Reconstruction of full glacial environments and summer temperatures from Lago della Costa, a refugial site in northern Italy

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Abstract

Vegetation and climate during the last ice age and the Last Glacial Maximum (LGM, ~ 23,000-19,000 cal BP) were considerably different than during the current interglacial (Holocene). Cold climatic conditions and growing ice-sheets during the last glaciation radically reduced forest extent in Europe to a restricted number of so-called “refugia”, mostly located in the southern part of the continent. On the basis of paleobotanical analyses the Euganean Hills (Colli Euganei) in northeastern Italy have previously been proposed as one of the northernmost refugia of temperate trees (e.g. deciduous *Quercus*, *Tilia*, *Ulmus*, *Fraxinus excelsior*, *Acer*, *Abies alba*, *Fagus sylvatica*, *Carpinus* and *Castanea*) in Europe. In this study we provide the first quantitative, vegetation independent summer air temperature reconstruction for Northern Italy spanning the time ~ 31,000-17,000 cal yr BP, which covers the coldest periods of the last glacial, including the LGM and Heinrich stadials 1 to 3. Chironomids preserved in a lake sediment core from Lago della Costa (7m a.s.l.), a small lake at the south-eastern edge of the Euganean Hills, allowed quantitative reconstruction of Full and Late Glacial summer air temperatures using a combined Swiss-Norwegian temperature inference model based on chironomid assemblages from 274 lakes. Chironomid and pollen evidence from Lago della Costa derives from finely stratified autochthonous organic gyttja sediments, which excludes major sediment mixing or reworking. After reconstructing paleo-temperatures, we address the question whether climate conditions were warm enough to permit the local survival of temperate tree species during the LGM and whether local expansions and pollen-inferred contractions of temperate tree taxa coincided with chironomid-inferred climatic changes. Our results suggest that chironomids at Lago della Costa have responded to major climatic fluctuations such as temperature decreases during the LGM and Heinrich stadials. The vegetation of the Euganean Hills shows responses to these climatic oscillations although the effects of temperature changes were probably also strongly influenced by changes in humidity. Reconstructed July air temperatures at Lago della Costa

never fell below 10-13 °C (error range of reconstruction $\sim \pm 1.5-1.6$ °C), which is considerably above the limit considered necessary for forest growth (8-10°C). Instead rather mild climatic conditions prevailed $\sim 31,000-17,000$ cal yr BP with average summer temperatures between ~ 12 and 16 °C, which most likely allowed survival of temperate tree taxa in the warmest (and moistest) microhabitats of the Euganean Hills during the LGM. Only assuming local survival it is possible to explain the repeated expansions and collapses of temperate trees at Lago della Costa which faithfully accompanied the climatic oscillations.

1. Introduction

Reconstructing the climate of the last ice age, especially of the Last Glacial Maximum (LGM), is crucial to understand the extinction, survival and immigration of taxa in the Mediterranean realm and elsewhere in Europe. During the last ice age climate and vegetation of the Mediterranean area were characterized by pervasive millennial-scale variability, and these variations have been correlated with Dansgaard-Oeschger cycles and Heinrich events (Cacho et al., 1999, 2000, 2006; Fletcher et al., 2010). Dansgaard-Oeschger cycles were characterized by rapid transitions from cool (stadials) to rather warm glacial climatic conditions (interstadials) in Greenland, the North Atlantic and the Mediterranean realms (Cacho et al., 1999; 2000; Sánchez-Goñi et al., 1999; Gouzy et al., 2004; Salguiero et al., 2010). During Heinrich events iceberg surges were released into the North Atlantic Ocean, with a slow-down effect on the thermohaline circulation (THC; Clark et al., 2002), triggering cool and dry climatic conditions around the North Atlantic and the Mediterranean Sea (Bond et al., 1993; Cacho et al., 1999, 2000). Warm and relatively humid conditions during at least some interstadials led to the development of grassland and shrub tundra in northwestern Europe, shrub- and forest tundra in northeastern Europe, open boreal forest in central Western Europe and the Alpine region, and open temperate forests in southern Europe (Fletcher et al., 2010). Besides the classic refugial areas in proximity of the Mediterranean Sea (Iberia, Italy

and Balkan; Bennett et al., 1991), micro-refugia further north may have allowed small populations of plants and animals to survive during the harshest periods of the last glaciation (Willis and Whittaker, 2000; Willis et al., 2000; Stewart and Lister, 2001; Babik et al., 2004). During the LGM (~ 23,000-19,000 cal BP) parts of the North Atlantic Ocean may have experienced conditions that were surprisingly mild (Abrantes et al., 1998). This finding is in agreement with sea surface temperature (SST) reconstructions from the Mediterranean Sea disclosing that the LGM was less cool if compared to the neighboring Heinrich events (Cacho et al., 1999, 2000), but still ~ 8 °C cooler than today (~ 11 vs. 19 °C, mean annual average; ENEA, 2015).

Past variations in mean summer air temperatures can be reconstructed by analyzing fossil chironomid headcapsules in lake sediments. The strong relationship between the distribution of chironomids and summer air temperature in the modern environment (Eggermont and Heiri, 2012) has led to the development of chironomid-based inference models for reconstructing past summer air temperature changes based on fossil assemblages (e.g. Lotter et al., 1997; Brooks and Birks, 2001; Heiri et al., 2011). In central and southern Europe, these so-called transfer functions have successfully been used to elucidate millennial- and centennial scale climate variations during the Lateglacial period (e.g. Heiri et al., 2014, 2015; Larocque-Tobler et al., 2011; Samartin et al., 2012). However, chironomid-based temperature reconstructions which extend into the LGM and preceding periods are rare (e.g. Engels et al. 2008, Haskett and Porinchu 2014, Helmens et al. 2015), and for southern Europe, not yet available.

Here we present a new chironomid record and quantitative chironomid-based July air temperature reconstruction covering the Last Glacial ~ 31,000-17,000 cal yr BP from a sediment core from Lago della Costa (7 m a.s.l.), a small lake at the south-eastern edge of the Euganean Hills (Colli Euganei), approximately 20 km southeast of Padua and 40 km west of the present-day shore of the Mediterranean Sea. Today the Euganean Hills have sheltered

microclimatic conditions, which allow the extrazonal occurrence of evergreen broadleaved Mediterranean tree stands (e.g. *Quercus ilex*), which are completely lacking in the remainder of the rather continental Po-Plain. Palaeobotanical evidence indicates that such favorable micro-climatic conditions may have allowed the survival of temperate trees during the harshest periods of the last ice age (Kaltenrieder et al. 2009). On the basis of the chironomid-inferred temperature reconstruction we address the question whether the climatic conditions around Lago della Costa were warm enough to support the survival of temperate trees (e.g. deciduous *Quercus*, *Tilia*, *Ulmus*, *Fraxinus excelsior*, *Acer*, *Abies alba*, *Fagus sylvatica*, *Carpinus* and *Castanea*) during the LGM, as suggested by pollen evidence from the same cores (Kaltenrieder et al. 2009). Furthermore, we address the question whether local expansions and contractions of temperate tree taxa coincided with climatic changes.

2. Material and Methods

2.1 Description of the region and the site studied

Lago della Costa (45° 16' 13'' N, 11° 44' 35'' E) is a small lake (3 ha) located at an elevation of 7 m a.s.l. on the south-eastern border of the Euganean Hills in the regional park 'Parco Regionale dei Colli Euganei' close to Arquà Petrarca (Fig. 1). It has no surface inlet, but has several subaqueous thermal springs, which possibly originate from ancient rainwater of the Small Dolomites and the Vicentino-Trentini plateaus (Piccoli et al., 1976). In addition to these subaqueous thermal springs, Lago della Costa was until modern times fed by freshwater input from precipitation, creeks and springs, which are now used for agricultural purposes (REGPARC, 2015). A small artificial outlet is located at the southern border of the lake. The Euganean Hills are situated 50-60 km south of the maximum extent of the last Alpine glaciations (Orombelli et al., 2004) and consist of about 100 individual hills of volcanic origin, which have a very distinct shape (cones, ridges) and variable elevations (Kaltenrieder et al., 2009) and thus provide small pockets of microenvironmentally favorable sites.

According to the pollen evidence, the Euganean Hills and their neighbouring areas are one of the northernmost refugia of thermophilous tree taxa in Europe (Paganelli and Miola, 1991; Krebs et al., 2004, Kaltenrieder et al. 2009). The Euganean Hills are presently covered by forests of *Quercus petraea*, *Q. pubescens*, *Q. ilex*, *Castanea sativa*, *Fraxinus ornus*, *Carpinus betulus*, *Acer pseudoplatanus*, *A. campestre*, *Fagus sylvatica*, *Sorbus torminalis* and exotic *Robinia pseudoacacia* (Kaltenrieder et al., 2009), a vegetation typical for warm temperate submediterranean to mesomediterranean southern Europe. The site has a Cfa climate type (Köppen, 1923) and mean annual precipitation is estimated to 720 mm near Lago della Costa (Kaltenrieder et al., 2009). Mean July and mean January temperatures are 23 °C and 2.2 °C in Padova (~ 19 km north-east of Lago della Costa), respectively (mean values for 1961-1990; SCIA, 2015).

2.2 Coring and sediments

In 2001 and 2003 two parallel cores (AP2 and AP5) were taken about 70 m away from the northwestern border of the present lake with a modified Streif – Livingstone piston corer (Merk and Streif, 1970, Kaltenrieder et al., 2009). 17.72 m of lake sediment were retrieved and the cores were correlated using lithostratigraphic markers. All analyses were conducted on core AP2. The core section analyzed mainly consists of calcareous gyttja with intercalated layers of silt, clay and marl. A detailed description of the sediment is provided in Kaltenrieder et al. (2009).

2.3 Radiocarbon dating and vegetation history

Radiocarbon ages for AP2 were obtained by Accelerator Mass Spectrometry (AMS) at the Institute of Physics of the University of Erlangen-Nürnberg (Germany) and at the Poznan Radiocarbon Laboratory (Poland) on selected plant macrofossils (Table 1). The resulting radiocarbon dates were converted to calendar years Before Present (cal yr BP) with the

program Calib version 7.1 using the INTCAL13 dataset (Reimer et al., 2013). Linear interpolation between the median of calibrated dates was used to estimate the age-depth relationship (Fig. 2).

2.4 Sampling and analysis of fossil chironomids

The core AP2 was sampled for chironomid analysis regularly every ~ 40-50 cm, using about 5-20 cm³ of wet sediment per sample. In total 25 samples were taken from the sediment cores of Lago della Costa. The sediment samples were sieved through a 100 µm size sieve without any chemical pretreatment. Chironomid head capsules in the sieve residue were sorted in a Bogorov tray under a stereomicroscope (30-50x magnification), dried and mounted in Euparal for taxonomic identification. The subfossils were identified at 100-400x magnification under a compound microscope. A minimum count sum of 50 head capsules per sample was aimed for (Heiri and Lotter, 2001). However, 6 samples yielded count sums below this threshold (18-47 headcapsules). Head capsules containing a complete mentum were counted as one specimen, head capsules containing half a mentum were counted as half, while head capsules with less than half a mentum were disregarded. Taxonomic identification followed Wiederholm (1983), Schmid (1993), Rieradevall and Brooks (2001) and Brooks et al. (2007).

2.5 Temperature reconstruction

Quantitative mean July air temperature estimates were produced based on the fossil chironomid assemblages using a combined Swiss-Norwegian temperature inference model (Brooks and Birks, 2001, Heiri and Lotter, 2010, Heiri et al., 2011) consisting of 274 lakes covering a July air temperature gradient of 3.5 to 18.4 °C and including information on the distribution of 154 chironomid taxa. This combined dataset has the advantage that it contains distributional data on most chironomid taxa expected to occur during the late Quaternary in

European lake sediments and that it covers a larger temperature range than most other existing regional calibration datasets.

A weighted averaging partial least squares model (WA-PLS; ter Braak and Juggins, 1993; ter Braak et al., 1993) with two components was used for reconstruction. The model features a cross-validated root mean square error of prediction (RMSEP) of 1.55 °C, a mean bias of -0.008 °C, a maximum bias of 1.35°C, and a cross-validated coefficient of determination (r^2) of 0.84 between observed and inferred July air temperatures. Cross validation was based on bootstrapping (9999 cycles) and calculations were based on square root transformed chironomid percentage data.

2.6 Reconstruction diagnostic statistics

To evaluate the reliability of the chironomid-inferred temperature reconstruction, five numerical criteria were examined for fossil assemblages (Birks et al., 2010): the sample specific error of prediction (SSPE); the chi-square distance to the closest modern analogue to identify if any fossil assemblages lack “good” modern analogues within the modern calibration data; the goodness-of-fit to temperature derived from canonical correspondence analysis (CCA) of the modern and fossil data with July air temperature data as the only constraining variable; the percentage of rare taxa (Hill's N2 (Hill, 1973) <5); and the percentage of taxa not occurring in the training set.

Chi-square distances and Hill's N2 values were calculated using C2 (Juggins, 2003), and CCA to calculate the goodness-of-fit of individual samples was carried out with the program CANOCO 4.5 (ter Braak and Šmilauer, 2002). Fossil assemblages with a squared chi-square distance to the most similar sample in the modern calibration dataset larger than the 2nd and the 5th percentile of all squared chi-square distances in the modern assemblage data were identified as samples with “no close” and “no good” analogue, respectively (Birks et al., 1990). Samples with a residual distance to axis 1 higher than the extreme 10 and 5% of

all residual distances in the modern calibration dataset when calculating a CCA with July air temperature as the sole constraining variable were considered to have a “poor” and “very poor” fit with temperature, respectively (Birks et al., 1990). All calculations were accomplished on square-root transformed percentage abundances.

3. Results and Interpretation

3.1 Chronology

The Lago della Costa age-depth relationship is based on calibrated radiocarbon ages from 6 terrestrial plant macrofossils (Table 1). Linear interpolation between the calibrated radiocarbon ages was used to assign individual ages to the samples (Fig. 2). The average 95% confidence interval of the calibrated ages encompasses ~ 730 yr, suggesting chronological uncertainties of ~ ± 370 yr for the record.

3.2 Environmental interpretation of chironomid remains deposited between ~ 31,000-17,000 cal yr BP

In total, 38 different chironomid taxa were identified within 25 examined samples. Twenty-two taxa had relative abundances lower than 5%. Downcore changes in the chironomid record of Lago della Costa are not very pronounced and a selection of taxa is shown in Fig. 3. The chironomids are grouped according to their altitudinal preferences in the Swiss Alps (Heiri & Lotter, 2010, Heiri et al. 2011) to support interpretation and highlight trends. Chironomid head capsules were poorly preserved throughout the entire record. All abundances mentioned in this section refer to relative abundances.

Between ~ 30,920-23,620 cal yr BP (1705-1139 cm) relatively warm-adapted taxa such as *Chironomus plumosus*-type, *Cladopelma lateralis*-type, *Parakiefferiella bathophila*-type, *Tanytarsus mendax*-type, and *Paratanytarsus penicillatus*-type prevail (Henrikson et al., 1982; Hofmann, 1984; Brodin, 1986; Brooks et al., 2007), but the relatively cool-adapted taxa

Paratanytarsus austriacus-type and *Tanytarsus lugens*-type are also present (Brooks et al., 2007; Heiri et al., 2011), suggesting that climate was possibly moderately warm. The dominance of *Chironomus plumosus*-type, a taxon tolerant of low oxygen concentrations (Brooks et al., 2007), might reflect oxygen depletion of the lake water, possibly as a result of enhanced lake stratification associated with relatively warm climatic conditions throughout the section. The dominance of *Chironomus plumosus*-type, a taxon which often dominates in deepwater habitats (Henrikson et al., 1982), as well as the presence of littoral taxa that are often associated with macrophytes such as for instance *Paratanytarsus penicillatus*-type, *Polypedilum nubeculosum*-type and *Paratanytarsus austriacus*-type (Brodin, 1982; Buskens, 1987; Brodersen et al., 2001) suggest that the lake at that time might have been relatively deep with a pronounced vegetated littoral. Continuous finds of Characeae oogonia (most probably *Chara*), which occur in oligo- to mesotrophic lakes (Haas, 1999; Ellenberg, 1996), as well as the presence of *Chironomus plumosus*-type, *Polypedilum nubeculosum*-type, *Cladopelma lateralis*-type, *Parakiefferiella bathophila*-type, and *Dicrotendipes*, which are usually found in meso- to eutrophic lakes (Brodin, 1982; Henrikson et al., 1982; Hofmann, 1984; Brooks et al., 2007) suggest that nutrient concentrations in the lakewater were probably in the mesotrophic range.

Between ~ 28,000-24,500 cal yr BP *Polypedilum nubeculosum*-type and *Cladopelma lateralis*-type display maximum abundances, probably due to warmer climatic conditions. This interpretation is supported by additional finds of warm-adapted taxa such as for instance *Pseudochironomus* and *Microchironomus*, which have rather high temperature optima between ~ 15.3-15.6 °C in the Swiss-Norwegian trainingset (Heiri et al., 2011). The presence of the aquatic macrophyte *Nymphaea* also points to relatively warm summer conditions (minimum mean July temperature of ~12 °C; Isarin and Bohncke, 1999; Kaltenrieder et al., 2009). Warm-adapted taxa such as for instance *Chironomus plumosus*-type, *Polypedilum nubeculosum*-type, *Cladopelma lateralis*-type and *Parakiefferiella bathophila*-type (Brooks et

al., 2007; Heiri et al., 2011) decline towards the end of the section, presumably as a result of cooler climatic conditions.

Chironomids were absent from the record between ~ 23,620-23,270 cal yr BP (1139-911 cm), possibly as a result of very cool climatic conditions as have been reported for the North Atlantic region towards the end of Heinrich event 2 (Bond et al., 1992; 1993). This interpretation is supported by the deposition of minerogenic silt and clay later on between ~ 23,350-23,300 cal yr BP (1075-917 cm), which might have originated from unstable slopes due to a thinning of vegetation in response to a climatic shift towards colder and drier climatic conditions (Kaltenrieder et al., 2009).

Between ~ 23,270-18,610 cal yr BP (911-599 cm), chronologically corresponding to the Last Glacial Maximum (LGM; sensu Mix et al., 2001), low abundances of *Chironomus plumosus*-type are possibly a result of slightly cooler temperatures than between 31,000-23,620 cal yr BP, which may have led to less stable stratification of the lake and resulted in higher hypolimnetic oxygen concentrations. This would have favored the expansion of the oxybiontic taxon *Tanytarsus lugens*-type which is commonly found at relatively cool temperatures (Brundin, 1956; Brooks et al., 2007, Heiri and Lotter 2010). This taxon reached relatively high abundances between 22,400-21,400 cal yr BP. Higher oxygen concentrations in the deep-water environment of the lake may also have favored the expansion of *Tanytarsus mendax*-type (Engels et al., 2011). The presence of warm-adapted littoral taxa typically encountered in meso- to eutrophic lakes such as *Cladopelma lateralis*-type, *Paratanytarsus penicillatus*-type and *Dicrotendipes* (Brodin, 1982; Henrikson et al., 1982; Hofmann, 1984; Brooks et al., 2007) suggests that climate was only moderately cool and the lake water was possibly still mesotrophic. Additionally, sporadic finds of *Glyptotendipes barbipes*-type, *Endochironomus albigenis*-type and *Pseudochironomus*, taxa with rather high temperature optima between 15.6-16.5 °C in the Swiss-Norwegian trainingset (Heiri et al., 2011), potentially point to climate warming at the beginning and the end of the section. Furthermore,

Psectrocladius sordidellus-type, *Paratanytarsus penicillatus*-type and *Dicrotendipes* suggest the presence of aquatic macrophytes (Brodersen et al., 2001), which is further supported by continuous finds of Characeae oogonia (Kaltenrieder et al., 2009).

After the LGM, between ~ 18,610-17,210 cal yr BP (599-199 cm), no chironomid remains have been found, possibly as a result of cooler climatic conditions at the onset of Heinrich event 1 sensu lato (HE1-sl; after Stanford et al., 2011) and/or increased minerogenic (silt and clay) sediment deposition that started at Lago della Costa between ~ 18,400-17,400 cal yr BP (540-260 cm). Glacier melting along the southern border of the Italian Alps and Pre-Alps due to warmer climatic conditions led to slope instabilities and increased surface water discharge (Ravazzi, 2006), which caused high sedimentation rates before 17,400 cal yr BP (Kaltenrieder et al., 2009).

Between ~ 17,200 and 17,000 cal yr BP (199-149 cm) autochthonous material (lake marl) prevailed again. Only two samples have been analyzed for this part of the record. The two samples are dominated by littoral taxa typically of meso- to eutrophic lakes that are adapted to relatively warm climatic conditions, such as *Parakiefferiella bathophila*-type, *Paratanytarsus penicillatus*-type and *Endochironomus albipennis*-type (Pinder and Reiss, 1983; Hofmann, 1984; Brooks et al., 2007) and characterized by low abundances of *Tanytarsus lugens*-type (Brundin, 1956) suggesting that climate became gradually warmer. Various invertebrates (e.g. aquatic Gastropoda, Bivalvia) repopulated the lake, which also points to climatic warming during the early deglaciation (Kaltenrieder et al., 2009).

3.3 Full and Late Glacial temperature development at Lago della Costa

Taxa identified at low taxonomic resolution as for instance unidentified Chironomini, Tanytarsini, Orthocladiinae, Tanypodinae, Pentaneurini, non-Pentaneurini and Chironomidae were excluded when inferring temperature. Of the remaining 38 fossil chironomid taxa 37 occur in the applied transfer function. The reconstructed July air temperatures cover the time

interval ~30,900-17,000 cal yr BP. Temperature reconstructions are lacking for sections with no fossil chironomid remains such as between ~23,600-23,300 cal yr BP (1139-911 cm) and between ~18,600-17,200 cal yr BP (599-199 cm). These chironomid-barren intervals fall roughly within the age ranges reported for Heinrich event 1 and 2 (Bond et al., 1992, 1993; Hemming, 2004; Stanford et al., 2011) and the deglaciation in the southern Alpine foreland (Tinner et al., 1999; Ravazzi et al., 2006, 2014; Vescovi et al. 2007), suggesting that the climatic deterioration associated with these events (de Abreu et al., 2003; Roucoux et al., 2005; Wohlfahrt et al., 2008; Stanford et al., 2011) may have affected the chironomid fauna of the lake.

To provide an indication of whether the sub-thermal springs that presently feed into the lake influenced chironomid-inferred temperatures for Lago della Costa we compared the reconstructed values with a temperature reconstruction from Lago di Origlio (416 m a.s.l.) situated ~ 230 km to the west of our study site (Samartin et al., 2012). Inferred temperatures for Lago di Origlio are corrected to the altitude of Lago della Costa (7 m a.s.l.) assuming an altitudinal lapse rate of 0.6 °C/100 m (Livingstone and Lotter, 1998; Livingstone et al., 1999). When comparing the temperature reconstruction for the time period of overlap (~ 17,500-17,000 cal yr BP), both sites show July temperature estimates around 12.6 °C at 8 m a.s.l., suggesting that chironomid-inferred July air temperatures at Lago della Costa correctly reflect past summer temperatures in the region. This outcome was expected, since the sub-thermal springs may have affected winter more than summer temperatures. We assume that under natural conditions upland freshwater input from precipitation, creeks and springs dominated runoff to Lago della Costa as was the case before the freshwater was used for agricultural purposes (REGPARC, 2015).

When applied to the Lago della Costa chironomid record, the transfer function reconstructed average July air temperatures of ~12.9 °C in the oldest core section dated to ~ 31,000-28,000 cal yr BP (older than the oldest radiocarbon age of 27,730 cal yr BP; Fig. 4a).

These temperature values are well below the modern July air temperature recorded for this region (23 °C; mean values for 1961-1990; SCIA, 2015). A distinct cooling of ~2.7 °C seems to have occurred before ~29,000 cal yr BP. However, this temperature change is inferred from only one single sample. The cooling is followed by a warming between ~28,000-23,500 cal yr BP with a temperature average around 14.5 °C and maximum temperatures of ~15.7 °C. Between 23,000-18,600 cal yr BP July air temperatures were on average 13.5 °C, considerably lower than in the previous section. Chironomid-inferred temperatures suggest a rather abrupt warming of about 1.6 °C at around 23,100 cal yr BP to ~14.4 °C. The warming is followed by an abrupt temperature decline of ~2.4 °C (to reach a minim of 12.1 °C) at ~21,400 cal yr BP. Afterwards temperatures increased again by ~2.9 °C to about 15 °C. The uppermost part of the record between 17,200-17,000 cal yr BP suggests a warming of ~1.5 °C to ~ 13.4 °C.

The temperature reconstruction for Lago della Costa was characterized by sample-specific error of prediction (SSPE) between 1.5-1.6 °C (Fig. 4a). An evaluation of the modern analogues for fossil assemblages in the modern trainingset disclosed that only 4% of the samples have “no good” and “no close” analogue (1 sample) and additional 40% of the samples have “no close” analogue (10 samples) (Fig. 4b). Goodness-of-fit statistics revealed that only 4% of the samples have a “poor fit” with temperature (1 sample). In 20% of the samples (5 samples) we did not reach a minimum count of 50 headcapsules recommended for chironomid analysis (Heiri and Lotter, 2001). Some of these samples are also characterized by a “no close” and “no good” analogue situation and a “poor fit” with temperature.

Assemblages with *Microchironomus* are unusual in the modern trainingset and this taxon only occurs in low abundances in three Swiss and three Norwegian lakes and is solely responsible for the proportion of rare taxa found in the record (5 samples). Some of the assemblages that include *Microchironomus* are characterized by a “no close” and “no good” analogue situation.

The maximum abundance of taxa not occurring in the modern trainingset was very low and $\leq 1.1\%$ in any given sample (1 sample).

4. Discussion

4.1 Regional paleoclimate trends ~ 31,000-17,000 cal yr BP

Reconstructed temperatures oscillated markedly during the period ~ 31,000-17,000 cal yr BP (Fig. 4), ranging from ca. 11-12 °C (with two minima around 30,000 and 21,500 cal yr BP) to 15-16 °C (with two maxima around 28,000-24,000 and 19,000 cal yr BP). A very similar succession of cold and warm events has been identified in marine sediment cores from the Mediterranean Sea (Cacho et al., 1999, 2000, 2001; Fig. 5d). The comparison of the MD95-2043 sequence from the Western Mediterranean (Fig. 1) with our Lago della Costa record suggests that the lack of chironomid remains (Fig. 4, 5c) around 24,000 and 18,000 cal yr BP was associated with very cold conditions. These two Mediterranean cold events as well as the cold phase around 30,000 cal yr BP were correlated with Heinrich events (HE; Heinrich, 1988) by Cacho et al. (1999, 2001, with HE-3 radiocarbon-dated to $31,000 \pm 1000$ cal yr BP, HE-2 to $24,200 \pm 3800$ cal yr BP and HE-1 to $16,900 \pm 3300$ cal yr BP; Hemming, 2004, Fig. 5d).

Heinrich events were characterized by massive iceberg discharges from the Laurentide Ice sheet through the Hudson strait, which caused cold surface water temperatures and strongly reduced thermohaline circulation in the North Atlantic Ocean (Bond et al., 1993; Clark et al., 2002). Reduced SST in the Mediterranean (Fig. 5d) may have lowered the atmosphere-sea surface thermal gradient, resulting in a weakening of the Mediterranean low-pressure systems (Kwiecien et al., 2009). This may have caused less frequent and less intense storms, significantly reducing moisture availability and hence intensifying aridity in the Mediterranean (Tzedakis et al., 2004; Kwiecien et al., 2009). Additionally, the Mediterranean thermohaline circulation was intensified during the cold periods of the Heinrich and

Greenland Stadials in comparison to warm intervals, which is in contrast to what has been observed in the North Atlantic Ocean (Cacho et al., 2001). This possibly facilitated a faster response of the Mediterranean basin to any climatic alteration than in the open ocean (Cacho et al., 1999, 2002).

Global ice-sheets reached their maximum volume throughout the past 120,000 years during the LGM at approximately 23,000-19,000 cal yr BP (Mix et al., 2001) which corresponds to the mid-point of marine oxygen isotope stage 2 (MIS-2; Lisiecki and Raymo, 2005). Glacier cover reached maximum extensions in the southern Alps between ca. 26,500-23,000 cal BP (Monegato et al., 2007). Given that Lago della Costa is situated in close proximity of the LGM ice margin (50-60 km), very low temperatures at Lago della Costa around 21,000 cal BP might be associated with maximum ice extension in the Alps and their forelands.

In between the four cold phases HE-1, LGM, HE-2, HE-3 (Fig. 5c) relatively mild conditions prevailed at Lago della Costa and in the Mediterranean realm. For instance July temperatures were above the average of ca. 13.5 °C during the period 28,000-25,000 cal yr BP, when Mediterranean SST reached maximum values for the period 17,000-31,000 cal yr BP (Fig. 5d). This warm phase is too long to be attributed solely to Greenland Interstadials (GI) 3 and 4 (Fig. 5f) which occurred at ca. 29,000-27,000 cal BP. However, during GI 3 and 4, temperatures at Lago della Costa were still rising, together with the Mediterranean SST, following the temperature minimum at ca. 30,000 cal BP. Temperatures also transiently increased at approximately 20'000-19,000 cal yr BP at Lago della Costa. In agreement, perialpine lakes north of the Alps became ice-free between ca. 20'000-19'000 cal yr BP (Heiri et al., 2014b), and in the Mediterranean Sea SST's began to rise after approximately 21'000 cal yr BP (Fig. 5d; Cacho et al., 1999, 2000, 2001). Rising summer insolation (Fig. 5g, Berger and Loutre, 1991), may have contributed to this warming, which was abruptly terminated by cooling associated with HE-1.

4.2 Comparison of absolute temperatures values from Lago della Costa with Mediterranean SST and climate modelling data

At ca. 30,000 cal BP alkenone-derived annual SST reached a minimum of approximately 10 °C in the Western Mediterranean Sea (Fig. 5d, Cacho et al., 1999, 2000, 2001), which is only marginally cooler than the July air temperatures of 11 °C reconstructed for Lago della Costa, suggesting a deviation of reconstructed from modern temperatures of ca. 12 °C (July temperatures of 11 vs. 23 °C) for Lago della Costa and 9 °C in the Alborean Sea (annual SST ca. 10°C vs. 19°C, Cacho et al. 2001). The second cold episode documented at Lago della Costa occurred during the LGM at ca. 21,000 cal yr BP. Again, climatic conditions in the Southern Mediterranean Sea were warmer than at our site in Northern Italy: Annual SST was ca. 11 °C south of Spain (MD95-2043) and north of Sicily (BS79-39, Fig. 1 and 5), whereas on average, reconstructed July temperatures 23,000-19,000 cal yr BP were ca. 13.5 °C at Lago della Costa. The deviation of these values from modern temperatures at Lago della Costa was approximately 10 °C (13.5 vs. 23 °C mean values for 1961-1990, SCIA, 2015), while annual SST was ca. 8 °C cooler than during the Late Holocene in the Alborean Sea south of Spain and in the Tyrrhenian Sea north of Sicily (11 vs. 19°C, Cacho et al. 2001). Similar cooling in the range of 6-9 °C in the mean temperature of the warmest month compared to pre-industrial conditions has been simulated for the study region in northern Italy in climate modelling experiments by Strandberg et al. (2011). Likewise, Vrac et al. (2007) simulated a decrease of ca. 10 °C in July temperatures for Southern Europe. Pollen evidence suggests temperatures of the warmest month between 6 and 12 °C cooler than present in the northern Mediterranean region (Jost et al. 2005, Kageyama et al. 2006).

During the relatively mild period between HE-3 and HE-2 at ca. 29,000-25,000 cal yr BP annual SST in the Alborean Sea reached average values of ca. 14.5 °C (Fig. 5d, Cacho et al., 1999, 2000), while at Lago della Costa the same value was reached for July temperatures. This estimation suggests conditions of 5° cooler than today for the Alborean Sea, while at

Lago della Costa inferred July air temperatures were ca. 9 °C cooler than at present. This difference in cooling of 4 °C between the two areas is higher than the difference observed during colder ice age periods (2-3 °C) and may point to variations in north-south gradients during the ice age, with a stronger temperature gradient at 29,000-25,000 cal yr BP.

Alternatively, differences between mean annual and summer temperatures may have changed between the different time intervals, which would suggest changes in continentality within the last ice in the central Mediterranean region.

4.3 Vegetation responses to late ice age cooling and warming events at Lago della Costa

Our chironomid record suggests July temperature means around 13.5 °C (vs. 23 °C today, mean values for 1996-1990; SCIA, 2015), fluctuating between ~ 11 and 16 °C, for the final period of the last ice age. During this climatically extremely harsh time, forests had endured at Lago della Costa, which is unequivocally documented by well-dated high-resolution macrofossil and pollen data (Kaltenrieder et al., 2009). In the plains around the lake, boreal *Larix-Betula* parklands with steppic elements prevailed (macrofossil and pollen evidence), while in the Euganean Hills north of the lake patches of warm-loving trees such as *Quercus*, *Tilia*, *Ulmus*, *Fraxinus*, *Acer*, *Abies*, *Fagus*, *Carpinus* and *Castanea* (pollen evidence) may have persisted. These thermophilous tree taxa have variable July minimum temperature requirements, ranging from ~ 12 to 18°C (Landolt, 1992; Köhl et al., 2002, 2007; Köhl and Moschen, 2012, Tab. 2). Minimum July temperatures are one of the most important factors limiting tree growth (Körner, 2003; Körner and Riedl, 2012) and treeline in the Alps, for instance, is located at mean July temperatures of 8-10 °C (Landolt, 1992; Lang, 1994). The sheltered topography of the Euganean Hills may have provided local microclimates and environments for temperate trees to survive the LGM and to rapidly expand during warmer climates. In general, the low abundance of temperate vegetation at Lago della Costa during

the period 31,000-17,000 (ca. 1-4%) is comparable to that at southern Italian sites (e.g. Lago Grande di Monticchio, Valle di Castiglione, Lagaccione; Watts et al., 1996; Allen et al., 1999, 2000; Follieri et al., 1988; Magri, 1999), while Greek sites show higher abundances (e.g. Ioannina, Xinias; Tzedakis, 1993, 1994; Bottema, 1979; Fletcher et al., 2010). At present, under the absence of ice masses in the proximity, Lago della Costa has similar (summer) climatic conditions than other refugial sites such as Monticchio or Ioannina (e.g. 23 °C vs 23.5 °C and 24.9 °C for July means; Watts et al., 1996, Allen et al., 2000, Tzedakis, 1994), respectively. Warm summer conditions and the mild winters allow the growth of Mediterranean *Quercus ilex* stands in the forests of the Euganean Hills (Lona, 1957; Neviani, 1961; Paganelli, 1996a, Paganelli, 1996b; Miola and Gallio, 1997; Kaltenrieder et al. 2009), a situation which is comparable to that at the established refugial sites further south in Europe (e.g. southern Italy, Greece).

4.3.1 Vegetation dynamics during coldest ice age periods

During periods with allochthonous sediment formation (e.g. silts, sands at 17,500-18,500 and ca. 23,400-23,200 cal yr BP; Fig. 2), the pollen signal of thermophilous taxa may have partly or primarily derived from reworked pollen (Ravazzi, 2006; Kaltenrieder et al. 2009). We therefore limit our comparison of chironomid-inferred July temperatures with pollen inferred temperate vegetation to parts of the sequence which are characterized by autochthonous organic sediment formation (lake marl, calcareous gyttja, see Kaltenrieder et al. 2009; Fig. 2). Pollen data suggest a contraction of temperate forests (to ca. 1%) during the very cold period ~ 30,500-29,500 cal yr BP. Temperate tree taxa also declined (to < 1%, though without any interruption) during the LGM, suggesting that this second cold period strongly affected temperate refugial stands (Fig. 5). The ostracode record of Lago della Costa (Kaltenrieder et al. 2009) suggests rather dry conditions during the LGM at Lago della Costa, with elevated abundances of *Cyprideis torosa* (Fig. 5). This species tolerates oligohaline to

hyperhaline conditions (Kaltenrieder et al. 2009). Together with the observations that chironomids were still abundant, and that chironomid assemblages were dominated by freshwater taxa such as *Cladopelma lateralis*-type and *Tanytarsus mendax*-type (Fig. 2), this suggests that the lake, or its tributaries, turned oligohaline during this interval. Thus aridity may have also contributed to the reduction of temperate vegetation during this period. At 23,000-19,000 cal yr BP forests were rather open at Lago della Costa (30-55% AP; Kaltenrieder et al., 2009, Fig. 5), which is comparable to the situation at Ioannina (30% AP; Tzedakis, 1993, 1994) and Xinias (20% AP; Bottema, 1979) in Greece, as well as at Lago Grande di Monticchio (20-50%; Watts et al., 1996; Allen et al., 1999, 2000), Valle di Castiglione (20-50% AP; Follieri et al., 1988) and Lagaccione (20% AP; Magri, 1999) in southern Italy.

4.3.2 Vegetation dynamics in response to mild ice age climates

Pollen data suggest that sparse temperate tree stands reached their maximum abundance > 2% ca. 26,000-23,500 cal yr BP, when chironomid-inferred July temperatures were relatively high, around 15-16 °C. At present the full development of deciduous forests on either sides of the Atlantic Ocean is related to summer SST between 12-18 °C (van Campo, 1984). Marine cores along a Western European latitudinal transect suggest that both Atlantic and Mediterranean forests expanded when summer SST reached 12 °C (Fletcher and Sánchez Goñi, 2008), which is in good agreement with our results (13.5 ± 1.5 °C). The extent of forest development in southern Europe might have been determined by the duration of favorable temperature and moisture conditions, whereas at high latitudes ice sheet melting, permafrost retreat, soil development and migration lags might have had a greater influence (Fletcher et al., 2010).

A second minor peak of temperate vegetation with pollen abundances > 2% occurred at 29,500-28,500, when chironomid-inferred July temperatures were around 13° C and thus

only on an average. The ostracode record from Lago della Costa, particularly the low abundance of *C. torosa*, however, suggests that moisture availability was higher during this period than in the preceding and following intervals (Kaltenrieder et al. 2009; Fig. 5b). It is thus likely that this expansion of temperate taxa may have been co-induced by high moisture availability. The increase in temperate tree taxa at Lago della Costa was associated with a general expansion of forest vegetation (AP ca. 50%, Kaltenrieder et al., 2009) which is comparable to that at Ioannina and Kopais in Greece (ca. 60% AP, Tzedakis et al., 2002, 2004), stronger than in southern Italy at Monticchio (25-30% AP, Watts et al., 1996; Allen et al., 1999) and weaker than in southeastern France (up to ca. 90% AP, Wohlfarth et al., 2008) and Hungary (70% AP, Sümegi et al., 2013). The period 29,500-28,500 cal yr BP may correspond to GI-3 and GI-4 (Fig. 5f), when vegetation recovered in European regions south of 50°N, whereas north of these latitudes no such link could be found (Fletcher et al., 2010). On the other hand, inferred temperatures were relatively high at 28,000-26,500 cal yr BP (ca. 15 °C), when temperate tree taxa occurrence was < 2%. However, the ostracode record suggests that moisture availability was reduced (Fig. 5). We therefore assume that in addition to (summer) temperature, moisture availability was decisive for growth of temperate tree taxa in the Eugean Hills during the ice age.

5. Conclusions

This study provides the first quantitative, vegetation independent summer air temperature reconstruction for Northern Italy spanning the time ~ 31,000-17,000 cal yr BP. This interval covers the coldest periods of the last glacial, including the LGM and Heinrich events 1 to 3. Chironomids at Lago della Costa have responded to major cooling and warming fluctuations that were possibly induced by climatic oscillations such as Heinrich events and the LGM. The vegetation of the Euganean Hills followed the rapid and strong climatic oscillations at the end of the ice age. Summer air temperatures at Lago della Costa probably never fell below 10-13

°C (error range of reconstruction $\sim \pm 1.5$ - 1.6 °C, Fig. 5c), which is above the limit considered necessary for forest growth (8-10°C, Lang, 1994). Instead rather mild summer conditions prevailed $\sim 31,000$ - $17,000$ cal yr BP with average temperatures ~ 13.5 °C, which most likely allowed survival of temperate tree taxa in the warmest (and/or moistest) microhabitats of the Euganean Hills, e.g. where today Mediterranean *Quercus ilex* stands occur. Only if the local survival of these tree species is assumed, is it possible to explain the repeated expansions and collapses of temperate trees at Lago della Costa which faithfully accompanied climatic dynamics during the Heinrich events, the LGM and intervening periods. Pollen-inferred expansions of temperate trees occurred during periods with warm and/or moist conditions and autochthonous sedimentation (e.g. gyttja, lake marl), making it extremely unlikely that the Lago della Costa vegetational record was affected by sediment mixing or reworking.

Average summer air temperatures of ~ 13.5 °C during the LGM at Lago della Costa would have allowed the survival of *Quercus petraea*, *Ulmus* and *Fraxinus excelsior* (minimum July air temperature requirements of 10-12 °C; Kühl et al., 2002, 2007; Kühl and Moschen, 2012; Tab. 2) even in the plain around the lake, where climatic conditions were probably colder and harsher than inside the sheltered Euganean Hills. The presence of *Acer* and *Tilia* in the pollen record, both insect pollinated species (no long distance wind dispersal), with minimum July air temperature requirements of 14-16 °C, suggests that summer temperatures in the refugia inside the Euganean Hills were probably 0.5-2.5 °C warmer (14-16 °C vs 13.5 °C, Kühl et al., 2002, 2007; Kühl and Moschen, 2012) than in the plains. Such microclimatic disparities may exist today as evidenced by strongly varying vegetation composition (e.g. from *Fagus sylvatica* over *Castanea sativa* to *Quercus ilex* stands) and could be explored by a fine meshed climatic survey of the Euganean Hills. We thus conclude that relatively warm summer air temperatures, moist conditions as well as mild winters (less severe frosts) as indicated by high winter insolation during the LGM most likely favored the

survival of small and isolated patches of temperate trees in the Euganean Hills, a particularly sheltered landscape with azonal microclimatic conditions in Northern Italy.

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Table 1: ^{14}C dates of Lago della Costa (AP2)

Lab. No.	Depth (cm)	Core	Material	^{14}C dates, conv. uncal BP	Calibrated age (cal yr BP)*	Cal. 95% confidence limits*
Erl-4815	176-178	AP2	Wood (twig)	14086 $\pm$ 100	17130	16778-17464
Poz-16254	606-622	AP2	Wood, deciduous twig, charcoal, <i>Betula</i> fruits and fruit scale, <i>Larix</i> needles	15400 $\pm$ 150	18660	18327-18949
Erl-4816	840-842	AP2	Coniferous periderm and wood (twig)	19285 $\pm$ 160	23230	22814-23651
Poz-16337	1082-1084	AP2	Deciduous (Pomoideae) twig	19400 $\pm$ 120	23358	22997-23691
Poz-16256	1264-1282	AP2	<i>Larix</i> needles and part of seed wing, <i>Betula</i> fruit	20170 $\pm$ 130	24239	23902-24558
Poz-16257	1500-1502	AP2	Periderm, wood	23600 $\pm$ 250	27734	27348-28210

Table 2: Temperature requirements of selected trees (after Kühl and Moschen, 2012).

Taxa	Mimimum mean July temperature (°C)	Minimum mean January temperature (°C)
<i>Quercus petraea</i>	12	-6
<i>Quercus pubescens</i>	17	-4
<i>Carpinus betulus</i>	16	-7.5
<i>Tilia cordata</i>	14	-18.5
<i>Acer pseudoplatanus</i>	16	-6.5
<i>Acer campestre</i>	15	-12
<i>Castanea sativa</i>	18	-2
<i>Fraxinus excelsior</i>	12	-13
<i>Fraxinus ornus</i>	17.5	-3.5
<i>Fagus sylvatica</i>	15	-6
<i>Ulmus</i> (<i>U. glabra</i> , <i>U. laevis</i> , <i>U. minor</i>)	10	-20
* <i>Abies alba</i>	10	-4

* After Landolt, 1992

Figure captions

Fig. 1. Location of Lago della Costa (star, 7m a.s.l.) and a selection of other terrestrial palaeorecords (brown circles), such as Lago di Origlio (Tinner et al., 1999; Samartin et al., 2012), Lago Grande di Monticchio (Watts et al., 1996; Allen et al., 1999), Ioannina (Tzedakis et al., 2004), Kopais (Tzedakis et al., 1999, 2002), Tenaghi Philippon (Tzedakis et al., 2002, 2006), Fehér lake (Sümegei et al., 2013), Les Échets (Wohlfahrt et al., 2008), and marine SST records (blue circles), such as BS79-38 (Cacho et al., 2001), and MD95-2043 (Cacho et al., 1999, 2000). The map was made using the free and open source Geographic Information System Quantum GIS (QGIS, 2015).

Fig. 2. Age-depth model of the Lago della Costa record. The six AMS ^{14}C ages were obtained from plant macrofossils. The ^{14}C dates were converted to calibrated years (cal yr BP) with the program Calib version 7.1 (Reimer et al., 2013). The age-depth model is based on linear interpolation.

Fig. 3. The Lago della Costa chironomid record. Relative abundance (%) of selected chironomid taxa are shown. The taxa are grouped according to their present distribution in the Alps.

Fig. 4. Chironomid-inferred July air temperature estimates (**A**, including sample specific error of prediction: SSPE) plotted versus reconstruction diagnostic statistics and samples with low count sum (**B**). Circles in B indicate samples with no close or no good nearest modern analogues in the calibration dataset (**a, b**), samples with a poor fit with temperature (**c**), samples with chironomids that are rare (**d**, $N_2 < 5$), or not represented in the calibration dataset (**e**) and samples with low count sum (**f**, < 50 headcapsules).

Fig. 5. Summary diagram. (**a**) Relative abundance of arboreal pollen from the Lago della Costa core (Kaltenrieder et al., 2009), (**b**) relative abundance of selected temperate tree pollen taxa (*Carpinus* t., *Tilia*, *Ulmus*, *Acer*, *Castanea*, *Fraxinus excelsior*, deciduous *Quercus*, *Fagus* and *Abies*) from the Lago della Costa core (Kaltenrieder et al., 2009), (**c**)

chironomid-inferred July air temperature estimates (including sample specific error of prediction: SSPE), **(d)** alkenone-derived sea surface temperature (SST) data from two sediment cores (MD95-2043 and BS79-38) from the western and central Mediterranean Sea (Cacho et al., 1999, 2001), **(e)** relative abundance of the ostracode *Cyprideis torosa* from the Lago della Costa core (Kaltenrieder et al., 2009), **(f)** oxygen isotope data from the NGRIP ice core from Greenland (Svensson et al., 2008), **(g, h)** mean summer (June-August) and mean winter insolation (December-February) values at 45°N (Berger and Loutre, 1991). Heinrich Stadial (HS)-2 and 3 indicate SST temperature variations interpreted as related to Heinrich events 2 and 3 by Cacho et al. (1999), HE-1 is indicated slightly later in this publication (centered on 16.6 ka), but according to Sánchez Goñi and Harrison (2010) the associated temperature decrease (the Heinrich Stadial 1) starts around 18 ka. The temperature decrease marked by HS-1 in **(d)** therefore coincides with the beginning of the stadial. Numbers over the graph indicate the position of the Greenland Interstadials (GI; Dansgaard et al., 1993; Björck et al., 1998; Blockley et al., 2012) and the horizontal bar labeled with LGM the age of the global LGM following MARGO project members (2009).

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Figure 1

Figure 2

Figure 4

Figure 5