DIATOM AND VEGETATION RESPONSES TO LATE GLACIAL AND EARLY-HOLOCENE CLIMATE CHANGES AT LAKE ESTANYA (SOUTHERN PYRENEES, NE SPAIN).

[1]Vegas-Vilarrúbia T., [2] González-Sampériz P., [3]Morellón M., [2] Gil-Romera G., [2] Pérez-Sanz A; [2]Valero-Garcés B.

[1] Dep. Ecology, Fac. Biology, University of Barcelona, Barcelona, Spain. Email: tvegas@ub.edu. Phone: +34 93 4031376

[2] Pyrenean Institute of Ecology, Spanish Scientific Research Council, (CSIC), Zaragoza, Spain.

[3] Instituto de Geociencias, CSIC,UCM. Facultad de Ciencias Geológicas, Univ. Complutense. Madrid, Spain.

ABSTRACT

We investigate Lake Estanya's diatom and pollen records from the Late Glacial (LG) to the Early Holocene (EH), in order to compare limnological and vegetation responses to common climate forcing. The biotic changes recognized in this study largely agree with the hydrological evolution of the lake described previously for the same period. The diatom record shows high sensitivity to fluctuations in both lake level and salinity concentration as consequence of climate shifts. In addition vegetation results indicate that the area could have played an important role as regional vegetation refuge. Shallow lake conditions during the Last Glacial Maximum (LGM) were punctuated by relatively deeper freshwaters between 19.3 and 18.6 cal kyr BP and at 18.0 cal kyr BP, as recorded by diatom shifts. A subsequent increasing aridity trend, coinciding with the Mystery Interval (MI), affected the diatom accumulation rates, which dropped to its minimum values between 17.2 to 14.7 cal kyr BP. Particularly dry and cold conditions during the LGM and MI are supported by the largest values of steppic pollen taxa of the whole sequence, which account for up to 40%. However, relatively high values of *Betula* during the Heinrich Event 1 suggest a plausible regional vegetation refuge. Abrupt cooling and warming episodes within the LG triggered remarkable ecological threshold crossings in the diatom communities, especially during the stadial/interstadial episodes. At this point, the vegetation reflect the onset of warm conditions during the Bølling/Allerød with the partial substitution of *Betula* by Marcescent and Evergreen *Quercus*, what probably indicates the arrival of

temperate taxa to the area and the likely migration of birch to higher altitudes. The Younger Dryas Stadial shows a complex ecological response. Diatoms are very poorly preserved, but aquatic taxa reach their highest values. An increase in Marcescent *Quercus* during this cold stage lends further support to the hypothesis that this is a regional vegetation refuge. Low lake levels recorded during the EH affected the development and preservation of diatom communities. A delay in the onset of humid conditions for the EH is also supported by the vegetation composition, characterized by the maximum expansion of *Juniperus*.

Keywords: Biological responses, Diatoms, Ecological threshold, Mediterranean basin, Multiproxy approach, Paleoecology, Paleolimnology.

1. INTRODUCTION

Forecasting the nature and magnitude of future biotic responses to climate change requires understanding of the complexity of system response to climate forcing at different temporal scales (IPCC 2007). Although it is often argued that the climate change predicted for this century is unprecedented due to its high rate of change and magnitude, some of the climate oscillations during the last glacial cycle (ca. 120.0-11.6 kyr BP) in the northern Hemisphere were also "abrupt" and "rapid", typically occurring at a centennial or decadal scale (Broecker 2000). For example, the North Atlantic Dansgaard/Oeschger cycles (Dansgaard et al. 1993; Grootes et al. 1993) and the Heinrich events (Bond et al. 1992; Broecker 1994) alternated gradual cooling with abrupt warming. Particularly, the rapid warming trend at the end of the Younger Dryas and the beginning of the Holocene (Dansgaard et al. 1989) has been proposed as a possible past climate analogue, because both magnitude and rates of change parallel those predicted for the present century (Jackson and Overpeck 2000; Steffensen el al. 2008; Vegas-Vilarrúbia et al. 2011)

The available Iberian records show rapid hydrological, environmental and climate changes during the last glacial cycle and suggest a strong link between the Western Mediterranean and the North Atlantic climate (Pérez-Obiol and Julià 1994; Valero-Garcés et al. 1998; Cacho et al 1999, 2001; González-Sampériz et al., 2006; Moreno et al. 2010, 2012). A conspicuous regional feature for the last 25,000 years is that most of the North Atlantic cooling events correspond to drought periods, as deduced from dust accumulation (Moreno et al. 2002), speleothem records (Moreno et al. 2009), lacustrine sequences (Moreno et al. 2012) and both marine (Fletcher and Sánchez-Goñi 2008) and continental pollen sequences (González-Sampériz et al. 2010; Carrión et al. 2010).

Biotic responses to climate change during the Late Glacial and Early Holocene in most western Mediterranean regions have been mostly assessed using palynological records while other key palaeolimnological variables like diatoms, ostracods or chironomids, which offer independent responses to palaeoclimatic variables, have been comparatively less well studied. Pollen records show that vegetation responses during periods of rapid climate change, particularly at a local scale, also depend on autoecological processes, the proximity to refuge areas and/or high regional topographical variability (Carrión et al. 2010). Lacustrine diatoms are very sensitive to changes in water balance and conductivity and consequently have a great potential to test hypotheses of climate fluctuations, especially in regions with

a marked alternation between dry and wet phases like closed basins in the Mediterranean region (Ryves et al 1996; Reed et al. 2010). Diatoms have short life cycles and show a rapid, species-specific responses to variations in the precipitation/evaporation ratio (P/E) that in turn affect important limnological variables, i.e. water temperature, lake level, salinity and nutrients concentration and lake productivity (Battarbee et al. 2001; Adrian et al. 2009). For instance, diatoms provided a clear evidence for the Younger Dryas reversal to cold and arid conditions in Ioannina sequence, northwest Greece, where vegetation response was apparently inhibited (Lawson et al. 2004; Wilson et al. 2008). In the Iberian Peninsula, diatom records are really scarce, particularly for the Late Glacial and Early Holocene. However, the existing sequences show, for example, a clear response to Early Holocene climatic shift in lakes from NW – Lake Lucenza (Leira and Santos 2002) and Lagoa Grande (Leira 2005)- and SW Iberia - Laguna Medina- (Reed et al., 2001), and more subdued changes in mountain areas (Lake Enol, Moreno et al. 2009). These records show a complex hydrological variability and associated response in the Iberian Peninsula.

Our approach to better understand the nature, speed and thresholds of biological responses to gradual and rapid past climate shifts is based on a multidisciplinary strategy applied to lacustrine sequences, including pollen, diatom, sedimentological and geochemical techniques to assess the terrestrial vegetation, lake biota and paleohydrological history, and the leads and lags of the different sub-systems to particular climatic events.

Lake Estanya sequence (Morellón et al. 2009a, b) provides an opportunity to illustrate this approach because the main hydrological and environmental changes during the last 20 kyr have been documented using several proxies (sedimentary facies, elemental and isotopic geochemistry and biogenic silica) and a robust age model. In this paper we investigate the nature of ecological responses of diatom communities and vegetation to climate changes recorded between ca. 20-9.5 kyr BP in Lake Estanya, and we evaluate the local and regional factors modulating the respective biotic responses.

2. REGIONAL SETTING

Balsas de Estanya (42º02´ N, 0º32´ E) is a karstic lake complex in a small (2.45 km^2) endorheic basin located at the southern foothills of the External Pyrenean Ranges in north-eastern Spain (Fig.1). These mountain ranges are mainly composed of Mesozoic formations, and large poljes and dolines occur as the

result of karstic processes affecting Upper Triassic carbonate and evaporite materials outcropping along geological structures (IGME 1982). The Balsas de Estanya consists of three dolines, two of them with water depths of about 7 m and 20 m and one seasonally flooded (Fig. 1b). The region has a Mediterranean continental climate with long summer droughts (León-Llamazares 1991). Mean annual temperature (MAT) is 14 ºC (from MAT of 4 ºC in January to 24ºC in July); mean annual precipitation (MAP) is 470 mm (from MAP of 18 mm in July to 50 mm in October). The Estanya lakes are located at 670 m a. s. l. at the boundary between the *Quercus rotundifolia* and the *Quercus faginea* forest communities corresponding to the transitional zone between the Mediterranean and Sub-Mediterranean bioclimatic regimes (Blanco-Castro et al. 1997) (Fig.1a). Nowadays, the lakes are embedded in a patchy landscape of natural vegetation alternating with cereal crops. Hygrophyte communities of *Phragmites australis, Typha angustifolia, Juncus* spp., and *Scirpus* spp. constitute the littoral belt (Avila et al. 1984; Cambra 1991).

This study focuses on the largest lake sub-basin, the "Estanque Grande de Abajo" (Lake Estanya), where several cores have been recovered and studied (Morellón et al. 2009a, b). It has a relatively small watershed (surface area of 106.5 Ha) and although there is no permanent inlet, several ephemeral creeks drain the catchment, providing clastic material and run-off to the lake (López-Vicente 2007). The modern hydrological balance of Lake Estanya is mainly controlled by evaporation output and groundwater inputs (Morellón et al 2009a; Pérez-Bielsa et al. 2012). Maximum depth is about 20 m and slopes are steep, as shown by the bathymetry (Figure 1). The basin is composed of two sinkholes separated by a shallower sill (3 m max. depth) that emerges during low lake level periods. Measured electric conductivities (EC) are 630 µS/cm in groundwater and 372 µS/cm in surface water (Morellón et al., 2009a). Waters are alkaline and sulphate and calcium rich, with a long residence time and a strong impact of evaporation upon the lacustrine system. The thermal regime is monomictic with thermal stratification and bottom anoxia from May to October. Concentrations of nitrogen and phosphorus are very low but experience a fast turnover, as suggested from the fairly high phytoplankton concentrations (> 10,000 cells/ml). The summer maximum of phytoplankton is dominated by *Planctonema lauterbornii* and other Chlorophyceae, while the cyanophyte *Anabaena inequalis* appears when nitrates are almost exhausted. At the end of summer Dinophyceae take over with *Peridinium volzii.* Centric diatoms *Cyclotella comta* and *Cyclotella comensis* proliferate in November during mixing of the water column and persist till spring, but disappear during summer (Ávila et

al. 1984).

3. MATERIALS AND METHODS

3.2. Diatom analysis

The composite sequence based on cores 1A and 5A from the deep sub-basin (Morellón et al., 2009a) was sampled for diatom and pollen analyses. Fifty nine samples for diatom analysis were collected at 10-cm intervals along the late glacial-Early Holocene interval. Diatoms were extracted from 0.1 g of dry sediment and oxidised with hydrogen peroxide. Specimens were mounted in Naphrax and analyzed with a Polyvar light microscope at 1000X magnification. Valve concentrations per unit weight of sediment were calculated using plastic microspheres (Battarbee 1986) and transformed to diatom accumulation rates (valves $\cdot$ cm^{-1} $\cdot$ yr^{-1}). At least 300-500 valves were counted in each sample whenever possible; when diatom content was very low, counting continued until reaching at least 1,000 microspheres. Species were expressed in terms of relative abundance (%) of each taxon (Flower 1993; Battarbee et al. 2001; Abrantes et al. 2005). Taxonomic identifications and a review of autecological requirements for the principal taxa were made using specialized literature (Krammer and Lange-Bertalot 1986, 1988, 1991, 2001; Van Dam 1994; Witkowski et al. 2000; Lange-Bertalot 2001 a,b; Krammer 2002; Hofmann et al. 2011). We used the centric to pennate diatom ratio (C/P) as an indicator of the relative abundance of planktonic to benthic habitat availability as a proxy for lake level, although it is also known to indicate trophic changes mainly in disturbed environments (Cooper 1995). The dissolution index, or the degree of diatom preservation expressed by the ratio of valves showing dissolution and/or breakage to total valves number, yielded a mean value of 70%. Both phenomena indicate the impact of diagenesis as well as the importance of silicification for diatom preservation (Flower 1993; Ryves et al. 2001). Sometimes differential preservation among species might not properly reflect the diagenetic properties of the sediment (Reed et al. 2010). In our case, the central areas of most *Cyclotella* taxa remained relatively well preserved, so they were easily identified and hence did not interfere with counting accuracy. Fragilariales were commonly well preserved, while other taxa show variable preservation, yet the most representative taxa could be identified reliably. Diatom diagrams were plotted with Psimpoll software and divided into biozones using the Optimal Splitting by Information Content Method (Bennett 1996). Only taxa showing abundances > 3% were illustrated.

Canonical Correspondence Analysis (CCA) was applied to elucidate the relationships between biological assemblages of species and their environment. We previously run a Detrended Correspondence Analysis on the species matrix and obtained a gradient length (range of the site scores) of 6.6 standard deviations, which is an approximate measure of the existent ecological gradient in species turnover units and supports an unimodal distribution of species abundance (Legendre and Legendre 1998). CCA was performed on species abundance (explained variables) and XRF data counts of S, Ca, Al, K, Si, Fe, Ti from Morellón et al. (2009b) (constrained, explanatory variables). Although element chemical concentrations in sediments do not directly reflect water chemical composition, both are strongly related. Sediment composition is strongly influenced by the same drivers controlling diatom variability i.e. changes in the trophic status, salinity, lake-level fluctuations, clastic inputs.We used the Paleontological Statistics Software Package PAST (Hammer et al. 2001); samples without quantifiable valve quantities were ignored. In CCA triplots, the length of the arrows representing environmental variables is proportional to their rate of change, small angles imply high positive correlations between variables, and arrows pointing in opposite directions will be negatively correlated. Species are represented by their niche centre along each axis, i.e. by the weighted average of the axis-scores of sites in which they occur. Thus, orthogonal projection of species along the arrow permits comparisons of the relative effects of a particular variable on a diatom species. Orthogonal projections close to an arrow tip indicate a strong effect of the variable on the pattern of variation of a species. Eigenvalues sum (trace) is tested for significance using the method of permutations to determine whether there is an overall relationship between species and environment (Legendre and Legendre 1998).

3.3. Palynological analysis

Palynological samples were extracted every 10-cm intervals, intercalated about 5 cm from diatom samples. Pollen analyses followed the classic chemical method (Moore et al. 1991) modified according to Dupré (1992), thus, including HCl, KOH, HF digestion and mineral-organic particles separation with Thoulet solution (2.0 gr/cm^3 density). *Lycopodium clavatum* tablets were added in order to calculate pollen concentrations (Stockmarr 1971) and a minimum of 250-300 terrestrial pollen grains were counted in all samples. Some samples (e.g. 850 and 600 cm depth) had very low pollen preservation and only 150-200 pollen grains could be counted. Palynological identification was completed under an optical microscope

(x400, x630 and x1000 magnification) using European pollen type keys (Moore and Webb 1978) and the IPE-CSIC (Zaragoza, Spain) pollen reference collection. A total taxonomic diversity of 114 taxa was found but only some groups and significant curves for interpretation were included in the pollen diagram, plotted using Psimpoll 4.27 and divided into biozones using the Optimal Splitting by Information Content Method (Bennett 2009).

4. RESULTS

4.1. Chronology

The chronology for the lake sequence was constrained by 21 accelerator mass spectrometry (AMS) radiocarbon dates (Morellón et al., 2009a, b). In this paper we have re-calibrated the original radiocarbon dates with the INTCAL09 curve (Reimer et al. 2011) using CALIB 6.0 software and improve the correlation between cores 1A and 5A. The reservoir effect correction was applied following the approach used in Morellón et al., (2009a,b) and consistently, age/depth relationship was obtained with a generalized mixed-effect regression (Heegaard et al. 2005). Based on this revised age-depth model for Lake Estanya record the ca. 10 m of sediment sequence spans from ca 19.5 k cal yrs BP to the present, and the average error confidence interval is ca 150 kyr (Fig. 2 A). The sequence analysed in this paper spans the Late Glacial to Early Holocene (ca. 19,5 to 9,5 cal kyr BP) (Fig. 2B). Linear sedimentation rates are four times higher for clastic-dominant intervals (1.6 mm/yr) than for fine-laminated intervals (0.4 mm/yr) (Fig.2). The detailed, chronological model and sedimentary and geochemical characteristics of the composite sedimentary record of L. Estanya are described in Morellón et al. (2009a,b).

4.2. Diatom analysis

4.2.1. Stratigraphy

Figure 3 displays diatom accumulation rates and summarizes relative species abundance and the five major diatom assemblage zones (DZ-EST 1 to DZ-EST 5) defined statistically. Diatom zone DZ-EST 2 includes a number of main shifts within the diatom record and is further subdivided into eleven subzones (Fig. 3b; subzones a- k).

DZ-EST 1 (970-950 cm; ca.19, 665– 19,463 cal yr BP)

In this zone, only pennate diatoms are present and in scant quantities ($3.53 \cdot 10^4$ to $2.39 \cdot 10^5$ valves $\cdot$ $cm^{-1} \cdot yr^{-1}$) (2 samples). Assemblages are dominated by the epipelic *Diploneis ovalis* (Hilse in Rabenhorst) Cleve 189 and the epiphytic *Epithemia adnata* (Kützing) Rabenhorst (1853). Other rarer taxa include *Mastogloia smithii* Thwaites in W. Smith (1856) and *Navicula subalpina* Reichard. C: P ratio is always < 1. These species have in common their preference for habitats with mid to high electrolyte content, manly alkaline waters in continental waterbodies.

DZ-EST 2 (950- 660 cm; ca. 19,463 – 13,477 cal yr BP)

In this zone the diatom accumulation rates increases markedly, from zero to $4.35 \cdot 10^7$ valves $\cdot$ $cm^{-1} \cdot yr^{-1}$, reaching high but very fluctuating values (29 samples). C: P ratio is always >1. The zone is characterized by rapid changes in diatom community, mostly dominated by the centric diatom *Cyclotella ocellata* Pantocsek (valves with 3 ocelli), which largely determines the trends in the diatom accumulation rates. At the transition between zones DZ-EST 1 and DZ-EST 2 (subzone k) *Cyclotella ocellata* replaces *Diploneis ovalis* and shows a first peak at 945 cm, followed by a strong decrease. The interval between 936 and 920 cm is barren of diatoms except for some traces of *Campylodiscus* Ehrenberg ex Kützing (1844) sp. fragments but soon thereafter, *C. ocellata* expands again and dominates until 860 cm (subzone j). The marked decline in subzone I coincides with the reappearance of *Diploneis ovalis* and the occurrence of other pennate taxa such as the epiphytic *Cocconeis placentula* Ehrenberg, the cosmopolitan *Encyonopsis subminuta* Krammer & E. Reichardt and *Encyonema caespitosum* Kützing, *Mastogloia smithii* and *Navicula* Bory sp. 9, although these latter species appear in very low percentages. They coexist with low abundances of *Cyclotella ocellata*, until this latter species expands again (subzone h) at the expense of pennate taxa and becomes dominant again between 810 -750 cm (subzone g). During subzone g another centric diatom, *C. distinguenda* Hustedt, a pelagic inhabitant of alkaline waters, coexists with *C. ocellata*, although in relatively low proportions. *C. distinguenda* becomes dominant in 760-750 cm (subzone f), but *C. ocellata* soon recovers hegemony (subzone e). After a short interval with only traces of diatoms (750 and 740 cm depth, subzone d), *C. ocellata* populations reappear and show two maxima at 710 (subzone c) and at 680 cm (subzone a) reaching the highest value of the whole zone DZ-EST 2. The strong decrease in

subzone b coincides with a slight increase of some pennate species such as Amphora *inariensis* Krammer, *Sellaphora pupula* (Kützing) Mereschkowsky, *Cocconeis placentula*, and some species of the genus *Mastogloia* Thwaites. The transition zone to DZ-EST3 (subzone a) is abrupt and characterized with the proliferation of small quantities of *Amphora veneta* var. *subcapitata* Kisselew, *Nitzschia* cf. *filiformis* (W. Sm.) Van Heurck, *Fallacia pygmaea* (Kützing) A.J.Stickle & D.G.Mann, *Tryblionella hungarica* (Grunow) D.G.Mann, *Denticula elegans* Kützing and some species of the genera *Navicula, Pinnularia* Ehrenberg and *Mastogloia*.

DZ-EST 3 (660- 610 cm; ca. 13,477-12,502 cal yr BP)

This zone is characterized by scarce diatom presence and valve accumulation rates ranging from zero to $8.77 \cdot 10^4$ valves $\cdot$ $cm^{-1} \cdot yr^{-1}$ (6 samples). Where diatoms occur, C: P ratio is always < 1. The species assemblage characterizing the transition between zones DZ-EST2 and DZ-EST3 is replaced by an assemblage of pennate diatoms typical of aerophytic and subaerial habitats such as *Hantzschia amphioxus* and *Luticola mutica*. Also *Navicula salinarum* (Grunow 1880), known from marine and inland tidal habitats, it is very common in ephemeral Spanish salt lakes (Reed 1998) and appears for the first time in the record;

DZ-EST 4 (610- 460 cm, ca. 12,502 – 9,543 cal yr BP)

Most of the zone is devoid of diatoms. At the onset of this zone there are small peaks of freshwater diatoms *as Cyclotella ocellata* and *Cyclotella distinguenda,* and larger peaks of *Mastogloia smithii,* common in fresh- and brackish waters, and *Mastogloia braunii* Grunow, common in brackish-waters of saline inland waters. C: P ratio keeps < 1. There are some diatom traces at 562.5 cm depth and an isolated diatom peak at 503 cm ($2.95 \cdot 10^5$ valves $\cdot$ $cm^{-1} \cdot yr^{-1}$), nearly exclusively composed by the cosmopolite species *Pseudostaurosira brevistriata* (Grunow) D.M.Williams & Round, characteristic of fresh- or, oligosaline and calcium-rich waters.

DZ-EST 5 (460 – 416.5 cm, ca. 9,543 – 9,375 cal yr BP)

The beginning of the zone is marked by the return of *Pseudostaurosira brevistriata* as dominant species and the presence of *C. ocellata*. Valve accumulation rates ranges between 2.37 $\cdot 10^3$ and 1.12 x 10^5 valves $\cdot$ cm^{-1} $\cdot$ yr^{-1}. *Pseudostaurosira brevistriata* shows a minimum at the upper part of the core, with minor increases of *Luticula mutica* (Kützing) D.G.Mann and *Hantzschia amphioxys* (Ehrenberg) Grunow and smaller peaks of *Epithemia adnata*, *Denticula elegans*, *Amphora* spp. and *Mastogloia* spp. Towards the top of the zone *Pseudostaurosira brevistriata* increases again at the expenses of the other species.

4.2.2. Canonical correspondence analysis

The overall test of significance shows that canonical relationship between response (diatoms) and explanatory variables (XRF data) is significant ($p = 0.03$, 1000 permutations). The eigenvalue of the first eigenvector is $\lambda_1 > 0.3$ indicating a rather strong gradient (Table 1) (ter Braak and Verdonschot 1995). The first eigenvectors account respectively for 34.7%, 25.4% and 18.2% of total variation in response variables. Eigenvector 1 is positively correlated with Ca, S and negatively with Fe; eigenvector 2 shows weak and inverse correlations with Ca and S, and eigenvector 3 has negative significant correlations with K, Fe and Ti (Table 1). Si, K, Ti and Fe are strongly correlated with each other, reflecting their origin as clastic input from the lake basin although Si may partially be biogenic silica. Ca is present in clastic carbonates and in endogenic phases formed within the lake through inorganic or biological processes, whereas S may be associated mainly with gypsum and sulphate deposition, but perhaps also with sulphide precipitation under temporary anoxic conditions. In the first triplot (Fig. 4a) Ca, Fe and S show the highest rates of change. Sites (depths) scores appear scattered along eigenvectors 1 and 2 and roughly 40% remain clumped at the upper quadrant of the graph, these sites belong to subzone DZ-Est 2. The order of the species' orthogonal projections onto main arrows and their prolongations indicate their relative response/sensitivity to shifts in the particular environmental variables In our case, all species located on the right side of the graphs 4b and 4d seem to react distinctly to shifts in Ca and S, whereas species located on the left side of the graph seem to be related with Fe and Ti shifts. Some of the species best related to changes in Ca are *Denticula elegans*, *Amphora libyca* Ehrenberg, *Navicula* sp. 9, *Encyonopsis microcephala* (Grunow) Krammer) and *Mastogloia smithii*, while those better related to S are *Cyclotella spp.* Some of the species best related to variations in K, Ti, and Fe are *Pinnularia borealis* (Ehrenberg), *Luticola nivalis*, *Cocconeis placentula*,

Diploneis ovalis and *Navicula salinarum*, as well as some undetermined species of *Mastogloia* and *Navicula* (4d).

4.3. Pollen analysis

Five pollen zones -PZ-EST 1 to PZ-EST 5- (Fig. 5) are described for the Late Glacial and the beginning of the Holocene in the L. Estanya sequence.

PZ-EST 1 (965-720 cm depth, 19,700-14,600 cal yr BP)

Pollen preservation is low in this zone of the sequence, with sterile samples located at 890, 860, 825, 805, 785 and 728 cm depth (marked by grey bands in the pollen diagram, Fig. 5). The non-sterile samples show similar palynological features: *Pinus* and *Juniperus* are the dominant taxa in the arboreal pollen group (AP), with fluctuating proportions at around 20%, and herbaceous components Steppe taxa (Chenopodiaceae, Caryophyllaceae, Urticaceae, *Rumex*, Cichorioideae, Asteroideae, Carduae, *Plantago*) and *Artemisia* dominate and reach the highest values of the sequence (40%). The presence of *Betula* reaching 10%, the occurrence of Marcescent *Quercus* in the upper part of this zone, the high values of *Ephedra dystachia* and the almost complete absence of Mediterranean shrubs are characteristic of this zone. The aquatics show very low percentages (< 5 %) and are dominated firstly by *Ranunculus* and then *Myriophyllum*.

PZ-EST 2 (720-610 cm depth, 14,600-12,500 cal yr BP)

This zone is characterized by a rapid development of forest taxa and a sharp decrease of *Artemisia* and Steppe taxa (less than 10%). The forest is mostly composed by *Pinus* and *Juniperus* (values up to 60% and 30% respectively), with a relative increase of Marcescent *Quercus* and "Other mesophytes" and a decrease in *Betula*. The hydro-hygrophytes group increases (mainly Cyperaceae, *Ranunculus* and *Potamogeton*). A sterile level occurs at the top of this section (620 cm depth).

PZ-EST 3 (610-570 cm depth, 12,500-11,600 cal yr BP)

At the beginning of this zone, the AP composition drastically changes with a decrease of conifers (pines and junipers, 10-20% and less than 10% respectively), while Marcescent *Quercus*, Evergreen *Quercus* and

Mediterranean shrubs develop. *Juniperus* slowly increases at the top of the zone. *Artemisia* and Steppe taxa continue with low values, while the aquatics increase notably, with Cyperaceae, *Typha* and *Potamogeton* showing the maximum percentages.

PZ-EST 4 (570-500 cm depth, 11,600-9,900 cal yr BP)

Juniperus spreads at the onset of this zone and becomes the dominant AP taxon (40 %) while all mesophytes, both *Quercus* types and Mediterranean shrubs values are very low. Simultaneously, *Artemisia* and Steppe taxa develop again while the proportions of aquatics decrease (both hygro- and hydrophytes). *Ephedra dystachia* and *E. fragilis* types record their last relevant proportions in the sequence whereas *Artemisia* and Steppe taxa values remain constant, somewhat decreasing, values. Aquatics present similar proportions to the previous zone, without significant changes.

PZ-EST 5 (500-400 cm depth, 9,900-8,900 cal yr BP)

The onset of this zone is defined by a sharp increase in *Corylus* and the development of Marcescent *Quercus*, "Other Mesophytes", Mediterranean shrubs and Evergreen *Quercus*. *Juniperus* abruptly decreases to less than 10% and pines recover to higher proportions (20-30%). Steppe taxa and *Artemisia* diminish and an important hydro-hygrophytes expansion (mainly Cyperaceae and *Potamogeton*) occurs.

5. DISCUSSION

Previous paleohydrological research carried out in the Lake Estanya sequence, based on sedimentology and geochemistry (Morellón et al. 2009a), demonstrated a large hydrological variability during the last ca. 20 cal kyr BP, and particularly, within the Late Glacial period. The period 20 – 9.5 cal kyr BP was characterized by arid conditions represented by shallow lake levels, predominantly saline waters and reduced organic productivity. According to this reconstruction, the most arid conditions occurred during the period 18 - 14.5 cal kyrs BP (including Heinrich event 1) and the Younger Dryas (12.9 – 11.6 cal kyrs BP). Fresher conditions characterized the 14.5 - 12.6 cal kyrs BP period, likely indicating higher effective moisture during the Bölling/Allerød. Finally, the onset of more humid conditions started at 9.4 cal kyrs, indicating a delayed hydrological response to the beginning of the Holocene.

As the identified diatom and pollen zones broadly coincide, we have structured the discussion in five periods of time in order to facilitate the comparison among them.

5.1. The Last Glacial maximum (LGM) (19.7-18.0 cal kyr BP) and onset of Termination I

The sedimentary and geochemical features indicate that Lake Estanya was relatively shallow, with a fluctuating water balance and deposition of alternating carbonate and gypsum sediments (Morellón et al., 2009). Several studies in lakes of the Iberian Peninsula and in marine records also suggest the occurrence of periods of relative positive hydrological balance during the LGM in a context of the cold and dry climate during LGM (see Cacho et al. 200, Moreno et al. 2012 and literature therein).

The diatom communities responded to these changes with alternating episodes of dominance of planktonic *Cyclotella ocellata* and others with more development of benthic and littoral taxa. The base of the sequence is dominated by the epipelic diatom *Diploneis ovalis* that in the CCA analysis appears associated with higher catchment erosion and runoff, and other benthic, alkaliphilous species like *Epithemia adnata*, associated in the CCA triplots with periods of higher and fluctuating carbonate and sulphate deposition. This assemblage is thus indicative of shallow, fluctuating conditions and alkaline waters. The substitution at 19.3 cal kyr BP of this assemblage by a planktonic community dominated by *Cyclotella ocellata* suggests more permanent and deeper waters. *C. ocellata* is considered a cosmopolitan species that thrives in different environments (Krammer and Lange-Bertalot 1986-2000), and in the European Diatom Database (EDDI) it is most frequently reported in deep alkaline lakes. However, in Spain *C. ocellata* has also been found in shallow lakes < 2m deep and is classified as a fresh- or oligosaline species, with a tolerance optimum of 0.81 mS/cm and with a tolerance range between 0.13 and 4.92 mS/cm (Reed 1998). At the end of this period (18.6 cal kyr BP) the decrease of diatom accumulation rates ($1.73 \cdot 10^5$ valves/gr·yr) and the occurrence of small proportions of most benthic and littoral taxa at the expenses of *C. ocellata* reflects an expansion of littoral habitats or closer proximity to the littoral source area both likely related to lower lake levels. At 18 cal kyr BP, a rapid increase in diatom accumulation rates points to a quick recovery of the diatom community and a shift to a relatively deeper fresher lake, as inferred from the appearance of *Cyclotella distinguenda*, an alkaliphilous diatom that has less tolerance to oligosaline conditions than *C. ocellata* (Reed 1998) (estimated tolerance optimum of 0.62 mS/cm range between 0.33 and 1.16 mS/cm). In

392 the CCA analysis the abundance of this species appears slightly more sensitive to salinity variations than *C.*
393 *ocellata*.
394 Pollen data are also coherent with fluctuating hydrological conditions, well marked by Hygrophytes and
395 Hydrophytes changes and periods of even subaerial exposure with more intense oxidation processes leading
396 to numerous palynological sterile levels. *Artemisia* and Steppe taxa (Chenopodiaceae, Caryophyllaceae,
397 Urticaceae, *Rumex*, Cichorioideae, Asteroideae, Carduae, *Plantago*) reach more than 40% of the whole
398 pollen content while AP values fluctuates between 20-40%, dominated by pines, suggesting cold and
399 generally arid conditions. Other studies in lakes of the Iberian Peninsula and of marine records also suggest
400 the occurrence of periods of positive hydrological balance in a context of cold and dry climate during LGM
401 (see Moreno et al. 2012 and literature therein). According to our chronology, the decrease of diatom
402 accumulation rates and rapid changes in community composition in Lake Estanya are synchronous with the
403 alkenone SST decrease recorded in the Alboran sea about 18.7 to 18 cal kyr BP (Cacho et al. 2001).
404
405 **5.2. The Termination 1 and Mystery interval (18 – 14.5 cal kyr BP)**
406 The sedimentological record of L. Estanya (Morellón et al. 2009b) shows an aridification trend and the
407 gradual establishment of a closed, permanent lake with alkaline conditions (18.0 – 14.5 cal kyr BP).
408 Consistently, with a drier climate trend, diatom accumulation rates decreases after peaking at about 18.0 cal
409 kyrs BP and reaches minimum values between 17.2 to 14.7 cal kyr BP (Figs. 3 and 4).
410 The interval called "Mystery Interval", including Heinrich event 1 (H1), is characterized as a global, cool
411 and arid period (Denton et al. 2006). The H1 onset (16.9 cal kyr BP) is clearly recorded in the sediment
412 record of L. Estanya by the substitution of finely laminated facies by clastic and banded gypsum facies
413 indicative of alternating flooding and desiccation with associated evaporative concentration, respectively
414 (Morellón et al 2009).
415 Other regional reconstructions also show colder and more arid conditions for this interval: the Alboran Sea
416 and Gulf of Cádiz (Cacho et al. 2001), El Portalet peatbog in the Pyrenees, (González-Sampériz et al.
417 2006), Lake Banyoles (Pérez-Obiol and Julià 1994; Valero – Garcés et al., 1998, Höbig et al., 2011) and
418 lake Siles (Carrión et al. 2002), for example. Our record does not show any diatom response to this
419 transition in terms of noticeable changes in community composition or accumulation rates (see clumped

samples and diatoms position in Fig. 6), where planktonic *Cyclotella* species remain dominant (Fig. 3, subzones d,e,f of Fig. 4). This fact is probably due to low sampling resolution during this period.

As during the LGM, palynological spectra from the "Mystery Interval" (MI) in L. Estanya (790-720 cm depth, Fig. 5) reflects a cool and arid climate, with a maximum expansion of Steppe taxa (especially *Artemisia*), the maintenance of high abundance of conifers, which dominate the AP cover and low presence or even absence of temperate taxa like Evergreen *Quercus* and Mediterranean shrubs. Values of *Pinus* below 30% could reflect long-distance pollen transport or the existence of little patches of pine forest in the proximity of the lake, while maximum values at around 10-20% (Huntley 6 Birks 1983) suggest that *Juniperus* developed both regionally and locally. *Ephedra dystachia* type and *Artemisia* have their maximum values of the whole sequence stressing the dominant arid conditions. The timing of *Artemisia* peaks are in agreement with regional data that establish the maximum expansion of *Artemisia* in the Pyrenees between 18-15 cal kyr BP (Jalut et al. 1992; Reille and Lowe 1993; González-Sampériz et al. 2006). The relatively high percentages of first *Betula* and then Marcescent *Quercus* at this time-interval in L. Estanya are not consistent with the general arid climate conditions during the MI. We consider the presence of these taxa as an indication of refuge areas for meso-thermophilous trees in the region. These refuge locations were likely associated with sites with higher water availability along river valleys fed by glacial melt water at the headwaters as it has been shown in other palaeoclimatic sequences of the Ebro Basin and Iberia (Valero-Garcés et al. 2000, 2004; González-Sampériz et al. 2004, 2005, 2010; Carrión et al. 2010).

5.3. Abrupt cooling episodes within the Bölling / Allerød interstadial (14.5-12.8 cal kyr BP)

The lack of accurate chronologies and high-resolution analyses in continental records has precluded the identification of cold episodes within the Bölling / Allerød interstadial in the Iberian Peninsula. The Portalet sequence in the central Pyrenees (González-Sampériz et al., 2006) provided the first evidence of abrupt and rapid climate changes in terrestrial sequences during the deglaciation, synchronous to the North Atlantic sequences. However, the timing and patterns of the abrupt climatic changes of the last deglaciation identified in the paleorecords of the IP and how they reflect North Atlantic variability are still a matter of debate (e.g.; Moreno et al. 2012). Sedimentological and geochemical data indicate that Estanya lake level

448 remained stable, with relatively shallow, saline conditions prevailing until 13.5 cal kyr BP, when lake
449 deposition returned to carbonate-rich facies up to 13.3 cal kyr BP indicative of a brief interval of brackish
450 water conditions and thus, a relatively more positive water balance in Lake Estanya (Morellón et al. 2009b).
451 Although the limited resolution hampers an accurate dating of the beginning or the end of these periods, our
452 data indicate a fast response of diatom communities of Lake Estanya to some of these rapid climatic
453 episodes. High diatom accumulation rates and dominance of *C. ocellata* observed between 14.5-13.5 cal kyr
454 BP suggest a positive hydrological balance throughout this period (see clumped samples and diatoms
455 position in Fig. 4), but punctuated by short episodes of decreasing diatom concentracions and associated
456 shifts in species assemblage composition (see position of samples 654 and 694, Fig. 4). For instance, a
457 decrease in diatom accumulation rates between 13.9 and 13.7 cal kyr BP is marked by the reappearance of
458 alkaliphilous diatoms inhabiting different littoral substrates at the expense of freshwater diatoms, pointing
459 to lake level instability and a partial return to shallower and brackish water conditions. Taking into account
460 dating uncertainties, this short episode leading to an ecological threshold cross broadly coincides with the
461 abrupt cooling of the Older Dryas reversal (14.1-13.9 cal kyr BP). The subsequent *C. ocellata* peak (13.6
462 cal kyr BP, one sample) could represent the first phase of the warm Allerød interstadial. Between 13.2 and
463 12.9 cal kyr BP (2 samples) *C. ocellata* disappears and the planktonic community is substituted by scant
464 populations of brackish/saline, subaerial and aerophytic diatom taxa, suggesting a second diatom ecological
465 threshold coinciding with shallower lake conditions, with some phases of subaerial exposure. Many species
466 dominating this assemblage are known from habitats with moisture variations and prone to drying out, i.e.
467 soils, sublittoral and damp sites and caves, mosses (Lange-Bertalot 2001 a,b; Poulíkova and Hasler 2007).
468 Additionally, from the presence firstly *Navicula salinarum* and secondly Hantzschia *amphioxys* with
469 estimated salinity optima of 8.9 and 39.0 mS/cm respectively (Reed 1998), we infer that environmental
470 conditions were probably brackish. This arid episode could correlate with the Intra Allerød Cooling Period
471 (13.2-12.9 cal kyr BP). A return of planktonic diatom community although in low abundances points to
472 slight recovery of lake level and could reflect the last phase of the Allerød Interstadial (12.9-12.7 cal kys
473 BP). The age model precluded a direct association of sedimentological and geochemical changes with the
474 known intra Bölling / Allerød interstadial variability (Morellón et al. 2009b). However, the diatom
475 fluctuations during this interstadial are consistent with the reconstructed paleohydrological and productivity

(δ^{13}Corg) evolution evidencing a trend towards moister and warmer conditions with minor changes promoted by short, abrupt climate changes, such as the Older Dryas (GI-1d) and the Inter Allerød Cold Period (GI-1b) (Morellón et al. 2009b).

Pollen data from zone PZ-EST2 (Fig. 5) also identify the warming and increasing humidity trend during the Bölling / Allerød interstadial, with a clear increase in the AP proportions that reach values of around 60-80%. Despite the continued dominance of pines and junipers, at a local and regional scale (Jalut et al. 1992; Montserrat 1992; González-Sampériz et al. 2005, 2006, 2008), relatively constant percentages of Marcescent *Quercus* and Evergreen *Quercus* and the development of "Other Mesophytes" indicate warmer temperatures. *Betula* proportions decrease notably suggesting the disappearance from the L. Estanya surroundings and its migration to the highlands, in agreement with the global increase in temperatures associated with this interstadial. A decreasing trend in Steppe taxa and the sharp drop of *Artemisia* also point to moister conditions. The development of the aquatic component (mainly *Ranunculus,* Cyperaceae and *Potamogeton*) would reflect a higher development of flooded environments in the basin area. The current resolution does not enable the detection of vegetation responses to abrupt climate changes within the B/A.

5.4. The Younger Dryas stadial (YD) (12.7 -11.6 cal kyr BP)

The YD stadial is characterized in L. Estanya by a lake-level drop and salinity increase as indicated by the return towards the gypsum-rich facies and decrease in organic productivity (marked by positive excursion of δ^{13}Corg and a sharp decrease in biogenic silica, compared to previous B/A values) (Morellón et al. 2009b). This salinity increase is reflected in the diatom record, by the appearance of *Mastogloia braunii* which occurs for the first time in Estanya. From ~12.7 to 9.5 cal kyr BP diatoms are nearly or totally absent. A likely explanation is that environmental conditions were inadequate for diatom colonization and/or subsequent preservation, due to, for example: i) extremely alkaline conditions in concentrated waters leading to frustules dissolution, perhaps exacerbated by an ephemeral lake state which tends to cause increased breakage (Flowers 1993; Reed 1998), ii) eventual episodes of desiccation and competition with macrophytes growth in an oligotrophic environment. Both hypotheses are supported by the sedimentary record of L. Estanya indicating a lake level drop around 12.8 cal kyr BP (Morellón et al. 2009b) and by the

palynological record showing abundance of macrophytes pollen. The near absence of valves in this part of the record prevents discerning diatom responses to the effects of cold and drought phases, characteristic of this stadial. A similar situation is recorded in L. Enol (northwest IP) for the same period (Moreno et al 2009), as samples are barren of diatoms and the sedimentary record reflects a cold environment probably depressing the lake's primary productivity.

The pollen spectra from L. Estanya sequence (PZ-EST3) do not have an unequivocal cold and arid signature as expected during the Younger Dryas. However, lacustrine sequences from the IP show different responses for the YD (Carrión et al. 2010). A drop in juniper's proportions and AP percentages as well as a new increase in Steppe taxa is strong evidence for colder and more arid conditions but *Artemisia* percentages remained similar. Besides, both Marcescent and Evergreen *Quercus*, and "Other Mesophytes" and Mediterranean shrub proportions increase, suggesting a migration of these species towards the lowlands as a result of lower temperatures at high altitude.

Finally, the aquatic taxa (macrophytes like *Potamogeton* and *Myriophyllum)* have their highest values of the whole sequence suggesting that the lake never completely dried out in spite of regional aridity. This increase in aquatic taxa during generally lower lake levels would rather reflect a higher development of shallow water habitats. Thus, alkaline waters more than drying conditions seem to explain the poor diatom preservation in L. Estanya during the YD interval. Considering that higher *Juniperus* values during the Bölling/Allerød probably implied its local presence around Estanya basin, we propose that colder temperatures during the YD caused an abrupt vegetation change with a reduction of this tree cover reduction in an open landscape. In addition, these colder temperatures facilitated a migration of mesothermophytes to lowlands, to refuge areas close to L. Estanya as occurred during Late Glacial times. This situation could explain the unexpected proportions of Mesophytes and Mediterranean taxa recorded in the L. Estanya pollen record during a cold and arid event like the YD. The abundance in the pollen record of aquatic macrophytes including *Potamogeton* and *Myriophyllum* also corroborates that the lake did not completely dry out in spite of regional aridity. This increase in aquatic taxa during generally lower lake levels would reflect a higher development of shallow water habitats with higher light penetration in the whole karstic complex, as a result of lower lake levels.

5.5. Early Holocene (11.5 – 9.3 cal kyr BP)

The sedimentary record shows that L. Estanya experienced a new water level drop after the YD, leading to development of a shallow, ephemeral saline lake-mud flat complex with alternating carbonate sedimentation during flooding and gypsum precipitation during desiccation phases (Morellón et al 2009b). Adverse conditions for diatom colonization and/or preservation were maintained, as reflected by the persistence of extremely low diatom accumulation rates and reduced diversity (Fig. 3).

Pollen data demonstrate that dry/arid conditions continued during the beginning of the Holocene (PZ-EST4, 11.5-9.9 cal kyr BP), with a maximum expansion of juniper, a clear decrease of Marcescent *Quercus*, Other Mesophytes and *Corylus*, a new increase of *Ephedra dystachia* type and *Artemisia* values, and an abrupt drop or even disappearance of both diversity and abundance of the aquatic taxa.

Scant amounts of diverse brackish diatom populations began to appear only after 9.5 kyr BP (5 samples), at the same time as $\delta\,^{13}C$ shifts indicate enhanced algal productivity consistent with the onset of more humid conditions (Morellón et al 2009b). Synchronously to these changes in diatom communities, *Corylus* and Marcescent *Quercus* develop (PZ-EST5) while *Juniperus* drops abruptly reaching values under 10% (compared to 50 % in previous zone PZ-EST4). Simultaneously both *Ephedra* types disappeared and the aquatics recovered with the development of mainly Cyperaceae and *Potamogeton*, indicating some increase in temperatures and general humid conditions.

A decoupling of the local hydrological response to global climate fluctuations is evidenced during this period (Morellón et al. 2009a). Both diatom and pollen show a delayed local hydrological response at about 9.5 cal kyr BP compared to the increasing temperatures of the onset of the Holocene. Increased seasonality, with higher summer insolation at mid-latitudes might have also amplified the hydrological response of Lake Estanya, which is particularly sensitive to evaporation. Relatively dry conditions for the Early Holocene have been recorded in other sequences of the Southern Pyrenees (e.g., Basa de la Mora: Pérez-Sanz et al., in press). Continental sequences of the Iberian Peninsula based on different proxies(Pérez-Obiol and Julià 1994; Giralt et al. 1999; Carrión 2002; Leira 2005; Fletcher et al. 2007; Morellón et al 2009a, Moreno et al. 2009), indicate that hydrological and ecological response to the onset of the Holocene has a large regional variability in the IP (see Carrión et al. 2010 and literature therein).

5.6. Biotic responses to environmental and climatic changes along the L. Estanya record

Diatom and vegetation communities show large and rapid changes during the Late Glacial to the Early Holocene in Lake Estanya (Fig. 6), synchronous with the main paleohydrological and climate changes reconstructed from sedimentological and geochemical data (Morellón et al., 2009a, b). Large environmental fluctuations during the Late Glacial and Early Holocene are clearly recorded in the diatom assemblages with periods of planktonic *C. ocellata* dominance alternating with periods of diverse non-planktonic assemblages. From the CCA analysis we infer that changes in clastic input and/or carbonate and sulphate deposition/redissolution coincide with significant changes in habitat conditions, since these processes determine changes in limiting factors for diatom species, as for instance lake-level, salinity, mixing dynamics and light penetration. For the same period Morellón et al. (2009 b) found clastic input, lake-level and water salinity and the main factors forcing the sedimentary evolution of the sequence, mostly climate-driven in a landscape with a relatively poor vegetation cover. These climate-driven environmental changes may have triggered distinct diatom responses and even ecological thresholds leading to repeated replacements of diatom assemblages along the record, especially during the Bölling / Allerød interstadial, in less than 100-200 years (Fig. 6). The irreversibility of changes in diatom assemblages suggests the existence of tipping points. The resulting assemblages are associated with the successive occurrence of very different and contrasting habitat conditions within the lake. Catalan et al. (2009) showed diatom ecological threshold to be associated with acid neutralizing capacity and ice-cover in European alpine-lake. Interestingly, our results show that in other types of lakes, environmental variability leading to diatom thresholds may imply different factors, as for instance climate-driven shifts in lake level beyond certain limits that may deeply affect salinity conditions and ecosystem structure and functioning. In our case diatom threshold responses seem to be coupled with climate thresholds (Maslin et al. 2013) caused by the abrupt climate events that took place during the studied period. A higher resolution approach and additional case studies would improve understanding of the magnitude and rate of change of the abrupt climate changes occurring during this time period in the region, as well as the explicit detection of the character of ecological thresholds, which cannot be properly identified at the resolution of the present study.

Pollen data show a landscape dominated by Steppe herbs and a fluctuating level of arboreal cover including evidence of refuge areas, coherent with regional Late Glacial vegetation (González-Sampériz et al., 2004,

2005, 2010). Vegetation responded during cool-cold and arid periods (Late Glacial and Mystery Interval) with the expansion of Steppe taxa while conifers (both *Juniperus* and *Pinus*) are the main arboreal component, and Mesophytes and *Quercus* evolution must be associated to regional refuge areas. This situation and the current resolution of this work does not enable the detection of potential abrupt responses of vegetation to the environmental changes occurred during this time.

5.7. Regional contextualization of the diatom record

Reconstructions of the late Glacial and Early Holocene in the Mediterranean Basin using diatom data are scarce. The Estanya diatom record is one of the first in the Iberian Peninsula to include that time periods. It is in general agreement with other circum-Mediterranean records, which show a chronologically similar pattern of climate change to north-western Europe and are characterised by alternations between cool,-arid and warm-wet phases (see Wilson et al 2008 and literature therein). In the few regional records available for the Late Glacial-Early Holocene period, diatom responses seem to be driven by both changing lake levels and productivity, or a combination of the two. In L. Ioannina (Greece) facultative fragilaroid taxa indicative of shallow water characterised Last Glaciation and Late Glacial periods indicating environmental and physical stress, at times interrupted by peaks of *C. ocellata* and of benthic, eutrophic taxa associated with episodes of lake deepening and rising productivity. The relative increase of planktonic taxa during the early Late Glacial interstadial (14.5-14 cal kyr BP) reflected rising lake levels, which was followed by a decline indicative of aridification during the Younger Dryas. During the Early Holocene a recovery of C. *ocellata* suggested a lake deepening (Jones et al. 2013). In Lake Ohrid (Macedonia/Albania) *Cyclotella fotii*, a species commonly found during former glacial phases, and *C. ocellata* prevailed during Late Glacial. The apparent weak response of these diatoms to Late Glacial warming from 14.7 cal kyr BP to the Holocene transition at 11.7 cal kyr BP was attributed to poor preservation but still needs confirmation (Reed et al. 2010). Diatom stratigraphy of Lago di Monticchio (southern Italy) is broadly described but shows that during the Last Glaciation and Late Glacial Interstadial planktonic *Cyclotella comensis*, fragilaroid taxa and other benthic diatoms dominated, indicating alkaline and oligotrophic to mesotrophic conditions. The disappearance of *C.comensis* during the Younger Dryas event was attributed to lowered nutrient concentrations in spite of increases in benthic fragilaroid taxa. From the Early Holocene, Laghi di

Monticchio evolved towards the modern-day fen that it is today, as reflected by diatoms characteristic of very shallow lakes or marshes like *Cocconeis placentula* and *Nitzschia amphibia* (Watts el al. 1996). In Lake Albano (central Italy), *Cyclotella* sp.1 prevailed until the Pleistocene/Holocene boundary, then completely disappeared from the record, suggesting lake conditions quite unlike those occurring during the majority of the Last Glaciation and Late Glacial that prevented the return of this species. It was replaced by significant but fluctuating proportions of *Stephanodiscus hantzschii*, *C.ocellata* and fragilaroid taxa, interpreted as responses to warming and changes in lake level and productivity. The Early Holocene was dominated by small *Stephanodiscus* taxa reflecting a much a more productive lake (Ryves et al.1996). Similarly to these regional trends, in L. Estanya diatoms responded to climate-driven lake-level changes, salinity fluctuations and habitat structure with assemblage replacements and sharp oscillation of diatom accumulation rates. The absence in L. Estanya of diatom species demanding eutrophic conditions and the prevalence of oligo-mesotrophic species suggest that fluctuations in lake productivity, as reflected in minor shifts in diatom accumulation rates of *C. ocellata*, were driven more by climate related factors (epilimnetic temperatures, evaporation, solar irradiation, etc) than by nutrient availability. Fragilaroid taxa, characteristic of late glacial sediments in Mediterranean lakes and also in lakes of northern and central Europe (Bradshaw et al. 2000, Lotter 2001, Birks et al. 2012) appeared in L. Estanya only in the context of the cool and dry Late Glacial-Holocene boundary.

6. CONCLUSIONS

- Lake Estanya contains an exceptional palaeoenvironmental and paleolimnological archive for the last 20 cal kyr in continental Iberia.
- As shown in other available circum-Mediterranean records, diatoms responded quickly to climate-driven lake -level and salinity fluctuations associated to the humid/dry shifts during the last glacial/interglacial transition. These climate changes triggered diatom responses particularly when ecological threshold were crossed, especially during the stadial/interstadial episodes. The species-specific responses observed suggest that the B/A interstadial could serve as a past analogue for limnological responses with regard to current climate change.

643 - Vegetation response during cool and arid periods (Late Glacial and Mystery Interval) was
644 characterized by an expansion of Steppe taxa. During the warmer and more humid phases of the
645 B/A interstadial, both Marcescent and Evergren *Quercus* and aquatic vegetation expanded
646 following the general climate improvement. Increased presence of Betula, Corylus and Quercus
647 during cold periods such as the "Mystery interval" and the Younger Dryas suggest the presence of
648 local refuge areas for mesophytes during the Lateglacial.
649 - Both diatom and regional vegetation show that wetter conditions typical of the Holocene onset were
650 delayed till 9.5 cal kyr BP, in agreement other continental sequences of the Iberian Peninsula. The
651 higher sensitivity of diatoms compared to vegetation to local abrupt climate changes during this
652 period suggest that in these mid altitude Mediterranean mountain settings the climate signal was
653 more rapidly transfer to the local limnological and hydrological subsystems than to the regional
654 vegetation.
655

656 **7. ACKNOWLEDGEMENTS**

657 This research has been funded through the projects LIMNOCLIBER (REN2003-09130-C02-02),
658 IBERLIMNO (CGL2005-20236-E/ CLI), LIMNOCAL (CGL2006-13327-C04-01), PALEODIVERSITAS
659 (CGL2006-02956/BOS), GLOBALKARST (CGL2009-08415), GRACCIE-CONSOLIDER (CSD2007-
660 00067), DINAMO (CGL2009-07992), DINAMO2 (CGL2012-33063); provided by the Spanish Inter-
661 Ministry Commission of Science and Technology. (CICYT); and PIRINEOSABRUPT (PM073/2007),
662 provided by the Diputación General de Aragón. Mario Morellón Marteles and Graciela Gil-Romera hold
663 post-doctoral contacts funded by the "JAE-Doc/CSIC" ref.- and "Juan de la Cierva" (grant ref. JCI2009)
664 programs respectively. Ana Pérez-Sanz has been supported by a PhD Fellowship provided by the Aragon
665 Government. We also thank Beatriz Bueno and Aída Adsuar for lab assistance. Finally, we are grateful to
666 Antonia Andrade Olalla for helping in initial pollen analyses and to Joan Gomà for assistance in diatom
667 taxonomic determinations. Two referee's constructive criticism and suggestions helped improved a former
668 version of this paper.
669

670 **8. REFERENCES**

671 Abrantes, F., Gil, I., Lopes, C., Castro, M., 2005. Quantitative diatom analyses: a faster cleaning procedure.
672 Deep Sea Research 52:189–198.
673 Adrian, R., O'Reilly, C.M., Zagarese, H., Baines, B. S., Hessen, D.O., Keller, W., Livingstone, D. M.,
674 Sommaruga, R., Straile, D., Van Donk, E., Weyhenmeyer, G.A., Winder, M., 2009. Lakes as sentinels of
675 climate change. Limnol Oceanography 54(6): 2283-2297.
676 Ávila, A., Burrel, J.L., Domingo, A., Fernández, E., Godall, J., Llopart, J.M., 1984. Limnología del Lago
677 Grande de Estanya (Huesca). Oecologia aquatica 7, 3–24.
678 Battarbee, R.W., 1986. Diatom analysis. In: Berglund BE (ed.) Handbook of holocene palaeoecology and
679 palaeohydrology. Wiley, Chichester, pp 527–570.
680 Battarbee, R.W., Jones, V., Flower, R.J., Cameron, N.G., Bennion, H., Carvalho, L., Juggins, S., 2001.
681 Diatoms. In: Smol, J.P., Birks, H.J.B., Last, W.M. (eds.). Tracking environmental change using lake
682 sediments. Kluwer, Dordrecht.
683 Bennet, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. New
684 Phytologist 132: 155-170.
685 Bradshaw, E.G., Jones, V.J., Birks, H.B.J., Birks, H.H., 2000. Diatom responses to late-glacial and Early-
686 Holocene environmental changes at Kråkenes, western Norway. Journal of Paleolimnology 23: 21-34.
687 Birks, H.H., Jones, V.J., Brooks, S.J., Birks, H.J.B., Telford, R.J., Juggins, S., Peglar, S.M., 2012. From
688 cold to cool in northernmost Norway: Lateglacial and Early Holocene multi-proxy environmental and
689 climate reconstructions from Jansvatnet, Hammerfest. Quaternary Science Reviews 33, 100-120.
690 Blanco-Castro, E., Casado, M., Costa, M., Escribano, R., García Antón, M., Génova, M.,
691 Gómez, A., Moreno, J., Morla, C., Regato, P., Sainz Ollero, H., 1997. Los bosques ibéricos. Una
692 interpretación geobotánica. Planeta, Barcelona (Spain), 572 pp.
693 Bond, G., Heinrich, H., Broecker, W., Labeyrie, L., McManus, J., Huon, S., Tantschie, R., Clasen, S.,
694 Simet, C., Tedesco, K., Klas, M., Bonam, G., Ivy, S., 1992. Evidence for massive discharges into the North
695 Atlantic Ocean during the last glacial period. Nature 360, 245-249.
696 Broecker, W.S., 2000. Abrupt climate change: causal constraints provided by the palaeoeclimate record.
697 Earth-Science Reviews 51, 137-154.

Broecker, W.S, 1994. Massive iceberg discharges as triggers for global climate change. Nature 372, 421-424.

Cacho, I., Grimalt, J.O., Pelejero, C., Canals, M., Sierro, F.J., Flores, J.A., Shackleton, N., 1999. Dansgaard- Oeschger and Heinrich event imprints in Alboran Sea paleotemperatures. Paleoceanography 14, 698-705.

Cacho, I., Grimalt, J.O., Canals, M., Sbaffi, L., Shackleton, N.J., Schönfeld, J., Zahn, R., 2001. Variability of the western Mediterranean Sea surface temperature during the last 25,000 years and its connection with the Northern Hemisphere climatic changes. Paleoceanography 16, 40-52.

Cambra, J., 1991.Contribució a l'estudi de les algues epifítiques dels estanys de Banyoles, Basturs i Estanya. Orsis 6, 27-44.

Carrión, J.S., 2002. Patterns and processes of Late Quaternary environmental change in a montane region of southwestern Europe. Quaternary Science Reviews 21, 2047–2066.

Carrión, J.S., Fernández, S., González-Sampériz, P., Gil-Romera, G., Badald, E., Carrión-Marcod, Y, López-Merino, L., López-Sáez, J.A., Fierro, E., Burjachs, F., 2010. Expected trends and surprises in the Late Glacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands. Review of Palaeobotany and Palynology, 162:458–475.

Cooper, S.R., 1995.Chesapeake Bay watershed historical land use: impact on water quality and diatom communities. Ecological Applications 5,703–723.

Corella, J.P., El Amrani A., Sigró J., Morellón M., Rico E.,Valero-Garcés, B., 2011. Recent evolution of Lake Arreo, northern Spain: influences of land use change and climate. J. Paleolimnolimnology 46, 469–485.

Dansgaard, W., White, J.W.C., Johnsen, S.J., 1989. The abrupt termination of the Younger Dryas. Nature 339, 532-534.

Dansgaard, W., Johnsen, S. J., Clausen, H. B., Dahl-Jensen, D., Gundestrup, N. S., Hammer, C. U., Hvidberg, C. S., Steffensen, J. P., Sveinbjörnsdottir, A. E., Jouzel J., Bond, G., 1993. Evidence for general instability of past climate from a 250-kyr ice-core record. Nature 364, 218 – 220.

Denton, G.H., Broecker, W., Alley, R.B., 2006. The Mystery Interval 17.5 to 14.5 kyr ago. In: Brigham-Grette, J., Kull, C., Kiefer, T. (Eds.), PAGES News 14-16.

726 Denton, G.H., Anderson, R. F.,Toggweiler, J. R., Edwards, R.L., Schaefer, J. M., Putnam, A. E., 2010.
727 The Last Glacial Termination. Science 328, 1652.
728 Dupré, M., 1992. Palinología. Sociedad Española de Geomorfología, 30 pp.
729 Fletcher, W.J., Sánchez Goñi, M.F., 2008. Orbital- and sub-orbital-scale climate impacts on vegetation of
730 the western Mediterranean basin over the last 48,000 yr. Quaternary Research 70, 451-464.
731 Flower, R.J., 1993. Diatom preservation: experiments and observations on dissolution and breakage in
732 modern and fossil material. Hydrobiologia 269/270, 473–484.
733 González-Sampériz, P., Valero-Garcés, B.L., Carrión, J.S., 2004. Was the Ebro valley a glacial refugium
734 for temperate trees? Anales de Biología 26: 13-20.
735 González-Sampériz, P., Valero-Garcés, B.L., Carrión, J.S., Peña-Monné, J.L., García-Ruiz, J.M., Martí-
736 Bono, C., 2005. Glacial and Lateglacial vegetation in northeastern Spain: New data and a review.
737 Quaternary International 140–141: 4–20.
738 González-Sampériz, P., Valero-Garcés, B.L., Moreno, A., Jalut, G., García-Ruiz, J.M.,
739 Martín-Bono, C., Delgado-Huertas, A., Navas, A., Otto, T., Dedoubat, J.J., 2006. Climate variability in the
740 Spanish Pyrenees during the last 30,000 yr revealed by the El Portalet sequence. Quaternary Research 66,
741 38–52.
742 González-Sampériz, P., Leroy, S.A.G., Fernández, S., García-Antón, M., Gil-García, M.J., Uzquiano, P.,
743 Valero-Garcés, B., Figueiral, I., 2010. Steppes, savannahs, forests and phytodiversity reservoirs during the
744 Pleistocene in the Iberian Peninsula. Review of Palaeobotany and Palynology, 162, 427-457
745 Grootes, P. M., Stuiver, M., White, James, W.C.J., Sigfus. J., Jouzel, J., 1993. Comparison of oxygen
746 isotope records from the GISP2 and GRIP Greenland ice cores. Nature, 366, 552-554.
747 Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software package for
748 education and data analysis. Palaeontologia Electronica 4(1), 9pp.
749 http://palaeoelectronica.org/2001_1/past/issue1_01.htm
750 Heegaard, E., Birks, H.J.B., Telford, R.J., 2005. Relationships between calibrated ages and depth in
751 stratigraphical sequences: an estimation procedure by mixed effect regression. The Holocene, 612–618.

Höbig, N., Weber, M.E., Kehl, M., Weniger, G.C., Julià, R., Melles, M., Fülöp, R.H., Vogel, H., Reicherter, K., 2012. Lake Banyoles (northeastern Spain): A Last Glacial to Holocene multi-proxy study with regard to environmental variability and human occupation. Quaternary International 274, 205-218.

Hofmann, G., M.Werum, H. Lange-Bertalot, 2011. Diatomeen im Süßwasser-Benthos von Mitteleuropa. A.R.G. Gantner Verlag K.G.

IGME, 1982. Mapa Geológico de España 1:50000 No. 289. Benabarre. Instituto Geológico y Minero de España, Madrid.

Huntley, B., Birks, H., 1983. An atlas of past and present pollen maps for Europe: 0-13.000 years ago. Cambridge: Cambridge University Press. 667pp.

Jackson, S.T., Overpeck, J.T., 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. Palaeobiology 26 (Suppl.), 194-220.

Jalut, G., Marti, J.M., Fontugne, M., Delibrias, G., Vilaplana, J.M., Julia, R., 1992. Glacial to interglacial vegetation changes in the northern and southern Pyrenees: deglaciation, vegetation cover and chronology. Quaternary Science Reviews 11, 449–480.

Jones, T.D., Lawson, I.T., Reed, J.M., Wilson, G.P., Leng, M.J., Gierg, M., Bernasconi, S.M., Rienk, H. Smittenberg, R.H., Hajdas, I., Bryant, Ch. L., Tzedakis, P.B., 2013. Diatom-inferred late Pleistocene and Holocene palaeolimnological changes in the Ioannina basin, northwest Greece. Journal of Paleolimnology 49,185–204.

Krammer, K., 2002. Diatoms of Europe. Diatoms of the European Inland Waters and Comparable Habitats. A.R.G.n Gantner Verlag K.G, Ruggell, p 584.

Krammer, K. , Lange-Bertalot, H., 1986. Süßwasserflora von Mitteleuropa. Band 2. Bacillariophyceae. Teil 1. Naviculaceae. Gustav Fischer Verlag, Stuttgart.

Krammer, K. ,Lange-Bertalot, H., 1988. Süßwasserflora von Mitteleuropa. Band 2. Bacillariophyceae. Teil 2. Bacillariaceae, Epithemiaceae, Surirellaceae. Gustav Fischer Verlag, Stuttgart.

Krammer, K. and Lange-Bertalot, H., 1991. Süßwasserflora von Mitteleuropa. Band 2. Bacillariophyceae. Teil 3. Centrales, Fragilariaceae, Eunotiaceae. Gustav Fischer Verlag, Stuttgart.

Krammer, K. and Lange-Bertalot, H., 2001. Süßwasserflora von Mitteleuropa. Band 2. Bacillariophyceae. Teil 4. Achnanthaceae, Kritische Ergänzungen zu Navicula (Lineolatae) and Gomphonema [new edition]. Gustav Fischer Verlag, Stuttgart.

Lange-Bertalot, H., 2001a. Diatoms of the Europe inland waters and comparable habitats. A.R.G. Gantner Verlag K.G., Ruggell, p 526.

Lange-Bertalot-Festschrift: Studies on Diatoms 2001b. Regine Jahn, John P. Kociolek, Andrzej Witkowski & Pierre CompèreGantner (Eds.), Ruggell.

Last, W.M., Vance, R.E., 1997. Bedding characteristics of Holocene sediments fromm salt lakes of the northern Great Plains, Western Canada. Journal of Paleolimnology17, 297–318.

Lawson, I.., Frogley, M., Bryant, C., Preece, R.,Tzedakis, P., 2004. The Late Glacial and Holocene environmental history of the Ioannina basin, north-west Greece, Quaternary Science Review 23, 1599–1625.

Leira, M., 2005. Diatom responses to Holocene environmental changes in a small lake in northwest Spain. Quaternary International 140/141, 90–102.

Leira, M., Santos, L., 2002. An Early Holocene short climatic event in the northwest Iberian Peninsula inferred from pollen and diatoms. Quaternary International 93/94, 3–12.

Legendre, P., Legendre, L.., 1998. Numerical Ecology, 2nd ed. Elsevier.

León-Llamazares, A., 1991. Caracterización agroclimática de la provincia de Huesca Ministerio de Agricultura. Pesca y Alimentación (M.A.P.A.), Madrid.

Lotter, A.F., 2001. The paleolimnology of Soppensee (central Switzerland), as evidenced by diatom, pollen, and fossil pigments analyses. Journal of Paleolimnology 25, 65-79.

López-Vicente, M., 2007. Erosión y redistribución del suelo en agroecosistemas mediterráneos: Modelización predictiva mediante SIG y validación con ^{137}Cs (Cuenca de Estaña, Pirineo Central). PhD Thesis, Universidad de Zaragoza. Zaragoza, 212 pp.

Montserrat J., 1992. Evolución glaciar y postglaciar del clima y la vegetación en la vertiente sur del Pirineo: Estudio palinológico. Instituto Pirenaico de Ecología-CSIC, Zaragoza.

Moore P.D. & Webb J.A. ,1978. An Illustrated Guide to Pollen Analysis. Wiley and Sons.

807 Morellón, M., Valero-Garcés, B.L., Anselmetti, F., Ariztegui, D., Schnellmann, M., Moreno, A., Mata, P.,
808 Rico, M., Corella, J.P., 2009a. Late Quaternary deposition and facies model for karstic Lake Estanya (NE
809 Spain). Sedimentology, 1505-1534.
810 Morellón M., Valero-Garcés B, Vegas-Vilarrúbia T, González-Sampériz P., Romero O., Delgado-Huertas
811 A., Mata P., Moreno A., Rico M., Corella JP., 2009b. Late Glacial and Holocene palaeohydrology in the
812 western Mediterranean region: The Lake Estanya record (NE Spain). Quaternary Science Reviews 28,
813 2582–2599.
814 Moreno, A., Cacho, I., Canals, M., Prins, M.A., Sánchez-Goñi, M.F., Grimalt, J.O.,Weltje, G.J., 2002.
815 Saharan dust transport and high latitude glacial climatic variability: the Alboran Sea record. Quaternary
816 Research 58, 318-328.
817 Moreno, A., Stoll H., Jiménez-Sánchez M., Cacho I., Valero-Garcés B., Emi Ito, Edwards L.E.R., 2010.
818 A speleothem record of glacial (25–11.6 kyr BP) rapid climatic changes from northern Iberian Peninsula.
819 Global and Planetary Change 71, 218–231.
820 Moreno, A., López-Merino, L., Leira, M., Marco-Barba, J., González-Sampériz, P., Valero-Garcés, B.,
821 López-Sáez, J.A., Santos, L., Mata, P., Ito, E., 2011. Revealing the last 13,500 years of environmental
822 history from the multiproxy record of a mountain lake (Lago Enol, northern Iberian Peninsula). Journal of
823 Paleolimnology 46, 327-349.
824 Moreno, A., González-Sampériz, P., Mario Morellón, M., Valero-Garcés, B., Fletcher W.J., 2012. Northern
825 Iberian abrupt climate change dynamics during the last glacial cycle: A view from lacustrine sediments.
826 Quaternary Science Review 36, 139-153.
827 Pérez-Bielsa, C., Lambán, L., Plata, J., Rubio, F., Soto, R., 2012. Characterization of a karstic aquifer using
828 magnetic resonance sounding and electrical resistivity tomography: a case-study of Estaña Lakes (northern
829 Spain). Hydrogeology Journal 20, 1045-1059.
830 Pérez-Obiol, R., Julià, R., 1994. Climatic change on the Iberian Peninsula recorded in a 30,000-yr pollen
831 record from Lake Banyoles. Quaternary Research 41, 91-98.
832 Pérez-Sanz, A., González-Sampériz, P., Moreno, A., Valero-Garcés, B., Gil-Romera, G., Rieradevall, M,
833 Tarrats, P., Lasheras-Álvarez, L., Morellón, M., Belmonte, A., Sancho, C., Sevilla-Callejo, M., Navas A.,

2013. Holocene climate variability, vegetation dynamics and fire regimen in the Central Pyrenees: the Basa de la Mora sequence (NE Spain). Quaternary Sciences Review 73, 149-169.

Poulíčková, A., Hašler, P., 2007. Aerophytic diatoms from caves in central Moravia (Czech Republic). Preslia 79, 185–204.

Reed, J. M., 1998. A diatom conductivity transfer function for Spanish salt lakes. Journal of Paleolimnology 19, 399–416.

Reed, J.M., Stevenson, A.C., Juggins, S., 2001. A multi-proxy record of Holocene climatic change in southwestern Spain: the Laguna de Medina, Cadiz. The Holocene 11, 707-719.

Reed, J.M., Cvetkoska, A., Levkov, Z., Vogel, H., Wagner, B., 2010. The last glacial-interglacial cycle in Lake Ohrid (Macedonia/ Albania): testing diatom response to climate. Biogeosciences 7, 3083–3094.

Reille, M., Lowe, J.L., 1993. A re-evaluation of the vegetation history of the eastern Pyrenees (France) from the end of the last glacial to the present. Quaternary Science Reviews 12, 47–77.

Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Bertrand, C.J.H., Blackwell, P.G., Buck, C.E., Burr, G.S., Cutler, K.B., Damon, P.E., Edwards, R.L., Fairbanks, R.G., Friedrich, M., Guilderson, T.P., Hogg, A.G., Hughen, K.A., Kromer, B., McCormac, G., Manning, S., Ramsey, C.B., Reimer, R.W., Remmele, S.,Southon, J.R., Stuiver, M., Talamo, S., Taylor, F.W., van der Plicht, J., Weyhenmeyer, C.E., 2004. IntCal04 terrestrial radiocarbon age calibration, 0–26 cal kyr BP. Radiocarbon 46, 1029–1058.

Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Burr, G.S., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., McCormac, F.G., Manning, S.W., Reimer, R.W., Richards, D.A., Southon, J.R., Talamo, S., Turney, C.S.M., van der Plicht, J., Weyhenmeyer, C.E., 2011. IntCal09 and Marine09 Radiocarbon Age Calibration Curves, 0-50,000 Years cal BP.

Riera, S., Wansard, G., Julià, R., 2004. 2000-year environmental history of a karstic lake in the Mediterranean Pre-Pyrenees: the Estanya lakes (Spain). Catena 55, 293–324

Ryves, D.B., Juggins, S., Fritz, S.C., Battarbee, R.W., 2001. Experimental diatom dissolution and the quantification of microfossil preservation in sediments. Palaeogeography, Palaeoclimatology, Palaeoecology 1172, 99–113.

Ryves, D.B., Jones, V.J., Guilizzoni, P., Lami, A., Marchetto, A., Battarbee, R.W., Bettinetti, R., Devoy, E.C., 1996. Late Pleistocene and Holocene environmental changes in Lake Albano and Lake Nemi (central Italy) as indicated by algal remains. Memorie dell' Istituto Iataliano di Idrobiologia. 55: 119- 148.

Taylor, K.C., Mayewski, P. A., Alley,R. B., Brook,E. J., Gow,A. J., Grootes,P. M., Meese,D. A., Saltzman,E. S., Severinghaus,J. P., Twickler, M. S., White,J. W. C, Whitlow, S., Zielinski,G. A., 1997. The Holocene-Younger Dryas Transition Recorded at Summit, Greenland. Science 278, 5-827.

Steffensen, J.P., Andersen, K.K., Bigler, M., Claussen, H.B., Dahl-Jensen, D., Fischer, H., Goto-Azuma, K., Hanson, M., Johnsen, S.J., Jouzel, J., Masson-Delmotte, V.,Popp, T., Rasmussen, S.O., Röthlisberger, R., Ruth, U., Stauffer, B., Siggaard-Andersen, M.L., Sveinbjörnsdóttir, A.E., Stockmarr J., 1973. Determination of spore concentration with an electronic particle counter. Danmarks geologiske Undersøgelse Årbog, 1972, 87–89.

Svenson, A., White, J.W.C., 2008. High resolution Greenland ice core data show abrupt climate change happens in few years. Science 321, 680-684.

ter Braak C. J. E, Verdonschot, Piet, E.M.,1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences 57/3, 255-289.

Valero-Garcés, B.L., Kelts, K.R., 1995. A sedimentary facies model for perennial and meromictic saline lakes: Holocene Medicine Lake Basin, South Dakota, USA. Journal of Paleolimnology 14, 123–149.

Valero-Garcés, B., Zeroual, E., Kelts, K., 1998. Arid phase in the western Mediterranean region during the last glacial cycle reconstructed from lacustrine records. In: Benito, G., Baker, V.R., Gregory, K.J. (Eds.), Paleohydrology and Environmental Change. Wiley, London, pp. 67-80.

Valero-Garcés, B., Gonzalez-Samperiz, P., Delgado-Huertas, A.,Navas, A., Machın, J., Kelts, K., 2000. Lateglacial and Late Holocene environmental vegetational change in Salada Mediana, central Ebro Basin, Spain. Quaternary International 73–74, 29–46.

Van Dam, H., Mertens, A., Sinkeldam, J., 1994. A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. Netherlands Journal of Aquatic Ecology 28,117-133.

Vegas-Vilarrúbia T., Rull V., Montoya E., Safont E., 2011. Quaternary palaeoecology and nature conservation: a general review with examples from the neotropics. Quaternary Science Reviews 30, 2361-2388.

889 Weninger, B., Jöris, O., 2004. Glacial radiocarbon calibration. The CalPal Program. In: Higham, T.,
890 Ramsey, C.B., Owen, C. (Eds.), Radiocarbon and Archaeology. Fourth International Symposium, Oxford
891 2002.
892 Witkowski, A., Lange-Bertalot, H., Metzeltin, D., 2000. Diatom flora of marine coasts. In: Lange-Bertalot
893 H (Ed.) Iconographia diatomologica, p 925.

894
895

896 **FIGURE CAPTIONS:**

897

898 Figure 1: (A) Topographic and geological map of 'Balsas de Estanya's catchment area. The location of the
899 study area is indicated with a star. (B) Bathymetry of the main lake, Estanque Grande de Abajo with coring
900 sites (1A to 5A).

901

902 Figure 2: Updated chronological model for the Lake Estanya sequence (A) and detail of the time interval
903 studied in this paper (19.7 to 9.3 cal kyr BP). The continuous line represents the age-depth function framed
904 by dashed lines (error lines). Sedimentary units and limits of cores used for the composite sequence are also
905 displayed at the right end.

906

907 Figure 3: A) Relative abundance (≥ 3%) of diatom taxa throughout the record. The dotted lines separate
908 diatom zones DZ-EST-1 to DZ-EST-5. Valve accumulation rates in valves · cm^{-2} · $year^{-1}$. Radiocarbon
909 (^{14}C) dates in calibrated years before present (BP). B) Zone DZ-EST-2 is subdivided in eleven subzones (a-
910 k). Correlation between diatom abundance and the δ18O GRIP Greenland ice-core showing main climatic
911 features on the new event chronology proposed by the INTIMATE group (Björk et al. 1998) and its
912 correspondence with the classic last deglaciation sequence of GISPS2 (Stuiver et al. 1995).

913

914 Figure 4: CCA ordination diagram representing XRF geochemical variables, site scores (depths)
915 and species scores across axes: 4a and 4b: axes 1 and 2; 4c and 4d, axes 2 and 3. A: *Cyclotella ocellata,* B*:*
916 *Cyclotella distinguenda,* C: *Amphora inariensis,* D: *Amphora lybica,* E: *Amphora veneta var. sub capitata,*

F: *Amphora* spp, G: *Brachysira vitrea,* H: *Cocconeis placentula,* I: *Cymbella sp.1,* J: *Denticula elegans,* K: *Diploneis ovalis,* L: *Encyonopsis caespitosa,* M: *Encyonopsis microcephala,* N: *Encynopsis subminuta,* O: *Ephitemia adnata,* P: *Fallacia cf pygmaea,* Q: *Hantzschia amphioxus,* R: *Hyppodonta hungarica,* S: *Luticula mutica,* T: *Luticula nivalis,* U: *Mastogloia braunii,* V: *Mastogloia smithii,* WW: *Mastogloia spp,* X: *Navicula salinarum,* Y: *Navicula subalpina,* Z: *Navicula* spp, AA: *Navicula* sp.2, BB: *Navicula sp. 11,* *CC: Navicula* sp. 4, DD: *Navicula* sp. 9, EE: *Nitszchia* cf. *filiformis,* FF: *Nitszchia hungarica,* GG: *Nitszchia incospicua,* HH: *Pinnularia borealis,* II: *Pinnularia spp,* JJ: *Pseudostaurosira brevistriata,* KK: *Sellaphora pupula.*

Figure 5: Pollen diagram of selected taxa and group taxa from the Lateglacial to Holocene transition of Estanya lake record. Other Mesophytes curve includes *Alnus, Carpinus, Salix, Ulmus, Populus, Tilia, Fagus, Acer, Fraxinus* and *Juglans*. Mediterranean shrubs is composed of *Pistacia, Rhamnus, Phyllyrea, Buxus* and *Sambucus,* and Steppe taxa by *Ephedra distachya, E. fragilis, Artemisia*, Cichorioideae, Asteroideae, Carduae, Chenopodiaceae and *Plantago.*

Figure 6: Summary record grouping diatoms, according to their known habitat preferences, and main pollen assemblages. Diatom and pollen records are correlated with paleohydrological, paleoenvironmental and paleoclimatic records: sedimentary units and lake level reconstruction are based on sedimentary facies and geochemically-based salinity estimations (Morellón 2009b), and finally the $\delta^{18}O$ GRIP Greenland ice-core showing the new event chronology proposed by the IMITATE group 2 and its correspondence with the classical last deglaciation sequence of GISPS2. Main climate events are delimited by the dotted lines and white/grey bars.

945

946
947

Table 1
Click here to download Table: Table 1.doc

Table 1: Eigenvalues and constraining percentages of main eigenvectors. Correlations between environmental variables and eigenvectors. Asterisks indicate significant correlations (p = 0,1, one-tailed probabilities).

	Axis 1	**Axis 2**	**Axis 3**
Eigenvalue	0.390	0.290	0.204
Percentage	34.7	25.4	18.2
Correlations			
Al	0.22	-0.12	-0.16
Si	-0.12	-0.02	-0.25
S	0.38*	0.25	0.11
K	-0.18	-0.12	-0.34*
Ca	0.47*	-0.22	0.26
Ti	-0.26	0.00	-0.31*
Fe	-0.44*	-0.06	-0.33*

Figure 1

Click here to download high resolution image

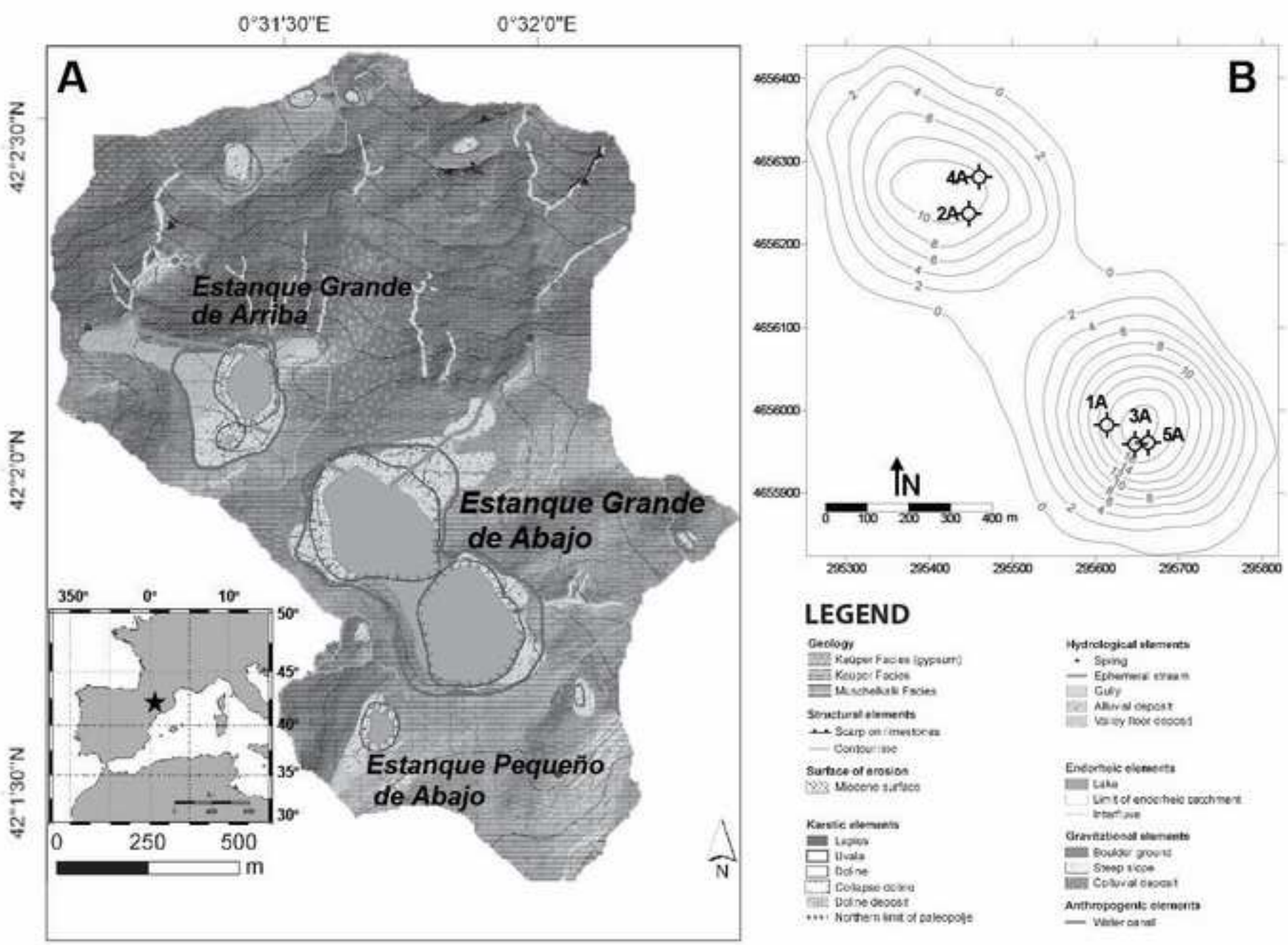

Figure 2

Click here to download high resolution image

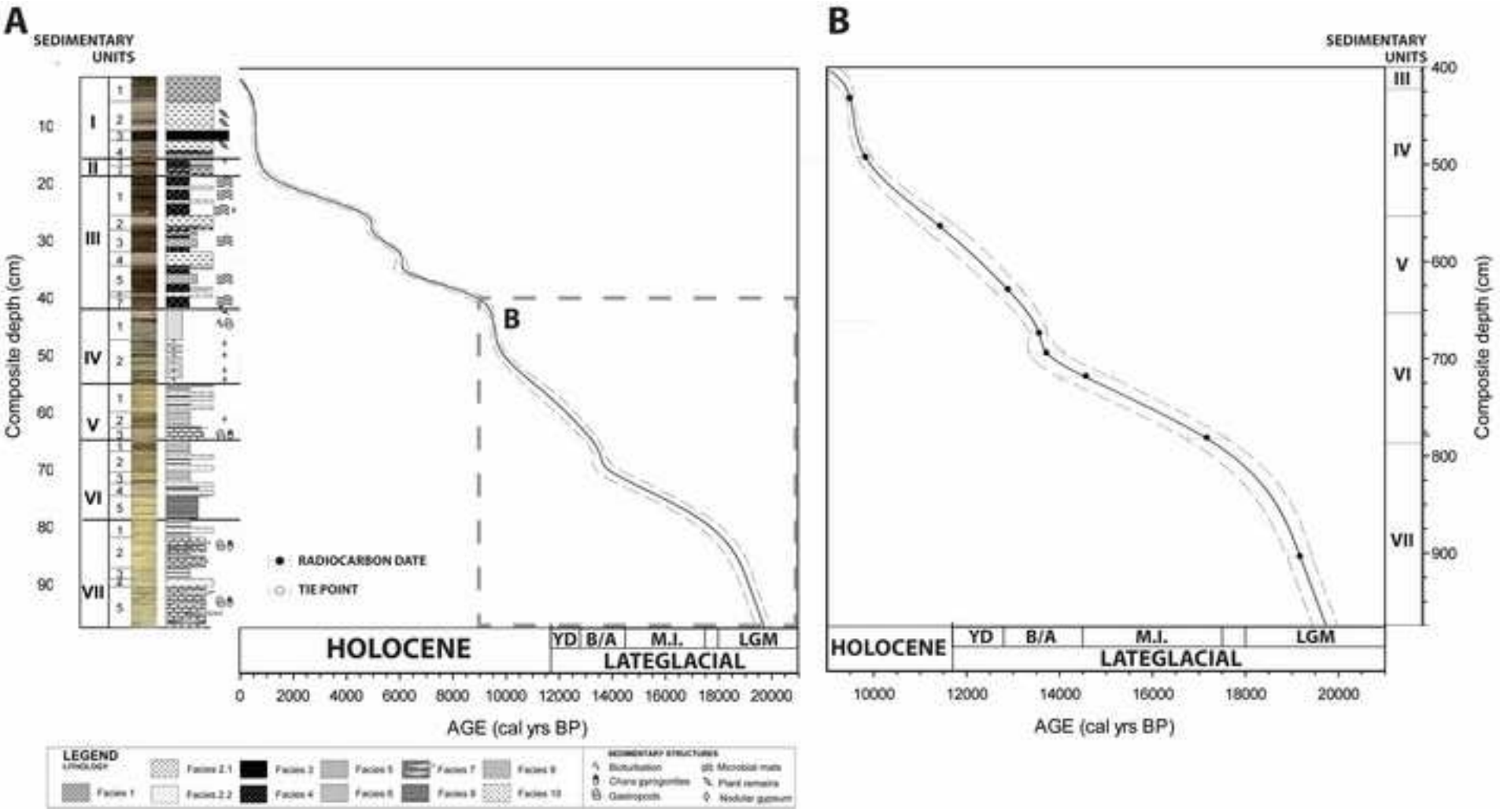

Figure 3

Click here to download high resolution image

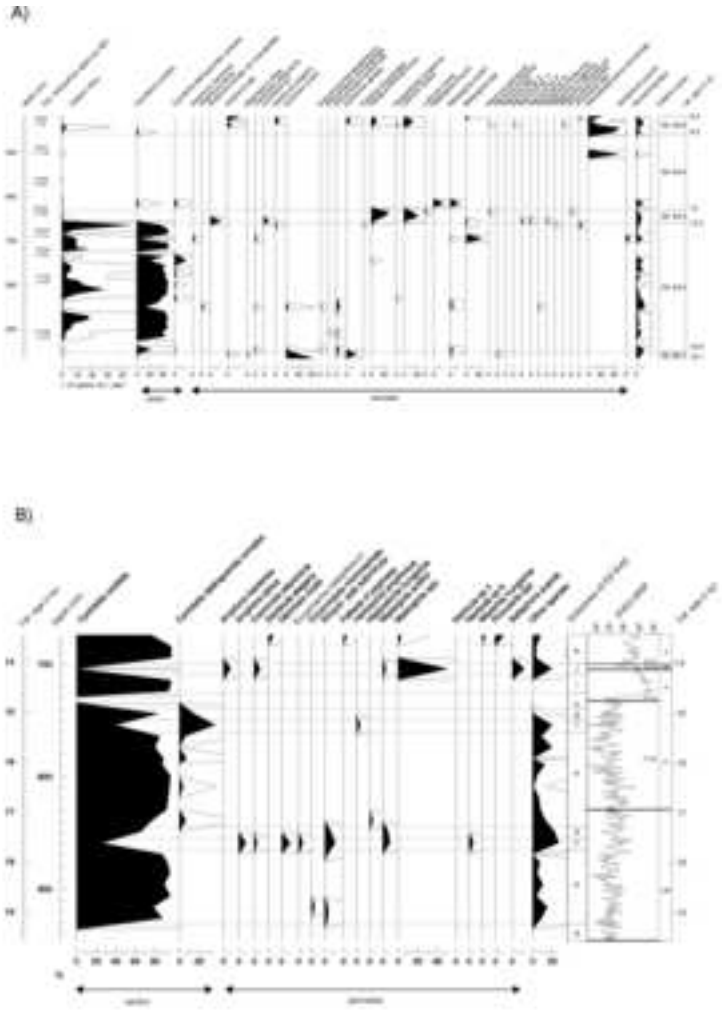

Figure 4

Click here to download high resolution image

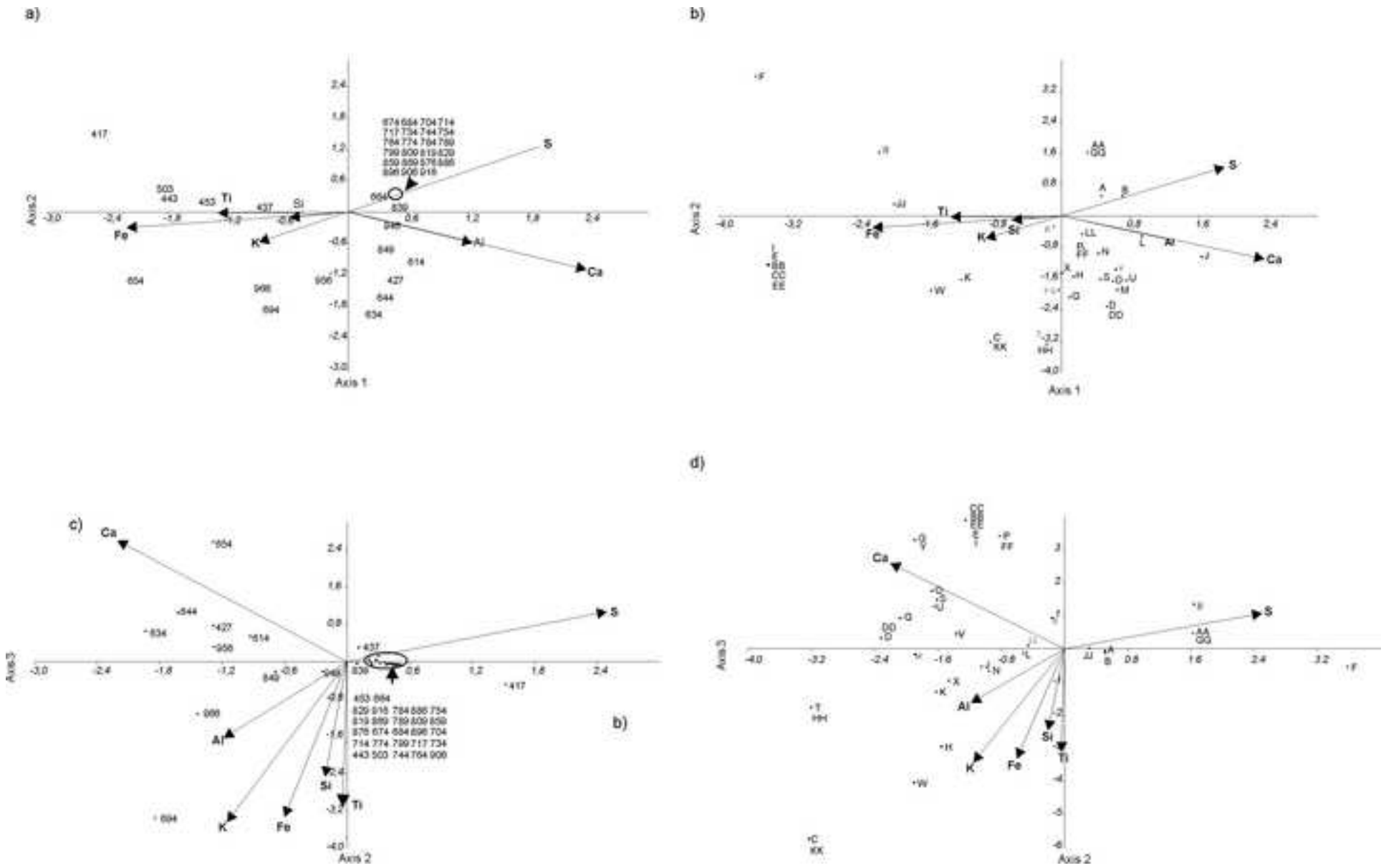

Figure 5

Click here to download high resolution image

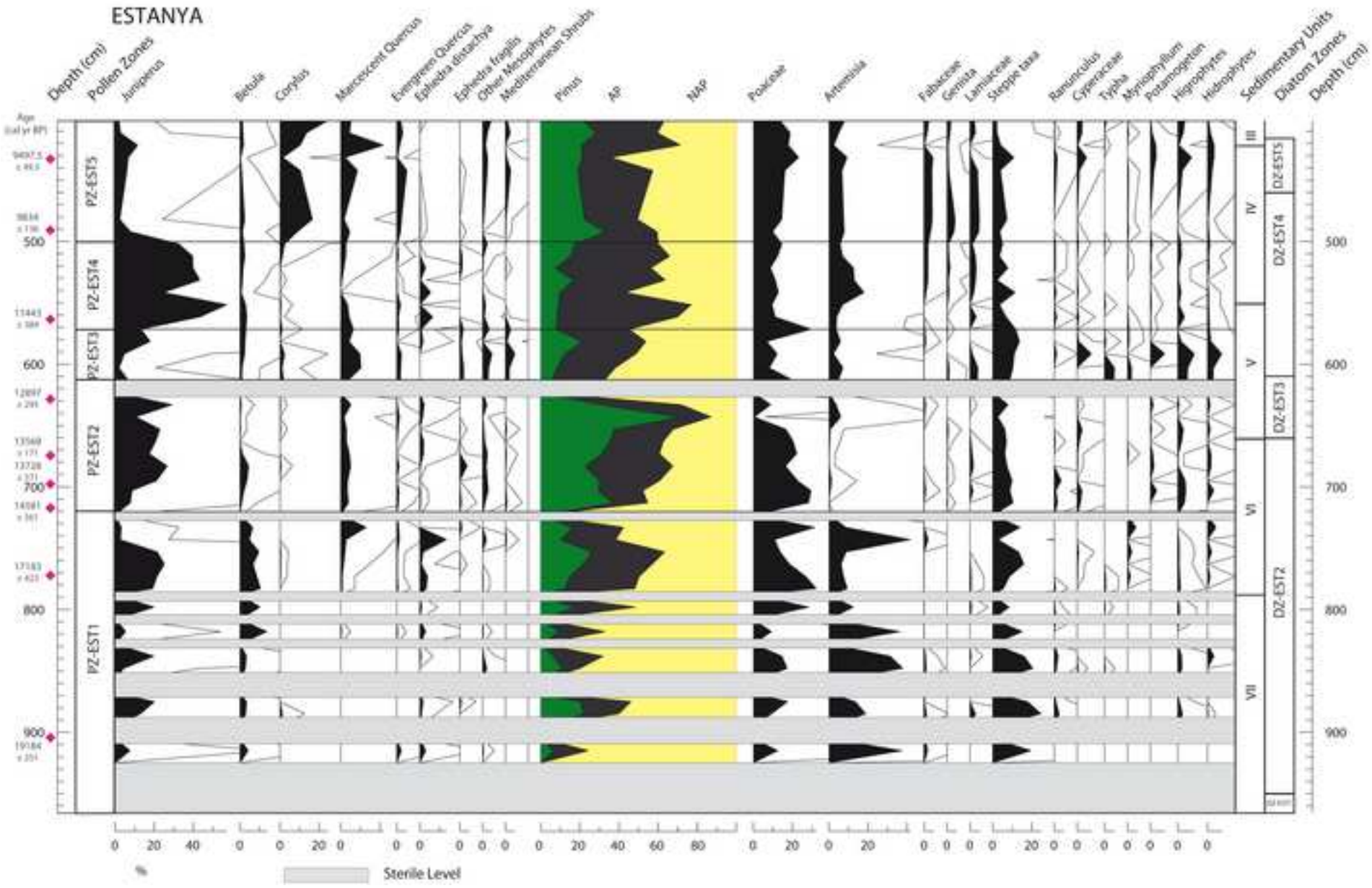

Figure 6

Click here to download high resolution image