fire dynamics since the last deglaciation at Moossee (Switzerland)'.

"2. In such paper discussing post-LGM and HE1 vegetation dynamics it is quite surprising not to see any references to paleoecological records in the same area/latitude covering these time slices and beyond such as La Grande Pile, Les Echets or Bergsee Lake (Becker et al 2006 is not the most uptodate reference). Please add."

We included the most up to date reference for Bergsee (Duprat-Oualid et al., 2017) in the manuscript. Indeed, Bergsee has a very profound chronology for the time window we are discussing. Since we start the discussion with the onset of deglaciation after 19000 cal. BP, La Grande Pile and Les Echets mostly fall beyond of what we want we are discussing in our paper. Their resolutions after 19,000 cal. BP is low and their chronological precisions rather inadequate. Nevertheless, these studies are still important key sites and 'classics' and we included the required references in the introduction.

"3. Paleodiversity analysis are interesting but are not really informative (only multimillenial patterns to the best) and are not much used in the discussion. I am wondering if it is really necessary to keep it in the paper?"

It was not our intention to discuss decadal or centennial patterns and trends in palaeodiversity. We rather wanted to show the long-term trends and the stability of the patterns. The results are still useful because they clearly indicate a higher pollendiversity with increasing human impact respectively openness. DE-PRI goes basically almost in line with DCA axis 1 and Poaceae %. This is a very interesting result and we think the curves are worth to keep and we elaborated the text.

"4. Use of Sporormiella and link to megafauna. First, Sporomiella is expressed as % of total pollen sum, which is somewhat problematic (eg. Baker et al 2013; Etienne & Jouffroy Bapicot, 2014) . Indeed, fungus and pollen does not belong to the same ecological community and expressing Sporormiella in percentage of the total pollen sum can lead to flawed results: for instance, the relatively high levels between 19 and 15.2 ka BP can either be related to higher presence of Sporomiella or to fluctuations in total pollen sum, or to change in sediment accumulation rate. Moreover, the chronology of the record is robust enough to calculate concentrations and accumulation rate, as it has been done for charcoal, which is also made possible by the use of Lycopodium in pollen slides preparation. I then strongly recommend to express Sporormiella in accumulation rate (nb.cm-2.yr-1), as it is the only way for authors to evidence their claim of more abundant coprophilous fungi between 19 and 15.2 ka BP and its potential link with megafauna presence and then extinction. As currently presented, the data do not support the interpretation. Second, the discussion about the link between continuous abundance (not evidenced in the current dataset) and the presence of Pleistocene megaherbivores is too affirmative in its current form (eg p10 l 363-365) and should be reformulated. Sporormiella is strictly coprophilous, and then megaherbivores are not the only explanation for potential high abundances. Moreover, with Sporormiella expressed ad % the authors cannot state that the extinction of megaherbivores is “also evidenced by decreasing numbers [of] dung spores after 16000 cal. BP” (p10 l 370- 371), since we do not know if the numbers of spores is actually decreasing (% are, which is different).”

We thank the reviewer for this important remark. We understand that it can be critical to only show the percentages of *Sporormiella*. However, in our case percentages and influx are very similar for all pollen, spore and other microfossils. Nevertheless, as suggested by the reviewer, we included the influx values in Fig. 4. Indeed, one can now see that the trends of the influx values are very similar to the percentages (due to the robust chronology). Thu, we are confident to state that the high values of *Sporormiella* are likely connected to the presence of megaherbivores. We also now include the percentages and influx values of *Cercophora* which support our interpretation. Theoretically, coprophilous fungi spores could also indicate the presence of other (smaller) animals. However, many studies in North America could show that e.g. *Sporormiella* values are indeed linked to high numbers of megaherbivores (Robinson et al. 2005; Davis and Shafer 2006; Gill et al. 2012), which is discussed in this manuscript. In Siberia, frozen dung next to an excavated mammoth carcass revealed high numbers of *Sporormiella* spores (Mol et al. 2006). Hence, we do believe that our *Sporormiella* and *Cercophora* values likely indicate high numbers of megaherbivores on the Swiss Plateau, so that the decreasing numbers of dung spores after 15,500 cal BP may be related to regional extinction of e.g. mammoths. However, to take into account the reviewer’s concerns, we slightly adjusted the text to be less affirmative.

“5. Main pollen diagram is described in the results section with a phase beginning at 19200 cal. BP. But Figure Figure 3 seems not to exhibit pollen data prior to 18800-19000 cal. BP? Please check & correct.”

We thank the reviewer for this comment. 19,200 cal. BP is actually the calibrated age of the oldest radiocarbon date (based on a *Salix herbacea* leaf fragment and rhizome). The reviewer is right: for this depth, we do not have a pollen sample (but a leaf). Hence, we corrected this misunderstanding by putting 19,000 for the first non-sterile pollen sample. The onset of the pollen diagram is now correctly set at 19,000 cal. BP in the text.

Climate impacts on ~~deglaciation and~~ vegetation and fire dynamics since the last deglaciation~~Last Glacial Maximum~~ at Moossee (Switzerland)

Fabian Rey[1,2,3], Erika Gobet[1,2], Christoph Schwörer[1,2], Albert Hafner[2,4], Sönke Szidat[2,5], Willy Tinner[1,2]

[1]Institute of Plant Sciences, University of Bern, CH-3013 Bern, Switzerland
[2]Oeschger Centre for Climate Change Research, University of Bern, CH-3013 Bern, Switzerland
[3]Geoecology, Department of Environmental Sciences, University of Basel, CH-4056 Basel, Switzerland
[4]Institute of Archaeological Sciences, University of Bern, CH-3012 Bern, Switzerland
[5]Department of Chemistry and Biochemistry, University of Bern, CH-3012 Bern, Switzerland

Correspondence to: Fabian Rey (fabian.rey@unibas.ch)

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Abstract. Since the Last Glacial Maximum (LGM, end ca. 19,000 cal BP) Central European plant communities were shaped by changing climatic and anthropogenic disturbances. Understanding long-term ecosystem reorganizations in response to past environmental changes is crucial to draw conclusions about the impact of future climate change. So far, it has been difficult to address the post-deglaciation timing and ecosystem dynamics due to a lack of well-dated and continuous sediment sequences covering the entire period after the LGM. Here, we present a new palaeoecological study with exceptional chronological time control using pollen, spores and microscopic charcoal from Moossee (Swiss Plateau, 521 m a.s.l.) to reconstruct the vegetation and fire history over the last ca. 19,000 years. After lake formation in response to deglaciation, five major pollen-inferred ecosystem rearrangements occurred at ca. 18,800 cal BP (establishment of steppe tundra), 16,000 cal BP (spread of shrub tundra), 14,600 cal BP (expansion of boreal forests), 11,600 cal BP (establishment of first temperate deciduous tree stands composed of e.g. *Quercus*, *Ulmus*, *Alnus*) and 8200 cal BP (first occurence of mesophilous *Fagus sylvatica* trees). These vegetation shifts were released by climate changes at 19,000, 16,000, 14,700, 11,700 and 8200 cal BP. Vegetation responses occurred with no apparent time lag to climate change, if the mutual chronological uncertainties are considered. This finding is in agreement with further evidence from Southern and Central Europe and might be explained with proximity to the refugia of boreal and temperate trees (< 400 km) and rapid species spreads. Our palynological record sets the beginning of millennial-scale land use with periodically increased fire and agricultural activities of the Neolithic period at ca. 7000 cal BP (5050 cal BC). Subsequently, humans rather than climate triggered changes in vegetation composition and structure. We conclude that *Fagus sylvatica* forests were resilient to long-term anthropogenic and climatic impacts of the mid and the late Holocene. However, future climate warming and in particular declining moisture availability may cause unprecedented reorganizations of Central European beech-dominated forest ecosystems.

1 Introduction

In the near term, rapid climatic and environmental changes hold a substantial risk to ~~irreversibly~~ modify irreversibly plant ecosystems in Europe (Schumacher and Bugmann, 2006; Kovats et al., 2014; Bugmann et al., 2015). Quantifying the response or resilience of ecosystems to environmental change in the past largely improves our capacity to assess future impacts of climate and global change (Henne et al., 2015). Specifically, palaeoecological data offer the great opportunity to study long-term climate-vegetation interactions under conditions that exceed the variability and duration recorded in historical archives or through measurements and experiments (Willis and Birks, 2006; Birks et al., 2016; Henne et al., 2018).

During the Last Glacial Maximum (LGM), large areas in Central and Southern Europe around the Alps, in the Jura Mountains, the Black Forest, the Vosges and the Apennines were covered by ice (Ehlers and Gibbard, 2004; Bini et al., 2009; Ehlers et al., 2011; Seguinot et al., 2018). The subsequent deglaciation is generally well-studied, however, timing issues remain due to dating uncertainties (e.g. Wirsig et al., 2016). Recent advances in Accelerator Mass Spectrometry (AMS) radiocarbon dating offer the possibility to produce reliable results with relatively small chronological uncertainties, when using samples with extremely low carbon contents (Szidat et al., 2014; Uglietti et al., 2016). Radiocarbon dates on terrestrial plant remains extracted from the very bottom of lake sediments from sites close to the LGM glacier margins may thus help to refine the onset of deglaciation. However, only very few sedimentary records providing reliable deglaciation ages (i.e. no bulk dating, only terrestrial macrofossils, see Finsinger et al., 2019) are available so far from the peri-alpine ~~lowlands~~ belt (e.g. Lister, 1988; Laroque and Finsinger, 2008; Lauterbach et al., 2012). Similarly, well-dated pollen profiles from Western and Central Europe covering the first two millennia of the Oldest Dryas (ca. 19,000–17,000 cal BP) are almost absent and the existing chronologies are therefore inadequate (e.g. Woillard, 1978; Welten, 1982; Ammann and Tobolski, 1983; de Beaulieu and Reille, 1984; de Beaulieu and Reille, 1992~~; Becker et al., 2006~~). Conversely, the temporal evolution of the vegetation after 17,000 cal BP is better known (e.g. Lotter, 1999; Tinner et al., 1999; Duprat-Oualid et al., 2017; Rey et al., 2017). Various sites south of the Alps indicate a first afforestation after 16,000 cal BP (e.g. Vescovi et al., 2007) and the main cause has been identified as the post Heinrich event (HE) 1 warming (Samartin et al., 2012). At around 16,000 cal BP shrub and probably~~possibly~~ even tree birches expanded into the steppe tundra north of the Alps (Lotter, 1999; Duprat-Oualid et al., 2017; Rey et al., 2017), forming open parklands or shrub tundra. North of the Alps, forests expanded after 14,700 cal BP as a consequence of the Bølling warming (see Ammann et al., 2013; van Raden et al., 2013), a process which was delayed by almost 1500 years compared to the lowlands south of the Alps (Vescovi et al., 2007). The reasons causing this long time-lag are not yet fully understood but might be related to a strong latitudinal temperature gradient and the presence of large ice masses (Heiri et al., 2014). The subsequent forested Late Glacial and Holocene vegetation history of the Swiss Plateau is best-studied and the chronological framework is rather robust (e.g. Lotter et al., 1999; Wehrli et al., 2007; Rey et al., 2017).

Taken together, despite the long tradition of palaeoecological research in ~~Switzerland~~ Central Europe with quite a high density of well-dated and highly resolved studies, a profound modern assessment of the major vegetation changes and their main causes is currently lacking. Here, the novel Moossee record has the great potential to shed new light on the timing of lake formation and on important vegetation reorganizations for the past ~~19,200~~19,000 years in a central area of the Swiss Plateau. In this study we aim (1) to reconstruct the timing of deglaciation and the establishment of first pioneer vegetation around the lake after the LGM, (2) to identify major postglacial changes in ecosystem evolution on the Swiss Plateau and to assess their causes, (3) to discuss the resilience and the vulnerability of Central European lowland forests in the past to inform the near future and (4) to emphasize the utility of exceptional temporal precision and resolution.

2 Study site

Moossee is a small eutrophic lake at 512 m a.s.l. (47°1′17.0′′N, 7°29′1.7′′E) located on the Swiss Plateau within the periphery of the Swiss capital Bern. The study area geologically belongs to the carbonate-rich molasse region with predominantly sandstone~~s~~ in between the Jura Mountains in the n~~N~~orth and the Alps in the s~~S~~outh (Schmid et al., 2004). The lake formed after the retreat of the Rhône glacier after the LGM and has a surface area of 0.31 km^2, with one main inflow in the w~~W~~est and one outflow in the e~~E~~ast (Fig. 1b). The maximum water depth is 22 m, with generally anoxic waters in the hypolimnion below 12 m (Guthruf et al., 1999). The lake used to be at least ten times larger in the past, but its size has shrunk due to peat formation over the millennia and artificial lake level lowering (by 4–5 m) since the late 18th century. Lake levels were lowered to drain the wetlands for peat exploitation and to gain agricultural land (von Büren, 1943; Guthruf et al., 1999; Harb, 2017, Fig. 1b). The climate at Moossee is oceanic with mean annual temperatures of 8.8 °C and an annual rainfall of 1059 mm (data from from Bern-Zollikofen at ca. 3 km distance, MeteoSwiss, 2017). July is the warmest month with a mean temperature of 18.6 °C. The wettest months are May–August with more than 100 mm of rainfall per month (MeteoSwiss, 2017).

Alnus glutinosa and *Fraxinus excelsior* form fragmented stands along the lake shore, whereas mixed *Fagus sylvatica* forests are dominant on the more elevated surrounding hills. The remaining and rather flat areas are either intensively used for agriculture or covered by settlements and infrastructure. The earliest archaeological findings around the lake date back to the Magdalenien and the Upper Palaeolithic ca. 15,950–14,750 cal BP (14,000–12,800 cal BC). At that time, two reindeer hunter camps (Moosbühl I and II) were located at the former lake shore (Bullinger et al., 1997; Harb, 2017; Nielsen, 2018, Fig. 1b). Many finds, including preserved lake-shore villages, are known from the Neolithic from ca. 6450 cal BP on (4500 cal BC), impressively documenting the strong prehistoric human activities in the region (Hafner et al., 2012; Harb, 2017, Fig. 1b). The following Bronze Age and Early Iron Age is represented with scattered artifacts and grave mounds in the proximity of the lake (Harb, 2017). In the Bern area the first urban centre~~er~~ was the oppidum Brenodor, which was built during the Late Iron Age or La Tène period (Ebnöther and Wyss, 2004). It persisted during the Roman Age as vicus Brenodurum. The Iron Age and Roman ruins (e.g. fortifications, bath, amphitheatre) are still visible in the town on the Enge peninsula at 5 km distance from Moossee (Ebnöther and Wyss, 2004). Finally, the medieval city centre~~er~~, which is part of the UNESCO World Heritage "Old City of Bern", was founded in 1191 AD around the Nydegg castle that already existed before (Hofer and Meyer, 1991).

3 Materials and methods

3.1 Coring and chronology

Six parallel sediment cores were retrieved at 19 m water depth with a~~n~~ UWITEC piston corer in the eastern part of the lake. Three cores (Moos A–C, core diameter: 60 mm, core length: 300 cm) reached coring depths of ca. 17.5 m. For the other three cores (Moos F–H, core diameter: 90 mm, core length: 200 cm), due to higher friction it was only possible to recover the uppermost 7 m. A master sequence with a total length of 16.44 m was defined using the Moos F–H cores for the uppermost 7 m and the Moos A–C cores for the remaining part. The sediment material below 13.5 m was not analyzed due to frequent sand layers in the lowermost part resulting in very low pollen concentrations.~~,~~

The chronology is based on 62 radiocarbon dates on terrestrial plant macrofossils and the Laacher See Tephra (LST; see Table 1). The radiocarbon content of terrestrial plant remains was measured at the ~~Laboratory for Radiocarbon Analysis (~~LARA laboratory ~~)~~ at the University of Bern using accelerator mass spectrometry (AMS, see Szidat et al., 2014). From 435–691 cm, additional varve counts were applied to refine the chronology. Here, the program OxCal 4.3 (V-sequence, Bronk Ramsey, 1994, 1995, 2001; Bronk Ramsey et al., 2001) and the IntCal13 calibration curve (Reimer et al., 2013) were used to estimate the age-depth model and its 95 % (2σ) probabilities (partly published, see Rey et al., 2019b). For the remaining part (0–435 cm and 691–1335 cm), a smooth-spline curve (smoothing level = 0.3) was calculated with the program clam 2.2 (Blaauw, 2010) to assess the final age-depth model (Fig. 2). The modelled curve runs within the 95 % (2σ) probabilities of the calibrated radiocarbon ages and the 2σ confidence envelope of a generalized mixed-effect regression (GAM, Heegaard et al., 2005).

3.2 Pollen, non-pollen palynomorphs and charcoal analysis

A total of 514 samples for pollen and microscopic charcoal analyses were taken from the sediment core from 1296 cm to the top. The standard sampling was 1 cm^3 every 10 cm. A higher resolution was implemented for the Oldest Dryas (18,800–14,700 cal BP) and for the Neolithic–Mid Bronze Age (7400–3200 cal BP, see Rey et al., 2019a). All palynological samples were treated with HCl, KOH, HF, acetolysis, sieved with a mesh size of 0.5 mm and mounted in glycerine following standard approaches (Moore et al., 1991). *Lycopodium* tablets (University of Lund batch no. 1031 with 20,848 ± 3457 spores per tablet) were added before the chemical treatment to estimate~~assess~~ microfossil concentrations (Stockmarr, 1971). Pollen, spores and non-pollen palynomorphs (NPPs) were identified under a light microscope at 400× magnification using palynological keys (Moore et al., 1991; Beug, 2004), photo atlases (Reille, 1992) and the reference collection at the Institute of Plant Sciences (University of Bern). *Betula nana* and tree *Betula* pollen grains were separated following Birks (1968) and Clegg et al. (2005). Cerealia-type pollen was identified according to size, pore diameter and annulus thickness (see Beug, 2004).

Pollen and spores were used to infer extra-local to regional vegetation dynamics (Conedera et al., 2006). A minimum pollen sum of 500 terrestrial pollen grains per sample was counted. For the lowest part of the sediment core, the minimum pollen sum was > 100 terrestrial pollen grains. *Sporormiella* and *Cercophora* (coprophilous fungal spores, see e.g. van Geel et al., 2003) was used as a proxy for grazing activities of herbivores (e.g. Gill et al., 2013; Rey et al., 2017) and livestock farming (e.g. Rey et al., 2013; Schwörer et al., 2015). The pollen and NPP results are presented in percentages of the terrestrial pollen sum excluding *Cannabis sativa* pollen (due to artificial pollen input by hemp retting, see Ranalli and Venturi, 2004) and pollen of aquatic plants (Fig. 3~~4~~).

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We used microscopic charcoal as a proxy for regional fire activity (Tinner et al., 1998; Adolf et al., 2018). Particles > 10 µm and < 500 µm were analyzed and counted on the pollen slides following Tinner and Hu (2003) and Finsinger and Tinner (2005). The data are presented as microscopic charcoal influx values (particles cm^{-2} yr^{-1}, Fig. 3~~4~~). Local pollen assemblage zones (LPAZ) were identified using optimal sum-of-squares partitioning (Birks and Gordon, 1985), while statistically significant zones were determined following the broken-stick method (Bennett, 1996). All calculations were run with the program R statistics (R Development Core Team, 2018). The data were~~as~~ plotted with the use of the programs Tilia 2.0.60 and CorelDraw.

3.3 Biodiversity estimations and ordination analysis

We first applied rarefaction analysis to calculate palynological richness (PRI), which is frequently used as a proxy for local to regional species richness (e.g. Birks and Line, 1992; Odgaard, 1999; Schwörer et al., 2015; Birks et al., 2016; Rey et al., 2019a). Rarefaction analysis assesses the number of taxa per sample after setting a constant minimum terrestrial pollen sum (Birks and Line, 1992), which was 116 in our case. Subsequently, the probability of interspecific encounter (PIE, Hurlbert, 1971) was taken as a measure of palynological evenness (van der Knaap, 2009). To assess distortion biases related to pollen production and dispersal on PRI (e.g. through high-pollen producers such as *Pinus sylvestris*, *Corylus avellana*), evenness-detrended palynological richness (DE-PRI) was calculated (see Colombaroli and Tinner, 2013). The aim of this procedure is to remove the evenness trend from PRI by applying an ordinary least square regression (OLS) between PRI and PIE and adding the deriving residuals (PRI - PIE) to the original PRI values (residuals + PRI). Only if PRI and DE-PRI indicate comparable trends and changes, we suppose that PRI is uninfluenced by evenness effects and thus primarily reflects species richness. The program R statistics (R Development Core Team, 2018) was applied for the calculations.

We used ordination analysis (Birks and Gordon, 1985; Ter Braak and Prentice, 1988) to identify gradients in vegetation composition over time using the program Canoco 5 (Šmilauer and Lepš, 2014). We first performed a detrended correspondence analysis (DCA, Birks and Gordon, 1985) by segments without down-weighting of rare species to assess the appropriate response model (i.e. unimodal vs. linear) for our pollen percentage data. Since there is important turnover in the species composition as indicated by the rather long gradient length of the first DCA axis (3.41 SD), we retained the unimodal response model (DCA, Šmilauer and Lepš, 2014).

4 Results and interpretation

4.1 Lithology and sedimentation

The lowermost part of the sediment sequence (1644–1300 cm, 19~~8~~,0~~9~~00 cal BP and older), which was not analyzed for pollen and microscopic charcoal, consists of clay and sand layers. From 1300 cm (19~~8~~,0~~9~~00 cal BP) upward, the sediment content changes to silty clay without sand layers until 980.5 cm (14,400 cal BP). According to the age-depth model (Fig. 2), the sedimentation rate is steadily decreasing at the same time, suggesting the establishment of relatively stable soil conditions shortly after deglaciation. From 980.5 cm (14,400 cal BP) to the top, the sediment consists of calcite-rich fine detritus gyttja. Between 712–429 cm (7550–2650 cal BP, see Rey et al., 2019a, b) the sediment is continuously varved. Some additional partly laminated sections are present at 980.5–768 cm (14,400–8900 cal BP) and at 415−134 cm (2350–300 cal BP). The sedimentation rate becomes rather stable from 980.5 cm (14,400 cal BP) onward and stays more or less constant until 429 cm (2650 cal BP). This stabilization is probably linked to forests growing in the catchment reducing the total erosional input. The uppermost 429 cm (2650 cal BP to the present) are characterized by a steep increase of the sedimentation rate, which is most likely related to increased erosion in response to forest openings and agricultural activities in the catchment of the lake.

4.2 Vegetation and fire history

The pollen sequence (Fig. 3) is subdivided into 21 local pollen assemblage zones (LPAZ) and five subzones (Moos-1a, 1b, 20a, 20b and 20c). The high number of statistically significant zones, especially in the upper part of the diagram (i.e. at 7300–2900 cal BP) is related to the exceptionally high sample resolution and the rather strong vegetation changes. For simplification and better comparison of the LPAZ, we added important climatic breaks (1–5) that are either related to temperature changes (breaks 1–4, see compilation of chironomid-based July air temperature estimate since the LGM in Finsinger et al. (2019) or increases of moisture availability (break 4, e.g. Tinner and Lotter, 2001; Joannin et al., 2013). This climate synopsis allows for the first time a tentative regional assessment and discussion of climate amplitude variation and its impacts on vegetation for the past 19,000~~19,200~~ years.

Herbaceous pollen grains from Poaceae, *Artemisia*, *Helianthemum*, *Thalictrum*, Chenopodiaceae, Rubiaceae and *Saxifraga aizoides*-type are dominant at the end of the LGM (climatic break 1, ca. 19,000~~19,200~~–18,800 cal BP, LPAZ Moos 1a, Finsinger et al. 2019). This indicates the establishment of open steppe/ tundra vegetation in the region including some first pioneer dwarf shrubs such as *Salix herbacea* (macrofossils found, see Table 1), ~~*Betula nana* and *Juniperus*~~ quickly after deglaciation~~ (not later than 19,200 cal BP as indicated by the oldest radiocarbon date in Table 1)~~. The slightly increased pollen percentages of *Pinus sylvestris*-type (up to 18 %) and single grains of *Abies alba* and *Picea abies* might point to reworking processes and/ or long-distance transport. High values~~percentages~~ of *Sporormiella* (percentages up to 6 %, influx up to 35 spores cm^{-2} yr^{-1}, see Fig. 4) as a proxy for local grazing (van Geel, 2006) may be indicative of the presence of Pleistocene megafauna such as *Mammuthus primigenius* (wolly mammoth), *Coelodonta antiquitatis* (wolly rhinoceros), *Rangifer tarandus* (reindeer) and others that were preferentially living in the cold steppe environment at that time (e.g. Nielsen, 2013). Charcoal influx values are extremely low (< 50 particles cm^{-2} yr^{-1}), suggesting rare or almost no fire activity in the region due to scarce vegetation cover.

From 18,800–16,000 cal BP (between climatic breaks 1 and 2, LPAZ Moos-1a), the pollen record indicates that an open, species-rich (see *Gypsophila repens*-type and *Rumex acetosa*-type pollen curves), herb dominated steppe tundra persisted around Moossee. A first slight increase of shrub pollen percentages (from 7 to 14 %) mainly from *Betula nana*, *Salix*, *Juniperus* and *Ephedra fragilis*-type suggest that patches of dwarf shrubs established in the region after 17,000 cal BP. This is underlined by findings of *Betula nana* remains (see Table 1). *Sporormiella* values~~percentages~~ remain high (at 1–5 % respectively around 20 spores cm^{-2} yr^{-1}) and *Cercophora* values peak (at 2.5 % respectively 20 spores cm^{-2} yr^{-1}, see Fig. 4), pointing to prevalence of wild animals grazing at the lake. Charcoal influx values stay low (10–40 particles cm^{-2} yr^{-1}), suggesting that regional fires were still absent.

Pollen percentages of tree *Betula* are markedly increasing (values up to 21 %) after the end of HE-1 (climatic break 2) during LPAZ Moos-1b (16,000–14,600 cal BP), suggesting the regional establishment of tree *Betula* stands or woods. Shrub pollen percentages (i.e. *Betula nana*, *Ephedra fragilis*-type, *Salix*, *Juniperus* and *Hippophaë rhamnoides*) stay at 12–20 %, whereas non-arboreal pollen (= NAP) values decrease but remain very high (55–75 %, see pollen percentages of *Artemisia*, *Heliathemum*, *Thalictrum* and Chenopodiaceae). This change points to an expansion of shrub tundra with *Betula nana*, *Salix*, *Juniperus* and maybe even some small growing *Betula* trees into the catchment of Moossee and is possibly related to climate warming after 16,200 cal BP (Samartin et al., 2012; Finsinger et al., 2019). The values of *Sporormiella* and *Cercophora* diminish and fade out at the same time, suggesting that some of the megaherbivores producing a lot of dung (e.g. *Mammuthus primigenius*) may have become extinct locally (see Nielsen, 2013; Cupillard et al., 2015). Charcoal influx prevail at low values (< 40 particles cm^{-2} yr^{-1}), indicating that despite higher total biomass and fuel availability, regional fire activity did not increase.

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Pollen data suggest that at the onset of the Bølling warming at ca. 14,700 cal BP (climatic break 3; van Raden et al., 2013; Finsinger et al., 2019), juniper shrub thickets or woods expanded (*Juniperus* pollen percentages > 65 %) and other woody taxa (peaks of *Hippophaë rhamnoides* and *Salix* pollen), leading to~~releasing~~ the gradual replacement of shrub and steppe tundra by boreal birch-pine forests (LPAZ Moos-2, ca. 14,600–14,400 cal BP, Fig. 3). Mixed *Juniperus* shrublands persisted for the subsequent 150–200 years until the onset of a marked expansion of tree *Betula* (pollen > 60 %), suggesting the establishment of birch forests around Moossee (ca. 14,400–13,750 cal BP, LPAZ Moos-3). This birch forest expansion resulted in~~released~~ an essential change in lithology (see Sect. 4.1). Subsequently, pollen of *Pinus sylvestris*-type steadily increases, suggesting the establishment of birch-pine forest around the lake (LPAZ Moos-4, 13,750–11,050 cal BP). These boreal forests prevailed through the Allerød warm period (13,900–12,900 cal BP, van Raden et al., 2013), the subsequent Younger Dryas (12,700–11,700 cal BP, Finsinger et al., 2019) and ~~the~~ during the first centuries of the Holocene, as suggested by the pollen assemblages. However, the dominance of *Pinus sylvestris*-type and the decrease of *Betula* pollen after 12,900 cal BP, followed by an increase of herb pollen (≤ 20 %, see Poaceae, *Artemisia*) and *Juniperus* pollen (2–3 %), points to a transformation of closed mixed boreal forests into more open, pine-dominated parklands. We interpret this change as a consequence of climate cooling during the Younger Dryas. *Sporormiella* fungal spores are only occurring sporadically which might indicate a low grazing activity in the close vicinity of the lake. Charcoal influx values increase temporarily (> 1000 particles cm^{-2} yr^{-1}) at the onset of mixed birch-pine forest formation and remain at elevated but stable values (> 100 particles cm^{-2} yr^{-1}), suggesting slightly enhanced fire activity after 13,400 cal BP.

The re-establishment of closed mixed birch-pine forests occurred shortly after the onset of the Holocene (climate break 4, ca. 11,700 cal BP, Finsinger et al., 2019) as indicated by the increase of arboreal pollen (> 80 %). Continuous curves of *Quercus*, *Alnus glutinosa*-type, *Corylus avellana* and *Ulmus* pollen suggest the presence of first temperate forest stands likely in response to the Holocene climate warming already at ca. 11,700–11,500 cal BP. However, temperate trees and shrubs (i.e. *Quercus*, *Corylus avellana*, *Ulmus*, *Tilia*, *Acer* and *Hedera helix*) expanded only after ca. 11,100 cal BP (LPAZ Moos-5, 11,050–8600 cal BP) as indicated by the pollen percentages, replacing the boreal forests within ca. 200–400 years (decrease of tree *Betula* and *Pinus sylvestris*-type pollen). This continental open forest and shrub vegetation was advantaged by the continental climate with hot and dry summers of the Early Holocene (Tinner and Lotter, 2001; Heiri et al., 2015). However, at 9000–8600 cal BP, *Fraxinus excelsior* pollen percentages increase and tree pollen indicative of mixed oak forests (*Quercus*, *Ulmus*, *Tilia*, *Acer* and *Fraxinus excelsior*, e.g. Welten, 1982) reach their highest values. Charcoal influx values remain low (Fig. 3), suggesting no significant increase of fire activity during the Early Holocene.

During LPAZ Moos-6 (8600–7250 cal BP), *Corylus avellana* declined, and less heliophilous trees such as *Fraxinus excelsior* and *Tilia* expanded. Likely in response to climate change around 8200 cal BP (climatic break 5, onset of mid Holocene), *Abies alba* and *Fagus sylvatica* pollen reach their empirical limit (i.e. continuous curves at 8400 and 8200 cal BP respectively), suggesting the local establishment of first stands of these tree species (Birks and Tinner, 2016). At the same time, *Alnus glutinosa*-type pollen percentages are steadily increasing, whereas percentages values of mixed oak forest and *Corylus avellana* start to decline. The pollen assemblages suggest that the decline of heliophilous deciduous forests continued after 7250 cal BP (LPAZ Moos-7 to 8, 7250–6400 cal BP), when mixed beech–silver fir forests expanded massively. The general prevalence of mesophilous tree species throughout LPAZ Moos-7 to LPAZ Moos-21 was likely caused by a gradual shift towards more oceanic climate conditions during the Mid–Late Holocene (Tinner and Lotter 2001, 2006), as e.g. reconstructed on the basis of higher lake levels (Magny, 2013; Joannin et al., 2013). However, this long-term dominance of dark mesophilous mixed beech–silver fir forests and the replacement of the formerly widespread mixed oak–linden–elm–maple forests was also affected by agricultural activities, starting as early as 7000 cal BP (5050 cal BC, first pollen grains of cultural indicators such as Cerealia-type and *Plantago lanceolata*).

The pollen stratigraphy indicates a stepwise intensification of land use over the millennia with NAP (including cultural indicator pollen) peaking at 5600 cal BP (3650 cal BC, LPAZ Moos-10, Neolithic), 3850 cal BP (1900 cal BC, LPAZ Moos-16, Early Bronze Age), 3500 cal BP (1550 cal BC, LPAZ Moos-18, Middle Bronze Age), 2600 cal BP (650 cal BC, LPAZ Moos 20b, Iron Age), 1800 cal BP (cal AD 150, LPAZ Moos 20b, Roman Period), 700 cal BP (cal AD 1250, LPAZ Moos 21, Middle Ages) as well as 200 cal BP (cal AD 1750, LPAZ Moos 21, Modern times). Each of these land-~~–~~use phases were generally accompanied by a decrease of tree pollen percentages of late successional *Fagus sylvatica* and *Abies alba* and by the expansion of light-demanding pioneers such as *Betula* trees and *Corylus avellana* shrubs. Mixed beech forests were able to recover after disturbances as suggested by the cyclical shape of the *Fagus sylvatica* curve. However, less resilient trees such as *Tilia*, *Ulmus*, *Taxus baccata* and the liana *Hedera helix* could not cope with the repeated forest disruptions mainly through logging, browsing, pollarding and massively increased fire disturbance (see Rey et al., 2019a for more details) and were strongly reduced or even disappeared after 4500 to 3500 cal BP (2550-1550 cal BC).

Most striking are the massive forest openings during the Iron Age/ Roman Period (> 30 % NAP, LPAZ Moos 20b, 2600–1600 cal BP (650 cal BC – cal AD 350)) and from the Middle Ages onward (> 60 % NAP, LPAZ Moos 21, 1050 cal BP (cal AD 900) – today) which we interpret as the influence of large settlements or urban centres~~ers~~ within close proximity (< 8 km) of the lake. The related strong increases of *Quercus* pollen percentages might point to forest management favouring oak for construction and forest pasture (acorn feeding, e.g. Gobet et al., 2000; Wick, 2015). Sporadic *Sporormiella* fungal spores suggest pastoral farming close to the lake. Charcoal influx values generally follow the land-~~–~~use phases showing two major peaks at 5600 cal BP (3650 cal BC) and 700 cal BP (cal AD 1250), pointing to two phases of highest fire activity during the past ~~19,200~~19,000 years (with up to 26,000 particles cm^{-2} yr^{-1}). The close link to pollen of crops and weeds as well as the related declines of forests, suggest that anthropogenic burning was related to slash-and-burn activities or maintenance of open fields (Tinner et al., 2005).

4.3 Biodiversity reconstruction and ordination

PRI (palnyological richness) and DE-PRI (eveness-detrended palynological richness) are very similar suggesting that overall, PRI is likely unaffected by evenness effects (Fig. 3). The agreement is particularly good during the periods 18,900–14,500 cal BP and 8600 cal BP to present. Here, both PRI and DE-PRI are slightly fluctuating around 15 pollen types per sample. Palynological evenness as inferred from PIE is stable (PIE at 0.8−0.9) in phases where PRI and DE-PRI are in agreement. Significantly lower values (PIE down to 0.5) are recorded from 14,500–8600 cal BP when pollen grains from few taxa are dominant (either *Juniperus*, *Betula*, *Pinus sylvestris*-type or *Corylus avellana*). There, palynological richness drops (PRI < 10 pollen types per sample) whereas DE-PRI stays stable at around 15 pollen types per sample. We thus assume that evenness distortions lead to underestimations of species richness during the period of strong *Juniperus*, *Betula*, *Pinus* (ca. 14,500–11,100 cal BP) and *Corylus* dominance (10,800–9000 cal BP, Fig. 3) and that such evenness distortions can be corrected by considering DE-PRI.

Both richness values (PRI, DE-PRI) generally increase (up to 20–25 pollen types per sample) during phases with higher human impact around 5650 cal BP (3700 cal BC), at 4650 cal BP (2700 cal BC), around 3850 cal BP (1900 cal BC) and 3500 cal BP (1550 cal BC) as well as after 2600 cal BP (650 cal BC). These increases are directly linked to human induced forest openings and the introduction of cultivated plants (e.g. Cerealia-type) as well as the expansion of weeds (e.g. *Plantago lanceolata*), apophytes (e.g. *Urtica*) and heliophilous shrubs (e.g. *Corylus avellana*). Interestingly, also the tundra phase (18,900–14,600 cal BP) was rather species rich suggesting that PRI and DE-PRI are correlated with openness. A rather low share (25.6 %) of the total pollen data variance is explained by DCA axis 1. Nevertheless, the DCA scores might indicate a signal of openness as the DCA axis 1 goes almost in line with the arboreal pollen (AP), ~~and~~ Poaceae percentages and DE-PRI (Fig. 3).

5 Discussion

5.1 ~~Climate-driven deglaciation and v~~Vegetation and fire dynamics from the last deglaciation ~~Oldest Dryas~~ to the Mid Holocene

The extent of the ice sheet around the Alpine arch during the LGM has been thoroughly studied in the past and the results are available as high-quality maps (e.g. Ehlers and Gibbard, 2004, see Fig. 1a). Radiocarbon dates on terrestrial plant remains preserved in the bottom part of lake sediment sequences can be used to track the onset of deglaciation (Wirsig et al., 2016; Rey et al., 2017). At Moossee, the earliest date gives a calibrated age of 19,200 cal BP (Table 1), which is well in line with the results from other ~~lowland~~ locations around the Alps (Table 2). The unpublished basal dates of Lago di Monate (lab. code BE-8023.1.1) and Gola di Lago (lab. code BE-12286.1.1) derive~~s~~ from ~~a~~ new lake sediment cores that are~~is~~ currently under investigation. Interestingly, most of the sites (including Moossee) with calibrated ages older than 18,000 cal years were located rather close to the margin of the former ice sheet (Fig. 1a, Table 2) and below < 500 m of ice (Bini et al., 2009). In contrast, sites with younger radiocarbon ages (17,270–17,820~~770~~ cal BP, e.g. Lotter and Zbinden, 1989; Tinner et al., 1999; Ravazzi et al., 2014) were ~~generally~~ either situated below a thicker ice sheet (750–1000 m) or higher up (Gola di Lago: ca. 970 m a.s.l.) and generally further away from the glacier tongues. However, the relatively small age difference between all these sites suggests that the collapse of the ice sheet in the peri-alpine belt ~~lowlands south and north of the Alps~~ occurred within 1000–1500 years, starting not later than 19,300 cal BP at the end of the LGM (23,000–19,000 cal BP for the Alps, Kaltenrieder et al., 2009; Hughes et al., 2013; Samartin et al., 2016). The huge loss of ice masses and the sudden retreat of glaciers were likely controlled by increasing summer insolation (Berger and Loutre, 1991) as well as constantly rising CO$_2$ and CH$_4$ concentrations in the atmosphere (Lourantou et al., 2010).

The pollen assemblage shows that pioneer plants colonized the bare grounds around Moossee shortly after glacial retreat (ca. 19,000 cal BP) to form quickly ~~form~~ open, species rich and herb-dominated steppe tundra communities (see biodiversity estimations and DCA in Fig. 3). First, arboreal plants (i.e. dwarf shrubs) could establish contemporaneously as indicated by a *Salix herbacea* leaf and *Betula nana* plant remains (see Table 1). Comparable vegetation patterns were found at several other sites ~~on the Swiss Plateau~~north of the Alps (e.g. Welten, 1982; Ammann, 1989; Hadorn, 1992; Duprat-Oualid et al., 2017), although only a few have radiocarbon-dated macrofossils of dwarf shrubs such as at Soppensee (*Dryas octopetala* leaves, Lotter, 1999, see Fig. 4), Wauwilermoos (twiglet of Ericaceae, Beckmann, 2004) and Burgäschisee (unidentified arboreal twiglets, Rey et al., 2017) older than 18,000 cal BP. South of the Alps, and close to the LGM refugia (Eastern Po Plain, Kaltenrieder et al., 2009), *Juniperus* shrublands spread on formerly glaciated areas above 400 m a.s.l. (e.g. Tinner et al., 1999, *Juniperus* stomata around 17,500 cal BP, high pollen values before 18,000 cal BP), possibly as a result of climate warming (+ 2.5–3 °C) around ca. 18,800 cal BP (Samartin et al., 2016; Finsinger et al., 2019). Post LGM climate warming may have also triggered tree species expansions south of the Alps at altitudes ≤ 350 m a.s.l. (*Larix decidua*, *Pinus* sp. and *Betula*) between 17,500–16,000 cal BP (see Finsinger et al., 2006; Monegato et al., 2007).

North of the Alps, a first important vegetation shift after the establishment of the steppe tundra occurred at ca. 16,000 cal BP with the expansion of shrub tundra around Moossee (see pollen of tree *Betula*, *Betula nana*, *Juniperus* and *Salix*, macrofossils of *Betula nana*). A similar vegetation shift has been recorded elsewhere in the Central European lowlands ~~on the Swiss Plateau~~ (Duprat-Oualid et al., 2017; Rey et al., 2017), pointing to a regional establishment of shrub tundra with ~~possibly~~ probably even some ~~first~~ tree birch stands. Plant macrofossil data from Soppensee (Lotter, 1999, see Fig. 4), suggest a coeval establishment of dwarf-~~–~~birch thickets on the Swiss Plateau, while several records of Welten (1982) point to increasing *Betula* abundances. Indeed, the chironomid-inferred July temperature estimates from Lago di Origlio (Samartin et al., 2012, corrected to the altitude of Moossee 521 m a.s.l. assuming a constant modern temperature rate of 6 °C km^{-1}, Livingstone and Lotter, 1998), indicate a July air temperature warming of 2–2.5 °C reaching temperatures of 10–11.5 °C that are suitable for tree growth (Lang 1994) after 16,000 cal BP, even after considering a latitudinal temperature gradient (see Figs. 4 and 5, Samartin et al., 2012; Finsinger et al., 2019). Other factors than summer temperatures such as cold air extrusions from the still existing Scandinavian ice sheet in the n~~N~~orth and a stronger latitudinal temperature gradient (Heiri et al. 2014) may have prevented the establishment of dense *Betula* forests north of the Alps (Rey et al., 2013). Indeed, south of the Alps, in more sheltered positions, wide~~-~~spread afforestation with *Pinus cembra* and *Larix decidua* started at around 16,500–16,000 cal BP (e.g. Tinner et al., 1999; Hofstetter et al., 2007; Vescovi et al. 2007; Pini et al., 2016, see Fig. 4~~5~~). South of the Alps, sites above 1000 m a.s.l. became ice-free but remained unforested (Vescovi et al., 2007; Pini, 2002), with treeline positions around 800–1000 m a.s.l.~~,~~ (Vescovi et al., 2007).

High and almost continuous abundances of coprophilous *Sporormiella* and *Cercophora* spores from the onset of the Moossee record until ca. 15,250 cal BP could be~~are~~ indicative of Pleistocene megaherbivores (e.g. *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Rangifer tarandus*). Similar results are recorded at Burgäschisee (Rey et al., 2017, see Fig. 4~~5~~) and fit well with numerous finds of remains of these animals (e.g. bones, tusks, antlers) in the region (Nielsen, 2013; Cupillard et al., 2015). On-site h~~H~~unter camps located at the former lake shore of Moossee (Fig. 1b), dated to 16,950–14,750 cal BP (14,000–12,800 cal BC, Harb, 2017; Nielsen, 2018), suggest intense hunting. Hunting combined with climate warming may have caused the regional extinctions of *Mammuthus primigenius*, *Coelodonta antiquitatis*~~,~~ and *Rangifer tarandus* during the Late Glacial (see Nielsen, 2013; Cupillard et al., 2015), as also evidenced by decreasing numbers dung spores after 15,500~~16,000~~ cal BP (Fig. 4).

Juniper shrublands expanded massively at Moossee after ca. 14,600 cal BP (onset of the Bølling) which is in agreement with the well-dated pollen record at Gerzensee (van Raden et al., 2013). Only ca. 200 years later, *Betula* forests took over and completed the initial afforestation which is widely recorded in pollen assemblages across the Swiss Plateau (e.g. Ammann, 1989; Rey et al., 2017) and unambiguously confirmed by *Betula pubescens* and *B.~~etula~~ pendula* macroremains at Soppensee (Lotter, 1999, see Fig. 4). Contemporaneously, sites up to 1800 m a.s.l. in the Alps turned ice-free (Welten, 1982; Ilyashuk, et al., 2009). South of the Alps, dense

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boreal forests with *Pinus sylvestris* and *Betula* established in the lowlands (Vescovi et al., 2007) and the tree line reached at least 1850 m a.s.l. (Tinner and Vescovi, 2007, Marta et al., 2013). This rapid deglaciation in the Alps and the forest expansion in Southern and Central Europe was caused by a sudden ca. 4 °C warming, as indicated by chironomid and stable isotope records (von Grafenstein et al., 1998, 1999; North Greenland Ice Core Project members, 2004; Heiri and Millet, 2005; Larocque and Finsinger, 2008; Fleitmann et al., 2009, see Fig. 5).

After ca. 13,600 cal BP (during the Allerød) mixed birch–pine forests were spreading at Moossee and all across Southern Central Europe (e.g. Clark et al., 1989; Lotter, 1999). In Northern Italy temperate tree stands established, probably in response to increasing summer temperatures (Vescovi et al., 2007, Lotter et al., 2012). The early spread of temperate trees south of the Alps (e.g. *Quercus*, *Tilia*, *Ulmus*) is evidenced by *Quercus* bud scales at Lago Piccolo di Avigliana (Finsinger et al., 2006) and Lago di Ragogna (Monegato et al., 2007). Summer warming (Heiri et al., 2015, see Fig. 5~~4~~) may also have triggered the increase of regional forest fires observed at Moossee and elsewhere north of the Alps (Rey et al., 2017).

Boreal forests prevailed around Moossee during the Younger Dryas cold period (ca. 12,600–11,700 cal BP), when a summer temperature cooling of ca. 2–4 °C north of the Alps (Lotter et al., 2000; Heiri et al., 2015; Finsinger et al., 2019, Fig. 5) initiated a recovery of cold steppe–tundra vegetation (e.g. *Artemisia*, Chenopodiaceae). At the same time, late successional pine trees increasingly outcompeted pioneer birch trees, forming open pine-dominated forests, a finding well supported by the macrofossil evidence (Lotter, 1999). Chironomid-based summer temperature reconstructions (Samartin et al., 2012; Heiri et al., 2014) suggest only a marginal cooling in southern Europe, which nevertheless affected temperate trees stands (Tinner et al., 1999; Finsinger et al., 2006; Vescovi et al., 2007). This different magnitude of climate cooling may be related to the sheltered location of these lakes in the lee of the Alps, preventing direct influences from the polar ice masses and the North Atlantic during the Younger Dryas (Samartin et al., 2012; Heiri et al., 2014).

After 11,700 cal BP at the onset of the Holocene, boreal forests became dense in the peri-alpine lowlands (Tinner et al., 1999; Rey et al., 2017). Chironomid-based July temperature estimates (Heiri et al., 2015; Finsinger et al., 2019), other biotic proxies (Lotter et al., 2000, Birks and Ammann, 2000) as well as oxygen isotope records (von Grafenstein et al., 1998, 1999; 2000; Schwander et al., 2000) suggest a sudden warming of 3–4 °C within only ca. 50 years (Tinner and Kaltenrieder, 2005). In response to this rapid and strong climate warming, stands of temperate trees (e.g. *Quercus*, *Alnus, Ulmus*) established north of the Alps at 11,600–11,100 (Fig. 3) to gradually replace the former mixed pine-birch forests shortly after 11,100 cal BP. By 10,500 cal BP mixed oak–linden–elm–maple forests prevailed. In the forelands of the southern Alps, first mixed oak–linden–elm stands had established already during the Late Glacial, so that the Early Holocene population expansions of temperate trees (e.g. *Quercus, Ulmus, Tilia*) were far more rapid and accomplished by ca. 11,500–11,300 cal BP (Tinner et al., 1999; Finsinger et al., 2006; Vescovi et al., 2007), i.e. 800–1000 years earlier than north of the Alps. This finding is in agreement with process-based dynamic vegetation simulations, which suggest that after a first establishment of boreal and temperate tree stands, population expansions usually last 500–1000 years before coming to a (high) biomass equilibrium with climate (Lotter and Kienast, 1992; Wick and Möhl, 2006; Henne et al., 2011; Schwörer et al., 2014).

The dominance of mixed oak–linden–elm–maple forests over millennia in Central Europe (see e.g. Hadorn, 1992; Lotter, 1999; Litt et al., 2009; Rey et al., 2017) was most likely favoured by continental climate as indicated by maximum summer and minimum winter insolation (Berger and Loutre, 1991), 1.5–2 °C warmer summers than today (e.g. Heiri et al., 2015) and generally drier conditions as reflected by lower lake levels (e.g.

Magny et al., 2012, see Fig. 5). This forest type persisted until ca. 8500–8000 cal BP (Figs. 3 and 5), when *Abies alba* and *Fagus sylvatica* tree stands established around Moossee. Both tree species are shade-tolerant and competitive under mesophytic conditions (Tinner and Lotter, 2006; Tinner et al., 2013; Lauber et al., 2014). Similarly, *Alnus* and *Fraxinus excelsior*, both well-adapted to wet soils and moist conditions (Lauber et al., 2014; Rey et al., 2017), expanded as well. The establishment and massive spread of mesophilous mixed beech forests after 7500 cal BP (see high number of *Fagus sylvatica* bud scales in Table 1) is well studied on the Swiss Plateau (e.g. Lotter, 1999; Wehrli et al., 2007) and the causes for this change have been intensely discussed in the past (Tinner and Lotter, 2006). Decreasing summer temperatures (Heiri et al., 2015; Finsinger et al., 2019) and increasing moisture availability (e.g. Magny et al., 2011; Magny et al., 2012; Joannin et al. 2013, see Fig. 5) suggest climate as the main trigger of this drastic change in Central European forest composition.

5.2 Vegetation and land-~~–~~use history during the Mid and Late Holocene

The onset of land use and agricultural activities around Moossee is documented as early as 7000 cal BP (5050 cal BC) by the first cultural indicator pollen such as Cerealia-type and *Plantago lanceolata* (see Figs. 3 and 5). Increases of microscopic charcoal, which fall~~s~~ into a phase with fairly closed mixed beech–oak forests (Figs. 3 and 5), suggest a drastic increase of fire activity at the onset of the farming. After 6500 cal BP (4550 cal BC) intensified agricultural activities caused a first dieback of the mixed beech forests. Our interpretation is in good agreement with coeval on-site archaeological evidence (e.g. log boat made of *Tilia* wood; Hafner et al., 2012; Harb, 2017). Many lowland sites south and north of the Alps indicate a contemporaneous opening of the forests. The strong link with increasing fire activities suggests that farmers used fire to gain arable and pastoral land (i.e. slash-and-burn, e.g. Tinner et al., 1999; Kleinmann et al., 2015; Rey et al., 2017, 2019a). Disruption and land-use phases generated typical successional cycles starting with arboreal pioneers (*Corylus avellana*, tree *Betula* and *Alnus*) rapidly spreading after disturbance. These light-demanding pioneers were regularly replaced by *Fraxinus excelsior* and *Ulmus*, which were in turn replaced by late-successional *Fagus sylvatica* and *Abies alba* (e.g. Kleinmann et al., 2015). Most strikingly, a recent high precision and high-resolution study was able to numerically demonstrate that land-~~–~~use phases and the subsequent forest successions were regionally to supra-regionally synchronous (Rey et al., 2019a). The most reasonable explanation for such a striking pattern is climate and its influences on human activities. Indeed, Rey et al. (2019a) found that land-~~–~~use phases generally coincided with warm and dry periods as indicated by lower lake levels in Western Switzerland and Eastern France (Magny, 2013) as well as higher solar irradiance (Steinhilber et al., 2009). This finding underlines that climate may have governed harvest success and through that prehistoric human population densities, an environmental effect that on the long-term was counteracted by stepwise introductions of technological innovations (e.g. metal tools, new crops; Tinner et al., 2003, Wirtz and Lemmen, 2003).

Our palaeobotanical data indicate a steady intensification of agricultural activities during the Late Holocene (from ca. 3850 cal BP (1900 cal BC) onward), which is primarily evidenced in regions on the Swiss Plateau that are climatically favourable for crop production (i.e. < 550 m a.s.l., Ammann, 1989; Hadorn, 1992; Rey et al., 2017). Many tree species were strongly affected by fire disturbance, browsing and/ or overexploitation and some of them (e.g. *Tilia*, *Taxus baccata*) even collapsed completely (Rey et al., 2017). Contrarily, several taxa such as *Quercus* and *Fagus* were promoted as fruit trees (Gobet et al., 2000; Wick, 2015), while others were introduced (e.g. *Juglans regia*, *Castanea sativa*) for the same reason (Tinner et al., 2003; Conedera et al., 2004). Thanks to the combined effects of open land creation and the introduction of new species, t~~T~~otal biodiversity increased

(Fig. 3), suggesting that human activities related to farming were crucial for the establishment of a mosaic of diverse communities (e.g. hay meadows, orchards, hedges).~~, thanks to the creation of large open habitats (Colombaroli and Tinner, 2013).~~ As a consequence, during the Late Holocene (i.e. the past 5000 years) humans gradually replaced climate as the driving factor of vegetation structure and composition. Woodlands increasingly impoverished, leading to~~, creating artificial communities (e.g.~~ monospecific *Picea*, *Quercus* or *Fagus* forest communities ~~forests, hedges, pastures, fields)~~ that are best suited for timber, fuel and fodder production~~land use~~. The strong increase of biodiversity in open habitats (meadows, fields, hedges) thus contrasted diversity losses in forests and woodlands (Colombaroli and Tinner, 2013). ~~However, w~~We can show that in regard to the dominant species, beech forests were able to recover even after the most intense anthropogenic disturbances (e.g. Iron Age, Roman Period, Middle Ages). Therefore, Central European beech may presumably prevail in the future if the amplitude of the anticipated climate warming remains within the Mid Holocene variability range (ca. + 2 °C compared to the 20th century, Heiri et al., 2015; Finsinger et al., 2019). However, if intense forestry should decline, e.g. as a consequence of nature protection measures, more diverse forests may re-establish. If climate should become > 2° C warmer, possibly causing a reduction of moisture availability (Kovats et al, 2014; Henne et al. 2018), drought-sensitive beech may rapidly decline, giving way to unprecedented forest communities that will likely include drought-~~–~~resistant deciduous species such as *Quercus pubescens*, drought-resistant evergreen broadleaved species such as *Quercus ilex* and warm-temperate conifers such as *Abies alba* (Bugmann et al., 2015; Henne et al., 2015; Henne et al., 2018).

6 Conclusions

We present a novel highly-resolved vegetation and fire history record from Central Europe that covers the entire post-LGM period. Radiocarbon dating on terrestrial plant remains (i.e. *Salix herbacea* leaf) resulted in a calibrated age of ca. 19,200 cal BP (18,890–19,520 cal BP, 95 % (2σ) probabilities) for the bottom of the sediment sequence. To our knowledge, together with the novel radiocarbon date from the bottom sediments of Lago di Monate of 19,300 cal BP (18,780–19,930 cal BP, 95 % (2σ) probabilities, see Table 2), this date provides the oldest age coming from peri-alpine lakes that were created by deglaciation after the ice collapse at the end of the LGM. Deglaciation was followed by the rapid establishment of pioneer steppe vegetation. After HE-1 (end ca. 16,700 cal BP, Stanford et al., 2011) shrubs (*Betula nana*~~, *Betula humilis*~~, *Juniperus*, *Salix*) and probably~~possibly~~ trees (likely *Betula pubescens*, *Betula pendula*) expanded, which is comparable to recent ecosystem changes in the Arctic in response to ongoing global warming (Pearson et al., 2013, Brugger et al., 2019). Starting points of important vegetation reorganizations at 16,000, 14,600, 11,600 and 8200 cal BP were strongly linked to climate change (temperature and/ or precipitation shifts). No apparent inertia nor lags of population establishments were detected, implying a very high sensitivity and adjustment capacity of plant communities to climatic and environmental changes at decadal scales. These rapid responses without any~~no~~ apparent lags (due to e.g. migration) are explained by the very efficient distribution mechanisms of plants (e.g. winged fruits or bird transport of acorns, see Firbas, 1949, Tinner and Lotter, 2006) and the proximity to the refugia (< 400 km) of temperate and boreal species (Kaltenrieder et al., 2009, Samartin et al., 2012, Gubler et al., 2018). The onset of varved sediments (7000 cal BP) was closely related to vegetation opening for land use. Land use gradually overrode climate as the dominant factor in determining vegetation composition and structure during the Late Holocene. Present-day beech forests have been shaped by anthropogenic disturbances over millennia and were resilient to Mid and Late Holocene climate change. However, recent climate warming may exceed the Mid and Late Holocene climate variability releasing sudden collapses and unprecedented reorganizations of Central European ecosystems.

Data availability

The complete pollen and microscopic charcoal data sets are~~will be~~ available through the Neotoma Palaeoecology Database (https://www.neotomadb.org). Pollen: http://dx.doi.org/10.21233/6N58-K786 (Rey et al., 2020a); Microscopic charcoal: http://dx.doi.org/10.21233/XD5R-PF83 (Rey et al., 2020b).~~ after acceptance of this paper. The data sets are currently processed in the database. However, there is a delay due to rearrangement of the database.~~

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Author contributions

F.R. carried out all pollen and most of the quantitative analyses, constructed the chronology, arranged all figures and led the writing. E.G. initially designed the research project and helped with interpreting the data sets. C.S. calculated the zonation and gave important scientific inputs. A.H. obtained funding and contributed with the discussion of local and regional archaeology. S.S. was responsible for radiocarbon dating. W.T. helped designing the research project, received funding and wrote major parts of the manuscript. All authors contributed and commended critically on the manuscript and gave final approval for publication.

Competing interests

The authors declare that they have no conflict of interest.

Acknowledgements

We thank Willi Tanner, Julia Rhiner, Sandra O. Brügger, Stéphanie Samartin, Lena Thöle and Petra Beffa for their valuable help during the corings, ~~Sönke Szidat and~~ Edith Vogel for executing the radiocarbon dating, André F. Lotter for his important inputs into the analysis of varved lake sediments, Stamatina Makri and Julian Laabs for helping with the maps, Werner E. Stöckli for providing the idea of gaining oldest bottom lake sediment dates, Adriano Boschetti and the Beyond Lake Villages (BeLaVi) project team for constructive discussions, Jacqueline van Leeuwen for double checking some pollen identifications and César Morales del Molino for his help with archiving the data sets. We are grateful to the editor Nathalie Combourieu-Nebout and two anonymous reviewers for their valuable comments on a previous version of the manuscript.

Financial support

This research study has been supported by the Swiss National Science Foundation (SNF 200021_149203/1).

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Table 1: Radiocarbon dates and calibrated ages from the Moossee record. Uncertainties of ^{14}C ages refer to 68 % probabilities (1σ) whereas ranges of calibrated and modelled ages represent 95 % probabilities (2σ).

Lab. code	Depth (cm)	^{14}C age (BP)[a]	Age range (cal BP)[b]	Modelled age range (cal BP)[c]	Material
BE-7363.1.1	78.6−75.9	150 ± 20	5~~0~~−280	-135−420	*Picea abies* needle
BE-7362.1.2	104.7−102.2	240 ± 70	5~~0~~−480	-230−700	Leaf indet
BE-7361.1.1	187.5−186.3	450 ± 20	495−525	475−545	Leaf fragments indet
BE-7360.1.1	241.6−239.8	1065 ± 20	930−1050	870−1110	*Alnus glutinosa* fruit
BE-7359.1.1	261.1−259.9	1110 ± 35	935−1170	820−1285	*Alnus glutinosa* fruit
BE-7358.1.1	324.4−321.1	1495 ± 40	1305−1520	1205−1620	*Betula* fruits, *Fagus sylvatica* bud scales
BE-7357.1.1	328.0−325.1	1535 ± 30	1360−1520	1270−1600	*Betula* fruits, *Fagus sylvatica* bud scales, *Salix* bud scale, bud scale indet
BE-7356.1.1	330.8−328.6	1555 ± 40	1360−1535	1285−1625	*Betula* fruit, *Fagus sylvatica* bud scale, *Populus tremula* floral bract
BE-7355.1.1	338.5−332.2	1620 ± 40	1410−1605	1320−1700	*Betula* fruits, *Fagus sylvatica* bud scale, *Populus tremula* floral bract, *Quercus* bud scales
BE-7354.1.1	346.9−339.8	1700 ± 40	1535−1705	1450−1785	*Betula* fruits, *Populus tremula* floral bract
BE-7353.1.1	386.5−385.9	2060 ± 35	1935−2120	1840−2215	Terrestrial fruit indet
BE-7352.1.1	416.2−409.3	2290 ± 50	2150−2400	2025−2525	*Betula* fruit, *Betula* fruits scales
BE-7351.1.1	435.0−432.7	2420 ± 35	2350−2700	2655−2705	*Fagus sylvatica* bud scales
BE-7350.1.1	439.0−438.1	2630 ± 50	2540−2860	2730−2775	*Betula* fruit, *Betula* fruit scale
BE-7349.1.1	441.4−439.7	2730 ± 35	2760−2920	2765−2810	*Abies alba* bud scale, *Fagus sylvatica* bud scales, terrestrial fruit indet
BE-7348.1.1	447.0−446.4	2795 ± 40	2790−2990	2875−2920	*Fagus sylvatica* bud scale
BE-7347.1.1	449.9−448.8	2810 ± 45	2790−3055	2910−2960	*Betula* fruit, *Fagus sylvatica* bud scales
BE-7346.1.1	453.0−452.5	2900 ± 45	2890−3170	2965−3020	Bud scale indet
BE-7345.1.1	461.1−460.0	3010 ± 40	3070−3340	3085−3135	*Abies alba* bud scale, *Alnus glutinosa* bud scale, *Betula* fruits, bud scale indet, petiole indet
BE-7344.1.1	468.3−466.9	3010 ± 40	3070−3340	3185−3240	*Alnus glutinosa* fruit, *Betula* fruits, *Populus tremula* floral bract
BE-7343.1.1	472.7−472.0	3070 ± 45	3165−3380	3245−3300	*Alnus glutinosa* bud scale
BE-7342.1.1	495.8−495.0	3245 ± 50	3375−3575	3490−3550	Leaf fragments indet
BE-7341.1.1	498.0−497.3	3315 ± 40	3455−3640	3520−3580	*Abies alba* bud scale, *Fagus sylvatica* bud scale
BE-7340.1.1	500.2−499.0	3295 ± 45	3405−3635	3555−3610	*Fagus sylvatica* bud scale, terrestrial fruit indet
BE-7339.1.1	502.9−501.3	3395 ± 40	3515−3820	3585−3650	*Abies alba* bud scale, *Betula* fruit, *Fagus sylvatica* bud scales, *Quercus* bud scale, bud scale indet, terrestrial fruit indet
BE-5380.1.1	520.2−519.5	3615 ± 35	3835−4070	3840−3885	*Alnus glutinosa* fruit, terrestrial plant remain indet
BE-5631.1.1	540.3−539.8	3765 ± 40	3985−4245	4065−4105	*Alnus glutinosa* fruit, leaf fragment indet
BE-5381.1.1	543.5−543.0	3710 ± 35	3930−4150	4110−4145	*Betula* fruit, *Fagus sylvatica* bud scales
BE-5632.1.1	548.4−547.7	3865 ± 40	4155−4415	4180−4220	*Fagus sylvatica* bud scales
BE-5382.1.1	553.1−552.4	3865 ± 35	4160−4415	4270−4305	*Fagus sylvatica* bud scales
BE-5383.1.1	569.8−569.2	4190 ± 35	4590−4840	4655−4685	*Abies alba* needle, *Fagus sylvatica* bud scale
BE-5633.1.1	572.4−571.6	4160 ± 40	4570−4830	4695−4720	*Alnus glutinosa* fruit, *Betula* fruit, *Fagus sylvatica* bud scale

Table 1: *(continued)*

Lab. code	Depth (cm)	^{14}C age (BP)[a]	Age range (cal BP)[b]	Modelled age range (cal BP)[c]	Material
BE-5384.1.1	578.7−578.3	4250 ± 20	4825−4855	4835−4860	*Populus tremula* floral bract, leaf fragments indet
BE-5385.1.1	604.6−604.0	4730 ± 20	5330−5580	5330−5360	*Alnus glutinosa* bud scale, *Alnus glutinosa* catkin, *Betula* fruits
BE-5634.1.1	606.3−605.8	4740 ± 40	5325−5585	5355−5385	*Alnus glutinosa* bud scale, *Alnus glutinosa* fruit
BE-5635.1.1	607.7−607.2	4690 ± 45	5315−5580	5395−5420	*Alnus glutinosa* bud scale, *Betula* fruit
BE-5636.1.1	612.0−611.5	4830 ± 70	5330−5720	5500−5530	*Betula* fruits, *Fagus sylvatica* bud scale
BE-5386.1.1	618.7−618.1	4970 ± 25	5615−5745	5640−5675	*Abies alba* seed, *Fagus sylvatica* bud scale, leaf fragments indet
BE-5387.1.1	624.2−623.6	5035 ± 40	5660−5900	5720−5755	*Abies alba* needle, *Abies alba* bud scale, petioles indet
BE-5388.1.1	625.9−625.2	5060 ± 35	5730−5905	5755−5790	*Alnus glutinosa* bud scale, *Betula* fruit, *Fagus sylvatica* bud scale, leaf fragments indet
BE-5637.1.1	630.8−630.3	5005 ± 50	5620−5895	5850−5885	*Betula* fruit, *Fagus sylvatica* bud scale
BE-5389.1.1	636.2−635.5	5235 ± 40	5915−6175	5965−6005	Petiole indet
BE-5638.1.1	641.3−640.8	5375 ± 40	6005−6280	6105−6140	*Alnus glutinosa* bud scale
BE-5390.1.1	646.2−645.5	5370 ± 60	6000−6285	6230−6270	*Fagus sylvatica* bud scale
BE-5639.1.1	652.7−652.1	5660 ± 45	6315−6550	6380−6420	*Fagus sylvatica* bud scales
BE-5391.1.1	656.2−655.8	5655 ± 25	6355−6495	6430−6475	*Fagus sylvatica* bud scale, bud scale indet, petioles indet
BE-5392.1.1	659.8−659.3	5760 ± 25	6490−6635	6495−6535	*Alnus glutinosa* catkin, *Alnus glutinosa* fruits
BE-5640.1.1	669.1−668.6	5875 ± 45	6565−6795	6625−6670	*Fagus sylvatica* bud scale
BE-5393.1.1	675.7−675.2	5940 ± 25	6680−6845	6740−6790	*Fagus sylvatica* bud scales, bud scales indet
BE-5394.1.1	678.3−677.8	5990 ± 40	6735−6940	6790−6845	*Fagus sylvatica* bud scale, leaf fragments indet
BE-5641.1.1	689.8−689.4	6135 ± 45	6910−7160	7010−7065	*Fagus sylvatica* bud scale, petiole indet
BE-5642.1.1	691.2−690.8	6210 ± 45	6995−7250	7035−7095	*Alnus glutinosa* fruit, *Tilia* anthers
BE-5395.1.1	767.0−765.0	7850 ± 110	8440−8990	8160−9270	Terrestrial fruit indet
BE-5396.1.1	798.0−796.0	8165 ± 25	9015−9245	8890−9370	*Tilia* fruit scale
BE-5397.1.1	867.0−865.0	9380 ± 30	10,520−10,690	10,440−10,805	*Pinus sylvestris* bud scale, *Populus tremula* floral bract, *Populus tremula* fruits, *Quercus* bud scale, *Ulmus* bud scale
BE-5398.1.1	883.0−881.0	9980 ± 60	11,250−11,710	10,960−11,890	*Betula* fruits, *Betula* fruit scales, *Pinus sylvestris* bud scales
	933.0−932.0		12,885−13,185[d]	12,740−13,350	Laacher See Tephra (LST)
BE-5399.1.1	949.0−947.0	11,675 ± 35	13,440−13,570	13,360−13,650	*Betula* fruits, *Betula* fruit scale, *Juniperus* needles
BE-5400.1.1	967.0−965.0	12,200 ± 70	13,810−14,350	13,520−14,600	*Betula* fruits, *Betula* fruit scale
BE-5401.1.1	983.0−981.0	12,350 ± 80	14,070−14,830	13,700−15,210	*Betula* fruits
BE-5402.1.1	1010.0−1008.0	12,720 ± 170	14,310−15,680	13,650−16,360	*Betula nana* leaf
BE-5403.1.1	1110.0−1105.0	14,000 ± 210	16,340−17,560	15,740−18,160	*Betula nana* fruit, *Betula nana* fruit scale, *Betula nana* leaf
BE-5404.1.1	1340.0−1335.0	15,900 ± 130	18,890−19,520	18,560−19,850	*Salix herbacea* leaf, rhizome indet

[a] Stuiver and Pollach, 1977

[b] Stuiver and Reimer, 1993; Reimer et al., 2013

[c] Bronk Ramsey, 1994, 1995, 2001; Bronk Ramsey et al., 2001; Heegaard et al., 2005

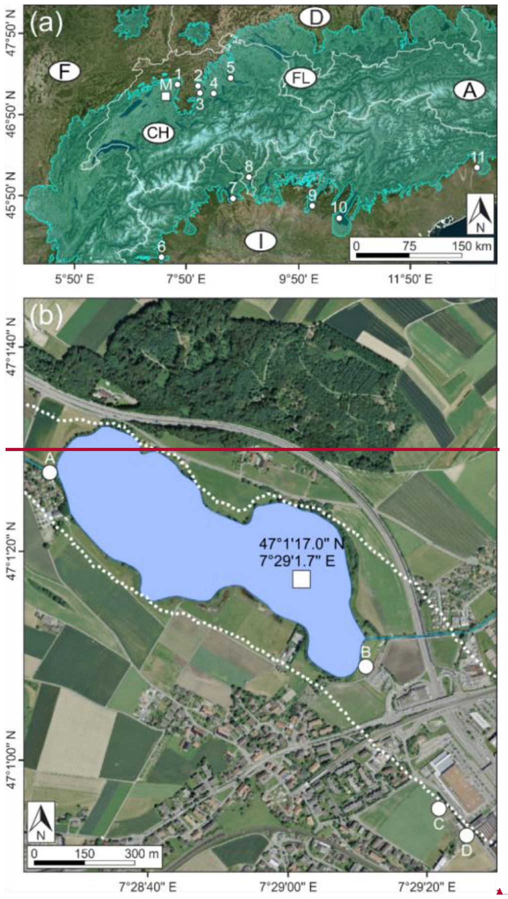
[d] van Raden et al., 2013

Table 2: Oldest radiocarbon dates from terrestrial plant remains found in sediment sequences from ~~lowland~~ lakes north and south of the Alps. Uncertainties of ^{14}C ages refer to 68% probabilities (1σ) whereas ranges of calibrated ages represent 95% probabilities (2σ).

Code (Fig. 1a)	Site name	Reference	^{14}C age (BP)[a]	Age (cal BP)[b]	Age range (cal BP)[b]	Material
M	Moossee	This issue	15,900 ± 130	19,180	18,890−19,520	*Salix herbacea* leaf, rhizome indet
1	Burgäschisee	Rey et al., 2017	15,380 ± 70	18,660	18,490−18,800	Twiglet indet
2	Wauwilermoos	Beckmann, 2004	15,300 ± 130	18,560	18,260−18,830	Ericaceae twig
3	Soppensee	Hajdas et al., 1993; Lotter, 1999	14,190 ± 120	17,270	16,900−17,620	Terrestrial plant remains indet
4	Rotsee	Lotter and Zbinden, 1989	14,600 ± 200	17,770	17,250−18,270	Terrestrial plant remains indet
5	Zürichsee	Lister, 1988	14,600 ± 250	17,760	17,110−18,370	Twiglet indet
6	Lago Piccolo di Avigliana	Larocque and Finsinger, 2008	14,930 ± 80	18,150	17,930−18,360	Wood indet
7	Lago di Monate	This issue	16,000 ± 250	19,310	18,780−19,930	Deciduous leaf fragments indet
8	Lago di Origlio	Tinner et al., 1999; Samartin et al., 2012	14,520 ± 80	17,700	17,480−17,930	Wood indet
9	Gola di Lago	This issue	14,640 ± 70	17,820	17,610−18,010	Deciduous leaf, twig fragments
10~~9~~	Lago d’Iseo	Lauterbach et al., 2012	14,950 ± 130	18,180	17,870−18,500	Terrestrial plant remains indet
11~~0~~	Lago di Garda	Ravazzi et al., 2014	14,350 ± 70	17,490	17,220−17,710	*Hippophaë* seed, leaf fragment indet
12~~1~~	Lago di Ragogna	Monegato et al., 2007	14,490 ± 130	17,660	17,310−17,980	*Larix* and *Pinus* remains

[a] Stuiver and Pollach, 1977

[b] Stuiver and Reimer, 1993; Reimer et al., 2013



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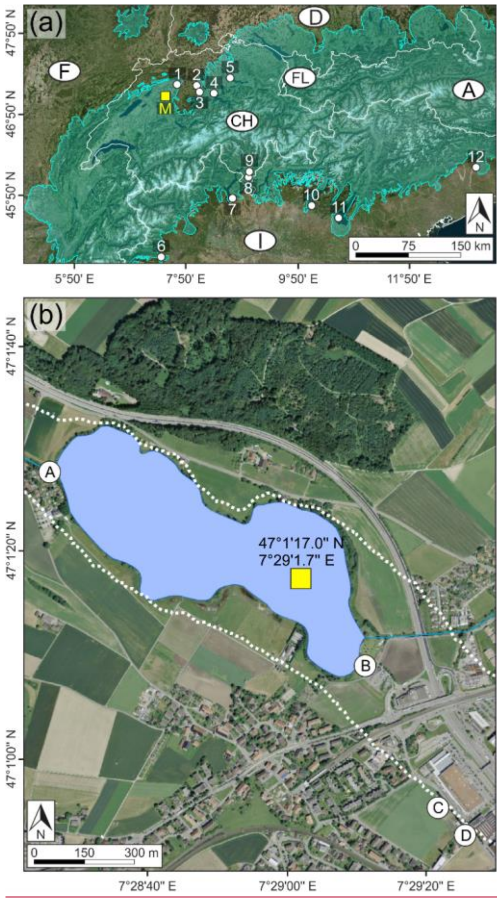

Figure 1: (a) Overview map of Switzerland (CH) and the neighbouring countries (white lines = national borders, source of the satellite image: Google Earth (modified)) including the glacier extent during the Last Glacial Maximum (LGM, light blue area; Ehlers and Gibbard, 2004), the study site Moossee (M, yellow box) and other discussed sites (white circles). 1 Burgäschisee (Rey et al., 2017); 2 Wauwilermoos (Beckmann, 2004); 3 Soppensee (Lotter, 1999); 4 Rotsee (Lotter and Zbinden, 1989); 5 Lake Zurich (Lister, 1988); 6 Lago Piccolo di Avigliana (Larocque and Finsinger, 2008); 7 Lago di Monate (this issue); 8 Lago di Origlio (Tinner et al., 1999); 9 Gola di Lago (this issue); 10~~9~~ Lago d'Iseo (Lauterbach et al., 2012); 11~~0~~ Lago di Garda (Ravazzi et al., 2014); 12~~1~~ Lago di Ragogna (Monegato et al., 2007). A = Austria, D = Germany, F = France, FL = Liechtenstein, I = Italy. (b) Detailed map of Moossee (blue area = present lake surface area, source of the aerial photograph: swisstopo (modified)), the extent of the former lake area (dotted white line; Harb, 2017), the coring coordinates (yellow~~white~~ box) and local archaeological sites (white circles; Harb, 2017). A Moossee West; B Moossee East; C Moosbühl II; D Moosbühl I.

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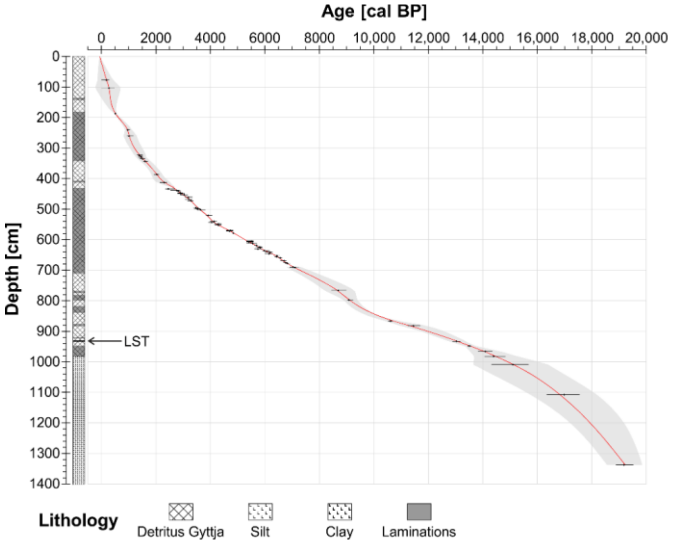


Figure 2. Age-depth model and lithology of Moossee. Black dots show the calibrated ages with 95 % (2σ) probabilities (IntCal13, Reimer et al., 2013). The red line is the modelled chronology using OxCal 4.3 from 435−691 cm (V-sequence, see Bronk Ramsey 1994, 1995, 2001; Bronk Ramsey et al., 2001) and clam 2.2 smooth spline at smoothing level = 0.3 from 0−435 cm and from 691−1335 cm (Blaauw, 2010). The 95 % (2σ) probabilities of the model (grey area) were calculated using again OxCal V-sequence (435−691 cm) and a generalized mixed-effect regression (GAM, 0−435 cm and 691−1335 cm, see Heegaard et al., 2005). LST = Laacher See Tephra (black line at 932−933 cm).

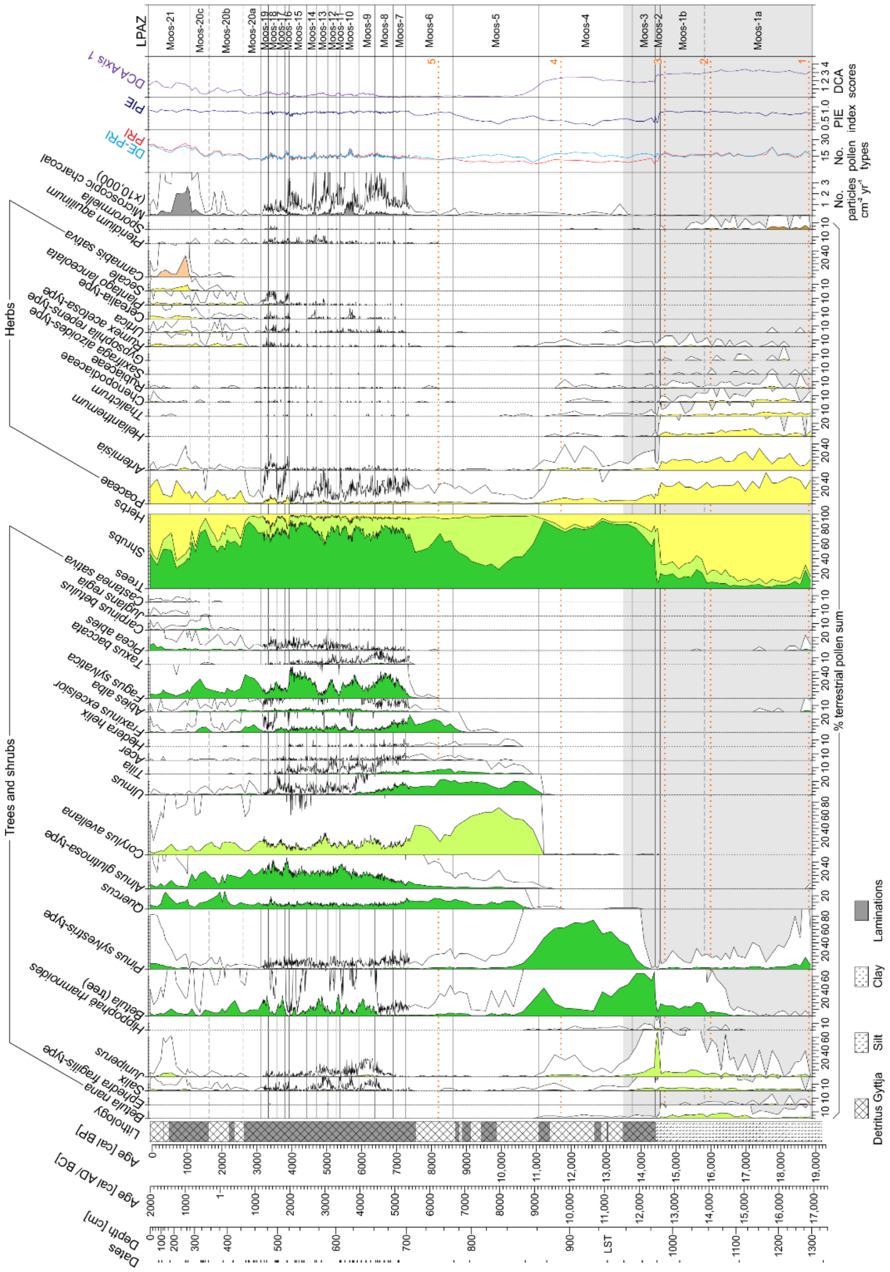
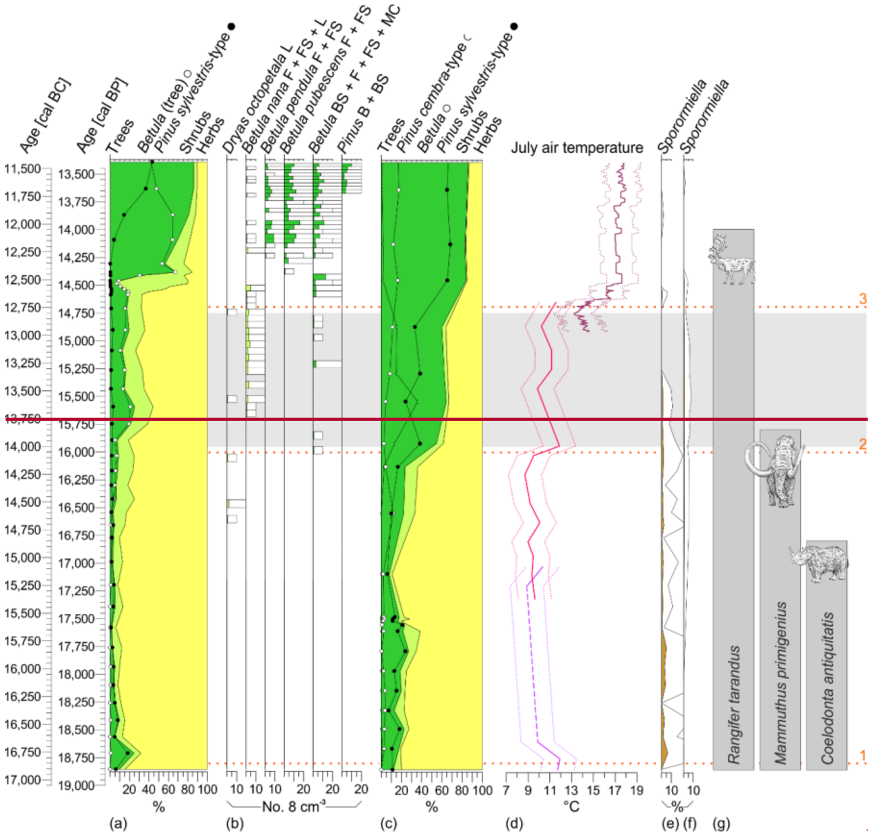


Figure 3. Moossee sediment sequence. Presented are the dates (small black lines), the lithology, percentages of selected pollen types, *Pteridium aquilinum* (fern spore) and *Sporormiella* (coprophilous fungal spore), microscopic charcoal influx values, the palynological richness (PRI, red line), the evenness-detrended palynological richness (DE-PRI, light blue line), the palynological evenness (PIE, dark blue line) as well as the detrended correspondence analysis (DCA, purple line). Empty curves show 10x exaggerations. LST = Laacher See Tephra. The horizontal light grey bar indicates the time window of Fig. 4. The orange horizontal dotted lines (1–5) mark important climatic breaks on the basis of temperature changes (see Finsinger et al., 2019) and/ or changing moisture availability.


Age [cal BC]
Age [cal BP]
Trees
Betula (tree) ○
Pinus sylvestris-type ●
Shrubs
Herbs
Dryas octopetala L
Betula nana F + FS + L
Betula pendula F + FS
Betula pubescens F + FS
Betula BS + F + FS + MC
Pinus B + BS
Trees
Pinus cembra-type ○
Betula ○
Pinus sylvestris-type ●
Shrubs
Herbs
July air temperature
Sporormiella
Sporormiella
11,500
11,750
12,000
12,250
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20 40 60 80 100
%
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No. 8 cm⁻³
20 40 60 80 100
%
7 9 11 13 15 17 19
°C
10 10
%
(a)
(b)
(c)
(d)
(e) (f)
(g)
3
2
1
Rangifer tarandus
Mammuthus primigenius
Coelodonta antiquitatis

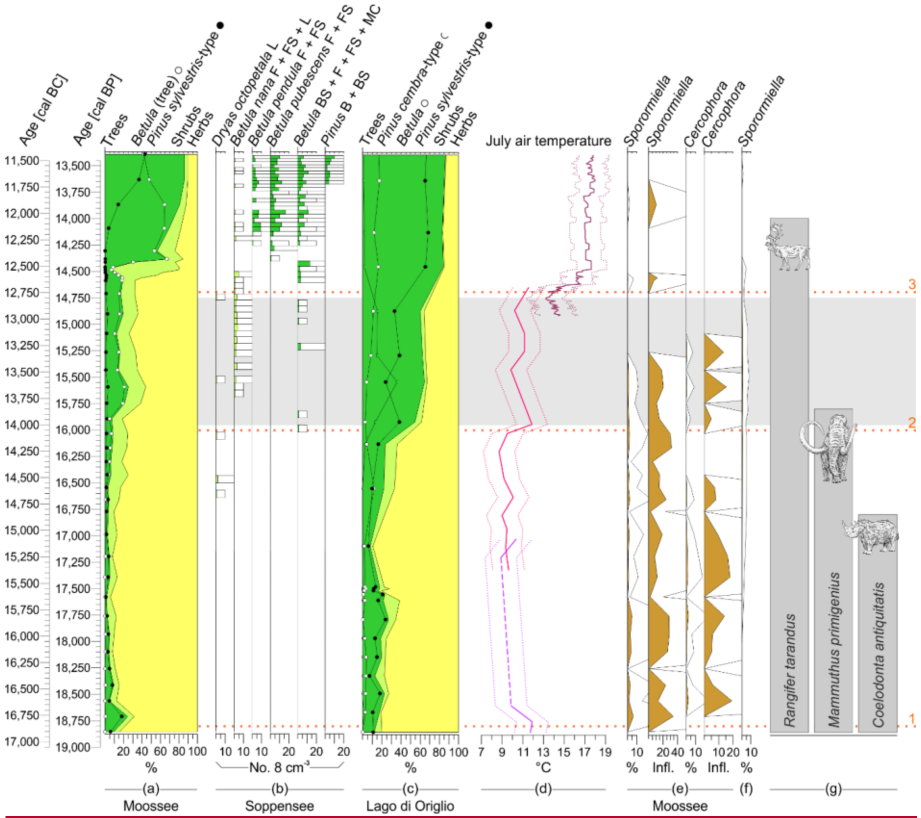

Figure 4. Composite. (a) Main pollen percentages of Moossee including pollen percentages of *Betula* (tree) and *Pinus sylvestris*-type. (b) Concentrations of selected plant macrofossils at Soppensee (Lotter, 1999). B = bud, BS = bud scale, F = fruit, FS = fruit scale, L = leaf, MC = male catkin. (c) Main pollen percentages of Lago di Origlio including pollen percentages of *Betula*, *Pinus sylvestris*-type and *Pinus cembra*-type (Tinner et al., 1999). (d) Mean July air temperature estimates for the altitude of Moossee (521 m a.s.l.) using chironomid-based temperature reconstructions from Lago della Costa (light purple lines, Samartin et al., 2016), Lago di Origlio (pink lines, Samartin et al., 2012) and a chironomid-inferred stacked temperature record representing mean July air temperature estimates in the Northern and Central Swiss Alps (dark red lines, Heiri et al., 2015). Temperatures were corrected under the assumption of a constant modern temperature rate of 6 °C km^{-1} (Livingstone and Lotter, 1998) and plotted according to Finsinger et al. (2019). The Origlio record is only shown for the oldest part (older than 14,600 cal yr BP). Dotted lines reflect standard error estimates. (e) *Sporormiella* and *Cercophora* percentages and influx values (spores cm^{-2} yr^{-1}) of Moossee. ~~(e) *Sporormiella* percentages of Moossee.~~ (f) *Sporormiella* percentages of Burgäschisee (Rey et al., 2017). (g) Presence and extinction of important Pleistocene megafauna (Nielsen, 2013; Cupillard et al., 2015). The horizontal light grey bar indicates the time window of local archaeological findings (reindeer hunter camps, Bullinger et al., 1997; Harb, 2017; Nielsen, 2018). Empty curves show 10x exaggerations (b, e, f). The orange horizontal dotted lines (1−3) mark important climatic breaks on the basis of temperature changes (see Finsinger et al., 2019).

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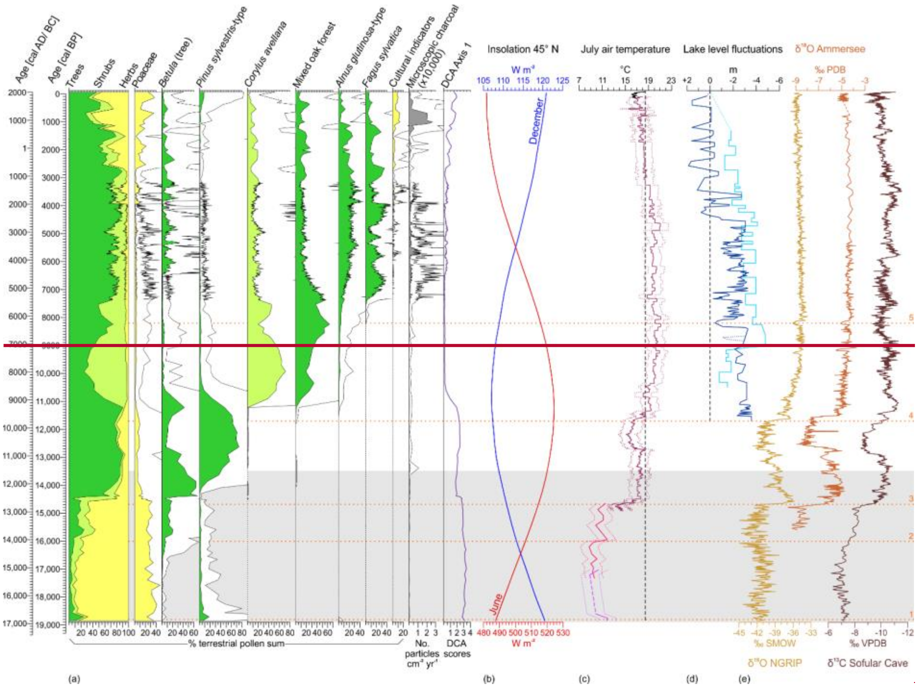

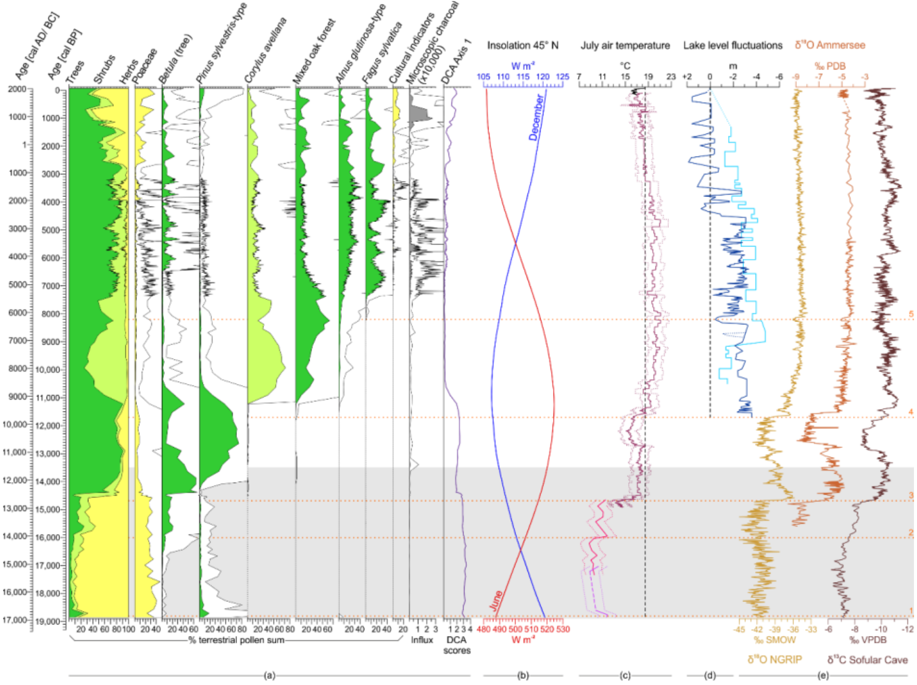

Figure 5. Composite. (a) Selected pollen percentages, microscopic charcoal influx values (particles cm^{-2} yr^{-1}) and the detrended correspondence analysis (DCA, purple line) of Moossee. Mixed oak forest = Σ *Quercus* + *Ulmus* + *Fraxinus* 1295

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***excelsior* + *Tilia* + *Acer*. Cultural indicators = Σ Cerealia-type + *Plantago lanceolata*. Empty curves show 10x exaggerations. (b) June (red line) and December (blue line) insolation for 45°N (Berger and Loutre, 1991). (c) Mean July air temperature estimates for the altitude of Moossee (521 m a.s.l.) using chironomid-based temperature reconstructions from Lago della Costa (light purple lines, Samartin et al., 2016), Lago di Origlio (pink lines, Samartin et al., 2012) and a chironomid-inferred stacked temperature record representing mean July air temperature estimates in the Northern and Central Swiss Alps (dark red lines, Heiri et al., 2015). Additionally, historical (1755–2018 AD) 30-yr moving average July air temperature measurements from Basel-Binningen (black line) are shown. Temperatures were corrected under the assumption of a constant modern temperature rate of 6 °C km^{-1} (Livingstone and Lotter, 1998) and plotted according to Finsinger et al. (2019). The black vertical dashed line indicates today's average July air temperatures (= 18.3 °C) in Bern/ Zollikofen (MeteoSwiss, 2017). The Origlio record is only shown for the oldest part (older than 14,600 cal yr BP). Dotted lines reflect standard error estimates. (d) Relative lake level reconstructions of Lac de Cerin (light blue line, Magny et al., 2011) and Lago di Ledro (dark blue line, Magny et al. 2012). The black vertical dashed line mark today's lake levels. (e) Stable isotopes records from NGRIP (light brown line, North Greenland Ice Core Project members, 2004), Ammersee (dark orange line, von Grafenstein et al., 1998, 1999) and Sofular Cave (brown line, Fleitmann et al., 2009). The horizontal light grey bar indicates the time window of Fig. 4. The orange horizontal dotted lines (1−5) mark important climatic breaks on the basis of temperature changes (see Finsinger et al., 2019) and/ or increased moisture availability.**