

**Climate and  
vegetation changes**

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# Climate and vegetation changes during the Lateglacial and Early-Mid Holocene at Lake Ledro (southern Alps, Italy)

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## Abstract

Adding to the on-going debate regarding vegetation recolonisation in Europe and climate change since the Lateglacial, this study investigates a long sediment core (LL081) from Lake Ledro (652 m a.s.l., southern Alps, Italy). Environmental changes that were reconstructed using multiproxy analysis (pollen-based vegetation and climate reconstruction, lake-levels, magnetic susceptibility and X-ray fluorescence (XRF) measurements) recorded climate and land-use changes during the Lateglacial and Early-Mid Holocene. The well-dated and high-resolution pollen record of Lake Ledro is compared with vegetation records from the southern and northern Alps to trace the history of distribution tree species. An altitude-dependent progressive time-delay of the first continuous occurrence of *Abies* (fir) and of the *Larix* (larch) development has been observed since the Lateglacial in the southern Alps. This pattern suggests that the mid-altitude Lake Ledro area was not a refuge and that trees originated from lowlands or hilly areas (e.g. Euganean Hills) in northern Italy. Preboreal oscillations (ca. 11 000 cal. BP), Boreal oscillations (ca. 10 200, 9300 cal. BP) and n.e. 8.2 kyr cold event suggest a centennial-scale short-lasting climate forcing in the studied area. *Picea* (spruce) expansion occurred preferentially around 10 200 cal. BP and 8200 cal. BP in the south-eastern Alps and, therefore, reflects the long-lasting cumulative effects of successive boreal and 8.2 kyr cold events. The extension of *Abies* is contemporaneous with the 8.2 kyr event, but its development in the southern Alps benefits from the wettest interval 8200–7300 cal. BP evidenced in high lake-levels, flood activity and pollen-based climate reconstructions. Since ca. 7500 cal. BP, low signal of pollen-based anthropogenic activities suggest a weak human impact. The period between ca. 5700 and ca. 4100 cal. BP is considered as a transition period to colder and wetter conditions (particularly during summers) that favoured a dense beech (*Fagus*) forest development which in return caused a distinctive yew (*Taxus*) decline. We conclude that climate was the dominant factor controlling vegetation changes and erosion processes during the Early and Mid Holocene (up to ca. 4100 cal. BP).

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# 1 Introduction

During the Last Glacial Maximum (LGM) and the Early-Mid Holocene, the vegetation history of the Alpine area record two main features: (1) treeline migration, and the spreading of taxa from various Glacial refuges, in response to long-lasting climate change, and, (2) mixed forcing from long- and short-term climate and anthropogenic changes.

During the last orbitally-driven deglaciation, conifers and broad-leaved tree species benefit from global climate improvement and glacier retreats in the Alps to conquer new available areas. A growing body of evidence suggests that these species survived the cold phases in the Po-Plain and along the southeastern Alpine border (Vescovi et al., 2007, 2010; Kaltenrieder et al., 2009, 2010). The spread of *Abies*, however, may have been different as it highlights the possible persistence at high altitudes in the southern slope of the Alps (Hofstetter et al., 2006). To address this question, researchers are searching for studies that cumulate three characteristics: (1) they have to be located southeast of the Alps for comparison with the nearby potential Euganean Hills refuge (Kaltenrieder et al., 2009), (2) a palaeo-vegetational archive must be present at high-chronological and temporal resolution for the Lateglacial, (3) and pollen grains must be received from a large range of altitudes in its catchment.

The Holocene climate in Europe is punctuated by numerous short-term cold events, such as Preboreal and Boreal oscillations (Björck et al., 1997, 2001; Fleitmann et al., 2007; Yu et al., 2010), the 8.2 kyr event (Wiersma and Jongma, 2010) and Neoglacial climate cooling at ca. 6000–4000 cal. BP (Magny et al., 2006b; Miller et al., 2010; Giraudi et al., 2011; Zanchetta et al., 2012; Vanni re et al., 2012). These rapid climatic changes are recorded throughout the Mediterranean region, but their characteristic effects can vary spatially (e.g. Magny et al., 2003, 2011; Roberts et al., 2011). In the context of low Holocene temperature variations in the Alps ( $\pm 1^\circ\text{C}$ ; Heiri et al., 2003), precipitation, reflected by lake-level changes (e.g. Magny, 2004), may be a relevant indicator for climate reconstruction at centennial scales. In addition, pollen-based

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climate reconstructions can enhance our understanding of precipitation changes over the Italian peninsula (e.g. Peyron et al., 2012). Recent palynological and anthracological records have pointed out the need to disentangle climate and human influences (e.g. Tinner et al., 2003; Valsecchi et al., 2008–2010; Cruise et al., 2009; Vanni re et al., 2011). In the open debate to assess the possible relationships between climatic change and impact of human societies, which has become a contemporary issue, palaeoenvironmental records are needed to gain a perspective of past processes.

In this study, we investigate well-dated and high-resolution pollen-based vegetation changes recorded in a long sediment core (LL081) from Lake Ledro (652 m a.s.l., southern Alps, Italy, Fig. 1). This lake combines the required characteristics (close to the Euganean Hills refuge, relatively large catchment area) and offers the opportunity to explore spatial expansion of tree species during the Lateglacial and the Early-Mid Holocene. We compare the pollen record with proxies that are indicative of runoff, soil erosion and lake-level changes (Magny et al., 2009, 2012). Therefore, we provide a complete analysis of climate and anthropogenic activities in the Ledro catchment to assess whether the environment responded to millennial and centennial-scale climate changes and/or to possible land-use dynamics. This study provides a low temporal resolution for the Lateglacial, as the focus is on the Holocene record. The younger part of the sequence, characterised by strong human impacts on the vegetation, are presented in a separate paper dealing with Late Holocene environmental changes in the Ledro area (Galop et al., 2012).

## 2 Study area

Lake Ledro (Lago di Ledro; 45°52' N, 10°45' E, 652 m a.s.l.) is a 3.7 km<sup>2</sup> large lake located in northern Italy (Fig. 1a), on the southern slope of the Alps (Fig. 1b). The maximum depth of this lake is 46 m. The catchment area is 111 km<sup>2</sup> and includes mountains that culminate at 1500–2250 m (Fig. 1c). The geological substratum comprises mainly Triassic, Liassic and Cretaceous limestone. Morainic tongues and

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conglomeratic deposits of calcareous and siliceous composition fill the valley bottom. The lake was formed due to a morainic dam (Beug, 1964), which is now cut by the outlet. Lake Ledro drains into nearby Lake Garda (65 m a.s.l.). Lateglacial and Holocene sedimentation is dominated by calcite precipitation and biogenic lake productivity accompanied with allochthonous material, such as clay and organic particles.

Vegetation around the lake is dominated by beech (*Fagus*) mixed with fir (*Abies*). Higher in the Ledro Valley, the montane belt (650–1600 m) is characterised by spruce (*Picea*). The subalpine belt (1600–2000 m) is replaced by grasslands above 2000 m. The mild climate allowed for the development of (1) a mixed oak forest with lime (*Tilia*) and elm (*Ulmus*) trees, and (2) Mediterranean vegetation, such as *Quercus ilex*, Ericaceae and olive trees which can reach 300 m a.s.l. as a grove forms. At Molina di Ledro, a village at the Lake Ledro outlet, the mean temperature of the coldest and warmest months are 0°C and 20°C, respectively. The annual precipitation ranges from ca. 750 to ca. 1000 mm.

### 3 Methods

#### 3.1 Selection of the coring site

Lake Ledro bathymetry (Fig. 2a) and sedimentary stratigraphy have been documented by a high resolution seismic reflection survey using a 3.5 kHz pinger source and an Octopus Marine acquisition system mounted on an inflatable boat. Conventional GPS navigation allowed tracking the acquisition of a dense grid of profiles imaging most of the basin fill (Fig. 2a and b; Simonneau et al., 2012). To encompass the entire Holocene sediments, coring site LL081 was selected in the deep basin, away from chaotic to transparent lens-shaped bodies reflecting mass wasting deposits (MWD) and in a relatively distal position from the two main deltas formed by lake tributaries. The coring site was characterised by well-stratified, acoustic facies showing continuous and high-frequency reflections (Fig. 2b).

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## 3.2 Core sampling and sedimentology

Coring recovery was done using an UWITEC coring platform with a percussion piston coring technique. Coring operations were directly guided by the quasi-3-D seismic stratigraphy. Twin cores were retrieved, and segments were extracted and stored at 4 °C at the University of Franche-Comté (France).

The cores were split longitudinally into two halves, photographed and logged with a GEOTEK Multi Sensor Core Logger to obtain geophysical measurements (gamma-ray wet bulk density, magnetic susceptibility (MS), p-wave velocity) at 5 mm intervals. The master core (MC), i.e. the ideal and complete lithologic succession using both parallel cores, was established based on lithological changes (with observation of key reference horizons) in combination with MS and gamma-density profiles.

MS, primary dependent on the magnetite concentration in sediments, was measured in electromagnetic units to determine the inorganic allochthonous sediment content (Gedye et al., 2000). The development of pedogenesis under forest cover may have favoured a mineral magnetic increase in soils (Jong et al., 1998), so low MS in sediments is expected during phases of stabilized, vegetated slopes (Whitlock et al., 2011), while increased magnetic concentrations may be related to changes in sediment sources and soil erosion (Dearing et al., 1996; Jong et al., 1998; Vanni re et al., 2003; Cruise et al., 2009). Nevertheless, when ferrimagnetic mineral concentration is low (magnetite and maghaemite), MS may be largely influenced by diamagnetic minerals (quartz, carbonates) (Thompson and Oldfield, 1986).

X-ray fluorescence core scanning was done on an AVAATECH instrument at the ETH Zurich and with a spatial resolution of 200- m. XRF-core scanning is a fast, non-destructive technique, which provides information about elemental variations directly from untreated sediment and reflects the amount of minerogenic material (L wemark et al., 2011). Among the various elements tested (Vanni re et al., 2012), and considering the geological setting of the catchment, we provide the Ca/Si ratio to distinguish between authigenic carbonate sedimentation from glacial face leaching, mostly

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comprising siliceous stones transported by the Glacial tongue in the valley. Ca and Si were thus anticorrelated ( $r = -0.55$ ;  $p < 0.001$ ). A Ca/Si ratio increase was interpreted to correspond to an increasing authigenic carbonate component linked with climate warming and/or to a lower siliceous proportion under decreasing runoff and humidity.

### 3.3 Radiocarbon dating

The Lateglacial and Early-Mid Holocene chronology is based on six Accelerator Mass Spectrometry (AMS)  $^{14}\text{C}$  ages measured on terrestrial organic material from cores LL081 (Table 1). Four  $^{14}\text{C}$  ages measured on a different core (LL082, Fig. 2a) are included according to lithological correlation (Vanni re et al., 2012). Macrofossils were collected from sediment samples sieved with a 100  $\mu\text{m}$  mesh screen. Radiocarbon ages were calibrated in years cal. BP by the Calib 6.0 software using the calibration curve IntCal09 (Reimer et al., 2009). Dates are expressed as intercepts with  $2\sigma$  ranges. Further age control is provided by the Lateglacial-Holocene transition ( $\sim 11\,700$  yr cal. BP), which is well established in the LL081 pollen stratigraphy. This transition is also observed in the littoral site of Ledro II where it is dated to  $10\,090 \pm 70$  BP, i.e. 11 700–11 240 cal. BP (Fig. 2a; Magny et al., 2012). Therefor, we used this transition to better constrain the age-depth model. The age-depth model is constructed using a smooth, cubic spline model (Fig. 3) available within the “Clam” software from Blaauw (2010).

### 3.4 Pollen analysis

#### 3.4.1 Pollen samples

Sediment samples (1  $\text{cm}^3$ ) were treated both chemically (HCl, KOH, HF, acetolysis) and physically (sieving) following standard procedures (Moore et al., 1991). *Lycopodium* spore tablets were added for estimating pollen concentrations (grains  $\text{cm}^{-3}$ ; Stockmarr, 1971). Pollen were poorly preserved in the lower part of the LL081 core. A total of

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124 pollen samples were analysed under a light microscope at standard magnification ( $\times 400$ ). A total of 123 pollen types were identified using photo atlases (Reille, 1992–1998; Beug, 2004) and the reference collection at the University of Franche-Comté. At least 300 terrestrial pollen grains were counted, excluding dominant terrestrial taxa and water and wetland plants, as well as pteridophyte spores. Percentages were calculated based on total pollen. Spores and algae were added to the total counted palynomorphs to calculate their percentage.

Using the TILIA 1.12 program (Grimm, 1992–2005), main pollen percentages are represented in Fig. 4a and b. Local pollen assemblage zones (LPAZ) were defined using the CONISS function of TILIA 1.12 (Tables 2 and 3). One solid and eight dashed lines define the limits between statistical first- and second-order splits. This dashed line has been accentuated to indicate the Holocene basal limit and to facilitate discussion of the diagram. Figure 5 presents a pollen diagram with selected major arboreal and non-arboreal taxa and the sum of anthropogenic indicators. Two ratios were established: total arboreal taxa ( $AP_t$ ) and arboreal pollen without *Pinus* ( $AP_{wp}$ ) (calculated by excluding pine pollen grains).

### 3.4.2 Pollen-based climate reconstruction

The Modern Analogue Technique (MAT; Guiot, 1990) was used to reconstruct climatic changes in the Mediterranean area (e.g. Davis and Brewer, 2009; Joannin et al., 2011; Peyron et al., 2011; Combourieu Nebout et al., 2012). MAT is based on a modern pollen dataset containing more than 3500 modern spectra, with 2000 samples from the Mediterranean area (Dormoy et al., 2009). Additional information about MAT methodology and its application to the Ledro pollen record are available in the work by Peyron et al. (2012). Annual precipitation was reconstructed based from the pollen dataset with *Pinus* excluded (dashed line in Fig. 5).

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## 4 Results and interpretation

### 4.1 Age model and sediment lithology

#### 4.1.1 Age-depth model

Age control during the Lateglacial is inferred from one radiocarbon date. It helps us to perform a consistent age model (Fig. 3) for the Younger Dryas and the beginning of the Holocene. The age-depth model is extrapolated to the base of the mastercore, so that these ages might just be used as estimation.

The age-depth curve shows low sedimentation rates from the beginning of the Holocene to ca. 7000 yr cal. BP, resulting in condensed deposits from 7 to 5.75 m depth. The average temporal resolution is approximately 73 yr/sample for this portion of the core. Sedimentation rates increase steadily upwards in the core.

#### 4.1.2 Changes in lithological and abiotic proxies

Changes in the abiotic proxies (MS, Ca/Si; Fig. 5) suggest phases with distinct sediment sources and erosive processes. The scheme appears robust when considering the strong contrast between multi-millennial trends, which can be unraveled from the data. While Ca is related to authigenic carbonate component, Si is related to detrital inputs. Three phases are distinguished.

From the base up to ca. 10 800 cal. BP, increasing Ca/Si ratio suggests high but decreasing erosional activity while relatively stable MS values do not indicate soil erosion in the not yet afforested area. From Up to approximately 5700 cal. BP, MS values are stable and low, suggesting that erosion was low. From ca. 5700 to 4100 cal. BP, coinciding peaks and drops in MS and Ca/Si (at ca. 5500 and 5000 cal. BP) are observed.

While core lithology did not reveal multi-millennial trends, carbonate marl facies (white to brown in colour) were intercalated with detrital material layers (dark colours) (Fig. 3; for further detail, see Simonneau et al., 2012). This pattern is obvious from two

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thick, dark detrital layers of 23 and 12 cm dated at ca. 5500 and 5000 cal. BP, respectively. All abiotic proxies shift in these layers, which are interpreted as the signature of two exceptional, most likely short-term, flood events discharging elements from soil and rocks and, eventually diluting the pollen concentration (Fig. 5). This scheme suggests continuous sedimentation of authigenic carbonate, sporadically interrupted by detrital events (Vanni re et al., 2012; Simonneau et al., 2012).

## 4.2 Pollen analysis

### 4.2.1 Pollen sequence and terrestrial vegetation dynamics

The history of Lake Ledro vegetation is divided into four LPAZ for the Lateglacial (LL-1 to LL-4) and two LPAZ (LL-5 and LL-6) with lower level subdivisions for the Holocene (Fig. 4a and b). Only general features could be identified in the three first LPAZ (LL-1 to LL-3) because samples with sufficient pollen grains are sparse.

According to the age-model, the sequence starts around 17 000 cal. BP (LL-1). The pollen record suggests that an open vegetation may have grown in the Lake Ledro landscape (Table 2), which was dominated by pine trees (ca. 60 %) and constituted of pioneer vegetation (*Betula*, *Juniperus* and *Ephedra*). *Artemisia*, Chenopodiaceae and Poaceae developed in a steppe-tundra, most likely located at a higher altitude. Rare grains of deciduous *Quercus*, *Corylus*, and *Salix* exemplify the regional presence of temperate trees at the end of the LGM and the following Lateglacial (LL-1 and LL-2), when climate was still cold and arid and the Alpine glaciers still in proximity.

From ca. 14 100 cal. BP (zone LL-3, Table 2), pollen-inferred vegetation around Lake Ledro indicates afforestation, illustrated by AP<sub>wp</sub> increase (up to 60 %). This afforestation includes development of thermophilous trees (deciduous *Quercus* and *Corylus*) and mixed-open and mixed-coniferous forests (*Betula*, *Pinus*, and *Larix*) during the Aller d/B lling interstadial. *Ulmus*, *Tilia*, and *Fraxinus excelsior* also appeared in the pollen record, together with *Abies* which develops in the montane belt. Considering the

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poor dispersal of fir pollen grains (Mazier, 2006) and diversity of thermophilous taxa at the end of this zone, the Lake Ledro landscape likely was below the treeline.

In zone LL-4 (ca. 12 700 to ca. 11 700 cal. BP), *Betula*, *Pinus* and *Larix* redeveloped while the amount of deciduous *Quercus*, *Abies*, *Ulmus* and *Tilia* decreased. Forest spread therefore ceased (low values of  $AP_{wp}$ ), and steppe and meadows increased (up to 10 % each). These patterns illustrate climate deterioration in the Younger Dryas (YD). Only coniferous woods (*Pinus* and *Larix*) seem to develop at the lake elevation. During this phase, abundant Volvocaceae (HdV-128) are recorded, typical for an open but less deep lake (Jouffroy-Bapicot, 2010).

At ca. 11 700 cal. BP (zone LL-5), rapid increases in deciduous *Quercus* and *Ulmus* correspond to local settlement of a thermophilous forest. The sharp increase in  $AP_{wp}$  thus suggests an upward migration of the treeline added to the effect of rapid climate improvement at the beginning of the Holocene. The pollen record shows high and low *Pinus* amount before and after 650 cm (ca. 9800 cal. BP), respectively.

The CONISS software identifies two subzones (Table 2). The first (LL-5a; ca. 11 000 to ca. 10 350 cal. BP) is characterised by abundant oak pollen grains and relatively abundant elm, hazel, and lime pollen grains. This expansion is associated with birch development, most likely on the lake shore, as suggest by higher *Betula* pollen rates in the littoral core from Ponale (Magny et al., 2012) than in deep sediments. *Corylus* and *Fraxinus excelsior* population expansion is delayed by 350 years compared to the concomitant increase in deciduous *Quercus*, *Ulmus* and *Tilia*. Sharp decreases in *Pinus* ( $\Delta 20\%$ ) and deciduous *Quercus*, *Ulmus* and *Corylus* occurred at ca. 11 200 cal. BP and in the subsequent samples (ca. 11 000 to ca. 10 800 cal. BP), respectively.

In subzone LL-5b (ca. 10 350 to ca. 9750 cal. BP), the  $AP_{wp}$  ( $\sim 87\%$ ) suggests a dense, mixed-oak forest progressively dominated by hazel (up to 34 %). A marked decrease in pine begins at the Preboreal-Boreal transition (ca. 10 800 cal. BP) and continues during the Boreal phase. Despite the proximity of the Mediterranean belt, sclerophilous taxa (*Quercus ilex* type) appearing in the zone LL-5b are scarce (which is the case until the top of the sequence).

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From ca. 9750 to 3950 cal. BP, deciduous *Quercus*, *Ulmus*, *Corylus*, *Tilia*, *Fraxinus excelsior*, *Acer*, *Picea*, *Abies*, *Alnus*, *Taxus*, *Fagus* and *Carpinus* successively developed and regressed and replaced each other. As a result, a remarkably stable plateau in AP values (between 81 and 96 %; LL-6) likely forced the CONISS function to group the four subzones (LL-6a-b-c-d).

Subzone LL-6a (ca. 9750–7700 cal. BP) is characterised by the *Picea* development (up to 20 %), the appearance of *Abies* pollen grains, steadily increases in deciduous *Quercus* and *Ulmus* and decrease in *Corylus* percentage. The decline in *Corylus* and *Tilia* correlates with the *Picea* main increase, and, when focussing on short oscillations, opposed percentage variations of *Corylus* and *Picea* are recorded ( $\Delta 20\%$  and  $\Delta 15\%$ , respectively). Since ca. 9750 cal. BP, temperate trees and shrubs developed and formed a mixed deciduous oak forest (Table 3). More specifically, deciduous *Quercus*, *Ulmus*, *Picea* and *Corylus* mainly composed the pollen assemblage from ca. 9750 to ca. 7700 cal. BP.

The first *Abies* maximum at ca. 7700 cal. BP and the gradual increase in the abundance of *Fagus* mark the beginning of subzone LL-6b (up to ca. 6000 cal. BP). Sharp variations in the percentage of *Abies* pollen are recorded with a maximum (25 %) at ca. 7200 cal. BP. *Alnus* also entered the forest composition. Between ca. 6700 to ca. 6000 cal. BP, *Tilia*, *Ulmus* and *Fraxinus excelsior* regressed, while *Corylus* re-expanded. On shorter time scales, lows in the percentages of *Picea* and *Abies* are observed concomitantly with an important increase in *Corylus* at ca. 6700 cal. BP and ca. 6000 cal. BP. Cereal-type pollen grains are first recorded at ca. 7500 cal. BP suggesting human activity in the Ledro landscape.

The subsequent subzone LL-6c (ca. 6000 to ca. 5300 cal. BP) starts with a *quasi* disappearance of *Picea* pollen (at ca. 5950 cal. BP), and an increase in *Taxus*. Deciduous *Quercus* decreases to a minimum of 10 %. The AP rate is slightly lower than that of previous LL-6 subzones, as temperate and coniferous trees are balanced by increased *Artemisia*, *Poaceae* and *Asteraceae* Cichoriodeae.

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From ca. 5300 to ca. 3950 cal. BP (LL-6d), the pollen-based vegetation is characterised by large amounts of deciduous *Quercus* and *Abies* and decreases of *Corylus* and *Picea*, while *Fagus* develops up to a maximum ( $\sim 30\%$ ), and *Carpinus* becomes more present. Human occupation is suggested by the presence of cerealia type pollen grains and a questionable apparition of *Juglans* (which is collected in northern Italy since the Early Neolithic; Rottoli and Castiglioni, 2009).

### 4.2.2 Pollen-based quantitative reconstruction of precipitation

Annual precipitation has been reconstructed for the interval of ca. 12200 to ca. 4000 cal. BP (Fig. 5) and shows a long-term progressive increase ( $\Delta 300$  mm). Pluri-secular variations also appear to be superimposed on this millennial-scale trend, such as a dry phase which begins during the YD and ends at ca. 11100 cal. BP and two drought phases at ca. 9100–8900 and 8100–7500 cal. BP.

## 5 Discussion

### 5.1 Pollen-based vegetation dynamics at Ledro and in northern Italy

#### 5.1.1 Vegetation changes before and during the Lateglacial interstade

To assess whether long-distance transported pollen grains signed the pollen record of Lake Ledro in LL-1 and LL-2 (Table 3), the results were compared with other pollen sites in the southern Alps. Kaltenrieder et al. (2009) observed that the Po Plain lowlands (i.e. below 800 m a.s.l.) were partly wooded by mixed deciduous-conifer woods since the last Glacial and even during the LGM (i.e. 23 to 18 kyr cal. BP). We can thus consider that rare pollen grains from mesothermic plants found at Lake Ledro, such as deciduous *Quercus*, *Corylus*, and *Fraxinus excelsior* possibly originated from these lowlands (up to the altitude of the lake, i.e. 652 m a.s.l.) during the Lateglacial. At the Palughetto basin (1040 m a.s.l.), Vescovi et al. (2007) found that *Pinus* pollen grains

are transported from lowlands. The *Pinus* percentage is higher at Ledro (up to 80 %), so we assume that pines reached lake elevation.

Pollen grains from thermophilous and montane trees start to increase at ca. 14 300 cal. BP. Considering that the age model is less robust for the pre-Holocene, this age is consistent with the temperature increase at the onset of the Allerød/Bølling interstadial (ca. 14 600 cal. BP), which favoured an upward migration of the treeline in northern Italy (Tinner and Vescovi, 2005). Moreover, pollen grains from thermophilous and montane trees at Lake Ledro initially increased slowly, and then become more abundant at the end of this period. This trend may indicate gradual climate improvement, latter reaching a maximum, as also shown in chironomid-inferred July air temperatures in the nearby Lago Lavarone (ca. 13 000–12 800 cal. BP; Heiri et al., 2005).

### 5.1.2 Impact of Younger Dryas cooling

Climate deterioration in the Younger Dryas favoured a mixed-open vegetation development (LL-4, Table 3). Heliophilous plants, such as *Artemisia*, developed with three maxima dated to ca. 12 400, 12 100 and 11 850 cal. BP. These three peaks may be related to three climate deteriorations inferred from  $\delta^{18}\text{O}$  records in the GRIP ice core (Dansgaard et al., 1993). Other heliophilous plants, such as pine and larch, seemed to be less favoured during these three phases; however, they reached their maximum when considering the entire YD. A similar pattern is recorded in the littoral core from Ponale (Magny et al., 2012).

### 5.1.3 Vegetation changes during the Early Holocene (ca. 11 700–7700 cal. BP)

The beginning of the Holocene is characterised in the pollen record of Lake Ledro by a rapid expansion of mixed-open broad-leaved forests in which pines are still abundant. More specifically, a mixed oak forest associated with elm and lime develops at lake altitude. Such a concomitant population expansion was also described in the Lago di Lavarone record (Filippi et al., 2007).

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Considering the pine reduction at the Preboreal-Boreal transition (ca. 10 800 cal. BP), a similar decrease of this cold-adapted, heliophilous tree is observed at Lago di Lavarone (Filippi et al., 2007) and Lago di Fimon (23 m a.s.l., Valsecchi et al., 2008). Pines is also linked with the light-demanding hazel expansion at Lago di Fimon (Valsecchi et al., 2008), Lago di Origlio (Finsinger et al., 2006) and Lago di Annone (Wick and Möhl, 2006). At higher elevations, the decrease in the abundance of pine occurred later, at ca. 9750 cal. BP, as in Totenmos (Heiss et al., 2005).

#### 5.1.4 Vegetation changes during the Mid Holocene (ca. 7700–3950 cal. BP)

The anthropogenic influence on the study area can be traced from cerealia type pollen grains and pollen-based vegetation that directly or indirectly resulted from anthropogenic activities. At Ledro, cereal-type pollen grains occurred sporadically from ca. 7500 cal. BP onwards. The low transportation potential of cereal-type pollen grains (Tweddle et al., 2005) suggests the establishment of Early Neolithic communities in the vicinity of the lake. However, other anthropogenic indicators are still sparse at that time. According to Bellini et al. (2008), agricultural activities began in Tuscany in the Neolithic (ca. 8000 cal. BP), and the openness of the landscape could also be a consequence of the anthropogenic clearing practices. In Northern Italy, Rottoli and Castiglioni (2009) reported the appearance of farming communities at ca. 7600–7500 cal. BP. According to these authors, Early Neolithic agriculture spread rapidly (over a few centuries) throughout the Alps, which is in accordance to the pollen record of Lake Ledro.

*Picea* and *Abies* proportion declined concomitantly with a significant increase in *Corylus* at ca. 6700 cal. BP and ca. 6000 cal. BP. These short-term vegetation replacements thus complete the relationship described in Sect. 5.2.4 (*Picea* development), as it illustrates the light-demanding hazel benefiting from spruce and fir regression. Peaks of cerealia type pollen grains just precede these vegetation changes by approximately 100 yr and around 50 yr at ca. 6800 and ca. 6050 cal. BP, respectively. Agricultural activities documented by cereal-type grains and anthropogenic indicators appeared at ca. 6000 cal. BP, providing a more complete description of human occupation around the

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when studying spatial patterns (latitude, longitude, and elevation) in migration and/or population expansion.

At the lowland Lago della Costa site (7 m a.s.l.; Kaltenrieder et al., 2009, 2010), *Abies* is continuously recorded from last Glacial. The first continuous record of fir pollen grains is dated to ca. 15 500 cal. BP in Lago Piccolo di Aveglia (353 m a.s.l.; Finsinger et al., 2006), ca. 13 000 cal. BP in Balladrum (390 m a.s.l.; Hofstetter et al., 2006), ca. 12 800 cal. BP in Lago di Origlio (416 m a.s.l.; Tinner et al., 1999), ca. 12 800 cal. BP in Lake Ledro, ca. 11 800 cal. BP in Lago di Lavarone (1100 m a.s.l.; Filippi et al., 2007), ca. 11 000 cal. BP in Pian di Gembro (1350 m a.s.l.; Pini, 2002) and in Piano (1439 m a.s.l.; Valsecchi and Tinner, 2010), ca. 10 800 cal. BP in Palughetto (presence of stomata; 1040 m a.s.l.; Vescovi et al., 2007), ca. 9100 cal. BP in Totenmoos (1718 m a.s.l.; Heiss et al., 2005) and at ca. 8500 cal. BP in Lej da San Murezzan (1768 m a.s.l.; Gobet et al., 2003). These estimated ages of the first continuous records of fir pollen grains (sometimes including *Abies* stomata) have been plotted according to the elevation of the sites on Fig. 6a. This shows a progressive delay with increasing altitude and a trend, that was quantified using linear regression ( $r = -0.93$ ;  $p < 0.001$ ), of approximately 225 m/1000 yr in the southern Alps. The fir pollen record of Lago del Greppo (1442 m a.s.l.; Vescovi et al., 2010) in the northern Apennines is clearly excluded and therefore suggests a distinct pattern for the fir spread in this area. Altitudinal abundance reflects the ecological optimum of trees, so that tree migration was faster at optimum elevation and slower at lower and higher elevations, rather than exhibiting a linear relationship with elevation (van der Knaap et al., 2005). This observation explains why *Abies* migration in the southern and northern Alps shows an inadequate linear regression with elevation (van der Knaap et al., 2005), as indicated by the scarcity of p-values. Discrepancies with results from our study is therefore expected to be due to location and number of sites (southern-northern Alps and 68 sites in van der Knaap et al.; southern Alps and 11 sites in our study), as other authors observed a clear relationship between *Abies* migration and latitude (a northward migration).

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This trend suggests that altitudinal conditions drove the spread of fir trees in the southern Alps, despite non-linear climate improvement and glacier retreat since the Lateglacial and various topographical, edaphical and microclimatical conditions. However, low percentages indicate that *Abies* did not form fir forests. This trend may also question whether fir formed refugee populations in the lowlands (*sensu stricto*) or hilly areas (Kaltenrieder et al., 2009). This study provides helpful data and insights from Lago della Costa, situated at the edge of the Euganean Hills (up to 800 m), where favourable micro-environmental conditions may have occurred. However, fir refugees cannot be excluded in the case of lowlands, which were at higher elevation when considering a lower sea level. Hofstetter et al. (2006) discussed the possible persistence of *Abies* at high altitudes during the Lateglacial on the southern slope of the Alps by excluding (but not completely) long-distance transport from the Apennines. However, the persistence of *Abies* at high altitudes is not corroborated by the present study.

### 5.2.2 *Larix* immigration and its development

*Larix* pollen grains reflect the larch development at a relatively low altitude during the Lateglacial (Lago della Costa, Kaltenrieder et al., 2009; Lago Ragogna, Monegato et al., 2007; Lago Piccolo di Aveglia, Finsinger et al., 2006). Larch development is delayed according to elevation in the southern Alps (Fig. 6b) and is reported from 800–900 m at the onset of the Allerød/Bølling interstadial (Vescovi et al., 2010) and between 1000 and 1700 m (Lago di Lavarone, Filippi et al., 2007; Pian di Gembro, Pini, 2002; Palughetto, Vescovi et al., 2007; Totenmoos, Heiss et al., 2005) during the Allerød/Bølling interstadial. However, Lake Ledro pollen record differs, as larch development occurred at lower altitude during this period. Thus, this trend needs to be confirmed, particularly for the interval between ca. 16 500–14 500 cal. BP.

From ca. 14 000–12 500 and ca. 11 500–9500 cal. BP, larch is abundantly found at Totenmoos in north-eastern Italy (1718 m a.s.l.; Heiss et al., 2005). During the YD, larch amounts reached their maximum at neighbouring Palughetto (1040 m a.s.l.; Vescovi et al., 2007) and Pian di Gembro (1350 m a.s.l.; Pini, 2002). Thus, low larch abundance

at Totenmoos suggests that the treeline was at lower altitude (i.e. between 1350 and 1718 m). This elevational pattern confirm that the treeline was above 1400 m in the southern Alps as suggested by Vescovi et al. (2007), and agrees with a treeline located at ca. 1500 m a.s.l. as suggested by Gobet et al. (2005). At Ledro, larch developed from 14 000 to 7500 cal. BP and simultaneously disappeared from the nearby Lago di Lavarone (1100 m a.s.l.; Filippi et al., 2007). However, charcoal fragments suggest that larch presence is continuously recorded during Holocene times at a higher altitude in the nearby Valle di Sol (up to 2200 m a.s.l.; Trentino, Favilli et al., 2010). Larch presence has also been documented for the last millennia in Lake Tovel (1177 m a.s.l.; Gottardini et al., 2004). This discrepancy may result from varying situations of the larch developments in alpine valleys or, more likely, to a bias in the pollen record because *Larix* has poor pollen distribution (Sjögren et al., 2008). A large part (25 %) of the Bronze Age lake-dwelling wood piles found in Lake Ledro littoral are larch wood (Pinton and Carrara, 2007), and larch woodland occurs today in the subalpine belt of the Ledro valley (Magny et al., 2009). The absence of *Larix* grains in the pollen diagram since ca. 7500 cal. BP is thus a distribution artefact, which also argues for a lower-than-today elevation of the treeline by the time of larch records in the lake.

### 5.2.3 *Corylus* development

*Corylus* developed later than oak (LL-5a), as it is generally observed in the southern Alps (Finsinger et al., 2006) at Lago Piccolo di Avigliana (353 m a.s.l.) and Lago di Origlio. Thus, this pattern is opposite from the northern Alps where hazel expanded before oak. In more details, the age for *Corylus* expansion given at Lago Piccolo di Avigliana and Lago di Origlio (between ca. 10 400 and ca. 10 200 cal. BP; Finsinger et al., 2006) does not correspond to the first hazel increase at Lake Ledro (ca. 11 200 cal. BP), nor to the second increase at ca. 10 750 cal. BP. At Ledro, hazel expansion is complicated by the fact that the first and second expansions are separated by a 300-yr long decline (from ca. 11 100 to ca. 10 800 cal. BP), which also affected deciduous *Quercus*, *Ulmus* and *Tilia*. This event temporally affected most of the

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temperate trees, suggesting that the first increase of *Corylus* has to be considered to integrate the discussion about hazel expansion in Europe (Fig. 6c). Hazel expansion, therefore, seems to be older than that observed at Lago di Annone (226 m a.s.l.; Wick and Möhl, 2006) and more in accordance with Lago di Fimon (Valsecchi et al., 2008).

5 However, when looking at other pollen records from the southern and northern Alps, and considering the reliability of age estimates, hazel expansion occurred in a short interval between 11 200 and 10 100 cal. BP (Fig. 6c). This corroborates the conclusions of Finsinger et al. (2006), who reported a broadly synchronic hazel expansion in the northern and southern Alps, as well as those of Giesecke et al. (2011), who observed  
10 a synchronic rise in *Corylus* in central and northern Europe.

#### 5.2.4 *Picea* development

The rare presence of *Picea* pollen in the Lake Ledro sediments, estimated to have occurred in Glacial times, is most likely due to wind dispersal. Van der Knaap et al. (2005) assumed that a low pollen levels indicates the approximate immigration time and the beginning of population expansion. Spruce development is dated to ca. 9100 cal. BP in  
15 Lake Ledro (Fig. 6d). This is more recent than records from Palughetto (1040 m a.s.l.; Vescovi et al., 2007) and Lago Ragogna (188 m a.s.l.; Monegato et al., 2007), which show spruce development during the Allerød/Bølling interstadial. The age for Lake Ledro spruce development is more similar to those from Lago di Lavarone (Filippi et al., 2007), Lago del Greppo (Vescovi et al., 2010), Totenmoos (Heiss et al., 2005) and  
20 Passo del Tonale (1883 m a.s.l.; Gehrig, 1997). This age is older than Pian di Gembro (1350 m a.s.l.; Pini, 2002), Lej da San Murezzan (Gobet et al., 2003) and Palù di Sonico (650 m a.s.l., Gehrig, 1997). Thus, no clear relationship between altitude and spruce development is observed in the southern Alps and a westward development is more  
25 apparent. At the scale of the southern and northern Alps, this pattern was observed by Ravazzi (2002) and shown statistically by van der Knaap et al. (2005).

Pini (2002) discussed increasing humidity in the Early Holocene, which favoured the development of *Picea* and *Abies* to form montane coniferous forests. According

to Pini (2002), *Picea* moved down from higher altitudes to colonise montane altitudes. The same observation was reported by van der Knaap et al. (2005) based on pollen records from the southern and northern Alps. In the present study, considering only the southern Alps, we suggest that spruce expansion was unrelated to altitude, and factors other than climate, are expected to be important. *Corylus* and *Picea* are anti-correlated ( $r = -0.58$ ;  $p < 0.001$ ) in the interval 9750–7700 cal. BP. This relationship is also established in Norway (Seppä et al., 2009), where the dominance of *Picea abies* was caused by its rapid population growth, competitive suppression of other taxa (particularly *Corylus* and *Tilia*), and local edaphic factors. We can thus postulate that both, climate and competitive capacity may have triggered spruce development at Ledro.

### 5.2.5 *Fagus* development

Focusing on *Fagus*, we found a bi-phased expansion from ca. 7500 to ca. 6000 cal. BP, and from ca. 5300 to ca. 4050 cal. BP. A bi-phased expansion is also observed at Lago di Fimon (Valsecchi et al., 2008) with similar ages for the onset of these phases, while ages for maximal content are not comparable. Valsecchi et al. (2008) discussed the relationship between *Fagus* establishment and climate vs. anthropogenic factors. They used cross-spectral analysis on pollen and charcoal to conclude that no single factor was determinant. Anthropogenic indicators, such as *Rumex* and *Plantago lanceolata*, are observed continuously in the pollen record of Lake Ledro since the Lateglacial. Thus, it appears to be preferable, in the present discussion of *Fagus* establishment, to focus on cereal-type pollen grains, which occurred sporadically during the bi-phased beech development. These occurrences are out of phase with *Fagus* variations and therefore suggest that beech development was most likely not related to human activities. Lago di Lavaronne, at higher altitude (i.e. 1100 m a.s.l.; Filippi et al., 2007), had a one-phase increase in *Fagus* at ca. 8000 cal. BP. The Lake Ledro catchment area provides pollen grains from higher altitudinal vegetation belts, so it is remarkable that the rise in beech differs both in age and pattern. This difference questions whether a

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common factor (i.e. human impact) could explain different *Fagus* development patterns from areas in close proximity. At Ledro, the existence of agriculture is confirmed by pollen analysis, while pastoral activity in the catchment area is not. Raw data thus indicate a minor anthropogenic influence, but we cannot clearly assess the anthropogenic role for influencing the bi-phased *Fagus* development.

## 5.3 Climate and human influences on vegetation in north-eastern Italy

### 5.3.1 Beginning of the Early Holocene (before ca. 11 000 cal. BP)

Before ca. 11 200 cal. BP (Fig. 5), Ca/Si values indicate the onset of less erosive activity, which is correlated with the pollen-based vegetation history showing rapid afforestation. Warmer, wetter climate conditions (shown by increasing pollen-based annual precipitation values; Fig. 5; Peyron et al., 2012) associated with the final stages of deglaciation, triggered forest expansion, which, in turn, limited erosional processes (Olsen et al., 2010) and Si delivery to the lake. Volvocaceae decreased during this phase of environmental change. This algae family is typical for an open, less deep lake (Jouffroy-Bapicot, 2010), and its decrease in abundance may indicate rising lake levels and more mesotrophic conditions in the lake.

A centennial-scale drop in percentages of deciduous *Quercus*, *Ulmus* and *Corylus* is recorded at ca. 11 100 cal. BP. This period corresponds to lower pollen-based annual precipitation and temperature estimates for the coldest month (Peyron et al., this volume) and to a deposit characterised by low Ca/Si values. Simultaneously, small and short successive rises and drops are recorded in the littoral section from Ponale (Fig. 5; Magny et al., 2012), suggesting cooler and drier conditions. The timing and duration of these events recorded in both biotic and abiotic proxies can be interpreted as the cold Preboreal oscillation, which temporarily recalls less favourable climate conditions as during YD. Palaeoenvironmental records obtained using stable isotopes from the Swiss Plateau revealed a Preboreal Oscillation (PBO) but no significant effect on low altitude vegetation (Gerzensee, 602 m a.s.l., Lotter et al., 2000). The pollen-based vegetation

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response is strongly recorded in the catchment of Lake Ledro, as it is generally more pronounced near vegetation ecotones at medium and higher altitudes than in lowlands (Wick, 2000). A cold oscillation has also been observed for the Preboreal chronozone in the pollen stratigraphy of Lago di Avigliana (Finsinger and Tinner, 2006). A cooling and drought event is also evidenced in pollen and lake-level records from Lago di Accesa (Magny et al., 2006a; Finsinger et al., 2010) and linked with the PBO. Magny et al. (2007) provided a lake-level synthesis for the PBO (ca. 11 300–11 150 cal. BP, as defined from the GRIP oxygen isotope record) and concluded that wetter climatic conditions prevailed in west-central Europe, while a marked climatic drought characterised the north-central Italy. A growing body of studies extends the occurrence of this dry phase toward southern Italy (e.g. Di Rita et al., 2012; Joannin et al., 2012). Lake Ledro pollen and sedimentological records are therefore in the line with a cooling and drying climate during the PBO for all of Italy.

### 5.3.2 Early-Mid Holocene (ca. 11 000–5700 cal. BP)

From ca. 10 800 to 5700 cal. BP, the forest cover, which was inferred from AP percentages, stabilised at approximately 90–95 %, and geochemical measurements show a high Ca/Si ratio. Again, biotic and abiotic proxies indicate that climate conditions in the Lake Ledro catchment enhanced forest cover large enough to limit runoff and erosion activity, though successive taxa replacement occurred with reduction of temperate trees and the expansion of montane trees. Increasing pollen-based annual precipitation values, which are  $> 800 \text{ mm yr}^{-1}$  since ca. 10 800 cal. BP, are triggered mainly by increasing summer precipitation (Peyron et al., 2012) associated with lower temperature in the warmest month. Lake level variations and flood frequency are in general low during this phase (Magny et al., 2012; Vanni re et al., 2012). Thus, vegetation and sediment records, on a multi-millennial scale, show generally stable climate conditions from ca. 10 800 to 5700 cal. BP.

However, the present study shows a more complex history along this interval. A peak in the Ca/Si ratio is recorded at ca. 10 200 cal. BP and correlates with an increase

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of light-demanding hazel and *Fraxinus excelsior*. This feature coincides with the cooling during the oldest Boreal oscillation (Magny et al., 2007). Another change started from ca. 9300 cal. BP onwards, as montane trees clearly expanded (mainly *Abies* and *Picea*). The well-known Boreal oscillations (9300–9050 and 8750 cal. BP; Magny et al., 2007) and 8.2 kyr cold events coincided with *Picea* and *Abies* expansion, respectively. These events are marked by Ca/Si drops, which indicate increasing runoff and are associated with rises in lake-level (Fig. 5; Magny et al., 2012), decreases in annual precipitation (mostly forced by winter precipitation changes) and decreases in temperature of the coldest month (Peyron et al., this volume). These cold and dry events occurred within the 9000–8000 cal. BP interval, which is interpreted as a partial return to cooler conditions following an orbitally driven delay in Northern Hemisphere deglaciation (Mayewski et al., 2004). Finally, montane coniferous forests may record the vegetation response to the long-lasting cumulative effect of these decadal-centennial successive events. Accordingly, spruce development in the south-eastern Alps preferentially occurred at approximately 10 000 cal. BP and 8200 cal. BP (Fig. 6d).

After ca. 8200, *Abies* develops in the Lake Ledro catchment as well as in Pian di Gembro (Pini, 2002). This tree is meso-hygrophile, and its development, which requires a minimum precipitation of 800 mm yr<sup>-1</sup> without long summer dryness, has also been shown important from ca. 8200 to 7200 cal. BP in Lago di Annone (Wick and Möhl, 2006). During this interval, a general increase in lake level is observed in Lake Ledro, where higher lake-levels coeval (and may trigger) with the low development of Volvocaceae at ca. 8200 and 7500–7300 cal. BP (Fig. 5). A general increase in the pollen-based reconstruction of annual precipitation is observed between ca. 8500–8200 and 7300–7100 cal. BP. This increase is mostly triggered by increased summer precipitation during the first half of this interval (Peyron et al., 2012). Based on spring to autumn floods, Vannièrè et al. (2012) observed an increase in flood activity from ca. 8000–7000 cal. BP. Taken together, and considering dating uncertainties, these observations corroborate the wet climate scenario for the Alps recognised in the Corchia's speleothem (Spötl et al., 2010). Base on reconstructed  $\delta^{18}\text{O}$  (Zanchetta et

al., 2007) and dendrochronological data provided by the East Alpine Conifer Chronology (Nicolossi et al., 2009), these authors observed rainy summers from ca. 8200 to 7300 cal. BP. According to Pini (2002), expansion of *Abies* at middle and high altitudes started from the lowlands at ca. 11 500 cal. BP and benefited from increasing humidity at ca. 8200 cal. BP. Pini (2002) questioned the direct relationship between sudden spruce and fir expansion with climate change. Our study indicates that spruce development is more likely influenced by several factors, such as the long-lasting, cumulative effects of decadal-centennial, successive climate events, which occurred from ca. 10 200 to 8200 cal. BP, and competitive capacity.

Large changes in *Abies* are noteworthy from ca. 7600–6700 cal. BP, which, within dating uncertainty, is not comparable to abrupt collapses of *Abies* during Misox events that developed at high-elevation sites in the southern Alps (Piano; Valsecchi and Tinner, 2010). At ca. 5700 cal. BP, the cerealia type sum suggests human occupation along the lakeshore. No relationship is observed between pollen-based human activities (i.e. crops), vegetation changes in the landscape (such as forest clearance), changes in pollen concentrations, and geochemical variations up to ca. 5700 yr cal. BP, so we conclude that climate was the dominant factor controlling vegetation changes during a phase of low human impact.

### 5.3.3 Final Mid Holocene (ca. 5700–4100 cal. BP)

From ca. 5700 to ca. 4100 cal. BP, more contrasted values in abiotic records are observed. Vegetation is still largely forested, but includes more anthropogenic indicators (mainly representing farming). As discussed above, vegetation and beech developments, are largely climatically controlled. Abiotic indicators show clear and strong changes, which leads us to separate this phase from the previous one. As the anthropogenic influence is low, two very thick and exceptional deposits recorded ca. 5800–5300 cal. BP (Vanni re et al., 2012), may indicate major climate instabilities, which most likely enhanced erosion in the catchment. Magny (2004) and Magny et al. (2012) have discussed the possible impact of wetter and cooler events between ca. 6000 and ca.

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5000 cal. BP in Europe, possibly related to rapid climate changes (RCC) suggested by Mayewski et al. (2004). Local declination of these RCC may thus have affected the precipitation regime in this part of the Alps and caused successive lake-level rises and stopped beech development between ca. 5800 and ca. 5300 cal. BP in the Ledro. This phenomenon may be linked with successive episodes of higher lake-level between ca. 5550 and ca. 5300 cal. yr BP at Lake Constance, coinciding with glacier advances (Magny and Haas, 2004) during the Neoglacial (Zanchetta et al., 2012).

At ca. 4500 cal. BP, the lake level showed an abrupt rise that continued onwards with a high average water table (Magny et al., 2012). Again, low development of Volvocaceae appears to be related to deeper water depth. According to Vannièrè et al. (2012), flood activity increases since ca. 4500 cal. BP onwards suggesting a major change in the palaeohydrological regime. These authors also report that the rupture reflects a non-linear climate response to the orbitally-driven gradual decrease in summer insolation (Zhao et al., 2010), which caused the millennial trend toward wet conditions during the Late Holocene. Lake-level rises therefore suggest higher humidity during summer (Magny et al., 2012) while both pollen-based summer and winter precipitation increased (Peyron et al., 2012). Valsecchi et al. (2008) reports tree-ring studies, which evidence a reduced beech growth (at its southern range) in response to dry summers (Jump et al., 2006). We observed that the beech forest development in the Ledro pollen record was (1) stopped between ca. 6000 and ca. 5300 cal. BP during wet, cooler summers, and (2) was strong thereafter due to wetter summers. As for Lago di Fimon, we can conclude that low beech population densities since ca. 7500 cal. BP indicate that population expansion was not favoured by the previous cold and wet phases (Valsecchi et al., 2008). However, in the context of minor anthropogenic influence in Ledro, beech expansion may have benefited wetter summers.

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## 6 Conclusions

We investigated pollen-based vegetation changes recorded in the sediments of Lake Ledro (652 m a.s.l.) since the Lateglacial, particularly for the last 12 000 yr. By comparing the continuous and high-resolution pollen records with those from other sites in the southern and northern Alps, we were able to discuss successive increases in taxa abundances. We considered their climatical and ecological requirements relative to their expansion in the southern Alps from various glacial refuges. A progressive, altitudinal time-delay for the first continuous occurrence of *Abies* was observed since the Lateglacial in the southern Alps. This tree expanded as single trees from the lowlands (or hilly areas) long before the development of dense fir forests. *Larix* development also is delayed according to altitude, though this trend is not sufficiently documented. This pattern confirms that the treeline was above 1400 m in the southern Alps during the Younger Dryas. Thus, it appears that despite its mid-altitude position, the Ledro catchment cannot be considered as a refuge. This conclusion suggests that trees originate from lowlands (e.g. Euganean Hills) and, with the upward migration of the treeline, colonised the area during the climate improvement in the Early Holocene. *Corylus* and *Picea* developments, which occurred at 11 200–10 100 and between 14 500 and 8200 cal. BP, respectively, do not show a delay according to altitude. The broadly synchronic *Corylus* expansion in the Alps is a common feature recognised in central and northern Europe. Expansion pattern of *Picea* is more surprising and occurred ca. 10200 cal. BP and 8200 cal. BP in the south-eastern Alps, and therefore reflected the long-lasting cumulative effects of successive Boreal and 8.2 kyr cold events.

Pollen analysis and pollen-based climate reconstructions were coupled with lake-level variations and abiotic proxies, such as magnetic susceptibility and elemental variation from the Lake Ledro long core, to reveal the local impacts of climate change and land-use activities. On a millennial-scale, climate is the dominant factor controlling vegetation and erosional processes during the Early and Mid Holocene (up to 4100 cal. BP). A steady climate change toward wetter conditions, allowed oak,

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hazel, spruce, fir, beech and yew to successively expand and regress. Human impact, recorded since 7500 cal. BP, is low. Sporadic occurrences of cereal-type pollen grains are out of phase with the observed bi-phased *Fagus* variations, suggesting that beech development is not related to human activities in the Ledro area and may have benefited from wetter summers. No important pastoral activity is observed during periods of declining yew abundance, which is more likely caused by a concomitant change to dense forest, mostly dominated by the shade-giving beech. A shift toward colder and wetter conditions (mostly during summers) is recognised from 5700 to 4100 cal. BP (i.e. during the Neoglacial period), but yet, human influence remained low.

On a centennial-scale, the Preboreal (11 000 cal. BP) and Boreal oscillations (10 200, 9300–9050 and 8750 cal. BP) are evidenced in biotic and abiotic records. They thus correspond to cold and/or dry climate installation, and forced short-term vegetation changes. The interval 9000–8000 cal. BP is a cold and dry interval, which is interpreted as a partial return to cooler conditions following an orbitally-driven delay in the northern Hemisphere deglaciation. Expansion of *Abies* is contemporaneous with the 8.2 kyr cold event but its development in the southern Alps benefited from the wettest interval 8200–7300 cal. BP, as evidenced in lake-levels, flood activity and pollen-based climate reconstruction.

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**Table 1.** AMS-radiocarbon dates with a  $2\sigma$  age range calibration from the Lake Ledro LL081 core.

Sample ID	Lab. code	Material	AMS 14C Age BP	Depth MC (cm)	Cal. yr BP ( $2\sigma$ )
B2a-43*	ETH-40411	Leaf remains	3575 ± 35	424.9	3730–3980
B2a-80	POZ-27891	Wood-Charcoal	4080 ± 35	461.6	4440–4810
A3b-91	POZ-30223	Wood-Charcoal	4550 ± 35	499.2	5050–5320
A3b-127*	ETH-39233	Leaf remains, needles	5200 ± 35	535.8	5900–6170
B2b-20	POZ-27892	Wood-Charcoal	5720 ± 40	562.4	6410–6630
A4a-19*	ETH-39234	Needles	6530 ± 40	589	7330–7560
A4a-46	POZ-30224	Wood-Charcoal	7270 ± 50	616	7980–8180
B2b-109	POZ-27894	Wood-Charcoal	8385 ± 35	641.5	9300–9490
A4a-73*	ETH-39235	Needles	8405 ± 40	643	9300–9520
B3a-75	POZ-27895	Wood-Charcoal	11 480 ± 60	759.3	13200–13470

\* Ages obtained from core LL082 and lithologically correlated.

**Table 2.** Inventory of local pollen zones with depth and estimated ages, main taxa, total arboreal pollen (AP), and common and rare pollen types. Note that two ratios ( $AP_t$  and  $AP_{wp}$ ) are used (arboreal pollen without *Pinus* ( $AP_{wp}$ ) was calculated by excluding pine pollen grains).

LPAZ	Depth (cm) <i>Age (yr cal. BP)</i>	Main taxa observed	Total of Arboreal Pollen %	Common pollen types (CPT) Rare pollen types (RPT)
LL-6d	505–435 <i>5300–3950</i>		$AP_t$ 89–96	CPT: <i>Pinus</i> , <i>Ulmus</i> , <i>Tilia</i> , <i>Fraxinus excelsior</i> , <i>Picea</i> , <i>Abies</i> , <i>Alnus</i> , <i>Fagus</i> and Poaceae
LL-6c	540–505 <i>6000–5300</i>		$AP_t$ 86–96	CPT: <i>Pinus</i> , <i>Ulmus</i> , <i>Tilia</i> , <i>Fraxinus excelsior</i> , <i>Picea</i> , <i>Abies</i> , <i>Alnus</i> , <i>Fagus</i> and Poaceae
LL-6b	601–540 <i>7700–6000</i>		$AP_t$ 87–95	CPT: <i>Pinus</i> , <i>Betula</i> , <i>Ulmus</i> , <i>Tilia</i> , <i>Fraxinus excelsior</i> , <i>Picea</i> , <i>Abies</i> , <i>Alnus</i> , <i>Fagus</i> and Poaceae RPT in LL-6b to 6d: <i>Acer</i> , <i>Carpinus</i> , <i>Taxus</i> , Ericaceae, <i>Ostrya</i> , <i>Pistachia</i> , <i>Quercus ilex</i> , <i>Salix</i> , <i>Juniperus</i> , <i>Hedera helix</i> , Cyperaceae, Apiaceae, Ast. Asteroideae, Ast. Cichorioideae, Brassicaceae, Cerealia type, <i>Triticum</i> , <i>Plantago lanceolata</i> , <i>Artemisia</i> , <i>Orlaya grandiflora</i> , Lamiaceae and <i>Typha</i>
LL-6a	648–601 <i>9750–7700</i>		$AP_t$ 81–96	CPT: <i>Pinus</i> , <i>Ulmus</i> , <i>Tilia</i> , <i>Fraxinus excelsior</i> , <i>Picea</i> , <i>Abies</i> , <i>Alnus</i> and Poaceae RPT: <i>Acer</i> , <i>Fagus</i> , <i>Larix</i> , <i>Carpinus</i> , Ericaceae, <i>Ostrya</i> , <i>Pistachia</i> , <i>Salix</i> , Cyperaceae, Ast. Asteroideae, Brassicaceae, <i>Artemisia</i> , <i>Plantago</i> , <i>Convolvulus</i> , Lamiaceae and <i>Typha</i>
LL-6	648–435 <i>9750–3950</i>	deciduous <i>Quercus</i> - <i>Corylus</i> - <i>Abies</i>		
LL-5b	661–648 <i>10350–9750</i>		$AP_t$ 95 $AP_{wp}$ 87	CPT: <i>Corylus</i> , <i>Ulmus</i> , <i>Tilia</i> , <i>Fraxinus excelsior</i> , <i>Abies</i> and <i>Alnus</i>
LL-5a	692–661 <i>11000–10350</i>		$AP_t$ 87–96 $AP_{wp}$ 53–87	CPT: <i>Betula</i> , deciduous <i>Quercus</i> , <i>Ulmus</i> , <i>Tilia</i> <i>Abies</i> , <i>Alnus</i> , <i>Larix</i> , <i>Corylus</i> , <i>Fraxinus excelsior</i> and <i>Artemisia</i>
LL-5	692–648 <i>11700–9750</i>	<i>Pinus</i> - deciduous <i>Quercus</i> - <i>Corylus</i> - Poaceae		RPT: <i>Tilia</i> , <i>Fraxinus excelsior</i> , <i>Larix</i> , <i>Pistachia</i> , <i>Quercus ilex</i> , <i>Salix</i> , Ast. Cichorioideae, <i>Plantago</i> , <i>Sanguisorba</i> , <i>Thalictrum</i> , <i>Typha</i> , Cyperaceae and <i>Artemisia</i>

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Table 2. Continued.

LPAZ	Depth (cm) Age (yr cal. BP)	Main taxa observed	Total of Arboreal Pollen %	Common pollen types (CPT) Rare pollen types (RPT)
LL-4	725–692 12 700–11 700	<i>Pinus</i> -Poaceae- <i>Artemisia</i>	AP <sub>t</sub> 75–95 AP <sub>wp</sub> 25–53	CPT: deciduous <i>Quercus</i> , <i>Corylus</i> , <i>Abies</i> , <i>Alnus</i> , <i>Larix</i> , <i>Amaranthaceae</i> and <i>Ast. Cichorioideae</i> RPT: <i>Cyperaceae</i> , <i>Ast. Asteroideae</i> , <i>Brassicaceae</i> , <i>Centaurea</i> , <i>Plantago</i> , <i>Alisma</i> , <i>Convolvulus</i> , <i>Thalictrum</i> , <i>Typha</i> and <i>Lamiaceae</i>
LL-3	795–725 14 100–12 700	<i>Pinus</i> - <i>Betula</i> - Poaceae- <i>Artemisia</i>	AP <sub>t</sub> 85–90 AP <sub>wp</sub> 30–55	CPT: deciduous <i>Quercus</i> , <i>Corylus</i> , <i>Betula</i> , <i>Cyperaceae</i> and <i>Plantago</i> RPT: <i>Ulmus</i> , <i>Abies</i> , <i>Alnus</i> , <i>Carpinus</i> , <i>Pistachia</i> , <i>Amaranthaceae</i> and <i>Larix</i>
LL-2	915–795 16 500?–14 100	<i>Pinus</i> -Poaceae- <i>Artemisia</i>	AP <sub>t</sub> 75–85 AP <sub>wp</sub> 15–30	CPT: <i>Juniperus</i> , deciduous <i>Quercus</i> , <i>Corylus</i> , <i>Betula</i> , <i>Amaranthaceae</i> , <i>Ast. Asteroideae</i> and <i>Ast. Cichorioideae</i> RPT: <i>Picea</i> , <i>Plantago</i> and <i>Lamiaceae</i>
LL-1	1003–915 17 000?	<i>Pinus</i> -Poaceae- <i>Artemisia</i>	AP <sub>t</sub> 65–75 AP <sub>wp</sub> 12–17	CPT: <i>Juniperus</i> , <i>Betula</i> , <i>Ephedra</i> , <i>Amaranthaceae</i> , <i>Ast. Asteroideae</i> and <i>Ast. Cichorioideae</i> RPT: <i>Brassicaceae</i> , <i>Centaurea</i> , <i>Hippophae</i> , <i>Alisma</i> , <i>Convolvulus</i> and <i>Lamiaceae</i>

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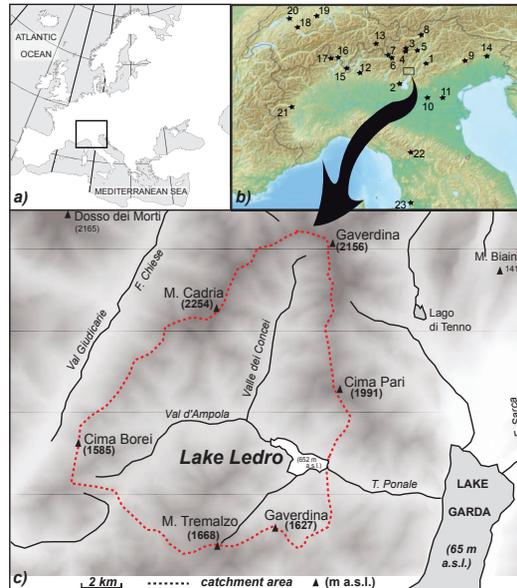
**Table 3.** Local pollen zones as established in Fig. 4a and b with indication of floristic composition, inferred vegetation change and correlation to biozones.

Lake Ledro LPAZ	Age (cal. BP)	Event	Inferred vegetation change	Correlation to biozones
LL-6d	5300	Abrupt ↗ <i>Fagus</i>	Dense oak-beech forest	Early Atlantic
LL-6c	6000	↗ <i>Taxus</i>	Mixed deciduous oak forest	Early Atlantic
LL-6b	7700	↗ <i>Abies</i> , first cereals	Montane trees development	Early Atlantic
LL-6a	9750	↗ <i>Tilia</i> , <i>Fraxinus excelsior</i> , <i>Picea</i>	Mixed deciduous oak forest	Early Atlantic
LL-5b	10350	↘ <i>Pinus</i> , deciduous <i>Quercus</i> and <i>Ulmus</i> abundant; Abrupt ↗ <i>Corylus</i>	Mixed deciduous oak forest development	Boreal
LL-5a	11700	Abrupt ↗ deciduous <i>Quercus</i> , <i>Ulmus</i> , <i>Corylus</i> ; ↘ <i>Pinus</i> and <i>Artemisia</i>	Mixed deciduous oak forest	Preboreal
LL-4	12700	↗ <i>Artemisia</i> and <i>Pinus</i>	Steppe-tundra, open forest	Younger Dryas
LL-3	~ 14 100	↗ <i>Betula</i> and deciduous <i>Quercus</i> then ↘ <i>Betula</i> ; regular presence of <i>Corylus</i> , <i>Tilia</i> , <i>Alnus</i>	Afforestation: mixed open forest	Allerød/Bøiling
LL-2	~ 16 500?	↘ <i>Artemisia</i> and Poaceae	Small afforestation	
LL-1	~ 17 000?	↗ <i>Pinus</i> and Poaceae	Pioneer/steppe-tundra	Oldest Dryas

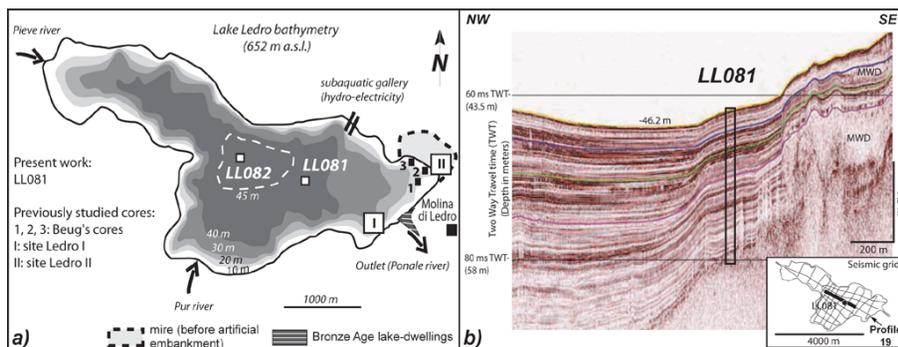
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**Fig. 1.** (a) The study site in the northern Mediterranean area; (b) location of pollen sites discussed in the paper for the Alps and northern Italy (1: Lake Lavarone, Filippi et al., 2007; 2: Lake Lucone, Valsecchi et al., 2006; 3: Passo del Tonale, Gehrig, 1997; 4: Valle di Sol, Favilli et al., 2010; 5: Lake Tovel, Gottardini et al., 2004; 6: Palù di Sonico, Gehrig, 1997; 7: Pian di Gembro, Pini, 2002; 8: Totenmoos, Heiss et al., 2005; 9: Palughetto Cansiglio Plateau, Vescovi et al., 2007; 10: Lago di Fimon, Valsecchi et al., 2008; 11: Lago della Costa, Kaltenrieder et al., 2009, 2010; 12: Lago di Annone, Wick and Möhl, 2006; 13: Lej da San Murezzan, Gobet et al., 2003; 14: Lago Ragogna, Monegato et al., 2007; 15: Lago di Origlio, Tinner et al., 1999; 16: Balladrum, Hofstetter et al., 2006; 17: Piano, Valsecchi and Tinner, 2010; 18: Gerzensee, Lotter et al., 2000; 19: Soppensee, Lotter, 1999; 20: Lobsigensee, Tinner et al., 2005; 21: Lago Piccolo di Avigliana, Finsinger et al., 2006; 22: Lago del Greppo, Valsecchi et al., 2010; 23: Lago dell’Accesa, Drescher-Schneider et al., 2007); (c) Catchment area of Lake Ledro (dotted line).



**Fig. 2.** Main characteristics of the Lake Ledro basin fill **(a)** Lake Ledro bathymetry showing the Pieve and Pur River deltas, and collection location of the LL081 (this study) and LL082 (Simoneau et al., 2012; Vanni re et al., 2012) sediment cores and of previously studied sites from Beug (1964) and Magny et al. (2009); **(b)** Seismic reflection profile from Lake Ledro illustrating well-preserved basin fill geometry at site LL081, i.e. away from tributary deltas and mass wasting deposits (MWD).

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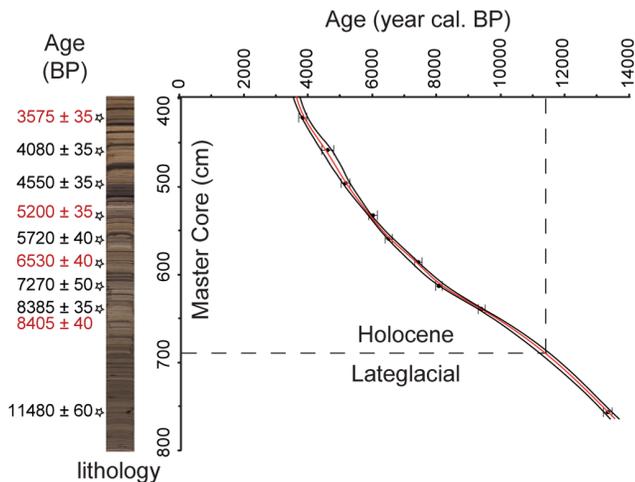
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**Fig. 3.** Lithology of the mastercore LL081 and age-depth model based on calibrated radiocarbon ages (black dots with 2-sigma errors) (AMS, see Table 1) from LL081 and LL082 (in red).



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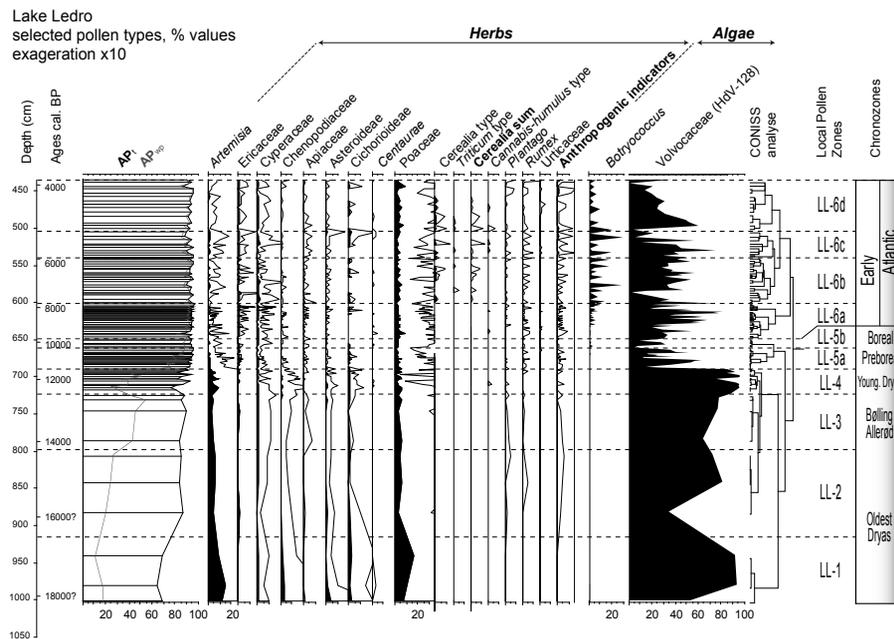


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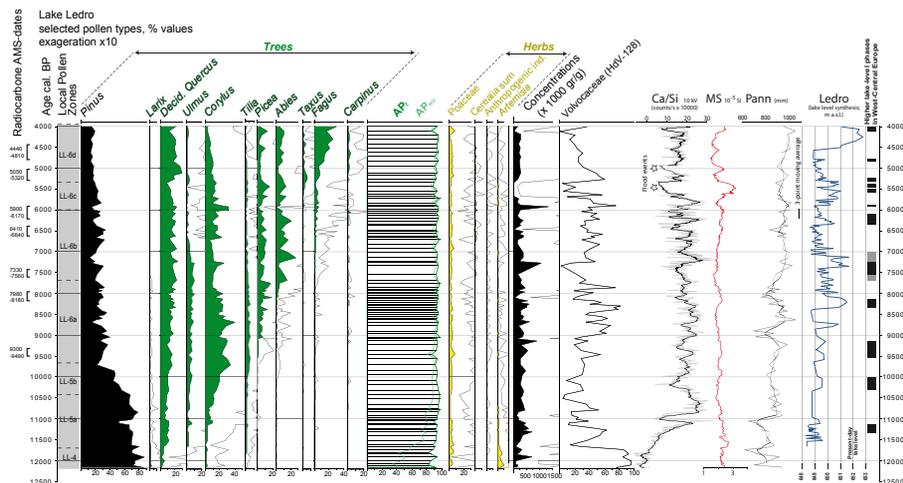
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**Fig. 5.** Main pollen taxa, total pollen concentration and abiotic parameters (Calcium/Siliceous, Magnetic Susceptibility) of Lake Ledro sediments represented by age (cal.BP). On the right, pollen-based annual precipitation (Pann) and lake-level changes reconstructed at Ledro are shown together with higher lake-level phases for West-Central Europe according to Magny (2004).

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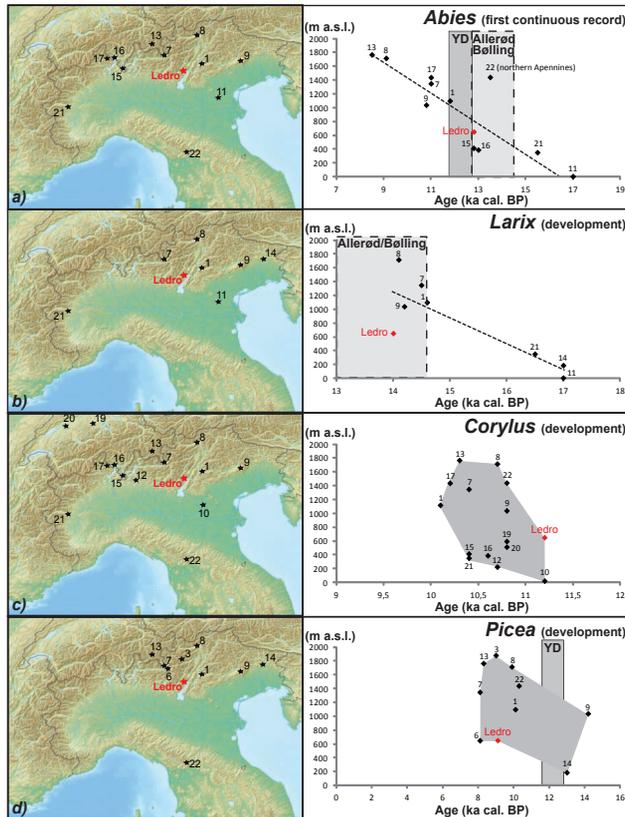
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**Fig. 6.** Compilation of pollen records (plus macrofossil and stomata data when available) from the southern Alps and Switzerland and the northern Apennines. Location of sites and graphs are provided, where age estimates are plotted against altitude, for the four tree taxa *Abies*, *Larix*, *Corylus* and *Picea*. The age scale differs for each graph. Site numbers refer to the caption from Fig. 1. **(a)** Ages of the first continuous *Abies* (fir) record; **(b, c, d)** Ages for the development of *Larix* (larch), *Corylus* (hazel) and *Picea* (spruce). YD = Younger Dryas.