Vegetation response to rapid climate change during the Lateglacial–Early Holocene transition at Gola di Lago, southern Switzerland

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BOREAS

Predicting the effects of ongoing climate warming on vegetation requires a long-term perspective of past ecosystem dynamics. We therefore analysed the sedimentary record from the mire Gola di Lago (985 m a.s.l.) in southern Switzerland, to better understand the vegetation response to past rapid climate change. We present a high-resolution pollen and plant macrofossil study from the Lateglacial to the Early Holocene (13 400–10 400 cal. a BP), a climatic transition that represents a close analogue to current global warming. The vegetation responses during this time match previously analysed palaeoecological sites south of the Alps. At the end of the Bølling-Allerød interstadial, the site was surrounded by open larch forest. The beginning of the Younger Dryas was characterized by the local presence and rapid expansion of *Pinus cembra*, whereas the second part was dominated by *Pinus sylvestris*, *Betula* and *Larix decidua*. These vegetation dynamics agree well with independent climate data indicating a cold and dry start and a subsequent shift to slightly warmer climate. The following rapid temperature increase at the beginning of the Holocene resulted in an increase in forest density and the establishment of novel temperate vegetation assemblages, without major changes in species diversity. Noteworthy, during the Younger Dryas–Early Holocene transition, long-lived cold-adapted tree line species such as *P. cembra* and *L. decidua* persisted over several centuries, while open boreal forests dominated by *P. sylvestris* and *Betula* expanded, indicating high resilience to climatic changes. The results of Gola di Lago suggest that climate warming led to a significant change in vegetation communities through species range shifts. Our study also indicates that some species may potentially be able to locally persist under current global warming, forming novel vegetation assemblages with newly establishing species.

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Ongoing global warming is already affecting ecosystems (Kovats *et al.* 2014) and further temperature increase will likely force species to either shift their distributional range or to adapt to the changing environmental conditions (Aitken *et al.* 2008; de Lafontaine *et al.* 2018). For rapid range shifts, plant species need efficient dispersal traits to track their suitable climate niche (McLachlan *et al.* 2005), consequently invading previously inhospitable habitats and existing communities (de Lafontaine *et al.* 2018; Birks 2019). During warm periods, temperate plant species tend to shift their distribution up-slope or pole-wards, whereas during cold periods their range is contracting and restricted to lower altitudes or latitudes and often limited to natural refugia, where adequate conditions for survival exist (Gobet *et al.* 2005; Médail & Diadema 2009; de Lafontaine *et al.* 2018). A key question is how large the amplitude of climatic fluctuations needs to be to overcome the inherent resilience of vegetation communities to external disturbances, which is an important feature for vegetation communities to survive in a changing environment (Moris *et al.* 2017a; Timpane-Padgham *et al.* 2017). A resilient forest ecosystem has the ability to absorb disturbances, maintaining its state (i.e. function and structure) during internal fluctuations and environmental changes, allowing the species' persistence in a changing habitat (Mumby *et al.* 2014; Moris *et al.* 2017a).

High-resolution studies of past vegetation dynamics are essential for a better understanding of the capacity of species to migrate and/or adjust to new environmental conditions under global change. After the Last Glacial Maximum (LGM) large-scale climate fluctuations (Heiri *et al.* 2015) caused dynamic species responses through range shifts and adaptation (Davis & Shaw 2001). The individuals living at the edge of the expansion range of a population lie at the ecological and geographical fore-front and are thus expected to react very sensitively to climatic fluctuations (de Lafontaine *et al.* 2018), which makes them especially suited to investigate species response to climate change. The transition from the Younger Dryas to the Early Holocene, around 11 700 cal. a BP (calibrated years before present), when temperatures increased about 3–4 °C in half a century, is a close analogue to current climate warming in terms of rates of change (von Grafenstein *et al.* 2000; Walker *et al.* 2012). Understanding the vegetational changes that occurred during this short transition can help to improve predictions of the possible vegetation response to current global warming.

In this study, we analyse the consequences of the Younger Dryas–Early Holocene climate warming on the vegetation around Gola di Lago. The site is located in the montane belt of the Swiss Southern Alps. A previous

study carried out by Zoller & Kleiber (1971) gives an overview of the vegetation history at Gola di Lago. According to the authors, the site was surrounded by open forests of *Larix decidua* and *Pinus cembra* during the Younger Dryas. With Early Holocene warming, those species were able to expand upslope and declined locally, whereas *Pinus sylvestris* was able to expand around the site together with temperate trees and shrubs. However, low numbers of macrofossils indicate that *L. decidua* stands were able to persist locally at Gola di Lago after the Younger Dryas, suggesting a certain resilience to environmental changes. Unfortunately, the time resolution provided by Zoller & Kleiber (1971) does not allow the vegetation responses during the Younger Dryas–Early Holocene transition to be studied in detail. Thus, the overall goal of this study is to analyse the vegetation responses to rapid temperature increase more in depth. Using palaeoecological tools, such as pollen, macrofossil and charcoal analysis, we provide a high-resolution study that covers the Lateglacial to the Early Holocene transition. More specifically, we aim to (i) compare the vegetation response at Gola di Lago with other sites from southern Switzerland and northern Italy, (ii) analyse the impact of the rapid temperature increase on the species diversity, and (iii) study the postglacial vegetation response at Gola di Lago, with a special focus on the resilient character of *L. decidua*.

Study site

The mire Gola di Lago (latitude 46°06′17″N, longitude 8°57′55″E, altitude 985 m a.s.l.) is located in Ticino (southern Switzerland). The site is a small (3 ha) minerotrophic peatland, with two permanent streams entering and one main stream draining the mire from south to north (Cheburkin *et al.* 2006; Fig. 1). Originally, Gola di Lago was a lake formed after the deglaciation and transitioned to a mire during the Late Holocene (Zoller & Kleiber 1971). The geology of the area is characterized by crystalline silicate rocks (Zoller & Kleiber 1971; Felber 1993). Current climate at Gola di Lago is cool temperate with mean annual temperature and precipitation of 8.3 °C and 1559 mm, respectively. January is the coldest and July the warmest month with mean temperatures of −1.5 and 15.8 °C, respectively (adjusted to the elevation of Gola di Lago from the nearby meteorological station at Lugano using standard lapse rates, means based on the norm period 1981–2010; MeteoSwiss 2020).

The vegetation within the mire is mainly composed of *Trichophorum cespitosum* and *Carex elata* (Cheburkin *et al.* 2006). Gola di Lago is situated in the montane belt of the Southern Swiss Alps, which is dominated by *Fagus sylvatica* and co-dominated by *Abies alba*. Locally, *Betula pendula* stands dominate the surroundings of the mire together with scattered *F. sylvatica*. Pure sweet chestnut (*Castanea sativa*) forests and mixed oak-sweet chestnut forests comprising e.g. *Corylus avellana*,

Fraxinus excelsior, *Tilia* and *Ulmus* occur in the colline belt, just below the site (Zoller 1960; Valsecchi *et al.* 2010). The subalpine belt above the site is dominated by *Picea abies* and *L. decidua*, whereas *Pinus* species are present sporadically in the Insubrian region (Zoller & Kleiber 1971; Valsecchi & Tinner 2010; Valsecchi *et al.* 2010).

Material and methods

Coring and chronology

In October 2019, four parallel cores were taken, 1 m apart from each other, where peat and mineral deposits were deepest. One-metre-long core sections were retrieved with a modified Streif-Livingstone piston-corer with a diameter of 8 cm for the upper part of the core and 5 cm diameter for the deepest part. The uppermost 0.5–1 m of sediment was taken with a Russian corer to avoid compaction of peat material. The cores were transported to the Palaeoecological Laboratory of the Institute of Plant Sciences at the University of Bern, where they were extruded, analysed and visually correlated according to lithostratigraphical features, resulting in a complete master core of 572 cm.

The chronology of the sequence is based on accelerator mass spectrometry (AMS) radiocarbon dating of terrestrial plant macrofossils. Overall, 11 macrofossil samples were dated, whereof eight dates are included in the analysed high-resolution sequence. The resulting ^{14}C dates were converted to calibrated ages (cal. a BP) in R (version 3.6.0; R Core Team 2020) using the package 'clam' (Blaauw 2010) with the IntCal20 calibration curve (Reimer *et al.* 2020). The age-depth model was also calculated with 'clam'. The dates were interpolated using a monotonic spline function and a mixed-effect model was used to calculate the 95% confidence-envelope (Heegaard *et al.* 2005).

Pollen, spores and charcoal analysis

For the high-resolution analysis, 56 contiguous subsamples of 1 cm^3 sediment were taken (350–294 cm). The pollen slides were prepared following standard procedures using HCl, KOH, HF and acetolysis (Moore *et al.* 1991). *Lycopodium* tablets (Stockmarr 1971) were added to the samples to calculate concentrations and influx. The pollen slides were analysed under a light microscope at 400-fold magnification. A minimum of 500 pollen grains, excluding aquatic pollen and spores, was counted per sample. Pollen grains, spores and stomata were identified using palynological keys (Moore *et al.* 1991; Beug 2004), the pollen atlas of Reille (1992) and the reference collection of the Institute of Plant Sciences at the University of Bern. For each pollen slide, microscopic charcoal particles >10 μm were counted following Finsinger & Tinner (2005) and Tinner & Hu (2003). The pollen and charcoal diagram was drawn in Tilia (version
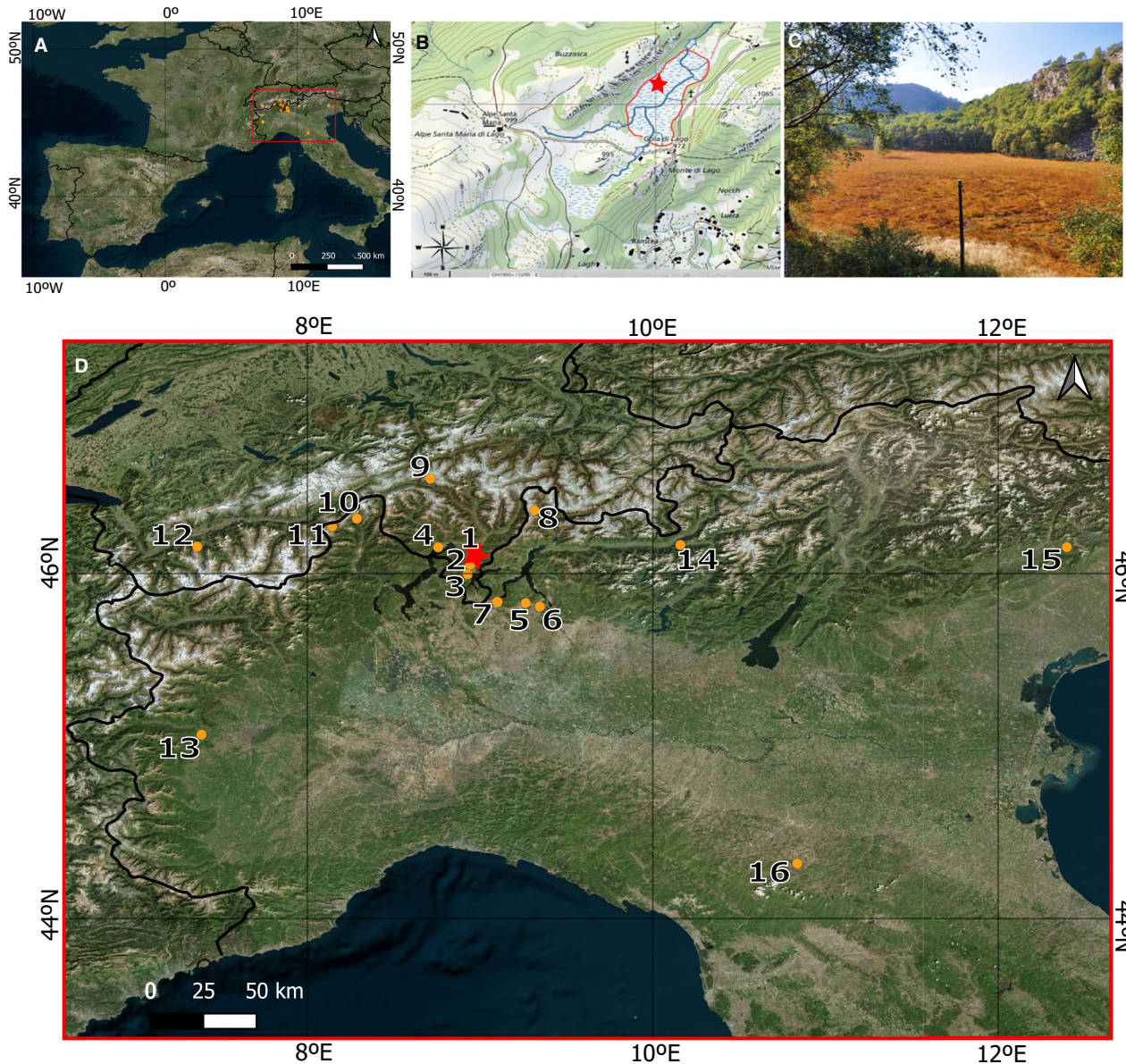
Fig. 1. A. General map of south-western Europe indicating the study area (base map source: Bing VirtualEarth). B. Topographic map of the mire Gola di Lago (https://map.geo.admin.ch). The red line highlights the extent of the mire, the red star indicates the coring location. Inflowing streams are indicated by blue lines. C. Picture of the study site, showing the mire Gola di Lago surrounded by birch trees. D. Map of Switzerland and northern Italy showing the sites mentioned in the text: 1 = Gola di Lago (our study site, marked with a red star); 2 = Lago di Origlio; 3 = Lago di Muzzano; 4 = Balladrum; 5 = Lago del Segrino; 6 = Lago di Annone; 7 = Lago di Como; 8 = Lago Basso; 9 = Lago Cadagno; 10 = Lago Inferiore del Sangiatto; 11 = Alpe Veglia; 12 = Gouillé Rion; 13 = Lago Piccolo di Avigliana; 14 = Pian di Gembro; 15 = Palughetto; 16 = Pavullo nel Frignano.

2.6.1.) and subdivided into statistically significant local pollen assemblage zones (LPAZ) using zonation of optimal partitioning with minimal sum-of-squares and broken-stick with R (version 3.5.3).

Macrofossil analysis

Fifty-six contiguous subsamples of 1 cm thickness and a volume of 12–20 cm^3 were taken at the same depths as the pollen subsamples (350–294 cm). These sediment samples were first frozen (−20 °C) to disaggregate the sediment matrix and then sieved with a mesh size of 200 μm. The macrofossils were identified and counted with a stereomicroscope using various identification keys (Schoch *et al.* 1988; Cappers *et al.* 2006) and the reference collection of the Institute of Plant Sciences at the University of Bern. The macrofossil diagram was drawn in Tilia (version 2.6.1.).

Numerical methods

Ordination analysis. – To identify the main ecological gradients driving the species assemblage, we analysed the pollen percentage data with different ordination methods in Canoco5 (version 5.2). We chose to use linear distribution models, because the first axis of the detrended correspondence analysis (DCA) measured 1.6 standard deviation units (SD units; Lepš & Šmilauer 2003). The pollen percentage data were log-transformed and analysed using principal component analysis (PCA). Microscopic charcoal influx (as a proxy for regional fire activity) was added passively to the PCA as a supplementary variable.

To quantify the vegetation change at Gola di Lago and identify the emergence of novel vegetation communities we estimated the degree of dissimilarity between terrestrial pollen assemblages. We first used non-metric multidimensional scaling (NMDS) with chord-distance as a dissimilarity measure to identify similar vegetation communities as classified by the LPAZ. We then calculated rate of change (RoC) between adjacent pollen samples and novelty based on chord-distance after Finsinger *et al.* (2017). Chord-distance was also used to quantify the degree of dissimilarity between individual pollen samples and all other subsequent samples in the record. The numerical analyses were carried out with Canoco5 and R, using code provided by Finsinger *et al.* (2017).

Floristic diversity analysis. – To reconstruct past biodiversity changes, we calculated palynological richness (PRI) and the probability of interspecific encounter (PIE; Birks & Line 1992). PRI is a measure for species richness and calculated with rarefaction analysis, which allows standardization of the number of pollen taxa (in our case to a minimal pollen sum of 508 pollen). PIE is a measure for species evenness and estimates to what extent the dominant taxa influence the total number of pollen types in a sample (van der Knaap 2009). The biodiversity analyses were performed with R (version 3.5.3) using the package 'vegan' (Oksanen *et al.* 2015).

Species response curves. – Response curves quantify the response of species to environmental drivers, allowing an estimation of the environmental optimum of a species and its tolerance to disturbance (Lepš & Šmilauer 2003). Using generalized additive models (GAMs) we analysed the responses of *L. decidua*, *P. sylvestris* type, *P. cembra*, tree *Betula* and *Betula nana* to charcoal influx (as a proxy for fire) and temperature (data set from Heiri *et al.* 2015). We created the models with Canoco5 (version 5.2), by using a maximum of two degrees of freedom, a Gaussian distribution and stepwise selection based on the Akaike information criterion.

Table 1. Sedimentology of the Gola di Lago record.

Depth (cm)	Age (cal. a BP)	Deposit
0–142	NA	Peat
142–205.5	NA	Gyttja
205.5–276.5	NA–10 082	Peat
276.5–364.5	10 082–15 350	Gyttja
364.5–398	13 350–17 630	Organic-rich clay
398–439	17 630–NA	Sandy clay
439–531	NA	Clay with sand
531–572	NA	Sandy clay

Results and interpretation

Lithology and chronology

The master core measures 572 cm. The bottom of the sediment (Table 1) consists of sandy clay (572–398 cm) with a section where the clay dominates (531–439 cm). From 398 to 364.5 cm the sediment consists of organic-rich clay, followed by gyttja (364.5–276.5 cm). Further upwards, the sediment consists of peat (276.5–0 cm) only interrupted once by gyttja at 205.5–142 cm. The age depth model (Fig. 2, Table 2) spans from 18 000 to 9300 cal. a BP (406–238 cm).

The sand and clay at the bottom of the sediment record indicate that soil or lake shore erosion was high. The
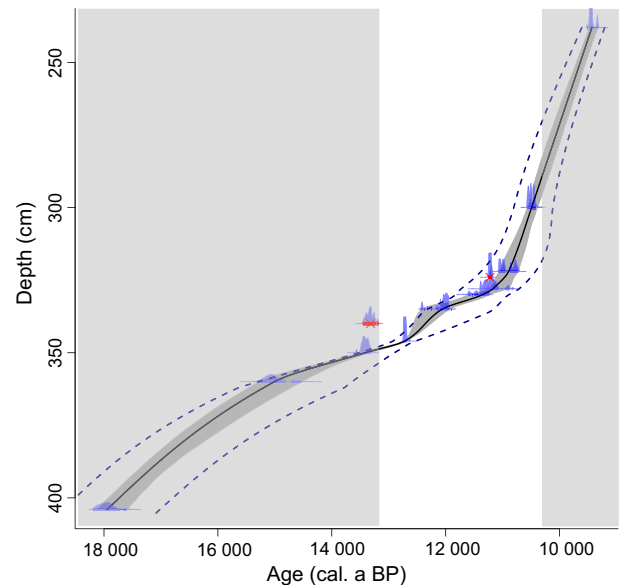

Fig. 2. Age-depth model from the mire Gola di Lago. The model is based on a monotonic spline interpolation (black line). The 95% confidence interval of the model based on Monte Carlo sampling of the weighted probability distributions is shown with the dark grey area along the interpolation line. The extended 95% confidence interval based on mixed-effect modelling is shown by the dashed blue lines. The calibrated ages of the terrestrial macrofossils are shown in blue and two dates were rejected (red). The white area represents the focus section of this study for the high-resolution analysis.

Table 2. Radiocarbon dates from the Gola di Lago sediment record. N = needles; BS = bud scales; F = fruits; LF = leaf fragments; TF = twig fragments; P = periderm. Modelled age in diagrams refers to the 'best' age estimate given by the model. *Rejected, due to ages being too old.

Lab. code	Depth (cm)	Material	^{14}C ages (a BP)	Calibrated age (cal. a BP, 2σ-range)	Modelled age (cal. a BP) in diagrams
BE-12291.1.1	238–239	*Abies* N, *Pinus* P, deciduous LF	8400±25	9317–9520	9434
BE-13068.1.1	300–301	Deciduous TF	9295±25	10 407–10 576	10 495
BE-12290.1.1	322–323	*Pinus* and *Larix* N, P, deciduous LF	9545±25	10 715–11 073	10 902
BE-12289.1.1	324–325*	*Larix* and *Pinus* N, P, *Betula* F	9800±30	11 190–11 250	Rejected
BE-13069.1.1	328–329	*Betula* F, conifer BS, conifer P, *Larix* N	9755±60	10 820–11 269	11 173
BE-12412.1.1	330–331	*Larix* N, *Betula* F, conifer BS, P	9920±50	11 232–11 607	11 362
BE-13070.1.1	335–336	Conifer P, conifer BS, *Betula* F, deciduous LF	10 230±25	11 890–12 437	12 068
BE-12411.1.1	340–341*	*Larix* N, *Betula* F, *P. cembra* N, BS, P	11 455±50	13 188–13 451	Rejected
BE-13876.1.1.	346–347	*Betula* F, *Larix* N, conifer P, deciduous bark	10 720±35	12 685–12 743	12 716
BE-12288.1.1	350–351	*Larix* and *Pinus* N, P, *Betula* BS	11 550±50	13 313–13 567	13 415
BE-12287.1.1	360–364	*Betula* F, conifer BS, conifer P	12 640±90	14 537–15 313	15 192
BE-12286.1.1	404–406	Terrestrial plant LF and TF	14 640±70	17 589–18 198	17 941

transition from clay to gyttja at 364.5 cm (15 350 cal. a BP) documents the shift from allochthonous to autochthonous sedimentation. Subsequent gyttja deposition over the entire focus period of this study (350–294 cm, 13 400–10 400 cal. a BP; Table 1) suggests rather stable depositional and environmental conditions (Tinner *et al.* 2016). As a consequence, the sedimentation rates are high until *c.* 15 000 cal. a BP, reflecting erosional input, then subsequently decline with catchment stabilization. The increase of sedimentation rates at 11 000 cal. a BP may reflect rising productivity. The average sample resolution is 51±46 years (mean±standard deviation).

Pollen, macrofossil and charcoal analysis

The pollen record (Fig. 3) consists of six statistically significant local pollen assemblage zones (LPAZ from GDL-1 to GDL-6). We used the same LPAZ to subdivide the macrofossil diagram (Fig. 4).

GDL-1 (13 400–12 500 cal. a BP). – Arboreal pollen remains stable around 80%, indicating open forest conditions during this period of the Lateglacial. *Pinus sylvestris* type and *P. cembra* pollen are dominant, reaching 50 and 20%, respectively. However, as *P. sylvestris* is a high pollen producer it is overrepresented in the pollen assemblage. Nevertheless, several *P. sylvestris* type and a single *P. cembra* needle as well as the continuous presence of *Pinus* stomata point to the local presence of these tree species. The continuous presence of *L. decidua* needles, as well as *B. pubescens* type fruits and *Betula* pollen above 10% indicate the local presence of these taxa around the lake. Few pollen grains (<5%) but no macrofossils of temperate taxa such as *Quercus robur* type, *Alnus glutinosa* type, *Tilia* and *Acer* suggest the presence of these taxa nearby, probably at lower elevations. *B. nana* and *Juniperus* type pollen are continuously present and a single *B. nana* type fruit was found, suggesting that this shrub was part of the open forest understory. Herb pollen

stays around 20% during this zone and is dominated by pollen of Poaceae and *Artemisia* and many other taxa co-occur, such as Caryophyllaceae, *Rumex acetosa* type and *Rumex acetosella* type, suggesting the presence of diverse grasslands. Relatively low microscopic charcoal influx values and only scattered finds of macroscopic charcoal particles point to low fire activity during this zone. An increase in microscopic charcoal influx from *c.* 12 800 cal. a BP onwards suggests rising regional fire activity.

GDL-2 (12 500–12 250 cal. a BP). – Arboreal pollen remains stable around 80%, whereas tree pollen drops from 70 to almost 60%. In this zone *P. cembra* pollen significantly increases to almost 40%, whereas *P. sylvestris* type pollen decreases to 20%. While tree *Betula* pollen decreases by 5%, macrofossil remains of tree *Betula* appear continuously, indicating its presence at the site. *Larix* stomata decrease almost to zero, indicating a contraction of larch populations at Gola di Lago. Similarly, pollen data suggest that temperate *Quercus* declined below the site. *Betula nana* type pollen increases by 5% and fruits are found more frequently. *Artemisia* pollen decreases to less than 5% during GDL-2 and towards the end of this zone increases again up to almost 10%. While *Artemisia* pollen abundances are low, *Ranunculus* seeds increase and Cyperaceae pollen reaches almost 5%, pointing to an expansion of shore vegetation possibly due to a lowering of the lake level. The simultaneous occurrence of a small increase in macroscopic charcoal particles and a microscopic charcoal influx peak at 12 450 cal. a BP suggest a minor increase in local and regional fire activity.

GDL-3 (12 250–11 400 cal. a BP). – At the beginning of this zone, tree pollen is at a minimum of 60% and increases to 80% towards the end of the zone. Arboreal pollen remains stable at 80% and increases by ~5% at the end of GDL-3 (*c.* 11 500 cal. a BP). The start of GDL-3 is characterized by the transition of high pollen

Fig. 3. Pollen and charcoal diagram of Gola di Lago. Pollen percentages (%) are based on the terrestrial pollen sum. Selected pollen types are listed only. The diagram is divided into six statistically significant local pollen assemblage zones (LPAZ). Empty curves show 10× exaggeration. Dotted lines show climatic periods.

abundance from *P. cembra* (drops from >30% in previous zone to 10%) to *P. sylvestris* type (increases from <30 to >40%). *Larix* stomata and *Larix decidua* macrofossil finds indicate that larch was present around the lake. Contiguous *B. pubescens* type and *B. nana* fruit finds point to their local presence at Gola di Lago. *Alnus glutinosa* fruits occur around 11 700 cal. a BP also indicating its presence around the lake. Pollen of

temperate taxa such as *Q. robur* type, *Ulmus* and *Tilia* are consistently found in low percentages (<5%). At the onset of the zone, *Artemisia* and Poaceae pollen increases up to almost 10% each, whereas pollen of the other herbaceous taxa becomes less important. Low pollen percentages of temperate species suggest the presence of temperate forests at lower altitudes. The *Pediastrum* algae peak around 11 800 cal. a BP,

Fig. 4. Macrofossil diagram of Gola di Lago. The concentrations of the selected macrofossils are calculated for the smallest sample volume (12 cm³). The concentration is given in particles per 12 cm³ or area per 12 cm³. The diagram is divided into six statistically significant local pollen assemblage zones (LPAZ). Empty columns show 10× exaggeration. Dotted lines show climatic periods.

together with the increase of Characeae oogonia, point to an increase in lake level. While macroscopic charcoal stays at low values throughout GDL-3, microscopic charcoal influx decreases continuously, suggesting a decrease in regional fire activity.

GDL-4 (11 400–10 700 cal. a BP). – Arboreal pollen slowly increases through the whole zone reaching ~90% around 10 900 cal. a BP, suggesting that forests became quite dense. *Pinus sylvestris* type pollen fluctuates around 45%, while pollen of temperate tree taxa such as *Q. robur* type, *Alnus glutinosa* type, *Ulmus* and *Corylus* increases. *Larix decidua* stomata and needles drop after 11 200 and 10 900 cal. a BP respectively, indicating a decrease in larch stands around the site. *Alnus glutinosa* and *Salix* macrofossils increase from 11 200 cal. a BP onwards, indicating the local presence of these species around the lake. Herb pollen decreases from 15 to 10%, mostly due to the continuous decrease of *Artemisia* and Poaceae pollen grains. An increase in monolete spores, Cyperaceae pollen and *Carex* fruits may have resulted from a further lake level rise. While macroscopic charcoal stays at low values throughout GDL-4, microscopic charcoal influx increases through the whole zone, suggesting a marked rise in regional fire activity.

GDL-5 (10 700–10 650 cal. a BP). – This zone lasts less than 60 years and is characterized by a sudden herb and shrub pollen increase (5%), driven by Poaceae and *Corylus*, as well as a decline in arboreal pollen to 75%, indicating a short-lived forest opening. High frequencies of *Najas* seeds and monolete spores are recorded. While microscopic charcoal stays at stable values, a small rise in macroscopic charcoal points to a minor increase in local fire activity.

GDL-6 (10 650–10 400 cal. a BP). – Arboreal pollen remains constantly high (90%), suggesting closed forest conditions. *Artemisia* pollen decreases (<5%) and Poaceae, *Ranunculus acris* type and Cyperaceae pollen become dominant among the herbs. *Betula nana* type fruits decrease and *B. nana* pollen percentages remain below 5%. *Corylus* pollen increases reaching 10%. *Larix decidua* stomata and macrofossils decrease in this zone, together with *P. cembra* pollen (>10%) and needles. The dominance of *P. sylvestris* type pollen (45–50%) and the presence of *P. sylvestris* type needles indicate that the forest around the lake was mainly composed of pine stands. The recorded macroscopic charcoal increase towards the end of this zone points to a rise in local fire frequency, while microscopic charcoal inferred regional fire activity declined.

Ordination

PCA axis 1 (Fig. 5A) explains 58.4% of the variation in the data and shows a gradient from temperate and even submediterranean taxa such as *Corylus*, *Quercus ilex* type and *Ulmus*, having low PCA axis 1 scores, to cold adapted or tolerant taxa such as Poaceae, *Artemisia* and *B. nana*, reaching high scores. PCA axis 2 is driven by the opposite pollen curves of *Pinus sylvestris* and *Pinus cembra*, perhaps reflecting a moisture gradient. The passive plotting of microscopic charcoal influx into the PCA (Fig. 5A) shows the positive correlation of fire activity with temperate taxa, suggesting that increasing biomass (as a result of Holocene warming) may have provided more fuel (Marlon *et al.* 2006).

NMDS axis 1 (Fig. 5B) describes the dissimilarity of different vegetation communities. The LPAZ encompassing the Younger Dryas cold period (GDL-2 and 3) have high axis 1 scores, whereas the Early Holocene LPAZ (GDL-4–6) have low scores, suggesting that climate warming caused substantial vegetational differences between these two periods. Species compositions before (GDL-1) and right after the Younger Dryas (GDL-4) have intermediate axis 1 values, suggesting similar vegetation composition under rather warm Bølling-Allerød interstadial and Early Holocene temperatures. When looking at dissimilarity between samples (Fig. 5C) as well as RoC and novelty over time (Fig. 6) the largest vegetation change occurs within the Younger Dryas cold period at *c.* 12 250 cal. a BP. It is also evident that the first part of the Younger Dryas (GDL-2) has a distinct vegetation composition dissimilar to the other samples in the record. The heatmap also shows that there was a gradual vegetation change in response to the rapid climate warming at the beginning of the Holocene, with distinct and novel vegetation communities establishing after *c.* 11 000 cal. a BP.

Diversity proxies

PRI shows no clear trend but large fluctuations throughout the record, e.g. a sharp decrease at 12 200 cal. a BP and a marked increase at 11 600 cal. a BP. PIE increases at *c.* 12 600 cal. a BP with the decline of dominant *P. sylvestris* type, to remain high until *c.* 11 500 cal. a BP, when it decreases slightly in response to the re-expansion of pine forests.

Species response curve

The GAMs show the response of different species to increasing charcoal influx and summer temperatures (Fig. 7). The response of *P. cembra* to fire is not shown, because it is not statistically significant. *Larix decidua* does not show major changes in response to increasing fire activity or July temperatures, likely due to very low pollen percentages throughout the record. Instead, both tree *Betula* and *B. nana* show a negative response to fire, while *P. sylvestris* type shows a positive response to fire and July temperatures. *Pinus cembra* and *B. nana*
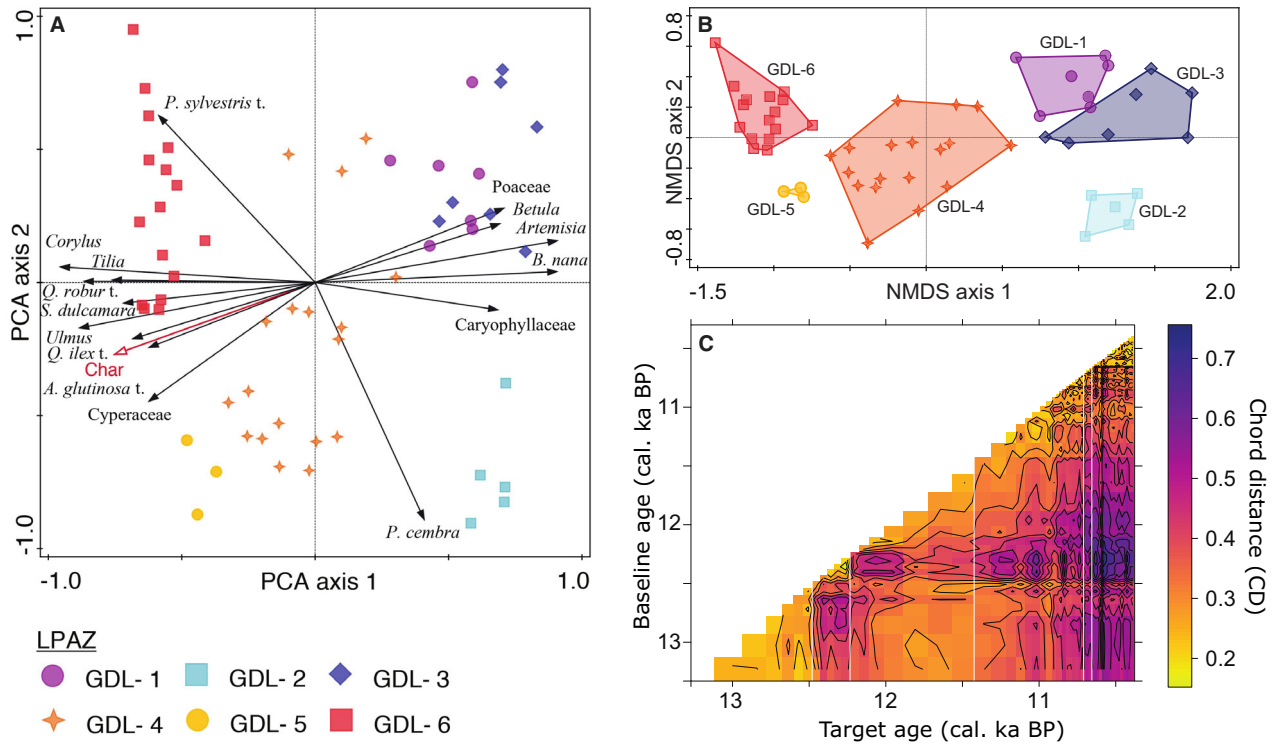
Fig. 5. Ordination and dissimilarity analyses of the Lateglacial–Early Holocene transition at Gola di Lago. A. Principal component analysis (PCA) biplot showing species (t., type; black arrows) and sample scores (symbols) grouped by local pollen assemblage zone (LPAZ). Charcoal influx (Char; red arrow) is added as a supplementary explanatory variable. The first axis explains 58.4% of the variance and the second axis 10.5%. B. Non-metric multidimensional scaling plot showing dissimilarity of samples in chord distance (CD) along two axes. The samples are grouped by LPAZ. C. Novelty analysis presented as a heatmap, showing the dissimilarity in CD between individual samples (baseline age) and all subsequent samples in the record (target age).

decrease with increasing July temperatures, as does tree *Betula* with July temperatures higher than 14 °C.

Discussion

Lateglacial–Early Holocene vegetation dynamics along an altitudinal transect

Our results indicate that at 13 400 cal. a BP Gola di Lago was forested by *Betula*, *L. decidua* and *P. sylvestris*. Similar vegetation conditions were reconstructed at Palughetto at comparable elevation in northeastern Italy (1040 m a.s.l.; Fig. 1; Vescovi *et al.* 2007) and at Pian di Gembro (1350 m a.s.l.; Fig. 1; Pini 2002) at higher elevation in the central Alps. Low pollen abundances from temperate taxa at Gola di Lago reflect the lowland vegetation below our site. The expansion of temperate

trees in the lowlands at *c*. 13 000 cal. a BP is observed in several records from southern Switzerland and Italy for instance at Lago di Origlio (Fig. 1; Tinner *et al.* 1999), Lago di Muzzano (337 m a.s.l.; Fig. 1; Tinner *et al.* 2005), Balladrum (Hofstetter *et al.* 2006), Lago di Como (198 m a.s.l.; Fig. 1; Martinelli *et al.* 2017), Lago di Annone (226 m a.s.l.; Fig. 1; Wick 1996) and Lago Piccolo di Avigliana (353 m a.s.l.; Fig. 1; Finsinger *et al.* 2006).

The onset of the Younger Dryas (*c*. 12 800 cal. a BP) is characterized by a temperature drop of about 3–4 °C and a shift to drier conditions within *c*. 150 years (von Grafenstein *et al.* 2000; Schwander *et al.* 2000; Heiri & Millet 2005; Rach *et al.* 2014). At Gola di Lago the Younger Dryas displays two distinct phases with pollen-inferred statistically different vegetation compositions during GDL-2 (12 500–12 250 cal. a BP) and GDL-3

Fig. 6. Comparison of biotic proxies at Gola di Lago. Pollen percentage and macrofossil concentrations based on the smallest sample volume (12 cm³) of (A) *Larix decidua*; (B) *Pinus cembra* (blue) and *Pinus sylvestris* (light blue); (C) *Betula nana* (light green) and tree *Betula* (green). D. Influx values (# cm⁻² a⁻¹) of microscopic charcoal. E. PCA axis 1 scores. F. Proxies for species diversity: palynological evenness (PIE), palynological richness (PRI). G. Novelty of pollen assemblage measured in chord distance compared to all previous samples in the record. H. Rate of change (RoC) between adjacent pollen assemblages measured in chord distance. I. July temperature reconstruction based on six chironomid records from the Alps (Heiri *et al.* 2015). M = macrofossil; P = pollen; PO = Preboreal oscillation.
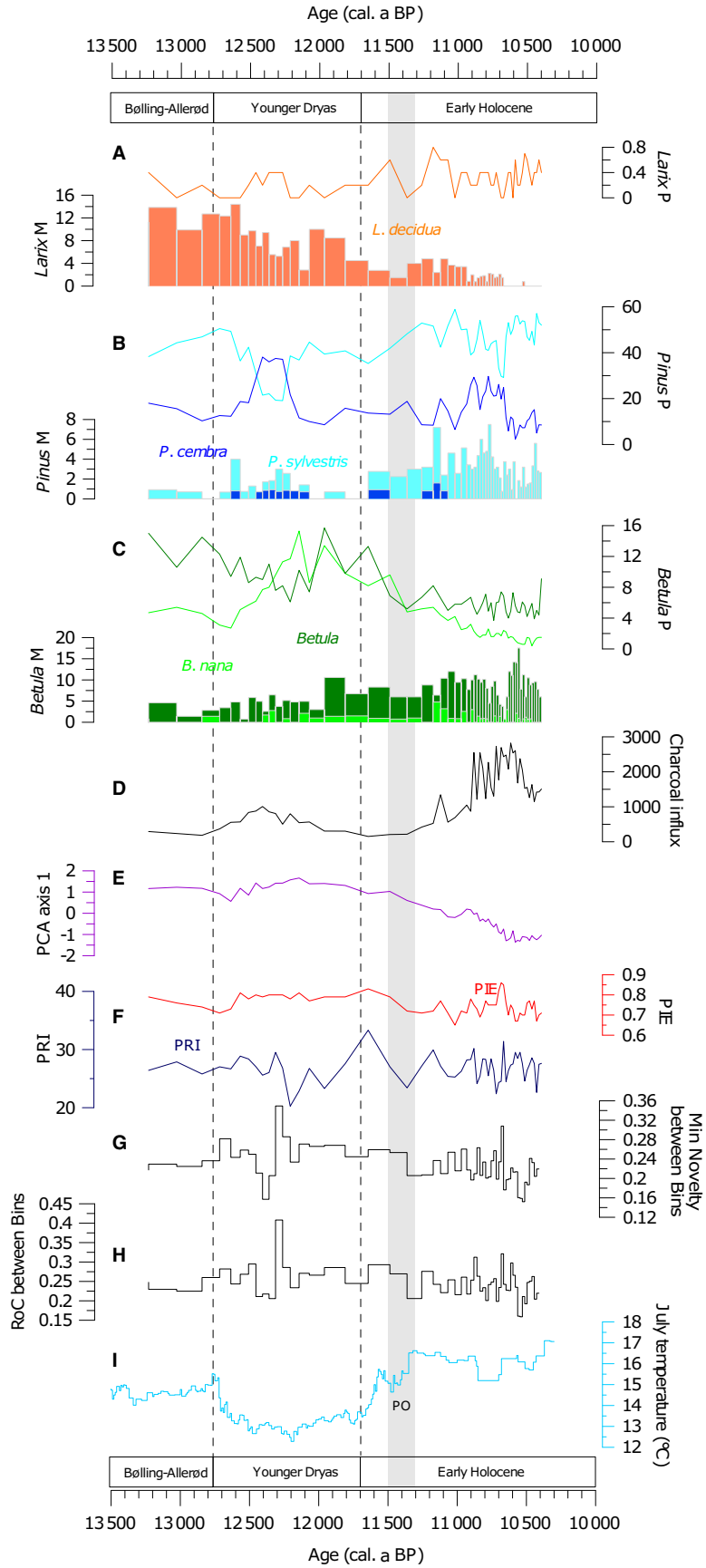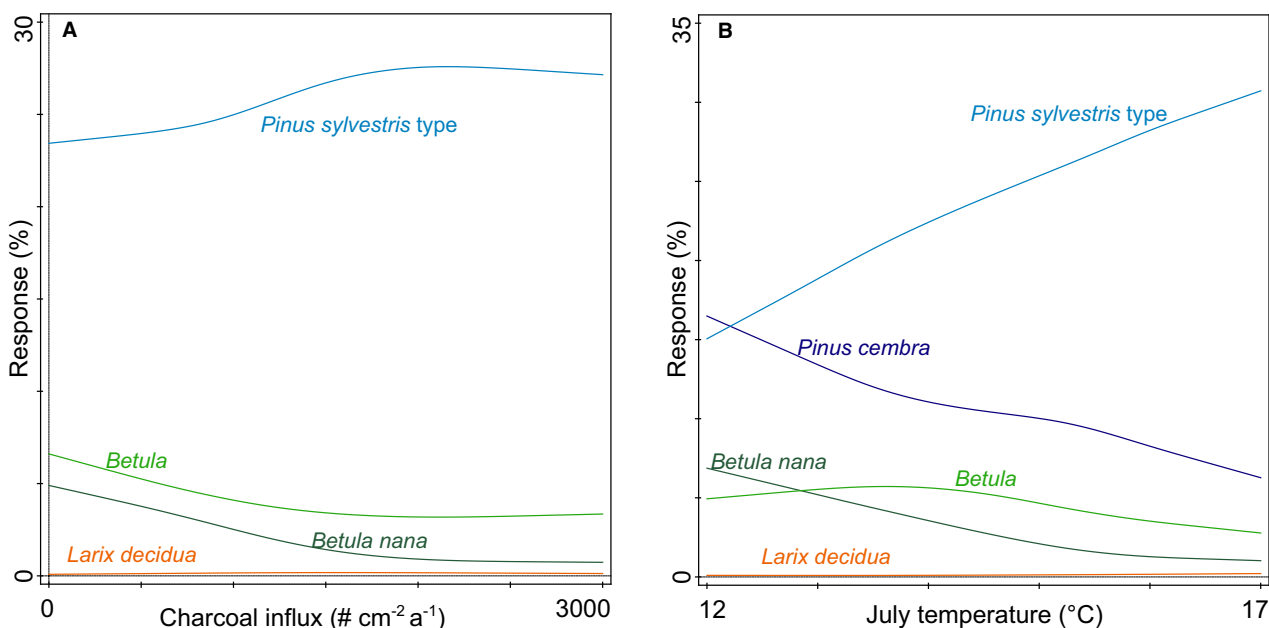
Fig. 7. Species response curves to environmental gradients. A. Pollen-inferred taxa response curves to charcoal influx as proxy for fire activity. B. Pollen-inferred taxa response curves to chironomid-inferred July temperature.

(12 250–11 400 cal. a BP). At the onset of the Younger Dryas, fires increased and steppe vegetation (e.g. *Artemisia*), as well as cold-adapted alpine and tree line species such as *P. cembra* expanded at Gola di Lago, while temperate tree stands below the site (e.g. *Ulmus*, *Quercus*) declined, indicating a downward shift of vegetation belts, likely in response to the cooler and drier climate conditions (Rach *et al.* 2014; Pauly *et al.* 2018). Likewise, the tree line was lowered by 100–200 m and was located between 1500–1800 m a.s.l. in southern Switzerland and northern Italy (Gobet *et al.* 2005; Vescovi *et al.* 2007).

Similar dynamics, although less pronounced, are also found at lower elevations, for instance at Lago di Annone and Lago del Segrino in Brianza (Fig. 1; Wick 1996), at Lago di Origlio in Ticino (Tinner *et al.* 1999) and at Lago Piccolo di Avigliana in Piedmont (Finsinger *et al.* 2006), where temperate trees declined, while cold-adapted *Betula*, *Juniperus* and steppic herbaceous taxa such as *Artemisia* expanded (Vescovi *et al.* 2007). Further south in the northern Apennines, the site Pavullo nel Frignano (675 m a.s.l.; Fig. 1; Vescovi *et al.* 2010) shows very similar dynamics to Gola di Lago, with a fire peak and a decline of *Pinus* and temperate tree species.

Subsequently, during the second part of the Younger Dryas and the Early Holocene transition (*c.* 12 250–11 400 cal. a BP), temperate trees re-expanded, *P. sylvestris* replaced *P. cembra* and steppic vegetation declined at Gola di Lago, likely in response to a slight increase in temperatures (Heiri *et al.* 2015). At several sites in southern Switzerland and northern Italy (e.g. Lago di Origlio, Tinner *et al.* 1999; Lago di Annone, Lago del Segrino, Wick 1996; Lago Piccolo di Avigliana,

Finsinger *et al.* 2006; and Pavullo nel Frignano, Vescovi *et al.* 2010), the second part of the Younger Dryas is also characterized by a slow re-expansion of temperate trees and a decrease of steppic herbaceous taxa.

At the onset of the Holocene around 11 700 cal. a BP, temperatures increased about 3–4 °C within *c.* 50 years (von Grafenstein *et al.* 2000; Schwander *et al.* 2000; Rasmussen *et al.* 2014; Heiri *et al.* 2015) leading to an upward movement of the tree line (Gobet *et al.* 2005). At Gola di Lago, Poaceae and *Artemisia* declined and *A. glutinosa* expanded locally (as documented by macrofossils) from 11 200 cal. a BP onwards. Open woodland conditions persisted when *P. cembra*, *L. decidua* and *Betula* started to decline, suggesting that their ranges shifted towards higher altitudes. Indeed, according to Paganelli & Borgato (2000) *P. cembra*, *L. decidua* and *Betula* established during the Early Holocene at Alpe Veglia (1700 m a.s.l.; Fig. 1) in the neighbouring Ossola valley. At Lago Cadagno (1921 m a.s.l.; Fig. 1; Vescovi *et al.* 2018) and at Lago Inferiore del Sangiatto (1980 m a.s.l.; Fig. 1; van Vugt 2019), two sites located in the Swiss and Italian Lepontine Alps, respectively, the establishment of *L. decidua* is dated to around 11 000 cal. a BP. Later, around 10 000 cal. a BP, *P. cembra* established in that region forming forests together with *L. decidua*. In the nearby Valais, in the western Central Swiss Alps, *L. decidua* stands established already around 11 350 cal. a BP at Gouillé Rion (2343 m a.s.l.; Fig. 1; Tinner & Kaltenrieder 2005), indicating a rapid upslope tree line shift of 800 m within a few centuries. The altitudinal tree line shift at the onset of the Early Holocene in the Lepontine Alps was therefore slower and less pronounced than in the more continental

Valais. It is likely that the Preboreal Oscillation, a period of 150–250 years characterized by a cooling of 1–2 °C that started at 11 300 cal. a BP (Wick & Tinner 1997; Heiri *et al.* 2004), was slowing down the Early Holocene afforestation process.

At Gola di Lago, Poaceae expanded and arboreal taxa declined at 10 700–10 650 cal. a BP. This change in vegetation composition is statistically significant, based on the zonation analysis, despite its short duration. Chronologically this shift falls into the Preboreal Oscillation (*c.* 11 500–11 300 cal. a BP), when dating uncertainties are considered (Wick & Tinner 1997; Heiri *et al.* 2004). We therefore assume that at Gola di Lago, the summer temperature decrease of the Preboreal Oscillation peaked during this short period. Compared to other sites in the Alps (Gouillé Rion; Wick & Tinner 1997) and to a climatic reconstruction including the Alpine forelands (Haas *et al.* 1998), the effect of the cooling on the vegetation at Gola di Lago and Lago Basso (2250 m a.s.l.; Fig. 1; Wick & Tinner 1997) in the southern Alps was only short-lived. Moreover, the vegetation response to this cooling has been only detected in a few studies, which might be due to the short duration of the event. Thus, more high-resolution studies are needed, to reveal such short climatic events and to understand their impact on the vegetation between different regions.

Impact of Lateglacial–Early Holocene rapid temperature increase on species diversity and vegetation communities

High biodiversity may ensure ecosystem functioning under environmental fluctuations (Yachi & Loreau 1999). On the other hand, climatic and environmental changes may adversely affect biodiversity, e.g. by species extinctions and range shifts (Nogués-Bravo *et al.* 2018; Giesecke *et al.* 2019). It is not clear yet, to what extent a changing climate influences species diversity and associated ecosystem functioning (Nogués-Bravo *et al.* 2018). Palynologically-inferred species richness at Gola di Lago fluctuated, but did not show a clear trend during the Lateglacial–Early Holocene transition (Fig. 6). Giesecke *et al.* (2019) analysed floristic diversity trends since the Lateglacial in Europe and concluded that rapid climatic changes do not necessarily translate into rapid shifts in richness patterns. Stable pollen richness recorded at Gola di Lago during the climate transition indicates that the temperature increase did not lead to diversity loss, in contrast to the hypothesis that global warming alone may lead to a general reduction in species diversity (Thuiller *et al.* 2005; Baldwin *et al.* 2014), even if in some areas species richness may increase with climate warming (Steinbauer *et al.* 2018). Interestingly, even though palynological diversity did not change, the dissimilarity as well as numerical zonation and ordination analyses (Figs 3, 5, 6) show that species composition was significantly different during contrasting climatic periods, pointing to a dynamic response of vegetation to

strongly changing climates without considerable species losses or gains. Particularly the sharp temperature decrease at the beginning of the Younger Dryas cold period led to a rapid change in vegetation communities, driven by a downward shift of cold-adapted tree line species such as *Pinus cembra*. The rapid warming at the beginning of the Holocene triggered vegetational changes that became prominent at the latest at *c.* 11 450 cal. a BP (LPAZ boundary). They involved the expansion of temperate taxa such as e.g. *Ulmus*, *Corylus* and *Alnus*, which initiated at the onset of the Holocene at *c.* 11 600–10 500 cal. a BP. However, this shift to temperate forests persisted over several centuries. This contrasts with Gouillé Rion, where vegetation adjusted more rapidly to climate change within *c.* 50–100 years at the onset of the Holocene (Tinner & Kaltenrieder 2005). One hypothesis that could explain these ecological patterns is that long-lived, persisting species can delay the establishment of newly arriving species after climatic changes. However, if there is no competition, either because there are no direct competitors present (e.g. above the tree line at Gouillé Rion) or because of disturbance events disrupting the vegetation inertia (e.g. high tree mortality caused by rapid temperature declines at the beginning of the Younger Dryas at Gola di Lago), invading species are able to rapidly shift their ranges in response to temperature changes. At Gola di Lago, even though reduced to lower abundances, the persistence of cold-adapted, already established species, such as *B. nana*, *L. decidua* and *P. cembra* during the Early Holocene, might have delayed the establishment of temperate taxa from lower elevations. Besides highly variable local habitat conditions (e.g. soils; Henne *et al.* 2011; Schwörer *et al.* 2014), genetic adaptations or phenotypic plasticity may have allowed the species to tolerate a certain degree of environmental change *in situ* (Nogués-Bravo *et al.* 2018), before they were replaced by more competitive species after a few centuries.

Indeed, the species response curves (Fig. 7) show that increasing temperatures significantly influenced forest composition over longer time scales, causing cold-adapted tree line trees such as *P. cembra* and *Betula* to decline, whereas the generalist tree *P. sylvestris* expanded. *Pinus sylvestris* is also the only analysed arboreal species that was not negatively affected by the increase in natural fire frequency recorded at the onset of the Early Holocene. Our results indicate that temperature played a key role in shaping vegetation composition, leading to open boreal forests with steppic elements under cooler temperatures and forest with temperate species under warmer temperatures. However, to our knowledge, Gola di Lago is the first site south of the Alps that did not record major biodiversity changes during the Younger Dryas–Early Holocene transition. Additional palaeoecological biodiversity studies at further sites are required to gain a more in-depth knowledge of this pattern. Overall, our results show

that within the study's time resolution of 51 years (mean) for the high-resolution sequence, vegetation was able to dynamically react to fast climatic changes (independently reconstructed by Heiri *et al.* 2015) through both rapid range shifts and local persistence, without displaying major biodiversity declines.

Postglacial vegetation at Gola di Lago and the resilient character of Larix decidua

Even though vegetation was generally able to respond fast to past climatic changes at Gola di Lago, there is nevertheless a significant lag of 250–300 years between the end of the Younger Dryas (*c.* 11 700 cal. a BP; Walker *et al.* 2012; Rasmussen *et al.* 2014) and a significant change in the vegetation communities as identified by zonation analysis (11 400 cal. a BP, Fig. 3) and PCA axis 1 scores (Fig. 6E). This could be due to chronological uncertainties in the Gola di Lago record and/or biological processes, i.e. the time needed (centuries) for long-lived species, such as trees, to establish and then expand to be recognized in the fossil record (MacDonald 1993; Aitken *et al.* 2008). Indeed, the pattern observed at Gola di Lago, seems to be a common feature in the lowland sites of the Insubrian region (e.g. Lago di Origlio or Balladrum; Hofstetter *et al.* 2006; Vescovi *et al.* 2007). Since the expanding temperate species were already present in the area at the end of the Bølling-Allerød interstadial (e.g. Lago di Origlio; Tinner *et al.* 1999), a migrational lag can be excluded. The high-resolution Lago di Origlio record suggests that the response of vegetation started already at 11 700 cal. a BP (e.g. local expansion of oak forests), but that several centuries were needed for *Quercus* populations to reach equilibrium conditions with climate (oak forest maximum at *c.* 11 400 cal. a BP; Tinner *et al.* 1999). Similar long-lasting population expansion processes regarding forest establishment have also been identified in dynamic vegetation models (e.g. Henne *et al.* 2011; Schwörer *et al.* 2014).

During the Early Holocene, pine forest expanded at Gola di Lago. However, the woodland remained open, since light demanding species such as *B. nana* and *L. decidua* persisted for at least 1000 years after the onset of the Holocene. *Betula nana* is a shade-intolerant species (Vasander *et al.* 1995) and can avoid competition with other species by growing in mires (Vasander *et al.* 1995; Ejankowski 2010). Nowadays, dwarf birch occurs at high latitudes and persists as a glacial relict species in mountain peat bogs in central Europe (Ejankowski 2010; Beck *et al.* 2016), but is absent from the Southern Alps and elsewhere in southern Europe, including Spain, Italy and the Balkans (excluding Romania; Drzymulska 2014). At Gola di Lago, *P. cembra* macrofossil findings suggest that this species was likely present in the surroundings of the lake for nearly half a millennium after the end of the Younger Dryas. Likewise, *L. decidua*

was continuously present at the site during the Younger Dryas and the Early Holocene, as indicated by contiguous macrofossils and stomata. Similar pollen abundances of *Larix* (~0.5%) are also reached at lowland sites such as Lago di Origlio, while stomata are very rare and confined to the Younger Dryas (Vescovi *et al.* 2007). According to the stomata findings at Gola di Lago, *L. decidua* expanded with the cooler temperatures of the Younger Dryas and then persisted at a relatively high and stable abundance for some centuries during the Early Holocene (between *c.* 12 100–11 200 cal. a BP). Macrofossil finds suggest that *L. decidua* started decreasing already at the onset of the Younger Dryas, recovering slightly in the second half of the Younger Dryas, before continuing the decline in the Early Holocene. Both stomata and macrofossil data indicate that around 11 000 cal. a BP, *L. decidua* decreased and survived at lower, yet fairly stable frequencies for several centuries until at least *c.* 10 500 cal. a BP, while *P. sylvestris* was spreading around the site. *Pinus cembra*, on the other hand, likely disappeared or became unimportant locally around 11 100 cal. a BP, *c.* 600 years before *L. decidua* collapsed. During the Holocene *L. decidua* and *P. cembra* forests successfully shifted their range towards higher altitudes in the Alps (Paganelli & Borgato 2000; Tinner & Kaltenrieder 2005), and both grow nowadays up to 2500 m a.s.l. (Da Ronch *et al.* 2016). However, patchy European larch stands are still present in the Insubrian Southern Alps on shallow soils down to 800 m a.s.l. (Leuschner & Ellenberg 2017). They can even grow at ~250 m a.s.l. in Austria, where enough precipitation occurs during the growing season (Gower *et al.* 1992; Da Ronch *et al.* 2016; Nothdurft & Engel 2020), indicating the broad range of its realized ecological niche. A study on European larch suggests that *L. decidua* suffers with decreasing continentality (Moris *et al.* 2017a), indicating that the very continental climate of the Early Holocene could have contributed to its local persistence. Moris *et al.* (2017a) claim that due to the high relative resilience of subalpine European larch forests, declines of *L. decidua* in response to climatic change may not be evident at first. Our palaeoecological results provide support for this hypothesis; moreover, we can show that, in agreement with previous studies, European larch communities are resilient to moderate-severity fires (Moris *et al.* 2017b; Fréjaville *et al.* 2018; Dupire *et al.* 2019). Thus, although a tree line species, *L. decidua* may persist in the montane and subalpine belts during the next centuries, even if fire incidence should increase in response to warmer and/or drier climates.

Conclusions

With our high-resolution sediment record from Gola di Lago, we were able to analyse in detail species' compositional turnover and the emergence of novel vegetation communities in response to sudden temper-

ature changes in the past. Our study reveals a rapid vegetation response to climatic cooling at the beginning of the Younger Dryas, characterized by a downward shift of cold-adapted tree line species such as *Pinus cembra*. We could distinguish two distinct vegetation communities during the Younger Dryas, which is in accordance with independent climate data indicating a cold and dry start followed by slightly warmer conditions. Additionally, we found that at Gola di Lago pollen type richness and evenness do not display major declines during the Younger Dryas–Early Holocene transition, suggesting that the rapid temperature increase did not lead to species richness loss. We also provide evidence for both rapid vegetation responses and partial inertia. Specifically, we showed that *Larix decidua* displayed some remarkable resilience to climate warming of 2–4 °C and was able to persist locally for a millennium during the Early Holocene despite the rapid expansion of temperate trees. European larch stands grow nowadays at the tree line in the Alps (Da Ronch *et al.* 2016), but can also occur at lower elevation (Da Ronch *et al.* 2016; Nothdurft & Engel 2020) showing a broad ecological niche. Together with our results, this indicates that long-lived *Larix decidua* might potentially be able to persist under current global warming conditions.

References

Aitken, S. N., Yeaman, S., Holliday, J. A., Wang, T. & Curtis-McLane, S. 2008: Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications 1*, 95–111.

Baldwin, A. H., Jensen, K. & Schönfeldt, M. 2014: Warming increases plant biomass and reduces diversity across continents, latitudes, and species migration scenarios in experimental wetland communities. *Global Change Biology 20*, 835–850.

Beck, P., Caudullo, G., de Rigo, D. & Tinner, W. 2016: *Betula pendula, Betula pubescens* and other birches in Europe: distribution, habitat, usage and threats. *In* San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T. & Mauri, A. (eds.): *European Atlas of Forest Tree Species*, 70–73. Publication Office of the EU, Luxembourg.

Beug, H.-J. 2004: *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete.* 542 pp. Verlag Dr. Friedrich Pfeil, Munich.

Birks, H. J. B. 2019: Contribution of Quaternary botany to modern ecology and biogeography. *Plant Ecology and Diversity 12*, 189–385.

Birks, H. J. B. & Line, J. M. 1992: The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. *The Holocene 2*, 1–10.

Blaauw, M. 2010: Methods and code for 'classical' age-modelling of radiocarbon sequences. *Quaternary Geochronology 5*, 512–518.

Cappers, R. T. J., Bekker, R. M. & Jans, J. E. A. 2006: *Digital Seed Atlas of the Netherlands.* 502 pp. Groningen Archaeological Studies, Barkhuis (in Dutch).

Cheburkin, A. K., González, A. Z. I., Krachler, M. & Shotyk, W. 2006: Spatial distribution of natural enrichments of arsenic, selenium, and uranium in a minerotrophic peatland, Gola di Lago, canton Ticino, Switzerland. *Environmental Science & Technology 40*, 6568–6574.

Da Ronch, F., Caudullo, G., Tinner, W. & de Rigo, D. 2016: *Larix decidua* and other larches in Europe: distribution, habitat, usage and threats. *In* San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T. & Mauri, A. (eds.): *European Atlas of Forest Tree Species*, 108–110, Publication Office of the EU, Luxembourg.

Davis, M. B. & Shaw, R. G. 2001: Range shifts and adaptive responses to Quaternary climate change. *Science 292*, 673–679.

Drzymulska, D. 2014: Postglacial occurrence and decline of *Betula nana* L. (dwarf birch) in northeastern Poland. *Estonian Journal of Earth Sciences 63*, 76–87.

Dupire, S., Curt, T., Bigot, S. & Fréjaville, T. 2019: Vulnerability of forest ecosystems to fire in the French Alps. *European Journal of Forest Research 138*, 813–830.

Ejankowski, W. 2010: Demographic variation of dwarf birch (*Betula nana*) in communities dominated by *Ledum palustre* and *Vaccinium uliginosum*. *Biologia 65*, 248–253.

Felber, M. 1993: *La storia geologica del tardo – terziario e del quaternario nel Mendrisiotto, Ticino meridionale, Svizzera.* Ph.D. thesis, ETH Zürich, 617 pp.

Finsinger, W. & Tinner, W. 2005: Minimum count sums for charcoal-concentration estimates in pollen slides: accuracy and potential errors. *The Holocene 15*, 293–297.

Finsinger, W., Giesecke, T., Brewer, S. & Leydet, M. 2017: Emergence patterns of novelty in European vegetation assemblages over the past 15 000 years. *Ecology Letters 20*, 336–346.

Finsinger, W., Tinner, W., van der Knaap, W. O. & Ammann, B. 2006: The expansion of hazel (*Corylus avellana* L.) in the southern Alps: a key for understanding its early Holocene history in Europe? *Quaternary Science Reviews 25*, 612–631.

Fréjaville, T., Vilà-Cabrera, A., Curt, T. & Carcaillet, C. 2018: Aridity and competition drive fire resistance trait covariation in mountain trees. *Ecosphere 9*, e02493, doi: https://doi.org/10.1002/ecs2.2493.

Giesecke, T., Wolters, S., van Leeuwen, J. F. N., van der Knaap, W. O., Leydet, M. & Brewer, S. 2019: Postglacial change of the floristic diversity gradient in Europe. *Nature Communications 10*, 5422, doi: https://doi.org/10.1038/s41467-019-13233-y.

Gobet, E., Tinner, W., Bigler, C., Hochuli, P. A. & Ammann, B. 2005: Early-Holocene afforestation process in the lower subalpine belt of the Central Swiss Alps as inferred from the macrofossil and pollen records. *The Holocene 15*, 672–686.

Gower, S. T., Kloeppel, B. D. & Reich, P. B. 1992: Carbon, nitrogen, and water use by larches and co-occurring evergreen conifers. *In* Schmidt, W. C. & McDonald, K. J. (eds.): *Ecology and Management of Larix Forests: A Look Ahead*, 110–117. Proceedings of an International Symposium, Whitefish, Montana, USA.

von Grafenstein, U., Eicher, U., Erlenkeuser, H., Ruch, P., Schwander, J. & Ammann, B. 2000: Isotope signature of the Younger Dryas and two minor oscillations at Gerzensee (Switzerland): palaeoclimatic and palaeolimnologic interpretation based on bulk and biogenic carbonates. *Palaeogeography, Palaeoclimatology, Palaeocology 159*, 215–229.

Haas, J. N., Richoz, I., Tinner, W. & Wick, L. 1998: Synchronous Holocene climatic oscillations recorded on the Swiss Plateau and at timberline in the Alps. *The Holocene 8*, 301–309.

Heegaard, E., Birks, H. J. B. & Telford, R. J. 2005: Relationship between calibrated ages and depth in stratigraphical sequences: an estimation procedure by mixed-effect regression. *The Holocene 15*, 612–618.

Heiri, O. & Millet, L. 2005: Reconstruction of Lateglacial summer temperature from chironomid assemblages in Lac Lautrey (Jura, France). *Journal of Quaternary Science 20*, 33–44.

Heiri, O., Ilyashuk, B., Millet, L., Samartin, S. & Lotter, A. F. 2015: Stacking of discontinuous regional paleoclimate records: chironomid-based summer temperatures from the Alpine region. *The Holocene 25*, 137–149.

Heiri, O., Tinner, W. & Lotter, A. F. 2004: Evidence for cooler European summers during periods of changing meltwater flux to the North Atlantic. *Proceedings of the National Academy of Sciences of the United States of America 26*, 15285–15288.

Henne, P. D., Elkin, C. M., Reineking, B., Bugmann, H. & Tinner, W. 2011: Did soil development limit spruce (*Picea abies*) expansion in the Central Alps during the Holocene? Testing a palaeobotanical hypothesis with a dynamic landscape model. *Journal of Biogeography 38*, 933–949.

Hofstetter, S., Tinner, W., Valsecchi, V., Carraro, G. & Conedera, M. 2006: Lateglacial and Holocene vegetation history in the Insubrian Southern Alps – New indications from a small-scale site. *Vegetation History and Archaeobotany 15*, 87–98.

van der Knaap, W. O. 2009: Estimating pollen diversity from pollen accumulation rates: a method to assess taxonomic richness in the landscape. *The Holocene 19*, 159–163.

Kovats, R. S., Valentini, R., Bouwer, L. M., Georgopoulou, E., Jacob, D., Martin, E., Rounsevell, M. & Soussana, J.-F. 2014: Europe. *In* Barros, V. R., Field, C. B., Dokken, D. J., Mastrandrea, M. D., Mach, K. J., Bilir, T. E., Chatterjee, M., Ebi, K. L., Estrada, Y. O., Genova, R. C., Girma, B., Kissel, E. S., Levy, A. N., MacCracken, S., Mastrandrea, P. R. & White, L. L. (eds.): *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects*, 1267–1326. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

de Lafontaine, G., Napier, J. D., Petit, R. J. & Hu, F. S. 2018: Invoking adaptation to decipher the genetic legacy of past climate change. *Ecology 99*, 1530–1546.

Lepš, J. & Šmilauer, P. 2003: *Multivariate Analysis of Ecological Data using CANOCO™*. 269 pp. Cambridge University Press, Cambridge.

Leuschner, C. & Ellenberg, H. 2017: *Ecology of Central European forests. Vegetation Ecology of Central Europe*, vol. *1*, 972 pp. Springer, Cham.

MacDonald, G. M. 1993: Fossil pollen analysis and the reconstruction of plant invasions. *Advances in Ecological Research 24*, 67–110.

Marlon, J., Bartlein, P. J. & Whitlock, C. 2006: Fuel-fire-climate linkages in the northwestern USA during the Holocene. *The Holocene 12*, 1059–1071.

Martinelli, E., Michetti, A. M., Colombaroli, D., Mazzola, E., De Carlo, S. M., Livio, F., Gilli, A., Ferrario, M. F., Höbig, N., Brunamonte, F., Castelletti, L. & Tinner, W. 2017: Climatic and anthropogenic forcing of prehistorical vegetation succession and fire dynamics in the Lago di Como area (N-Italy, Insubria). *Quaternary Science Reviews 161*, 45–67.

McLachlan, J., Clark, J. S. & Manos, P. S. 2005: Molecular indicators of tree migration capacity under rapid climate change. *Ecology 86*, 2088–2098.

Médail, F. & Diadema, K. 2009: Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *Journal of Biogeography 36*, 1333–1345.

MeteoSwiss 2020: *Climate normals Lugano, Reference period 1981 – 2010. Climate diagram and table of climatological measurements for this station (Lugano), climasheet 2.1.3.* https://www.meteoswiss. admin.ch/home/climate/swiss-climate-in-detail/climate-normals/ climate-diagrams-and-normals--per-station.html (accessed: 12.01.2021).

Moore, P. D., Webb, J. A. & Collinson, M. E. 1991: *Pollen Analysis*. 216 pp. Blackwell Scientific Publications, London.

Moris, J. V., Vacchiano, G., Ascoli, D. & Motta, R. 2017a: Alternative stable states in mountains forest ecosystems: the case of European larch (*Larix decidua*) forests in the western Alps. *Journal of Mountain Science 14*, 811–822.

Moris, J. V., Vacchiano, G., Enri, S. R., Lonati, M., Motta, R. & Ascoli, D. 2017b: Resilience of European larch (*Larix decidua* Mill.) forests to wildfires in the western Alps. *New Forests 48*, 663–683.

Mumby, P. J., Chollett, I., Bozec, Y.-M. & Wolff, N. H. 2014: Ecological resilience, robustness and vulnerability: how do these concepts benefit ecosystem management? *Current Option in Environmental Sustainability 7*, 22–27.

Nogués-Bravo, D., Rodríguez-Sánchez, F., Orsini, L., de Boer, E., Jansson, R., Morlon, H., Fordham, D. A. & Jackson, S. T. 2018: Cracking the code of biodiversity responses to past climate change. *Trends in Ecology and Evolution 33*, 765–776.

Nothdurft, A. & Engel, M. 2020: Climate sensitivity and resistance under pure- and mixed-stand scenarios in Lower Austria evaluated with distributed lag models and penalized regression splines for tree-ring time series. *European Journal of Forest Research 139*, 189–211.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., Ohara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E. & Wagner, H. 2015: *Vegan: community ecology package. R package.* Available at: https://cran.r-project.org.

Paganelli, A. & Borgato, S. 2000: *Risultati delle ricerche palinologiche condotte sui campioni delle trivellazioni eseguite sull'Alpe Veglia: (Alpi occidentali, Provincia di Verbania)*. 20 pp. Parco Naturale Alpe Veglia e Alpe Devero, Varzo.

Pauly, M., Helle, G., Miramont, C., Büntgen, U., Treydte, K., Reinig, F., Guibal, F., Sivan, O., Heinrich, I., Riedel, F., Kromer, B., Balanzategui, D., Wacker, L., Sookdeo, A. & Brauer, A. 2018: Subfossil trees suggest enhanced Mediterranean hydroclimate variability at the onset of the Younger Dryas. *Scientific Reports 8*, 13980, doi: https://doi.org/10.1038/s41598-018-32251-2.

Pini, R. 2002: A high-resolution Late-Glacial – Holocene pollen diagram from Pian di Gembro (Central Alps, Northern Italy). *Vegetation History and Archeobotany 11*, 251–262.

R Core Team 2020: *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna.

Rach, O., Brauer, A., Wilkes, H. & Sachse, D. 2014: Delayed hydrological response to Greenland cooling at the onset of the Younger Dryas in western Europe. *Nature Geoscience 7*, 109–112.

Rasmussen, S. O., Bigler, M., Blockley, S. P., Blunier, T., Buchardt, S. L., Clausen, H. B., Cvijanovic, I., Dahl-Jensen, D., Johnsen, S. J., Fischer, H., Gkinis, V., Guillevic, M., Hoek, W. Z., Lowe, J. J., Pedro, J. B., Popp, T., Seierstad, I. K., Steffensen, J. P., Svensson, A. M., Vallelonga, P., Vinther, B. M., Walker, M. J. C., Wheatley, J. J. & Winstrup, M. 2014: A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE even stratigraphy. *Quaternary Science Reviews 106*, 14–28.

Reille, M. 1992: *Pollen et spores d'Europe et d'Afrique du nord*. 520 pp. Laboratoire de Botanique historique et Palynologie, Marseille.

Reimer, P. J. & 41 others 2020: The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon 62*, 725–757.

Schoch, W. H., Pawlik, B. & Schweingruber, F. H. 1988: *Botanische Makroreste. Ein Atlas zur Bestimmung häufig gefundener und ökologisch wichtiger Pflanzensamen.* 227 pp. 4. Band. Paul Haupt, Bern.

Schwander, J., Eicher, U. & Ammann, B. 2000: Oxygen isotopes of lake marl at Gerzensee and Leysin (Switzerland), covering the Younger Dryas and two minor oscillations, and their correlation to the GRIP ice core. *Palaeogeography, Palaeoclimatology, Palaeoecology 159*, 203–214.

Schwörer, C., Henne, P. D. & Tinner, W. 2014: A model-data comparison of Holocene timberline changes in the Swiss Alps reveals past and future drivers of mountain forest dynamics. *Global Change Biology 20*, 1512–1526.

Steinbauer, M. J. & 52 others 2018: Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature 556*, 231–234.

Stockmarr, J. 1971: Tablets with spores used in absolute pollen analysis. *Pollen et Spores 13*, 615–621.

Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T. & Prentice, I. C. 2005: Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America 102*, 8245–8250.

Timpane-Padgham, B. L., Beechie, T. & Klinger, T. 2017: A systematic review of ecological attributes that confer resilience to climate change in environmental restoration. *PLoS One 12*, e0173812, doi: https://doi.org/10.1371/journal.pone.0173812.

Tinner, W. & Hu, F. S. 2003: Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. *The Holocene 13*, 499–505.

Tinner, W. & Kaltenrieder, P. 2005: Rapid responses of high-mountain vegetation to early Holocene environmental changes in the Swiss Alps. *Journal of Ecology 93*, 936–947.

Tinner, W., Conedera, M., Ammann, B. & Lotter, A. F. 2005: Fire ecology north and south of the Alps since the las ice age. *The Holocene 15*, 1214–1226.

Tinner, W., Hubschmid, P., Wehrli, M., Ammann, B. & Conedera, M. 1999: Long-term forest fire ecology and dynamics in southern Switzerland. *Journal of Ecology 87*, 273–289.

Tinner, W., Vescovi, E., van Leeuwen, J. F. N., Colombaroli, D., Henne, P. D., Kaltenrieder, P., Morales-Molino, C., Beffa, G., Gnaegi, B., van der Knaap, W. O., La Mantia, T. & Pasta, S. 2016: Holocene vegetation and fire history of the mountains of Northern Sicily (Italy). *Vegetation History & Archaeobotany 25*, 499–519.

Valsecchi, V. & Tinner, W. 2010: Vegetation responses to climatic variability in the Swiss Southern Alps during the Misox event at the early mid Holocene transition. *Journal of Quaternary Science 25*, 1248–1258.

Valsecchi, V., Carraro, G., Conedera, M. & Tinner, W. 2010: Late-Holocene vegetation and land-use dynamics in the Southern Alps (Switzerland) as a basis for nature protection and forest management. *The Holocene 20*, 483–495.

Vasander, J., Vasander, H. & Laiho, R. 1995: Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. *Journal of Applied Ecology 32*, 785–802.

Vescovi, E., Ammann, B., Ravazzi, C. & Tinner, W. 2010: A new Late-Glacial and Holocene record of vegetation and fire history from Lago del Greppo, Northern Apennines, Italy. *Vegetation History & Archaeobotany 19*, 219–233.

Vescovi, E., Ravazzi, C., Arpenti, E., Finsinger, W., Pini, R., Valsecchi, V., Wick, L., Ammann, B. & Tinner, W. 2007: Interactions between climate and vegetation during the Lateglacial periods as recorded by lake and mire sediment archives in Northern Italy and Southern Switzerland. *Quaternary Science Reviews 26*, 1659–1669.

Vescovi, E., Tinner, W., Beer, R., van Leeuwen, J. F. N., Steinhauser, U., Ziegler, S., Gilli, A., Wirth, S. B., Samartin, S., Jacquat, C. & Carraro, G. 2018: Vegetation history of the Upper Leventina Valley from Neolithic to Roman times, recorded by pollen, spores, plant macro-fossil, and charcoal. *Zurich Studies in Archaeology 12*, 207–225.

van Vugt, L. 2019: *12,000 years of vegetation dynamics influenced by climate and land use at Lago Inferiore del Sangiatto, Italian Lepontine Alps*. M.Sc. thesis, University of Bern, 59 pp.

Walker, M. J., Berkelhammer, M., Björck, S., Cwynar, L. C., Fisher, L. C., Long, A. J., Lowe, J. J., Newham, R. M., Rasmussen, S. O. & Weiss, H. 2012: Formal subdivision of the Holocene Series/Epoch: a discussion paper by Working Group on INTIMATE (Integration of ice-core, marine and terrestrial records) and the Subcommission on Quaternary Stratigraphy (International Commission on Stratigraphy). *Journal of Quaternary Science 27*, 649–659.

Wick, L. 1996: Late-Glacial and Early-Holocene palaeoenvironments in Brianza, N Italy. *Il Quaternario 9*, 653–660.

Wick, L. & Tinner, W. 1997: Vegetation changes and timberline fluctuations in the Central Alps as indicators of Holocene climatic oscillations. *Arctic and Alpine Research 29*, 445–458.

Yachi, S. & Loreau, M. 1999: Biodiversity and ecosystem productivity in a fluctuating environment: the insurance theory. *Proceedings of the National Academy of Sciences of the United States of America 96*, 1463–1468.

Zoller, H. 1960: Pollenanalytische Untersuchungen zur Vegetationsgeschichte der insubrischen Schweiz. *Denkschriften der Schweizerischen Naturforschenden Gesellschaft 83*, 45–156.

Zoller, H. & Kleiber, H. 1971: Vegetationsgeschichte Untersuchungen in der montanen und subalpinen Stufe der Tessintäler. *Sonderausdruck Verhandlungen der Naturforschenden Gesellschaft in Basel 81*, 90–154.