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Research Article

Changes in climate drove vegetation and land use dynamics at the onset of farming in Europe

Lieveke van Vugt[a,b], Erika Gobet[a,b], César Morales-Molino[a,b,c], Kathrin Ganz[a,b], Tryfon Giagkoulis[d], Antonietta Knetge[a,e], André F. Lotter[a,b], Hendrik Vogel[b,f], Martin Grosjean[b,g], Amy Bogaard[h], Kostas Kotsakis[d], Albert Hafner[b,i] and Willy Tinner[a,b]

[a]Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland; [b]Oeschger Centre for Climate Change Research, University of Bern, Hochschulstrasse 4, 3012 Bern, Switzerland; [c]Grupo de Ecología y Restauración Forestal (FORECO), Departamento de Ciencias de la Vida, Facultad de Ciencias, Universidad de Alcalá, 28805, Alcalá de Henares, Spain; [d]Department of Archaeology, Aristotle University of Thessaloniki, 54124 Thessaloniki, Greece; [e]Botany Department, Trinity College Dublin, Dublin 2, Ireland; [f]Institute of Geological Sciences, University of Bern, Baltzerstrasse 1+3, 3012 Bern, Switzerland; [g]Institute of Geography, University of Bern, Hallerstrasse 12, 3012 Bern, Switzerland; [h]School of Archaeology, University of Oxford, 1 South Parks Road, Oxford OX1 3TG, UK and [i]Institute of Archaeological Sciences, University of Bern, Mittelstrasse 43, 3012 Bern, Switzerland

Abstract

Here we present the first high-resolution continuous palaeoecological study from Greece covering the Mesolithic–Neolithic transition at Limni Zazari, a small lake in western Macedonia. We study how interactions between vegetation and climate might have affected the introduction of agriculture to Europe ca. 8500 years ago. We found that mixed deciduous oak woodlands established around the lake once moisture availability began to increase at ~10,300 cal yr BP. Between 8600 and 8000 cal yr BP, climate change, causing drier conditions, led to the decline of the woodlands and the expansion of steppe and grassland vegetation. Concurrently, in agreement with the archaeological record, pollen indicative of arable and pastoral farming indicate the onset of Neolithic farming. After 8000 cal yr BP the forest composition changed, with a major expansion of pine forests and increases in disturbance-adapted trees like *Ostrya* and *Fagus*. This change might be linked to changes in moisture availability, but it is likely that land use also facilitated these shifts. We conclude that the introduction of Neolithic farming was advantaged by climate-induced vegetation changes. While the vegetation structure around Zazari was very sensitive to changes in moisture, early anthropogenic disturbances led to changes in the vegetation composition that are still important today.

Keywords: Southern Balkans, Neolithic, palaeoecology, climate change, 8.2 ka event, vegetation history, Mediterranean ecosystems, Greece

INTRODUCTION

Agriculture was first introduced to Europe in Greece over 8500 years ago and spread from there to the Balkans and central Europe (Reingruber, 2018; Betti et al., 2020). With the start of the Neolithic, new crops (e.g., wheat, barley, lentil, and flax), domesticated animals (e.g., sheep, goats, and cattle), and novel land use practices were introduced into the region (Zohary et al., 2012a; Halstead and Isaakidou, 2013). As a result, people started to permanently alter the landscape around them (Stephens et al., 2019). Previous studies suggest that Neolithic farmers had a limited impact on the natural vegetation of Northern Greece, and that significant anthropogenic disturbances can only be observed with the start of the Bronze Age (~5000 cal yr BP), as the natural forests started to change and decline (Willis, 1994; Panagiotopoulos et al., 2013; Masi et al., 2018; Gassner et al., 2020).

Rapid climate change (RCC) events are often proposed as an important environmental factor driving cultural changes and migrations in the eastern Mediterranean (Staubwasser and Weiss, 2006; Weninger et al., 2009; Berger et al., 2016; Rohling et al., 2019). Some authors consider the pronounced and abrupt climatic "8.2 ka event" to be an important driver for the fast spread of agriculture from Anatolia to Greek Macedonia (Weninger et al., 2006). The "8.2 ka event" lasted for about 160 years (8250–8090 cal yr BP; Rasmussen et al., 2014) and was a period characterised by colder conditions throughout the Northern Hemisphere (Alley et al., 1997; Alley and Ágústsdóttir, 2005). However, recent archaeological finds show that the Neolithic had already started several hundred years earlier around 8600–8500 cal yr BP (e.g., Mavropigi-Filotsairi, Paliambela Kolindros, and Revenia-Korinos; Karamitrou-Mentessidi et al., 2015; Tsartsidou and Kotsakis, 2020; Maniatis and Adaktylou, 2021) in western Greek Macedonia and even earlier on Crete (Knossos; Douka et al., 2017). Still, Neolithic farmers would have been reliant on the landscape around them and changes in climate could have altered the natural vegetation and/or influenced crop production (Krauss et al., 2018). The domesticated crops developed by the first farmers in the Levant, Anatolia, and Upper Mesopotamia required open vegetation conditions and were adapted to warmer and drier climates than those in Europe

Corresponding author: Lieveke van Vugt; Email: lieveke.vanvugt@unibe.ch

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(Willcox, 2005). Shifts to warmer and/or drier climatic conditions as well as related forest openings may have advantaged the establishment of farming in Northern Greece. However, once established in Greece, the new crops needed to be adapted to the relatively cool conditions and shorter growing season of continental Europe, before spreading farther north (Krauss et al., 2018). Additionally, stable climatic conditions were extremely important for harvest success. For example, Bronze Age societies in the Peloponnese flourished under favourable climate conditions, but were sensitive to droughts (Weiberg et al., 2021). Furthermore, observations from the past decades as well as palaeoecological studies show how sensitive Mediterranean forests are to changes in precipitation (Tinner et al., 2009; Beffa et al., 2016; Cramer et al., 2018; Gazol et al., 2018) and there is increasing concern about the resilience of forests to the projected rise in droughts based on the current climate change scenarios (IPCC, 2022).

The combination of palaeoecological and archaeological studies can help us to explore and better understand the underlying mechanisms of long-term human–environment dynamics (Crabtree and Dunne, 2022; Silva et al., 2022). Previous palaeoecological contributions to the vegetation history of Northern Greece confirm the complex interactions between climate, vegetation, and early agriculture (e.g., Bottema, 1974; Glais et al., 2016; Gassner et al., 2020); however, the temporal resolution of these records does not allow the disentanglement of the different factors involved. High-resolution, continuous, multiproxy studies with robust chronologies from sites close to prehistoric settlements are necessary to study the impact of climate change on the environment and human societies (Berger et al., 2016). One site suitable for such a high-resolution study is Limni Zazari, a small lake in Northern Greece, where the onset of farming activities coincides with a period of forest opening and possibly lower lake levels between 8600 and 8200 cal yr BP (Gassner et al., 2020). Multiple Neolithic and Bronze Age settlements have been excavated close to the site, with some assigned to the Early Neolithic (~8500–7800 yr BP; Kokkinidou and Trantalidou, 1991; Chrysostomou et al., 2015; Chrysostomou, 2015).

This study aims to provide a better understanding of the environmental history during the transition from Mesolithic (~9700–8500 cal yr BP) hunter-gatherer to Neolithic (~8500–5300 cal yr BP) farming societies in Northern Greece by studying lake sediments from Limni Zazari at a high resolution. We use pollen and microscopic charcoal to reconstruct the Mesolithic and Neolithic vegetation and regional fire dynamics from ca. 10,900 to 5060 cal yr BP. To reconstruct the environmental conditions in and around the lake we study the biogeochemical composition of the sediments by using X-ray fluorescence (XRF) elemental composition scanning and hyperspectral imaging (HSI) of pigments in the sediment cores. The results of the different analyses are compared with other palaeoenvironmental and palaeoclimatic studies from the eastern Mediterranean to understand the effects of climate change on vegetation dynamics during the Mesolithic–Neolithic transition. We are especially interested in answering the question of how climate change might have influenced the onset of the Neolithic. Additional focus is placed on human impact on the vegetation, with special emphasis on the timing and nature of the earliest Neolithic land use.

STUDY SITE

Limni Zazari is a small and shallow lake (surface: 2 km^2; maximum depth: 6.3 m) in the Eordea basin in Macedonia, Greece (606 metres above sea level; 40°37′31′′N, 21°32′50′′E, Fig. 1). Geologically, the Eordea basin belongs to the north Pelagonian zone and consists of crystalline limestones and marbles, with recent alluvial and lacustrine deposits around the lakes (Pavlides and Mountrakis, 1987). Today, Zazari has an inlet and outlet, but it is likely that in the past the lake was hydrologically closed. During the 1950s, a stream was rerouted to flow into Zazari and an outlet was constructed connecting the lake with Limni Chimaditis (Fig. 1). During this period, the extensive peatlands and marshes around Chimaditis were drained to create arable land (Papastergiadou et al., 2008). In the past, the marshes would flood during the winter and dry up during the summer (Bottema, 1974). The vegetation around the lake is dominated by grassland and shrubs, with scattered deciduous trees such as *Quercus pubescens*, *Quercus frainetto*, *Carpinus orientalis*, *Fraxinus excelsior*, and *Fraxinus angustifolia*. Such communities belong to the sub-Mediterranean vegetation type as defined by the occurrence of, for example, *Q. pubescens*, *Q. frainetto*, and *C. orientalis* (Lang et al., 2023a). Various reeds and herbs (e.g., *Phragmites australis*, *Artemisia*) grow on the lakeshore. The lowlands in the region are used for arable land, with the hills to the northwest of the lake covered with lowland sub-Mediterranean mixed oak forests. At higher elevations, forest composition changes to oro-Mediterranean beech forests and coniferous forests with *Pinus nigra* and *Pinus sylvestris*. Several Neolithic and Bronze Age settlements have been found in the area around Zazari and Chimaditis (Fig. 1). The earliest settlements are typologically dated to the Early Neolithic (~6500–5800 BCE; 8450–7750 cal yr BP) and occupation shifted between different sites, including dryland sites and pile dwellings (Chrysostomou et al., 2015; Chrysostomou, 2015).

The climate at Limni Zazari is warm-temperate Mediterranean (Csa according to Köppen Geiger; Beck et al., 2018) with a mean annual air temperature of 12.3°C, mean temperatures of 22.5°C for July and 2.6°C for January, and an average annual precipitation of 541 mm (Limnochori weather station, 1974–2004: Grimpylakos et al., 2013). Most of the precipitation falls during the winter months whereas the summers are rather dry.

METHODS

Sediment cores and radiocarbon dating

The sediment cores used in this study were retrieved in 2016, and an overview of the vegetation and environmental history covering the past 20,000 years at low temporal resolution was recently published (Gassner et al., 2020). We added 12 new radiocarbon samples of terrestrial plant macrofossils to those published in Gassner et al. (2020) in order to increase the robustness and detail of the overall chronology (Table 1, Supplementary Table S1, Supplementary Fig. S1). The samples were dated with accelerator mass spectrometry (AMS) in the Laboratory for the Analysis of Radiocarbon with AMS (LARA) at the University of Bern. We used the R package "rBacon" (Blaauw and Christen, 2011), with the IntCal20 calibration curve (Reimer et al., 2020), to calibrate the radiocarbon dates to years before present (cal yr BP) and to construct the age–depth model (Fig. 2, Supplementary Fig. S1). In total, 12 radiocarbon dates were located within the focus period (10,900–5060 cal yr BP) of this paper, five of them new (Table 1).

Pollen, stomata, and charcoal analyses

For the palynological and microscopic charcoal analyses, we took a total of 199 sediment samples of 1 cm^3. The sampling is in

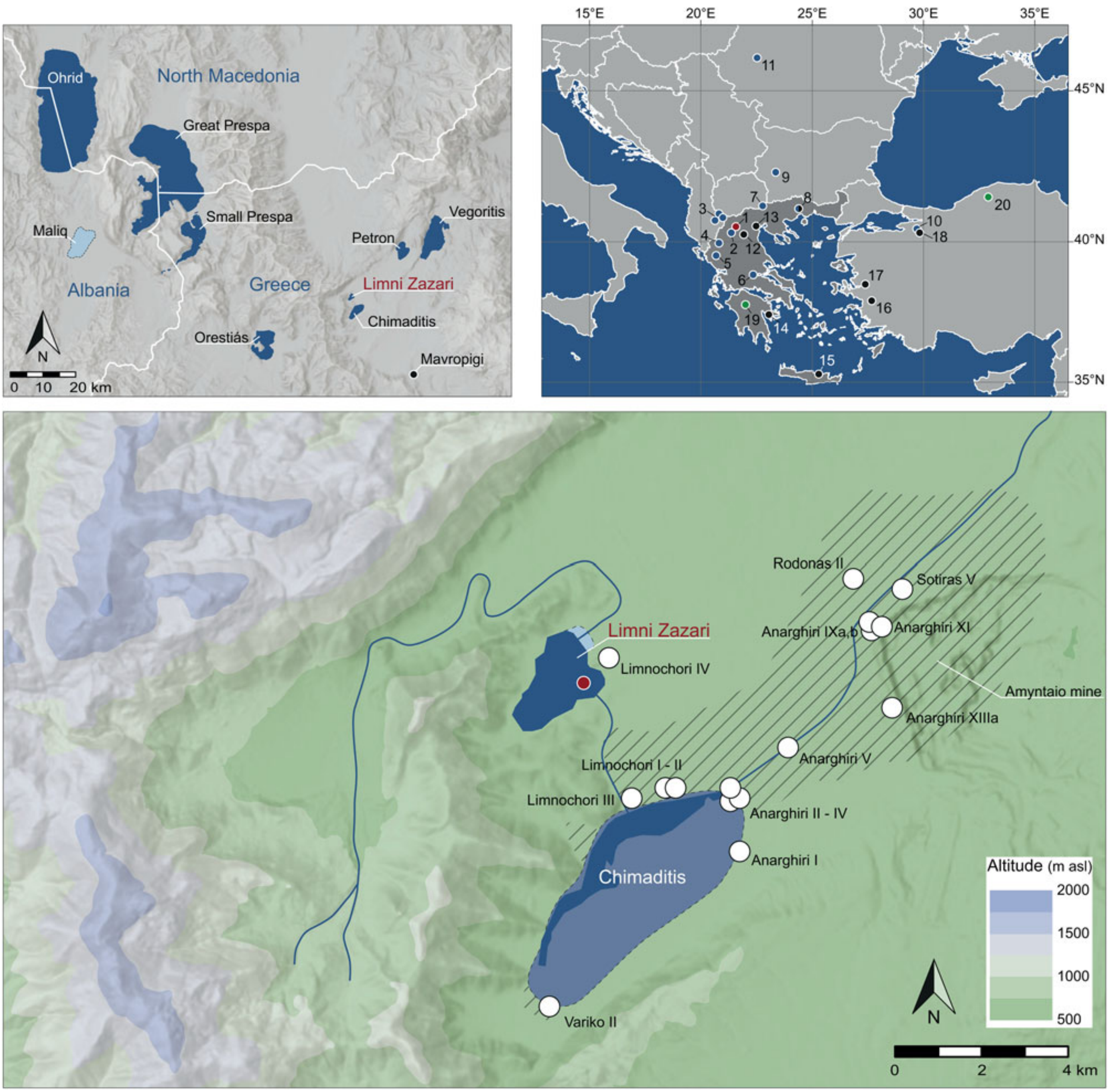

Figure 1. Study site (sources: EEA, 2016; Esri, 2023). Top left: Overview of the wider region around Limni Zazari. Top right: Overview of regionally important sites for this study. Lakes and marshes (blue dots): 1, Limni Zazari (red dot); 2, Limni Orestiás; 3, Lake Ohrid, Limni Prespa, and former Lake Maliq; 4, Limni Gramousti; 5, Limni Ioannina; 6, Limni Xinias; 7, Lake Dojran; 8, Tenaghi-Philippon marsh; 9, Rila mountains; 10, Lake Iznik; 11, Lake Brazi. Archaeological sites (black dots): 8, Dikili Tash; 12, Mavropigi-Filotsairi; 13; Paliambela Kolindros, Revenia-Korinos; 14, Franchthi cave; 15, Knossos; 16, Çukuriçi Höyük; 17, Ulucak; 18, Barçin. Speleothems (green dots): 19, Limnon cave; 20, Sofular cave. Bottom: The surroundings of Limni Zazari, with the coring site (red dot) and different archaeological sites dated between ca. 6500 and 1500 BCE (~8450–3450 yr BP, white dots; Kokkinidou and Trantalidou, 1991; Chrysostomou et al., 2015; Giagkoulis, 2019). The shaded area is the approximate extent of the peatlands in 1945; during the 1960s these were drained (Bottema, 1974; Papastergiadou et al., 2008).

contiguous 1 cm steps between 275 and 476 cm, with 1 cm missing (at 380 cm) as a result of cutting the 3-m-long core into 1-m-long segments. We prepared the samples following standard procedures (Moore et al., 1991) with mounting in glycerine and by adding a known number of *Lycopodium* spores to the samples beforehand to estimate concentrations and influx (i.e., accumulation rates; Stockmarr, 1971). Pollen, spores, stomata, and algae were identified under a light microscope at 400× or 1000× magnification using different keys (e.g., Trautmann, 1953; Moore et al., 1991; Jankovská and Komárek, 2000; Beug, 2004; van Geel and Aptroot, 2006) and the reference collection at the Institute of Plant Sciences, University of Bern. Cerealia type pollen were grouped into different size classes according to Bottema (1992): 40–49 µm (may include many wild grasses in the study region), 50–59 µm (may include various wild grasses), and ≥60 µm (includes only cultivated cereals). We distinguished three different types of *Quercus* pollen: *Q. frainetto* type, which includes *Q. frainetto*, *Quercus petraea*, and *Q. pubescens* in the study area; *Quercus cerris* type, including *Q. cerris* and *Quercus trojana*; and *Quercus ilex* type, including

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Table 1. New radiocarbon dates for the high-resolution sequence from the master core of the Limni Zazari sediment record. For the complete table with all the radiocarbon dates used see the supplementary material (Supplementary Table S1) and Gassner et al. (2020).

Depth (cm)	Lab. code	Material	^{14}C age (yr BP)	Calibrated age (cal yr BP, 2σ-range)	Median age (cal yr BP)	Modelled age in diagrams (cal yr BP)
338–339	BE-16306.1.1	Leaf fragments, bud scale	5565 ± 35	6294–6403	6349	6390
366–370	BE-16307.1.1	(Charred) leaf fragments, *Pinus* seed wing, anther	6210 ± 90	6884–7319	7098	7048
388–389	BE-16308.1.1	Bud scale, bark, charred grass, terrestrial plant indet.	6830 ± 60	7575–7785	7660	7618
429–432	BE-16309.1.1	(Charred) leaf fragments, grass cf.	7735 ± 100	8347–8975	8525	8769
461–463	BE-16310.1.1	Charred leaf fragments, bud scale, (charred) bark, seed wing	8720 ± 65	9540–10107	9691	9917

Q. ilex and *Quercus coccifera* (Beug, 2004). Generally, the terrestrial pollen sum, excluding pollen of aquatic plants and spores, was over 500. Microscopic charcoal (>10 μm) was analysed following Tinner and Hu (2003) and Finsinger and Tinner (2005) to reconstruct regional fire activity (Whitlock and Larsen, 2001; Conedera et al., 2009). We subdivided the pollen diagram into local pollen assemblage zones (LPAZ) by using the zonation method of optimal partitioning by the sum-of-squares criterion (Birks and Gordon, 1985) and by identifying statistically significant zones with the broken-stick model (Bennett, 1996).

Biogeochemical analysis

The methodology and equipment used for the geochemical XRF spectroscopy and HSI analyses are described in detail by Gassner et al. (2020). The sampling resolutions were 5 mm for XRF and 0.069 mm for HSI scanning, but we smoothed the HSI to a resolution of 2 mm for the diagrams. We use the element counts of titanium (Ti) as a proxy for terrigenous sediment input from the watershed (e.g., Haug et al., 2001). The ratio of Zr/Al is used as a proxy for sediment grain size, with high values indicating larger grain sizes; this ratio can also be used as a proxy for

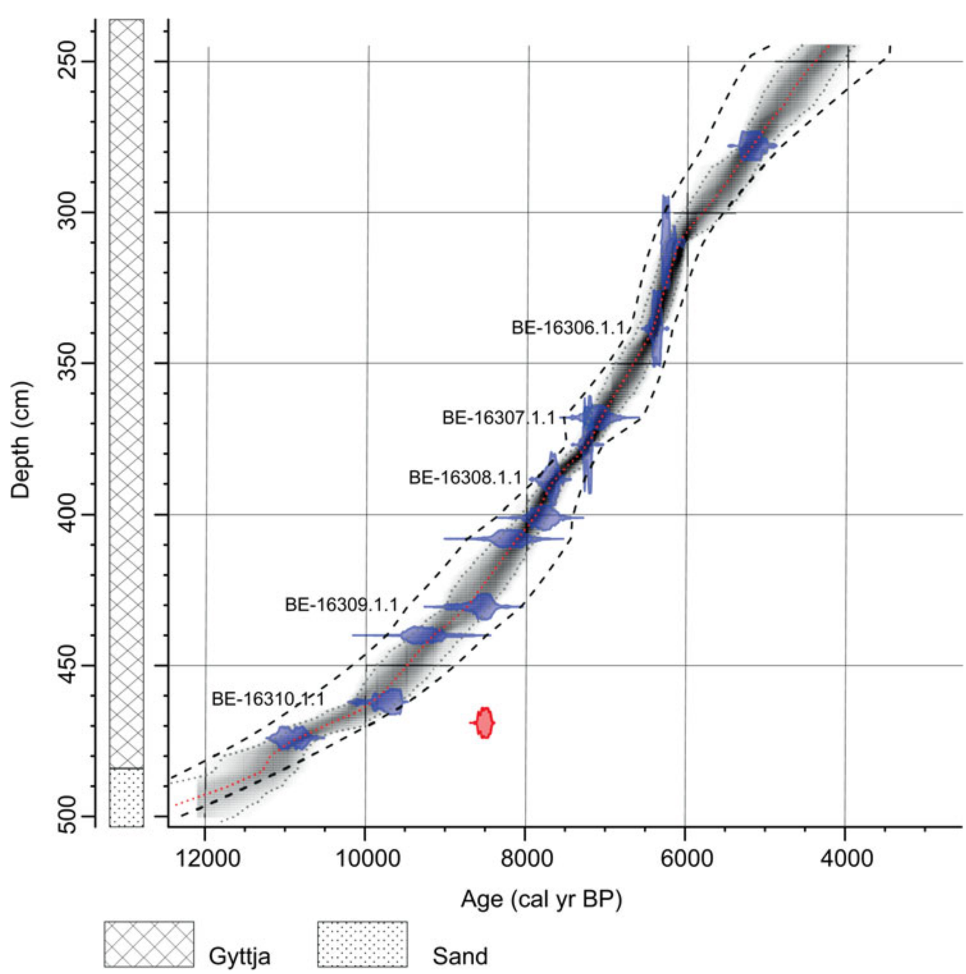

Figure 2. Age–depth model and lithology for the Mesolithic and Neolithic high-resolution sequence of Limni Zazari. The blue horizontal integrals show the probability density functions of the individual radiocarbon dates (IntCal 20; Reimer et al., 2020), the red dotted line represents the modelled chronology (Bacon; Blaauw and Christen, 2011), the grey envelop shows the 95% confidence interval, and the black dashed lines show the 95% confidence intervals from the generalised additive model (GAM; Heegaard et al., 2005) considering both age and depth uncertainties. The five radiocarbon dates from Table 1 are marked with their laboratory code; the unmarked dates were published in Gassner et al. (2020). The age–depth model for the complete core and the full table of radiocarbon dates can be found in the supplementary material (Supplementary Fig. S1, Supplementary Table S1).

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shoreline proximity to the coring site and thus low lake-level stands (Haberzettl et al., 2007). We assume that calcium (Ca) is predominantly related to endogenic calcite precipitating in the lake during periods of increased precipitation, high evaporation, and/or elevated temperatures. This is common for many lakes in the southern Balkans with karst-dominated catchments (e.g., Vogel et al., 2010; Francke et al., 2013). We use the ratio of Ca/Ti as an indicator for sedimentary calcite content, which serves as a proxy for moisture availability, with higher values indicating wetter and warmer conditions. The ratio of Rb/K is used as a proxy for chemical alteration of lithogenic sediments being deposited at the coring site, with higher values pointing towards more intensely weathered sediments (e.g., Burnett et al., 2011). From the HSI analysis, we use $RABD_{673}$ as an indicator of "green pigments" (chlorophyll-a and diagenetic products) and aquatic primary production, and $RABD_{845}$ as a proxy for bacteriopheophytin *a* (Bphe *a*) and meromixis (Zander et al., 2022).

Numerical methods

Ordination analysis and cross-correlations

To infer environmental gradients in the pollen assemblages, we used a principal component analysis (PCA) performed in Canoco 5.15 (ter Braak and Šmilauer, 2012). Before the PCA, we log transformed the percentage data to reduce the effects of dominant species. Several types of data were added passively to the analysis as supplementary variables, including microscopic charcoal influx as a proxy for fire activity, *Sporormiella* type influx as a proxy for grazing, July and January insolation (Laskar et al., 2004), and the ratio of calcium and titanium counts (ln(Ca/Ti)) as a proxy for moisture availability and temperature (higher values indicate wetter and warmer conditions).

We calculated cross-correlations (Green, 1981; Tinner et al., 1999) to identify leads and lags between fire (microscopic charcoal influx), moisture availability (−ln(Ca/Ti)), and vegetation (pollen percentages) by using R (R Core Team, 2023). The sign of ln(Ca/Ti) was reversed, to emphasise the response of vegetation to a decrease instead of an increase in moisture. Additionally, the −ln(Ca/Ti) was smoothed and resampled to match the resolution of the pollen samples. We analysed two time periods: 8700–7130 cal yr BP (ZAZ-3 to 6, 56 samples, 1 lag = 27.3 ± 5.7 yr) and 7720–6310 cal yr BP (ZAZ-6 to 8, 60 samples, 1 lag = 22.9 ± 7.2 yr) to assess the role of fire and moisture as drivers of vegetation change. For each period we calculated the cross-correlation coefficients for fire (as inferred from microscopic charcoal influx) versus vegetation (pollen percentages) and for moisture availability (−ln(Ca/Ti)) versus vegetation (pollen percentages) at ±10 lags and plotted them as correlograms. The 95% confidence intervals of the correlations were estimated by computing ±2 SE of the correlation coefficients, which corresponds to a two-sided significance level of $\alpha = 5\%$ (Tinner et al., 1999).

Biodiversity analysis and anthropogenic impact

Species diversity is a complex function of species richness and species evenness (Legendre and Legendre, 2012). To investigate biodiversity trends in the past, we calculated the palynological richness index (PRI), the evenness detrended palynological richness index (DE-PRI; Colombaroli and Tinner, 2013), and the probability of interspecific encounter (PIE; Hurlbert, 1971). PIE can be used as a proxy for evenness to estimate to what extent the total number of taxa in a sample is influenced by dominant taxa, and DE-PRI reduces the effects of unevenness on palynological richness. To account for differences in sample size (i.e., pollen sums) we used a rarefaction analysis (Birks and Line, 1992) with a minimum pollen sum of 487 (excluding aquatic taxa and ferns) by using the "vegan" package in R (version 2.6-4; Oksanen et al., 2020).

We calculated the land use probability (LUP) index (Deza-Araujo et al., 2022) to investigate and quantify the impact of human land use. The LUP is a probabilistic way to weight and summarise cultural indicator pollen taxa. We used the anthropogenic indicator values (AIV) of LUP for the indicator taxa of the sub-Mediterranean vegetation belt as published by Deza-Araujo et al. (2022), except for the Cerelia type pollen where we adjusted the AIV to reflect the different categories of Cerealia pollen weighted according to their diagnostic value (40–49 μm, AIV 5; 50–59 μm and ≥60 μm, AIV 10).

RESULTS

Chronology

The age–depth model for the high-resolution sequence from 10,900 to 5000 cal yr BP contains 12 radiocarbon dates (Fig. 2, Table 1) and is based on the model for the entire core (Supplementary Table S1, Supplementary Fig. S1). We rejected four radiocarbon dates from the complete model as they were clearly too young or did not fit the model (Supplementary Fig. S1). Sediment accumulation rates range between 20 and 40 yr/cm, except for one section between 310 and 340 cm with increased accumulation rates of ca. 10 yr/cm.

Biogeochemical proxies

At the start of the high-resolution record (10,900 cal yr BP), terrigenous sediment input (Ti) is moderately high; lake levels (ln(Zr/Al+1)) were likely lowered and sediments entering the lake experienced little chemical weathering prior to transport (low ln(Rb/K)), pointing towards drier and cooler conditions (Fig. 3). After 10,300 cal yr BP, increases in ln(Ca/Ti) and ln(Rb/K) suggest an increase in moisture, followed by a decrease in ln(Zr/Al+1) indicating higher lake levels. Periods of hypolimnetic anoxia or even meromixis (increased $RABD_{845}$) and increased aquatic productivity (higher $RABD_{673}$) are observed from ca. 9800 cal yr BP onwards. These conditions persisted until 8600 cal yr BP, when a period with high terrigenous sediment input and reduced Ca precipitation started. The biogeochemical proxies together suggest a period of lower lake levels, drier conditions, cessation of hypolimnetic anoxia, and reduced primary production between 8600 and 7800 cal yr BP. Afterwards, the previous conditions mostly returned, but primary production was now elevated and periods of hypolimnetic anoxia were more common. Between 7100 and 6150 cal yr BP, terrigenous sediment influx is higher and chemical weathering is reduced, indicating increased erosion. A reduction in endogenic calcite precipitation, together with high terrigenous sediment input, takes place during the last ca. 150 years of this phase (ZAZ-9), suggesting another period with drier conditions and lower lake levels between 6300 and 6150 cal yr BP.

Vegetation and fire history

We found 11 statistically significant LPAZ in the high-resolution Limni Zazari record (Figs. 4 and 5, ZAZ-1 to ZAZ-11). For ease of comparison, all data sets and diagrams use the LPAZ.

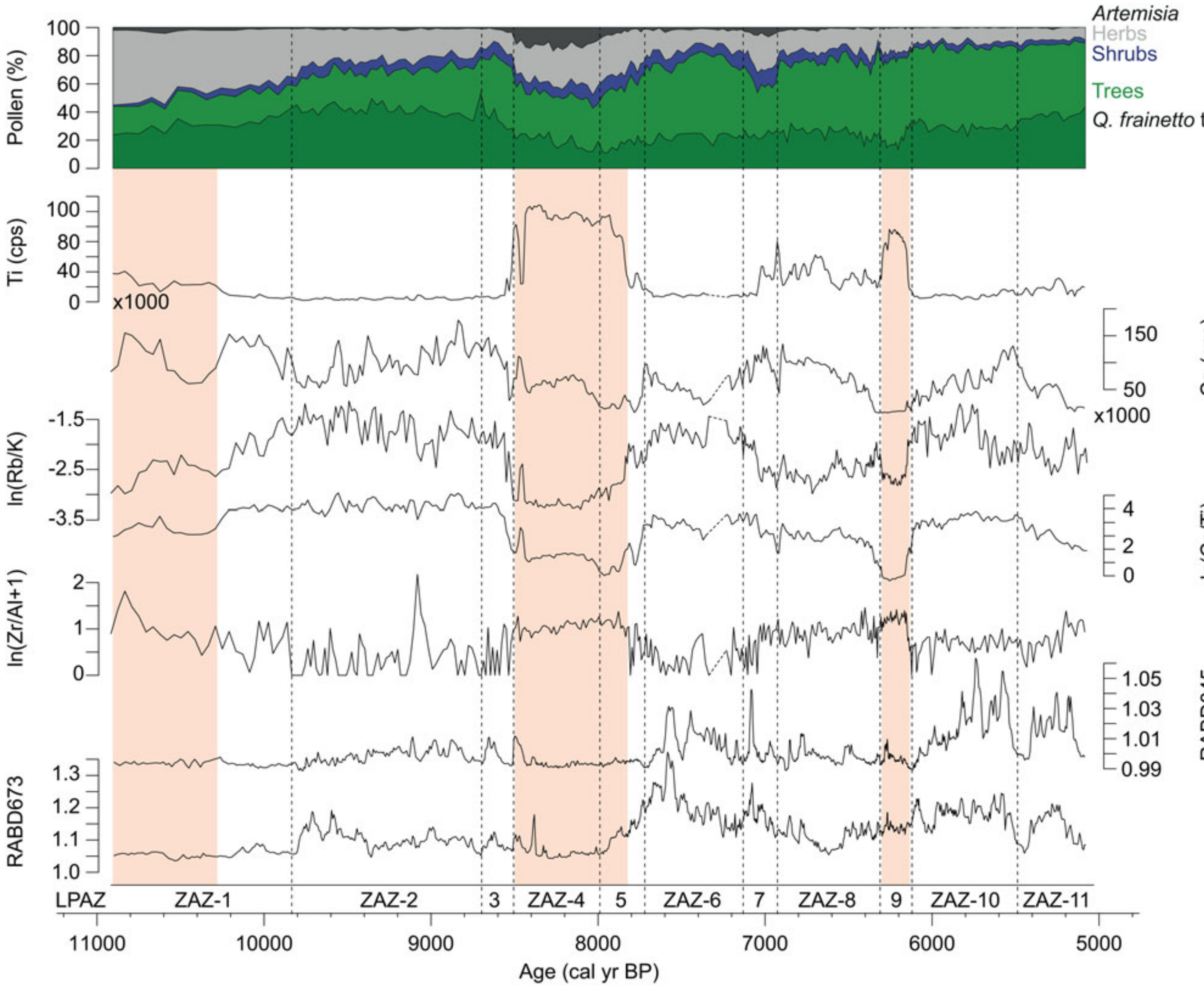

Figure 3. Comparison of the summary pollen diagram from Limni Zazari with X-ray fluorescence and hyperspectral imaging measurements. Titanium (Ti) counts are used as a proxy for lithogenic input; increased calcite (Ca, ln(Ca/Ti)) content is linked to more humid and/or warmer conditions, with higher values indicating wetter and warmer conditions; the ratio of rubidium and potassium (ln(Rb/K)) is used as a proxy for the chemical alteration of sediments deposited, with higher values indicating less alteration; the ratio of zirconium and aluminium (ln(Zr/Al+1)) is used as an indicator for increased grain size and lake level low stands, with higher values indicating coarser grain size and lower lake levels; $RABD_{673}$ is used as a proxy for aquatic productivity and $RABD_{845}$ for meromixis (see Supplementary Fig. S4 and Gassner et al. [2020] for the full record). LPAZ, statistically significant local pollen assemblage zones. The orange-coloured bars highlight periods with drier conditions.

Between 10,900 and 9900 cal yr BP (ZAZ-1), the pollen data suggest that the vegetation around Zazari developed from a species-rich herbaceous steppe (non-arboreal pollen >50%; high pollen richness, e.g., Poaceae, *Rumex acetosella* type, *Galium* type, *Achillea* type, *Artemisia*, Chenopodiaceae) to open parklands with shrubs and tree stands (*Pistacia*, *Q. frainetto* type). Around 9900 cal yr BP (ZAZ-2), arboreal pollen (AP) reaches values of 80%, indicating the establishment of sub-Mediterranean mixed oak woodlands (e.g., *Q. frainetto* type, *Q. cerris* type, *Tilia*, *Ulmus*, *Corylus*). These woodlands were initially rather open but became closed around 8700 cal yr BP (ZAZ-3) with high pollen percentages of deciduous oaks and *Tilia*. Low percentages of *Pinus* suggest that pines were growing in the wider catchment. Charcoal influx is low at the start of the record but increases from 9900 cal yr BP onwards with frequent peaks, indicating a change from low (ZAZ-1) to increased fire activity (ZAZ-2).

Starting at 8600 cal yr BP (transition from ZAZ-3 to 4), oaks (*Q. frainetto* type, *Q. cerris* type, *Q. ilex* type) along with *Tilia* decline and AP rapidly falls to ca. 60%. Concurrently, steppe taxa (e.g., *Artemisia*, Poaceae, Chenopodiaceae) and *Polygonum aviculare* type expanded, suggesting a marked opening of the mixed oak woodlands and a return of the parklands within less than 100 years. Interestingly, *Abies* pollen percentages did not decrease, but show a small increase to 3–4% during this period. Simultaneously with the opening of the woodlands, pollen richness and pollen evenness increased (Fig. 4), suggesting higher diversity. Also, cultural indicator taxa (e.g., *Plantago lanceolata* type, first appearance of Cerealia type ≥60 μm) and the LUP increase, suggesting the start of agricultural activities in the area at ca. 8500 cal yr BP. Charcoal influx shows no major change, indicating that fire activity remained stable. Between 8000 and 7300 cal yr BP (ZAZ-5, 6), AP increases again (>80%) and the steppe pollen decreases, showing a return to forested conditions. However, the composition of the forest changed; pollen percentages of *Pinus* (>30%) together with *Q. frainetto* type (~25%) now dominate, suggesting a change to mixed oak–pine forests.

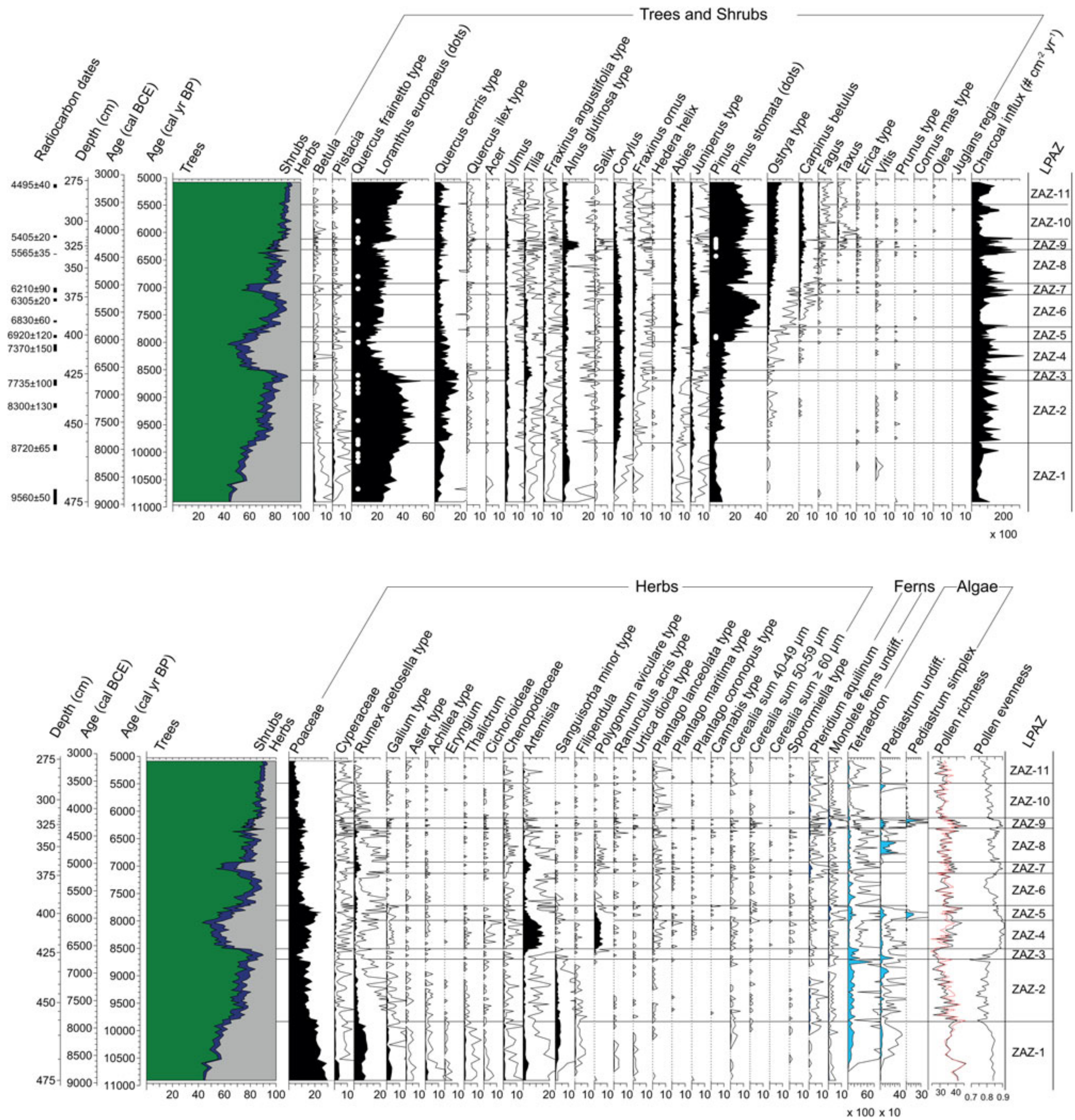

Figure 4. Selected pollen, spore, and green algae percentages of Limni Zazari based on the terrestrial pollen sum, together with the radiocarbon dates, microscopic charcoal influx, pollen richness (black solid line = palynological richness, red dotted line = detrended palynological richness), and pollen evenness. Empty curves show 10× exaggeration. LPAZ, statistically significant local pollen assemblage zones.

Also, other tree taxa such as *Ostrya* type and *Carpinus betulus* increase or reach their empirical pollen limit (a proxy for local establishment; Lang et al., 2023b). Medium-sized Cerealia pollen (inc. *Hordeum* type and *Triticum* type; Fig. 5) appear more regularly, suggesting a continuation of agricultural activities. Between 7600 and 7200 cal yr BP (ZAZ-6), charcoal influx is low and the regular fire peaks from before have disappeared, indicating reduced fire activity.

Between 7300 and 6900 (ZAZ-6, 7), tree pollen percentages show a marked decline (from 80 to 55%) mostly driven by decreasing *Pinus* pollen, but also *Abies* and *Tilia* show lower percentages. Pollen percentages of *Juniperus* type and herbaceous taxa (Poaceae, *R. acetosella* type, *Artemisia*) increase, whereas the cultural indicators and the LUP remain stable. Conifers may have declined in response to fire, as concurrently charcoal influx increases. Subsequently, tree pollen percentages rapidly increase, but the forest does not fully recover. AP fluctuates between 75 and 85%, suggesting a period of minor woodland openings that lasts until ca. 6150 cal yr BP (ZAZ-8, 9). *Pinus* and *Tilia* percentages were mainly affected by the disturbances, whereas taxa like *Ostrya* type, *C. betulus*, and *Fagus* increased. Large Cerealia pollen (≥60 µm) appear regularly, pointing to agricultural activities

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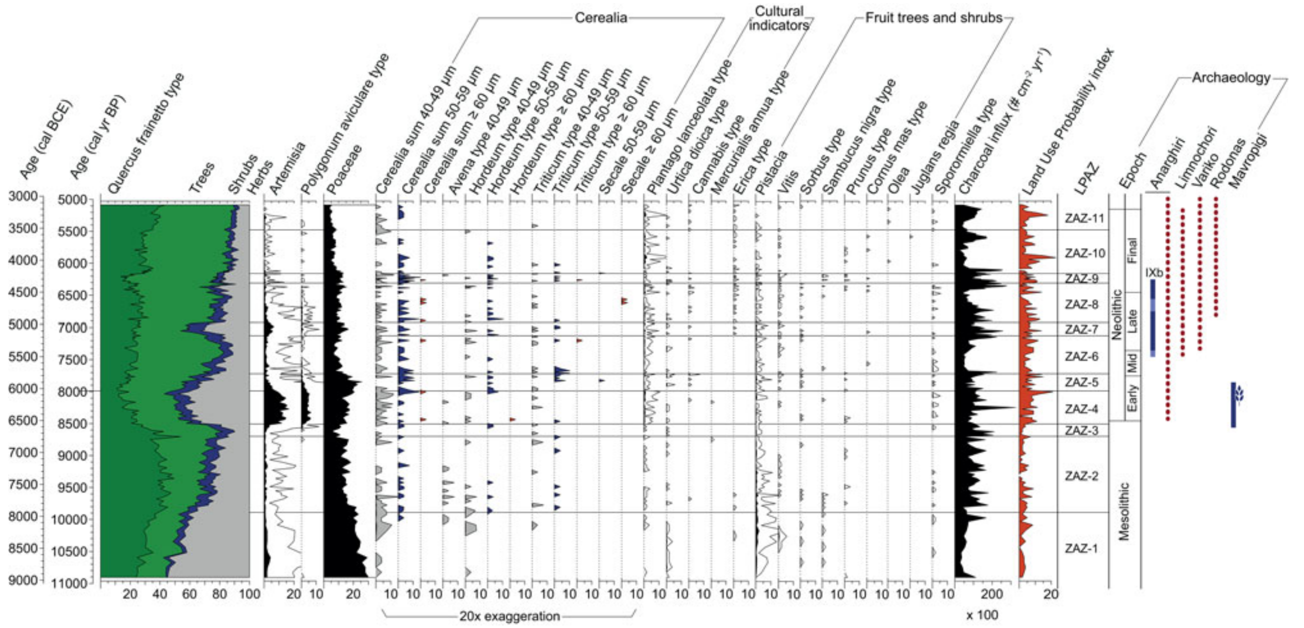

Figure 5. Selected pollen and spore percentages of Limni Zazari based on the terrestrial pollen sum, together with the microscopic charcoal influx and the land use probability index (Deza-Araujo et al., 2022). Empty curves show 10× exaggeration; the coloured Cerealia curves show 20× exaggeration. Archaeology: phases of different Neolithic settlements in the area around Limni Zazari (Fig. 1). Red dotted bars are based on typo-chronology, blue bars are radiocarbon dated (Kokkinidou and Trantalidou, 1991; Chrysostomou et al., 2015). The blue cereal ear represents the first dated cereal grains from the early Neolithic settlement Mavropigi-Filotsairi (Fig 1; Karamitrou-Mentessidi et al., 2015). LPAZ, statistically significant local pollen assemblage zones.

nearby. Charcoal influx shows large and irregular peaks, indicating periods of high fire activity. During the last 150 years of this phase (6310–6160 cal yr BP; ZAZ-9), percentages of riparian taxa (*Alnus glutinosa* type, *Salix*) increase for a short period and *Pinus* stomata appear frequently, indicating a change in the lakeshore vegetation. *Taxus* reaches its empirical limit, pointing to the establishment of this temperate coniferous tree (Landolt et al., 2010) in the region.

Afterwards (6160–5060 cal yr BP; ZAZ-10, 11), AP reaches over 90% suggesting that the mixed oak–pine forests fully closed. With the closing of the forest, pollen richness and pollen evenness decrease, suggesting a decline in diversity. Cerealia type appears less regularly and the largest category is not present anymore, indicating a decrease in agricultural activities. Charcoal influx is relatively low but suggests two periods of moderate fire activity.

Numerical analyses

PCA axis 1 (Fig. 6) explains 38% of the variance in the pollen assemblages and represents a gradient from steppe and parklands dominated by deciduous oaks (<50% AP; negative PC1) to closed pine–deciduous oak forests (>90% AP; positive PC1). The sample scores of axis 1 plotted against time show a clear change around 8000 cal yr BP, at the same time as the shift in forest composition, suggesting a major change in the vegetation around this time (Fig. 7). Axis 2 explains a further 16% of the variance and might be related to changes in moisture availability (high correlation with ln(Ca/Ti)) and/or land use (LUP). The sample scores of axis 2 plotted against time show the biggest change between 8500 and 7700 cal yr BP, a period with drier conditions, open parklands, and the first agriculture, further suggesting an important role for moisture availability and/or land use.

The cross-correlation analysis (Fig. 8, Supplementary Fig. S3) underscores the importance of moisture availability on vegetation dynamics, showing negative correlations between increased −ln(Ca/Ti) and AP as well as *Q. frainetto* type, suggesting that decreased moisture availability affected forest growth (note the inversed sign for ln(Ca/Ti)). The strong positive correlation of *Artemisia* and *P. aviculare* type already before lag 0 may indicate that another factor than moisture availability could have influenced the vegetation ca. 40–60 years (minimum at lags −2 and −3) before the lake-level shift. Given that *P. aviculare* is classified as a human indicator taxon (Behre et al., 2023) it may point to human impact, which would also explain the correlation with *P. lanceolata* type and the LUP. However, in Greece, *P. aviculare* is also associated with marshes and areas that seasonally flood and dry out (Bottema, 1974; Strid, 1986; Willis, 1992), suggesting moisture availability may have played a role. The cross-correlations between charcoal influx and different pollen taxa during the Neolithic show that fires promoted the expansion of herbs (e.g., *Artemisia*) at the expense of trees (e.g., AP, *Pinus*).

DISCUSSION

Early Holocene vegetation dynamics driven by changes in moisture

In Europe and the Mediterranean region, climate is generally regarded as the main driver of vegetation change before the introduction of farming, with changes in temperature, precipitation, but also seasonality playing an important role (e.g., Eastwood, 2004; Tinner et al., 2009; Davis et al., 2015; Roberts et al., 2018; Giesecke et al., 2019; Lang et al., 2023c). Our high-resolution record starts during the Early Holocene at 10,900 cal yr BP when the landscape was dominated by forest-steppe vegetation with scattered mixed oak stands. Climatic conditions during the Early Holocene were still rather continental with warm summers and cold winters (Laskar et al., 2004; Vogel et al., 2010; Francke et al., 2013), and moisture availability was relatively low at the

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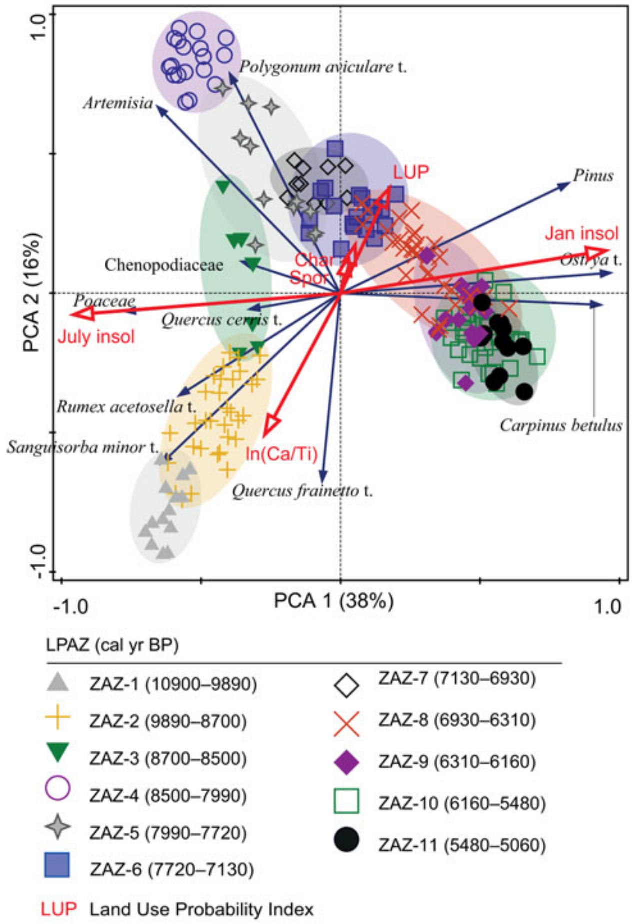

Figure 6. Principal component analysis (PCA). PCA scatterplot of the samples and selected taxa. Microscopic charcoal influx (Char) as a proxy for fire, *Sporormiella* type influx (Spor) as a proxy for grazing, the land use probability index (LUP; Deza-Araujo et al., 2022), July and January insolation (July insol, Jan insol; Laskar et al., 2004), and the natural logarithmic transformed ratio of calcium and titanium counts (ln(Ca/Ti)) as a proxy for hydrological conditions (higher values indicate wetter conditions) are supplementary explanatory variables and were projected passively onto the ordination (red arrows). Samples are grouped according to the local pollen assemblage zones (LPAZ).

start of our high-resolution record (Fig. 7; Peckover et al., 2019). The continental climate explains the prevalence of grassland steppe, where only few temperate deciduous trees were able to grow on moister habitats (e.g., riparian areas, north-facing slopes). The drought-adapted forest-steppe was diverse and dominated the landscape until 9800 cal yr BP, when forests started to close. During the Early Holocene, forest-steppe or maquis vegetation was widespread in the eastern Mediterranean (e.g., Lake Dojran, Limni Prespa, Lake Iznik; Fig. 1; Panagiotopoulos et al., 2013; Miebach et al., 2016; Masi et al., 2018), but also in the central and western Mediterranean (e.g., Sadori and Narcisi, 2001; Tinner et al., 2009; Lang et al., 2023d).

The closing of the forest at Zazari was delayed compared to the onset of the Holocene (~11,650 cal yr BP) and to the onset of wetter/warmer conditions indicated by increased carbonate deposition in Zazari starting at ca. 10,300 cal yr BP (Fig. 3). The change from forest-steppe or mixed deciduous oak parklands (50–70% AP, see Magyari et al., 2010; Lang et al., 2023d) via open woodlands (70–80% AP) to mixed deciduous oak forests (AP >80%) only started at ca. 9800 cal yr BP. The delay in the formation of closed forest can be observed in several records of the central-eastern Mediterranean (Fig. 1; e.g., Lake Maliq, Dojran, Volvi, Prespa, Tenaghi Philippon, and Iznik; Wijmstra, 1969; Denèfle et al., 2000; Panagiotopoulos et al., 2013; Glais et al., 2016; Miebach et al., 2016; Masi et al., 2018; Ganz et al., 2024) and is even more pronounced further to the east, with forests in central Anatolia first closing at ca. 8000 cal yr BP (Roberts et al., 2001). Similarly, afforestation was delayed until 8000–7000 years ago at the warmest thermo-Mediterranean sites in the western and central Mediterranean (e.g., Fletcher et al., 2007; Tinner et al., 2009; Lang et al., 2023d). This Early Holocene delay in afforestation is generally attributed to low humidity and limited moisture availability caused by a maximum in boreal summer insolation (Fig. 7; Tzedakis, 2007; Kotthoff et al., 2008; Tinner et al., 2009). In agreement with today's moisture gradient, sites located to the west of the Pindus mountains were less affected and forests closed at the onset of the Holocene (e.g., Ioannina and Gramousti; Fig. 1; Willis, 1992; Lawson et al., 2004). This moisture gradient is caused by the Pindus mountains, with higher orographic precipitation and thus moisture availability west of the Pindus (Lawson et al., 2004).

At Zazari, deciduous oaks (especially *Q. frainetto* type) rapidly expanded from 10,100 cal yr BP to form semiclosed woodlands from 9800 cal yr BP onwards. We assume that moisture availability started to increase after 10,300 cal yr BP (Figs. 3 and 7), synchronous with the start of a more humid phase in the central-south Mediterranean (Magny et al., 2013). Indeed, afforestation by *Quercus* and the onset of sapropel S1 formation at about 10,000 cal yr BP has been attributed to increasing precipitation in the eastern Mediterranean (e.g., Rossignol-Strick, 1999; Kotthoff et al., 2008; Tinner et al., 2009; Masi et al., 2018). In support of this argument, increasing moisture availability was reconstructed from different types of proxies from Greece and the southern Balkans (Figs. 1 and 7); for example, in speleothems (e.g., Limnon cave; Peckover et al., 2019), lake-level reconstructions (e.g., Limni Xinias; Digerfeldt et al., 2007), and in stable isotopes (e.g., Lake Ohrid and Dojran; Francke et al., 2013; Lacey et al., 2015). However, at Zazari it did take about 500 years for the forest to close; possible causes for this lag might be a gradual increase in moisture availability and/or changes in the seasonality of the precipitation with the majority of the precipitation falling outside the growing season (Stevens et al., 2001; Tzedakis, 2007; Roberts et al., 2008; Peyron et al., 2011). With the establishment of the mixed oak woodlands, a new fire regime with regular fires established, likely linked to an increase in available biomass (Turner et al., 2008; Vannière et al., 2011; Lawson et al., 2013).

Forest disturbance driven by rapid climate change

The forest opening phase from 8600 to 8000 cal yr BP is one of the most striking features of our record. Pollen percentages and influx both show a significant reduction in deciduous oak forests and the expansion of *Artemisia*–*P. aviculare* type-dominated open lands (Fig. 7). This period is also well reflected in the biogeochemical proxies as a period of low carbonate deposition, increased soil erosion, and lower lake levels suggesting colder and drier conditions (Figs. 3 and 7). It is synchronous with a distinct RCC event in the eastern Mediterranean dated to ca. 8600–8000 cal yr BP that is characterised by cooler and drier conditions (Rohling et al., 1997; Mayewski et al., 2004; Migowski et al., 2006; Marino et al., 2009; Göktürk et al., 2011; Aufgebauer et al., 2012; Francke et al., 2013; Schemmel et al., 2016). The so-called "8.2 ka BP event" is a much shorter-lived event

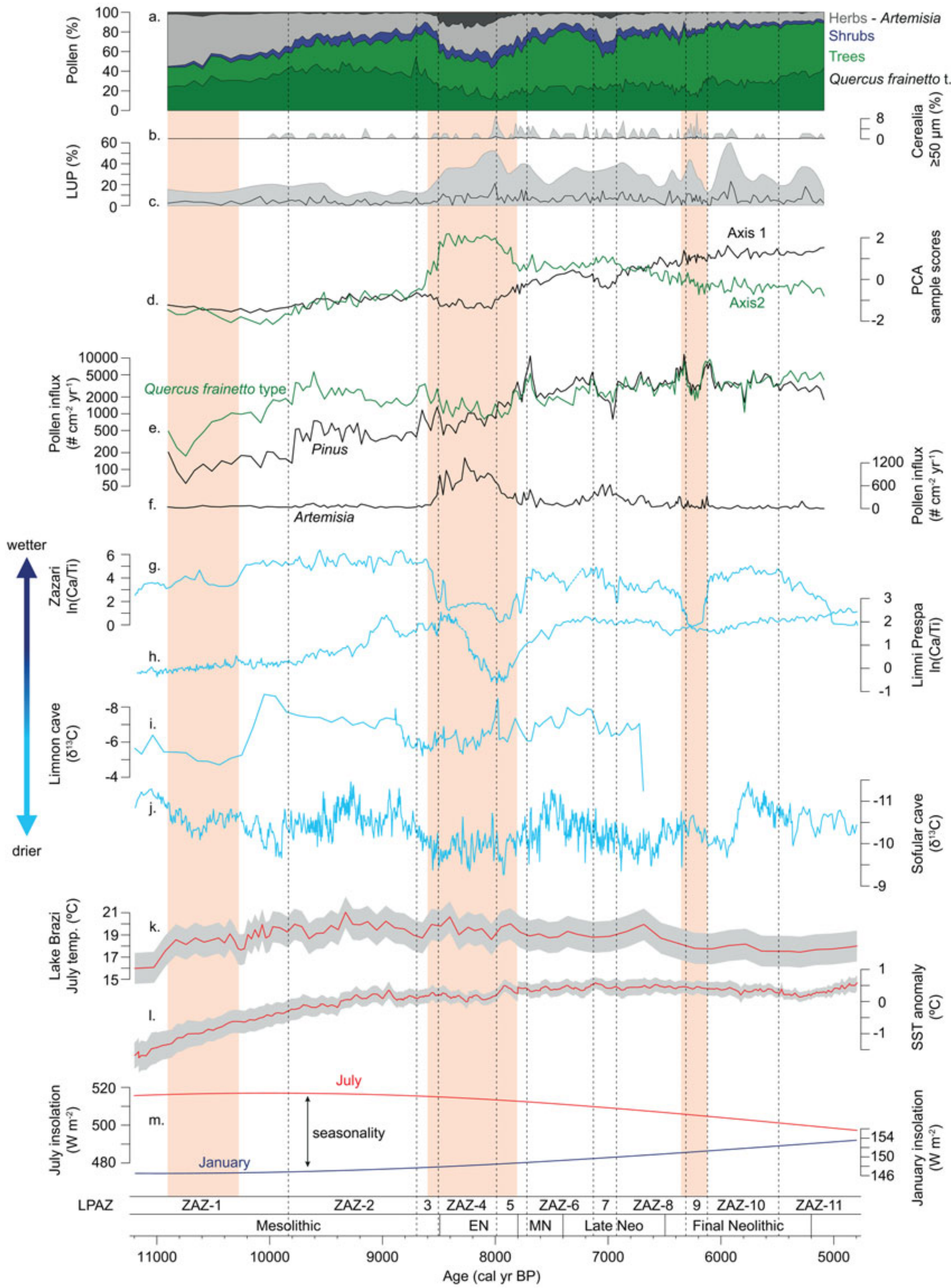

Figure 7. Comparison of the vegetation and environmental history of Limni Zazari with different climate records: (a) summary diagram of the vegetation history; (b) sum of Cerealia ≥50 μm pollen percentages (10× exaggeration in grey); (c) land use probability (LUP) index (5× exaggeration in grey with loess smoothing, span = 0.1); (d) PCA axis 1 and axis 2 sample scores; (e) pollen influx of *Quercus frainetto* type and *Pinus* on a logarithmic scale; (f) pollen influx of *Artemisia*; (g) ln(Ca/Ti) at Limni Zazari as a proxy for climatic conditions, higher values indicating wetter and warmer conditions; (h) log-transformed ratio between calcium and titanium X-ray fluorescence counts from Limni Prespa as a proxy for climatic conditions; (i) $\delta^{13}C$ values from the Limnon cave (Peloponnese, Greece) stalagmite record as a proxy for winter precipitation (Peckover et al., 2019); (j) $\delta^{13}C$ values from the Sofular cave (Türkiye) stalagmite as a proxy for spring–summer–autumn effective moisture availability (Fleitmann et al., 2009; Göktürk et al., 2011); (k) chironomid-based July air temperature reconstruction from Lake Brazi (Carpathians, Romania; Tóth et al., 2015); temperatures were transformed to the altitude of Limni Zazari (0.6°C/100 m); (l) stack of Mediterranean sea-surface temperature (SST) anomalies (Marriner et al., 2022); (m) July and January insolation for 40.6°N (Laskar et al., 2004). Dashed lines are the local pollen assemblage zone (LPAZ) boundaries; the orange-coloured bars represent the different dry phases found in the biogeochemical proxies (Fig. 3).

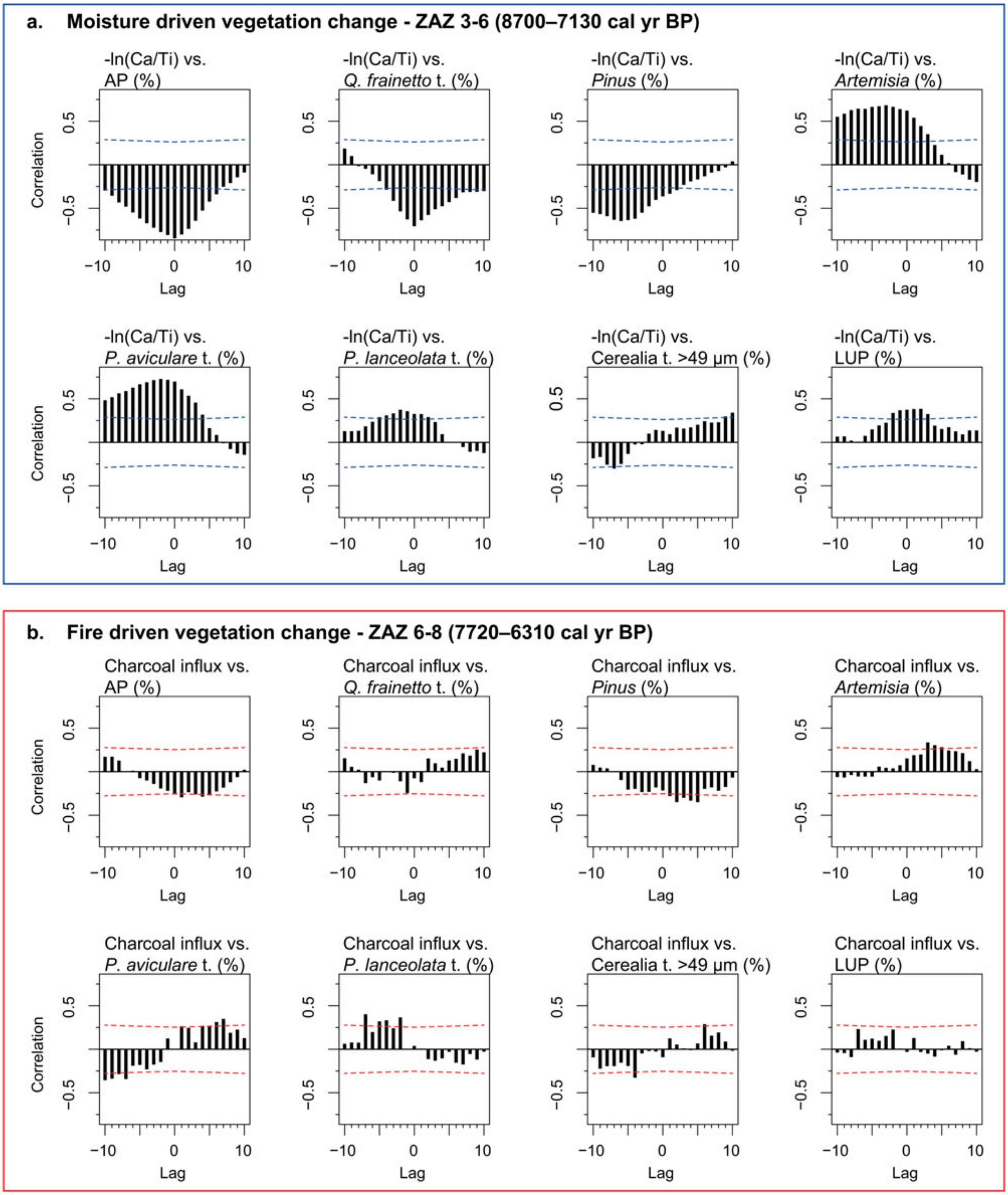

Figure 8. Cross-correlation diagrams from Limni Zazari with: (a) −ln(Ca/Ti) as a proxy for moisture availability versus selected pollen percentages (arboreal pollen, *Quercus frainetto* type, *Pinus*, *Artemisia*, *Polygonum aviculare* type, *Plantago lanceolata* type, Cerealia type) and the land use probability index (LUP) for zones ZAZ-3 to ZAZ-6 (8700–7130 cal yr BP); 1 lag corresponds to 27.3 ± 5.7 years. The sign of ln(Ca/Ti) was reversed, to emphasise the response of vegetation to a decrease instead of an increase in moisture; (b) microscopic charcoal influx (particles per cm^2/yr) as a proxy for fire activity versus selected pollen percentages and the LUP for zones ZAZ-6 to ZAZ-8 (7720–6310 cal yr BP); 1 lag corresponds to 22.9 ± 7.2 years. The dotted horizontal lines mark the significance level ($P < 0.05$).

(~8250–8090 cal yr BP) associated with widespread Northern Hemisphere cooling and is superimposed onto the longer 8600–8000 cal yr BP RCC event (Alley et al., 1997; Rohling and Pälike, 2005; Rasmussen et al., 2014). During the longer 8600–8000 cal yr BP RCC event, sea-surface temperature reconstructions show a cooling of 2–4°C in the Aegean Sea (Rohling

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et al., 2002; Marino et al., 2009). Pollen-based temperature reconstructions from Tenaghi Philippon and Maliq also suggest a lowering of winter temperatures by ca. 3–4°C and a reduction in annual precipitation of 200–250 mm (Bordon et al., 2009; Pross et al., 2009). Pollen-independent terrestrial temperature reconstructions, though rare, do not show significant changes in July or annual temperature (Lake Brazi and Limni Dojran; Fig. 7; Tóth et al., 2015; Thienemann et al., 2017). Since pollen-inferred climate reconstructions cannot be used to study the impact of climate on vegetation, as it would lead to circularities, this scarcity of independent evidence makes it difficult to assess how pronounced the cooling at Zazari was. However, the disappearance of *Q. ilex* type during this period (Fig. 4) might have been caused by lower winter temperatures and especially frost (Lang et al., 2023b). Studies into moisture availability and hydrologic conditions are more widespread, with several lake records and speleothems from the eastern Mediterranean suggesting a period with drier conditions and lower lake levels (Fig. 7; Göktürk et al., 2011; Aufgebauer et al., 2012; Francke et al., 2013; Peckover et al., 2019). The leaf wax record from Tenaghi Philippon (Fig. 1), ca. 200 km to the east of Zazari, attributes the drier conditions to reduced summer precipitation and lower humidity between 8700 and 8200 cal yr BP (Schemmel et al., 2017).

Particularly drier summer conditions would have negatively impacted the mixed broadleaved forests as they are sensitive to summer droughts and would have enabled *Artemisia* to quickly expand around the lake (Fig. 7). Our cross-correlations clearly show how susceptible the mixed oak forests are to changes in moisture availability (Fig. 8). It is likely that parts of the marshes surrounding Chimaditis (Fig. 1) dried out (Bottema, 1974), further expanding the available space for *Artemisia*-dominated steppe. A reduction in mixed broadleaved forests and a steppe expansion can be observed in several records in the southern Balkans (e.g., Prespa, Maliq, Tenaghi Philippon; Fig. 1; Denèfle et al., 2000; Pross et al., 2009; Panagiotopoulos et al., 2013), showing that the response to the RCC was not confined to Zazari. Interestingly, Dojran (Fig. 1) does not show any changes in the pollen percentages, but the pollen influx of *Quercus robur* type (same as *Q. frainetto* type) was reduced during the RCC event (Masi et al., 2018).

Intriguing is the large role that *P. aviculare* type plays at Zazari, as it already expanded together with *Artemisia* and *P. lanceolata* type a few decades before conditions became most arid (Fig. 8). This pollen type is associated with anthropogenic disturbances, as many of the taxa included are ruderals, spreading after forest openings or under livestock grazing (Strid, 1986; Bottema and Woldring, 1990; Brechbühl et al., 2024). It is likely that Neolithic farmers started to play an active role in the vegetation dynamics around this time, as the LUP index shows a clear increase after ca. 8500 cal yr BP (Figs. 5 and 7; LUP does not include *P. aviculare* type and *Artemisia*). On the other hand, the PCA and the cross-correlations (Figs. 6 and 8) suggest that climate was the most important driver. *Polygonum aviculare* type was present during the Late Glacial period and only disappeared at the onset of the Holocene, suggesting that under cold and dry conditions it was part of the native flora (Gassner et al., 2020); today, *P. aviculare* is also associated with marshes and seasonally wet/dry areas (Bottema, 1974; Strid, 1986; Willis, 1992).

After 8000 cal yr BP, the forest expanded and the previous vegetation structure was re-established, while vegetation composition changed significantly. Deciduous oaks only partly recovered, whereas pines rapidly expanded within the catchment of Zazari (Fig. 4). Similar vegetation changes occurred in the mountains of southwestern Bulgaria (Tonkov, 2021) and (less pronounced) at Prespa and Iznik (Panagiotopoulos et al., 2013; Miebach et al., 2016), suggesting a widespread shift. Several authors have proposed a change in precipitation across the Mediterranean linked to changes in atmospheric circulation (e.g., Eastwood et al., 2007; Magny et al., 2013; Schemmel et al., 2017). Plant waxes from Tenaghi Philippon (Fig. 1) suggest a shift from low to higher summer precipitation around 8000 cal yr BP (Schemmel et al., 2016, 2017), and Tonkov et al. (2016) attributed the establishment of a coniferous belt in the Bulgarian Rilin mountains (Fig. 1; including *Pinus* and *Abies*) to a climate shift towards cooler summers, warmer winters, and increased precipitation in the northern Mediterranean region. Besides climate, the start of anthropogenic disturbances during the RCC event likely played a role as well, with human impact ultimately leading to irreversible shifts in Mid- and Late Holocene plant communities.

Earliest farming and the impact of Neolithic land use on the vegetation composition

The earliest radiocarbon evidence for the start of the Neolithic is dated to ca. 8600–8500 cal yr BP in Greek Macedonia at the sites of Mavropigi-Filotsairi, Revenia-Korinos, and Paliambela Kolindros (Fig. 1), followed by a general increase in dates at 8400 cal yr BP (Maniatis, 2014; Weiberg et al., 2019; Reingruber, 2020). The appearance of the first documented Neolithic settlements coincides with the drought-driven forest opening, the increase of *P. lanceolata* type pollen, the first appearance of the largest Cerealia type pollen, and the increase of LUP at Zazari (Figs. 5 and 7). It is likely that the opening of the forest and the return to the parklands or forest-steppe facilitated the establishment of the first farming activities. Specifically, the RCC event promoted environmental conditions similar to the Levant and Anatolia, where people also preferred open parklands for their settlements, as crop cultivation and pastoralism were easier and there was no need to clear the forest first (Tinner et al., 2009; Krauss et al., 2018). Furthermore, it seems that during the RCC event, Neolithic farmers moved away from central/southeastern Anatolia and started to settle the coasts of the Aegean (e.g., Barçin, Çukuriçi Höyük, Ulucak, Mavropigi, Fig. 1; Maniatis, 2014; Weninger et al., 2014; Horejs et al., 2015; Clare, 2016). During the RCC event, coastal areas would have had more favourable climatic conditions, with less severe winters and less drought, and would have posed lower risks to the Neolithic lifestyle (Clare, 2016).

Even though Cerealia type pollen (inc. *Hordeum* type, *Triticum* type, *Avena* type) already occurs from the start of our record more than 10,000 years ago, this pollen pattern cannot be interpreted as evidence for cereal cultivation. The smaller Cerealia type pollen (<60 μm) includes various wild grasses, including the wild ancestors of barley and wheat (Bottema, 1992; Beug, 2004). These grasses were a common component of the steppe and deciduous oak parklands in the eastern Mediterranean (Harlan and Zohary, 1966), and can be found throughout the Holocene and the Late Glacial period in Northern Greece (e.g., Huttunen et al., 1992; Lawson et al., 2004; Kouli and Dermitzakis, 2008). Furthermore, archaeobotanical remains from Franchthi cave show that wild barley (*Hordeum vulgare* ssp. *spontaneum*) and oats (*Avena* sp.) were regularly collected by Mesolithic foragers (Hansen and Renfrew, 1978; Kotzamani and Livarda, 2018). The largest Cerealia type pollen

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(≥60 μm, exclusively cultivated cereals; Bottema, 1992) only appeared after 8500 cal yr BP in our record, after the archaeologically inferred onset of the Neolithic and concurrent with the first radiocarbon-dated cereal macrofossils from the wider region (e.g., Mavropigi, Revenia; Figs. 1 and 5; Maniatis, 2014; Chrysostomou et al., 2015; Karamitrou-Mentessidi et al., 2015; Tsartsidou and Kotsakis, 2020; Maniatis and Adaktylou, 2021). The majority of the larger Cerealia type pollen in our record belong to *Hordeum* type, with *Triticum* type appearing less regularly (Fig. 5). This is in contrast with the archaeobotanical record from Northern Greece, where macrofossils of glume wheats and einkorn (*Triticum*) dominated the settlement assemblages, although barley (*Hordeum*) is also well represented (Marinova and Valamoti, 2014; Kotzamani and Livarda, 2018; Valamoti, 2023). Grains of rye (*Secale*) and oat (*Avena*) are very rare in Neolithic archaeobotanical assemblages (Zohary et al., 2012b; Valamoti, 2023); most likely these cereals were not cultivated and our *Avena* type and *Secale* pollen stem from wild varieties. Our interpretation is supported by the generally low LUP values prior to 8600 cal yr BP; LUP does include Cerealia type pollen <60 μm, but gives more weight to the combined occurrence of crops and weeds (Deza-Araujo et al., 2022).

From ca. 8000 cal yr BP (~6050 BCE), the number of settlements in the area around Zazari rose, with about half classed as lakeside settlements (Chrysostomou et al., 2015). The higher values of Cerealia type pollen between 8000 and 5900 cal yr BP and the regular small-scale forest openings between 7400 and 6100 cal yr BP are most likely linked to the increased activities associated with these settlements. Although most of the settlements are dated based on pottery typology, radiocarbon dates from Anarghiri IXb are concentrated during the period of forest disturbances (Fig. 5; Giagkoulis, 2019). Interestingly, Anarghiri IXb changed from a wetland site to a dryland site at some point between ca. 6650 and 5200 cal yr BP (4700–3250 BCE; Giagkoulis, 2019). Indeed, around the same time, a short dry period from 6310 to 6160 cal yr BP at Zazari is also indicated by grain-size proxies suggesting lower lake levels and a decrease in carbonate deposition pointing to drier and colder climate conditions (Figs. 3 and 7). Towards the end of the Neolithic (~6450–5200 cal yr BP; ~4500–3250 BCE), settlement densities decreased (Chrysostomou et al., 2015); unfortunately, there are no precise dates for when the settlements around Zazari were abandoned. However, the closing of the forest around 6100 cal yr BP, a general decline in radiocarbon dates in Northern Greece (Weiberg et al., 2019), and the abandonment of several Neolithic sites (Renfrew, 1971; Andreou et al., 1996; Kotsakis, 2018) would suggest limited anthropogenic activity towards the end of the Neolithic. Nevertheless, surveys show that settlements were still present, but smaller and more widely dispersed across the landscape (Weiberg et al., 2019).

Neolithic farming in Northern Greece is often characterised as intensive farming on small garden-like plots, supplemented with nuts and fruits from foraging in the forest (Bogaard, 2005; Bogaard et al., 2013; Marinova and Ntinou, 2018). In agreement, the short-lived forest disturbances between 7400 and 6100 cal yr BP and the relatively low values of cultural indicator taxa at Zazari (Fig. 5) suggest small-scale activities with minor to moderate impact on the local vegetation structure and compares well with the use of small plots for crop cultivation. The lower pollen percentages of *Q. frainetto* type from 8100 to 6200 cal yr BP could reflect the use of deciduous oaks as the main woodland resource in Neolithic settlements in Northern Greece (Marinova et al., 2012; Marinova and Ntinou, 2018). Also, at Anarghiri IXb oaks were predominantly used for the construction of the settlement and made up approximately 80% of the wooden piles analysed (Giagkoulis, 2019, 2020).

Although the forest quickly recovered after small to moderate anthropogenic disturbances, its composition gradually changed and its diversity increased (Fig. 4). The decline of disturbance-sensitive *Tilia* and the expansion of disturbance-adapted *Ostrya* type (includes *Ostrya carpinifolia* and *C. orientalis*) is likely linked to human impact. Both *Ostrya* type species are light-loving, excellent resprouters, and were often used for fodder production; it is likely they benefitted from fire, cutting, and grazing disturbances (Horvat et al., 1974; Gobet et al., 2000; Pasta et al., 2016; Sikkema and Caudullo, 2016). Also, *Fagus* and *C. betulus* are rather disturbance tolerant and may have been favoured by anthropogenic disturbance (Brechbühl et al., 2024). However, climatic change may have co-determined the expansion of these tree species (Bottema, 2003); for example, *O. carpinifolia* generally prefers humid summer conditions (Pasta et al., 2016; Lang et al., 2023b). Likewise, *Fagus* is even more mesophilous than *O. carpinifolia*, which may have advantaged its Late Holocene expansion as also observed in other Mediterranean areas (Morales-Molino et al., 2021). Fire seems to have played a moderate role in the vegetation dynamics at Zazari, negatively affecting trees and promoting herbs (Fig. 8). The higher diversity of the vegetation can be partly explained by the openness of the forest, as it generally leads to a more even distribution of the pollen types, higher pollen richness, and thus more diverse conditions (Giesecke et al., 2014). In addition, Neolithic land use likely led to the formation of new vegetation communities, which also increased the diversity of the vegetation (Marinova et al., 2012).

CONCLUSIONS

Limni Zazari provides the first continuous, high-resolution multiproxy palaeoecological and palaeoenvironmental reconstruction of the Mesolithic–Neolithic transition for Northern Greece by combining pollen, microscopic charcoal, and biogeochemical proxies. Such uninterrupted time series can provide novel ecological insights into the response of vegetation to discrete disturbance events such as drought, frost, or fire. We can show that the natural forests in this region were sensitive to changes in climate and reacted quickly to RCC events with reduced moisture availability. Drier conditions between 8600 and 8000 cal yr BP opened the woodlands and enabled the re-expansion of forest-steppe vegetation. The introduction of farming in Northern Greece and thus mainland Europe was likely advantaged by this climate-induced vegetation change that had already started before the “8.2 ka event”. We assume that early farmers took advantage of the openings in the deciduous oak forests to cultivate cereals on small plots between the tree stands. Conversely, Neolithic farmers only had a small impact on the forest structure, e.g., by using fire to open the vegetation to grow crops and graze animals. Changes in vegetation composition were facilitated by land use, creating legacy effects that after 8000 years still persist today. Climate change projections predict decreasing precipitation for the Mediterranean region if greenhouse gas emissions are not drastically reduced (IPCC, 2022). According to our data, a reduction in moisture availability and related increase in fire incidence will severely affect the forest cover and related ecosystem services in Northern Greece. More detailed precipitation and temperature records would be very valuable to better understand the drivers of Holocene ecosystem and land use changes.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/qua.2024.40.

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Competing interests. The authors declare that there are no conflicts of interest.

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