

**Climate variability
since MIS 5 in
SW Balkans**

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Climate variability since MIS 5 in SW Balkans inferred from multiproxy analysis of Lake Prespa sediments

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Abstract

The transboundary Lake Prespa (AL/FYROM/GR) has been recognized as a conservation priority wetland. The catchment area has a remarkably diverse flora that points to its refugial properties. A lake sediment core retrieved from a coring location in the northern part of the lake was investigated through geophysical, sedimentological, geochemical, and palynological analyses. Based on tephrochronology, radiocarbon and electron spin resonance (ESR) dating, and cross correlation with other Northern Hemisphere records, the age model suggests that the basal part of core Co1215 reaches back to 92 ka cal BP. Here we present the response of this mid-altitude site (849 m a.s.l.) to climate oscillations during this interval and assess its sensitivity to millennial-scale variability. Endogenic calcite precipitation occurred in Marine Isotope Stages (MIS) 5 and 1 and is synchronous with periods of increased primary production (terrestrial and/or lacustrine). Periods of pronounced phytoplankton blooms (inferred from green algae and dinoflagellate concentrations) are recorded in MIS 5 and MIS 1 and suggest that the trophic state and lake levels underwent substantial fluctuations. Three major phases of vegetation development are distinguished: the forested phases of MIS 5 and MIS 1 dominated by deciduous trees with higher temperatures and moisture availability, the open landscapes of MIS 3 with significant presence of temperate trees, and the pine dominated open landscapes of MIS 4 and MIS 2 with lower temperatures and moisture availability. Forest dynamics, cover and density are discussed in an altitudinal context and the existence of temperate tree refugia is examined.

1 Introduction

The Balkan Peninsula is currently very heterogeneous in terms of its landscapes, climate and habitats (Grove and Rackham, 2003). This heterogeneity has shaped the fauna and flora through time and accounts for the impressive floral and faunal biodiversity, also found on the Iberian and Italian peninsulas (Blondel et al., 2010). These

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three Mediterranean peninsulas, in particular the Balkans, are thought to have provided shelter for species over recurring glacial-interglacial cycles (Griffiths et al., 2004).

A recent review of the vegetational response in Europe during the last glacial (Fletcher et al., 2010) demonstrated that millennial-scale events, such as Dansgaard–Oschger (D–O) cycles and Heinrich (H) events are clearly identifiable in both terrestrial and marine pollen diagrams. Two features are apparent from this regional review of MIS 4 to MIS 2. Firstly, long and continuous sequences registering millennial-scale variability during this period are located almost exclusively within the Mediterranean region. Indeed, owing to its latitudinal location, this region has provided exceptional records that span several glacial cycles such as the renowned pollen sequence of Tenaghi Philippon (Wijmstra, 1969). The second feature is the limited number of glacial records originating from the Balkans in comparison with sites from the Italian and Iberian peninsulas. Several long and continuous pollen sequences encompassing multiple glacial cycles have been obtained from Greece (Wijmstra, 1969; Okuda et al., 2001; Tzedakis et al., 2002). Some of them confirm the notion of glacial refugia for temperate trees (e.g. the loannina basin located in northwestern Greece). There are no pollen records covering the Last Glacial cycle outside Greece with the exception of Lake Ohrid (Lézine et al., 2010). However, most cores retrieved from the latter reveal disruptions in the sedimentation patterns (Vogel et al., 2010; Lézine et al., 2010).

The Lateglacial pollen record from neighboring Lake Prespa (Fig. 1) provides insights into the vegetation and climate conditions at a centennial-scale from an altitude of 849 m a.s.l. (Aufgebauer et al., 2012; Panagiotopoulos et al., 2013). Ensuing isotopic and hydrological studies on a c. 16 m core (Co1215) confirmed the sensitivity of the site to climate variability (Wagner et al., 2012; Leng et al., 2013) and a recent lithological and tephrostratigraphical study on a c. 18 m long core (Co1215) indicates that the sediment accumulation in the central northern part of the lake is undisturbed and covers the last c. 92 ka cal BP (Damaschke et al., 2013).

Here we present geophysical lithological, geochemical and palynological data of core Co1215 with a focus on biological proxies and ecological processes. Our multi-proxy

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approach aims at understanding the complex responses of the Lake Prespa catchment to climate variability during the Last Glacial. In order to assess the impacts of orbital- and suborbital-scale variability we first examine the response of the study area on a local level, and then compare it to selected regional and global reference archives. Finally, we discuss implications of the climate reconstruction for modern human dispersal into Europe and other environmental constraints posed on hominid migrations/populations.

2 Physical setting

The Prespa Lakes (Megali and Mikri Prespa) and the surrounding streams and springs, enveloped by mountains forming several peaks around or above 2000 m a.s.l., are shared between Albania, the Former Yugoslav Republic of Macedonia, and Greece (Fig. 2). Lake Megali Prespa, hereafter referred to as Lake Prespa, has no surface outflow and is separated by an alluvial isthmus from Lake Mikri Prespa. The lake has a catchment area of 1300 km², a mean water depth of 14 m (48 m maximum), and a surface area of 254 km² (Matzinger et al., 2006). Lake Prespa is situated at 849 m a.s.l. and drains through karst channels traversing the Galičica and Mali Tate mountains into Lake Ohrid standing at 693 m a.s.l. Hence, it belongs hydrologically to the Adriatic drainage region, although recent faunal studies suggested a closer biogeographical affiliation with lakes eastwards belonging to the Aegean drainage region (Wilke et al., 2010).

The geology of the area mainly comprises Mesozoic limestones and granites. The climate is transitional and can be classified as sub-Mediterranean with continental influences. Mean July and January temperatures in the lowlands are 21 and 1° C, respectively, with a mean annual temperature of 11° C. Precipitation varies from 750 mm in the lowlands to over 1200 mm in the mountains and peaks in winter when snowfalls are frequent (Hollis and Stevenson, 1997). Consequently, streams and springs are fed by late spring snowmelt resulting in peak lake levels in May and June. Total inflow

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comprises stream and spring discharge (56%), direct precipitation (35%) and Mikri Prespa inflow (9%). In the absence of natural surface outlet, water from Lake Prespa is mostly evaporated (52%), fed through the karst aquifer (46%) to Ohrid springs, and 2% is used for irrigation (Matzinger et al., 2006). Increasing anthropogenic pressure combined with precipitation patterns and the closed nature of the watershed account for the annual lake level change and an estimated residence time of 11 yr (Matzinger et al., 2006). Apart from seasonal variations, lake levels have oscillated historically (up to several meters) as evidenced by existing national records and inundated settlement ruins from the 11th century (Wagner et al., 2012). Level fluctuations of Lake Prespa are expected to influence the sedimentation regime given the shallow water depth with reference to the large surface area. At present, Lake Prespa is a mesotrophic lake and overturning of the water column has been documented to occur between fall and spring, while thermal summer stratification results in dissolved oxygen depletion below 15 m (Matzinger et al., 2006). However, the lake underwent substantial changes in its trophic, mixing and level status in the past (Aufgebauer et al., 2012). The presence of gyres on the surface of Lake Prespa is assumed to propagate currents in the water column leading, in concert with geostrophic effects, to the formation of a contourite drift (Wagner et al., 2012).

The diverse topography of the Lake Prespa catchment and its location at a transitional climate zone gave rise to an assemblage of central European, Mediterranean and Balkan endemic plant species (Polunin, 1980). Panagiotopoulos et al. (2013) described the diversity and origin of the modern flora found at Prespa and discussed the refugial character of the study site.

3 Material and methods

Here we present a dataset of core Co1215 (40°57'50" N, 20°58'41" E) with a composite length of 1776 cm recovered from a location at the northern part of Lake Prespa (14.5 m water depth) in November 2009 and June 2011 (Fig. 2). The coring location displays

relatively undisturbed sedimentation, revealed after a shallow hydro-acoustic survey (Wagner et al., 2012). The core was recovered from a floating platform equipped with a gravity corer for surface sediments and a 3 m long percussion piston corer for deeper sediments (UWITEC Co. Austria). One core half was used for non-destructive analyses (e.g. XRF scanning) and then archived at the Institute of Geology and Mineralogy at the University of Cologne; the other half was subsampled at 2 cm intervals and the samples were freeze-dried and homogenized using an agate ball mill.

3.1 Geophysical and geochemical analyses

X-ray fluorescence (XRF) scanning was performed at 2 mm steps with an analysis time of 10 s per measurement using an ITRAX core scanner (COX Ltd. Sweden). The count rates of individual elements presented here were used as semi-quantitative estimates of their relative concentrations (for more details see Aufgebauer et al., 2012). Total carbon (TC) and total inorganic carbon (TIC) were measured with a DIMATOC 200 (DIMATEC Co. UK) and total organic carbon (TOC) was calculated by subtracting TIC from TC. The identification of carbonate types (e.g. calcite, siderite) was determined by X-ray diffraction (XRD) analysis (Leng et al., 2013).

3.2 Palynological analyses

Palynological analyses were performed on 170 subsamples taken at 2–16 cm intervals. After measuring their volume, samples were sieved (112 μm), *Lycopodium* tablets (Stockmarr, 1971) were added in order to calculate concentrations, and subsequently they were processed using standard palynological techniques. Identification of palynomorphs was performed with relevant keys and atlases, as well as the reference collection of the Laboratory of Palynology of the Seminar of Geography and Education at the University of Cologne (Panagiotopoulos et al., 2013; and references therein). An average of 500 (with a minimum of 300) terrestrial pollen grains were counted per sample (with the exception of two samples at 546 and 890 cm with a pollen sum of

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171 and 177, respectively). The average temporal resolution between pollen samples, derived from the presented age model, is ca. 500 yr (ranging between 50 and 1250 yr). Relative percentages were based on the sum of terrestrial pollen (excluding aquatics and spores). The term aquatics (or aquatic vegetation) in this study comprises vascular plants (macrophytes); and phytoplankton comprise green algae and dinoflagellates. The latter are presented in concentrations and the former both in concentrations and percentages based on a pollen sum including the main pollen sum and aquatics. Nomenclature and taxa group terminology follows Panagiotopoulos et al. (2013). Apart from *Artemisia*, which is plotted separately, the Asteraceae curve comprises differentiated Asteroideae, Cichorioideae and Centaurea pollen percentages. Poaceae groups together Poaceae (wild types) and Cerealialia (cultivars > 40 µm). Although *Phragmites* pollen grains were not differentiated, the modern vegetation of Prespa suggests that *Phragmites* grains must form part of the Poaceae (wild type) group. *Quercus* comprises differentiated deciduous (*Quercus robur*-type and *Quercus cerris*-type) and evergreen types.

The *Pediastrum* species encountered (*P. boryanum* spp., *P. simplex*) are freshwater planktic green algae, which have a cosmopolitan distribution and wide ecological tolerance (Komárek and Jankovská, 2001). Both species are dominant in eutrophic lakes under temperate climates, although the latter is also commonly found in tropical regions (Komárek and Jankovská, 2001). *Botryococcus* species are dominated by *B. braunii* mostly in association with *B. neglectus* and *B. pila*. The synchronous occurrence of *Pediastrum* and *Botryococcus* species is characteristic of large eutrophic lakes with open water surface and extensive submerged and littoral vegetation typical for climatic optima (Jankovská and Komárek, 2000).

Dinoflagellate cysts were counted in pollen slides and can be attributed tentatively to *Gonyaulux*-type. Two morphotypes were distinguished; a dominant one with pronounced and protruding ornamentation present throughout the core and one with very limited or absent ornamentation and intermittent presence. Further studies (including SEM imaging) are needed to determine the species. Kouli et al. (2001) reported

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the presence of two identified freshwater dinoflagellates (*Gonyaulux apiculata* and *Spiniferites cruciformis*) from Lake Kastoria. As this lake is situated 20 km southwards from Lake Prespa, it is assumed the dinoflagellates encountered at Prespa (*Gonyaulux*-type) belong to *G. apiculata*.

3.3 Chronology

The age model of core Co1215 is based on accelerator mass spectrometry (AMS) ¹⁴C dates, tephrochronology, electron spin resonance (ESR) dating and cross correlation with the NGRIP ice core record and described in detail in Damaschke et al. (2013) (Fig. 3). Radiocarbon dates were calibrated into calendar years (a cal BP) using the INTCAL09 calibration curve (Reimer et al., 2009) and for the uppermost sample using the Levin14c dataset (Levin and Kromer, 2004). All ages presented in this paper are calendar ages. Aufgebauer et al. (2012), Wagner et al. (2012) and Damaschke et al. (2013) elaborate on the composition and correlation of the identified tephra layers, as well as on the ESR dating of a shell horizon at 1458–1463 cm. The ESR dating provided the only independent chronological tie-point below 858 cm (representing the last identified tephra layer) in core Co1215. Two additional tie points demarcating the maximum age of the lowermost part of the core were fixed by tuning two TOC peaks to Dansgaard–Oeschger (D–O) warming events 21 and 22 of the NGRIP GICC05modelext (Damschke et al., 2013). According to the proposed age model, the base of the sediment sequence can be extrapolated to c. 92 ka cal BP.

4 Results

The upper 320 cm of core Co1215, spanning the past 17 ka, were described with respect to lithology, geochemistry and chronology in Aufgebauer et al. (2012) and with respect to palynological and microscopic charcoal data in Panagiotopoulos et al. (2013). Wagner et al. (2012) and Leng et al. (2013) presented sedimentological

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and geochemical data for the upper 1576 cm and provided some first age estimations of the sequence. This study presents sedimentological, palynological, geophysical, and geochemical parameters for the longest (1776 cm) composite core to date, after the addition of 2 m recovered during fieldwork in June 2011.

5 Considering the distinct and overlapping lithological and palynological units, the ensuing discussion utilizes the marine isotope stages (MIS) chronological framework (Lisiecki and Raymo, 2005) to facilitate comparison between different proxies as well as other regional or global archives.

4.1 Lithology and geochemistry

10 Three lithofacies (L3, L2, L1) occur in Co1215, and have been distinguished based on color, grain-size composition and chemistry (Fig. 3). Lithofacies 3 (1776–1516 and 204–0 cm) sediments are characterized by olive-brown colored bioturbated silt, relatively high organic matter and calcium carbonate (calcite) and low to intermediate clastic content. Lithofacies 2 (1516–1380, 1066–662, and 292–204 cm) has gray-olive, non-laminated silts with intermediate organic content, and generally low carbonate content but with distinct TIC (calcite and siderite) and Fe spikes. Sporadic occurrence of
15 sand and gravel was recorded in L2. Lithofacies 1 (662–292 and 1380–1066 cm) sediments are gray, bioturbated, dominated by silt and with very low organic content. Conspicuous TIC (siderite) and (Fe) spikes are present between 1380 and 1066 cm, and
20 an irregular black-greenish lamination associated with black spots and high Fe and Mn (between 662 and 292 cm). Coarse sand and gravel were present intermittently throughout L1.

4.2 Pollen Assemblage Zones (PAZs)

Ten local pollen assemblage zones (P-1 to P-10) and several subzones were delimited
25 based on visual inspection of the pollen record and supported by CONISS analysis for pollen taxa (> 2%) included in the pollen sum as implemented in TILIA (Grimm, 1992).

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Zone numbers and letters were assigned with ascending order from top to bottom (Fig. 4).

Arboreal pollen (AP) percentages above 80 % with a significant deciduous-tree component (20 % *Quercus*, 10 % *Carpinus* and 10 % *Fagus*) are recorded in zone P-10 (1776–1680 cm). In P-9 (1680–1580 cm), non-arboreal pollen (NAP) percentages rise up to 60 % abruptly (30 % *Artemisia*, 15 % Poaceae and 10 % Chenopodiaceae), while tree values (mostly conifers) contract (AP < 40 %) and recover at the top of the zone (~ 80 %). Aquatic pollen percentages (excluded from the main pollen sum) and phytoplankton concentrations reach maximum values in zone P-9 forming prominent peaks. The ensuing P-8 (1580–1390 cm) marks the last consecutive zone with AP percentages crossing the 80 % threshold. P-8b (1580–1480 cm) is characterized by high arboreal values (> 80 %) and a gradual transition to conifer-dominated pollen spectra (from 20 % to 60 % *Pinus*). An abrupt expansion of NAP percentages (21 % Poaceae and 10 % *Artemisia*) and a subsequent contraction occur in P-8a (1480–1390 cm). *Pinus* dominance (up to 60 %) continues in P-7 (1390–1180 cm), while NAP rise above 50 % towards the top of the zone. In P-6 (1180–1027 cm) the *Pinus*-dominated AP percentages decline and NAP percentages stay above 50 % throughout the zone (*Artemisia*, Chenopodiaceae and Poaceae values mostly above 10 %). *Pinus* and *Quercus* percentages rise towards the top of the zone (peaking at 18 %) in parallel with Poaceae (peaking at 20 %) and Aquatics (*Typha* reaches absolute maximum values of 3 % within P-6). In P-5 (1027–760 cm), several peaks above 70 % are recorded in AP percentages and an absolute maximum of NAP values (NAP = 90 % comprising 43 % *Artemisia*) at the top of the zone. AP percentages are dominated by *Pinus* (up to 60 %), however a significant *Quercus* component is present (peaking at 19 % and contracting down to 2 %) and several other deciduous trees are almost continuously present despite very low values (e.g. *Carpinus* and *Ulmus*). Conspicuous NAP spikes (mostly *Artemisia*) are characterizing P-5 and the succeeding P-4 (760–525 cm). In P-4, AP values show abrupt fluctuations and decline (below 50 %) at the top of the zone. Asteraceae percentages peak (27 %) towards the top of the zone, whereas deciduous tree

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values decline. In P-3 (525–364 cm), *Quercus* percentages contract further and absolute minima (< 1%) are recorded at the top of the zone. Abrupt fluctuations of *Pinus* values, continuous *Hippophae* presence and increasing Aquatics percentages characterize zone P-3.

The ensuing zone, P-2 (364–240 cm), marks the gradual expansion of deciduous tree percentages and the parallel decline of *Pinus*. Two conspicuous *Artemisia* and *Chenopodiaceae* peaks are registered in P-2c (364–277 cm) and P-2a (240–204 cm) separated by a subzone, P-2b (277–240 cm), with relatively high AP percentages (> 65%). Zone P-1 (204–0 cm) is characterized by high AP percentages (up to 95%) that decrease (70%) at the top of the record. *Abies* and several deciduous trees percentages rise above 10% (e.g. *Quercus*, *Carpinus*, *Corylus* and *Fagus*), while *Pinus* declines substantially (min. 5%). Mediterranean taxa (e.g. *Phillyrea*, *Pistacia* and *Olea*) are continuously present in this zone. Aquatics and phytoplankton concentrations peak within P-1.

5 Discussion

5.1 The Prespa paleoarchive

5.1.1 Vegetational and limnological feedbacks to climate variability at a local scale

The pollen record (Fig. 4) reveals two distinct phases (P-10 and P-8b) of high and sustained arboreal pollen percentages (AP > 70%) at the base and one (P-1) at the top of core Co1215. During these intervals, deciduous trees dominated the pollen spectra and displaced *Pinus* suggesting warmer and moister conditions. According to the age model, P-10 and P-8b correspond to MIS 5 and P-1 to the Holocene. The forested landscape inferred is substantiated by relatively high arboreal pollen concentration (proportional to tree population density) and low to intermediate Ti counts which indicate

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fluctuating allochthonous clastic material input (i.e. Ti; Fig. 5b and d). In contrast, in P-7, P-6, P-4 (upper part), P-3 and P-2c AP percentages stay below the 70 % boundary suggesting these time periods represent an open landscape and glacial conditions. As pollen percentages are dependant of each pollen type included in the pollen sum, some taxa such as *Pinus* with its exceptional pollen productivity and dispersal properties are over-represented in the relatively open landscapes encountered during full glacial conditions. These pollen zones, corresponding to MIS 4 (P-7 to P-6) and MIS 2 (P-4 to P-2c), contain extremely low arboreal pollen concentrations (below 200 000 grains cm⁻³) and have a high clastic content. Arboreal relative percentages (reflecting mostly forest composition) were dominated by *Pinus* during MIS 4 and MIS 2. Although *Quercus* pollen is present throughout the record, pointing to the refugial properties of the area, distinct minima occur within zones P-6, P-5 and P-3. A prolonged phase of moderate *Quercus* percentages occurs between P-6 and P-4 and correlates with MIS 3. During this interval of abrupt AP percentage fluctuations, total tree abundance (percentages and concentrations) was high in comparison with the preceding (MIS 4) and ensuing (MIS 2) intervals.

It is apparent that climate oscillations control the response of vegetation within the Prespa watershed influencing spatial patterns and floristic composition through time. However, there are other environmental parameters, such as geomorphology, slope exposure, soil formation, lake level, pH and nutrient availability, which determine vegetation development in the terrestrial and aquatic ecosystems. Semi-aquatic and aquatic vascular plant pollen percentages in Prespa (Fig. 4) can be employed as a proxy to infer fluctuations in lake levels (e.g. Harrison and Digerfeldt, 1993). Poaceae percentages are assumed to contain a portion of grassland (upland) and reed-bed taxa (e.g. *Phragmites* sp.) growing at the littoral zone. In Co1215, Poaceae maxima are synchronous with *Artemisia* peaks (a proxy of increasing aridity) throughout the core. At first sight, this appears to be contradictory as grasslands usually expand with increasing precipitation. Hence, we assume that *Phragmites* sp. contribute a significant percentage to Poaceae expansions during these zones and consequently these abrupt expansions

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are estimated to be synchronous to fluctuating lake levels. Along with peaking *Typha* and Cyperaceae percentages, Poaceae percentages are used to infer intervals of spreading reed beds and sedgeland. At this point, it should be underlined that changes inferred from aquatic pollen are relative and indicative of trends (e.g. a lowering of the lake level). They do not necessarily coincide with low or high stands of Lake Prespa (namely with actual water depth). In fact, the concomitant occurrence of *Nymphaea*, *Sparganium*, *Myriophyllum* and *Potamogeton* pollen suggest rather deep waters (> 6 m) at the coring site (Harrison and Digerfeldt, 1993) throughout the study period. Therefore, different lines of evidence (i.e. sedimentological, seismic, geochemical, geophysical and isotopic data) are compiled to infer changes in the littoral and aquatic environment of Lake Prespa through time.

Green algae and dinoflagellate concentrations (Fig. 5d and e) are considered to represent periods when frequent phytoplankton blooms occurred. Rising temperatures and light intensity, nutrient availability, and the onset of lake stratification constitute the major parameters controlling (springtime) phytoplankton blooms (Wetzel, 2001). In mesotrophic and eutrophic lakes, diatoms and cyanobacteria (blue-green algae) account for dense blooms as a result of excess nutrient accumulation, notably phosphorus. On an annual basis, phytoplankton blooms are usually terminated with the gradual depletion of soluble nutrients (e.g. phosphorus, nitrogen, silicon) available for algae growth in the epilimnion (Wetzel, 2001). In Co1215, high plankton concentrations occur in MIS 5, MIS 3 and MIS 1. In general, these intervals coincide with increased forest cover suggesting higher moisture availability and/or temperatures in the catchment. However, absolute maximum values occurred during a short interval in MIS 5 concurrent with an abrupt arboreal retreat (P-9). Matzinger et al. (2006) discussed the dramatic impact of changes in lake volume on the concentration of dissolved nutrients (in particular the focusing on phosphorus) considering the relatively shallow depth of Lake Prespa with respect to its surface area. In the presence of low lake-levels, increased wave and current activity and thus enhanced mixing and oxygenation are

expected. In addition, increased nutrients (e.g. phosphorus) and oxygenation could lead to high lake productivity and extensive blooms.

The lake productivity proxies in Co1215 (Figs. 4 and 5d, e) comprise green algae (*Pediastrum* and *Botryococcus* species), dinoflagellates (*Gonyalux*-type) and aquatic vascular plants (emerged, submerged and floating; Fig. 4). Along with terrestrial pollen (Fig. 5a and d), they are assumed to indicate changes in organic matter (OM) sources within the Prespa catchment. Atomic C/N values between 4 and 10 imply that sedimentary OM in Co1215 originated from non-vascular plants and is probably affected by decomposition (Meyers, 1994). The synchronous C/N, TOC, AP/NAP and plankton fluctuations (Fig. 5a, c, f) downcore and peak C/N values corresponding to forested intervals (i.e. MIS 5 and MIS 1) suggest that diagenesis did not alter significantly the source signal of OM for the past 92 ka. Indeed, Rock Eval analysis of the Prespa sediments confirmed that although oxidation did play an active role, the source of OM was found to be a function of climate/hydrology (Leng et al., 2013). High rates of OM oxidation are mostly found during MIS 4 and MIS 2 and coincide with phases of open catchment vegetation, low primary production and siderite precipitation in the lake sediments (Leng et al., 2013).

Carbonate minerals formed intermittently in Lake Prespa throughout the period examined (Fig. 5g). Calcite precipitation occurred sporadically in MIS 5 and continuously in MIS 1 (Holocene). Calcite precipitation is often controlled by pH shifts induced by photosynthesis (higher pH and removal of carbon dioxide causing precipitation). Subsequent respiration and decomposition of OM lower the pH releasing CO₂ and thus promote CaCO₃ dissolution. Usually, most of the autochthonous precipitated calcite is dissolved in the anoxic and more acidic hypolimnion (Cohen, 2003). Dittrich and Koschel (2002) have shown that sedimentation of phosphorus and calcite precipitation are closely linked; and that artificial addition of Ca(OH)₂ in the hypolimnion during summer in a stratified hardwater lake intensified calcite precipitation and lowered the trophic state enhancing the internal phosphorus sink. The absence of calcium carbonate in the Glacial is assumed to be a result of low trophic status, dissolution due to

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aerobic decomposition of organic matter and inhibited ion supply from the catchment (Aufgebauer et al., 2012). However, siderite (FeCO_3) peaks in Co1215 are scattered within the Last Glacial. The TIC peaks throughout MIS 4 to MIS 2 occur alongside Fe peaks and suggest changing redox conditions and burial processes, such as proposed for peaks in Mn (Wagner et al., 2010).

5.1.2 Temporal and spatial development of local ecosystems

MIS 5 (c. 92–71 ka cal BP; P-10 to P-8)

In terms of forest dynamics within the Prespa catchment, the AP/NAP curve (Fig. 5a) outlines the rather limited duration of closed-canopy phases in Co1215. High percentages of *Abies* along with *Quercus*, *Carpinus*, *Fagus*, and other deciduous trees point to sufficient moisture availability and temperatures for growth in P-10 (c. 92–87 ka cal BP). However, the conspicuous absence or appearances of isolated grains of Mediterranean taxa suggest that (winter) temperatures were not favorable for their survival/expansion. A similar picture of advancing temperate forest and absence of sclerophyllous species occurs within P-8 (c. 81–71 ka cal BP). Continuous presence of the latter is confined to P-1 (Holocene) and marks in effect the warmest interval in the core. Two periods (P-9 and P-8a) of rapid herb expansion interrupt forest continuity at the base of Co1215. The collapse of conifer populations, the relative stable *Quercus* and rising *Betula* percentages and pronounced peaks of *Artemisia* and Chenopodiaceae attest to increased aridity, dropping temperatures and a descending treeline in P-9 (c. 87–81 ka cal BP). A parallel AP concentration decrease supports the notion of thinning tree stands. A similar arboreal (mainly *Pinus*) response with maximum Poaceae (Fig. 4) percentages is evident in P-8a (c. 75–71 ka cal BP). In both zones, pollen spectra resemble the ones belonging to Younger Dryas (P-2a) discussed extensively elsewhere (Panagiotopoulos et al., 2013). Calcite precipitation during MIS 5 is mostly confined to a short interval between 87–82 ka cal BP and two isolated peaks at 91 and 74 ka cal BP. High and fluctuating TOC throughout MIS 5 implies high catchment productivity. The

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apparent decoupling of organic and inorganic carbon preserved in Lake Prespa sediments points to increased accumulation and/or deposition of organic matter and intensified dissolution, respectively. The first TIC peak at the base of Co1215 is the only interval in MIS 5 coincident with a forested watershed phase (high AP percentages and concentrations) and relatively high green algae content (*Pediastrum*) suggesting high temperatures, limited decomposition and seasonal bottom water anoxia. Between 87 and 82 ka cal BP, three distinct TIC (calcite) peaks are expressed concurrently in fluctuating C/N and TOC. However, the TIC peaks between 87–82 and 74 ka cal BP occur during periods of declining tree cover and apparently lower lake levels.

MIS 4 (c. 71–57 ka cal BP; P-7 and P-6)

Pinus dominance established in zone P-8a continues in P-7 (c. 71–64 ka cal BP), and deciduous tree and *Abies* percentages decline gradually reaching minimums within the subsequent zone (P-6; c. 64–57 ka cal BP). AP concentrations are very low and the relatively stable Ti values suggest limited clastic material input in contrast to MIS 5. IRD, first recorded at the end of MIS 5 (P-a), is present throughout this interval and suggest ice-floe transport. Chenopodiaceae, *Artemisia* and Poaceae values culminate in this order upcore in P-6. The declining TOC and C/N ratio suggest retreating catchment vegetation and/or increased degradation of OM due to enhanced mixing promoted by a colder climate and/or a lower lake level. The synchronous *Typha* and Poaceae maxima at the top of P-6 point to a lake level lowering. Two pronounced siderite peaks concomitant to Fe peaks indicate changes in the redox front conditions and correspond to distinct minima in AP percentages (at 66 and 63 ka cal BP). The apparent opening of the landscape and/or lowering of treeline imply a cold climate regime and a deficit in moisture required for tree growth within the catchment. Trees (mostly hardy pines) were restricted to favorable habitats provided by the diverse topography of the Prespa area. The ensuing decline of herb percentages and a notable *Quercus* peak mark the top of P-6.

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MIS 3 (c. 57–29 ka cal BP; P-5 and partly P-4)

The onset of MIS 3 is characterized by the expansion of deciduous tree percentages (primarily *Quercus*). The parallel increase of AP concentrations points to a rise in primary production in the Prespa catchment. Relatively high C/N values (above 6) up to c. 50 ka cal BP imply an increased input of terrestrial OM and/or inhibited decomposition. The siderite and Fe peak at c. 55 ka cal BP corresponds to a period of decreasing AP abundance and clastic content suggesting enhanced mixing of the water column. The presence of IRD, which is continuous throughout MIS 3, indicates the occurrence of (at least partial) ice cover at Prespa. Although pines constitute the majority of trees at Prespa, the continuous *Abies*, *Betula*, *Quercus* and *Carpinus* curves along with intermittent presence of others (e.g. *Alnus*, *Corylus*, *Ulmus*, *Tilia*) suggest their likely survival within the catchment. A pronounced minimum in AP percentages at the top of P-5 (at 39 ka cal BP) coincides with the deposition of the substantial (19 cm) Y5 tephra layer. Following this abrupt event, trees return briefly to values preceding the perturbation (at the base of P-4) and decline significantly (down to 20%) thereafter. From c. 40 ka cal BP till the end of MIS 3, the geochemical proxies and the AP percentages show abrupt fluctuations. AP minima and siderite precipitation are accompanied by changes in the redox conditions and the mixing regime of Lake Prespa. The low TOC and C/N values (below 6) during this period suggest that primary productivity declined and/or decomposition of OM increased. At c. 31 ka cal BP *Artemisia* and Chenopodiaceae peak while a synchronous siderite precipitation event marks the end of MIS 3.

MIS 2 (c. 29–14 ka cal BP; partly P-4 to P-2c)

At the top of P-4, Asteraceae (excluding *Artemisia*) reach maximum values, ensuing the distinct *Artemisia* and Chenopodiaceae peaks. Arboreal pollen concentrations show minimum values and resemble conditions similar to MIS 4. The relatively high tree percentages in P-3 comprise mostly pines. *Abies* and *Quercus* are the only other trees in the catchment with most likely continuous presence, but with very limited abundances.

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Quercus absolute minima (< 1 %) are recorded at the top of this zone (P-3) suggesting cold and dry conditions. The synchronous *Pinus* and *Abies* peaks point to the critical role of extremely low temperatures rather than moisture availability, in light of no significant peak in steppe elements (i.e. *Artemisia* and Chenopodiaceae). In P-2c (c. 19–15 ka cal BP), distinct peaks of *Artemisia* and Chenopodiaceae indicate periods of increased aridity. The very low TOC content and C/N values imply retreating tree cover in the surroundings of Lake Prespa and a high decomposition of OM. The TIC peaks are concurrent with AP percentage minima, as well as increased and abruptly fluctuating iron counts, suggesting abrupt shifts in temperatures, moisture availability, redox conditions at the hypolimnion. In addition, the very low phytoplankton concentrations point to restricting temperatures and/or nutrient availability for their growth.

MIS 1 (c. 15 ka cal BP to Present; partly P-2b to P-1)

The Lateglacial transition and the onset of the Holocene marked the termination of the last glacial and the return to interglacial conditions at Prespa. During MIS 1, the Prespa catchment underwent substantial changes in floristic composition as forests expanded (ascending treeline) and diversified. The restricted erosion activity, inferred from decreasing titanium counts, and maximum AP concentrations of (absolute max of 23×10^5 grains cm^{-3}) suggest the closing of the tree canopy within the catchment. High macrophytes concentration indicates fluctuating lake levels during the Lateglacial and the Holocene. Aufgebauer et al. (2012) and Panagiotopoulos et al. (2013) describe in detail the vegetational and limnological response to climate change during this interval. Holocene sediments with high TOC content suggest high primary production in the Prespa watershed, as well as enhanced deposition of OM and thus seasonal stratification and hypolimnion anoxia. Relatively high phytoplankton (green algae and dinoflagellates) concentrations during this interval imply increased nutrient accumulation and/or higher temperatures. This increase in lake productivity was coincident with forest expansion (P-1 in Fig. 4) and decreasing allochthonous input. High and synchronous TIC content was attributed to authigenic calcite precipitation corresponding

to higher temperatures and productivity in the lake (Aufgebauer et al., 2012). However, during the Early Holocene TIC values (Fig. 6g) remained low implying that increased dissolution of calcium carbonates occurred with seasonal stratification.

5.1.3 Understanding ecological processes, triggers and thresholds

5 Three noteworthy events involving lentic organisms are encountered in the Prespa sequence (phytoplankton blooms, dinoflagellate migration and formation of a shell horizon) and their potential ecological-indicator value is assessed.

The *Pediastrum* and subsequent dinoflagellate peaks at 85 ka and 84 ka cal BP (1648 and 1624 cm) are the only recorded incidents of planktonic population expansion of this order (maxima of 19×10^5 coenobia cm^{-3} and 14×10^5 dinoflagellates cm^{-3} , respectively). Calcite peaks between 87 and 82 ka cal BP, an abrupt opening of the landscape (AP, Ti) and peaking macrophyte (e.g. *Typha* and Cyperaceae) and plankton percentages suggest that the catchment underwent dramatic changes within this interval. The descending treeline left large areas of the surrounding limestone slopes barren and exposed to chemical weathering and erosion. Rising percentages of emergent aquatic vegetation point to fluctuating lake levels and frequent flooding of the littoral zone. Increased aridity and lower annual temperatures inferred from corresponding pollen spectra suggest that these flooding events can be related to seasonal releases of snowmelt from local ice caps (Woodward and Hughes, 2011). Owing to bedrock composition of the Prespa catchment, lake-water likely became supersaturated with respect to calcium during these events. Pronounced calcium peaks concurrent to TIC peaks back this interpretation. Moreover, relative high fine-sand content (up to 14 vol% at 1578 cm) corroborates the notion of increased wave and current activity indicating lowering lake levels and/or increased aeolian activity. Therefore, the expansion of sedgeland (Cyperaceae) and reed beds (e.g. *Phragmites* and *Typha*) attest to lower lake levels and most likely also accounted for increasing OM accumulation allowing riparian trees (i.e. *Salix* and *Alnus*) to reclaim land and in effect pushing the reed beds further into the lake. It should also be noted that during this period summer insolation

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and light intensity were increasing (Fig. 5a). This could imply that aridity promoted by enhanced seasonality (rather than lower temperatures) was the decisive parameter controlling the aforementioned environmental response. However, the conspicuous absence of Mediterranean taxa pollen points to a rather dry and cold climate regime similar to the one inferred during the Lateglacial to Holocene transition (Panagiotopoulos et al., 2013).

The acceleration of calcium ion accumulation and generally enriched nutrient concentrations caused by a presumed lower stand of Lake Prespa provided ideal conditions for algal growth (see Sect. 5.1.1). The unprecedented phytoplankton blooms (inferred by peaking *Pediastrum* and dinoflagellates concentrations) were in turn instrumental in triggering the formation of calcite (nucleation) and thus catalyzed its precipitation. The concomitant double TOC peak and low terrestrial productivity suggest that phytoplankton was the major source of OM deposited. Considering that both planktonic species preserved in pollen slides are composed of robust sporopollenin and cellulose (for green algae and dinoflagellates, respectively), the relative high C/N ratio (above 12) can be partly attributed to these properties and due to restricted decomposition of OM. Increased macrophyte biomass (Fig. 5e) within this interval probably accounted for the high C/N ratio as terrestrial biomass retreated substantially. Indeed, relatively high macrophyte percentages (e.g. *Typha*, *Cyperaceae* and *Sparganium*) and concentrations are registered between c. 87–81 ka cal BP (P-9; Fig. 4).

In contrast to green algae, dinoflagellates are not found in the period prior to 87 ka cal BP (1672 cm). Thus, it is postulated that they were most likely introduced (reintroduced?) into the lake by migrating (avian) fauna. In fact, Wilke et al. (2010) reported the appearance of bivalves (*Dreissena* spp.) in artificial water reservoirs – constructed during the last decades in Greece – implying the occurrence of such re/introduction events on a regular basis. The third event accounts for the TIC peak (calcite) at 74 ka cal BP comprising a horizon of *Dreissena* (*presbensis*) fragments and was tentatively attributed to low lake levels (Wagner et al., 2012).

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A *Dreissena* shell layer (1463–1458 cm) formed at 74 ka cal BP and corresponds to the last calcite peak in MIS 5. *Dreissena* spp. are native to several Balkan lakes (Albrecht et al., 2007) and in contrast to their infamous relative, namely the invasive zebra-mussel (*D. polymorpha*), form an integral and vital link in the trophic chain of these ecosystems. These freshwater bivalves exhibit a similar feeding strategy to their marine counterparts (i.e. filtering particles suspended in the water column) and preferably attach to solid substrates (Griffiths et al., 2004). Sparse *Dreissena* fragments were also encountered and dated in the uppermost centimeters of Co1215. Considering the current water depth and distance to the shore, these fragments were most likely transferred to the coring location with waves and currents. A similar transfer mechanism and lower lake levels can be invoked to explain the formation of the mollusk horizon. Wagner et al. (2012) interpreted the undulating reflections found in hydro-acoustic profiles from Lake Prespa during this interval as the result of intensified wave/current activity and low lake levels. Accordingly, the opening of catchment vegetation and decreasing percentages of deciduous trees in P-8a (c. 75–71 ka cal BP) point to a moisture deficit and dropping temperatures. In general, aquatic vegetation abundance is rather low with the exception of a pronounced Poaceae maximum that could indicate a high *Phragmites* percentage (see Sect. 5.1.1). In addition, measured phytoplankton concentrations are peaking within this zone (P-8a). It seems plausible that the expansion of the littoral zone caused by a lake-level lowering is responsible for the population growth of *Dreissena* providing suitable habitats and nourishment. Based on genetic and mismatch analyses, Wilke et al. (2010) modeled the spatial and demographic expansion of *Dreissena* at Prespa and reported estimated ages of 72 and 113 ka for these expansions, respectively. It can be argued that demographic expansion of *D. presbensis* at Prespa is related to the unprecedented event of 74 ka cal BP marking the end of MIS 5.

5.2 Comparison with regional and global records

5.2.1 Mediterranean records

On a regional scale, the Prespa pollen record is probably best compared to the Monticchio (Allen et al., 1999) and Ioannina (Tzedakis et al., 2002) pollen archives (Fig. 6), as both records have a similar climate (sub-Mediterranean), elevation (middle-altitude, located at 656 m a.s.l. and 470 m a.s.l., respectively), sedimentation regime (absence of hiatus), sample resolution (detecting millennial-scale variability), and timescale (reaching back to MIS 5). Despite the differences in elevation, topography, sedimentation, chronology and plant composition some general conclusions can be drawn from the comparison between the three pollen records. It should be noted that the Monticchio sequence features an independent chronology based on tephrostratigraphy and varve counting. Whereas, orbital tuning was applied beyond the range of radiocarbon dating in core I-284 (Ioannina), which differs from the tuning procedure for the basal part of Co1215. As evidenced in Sect. 5.1, pollen relative percentages can be misleading in respect to the actual forest coverage of the examined paleolandscapes. Consequently, the ensuing discussion focuses on prominent features that can be traced across several proxies and/or archives.

Further regional records include the oxygen stable isotopes measured in speleothems from Soreq cave (Bar-Matthews et al., 2000) and the Alkenone-derived SST curve from core MD01-2444 at the Iberian margin (Martrat et al., 2007).

The temperate tree (AP – *Juniperus* + *Pinus*, mostly *Quercus*) curve of I-284 (Fig. 6 D), the site with the lowest altitude, provides a closer match to the AP curves of Prespa and Monticchio. This is partly due to the rather limited role of *Pinus* at the Ioannina basin and the dominance of deciduous *Quercus* in the pollen spectra (Tzedakis et al., 2002). A similar picture emerges from Monticchio (Allen et al., 2000), where *Pinus* relative abundance is limited and attains maximum values only around the LGM (> 40 %) while *Quercus* percentages dominate pollen spectra (i.e. MIS 5, MIS 3 and MIS 1). In comparison, core Co1215 has the highest (lowest) *Pinus* (*Quercus*) percentages.

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Among other factors, it has been suggested that mid-altitude sites were better suited in sustaining refugial temperate tree populations due to the effect of orographic precipitation (Bennett et al., 1991). Tzedakis et al. (2004) studied three pollen records from contrasting bioclimatic areas in Greece and demonstrated the importance of local topography and ecological thresholds in controlling the response of the vegetation to climate variability. The Lake Prespa catchment sustained temperate tree populations throughout the Last Glacial (Fig. 4). However, the intermittent appearance and very low values of some drought-sensitive taxa, such as *Fagus*, *Ulmus* and *Tilia*, during MIS 4 to MIS 2 imply that environmental conditions were challenging for growth at an altitude of 849 m a.s.l. (minimum). Taking into account the individual characteristics of each record examined here, it can be argued that the Lake Prespa catchment at 849 m a.s.l. seems to form roughly the upper distribution limit of drought-sensitive trees at these latitudes in Mediterranean mountains.

The *Quercus* curve of Co1215, although continuous, registers very low oak values in specific in MIS 4 and MIS 2 (Fig. 6f). These intervals show the maximum contraction of *Quercus* percentages in all three pollen records, suggesting cold and dry conditions, and a rather open landscape (Fig. 5d). The $\delta^{18}\text{O}$ record from Israel is in agreement with pollen records, and depicts pluvial conditions in MIS 5 and MIS 1 (Fig. 6c). As precipitation in that area originated from the Mediterranean Sea (Bar-Matthews et al., 2003), and given its independent ^{230}Th -U dating, it appears that the conditions described above were synchronously prevalent across the (central and eastern) Mediterranean.

The deposition of two Sapropel layers (S3 and S1) in the eastern Mediterranean coincided with peaks in the speleothem oxygen-isotope record and AP percentage maxima in all pollen records (implying a notable increase in rainfall). It was originally proposed that these organic rich layers, which formed under anoxic conditions in the eastern Mediterranean basin, originated during periods of increased Nile River runoff fed by enhanced monsoon intensity (Rossignol-Strick, 1985). It was demonstrated that increased Nile discharge was not the exclusive cause of sapropel formation (Rohling and Hilgen, 1991). However, Rossignol-Strick (1985) described first

the temporal connection between sapropel formation and orbital forcing. Hilgen (1991) correlated sapropels to precession minima (when perihelion occurs in boreal summer and aphelion in boreal winter) and eccentricity maxima. With this orbital configuration, the seasonal insolation contrast (enhanced summer and subdued winter insolation) is greater and thus it affects atmospheric and oceanic circulation (e.g. monsoonal intensification). At Prespa, increased lake and catchment primary production are associated to June insolation maxima during MIS 5, MIS 3 and MIS 1 (Fig. 5). AP percentage maxima concurrent to sapropel deposition are preceded by pronounced retractions (GS 22 and YD) of trees evident in all records presented.

5.2.2 Global records

Millennial-scale climate variability was expressed in the North Atlantic during the Last Glacial at a suborbital scale. Events of extreme iceberg discharges from the Laurentide Ice Sheet to the Hudson Strait occurred during this period and are detected as distinct layers of ice-rafted debris (IRD) in marine cores from the North Atlantic (Heinrich, 1988). Bond et al. (1993) recognized six Heinrich events (H1–H6) and additional ones were also proposed (Hodell et al., 2008). Dansgaard–Oeschger (D–O) cycles, characterized by a rapid warming and subsequent cooling, are another type of millennial-scale climate oscillations first recorded in Greenland ice cores spanning the last glacial period (Dansgaard et al., 1984).

Numerous investigations around the globe have detected the imprint of these short-lived climate oscillations in different proxies in the marine as well as in the terrestrial realm (Dansgaard et al., 1984). Marine cores from the Iberian continental margin have been instrumental in establishing the link between ice and other terrestrial records showing the synchronous response of European vegetation to Greenland climate oscillations (Cacho et al., 1999; Sánchez Goñi et al., 2000). Allen et al. (1999) associated millennial-scale variability at Monticchio with the one observed in Greenland ice-cores and argued that the Mediterranean region responded to changes in North Atlantic climate rapidly. At Ioannina, Tzedakis et al. (2002) suggested that AP absolute

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minima should correlate to Heinrich events recorded in marine cores from the Iberian margin.

At Prespa, Wagner et al. (2010) correlated peaks in Mn and Zr/Ti from cores Co1202 and Co1204 (retrieved from Prespa and Ohrid, respectively; Fig. 2) with cold intervals associated with Heinrich events in the North Atlantic. Sediments of the longest core from Lake Prespa to date (Co1215) react sensitively to suborbital climate oscillations and capture these global signals in different proxies. Synchronous peaks in Fe and TIC correlate well with H6, H4, H3, and H2, but there are absent during H5 and H1 implying the complex interplay between climate and environmental parameters and limnological processes. Despite the resolution constraints, the *Quercus* curve picks up several D–O warming events (Fig. 6f), while Heinrich events are imprinted as distinct minima in AP percentages. Heinrich event 4, which is concurrent to the deposition of the Y5 tephra layer (de Vivo et al., 2001; Lowe et al., 2012), had the greatest impact (AP percentages absolute minimum) on the vegetation at the Lake Prespa catchment. This observation is in agreement with the SST record from the Iberian margin (Fig. 6b), which was associated with the lowest sea surface temperatures ($\sim 10^{\circ}\text{C}$) within the period studied. Consequently, the Campanian/Ignimbrite eruption was not solely responsible for the conditions experienced downwind, but probably enhanced the impacts experienced by local ecosystems. The combined effect of H4 and the volcanic ash also affected the other two pollen sites as registered by significant declines of AP percentages.

5.3 Environmental constraints posed on hominid populations

Modern human colonization of Europe is in the spotlight for researchers from a variety of disciplines. Genetic studies (involving mitochondrial and Y-chromosome DNA) confirmed the African origin of modern humans and estimated their dispersal out of the continent between c. 80 and 60 ka BP (Mellars, 2006). Although skeletal remains from Skhul and Qafzeh caves in Israel indicate an early and apparently short-lived colonization of the Levant in MIS 5 (c. 100 ka BP), there are no signs of dispersal at such an early stage into Europe (Mellars, 2011; Richter et al., 2012).

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The Aurignacian technocomplex, associated with many distinctive features of “modern” cultural behavior, took place at c. 40 ka (Upper Paleolithic) according to the archaeological record and has been traditionally linked with the dispersal of modern humans into Europe (Mellars, 2011; Richter et al., 2012). This period differs considerably from the preceding Middle Paleolithic that is considered to be formed of Neanderthal communities (Mellars, 2011). Mellars (2004) pointed out that major constraints in the process of unraveling these migration trajectories have been the quality of dated material and the implicit limitations of radiocarbon dating and calibration techniques at the time. Despite the continuous advances in ^{14}C calibration (Reimer et al., 2009), the selection and treatment of dated material (e.g. shell, bone) is critical and can bias the acquired ages.

One well-established migration route for subsequent modern human dispersals westwards into Europe is considered to be the Danube River valley (Conard, 2002; Conard and Bolus, 2003; Mellars, 2004; Zilhão et al., 2007). The Peștera cu Oase site located in close proximity to the Danube in the southwestern Carpathians (Fig. 1) yielded one of the oldest directly dated human finds in the Balkans with an age of c. 40 ka cal BP (Trinkhaus et al., 2003; Zilhão et al., 2007). Recent evidence from a site in the UK (Higham et al., 2011) provided estimates of a human maxilla with an age of c. 43 ka cal BP making it the oldest known modern human fossil in northwestern Europe to date. Assuming that one of the primary dispersal routes crossed the Balkan peninsula, it should be expected that modern human finds in this and surrounding areas should be at least of the same age. Indeed, deciduous molars of modern human origin from Grotta del Cavallo (associated with the Uluzzian industry) were dated indirectly at c. 44 ka cal BP (Benazzi et al., 2011). The only known sites associated with this technology outside of the Italian peninsula are located in the Peloponnese, Greece (layer V at Klissoura, Cave 1; Koumouzelis et al., 2001; Lowe et al., 2012), and consequently a Levantine origin can be assumed (Mellars, 2011), although the Uluzzian is absent in the Near East.

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The pollen record from Lake Prespa reveals a period of relative high AP and *Quercus* percentages between 60 and 35 ka cal BP that are interpreted as the signature of increased precipitation and higher temperatures (Fig. 6g). The oxygen isotope record from Israel registers a concurrent increase in precipitation at the Levant that coincides with the onset of MIS 3 (Fig. 6c). These findings, apparent in regional and global archives, suggest that climatic conditions were favorable for sustained forest growth within this interval at Prespa. Müller et al. (2011) argued that the summer insolation maximum at c. 58 ka cal BP resulted in a northward displacement of the Intertropical Convergence Zone (associated with increased rainfall in northern Africa) and thus facilitated modern human dispersal out of the continent during the period between 55 to 50 ka cal BP (GI 14-13). Based on a collapse of AP percentages at the Tenaghi Philippon record concurrent to Heinrich event 5 (Fig. 6b), the authors suggested that modern human populations invaded Europe taking advantage of the demographic vacuum left by retreating Neanderthals during this centennial event.

The impact of the H5 event (c. 48 ka cal BP) at Prespa, as is the case for Ioannina, was apparently less severe on arboreal vegetation given the dating and sampling constraints. As a consequence, the climatic and environmental conditions across the southwestern part of the Balkan Peninsula remained favorable for modern human occupation during most of the MIS 3. A precipitation gradient between western and eastern Greece exists today and was present during the last glacial as it was demonstrated in pollen archives from Greece (Tzedakis et al., 2004). Differences in local parameters, such as topography and plant composition, can therefore hamper the comparison between different records and proxies (even within similar climate regimes). Thus, the need of a dense network of paleorecords from a region is critical for the accurate reconstruction of climatic and environmental conditions along potential corridors of human migration.

It should also be noted, that ice accumulation during glacial times was a major factor in shaping coastal planes and determining the paleocoastline (Waelbroeck et al., 2002). Sea-level fluctuations (of up to 100 m, see the 100 m contour line marked in

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in enhanced erosional activity in the catchment and restricted lake productivity. Siderite formation occurs sporadically throughout the glacial and signified substantial changes in lake mixing and redox conditions. Several of these peaks depicted in the TIC curve are concurrent to short lived cold events and probably represent far field responses to the North Atlantic events. During periods of enhanced lake productivity (MIS 5 and MIS1) calcite is precipitated in the lake and the lake-mixing regime is altered.

The Lake Prespa record appears to be in good agreement with regional and global archives depicting orbital and suborbital climate variability. Despite the limitations of the age model of Co1215 (i.e. tuning with NGRIP curve at the basal part), major climate events are in phase with other archives in the eastern Mediterranean featuring independent chronologies (e.g. speleothem record). The Prespa record as well as other reference archives from the Mediterranean point to a time window encompassing MIS 3 when the climate conditions were likely favorable for modern human dispersal from the Levant into Europe.

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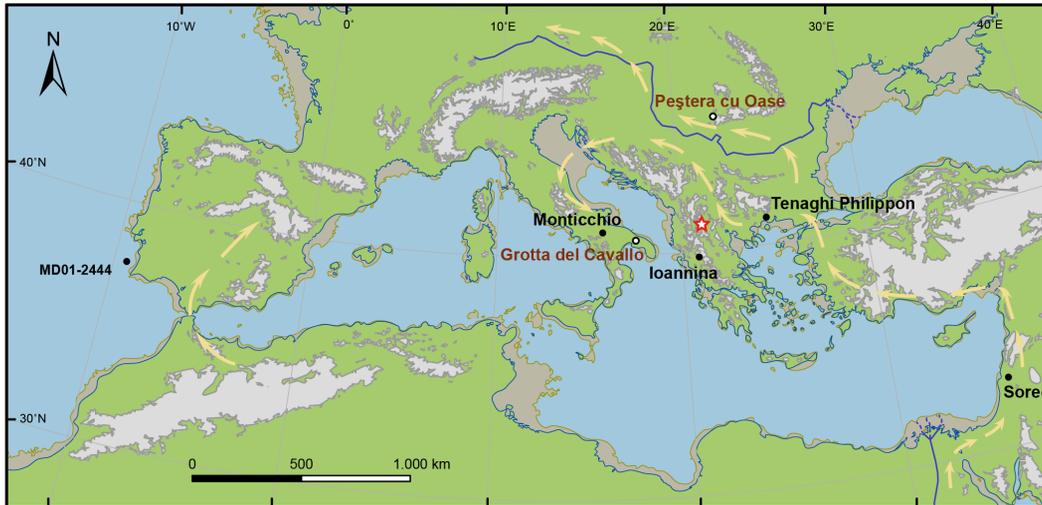


Fig. 1. Locations of selected records discussed and of Lake Prespa (star); archaeological sites are marked with an open circle. Note the paleocoastline during MIS 3 at 100 m below present sea level (in brown) and possible dispersal routes of modern humans (arrows).

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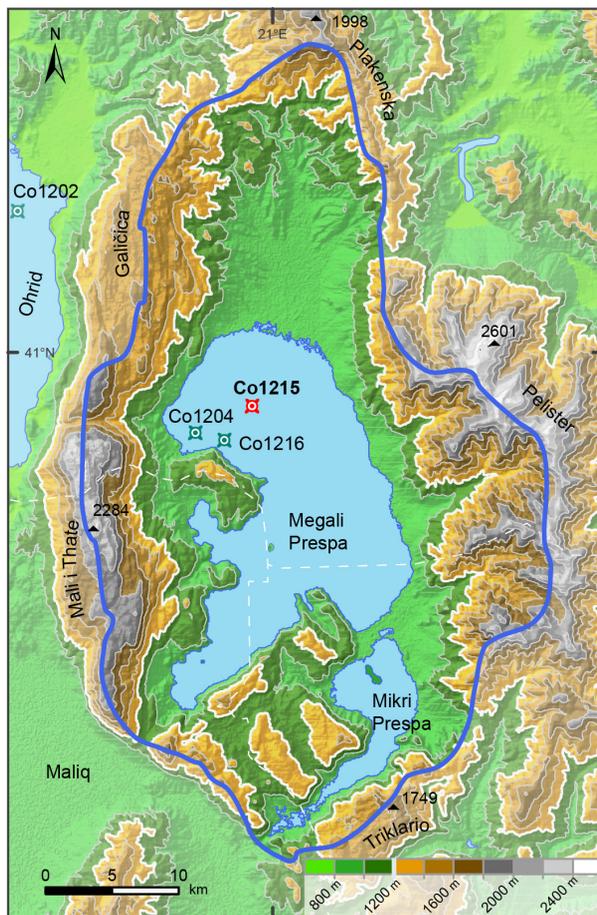


Fig. 2. Topography of Lake Prespa. Lake catchment (blue line) and core locations (Co1215, this study) are shown (SRTM Data: Jarvis et al., 2008).

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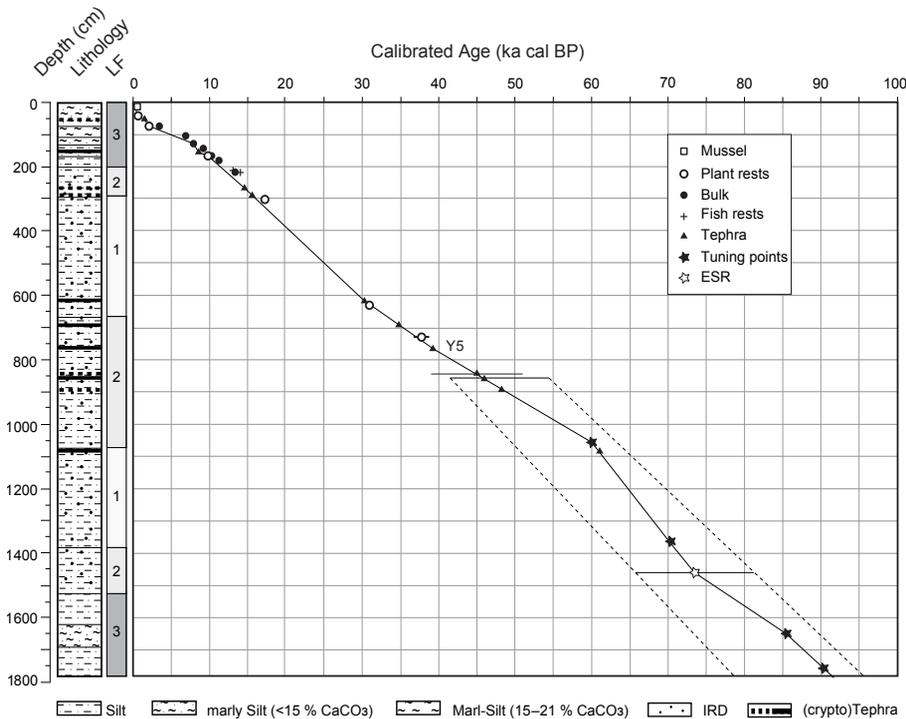


Fig. 3. Age model of core Co1215 with lithology. Reliable age control points were interpolated on a linear basis.

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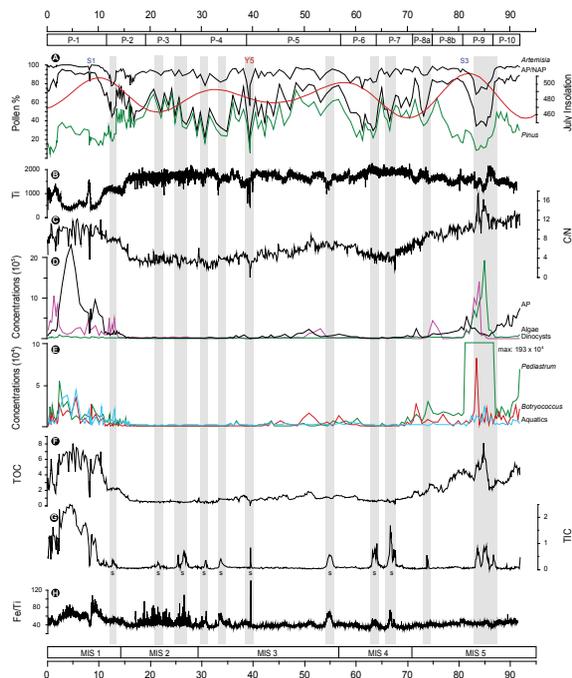


Fig. 5. Selected biological, geophysical and geochemical proxies from Lake Prespa (core Co1215) plotted against age. (A) *Artemisia* (dashed line), AP/NAP (black), and *Pinus* (green) pollen percentages; mean July insolation at 40° N (W m^{-2} ; red); sapropels (S1, S3); and Y5 tephra layer, (B) Titanium (Ti) counts, (C) Atomic C/N, (D) Concentrations ($\times 10^5$) of arboreal pollen (AP; black), green algae (green) and dinoflagellates (purple), (E) Concentrations ($\times 10^4$) of aquatics (blue), *Botryococcus* (red) and *Pediastrum* (green). Note the difference in scale, (F) Total organic carbon (wt. %); siderite (s) peaks are marked, (G) Total inorganic carbon (wt. %), (H) Iron/titanium (Fe/Ti). Shaded intervals correspond to carbonate peaks precipitated at Lake Prespa during the Last Glacial.

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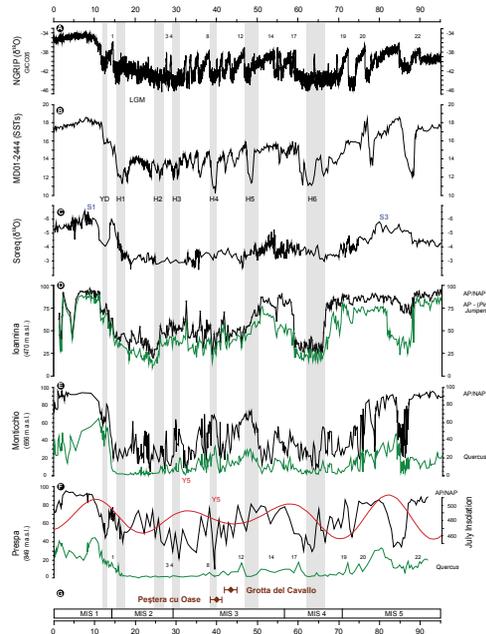


Fig. 6. Comparison of Prespa proxies with regional and global records. (A) Ice oxygen isotopes (‰) measured in NGRIP (GICC05) with Dansgaard–Oeschger (D–O) warming events/Greenland interstadials (GI) numbered; Last Glacial Maximum is indicated, (B) alkenone derived (U_{37}^K) sea surface temperatures (SSTs) measured in core MD01-2444 from the Atlantic Ocean, (C) oxygen isotopes (‰) measured in speleothems from Soreq cave (Israel) and sapropel depositions (S1, S2) in the eastern Mediterranean Sea, (D) AP/NAP (black) and AP minus *Pinus* and *Juniperus* (green) pollen percentages in I-284 from Lake Ioannina (Greece), (E) AP/NAP (black) and *Quercus* (green) pollen percentages from Lago Grande di Monticchio (Italy), (F) AP/NAP (black) and *Quercus* (green) pollen percentages from Lake Prespa; mean July insolation at 40° N ($W m^{-2}$; red), (G) calibrated radiocarbon ages from neighboring sites with modern human remains. Gray bars correspond to Heinrich events in MD01-2444.

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