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Climate and vegetation changes during the Lateglacial and early–middle Holocene at Lake Ledro (southern Alps, Italy)

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Abstract. Adding to the on-going debate regarding vegetation recolonisation (more particularly the timing) 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 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–middle 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 tree species distribution. 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 the 8.2 kyr cold event suggest a centennial-scale climate forcing in the studied area. *Picea* (spruce) expansion occurred preferentially around 10 200 and 8200 cal BP in the south-eastern Alps, and therefore reflects the long-lasting cumulative effects of successive boreal and the 8.2 kyr cold event. 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, a weak signal of pollen-based anthropogenic activities suggest 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 middle Holocene (up to ca. 4100 cal BP).

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1 Introduction

During the Last Glacial Maximum (LGM) and the early–middle Holocene, the vegetation history of the Alpine area records two main features: (1) treeline migration, and the spreading of taxa from various Glacial refugia, 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 benefitted from global climate improvement and glacier retreat in the Alps to colonise new available areas. A growing body of evidence suggests that these species survived the cold phases in the Po Plain and along the south-eastern Alpine border (Vescovi et al., 2007, 2010; Kaltenrieder et al., 2009, 2010). The spread of *Abies*, however, may have been different with 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 meet three criteria: (1) they have to be located in the key zone of south-eastern Alps, which was a potential route for tree immigration from southern Italy and the Balkans and for comparison with the nearby potential Euganean Hills refuge (Kaltenrieder et al., 2009); (2) a palaeovegetational 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; Vannière 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; Fletcher et al., 2010; Roberts et al., 2011). In the context of low Holocene temperature variations in the Alps (±1 °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 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; Vannière 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 (111 km^2)) and offers the opportunity to explore spatial expansion of tree species during the Lateglacial and the early–middle Holocene. We compare the pollen record with proxies that are indicative of run-off, 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 early Lateglacial (higher in the upper part) as the focus is on the Holocene record. The younger parts of the sequence, characterised by strong human impacts on the vegetation, will be presented in a separate paper dealing with late Holocene environmental changes in the Ledro area.

2 Study area

Lake Ledro (Lago di Ledro; 45°52′ N, 10°45′ E, 652 m a.s.l.) is a 3.7 km^2 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^2 and includes mountains that culminate at 1500–2250 m (Fig. 1c). The geological substratum comprises mainly Triassic, Liassic and Cretaceous limestone. Morainic tongues and 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 dominated by *Larix* (larch) and *Picea*, and 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 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

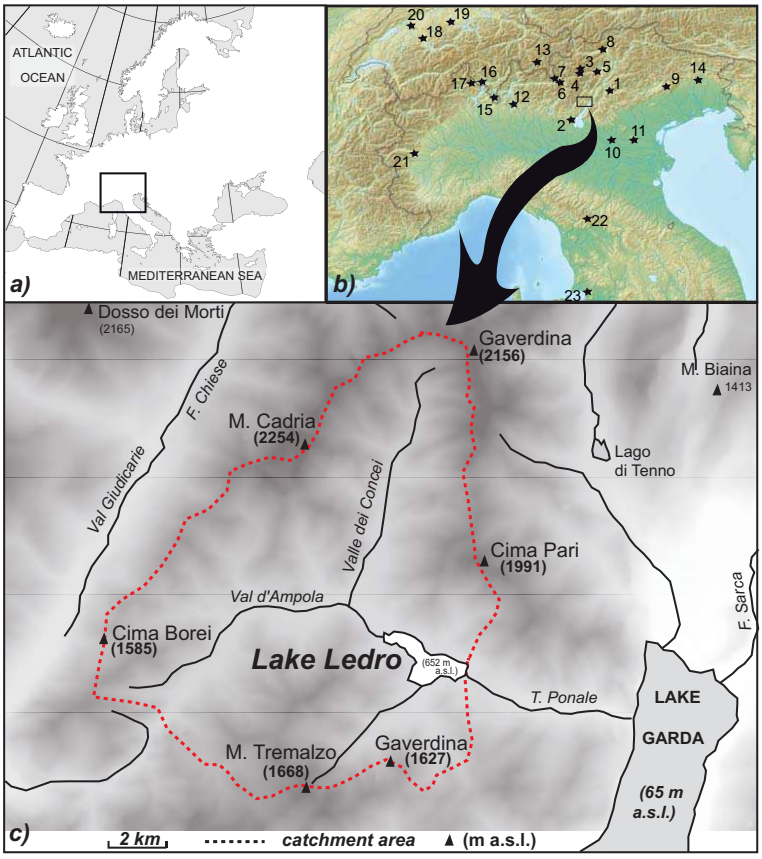


Fig. 1. (a) The study site in the northern Mediterranean area. **(b)** Location of pollen sites discussed in the paper for the Alps and northern Italy – 1: Lake Lavarone (Filippi et al., 2007); 2: Lake Lucone (Valsecchi et al., 2006); 3: Passo del Tonale (Gehrig, 1997); 4: Valle di Sol (Favilli et al., 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 and Vescovi, 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).

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., 2013). To encompass the entirety of 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).

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-3D 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, primarily 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

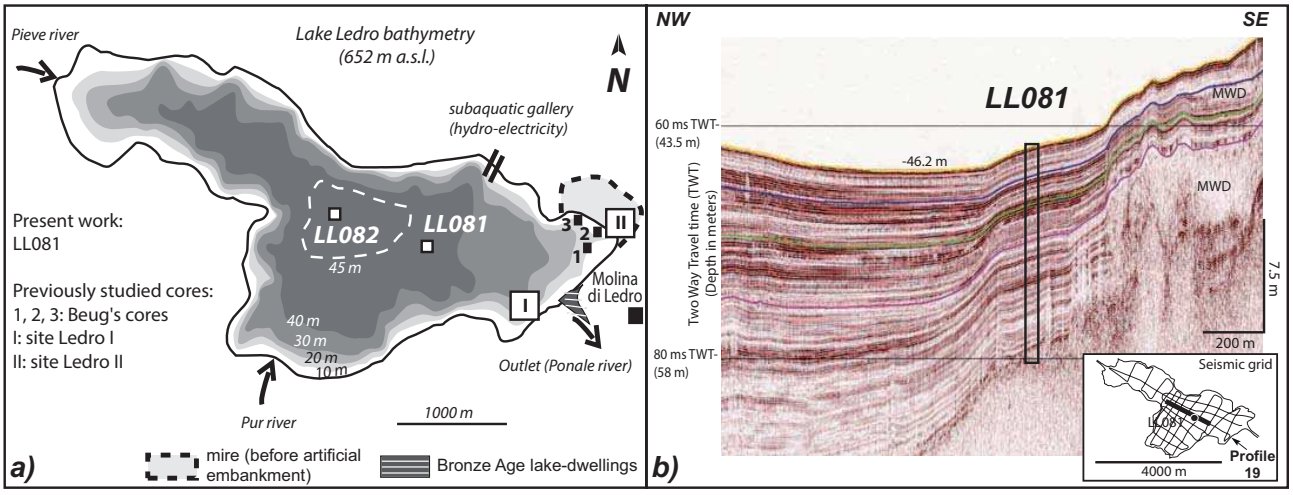


Fig. 2. Main characteristics of the Lake Ledro basin fill: **(a)** Lake Ledro bathymetry showing the Pieve and Pur River deltas, and collection location of the LL081 (this study) and LL082 (Simmoneau et al., 2012; Vannière et al., 2012) sediment cores and of previously studied sites from Beug (1964) (1–3) and Magny et al. (2009) (I–II); **(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).

cover may have favoured a mineral magnetic increase in soils (Jong et al., 1998), so low MS in sediments is expected during phases of stabilised, 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; Vannière 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 µm. XRF core scanning is a fast, non-destructive technique which provides information about elemental variations directly from untreated sediment and reflects proportions of different minerogenic components (Löwemark et al., 2011). Among the various elements tested (Vannière 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 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 run-off and humidity.

3.3 Radiocarbon dating

The Lateglacial and early–middle Holocene chronology is based on six accelerator mass spectrometry (AMS) ^{14}C ages measured on terrestrial organic material from cores LL081 (Table 1). Four ^{14}C ages measured on a different core (LL082, Fig. 2a) are included according to lithological correlation (Vannière et al., 2012). Macrofossils were collected from sediment samples sieved with a 100 µm mesh screen. Radiocarbon ages were calibrated in yr cal BP by the Calib 6.0 software using the calibration curve IntCal09 (Reimer et al., 2009). Dates are expressed as intercepts with 2σ 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). Therefore, 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 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 cm^{-3}; Stockmarr, 1971). Pollen grains were poorly preserved in the lower part of the LL081 core. A total of 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.

Table 1. AMS radiocarbon dates with a 2σ age range calibration from the Lake Ledro LL081 core.

Sample ID	Lab. code	Material	AMS 14C Age BP	Depth MC (cm)	Cal yr BP (2σ)
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	$11\,480 \pm 60$	759.3	13 200–13470

* Ages obtained from core LL082 and lithologically correlated.

As the dominant taxa can reduce the significativity of the other taxa counted, we constantly counted a minimum of 300 terrestrial pollen grains excluding the most dominant terrestrial taxa as well as water and wetland plants, and pteridophyte spores. Therefore, the dominant taxa were successively *Pinus*, *Corylus* and deciduous *Quercus*. During the calculation process, terrestrial pollen percentages were calculated based on total pollen (i.e. including all terrestrial taxa), which is on average 706 grains per sample. 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. 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}).

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., 2013). 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). To reduce uncertainties, we have applied to the analogues selection a constraint by biomes (Peyron et al., 1998). The biomes assigned to the selected modern analogues are compared to the biome assigned to the fossil assemblage, and only the analogues with consistent biomes are retained for the analogue matching step. 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 (dashed line in Fig. 5).

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 which permits the extension of the age model (Fig. 3) to 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. The average temporal resolution for the upper part is estimated to 77 yr/sample.

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, and strong contrast between multi-millennial trends, which can be unravelled 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

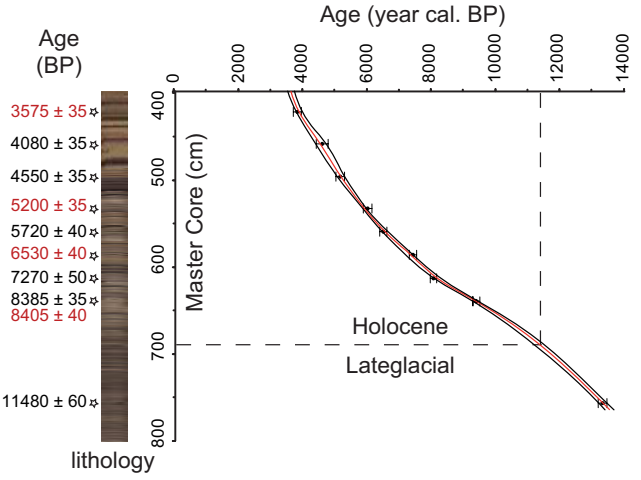


Fig. 3. Lithology of the mastercore LL081 and age–depth model based on calibrated radiocarbon ages (black dots with 2σ errors) (AMS, see Table 1) from LL081 and LL082 (in red).

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., 2013). This pattern is obvious from two 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 (Vannière et al., 2012; Simonneau et al., 2013).

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 a mixed open forest may have grown in the Lake Ledro landscape (Table 2), which was dominated by *Pinus* (pine) trees (ca. 60%) and consist 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 were still in proximity.

From ca. 14 100 cal BP (zone LL-3, Table 2), pollen-inferred vegetation around Lake Ledro indicates a change in the woody taxa composition, illustrated by AP_{wp} increase (up to 60 %). This change includes development of thermophilous trees (deciduous *Quercus* and *Corylus*) and mixed open and mixed coniferous forests (*Betula*, *Pinus*, and *Larix*) during the Allerød/Bølling interstadial. *Ulmus*, *Tilia*, and *Fraxinus excelsior* also appeared in the pollen record, together with *Abies* which develops in the montane belt. Considering the poor dispersal of *Abies* (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 than today (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 clustering method identifies two subzones (Table 2). The first (LL-5a; ca. 11 000 to ca. 10 350 cal BP) is characterised by abundant deciduous *Quercus* (oak) pollen grains and relatively abundant *Ulmus* (elm), *Corylus* (hazel) and *Tilia* (lime) pollen grains. This expansion is associated with birch development, most likely on the lake shore, as suggested 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 yr compared to the concomitant increase in deciduous *Quercus*, *Ulmus* and *Tilia*. Sharp decreases in *Pinus* (Δ 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 *Corylus* (up to 34 %). A marked decrease in *Pinus* (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,

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 *Pinus* (pine) pollen grains.

LPAZ	Depth (cm) Age (yr cal BP)	Main taxa observed	Total of arboreal pollen %	Common pollen types (CPT) Rare pollen types (RPT)
LL-6d	505–435 5300–3950		AP_t 89–96	CPT: *Pinus*, *Ulmus*, *Tilia*, *Fraxinus excelsior*, *Picea*, *Abies*, *Alnus*, *Fagus* and Poaceae
LL-6c	540–505 6000–5300		AP_t 86–96	CPT: *Pinus*, *Ulmus*, *Tilia*, *Fraxinus excelsior*, *Picea*, *Abies*, *Alnus*, *Fagus* and Poaceae
LL-6b	601–540 7700–6000		AP_t 87–95	CPT: *Pinus*, *Betula*, *Ulmus*, *Tilia*, *Fraxinus excelsior*, *Picea*, *Abies*, *Alnus*, *Fagus* and Poaceae RPT in LL-6b to 6d: *Acer*, *Carpinus*, *Taxus*, Ericaceae, *Ostrya*, *Pistachia*, *Quercus ilex*, *Salix*, *Juniperus*, *Hedera helix*, Cyperaceae, Apiaceae, Ast. Asteroideae, Ast. Cichorioideae, Brassicaceae, Cereal-type, *Triticum*, *Plantago lanceolata*, *Artemisia*, *Orlaya grandiflora*, Lamiaceae and *Typha*
LL-6a	648–601 9750–7700		AP_t 81-96	CPT: *Pinus*, *Ulmus*, *Tilia*, *Fraxinus excelsior*, *Picea*, *Abies*, *Alnus* and Poaceae RPT: *Acer*, *Fagus*, *Larix*, *Carpinus*, Ericaceae, *Ostrya*, *Pistachia*, *Salix*, Cyperaceae, Ast. Asteroideae, Brassicaceae, *Artemisia*, *Plantago*, *Convolvulus*, Lamiaceae and *Typha*
LL-6	648–435 9750–3950	deciduous *Quercus*-*Corylus*-*Abies*		
LL-5b	661–648 10 350–9750		AP_t 95 AP_{wp} 87	CPT: *Corylus*, *Ulmus*, *Tilia*, *Fraxinus excelsior*, *Abies* and *Alnus*
LL-5a	692–661 11 000–10 350		AP_t 87–96 AP_{wp} 53–87	CPT: *Betula*, deciduous *Quercus*, *Ulmus*, *Tilia Abies*, *Alnus*, *Larix*, *Corylus*, *Fraxinus excelsior* and *Artemisia*
LL-5	692–648 11 700–9750	*Pinus* – deciduous *Quercus*-*Corylus*-Poaceae		RPT: *Tilia*, *Fraxinus excelsior*, *Larix*, *Pistachia*, *Quercus ilex*, *Salix*, Ast. Cichorioideae, *Plantago*, *Sanguisorba*, *Thalictrum*, *Typha*, Cyperaceae and *Artemisia*
LL-4	725–692 12 700–11 700	*Pinus*-Poaceae-*Artemisia*	AP_t 75–95 AP_{wp} 25–53	CPT: deciduous *Quercus*, *Corylus*, *Abies*, *Alnus*, *Larix*, Amaranthaceae and Ast. Cichorioideae RPT: Cyperaceae, Ast. Asteroideae, Brassicaceae, *Centaurea*, *Plantago*, *Alisma*, *Convolvulus*, *Thalictrum*, *Typha* and Lamiaceae
LL-3	795–725 14 100–12 700	*Pinus*-*Betula*-Poaceae-*Artemisia*	AP_t 85–90 AP_{wp} 30–55	CPT: deciduous *Quercus*, *Corylus*, *Betula*, Cyperaceae and *Plantago* RPT: *Ulmus*, *Abies*, *Alnus*, *Carpinus*, *Pistachia*, Amaranthaceae and *Larix*
LL-2	915–795 16 500?–14 100	*Pinus*-Poaceae-*Artemisia*	AP_t 75–85 AP_{wp} 15–30	CPT: *Juniperus*, deciduous *Quercus*, *Corylus*, *Betula*, Amaranthaceae, Ast. Asteroideae and Ast. Cichorioideae RPT: *Picea*, *Plantago* and Lamiaceae
LL-1	1003–915 17 000?	*Pinus*-Poaceae-*Artemisia*	AP_t 65–75 AP_{wp} 12–17	CPT: *Juniperus*, *Betula*, *Ephedra*, Amaranthaceae, Ast. Asteroideae and Ast. Cichorioideae RPT: Brassicaceae, *Centaurea*, *Hippophae*, *Alisma*, *Convolvulus* and Lamiaceae

sclerophilous taxa (*Quercus ilex* type) appearing in the zone LL-5b are scarce (which is the case until the top of the sequence).

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

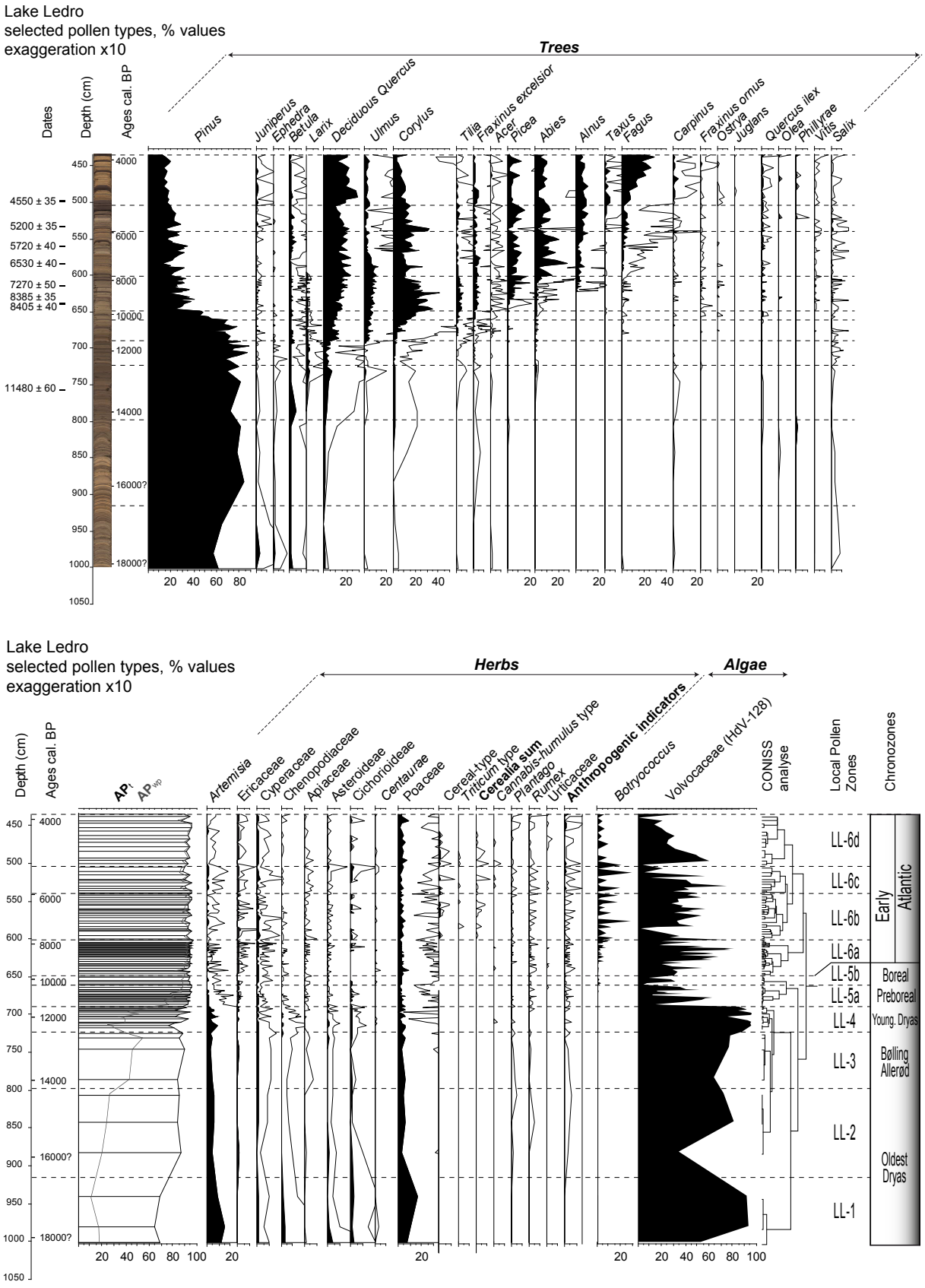


Fig. 4. Pollen diagram by depth showing percentages of main pollen taxa. Pollen zones are based on CONISS. 10* exaggerations of the pollen curves are also shown.

Subzone LL-6a (ca. 9750–7700 cal BP) is characterised by the *Picea* development (up to 20%), the appearance of *Abies* pollen grains, steady 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 (Δ 20 % and Δ 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. The pollen diagram from the littoral section of Ponale (Magny et al., 2012) provides an earlier presence of *Alnus* than the deep core. This may indicate that this taxa was living around the lake margin before entering the forest composition, as shown by its rapid immigration and development in subzone LL-6b. 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 near 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 reductions in temperate and coniferous trees are balanced by increased *Artemisia*, Poaceae and Asteraceae Cichoriodeae.

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 cereal-type pollen grains and a questionable apparition of *Juglans* (which has been 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. 12 200 to ca. 4000 cal BP (Fig. 5) and shows a long-term progressive increase (Δ 300 mm). Plurisecular 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. 11 100 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 influenced 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 *Pinus* (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, later 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 forest 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. Other heliophilous plants, such as *Pinus* (pine) and *Larix*, 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).

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 ↗ *Fagus*	Dense oak–beech forest	Early Atlantic
LL-6c	6000	↗ *Taxus*	Mixed deciduous oak forest	Early Atlantic
LL-6b	7700	↗ *Abies*, first cereals	Montane trees development	Early Atlantic
LL-6a	9750	↗ *Tilia, Fraxinus excelsior, Picea*	Mixed deciduous oak forest	Early Atlantic
LL-5b	10 350	↘ *Pinus*, deciduous *Quercus* and *Ulmus* abundant; abrupt ↗ *Corylus*	Mixed deciduous oak forest development	Boreal
LL-5a	11 700	Abrupt ↗ deciduous *Quercus, Ulmus, Corylus*; ↘ *Pinus* and *Artemisia*	Mixed deciduous oak forest	Preboreal
LL-4	12 700	↗ *Artemisia* and *Pinus*	Steppe tundra, open forest	Younger Dryas
LL-3	∼ 14 100	↗ *Betula* and deciduous *Quercus* then ↘ *Betula*; regular presence of *Corylus, Tilia, Alnus*	Afforestation: mixed open forest	Allerød/Bølling
LL-2	∼ 16 500?	↘ *Artemisia* and Poaceae	Small afforestation	
LL-1	∼ 17 000?	↗ *Pinus* and Poaceae	Pioneer/steppe tundra	Oldest Dryas

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 *Pinus* (pines) are still abundant. More specifically, a mixed oak forest associated with *Ulmus* (elm) and *Tilia* (lime) develops at lake altitude. Such a concomitant population expansion was also described in the Lago di Lavarone record (Filippi et al., 2007).

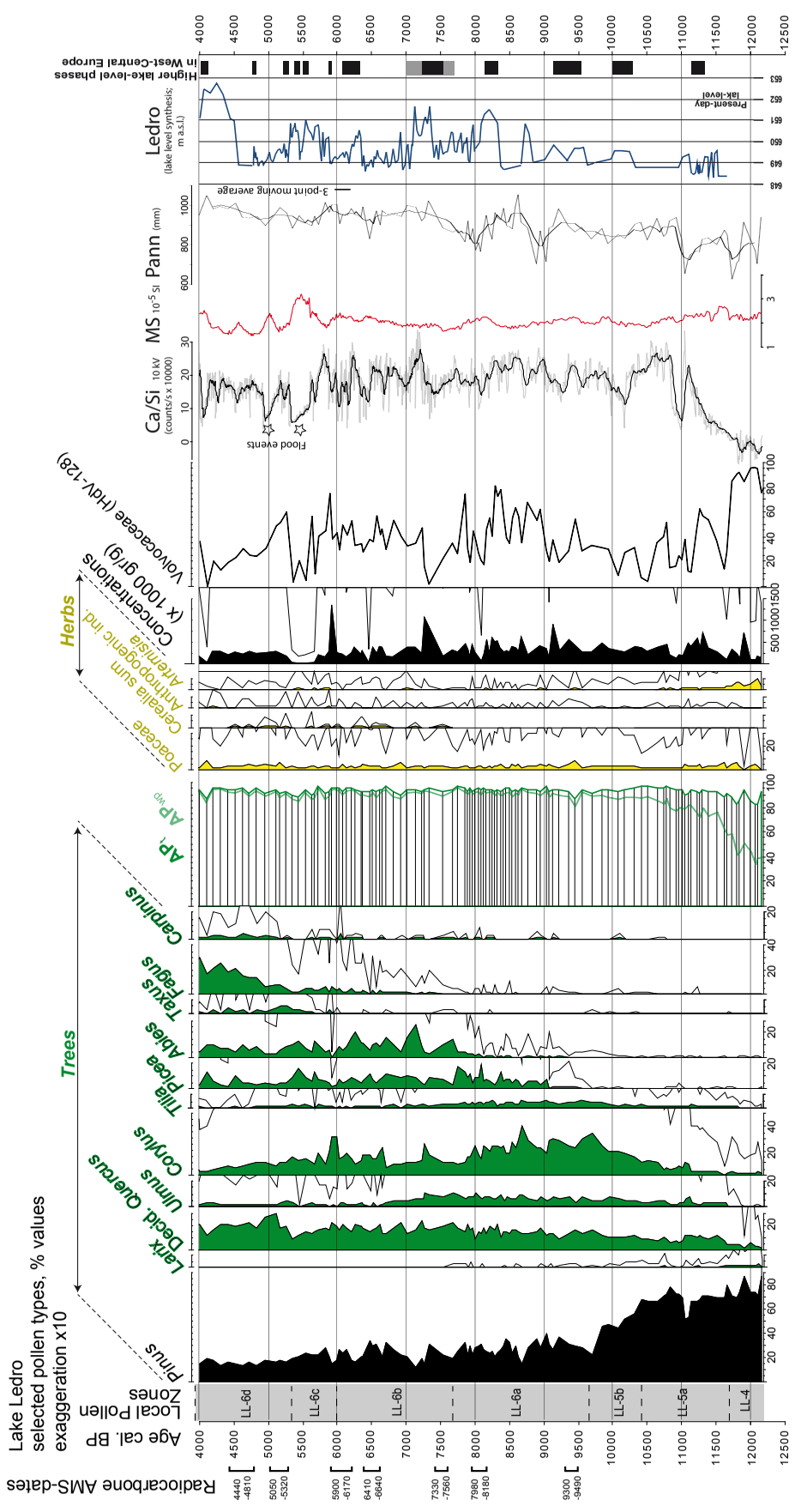
Considering the *Pinus* (pine) reduction at the Preboreal–Boreal transition (ca. 10 800 cal BP), a similar decrease of this cold-adapted, heliophilous tree is observed at Lago di Lavarone (Filippi et al., 2007) and Lago di Fimon (23 m a.s.l., Valsecchi et al., 2008). *Pinus* (pine) is also linked with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

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

The anthropogenic influence on the study area can be traced from cereal-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 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 accord with the pollen record of Lake Ledro.

Picea and *Abies* proportion declined concomitantly with a significant increase in *Corylus* at ca. 6700 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 *Corylus* benefitting from *Picea* (spruce) and *Abies* regression. Peaks of cereal-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. However, the abruptness and brevity of these changes may suggest catastrophic events, such as fire, which may also be triggered by humans. *Picea* and *Abies* redeveloped afterwards, associated with the appearance of *Taxus* in the pollen diagram.

The *Taxus* amount increase was reported previously by Beug (1964). The age–depth model indicates an age of ca. 5500 cal BP for this tree development, which occurred at the onset of the second increase of *Fagus*. *Taxus* is not present in the record from Lago di Lavarone (Filippi et al., 2007), but


Lake Ledro
selected pollen types, % values
exaggeration x10
Age cal. BP
Local Pollen Zones
Radiocarbone AMS-dates
Trees
Herbs
Pinus
Betula
Betula nana
Betula pubescens
Betula pendula
Betula sect. Albae
Betula sect. Nanae
Betula sect. Fruticosae

exists at Lago di Annone (Wick and Möhl, 2006) and Lago della Costa (ca. 6000 cal BP; Kaltenrieder et al., 2010).

5.2 Immigration and development of key taxa in the southern Alps

5.2.1 *Abies* immigration

To discuss the persistence and spread of *Abies*, pollen diagrams from the southern Alps were compiled in Fig. 6. These records generally show that *Abies* pollen grains are first recorded continuously with low percentages (below 1 %) for millennia before *Abies* development marked by higher percentages. Furthermore, pollen productivity and the transport potential of *Abies* are low (Huntley and Birks, 1983). For these two reasons, low and continuous percentages can therefore be interpreted as significant. This characteristic is confirmed by Van der Knaap et al. (2005), who indicated that the assumed pollen-percentage thresholds (between 0.5 and 8 %) are similarly robust 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 *Abies* pollen grains is dated to ca. 15 500 cal BP in Lago Piccolo di Avigliana (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 *Abies* 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 *Abies* 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 *Abies* 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).

This trend suggests that altitudinal conditions drove the spread of *Abies* 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 *Abies* forests. This trend may also question whether *Abies* formed refugial populations in the lowlands (senso 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 microenvironmental conditions may have occurred. However, *Abies* refugia 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 *Larix* 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 Avigliana, Finsinger et al., 2006). *Larix* 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, the Lake Ledro pollen record differs, as *Larix* 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, *Larix* is found in high abundance at Totenmoos in north-eastern Italy (1718 m a.s.l.; Heiss et al., 2005). During the YD, *Larix* 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 *Larix* abundance at Totenmoos suggests that the treeline was at lower altitude (i.e. between 1350 and 1718 m). This elevational pattern confirms 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, *Larix* 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, taxonomic identification of macrocharcoal fragments suggest that *Larix* 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). *Larix* 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 *Larix* 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 *Larix* wood (Pinton and Carrara, 2007), and *Larix* 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 *Larix* records in the lake.

5.2.3 *Corylus* development

Corylus developed later than deciduous *Quercus* (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 the opposite that of the northern Alps, where *Corylus* expanded before deciduous *Quercus*. In more detail, 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 *Corylus* increase at Lake Ledro (ca. 11 200 cal BP), nor to the second increase at ca. 10 750 cal BP. At Ledro, *Corylus* 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 temporarily affected most of the temperate trees, suggesting that the first increase of *Corylus* has to be considered to integrate the discussion about *Corylus* expansion in Europe (Fig. 6c). *Corylus* 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). However, when looking at other pollen records from the southern and northern Alps, and considering the reliability of age estimates, *Corylus* 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 *Corylus* expansion in the northern and southern Alps, as well as those of Giesecke et al. (2011), who observed 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 level indicates the approximate immigration time and the beginning of population expansion. *Picea* development is dated to ca. 9100 cal BP in 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 *Picea* development during the Allerød/Bølling interstadial. The age for Lake Ledro *Picea* 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 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 *Picea* development is observed in the southern Alps and a westward development is more 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 *Picea* 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 *Picea* development at Ledro.

5.2.5 *Fagus* development

Focusing on *Fagus* (beech), 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

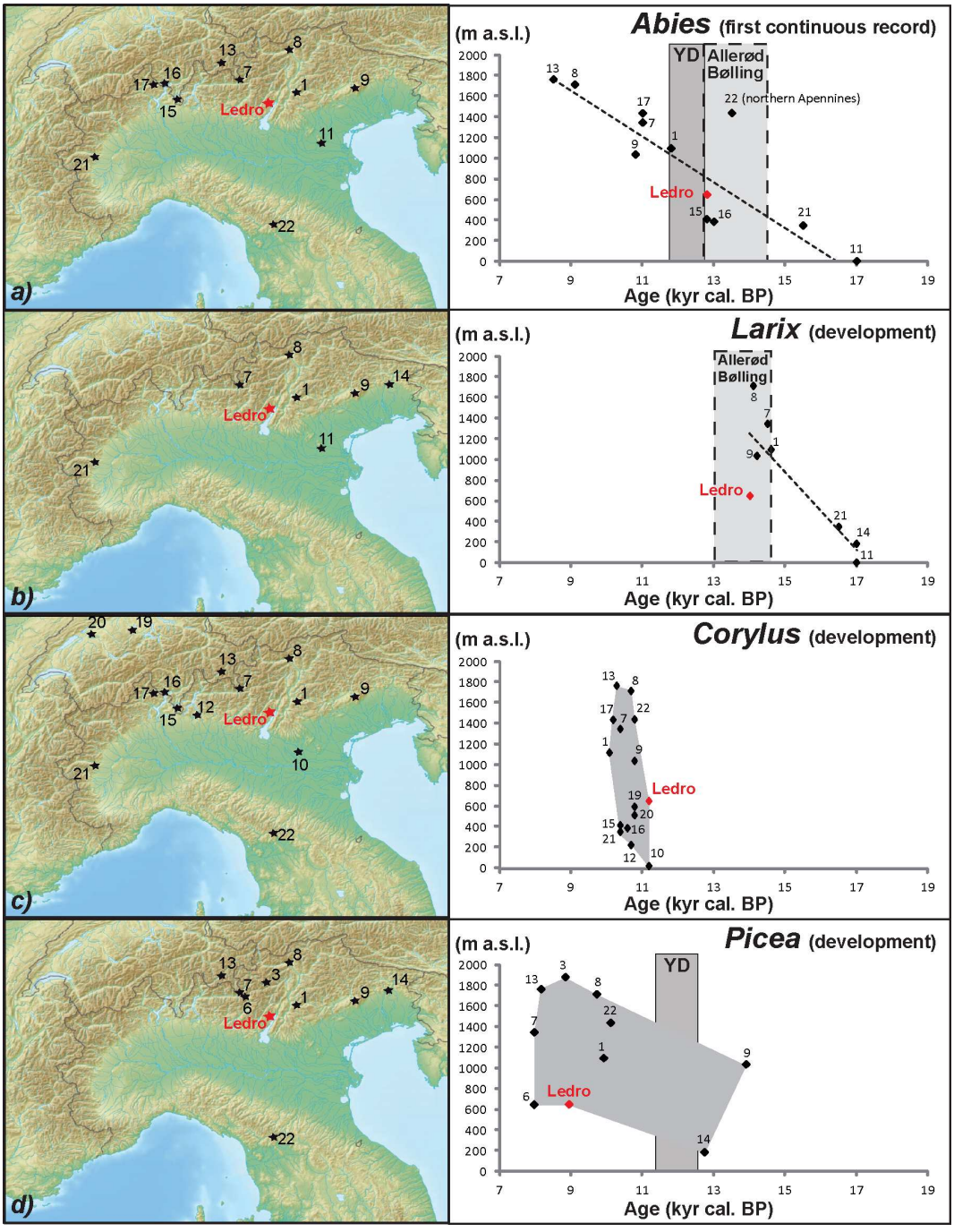


Fig. 6. Compilation of pollen records (plus macrofossil and stomata data when available) from the southern Alps and Switzerland and the northern Apennines. Location of sites and graphs are provided, where age estimates are plotted against altitude, for the four tree taxa *Abies*, *Larix*, *Corylus* and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

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 *Fagus* development. These occurrences are out of phase with *Fagus* variations and therefore suggest that *Fagus* 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 *Fagus* differs both in age and pattern. This difference raises the question whether a 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., this volume) 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., 2012) 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 than 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 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 north-central Italy. A growing body of studies extends the occurrence of this dry phase toward southern Italy (e.g. Joannin et al., 2012; Di Rita et al., 2013). 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–middle 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 run-off 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 have been $> 800\,\mathrm{mm\,yr^{-1}}$ 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; Vannière 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 of light-demanding *Corylus* 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 the 8.2 kyr cold event coincided with *Picea* and *Abies* expansion, respectively. These events are marked by Ca / Si drops, which indicate increasing run-off 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, *Picea* development in the south-eastern Alps preferentially occurred at approximately 10 000 and 8200 cal BP (Fig. 6d).

After ca. 8200 cal BP, *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^{-1} 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 are 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, Vannière 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). Based on reconstructed $\delta^{18}O$ (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 benefitted from increasing humidity at ca. 8200 cal BP. Pini (2002) questioned the direct relationship between sudden *Picea* and *Abies* expansion with climate change. Our study indicates that *Picea* 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 cereal-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 middle 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 *Fagus* 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 (Vannière 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. 5000 cal BP in Europe, possibly related to rapid climate changes (RCC) suggested by Mayewski et al. (2004). Local expression of these RCC may thus have affected the precipitation regime in this part of the Alps and caused successive lake level rises and stopped *Fagus* 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 Vannière et al. (2012), flood activity has increased 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., this volume). Valsecchi et al. (2008) report tree-ring studies, which evidence a reduced *Fagus* growth (at its southern range) in response to dry summers (Jump et al., 2006). We observe that the *Fagus* forest development in the Ledro pollen record was (1) stopped between ca. 6000 and ca. 5300 cal BP during wet, cooler summers (based on the pollen-based temperature of the warmest month; Peyron et al., 2012), and (2) was strong thereafter due to wetter and warmer summers. As for Lago di Fimon, we can conclude that low *Fagus* 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, *Fagus* expansion may have benefitted from wetter summers.

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 *Abies* 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 a refugial for *Abies*, *Larix* and *Picea*. 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. The expansion pattern of *Picea* is more surprising and occurred ca. 10 200 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 middle Holocene (up to 4100 cal BP). Accordingly, a steady climate change toward wetter conditions allowed deciduous *Quercus*, *Corylus*, *Picea*, *Abies*, *Fagus* and *Taxus* (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 *Fagus* development is not related to human activities in the Ledro area and may have benefitted from wetter summers. No important pastoral activity is observed during periods of declining *Taxus* abundance, which is more likely caused by a concomitant change to dense forest, mostly dominated by the shade-giving *Fagus*. A shift toward colder and wetter conditions (mostly during summers) is recognised from 5700 to 4100 cal BP (i.e. during the Neoglacial period), 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 benefitted from the wettest interval, 8200–7300 cal BP, as evidenced in lake levels, flood activity and pollen-based climate reconstruction.

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