Diatom responses to warming, heavy rains and human impact in a Mediterranean lake since the preindustrial period

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HIGHLIGHTS

- Diatoms responded to climate and human impact in a Mediterranean lake since 1716 CE.
- The planktonic *Cyclotella cyclopuncta* dominated the community from 1716 to 1971 CE.
- New plankton species appeared but did not outcompete *C. cyclopuncta* until the 1970s.
- Storms and warming destabilized the planktonic diatom community from the 1970s on.
- Knowing the extreme events effects on the biota is crucial to predict future scenarios.

GRAPHICAL ABSTRACT
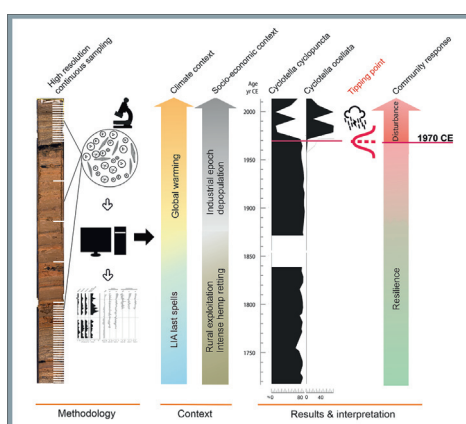
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ABSTRACT

In the Mediterranean region, annual mean air temperature will continue to increase during the 21st century, while seasonal precipitation is expected to decrease and extreme events to be more frequent. Human-induced climate change will severely impact aquatic ecosystems. A subdecadal stratigraphic diatom record of Lake Montcortès (central Pyrenees) was investigated, focusing on the potential responses of diatoms to anthropogenic warming and catchment alteration. The study includes the end of the Little Ice Age (LIA), the transition to the industrial and postindustrial eras, and the recent global warming and its current acceleration. Sediment samples were treated and diatoms taxonomically identified. Relationships between diatom taxa abundances and climatic (temperature and precipitation) and environmental (land use, soil erosion, and eutrophication) variables were investigated using multivariate statistical methods. The results indicate that, from ca. 1716 to 1971 CE, the diatom community was dominated by *Cyclotella cyclopuncta* and showed small perturbations, despite the pressure of important stressors such as strong cooling episodes, droughts and an intense use of the lake for hemp retting during the 18th and 19th centuries. However, during the 20th century, other centric species gained relevance, and from the 1970s on, *Cyclotella ocellata* competed with *C. cyclopuncta* for dominance. These changes coincided with pulse-like disturbances in the form of extreme rainfall events along with the gradual 20th century increase in global temperature. These perturbations affected the planktonic diatom community and led to instability dynamics. The benthic diatom community did not reflect any comparable shifts under the effect of the same climatic and environmental variables. Because heavy rainfall episodes are likely to intensify with current climate change in the Mediterranean region, their importance as stressors of planktonic primary producers should be taken into account as potential disrupters of biogeochemical cycles and trophic networks of lakes and ponds.

1. Introduction

The present study takes place on the Iberian Peninsula (IP) (West Mediterranean region), specifically in the Pyrenean mountain range (Fig. S1; ICGC, accessed October 2022), and addresses the impact of global warming on Lake Montcortès, an example of a deep Mediterranean lake. It is a karstic waterbody located in the central Pyrenees. In the Mediterranean region, human-induced climate warming will heavily impact aquatic communities and ecosystems (Lange, 2020). Reduction in precipitation, increased frequency and intensity of drought and extreme rainfall events, and higher water demand by both communities and irrigation-dependent agriculture are among the most expected threats from climate change to freshwater bodies (Bucak et al., 2017; Lange, 2020). Regional climate projections predict contrasting scenarios of temperature increases up to 5 °C and increases in the annual average temperature between 2 °C in winter and 3–6 °C in summer by 2100 CE. Additionally, precipitation decreases with strong spatial and temporal variability and a decrease in seasonal rainfall are expected (15 %–25 %) by the end of the 21st century (Barrera, 2011; Calbó et al., 2010; IPCC, 2021; López-Moreno and Beniston, 2009). In the Mediterranean sector of the Iberian Peninsula, rainfall has also experienced a decrease in annual totals and in the number of days of precipitation (Gallego et al., 2011; Valdes-Abellan et al., 2017), although an increase in the frequency of high and very high events has been detected (Serrano-Notivoli et al., 2018). For the next decades (2021–2050 CE), average temperature increases of approximately 1.3 °C to 2.3 °C and precipitation decreases of −5 % to −20 % (Fernández et al., 2017) are expected compared with the previous 1971–2020 CE period.

During the last century, a sustained increase in temperature was detected in this sector of the Pyrenees, with an intensification starting in the 1970s (Pérez-Zanón et al., 2017). The IP has more than a thousand lakes and natural lagoons. Despite being small in relation to their European counterparts, they provide important services in strategic sectors. For most Iberian lakes, detailed, long-term ecological and environmental studies are still scarce (Barrera et al., 2012). However, such knowledge is crucial to reconstruct how these lacustrine ecosystems have evolved under the influence of climate and human pressure, especially over the last two centuries, and to anticipate global change scenarios based on their degree of resilience.

Many biotic and abiotic proxies unequivocally capture climatic signals and can easily be recovered from sedimentary archives. Among them, diatoms (Bacilliarophyta) have been extensively used as indicators of environmental conditions in lakes (e.g., nutrient, pH, ionic concentration, and water level) (Stoermer and Smol, 1999) because they are diverse, remain well preserved in the sediments and have short lifespans that allow them to rapidly respond to environmental shifts (Smol et al., 2001). Furthermore, evidence exists that changes in diatom communities are representative of ecosystem-scale processes (Smol et al., 2005).

Evidence of climate-driven shifts in diatom communities is not always direct because factors that directly control diatom changes can also be strongly affected by climatic variations. In fact, it is still not clear whether temperature variations have a direct effect on diatom body size (Adams et al., 2013; Winder et al., 2009) or on photosynthetic rates (Fanesi et al., 2016). Among the best-documented indirect factors that affect diatom communities are variations in snow cover and spring melt through the increase in lake turbidity and nutrient transfer, rainfall through enhanced runoff, or wind modulation of thermal structure and mixing of lakes (Anderson, 2000; Rühland et al., 2015). For instance, in remote and cold lakes of the Arctic Circle and alpine regions, unprecedented and unidirectional changes in the specific composition of diatom communities since 1850 CE and after 1998 CE, respectively, were attributed to variations in ice cover and related variables (Smol and Douglas, 2007; Smol et al., 2005) and strengthening of thermal stratification (Weckström et al., 2016). In continental Lake Baikal with a milder climate, higher abundances of the dominant diatom *Synedra acus* and disappearance of several endemic species over the past 20 years were likewise attributed to warming of the surface water, decrease in ice sheet duration and alterations of the mixing regime (Roberts et al., 2018). In Mediterranean Lake Redon (central Pyrenees), some epilimnetic diatom

species responded to atmospheric temperature fluctuations during the growing ice-free season from 1900 CE onwards (Catalan et al., 2002). Regional factors other than climate may also equal or exceed the impact of climate shifts on diatoms. For instance, a study of six shallow lakes in the Sierra Nevada Mountains (southern IP) showed notable variations in diatom composition at the turn of the 20th century and after 1970 CE. These shifts were concurrent with a drier and warmer climate and with the alkalinizing effect of Saharan dust deposition events, making it difficult to identify the effects associated with each stressor (Pérez-Martínez et al., 2020).

The examples mentioned above are from remote lakes of the globe with relatively little exposure to human impacts. The panorama changes in regard to ecological responses to climate change in lakes near densely populated areas with agriculture, increasing livestock or manipulated basins, since such systems are subjected to strong stressors that can override or modify both vulnerability and responses to current warming. Prominent examples include the European lakes Genève, Annecy and Bourget (Perga et al., 2015). These lakes reached high levels of eutrophication in the early 20th century, but eutrophic conditions receded later with management. Subsequently, the effects of the increase in atmospheric temperature became apparent, and diverse diatom responses were observed in the two most nutrient-rich lakes, suggesting that higher amounts of nutrients may increase diatom vulnerability to warming. In Pyrenean Lake Isoba, a regional decrease in precipitation and lake level after 1986 CE caused a shift towards the dominance of periphytic and epiphytic diatoms, but after 1997 CE, the environmental impacts from the introduction of local cattle completely changed the waterbody, thus blurring the signal of climate change (Gardoki et al., 2023).

These and more examples show that determining diatom responses to climate change can be a complex task because there are multiple climate and nonclimate factors involved that can trigger a contingent response in diatom species and communities. In a global change context, confronting complexity will be an unavoidable challenge in any study that attempts to discriminate between the effects of anthropic climate change and any of the multiple factors, natural or not, that affect any of the existing biological communities. Taking advantage of the annual resolution of varved records (Zolitschka et al., 2015), in this paper, the stratigraphic diatom record of Mediterranean Lake Montcortès (central Pyrenees) was investigated in detail, encompassing the end of the Little Ice Age (LIA), the transition to the industrial and postindustrial eras, and the recent global warming and its acceleration. Decadal and subdecadal shifts in the composition of diatom communities that may have occurred over the last 300 years could be related to regional climatic variations, different phases of human activities and intense meteorological events of comparable temporal resolution. Specifically, this study focuses on the responses of individual diatom species to anthropogenic warming and eutrophication, which are the most emblematic human impacts of the last two centuries. It is also examined whether there are species that could be useful as potential proxies of these impacts in Lake Montcortès. Chronologically, the time lapse of this study spans from ca. 1716 until 2013 CE.

During the last decade, Lake Montcortès has been thoroughly investigated from different perspectives, and modern analogues as well as paleoecological, paleoenvironmental and paleoclimatic reconstructions are available (Corella et al., 2011, 2012, 2014, 2019; Montoya et al., 2018; Rull et al., 2011, 2017, 2022; Rull and Vegas-Vilarrúbia, 2014, 2015; Scussolini et al., 2011; Trapote et al., 2018a, 2018b; Vegas-Vilarrúbia et al., 2018, 2020, 2022). This wealth of information has furnished proxy data of interest with which to correlate changes in the diatom record (see Section 2.3).

2. Materials and methods

2.1. Environmental settings

Lake Montcortès (42°19′50″ N - 0°59′41″ E; 1027 m elevation) is a karstic lake located on the southern flank of the central Pyrenees (Fig. S1A). It is kidney-shaped with a perimeter of 1320 m, a surface area

of 0.14 km^2 and a maximum water depth of 32 m (Corella et al., 2019). Its inlet is ephemeral, and its outlet is inactive at present. The basin is located on a carbonated and evaporitic Mesozoic substrate characterized by Triassic limestones, marls and evaporates and Oligocene carbonate conglomerates (Corella et al., 2011; Rosell, 1994). Lake hydrology is mainly governed by underground water inflows heavily laden with carbonates and sulfates (Corella et al., 2011). The thermal-mixing regime is mainly meromictic (infrequent turnover), but occasional turnover of the water column may take place in winter (Vegas-Vilarrúbia et al., 2018). Meromixis creates hypolimnetic anoxic conditions that are suitable for varve formation and preservation. These varves are formed by couplets of light calcite and brownish organic layers containing abundant diatoms (Corella et al., 2011) that are deposited in summer/fall and winter/spring, respectively (Trapote et al., 2018b). At present, seasonal calcite sedimentation patterns are strongly linked with primary producers and are sensitive to temperature shifts (Trapote et al., 2018b; Vegas-Vilarrúbia et al., 2018, 2020).

The lake is very sensitive to climate change due to its position in the climatic transition area between the Mediterranean lowlands and the Middle Montane Belt within the sub-Mediterranean bioclimatic domain (Vigo and Ninot, 1987). Currently, forest formations of evergreen and deciduous oak trees and conifer forests surround the lake, and its nearest vicinity is dominated by herbaceous vegetation represented by pastures, hay meadows and crops of cereal and alfalfa. The lake's shoreline has a homogeneous, dense vegetation belt dominated by *Phragmites australis*, *Juncus* sp. and *Scirpus* sp. (Mercadé et al., 2013; Rull et al., 2011). The aquatic habitat is mainly pelagic due to the steep morphology of the lake. Between 2013 and 2016 CE, planktonic Chlorophytes prevailed in summer, Cryptophytes in winter and planktonic diatoms, dominated by centric species, flourished in spring and summer. The highest phytoplankton biovolume values reached $\leq 6 \times 10^6$ μm^3/mL during summer. Total phosphorus (TP) ranged from 0.05 to 0.08 mg/L; total nitrogen (TN), from 24 to 71 mg/L; Secchi disc values, from 3.5 to 8.5 m; and pH values, from 7.2 to 8.4 (Trapote, 2019). A previous reconstruction at the millennial scale of the diatom community of Lake Montcortès is also available and shows a marked alternation between two centric species, *Cyclotella comta* and *Cyclotella cyclopuncta*, which were suggested to reflect changes in the trophic state of the lake (Scussolini et al., 2011).

Lake Montcortès is located in the Baix Pallars municipality, which houses ca. 342 habitants, with only 23 living in the town of Montcortès (Idescat (Institut d'Estadística de Catalunya), 2015). Currently, land use is limited to cereal crops and livestock pastures (Fig. S1B; Mercadé et al., 2013). The lake has historically been an important water resource for numerous surrounding villages and farmhouses and an important center of hemp retting during the 18th and 19th centuries (Rull and Vegas-Vilarrúbia, 2014; Rull et al., 2022).

2.2. Coring, dating, sample treatment, counting and identification

Core MONT500-07-13-G05 was extracted from the deepest part of the lake basin (Fig. S1B) in July 2013 using a UWITEC 60 mm diameter gravity corer. The total length of the core was 114 cm. It was maintained on the lakeshore for three days to allow consolidation of the upper layers before its transport to the laboratory. In previous studies, an age-depth model was created for the last six centuries using ^{210}Pb and ^{14}C radiometric dating and independent varve counting (Corella et al., 2011, 2014). Varve counting was accomplished on a composite sequence obtained from cores MON12-3A-1G and MON12-2A-1G and by double counting in 14 overlapping thin sections. Less than 1 % of varves were interpolated using annual sedimentation rates from well-preserved adjacent varve sections (Corella et al., 2012, 2014). This age model was transferred from core MON12-3A-1G to targeted core MONT-0713-G05 by stratigraphic correlation based on comprehensive examination of sedimentary structures, varve thickness patterns and characteristic features seen in specific varves that allowed the identification of 96 marker horizons (i.e., flood layers and/or distinct sublayering in calcite layers). Further details of this age-depth model are provided in Trapote et al. (2018a).

The present study focuses on the diatoms in the first 77 cm from the top of the core and comprised 52 sediment samples. The samples were obtained every consecutive 0.5 cm using a 0.5 cm diameter syringe, which was a trade-off between sampling the minimum sediment volume necessary for diatom analysis and obtaining the highest possible resolution. To avoid sample dilution effects, sediment-laden turbidites (15–44 cm and 45–60 cm depth from the top in the sediment core) were bypassed following Corella et al. (2015). Each sample covered 6 years on average, thus achieving subdecadal resolution. Samples were identified with the more recent year of their encompassed period (e.g., the sample dated from ca. 2007 to 2013 CE was named "2013 CE"). The deepest sample (76.5 cm) dated back to ca. 1716–1717 CE. Hence, the study encompassed ca. 297 years.

Diatoms were extracted from 0.1 g of dry sediment. A few drops of HCl 37 %, 20 mL H$_2$O$_2$ 30 %, and 5 mL Na$_4$P$_2$O$_7$ 0.5 % were added to each sample to eliminate carbonates, organic matter and clay particles, respectively. A known quantity of microspheres was added to each sample to be used as external markers, enabling flux estimations (Battarbee et al., 2001). Specimens were mounted in Naphrax and analyzed with a light microscope Polyvar equipped with differential interference contrast (DIC) optics at 1000× magnification. For each sample, 500 to 600 valves were counted. Diatom lifestyles and taxonomic determinations were accomplished with the help of different iconographic references (Bayarri-Borja, 2005; Guiry and Guiry, 2018; Hofmann et al., 2011; Krammer, 2002; Krammer and Lange-Bertalot, 1986, 1991a, 1991b; Lerin, 2011; Prygiel and Coste, 2000; Rivera-Rondón and Catalan, 2017) and consistent databases (Rimet et al., 2016; Spaulding et al., 2021). Samples from 45 to 60.5 cm were processed and mounted but could not be inventoried because they were greatly diluted.

Two *Cyclotella* species were far more abundant than the remaining taxa across all samples (see Fig. 1). Thus, the initial counting was extended but now excluded *Cyclotella cyclopuncta* and, from ca. 1971 CE on, also *Cyclotella ocellata*, from the counting until reaching approximately 300 non-*Cyclotella* valves. The results are expressed as the flux towards the sediment per year (valves cm^{-2} year^{-1}) for each species, for all pennate diatoms together (pennate flux), for all centric diatoms together (centric flux), and for all diatom species together (diatom flux); the relative abundance of valves for each species with respect to the total number of valves (%); and the centric to pennate ratio (C/P) as an indicator of relative shifts in planktonic and benthic habitat conditions (Cooper, 1995a, 1995b; Wolin and Duthie, 1999). However, it should be noted that some pennate diatoms can have a planktonic lifestyle. In our study, this may be the case for *Fragilaira tenera*, a pennate diatom that has been found in both pelagic (e.g., in Cremer and Wagner (2004) and in Noble et al. (2013)) and benthic communities (e.g., in Hofmann et al. (2011)) in other studies.

Two matrices with the relative abundances of the different species were created, one (CYCLO) including all species with a maximum relative abundance ≥0.3 % to explore the diatom community and another (NOCYCLO) with species with a maximum relative abundance ≥3 % when leaving out the valves of *C. cyclopuncta* and, from ca. 1971 CE on, also those of *C. ocellata*, to focus on nondominant taxa. Basic calculations were performed with Microsoft Office Excel 2016. Diagrams were created based on diatom species abundances and zone limits were delimited for plotting and analysis of the paleoecological data using Psimpoll 4.27 software (Bennett, 2002), the method of optimal splitting by information content (Bennett, 1996) and the diatom species relative abundances. The graphs were edited with Adobe Illustrator 2022.

2.3. Climate variables

To examine the influence of climate shifts on the diatom communities of Lake Montcortès over time, several records of precipitation and temperature were examined and compared. For the period between 1910 and 2013 CE, the instrumental series of daily accumulated precipitation (PREC) and average, maximum, and minimum temperature values (TM, TX and TN, respectively) from the central Pyrenees region (Pérez-Zanón
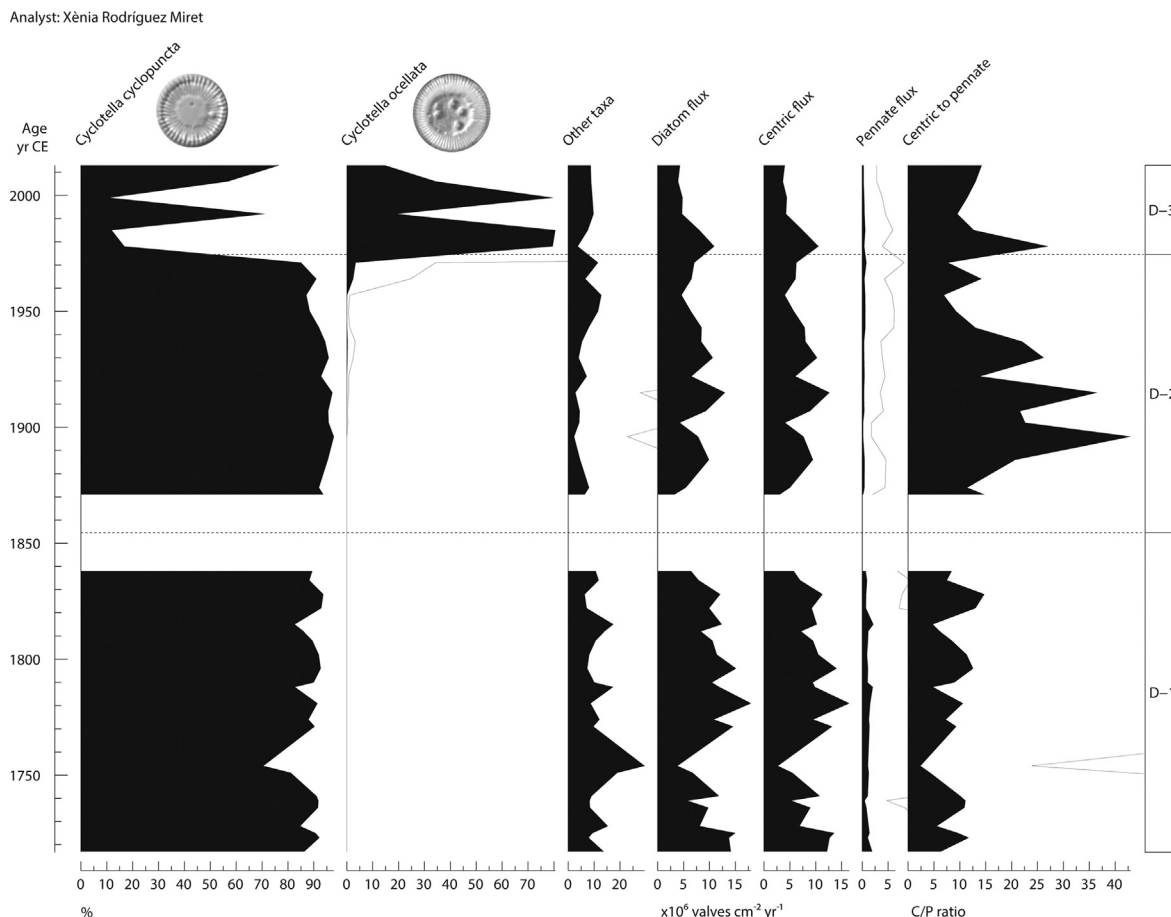
Analyst: Xènia Rodríguez Miret

Fig. 1. Relative abundances of *Cyclotella cyclopuncta* and *Cyclotella ocellata*, diatom fluxes and C/P ratio. 'Other taxa': species other than *C. cyclopuncta* and *C. ocellata* merged. Solid lines represent x10 exaggeration. Horizontal dashed lines delimit statistically differentiated zones. The 1838 to 1871 CE period (blank space) is devoid of diatom samples due to the presence of an approximately 16 cm thick turbidite. *n* = 44.

et al., 2017) were used. These climatic series represent the longest high-quality and homogenized set of instrumental climate data available for this region and were obtained from the Spanish State Meteorological Agency (AEMET), the Meteorological Service of Catalonia (SMC) and the Spanish Daily Temperature Series (SDATS) (Brunet et al., 2006; Pérez-Zanón et al., 2017) available at http://www.c3.urv.cat/climadata.php. For the period between 1716 and 1910 CE, instrumental measurements were lacking. Therefore, the monthly accumulated precipitation (PPT) and the monthly average temperature (Tm) data from the city of Barcelona (BCN) could be used as a surrogate, which included data from 1780 to 2013 CE (Prohom et al., 2012, 2016). Because Barcelona is located on the coast of northeastern Spain, analyses were performed to test the concordance of the PPT and the Tm series with the precipitation and mean temperature series from the meteorological station closest to Montcortès in La Pobla de Segur (PdS) (https://www.meteo.cat/observacions/llistat-xema) and with the TM and PREC values from the central Pyrenees region (Pyr) (Pérez-Zanón et al., 2017) for the instrumental period when these series coincided (1997–2021 CE, *n* = 25), (Fig. S2). The BCN-PdS correlation between the annual mean temperature values of BCN and PdS was *r* = 0.624 (*p* value = 0.001), and between the values of annual precipitation, it was *r* = 0.482 (*p* value = 0.017), which are quite acceptable, considering the differences between both locations. The BCN-Pyr correlation between the annual mean temperature values of BCN and Pyr was *r* = 0.883 (*p* value = 0.000), but between the values of annual precipitation, it was not significant. Finally, to cover the time period between 1716 and 1780 CE, the Northern Hemisphere air surface temperature (NHTA) reconstruction from Mann et al. (2009) could be used, as it properly captures the mean regional climatic features of the study period. In fact, the correlation

value between Tm and NHTA series for the period of overlap (1780–2005 CE, *n* = 226) was *r* = 0.660 (*p* value = 0.000) (Fig. S3).

The anomalies of the climate variables were calculated by extracting the average value of the study period from the observed values. Different climate variables have different temporal resolutions. Therefore, to make these data coincide with the temporal intervals included in each diatom sample, average values of the climate variables were calculated for each single interval.

2.4. Environmental variables

One of the main aims of the investigation was to examine, based on species abundances and biodiversity, whether diatom communities could have responded to the environmental changes induced by human activities in the lake basin since 1716 CE, including pastures, cultivation, burning or hemp retting, which take place at longer time scales. Although responses of diatom populations to environmental changes are very fast (e.g., daily, seasonal), changes in the diatom communities can happen at larger scales (e.g., suprannual, decadal) and can match, be related or be synchronous with comparable changes in other proxies (Rull, 2020). To this end, well-documented environmental proxies were used (Table 1), whose data were extracted from previous studies at Montcortès (Trapote, 2019). Specifically, the following proxies were chosen: the abundances of *Typha* pollen and *Pediastrum* cells were chosen as indicators of changes in nutrient conditions (Jankovská and Komárek, 2000; Miao and Sklar, 1998; Newman et al., 1996), distinct pollen grains for crops and ruderal herbs, *Cannabis* pollen for hemp retting (Rull and Vegas-Vilarrúbia, 2014), best-represented charcoal particles representing regional fires (Whitlock and

Table 1

Paleoecological variables selected as environmental proxies (Trapote, 2019; Vegas-Vilarrúbia et al., 2018).

Proxy type	Units	Variable	Related process
Pollen grains	%	Pastures: *Artemisa* (Ar)	Changes of land use
Pollen grains	%	Crops: *Secale* (Se), Cerealia (Ce)	
Pollen grains	%	Ruderal herbs/weeds: *Galium* (Ga), *Urtica* (Ur)	
Pollen grains	%	*Cannabis* (Cn)	Cultivation and retting
Coprophilus fungus	%	*Sporormiella* (Sp)	Livestock
Algae, macrophytes	%	*Pediastrum* (Pe), *Typha* (Ty)	Changes in the lake's trophic state
Fungus spores	%	*Glomus* fungi (Gl)	Regional fire, soil erosion, runoff
Charcoal I (<100 μm)	Particles·cm^{-2}·yr^{-1}	<100 μm (Ch)	
Elemental composition	XRF, counts per second (cps)	Iron (Fe)	Detrital inputs
Elemental composition	XRF, counts per second (cps)	Titanium (Ti)	Runoff
Elemental composition	XRF, counts per second (cps)	Bromine (Br)	Allochthonous organic matter accumulation
Elemental composition ratio	Unitless	Calcium to titanium ratio (Ca/Ti)	Phytoplankton photosynthetically induced carbonate precipitation
Elemental composition ratio	Unitless	Silicon to titanium ratio (Si/Ti)	Diatom productivity
Component 2, principal component analysis	Unitless	Component 2 (C2), principal component analysis	Hypolimnetic oxygenation shifts

Larsen, 2001), *Glomus* fungus spores for soil erosion (Kołaczek et al., 2022; van Geel et al., 1989), and coprophilous fungi such as *Sporormiella* for the presence of livestock (Lee et al., 2022; Raczka et al., 2016). The temporal resolutions of these selected records and the diatom records of the present study are coincident, as both studies obtained their samples from the same sediment core and at the same depths. Additionally, we used several elemental components of the sediment obtained by X-ray fluorescence analyses from a former paleolimnological study of Lake Montcortès (Vegas-Vilarrúbia et al., 2018). The calcium to titanium ratio (Ca/Ti) was taken as indicator for planktonic photosynthetically induced calcite precipitation; the silica to titanium ratio (Si/Ti), for diatom production; mean bromine (Br), for allochthonous organic matter accumulation at the sediment; and iron (Fe) and titanium (Ti), for erosion of the catchment. As a proxy for historical oxygenation shifts in the hypolimnion, we used the second component (C2) resulting from a principal component analysis (PCA) performed on elemental ratios (Fe/Ti and Fe/Mn) and bacterial pigments data. The positive side of C2 was associated with enhanced precipitation of iron oxides under oxic conditions and the negative C2 side with increasing anoxia and stratification status.

2.5. Statistical analysis

2.5.1. Change-point analysis

Change-Point Analysis (CPA) was performed on the diatom series to refine the detection of changes over time (Taylor, 2000). This procedure examines the data searching for changes in the average and the standard deviation. When only a single value per period is available (i.e., for *C. ocellata*, *C. cyclopuncta*, diatom flux and the C/P ratio), CPA groups consecutive periods together to form pairs and then estimates the standard deviation of each pair. CPA iteratively uses a combination of cumulative running sums of differences between mean and individual values. The point farthest from 0 denotes a Change-Point (CP), being this the first and more noticeable change detected (level 1). Then, the series is broken into two subseries at this CP, which are analyzed for additional significant CPs (level 2). The number of levels depends on the number of changes found by applying the CPA algorithm. The mean Square Error (MSE) is used as an estimator of when the changes have occurred. Bootstrapping provides confidence levels and pinpoints the confidence intervals in which the first change occurs. To subdue the effect of outliers found on the variation of the series, this procedure uses ranks instead of the actual values.

2.5.2. Ordination analysis

To explore the possible influence of climate and environment on the diatom community, ordination analyses were performed using the diatom relative abundance matrices and the potentially explicative climate and environmental variables. Two explanatory datasets named NGXA2 and PT were used. NGXA2 consisted of the NHTA data and the variables described in Table 1: the time series of the selected palynological variables, the XRF

elemental data and ratios and the second component C2 of the PCA in Vegas-Vilarrúbia et al. (2018). It entailed from 1717 to 2006 CE samples because the NHTA time series lacked data beyond 2006 CE (Mann et al., 2009). Consequently, only the ca. 2013 CE diatom sample had to be excluded. The PT dataset included the Tm and PPT climate records as well as the NHTA data, being the overlapping period from 1788 to 2006 CE samples. The two diatom matrices, CYCLO and NOCYCLO, contained the diatom response datasets (see Section 2.2). For the analyses on the NOCYCLO matrix, *C. ocellata* was excluded from all samples. Both explanatory datasets were scaled to zero mean and unit variance. Both response datasets were transformed with the Hellinger distance for the RDA analyses (Legendre and Gallagher, 2001).

Detrended correspondence analyses (DCAs) were performed to determine whether linear or nonlinear ordination methods were more suitable according to the degree of heterogeneity of diatom datasets (Legendre and Legendre, 2012; Ter Braak and Prentice, 1988). For the period included in each explanatory dataset (i.e., the NGXA2 and PT datasets), a DCA was performed for each of the two diatom matrices (i.e., 4 DCAs in total). In all cases, the maximum length of the axes was lower than 3 standard deviations (Table S4). These results indicated homogeneous datasets for which linear methods were suitable. Hence, redundancy analysis (RDA) was chosen to explore the datasets. PAST v.4 software (Hammer et al., 2001) was used to perform the canonical ordination analyses. Creation of the ordination biplots was performed with Adobe Illustrator 2022 software.

3. Results

3.1. Analysis of the diatom stratigraphy

Figs. 1 and 2 display the diatom stratigraphic record of this study. The diatom diagrams were divided into three different diatom zones (D-1 to D-3) by merging the three independent zone splits resulting from the diatom, centric and pennate fluxes and the C/P ratio; the CYCLO matrix; and the NOCYCLO matrix (Table S1).

Throughout the study period, centric diatoms were generally much more abundant within the diatom community than their pennate counterparts, with an average C/P ratio of 13.0 and a standard deviation of 8.19. However, the main benthic habitat of Lake Montcortès is the littoral zone, while the coring site was located in the deep pelagic zone of the lake (Fig. S1B). The steep bathymetry at more distant sites can reduce the relative importance of benthic versus pelagic diatoms at the whole-ecosystem level (Althouse et al., 2014); thus, possible variations in the benthic diatom record might be underrepresented in the examined samples.

3.1.1. Diatom zone D-1: 77–61 cm, ca. 1716–1838 CE (122 years, 23 samples, average resolution (±SD): 5.30 ± 3.43 years/sampling interval)

The average diatom, centric and pennate fluxes were the highest when compared to the other zones, whereas the mean C/P ratio was the lowest
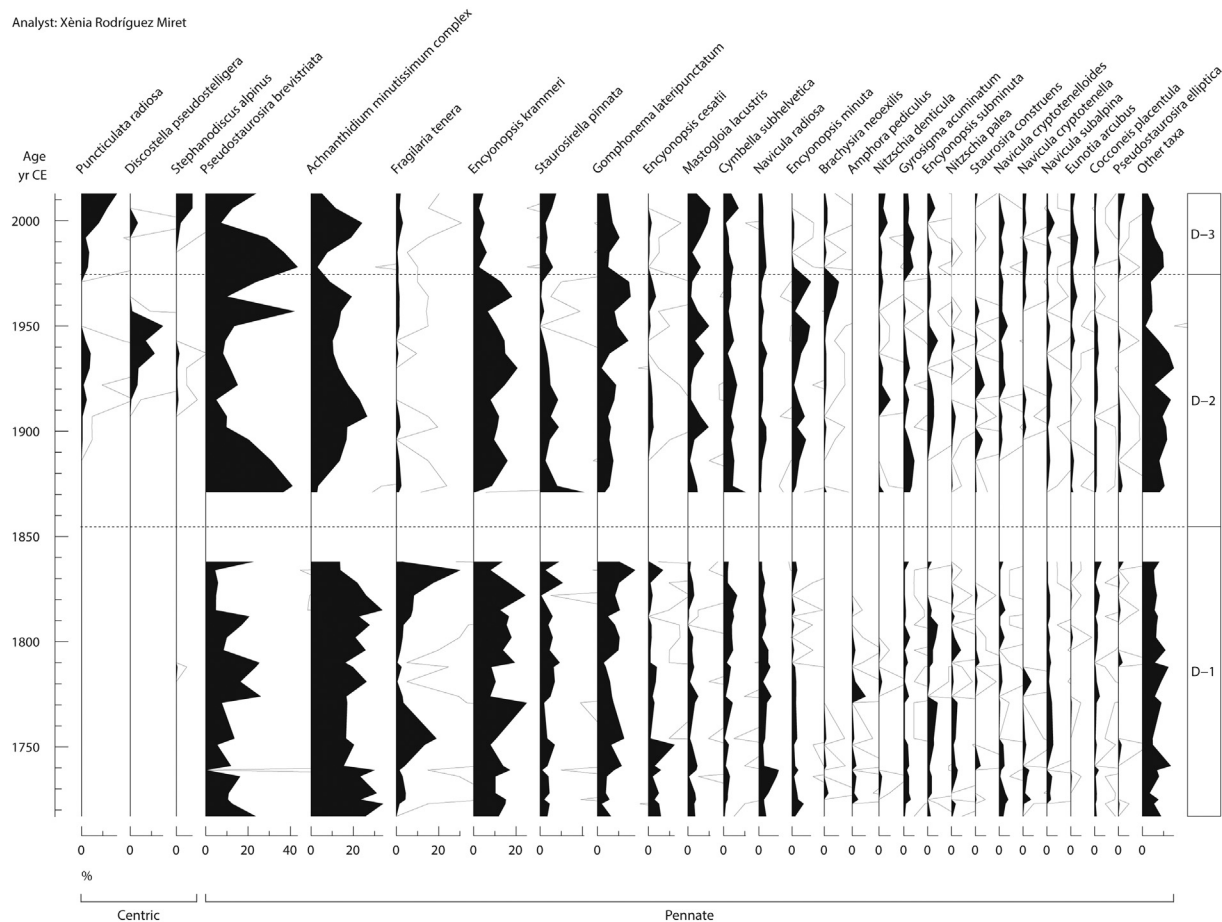
Fig. 2. Relative abundances of diatom species with maximum abundance ≥ 3 % when dominant species are excluded (NOCYCLO). 'Other taxa': species with maximum abundances ≤ 3 % when dominant species are excluded merged. Solid lines represent x10 exaggeration. Horizontal dashed lines delimit statistically differentiated zones. The 1838 to 1871 CE period (blank space) is devoid of diatom samples due to the presence of an approximately 16 cm thick turbidite. n = 44.

value across the three zones (Table S2). Throughout this period, the diatom community was largely dominated by the planktonic *Cyclotella cyclopuncta*, which had RAs generally higher than 85 % (Fig. 1). On average, the second most abundant species in this diatom zone, far below *C. cyclopuncta*, was the *Achnanthidium minutissimum* complex, with RAs ranging from 1.39 % to 5.86 %, followed by *Pseudostaurosira brevistriata* and *Encyonopsis krammeri*, with RAs ranging from absent to 4.10 % and from 0.87 % to 3.15 %, respectively. *Amphora pediculus* was found exclusively and in multiple samples in this diatom zone, although its RAs were low (Fig. 2). The *A. minutissimum* complex, *E. krammeri*, *Gomphonema lateripunctatum* and *Fragilaria tenera* had their greatest average RA (ARA) compared to the other zones (Fig. 2; Table S3).

Because of the strong dominance of *C. cyclopuncta*, both the centric and the total diatom fluxes were tightly linked to the flux of *C. cyclopuncta* alone. Nonetheless, there were relevant fluctuations both in the RA and particularly in the flux of *C. cyclopuncta* (Figs. 1 and S4). The most severe fluctuation occurred between ca. 1742 and 1754 CE, when there was a noteworthy decline in the flux of centric diatoms, but not in the pennate flux of the lake, leading to the lowest C/P ratio across the whole study period. During this decline, *C. cyclopuncta*'s RA diminished to 70.5 %, while the rest of the community gained relevance; particularly *F. tenera*, which notably increased in flux and RA to 5.59 % (Figs. 2 and S5B). Some decades later, *C. cyclopuncta*'s RA experienced two further minima, one in the late 1780s and another in the 1810s (Fig. 1). The pennate flux reached its maximum values across the whole study period during these two minima and, as a result, the C/P ratio had two of its lowest values. In the 1780s minimum, *P. brevistriata* gained relevance in the community (Fig. 2). In the

minimum of the 1810s, the *A. minutissimum* complex achieved its maximum RA. *F. tenera* experienced a second prominent growth period in the early 1830s, reaching a relative abundance of 3.55 %.

3.1.2. Diatom zone D-2: 45–3 cm, ca. 1869–1971 CE (102 years, 15 samples, average resolution: 6.80 ± 2.43 years/sampling interval)

The transition from Zone D-1 to Zone D-2 showed conspicuous changes. After a period characterized by the presence of abundant turbidites, the diatom community experienced one of its most noticeable transformations in terms of fluxes and C/P ratios (Fig. 1) and community-specific composition (Fig. 2). The centric and especially the pennate fluxes greatly decreased and, consequently, the C/P ratio increased (Fig. 1). Despite its flux being reduced, *C. cyclopuncta* gained relevance within the diatom community (Figs. 1 and S4). The *A. minutissimum* complex, *E. krammeri*, and *G. lateripunctatum* populations decreased notably, reducing their RAs as well (Figs. 2 and S5B). The same occurred for *F. tenera*, yet its reduction started by the end of the 1830s in Zone D-1. In contrast, *P. brevistriata*, *Staurosirella pinnata* and *Cymbella subhelvetica* gained relevance in the transition to Zone D-2.

In Zone D-2, the mean C/P was the highest among the three zones (Table S2). *C. cyclopuncta* remained dominant in the diatom community and its RA was even higher than that in Zone D-1, above 90 %, having its greatest ARA across the three zones (Fig. 1; Table S3). *P. brevistriata* was the second most abundant species, with RAs ranging from 0.14 % to 5.42 %. The *A. minutissimum* complex and *E. krammeri* were the third and fourth most abundant species, with RA ranging from 0.18 % to 1.83 % and from 0.04 % to 1.49 %, respectively. *P. brevistriata*, the *A. minutissimum*

complex and *F. tenera* had their minimum relevance in the community during this period (Fig. 2; Table S3).

From the 1870s to the late 1880s, the pennate flux and especially the diatom and centric fluxes increased again but were still generally lower than those of Zone D-1 (Fig. 1). The *A. minutissimum* complex and *E. krammeri* populations grew faster than others and slowly recovered relevance in the community (Figs. 2 and S5B). On the other hand, the absolute and relative abundances of *P. brevistriata*, *S. pinnata* and *C. subhelvetica* showed a downwards trend. After the 1880s, there was a remarkable change in the background diatom community, especially regarding the plankton (Figs. 2 and S5A). At the beginning of the 20th century, *C. cyclopuncta* showed its highest RA values, ranging from 92.8 % to 97.7 %, but from ca. 1930 CE on, it decreased until reaching 85.1 % in ca. 1971 CE (Fig. 1). Similar trends were observed in the centric flux and, as a result, in the C/P ratio. Interestingly, four centric diatoms other than *C. cyclopuncta*, namely *Cyclotella ocellata*, *Discostella pseudostelligera*, *Puncticulata radiosa* and *Stephanodiscus alpinus*, appeared and gained some relevance at the beginning of the 20th century (Fig. 2). Nevertheless, during the 1940s and 1950s, their populations decreased again except for that of *C. ocellata*, which increased during the 1960s and reached a relative abundance of 3.43 % in ca. 1971 CE. *D. pseudostelligera* had its greatest ARA in this zone (Fig. 2; Table S3), having its maximum RA in ca. 1950 CE with 1.80 %.

3.1.3. Diatom zone D-3: 3–0 cm, 1971–2013 CE (42 years, 6 samples, resolution: 7.00 ± 0.00 years/sampling interval)

During this period, the diatom flux was almost entirely dependent on the centric flux, and both the centric and the pennate fluxes showed a decreasing trend (Fig. 1). As a result, the fluxes reached their lowest average values across all zones (Table S2). Strikingly, *C. cyclopuncta* and *C. ocellata* alternately dominated the diatom community of the lake, changing their dominances by up to three times within this relatively short period (Figs. 1 and S4). *C. cyclopuncta*'s RA fluctuated between 14.7 % and 80.5 %, while *C. ocellata*'s RA fluctuated between 11.0 % and 76.6 %, thus showing their lowest and highest ARA across the whole study period, respectively. *P. brevistriata* and the *A. minutissimum* complex were the third and fourth most abundant taxa, respectively, with RA ranging from 0.67 % to 2.81 % and from 0.11 % to 2.25 %. *P. brevistriata* had its highest ARA during this period, whereas *E. krammeri* had its minimum relevance in the diatom community (Fig. 2; Table S3).

In this zone, *P. radiosa*, *S. alpinus* and *D. pseudostelligera* reappeared again (Figs. 2 and S5A). *D. pseudostelligera* was much scarcer than in Zone D-2. In contrast, *P. radiosa* and *S. alpinus* were increasingly present in the community, especially from the late 1990s on, and their populations grew despite the decreasing trend in both centric and pennate fluxes. These two species had their greatest ARA in this zone (Fig. 2; Table S3), yet they were not highly relevant in the planktonic community, having RA values as high as 1.45 % for *P. radiosa* and 0.67 % for *S. alpinus*.

3.2. Change point analysis

CPA allowed to highlight the most relevant changes in the species and attributes of the diatom community. Outliers (3σ) were detected only for *C. cyclopuncta* and *C. ocellata* time series and coincided with the minimum and maximum abundance values, respectively, which occurred from the 1970s onwards. Table 2 displays the main results of the CPA scoring levels 1 and 2. The second column identifies the first sample following the most important changes, indicating that around that time, the average shifted. High confidence levels are evidence that the changes actually did occur. Narrow confidence intervals indicate that pinpointed changes are more accurate in time estimation. The most significant and conspicuous results were the appearance of *C. ocellata* around ca. 1902 CE; the first abrupt decrease of *C. cyclopuncta* by ca. 1978 CE; and the fluctuations of important pennate species

Table 2
Results of the CPA showing the most significant changes in the diatom community. Asterisks indicate time series with outliers.

Variable	First sample after change	Confidence level (%)	Confidence interval	Level
CYCLO matrix	1886 CE	100	(1725 CE,1896 CE)	1
NOCYCLO matrix (but only pennate taxa)	1930 CE	100	(1922 CE, 1930 CE)	1
	1999 CE	98	(1999 CE,1999 CE)	2
Diatom flux	1834 CE	100	(1781 CE, 1896 CE)	1
	1886 CE	100	(1886 CE,1902 CE)	1
C/P ratio	1943 CE	95	(1902 CE, 1957 CE)	2
*C. ocellata**	1902 CE	100	(1902 CE,1902 CE)	1
*C. cyclopuncta**	1978 CE	94	(1978 CE, 1978 CE)	2

(e.g., *P. brevistriata*, *A. minutissimum* and *E. krammeri*) around ca. 1930 and 1999 CE (Table 2). Relevant changes in the diatom community as a whole (i.e., the CYCLO matrix) are difficult to interpret because of the wide confidence interval.

### 3.3. Canonical correlation analysis

Redundancy analyses (RDA) were performed to analyze the relationships between the diatom taxa and the considered environmental and climate variables. Fig. 3 displays the biplots resulting from the two NGXA2 RDAs. With respect to the relationships of the response variables in the CYCLO matrix with the NGXA2 dataset (1717 to 2006 CE samples), the NGXA2 dataset explained 69.0 % of total variance of the CYCLO matrix (*p*-value = 0.004). The resulting RDA biplot showed that most of the constrained variance was mainly explained by Axis 1, which explained 58.9 % of the total variance (Fig. 3A). NHTA, Br, the Ca/Ti and the Si/Ti ratios on the one hand and *Secale* (Se), *Artemisia* (Ar), *Cannabis* (Cn), *Sporormiella* (Sp), charcoal I (Ch), Fe and the C2 component (C2) on the other were negatively correlated and were the variables best related to Axis 1. On the same axis, *C. ocellata* had a positive relationship with NHTA, Br, Ca/Ti and Si/Ti and a negative relationship with Se, Ar, Cn, Sp, Ch, Fe and C2. In contrast, *C. cyclopuncta* was positively correlated with Se, Ar, Cn, Sp, Ch, Fe and C2 and negatively correlated with NHTA, Br, Ca/Ti and Si/Ti. The remaining diatom species were positioned close to the 0 value of Axis 1, revealing a weak or null correlation with the constrained environment.

In the case of the RDA of the NOCYCLO matrix with the NGXA2 dataset, the explanatory variables explained 58.3 % of total variance (*p*-value = 0.001). The first and second axes explained 20.6 % and 12.8 % of the total variance, respectively (Fig. 3B), which is notably lower than the variance explained by Axis 1 of the CYCLO RDA (Fig. 3A). The NHTA, Br and Si/Ti vectors increased towards the negative end of both axes and the Se, Cn, Ur, Ty, Ch and Pe towards the positive end of both axes. Ar and Ga were positively correlated with the first axis, and Ca/Ti and Fe were negatively and positively related, respectively, to the second axis. *A. pediculus* and particularly *F. tenera* had negative correlations with NHTA, Br, Si/Ti and Ca/Ti and a positive relationship with Cn, Se, Ch, Ty, Ur and Pe. The opposite pattern was found for *Nitzschia denticula*, *Mastogloia lacustris*, *Eunotia arcubus*, *S. alpinus* and, especially, for *P. radiosa*.

Fig. 4 displays the biplots resulting from the two PT RDAs. The PT dataset (1788 to 2013 CE samples) explained 34.8 % of total variance of the CYCLO matrix (p-value = 0.006). In the RDA biplot, 33.3 % of the total variance was explained by the first axis and 0.87 % by the second axis (Fig. 4A). Axis 1 was mostly linked with NHTA and Tm. *C. ocellata* was strongly and positively correlated with NHTA and Tm; conversely, *C. cyclopuncta* was negatively correlated with NHTA and Tm. The influence of climate on the rest of the diatom community was feebler or nonexistent. On the other hand, the PT dataset explained 22.7 % of total variance of the NOCYCLO matrix (*p* value = 0.001). In the RDA biplot, the first and second

axes explained 14.4 % and 6.22 % of the total variance, respectively (Fig. 4B). NHTA, Tm and more weakly PPT were positively correlated on Axis 1. *P. radiosa* and *F. tenera* had positive and negative correlations, respectively, with NHTA, Tm and PPT, whereas *M. lacustris* and *E. krammeri* had positive and negative relationships, respectively, with the aforementioned variables.
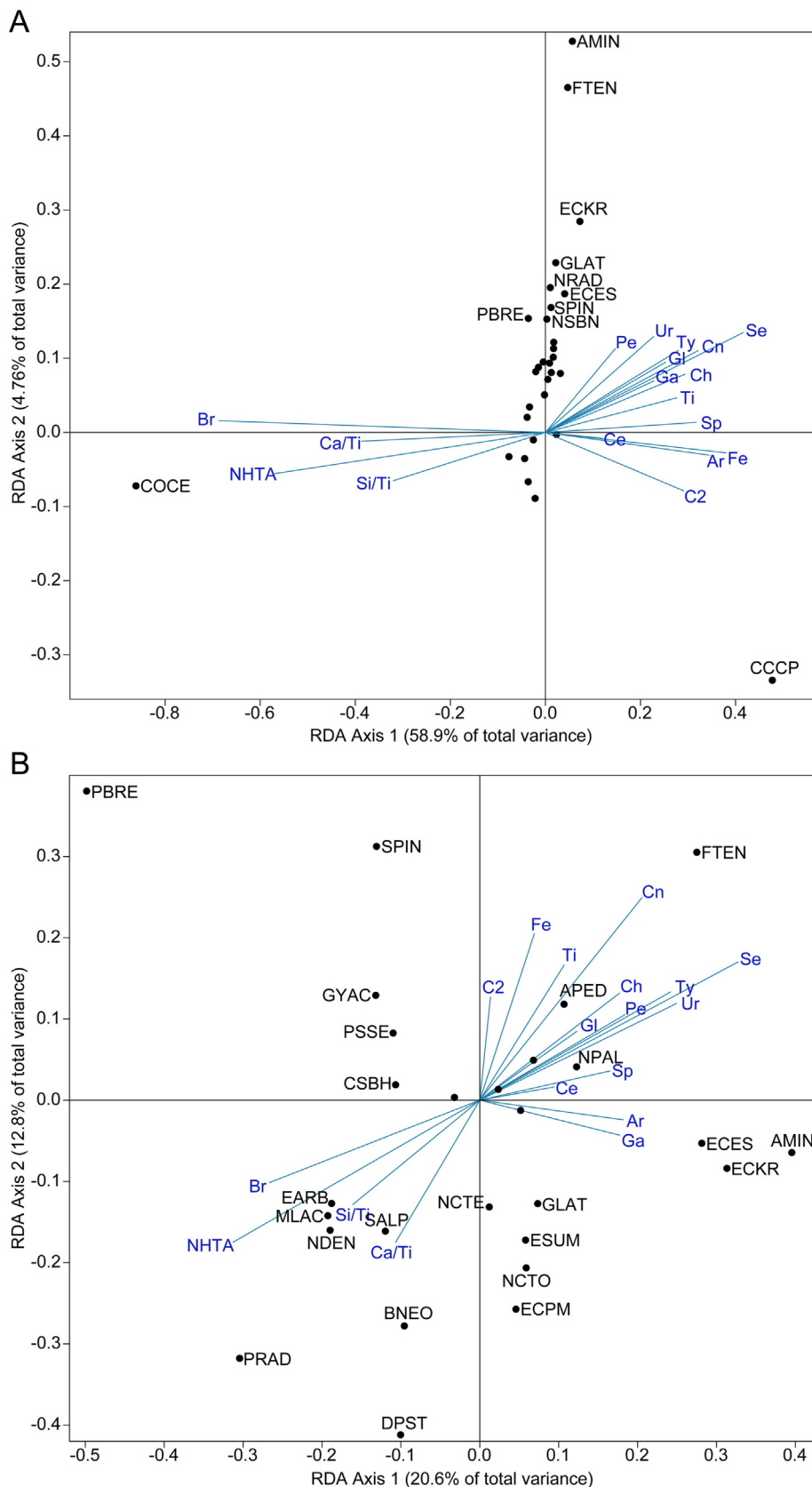
4. Discussion

4.1. Responses of diatom species to environmental and climatic shifts

The high resolution, temporal precision and continuity of the data due to the varved nature of the lake's sediment and the reliability of the age model (see Section 2.2) are remarkable strengths of this study. The attained subdecadal resolution allowed to detect subtle and abrupt changes in the diatom community that could not be detected in previous research (Scussolini et al., 2011). Nonetheless, "a priori", one could have expected to find more intense responses of the diatom communities to the many changes that have occurred since ca. 1716 CE, i.e., LIA cooling, anthropogenic global warming, transition from the rural to the industrial and postindustrial epochs, and the depopulation of the Pallars region. As shown by the diatom diagrams (Figs. 1 and 2) and the CPA (Table 2), the planktonic diatom community showed moderate fluctuations before ca. 1900 CE, denoting resilience (Holling, 1973; Gunderson, 2000) and therefore persistent relationships among species until its destabilization in the last three decades. Contrarily, the benthic community did not experience any noteworthy transformation, despite some small changes in a few pennate species during the 20th century.

The RDA allowed to inquire into the likely effects of the chosen climatic and environmental variables on the entire diatom community. Interestingly, in Fig. 3A and B, the NHTA, Br, Ca/Ti and Si/Ti vectors opposed to the vectors of the palynological variables, Fe, Ti and C2 on Axis 1 clearly divided the biplots into two halves that approximately corresponded to the periods before and after the 20th century and pinpointed which explanatory variables diatoms may be related with in each period. The results of the RDAs indicate moderate responses of only some diatom species (Table S5). The strongest response, by far, was that of *Cyclotella ocellata* in a context of temperature shifts, higher phytoplanktonic productivity and increased oxygen depletion after ca. 1971 CE, followed by that of *Cyclotella cyclopuncta* to variables indicative of intense human exploitation of the lake's basin, increased run-off or rainfall and detrital input. Furthermore, the presence of the benthic *Amphora pediculus* only in Zone D-1 of the diagram (Fig. 2) suggests a stronger link to human impact than the one shown by the RDA (Fig. 3). In fact, *A. pediculus* has been previously described as a tolerant N-autotrophic, eutraphentic, fresh-brackish and beta-mesosaprobic species (Van Dam et al., 1994). Overall, the high percentages of total explained variance suggest a strong influence, particularly on the planktonic dominant diatom species, from the changes that have occurred to the explanatory variables since 1716 CE. The percentage of total variance that remained unexplained by the RDAs indicates that other factors that have not been considered in this study (e.g., interspecific competition or predation) possibly also affected the diatom community of Lake Montcortès, particularly the nondominant species.

4.2. Inferences from the diatom record of Lake Montcortès

4.2.1. Cold and dry spells during the LA

On the IP, the LIA (1300–1850 CE) was characterized by frequent shifts between warm and cold conditions and remarkable spatial and temporal variability in precipitation with severe droughts, floods, and cold/heat waves. The investigated diatom record started ca. 1716 CE, after the coldest period of the LIA, associated with the Maunder solar activity minimum that occurred from 1645 to 1715 CE (Alcoforado et al., 2000; Oliva et al., 2018; Rodrigo and Barriendos, 2008; Rodrigo et al., 1999 and literature therein).

The first minimum of *C. cyclopuncta* occurred between ca. 1742 and 1754 CE and was coeval with a drop in the flux of this species. Concomitantly, the *Fragilaria tenera* population notably grew and gained relevance in the community. The RA of the green algae *Pediastrum* was also very low during those years (Fig. 5; Trapote et al., 2018a). This *C. cyclopuncta* minimum was coincident with a first peak in hemp retting (Rull et al., 2022) and a long-lasting, extreme drought that caused the loss of crops and livestock, a tremendous famine and riots (Domínguez-Castro et al., 2012). Concurrently, charcoal particles indicate a burning maximum (Fig. 5; Rühland et al., 2015; Trapote et al., 2018a). In addition, catchment erosion decreased and biogenic calcite precipitation increased compared to adjacent years, according to the analyzed proxies (Fig. 6). Three years of severe drought probably induced high evaporation and ionic concentration of the water of the meromictic Lake Montcortès. This, together with an extra supply of atmospheric nitrogen, ashes and abrupt entries of carbon from dead and charred organic matter accumulated in the catchment once precipitation started again, may have caused significant and long-lasting shifts in the balance of critical nutrients and water transparency. These conditions may have benefited the growth of *F. tenera* and reduced *C. cyclopuncta* abundance, which did not lose its dominance. *F. tenera* has been considered to be an indicator of enriched nutrient conditions in mountain lakes elsewhere (Sheibley et al., 2014). Moreover, hemp fibers probably increased the surface area available for the growth of epiphytic *Fragilaria* species during the retting, as seems to have been the case at eutrophic Lago Grande di Avigliana (Northern Italy) (Finsinger et al., 2006).

Later, *C. cyclopuncta* experienced two further minima in the late 1780s and the 1810s. Interestingly, the first *C. cyclopuncta* minimum by 1780s occurred during a decade of relatively stronger oxygen depletion and high productivity in Lake Montcortès (Vegas-Vilarrúbia et al., 2018) and a maximum activity in hemp retting (Fig. 5; Rull et al., 2022; Vegas-Vilarrúbia et al., 2022). The green algae *Pediastrum* showed its highest RA across the studied period during this *C. cyclopuncta* minimum (Fig. 5; Trapote et al., 2018a). The 1810s minimum coincided with general and unfavourable climatic conditions driven by a new decrease in solar activity associated with the Dalton solar minimum (1790–1830 CE) that affected the region with lower-than-average global temperatures and readvances of Pyrenean glaciers (Oliva et al., 2018). This second *C. cyclopuncta* minimum was also contemporaneous with a further overlapping decrease of 2–3 °C in the summer temperature of the Pyrenees, seemingly due to the catastrophic volcanic eruption of Mount Tambora in 1815 CE (Trigo et al., 2009); the ejected ash and pyroclastic flows favoured a further decrease in solar radiation across the globe. There is evidence that thermal-mixing events of the lake's water column began to be more intense after ca. 1810 CE (Vegas-Vilarrúbia et al., 2018), presumably as a consequence of harsh cooling due to solar forcing, and later maintained by climatic instability until approximately 1840 CE. *Pediastrum* and *Typha* showed relatively high RAs in the lake during this minimum (Fig. 5; Trapote et al., 2018a), which is in agreement with the possibility that the lake was more eutrophic at that time.

Interestingly, the benthic diatom community seemed to respond favorably to the new environmental conditions. The *C. cyclopuncta* minimums of 1780s and 1810s, unlike that of the 1740s, were not related to a particularly low flux of *C. cyclopuncta* but to a remarkable increase in the pennate fluxes, especially that of *Pseudostaurosira brevistriata* in the 1780s and that

Fig. 3. Redundancy analysis (RDA) linking the diatom response variables with the NGXA2 dataset within the MONT-0713-G05 sediment core. CYCLO (A) and NOCYCLO (B) matrix relationships with the NGXA2 data, from 1717 to 2006 CE samples. Only species having a higher score than 0.10 in absolute terms on any of the two axes (or 0.15 for the second axis in subgraph A) are labelled. Ar: *Artemisia*; Br: Bromine; C2: Component 2, PCA; Ca/Ti: Calcium to titanium ratio; Ce: Cerealia; Ch: Charcoal I; Cn: *Cannabis*; Fe: Iron; Ga: *Galium*; Gl: *Glomus*; NHTA: Northern Hemisphere temperature anomalies; Pe: *Pediastrum*; Se: *Secale*; Si/Ti: Silicon to titanium ratio; Sp: *Sporomiella*; Ti: Titanium; Ty: *Typha*; Ur: *Urtica*. AMIN: *Achnanthidium minutissimum* complex; APED: *Amphora pediculus*; APEL: *Amphipleura pellucida*; BNEO: *Brachysira neoexilis*; CCCP: *Cyclotella cyclopuncta*; COCE: *Cyclotella ocellata*; CPLA: *Cocconeis placentula*; CSBH: *Cymbella subhelvetica*; DPST: *Discostella pseudostelligera*; EARB: *Eunotia arcubus*; ECES: *Encyonopsis cesatii*; ECKR: *Encyonopsis krammeri*; ECPM: *Encyonopsis minuta*; ESUM: *Encyonopsis subminuta*; FTEN: *Fragilaria tenera*; GLAT: *Gomphonema lateripunctatum*; GYAC: *Gyrosigma acuminatum*; MLAC: *Mastogloia lacustris*; NCTE: *Navicula cryptotenella*; NCTO: *Navicula cryptotenelloides*; NDEN: *Nitzschia denticula*; NPAL: *Nitzschia palea*; NPSL: *Navicula pseudolanceolata*; NRAD: *Navicula radiosa*; NSBN: *Navicula subalpina*; PBRE: *Pseudostaurosira brevistriata*; PINN: *Pinnularia* sp.; PRAD: *Puncticulata radiosa*; PSSE: *Pseudostaurosira elliptica*; SALP: *Stephanodiscus alpinus*; SCON: *Staurosira construens*; SPIN: *Staurosirella pinnata*. n = 43.
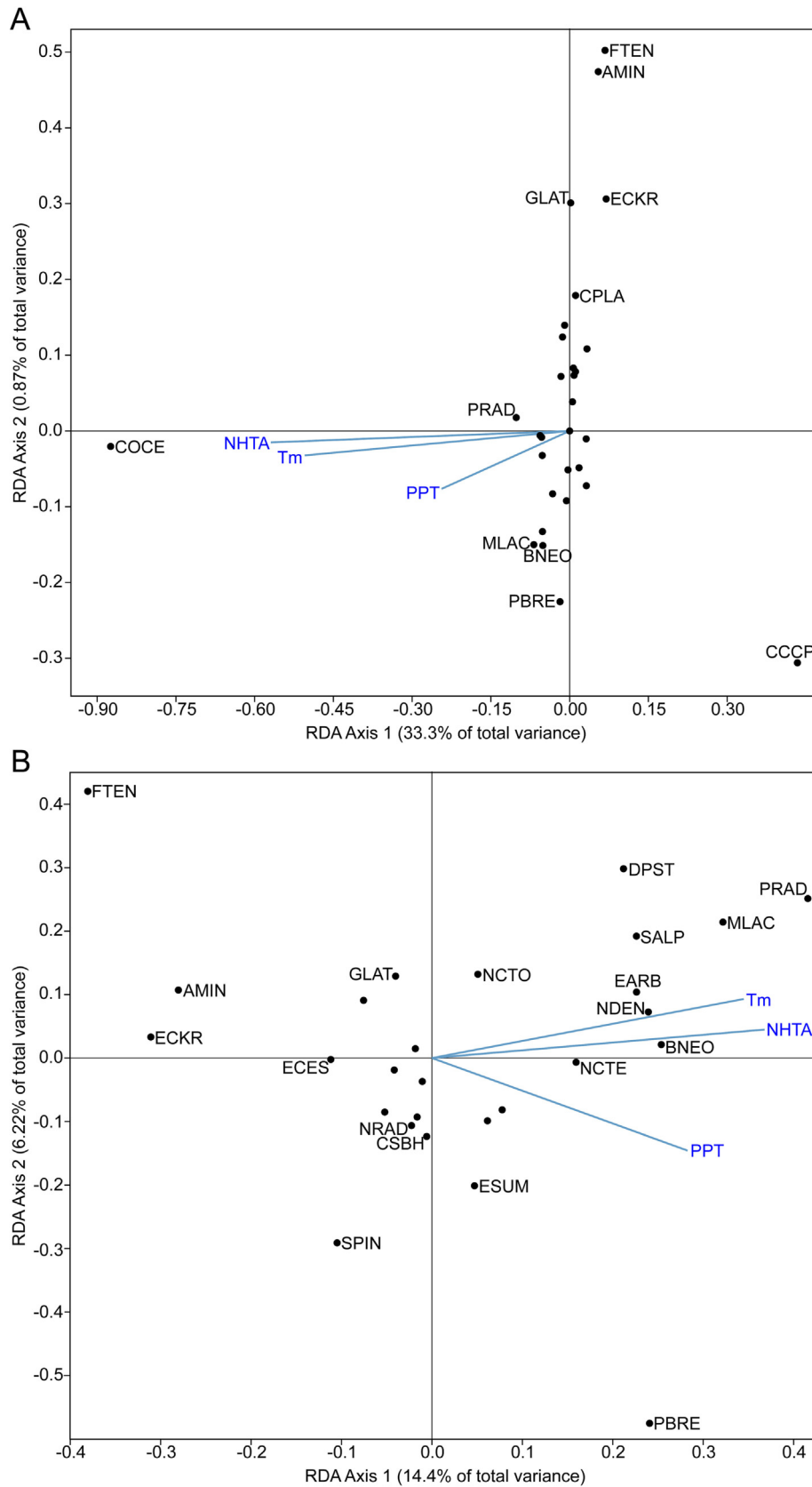
Fig. 4. Redundancy analysis (RDA) linking the diatom response variables with the PT dataset within the MONT-0713-G05 sediment core. CYCLO (A) and NOCYCLO (B) matrix relationships with Barcelona's instrumental climate data and the NHTA, from 1788 to 2006 CE samples. Only species having a higher score than 0.10 in absolute terms on any of the two axes (or 0.15 for the second axis in subgraph A) are labelled. NHTA: Northern Hemisphere temperature anomalies; PPT: Anomalies for the instrumental monthly accumulated precipitation in Barcelona; Tm: Anomalies for the instrumental monthly average temperature in Barcelona. Taxa abbreviations are depicted in Fig. 3 caption. $n = 31$.
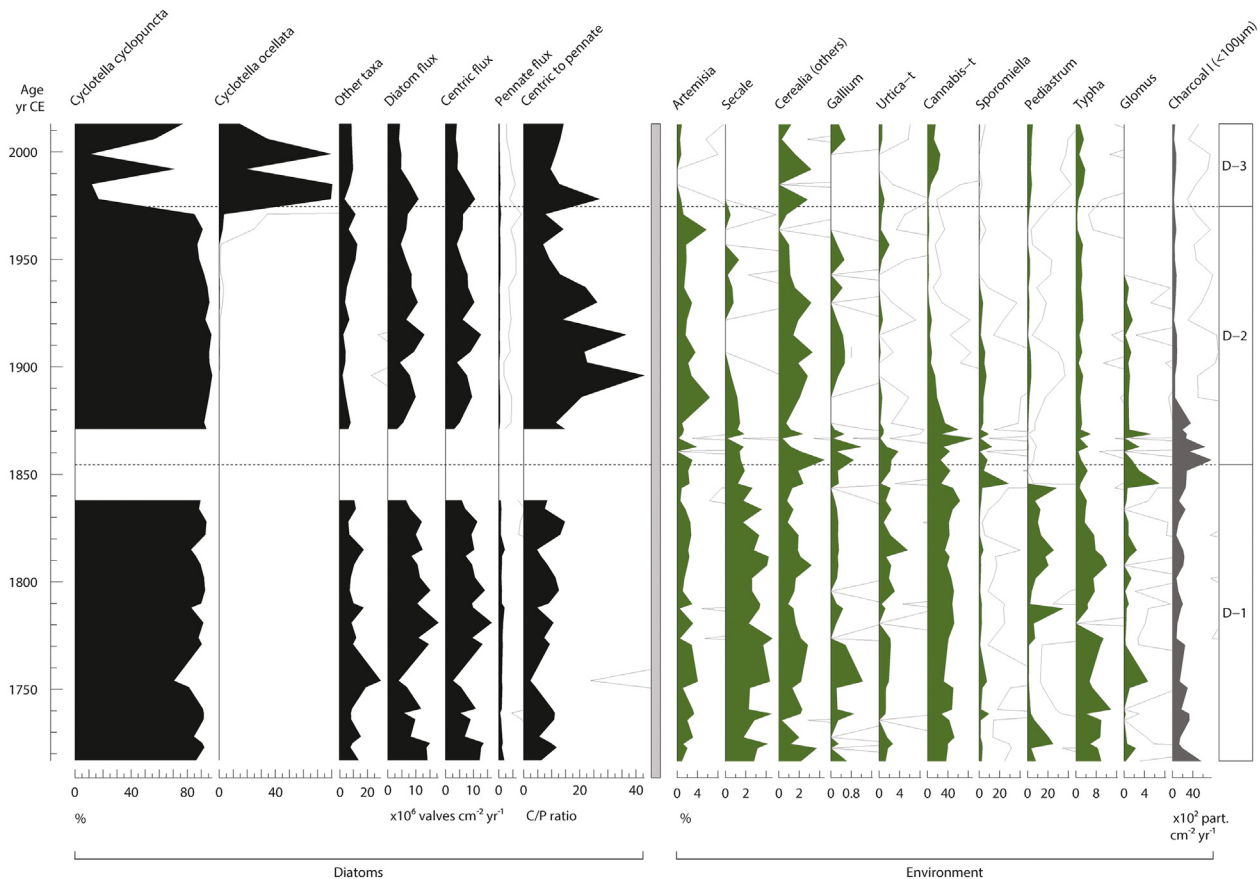
Analyst: Xènia Rodríguez Miret

Fig. 5. Relative abundances of *Cyclotella cyclopuncta* and *Cyclotella ocellata*, diatom fluxes and C/P ratio, together with selected environmental variables from Trapote (2019) (see Section 2.3). 'Other taxa': species other than *C. cyclopuncta* and *C. ocellata* merged. Solid lines represent x10 exaggeration. Horizontal dashed lines delimit statistically differentiated zones. The 1838 to 1871 CE period (blank space) is devoid of diatom samples due to the presence of an approximately 16 cm thick turbidite. *n* = 44 for diatom-related variables; *n* = 52 for environmental variables.

of the *Achnanthidium minutissimum* complex in the 1810s (Figs. 2 and S5B). However, it is not clear whether this was a direct effect of lower temperatures, weakening of the lake's stratification or other reasons, such as a possible higher water transparency.

The minimum mean C/P ratio occurred in this Zone D-1 (Table S2), and the minimums of *C. cyclopuncta* abundances detailed above led to the lowest C/P ratios across the whole period analyzed in this study (Fig. 1). These circumstances indicate that the planktonic community may have been less relevant during this period compared to subsequent periods, and especially during *C. cyclopuncta* minimums.

4.2.2. Cannabis sativa exploitation and the end of the LIA

The following years until ca. 1838 CE were characterized by a decrease in the diatom fluxes and a gain in relevance of *F. tenera*, *P. brevistriata* and *Gomphonema lateripunctatum*. CPA reflected this variation with a level 1 change in the diatom flux (Table 2). This period was climatically defined by slight temperature increases and more persistent rain, storms and floods (Fig. 7; Oliva et al., 2018). Concomitantly, *Cannabis* pollen RA reached its first maximum precisely in ca. 1840 CE due to intense hemp retting (Fig. 5; Rull et al., 2022; Trapote et al., 2018a), and the number of inhabitants of Montcortès town tripled to 175 people (Sabartés i Guixés, 1993). Overall, water hemp retting has been blamed for nutrient enrichment, enhanced turbidity, oxygen depletion and significant changes in plankton community composition (Anderson et al., 1984; Cheng et al., 2007; van der Werf and Turunen, 2008). In fact, some aquatic eutrophication indicators, e.g., Cyperaceae, *Typha*, *Pediastrum*, *Tetraedron*, subfossil pigments of sulfate-reducing bacteria and cyanobacteria, have been reported to have increased or reached their highest values in Lake Montcortès coinciding with

maximum *Cannabis* pollen values, thus suggesting eutrophic conditions in the aquatic habitat at that time (Trapote et al., 2018a; Vegas-Vilarrúbia et al., 2018). The decrease in diatom fluxes in Zone D-2 with respect to Zone D-1 and the shifts in the relative abundance of species within the community, although moderate, coincided with the lowest values of biogenic calcite precipitation across the whole studied period (Fig. 6). These changes occurred in a context of environmental instability. The transition between both zones coincided with the end of the LIA in 1850 CE and the transition to posterior warming (Oliva et al., 2018), which was characterized by climatic variability with very frequent heavy rainfall, severe storms and turbiditic deposition of fresh sediments (Corella et al., 2014; Oliva et al., 2018). Accordingly, catchment erosion was high (Fig. 6). The temperature was still low but generally higher than that in Zone D-1 (Fig. 7; Mann et al., 2009; Oliva et al., 2018). The transition to Zone D-2 was also defined by a second peak in hemp abundance in the late 1860s, which was the highest throughout all diatom zones (Fig. 5). The taxa that seemingly were negatively impacted by these environmental changes were the *A. minutissimum* complex, *Encyonopsis krammeri*, and *G. lateripunctatum* populations, while the opposite occurred for *P. brevistriata*, *Staurosirella pinnata* and *Cymbella subhelvetica*.

As hemp abundance began to decrease from the 1870s on, commercial activities stagnated, and part of the population was forced to migrate (Sabartés i Guixés, 1993). Cultivation of *Secale* decreased, whereas the opposite occurred for other cultivated grasses (Fig. 5). Charcoal I, indicator of regional fires and soil erosion, also diminished progressively (Fig. 5), and the same trend was found for the heavy rainfall frequency (Corella et al., 2014). During this period, both centric and pennate fluxes slightly recovered but did not reach the average levels observed in Zone D1. The
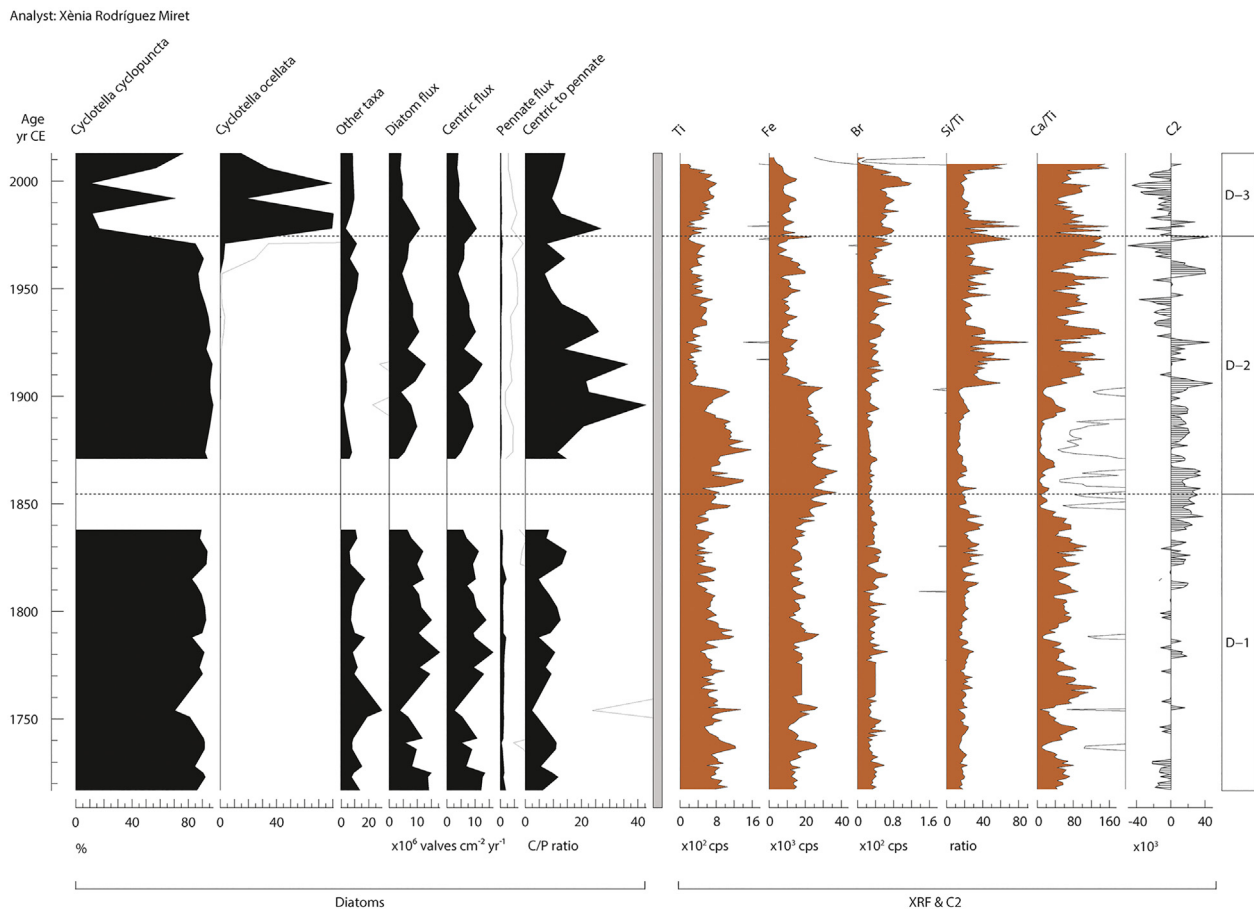
Fig. 6. Relative abundances of *Cyclotella cyclopuncta* and *Cyclotella ocellata*, diatom fluxes and C/P ratio, together with several elemental components of the sediment and the C2 component from Vegas-Vilarrúbia et al. (2018) (see Section 2.3). 'Other taxa': species other than *C. cyclopuncta* and *C. ocellata* merged. Solid lines represent x10 exaggeration. Horizontal dashed lines delimit statistically differentiated zones. The 1838 to 1871 CE period (blank space) is devoid of diatom samples due to the presence of an approximately 16 cm thick turbidite. n = 44 for diatom-related variables; $n = 289$ for NHTA; $n = 292$ for Ti, Si/Ti and Ca/Ti; $n = 295$ for Fe and Br; $n = 290$ for C2.

A. minutissimum complex and *E. krammeri* populations increased more than the other taxa and progressively became more relevant in the diatom community, whereas the opposite occurred for the *P. brevistriata* and *S. pinnata* populations (Figs. 2 and S5B).

4.2.3. Early 20th century: rising temperatures and recovering from eutrophication

The most outstanding feature of the period from the beginning of the 20th century to the 1970s was the gain of prominence of other centric species in the diatom community, albeit *C. cyclopuncta* persisted as the most dominant species by far. This new upturn could be partly due to the amelioration of climatic conditions, which seemed to have favoured the appearance and increases in the RA of other planktonic species, namely, *C. ocellata*, *Discostella pseudostelligera*, *Puncticulata radiosa*, and *Stephanodiscus alpinus*. The irruption of *C. ocellata* around 1900 CE was registered as a level 1 variation in the CPA (Table 2). Consequently, the average C/P ratio was the highest among the three periods, with a CPA level 1 variation around this date as well, suggesting a stronger stability of the water column. In fact, this period was characterized by a gradual recovery of temperature in the Northern Hemisphere (Fig. 7; Mann et al., 2009), which was also reflected in the maximum and minimum temperatures of the instrumental record of the central Pyrenees and a decrease in the number of colder years after 1950 CE (Pérez-Zanón et al., 2017). Mean regional precipitation suffered pronounced interdecadal shifts (Pérez-Zanón et al., 2017), whereas heavy rainfall was much less frequent (Corella et al., 2014) and catchment erosion notably decreased (Fig. 6). These climatic shifts likely enhanced water clarity and strengthened the vertical thermal gradient, especially between 1930 and 1940 CE, allowing for a greater

stability of the aquatic environment (Vegas-Vilarrúbia et al., 2018). Around that time, a level 1 change in the benthic diatom community was observed in the CPA analysis (Table 2). On the other hand, the cessation of retting activities (Rull et al., 2022; Trapote et al., 2018a) probably led to a progressive and natural recovery from eutrophication. The steady establishment of more permanent meromictic conditions with gradual warming (Vegas-Vilarrúbia et al., 2018) caused a reduction in the internal turnover of phosphorus, nitrogen and silica (own unpublished data). These changes in the lake's nutritional status might partly account for the shifts in the relative abundances of the newly appeared planktonic species. Accordingly, some studies have found a link between lake reoligotrophication and both *S. alpinus* and *P. radiosa* reappeareance in its diatom community (Horn et al., 2011; Rippey et al., 1997). *D. pseudostelligera* has been found to be related to lower population density and agriculture (Reavie and Cai, 2019), but the relationship between this species and the P content is ambiguous (Kireta and Saros, 2019). In addition, both diatom production and biogenic calcite precipitation augmented (Fig. 6).

4.2.4. Second half of the 20th century: do heavy storms matter?

From the 1980s onwards, the diatom flux constantly and notably decreased, coinciding with a reduction in thermal-mixing events and reinforcement of meromictic conditions (Vegas-Vilarrúbia et al., 2018). The most conspicuous fact was the occasional loss of dominance of *C. cyclopuncta*, giving way to the irruption of *C. ocellata* as a strong competitor. *C. ocellata* had not been recorded in Lake Montcortès before the 20th century (Scussolini et al., 2011) and it was not until the 1970s when its abundance abruptly increased and the alternance between both species began. This upturn was reflected in the CPA by the outliers, which
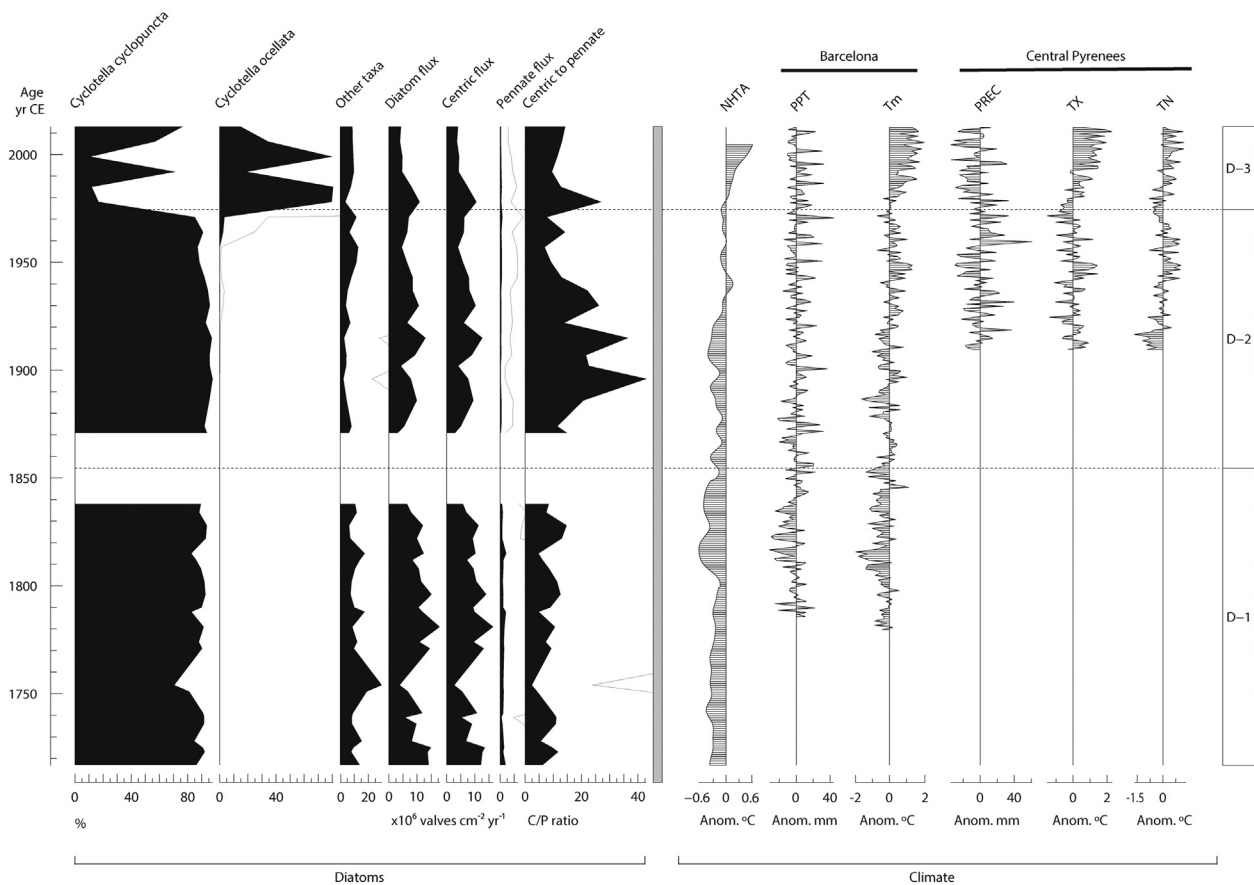
Fig. 7. Relative abundances of *Cyclotella cyclopuncta* and *Cyclotella ocellata*, diatom fluxes and C/P ratio, together with selected climatic variables from other studies (see Section 2.2). 'Other taxa': species other than *C. cyclopuncta* and *C. ocellata* merged. Solid lines represent x10 exaggeration. Horizontal dashed lines delimit statistically differentiated zones. The 1838 to 1871 CE period (blank space) is devoid of diatom samples due to the presence of an approximately 16 cm thick turbidite. n = 44 for diatom-related variables; n = 289 for NHTA; *n* = 228 for PPT; *n* = 234 for Tm; *n* = 104 for central Pyrenees.

corresponded with the abrupt minimum and maximum in *C. cyclopuncta* and *C. ocellata* abundances, respectively. The evidence of changes in the relative abundances of both diatoms in each of the 6 samples of the Zone D3 is overwhelming. *C. ocellata* is a cosmopolitan (Burge et al., 2016), eurythermic (Zhang et al., 2016) and mesotrophic species (Wagner et al., 2009). Much less is known about the autecology of *C. cyclopuncta*. The exchange of dominance between the two centric small-sized diatoms occurred in the context of temperature increases and lower rainfall (Fig. 7; Corella et al., 2014; Pérez-Zanón et al., 2017). Since the 1980s, winter mixing has become less frequent, and meromictic conditions have become more stable, reinforcing the natural reoligotrophication of Lake Montcortès after depopulation (Vegas-Vilarrúbia et al., 2018). As both diatom species are similar in size, the ability to stay afloat with the growing thermal stability of the lake can be ruled out as the factor deciding the dominance of one species over the other (Saros et al., 2012; Winder et al., 2009).

Interestingly, the samples showing *C. ocellata*'s prevalence include the ca. 1978 to 1985 CE and ca. 1992 to 1999 CE intervals, which were characterized by extraordinary rainfall events. In particular, the rainy years included 1992 CE, with an average value of precipitation of 23.2 %, which was higher than that of the reference period (1961–1990 CE) and 1979 and 1996 CE (OPCC-CTP, 2018; Serrano-Muela et al., 2013). In the central Pyrenees, extreme rainfall events occurred in November 1982 with >200 mm over 3 days and in August 1996 with >220 mm over 125 h. Both episodes generated destructive floods in the main Pyrenean rivers (García-Ruiz et al., 1996).

Fortunately, the stratigraphy of the sediment of Lake Montcortès from which the samples had been extracted could be examined (Corella et al.,

2014). The authors tested the concordance of the detrital microfacies intercalated within the varved record in Lake Montcortès with the instrumental daily rainfall records gathered from the nearby Cabdella meteorological station. Interestingly, they found temporal coincidence of the recorded extreme precipitation events with the deposition of 11 detrital layers between 1917 and 1994 CE (Corella et al., 2014). The signals of the two heaviest storms (1982 CE, 252 mm, and 1937 CE, 160 mm) were visible in the varved record of Lake Montcortès and support the hypothesis that the abrupt changes in the planktonic diatom community were related to extreme episodes of rainfall. This suite of remarkably higher-than-average years of precipitation may have changed the pelagic habitat of the lake for several years by altering the water temperature and mixing depth, decreasing light penetration and enhancing the input of allochthonous phosphorus to the lake. This suggests that the pulses of *C. ocellata* could have been an opportunistic response to alterations of key ecological factors that provided this species with a temporary competitive advantage at the expense of *C. cyclopuncta*. There is some evidence available in favour of this tipping-point hypothesis. *C. ocellata* has shown complex responses to climate-driven shifts in temperature, light and nutrients under experimental conditions (Malik and Saros, 2016). Particularly when nutrients were added, *C. ocellata* grew better but under low light conditions. This suggests that this species may have been able to outcompete *C. cyclopuncta* when torrential rainfall increased sediment loading from runoff, hence reducing light availability (Stockwell et al., 2020). These two species notably differ in their optima and tolerances to total phosphorus content, presenting a further handicap to *C. cyclopuncta*. In Swiss lakes, *C. cyclopuncta* and *C. ocellata* showed optimal TP values of 9 µg/L and 57 µg/L and tolerance values of

6–15 μg/L and 35–93 μg/L, respectively (Bigler et al., 2007). On the other hand, storms are known to impact phytoplankton by prompting the external loading of phosphorus with runoff and by increasing internal loading through mixing events (Stockwell et al., 2020). Thus, it is reasonable to suppose that in Lake Montcortès, an unprecedented combination of higher phosphorus availability and light attenuation in the context of warmer water triggered the expansion of *C. ocellata* at the expense of *C. cyclopuncta*. From its arrival to the lake until the 1970s, this species might have been surviving in very low proportions, even during adverse conditions such as P limitation through auxospore production (Perez-Martinez et al., 1992). Nonetheless, other explanations are also possible.

Finally, it is worth mentioning that recent research in Lake Montcortès has confirmed the expansion and diversification of centric diatoms at least since 2013 CE, which account for >50 % of the diatom community during most of the year (Trapote, 2019; Trapote et al., 2018b). The main centric species present today are *C. cyclopuncta*, *C. ocellata*, *P. radiosa* and *Stephanodiscus hantzschii*. *C. cyclopuncta* still dominates the community, whereas *C. ocellata* is less abundant but maintains constant proportions, and *P. radiosa* shows small proportions except during spring bloom episodes.

4.3. Long-term stability dynamics of the diatom community

From an ecological perspective, the diatom community dynamics of Lake Montcortès is an interesting example of resilience (Holling, 1973; Gunderson, 2000) and alternative states (Beisner et al., 2003) in which it is recognizable. The complete set of these varieties has been called attraction domain (Grimm et al., 1992; Rull, 2020).

From the 18th century until the 1970s, the planktonic diatom community was resilient, showing high structural persistence at the subdecadal scale and only smooth responses to human-induced alterations, harsh cooling episodes and, from the 1920s onwards, acclimation to warming and oligotrophication in the context of climate change and depopulation of the Pallars region. It is possible that certain limnological characteristics provide certain buffer when temperature (e.g., due to steep topology) or nutrient circulation and availability (e.g., due to meromixis) change progressively. However, after the 1970s, tipping points appeared in the form of extreme rainfall events that abruptly changed the value of key environmental parameters (e.g., light, nutrients…), probably disturbing the planktonic diatom community and pushing it to an alternative state dominated by *C. ocellata* instead of *C. cyclopuncta* (Fig. 8). Interestingly, the community shifted from and slowly returned to *C. cyclopuncta*-dominated state at least twice until 2013 CE. Noteworthy was also the lack of return of the community to the predisturbance stable state (i.e., before ca. 1964 CE) when the impact was over. *C. cyclopunta* lost prominence despite its dominance, *C. ocellata* became codominant, and other centric diatoms gained relevance. Summing up, it seems to exist an attraction domain launching three alternative states: 1. *C. cyclopuncta* as the only significant planktonic and dominant species (i.e., the predisturbance state); 2. dominance of *C. ocellata* in coexistence with *C. cyclopuncta*; 3. dominance of *C. cyclopuncta* in coexistence with *C. ocellata*.

The benthic diatom community did not reflect any comparable instability dynamics during the whole studied period (Figs. 2 and S5B). There were fluctuations in the RA of some species, e.g., *P. brevistriata* and the *A. minutissimum* complex, but not a significant shift. However, some of the relevant benthic species did experience changes in their relative abundance when the planktonic abrupt shifts began (Fig. 8B).

Paradoxically, the 20th century was the period with the least storm frequency of the last 200 years (Corella et al., 2014). The effects of subjacent factors acting at the beginning of the 20th century, such as the ongoing increase in temperatures due to global warming and trophic changes due to a decrease in anthropogenic pressure, probably created the necessary antecedent conditions to destabilize the diatom community and to produce alternative states within the same attraction domain. In fact, the community seems not to have returned to the ecological state prior to the 1970s in the following 50 years and may not have finished to change. In the future, the persistent environmental effects of these chronic stressors could approach the community to its resilience threshold, so that extreme storms could finally trigger a
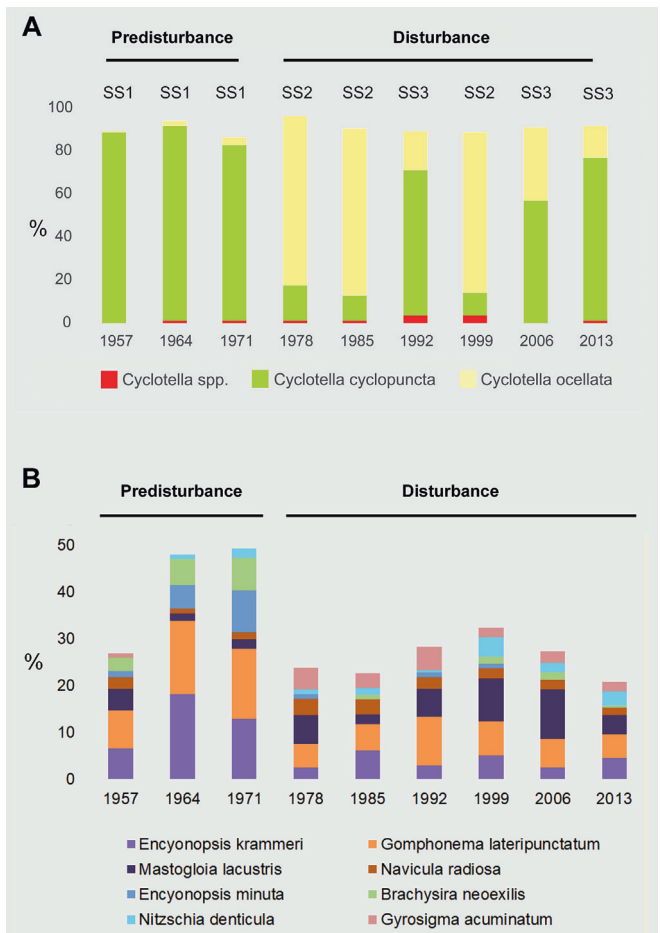
Fig. 8. Disturbance dynamics of the diatom community in Lake Montcortès since ca. 1957 CE. A) Structural alternative stable states (SS) of the diatom community from ca. 1957 to 2013 CE. B) Relative abundances (excluding the two dominant *Cyclotella* species) from ca. 1957 to 2013 CE of the most relevant pennate diatom species showing differences after ca. 1971 CE (plankton disturbance).

regime shift (Capon et al., 2015), i.e., the replacement of the actual community by another belonging to a different attraction domain. The presence of new species would facilitate the community turnover.

From these results, a link with the stochastic occurrence of heavy storms and their effects on the planktonic diatom community can be inferred. They are highly indicative and consistent with the hypothesis that intense storms can restructure phytoplankton communities and their dynamics in the short and long term (Stockwell et al., 2020). Undoubtedly, these insights are important for Mediterranean freshwater bodies, where heavy rainfall events are likely to intensify by 10 to 20 % in all seasons except summer because of climate change (Lange, 2020; United Nations Environment Programme/Mediterranean Action Plan and Plan Bleu, 2020). Phytoplankton, including diatoms, are primary producers and therefore essential players in ecosystem functions that can become quite disturbed, thus impairing biogeochemical cycles and trophic networks. Research on this subject is rather scarce because of the difficulty of precisely knowing the timing, intensity and duration of a heavy storm, making its planning and execution very challenging, but necessary.

4.4. Comparison with other lakes

Detailed paleolimnological studies of Mediterranean lakes focusing on the biological responses to the climate and anthropogenic changes of the last decades are still scarce. A reason for this gap is that the main research interest of the available studies has been to infer climate changes from biological records (López-Merino et al., 2011; Roberts et al., 2012), instead of

analyzing the biological responses against independent climate records, or that the temporal scale is too low.

A question raised in the analyses of our results was whether the abrupt changes registered in the planktonic diatom community during the second half of the 20th century represented a regime shift or not. From an empirical and behavioral perspective, the tendency of the community to return to a *C. cyclopuncta*-dominated alternative state despite the increasing influence of other planktonic species did not support the hypothesis that a regime shift, or a real community change, has occurred. Other studies applied mathematical procedures to test whether abrupt ecosystem changes that occurred over the last centuries would meet the essential properties of a regime shift (e.g., Andersen et al., 2009; Bunting et al., 2016; Randsalu-Wendrup et al., 2016). For instance, the study of the paleoecological trajectory of Lake Varese (North-Western Italy) showed that continuous and abrupt responses of the pelagic assemblages to environmental drivers can occur synchronously (Bruel et al., 2018). The tipping point causing a regime shift in Lake Varese was a striking P increase in a context of lake restauration from eutrophication and ongoing climate change. These results support the aforementioned hypothesis for Lake Montcortès on the importance of a precondition created by climate warming to trigger unexpected response, when extreme events occur. In the same paper, the authors report desynchronized environmental responses of the pelagic and the benthic habitats and suggest that these may be most common in deep lakes because of the spatial segregation of both habitats. This explanation may be useful to understand the different responses obtained in the planktonic and benthic diatoms of Lake Montcortès.

Many abrupt ecological changes in diatom communities that occurred in the second half of the 20th century are comparable to the ones that took place in Lake Montcortès. However, most investigations that were able to evidence a regime shift worked with multiple lines of evidence by using different trophic levels, which seems to be a more powerful approach. For instance, in the perialpine Lake Joux (Swiss Jura), a paleoecological study tested the occurrence of regime shifts by tracking changes throughout the lake food web (Monchamp et al., 2021) and detected an unprecedented multitrophic regime shift triggered by the onset of rapid cultural eutrophication in the 1950s, after several centuries of relatively stable communities despite growing anthropogenic impacts. In alpine lake Bâlea (Southern Carpathians, Romania), the benthic diatoms and the chironomid species that dominated the ecosystem before 1926 CE were outcompeted by other species (Szabó et al., 2020). The transformation of the chironomid community was caused by a summer mean temperature increase, whereas new planktonic community reached their highest abundance between 1950 and 1990 CE due to nitrogen fertilization. A paleolimnological study at Piburger See (Austria) revealed that algal growth, increases in centric diatoms and blooms in *Asterionella formosa* coincided with a significant enhancement of the epilimnetic temperature during the mid-1940s and also since the late 20th century (Thies et al., 2012). Interestingly, a recent paleolimnological study in shallow Lake Isoba (North-Western Spain) reported an abrupt raise of *C. ocellata* between 1925 and 1986 CE, and a drastic change in the diatom assemblage towards a clear dominance of benthic, periphytic and epiphytic diatoms after 1986 CE (Gardoki et al., 2023). Contrarily to the case of Lake Montcortès, this change represented a major shift in the ecological status of Lake Isoba and coincided with a decrease in precipitation, a drop of lake level and the intensification of human impact caused by changes in the transhumant practices.

Research on the effect of climatic extreme events on freshwater ecosystems is gaining relevance around the globe but is still scarce, as could be stated in the review of Stockwell et al. (2020) and in this study. Studies of present and past extreme climatic phenomena (e.g., storms, droughts or hurricanes) are essential to assess the magnitude, timing and duration of the derived ecological effects (e.g., Liess et al., 2016; Mesman et al., 2022; Virta and Teittinen, 2022). The eventual contribution of paleoecological and paleoenvironmental studies to the impact of extreme events on lacustrine communities rely firstly on the translation of the corresponding climatic signal to the lake sediments; for instance, in the form of detrital inputs (e.g., Corella et al., 2014). Secondarily, a good match between this signal and the response of the targeted proxy is needed, and this condition presupposes that the proxy is physically deposited in temporal correspondence with the extreme event under study. By now, methodological limitations exist to sample diatoms and other organisms for such high-resolution reconstructions, even in varved sediments (Vegas-Vilarrúbia et al., 2020). Hyperspectral techniques might provide interesting solutions soon, as they are able to detect specific chemical compounds and substances, based on their unique spectral fingerprints (Butz et al., 2015).

5. Conclusions

A ca. 300 year-long diatom record from Lake Montcortès was evaluated at among the highest resolution (subdecadal) achieved so far for a lake on the Iberian Peninsula. The varved nature of the lacustrine sediments and the multidisciplinary approach, including climatic data from instrumental recording, allowed tracking the responses of diatoms to the effects of pre- and postindustrial climate and human activities at the subdecadal level.

The results do not support the use of any of the identified diatom species as proxies to track or predict single variables intended to describe trophic or climatic changes in Lake Montcortès. In numerous cases, the relationship between the abundance of a determined species and a particular explanatory variable was rather weak or nonexistent. The apparent absence of a response may hide the existence of simultaneous responses to multiple factors that cancel each other out and stabilize the coexistence of species in a complex microbial ecosystem.

Contrary to what was expected, the diatom community as a whole also changed surprisingly little until the 20th century. Either the derived impacts were not strong enough to significantly modify the structural characteristics of the community; there was a legacy of conditions and regulatory mechanisms that allowed the community to preserve at least its structure within the determinants of growth of the prevalent diatom species; or the limnological conditions of the lake allowed for a certain buffer against gradual increases in temperature (e.g., due to steep topology) or nutrient circulation and availability (e.g., due to meromixis).

The most revealing diatom community dynamics in Lake Montcortès occurred after the 1970s with the competition of two species of *Cyclotella* for the dominance of the community and the arrival of new centric diatoms. The derived instability dynamics of the planktonic diatom community may have been triggered by the concurrent extreme rainfall episodes that occurred between 1982 and 1996 CE and whose effects may have been amplified by the gradual impact of global warming on environmental conditions. Future research should attempt to further verify causation, set the mechanistic basis and attempt to understand the ecosystem dynamics.

The results are consistent with predictions in which extreme events should have large impacts on ecosystem structure (Stockwell et al., 2020). In the Mediterranean region, the increase in the intensity and frequency of torrential storms with climate change constitutes an important challenge to the integrity of many biotic communities that thrive in a continuously shifting regime owing to climate change. The unpredictability of these events and the derived scope of biotic consequences will add notable difficulties to the management of lacustrine water masses.

Overall, the acquisition of high-resolution decadal and subdecadal data can guide current research on the effects of extreme weather events on biotic communities, since derived long-lasting changes can develop beyond annual or seasonal scales and promote changes at the ecosystem level. This investigation is an example of this approach and highlights the relevance, persistence and direction of shifts that occurred to a biotic community under demonstrated climatic perturbations. Such information is crucial to predict future scenarios of ecological change, especially in regions of the world with a high frequency of abrupt climatic disturbances.

CRediT authorship contribution statement

XRM: Conceptualization, methodology, formal analyses, investigation, writing – original draft, writing – review & editing. MCT and JS: Methodology, data provision, writing – review & editing. TVV: Idea,

conceptualization, methodology, investigation, visualization, writing – original draft, writing – review & editing, funding acquisition, project coordination and administration.

Data availability

Data will be made available on request.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.163685.

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