Vegetation History and Archaeobotany
https://doi.org/10.1007/s00334-019-00734-5

ORIGINAL ARTICLE

20,000 years of interactions between climate, vegetation and land use in Northern Greece

Sylvia Gassner[1,2] · Erika Gobet[1,2] · Christoph Schwörer[1,2] · Jacqueline van Leeuwen[1,2] · Hendrik Vogel[2,3] · Tryfon Giagkoulis[4] · Stamatina Makri[2,5] · Martin Grosjean[2,5] · Sampson Panajiotidis[6] · Albert Hafner[2,4] · Willy Tinner[1,2]

Received: 31 May 2018 / Accepted: 23 May 2019

Abstract

Detailed knowledge about the history of vegetation, fire and land use is scarce in Northern Greece. We analysed lake sediments from Limni Zazari (Northern Greece) to reconstruct the past local vegetation and fire history with a special focus on land use and its impacts on erosion and lake eutrophication. Our data suggest a rather dense steppic vegetation after ca 20,000 cal BP (18050 cal BC). Forest expansion with *Pinus sylvestris* and admixed *Quercus pubescens* started around 14,500 cal BP (12550 cal BC). After the onset of the Holocene, mixed deciduous sub-mediterranean oak forests expanded, accompanied by rapidly decreasing soil erosion rates and increasing aquatic biological productivity. Pollen of cereals and *Plantago lanceolata* suggests continuous farming activities in the region after 8,200 cal BP (6250 cal BC), in agreement with archaeological evidence. Fairly closed mixed pine-oak forests dominated the landscape until ca 3,500 cal BP (1550 cal BC) that were only temporarily reduced during the Neolithic around 7,100 and 6,500 cal BP (5150 and 4550 cal BC). Land cover changes and aquatic biogeochemistry were closely linked during this period. Forest phases corresponded to lake eutrophication and hypolimnetic anoxia (meromixis), whereas during periods of deforestation (e.g. around 8,200 cal BP/6250 cal BC) soil erosion rates and lake mixing increased, while aquatic productivity decreased. After 3,500 cal BP (1550 cal BC) humans disrupted forests and open land vegetation expanded (e.g. *Artemisia, Rumex*-type, Cichorioideae, Chenopodiaceae). With the onset of the Iron Age (ca. 3,050 cal BP/1100 cal BC) grassland communities expanded massively and pine-oak forests gradually declined. Anthropogenic pressure on forests increased even more during the past 500 years. Finally, forest recovery during the recent decades led to decreased erosion and increased lake productivity. We conclude that over the millennia, intense pastoral and arable activities shaped both aquatic and terrestrial environments, ultimately creating a humanized vegetation mosaic in which the original natural mixed deciduous oak forests only form relict stands. Future climate warming and decreasing anthropogenic pressure may release a rapid spread of mixed deciduous oak forests around Limni Zazari.

Keywords Aquatic productivity · Fire history · Land use · Neolithisation · Palaeoecology · Vegetation history

---

Communicated by F. Bittmann.

✉ Christoph Schwörer
christoph.schwoerer@ips.unibe.ch

[1] Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland

[2] Oeschger Centre for Climate Change Research, University of Bern, Hochschulstrasse 4, 3012 Bern, Switzerland

[3] Institute of Geological Sciences, University of Bern, Baltzerstrasse 3, 3012 Bern, Switzerland

[4] Institute of Archaeological Sciences, University of Bern, Mittelstrasse 43, 3012 Bern, Switzerland

[5] Institute of Geography, University of Bern, Hallerstrasse 12, 3012 Bern, Switzerland

[6] Faculty of Forestry and Natural Environment, Aristotle University of Thessaloniki, 541 24 Thessaloniki, Greece

Introduction

The linkages between climate, vegetation and land use during the past 20,000 years in lowland Northern Macedonia, Greece, have been of scientific interest for decades (e.g. Wijmstra and Smit 1976; Willis 1992). However, in the study area, which includes the four lakes Chimaditis, Petron, Vegoritis and Zazari and is therefore denominated the Four Lake District or Amindeon Basin, vegetation records covering the entire time after the ice age (i.e. the past 20,000 years) are temporally rather coarsely resolved. This can be partly attributed to a focus on multi-millennial vegetation dynamics over long time scales, for instance for the two large lakes lying north-west of our study site, Ohrid and Prespa (> 500,000 years, e.g. Sadori et al. 2016). Major overview contributions to reconstructing past vegetational changes in our study area (e.g. Limni Chimaditis, Limni Vegoritis) were made by Bottema (1974, 1982, 1995, 2003). Yet, the chronology for Limni Chimaditis (2 km from Limni Zazari) is based on ^{14}C bulk dating and thus only tentative (i.e. influenced by hard-water effects, Bottema 2003).

From the Near East where farming originated in the Fertile Crescent, Neolithisation rapidly spread via Anatolia to the Balkan region (Guilaine 2003; Schier 2009), possibly in two pathways northward to Central Europe (Ammerman and Cavalli-Sforza 1971; Hofmanová et al. 2016). Nonetheless, there are indications for a coeval emergence of Neolithisation patterns, suggesting that the dynamics of European Neolithisation are not yet fully understood (e.g. Reingruber 2008; Kotsakis 2014). For South-Western Europe for example, another pathway from Crete via the Ionian Sea towards Northern Italy and Southern France has recently been described by Guilaine (2018). Neolithisation dynamics in the Southern Balkans provide the basis for expansion of agriculture into Central and Northern Europe, because they preceded similar developments there by ca 1,000–2,000 years. The introduction of farming in South Eastern Europe started around 8,500 cal BP (ca. 6550 cal BC, e.g. Hofmanová et al. 2016), triggering socio-economic shifts that led to increased land use and a resulting change in ecosystems and vegetation. The first early farming communities in the Four Lakes District of Macedonia also appeared in the mid-7th millennium BC (Chrysostomou et al. 2015), therefore our study area in Northern Greece is regarded as a passage way between the Fertile Crescent and Central and Northern Europe (Tringham 2000).

Knowledge about Neolithisation and its possible climatic triggers in the Four Lakes District in Macedonia and elsewhere in Europe is still fragmented. In particular it is unknown if Neolithisation involved gradual local adaptation processes over centuries (e.g. of crops, husbandry, resources for material culture) or if people immigrated with a complete and rather rigid tool box that was instantaneously successful (Neolithic package, e.g. Budja 2004; Krauß et al. 2018; Mathieson et al. 2018). This latter model might have been successful in Mediterranean areas, where environmental conditions correspond to the region where farming developed, yet it seems very unlikely for cool-temperate and moist Europe north of the Alps. To further understand the dynamics and processes of Neolithisation in the Southern Balkan region, an interdisciplinary approach involving archaeology, dendrochronology and palaeoecology is necessary.

The principle aim of this study is to explore the linkages between climate, land use, vegetation and the fire regime at Limni Zazari. We use state-of-the-art multi-proxy palaeoecological approaches covering the past 20,000 years from Limni Zazari in Macedonia, Northern Greece to (1) create a robust chronology unaffected by hard-water effects, (2) disentangle the main drivers of vegetation dynamics (climate vs. human impact), (3) identify the first signs of anthropogenic land use linked to Neolithisation, (4) investigate anthropogenic ascendancy during periods of first advanced European civilizations from 3,500 cal BP onwards and (5) study human induced changes of the landscape, including soil erosion and biogeochemical processes in the lake.

Study site

Limni Zazari is a small, shallow lake located in the Eordea basin in Macedonia, Northern Greece, close to the border with Albania and the Republic of North Macedonia (40°37′31″N, 21°32′50″E, 606 m a.s.l., Fig. 1). The Eordea basin is part of the Pelagonian Plain, to the east of the Pindus range, dominated by calcareous bedrock and framed by mountains towards the north-west. Climate conditions are temperate continental with generally dry and cool conditions in summer and cold winters. Average annual precipitation amounts to 516.7 mm and the mean annual air temperature is 12.3 °C, while the mean monthly air temperatures for January and July are 2.6 and 22 °C, respectively (Seferlis et al. 2009). Vegetation around the lake mostly consists of grassland and shrubs, as well as scattered deciduous trees such as *Quercus pubescens, Carpinus orientalis* and *Fraxinus excelsior* (Fig. 1). In close proximity to the lake shore, reeds and herbs are prevalent, e.g. *Phragmites australis,* Poaceae, and *Artemisia*. The shores of Limni Zazari are confined by arable land to the East and West with a few *Populus* trees, whereas shrubby hills with single *Q. pubescens* and Rosaceae define the north-western shore. Towards the south of the lake the village of Limnochori reaches the water front. The south-facing hills approximately 2 km to the north-west of the lake consist of lowland forests, including mainly broadleaved taxa dominated by *Q. pubescens*

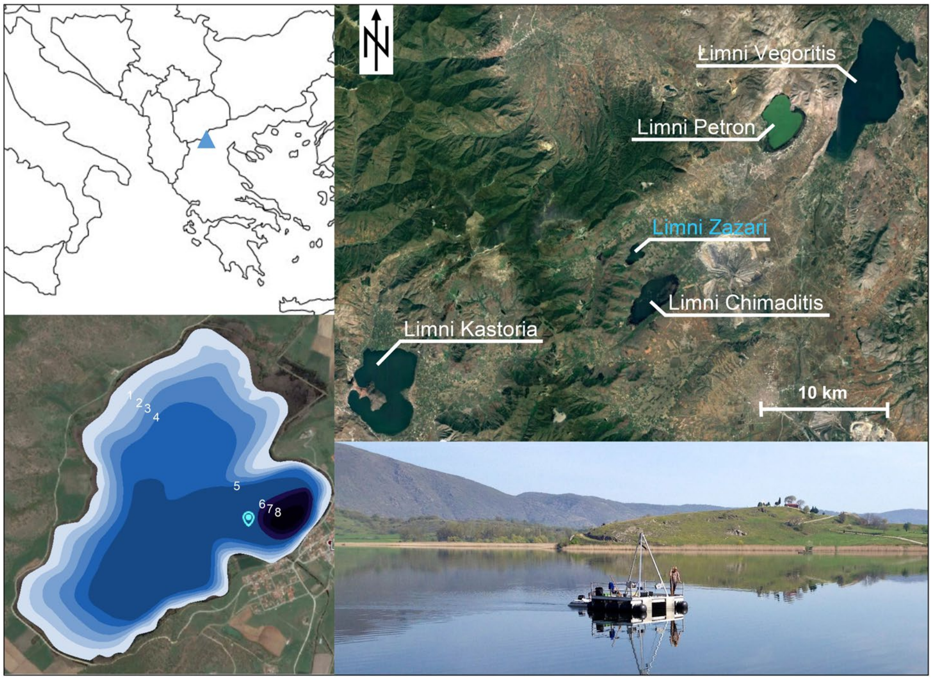


Fig. 1 Study site. Overview (top left), bathymetric map with white figures indicating water depth in m (bottom left), topographic view of study site and neighbouring lakes (top right, adjusted from Google Earth, 2017), photograph of Limni Zazari (bottom right; A. Lotter 2016)

and *Q. cerris*, together with *Fagus sylvatica,* admixed *Acer* as well as *Hedera helix*. At higher elevations, forest composition shifts to beech maple forests with *Corylus avellana* above 1,300 m a.s.l., while different pine species predominate above 1,500 m a.s.l.

The lake covers over 2 km^2 and has a mean and maximum water depth of 4.3 m and 6.3 m, respectively. An inlet at the north-eastern shore can be regulated through a floodgate, while in the south a ditch constructed in the 1960s transports excess water from Limni Zazari to Limni Chimaditis. Limni Zazari is considered a eutrophic lake, which can be related to anthropogenic influence, i.e. agricultural run-off (Skoulikidis et al. 1998). Several archaeological excavation sites are located close to Limni Zazari and Limni Chimaditis (Limnochori, Anarghiri), and another one is situated next to Limni Vegoritis (Agios Panteleimon), all located in the Four Lakes District or Amindeon Basin. Further important archaeological sites (Dispilió, Mavropigi) are situated within a 20 km radius of Limni Zazari, outside the Amindeon Basin. In this region the archaeological sites show comparable archaeological evidence, suggesting that in the past the settlements of both regions shared cultural characteristics (Karkanas et al. 2011; Chrysostomou et al. 2015).

Methods

Fieldwork

We retrieved two parallel sediment cores from Limni Zazari (40°37′31″N, 21°32′50″E) at a water depth of 5.3 m using a UWITEC piston corer (6 cm diameter, Fig. 1) in April 2016. The two parallel cores (ZAZ-1, ZAZ-2) were matched to a composite sequence of 6 m, by means of visual parallelization based on lithological marker horizons. Bathymetric data from Rosenmeier (2005) was used for the bottom left of Fig. 1. Modern pollen assemblages in surface sediments are related to the observable vegetation composition in the landscape (Davis 1963), based on an overview field survey of modern vegetation in the pollen catchment of Limni Zazari.

Chronology

The age-depth model relies on dated terrestrial plant macrofossils, which have been obtained through sediment sieving with a mesh size of 200 µm. All sediment subsamples were 2 cm thick, had a volume of 8–20 cm^3 and were frozen prior to sieving. Due to low macrofossil concentrations, the lower 141 cm were sampled contiguously. In total, 135 subsamples were sieved and analysed under a binocular microscope using a magnification between 6 and 50× and plant macrofossils were identified with standard plant morphology keys (e.g. Cappers et al. 2006). A total of 12 macrofossil samples were dated using accelerator mass spectrometry (AMS) at the LARA AMS Laboratory, Bern (Table 1). The obtained ^{14}C dates (BP) were then calibrated (cal BP) using CALIB 7.1 (Stuiver et al. 2017) with the IntCal13 calibration curve (Reimer et al. 2013). The final age-depth model (Fig. 2) was calculated with the program clam using a smooth spline (Blaauw 2010).

Table 1 Radiocarbon dates, calibrated and modelled ages

Sample code	Depth (cm)	^{14}C age (BP)	Age (cal BP, 2σ range)	Age in diagram (cal BP)	Dry weight (mg)	Material
BE-6440.1.1	110–108	725 ± 40	565–730	680	1.1	Bud, seed, leaf fragments
BE-6725.1.1	212–210	2,770 ± 20	2,792–2,925	2,860	3.3	Leaf fragments
BE-6439.1.1	279–277	4,495 ± 40	4,980–5,301	5,160	1.4	*Betula* seed, leaf fragments, 2 bud scales
BE-6438.1.1	311–309	5,405 ± 20	6,189–6,278	6,240	2.6	*Pinus* seed, 1/2 seed, leaf fragment
BE-6724.1.1	378–376	6,305 ± 20	7,173–7,268	7,230	3	Twig, epidermis, leaf fragments
BE-6979.1.1	402–400	6,920 ± 120	7,572–7,968	7,770	0.4	Charcoal
BE-6978.1.1	410–406	7,370 ± 150	7,874–8,447	8,190	0.4	Leaf fragments, bud scale
BE-6980.1.1	441–439	8,300 ± 130	9,007–9,529	9,280	0.4	Leaf fragment
BE-6977.1.1	471–467	7,730 ± 50	8,419–8,592	Rejected	1	Leaf fragments, charcoal
BE-6437.1.1	476–472	9,560 ± 50	10,711–11,106	10,930	1.4	*Asteraceae* seed, bud, leaf fragments
BE-6976.1.1	515–505	3,830 ± 90	3,977–4,511	Rejected	1.6	Bud scale, charcoal
BE-6346.1.1	565–560	15,830 ± 40	18,934–19,226	19,080	49.9	Twigs, bud

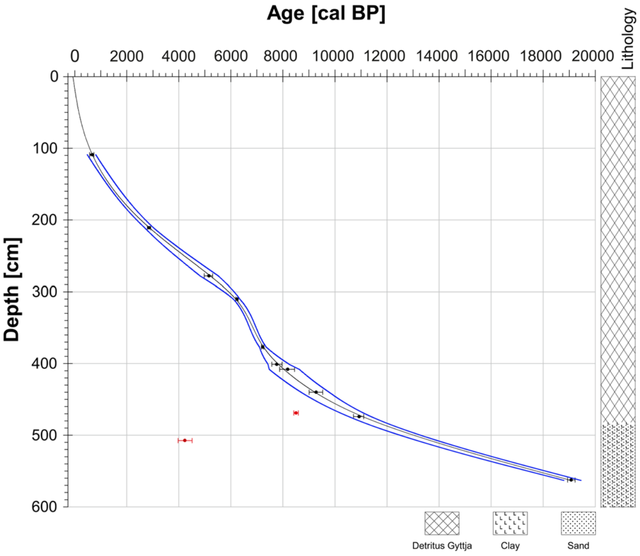


Fig. 2 Age-depth model for Limni Zazari. Black dots represent calibrated ages of plant macrofossils with 2 sigma error bars (IntCal13, Reimer et al. 2013). Connecting black line shows the modelled chronology (smooth spline, smoothing factor 0.3; Clam 2.2, Blaauw 2010). Blue envelope represents the 95% confidence interval (GAM, Heegaard et al. 2005)

A 95% probability distribution envelope was added using the GAM model by Heegaard et al. (2005).

Pollen and charcoal analysis

61 subsamples of 1 cm^3 were taken at 10 cm intervals from the sediment cores and prepared for pollen and charcoal analysis. Due to variable sedimentation rates, subsampling resolution was increased to 5 cm at the base of the core between 490 and 550 cm and decreased at the top 100 cm. Sediment subsamples were treated chemically (KOH, HCl, HF and acetolysis) and physically (0.5 mm sieving and decanting) and stored in glycerine following standard procedures (Moore et al. 1991). Prior to treatment, *Lycopodium* tablets were added to estimate pollen and microscopic charcoal concentrations (particles cm^{-3}) and influx (particles cm^{-2} year^{-1}; Stockmarr 1971). Pollen was identified and counted under a light microscope with a magnification of 400×, using the reference collection of the Institute of Plant Sciences of the University of Bern and palynological keys (e.g. Moore et al. 1991; Reille 1992; Beug 2004). Oak pollen was differentiated between the two pollen types *Quercus frainetto*-type (corresponding to *Q. pubescens*-type elsewhere in southern Europe) and *Q. cerris*-type, while the *Q. ilex*-type was not found. *Q. robur* is presumably not native to the study region (Eaton et al. 2016), albeit its occurrence cannot be excluded fully and has been recorded at Lake Ohrid for the Eemian interglacial (Sinopoli et al. 2018). However, we assume that most pollen of *Q. frainetto*-type derives from *Q. frainetto*, *Q. pubescens* and somewhat less likely, from *Q. petraea*. The *Q. cerris*-type includes pollen of *Q. cerris, Q. suber, Q. macrolepis* and *Q. trojana*. Most of the species within the *Q. cerris*-type are deciduous or semi-deciduous, except for evergreen *Q. suber*, which we assume is not native locally. *Abies* poses similar problems, since *Abies alba* grows with *A. borisii-regis* in the region, while *A. cephalonica* reaches here its northernmost extent (Lang 1994b; Caudullo and Tinner 2016). Thus, it is impossible to assign the pollen exclusively to one of these *Abies* species, although it most likely originated from *A. alba* (Lang 1994b). Generally, a minimum pollen count of 500 terrestrial pollen grains per subsample was achieved for the

largest part of the core (160–500 cm), while a pollen sum of 200 could be achieved in subsamples with very low pollen concentrations. Microscopic charcoal particles (> 10 µm) were counted following the procedure outlined in Finsinger and Tinner (2005) and Tinner and Hu (2003). We identified local pollen assemblage zones (LPAZ) using optimal sum of squares partitioning (Birks and Gordon 1985) with the program ZONE 1.2. We used the program BSTICK (Bennett 1996) to define statistically relevant zones.

Statistical analysis

To identify gradients in the species and sample distribution, we performed ordination analysis on pollen percentages with the program Canoco 4.5 (ter Braak and Smilauer 2002). First, a detrended correspondence analysis (DCA) was performed, to select the optimal response model. A gradient length of the first DCA axis of 2.727 indicates that both linear and unimodal methods can be applied (Legendre and Birks 2012). We decided on a principal component analysis (PCA) for the following ordination analysis (Birks and Gordon 1985; ter Braak and Prentice 1988).

Geobiochemical analysis

Geochemical compositions were assessed by means of XRF-scanning at the Institute of Geological Sciences of the University of Bern using an ITRAX XRF scanner (Cox Ltd., Sweden) equipped with a Cr X-ray tube. Analysed elements include bromine (Br), titanium (Ti) and zirconium (Zr) at a resolution of 0.5 cm and integration time of 50 s at 30 kV and 50 mA. Element intensities/relative concentration changes are reported as counts. According to Ziegler et al. (2008), Br is often enriched in organic matter and can be used as an approximation for sedimentary organic carbon. We use Ti and Zr as markers of terrigenous sediment delivery from the watershed (e.g. Haug et al. 2001). Ti and Zr values are reflecting sediment grain size, with high values pointing towards a higher grain size fraction due to sediment mobilization, e.g. by wave action at receding shorelines. Hence, they may indicate low lake-level stands (Haberzettl et al. 2007).

Hyperspectral Imaging (HSI) scans were performed on the fresh sediment half-cores using a Specim PFD-xx-V10E hyperspectral single core scanning system (Butz et al. 2015; 68 µm/pixel, spectral resolution of 2.8 nm; camera slit width 30 µm; spectral sampling 1.57 nm). Data post-processing followed Butz et al. (2015) using ENVI/IDL 5.4/8.6. Sedimentary photopigments (chlorophyll-a and derivatives, bacteriopheophytin-a) and clay minerals (illite, chlorite, biotite) were diagnosed with well-established spectral indices (Rein and Sirocko 2002; Trachsel et al. 2010) and modified with the continuum removal according to Butz et al. (2015, 2017). We used three spectral indices: (1) The relative absorption band depth with the minimum reflectance at 673 nm (RABD673; Eq. 1) indicative of 'green pigments' (chlorophyll-a and diagenetic products; Rein and Sirocko 2002; Butz et al. 2017) and aquatic productivity, (2) the RABD845 (Eq. 2) which is indicative of bacteriopheophytin-a and meromixis (Bphe-a; Butz et al. 2015, 2017) and (3) the spectral index R570/R630 (slope between reflectance at 570 nm and 630 nm; Rein and Sirocko 2002; Trachsel et al. 2010; Butz et al. 2015) for clay minerals (illite, chlorite, biotite; reflectance minimum at R690 nm here referred to as 'lithogenic influx').

$$\mathrm{RABD673\,nm} = \left(\frac{36 * R587.09\,\mathrm{nm} + 54 * R730.66\,\mathrm{nm}}{90} \right) \Big/ R671.85\,\mathrm{nm} \tag{1}$$

$$\mathrm{RABD845\ nm} = \left(\frac{34 * R789.83\,\mathrm{nm} + 34 * R900.34\,\mathrm{nm}}{68} \right) \Big/ R845.91\ \mathrm{nm} \tag{2}$$

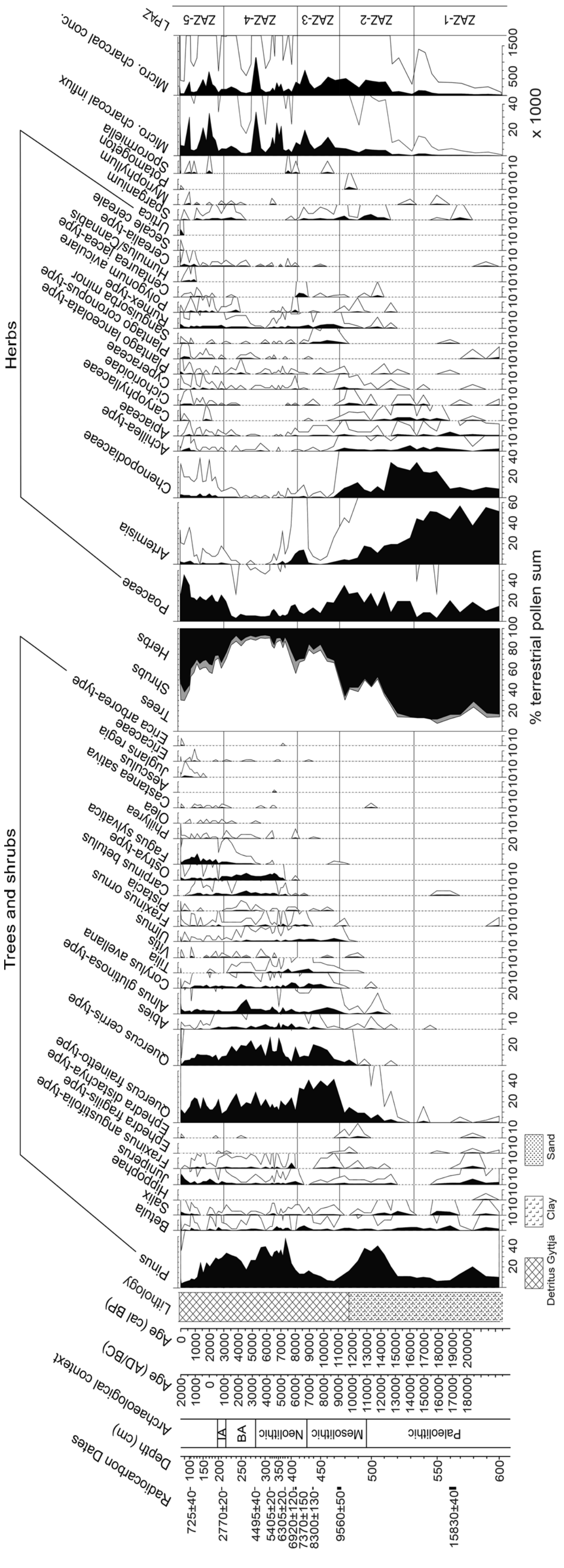
Results and interpretation

Chronology, lithology, XRF and HSI

We constructed the age-depth model (Fig. 2) on the basis of 10 terrestrial macrofossil radiocarbon dates (Table 1). Two further dates did not fit into the modelled GAM envelope of the 95% confidence interval and were therefore rejected. Sedimentation rates are mostly constant (0.01–0.05 cm year^{-1}), apart from higher sedimentation rates between 8,000 and 6,000 cal BP (6050–4050 cal BC; Fig. 2) and at the top (500 cal BP–present). The oldest macrofossil in our record dates to 19,100 cal BP (17150 cal BC), at 560–565 cm core depth. Linear extrapolation of the age-depth model was performed down to 20,000 cal BP (18050 cal BC) only.

The bottom of the sediment core, from 603.5 to 484 cm (ca. 20,000–11,800 cal BP/18050–9850 cal BC), consists of sandy clay (Figs. 2, 3, 4, 5). There Ti, Zr and lithogenic clay amounts (R570/R630) are low, 'green pigments' at moderate levels and Bphe-a values are high (Fig. 5), all together suggesting a fairly stable landscape with low erosion rates and a deep lake with meromictic conditions and moderate primary productivity. Above 590 cm sediment depth, primary productivity (RABD673) decreases, Br values are low and meromixis disappears (low RABD845, Fig. 5). Peaks in Zr, Ti and 'lithogenic components' (R570/R630) suggest enhanced soil erosion. The lithostratigraphy from 484 cm upwards changes from sandy clay to silty gyttja (Figs. 3, 4), also comprises the predominant lithology in the remainder of the core upwards. Br and 'green pigments'

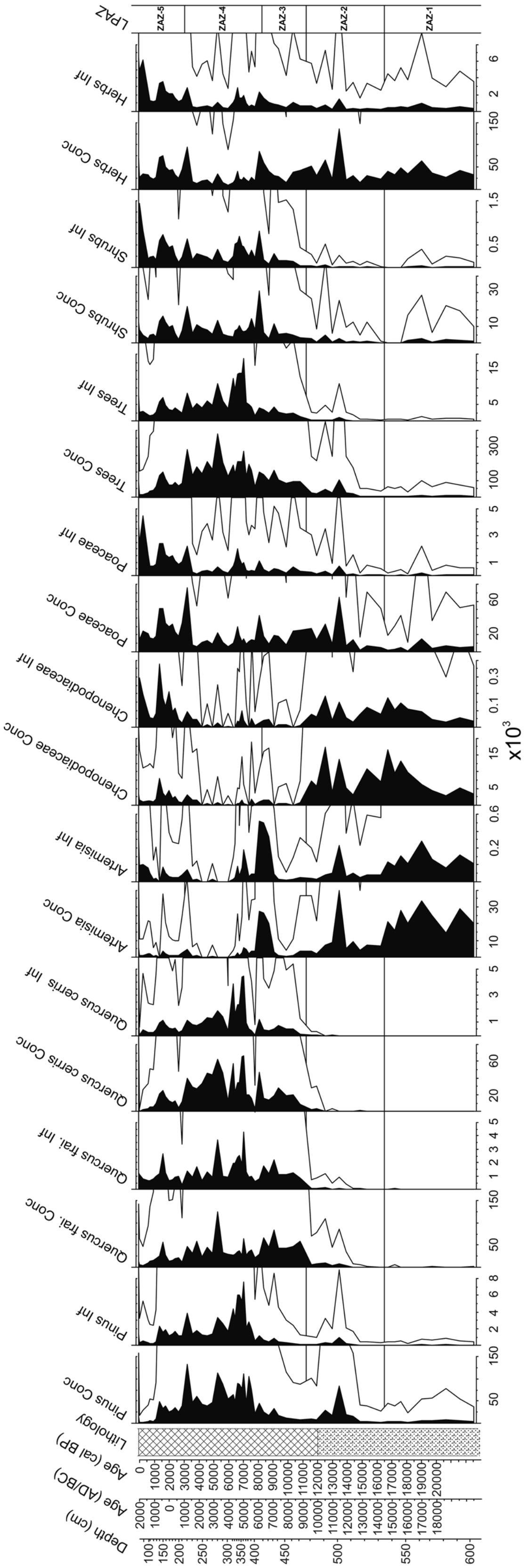
Fig. 3 Pollen diagram of Limni Zazari showing selected pollen taxa ▶ as percentages of the terrestrial pollen sum (i.e. aquatic pollen and all spores excluded). White curves show a ×10 exaggeration. Microscopic charcoal concentration and influx curves are shown as fragments cm^{-3} and fragments cm^{-2} year^{-1} (Analysis S. Gassner 2017). Archaeological context column showing Iron Age (IA) and Bronze Age (BA) for nearby archaeological sites



increase from ~ 11,500 cal BP (9550 cal BC) onwards, mirroring the change from clastic sediment to gyttja and indicating a highly productive lake system with generally low erosion rates (low Zr, Ti and R570/R630). Two 2 mm wide sand layers occur at a depth of 473 and 474 cm, which may have formed either due to low lake levels, landslips from the shoreline, or erosional input, e.g. through increased surface runoff in response to higher precipitation (Haberzettl et al. 2007). Although this middle part (480–248 cm) is generally characterized by high primary productivity (high Br and 'green pigments'), frequent meromixis (high RABD845) and low erosion rates (low Ti, Zr and R570/R630), several distinct maxima in Ti, Zr and lithogenics occur between 430 and 400 cm (9,000–7,700 cal BP/7050–5750 cal BC) and 370–310 cm (7,100–6,200 cal BP/5150–4250 cal BC). These maxima suggest erosion pulses, which coincided with a decrease in aquatic productivity and temporary breakdowns of meromixis and, possibly, lower lake levels (Haberzettl et al. 2007). In the upper part of the core, from 248 to 97.5 cm (4,150–550 cal BP/2200 cal BC–cal AD 1400), increasing trends in Zr, Ti and lithogenics suggest increasing catchment erosion while aquatic productivity decreased at the same time. The uppermost part of the sediment core (97.5–0 cm) consists of brown silty gyttja, regularly interrupted by dark brown gyttja. The lake was well oxygenated (low RABD845) and aquatic productivity was intermediate to high (RABD673 values; distinctive peak in the uppermost part); erosion rates remained high (high Zr, Ti and lithics, Fig. 5) with a sharp drop of R570/R630 at the very top.

Vegetation and fire history

We determined five statistically significant local pollen assemblage zones (LPAZ) in the Zazari record (Fig. 3, ZAZ-1-ZAZ-5). Our vegetation survey is consistent with the surface pollen assemblage, indicating an open landscape with meadows (non-arboreal pollen, NAP such as *Achillea*-type, *Centaurea jacea*-type and Poaceae), and isolated oak forest patches (*Q. frainetto*-type, *Q. cerris*-type). In general, arboreal pollen (AP, including trees and shrubs) percentage, concentration and influx values have similar trends, whereas the NAP percentage trend agrees with NAP influx but differs from NAP concentrations (Fig. 4), probably as a



◂ **Fig. 4** Concentration (particles cm^{-3}) and influx (particles cm^{-2} year^{-1}) values for selected pollen taxa. White curves show a ×10 exaggeration of actual values

consequence of fast sediment accumulation during phases of erosional input such as in the last 500 years.

ZAZ-1: 20,000–16,300 cal BP (18050–14350 cal BC)

The Zazari record shows high pollen percentages for herbs (80–90%), dominated by *Artemisia*, Chenopodiaceae and Poaceae, indicating steppic conditions during the transition from the Last Glacial Maximum (LGM, ca 23,000–19,000 cal BP/21050–17050 cal BC; Kaltenrieder et al. 2009) to the early Late Glacial period at the onset of the Oldest Dryas (Fig. 3). *Artemisia* has the highest pollen percentages (> 40%), pointing to its prevalence in the steppe. Chenopodiaceae became increasingly important, perhaps in response to declining moisture availability at ca 19,000–16,000 cal BP (17050–14050 cal BC; El-Moslimany 1987). Pollen grains of the pioneer shrub *Hippophaë* were found in this zone, along with first occurrences of pollen from pioneer arboreal taxa like *Betula, Pinus, Salix*, but also mid to late successional thermophilous trees such as *Fraxinus excelsior*-type, *F. ornus, Q. frainetto*-type and *Carpinus betulus*. AP does not exceed 10% but confirms the close proximity of refugia during the LGM (Bottema 1974; Willis 1992). The finding of twigs that date to an age of 19,100 cal BP (17150 cal BC) is evidence for woody species close to the lake at that time. The continuous presence of *Juniperus* pollen until approximately 17,500 cal BP (15550 cal BC) indicates the local occurrence of this light-demanding shrub or small tree (Ellenberg 1996). Charcoal concentration (particles cm^{-3}) and influx (particles cm^{-2} year^{-1}) are low throughout ZAZ-1, indicating low fire activity in the region during this time.

ZAZ-2: 16,300–11,100 cal BP (14350–9150 cal BC)

At around 16,000 years ago, *Artemisia* markedly declined to ca 20%, whereas Chenopodiaceae expanded in the steppes (> 30%, NAP > 80%), with Poaceae (ca 15%) as another important component. The first continuous appearance of Cyperaceae pollen at ca 16,000 cal BP (14050 cal BC) together with pollen of aquatic plants such as *Sparganium* may point to increasing moisture availability, lake level changes or increased nutrients in the lake (Rodwell 1998). At approximately 14,500 cal BP (12550 cal BC), at the onset of the Bølling-Allerød interstadial (Ammann et al. 2013), AP strongly increase (percentages, concentration and influx values), peaking

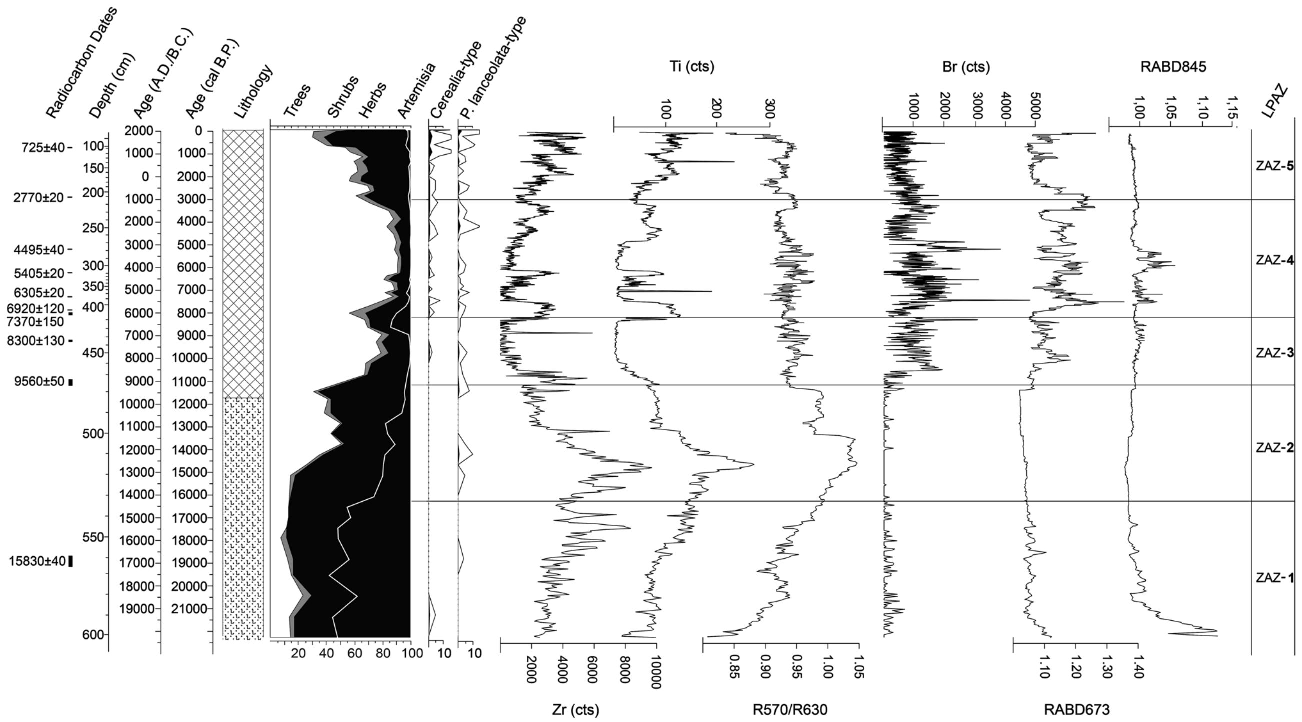


Fig. 5 Comparison of summary pollen diagram with selected taxa from Limni Zazari with XRF (Zirconium (Zr), Titanium (Ti), Bromine (Br); Analysis: H. Vogel 2017) as well as HSI data (R570R630, RABD673, RABD845; Analysis: S. Makri 2017)

at 14,000 cal BP (12050 cal BC; 50% of total pollen sum), indicating the spread of tree stands or open forests in the region. Indeed, the ratio of AP to NAP is comparable to the surface pollen sample (Fig. 3) reflecting a rather open landscape. The spread of tree stands ca 14,500 years ago strongly disfavoured Chenopodiaceae, while Poaceae increased. This points to a reorganization of open land vegetation with a marked reduction of dry steppe habitats around 14,500 cal BP (12550 cal BC). The increase of *Pinus sylvestris*-type around 14,500 cal BP (12550 cal BC) is simultaneous with the first continuous presence of *Q. frainetto*-type. Subsequently, *Q. frainetto*-type increases to 10–20% towards the end of ZAZ-2 at ca 12,000 cal BP (10050 cal BC). This suggests that mixed pine oak forests had established locally already during the Late Glacial. Temperate tree taxa such as e.g. *Alnus glutinosa* and *Abies* were also growing in the catchment of the lake between 14,000 and 11,500 cal BP (12050–9550 cal BC), as well as *Corylus avellana*. Tree pollen percentages decline to below 40% around 12,500 cal BP (10550 cal BC), whereas steppic herb and shrub pollen (e.g. Chenopodiaceae, *Ephedra fragilis*) increase, pointing to a shift in vegetation composition, possibly as a result of the Younger Dryas cooling, when climate conditions became drier (e.g. Ammann et al. 2000). A rise in charcoal particle influx occurred at approximately 14,300 cal BP (12350 cal BC), suggesting an increase of fire activity in the region together with the spread of *Pinus*.

ZAZ-3: 11,100–8,200 cal BP (9150–6250 cal BC)

High AP (up to 80%) indicates a forested landscape at the onset of the Holocene. Dominance of *Q. frainetto*-type (up to 40%) and *Q. cerris*-type (peaking at 9,000 cal BP/7050 cal BC with 20%) suggests the occurrence of mixed deciduous oak forests in the area. Poaceae pollen around 10–20% as well as the occurrence of *Sanguisorba minor*, *Rumex*-type and *Centaurea jacea*-type indicate the presence of local open grassland communities, coinciding with first occurrence of *Sporormiella* fungal spores at 10,250 cal BP (8300 cal BC). Around 9,500 cal BP (7550 cal BC) Cerealia-type pollen occurred. Right before the end of the zone, forests were disrupted around 8,600 cal BP (6650 cal BC). The AP decline (below 70%) is mainly driven by *Q. cerris*-type together with an increase of *Artemisia* (14%) and a prominent peak of *Centaurea jacea*-type. At the same time, *Fraxinus ornus* pollen passes the empirical limit and *Tilia* increases to 4%. Both taxa are insect-pollinated and thus underrepresented in pollen records. Of special interest is the expansion of *Tilia*, which is significantly more moisture-demanding than *Q. cerris* (Pignatti 2005) as well as sub-mediterranean *Q. frainetto* or *Q. pubescens* (> 40%). Distinct anthropogenic indicators such as Cerealia-type or *Plantago lanceolata*-type are missing or low, therefore this first Holocene forest disruption cannot be unambiguously attributed to anthropogenic activities such as e.g. forest clearance for farming. The pollen percentage curve of the water plant *Sparganium* remains stable and is interrupted only at the very end of the zone at ca 8,200 cal BP (6250 cal BC), possibly in response to Zazari lake level changes. The forest disruption at around 8,600 cal BP (6650 cal BC) coincided with a strong peak in charcoal concentration and influx (735,000 particles per cm^3; 19,300 particles per cm^2/yr), suggesting a marked increase in regional fire activity.

ZAZ-4: 8,200–3,000 cal BP (6250–1050 cal BC)

After the decline of tree pollen to below 70% and an increase of shrub pollen (*Corylus avellana* and *Juniperus*) to above 8% around 8,100 cal BP (6150 cal BC), tree pollen percentages recovered. *Pinus* (peaking at 7,500 cal BP/5550 cal BC with 40% of the total pollen sum) and *Q. frainetto*-type were driving this new forest expansion. The first continuous occurrence of Cerealia-type and *Plantago lanceolata*-type pollen, the recurrence of *Sporormiella* as well as an increase of Poaceae and *Polygonum aviculare* (a perennial ruderal plant) suggest the establishment of farming after 8,200 cal BP (6250 cal BC). The occurrence of the arboreal taxa *Carpinus betulus* and *Ostrya*-type (7,500 cal BP/5550 cal BC) may also indicate the use of woods (Gobet et al. 2000). During the time period 7,400 to 6,500 cal BP (5450–4550 cal BC), which can be attributed to the Late Neolithic in the Amindeon basin (Chrysostomou et al. 2015), forests reached their maximum density over the whole 20,000-year record, with tree pollen percentages close to 90%. The striking peak in *Vitis* pollen percentage around 6,000 cal BP (4050 cal BC) indicates the cultivation of grapes in this region as documented from archaeobotanical findings (6,400 to 6,000 cal BP/4450–4050 cal BC; Valamoti and Kotsakis 2007). At approximately 5,300 cal BP (3350 cal BC) the highest charcoal influx suggests a peak in regional fire activity, which preceded the spread of *Fagus sylvatica*, accompanied by *Pistacia,* a mediterranean shrub. Open land taxa (e.g. Poaceae, Chenopodiaceae, *Artemisia*) were not very abundant (under 10% of the total pollen sum) until ~ 4,200 cal BP (2250 cal BC), when they increased after a distinct rise of *Plantago lanceolata*-type, most likely in response to increased farming activities. Towards the end of this zone around 3,100 cal BP (1150 cal BC) AP declines (70%) and NAP (e.g. Chenopodiaceae, *Rumex*-type) increases markedly, most likely as a result of farming at the onset of the Greek Iron Age (1100 cal BC; Chrysostomou et al. 2015). This vegetational shift occurred contemporaneously with the spread of *Sparganium* in the lake or at the shore, possibly in response to changing lake levels. Several strong peaks in charcoal concentration and influx point to increased fire activity (mainly frequency; e.g. Tinner et al. 1998) in this zone. The two most prominent charcoal peaks at 7,000 cal BP and 5,300 cal BP (5050 cal BC and 3350 cal BC) are accompanied by low anthropogenic indicator values (e.g. Cerealia-type pollen) but correspond to short term openings of the mixed oak forests.

ZAZ-5: 3,000–66 cal BP (1050 cal BC—cal AD 2016)

The increase in NAP (> 60%, e.g. Poaceae) and the decrease of AP (< 40%, e.g. *Pinus, Q. cerris*-type, but not *Fagus*) during this zone suggests a further intensification of agricultural activities. Mesophilous and rather disturbance resistant *Fagus* may have increased in response to increasing moisture availability and/or increasing disturbance. The spread of open land taxa during this time was mostly driven by grasslands (Poaceae > 40%) and Cerealia-type as well as other minor taxa (e.g. *Sanguisorba minor* and *Humulus/Cannabis*-type). Arboreal taxa associated with land use such as *Juniperus*, *Ostrya*, *Olea* and *Castanea sativa* occurred, and at 1,700 cal BP (cal AD 250) also *Juglans* expanded. From ca 600 cal BP (cal AD 1350) onwards, NAP values abruptly increase to ca 70%, suggesting a further intensification of land use. Towards the end of the record (during the last century), *Juniperus* and *Urtica* expanded markedly. Charcoal concentrations and influx suggest high regional fire activity, peaking at around 2,500 cal BP (550 cal BC) and 600 cal BP (cal AD 1350). The fire activity increase coincided with strong AP declines and thus, forest disruptions (Fig. 3).

Ordination

PCA axis 1 explains 55.9%, while axis 2 explains 18.1% of the data variance. The species plot suggests that axis 1 is associated with vegetation openness, showing a clear gradient from open, steppic environments (e.g. *Artemisia*, *Achillea*-type, Chenopodiaceae) to closed sub-mediterranean mixed oak forests (Fig. 6). High axis 2 values are associated with human activities, with taxa indicative of anthropogenic environments such as Poaceae, *Juglans*, *Fagus* and Cerealia-type. Low axis 2 values are mainly linked to coniferous species (e.g. *Pinus*, *Abies*), that are often affected by disturbance (e.g. *A. alba*; Tinner et al. 2000) or less competitive than deciduous species (*Pinus*; Ellenberg 1996). The clusters formed by the sample scores are following the LPAZ zonation for Limni Zazari, with high axis1 values for the oldest zone ZAZ-1 including highest NAP (purple circles, Fig. 6) and low axis1 values for ZAZ-3 and ZAZ-4 with

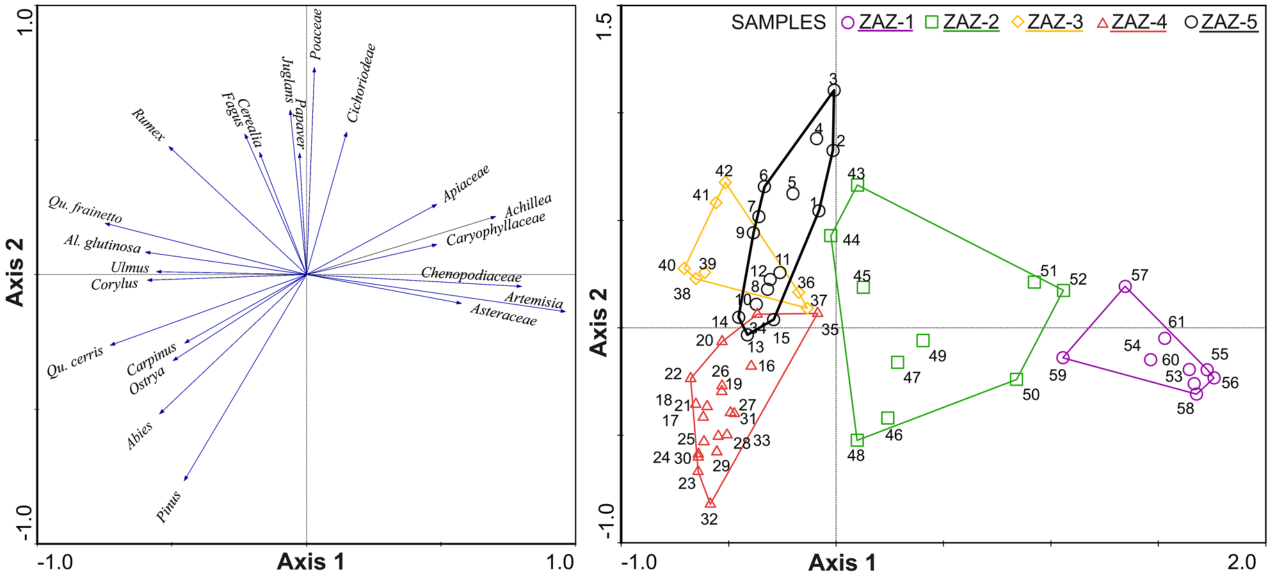


Fig. 6 Ordination analysis. PCA scatterplot of selected species (left) and samples (right). Axis 1 explains 55.9% of the variance in the vegetation data and likely represents a gradient from cold, steppic environments to thermophilous forests. Axis 2 explains 18.1% of variance and is probably related to forest cover and human impact. Samples are grouped (different colours) according to the local pollen assemblage zones (ZAZ 1–5)

lowest NAP (yellow diamonds and red triangles, Fig. 6). Conversely, ZAZ-5 shows highest and ZAZ-4 lowest axis 2 values, mirroring anthropogenic impact (Fig. 6).

Discussion

Climate driven vegetation changes

Climate is widely regarded as the main driver for vegetational change on millennial to centennial timescales (e.g. Tinner and Lotter 2001; Williams et al. 2002), specifically before the introduction of farming. In agreement, the pollen record of Limni Zazari suggests that during the Late Glacial, vegetation dynamics were mainly driven by climatic changes. Chronological uncertainties impede a thorough discussion of the time preceding the first ^{14}C date at 19,230–18,930 cal BP (17280–16980 cal BC). However, HSI data suggest that during this period when *Artemisia* dominated in the steppes, the lake was deep and meromictic and catchment erosion was low. The first marked vegetation change after the LGM was the expansion of drought-adapted Chenopodiaceae into the *Artemisia* dominated steppe at 19,000–18,000 cal BP (17050–16050 cal BC). The expansion of Chenopodiaceae coincided with a first substantial climate warming at the end of the LGM, as recorded in Southern Europe, the Mediterranean realm (Fig. 7; Samartin et al. 2016) and in other regions of the northern hemisphere (e.g. North Atlantic; Bond et al. 1992). Interestingly our Zr record suggests lower lake levels and/or enhanced catchment erosion, which we interpret as locally drier conditions, possibly in response to climate warming at the onset of the Late Glacial at 19,000–18,000 cal BP (17050–16050 cal BC; Samartin et al. 2016). We therefore assume that drought-tolerant Chenopodiaceae expanded on dry habitats, e.g. on south-facing slopes, while less drought-tolerant *Artemisia* continued to dominate on slightly moister locations (e.g. lake shores, north-facing slopes, the plain east of the lake). Possibly, differences in seasonal moisture availability also played a role (El-Moslimany 1987), given that summer insolation rapidly increased at 20,000–16,000 cal BP (18050–14050 cal BC; Fig. 7). Twigs dated at 19,230–18,930 cal BP (17280–16980 cal BC) unambiguously prove the occurrence of woody plants in the proximity of Zazari (Table 1), even if they were very rare (NAP ca 80%). In agreement, Lawson et al. (2005) reconstructed cold and dry steppic conditions for Nisi Fen (475 m a.s.l.), located 20 km north of Limni Zazari. Similarily, dry and cold climatic conditions for this period were reconstructed by multi-proxy investigations (δ^{18}O, biogeochemistry, palynology) from lakes Prespa and Ohrid, two large and well-examined lakes in the proximity of our study area (ca. 40 km; Vogel et al. 2010; Aufgebauer et al. 2012). Overall, quantitative climate reconstructions (e.g. Peyron et al. 1998; Samartin et al. 2012, 2016) suggest cool and dry conditions, with an annual average air temperature anomaly compared to today of around – 10 ± 5 °C and a precipitation anomaly of around -600 ± 200 mm compared to today for Italy and Greece.

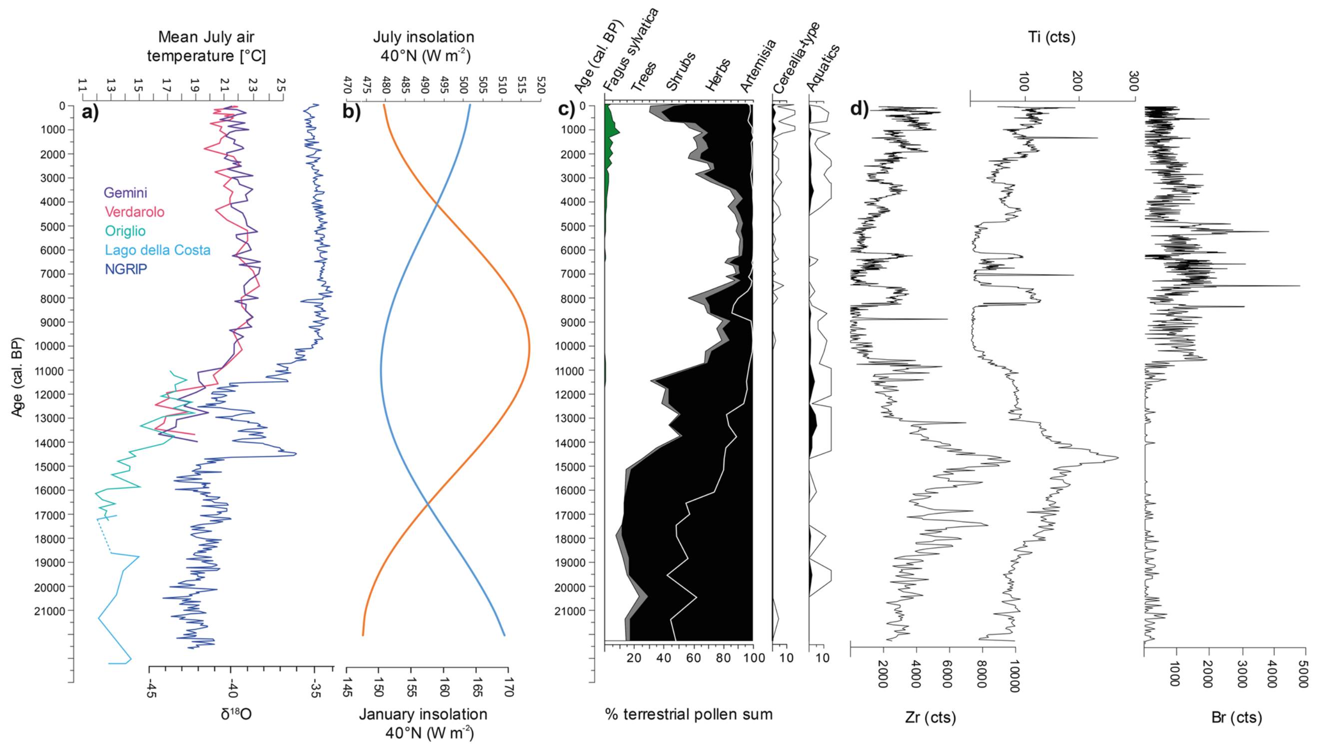


Fig. 7 Comparison of summary pollen diagram with selected taxa from Limni Zazari with XRF data and climatic reconstructions. **a** reconstructed July air temperatures at sea level based on chironomid data from the Mediterranean region (lilac and pink curves: Lago Gemini and Lago Verdarolo; Samartin et al. 2017; turquoise curve: Lago di Origlio; Samartin et al. 2012; light blue curve: Lago della Costa; Samartin et al. 2016) as well as NGRIP (dark blue curve; NGRIP members 2004), **b** insolation curve for July (red curve) and January (blue curve) in W m^{-2} for 40°N (Laskar et al. 2004), **c** pollen data, **d** XRF counts for Zirconium (Zr), Titanium (Ti) and Bromine (Br) (Analysis: H. Vogel 2017)

The expansion of arboreal pioneer species such as *Salix* was interrupted around lake Zazari between 17,500 and 16,000 cal BP (15550–14050 cal BC), when climate became colder (Heinrich Event 1) in Southern Europe and the Mediterranean realm (Combourieu Nebout et al. 2009; Samartin et al. 2012), the Arabian Sea (Pattan et al. 2017) and the North Atlantic (Bond et al. 1992). At Zazari, increases in Zr, Ti and lithogenics (R570/R630) fall into this period (17,000 to 16,000 cal BP; 15050–14050 cal BC), suggesting that climate cooling affected soil stability (Fig. 7). At the end of the Heinrich Event 1, summer temperatures became ca 2 °C warmer in Northern Italy close to the Adriatic Sea (Samartin et al. 2012). This warming released an expansion of forests in Northern Italy and Southern Switzerland (e.g. Lago Piccolo di Avigliana) up to ca 800 m a.s.l. (Vescovi et al. 2007). No similar woodland expansion occurred at our site (AP < 30%), however, vegetation changed significantly also in Northern Greece, with a strong expansion of Poaceae-dominated grasslands at the expense of *Artemisia* (statistically significant zone boundary).

Subsequently, *Pinus* expanded massively around 14,500 cal BP (12550 cal BC) and oak stands established in the Four Lakes District, likely creating parklands. Gradual (summer) warming in Southern and Central Europe ca 14,500–12,600 cal BP (12550–10650 cal BC; e.g. Vescovi et al. 2007; Heiri et al. 2015) was most probably responsible for the forest expansion. Zr and Ti values drop during that time, indicating enhanced soil stability. At Limni Zazari boreal tree species such as pine and birch expanded together with temperate trees (e.g. *Q. frainetto*-type, *Abies*, *Fraxinus*, *Alnus glutinosa*-type). A similar vegetational shift is documented in other palynological records from Northern Greece (e.g. Bottema 1974; Lawson et al. 2005), Northern Italy and Southern Switzerland (e.g. Vescovi et al. 2007). Our results contrast with the interpretation of Bottema (2003) that open steppic conditions prevailed until ca 10,500 cal BP (8550 cal BC) in the Four Lakes District. However, Bottema's records do not cover the Bølling–Allerød interstadial and are based on bulk dating of sediments (likely affected by hard water and old carbon errors; Grimm et al. 2009). Our record relies on a robust chronology with AMS radiocarbon dating of terrestrial macrofossils and is consistent with other well-dated palynological studies from the Mediterranean region (e.g. Hofstetter et al. 2006; Vescovi et al. 2007). The increase in fire activity during the Bølling-Allerød interstadial was likely the result of increasing fuel availability and warmer summer air temperatures in response to higher summer insolation (Fig. 7; Kutzbach and Webb 1993). Gradual (summer) warming came to an end during the Younger Dryas cooling (~ 12,600–11,700 cal BP/~ 10650–9750 cal BC), when forest cover transiently declined at Limni Zazari and elsewhere in Southern and Central Europe (e.g. Ammann et al. 2000; Vescovi et al. 2007).

Climate warming of 2–4 °C at the beginning of the Holocene at 11,650 cal BP (9700 cal BC; Heiri et al. 2015; Samartin et al. 2017) caused the expansion of sub-mediterranean mixed oak forests that replaced the pine dominated forests of the Bølling-Allerød interstadial around Limni Zazari. Associated with the expansion of oaks was the expansion of other temperate trees such as *Abies*, *Tilia* and *Ulmus*. Warmer temperatures in combination with reduced moisture availability due to changes in the precipitation regime (Kotthoff et al. 2008) probably favoured the spread of drought-tolerant deciduous oak species during that time.

8,200 years ago, air temperatures declined in Europe and elsewhere in the northern hemisphere by ~ 2 °C (von Grafenstein et al. 1998; Tinner and Lotter 2001) and precipitation regimes were strongly altered (e.g. Seppä and Birks 2001). This transient climatic event most likely contributed to a temporary decline of forests and expansion of *Artemisia* dominated grasslands at Limni Zazari. The vegetational response to the climate reversal at ca 8,200 cal BP (6250 cal BC) is well documented in other pollen records from Southern Europe, e.g. in Sicily (Tinner et al. 2009) and Greece (e.g. Tenaghi Philippon; Pross et al. 2009). In the Mediterranean, forest declines were primarily a result of declining moisture availability (Kotthoff et al. 2008). Although forest openings culminated at around 8,200 cal BP (6250 cal BC) at our study site (statistically significant zone boundary), vegetation changes had already started at 8,600 cal BP (6650 cal BC; e.g. expansion of *Artemisia*). Geochemical proxies from Limni Zazari (Zr, Ti) suggest increased erosion and a breakdown of meromixis, possibly in response to low lake levels and greater wind fetch as well as weaker soil protection as a result of declining forest cover (temporary decrease in AP). At Tenaghi Philippon in north-eastern Greece, relatively dry conditions occurred 8,700–8,200 cal BP (6750–6250 cal BC), followed by more humid ones. Interestingly, in Sicily *Artemisia* and Asteraceae as well as *Eupatorium* also expanded at 8,600–8,500 cal BP (6650–6550 cal BC), ca 300–400 years before climate cooling around 8,200 years ago (Tinner et al. 2009).

Another striking feature of the Limni Zazari pollen record is the late expansion of *Fagus sylvatica* (Figs. 3 and 7). The tree species had already spread in the Mediterranean region between 10,000 and 7,000 years cal BP (8050–5050 cal BC; Tinner et al. 2016; de Beaulieu et al. 2017). First pollen grains of *F. sylvatica* occur in our record at approximately 11,500 cal BP (9550 cal BC) at the onset of the Holocene. However, *F. sylvatica* disappeared almost completely around 10,700 cal BP (8750 cal BC) to reappear at 6,000–5,000 cal BP (4050–3050 cal BC), before finally expanding around 2,800 cal BP (850 cal BC). Mesophilous *F. sylvatica* classifies as a late successional or climax species, with a wide ecological range preferring mild winters without late frosts and moist summers, while being indifferent to browsing (Ellenberg 1996; Packham et al. 2012). Early palynological studies suggested that postglacial climate change played a key role in the late expansion of beech (e.g. Firbas 1949). *Fagus* expansions in pollen records across Europe have also been related to climate change, in particular to an increase of moisture availability and a decrease of frost occurrence, in the modern literature (e.g. Tinner and Lotter 2006; Magri 2008). The expansions occurred pulse-wise across the continent and were connected to cold-humid climate spells, e.g. at 2,800 cal BP (850 cal BC) in northern Central Europe (Tinner and Lotter 2006). However, in some areas of Europe including Southern Europe, the expansion of *F. sylvatica* was associated with human impact and small-scale forest openings (e.g. Valsecchi et al. 2008). Similarly, at Limni Zazari the expansion of this tree species is connected to land use activities, as e.g. indicated by the continuous occurrence of cereal pollen grains. Abundance peaked at 2,800 cal BP (850 cal BC), when climate became particularly cold and/or moist in Europe and elsewhere in the northern hemisphere (van Geel et al. 1998; Tinner et al. 2015). We conclude that the *F. sylvatica* dynamics at our site probably resulted from a combination of factors, with moisture availability and human impact being the most important ones.

The role of humans

Greece and the Balkans were crucial for the Neolithisation of Europe, given that technological innovations originating from the Levant, Upper Mesopotamia and Anatolia including plant crops such as cereals or linen were transmitted to the rest of the continent by first adoptions in this region (Lang 1994a). Our pollen record suggests that in the Zazari area relevant farming activities started ca 8,200 years ago (continuous presence of Cerealia-type pollen, coinciding with *Sporormiella* spores). This finding is in good agreement with first Early Neolithic archaeological evidence at 11 excavation sites in the Four Lakes District (dated to 6500–5800 cal BC; Chrysostomou et al. 2015), as well as from Mavropigi at ~ 20 km distance (Karamitrou-Mentessidi et al. 2013, 2015) at about 6550 cal BC. A marked increase in fire activity (charcoal influx 19,300 particles cm^{-2} $year^{-1}$) at approximately 8,600 cal BP (6650 cal BC) might be related to first burning of forests for agricultural purposes, although this interpretation remains speculative because there is no clear evidence for human impact (e.g. pollen of crops and weeds) and given the linkage of vegetational change with climate impacts (see discussion above) this issue remains ambiguous. It is likely that human and climate impacts acted together on vegetation and fire regime, exacerbating the opening signal (e.g. forest clearings with fire during dry climate phases). Early Neolithic pottery findings in the Amindeon basin suggest a gradual Neolithisation process (Chrysostomou et al. 2015), a result which is in agreement with our data. Similarly, ancient DNA samples of early farmers from Europe and Asia suggest only moderate migration from Asia Minor (Hofmanová et al. 2016).

Somewhat paradoxically, forests recovered after 8,200 cal BP (6250 cal BC), when farming established in the region. A similar pattern has been found in coastal Sicily (Tinner et al. 2009) and has been associated there with increasing mid and late Holocene moisture availability (Curry et al. 2016) that increased forest resilience to human impact, an explanation which may also apply to Zazari. However, on the basis of the pollen record (e.g. Cerealia-type) we assume continuous settlement activities close to Limni Zazari after 8,200 cal BP (6250 cal BC), which is in agreement with archaeological evidence in Western Macedonia (Kokkinidou and Trantalidou 1991). Our non-continuous findings of *Sporormiella* might lead to the conclusion that rearing of herbivores close to the lake might only have played a minor role, however, archaeological evidence (i.e. animal bones) suggests the opposite (Limnochori excavation; Giagkoulis personal communication 2018). Increased anthropogenic burning after 7,000 cal BP (5050 cal BC) was likely applied to open the landscape and produce fertile soils for agriculture, a slash-and-burn economy type which was characteristic for other areas in Europe (e.g. Clark et al. 1989; Rey et al. 2017) until the Iron Age, when it peaked at ca 2,600 cal BP (650 cal BC; e.g. Tinner et al. 2009), before being replaced by more advanced land use approaches (e.g. large-scale timber and fruit tree production) during and after the Roman epoch (Conedera et al. 2004).

Linkages and interactions between climate and societal systems

Prehistorical societal dynamics may have been controlled by climate, as suggested for the arid period around 8,200 years ago, which possibly triggered socio-economic movement from Anatolia to Macedonia (e.g. Weninger et al. 2006). This hypothesis was put forward to explain cultural innovations such as the introduction of agriculture in Northern Greece, which likely came from Anatolia (e.g. Özdoğan 2011). On the other hand, it has been argued that a change in climate, even one with a large impact such as the dry spell ca 8,200 years ago, may not necessarily trigger population movements (Lespez et al. 2013). The archaeological evidence suggests that local adaptation processes were important (Dikili Tash, Eastern Macedonia, Greece) and that it is highly unlikely that the onset of Neolithic settlements in Greece was triggered by the climate reversal around 8,200 cal BP (6250 cal BC), since by that time early settlements had already been established (Lespez et al. 2013; Gkouma and Karkanas 2018). Another hypothesis assumes that growing population density in the Levant or Eastern Mediterranean led to the spread of Neolithic farmers to central Anatolia and Cyprus (Belfer-Cohen and Goring-Morris 2011), suggesting that social conflict and an increasing need for land was the main driver of change. It is difficult to address these competing hypotheses (gradual local adaptation of innovations versus climate-driven migration versus economy-driven migration) by palaeoecological means alone. To disentangle environmental and social forcing on human population dynamics in the Neolithic, an integrative approach using high-resolution palaeoecological proxies as well as precisely dated archaeological findings is urgently needed.

Conclusions

Modern multiproxy palaeoecological studies from Northern Greece allow novel insights into the vegetation and fire history, landscape evolution, geomorphic activity (erosion), and aquatic productivity over the past 20,000 years. After vegetation reorganizations in response to climate warming at ca 19,000 and 16,000 cal BP (17050 and 14050 cal BC), further warming around 14,500 cal BP (12550 cal BC) promoted the expansion of boreo-nemoral pine-oak forests in which temperate trees such as *Abies* formed isolated patches. Similarly, climate change during the early Holocene allowed the establishment of sub-mediterranean deciduous oak forests (e.g. *Quercus frainetto*, *Q. pubescens*, *Q. trojana*, *Q. cerris*) with temperate taxa (e.g. *Abies*, *Corylus*, *Tilia*, *Ulmus*, *Fraxinus*, *Acer*) at the expense of pine forests or stands. Reconstructed first farming activities around 8,200 years ago at Limni Zazari are in good agreement with the archaeological evidence. We conclude that, until the onset of the Neolithic ca 8,600–8,200 years ago, vegetation was in dynamic equilibrium with climate. The rather gradual pollen-inferred increase of farming activities during the early Neolithic argues for local adaptation processes instead of a Neolithic "revolution" as e.g. released by mass movements of people. Our results imply that heat and drought-adapted *Q. pubescens*, *Q. frainetto* and *Q. trojana* may benefit from global warming given that they dominated the vegetation in the Early Holocene in Northern Greece, when summer temperatures were higher and the climate was drier than today.

Acknowledgements We gratefully thank the coring team Willi Tanner, André Lotter, Sandra Brügger and Sebastian Eggenberger for the field work. Tiziana Pedrotta is acknowledged for help during XRF analysis, Pim van der Knaap for help with botanical identifications, Sandra Brügger and Fabian Rey for help with figure design. We acknowledge the University of Bern for financing field work (ID-Grant 2015/003 to A. Hafner and W. Tinner). S. Makri was funded through the Hans Sigrist Foundation and SNF Grant (200021_172586).

References

Ammann B, Birks HJB, Brooks SJ et al (2000) Quantification of biotic responses to rapid climatic changes around the Younger Dryas—a synthesis. Palaeogeogr Palaeoclimatol Palaeoecol 159:313–347

Ammann B, van Leeuwen JF, van der Knaap WO, Lischke H, Heiri O, Tinner W (2013) Vegetation responses to rapid warming and to minor climatic fluctuations during the Late-Glacial Interstadial (GI-1) at Gerzensee (Switzerland). Palaeogeogr Palaeoclimatol Palaeoecol 391:40–59

Ammerman AJ, Cavalli-Sforza LL (1971) Measuring the rate of spread of early farming in Europe. Man 6:674–688

Aufgebauer A, Panagiotopoulos K, Wagner B et al (2012) Climate and environmental change in the Balkans over the last 17 ka recorded in sediments from Lake Prespa (Albania/F.Y.R. of Macedonia/Greece). Quat Int 274:122–135

Belfer-Cohen A, Goring-Morris AN (2011) Becoming farmers: the inside story. Curr Anthropol 52:209–220

Bennett KD (1996) Determination of the number of zones in a biostratigraphical sequence. New Phytol 132:155–170

Beug H (2004) Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Pfeil, München

Birks HJB, Gordon AD (1985) Numerical methods in quaternary pollen analysis. Academic Press, London

Blaauw M (2010) Methods and code for 'classical' age-modelling of radiocarbon sequences. Quat Geochronol 5:512–518

Bond G, Heinrich H, Broecker W et al (1992) Evidence for massive discharges of icebergs into the North Atlantic Ocean during the last glacial period. Nature 360:245–249

Bottema S (1974) Late Quaternary vegetation history of northwestern Greece. Dissertation, University of Groningen

Bottema S (1982) Palynological investigations in Greece with special reference to pollen as an indicator of human activity. Palaeohistoria 24:257–288

Bottema S (1995) The younger Dryas in the eastern Mediterranean. Quat Sci Rev 14:883–891

Bottema S (2003) The vegetation history of the Greek Mesolithic. In: Galanidou N, Perlès C (eds) The greek mesolithic: problems and perspectives. British School at Athens Studies 10. British School at Athens, London, pp 33–49

Budja M (2004) The transition to farming and the 'revolution' of symbols in the Balkans. From ornament to entoptic and external symbolic storage. Doc Praehist 31:59–81

Butz C, Grosjean M, Fischer D, Wunderle S, Tylmann W, Rein B (2015) Hyperspectral imaging spectroscopy: a promising method for the biogeochemical analysis of lake sediments. J Appl Remote Sens 9(096031):1–20

Butz C, Grosjean M, Goslar T, Tylmann W (2017) Hyperspectral imaging of sedimentary bacterial pigments: a 1700 year history of meromixis from varved Lake Jaczno, northeast Poland. J Paleolimnol 58:57–72

Cappers RTJ, Bekker RM, Jans JEA (2006) Digitale Zadenatlas van Nederland. Groningen Archaeological Studies 4. Barkhuis Publishing, Groningen

Caudullo G, Tinner W (2016) *Abies*—Circum-Mediterranean firs in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A (eds) European atlas of forest tree species. Publication Office of the European Union, Luxembourg, pp 50–51

Chrysostomou P, Jagoulis T, Maeder A (2015) The 'Culture of Four Lakes': prehistoric lakeside settlements (6th-2nd mill. BC) in the Amindeon Basin, Western Macedonia, Greece. Archäol Schweiz 38:24–32

Clark JS, Merkt J, Müller H (1989) Post-glacial fire, vegetation, and human history on the northern alpine forelands, south-western Germany. J Ecol 77:897–925

Combourieu Nebout N, Peyron O, Dormoy I, Desprat S, Beaudouin C, Kotthoff U, Marret F (2009) Rapid climatic variability in the west Mediterranean during the last 25,000 years from high resolution pollen data. Clim Past 5:503–521

Conedera M, Krebs P, Tinner W, Pradella M, Torriani D (2004) The cultivation of *Castanea sativa* (Mill.) in Europe, from its origin to its diffusion on a continental scale. Veget Hist Archaeobot 13:161–179

Curry B, Henne PD, Mesquita-Joanes F et al (2016) Holocene paleoclimate inferred from salinity histories of adjacent lakes in southwestern Sicily (Italy). Quat Sci Rev 150:67–83

Davis MB (1963) On the theory of pollen analysis. Am J Sci 261:897–912

De Beaulieu JL, Brugiapaglia E, Joannin S et al (2017) Lateglacial-Holocene abrupt vegetation changes at Lago Trifoglietti in Calabria, Southern Italy: the setting of ecosystems in a refugial zone. Quat Sci Rev 158:44–57

Eaton E, Caudullo G, Oliveira S, de Rigo D (2016) *Quercus robur* and *Quercus petraea* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A (eds) European atlas of forest tree species. Publication Office of the European Union, Luxembourg, pp 160–163

Ellenberg H (1996) Vegetation Mitteleuropas mit den Alpen: in ökologischer, dynamischer und historischer Sicht, 5th edn. Ulmer, Stuttgart

El-Moslimany AP (1987) The late Pleistocene climates of the Lake Zeribar region (Kurdistan, western Iran) deduced from the ecology and pollen production of nonarboreal vegetation. Plant Ecol 72:131–139

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

Firbas F (1949) Spät- und nacheiszeitliche Waldgeschichte Mitteleuropas nördlich der Alpen, vol 1. Allgemeine Waldgeschichte. Fischer, Jena

Gkouma M, Karkanas P (2018) The physical environment in Northern Greece at the advent of the Neolithic. Quat Int 496:14–23. https://doi.org/10.1016/j.quaint.2016.08.034

Gobet E, Tinner W, Hubschmid P, Jansen I, Wehrli M, Ammann B, Wick L (2000) Influence of human impact and bedrock differences on the vegetational history of the Insubrian Southern Alps. Veget Hist Archaeobot 9:175–187

Grimm EC, Maher LJ, Nelson DM (2009) The magnitude of error in conventional bulk-sediment radiocarbon dates from central North America. Quat Res 72:301–308

Guilaine J (2003) De la vague à la tombe, la conquête néolithique de la Méditerranée (8000-2000 avant J.-C.). Le Seuil, Paris

Guilaine J (2018) A personal view of the neolithisation of the Western Mediterranean. Quat Int 470:211–225. https://doi.org/10.1016/j.quaint.2017.06.019

Haberzettl T, Corbella H, Fey M et al (2007) Lateglacial and Holocene wet—dry cycles in southern Patagonia: chronology, sedimentology and geochemistry of a lacustrine record from Laguna Potrok Aike, Argentina. Holocene 17:297–310

Haug GH, Hughen KA, Sigman DM, Peterson LC, Röhl U (2001) Southward migration of the intertropical convergence zone through the Holocene. Science 293:1,304–1,308

Heegaard E, Birks HJB, Telford RJ (2005) Relationships between calibrated ages and depth in stratigraphical sequences: an estimation procedure by mixed-effect regression. Holocene 15:612–618

Heiri O, Ilyashuk B, Millet L, Samartin S, Lotter AF (2015) Stacking of discontinuous regional palaeoclimate records: chironomid-based summer temperatures from the Alpine region. Holocene 25:137–149

Hofmanová Z, Kreutzer S, Hellenthal G et al (2016) Early farmers from across Europe directly descended from Neolithic Aegeans. Proc Natl Acad Sci USA 113:6,886–6,891

Hofstetter S, Tinner W, Valsecchi V, Carraro G, Conedera M (2006) Lateglacial and Holocene vegetation history in the Insubrian Southern Alps—New indications from a small-scale site. Veget Hist Archaeobot 15:87–98

Kaltenrieder P, Belis CA, Hofstetter S, Ammann B, Ravazzi C, Tinner W (2009) Environmental and climatic conditions at a potential Glacial refugial site of tree species near the Southern Alpine glaciers. New insights from multiproxy sedimentary studies at Lago della Costa (Euganean Hills, Northeastern Italy). Quat Sci Rev 28:2,647–2,662

Karamitrou-Mentessidi G, Efstratiou N, Kozłowski JK et al (2013) New evidence on the beginning of farming in Greece: the Early Neolithic settlement of Mavropigi in western Macedonia (Greece). Antiquity 87(336), Project Gallery. http://antiquity.ac.uk/projgall/mentessidi336/

Karamitrou-Mentessidi G, Efstratiou N, Kaczanowska M, Kozłowski JK (2015) Early neolithic settlement of Mavropigi in western greek Macedonia. Eurasian Prehist 12:47–116

Karkanas P, Pavlopoulos K, Kouli K, Ntinou M, Tsartsidou G, Facorellis Y, Tsourou T (2011) Palaeoenvironments and site formation processes at the Neolithic lakeside settlement of Dispilio, Kastoria, Northern Greece. Geoarchaeology 26:83–117

Kokkinidou D, Trantalidou K (1991) Neolithic and Bronze Age settlement in western Macedonia. Annu Br Sch Athens 86:93–106

Kotsakis K (2014) Domesticating the periphery. Pharos 20:41–73

Kotthoff U, Müller UC, Pross J, Schmiedl G, Lawson IT, van de Schootbrugge B, Schulz H (2008) Lateglacial and Holocene vegetation dynamics in the Aegean region: an integrated view based on pollen data from marine and terrestrial archives. Holocene 18:1,019–1,032

Krauß R, Marinova E, De Brue H, Weninger B (2018) The rapid spread of early farming from the Aegean into the Balkans via the Sub-Mediterranean-Aegean Vegetation Zone. Quat Int 496:24–41

Kutzbach JE, Webb T III (1993) Conceptual basis for understanding Late-Quaternary climates. In: Wright HE Jr, Kutzbach JE, Webb T III, Ruddiman WF, Street-Perrott FA, Bartlein PJ (eds) Global climates since the last glacial maximum. University of Minnesota Press, Minneapolis, pp 5–11

Lang G (1994a) Quartäre Vegetationsgeschichte Europas: Methoden und Ergebnisse. Fischer, Jena

Lang KJ (1994b) *Abies alba* Mill.: differentiation of provenances and provenance groups by the monoterpene patterns in the cortex resin of twigs. Biochem Syst Ecol 22:53–63

Laskar J, Robutel P, Joutel F, Gastineau M, Correia ACM, Levrard B (2004) A long-term numerical solution for the insolation quantities of the Earth. Astron Astrophys 428:261–285

Lawson IT, Al-Omari S, Tzedakis PC, Bryant CL, Christanis K (2005) Lateglacial and Holocene vegetation history at Nisi Fen and the Boras mountains, northern Greece. Holocene 15:873–887

Legendre P, Birks HJB (2012) From classical to canonical ordination. In: Birks HJB, Lotter AF, Juggins S, Smol JP (eds) Tracking environmental change using lake sediments, vol 5. Data Handling and Numerical Techniques. Springer, Dordrecht, pp 201–248

Lespez L, Tsirtsoni Z, Darcque P et al (2013) The lowest levels at Dikili Tash, northern Greece: a missing link in the Early Neolithic of Europe. Antiquity 87(335):30–45

Magri D (2008) Patterns of post-glacial spread and the extent of glacial refugia of European beech (Fagus sylvatica). J Biogeogr 35:450–463

Mathieson I, Alpaslan-Roodenberg S, Posth C et al (2018) The genomic history of southeastern Europe. Nature 555:197–203

Moore P, Webb J, Collison M (1991) Pollen analysis. Blackwell Scientific Publications, Oxford

NGRIP (North Greenland Ice Core Project) Members (2004) High-resolution record of Northern Hemisphere climate extending into the last interglacial period. Nature 431:147–151

Özdoğan M (2011) Archaeological evidence on the westward expansion of farming communities from eastern Anatolia to the Aegean and the Balkans. Curr Anthropol 52(Suppl 4):S415–S430

Packham JR, Thomas PA, Atkinson MD, Degen T (2012) Biological flora of the British Isles: *Fagus sylvatica*. J Ecol 100:1,557–1,608

Pattan JN, Parthiban G, Garg A, Moraes NRC (2017) Intense reducing conditions during the last deglaciation and Heinrich events (H1, H2, H3) in sediments from the oxygen minimum zone off Goa, eastern Arabian Sea. Mar Pet Geol 84:243–256

Peyron O, Guiot J, Cheddadi R et al (1998) Climatic reconstruction in Europe for 18,000 yr B.P. from pollen data. Quat Res 49:183–196

Pignatti S (2005) Valori di bioindicazione delle piante vascolari della flora d'Italia. Dipartimento di Botanica ed Ecologia dell'Università, Camerino

Pross J, Kotthoff U, Müller UC et al (2009) Massive perturbation in terrestrial ecosystems of the Eastern Mediterranean region associated with the 8.2 kyr B.P. climatic event. Geology 37:887–890

Reille M (1992) Pollen et spores d'Europe et d'Afrique du Nord. Laboratoire de Botanique Historique et Palynologie, Marseille

Reimer PJ, Bard E, Bayliss A et al (2013) IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55:1,869–1,887

Rein B, Sirocko F (2002) In situ reflectance spectroscopy analysing techniques for high-resolution pigment logging in sediment cores. Int J Earth Sci 91:950–954

Reingruber A (2008) Die Argissa Magula: das frühe und das beginnende mittlere Neolithikum im Lichte transägäischer Beziehungen. Die deutschen Ausgrabungen auf der Argissa Magula in Thessalien 2. Habelt, Bonn

Rey F, Gobet E, van Leeuwen JFN et al (2017) Vegetational and agricultural dynamics at Burgäschisee (Swiss Plateau) recorded for 18,700 years by multi-proxy evidence from partly varved sediments. Veget Hist Archaeobot 26:571–586

Rodwell JS (1998) British plant communities. Aquatic Communities, Swamps and Tall-Herb Fens, vol 4. Cambridge University Press, Cambridge

Rosenmeier MF (2005) Bathymetric survey data of Lake Zazari. http://www.lakemaps.org. Accessed 14 May 2019

Sadori L, Koutsodendris A, Panagiotopoulos K et al (2016) Pollen-based paleoenvironmental and paleoclimatic change at Lake Ohrid (south-eastern Europe) during the past 500 ka. Biogeosciences 13:1,423–1,437

Samartin S, Heiri O, Lotter AF, Tinner W (2012) Climate warming and vegetation response after Heinrich event 1 (16 700-16 000 cal yr BP) in Europe south of the Alps. Clim Past 8:1,913–1,927

Samartin S, Heiri O, Kaltenrieder P, Kühl N, Tinner W (2016) Reconstruction of full glacial environments and summer temperatures from Lago della Costa, a refugial site in Northern Italy. Quat Sci Rev 143:107–119

Samartin S, Heiri O, Joos F, Renssen H, Franke J, Brönnimann S, Tinner W (2017) Warm Mediterranean mid-Holocene summers inferred from fossil midge assemblages. Nat Geosci 10:207–212

Schier W (2009) Extensiver Brandfeldbau und die Ausbreitung der neolithischen Wirtschaftsweise in Mitteleuropa und Südskandinavien am Ende des 5. Jahrtausends v. Chr. Prähist Z 84:15–43

Seferlis M, Clement B, Aidoud A (2009) Effect of climate change and human activities on lake marginal wetlands: land use and lake dynamics during the last 60 years in Cheimaditida-Zazari catchments, Macedonia, Greece. Report on effects of climate change and human activities on lake marginal wetlands (WP1, task 4.2). Integrated project to evaluate the impacts of global change on European Freshwater Ecosystems (EURO-LIMPACS)

Seppä H, Birks HJB (2001) July mean temperature and annual precipitation trends during the Holocene in the Fennoscandian tree-line area: pollen-based climate reconstructions. Holocene 11:527–539

Sinopoli G, Masi A, Regattieri E, Wagner B, Francke A, Peyron O, Sadori L (2018) Palynology of the last interglacial complex at Lake Ohrid: palaeoenvironmental and palaeoclimatic inferences. Quat Sci Rev 180:177–192

Skoulikidis NT, Bertahas I, Koussouris T (1998) The environmental state of freshwater resources in Greece (rivers and lakes). Environ Geol 36:1–17

Stockmarr J (1971) Tablets with spores used in absolute pollen analysis. Pollen Spores 13:615–621

Stuiver M, Reimer PJ, Reimer RW (2017) CALIB 7.1 [WWW program]. http://calib.org

Ter Braak CJF, Prentice IC (1988) A theory of gradient analysis. Adv Ecol Res 18:271–313

Ter Braak CJF, Smilauer P (2002) CANOCO. Software for canonical community ordination. Microcomputer Power, Ithaca

Tinner W, Hu FS (2003) Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. Holocene 13:499–505

Tinner W, Lotter AF (2001) Central European vegetation response to abrupt climate change at 8.2 ka. Geology 29:551–554

Tinner W, Lotter AF (2006) Holocene expansions of *Fagus silvatica* and *Abies alba* in Central Europe: where are we after eight decades of debate? Quat Sci Rev 25:526–549

Tinner W, Conedera M, Ammann B, Gaggeler HW, Gedye S, Jones R, Sagesser B (1998) Pollen and charcoal in lake sediments compared with historically documented forest fires in southern Switzerland since AD 1920. Holocene 8:31–42

Tinner W, Conedera M, Gobet E, Hubschmid P, Wehrli M, Ammann B (2000) A palaeoecological attempt to classify fire sensitivity of trees in the southern Alps. Holocene 10:565–574

Tinner W, van Leeuwen JF, Colombaroli D et al (2009) Holocene environmental and climatic changes at Gorgo Basso, a coastal lake in southern Sicily, Italy. Quat Sci Rev 28:1,498–1,510

Tinner W, Beer R, Bigler C et al (2015) Late-Holocene climate variability and ecosystem responses in Alaska inferred from high-resolution multiproxy sediment analyses at Grizzly Lake. Quat Sci Rev 126:41–56

Tinner W, Vescovi E, van Leeuwen JF et al (2016) Holocene vegetation and fire history of the mountains of Northern Sicily (Italy). Veget Hist Archaeobot 25:499–519

Trachsel M, Grosjean M, Schnyder D, Kamenik C, Rein B (2010) Scanning reflectance spectroscopy (380-730 nm): a novel method for quantitative high-resolution climate reconstructions from minerogenic lake sediments. J Paleolimnol 44:979–994

Tringham R (2000) Southeastern Europe in the transition to agriculture in Europe: bridge, buffer, or mosaic. In: Price TD (ed) Europe's first farmers. Cambridge University Press, Cambridge, pp 19–56

Valamoti SM, Kotsakis K (2007) Transitions to Agriculture in the Aegean: the archaeobotanical evidence. In: Colledge S, Connolly J (eds) The origins and spread of domestic plants in Southwest Asia and Europe. Left Coast Press, Walnut Creek, pp 75–91

Valsecchi V, Finsinger W, Tinner W, Ammann B (2008) Testing the influence of climate, human impact and fire on the Holocene population expansion of *Fagus sylvatica* in the southern Prealps (Italy). Holocene 18:603–614

Van Geel B, Raspopov OM, van der Plicht J, Renssen H (1998) Solar forcing of abrupt climate change around 850 calendar years BC. In: Peister BJ, Palmer T, Bailey ME (eds) Natural catastrophes during bronze age civilisations: archaeological, geological, astronomical and cultural perspectives. BAR International Series 728. Archaeopress, Oxford, pp 162–168

Vescovi E, Ravazzi C, Arpenti E et al (2007) Interactions between climate and vegetation during the Lateglacial period as recorded by lake and mire sediment archives in Northern Italy and Southern Switzerland. Quat Sci Rev 26:1,650–1,669

Vogel H, Wagner B, Zanchetta G, Sulpizio R, Rosén P (2010) A paleoclimate record with tephrochronological age control for the last glacial-interglacial cycle from Lake Ohrid, Albania and Macedonia. J Paleolimnol 44:295–310

Von Grafenstein U, Erlenkeuser H, Müller J, Jouzel J, Johnsen S (1998) The cold event 8200 years ago documented in oxygen isotope records of precipitation in Europe and Greenland. Clim Dyn 14:73–81

Weninger B, Alram-Stern E, Bauer E et al (2006) Climate forcing due to the 8200 cal yr BP event observed at Early Neolithic sites in the eastern Mediterranean. Quat Res 66:401–420

Wijmstra TA, Smit A (1976) Palynology of the middle part (30-78 metres) of the 120 m deep section in northern Greece (Macedonia). Plant Biol 25:297–312

Williams JW, Post DM, Cwynar LC, Lotter AF, Levesque AJ (2002) Rapid and widespread vegetation responses to past climate change in the North Atlantic region. Geology 30:971–974

Willis KJ (1992) The late quaternary vegetational history of northwest Greece. New Phytol 121:119–138

Ziegler M, Jilbert T, De Lange GJ, Lourens LJ, Reichart G (2008) Bromine counts from XRF scanning as an estimate of the marine organic carbon content of sediment cores. Geochem Geophys Geosyst. https://doi.org/10.1029/2007gc001932