

Impact of Holocene climate changes on alpine and treeline vegetation at Sanetsch Pass, Bernese Alps, Switzerland

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“We have a responsibility to protect the rights of generations, of all species, that cannot speak for themselves today. The global challenge of climate change requires that we ask no less of our leaders, or ourselves.”

W. Maathai, Nobel Peace Prize winner 2004

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“Climate change is already having an impact on biodiversity, and is projected to become a progressively more significant threat in the coming decades.... Climate change is projected to cause species to migrate to higher latitudes (i.e. towards the poles) and to higher altitudes, as average temperatures rise. In high-altitude habitats where species are already at the extreme of their range, local or global extinction becomes more likely as there are no suitable habitats to which they can migrate... The linked challenges of biodiversity loss and climate change must be addressed by policymakers with equal priority and in close coordination...”¹

Preface and Introduction

In respect to biodiversity assessments at high altitude habitats, this work aims to contribute to the knowledge and understanding of the impact of climate changes on treeline and alpine vegetation. Human land use interferes in the reaction of vegetation to climate change, which is why the impact of the combined interactions is of special interest. Hopefully, results of this study together with findings from other investigations will help maintain biodiversity under future anthropogenic global warming, through knowledge about potential natural vegetation and response of alpine and treeline vegetation to climatic changes and human impact in the past. Appropriate adaptation strategies may be derived thereof.

Whereas recent multiproxy and modelling studies (e.g. Heiri et al., 2004; Lotter et al., 2006; Colombaroli et al., 2010; Henne et al., 2011; Röpke et al., 2011) have broadened our knowledge about vegetation, climate and environmental history in several areas of the Alps, little new research has been done in the Northwestern Swiss Alps. To gain knowledge about high altitude Holocene forest dynamics in this area, the paleoecology group of the University of Bern launched a project covering a transect of three sites in the Bernese Oberland and the Wallis. Of these, the lowest one is Lauenensee (1,381 m a.s.l.), a lake located in the upper montane vegetation belt. Iffigsee (2,065 m a.s.l.) is located at today's potential treeline and has a long history of human impact, as documented by archaeological findings below and near the Schnidejoch (Grosjean et al., 2007; Hafner et al., 2009). The small pond Emines close to Sanetsch Pass is the highest site in the study area, and thus at an optimal position for studies about the upper limit of Holocene treeline. The manuscript on hand presents the research questions, the methods as well as important results and conclusions concerning the investigations at Emines. Conclusions drawn from

¹ Secretariat of the Convention on Biological Diversity (2010): Global Biodiversity Outlook 3. Montreal: 94 pp.

the transect (i.a. the maximum extent of Holocene treeline) including findings collated for the whole region will be presented in the near future in Chrisoph Schwörer's Ph.D. thesis.

Manuscript: Impact of Holocene climate changes on alpine and treeline vegetation at Sanetsch Pass, Bernese Alps, Switzerland

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Abstract

In order to infer reactions of treeline and alpine vegetation to climatic change, past vegetation changes are reconstructed on the basis of pollen, macrofossil and charcoal analysis. The sampled sediment cores originate from the small pond Emines, located at Sanetsch Pass (connecting the Valais and Bern, Switzerland) at an altitude of 2,288 m a.s.l. Today's treeline is at ca. 2,200 m a.s.l. in the area, though due to special pass (saddle) conditions it is locally depressed to ca. 2,060 m a.s.l. Our results reveal that the area around Emines was covered by treeless alpine vegetation during most of the past 12,000 years. Single individuals of *Betula*, *Larix decidua* and possibly *Pinus cembra* occurred during the Holocene. Major centennial to millennial-scale responses of treeline vegetation to climatic changes are evident. However, alpine vegetation composition remained rather stable between 11,500 and 6,000 cal. BP, showing that Holocene climatic changes of +/- 1 °C hardly influenced the local vegetation at Emines. The rapid warming of 3-4 °C at the Late Glacial/Holocene transition (11,600 cal. BP) caused significant altitudinal displacements of alpine species that were additionally affected by the rapid upward movement of trees and shrubs. Since the beginning of the Neolithic, vegetation changes at Sanetsch Pass resulted from a combination of climate change and human impact. Anthropogenic fire increase and land-use change combined with a natural change from subcontinental to more oceanic climate during the second half of the Holocene led to the disappearance of *Pinus cembra* in the study area, but favoured the occurrence of *Picea abies* and *Alnus viridis*. The mid to late Holocene decline of *Abies alba* was primarily a consequence of human impact, since the mesic species should have benefitted from shift to more oceanic conditions. Future alpine vegetation changes will be a function of the amplitude and rapidity of global warming as well as human land use. Our results imply that alpine vegetation at our treeline pass site was never replaced by forests since the last ice-age. This may change in the future if anticipated climate change will induce upslope migration of trees. The results of this study emphasise the necessity of climate change mitigation in order to prevent biodiversity losses as a consequence of unprecedented community and species displacement in response to climatic change.

Keywords: treeline, alpine vegetation, paleoecology, climate change, human impact, upslope migration, Bernese Alps

1. Introduction

Climatologists and ecologists generally agree that anthropogenic climate change will have a strong impact on the species composition and distribution of plant ecosystems. In this regard, it is broadly acknowledged that temperature-limited ecosystems like the treeline ecotone will be particularly affected (e.g. Grace et al., 2002; Lloyd and Fastie, 2002; Dullinger et al., 2004). Qualitative and quantitative responses of treeline vegetation to climatic changes depend on its definition. Being composed of trees, shrubs and herbaceous species, the extension of treeline vegetation is defined by the terms timberline, treeline and krummholz zone (Körner et al., 1999; Tinner and Theurillat, 2003; Tinner, 2007). In contrast to timberline, which is defined by closed forest, the term treeline refers to the highest elevation reached by single trees. In more detail, the position of treeline is commonly defined by trees characterised by a minimum height between 2 and 8 m. Tree species growing above treeline and consequently being smaller than 2 m belong to the so called krummholz zone, whose limit is defined by the absolute occurrence of tree species (Tinner and Theurillat, 2003; Tinner, 2007). The treeline ecotone is the boundary that separates the subalpine coniferous forest (below timberline) from open alpine landscapes (above treeline) (Lotter et al., 2006). Position of treeline and timberline is closely related to the length of the growing season, which in turn is correlated to temperatures $\geq 5^{\circ}\text{C}$ during 100 days of the year (Körner et al., 1999).

Other studies in comparable environments have already analysed the responses of treeline vegetation to Holocene climate change and human impact on the basis of macrofossil, pollen and stomata analysis (Markgraf, 1969; Lang and Tobolski, 1985; Ammann and Wick 1993; Wick et al., 2003; Heiri et al., 2004, 2006; Lotter et al., 2006). However, such responses are complex as there are various feedbacks with climate and land use (e.g. Grace et al., 2002; Lloyd and Fastie, 2002; Holtmeier and Broll, 2005). Treeline and alpine vegetation is especially endangered by the predicted annual mean warming of 2.3 to 5.3 °C for Europe during the 21st (IPCC, 2007a) century because its high-altitude habitats are anthropogenically restricted and fragmented, and thus upward movement of treeline species might be impossible (Tinner and Kaltenrieder, 2005). Colombaroli et al. (2010) showed that increased anthropogenic fire impact may impede the upslope movement of treeline. Conversely, rapid upward migration of trees may cause displacement of alpine communities and species (Theurillat et al., 1998), and thus irrecoverable biodiversity losses. Environmental instability may further be caused by landslides and rockfalls induced by melting of permafrost (Williams, 1995). Walther et al. (2005) already observed an

accelerated upward shift of alpine plants and a change in species composition in the southeastern Swiss Alps. In this regard, future changes in treeline vegetation may be abrupt with possible negative consequences for biodiversity (e.g. Grace et al., 2002; Tinner and Kaltenrieder, 2005; IPCC, 2007b; Colombaroli et al., 2010).

We have chosen the new site Emines for two main reasons: the site is situated slightly above today's treeline. On the basis of previous studies we expect that this altitudinal position should capture upward movements of treeline exceeding 100-200 altitudinal meters during periods warmer than today. Since the nearby Glacier de Tsanfleuron was located quite close to the study site during the Little Ice Age (distance of about 500 m; Sharp et al., 1989; Gremaud et al., 2009), we also expect a very high Holocene environmental sensitivity of the site to periods colder than today.

For these reasons, on the basis of pollen, macrofossil and charcoal analysis, the present paper addresses the following research questions: (1) Was the site overrun by a Holocene glacier advance that exceeded the LIA event? (2) Did treeline ever reach the site which is situated above today's treeline? (3) Have there been changes in alpine and treeline vegetation at the study site during the Holocene? (4) If yes, how did vegetation respond to climate changes? (5) Are the vegetational changes during the mid and late Holocene caused by climatic shifts or rather by human impact? (6) What are the implications for alpine and treeline vegetation and biodiversity under the anticipated climate change scenarios?

2. Study area

The sediment cores used for the analysis presented in this study originate from the small pond Emines at Sanetsch Pass (Valais, Switzerland). The pond is located on an altitude of 2,288 m a.s.l. at the coordinates 46° 19' 54" N, 7° 17' 10" E (Fig. 1). It has a surface area of only about 0.5 ha. The site is surrounded by a typical alpine karrenfield that formed since the end of the last ice age (Fig. 2). Geographically, the study site is located ca. 2.5 km east of the end of Glacier de Tsanfleuron (Fig. 1). It is important to note that the pond persisted during the Little Ice Age (LIA) at AD 1860, even though the glacier tongue was only 500 m from the study site at that time (Sharp et al., 1989; Gremaud et al., 2009).

Tectonically, the Sanetsch-Tsanfleuron area belongs to the Helvetic domain of the Alps. It is formed by a number of napes that consist of Paleogene and Mesozoic rocks, among which limestone belong to the most important ones. The study site itself is part of the Mont-Gond nappe, which overlies the Diablerets nappe (Gremaud et al., 2009).

The present climate at Emines is characterised by 0.67 °C annual mean temperature and an annual precipitation of 1890 mm. These data were interpolated to a 1 ha grid using the DAYMET model (Thornton et al., 1997; data source: Swiss Federal Institute for Forest, Snow and Landscape Research).

The regional treeline is formed by *Larix decidua* and *Pinus cembra*. Due to the harsh climate and poor pedogenesis, only treeless alpine vegetation can presently grow at Sanetsch Pass (Fig. 2). The area around the pond is covered by *Seslerio* communities, which are characterised by species like *Sesleria caerulea*, *Leontopodium alpinum* or *Carex sempervirens*.

Present highest timberline and treeline elevations in the area (Valais side) are located at ca. 2,200 m a.s.l. Possibly as a consequence of the windy pass situation, local timberline and treeline are lower, at ca. 1,950 m and 2,060 m a.s.l., respectively. Passes can funnel and concentrate winds causing unusually low, wind-depressed treelines well below the normal elevation (Arno and Hammerly, 1984). It is difficult to assess this effect at Sanetsch Pass, though on the basis of current tree growth it may have comprised ca. 140 altitudinal meters. However, the current depression of timberline and treeline at the pass may have also been caused by particularly intense land use connected to the exchange of goods between the Cantons of Bern and Valais. Consequently, the study site is ca. 230 m above today's locally lowered treeline and 90 m above normal (climate-controlled) treeline.

3. Materials and methods

3.1. Coring and radiocarbon dating

In September 2010, two parallel cores were taken with the help of a modified Streif-Livingstone piston corer with a tube diameter of 5 cm from a small raft, attached on rubber boats. The first core (SAN1) was taken at the deepest water depth, which was 1.5 m at that time, whereas the second core (SAN2) was taken at one meter distance at 1.3 m water depth.

The age-depth model used for the pollen and macrofossil diagrams is based on accelerator mass spectrometry (AMS) radiocarbon dating of terrestrial plant macrofossils measured at the Poznan Radiocarbon Laboratory (Poland). The program CALIB 6.0.2 (Stuiver et al., 2005) is used to convert radiocarbon dates (yr BP conv.) into calibrated dates (cal. yr BP). In addition, pollenstratigraphical methods are used to verify the resulting age-depth model. Pollenstratigraphically inferred dates are enclosed in brackets.

3.2. Pollen, charcoal and macrofossils

For pollen and charcoal analysis, samples of 1 cm³ were taken from the sediment core usually every 4 cm. Sediments at a depth between 54 and 14 cm have a sample resolution of 8 cm, whereas the top samples were sampled with varying resolution between 1 and 4 cm. Samples were treated following standard preparation methods for pollen samples (Moore et al., 1991) and mounted in glycerine. Pollen types were identified following the reference collection at the Institute of Plant Sciences of the University of Bern as well as pollen keys and photo atlases (Moore et al., 1991; Reille, 1992; Beug, 2004). Only pollen of terrestrial plant species are included in the pollen sum, and thus used to calculate pollen percentages. Microscopic charcoal particles >10 µm were counted on the pollen slides following Tinner and Hu (2003) and Finsinger and Tinner (2005). For the calculation of pollen and charcoal concentrations, *Lycopodium* tablets were added to the sediment samples previous to the treatment (Stockmarr, 1971). Pollen (grains cm⁻² yr⁻¹) and charcoal influx (fragments cm⁻² yr⁻¹) were estimated based on the age-depth model.

Following the zonation method of optimal partitioning (Birks and Gordon, 1985), the pollen diagrams are subdivided in local pollen assemblage zones (LPAZ), as identified by the program ZONE 1.2, written by Steve Juggins. In addition, the program BSTICK (Bennett, 1996) was used to find the number of statistically significant zones. The calculation of the LPAZ is based on all species included in the pollen sum.

For macrofossil analysis, the whole core was continuously sampled with a sample resolution of 4 cm and in some sections even 2 cm with exception of sediment depths between 126 and 134 cm. Macrofossils were separated from other fine-grained sediment components using a sieve with a 0.2 mm mesh width and identified using reference specimens at the Institute of Plant Sciences of the University of Bern. Concentrations are calculated and depicted per 44 cm³ of sediment. Due to low numbers of determinable macrofossils, it was not possible to calculate local macrofossil assemblage zones (LMAZ). Therefore, the macrofossil diagram is subdivided based on the LPAZ determined from the terrestrial pollen record.

4. Results

4.1. Lithology and chronology

The lowest part of the cores reaching from 218 to 193 cm consists of sandy silt. This layer is followed by a section of silty clay which includes some sand layers. From 148 to 136 cm, the cores consist of silty gyttja, and from 136 to the top of gyttja (Tab. 1), suggesting a

more stable sedimentation above 148 cm sediment depth, corresponding to ca. 11,100 cal. BP and especially above 136 cm sediment depth (9,100 cal. BP). Due to a lack of terrestrial plant macrofossils only three radiocarbon dates at a sediment depth of 148-144 cm, 138-134 cm and 42-34 cm were measured (Tab. 2). As a result, the age-depth model relies on a simple linear interpolation. Based on the pollen and macrofossil record (Fig. 4-6) and comparison with the pollen stratigraphy with well dated pollen records in the Valais and Bernese Alps region (e.g. Tinner et al., 1996; Tinner and Theurillat, 2003; Lotter et al., 2006) the age of the sediment base is estimated to be 12,000 cal. BP. The resulting age-depth model is shown in Figure 3. The beginning of the Holocene at ca. 11,600 cal. BP (Schwander et al., 2000) can be assigned to a sediment depth of 165 cm (Fig. 4 and Fig. 5). In addition, *Abies alba* expanded in the region at about 8,900 cal. BP (Tinner et al., 1996; Wick et al., 2003; van der Knaap et al., 2005; Lotter et al., 2006), resulting in a biostratigraphical age of about 8,900 years cal. BP for the sediment depth of 130 cm. Using the same methods and references, further pollenstratigraphical dates are inferred on the basis of the expansion of *Picea abies* and *Fagus sylvatica*. Table 2 summarises all information of the radiocarbon date as well as pollen stratigraphical age estimates. Dates inferred by pollen stratigraphy suggest that the linear radio-carbon based age-depth model well approximates the sediment age with maximum deviations up to a few hundred years (Fig. 3).

4.2. Pollen, macrofossils and charcoal

All pollen and macrofossil diagrams (Fig. 4-6) are subdivided into five statistically significant pollen-assemblage zones (SAN-1 – SAN-5):

SAN-1 (12,000 – 9,800 cal. BP)

The oldest zone is dominated by *Pinus sylvestris* pollen type, which usually accounts for more than 80% of the pollen sum (Fig. 4). In addition, the subalpine taxa *Pinus cembra* and *Betula* account for pollen percentages up to 13% and 5%, respectively. *Artemisia*, Poaceae and *Plantago alpina* are the most frequent herbaceous taxa (Fig. 5). However, pollen of cold-adapted herbs decrease around 11,600 cal. BP, when sediments change from sandy material to silty gyttja, and arboreal pollen (AP) subsequently reach up to 98%.

No macrofossils are found in the oldest part of the sequence (Fig 6). The earliest ones are two *Gnaphalium* seeds around 11,400 cal. BP. They are followed by leaf fragments of *Salix herbacea* and Caryophyllaceae seeds at about 10,900 cal. BP. At the same time, there

is a general increase in terrestrial and aquatic plant remains as well as in insect remains. Microscopic charcoal influx is low (around 1000 fragments $\text{cm}^{-2} \text{yr}^{-1}$) at the beginning of the sequence. However, there is a sharp increase with an influx peak (8,500 fragments $\text{cm}^{-2} \text{yr}^{-1}$) around 11,300 cal. BP.

SAN-2 (9,800 – 8,700 cal. BP)

At the beginning of this zone, *Pinus sylvestris* pollen type declines, while *Corylus avellana* pollen percentages increase significantly. In addition, *Ulmus* gains importance reaching up to 11% of the pollen sum. *Pinus cembra* pollen influx and pollen percentages decline again rapidly after having peaked at 9,000 cal. BP. *Abies alba* pollen abundance increases towards the end of the zone. The percentages of non-arboreal pollen gradually increase, with species of Poaceae and Cyperaceae becoming the most important. Concerning macrofossils, five winged fruits of *Betula* are found at the transition between SAN-1 and SAN-2. Again, *Salix herbacea* was present at Sanetsch Pass as indicated by leaf fragments. Other herbaceous taxa recorded in the macrofossils are *Gnaphalium*, *Potentilla argentea*-type and *Carex*. Moreover, a constant decline in microscopic charcoal influx (from 1,400 to 200 fragments $\text{cm}^{-2} \text{yr}^{-1}$) is recorded in this zone.

SAN-3 (8,700 – 6,100 cal. BP)

Abies alba becomes the dominant pollen type at the expense of *Pinus cembra* and *Corylus avellana*, the latter two fluctuating between pollen percentages of 2% and 12%, and between 4% and 14% respectively. *Ulmus* and *Tilia* pollen percentages decline continuously, while *Alnus glutinosa* increases. Furthermore, *Picea abies* pollen percentages and influx increase towards the end of this zone. One single *Larix* pollen grain is recorded at 8,100 cal. BP. Pollen of herbaceous taxa become more significant (e.g. Apiaceae, Campanulaceae, Cichorioideae, Cyperaceae, Brassicaceae, *Helianthemum*, *Plantago alpina*, Poaceae, *Rumex acetosa*, *Thalictrum*). A *Larix* needle is found at about 8,300 cal. BP. After ca. 7,700 cal. BP macrofossils of herbaceous taxa disappear (e.g. *Gnaphalium*, *Carex*). Microscopic charcoal influx remains on a low level during SAN-3.

SAN-4 (6,100 – 4,500)

Picea abies pollen increases about 6,400 cal. BP, and only a few centuries later, it is one of the dominant pollen types in the sequence, together with *Pinus sylvestris*-type and *Abies alba*. *Alnus viridis* and *Plantago alpina* pollen increase as well, while *Pinus cembra* pollen

percentages and pollen influx collapse. *Abies alba* pollen decreases towards the end of this zone. Bud scales of conifers as well as *Betula* fruits are found around 6,000 and 5,700 cal. BP, respectively. Herbaceous taxa that re-appear in the macrofossil record are *Campanula* seeds, *Potentilla argentea*-type (seeds), and *Selaginella selaginoides* (macrospores). Furthermore, macroscopic charcoal increases since about 5,100 cal. BP, in agreement with a peak of microscopic charcoal influx at about 5,300 cal. BP.

SAN-5 (4,500 – 0 cal. BP)

Picea abies becomes the dominant pollen type, whereas influx and percentage of *Pinus sylvestris*-type level out at lower values and *Abies alba* declines to only a few percentages of the pollen sum. In addition, pollen percentages of *Alnus glutinosa* fluctuate between 14% and 1%. Pollen percentages of *Pinus sylvestris*-type further decrease at 1,100 cal. BP (Middle Ages), whereas values of *Picea abies* decrease only after 350 cal. BP (Modern times). Percentage values of herbaceous taxa increase up to 45% as lowland cultural indicators like *Cannabis*, *Cerealia*, *Plantago lanceolata* and *Urtica* appear or become more abundant in the pollen diagram. Local alpine grazing indicators such as Cichorioideae, Poaceae, *Ligusticum mutellina*, and *Plantago alpina* additionally reach high values. Two *Betula* fruits are found around 4,100 cal. BP. Mirroring the increase of these anthropogenic or grazing indicators, microscopic charcoal influx also increases.

4.3. Interpretation and discussion

4.3.1. Lithology and Chronology

The lithology and chronology (Tab. 1) show that despite the flow of glacier ice around the site during the LIA, sediment accumulation at Emines was not disturbed during the entire Holocene. Sharp et al. (1989), who studied the drainage system of the Tsanfleuron glacier, suggested that the glacier reached its maximal Holocene position during the LIA. Our study confirms this result for Glacier de Tsanfleuron and is in agreement with several other reconstructions of glacier dynamics in the Swiss Alps (e.g. Joerin et al., 2006; Joerin et al., 2008; Gremaud et al., 2009).

4.3.2. Pollen-inferred vegetation history

The quantity of arboreal pollen is recognised as the most decisive criterion for treeline position in palynology (e.g. Zoller, 1960, 1977a, 1977b; Bortenschlager, 1977, 1984; Welten, 1982). When excluding lowland arboreal species, pollen percentages of non-

arboreal pollen >30% indicate treeless alpine vegetation, whereas percentages of arboreal pollen >70-80% are typical for timberline conditions (Tinner and Theurillat, 2003). According to this criterion, the area around the pond has been forested between 11,300 and 9,500 cal. BP. However, forested conditions at Sanetsch Pass are unlikely throughout the Holocene, as the percentages of subalpine arboreal species in the total pollen sum as well as tentative influx values are low (Fig. 4). Especially during the early Holocene, high percentages of subalpine arboreal species might be primarily a result of low local alpine vegetation density. In agreement, Lang (1994) showed that such threshold values may be ambiguous when applied to alpine environments.

Pollen interpretation can be enhanced by considering the vegetation ecology of the area: today *Pinus cembra* and *Larix decidua* are forming the forest belt above the subalpine *Picea abies* belt. The supra-subalpine *Pinus cembra* – *Larix decidua* belt encompasses about 300 altitudinal meters in the study area (ca. 2000-2300 m a.s.l., Landolt, 1992), thus the presence of this forest type at ca. 11,500-6,000 cal. BP below Emines points to maximum Holocene treeline and timberline positions in the area.

A method to overcome interpretation difficulties of pollen percentage diagrams is the use of pollen influx, though such an interpretation depends on the quality of the chronology (Lang, 1994). Van der Knaap et al. (2001) studied pollen influx at four different transects in the Swiss Alps using pollen traps. Their transect near Zermatt (Valais, Switzerland) is the only one suitable for comparison because only there, the forest limit is sufficiently intact and some pollen traps were located far enough above today's timberline. In addition, this transect also covers scattered trees as well as closed forests. Tinner and Theurillat (2003) suggested that *Pinus cembra* reaches an influx of 1,000 pollen grains $\text{cm}^{-2} \text{yr}^{-1}$ in closed forests, 700 at timberline and 400 in alpine treeless vegetation. In contrast, *Betula* influx in closed forests is only 200 grains $\text{cm}^{-2} \text{yr}^{-1}$, 150 at timberline and up to 100 in alpine grasslands (van der Knaap et al., 2001; Tinner and Theurillat, 2003). Similar results for *Pinus cembra* influx were obtained by Bortenschlager et al. (1998) in western Austria, as they recorded 1,000 grains $\text{cm}^{-2} \text{yr}^{-1}$ in closed forests and 350-500 at higher elevation. Applying these results to our tentative influx estimates (Fig. 4), it is apparent that the pond was mostly located above timberline during the past 12,000 years. However, the *Pinus cembra* influx values would suggest forest conditions between 11,300 and 9,000 cal. BP (up to 3,300 grains $\text{cm}^{-2} \text{yr}^{-1}$). Comparably, *Betula* influx during the early Holocene is up to 400 grains $\text{cm}^{-2} \text{yr}^{-1}$ indicating forest conditions. The total influx of tree pollen is distinctly above 2,000 grains $\text{cm}^{-2} \text{yr}^{-1}$ between 11,700 and 8,500 cal. BP as well as between 6,500

and 4,600 cal. BP, suggesting the pond's position below timberline. However, reliable influx estimates require an excellent chronology, which is hardly given here. We must thus rely on the sparse macrofossil evidence to refine our pollen-based reconstruction.

4.3.3. Macrofossil-inferred vegetation history

Based on the assumption that even single findings of a species already indicate its local presence, results from macrofossil analysis significantly add to the interpretation of pollen records near treeline (Lang and Tobolski, 1985). However, this principle may not be applied to winged *Betula* fruits, as these macrofossils might have found their way into the pond by wind transport. The interpretation of the single *Larix* needle finding at about 8,300 cal. BP is also difficult, as the deciduous tree leads to sediments rich in macrofossils if the species is locally present (Wick and Tinner, 1997; Tinner and Theurillat, 2003). Besides, long distance transport may be possible as the needles shed in autumn are dry and light (e.g. Wick, 1994). Nevertheless, it is remarkable that the detection of the only *Larix* pollen grain almost coincides with this needle finding (Fig. 4 and Fig. 6).

Between 11,400 and 10,900 cal. BP, the presence of *Gnaphalium* seeds, deciduous leaves and moss fragments suggests an open landscape with pioneer and snow bed vegetation. Subsequently, from 10,900 to 8,300 cal. BP the area around the pond was covered by alpine meadow and snow bed vegetation with at most a scattered occurrence of trees as suggested by macrofossils of *Salix herbacea*, Caryophyllaceae, *Galium*, *Gnaphalium*, *Potentilla argentea*-type, *Carex*, *Betula* and *Larix*. At about the same time, an increase of insect species indicates more habitable climate conditions. Nevertheless, *Salix herbacea* points to a harsh climate with long snow coverage during winter (e.g. Wijk, 1986), which excludes the presence of forests. The mid Holocene was still characterised by a sparse alpine-meadow vegetation cover, shown by the general low occurrence of macrofossils, and especially by the absence of tree or shrub macrofossils. Fruits, bracts and utricles of *Carex* are the only terrestrial plant remains after 8,300 cal. BP, and at 7,700 cal. BP even those disappeared. Only between 6,100 and 5,700 cal. BP, *Betula* fruits and a conifer bud scale suggest local re-appearances of single trees. In addition, *Betula* fruits re-occurred around 4,100 cal. BP. Finally, findings of 31 seeds of *Potentilla argentea*-type, which is adapted to a rather dry and open landscape (Lauber and Wagner, 2006), but no findings of arboreal plant macrofossils, indicate that the vegetation of Sanetsch Pass was characterised by open alpine meadows during the late Holocene.

4.3.4 Charcoal inferred fire history and ecology

Under natural conditions, fire occurrence generally is a function of ignition frequency, biomass availability and fuel dryness, which in turn is controlled by moisture, and thus also temperature (Carcaillet, 1998; Colombaroli et al., 2010). Consequently, due to the harsh climate and low ecosystem productivity at Sanetsch Pass, fire occurrence may be primarily linked to the precipitation regime and available biomass until the beginning of the Neolithic. The peak in microscopic charcoal influx between 11,600 and 11,100 cal. BP (up to 8,500 fragments $\text{cm}^{-2} \text{yr}^{-1}$) as well as the first occurrence of macroscopic charcoal particles around 11,300 are mirrored in peaks of the *Pinus sylvestris*-type and *Pinus cembra* influx curves and may reflect increased biomass availability and regional fire frequency during the early Holocene. The second largest peak of microscopic charcoal influx around 6,000-4,800 cal. BP (up to 1,800 fragments $\text{cm}^{-2} \text{yr}^{-1}$) coincided with the Holocene maximum of *Pteridium aquilinum*, a species which is often associated with forest fires and/or forest grazing (Tinner et al., 1999). At about the same time, alpine grazing indicators (e.g. Cichorioideae, *Plantago alpina*, Poaceae) increase, suggesting that fires might have been set by humans. Finally, increased regional fire activity since about 2,700 cal. BP was probably also caused by humans, as indicated by a second peak of grazing indicators (e.g. *Plantago alpina*, *Plantago lanceolata*, Poaceae, *Urtica*) (Fig. 7) and the expansion of cultural indicators such as *Cannabis*, *Cerealia* and *Plantago lanceolata* (Fig. 5). The frequent occurrence of macroscopic charcoal since 5,100 confirms an increased fire activity during the human land-use period.

4.3.5. Treeline position in the Alps

The results concerning treeline fluctuations can be compared to previous treeline studies in the Swiss Central Alps and in the Northern Alps. Studies at Gouillé Rion (Valais, Swiss Central Alps, 2,343 m a.s.l.) suggest that timberline climbed about 800 m during the Late Glacial/Holocene transition (Tinner and Kaltenrieder, 2005). Timberline and treeline in the Central Alps reached their uppermost position during the period from 8,700 to 5,000 cal. BP (Wick and Tinner, 1997), when timberline and treeline were at about 2,420 and 2,530 m a.s.l., respectively (Tinner and Theurillat, 2003). Between 5,500 and 4,500 cal. BP treeline sank only by about 100 m, while timberline was lowered by 300 m, which led to an enlargement of the treeline ecocline belt (Tinner and Theurillat, 2003). The results of Tinner et al. (1996) suggest that the lowering of the timberline was caused by the onset of a more intense land-use system based on alpine summer farming. Only treeline is then in

equilibrium with climate, as the lowering of timberline can rather be attributed to human impact (Tinner and Theurillat, 2003). Important arboreal species forming the central alpine treeline during the oldest part of the Holocene were *Larix*, *Juniperus* and *Salix*. At about 10,200 cal. BP *Pinus cembra* started to expand. Treeline was composed of *Pinus cembra*, *Larix* and *Betula* during the subsequent period. *Picea abies*, *Juniperus*, *Alnus viridis* and single *Larix* trees formed the treeline during the youngest Holocene period (e.g. Tinner et al., 1996; Wick and Tinner, 1997; Tinner and Theurillat, 2003; Kaltenrieder et al., 2005). At Lac de Fully (Valais, Swiss Central Alps, 2,135 m a.s.l.) *Betula* was the only tree to form larger stands prior to ca. 8,200 cal. BP, when *Larix decidua* and *Pinus cembra* expanded (Finsinger and Tinner 2007). The authors suggest that local climatic conditions may have delayed the expansion of closed stands of coniferous trees in the catchment of Lac de Fully until c. 8,200 cal. BP, when climate shifted to more humid and less continental conditions. Lac de Fully is located at the bottom of a former glacier cirque bordered by mountain chains reaching 2,300 to 3,000 m a.s.l. and this particular topographic setting may have delayed forest expansion due to locally unfavorable climatic conditions. In contrast to the Central Swiss Alps, it is supposed that treeline in the Northern Swiss Alps reached its maximum position of 2,250 m a.s.l. only between 6,000 and 3,000 cal. BP (Wick et al., 2003; Lotter et al., 2006). However, these findings are mainly based on the local presence of *Picea abies* macrofossils at Bachalpsee (2265 m a.s.l.) (Lotter et al., 2006). As a time lag of more than 2,000 years between the maximum treeline position in the Central and in the Northern Alps is currently inexplicable, an altitudinal transect of pollen and macrofossil records across the Northern Alps is needed to verify the timing of the maximal treeline position in the Northern Alps. Just as in the Central Alps, a lowering of timberline due to human impact during the younger Holocene is also recorded in the Northern Alps (Wick et al., 2003; Lotter et al., 2006). Regarding species composition, treeline was formed by *Pinus cembra* and *Abies alba* during the early Holocene. At about 6,300 cal. BP *Picea abies* expanded. *Pinus cembra* and *Abies alba* were the dominant treeline ecotone species until 3,700 cal. BP, when *Abies alba* lost importance. In contrast to the Central Swiss Alps, *Larix* never played an important role in the Northern Alps, although single specimens were present (Wick et al., 2003; Lotter et al., 2006). Local extinction of *Pinus cembra* and *Abies alba* and mass expansion of *Picea* and *Alnus viridis* in the Swiss Northern Alps is observed during the late Holocene (Wick et al., 2003). Comparing findings from the Northern and Central Alps with those presented in this study, it is evident that treeline vegetation history at Sanetsch Pass resembles very much

that of the Valais. Specifically this is the case due to the presence of a well-developed supra-subalpine belt with *Pinus cembra* 11,800-7,000 cal. BP together with highest treeline positions during the early and mid Holocene. Similar vegetational developments were also reconstructed in the continental French (Genries et al., 2009; Blarquez et al., 2010; Ponel et al., 2011) and Austrian (Wahlmüller, 1990; Oeggel, 1992; Wahlmüller, 2005) Alps, showing that the occurrence of *Pinus cembra* and *Larix decidua* forests during the early and mid Holocene was wide-spread in the Alps.

4.3.6. Vegetation changes and regional paleoclimate

Reaction of alpine and treeline vegetation to changing temperatures can be studied by comparing independent paleoclimatic proxies from the Alps. Non-pollen and non-macrofossil evidence points to conditions warmer than present between ca. 10,000-8,400 and 7,600 to 4,000 cal. BP in the Alps (von Grafenstein et al., 1998, 1999; Heiri et al., 2003, 2004; Joerin et al., 2008). The cooling between 8,400 and 7,600 cal. BP reached today's temperature levels (if compared with the period 1960-1990), whereas the warmer periods exceeded today's averages by ca. 1°C. Between 11,500 and 10,000 cal. BP and between 4000 and 0 cal. BP, temperatures in the region oscillated around the today's mean by about +/- 0.5 °C (von Grafenstein et al., 1998; Heiri et al., 2003, 2004). This general trend is reflected in the reconstructed treeline position at our site, suggesting highest stands during the early and mid Holocene. The most prominent difference is the rather early collapse of the supra-subalpine belt at our site (ca. 7,000-6000 cal. BP), since other treeline studies in the region suggest lowering of treeline only after ca. 5000-4000 cal. BP (e.g. Tinner et al., 1996; Finsinger and Tinner, 2007; Lotter et al., 2006). Given the huge chronological difference of 2000 years it is unlikely that this early demise of forests is just a result of dating uncertainty at Emines. Instead it may reflect more intense anthropogenic activities in the Sanetsch Pass area than in more remote localities. Mesolithic farming and animal husbandry has been recorded in the Valais since 7,000 cal. BP (Welten et al., 1982; Tinner et al., 2007; Hafner, 2009). Alpine vegetation composition, however, remained rather stable between 11,500 and 6,000 cal. BP, showing that Holocene climatic changes prior to Neolithic impact hardly influenced the local vegetation at Emines.

In addition to these rather low amplitude climatic oscillations of the Holocene, a much more pronounced climatic warming occurred at the Late Glacial/Holocene transition at ca. 11,600 cal. BP. Oxygen isotopes of lake marl at Gerzensee and Leysin (Switzerland) show that at the Younger Dryas/Pre-Boreal transition the temperature rose about 3 to 4 °C within

only half a century (Schwander et al., 2000; von Grafenstein et al., 2000). Similar results emerged from biotic reconstructions (Lotter et al., 2000; Heiri et al., 2003). Thus, the warming at the Younger Dryas/Pre-Boreal transition was within the same temperature range as the predicted temperature rise of 2.3 to 5.3 °C for the 21st century (IPCC, 2007a). It is likely that the pond became ice free in response to climate warming at the end of the Younger Dryas, when the Tsanfleuron glacier retreated to its Holocene position. According to our tentative chronology local alpine flora and fauna established around the lake 200 years later, at ca. 11,400 cal. BP (based on *Gnaphalium* seeds, Caryophyllaceae seeds, *Salix herbacea* leaves, leaf fragments, mosses and insect species, Fig. 6). Below the lake steppic tundra environments (e.g. *Artemisia*, *Thalictrum*, *Plantago alpina*, *Filipendula*) were rapidly replaced by forests (e.g. *Pinus cembra*, *Betula*, Fig. 4 and Fig. 5). Thus, in contrast to the smaller Holocene climatic variation of ca. +/- 1°C, the temperature increase at the end of the Younger Dryas of + 3-4 °C caused significant altitudinal displacements of alpine species that were additionally under pressure by the rapid upward movement of trees and shrubs (ca. 800 m within 200 years, see Tinner and Kaltenrieder, 2005). It is difficult to assess how rapidly alpine plant species were able to track the climatic change, however our tentative chronology suggests that they were able to migrate at similar speed as the tree expansion.

4.3.7. Anthropogenic or climate impact?

After 6,000 cal. BP regional vegetation composition changed remarkably, as *Pinus cembra* and *Abies alba* nearly vanished and *Picea abies* and *Alnus viridis* dominated regionally (Fig. 4).

This forest vegetation change was closely connected to the expansion of culturally enhanced taxa such as e.g. *Plantago alpina* and *Potentilla argentea*-type in the alpine meadows and Cerealia, *Cannabis*, *Plantago lanceolata*, and *Urtica* in the warmer subalpine, mountain and colline belts. Given that the climate after 5,500 cal. BP was not stable (cooling, increase of precipitation; Wick et al., 2003) the question arises whether climate or human impact was the main driver of vegetation changes at Sanetsch Pass during the second half of the Holocene.

On the basis of the increase of alpine grazing indicators (e.g. Cichorioideae, *Plantago alpina*, Poaceae) and regional fire activity in the pollen and microscopic charcoal records, the beginning of substantial Neolithic activities at Sanetsch Pass can be dated to about 6,100 -5,300 cal. BP (Fig. 7). Especially significant increases of *Plantago alpina* have been

associated with the onset of summer farming in the area (Tinner et al., 1996) and are dated at 6,100 cal. BP at Emines. The relevance of this vegetational change is underscored by statistical significance of the zone boundary between LPAZ 3 and 4. Increased occurrence of macroscopic charcoal since 5,100 cal. BP also suggests a higher fire activity close to the pond (Fig. 6). This is remarkably earlier than at other sites in the region (e.g. Tinner et al., 1996; Kaltenrieder et al., 2005; Heiri et al., 2003; Wick et al., 2003; Lotter et al., 2006; Finsinger and Tinner, 2007) and may be explained by the favourable pass position. At Schnidejoch, a pass located close to Emines, Hafner (2009) found archeological evidence of human presence as early as 6,500 cal. BP. Later on, a further simultaneous increase of grazing and cultural indicators (e.g. *Plantago alpina*, *Cannabis*, *Plantago lanceolata*, *Cerealia*) as well as erosional indicators (*Botrychium*) point to a second significant intensification of land use at and below the site (Fig. 5-7) during the Bronze Age, which is typical for the entire region (e.g. Welten, 1982; Tinner et al., 1996; Wick et al., 2003; Lotter et al., 2006; Finsinger and Tinner, 2007).

Simultaneous with the beginning of Neolithic activities at Sanetsch Pass, pollen data document the demise of the *Pinus cembra* forests and the expansion of *Alnus viridis* thickets and *Picea abies* below the site, when *Abies alba* forests were significantly reduced. Several studies showed that *Abies alba* and *Pinus cembra* are very sensitive to prolonged fire disturbance (e.g. Tinner et al., 1999; Gobet et al., 2003; Wick and Möhl, 2006). Since *Alnus viridis* is strongly advantaged by the frequent occurrence of forest fires and disturbance, the expansion of *Picea abies* and *Alnus viridis* in the Valais are mainly attributed to increasing human activities (Markgraf, 1969, 1970; Welten 1982; Tinner et al., 1996; Gobet et al., 2003). Increased fire frequency since the beginning of the Neolithic caused by human impact is well documented in different studies from the Alps (e.g. Gobet et al., 2003; Carcaillet et al., 2009).

Not only human impact but also climate set new conditions for alpine and treeline vegetation. In the Northern Alps, climate changed from subcontinental to more oceanic, implying a cooler and wetter climate since about 5,500 cal. BP (Wick et al., 2003). This climatic change was mainly caused by a reduction of the axial tilt (obliquity, i.e. the angle between the equator and the orbital plane), reducing the incoming summer radiation on the Northern Hemisphere (e.g. Wanner et al., 2008). Different studies suggest that at higher altitudes *Pinus cembra* may have declined in response to wetter and cooler conditions, whereas *Picea abies* and *Alnus viridis* may have been advantaged by cooler and moister climatic regimes (Heiri et al., 2006; Lotter et al., 2006; Valsecchi and Tinner, 2010).

However, there is no evidence for such a link in regard to the local alpine vegetation at Emines, where vegetation dynamics appear less pronounced. Original alpine communities could persist throughout the Holocene, withstanding climatic trends, although abundances of anthropogenically favoured taxa (e.g. *Plantago alpina*) strongly increased. In summary, the dominant influence of climate change on vegetation dynamics at our site is only valid until the beginning of the Neolithic, when increased fire frequency and intensified land use (Bronze Age) altered species composition and lowered timberline in the region (Tinner et al., 1996; Tinner and Theurillat, 2003; Colombaroli et al., 2010).

5.3.4 Possible consequences of anthropogenic climate change on alpine vegetation

Theurillat and Guisan (2001) reviewed the impact of future climate change on vegetation in the European Alps and concluded that alpine vegetation may tolerate a climate change in the order of 1 to 2 °C. Results of our study are in accordance with these findings, as little or no changes in vegetation at Sanetsch Pass are detected as a response to 1 to 2° C Holocene climate variability. However, Theurillat and Guisan (2001) propose that human land use is very likely to affect resilience of alpine communities, though our data show that original alpine communities may withstand even intense human impact. An annual mean warming of up to 5.3 °C for Europe is predicted by the IPCC (2007a), which exceeds by far the Holocene climatic variability, but is in the scale of the Early Holocene warming. Such a climate change would cause a large scale displacement of species and a rapid upslope movement of the treeline under natural conditions (Tinner and Kaltenrieder, 2005). Thus, landscape fragmentation and habitat loss caused by human land use may result in unpredictable, negative consequences for biodiversity (e.g. Theurillat and Guisan, 2001; Dirnböck et al., 2003; Tinner and Kaltenrieder, 2005; IPCC, 2007b). A projection (Theurillat and Guisan, 2001) suggests that an increase of 3.3 °C in mean annual air temperature would correspond to an altitudinal shift of vegetation belts by 600 m, which in turn would reduce the area of the Swiss alpine vegetation belt by 63 %. Comparably, the examples of the Late Glacial/Holocene warming presented in this study shows that climatic changes have high impacts on treeline and alpine vegetation by shifting treeline altitude as well as species composition.

Future land use will be decisive. For instance, Colombaroli et al. (2010) conclude that human induced increase of fire activity as well as alpine grazing may inhibit upslope migration of trees under anthropogenic warming, suggesting that alpine species survival might depend on the human disturbance regime. In agreement, a recent study shows that

shallow soil above the Holocene maximum treeline position may mitigate the effect of climatic warming for alpine species, impeding the establishment of closed forests as long as soils do not deepen (Henne et al., 2011). This may correspond to the situation during the early Holocene, when trees, shrubs and alpine species coexisted for centuries below treeline (Tinner and Kaltenrieder, 2005).

5. Conclusions

As the site at Emine was ice-free during the whole Holocene, the sediment cores contain information about vegetation changes throughout this period. The paleobotanical data show that the vegetation at Sanetsch Pass predominantly consisted of sparse alpine meadows during the past 12,000 years. Arboreal species reached the pond during the early Holocene and probably occurred sporadically throughout the Holocene. At the beginning and throughout the Holocene, alpine and treeline vegetation experienced substantial changes. However, during the period 11,500–6,000 cal. BP these changes were in equilibrium with climate, while afterwards human impact became more important. Today's alpine meadows are quasi-natural and persisted throughout the Holocene.

On the basis of our results, we conclude that future changes in alpine and treeline vegetation will be a function of the amplitude and rapidity of anticipated climate change as well as forest and land-use management practices. A temperature increase above 2° C will create unprecedented responses, forcing alpine vegetation to colonise altitudes never reached during at least the past 100,000 years. Shrinking habitats with increasing altitude as well as human land use may cause substantial losses of alpine species. Our results emphasise the necessity of climate change mitigation, as adaptation strategies alone may not prevent species extinction under rapid, high amplitude global warming. Further research is needed to allow conclusions for the whole region (e.g. the maximum extent of Holocene treeline and elasticity of alpine and treeline vegetation to climatic changes). In addition, this study emphasises the need of combined climate and human impact research to determine possible future forcing of anthropogenic climate change to high altitude habitats.

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Table 1: Sedimentology

Depth (cm)	Age (cal. yr BP)	Sediments
0-136	0 - 9,129	Gyttja
136-148	9129 – 11,086	Silty gyttja
148-193	11,086 – 11,674	Silty clay with sand layers
193-218	11,674 – 12,000	Silty sand

Table 2: Radiocarbon dates and pollenstratigraphical dates

Source	Laboratory code	Sample ID	Depth (cm)	Material	¹⁴ C age (yr BP conv.)	Age (cal. Yr BP) (2σ range)	Age (cal. yr BP)
¹⁴ C dating	- Poz-40964	- SAN 38	34-42	- <i>Potentilla argentea</i> -type seeds	3,235 ± 35	3382 - 3556	3,451
Pollen	-	-	78	-	-	-	5,400
Pollen	-	-	92.5	-	-	-	7,080
Pollen	-	-	130	-	-	-	8,900
¹⁴ C dating	- Poz-41029	- SAN 136	134-138	- Wood, <i>Potentilla argentea</i> -type seeds, <i>Salix herbacea</i> leaves, <i>Gnaphalium</i> seeds	8,180 ± 50	9013 - 9276	9,129
¹⁴ C dating	Poz-39385	SAN-146	144-148	<i>Salix herbacea</i> leaf, Caryophyllaceae seeds	9,480 ± 70	10565 - 11089	10,760
Pollen	-	-	165	-	-	-	11,600

Figure captions

Figure 1:

Map of the study area at Sanetsch Pass, showing the location of the investigated pond (star) and the location of Glacier de Tsanfleuron (square) (Source of map: Bundesbehörden der Schweizerischen Eidgenossenschaft, 2007; Reproduced by permission of swisstopo (BA110400)). Inset: Map of Switzerland showing the location of the study site (cross) (Modified after Reinhardt et al., 2005). The study site is located only about 2.5 km from the most eastern tongue of Glacier de Tsanfleuron. However, it was ice free even at the largest extent of the glacier during the LIA, at 1860.

Figure 2:

The pond with a surface area of about 0.5 ha is surrounded by a typical alpine karrenfield. The study area is sparsely covered by alpine vegetation. Picture by C. Schwörer.

Figure 3:

Age-depth model. Grey circles indicate calibrated ^{14}C dates (based on terrestrial macrofossils). White diamonds indicate pollenstratigraphical dates (based on comparison with well radiocarbon-dated pollen diagrams from the Central and Northern Alps). The error bars indicate 2σ ranges for the calibrated ^{14}C dates.

Figure 4:

Pollen percentage and influx diagram (selected taxa) showing arboreal pollen types. Water plants and ferns are excluded from the pollen sum, which is used for percentage values calculation. Influx values are given for selected subalpine tree- and shrub species (grey curves). Empty curves show 10x exaggerations.

Figure 5:

Pollen percentage diagram (selected taxa) showing herbs and ferns. Water plants and ferns are excluded from the pollen sum, which is used for percentage values calculation. Empty curves show 10x exaggerations.

Figure 6:

Macrofossil concentrations per 44 cm^{-3} . Plant material is counted up to a number of 50

fragments. Insect numbers exceeding 10 are divided in classes ≥ 10 and ≥ 25 . Empty curves show 5x exaggerations.

Figure 7:

Pollen percentage diagram showing selected grazing indicators. Water plants and ferns are excluded from the pollen sum, which is used for percentage values calculation. Grey pollen curves indicate influx values. Empty curves show 10x exaggerations.

Figure 1

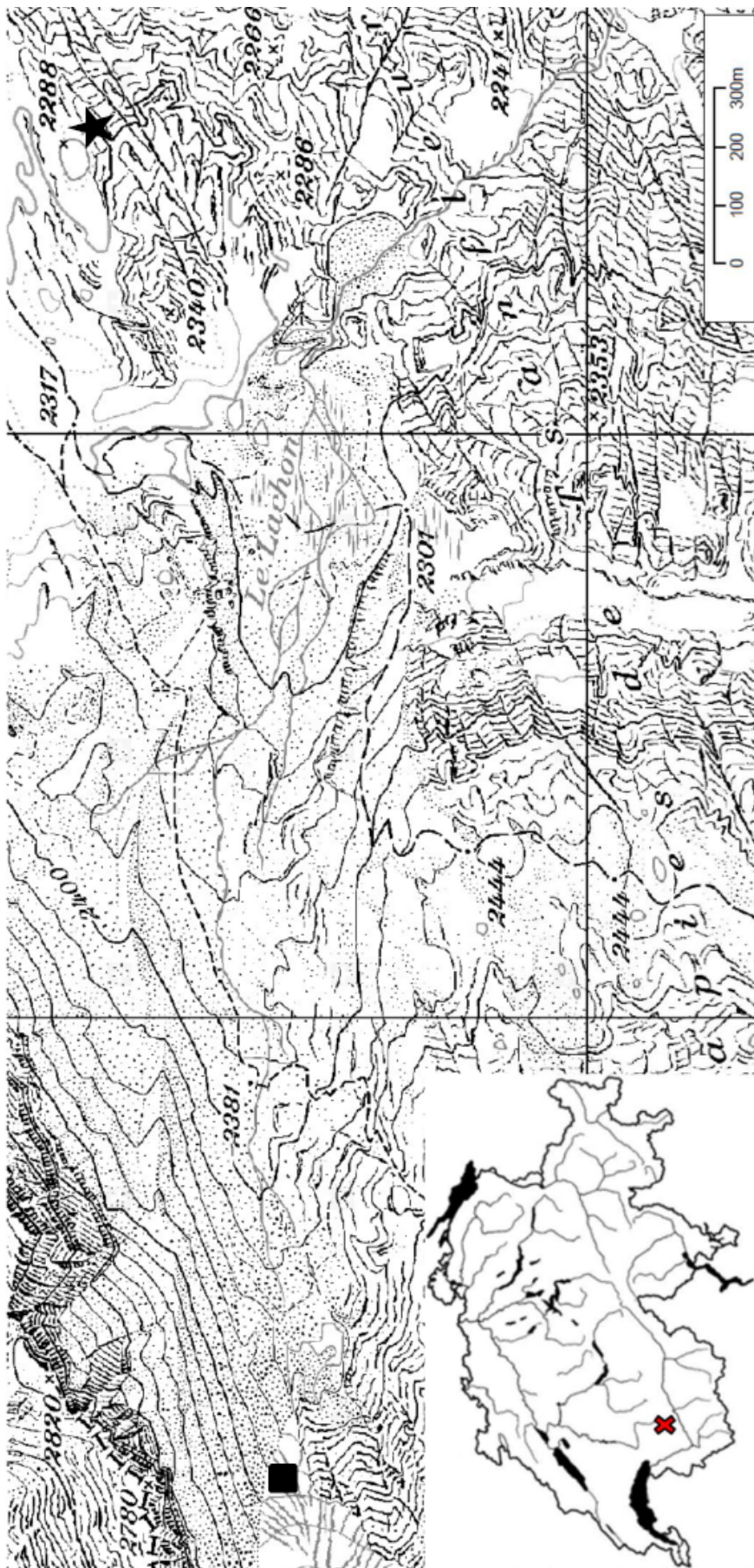


Figure 2

Figure 3

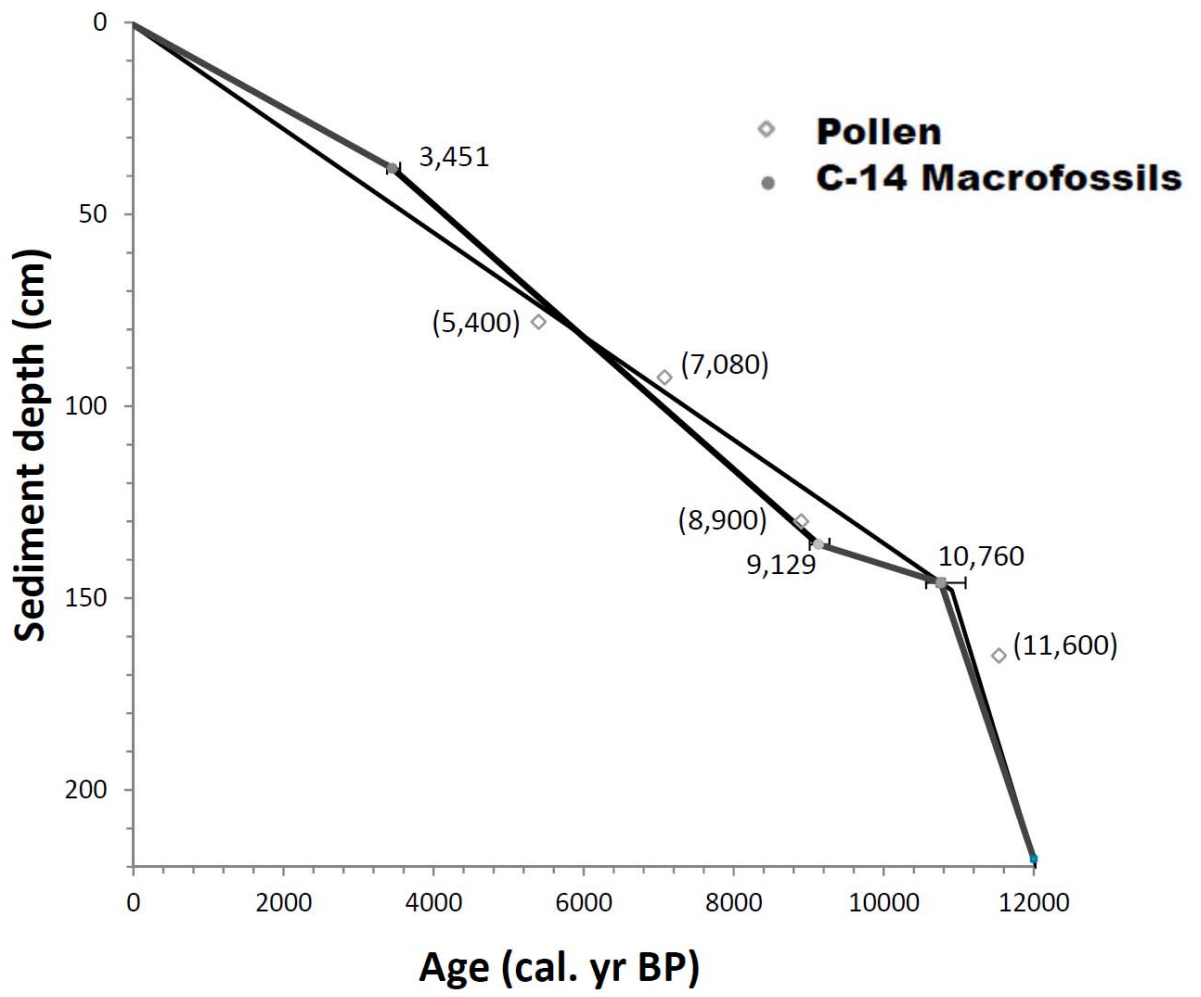


Figure 4

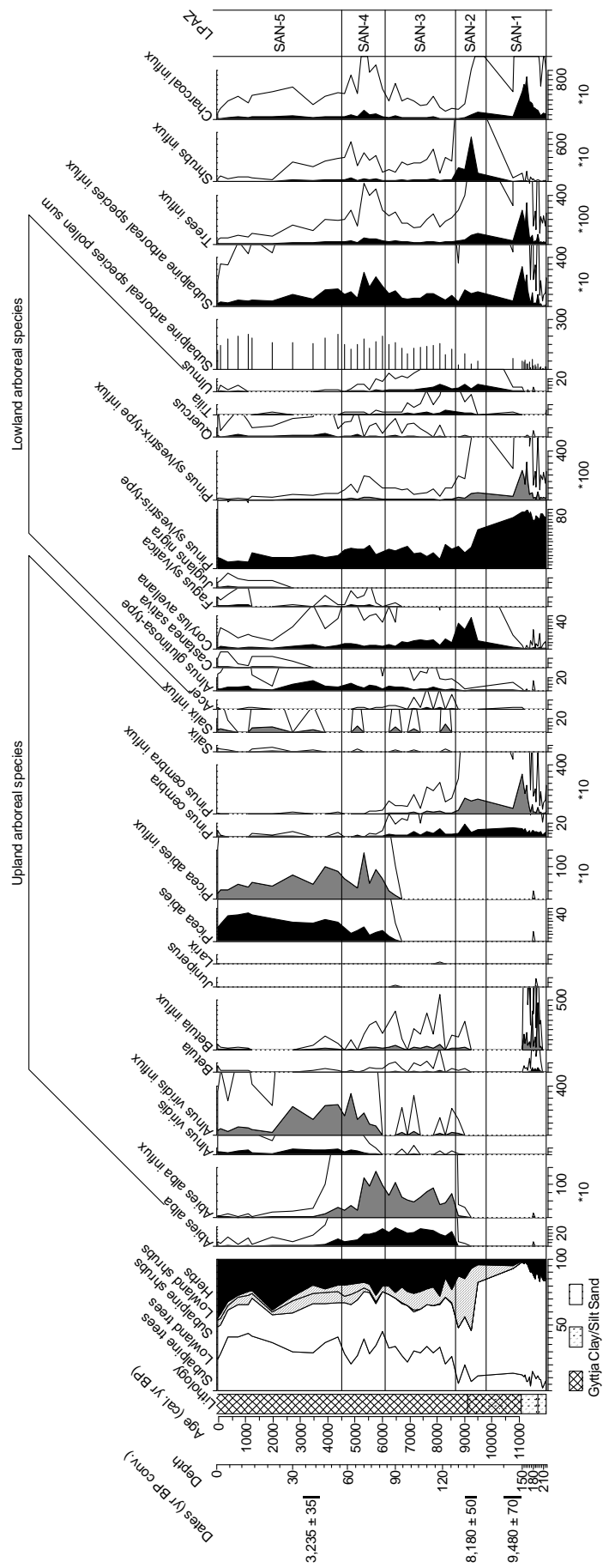


Figure 5

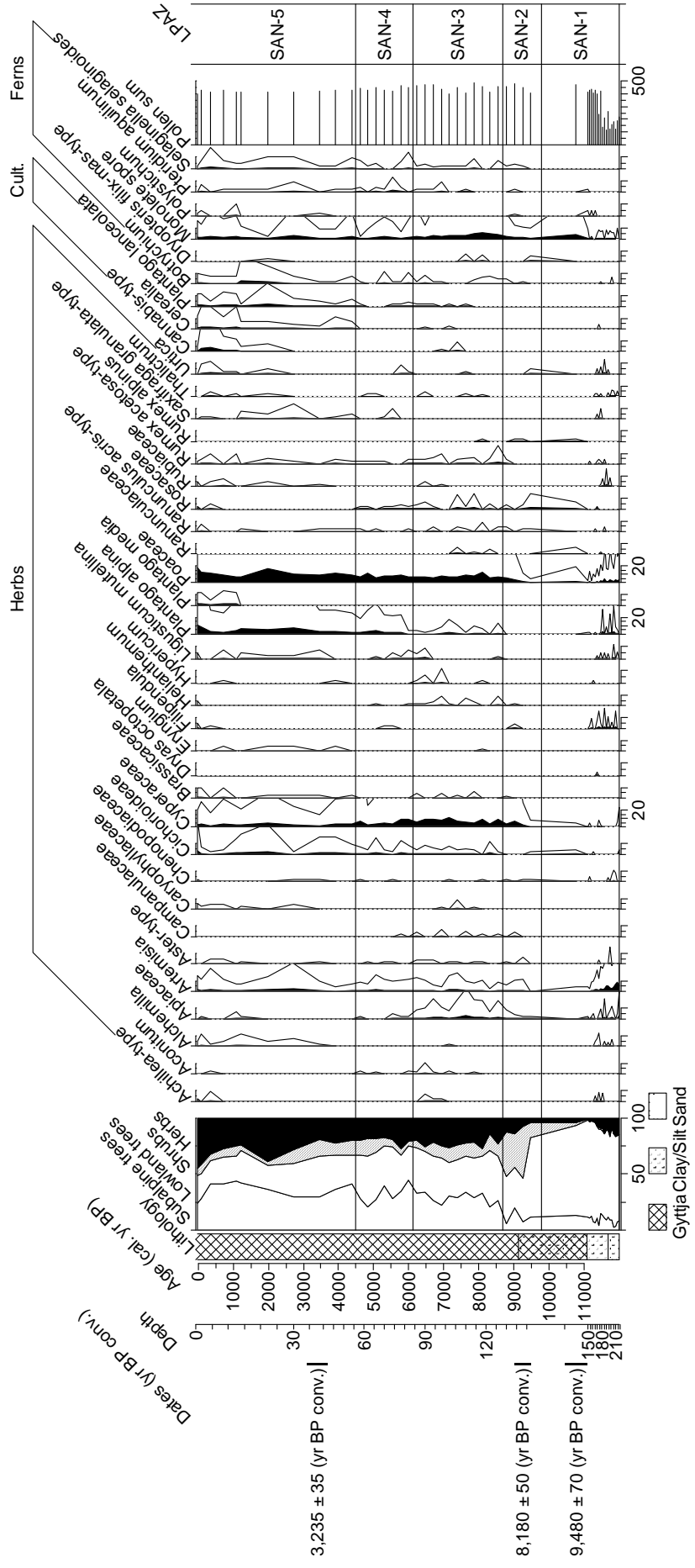


Figure 6

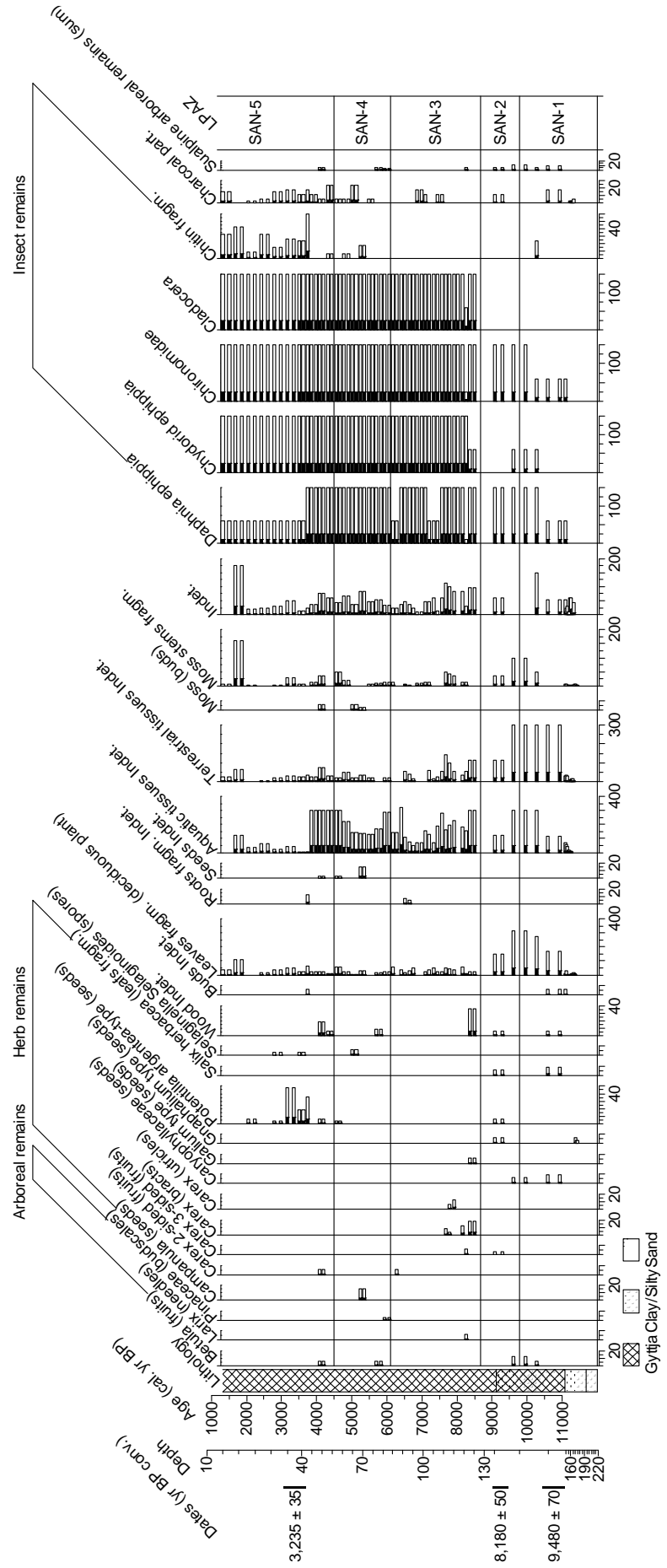
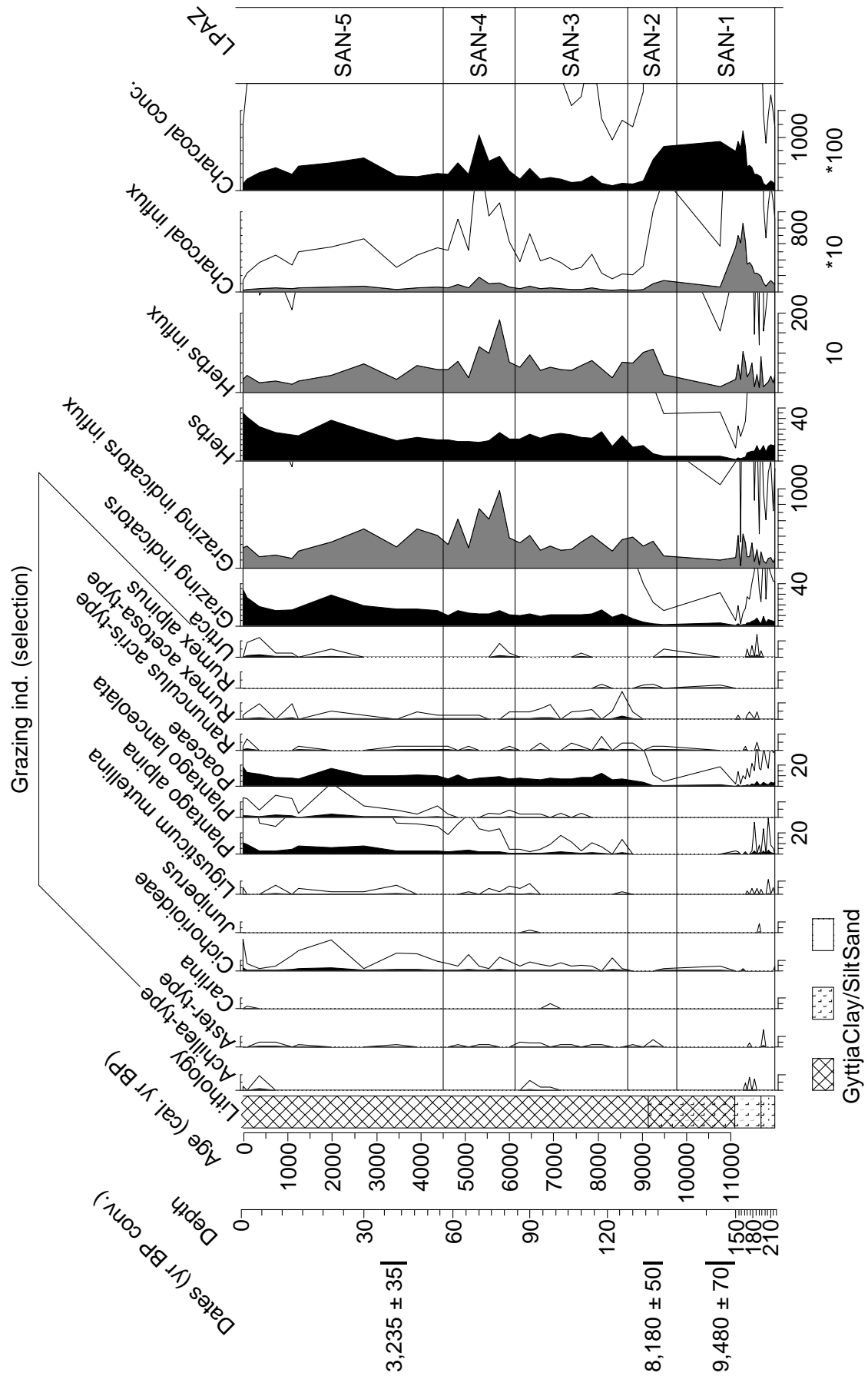


Figure 7



Summary of the manuscript

Vegetation at high altitudes is especially endangered by the prospected anthropogenic global warming. This is the motivation of the present study to address the main question, which is about the responses of alpine and treeline vegetation to Holocene climatic changes and or human land use by paleoecological methods. The sampled sediment cores used for the analysis originate from the small pond Emines, which is located at Sanetsch Pass (connecting the Valais and Bern, Switzerland) on an altitude of 2,288 m a.s.l. Possibly as a consequence of the windy pass situation, timberline and treeline at the study site are presently at ca. 1,950 m and 2,060 m a.s.l., respectively. Thus, Emines is located 230 m above today's locally lowered treeline.

Nowadays, the most eastern tongue of Glacier de Tsanfleuron is only at a distance of 2.5 km from the study site. However, the pond was ice free even at the largest extent of the glacier during the Little Ice Age (LIA) at 1860 AD, even though the glacier tongue was only about 500 m distant at that time.

Pollen samples were taken from the core and treated in the lab following standard preparation methods for pollen samples. For the calculation of pollen and charcoal influx, *Lycopodium* tablets were added to the sediment samples previous to the treatment. Macrofossil slices were collected using a sieve with a 0.2 mm mesh width. Identification of pollen and macrofossils largely followed the reference collection at the Institute of Plant Sciences of the University of Bern. For the charcoal analysis, only fragments larger than 10 µm were counted.

Due to a lack of terrestrial plant macrofossils only three radiocarbon dates could be measured. The age of the sediment base is estimated using the results from pollen and macrofossil analysis. To verify the age-depth model, further pollenstratigraphical dates are inferred by comparisons with well radiocarbon-dated pollen diagrams from the Central and Northern Alps. The age-depth model and dates inferred by pollen stratigraphy deviate by a few hundred years at most.

Collated results from pollen and macrofossil analysis show that the vegetation at Sanetsch Pass predominantly consisted of sparse alpine meadows during the past 12,000 years. However, with respect to treeline, individuals of *Betula*, *Larix decidua* and possibly *Pinus cembra* reached the pond after 10,300 cal. BP and persisted with varying abundance throughout the Holocene. Pioneer vegetation at Emines established at 11,300 cal. BP. Between 10,900 to 8,300 cal. BP the area around the pond was covered by alpine meadow and snow bed vegetation with e.g. *Salix herbacea*, Caryophyllaceae, *Galium*, *Gnaphalium*,

Potentilla argentea-type, *Carex* as well as scattered occurrence of *Betula* and *Larix*. Hardly any macrofossils are found during the mid Holocene indicating that Sanetsch Pass was still characterised by a sparse alpine-meadow vegetation cover, which persists also during late Holocene, although *Betula* fruits and *Potentilla argentea*-type seeds suggest a slightly denser alpine vegetation cover.

Sediment accumulation at Emnes was not disturbed during the entire Holocene implying that no glacier advance during the past 12,000 years substantially exceeded that of the LIA. Analysis of vegetation reaction at Emnes to small scale climate fluctuation during the Holocene showed that climatic change of ± 1 °C hardly influenced the vegetation composition. In contrast, the rapid warming of 3-4 °C at the Late Glacial/Holocene transition (11,600 cal. BP) caused significant altitudinal displacements of alpine species that were additionally forced by the rapid upward movement of trees and shrubs. Combination of human land use (i.a. increased fire regime) and a shift from subcontinental to a more oceanic climate during the second half of the Holocene caused the decline and even local extinction of *Pinus cembra* and *Abies alba* and advantaged *Picea abies* and *Alnus viridis*. *Pinus cembra* and *Abies alba* are very sensitive to increased fire regimes whereas *Alnus viridis* benefits from such disturbances. In addition, *Abies alba* and *Picea abies* are advantaged by the increased moisture conditions of the late Holocene. Thus, vegetation changes at Emnes were only in equilibrium with climate during the period 11,500–6,000 cal. BP, while afterwards human impact became important. Original alpine communities could persist throughout the Holocene, though during the past 6,000 years species promoted by grazing (e.g. *Plantago alpina*, *Potentilla argentea*-type; Cichorioideae) became more abundant.

Future alpine vegetation changes will be a function of amplitude and rapidity of global warming and forest and land-use management practices. Rising temperatures may induce an upslope migration of species. However, an increased fire regime, landscape fragmentation or shallow soils above the Holocene maximum treeline position may not allow a sufficient upward shift of trees. Habitat loss and species extinction at high altitude habitats will possibly be the consequence either way. This work demonstrates that vegetation at treeline is very sensitive to climate forcing and may react even more sensitive when climate changes are amplified through human impact. In this context, the results emphasise the necessity of climate change mitigation in order to prevent biodiversity losses under rapid, high amplitude anthropogenic global warming.

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Declaration

under Art. 28 Para. 2 RSL 05

Last, first name: Nadine, Berthel

Matriculation number: 09-105-842

Programme: M.Sc. in Climate Sciences
Master Thesis

Thesis title: Impact of Holocene climate changes on alpine and treeline
vegetation at Sanetsch Pass, Bernese Alps, Switzerland

Thesis supervisor: Prof. Dr. Willy Tinner

Thesis co-supervisor: Dr. Oliver Heiri

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person, except where due acknowledgement has been made in the text. In accordance with academic rules and ethical conduct, I have fully cited and referenced all material and results that are not original to this work. I am well aware of the fact that, on the basis of Article 36 Paragraph 1 Letter o of the University Law of 5 September 1996, the Senate is entitled to deny the title awarded on the basis of this work if proven otherwise.

.....
Place, date

.....
Signature

Appendix: Complete pollen and spore percentage

