

## Climatic fluctuations over the Holocene in southern Iberia (Sierra Nevada, Spain) reconstructed by fossil cladocerans

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### ABSTRACT

A combination of microfossil assemblages, abundance of fossil ephippia and mean body size provides the longest paleoclimatic reconstruction based on cladoceran subfossils in the Iberian Peninsula. Species turnover in Laguna de Río Seco (Sierra Nevada, southern Spain) was controlled by changes in lake levels in response to fluctuations in hydroclimatic variability over the last ~8600 years. Our archive documents a wet period in the Early and Middle Holocene (~8600–5000 cal yr BP), characterized by eurytopic and plant-associated species. A drier stage occurred from ~5000 cal yr BP and implied a reduction in lake level and higher occurrence of species highly adapted to more ephemeral environments. Proportions of total chydorid ephippia (TCE), indicating rates between asexual and sexual reproduction, are well-correlated with a progressive trend towards aridification. Lower TCE was registered before ~5000 cal yr BP as a result of a favourable environment under higher lake level, while higher TCE started with the upcoming arid stage (~5000 cal yr BP) due to environmental stress. Besides these hydrological signatures, data on *Daphnia* size broadly indicate a warmer period ~8600–4000 cal yr BP and a colder stage ~4000–255 cal yr BP. Further investigations using this indicator in the Sierra Nevada will provide more precise reconstructions of past climatic conditions in southern-latitude and alpine ecosystems.

### 1. Introduction

The cladocerans (Crustacea: Branchiopoda) are a major component of the planktonic and benthic crustacean fauna in lentic environments. They play a pivotal intermediary role in the aquatic food webs between primary producers and predators such as planktivorous fishes and/or invertebrates. Besides bottom-up and top-down forces, they are sensitive to changes in chemical composition and other abiotic factors namely temperature, turbidity, substrate, or water depth (see review in [Jeppesen et al., 2001](#); [Rautio, 2007](#); [Rautio and Nevalainen, 2013](#)). Moreover, they are the zooplankton group that is most readily preserved and identified in sediments and their importance for paleolimnological reconstructions has long been recognized ([Rautio and Nevalainen, 2013](#)). Links of cladoceran with temperature (climate) ([Belle et al., 2021](#)), water level (rainfall) ([Dietze et al., 2016](#)), pH (acidification) ([Zawisza et al., 2019](#)), nutrients (eutrophication) ([Leoni et al., 2021](#); [López-Blanco et al., 2021](#)) or planktivorous fish densities (alien species introduction) ([Jeppesen et al., 1996](#)) have revealed exceptional information

about past environments. These complex interactions of cladocerans with both biotic and abiotic variables, make their response more difficult to recognize ([Rautio, 2007](#)) but at the same time, enable them to respond to very particular questions in paleosciences research.

Paleoclimatic investigations have recently focused on climate change hotspots like the Mediterranean region ([Giorgi and Lionello, 2008](#)) since warming has amplified drying in the last decades in this area ([Cook et al., 2016](#)). For instance, the Iberian Peninsula has presented a significant tendency towards more arid conditions in the last decades ([Páscoa et al., 2017](#)) and drought projections revealed a potential risk of megadroughts in the future ([García-Valdecasas Ojeda et al., 2021](#)). Thus, paleoclimatic reconstructions are desirable to place the ongoing and predicted changes within multi-centennial-to-millennial timescales. Yet, despite the increasing research interest in reconstructing past environmental conditions in the Iberian realm (e.g. [Rodrigo-Gámiz et al., 2022](#); [Tarrats et al., 2018](#); [Vegas-Vilarrúbia et al., 2022](#)), studies using cladoceran subfossils are scarce in this area and have focused on short timescales. [García-Girón et al. \(2018\)](#) investigated the relationship

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between contemporary and subfossil cladoceran using surface sediments from 25 flatland ponds in the Iberian Plateau to find suitable indicators to track ecological changes over time. López-Blanco et al. (2013) also analysed biases between contemporary and fossilized cladocerans from sediments in a karstic sinkhole in the Iberian Ranges and inferred rainfall oscillations during the last millennium (López-Blanco et al., 2012; López-Blanco and Romero-Viana, 2019; Romero-Viana et al., 2009). Cladoceran subfossils were also used in central Spain (Lake El Tobar, Iberian Ranges) as indicators of anthropogenic impacts that involved changes in nutrients and species colonization in the last decades (López-Blanco et al., 2016a, 2011). However, of particular interest are remote and high-elevation lakes in southern mountainous areas of Iberia since they have shown an exceptional sensibility to anthropogenic warming, as revealed by changes in this crustacean assemblage in response to rising air temperatures and intensification of atmospheric deposition of Saharan dust during the last 180 years (Jiménez et al., 2019, 2018). These lacustrine ecosystems have been subjected to a large number of paleoecological investigations using biological and geochemical proxies that revealed several climatic oscillations and anthropogenic impacts since the last 11,700 cal yr BP (see review in Jiménez-Moreno et al., 2022). However, the biotic response of cladocerans to these environmental changes recorded throughout the Holocene remains unknown.

Here, we present the first cladoceran-based paleoecological reconstruction for the Holocene in the Iberian Peninsula, relying on the lacustrine sequence of the Laguna de Río Seco (LdRS), located in the highest mountain range in the southern Iberian Peninsula (Sierra Nevada). The main goals of this article are: (1) to describe the subfossil cladoceran assemblage and changes throughout the Holocene in this high-mountain lake, (2) to discover the main environmental factors controlling the species turnover at long-time scales, (3) to understand the main environmental stimuli for gamogenetic reproduction in chydorids and, (4) to explore the utility of morphological measurements for palaeoecological applications. The ultimate objective is to reconstruct climate changes during the Holocene, which is achieved not only by measuring the cladoceran response to environmental factors in terms of species abundance but also as rates between parthenogenetic and

gamogenetic reproduction and changes in body size in both planktonic and benthic species. This study will help to broaden the paleoecological reconstructions acquired from previous studies, obtaining a more holistic overview of this ecosystem in the past.

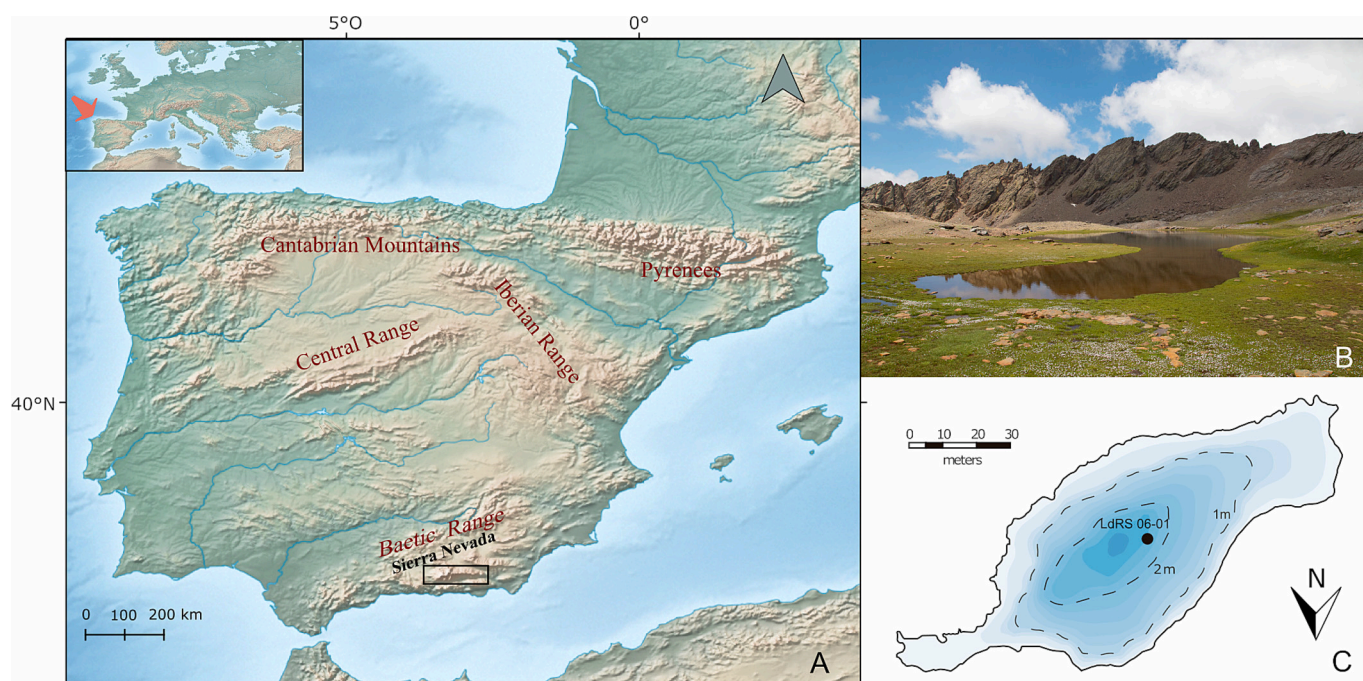
## 2. Material and methods

### 2.1. Study site

The massif of Sierra Nevada is part of the Baetic System, which is the highest mountain range in the southern Iberian Peninsula, situated at ca. 30 km north of the Mediterranean Sea (Fig. 1). Alpine wetlands and lakes formed in Sierra Nevada during the glacial retreat following the last glacial cycle (Castillo Martín, 2009) (maximum advance pulses ca. 30,000 cal yr BP and 20,000–19,000 cal yr BP) (Gómez-Ortiz et al., 2022). These lakes are generally oligotrophic systems characterized by cold, oxygen-saturated waters, with weak mineralization and low alkalinity (Sánchez-Castillo et al., 1989).

A Mediterranean climate characterizes the study area with warm, dry summers and cool, wet winters. The mean annual temperature is ca. 4.4 °C, ranging from ca. -4 °C in the coldest month to ca. 18 °C in the warmest period (instrumental series data 1965–1993 Prado Llano-Albergue University at 2500 m asl; ca. 15 km from the study site). Total annual rainfall is  $725 \pm 25$  mm, most of the precipitation (75%) falls as snow between October and May (AEMET, 2020; IEcolab, 2020) and it is mostly controlled by the North Atlantic Oscillation (NAO) (García-Alix et al., 2017; Ramos-Román et al., 2016) as also shown in other places in Iberia (López-Blanco et al., 2016b; López-Blanco and Romero-Viana, 2019).

Laguna de Río Seco (LdRS) (37°03'7N, 3°20'44W), is a small (~0.42 ha, max. depth ~3 m) and meso-oligotrophic lake (TP = 15.99 µg/L, TN = 402.52 µg/L; Chlorophyll: ~0.5–2 µg/L; Secchi depth equals maximum depth) (Barea-Arco et al., 2001; Jiménez et al., 2019; Morales-Baquero and Conde-Porcuna, 2000), which is situated on one of the south-facing cirques of the Sierra Nevada mountains at an altitude of 3020 m asl. The lake is too shallow to thermally stratify during the ice-free season, which typically lasts from June to October. It has temporal



**Fig. 1.** Location of the Sierra Nevada mountains in relation to the main mountain ranges in the Iberian Peninsula (A). Photograph (B) and bathymetry of the Laguna de Río Seco (LdRS) depicting the location of coring site LdRS06-01 (C).

inlets that during the ice-free season supply snowmelt and rain water to the basin. The main hydrological output is a small outlet in the southwestern part of the lake, which is only active during high lake levels. The pH is slightly acidic but close to neutrality and the conductivity does not reach values higher than 100  $\mu\text{S}/\text{cm}$ , as the catchment is mainly composed of metamorphosed siliceous rocks, mainly micaschists. This lake is situated above the treeline and partially covered by alpine meadows. Macrophytes are absent in the lake but the shores are surrounded by bryophytes (*Drepanocladus fluitans*) (Fig. 1B). LdRS is a fishless lake and planktonic communities are rather simple (Morales-Baquero and Conde-Porcuna, 2000). Zooplankton is dominated by the herbivorous zooplankter *Mixodiatomus laciniatus* and by the cladoceran *Daphnia pulex* (Pulido-Villena et al., 2005). The calanoid *Diatomus cyaneus* and the cyclopoid *Acanthocyclops vernalis* are occasionally found in this lake (Pulido-Villena, 2004). The littoral cladoceran community is mainly composed of *Chydorus sphaericus*, *Alona quadrangularis* and *Coronatella elegans* (unpublished results).

## 2.2. Sediment sampling and cladoceran analysis

A 150-cm sediment core (LdRS 06–01) was taken from the deepest part of the lake (1.7 m) (Fig. 1C) in September 2006. Stratigraphy, an initial chronological model, and pollen analyses were previously

described by Anderson et al. (2011), while a revision of the chronological model by adding more radiocarbon dates was recently described in Jiménez-Moreno et al. (2023a). The sedimentary record reached the lake bedrock and thus recovered the entire sedimentary sequence, spanning the last ca. 21,000 cal yr BP (Jiménez-Moreno et al., 2023a) (Fig. 2). It contains banded peaty clays and silty clays above ca. 133 cm and glacial clay and sand from ca. 133 cm to the core bottom (Anderson et al., 2011).

A total of fifty samples distributed from the 10 cm downcore were selected for cladoceran analysis following the protocol described in Szeroczyńska and Sarmaja-Korjonen (2007). Sediment samples from the topmost part of the core above 10 cm were already run out and used in previous analysis in this lake. One  $\text{cm}^3$  of wet sample was deflocculated in a warm (ca. 80 °C) water bath with a 10% solution of potassium hydroxide (KOH) for 30 min and subsequently sieved with a 40  $\mu\text{m}$  mesh-size sieve. Sieved residues were poured into a test tube and centrifuged for 10 min at 3500 rpm. After the centrifuge, the supernatant was decanted and a small quantity of ethanol was added and mixed. A slide was put on a hot plate, and liquefied glycerol jelly with some drops of safranin was added. Finally, a cover slip was placed on the slide. Samples were counted at 200–400 magnifications using a ZEISS Primostar 3 microscope. A minimum of 100 individuals (Kurek et al., 2010) and between 150 and 400 subfossils, were identified and counted. Only

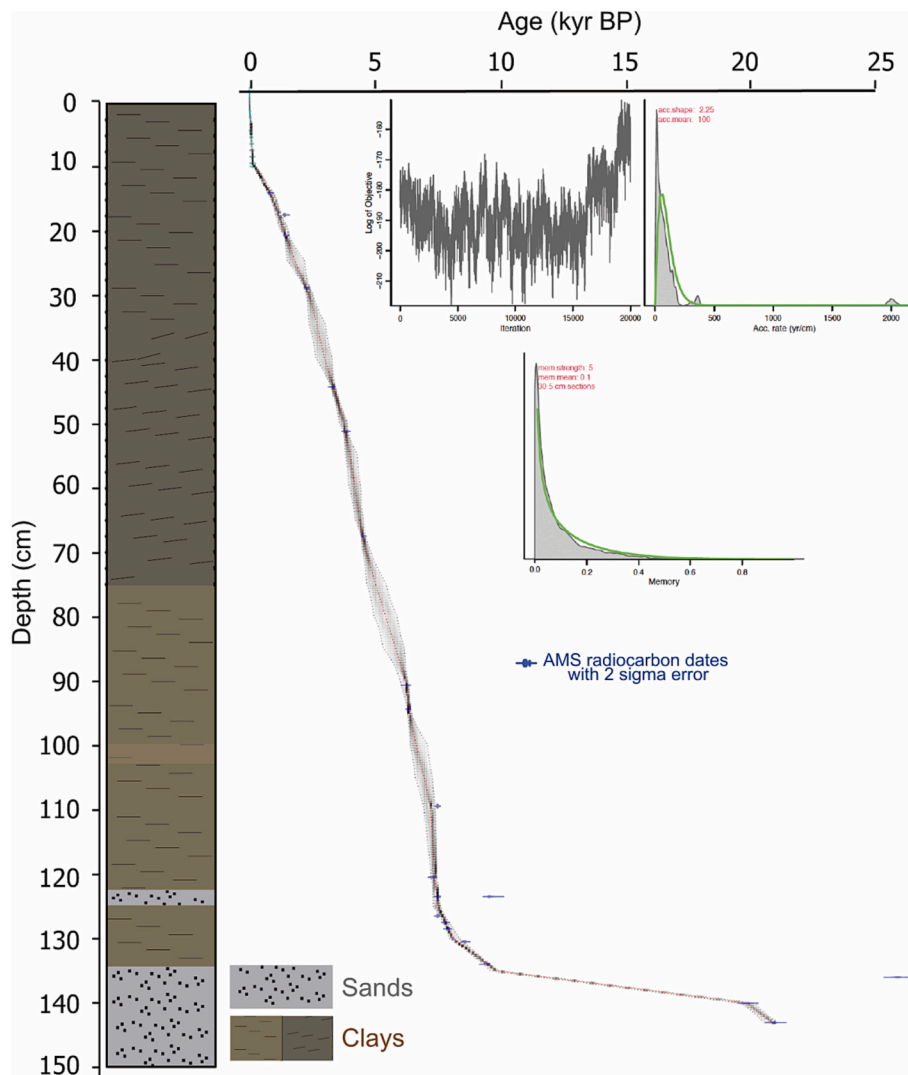


Fig. 2. Lithological column and Bayesian-based age-depth model of the Laguna de Río Seco sediment core (LdRS 06–01) plotted alongside the two-sigma age ranges of the radiocarbon dates (modified from Jiménez-Moreno et al., 2023a).



the three deepest samples (134.5; 139.5 and 143.5 cm) of the core were extremely scarce in fossils (50 cladoceran remains) and therefore, they were not considered for percentage determinations and multivariate analysis. Major stratigraphic subfossil cladoceran zones were identified using a constrained cluster analysis (CONISS) performed with the software TILIA v. 3.0.1 (Grimm, 1987). The total sums of 1.3 and 1.1 were chosen to identify the major zones and subzones, respectively.

For ephippium analysis (Sarmaja-Korjonen, 2003, 2004) chydorid carapaces (representing asexual reproduction) and ephippia (representing sexual reproduction) were enumerated from the same samples during the routine counting of cladocerans. The relative proportions of ephippia of individual species and total chydorid ephippia (TCE) were calculated from the number of chydorid carapaces and chydorid ephippia to represent the proportion of sexual of all chydorid reproduction. Ephippia of planktonic taxa such as *Daphnia* preserve in LdRS but as their parthenogenetic carapaces do not preserve, they were not used in estimating proportions of sexual and asexual reproduction. A Mann-Kendall trend test (PAST software) was applied to TCE to detect significant trends over the studied period.

### 2.3. Data screening and multivariate analysis

Redundancy analysis (RDA) was used to relate sedimentary cladoceran assemblage composition to biological, organic, and/or inorganic variables from the same sediment core (Anderson et al., 2011; García-Alix et al., 2018; Jiménez-Espejo et al., 2014). Table 1 compiles the initial environmental information considered for multivariate analysis. Before statistical analyses, environmental data were screened for normality using the Shapiro–Wilk test in Past 4.11. Inorganic and C/N data were log-transformed while percentages of pollen of aquatic and wetland species, as well as  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data, were square-root transformed.  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and fern spores data were skewed even after the transformation and were also highly correlated to other environmental variables in the dataset. Therefore, they were omitted from further analysis. Cladocera taxa with a relative mean lower than 1% were removed from the data set to reduce the weight of rare species. This threshold eliminated *A. quadrangularis* from the multivariate analysis. The remaining species were square-root transformed to minimize the impact of dominant taxa.

Prior to RDA analysis, a detrended correspondence analysis (DCA) was performed to assess the gradient length of the cladoceran data and, based on the results (gradient length = 0.6 SD), it was determined that linear ordination was more appropriate (Legendre and Birks, 2012). To summarize the species-environmental relationships and detect multicollinearity between independent variables, a series of initial RDAs were

**Table 1**

Compilation of biological, organic, and inorganic variables from the LdRS sediment core considered in the initial screening of the environmental data before the RDAs.

Variable	Type of indicator	Ecological meaning	Reference
Aquatic and wetland pollen (Cyperaceae, <i>Potamogeton</i> , <i>Botryococcus</i> , <i>Botrychium</i> , Ferns, <i>Sporormiella</i> )	Biological	Lake-level changes	Anderson et al. (2011)
C/N, $\delta^{13}\text{C}$ , $\delta^{15}\text{N}$	Organic	Origin (terrestrial or aquatic) of organic matter	García-Alix et al. (2018)
Ca, Fe, K, Sr, Ba, Cr, Co, Cu, Zn and Mn/Al ratio, Mg/Al ratio, Zr/Th ratio, Pb/Al ratio	Inorganic	Elemental composition of sediment, terrigenous input, and environmental interactions	Jiménez-Espejo et al. (2014)
<i>Olea</i> pollen	Biological	Anthropogenic impact	Anderson et al. (2011)

performed and the variance inflation factor (VIF) was used to eliminate highly correlated variables. In the initial RDA, all environmental variables were considered and the variables with the highest VIF were removed from the analysis. This procedure was repeated until all the variables highly correlated (VIF > 5) were eliminated from the analysis (Zuur et al., 2010). The significance of each environmental variable was tested with a Monte Carlo permutation test (999 unrestricted permutations), with significance levels of  $p < 0.01$  and  $p < 0.05$ . Only significant paleoenvironmental variables were plotted in diagrams. Additionally, in order to determine the relationship of the main cladoceran taxa to significant environmental variables, species response curves using generalized linear models with Poisson distributions were generated in CANOCO 5.

### 2.4. Morphometric analysis

To assess the potential effects of temperature and predation on the phenotypic plasticity of planktonic and benthic species, ephippia of *Daphnia pulex*-group and carapaces of *Chydorus sphaericus* were digitally photographed and measured using Image J (Rueden et al., 2017). To ensure that sufficient variation was captured in each assemblage (Brahney et al., 2011; Korponai et al., 2020; López-Blanco et al., 2020), between 30 and 50 *Daphnia* ephippia were measured. As *Chydorus* was more abundant, a minimum of 45 carapaces were measured and digitally photographed in each sample.

Mean values were calculated from the 30–45 replicates for each measurement (*Daphnia* ephippia and *Chydorus* carapace) and compared with data retrieved from the chironomid record published in Jiménez-Moreno et al. (2023a) using the same sedimentary core from LdRS and the same samples as those processed for cladoceran analyses. These data include the inferred summer temperature ( $^{\circ}\text{C}$ ) in LdRS and the total number of chironomid head capsules per  $\text{cm}^3$  that was taken as a potential indicator of predatory pressure.

## 3. Results

### 3.1. Cladocerans and chydorid ephippia

A total of five cladoceran taxa were identified in the sediment core of LdRS, which are illustrated in Fig. 3. According to the cluster analysis, the cladoceran stratigraphy was divided into two local fauna zones (CL1 and CL2) and two subzones (CL2a and CL2b). The fauna in zone CL1 (~8600–5000 cal yr BP) included pioneer chydorids such as *C. sphaericus* and higher abundances of *Flavalona rustica* and its tuberculate forms. Zone CL2 (~5000–256 cal yr BP) was generally characterized by an increase in the relative abundance of *Coronatella elegans* to the detriment of *C. sphaericus*. *Daphnia pulex*-group slightly increased its relative abundance in CL2a and CL2b. *Flavalona rustica* and *F. rustica* tuberculata showed a continuous presence until the upper part of CL2a. However, from this zone upwards their occurrence is irregular. The presence of *A. quadrangularis* is occasional along the whole sedimentary sequence. Note that *Daphnia pulicaria* is the only *Daphnia* present in the modern lake but for fossil samples, we used hereinafter the more conservative term *Daphnia pulex*-group, as the stout spines were present in the postabdominal claws in our samples but further morphological analyses to differentiate the distinct members of the *Daphnia pulex*-group were not performed.

The number of ephippia encountered in the samples varied between 7 and 100 (mean 39) and the number of carapaces varied between 71 and 255 (mean 143). These ephippia belonged to the *Daphnia pulex*-group, *C. elegans* and *C. sphaericus*. No ephippia of *A. quadrangularis* and *F. rustica* were encountered. The stratigraphy of chydorid carapaces and ephippia (indicating a shift from asexual to sexual reproduction) (*C. elegans* and *C. sphaericus*) was divided into two local zones (Eph 1 - Eph 2) and two subzones (Eph 1a - Eph 1b) (Fig. 4). The Early and Middle-Holocene sediments until ~5000 cal yr BP (Eph 1) were

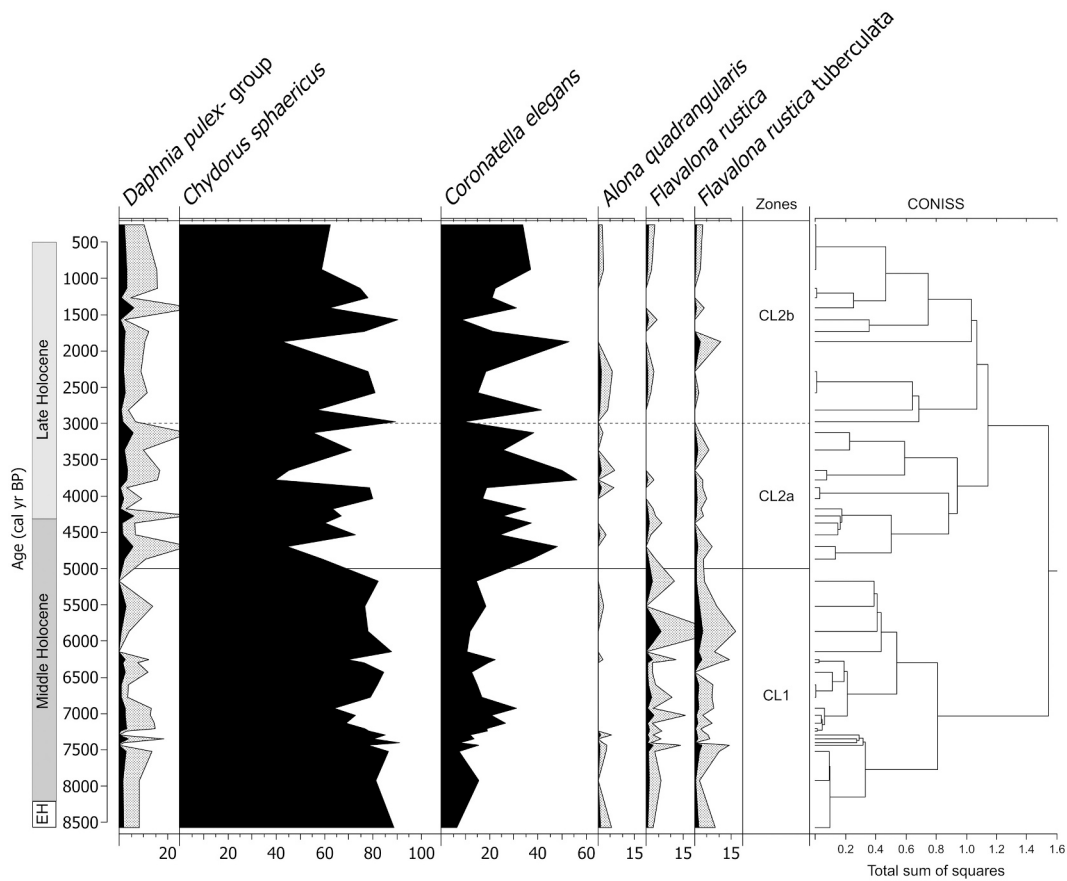


Fig. 3. Cladoceran sub-fossils from the Laguna de Río Seco (LdRS 06-01), expressed in relative abundance (%). Local cladoceran assemblage zones (CL) are based on the indicated constrained cluster analysis on percentages. Gray shadings indicate a 5× exaggeration scale.

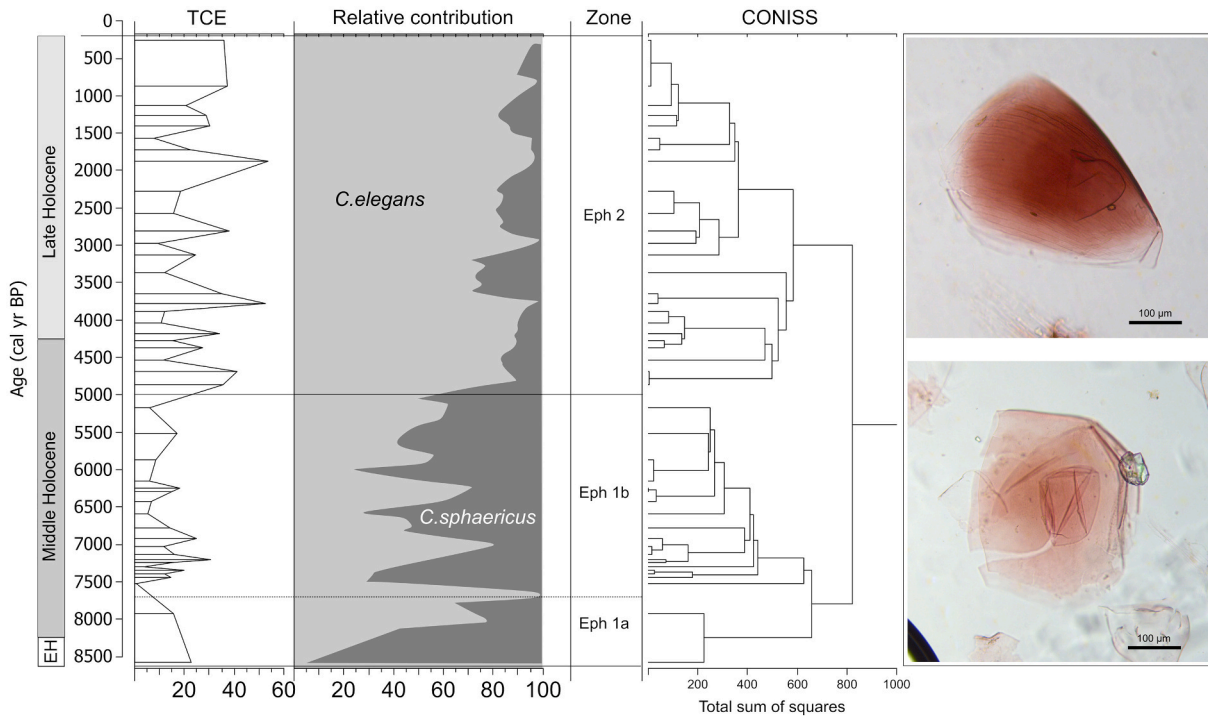


Fig. 4. Total Chydorid Ehippia (TCE) and relative contribution (%) of *C. elegans* and *C. sphaericus* throughout time. Ehippia zones (Eph) based on the indicated constrained cluster analysis and photographs of the main contributors to the egg bank, *C. elegans* in the upper part and *C. sphaericus* lower part.

generally characterized by lower values of TCE with mean values of ca. 13.5%. In this zone, there was a higher contribution of *C. sphaericus* to the total with maximums of 20.64% at ~7200 cal yr BP, 7.9% at ~7400 cal yr BP and 17.18% at ~8600 cal yr BP. Middle and Late-Holocene sediments (Eph 2; ~5000 cal yr BP) exhibited oscillations but generally high TCE percentages, with mean values of ca. 26.3%. Here, there is a higher contribution of *C. elegans* (mean ca. 92%) to the total. The Mann-Kendall test showed a statistically significant increasing trend of TCE over the Holocene.

### 3.2. Multivariate analyses

The initial RDA analyses with the backward selection eliminated ten environmental variables (Ca, Fe, K, Sr, Ba, Cr, Co, Zn, *Potamogeton* and Mg/Al and Zr/Th ratios) whose VIFs were >5. The final RDA identified three significant environmental variables (C/N ratio, Cyperaceae and *Botrychium*) at  $p < 0.01$  and one variable (*Botryococcus*) at  $p < 0.05$  levels (Fig. 5). RDA axis 1 and 2 explained 31.99% but only RDA axis 1 was found to be significant. The most positive values of RDA axis 1 grouped samples from the Early Holocene, where pioneer species like *C. sphaericus* and *F. rustica* were abundant. Notwithstanding, the most negative values are occupied by samples from the Middle and Late Holocene that were richer in *C. elegans*, a species that thrives well in shallow and ephemeral ecosystems. According to the species ecology and the distribution of significant environmental variables in the space defined by the RDA, axis 1 illustrates cladoceran species' response to lake level changes, which are related to the decline of aquatic vegetation and increasing C/N ratio during the Holocene.

Results of the generalized linear models (GLM) for the most abundant species (*C. sphaericus*, *C. elegans*, *F. rustica* and *Daphnia pulex*-group) are summarized in Fig. 6. *C. sphaericus* was significantly and positively related to algae and wetland vegetation but negatively related to the C/N ratio. *F. rustica* shows a similar pattern and it was significantly and positively related to Cyperaceae, but negatively to C/N ratio. However, *C. elegans* was significantly but negatively related to algae and aquatic vegetation but positively related to the C/N ratio. The only planktonic

species, *Daphnia pulex*-group, was significantly related to Cyperaceae and C/N ratio.

### 3.3. Morphological measurements

Results of *Daphnia* ephippia size and *Chydorus* carapace length are shown in Fig. 7. *Daphnia*'s mean body (ca. 900 measurements) (Fig. 7C) was between 0.96 and 1.16 mm with the largest body size in the Middle Holocene (~8000–4200 cal yr BP) and a decreasing trend towards the Late Holocene.

Body size measurements of *C. sphaericus* (ca. 1485 measurements) displayed a different pattern. It showed continuous changes during the studied period but with a decreasing tendency from the Early to the Late Holocene (Fig. 7A, note the reverse axis). In the Early Holocene (~10,000–7400 cal yr BP), carapace length reached maximum values ( $375.28 \pm 9.62 \mu\text{m}$ ) but decreased until ~7200 cal yr BP, when *Chydorus* body size was  $325.57 \pm 9.08 \mu\text{m}$ . Then, there was a period of oscillations with the smallest carapaces found at 5500, 4000 and 1500 cal yr BP (minimum values of  $326.89 \pm 9.2 \mu\text{m}$ ).

## 4. Discussion

Cladoceran assemblages in the Laguna de Río Seco exhibit a habitat and resource response during the Holocene, which is coupled with lake level changes following regional hydroclimatic variability. Supplementary proxies such as mean body size and abundance of fossils ephippia offer additional information for paleoecological interpretations in the highest mountain range in southern Iberia.

### 4.1. Cladocerans and hydroclimatic variability

As expected for a remote and alpine ecosystem with extreme environmental conditions and very little disturbance by allochthonous colonization, the cladoceran assemblage in Laguna de Río Seco is characterized by a low number of species and dominated by benthic taxa (the chydorid group). Based on the compilation of geochemical and

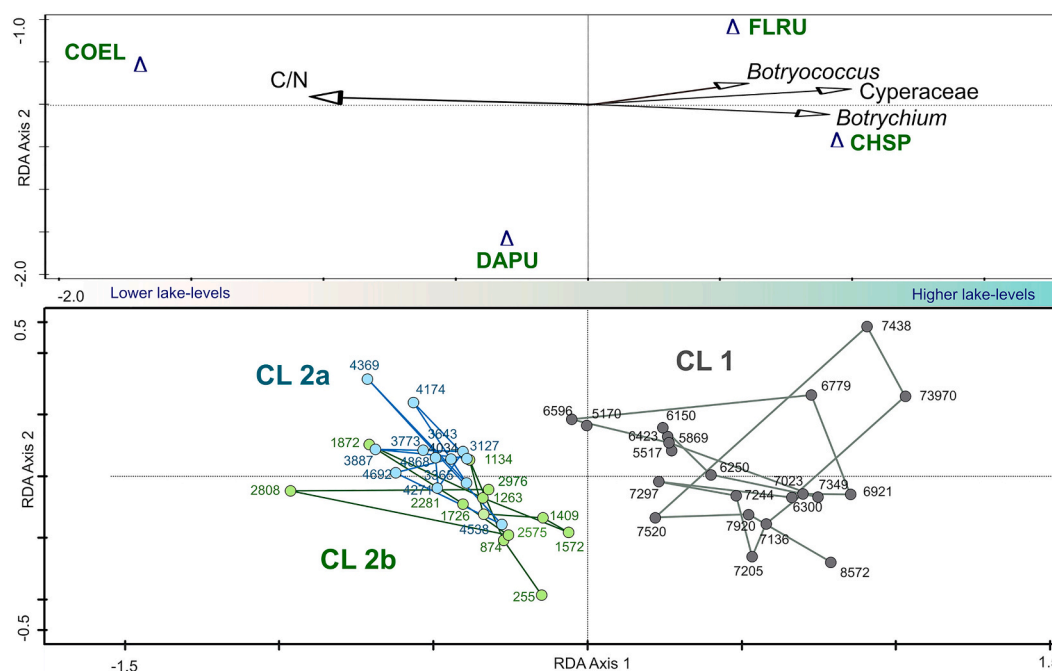
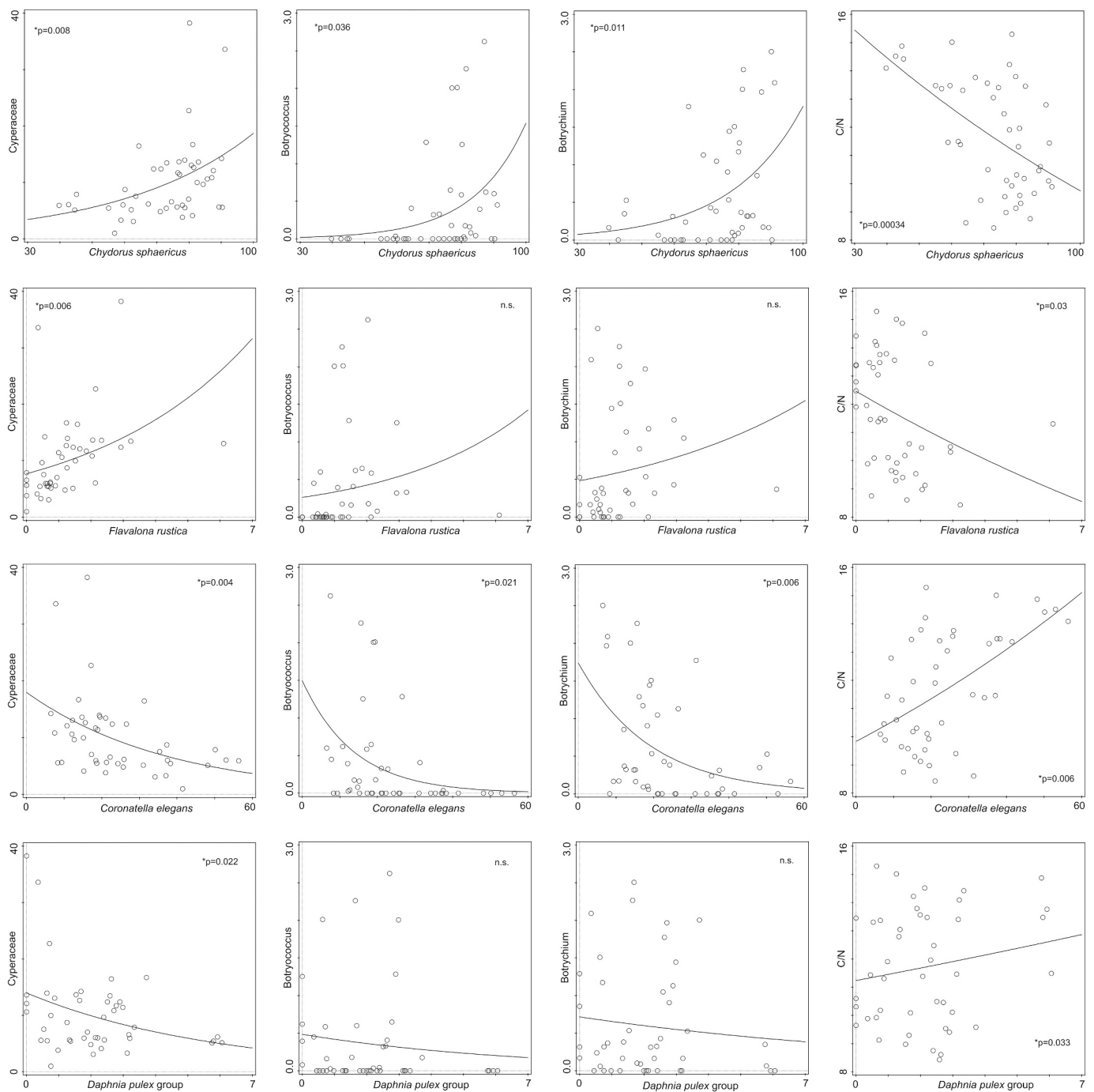


Fig. 5. RDA analysis for cladoceran assemblages of LdRS 06–01. In the upper panel, RDA with backward selection shows significant environmental variables at  $p < 0.01$  and  $p < 0.05$  and the relative position of the species (FLRU: *F. rustica*; CHSP: *C. sphaericus*; DAPH: *Daphnia pulex*-group.; COEL: *C. elegans*). In the lower panel, sample distribution in the space defined by the RDA, coloured lines indicated the environmental trajectory of the samples, as shown in the cladoceran biozones in Fig. 2.

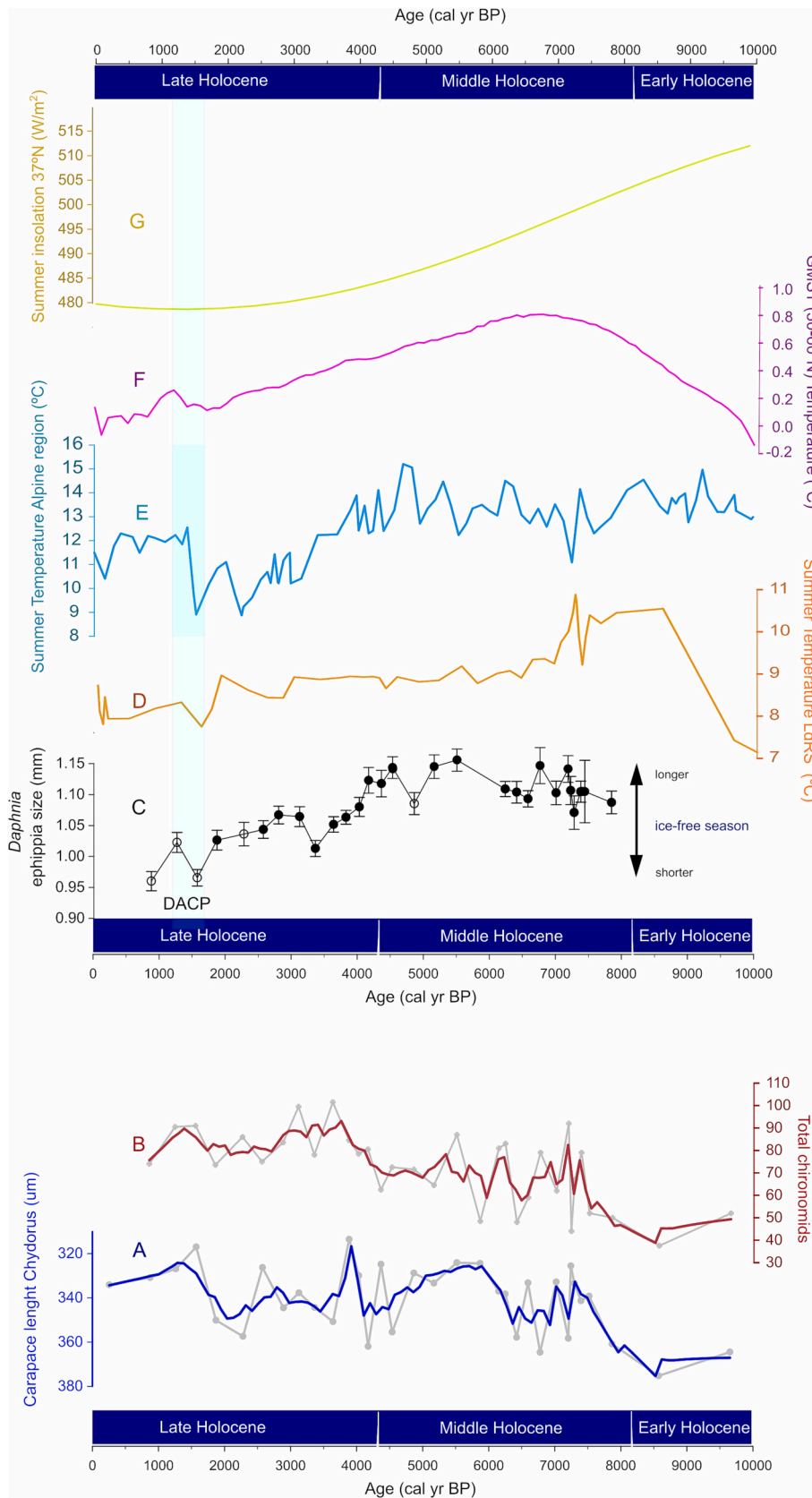


**Fig. 6.** Results of the generalized linear models (GLM) of significant ( $p < 0.05$ ) responses of *Chydorus sphaericus*, *Coronatella elegans*, *Flavalona rustica* and *Daphnia pulex*-group to the main significant environmental variables detected in the RDA analysis (*Botryococcus*, Cyperaceae, *Botrychium* and the C/N ratio).

biological data, two different assemblages are described. A higher lake-level assemblage is formed by *C. sphaericus* and *F. rustica* (Figs. 3 and 5). *C. sphaericus*, although typically littoral, it is an eurytopic species that is well-known to develop truly pelagic populations (Bonacina and Bonomi, 1984; López-Blanco et al., 2013; Marcé et al., 2005). *F. rustica* has been found in the littoral part of deep lakes (Alonso, 1996) and between *Sphagnum* moss-covered ditches (Błędzki and Rybak, 2016). This assemblage occurs with the greatest frequency at higher relative abundance of algae, aquatic and wetland pollen, and at a lower value in the C/N ratio (Figs. 4 and 5). According to Anderson et al. (2011), the occurrence of the pelagic chlorophyte *Botryococcus* and pollen of Cyperaceae, *Potamogeton* and *Ranunculus* were either related to more

permanent water or higher lake level in LdRS. Under these conditions, *C. sphaericus* and *F. rustica* might use preferentially periphyton and/or planktonic algae as food resources.

The lower lake-level assemblage is formed by *C. elegans* and *A. quadrangularis*, which are both known to be typical taxa from vegetation-bare and temporal environments (Błędzki and Rybak, 2016). In fact, the elegans-group was recently suggested to form a separate subgenus within the genus *Coronatella*, named *Coronatella (Ephemeralona)* after the Latin “ephemeral” –temporary-, as most species of the group inhabit this kind of water bodies (Sinev, 2020). *C. elegans* have significantly higher relative abundance at higher C/N ratio values (Figs. 5 and 6). Higher values in the C/N ratio indicates the



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**Fig. 7.** Age-profile comparison of Laguna de Río Seco sediment core (LdRS 06–01) where the lower panel shows a comparison between changes in the body size of *Chydorus* ( $\mu\text{m}$ ) (A) and (B) the number of chironomid headshields (number/ $\text{cm}^3$ ) (Jiménez-Moreno et al., 2023a). The upper panel displays a comparison between (C) changes in *Daphnia* ephippia length (mm) and (D) Chironomid-inferred July air temperatures from the LdRS sediment record (Jiménez-Moreno et al., 2023a) (E) Stacked summer air temperature for the Alpine region (Heiri et al., 2015), (F) Global Mean Surface Temperature for 30–60°N (Kaufman et al., 2020), and (G) 37°N mean monthly summer insolation (21 June–21 July) obtained online (<http://vo.imcce.fr/insola/earth/online/earth/online/index.php>) from Laskar (2004). Blue shading depicts the Dark Ages Cold Period (DACP). Note that empty symbols in the *Daphnia* ephippia size curve denotes samples where the minimum of measurable remains were not achieved. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

predominance of a terrestrial origin of the organic matter and occurred under drier conditions and lower lake levels in LdRS, as well as in other alpine wetlands in the area (García-Alix et al., 2012; Jiménez-Espejo et al., 2014). The habitat of *C. elegans* is not bonded to vegetation/pelagic algae and may use detritus of fine organic matter as a food source, as indicated by its significant negative correlation with *Botryococcus* and wetland vegetation (Figs. 5 and 6). Ecological information on *C. elegans* in the Mediterranean region indicates an association with sediment-rich, turbid, low mineralized waters and with poor development of vegetation (Alonso, 1996; Marrone et al., 2006; Sahuquillo and Miracle, 2013), which agrees well with our inferences.

According to the species ecology and its relationship to the environmental variables aforementioned, the RDA axis 1 (Fig. 5) illustrates cladoceran species' response to lake level changes. Rather, as deduced from above, cladocerans might not directly respond to lake depth per se, but to those environmental factors such as habitat and food resources, modulated by fluctuating lake levels that are somehow reflected in RDA axis 1. Thus, the scores of this axis allow reconstructing different stages in the lake development in relation to water depth (Figs. 8 and 9). In the Early and Middle Holocene (~8600 to 5000 cal yr BP), when a pristine lake with rooted vegetation existed, cladocerans such as *C. sphaericus* dominated the assemblage. This species has been found among the pioneer taxa in post-glacial conditions due to its broad ecological spectrum and tolerance to low temperatures and open-water conditions (Duigan and Birks, 2000; Zawiska et al., 2019). Lake depth was higher than today, with two different periods separated by a small decline in depth ~ 7000 cal yr BP (Fig. 8). This reconstruction is consistent with studies at local (Anderson et al., 2011; García-Alix et al., 2012; Jiménez-Espejo et al., 2014; Jiménez-Moreno and Anderson, 2012), regional (García-Alix et al., 2021; Mesa-Fernández et al., 2018; Morellón et al., 2009; Ramos-Román et al., 2018; Toney et al., 2020; Jiménez-Moreno et al., 2023b) and European scale (Ilvonen et al., 2022; Magny et al., 2002) that indicated a higher Early and Middle Holocene relative humidity (Fig. 9).

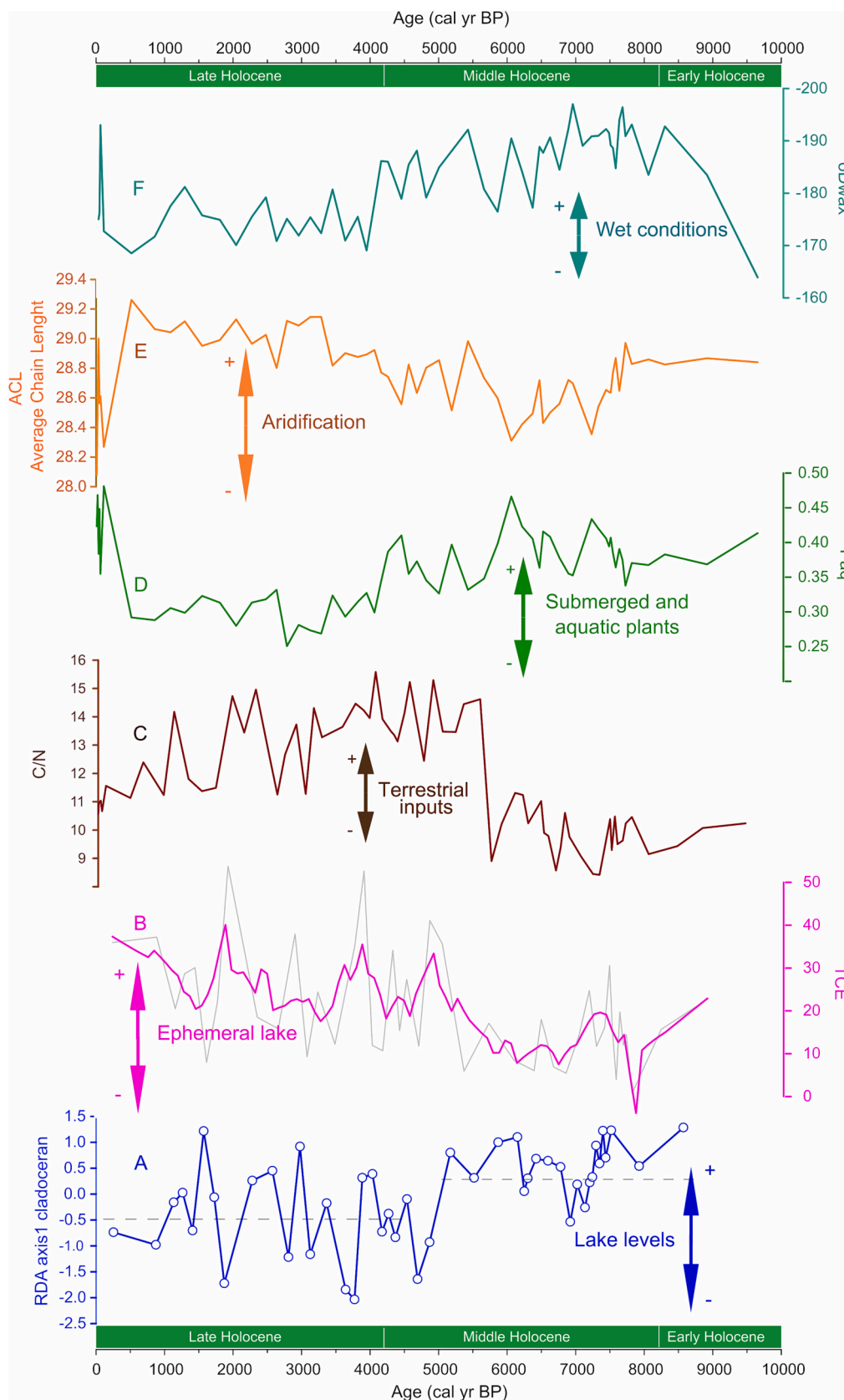
At ~5000 cal yr BP, there was a clear shift towards lower lake level inferred by the increase in species that thrives well in shallow ecosystems, such as *C. elegans* (Figs. 3 and 8). Anderson et al. (2011), Ramos-Román et al. (2018) and Schröder et al. (2018) also inferred lower lake levels from this period onwards in LdRS, Padul, and Laguna de Medina, respectively, all of them in southern Spain and using proxies with independent links to lake level variability. In more central and northern locations in Spain, like the marshlands of Las Tablas de Daimiel (Dorado Valiño et al., 2002) or the Pyrenees (Morellón et al., 2009; Pérez-Sanz et al., 2013), there was also evidence of an increasing aridity over the last 5000 cal yr BP. However, this lower-level stage is interrupted in our sedimentary record by some higher-level peaks, particularly between ~3000–1600 cal yr BP (Figs. 8 and 9). A wet and cool event at a global scale and starting at ~2800 cal yr BP was synchronous to the Iberian-Roman Humid Period (IRHP) (~2600–1600 cal yr BP) (Martín-Puertas et al., 2009) and could also be ascribed, but with limitations due to our sample resolution, to the humid phase detected by the increase of heleoplanktonic cladocerans in LdRS. Likewise, a wet period between ~2600–1450 cal yr BP was inferred in Laguna de La Mula and Laguna Hondera, both in the Sierra Nevada, by changes in arboreal pollen, magnetic susceptibility and high values in the K/Al and K/Ti ratios (Jiménez-Moreno et al., 2013; Mesa-Fernández et al., 2018) (Fig. 9). From this period onwards, a high relative abundance of *C. elegans* together with increasing values in the TCE (see the section below; Fig. 8)

are consistent with a shallower ecosystem under a context of reduced regional moisture provided by multiple paleoecological indicators (see review in Jiménez-Moreno et al., 2022). Solar activity and atmospheric-oceanic dynamics have been suggested as potential climate forcings in other Sierra Nevada records (García-Alix et al., 2017, 2020; Jiménez-Espejo et al., 2014; Ramos-Román et al., 2018; Toney et al., 2020). The good correspondence between inferred lake levels in LdRS, the Total Solar Irradiance (TSI) anomaly and the Ocean Drift Ice Index during the Holocene might also suggest a link between all of them in this record (Fig. 9).

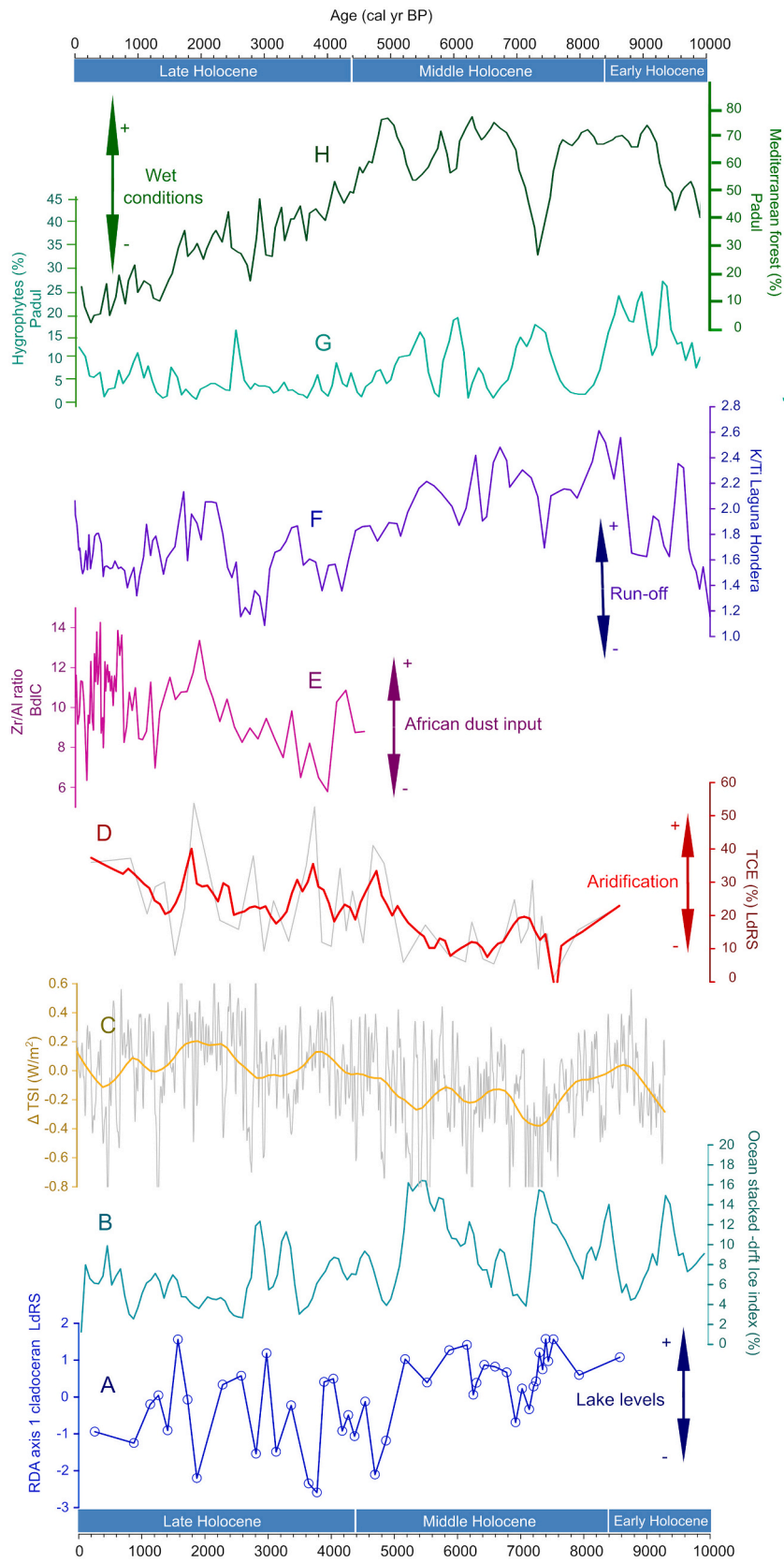
#### 4.2. Chydrid reproduction and aridification

Natural disturbances can also activate changes in the genetic structure of cladocerans (Jeppesen et al., 2001). They mostly reproduce parthenogenetically but stressful conditions can trigger gamogenesis or sexual reproduction as a mechanism to increase the adaptability of the offspring. Among the multiple forces, temperature is the main factor controlling the development of resting eggs or ephippia in northern latitudes and/or high-altitude lakes (Nevalainen, 2008; Sarmaja-Korjonen, 2004). There, the TCE has been used as an indicator of the length of the ice-free season, as higher TCE detected in the Early Holocene/Little Ice Age indicated severe climate or short open-water season. However, the TCE curve in LdRS (Fig. 4) is not linked either to temperature or to the open-water season length. In fact, higher TCE in LdRS (maximum ca. 54% and mean values ca. 20%) in comparison with studies in northern latitudes (i.e., maximum of 26.1% in Nevalainen et al., 2011) suggests more frequent gamogenesis in southern latitudes and probably different causes behind the onset of diapause. The high coherence between the TCE and the inferred lake levels in the section before (Figs. 4 and 8) suggests that the main stimuli for gamogenesis in LdRS were the decline in lake level starting at ~5000 cal yr BP (Fig. 4 transition Eph 1 and Eph 2). This is consistent with the ecological data of the main contributors of resting eggs to the sediment. *C. elegans*, which is the most abundant species in the Late-Holocene sediments and more adapted to shallow environments, showed higher contribution to the egg bank in the Late Holocene (Fig. 4). However, ephippia of *C. sphaericus* showed the reverse tendency, with maxima contribution in the Early-Holocene sediments (Fig. 4). Presently, males and ephippial females in populations of *C. elegans* are very frequent in the Iberian Peninsula (Alonso, 1996), some of them reached proportions up to 77% in mid-spring, when water bodies were close to dry (Sahuquillo, 2012). The production of desiccation-resistant forms such as ephippia was the strategy found by *C. elegans* for surviving droughts and a mechanism of adaptation and success in highly ephemeral conditions as those inferred for the Late-Holocene sediments in LdRS. Thus, higher diapausing rates are triggered here under harsh and more temporary conditions, which allows using the TCE curve as indicator of aridification throughout time.

The TCE is relatively low (~13%) in the Early and Middle Holocene (~8600–5000 cal yr BP) (Fig. 4) as chydorids reproduce primarily by parthenogenesis during favourable and wetter climatic stages corresponding to relatively higher lake levels. Environmental stress, such as an oncoming arid stage and a reduction of lake level (~5000 cal yr BP), triggers sexual reproduction, which increases the number of total ephippia (~26%) (Fig. 4) and favours species highly adapted to more temporary environments (Fig. 3). The statistically significant increasing trend of TCE over the Holocene (Figs. 8 and 9) provided evidence of environmentally unstable and stressful conditions under the regional



**Fig. 8.** Comparison between lake levels inferred in Laguna de Río Seco (LdRS) from cladoceran subfossil analyses performed in this study. (A) Scores of RDA axis 1 based on cladoceran analysis, and (B) Total Chydorid Ehippia (TCE) (%), with selected organic and biomarkers proxies from same sediment core, LdRS 06–01. From bottom to upper panel: (C) the C/N ratio (García-Alix et al., 2018), (D) aquatic plants portion deduced from C<sub>23</sub>-C<sub>25</sub>-C<sub>29</sub> and C<sub>31</sub> n-alkanes (Paq), (E) Average Chain Length between C<sub>25</sub> and C<sub>33</sub> n-alkanes (ACL), (F) Hydrogen isotopic composition of the terrestrial C<sub>29</sub> and C<sub>31</sub> n-alkanes (δD<sub>wax</sub>) (Toney et al., 2020).



(caption on next page)

**Fig. 9.** Comparison between lake levels inferred in Laguna de Río Seco (LdRS) from cladoceran subfossil analyses performed in this study: (A) RDA axis 1 based on cladoceran analysis, and (D) Total Chydorid Ehippia (TCE) (%) (raw data in gray and smoothed data in red) with selected regional and global proxies. From bottom to upper panel: (B) Ocean stacked percentage of the Drift Ice Index (Bond et al., 2001), (C) Total Solar Irradiance (TSI) anomaly reconstruction for cosmogenic radionuclide from Greenland ice core (Steinilber et al., 2009), (E) the Zr/Al ratio from the Borreguil de la Caldera (BdlC) (García-Alix et al., 2018), (F) the K/Ti ratio from Laguna Hondera (LH) (Mesa-Fernández et al., 2018), (G) hygrophytes pollen percentages (%), and (H) Mediterranean forest pollen percentages (%) from Padul (Ramos-Román et al., 2018), being all these three last locations in the Sierra Nevada mountains. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

aridification inferred for the last centuries in the Sierra Nevada. Values in the Zr/Th, Zr/Al and Ca/Al ratios increased in LdRS, Laguna Hondera and Borreguil de la Caldera, as a result of enhanced eolian dust emission from the Sahara (García-Alix et al., 2017; Jiménez-Espejo et al., 2014; Mesa-Fernández et al., 2018). Pollen records also showed an increase in xerophytes and a decrease in hygrophilous forest species after ~6000–5000 cal yr BP (Jiménez-Moreno et al., 2022, 2023b), and the *n*-alkane record and the hydrogen isotopes values from LdRS also displayed a gradual increase of the Average Chain Length (ACL) and higher  $\delta D_{wax}$  (Fig. 8), suggesting drier conditions for the Late Holocene as well (Toney et al., 2020).

#### 4.3. *Daphnia ehippia* and temperature

As expected for an alpine fishless lake, large *Daphnia ehippia* (mean size = 1.08 mm) are present in our sequence due to the absence of fish planktivory that tends to selectively consume the larger and more visible cladocerans like the daphniids (Brooks and Dodson, 1965). Predatory chironomids feed mainly on micro invertebrates in the early instars to diverse fauna from the meiobenthos (Schmid and Schmid-Araya, 1997) and did not affect *Daphnia* size in our sedimentary record (Fig. 7). However, *Daphnia* size in LdRS might have been influenced by temperature, as shown by the comparison between the morphological measurements of this planktonic species and the selected temperature-derived records shown in Fig. 7. Despite differences due to distinct ecological meanings of the signals (annual, seasonal), these data suggest that the size of *Daphnia ehippia* mirrors the available records of temperature and the dorsal length of daphnid ehippia might have increased with increasing temperature. Other paleolimnological studies (Korponai et al., 2011; Manca and Comoli, 2004; Nevalainen et al., 2013) also found a relationship, but negative, between *Daphnia* size and temperature, measuring larger remains in colder climate periods than in warmer. Our data from the LdRS seems to be an exception to the widespread temperature-size rule (TSR; Atkinson, 1994) but is well explained and supported by both in vitro and in situ data from the study site. In vitro experiments with clones of *Daphnia cf. pulex* from Borreguil Lake in the Sierra Nevada agree well with our in-sediment measurements and found significantly larger body size at higher temperatures (Ramos-Rodríguez et al., 2022). As the preferred temperature range for *D. cf. pulex* is 16–21 °C (Ramos-Rodríguez et al., 2022), extreme cold conditions as those registered in the Holocene sequence of the LdRS could impair growth and the size-temperature relationship could differ from the TSR due to the physiological constraints for the organism, as also documented in other studies (Atkinson, 1994; Atkinson et al., 2003; Walczyńska et al., 2016). In LdRS, although *D. pulicaria* is present from the beginning of the ice-free season, ehippial eggs are produced from September onwards as a part of a strategy to guarantee the persistence of the species in the sediment and have the possibility to hatch in the next ice-free season (Pérez-Martínez et al., 2007, 2013). In situ data demonstrated that each year, only one generation of *D. pulicaria* exists in this lake, increasing its size as the growing season advances (Pérez-Martínez et al., 2007). The diapause onset showed a high temporal synchronization in this lake being the day length the main cue for diapausing (Pérez-Martínez et al., 2007). Therefore, larger ehippia are produced under longer open-water seasons because individuals have more time to grow when the resting egg is formed. On the other hand, smaller ehippia are produced in September if the thaw, under colder climate, is delayed until July. These in-lake data from the LdRS support

the use of the *Daphnia ehippia* dorsal length in this lake as an indicator of the ice-free season length, which is modulated by temperature.

*Daphnia ehippia* were larger in the Middle-Holocene sediments, which might indicate a longer opening season, in a classic warm Holocene between ~8000–4000 cal yr BP in agreement with other continental records (see review in Cartapanis et al., 2022). Midges and cladoceran-based temperature reconstructions in Scandinavia (Luoto et al., 2010; Nevalainen et al., 2011) also inferred the warmest period of the Holocene between ~8000–4000 cal yr BP while a summer temperature reconstruction for the Alpine region indicated a longer Holocene Thermal Maximum (HTM) between ~9200–4700 cal yr BP (Heiri et al., 2015). The largest ehippia (1.16 ± 0.18 mm) were encountered at ~5500 cal yr BP, which according to the temperature-size relationship described above, might situate the warmest period within our studied interval around this age. A global mean surface temperature (GMST) reconstruction situated the warmest period of the Holocene at ~6500 cal yr BP (Kaufman et al., 2020). However, local qualitative (Ramos-Román et al., 2018) and quantitative (Jiménez-Moreno et al., 2023a) temperature reconstructions in other Sierra Nevada sedimentary records (Fig. 7) provide evidence of different timing for the HTM, and situated this warm period during the Early Holocene. Unfortunately, our data did not register the Early-Holocene conditions required for the establishment of local comparisons of the signals at this period. Differences in the temperature reconstructions using pollen, chironomids (Jiménez-Moreno et al., 2023a) and cladocerans in LdRS are probably due to the distinct nature of each proxy and the sedimentary signal recorded. The chironomid record reflects the summer air temperature (July), while *Daphnia* size depends more on the late-spring air temperature, which controls the beginning of the thaw, and therefore, the open-season length and the size of ehippia by the end of each September. The signal of pollen is more regional and, as noticed by Jiménez-Moreno et al. (2023a), apart from temperature, vegetation receives influence on humidity and evapotranspiration, which can explain the non-synchronic signal of pollen in comparison with other biological proxies. The Late Holocene, according to our data, was marked by a shorter opening season, within a gradual cooling at ~4000 cal yr BP inferred by a decrease in ehippia size. Within this period, the smallest remains were measured (0.97 ± 0.013 mm) at ~1572 cal yr BP, coinciding with the Dark Ages Cold Period (DACP) (1550–1185 cal yr BP), where rather anomalous and colder conditions were registered in Europe (Helama et al., 2017) and were likely to have promoted the development of a glacier in the Mulhacén cirque in Sierra Nevada (Oliva and Gómez-Ortiz, 2012).

This relationship between *Daphnia* size and temperature, although regarded as a high-potential approach at broadly detecting cold and warm phases during the Holocene, needs to be validated by analyzing higher resolution records containing enough planktonic remains and registering the coldest and warmest periods for the last 11,700 cal yr BP. Besides temperature, other factors such as food availability are likely to have effects on *Daphnia* size. However, they are difficult to evaluate in sediments, given the taphonomic processes affecting many algal groups and other intrinsic factors of daphnids, such as the epibiont *Korshikoviella gracilipes* that regularly attaches to *D. pulicaria* in LdRS, acting as a food source (Pérez-Martínez et al., 2001).

#### 4.4. Controls on Chydorus size

A priori, chydorids are less sensitive to top-down controls than



planktonic species and in fishless lakes, but they might theoretically preferentially respond to abiotic factors like temperature (Korponai et al., 2020; Perrin, 1988). However, these small-bodied zooplankton individuals are also preferred by invertebrate predators (Carpenter and Kitchell, 1988). The good correspondence between *Chydorus* carapace size and the total number of chironomid head capsules (Fig. 7) could suggest a predation effect on *Chydorus*, since smaller individuals of *C. sphaericus* are found when total midges increase. Conversely, larger carapaces are present under a low number of larval chironomids. This might indicate a size-selective preference of midges and that the greatest predation on *Chydorus* falls on the larger ones, eliminating the large body-size specimens from the populations. Nonetheless, the cyclopoid copepod *A. vernalis* has occasionally been found in the LdRS (Pulido-Villena, 2004) and it is known to predate on both planktonic and littoral cladocerans like *Bosmina*, *Diaphanosoma* and *Ceriodaphnia* (Balcer et al., 1984; Li and Li, 1979). Complex food web relationships, cascade effects or chemical variables not considered in this study might have also influenced the size of benthic cladocerans.

## 5. Conclusions

This study shows a compilation of data derived from the analysis of cladoceran microfossils, which include relative abundances, chydorid ephippia, and morphometric measurements, providing the longest cladoceran-based paleoecological reconstruction in the Iberian Peninsula covering the last ~8600 cal yr BP. Species turnover at millennial timescales was indirectly controlled by changes in lake level, in response to precipitation variability during the Holocene. A wetter stage was inferred between ~8600–5000 cal yr BP, under a stable phase for chydorid reproduction, as parthenogenesis was the main reproduction mode. A positive relationship between *Daphnia* size and temperature provides evidence of longer ice-free seasons under warm temperatures in this period. This stage and the next period agree well with the general idea of a dichotomy in hydroclimatic variability during the Holocene, which has been provided by multiple paleoindicators at different spatial scales.

An arid phase with a progressive reduction in lake level started around ~5000 cal yr BP favoured species more adapted to temporary environments and triggered sexual reproduction. Smaller *Daphnia* remains might indicate shorter ice-free seasons and a temperature decline starting at ~4000 cal yr BP, with the smallest individuals measured at ~1500 cal yr BP, coinciding with the onset of the DACP. The most remarkable feature of this phase (~5000–255 cal yr BP) is a tendency towards increasing aridity only interrupted by peaks in precipitation around ~3000–1600 cal yr BP, broadly coinciding with the IRHP. The increasing trend in TCE over the whole Holocene and particularly during the Late Holocene is in concordance with the progressive aridification inferred by other biological and geochemical indicators and Saharan eolian dust deposition in the Sierra Nevada wetlands.

Our study indicates that the remains of these invertebrates provided excellent proxy data on past lake-level changes, in particular, the TCE is a promising indicator of aridification in southern-latitude alpine ecosystems. A combination of intra-lake datasets together with modern sampling could validate the use of *Daphnia* size as a paleothermometer, providing high-resolution records of temperature throughout time.

## CRediT authorship contribution statement

**Charo López-Blanco:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing, Visualization. **Antonio García-Alix:** Conceptualization, Funding acquisition, Investigation, Project administration, Supervision, Validation, Writing – review & editing, Resources, Visualization. **Gonzalo Jiménez-Moreno:** Funding acquisition, Investigation, Resources, Writing – review & editing, Visualization. **Marta Rodrigo-Gámiz:**

Investigation, Writing – review & editing, Visualization. **R. Scott Anderson:** Investigation, Writing – review & editing, Visualization.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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