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Late Quaternary record of the vegetation and catchment-related changes from Lake Paravani (Javakheti, South Caucasus)

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ABSTRACT

Here we present a palynological and sedimentological record from a 96-cm sediment core covering the last 13 ka aiming to document palaeoecological changes in the central South Caucasus driven by climate and/or human impact. The core was retrieved from Lake Paravani (2073 m asl, 41°27′N, 43°48′E), located in the steppic grasslands of South Caucasus in the Samsari-Javakheti volcanic plateau. The geomorphological features observed on the plateau, including moraine deposits, suggest the presence of local glaciers reaching the lake level during the Last Glacial periods. Based on sediment and pollen data, three palaeoecological phases have been identified. The first phase spanning the Younger Dryas and the Early Holocene, corresponds to a steppic environment with a limited lake productivity driven by a cold and particularly dry climate. According to the Age–depth model, this phase ends near 8500 cal BP with the decline of Chenopodiaceae. The second phase starts with an important expansion of trees at 8300 cal years BP. The delayed afforestation recorded in Lake Paravani is a pattern that has now been recognised widely through the Black Sea region's more continental areas. As soon as the climatic and edaphic conditions were favourable, the main deciduous and coniferous trees expanded concurrently due to the proximity of glacial forest refugia located in western Caucasus. This second phase marked by a climatic optimum is also characterized by an increase in lake productivity. The third phase starts at 2000–3000 cal BP and corresponds to the decline of forests on the plateau and the expansion of herbaceous formations, leading to the present-day steppic environment. This deforestation phase is driven by the deterioration of the climate conditions and human impact.

1. Introduction

The South Caucasus region (Figs. 1 and 2) exhibits a wide range of physical environments and ecological conditions (Gulisashvili, 1964; Volodicheva, 2002), and is characterized by a high diversity of temperature and precipitation conditions. The western part includes subtropical forests and is characterized by a high annual rainfall (up to 2800 mm/yr) (Lominadze and Chirakadze, 1971; Denk et al., 2001), while the eastern part includes steppes and semi-desert formations with low rainfall (400 mm/yr or less). The Javakheti Plateau (1700–2000 m asl), located in the central part of South Caucasus is a volcanic plateau composed of basaltic–andesitic lavas that erupted during the Upper Pliocene to Lower Pleistocene (Lebedev et al., 2008). The youngest volcanic activity on the plateau resulted in a 40 km-long volcanic ridge, the Samsari Range

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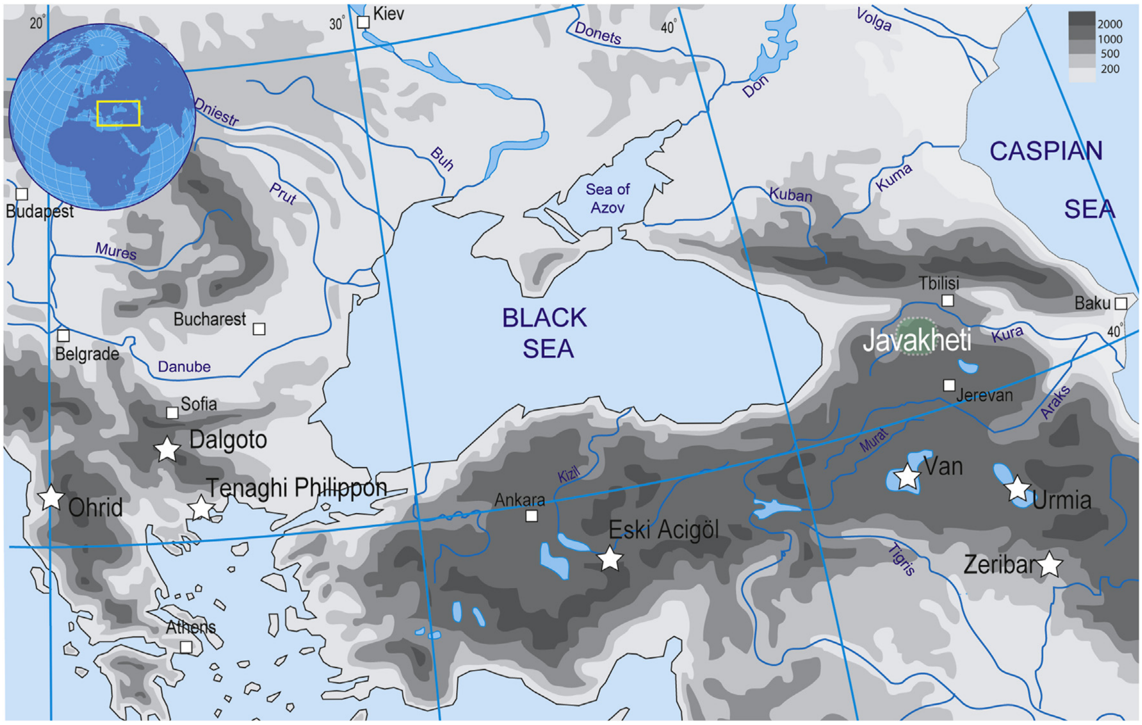

Fig. 1. Physiographic map of Eastern Europe and Black Sea region showing the location of the Javakheti Plateau, and continental pollen records discussed in the text (white stars). (The map is adapted from GeoAtlas).

(3000 m asl), composed of more than 20 well-preserved cones formed between 700 ka and 30 ka (Lebedev et al., 2008). The plateau is surrounded by various forest types; however the plateau itself remains quasi-treeless. Evidence such as, historical archives, archaeobotanical and archaeozoological data from archaeological sites suggest that the plateau was more forested until recent times (Matcharashvili et al., 2004; Kvavadze and Kakhiani, 2010). The few patches of trees near Lake Kartsakhi (Fig. 2) probably represent a

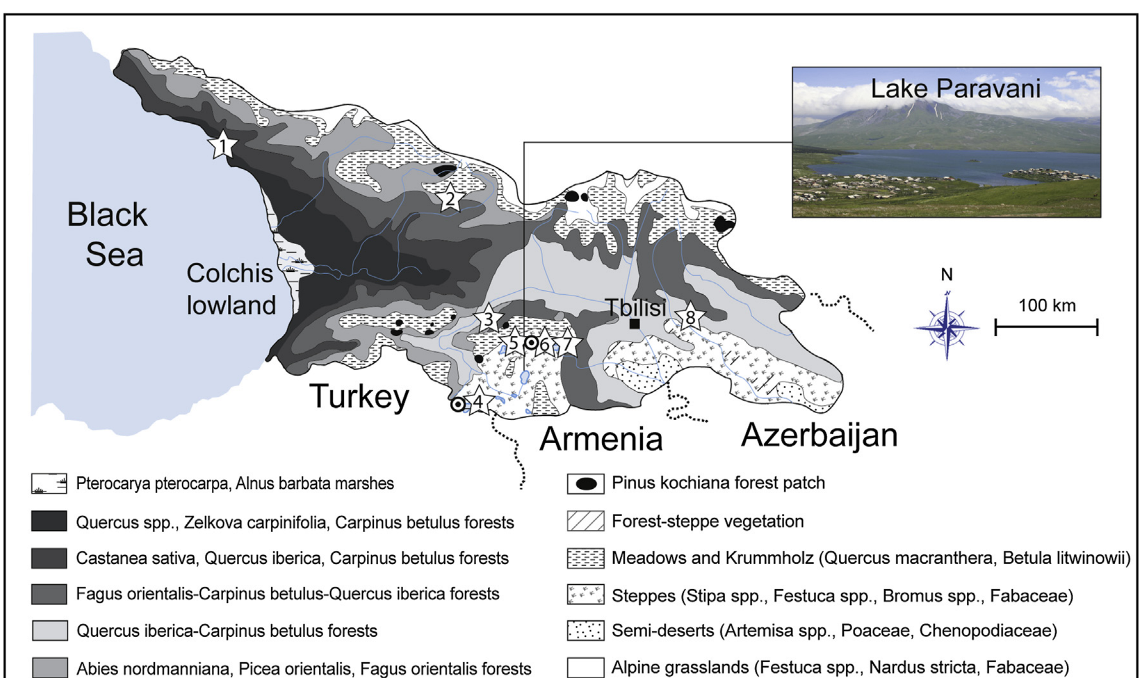

Fig. 2. Map of Georgia showing the main natural vegetation groups (modified from Bohn et al., 2000). In the western part, the vegetation is dominated by refugia forests with relict trees (vegetation groups 1, 2, 3). In the Southeastern part, the vegetation includes deciduous forests (4, 5) but is mainly dominated by meadow (9), steppe (10) and semi-desert (11) formations. The stars represent the Georgian pollen records discussed in the text: 1. Sukhumi marine core, 2. Lake Cheliagele, 3. Lake Gomnis, 4. Kartsakhi mire, 5. Nariani wetland, 6. Lake Aligol, 7. Lake Imera, 8. Sagarejo sequence. The black double circles represent the 2 small areas of natural sub-alpine forest (Lake Kartsakhi and Mt Tavkvetili).

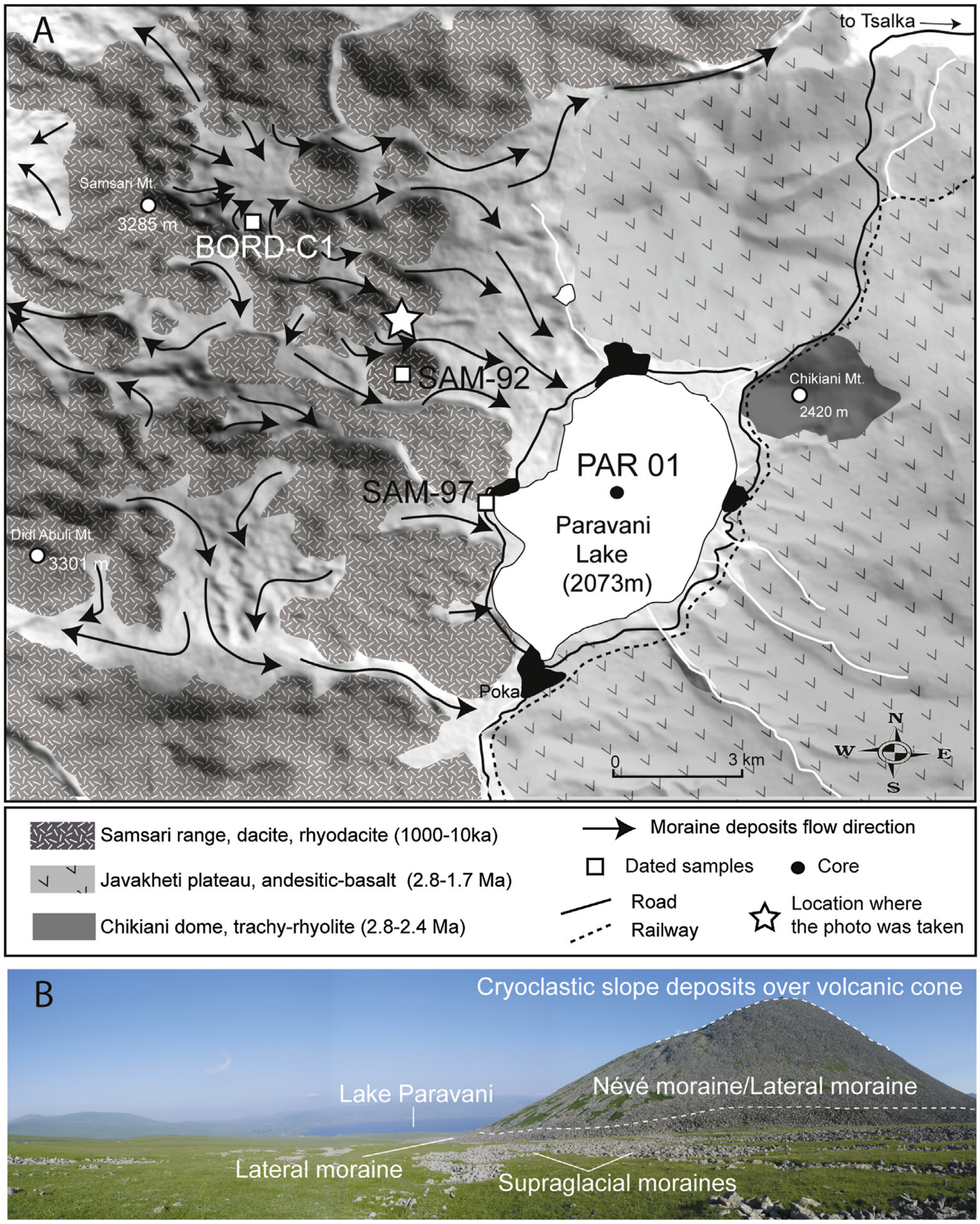

Fig. 3. **A**. Geological map of the Lake Paravani area, showing the locations of the core site, and lava samples for $^{40}Ar/^{39}Ar$ and K/Ar dating. **B**. Photo of the moraine deposits in the surroundings of Lake Paravani. The terminal and lateral moraines define the Last Glacial Maximum extent with a lake Paravani surrounded by glacial tongues. This sector is considered as a proglacial area with fluvio-glacial material deposited by melt-water pulse and debacle episodes.

remnant of the past forest (Nakhutsrishvili, 1999). Numerous archaeological sites attest to the recurrent occupation of this area during Prehistoric and Proto-Historic times (Kikodze and Koridze, 1978; Kvavadze and Kakhiani, 2010) and therefore, the effect of human activities is considered as a potential driver of deforestation of the plateau. However, the previous pollen studies from Lakes Imera and Aligol (Fig. 2) located on the Tsalka Plateau (Connor and Sagona, 2007; Connor, 2011) and from other small lakes or wetlands such as Nariani and Kartsakhi (Fig. 2) located on the upper Javakheti Plateau (Margalitadze, 1977, 1995) have not given support to the hypothesis of a past Holocene afforestation on the Javakheti Plateau followed by recent expansion of grasslands.

In the present study, we focus on investigating the palaeoecological and environmental changes recorded in lake sediments, along with climate change and/or human impact to document the vegetation and specifically the forest history of the upper Plateau. Previous studies of pollen records from small lakes and wetlands in the Javakheti Plateau allowed the reconstruction of the vegetation dynamics since the Lateglacial; however, their interpretation was hindered because of the low recording of tree pollen grains (Connor, 2011).

Here, we present the first palaeoenvironmental study from Lake Paravani located in the upper Javakheti area (2073 m asl, 41°27′N 43°48′E; 37.5 km^2) from a 96-cm sediment core retrieved in the central and deepest part of the lake. We discuss past vegetation and lake-watershed sedimentation dynamics including proxies from our core (pollen, magnetic susceptibility, grain-size analysis and mineralogical analysis) and from other regional records (see Figs. 1 and 2). In order to define factors controlling the peculiar environmental changes documented in our core, we discuss the

Table 1
List of AMS ^{14}C dates from Paravani core PAR01. ^{14}C ages were calibrated using INTCAL09 (Stuiver and Reimer, 1993; Reimer et al., 2009).

Lab. code	Sample	Mean depth	Type	mg C	$\delta^{13}C$	Radiocarbon age BP	Age cal BP
SacA 16247	PAR09-P1-0-2	1	Bulk	0.66	−22.80	0 ± 0	0
SacA 20045	PAR09-P1-12-13	12.5	Bulk	0.60	−23.60	525 ± 30	509–628
SacA 16248	PAR09-P1-25-27	26	Bulk	0.93	−14.40	490 ± 45	474–632
SacA 20046	PAR09-P1-35,5-36,5	36	Bulk	0.57	−23.10	2430 ± 40	2351–2702
SacA 20047	PAR09-P1-45,5-46,5	46	Bulk	0.63	−26.80	5345 ± 35	6000–6269
SacA 16249	PAR09-P1-54-56	55	Bulk	0.81	−26.80	5355 ± 40	6001–6275
SacA 20048	PAR09-P1-61,5-62,5	62	Bulk	0.46	−27.20	6325 ± 30	7171–7313
SacA 16250	PAR09-P1-68-70	69	Bulk	0.77	−28.80	7400 ± 50	8050–8355
SacA 20049	PAR09-P1-81,5-82,5	82	Bulk	0.72	−27.20	10 740 ± 45	12 563–12 739
SacA 16251	PAR09-P1-94-96	95	Bulk	0.96	−24.30	10 690 ± 50	12 548–12 710

geomorphological and volcanic settings of the Javakheti Plateau and Lake Paravani watershed including field observations and radiometric dating methods.

2. Regional and local setting

2.1. Geological and hydrological context

The Lake Paravani is located on the Javakheti Plateau and is enclosed by the Samsari-Javakheti range (Fig. 3). The presence of these volcanic reliefs provided a favourable environment for the development of local glaciers in this region, that previously reached relatively low altitudes (ca 1450–1500 m asl) as observed in southern Armenia and Iran (Kuhle, 2007; Ollivier et al., 2010). At the present time, there are many glaciers in the northern and central parts of the Greater Caucasus (Volodicheva, 2002), while there is none on the Javakheti Plateau. Evidence of Upper Pleistocene glaciations consisting of glacial cirques and moraine fields are abundant in the Samsari-Javakheti volcanic plateau and in the Lake Paravani watershed down to the lake shores (Fig. 3). Therefore, in order to better constrain the geomorphological history of the lake area, three samples (SAM-92, SAM-97 and BORD-C1) belonging to the youngest part of the Samsari volcanic activity (Fig. 3) were dated using the K/Ar method (Guillou et al., 1998, 2004; Scaillet and Guillou, 2004) and $^{40}Ar/^{39}Ar$ method (Nomade et al., 2005; Messager et al., 2011). The weighted mean ages (combined $^{40}Ar/^{39}Ar$ and K/Ar dating methods) for SAM-97 and SAM-92 are 244 ± 8 ka and 309 ± 11 ka, respectively (see Supplementary material SD1, SD2). The age of BORD-C1 is 189 ± 11 ka ($^{40}Ar/^{39}Ar$ dating methods). The averaged ages of the volcanic rocks covered by the moraines give insights of the potential maximum age for these glacial deposits located in the eastern part of the Lake Paravani, thus suggesting that the glacial landscape is contemporaneous, or younger than the MIS 6 glacial period. Most of the fresh-looking moraines date probably to the Last Glacial period MIS 4–2.

The Javakheti Plateau contains the largest number of lakes and marshes in the Caucasus (Matcharashvili et al., 2004) including the largest lakes in Georgia (Fig. 2). Most of the lakes are interconnected by surface rivers and tributaries, and by groundwater systems. Lake Paravani is 2–3 m deep and has a surface area of 37.5 km^2. The lake receives the major part of its inflow from snowmelt and a number of unknown sub-aquatic seepages located along the western shore of the lake. The lake surface outflow corresponds to the Paravani River in the southern end of the lake, and flows into the Mtkvari (Kura) River.

2.2. Climate and modern vegetation

The exceptionally stable climatic conditions of the western part of South Caucasus played a major role in sheltering tree refugia during glacial phases (Denk et al., 2001). Consequently, many Tertiary-relict species, such as *Pterocarya fraxinifolia* and *Diospyros lotus* (which have largely disappeared from western Eurasia), are today only observed in the Colchic area, in the western part of South Caucasus (Ketskhoveli, 1959; Kolakovskii, 1961; Dolukhanov, 1989; Denk et al., 2001). The central part of South Caucasus is occupied by deciduous and coniferous forests along with forest-steppe and grasslands (Fig. 2). The eastern part comprises steppes and semi-deserts with low rainfall (400 mm/yr or less). The climate of the Javakheti Plateau is continental with long, cold winters and short, cool summers, with mean annual temperatures of 5.3 °C. The annual precipitation is 500–600 mm with a maximum in late spring and early summer and minimum in January (Matcharashvili et al., 2004). Presently, the Javakheti Plateau is covered by herbaceous vegetation composed of three communities: mountain steppe, meadows, and mountain xerophilous vegetation (Nakhutsrishvili, 1999; Bohn et al., 2000).

The most widely distributed vegetation community is mountain steppe, and is dominated by grasses (Poaceae family, e.g. *Festuca* spp. or *Stipa* spp.). The origin of the Javakheti Plateau open vegetation is still debated. The grasslands are thought to have developed during the late Holocene as a result of farming activities such as grazing (Nakhutsrishvili, 1999). These secondary herbaceous ecosystems are nowadays maintained by grazing and especially by haymaking. The second hypothesis states that the grasslands were dominant during the Lateglacial and throughout the entire Holocene (Margalitadze, 1995). Forest communities are mostly absent from the plateau and only two small areas of sub-alpine forest still exist (Fig. 2): a patch of *Betula litwinowii*, *Populus tremula*, *Sorbus aucuparia* and many shrubs of the Rosaceae family, located on the eastern part of Lake Kartsakhi (Matcharashvili et al., 2004) and a patch of dwarf beech forest located on the side of Mt Tavkvetili (Arabuli et al., 2008).

3. Material and methods

3.1. Core site and chronology

A 96 cm-long core PAR09-1 was recovered from the central part of Lake Paravani (41°27′N 43°48′E, 2073 m asl), at 3 m water-depth using a gravity corer (UWITEC, Mondsee, Austria).

Core chronology is based on 10 AMS ^{14}C ages determined on bulk sediment samples using acid–base–acid pretreatment (See Table 1). The age–depth relationship was constructed using an age–depth model based on autoregressive Gamma Process called “Bacon” (Blaauw and Christen, 2011). The Bacon model is based on Bayesian statistics, and controls the accumulation rate between the dating points with an arbitrary subdivision along the sediment that corresponds to the section thickness (Δ_C). For each individual section, the accumulation rate is modelled, constrained by the dates and the prior information of accumulation rate and memory. The memory parameter is the variability of the accumulation rate

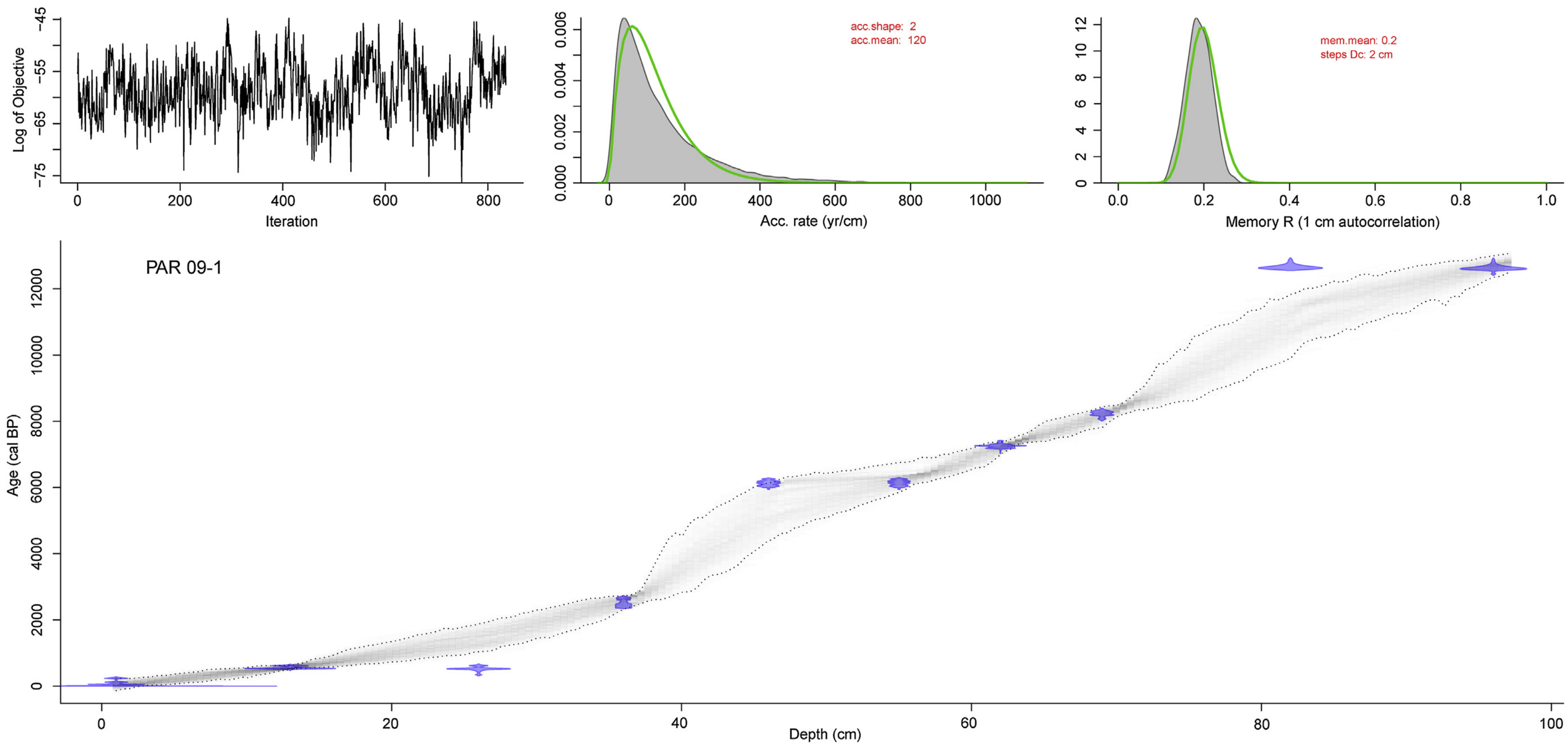

Fig. 4. Posterior age–depth model for core Paravani PAR09-1 (grey), overlaid on the calibrated distribution of the individual dates (blue). Grey dots indicate the model's 95% probability interval. Top panel: Time-series (at right) of the log-posterior for the sub-samples MCMC (Blaauw and Christen, 2011), prior (green) and posterior (grey) distributions of accumulation rate (Center) and memory (Left). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

between 1 cm depth increments. If the values are low, there is almost no memory and the accumulation rate is independent of neighbouring depths. The accumulation rate model along the core requires environmental knowledge (i.e. changes in lithology) to be used as prior information for the model's parameter input (Blaauw and Christen, 2011). Based on the length of our core and the time period covered by the record as indicated by the lowermost ^{14}C age of 12 548–12 739 cal. BP, we expect a low accumulation rate and therefore, we initially set our prior for the mean accumulation rate to 120 yr/cm, and the Δ_C at 2 cm to potentially depict any fine-resolution changes in accumulation rate. Accordingly, the memory mean was set to a low value of 0.2 to allow more variability in the accumulation rate from one depth to the other. The age–depth model was calculated for 49 sections.

3.2. Grain size, magnetic susceptibility and mineralogy

For grain-size analyses, the samples were measured without chemical preparation or sieving due to the absence of calcium carbonate and a coarse fraction. Grain size was determined with a laser particle analyser (Malvern Instruments Mastersizer 2000 model) with a wet dispersion unit (Hydro 2000MU), following the Folk & Wards method (1957). Additional hydrogen peroxide treatment was used for some samples to remove the influence of organic matter.

For magnetic susceptibility (MS) analyses, the core was sampled using 2 cm^3 sampling plastic cubes at 2 cm resolution. MS was measured at the Laboratoire des Sciences du Climat et de l'Environnement (LSCE) at Gif-sur-Yvette (France) using a Bartington© MS3 model, and the obtained SM values were normalized to samples weight.

Five dry samples were prepared for mineralogical analyses (Par P1: 18–20 cm, 34–36 cm, 56–58 cm, 76–78 cm, 86–88 cm). The mineralogy of the sample powder was determined by X-ray diffraction (XRD) using the $CuK\alpha_{1,2}$ radiation with dwell time of 2 s and step size of 0.04°2 between 5° and 70° on a Siemens D5000 diffractometer, equipped with a diffracted-beam graphite monochromator designed to minimize the fluorescence effect. The mineralogical phase determination was carried out with X'Pert HighScore version 2.0 software using the International Center for Diffraction Data (ICDD).

3.3. Pollen analysis

Sixty-one samples were taken at 1–2-cm intervals for pollen analyses. For each sample, 1–2 g of sediment was processed following the standard methods in palynology using HCl, KOH baths (Fægri and Iversen, 1989) and heavy liquid flotation (Girard and Renault-Miskovsky, 1969; Goeury and Beaulieu, 1979). Two densities have been used for the flotation: i.) d. 2.35 g ml^{-1} to recover phytoliths and diatoms (for further analysis) and ii.) d. 2 g ml^{-1} to recover palynomorphs. After flotation, if significant amounts of silica particles remained, an HF bath was finally used. After treatment, the residue was suspended in glycerol, mounted onto microscope slides and counted using "Zeiss standard™" and "Leica DM 1000" microscopes. Pollen grains were identified using atlases of European and Mediterranean pollen types (Reille, 1992; Beug, 2004). The Pollen Indicator of Human Activities was calculated with the frequencies of *Cerealia*-type, *Plantago* group and *Juglans*. The pollen concentration ranges from 20 000 to 40 000 grains g^{-1} in the lower part (below 71 cm) and from 100 000 to 300 000 pollen grains g^{-1} in the middle and upper parts of the sequence (up to 71 cm). The pollen sum (reported on the diagram) used for percentage calculations was based on the total terrestrial pollen (AP + NAP), excluding spores of mosses and pteridophytes. The diagram was produced using Gpalwin software (Goeury, 1997).

4. Results and interpretation

4.1. Age–depth model

The final age–depth model for core PAR09-1 reconstructs a generally smooth accumulation history (Fig. 4). The age model error increases significantly when the distance between two dating points is large (e.g. between 70 and 96 cm). Two ^{14}C ages corresponding to samples at 26 and 82 cm were identified as outliers by the model and were not included in the age–depth model. Indeed, these samples showed age anomalies (younger ages for their corresponding depth, Table 1), which may be attributed to sample contamination. The very low $\delta^{13}C$ of the sample located at 26 cm leads to reject the ^{14}C date. Posterior distribution for accumulation rate and memory were obtained and are presented in Fig. 4 (top panel centre and left). The posterior for memory indicated that the prior value of a low correlation between sediment accumulations at a distance of 1 cm (equivalent of 120 years) seems accurate. The average distribution of accumulation rate is similar to the prior distribution, thus indicating that the prior used for accumulation rate is sufficiently strong. Although the sedimentation rate was temporally variable, some sections, for instance 45–55 cm were distinguished with a relatively constant sedimentation rate. For the uppermost section from 0 to 40 cm, the average sedimentation rate derived from the Bacon model was 0.12 mm/yr. The mean accumulation rate for the section between 40 and 46 cm was significantly lower with 0.03 mm/yr. The following section between 46 and 55 cm is marked by a higher accumulation rate (0.068 mm/yr) and the average accumulation rate for the following 30 cm remains similar ~ 0.06 mm/yr. The oldest part of the sediment (from 85 cm) was characterized by a higher sedimentation rate of 0.09 mm/yr.

Although, we are quite aware that the length of the time interval recorded by the relatively short sediment sequence of PAR09-1 implies a high probability for a hiatus in the sedimentary record, the temporal variations of the proxies studied in PAR09-1 show no evidences for the presence of a hiatus. Additionally, similar changes and transitions in the environmental history recorded in lake Paravani and discussed below are observed in another sequence located near Lake Tabatskuri (Messager et al., Unpublished data).

4.2. Core lithology and mineralogy

The stratigraphy of Lake Paravani sediments allowed the PAR09-1 core to be subdivided into 3 different units based on the Munsell soil colour charts (Table 2 and Fig. 5).

i.) The lowest stratigraphic unit (depth: 96–68.5 cm) consisted of compact grey silt interrupted by light grey silt at 84.6–

Table 2
Lithological units defined using the Munsell soil colour charts (1975).

Depth (cm)	Description	Colour	Colour code (Munsell)
0–29	Gyttja	Brown/Dark brown	10YR4/3
29–30	Organic silt	Greyish brown	10YR5/2
30–31.5	Gyttja	Brown/Dark brown	10YR4/3
31.5–68.5	Organic silt	Greyish brown	10YR5/2
75.5–68.5	Compact grey silt	Olive grey	5Y4/2
75.5–76	Light-grey silt	Light grey	2,5Y7/2
76–76.5	Olive Silt	Light olive brown	2,5Y5/4
76.5–77	Blackened silt	Very dark greyish brown	2,5Y3/2
77–84.2	Compact grey silt	Olive grey	5Y4/2
84.2–84.6	Light-grey silt	Light grey	2,5Y7/2
84.6–96	Compact grey silt	Olive grey	5Y4/2

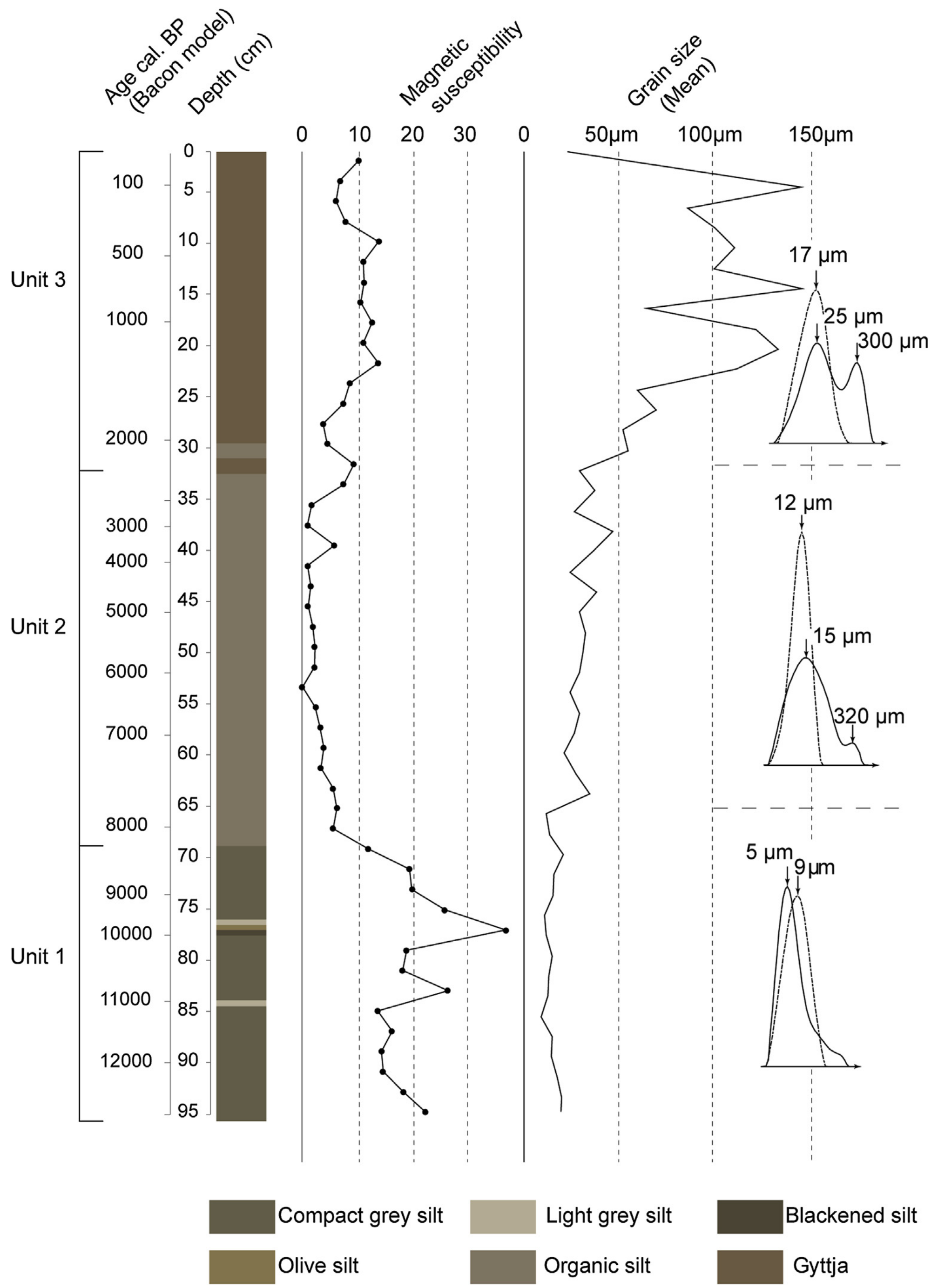

Fig. 5. Lithology, magnetic susceptibility (10^{-5} SI) and grain-size curves from PAR01 versus core depth in cm and age. The cumulative in the middle (mean) and frequency curves on the right (main grain-size populations) are represented for the grain-size analysis.

84.2 cm, blackened silt at 77–76.5 cm, olive silt at 76.5–76 cm and light grey silt at 76–75.5 cm. The sediments of this unit are characterized by a low mean size (10–25 µm) and uni-modal grain size distributions. The magnetic susceptibility displays varying but high values ranging from 13.8 to 37.

ii.) The next unit (depth 68.5–31.5 cm) consisted of greyish brown organic silt. This unit is characterized by a higher mean size (25–50 µm) and uni-modal grain size distribution curve (15 µm) with a minor shoulder (320 µm), however, the transition to higher grain size occurred at 64 cm (4 cm above the lithological transition between Unit 1 & 2). The magnetic susceptibility shows low and stable mean values (0–8.6) after a transition phase at 70–69 cm with values around 12.

iii.) From 31.5 cm upward, the sediments consisted of brown and dark brown gyttja interrupted by a greyish organic silt layer between 30 and 29 cm. This upper unit is characterized by a coarser mean size (50–150 µm) and bi-modal frequency curves (25 and 300 µm), and is marked by varying and higher mean magnetic susceptibility values (6.1–13.9).

The main grain-size peak (5–25 µm) observed in the three units can be related to a constant mineral input. The frequency

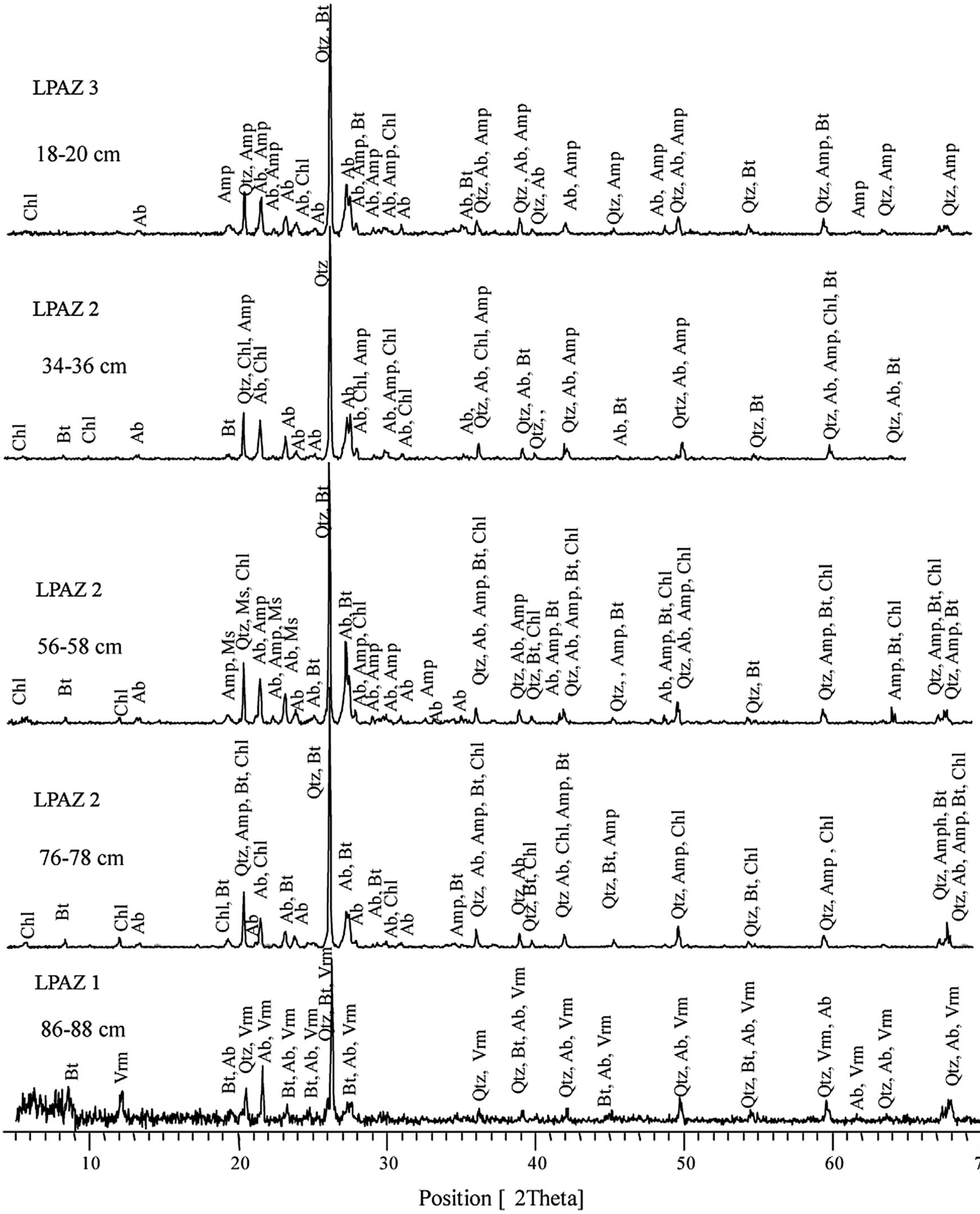

Fig. 6. Bulk X-ray powder diffraction patterns of the sediments samples PAR01 18–20, 34–36, 56–58, 76–78, 86–88 at different depths. The mineralogical assemblages are dominated by silicates with quartz (Qtz), amphibole (Amp), albite (Ab), muscovite (Ms), biotite (Bt), clinochlore (Chl) and clay minerals as vermiculite (Vm).

curves of Units 2 and 1 became quasi-uni-modal after processing with hydrogen peroxide, therefore, the minor peak (300–320 μm) can be related to organic matter micro-remains. The increase of the coarse-sized particles in unit 3 of the Lake Paravani record appears to be directly controlled by organic matter input and production from biological activities (i.e. vegetal tissues, chironomid chitin remains and diatoms observed in the sediments). The magnetic susceptibility variations mirror the pattern observed in the grain size analysis. The higher input of organic matter is responsible for the decrease in the concentration of magnetic minerals.

The mineralogical assemblage is homogeneous along the core (Fig. 6), with quartz (Qtz), amphibole (Amp), biotite (Bt), feldspar (Alb) and various clay minerals. The sampling resolution was sufficient to characterize the mineralogical input along the core sequence because of the very homogeneous mineral-assemblages. The only noticeable difference is the presence of vermiculite instead of chlorite in the lowermost part of the core, probably due

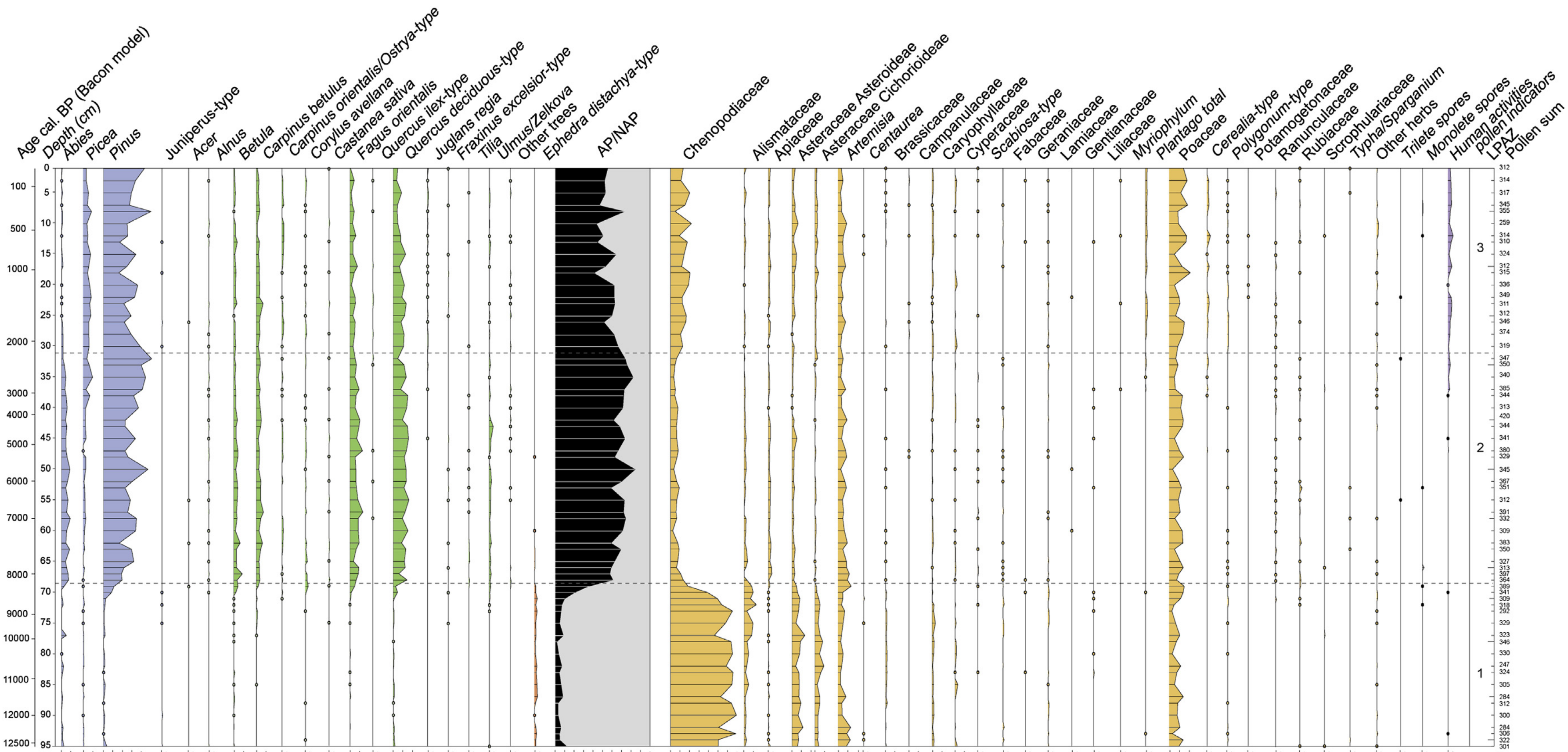

Fig. 7. Diagram of selected pollen data from Lake Paravani versus age in ka cal. BP. LPAZ: Local Pollen Assemblage Zones, AP: Arboreal Pollen, NAP: Non Arboreal Pollen. Pollen values lower than 0.35% are represented by dots.

to biotite and/or chlorite alteration. As most of the Javakheti Plateau is made of andesite and basalt, without either quartz, amphibole or biotite, the presence of these minerals clearly point toward a unique source for the detrital material found in the lake: the Samsari Ridge volcanoes located immediately west of the lake shores (Fig. 3).

4.3. Pollen results

The results of the pollen analyses (pollen diagram) are presented in Fig. 7. In a pollen diagram from a given site, a Local Pollen Assemblage Zone (LPAZ) is defined as a body of sediment with a consistent and homogeneous fossil pollen content different from the adjacent zones (Birks and Birks, 1980). Three main LPAZs (Local Pollen Assemblage Zones) have been distinguished in the Paravani pollen record:

- LPAZ1 (depth: 96–68.5 cm): The first zone is characterized by a prevalence of herbaceous pollen taxa. In this PAZ, pollen assemblages are dominated by Chenopodiaceae and other herb taxa, such as Poaceae, Asteraceae (Asteroideae, Cichorioideae and *Artemisia*), Cyperaceae, Brassicaceae and Caryophyllaceae, indicating open vegetation. The xeric and steppic taxon, *Ephedra distachya* t., is present in every sample of this zone (1–3%). In the lowest part of this LPAZ (at 96–95 cm), tree and shrub pollen grains (*Abies*, *Pinus*, *Betula*, *Quercus*, *Alnus* and *Juniperus*) reach 11%. After that, trees are only represented by a few pollen grains of coniferous or deciduous taxa. The end of LPAZ1 is characterized by a marked decrease in Chenopodiaceae and Asteraceae pollen frequencies. This decline of herbaceous pollen corresponds to the emergence and slight increase in tree pollen grains in the Lake Paravani sediments. This period corresponds also to significant values in *Betula* and the highest representation of *Corylus*. The continuous curve of *E. distachya* t. ends at the top of LPAZ1. Alismataceae pollen values increase in this transitional phase.
- LPAZ2 (depth 68.5–31 cm): At the very beginning of this zone, a simultaneous expansion of *Pinus*, *Abies* and deciduous trees, such as *Quercus*, *Fagus*, *Betula* and *Carpinus*, is recorded. All the main arboreal taxa, except *Picea*, attain high percentages, suggesting rapid colonization change in the surroundings of Lake Paravani. Then, *Pinus*, *Abies* and the main deciduous trees (e.g. *Quercus*, *Fagus*, *Carpinus* and *Betula*) display a continuous curve with stable frequencies. Other arboreal taxa, such as *Ulmus*/*Zelkova*, *Corylus* and *Castanea*, are frequently recorded. *Picea* presents a semi-continuous curve but its pollen frequencies remain low (1.5%–3%). The end of LPAZ2 is characterized by a gradual but slight decrease of *Abies* and *Fagus* pollen frequencies. On the other hand, *Pinus* and *Picea* pollen are more frequently recorded. An expansion of *Pinus* and *Picea* occurred at that time in the Paravani region, synchronous with a decline of *Abies* and deciduous mid-altitude trees.
- LPAZ3 (depth 31–0 cm): Pollen data for this zone indicate the local extinction of *Abies* and the decline of deciduous trees such as *Quercus*, *Fagus* and *Carpinus*, while a rise in herb pollen (NAP) is recorded. Herbaceous pollen taxa such as Chenopodiaceae, Asteraceae (Asteroideae and Cichorioideae) as well as Poaceae show increasing frequencies. Pollen indicators of human activities display a semi-continuous curve. The vegetation change corresponds to an opening of the landscape in the Lake Paravani area. The end of this phase is marked by increasing percentages of *Pinus*, probably reflecting the plantations of *Pinus kochiana* during the Soviet-Era. At the end of this zone, deciduous tree pollen values are low (9–18%) and confirm the decline of the broad-leaved forests on the Javakheti Plateau.

5. Discussion

5.1. Comparison of fossil and modern spectra

Lake Paravani has a large surface area (37.5 km^2) and therefore the tree pollen rain can be well-recorded compared to smaller lakes in which the local herbaceous vegetation is over-represented (Connor, 2011). However, its large size could also induce some misinterpretations about the local tree-cover because the spectra represent rather regional pollen rain (Prentice, 1985). In order to better constrain the pollen source area, the fossil spectra from Lake Paravani core have been compared to modern pollen spectra established in Georgia (Connor and Sagona, 2007; Connor, 2011). Two particular points are discussed using this modern analogue approach: i.) the origin of Chenopodiaceae signal, and ii.) the origin of tree pollen assemblages.

i) The pollen assemblages from the lower Lake Paravani sediments display very high rates in Chenopodiaceae (60–70%). Since Chenopodiaceae plants are wind-pollinated and produce a large amount of pollen, their representation in the Javakheti palaeoflora can therefore be questioned. Nevertheless, the Chenopodiaceae values in the lowermost part of the Lake Paravani core are more similar to Chenopodiaceae values (70–80%) recorded in modern semi-desert in which Chenopodiaceae plants are widespread, than to Chenopodiaceae values recorded in modern Javakheti grasslands (<5%) (Connor and Sagona, 2007). The high percentages of Chenopodiaceae in the lower part of the record indicate that these xerophilous plants were significantly represented in the Lake Paravani area, while long distance pollen transport (probably from the eastern arid lowlands) contributed also to the high values.

ii) The pollen data from the middle part of the core, reveal significant values in arboreal pollen (60% < AP < 70%). *Pinus* is well represented (20–45%) as well as several deciduous trees such as *Quercus* (10–15%), *Abies* (5–10%) and *Fagus* (5–12%). While the region is mostly devoid of trees at the present time, the modern pollen spectra from the Javakheti highlands show an important amount of tree pollen (AP: 40–60%, Connor and Sagona, 2007; Connor, 2011). However, in modern spectra, the high values in *Pinus* (~20%) representing 50% of the AP values, reflect the large pine plantations dating back to the Soviet era. The other trees such as *Quercus*, *Abies* and *Fagus* are recorded with only low values (<5%). As a result, the high percentages of arboreal pollen recorded in the Lake Paravani core confirm that mesophilous and coniferous belts were better developed in the landscape. The assemblages correspond to pollen influx originating from forest communities located in Javakheti, probably at lower elevations (Kvavadze, 1993; Connor and Sagona, 2007) compared to the lake elevation (2100 m asl). The highest belts (coniferous or mixed forest) might have reached the Lake Paravani watershed during the most favourable climatic periods.

5.2. The arid and steppic environment of the Lateglacial

In the Lake Paravani sequence, the mineralogical and grain-size analyses show that the lower deposits are mainly composed of detrital mineral input originating from the erosion of the moraine deposits in the Samsari lava zone. High values of magnetic susceptibility (Fig. 5) confirm the abundance of magnetic mineral input from the Samsari rhyodacites and dacites (Fig. 3). The sediments are devoid of any organic matter, which reflects limited productivity in the lake water, poorly developed soils and sparse vegetation in the catchment. The Lake Paravani environment might have experienced harsh climate conditions. The large number of moraine deposits covering the basaltic rocks of an age younger than 200 ka points to the presence of active local glaciers during the upper Pleistocene. These local glaciers probably persisted in the Lake Paravani area during the Younger Dryas period, or later. The persistence of glaciers late in the Holocene has already been recorded in the southern range of Russia, where glacial retreat started between 12 000–9000 cal. BP (Mel'nikova, 1987; Sevastianov et al., 1990; Bondarev et al., 1997).

The vegetation recorded by pollen data in the lower deposits of the sequence was dominated by steppic taxa such as Chenopodiaceae, Poaceae and Asteraceae (Asteroideae, Cichorioideae and *Artemisia*). Pollen assemblages dominated by Chenopodiaceae (Fig. 8) were also identified in Lateglacial records from Lake Van (Turkey, 1650 m asl, Wick et al., 2003; Litt et al., 2009) and Lake Zeribar (Iran, 1300 m asl, Van Zeist and Bottema, 1977). These dry steppes, which typically developed during the glacial phases in the Middle East (Djamali et al., 2008), indicate a particularly arid climate. The frequent occurrence of *Ephedra* in the base of the Lake Paravani sequence supports this climatic interpretation. Similar assemblages are also recorded in the modern semi-desert grasslands (Fig. 2) in the arid continental areas of Southeastern Georgia (Connor et al., 2004). The arboreal pollen sum >10% observed at the very beginning of the sequence (dated to more than 12 500 cal. BP) could reflect the end of a milder period, the Bølling–Allerød interstadial warming phase (Von Grafenstein et al., 1999), but this AP sum is only recorded in a single sample (Fig. 7).

The subsequent pollen spectra clearly depict a very open landscape representing a severe glacial climate corresponding to the Younger Dryas cold event. The environmental response of this Lateglacial stadial is recorded in many lacustrine sequences from North and Central Europe (Lotter, 1999). In Southeastern Europe, the responses to the Younger Dryas were varied and expressed local and regional climate and environmental conditions (Bottema, 1995). The pollen sequences of Tenaghi Philippon (Greece, 40 m asl, Fig. 1) and Lake Ohrid (Albania, 697 m asl, Fig. 1) show a quasi-continuous and increasing temperate deciduous trees from the end of the Pleniglacial to the Mid-Holocene (Wijmstra, 1969; Pross et al., 2007; Lézine et al., 2010; Müller et al., 2011). In contrast, several lake pollen-records from Central and Eastern Anatolia displayed a spread of herbaceous communities and a decrease in arboreal vegetation. This vegetation dynamic reflects increased climate aridity in the Eastern Mediterranean during the Younger Dryas (Bottema, 1995; Wick et al., 2003; Wright et al., 2003). The contrast between the different sequences in Southeastern Europe can be explained by several factors, like distance from glacial tree refugia, topography and/or orography. The Black and Mediterranean Seas seem, however, to have played a major role in modulating the local expression of the Younger Dryas. The comparison of Lake Eski Acigöl (Turkey, 1270 m asl, Roberts et al., 2001) and Lake Van (Wick et al., 2003) suggests that the Younger Dryas was more pronounced in Lake Van than in central Anatolia (Fig. 1), which reflects a moisture gradient between coastal and inland parts of the east Mediterranean region during the Younger Dryas (Jones et al., 2007). The Lake Aligol pollen record (Georgia, 1534 m asl, Fig. 2) shows a prevalence of Chenopodiaceae and *Artemisia*, as well as *Ephedra*

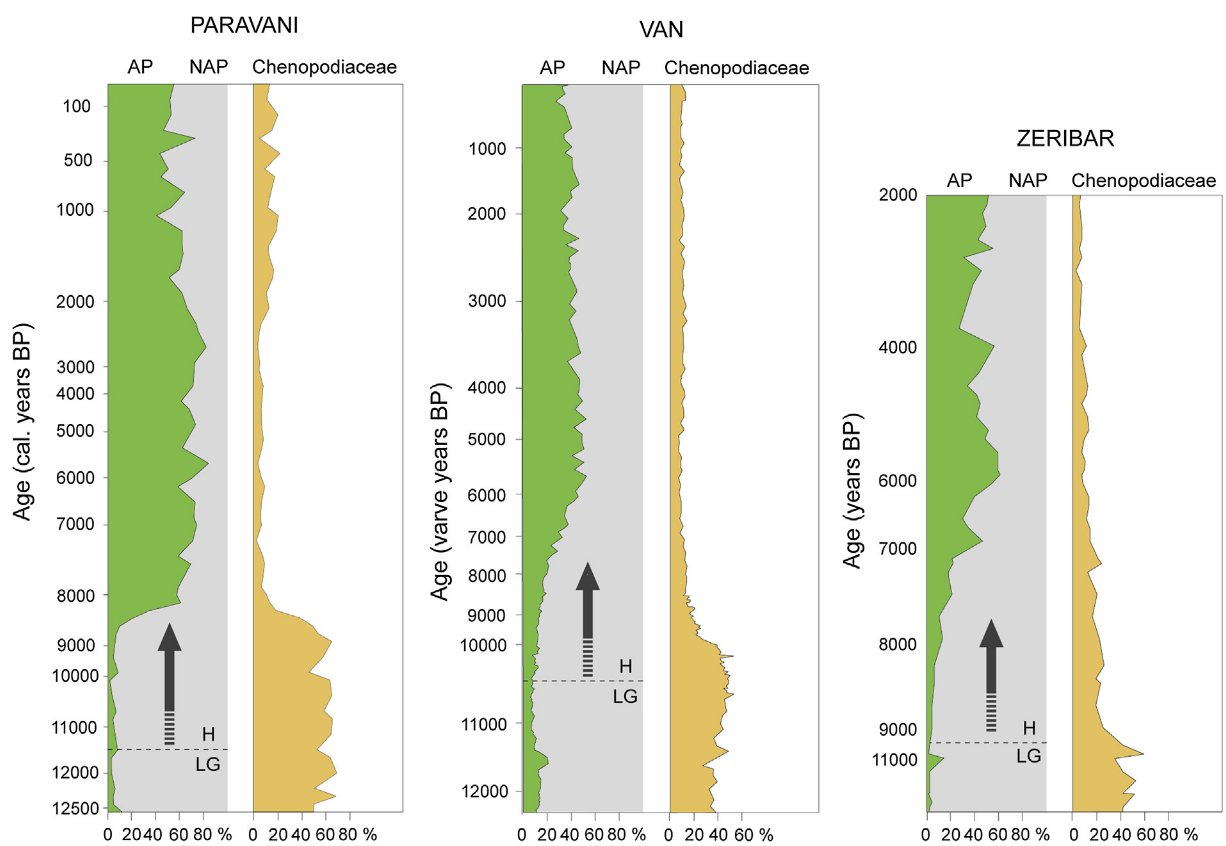

Fig. 8. Timing of afforestation (AP/NAP) and Chenopodiaceae variations, recorded in Lake Paravani, Lake Van (Wick et al., 2003) and Lake Zeribar (Van Zeist and Bottema, 1977). The lower dotted line indicates the Lateglacial–Holocene boundary (Wright et al., 2003) and the arrows represent the delay of forest expansion. The sedimentation rate and the age/calibration are not standardized amongst the different sequences. The Lake Zeribar diagram is based on pollen data from the EPD (European Pollen Database). The AP, NAP and Chenopodiaceae curves of Lakes Van and Zeribar are calculated as well as in the original articles (Van Zeist and Bottema, 1977; Wick et al., 2003).

indicating a “hyper arid desert or semi-desert steppe landscape” (Connor and Sagona, 2007). Connor (2011) have demonstrated through numerical analysis applied on the pollen data from this lake, that low winter temperatures was the main factors limiting the tree development during the Younger Dryas. In contrast, increasing aridity during the Younger Dryas is considered to be the main factor limiting tree growth in the Lake Paravani area which records higher Chenopodiaceae values (80–70%) compared to Aligol (10–30%). The Arsiani Ridge, located west of the lake-watershed and with a N–S orientation, played an important role in restricting the influence of sea-moisture and precipitation originating from the Black Sea during this period. The hypothesis of increasing aridity is also supported by the high values in Chenopodiaceae and the ^{18}O record during the Younger Dryas in the Lake Van sequence (Wick et al., 2003).

For the Lateglacial period, trees have been documented by a few occurrences in Lake Paravani as well as in Lake Aligol (*Abies*, *Pinus*, *Quercus*, *Carpinus*). The tree pollen grains might originate from the Colchis region (Western Georgia) in which “glacial tree refugia” existed (Shatilova and Ramishvili, 1990; Shatilova et al., 2011). For instance, the Sukhumi record on the Black Sea coast (Georgia, 0 m asl) presents a pollen sequence covering the Pleistocene–Holocene transition in which the tree pollen curve never decreased lower than 40% (Kvavadze and Rukhadze, 1989). The comparison of western and eastern Georgia records confirms the humidity (or alternatively aridity) contrast existing between the continental and coastal regions of the Caucasus.

Interestingly, in the Lake Paravani record, the *Juniperus* expansion is not observed during the Younger Dryas interval, a pattern also observed in the pollen diagrams of Nariani (Georgia, 2100 m asl) and Kartsakhi wetlands (Georgia, 1850 m asl, Margalitadze, 1977, 1995). Even if several species of *Juniperus* are present in Eastern Georgia, this shrub is nowadays rare in the Javakheti highlands. However, in the lowest part of Lake Aligol record, *Juniperus* was associated with Chenopodiaceae and declined at the very beginning of the Younger Dryas (Connor, 2011). In the South Georgian Uplands, *Juniperus* probably declined at the end of the Lateglacial which explains its absence in Lake Paravani record dating back only to 12 500 cal. BP. Another original feature in our record is the low percentages of *Pinus* pollen during the Younger Dryas. A similar pattern was recorded in Sagarejo (Fig. 2) deposits located in the Kakheti region (Georgia, 550 m asl), where the percentages of *Pinus* pollen were high (50–60%) during the Pleniglacial and declined (20%) during the Lateglacial (Gogichaishvili, 1984). The high values in *Pinus* recorded for glacial periods in Kakheti lowland can also be due to the pollen contribution of *Pinus eldarica*, a xerophilous pine occurring in arid steppes (Connor, 2011). Indeed, pines seem to have been an important component of Late Pleistocene vegetation in Eastern Georgia but was restricted to their refugia during the Younger Dryas event.

5.3. A persistent steppic environment followed by a late and rapid forest expansion

In the core corresponding to the Early Holocene, the magnetic susceptibility values remain high and the grain-size curve remains stable (Fig. 5). The very beginning of the Holocene in the Lake Paravani record is not marked by increasing abundances of trees as typically observed in Northern and Central Europe (Watts et al., 1996). In fact, steppic vegetation continued to dominate the Lake Paravani environment during the Early Holocene (Fig. 7). This pattern has already been described in several palaeoenvironmental records from Southeastern Europe (Wright et al., 2003). In the Lake Van pollen record, the Early Holocene is characterized by the replacement of Chenopodiaceae steppes by Poaceae steppes rather than forest colonization (Wick et al., 2003). In the Trialeti range, 50 km from Lake Paravani (Fig. 2), the pollen record from the Lake Gomnis (Georgia, 1850 m asl) indicates that a steppic vegetation prevailed until the Mid-Holocene (Margalitadze, 1971, 1995). This pattern points to dry conditions occurring at high elevation up to 1850 m asl (Wright et al., 2003). The comparison of the pollen records from Lake Paravani and Lake Aligol, located on the lower Javakheti Plateau, is made difficult by the fact that the tree pollen grains are not well-recorded in Lake Aligol because of lake level variations (Connor, 2011). However, the few tree pollen grains recoded in Lake Aligol between 12 000 and 11 000 cal. BP tend to demonstrate that a pioneer phase composed of *Corylus* and *Betula* follows the steppic environment (Connor and Sagona, 2007). In Lake Paravani, the end of the steppic phase is characterized by a rapid expansion of deciduous (including *Corylus* and *Betula*) and coniferous trees without any marked pioneer phase (Fig. 7). The possibility of a hiatus in our record that might explain the absence of a pioneer phase is not supported by lithological and environmental proxies from our core. Magnetic susceptibility and pollen assemblages show gradual changes (Figs. 5 and 7), suggesting a continuous sedimentation process. The sample in which the radiocarbon date of 8050–8355 cal. BP was obtained (mean depth of 69 cm) yields a pollen assemblage indicating that the forest expansion was not reached (AP: 30%) at that time, while the subsequent samples display a more forested signal (AP≥60%) confirming the late afforestation. Similar pattern is observed in Lake Zeribar and Lake Urmia (Iran, 1275 m asl Bottema, 1986) sequences where the abrupt increase in tree pollen frequencies (Fig. 8) corresponds to the expansion of Zagros oak forest during the transition from the Early to Middle Holocene (Van Zeist and Bottema, 1977; Bottema, 1986; Djamali et al., 2008, 2010). Additionally, in marine pollen sequences from the western (Atanassova, 2005) and the southern Black Sea (Shumilovskikh et al., 2012), an abrupt increase of deciduous tree pollen occurred between 8000 and 8300 cal. BP. The observed delayed forest expansion in the southeastern regions of Europe is argued to result from a late onset of precipitation at the beginning of Holocene (Van Zeist and Bottema, 1977; Wright et al., 2003; Atanassova, 2005; Djamali et al., 2008; Litt et al., 2009). Understanding the mechanisms at the origin of the late or alternatively early afforestation in Southeastern Europe is challenging because of the diversity of the pollen sequences recording these patterns, including both dry-continental and high altitude environments. The delay of the forest expansion in Lake Paravani (Fig. 8) can probably be linked to persistent arid conditions during the growing season as suggested by the rare trees and the high Chenopodiaceae values. The hypothesis of insufficient moisture in Southeastern European Mountains was also proposed to explain the delayed expansion of conifers recorded in Lake Dalgoto (Bulgaria, 2310 m asl) that reached these high altitudes only after 6500 BP (Stefanova and Ammann, 2003). This delay in woodland expansion is mainly recorded in intra-mountain areas (van Zeist and Bottema, 1991; Roberts and Wright, 1993; Wick et al., 2003), and was also recently recorded in lowland Bulgaria (Connor et al., 2013). It might be related to climate aridity, a factor that limited the tree growth of mesophilous woodlands during the Early Holocene (Roberts and Wright, 1993). In the Lake Paravani pollen record corresponding to the Early Holocene, the significant values in Alismataceae, a family of hygrophilous plants, is analogous to its current expansion nowadays in very shallow lakes like Lake Madatapa (20–40 cm depth, 20 km south of Paravani). These results suggest a low lake level for Lake Paravani at this time. However, proxy-based records from other lakes in Southeastern Europe (e.g. Eski Acigöl) seem to show an increase in global precipitation (Roberts et al., 2001).

In the Lake Paravani area, various tree taxa concurrently colonized the different altitudinal vegetation belts immediately after the climatic and edaphic conditions were suitable for tree growth and expansion, thus suggesting that the vegetation responds to the climatic changes only when "species-related threshold levels are crossed" (Wick et al., 2003). The simultaneous expansion of tree taxa such as *Fagus*, *Abies* or *Carpinus*, as early as 8050–8355 cal. BP (radiocarbon date), is an exceptional pattern. The early expansion of mesic tree taxa is typically recorded in regions of glacial tree refugia such as the Balkans (Denèfle et al., 2000; Tzedakis et al., 2002; Lézine et al., 2010) and Italy (Magri et al., 2006). In the Romanian Carpathians, where glacial tree refugia were documented, many trees inhabited this area between 8 and 9 ka uncal BP, except *Fagus* which appeared four millennia later (Tanţău et al., 2003). *Fagus* pollen is a good indicator of the local presence of beech in lowlands, because of its low dispersal capacity (Heim, 1970), while in the Javakheti mountains, *Fagus* pollen may originate from lower elevation forests of *Fagus orientalis* (Kvavadze, 1993; Connor, 2011). In the Lake Paravani pollen sequence, *Fagus* is well-recorded (up to 10%) implying that the mid-altitude beech forest expanded at that time on the Javakheti Plateau. *Fagus* trees may have contributed to a high altitude forest belt reaching the Lake Paravani basin. In Europe, the origin of the *Fagus sylvatica* expansion during the Holocene is still debated (Tinner and Lotter, 2006). Anthropogenic disturbance has often been considered as one of the main factors favouring *F. sylvatica* development (Küster, 1997). The Lake Paravani pollen record demonstrates that in the South Caucasus, the early development of this tree genus appears to be linked to climatic and biogeographical factors.

The significant percentages of *Quercus*, *Carpinus* and *Ulmus*/*Zelkova* pollen grains could reflect the mid-altitude oak forest belt that probably developed on the lower plateau, such as Tsalka Plateau (Connor and Sagona, 2007). The pollen grains identified as *Quercus* (deciduous-type) could be related to *Quercus iberica* (low or midland oak) or *Quercus macranthera* (upland oak). Considering the topography of the Lake Paravani area, *Q. macranthera* trees, able to grow between 1800 and 2400 m (Volodicheva, 2002), might have contributed significantly to the high-altitude forests at that time.

Abies pollen grains are well represented as early as 8200 cal BP. The relatively poor dispersal of *Abies* pollen grains suggests that values $\geq$2% are probably a reliable indicator of local presence, and that values $\geq$5% indicate that *Abies* was a significant member of the surrounding forest (Huntley and Birks, 1983). Therefore, if high *Abies* pollen percentages are recorded in sediments, this would imply a significant fir population. Modern pollen spectra from the Javakheti Plateau indicate that *Abies* is not well represented (Connor, 2011), however, in the Lake Paravani record, the *Abies* values reach 10%. We can therefore conclude that the *Abies* forests were better developed at 8000 cal BP in the Lake Paravani surrounding areas compared to the present.

The glacial and post-glacial history of the main tree species in this part of Caucasus is significantly linked to main tree refugia located in the Colchis lowland (Fig. 2). This region was a major refugium for temperate trees in the Quaternary, due to its exceptional climate with high precipitation and temperatures even during the glacial phases (Shatilova and Ramishvili, 1990; Kvavadze et al., 1992). The palynological record from the Sukhumi 36 core (Georgia, 0 m asl), located on the coast of the Colchis lowland, has shown that deciduous (*Fagus*, *Quercus*, *Carpinus*) and coniferous (*Abies*, *Pinus* and *Picea*) trees were well developed even during the Younger Dryas (Kvavadze and Rukhadze, 1989; Kvavadze and Connor, 2005). These arboreal glacial-refugia permitted a rapid expansion of *Castanea*, *Fagus*, *Picea* and *Abies* in the mountains bordering the lowland, as revealed by pollen-based modelling of plant distribution in Georgia (Connor and Kvavadze, 2008). In Lake Cheliagele (Georgia, 1100 m asl), located further west than Paravani (Fig. 2), *Abies*, *Fagus* and *Carpinus* were well-developed as early as 6900 uncal BP (Ammann, 2009). The Lake Paravani area is isolated from the Colchis lowland, but is located only 100 km from the modern Hygro-thermophilous mixed forests (Fig. 2, Bohn et al., 2000). The deciduous and coniferous tree taxa preserved in Western Georgia were therefore able to concurrently reach the Javakheti Mountains as soon as regional climatic conditions were favourable.

Organic matter accumulation increased markedly in the core sediments after 8500 cal BP. Magnetic susceptibility data show decreased values at the same level and the grain-size is characterized by a bi-modal frequency curve with peaks attributed to organic macro-remains (Fig. 5). This change represents an increase in lake-surface productivity, a pattern observed in many other lakes of Southeastern Europe (Roberts et al., 2001; Wick et al., 2003) and a decrease in the sediment erosion in the watershed, following the onset of the forested phase (Fig. 7). The expansion of beech and fir trees recorded in Paravani pollen data shows that moisture was significantly higher during this period of climatic optimum. The recorded values of fir show that the threshold of 800 mm of precipitation required by this conifer (Nakhutsrishvili, 1999) was attained in the wettest areas of the Javakheti Plateau. The mean annual temperatures in Eastern Georgia have been estimated to 6 °C and the precipitation to 200–400 mm higher than today during the Atlantic period (Kvavadze and Connor, 2005). Nonetheless, more recent modelling suggests that temperatures might be difficult to reconstruct from pollen data in the region and that the change in precipitation might be less than previously estimated (Connor and Kvavadze, 2008). In the Lake Paravani record, the balance between the different forest formations and the grassland established at that time appears to remain stable until 3200 cal BP.

5.4. The palaeoecological changes of Late Holocene

During the Late Holocene, a significant vegetation change occurred between 3200 and 2000 cal. BP. This period corresponds to the decline of *Abies* and *Pinus* and the progressive expansion of *Picea*. The replacement of *Abies* by *Picea* was previously recorded just after 3000 cal. BP in the Lake Aligol located in lower Javakheti (Connor and Sagona, 2007). The climatic and/or anthropogenic causes of the modification in coniferous communities is still questioned in Europe, however, cold climate conditions are believed to be at the origin of the *Picea* expansion in Northern Europe (Bradshaw and Lindbladh, 2005). Furthermore, the species "*Picea orientalis*" is a drought-tolerant spruce tree able to grow at temperatures as low as −5.7 °C (Mudie et al., 2007). In the Tsalka area (lower Javakheti), a depression of the timberline linked to a cooling climate is observed between 4000 and 3000 cal. BP (Connor and Sagona, 2007). This expansion of *P. orientalis* appears to be linked to much colder climatic conditions, but anthropogenic deforestation coincident with agricultural activities could have also generated new places for *Picea* expansion. In fact, in the Lake Paravani record, this change in forest composition coincides with the first significant records of palynological indicators of human activities (Fig. 7). As indicated by previous pollen records, clearing of high altitude deciduous forests (especially beech forest), might have favoured the expansion of *Picea* in Javakheti uplands (Margalitadze, 1971; Connor, 2011). The combined effects of human activities and climate are probably responsible for *Picea* expansion in the region. A large number of Early and Middle Bronze Age (3000–1500 BC) settlements (Sagona, 2004; Connor and Sagona, 2007), such as domestic sites and kurgans (burial mounds), are present in the Javakheti Plateau and especially in Lake Paravani area. The results of investigations carried out on these archaeological sites point to the development of "high mountains agriculture" at the beginning of the Bronze Age period (Kvavadze and Kakhiani, 2010). The agro-pastoral activities of these populations might have affected the Javakheti Plateau environment.

The decline of beech forest during this period (Fig. 7) could be due to forest clearance by populations to prepare agriculture areas. However, the anthropogenic signal recorded in Lake Paravani remains low and especially until 2000 cal BP. The local impact of agricultural and pastoral activities was better revealed in small lakes such as Aligol and Imera (Tsalka Plateau) in which the pollen of cereals and weeds were better recorded (Connor and Sagona, 2007; Connor, 2011). The nature and the intensity of activities of Early and Middle Bronze Age populations in Paravani highlands (cereals cultivation, cattle grazing) remain unknown. These activities require further archaeobotanical and archaeozoological investigations to compare them with the palaeoecological signal recorded in the Lake Paravani as well as in lower elevation lakes such as Aligol and Imera (1500 m asl).

The beginning of the last two millennia corresponds to the decline of *Quercus* and an expansion of herbaceous plants such as Chenopodiaceae, Poaceae and Asteraceae (Asteroideae and Cichorioideae). The herbs from the Asteraceae group, well represented nowadays in the Javakheti steppes, are a good indicator of grasslands expansion during the last two millennia. The spread of herbaceous vegetation is probably related to human impact from the increasing settlements and agricultural practices on the Javakheti Plateau. The opening of the landscape resulted in an increased erosion since 2000 cal BP, as recorded by magnetic susceptibility (Fig. 5). During the last century, despite the artificial increase in *Pinus* due to Soviet-era plantations, the trees including deciduous trees declined and led to the expansion of the steppic environment, which is dominant today. While grasslands still played a significant role in the Javakheti Plateau vegetation during the entire Holocene (Connor, 2011), the spread of the dominant grassland appears to be a very recent process (last few centuries). According to previous pollen data from Javakheti uplands, grasslands were predominant during the whole Holocene because arboreal pollen values are never significant in pollen records from small lakes and wetlands (Margalitadze, 1977, 1995). These new data based on Lake Paravani record tend to support the hypothesis that grasslands became predominant in the Javakheti highland as a result of recent deforestation (Nakhutsrishvili, 1999; Volodicheva, 2002; Matcharashvili et al., 2004).

6. Conclusion

Our study from Lake Paravani provides a record of the vegetation dynamics and climate history during the Younger Dryas and the entire Holocene, in Eastern Georgia. The general patterns of vegetation change are consistent with previous studies from western and eastern mountains of South Caucasus (Margalitadze, 1971, 1995; Connor and Sagona, 2007; Connor, 2011), but also reveal the variability of Holocene forest dynamics among the Transcaucasian regions (Margalitadze, 1995). Climate variations were the main factors controlling the vegetation dynamics until 3000 cal. BP. The proximity of glacial tree refugia (located in Western Georgia) combined with the effect of high elevation of the site, have induced a unique vegetation history. During the last three millennia, the roles of climate and human impacts are difficult to disentangle but have probably caused changes in forest composition and its definitive decline. New lake records are needed in the South Caucasus to refine our knowledge of the vegetation history of this biogeographically important region, and to improve the chronological constraints of post-glacial palaeoclimate variability.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2013.07.011.

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