Inferring the occurrence of regime shifts in a shallow lake during the last 250 years based on multiple indicators

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ABSTRACT

Regime shifts are ecosystem-scale phenomena. In lake studies, most supporting evidence is frequently based on a single state variable. We examined the sediment record of the shallow lake Blanca Chica (Argentina) to explore the response of multiple proxies belonging to different trophic levels (nutrients, chlorophyll and carotenoid pigments, diatoms, Cladocera remains, and Rotifera resting eggs) over the last 250 yr. We explored different ecological indicators to assess changes consistent with regime shifts. To do so, first we identified the timing of transitional periods on multiple-proxies. Then, we explored (1) the nature of the change (linear versus non-linear dynamics), (2) different indicators of a shift across the food web: multimodality and resilience indicators (standard deviation and autocorrelation), and (3) examined the synchronicity of the detected indicators at multiple-trophic levels. Generalized additive models fitted to the ordination scores of the assemblages analyzed revealed two transitions: ca. 1860–1900, and 1915–1990. Ecological indicators of regime shifts revealed that the first transition is consistent with a threshold state response (change in the ecosystem state manifest as a jump when the driver exceeds a state threshold), and the second one with a critical transition (hysteretic transition in which the system change to an alternate stable state). After the first transition lake structure shifted from littoral to pelagic species dominance (evidenced by Cladocera and diatom assemblages), and turbidity increased, indicating a rise in lake water level. This transition was non-linear, showed multimodality, and is most likely driven by an increase in precipitation registered in the region since 1870. During the second transition, nutrient levels rose, all indicators showed multimodality, non-linear dynamics and an increase in standard deviation prior to the regime shift. These dynamics are consistent with a critical transition in response to eutrophication, and coincides with a post-1920 change in land use. Our results show that several ecological indicators of regime shifts need to be examined to perform an accurate diagnosis. We highlight the relevance of a multi-proxy approach including multiple-trophic level responses as the appropriate scale of analysis to determine the occurrence, type and dynamics of regime shifts. We also show that resilience indicators and critical transitions can be detectable in the whole food web and that shallow lakes can undergo different types of regime shifts.

1. Introduction

Lakes, like other ecological systems, can undergo rapid and drastic changes that have been interpreted under the catastrophic theory paradigm as abrupt change, regime shifts, and/or multiple stable states (Scheffer and Carpenter, 2003; Bestelmeyer et al., 2011; Petraitis and Dudgeon, 2015) (Box 1, Supplemental Information). Shifts in the ecosystem state are generally triggered by external drivers (stochastic or deterministic), sometimes involving internal feedbacks. Regime shifts can include multiple stable states, but also other type of transitions; indeed, can be either: 1- smooth (linear), 2- non-linear (threshold state response) or 3- discontinuous (critical, hysteretic) transitions (i.e.

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multiple/alternative stable states) (Andersen et al., 2009). Regime shifts can occur when a threshold is exceeded by the driver (linear dynamic, driver threshold), the ecosystem state (non-linear dynamic, state threshold) or when attractors/critical points are reached in systems with hysteresis (Andersen et al., 2009).

Analysis of regime shifts is one of the most complex problems of ecology, as there is no unique model for regime shifts nor a unique statistical test for identification. Lakes are important model ecosystems to study this phenomena as they exhibit an array of multiple ecological responses to different interacting pressures like eutrophication, acidification or climate change (Spears et al., 2017). Shallow temperate lakes can shift between a clear macrophyte-dominated state and a turbid phytoplankton-dominated state; therefore, are frequently cited as examples of regime shifts and multiple stable states (Scheffer et al., 1993). Although regime shifts, alternative/multiple stable states, and threshold are widely used concepts, a study reviewed the evidence of regime shifts in 135 freshwater lakes demonstrated that there was little empirical evidence of them or a change from multiple stable states (Capon et al., 2015). In many cases, multiple stable states have been widely reported despite a lack of probabilistic evidence and/or based on changes in only one state variable (Capon et al., 2015; Spears et al., 2017). To demonstrate pressure-induced non-linear changes, several criteria and requirements should be met. First, it is necessary that datasets have sufficient duration, extent, spatial and temporal resolution to adequately link pressures to ecological responses (Capon et al., 2015). Second, indicators of multiple stable states (or state-threshold shifts) should be detected; like multimodality (see Box 1, Supplemental Information), anomalous variance, hysteresis, discontinuous jumps, one jump paths or non-linear responses among others (Petraitis, 2013). However, some indicators can be common to different types of transitions; for example, catastrophic and non-catastrophic transitions can both present increased variance and autocorrelation (Scheffer et al., 2009; Kéfi et al., 2013). Thus, several indicators need to be considered for a proper discrimination. Eventually, four characteristics were accepted to define the different types of regime shift: 1-the change has to be sudden, 2- physical and biological variables should be involved, 3- the ecological change should occur at multiple trophic levels, and 4- with high amplitude, but low frequency (Lees et al., 2006).

Shallow lakes are highly vulnerable to the impact of human activities and climate change. For this reason, Early Warning Indicators (EWI) have been developed to anticipate and predict critical transitions (Dakos et al., 2012). These resilience indicators are based on different statistical moments (like variance, autocorrelation, return rates, among others). Although there is a broad theoretical and experimental support of EWI, there is still some concern about their application in real-world ecological systems. EWI can only be applied to systems with non-linear dynamics (Litzow and Hunsicker, 2016). Furthermore, the trophic level analyzed matters: there is little evidence that EWI precedes non-linear transitions at a population level, but generally more evidence at the community or ecosystem level (Burthe et al., 2016). In other cases, EWI failed to anticipate a catastrophic shift simply because the perturbation is too large and there is no forewarning indicator (Hastings and Wysham, 2010). In contrast, other studies have demonstrated that these leading indicators have anticipated non-linear transitions, and revealed the mechanisms involved (flickering or critical slowing down, Box 1, Supplemental Information) (Carpenter et al., 2011). Finally, researchers or managers must take several decisions when applying this methodology that can affect its outcome (Spears et al., 2017). Thus, the occurrence and detection of EWI depend on several characteristics like the dynamic of the system (non-linear), the length of the data set, the type and dimension of the perturbation/driver exerting pressure on the system and the trophic levels involved (k or r species, population, community) (Hastings and Wysham, 2010; Capon et al., 2015; Burthe et al., 2016; Litzow and Hunsicker, 2016).

Lacustrine sediment records offer the possibility to study ecosystem responses across multiple trophic levels and along extended periods of time, thus addressing the above-mentioned limitations. Sediment records have their own limitations (e.g., sediment mixing, compression, and irregular time aggregation); however, high-resolution paleolimnological studies (i.e., < 10 yr aggregation per core interval) that consider multiple proxies offer a unique opportunity to explore regime shifts and resilience indicators detected at one trophic level and how this may dissipate to higher trophic levels (Carpenter et al., 2011; Frossard et al., 2015). In this work, we examined the sediment core archive of the shallow Lake Blanca Chica to understand changes in lake function and to detect indicators of regime shifts. To do so, we first identified the timing of the transitional periods that occurred during the last 250 years across multiple-proxies: geochemical indicators, primary producers, zooplankton and zoobenthos. We then explored (i) the nature of the change (linear versus non-linear dynamics), (ii) different indicators of a shift across the food web: multimodality and EWI, and (iii) examined the synchronicity of the detected indicators at multiple-trophic levels.

2. Material and methods

2.1. Study site

Blanca Chica Lake (36° 50′ 00.9″S; 60° 28′ 00.9″W) is a shallow (1–2 m), warm temperate, and polymictic lake located in the Pampa plain (also called Pampean Region or Pampas) (Central Argentina, South America) (Fig. 1). This region contains multiple shallow lakes, and constitutes one of the largest area of wetlands of South America (Iriondo, 1989). Regional climate is mainly determined by the South American Monsoon System that defines the precipitation regime (Garreaud et al., 2009).

Blanca Chica is a turbid (Secchi Disc depth: 0.2–0.3 m, Chl a concentration: 90–500 mg m^{-3}) and eutrophic (TP: 0.3–1.2 ppm) lake of alkaline waters (pH: 8–9.8). The fish community is dominated by *Odontesthes bonariensis* and *Cheirodon interruptus*. Zooplankton is composed of small-medium sized Cladocera, Rotifera, and Copepoda species like *Bosmina* sp. or *Brachionus havanensis* (Sanzano et al., 2014).

According to gridded climate models centered on Blanca Chica (CRU TS 3.10, http://www.cru.uea.ac.uk/; (Harris et al., 2014)), the annual mean air temperature is 15.4 °C (average: maximum (January): 26.1 °C; minimum (July): 4.1 °C). Rainfall is strongly seasonal, with ca. 70% of yearly precipitations falling during summer (gridded annual precipitation CE 1901–2014: range: 492–1390 mm year^{-1}; average: 880 mm year^{-1}). The lake is highly sensitive to changes in hydrology, having neither tributaries nor natural surface outlet. Satellite images indicate that its surface can increase or retract with precipitation above average or intervals of drought, respectively (Fig. 1). Climatic oscillations, alternating between wet and dry periods, have been recorded historically and instrumentally along the Pampean region (Piovano et al., 2009; Córdoba et al., 2017).

2.2. Sediment sampling and core chronology

Sediment coring was conducted on October 2015 using a vibracorer; a 60 cm undisturbed sediment core was collected in the deepest part of the lake. Sub-sampling (every 1 cm interval) was carried out on the entire core.

Radionuclide activities of ^{137}Cs, ^{210}Pb and ^{226}Ra were analyzed at the Radiochronology Laboratory of the Laval University, Canada. The calculation of excess ^{210}Pb (^{210}Pb$_{ex}$) was done by subtracting the specific activity of ^{226}Ra from total ^{210}Pb. ^{210}Pb$_{uns}$ flux was determined from the specific activity profile obtained from core inventories (Sanchez-Cabeza and Ruiz-Fernández, 2012). Because the appropriate choice of the calculation model is not *a-priori* known, ^{210}Pb ages and sediment accumulation rates (SAR) were calculated with the CRS, CIC, CFCS and SIT numerical models (Appleby, 2001; Carroll and Lerche, 2003; Appleby, 2008). The details of the models calculations, the
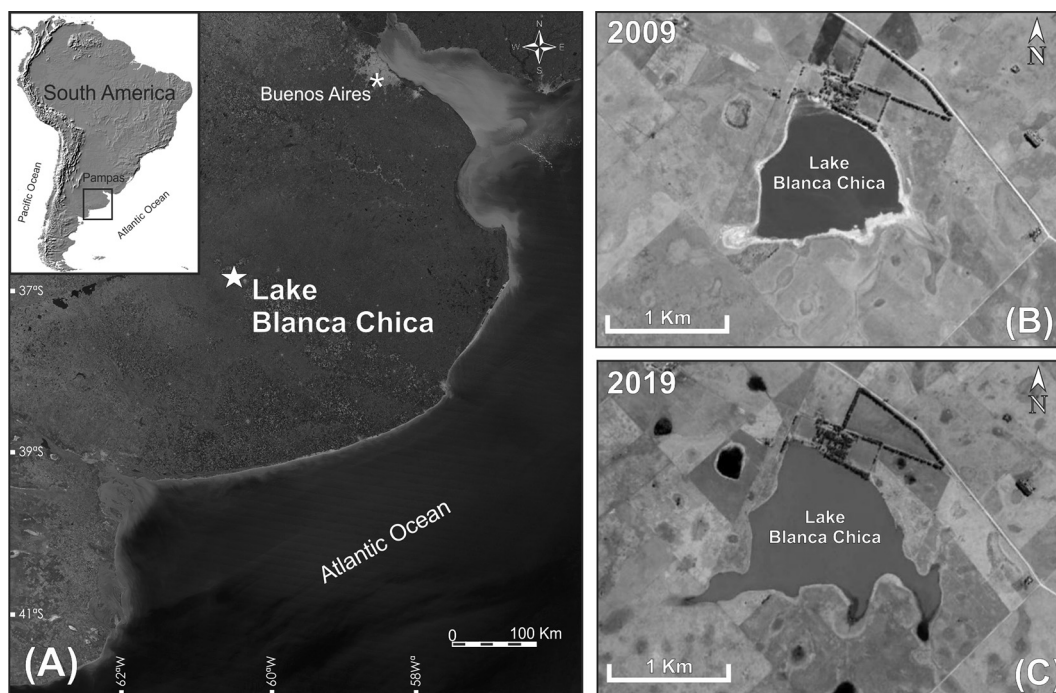
Fig. 1. (A) Location of Blanca Chica Lake in the Pampa Plain ("Pampas" in the central part of Argentina, South America). (B and C) Satellite images of the lake surface in contrasting low (2009) and high (2019) lake-level stands.

inventory and the mean annual flux of $^{210}Pb_{ex}$ are reported in Appleby (2001), Carroll and Lerche (2003) and Sanchez-Cabeza and Ruiz-Fernandez (2012). Extrapolated ages below the limit of ^{210}Pb dating were calculated using Basal SAR as background values for each model. Independent environmental chronomarkers were used to constrain the upper and lowermost part of the ^{210}Pb chronologies: a) ^{137}Cs maximum peak at 6–7 cm as a time marker of CE 1964/65, b) T1$_{BCh}$: first occurrence of *Eucalyptus* pollen in the sedimentary record as a result of an

extensive forestation of this exotic tree since 1880 in Argentina, and c) T2$_{BCh}$: defined as a lithology change corresponding to extreme regional dry pulses registered across the Pampean Plain at the end of the Little Ice Age, and recognized in other lakes, e. g. Mar Chiquita, Melincué (Piovano et al., 2002; Guerra et al., 2015), and estimated to be AD 1775 ± 10 yrs.

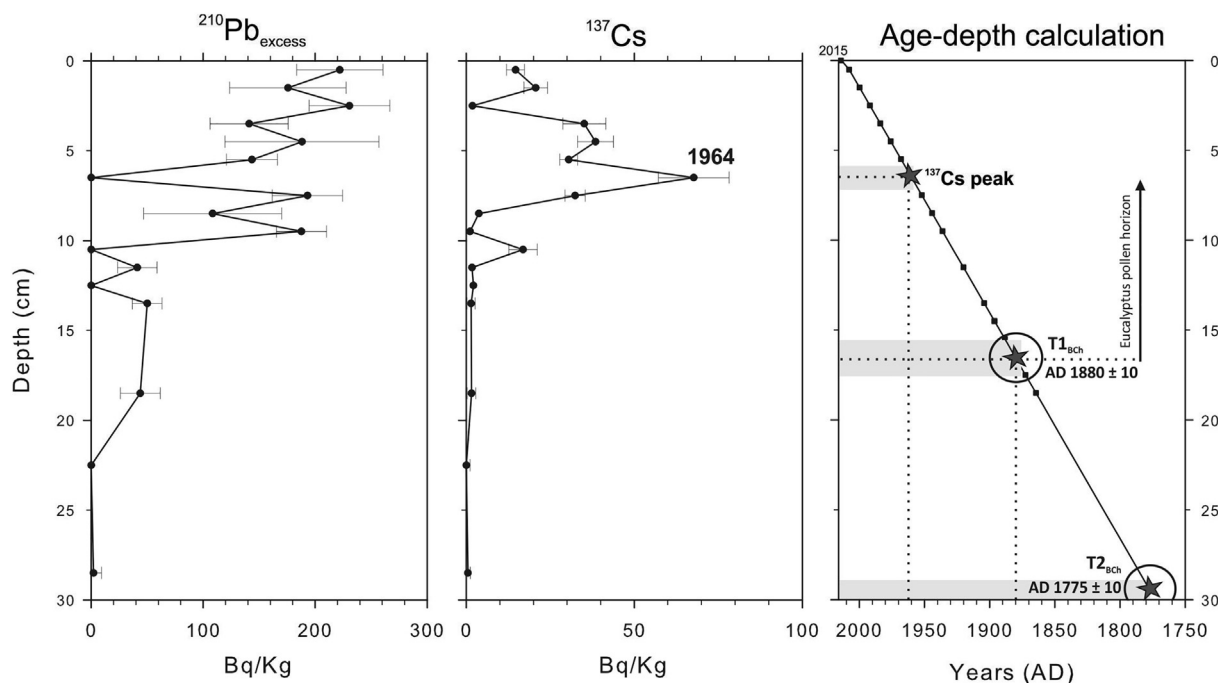**Fig. 2.** ^{210}Pb and ^{137}Cs specific activities and depth-age model for the sediment core of Blanca Chica Lake. Sediment age was estimated using the Constant Flux/Constant Sedimentation model (CFCS) and three chronostratigraphic markers: the 1964 maximum peak of ^{137}Cs registered in the South Hemisphere, the introduction of the exotic tree *Eucalyptus* (T1$_{BCh}$, CE 1880) and a lithological change associated to striking regional dry pulses registered across the Pampean Plain during the end of the Little Ice Age (T2 $_{BCh}$, CE 1775).
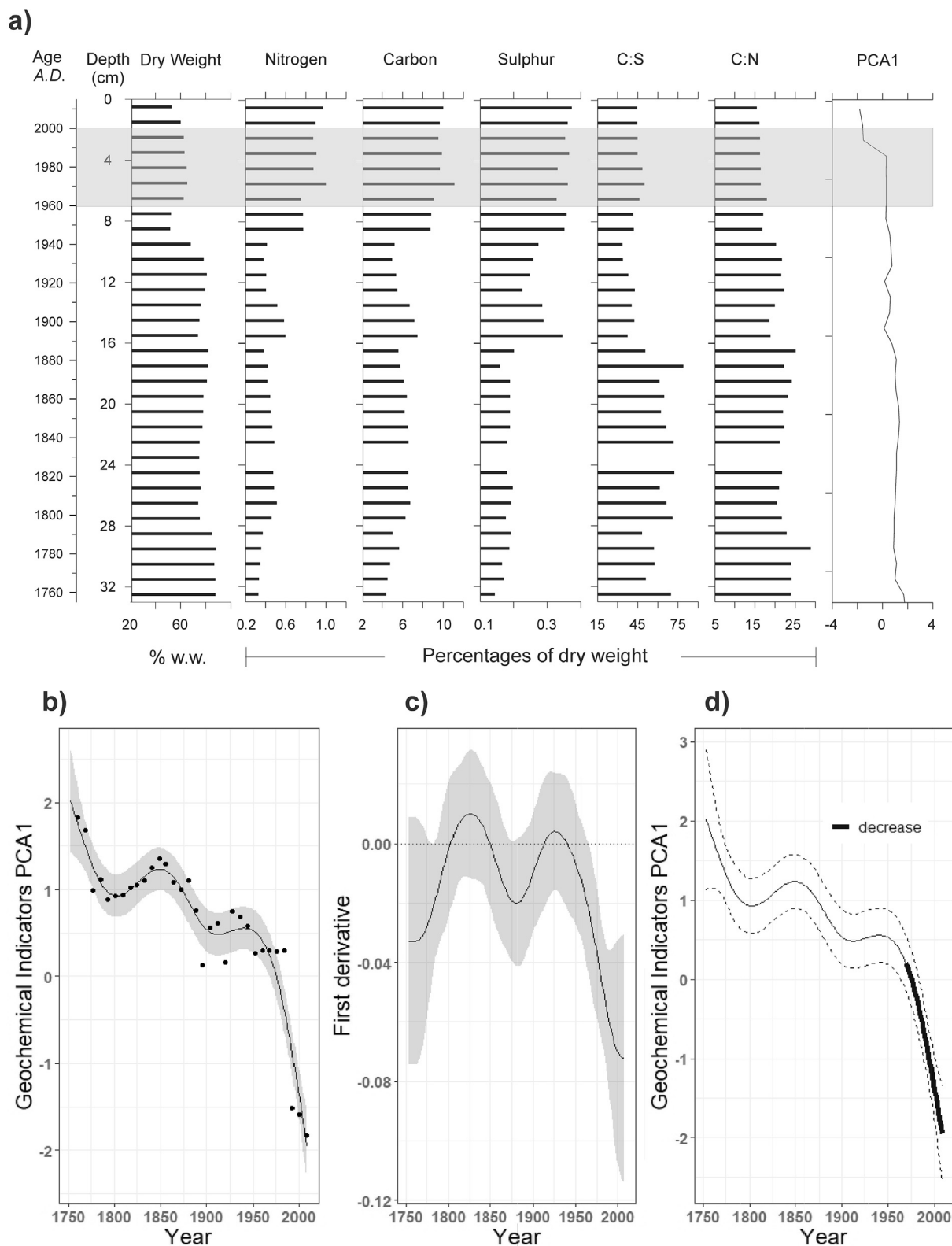
Fig. 3. a Geochemical proxies stratigraphy for Blanca Chica Lake and the scores for the first axis of principal component analysis. The shaded area corresponds to the transition detected by fitting GAM to the time series of ordination scores. Note the different scaling of the *x*-axes. **b** GAM-based trend fitted in the scores of PCA and 95% confidence intervals. **c** First derivative of the fitted trend and its 95% simultaneous confidence interval. Where the trend and its interval bounded away from zero, the model detects a significant temporal change in the response. **d** Periods of transition detected according to the first derivative of the fitted trend and the simultaneous interval, highlighting the decreasing trend.

2.3. Palaeolimnological analyses

Results described in this study correspond to the top 30 cm of the core and include the analyses of geochemical indicators, chlorophyll and carotenoid pigments, diatoms, Cladocera and Rotifera remains. Other remains lacking a taxonomical relationship were also found (e.g., plant seeds, gastropod and fish scales) in low numbers in most of the cases; thus, described in Supplemental information (Miscellaneous rests). Below 30 cm (ca. AD1775, Fig. 3) no pigments were detected and the other biological proxies were too low in number or severely damaged to be quantified.

2.3.1. Geochemistry

Dry mass was estimated after drying 1 g of wet sediment at 60 °C for 24 h; afterwards, the organic content was obtained by loss-on-ignition at 460 °C for 6 h. Total concentrations of carbon, sulphur, and nitrogen were measured on the dry sediment using an "Elemental Analyzer" (NA 1500 Fisons, Carlo Erba) (Lami et al., 2000).

2.3.2. Photosynthetic pigments

Pigments were extracted with 5 ml of a 90:10 acetone:MilliQwater solution overnight in dark, after flushing with nitrogen from ca. 1 g of wet sediment. Sediments were then centrifuged at 3000 rpm for 10 min. Photosynthetic pigments from different taxonomic affinities were detected by High Pressure Liquid Chromatography with an Ultimate 3000 system (Thermo Scientific, Waltham). The elution program and the methodology for pigment identification and quantification followed previous protocols (Lami et al., 2009); the method allowed to resolve on the chromatogram the critical couple lutein-zeaxanthin.

2.3.3. 2.3.3 Diatom

Diatoms were prepared using standard H_2O_2-HCl digestion and mounted with Naphrax (Battarbee et al., 2001). For each sample, at least 300 valves were counted and identified at $100\times$ magnification with a light microscope (dark field, phase contrast) (Zeiss Axiolab, Gottingen, Germany). Several keys were used for taxonomic identification (Krammer and Lange-Bertalot, 1986–1991; Lange-Bertalot and Metzeltin, 1998; Lange-Bertalot, 2000; Metzeltin and Lange-Bertalot, 2007; Cantonati et al., 2017).

2.3.4. Animal remains and seeds

Each sample (2–8 cm^3 of sediment) was gently washed through a 50 µm sieve; the material retained (seeds, gasteropods, fish scales) was identified and counted under a stereomicroscope at 10-40x magnification. Chitinous Cladocera remains, and resting eggs of Rotifera were analyzed in a quarter, approximately, of the sample under an optic microscope (Zeiss Primo Star) at 100-200x magnification. Previously, the sample was sieved (50 µm), and heated (70–80 °C) in 10% KOH, a deflocculating agent, during 45 min (Korhola and Rautio, 2001). Subsamples (200 µl) were taken and counted at least 400 remains. Each type of remain were enumerated separately, and the minimum possible number of individuals were calculated. Several keys were used for taxonomic identification (Paggi, 1979; Kotov, 2003; Segers, 2004; Smirnov et al., 2006; Szeroczyńska and Sarmaja-Korjonen, 2007).

2.4. Statistical analysis

All analyses were performed using R version 3.5.1 (R Core Team, 2017).

2.4.1. Detection of transitions

Multivariate ordination methods, Principal Component Analysis (PCA) or Correspondence Analysis (CA) (package *vegan* (Oksanen et al., 2015)), were performed in the time series of geochemical and biological indicators, depending on the characteristics of each data set. For frequency data (e.g., rotifer, cladoceran remains) CA was conducted. PCA

was applied to dimensionally homogeneous (e.g., carotenoid pigments) and heterogeneous indicators (e.g., geochemical indicators), after normalization of the data (using log or square root transformations). Geochemical indicators were first normalized and then scaled to remove the effect of different units. The number of ordination axes (CA and PCA) were chosen according to Kaiser-Guttman criterion and the Broken stick model (Borcard et al., 2011).

Generalized Additive Models (GAMs) were used to estimate trends as a smooth function of time on the selected ordination axes. To fit GAMs, restricted maximum likelihood (REML) was used for smoothness selection. To account for correlation between residuals, a continuous time first-order autoregressive process (CAR(1)) was chosen (Simpson, 2018). To identify periods of transition, we estimated simultaneous confidence intervals from the posterior distribution of the model (Bayesian approach), and the first derivative of the fitted trend (Simpson, 2018). Periods of significant change are identified as those time points where the simultaneous confidence interval on the first derivative bounded away from zero (Simpson, 2018). The estimation of the models and derivatives were performed using the *mgcv* and *gratia* packages.

2.4.2. Multimodality

Tests for multimodal distribution (Box 1, Supplemental Information) have been previously performed as informal tests for nonlinearity (Scheffer and Carpenter, 2003; Wang et al., 2012). Statistically, the frequency distribution of a variable is multimodal if there are alternative attractors (bistable systems with hysteresis) or a threshold state response (Scheffer and Carpenter, 2003). This method was used as an auxiliary tool to understand the nature of the transition and the occurrence of multimodality. For that purpose, probability density functions (Gaussian kernel density estimation) were estimated from the scores of ordination axes for each indicator (Wang et al., 2012) for each subset of data (post- and transitional periods, if the data length of posttransition was sufficient). In order to avoid spurious results, optimum bandwidth was selected following the rule of thumb of neither overfitting the data, nor filtering out the low frequencies. The detection of multimodality was used as an EWI of a critical transition or a threshold state response.

2.4.3. Early warning indicators

Trends of standard deviation (SD) (variance) and autocorrelation at lag-1 (AR(1)) were estimated as early leading indicators of a regime shift using the R package "earlywarning" (Dakos et al., 2012). Palaeoecological time series represent time-aggregated ecological signals, only SD and AR are sufficiently robust to be tracked in palaeolimnological studies of high resolution (1–10 yr) (Frossard et al., 2015). However, several factors can also weaken the detection of SD and AR like core compaction, mixing, uneven degradation or integration of core intervals (Taranu et al., 2018). SD and AR were estimated on the scores of ordination axes. Data was log-transformed and filtered using a Gaussian smoothing and sensibility analyses were performed to selects the optimum band width that maximizes the estimated trend. Analyses were performed using different size of rolling windows (10, 20, 30, 40, 50 & 60), that represent a percent of the data set; for example, a rolling window of 20% represents 4 samples and a time span of 32 yr in a time series of 32 data points. Trends for each rolling window were calculated using the Mann-Kendall rank correlation test (Kendall τ). Surrogate datasets were produced by fitting linear autoregressive moving average model (ARMA) based on AIC (Akaike's Information Criteria), using 100 simulated datasets (Dakos et al., 2012). The Kendall τ of the original time series was compared to the number of cases in which the statistics was equal or smaller than the estimates of the simulated records. The estimated trends were tested under the null hypothesis that the trend estimates of the indicators are due to chance alone, with $p < 0.05$. As different outcomes could be computed depending on the rolling window size selected (Spears et al., 2017; Bruel et al., 2018), we have

considered that an increased in SD have occurred when significant Kendall τ were detected over the majority of the rolling windows considered.

2.4.4. Testing for a change before and after transitions

The scores of PCA/CA and the SD of each indicator from post- and transitional periods were compared through *t*-tests. If a regime shift did occurred, the scores of the ordination axis should differ (Wang et al., 2012; Bruel et al., 2018). This analysis was done considering a maximum of 10 and a minimum of 5 data points as the cut-off length and a significance level < 0.05. SD estimated from a rolling window of 20% was chosen to avoid increase variation as an artifact of a shorter sliding time window.

3. Results

3.1. Core chronology

^{137}Cs specific activity sediment profile had a pronounced peak at the depth of 6–7 cm with a value of 67.6 ± 10.5 Bq kg^{-1} (Fig. 2). Despite that maximum ^{137}Cs fallout from atmospheric nuclear weapon tests in the Northern Hemisphere (UNSCEAR, 2000) was registered in 1963, the most intense ^{137}Cs fallout peaks in the Pampa Plain (samples collected in Buenos Aires City) occurred slightly later (1964–1966); as a consequence of stratospheric and tropospheric fallout and input from the South Pacific nuclear tests (Ribeiro Guevara and Arribere, 2002). Thus the maximum ^{137}Cs peak at 6–7 cm in Blanca Chica core was assigned as AD 1964/65.

^{210}Pb$_{ex}$ specific activities ranged from 230.6 Bq kg^{-1} to 0.0 Bq kg^{-1} in core Blanca Chica (average = 101.6 Bq kg^{-1}; Fig. 2). The ^{210}Pb$_{ex}$ inventory was estimated to be 11,426 Bq m^{-2}, which corresponds to a mean ^{210}Pb$_{uns}$ supply rate of about 356 ± 21 Bq m^{-2} yr^{-1}. ^{210}Pb$_{ex}$ activities decline with increasing sediment depth. The trend deviates significantly from the theoretical exponential distribution, showing multiple peaks throughout the core (Fig. 2). This non-exponential and non -monotonic ^{210}Pb vertical profile patterns observed in Blanca Chica core should be the consequence of severely hydrological changes that caused several variations in the sediment flux, precluding the direct use of any ^{210}Pb classical mathematical models to derive ages (Appleby, 2008; Sanchez-Cabeza and Ruiz-Fernández, 2012). In fact, CRS, CIC, and SIT models derived-chronologies show inconsistencies and uncertainties, and, therefore, they cannot be used for developing ^{210}Pb ages in this sedimentary record. On the contrary, the Constant Flux/ Constant Sedimentation (CFCS) age-depth model provided the most consistent results with the time markers (Fig. 2). Chronostratigraphic markers (T1$_{BCh}$ & T2 $_{BCh}$) allowed to constrain the upper and lowermost parts of the ^{210}Pb age models. Thus, ages were calculated using the CFCS model applied to the sediment sequence to provide a continuous age-depth relationship, fitting the independent, and well-defined ^{137}Cs time marker of 1964/65 (Fig. 2).

3.2. Transitions in multiple geochemical and biological indicators

Biplots of ordination analyses for all indicators can be found in Supplemental Information, Fig. S1.

Geochemical variables, carbon (C), nitrogen (N), sulphur (S), and the nutrient ratios C:N, and C:S showed contrasting patterns along the sedimentary record (Fig. 3a). PCA1 (first component) was able to capture 75% of the geochemical dataset variance. C and the C:N ratio had the highest loads to PCA1, but with opposite signs. The fitted GAM in the time series for the PCA1 scores explained most of the deviance, and the smooth term had a highly significant effect (Table 1, Fig. 3b). The first derivative of the fitted trend, and its simultaneous confidence interval deviated from zero ca. 1960–2000, indicating a period of transition (Fig. 3c, d). During the transition, the concentration of nutrients increased, but the inverse relationship occurred for C:N and C:S

Table 1
Results from Generalized Additive Models (GAM) fitted to the scores from the ordination methods (PCA or CA) of different indicators from the core of Blanca Chica Lake. The estimated degrees of freedom (edf), *F*-statistic, *p*-values of the smooth term and percent (%) of deviance explained by the fitted model are shown. The significance level was set on *p*-values < 0.05, ns: non-significant results. All the fitted models were estimated using continuous-time AR(1) and REML smoothness selection.

	edf	F	p-values	% Deviance explained
Geochemical Indicators PCA1	6.7	35.64	≪0.0001	92
Carotenoids PCA1	7.25	61.91	≪0.0001	95
Chorophylls PCA1	7.69	112.3	≪0.0001	98
Diatoms PCA1	7.60	46.85	≪0.0001	95
Diatoms PCA2	7.55	42.02	≪0.0001	95
Cladocera Chitinous Remains CA1	4.28	8.02	< 0.0001	65
Rotifera CA1	2.5	20.29	≪0.0001	73
Rotifera CA2	1	0.79	ns	3.05

ratios (Fig. 3a,c). In particular, C:N values turned from ∼ 20 to ∼ 10 after 1960, representing a shift from a heterotrophic to an autotrophic lake metabolism (Fig. 3a, c, d).

Photosynthetic pigments, carotenoids and chlorophylls, showed rather good preservation along the time interval covered by the core as shown by the ratio 430:410 (Supplemental Information, Fig. S2). Both types of pigments increased their contribution from the bottom towards the top of the sedimentary record, and in addition, the detected transitions took place over the same time periods. The changes reflect a variation in composition of the primary producer assemblage, as indicated by carotenoids, and in the total primary productivity, as indicated by chlorophylls. Ordination analysis in fossil carotenoids explained 75% data variance in the first component (PCA1). All pigments contributed with negative scores to PCA1, zeaxanthin (cyanobacteria) being the one with the lowest score (Fig. 4a). The GAM fitted to the time series of PCA1 scores resulted in a significant trend, explaining a high percent of data deviance (Table 1, Fig. 4b). Two transitional periods were detected: ca. 1750–1780 and 1920–1950 (Fig. 4b,c,d). The period after the first transition (ca.1750–1900) is characterized by a low pigment concentration, an equitable contribution of the different carotenoid pigments and a low contribution of cyanobacteria related pigments. After the transitional period (1950), all carotenoids increased their concentration and cyanobacteria related pigments dominated the primary producer assemblage (Fig. 4a). Ordination analysis on chlorophyll pigments explained 94% of the variance (PCA1). Pheophorbide *a* and chlorophyll *a* accounted with the lowest loading to the PCA1 whereas pheophytin *a* did it with the highest (Fig. 5a). The effect of the smooth term was significant and the fitted GAM highly explained data deviance (Table 1, Fig. 5b). The same two transitional periods were observed for the chlorophyll pigments: ca. 1750–1780 and 1915–1952 (Fig. 5c,d). The period after the first transition is distinguished by a low contribution of the different chlorophyll pigments and the one after the second transition by an increased in the overall primary productivity (Fig. 5a).

Diatom assemblage displayed a changed in its composition along the sedimentary record. The first two axes (PCA1 & PCA2) of the ordination analysis explained 73% of data variance, whereas PCA1 reflects inter-species dynamics, PCA2 accounts for different environmental conditions. PCA1 reflects the antagonistic relationship between the widely distributed *Cyclotella meneghiniana* (Hassan et al., 2009) and *Aulacoseira granulata* (occurring under turbid and turbulent conditions (Izaguirre et al., 2012)). The former contributed with highest positive scores and the later with the most negative scores (Fig. 5a). The GAM fitted to the diatom PCA1 scores (Fig. 6b), explained 95% of the deviance (Table 1), detecting two transitional periods: ca. 1850–1930 and 1960–1990 (Fig. 6c,d). In both cases, the trend can be related to the
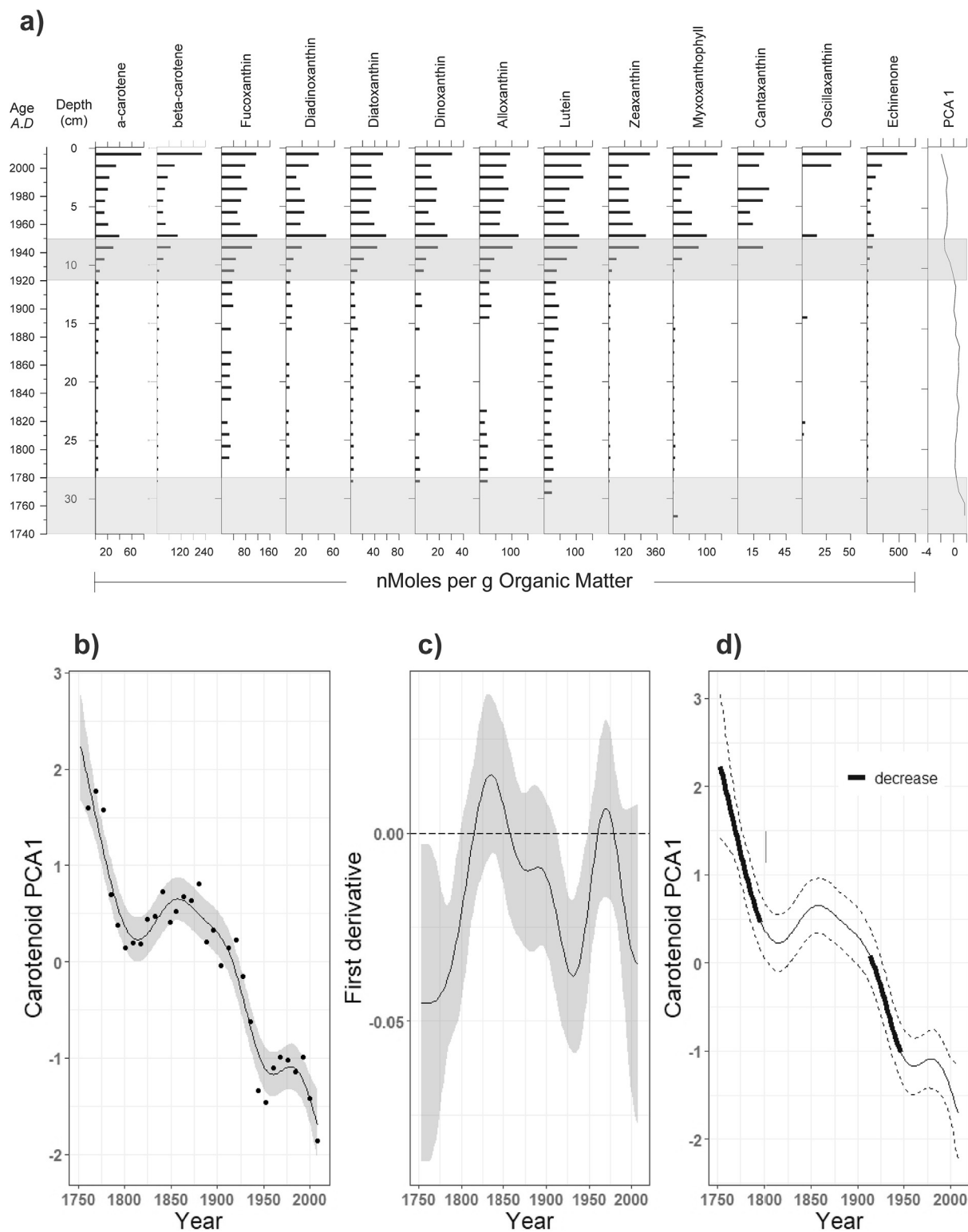
Fig. 4. a Carotenoid pigment stratigraphy of Blanca Chica Lake and the scores of principal component analysis. The shaded area corresponds to the transition. **b** GAM-based trend fitted in the scores of PCA and 95% confidence intervals. **c** First derivative of the fitted trend and its 95% simultaneous confidence interval. **d** Periods of transition, highlighting the decreasing trend. For further details, see Fig. 3.

dynamics of *C. meneghiniana*, that shows a decreasing trend (1850–1880) followed by an increasing trend (1900–1930) and a second decreasing trend after 1960 (Fig. 6a,b,c,d). On the other hand, PCA2 reflects the contribution of diatom species that track increasing nutrient levels under a clear light environment as benthic *Navicula veneta*, *Nitzschia palea*, *Navicula peregrina* and *Nitzschia frustulum*

accounted for the highest scores to axis 2, whereas *C. meneghiniana* and *A. granulata* the lowest (Fig. 5a). The GAM fitted in the PCA2 scores also explained a high percent of the deviance (Table 1, Fig. 6b), bounding away from zero between ca.1910–2008 in association with the increase of *N. peregrina*, *N. frustulum*, *N. veneta* and *N. palea* up to 1970. Afterwards, these species faced a decreasing trend concomitant with the
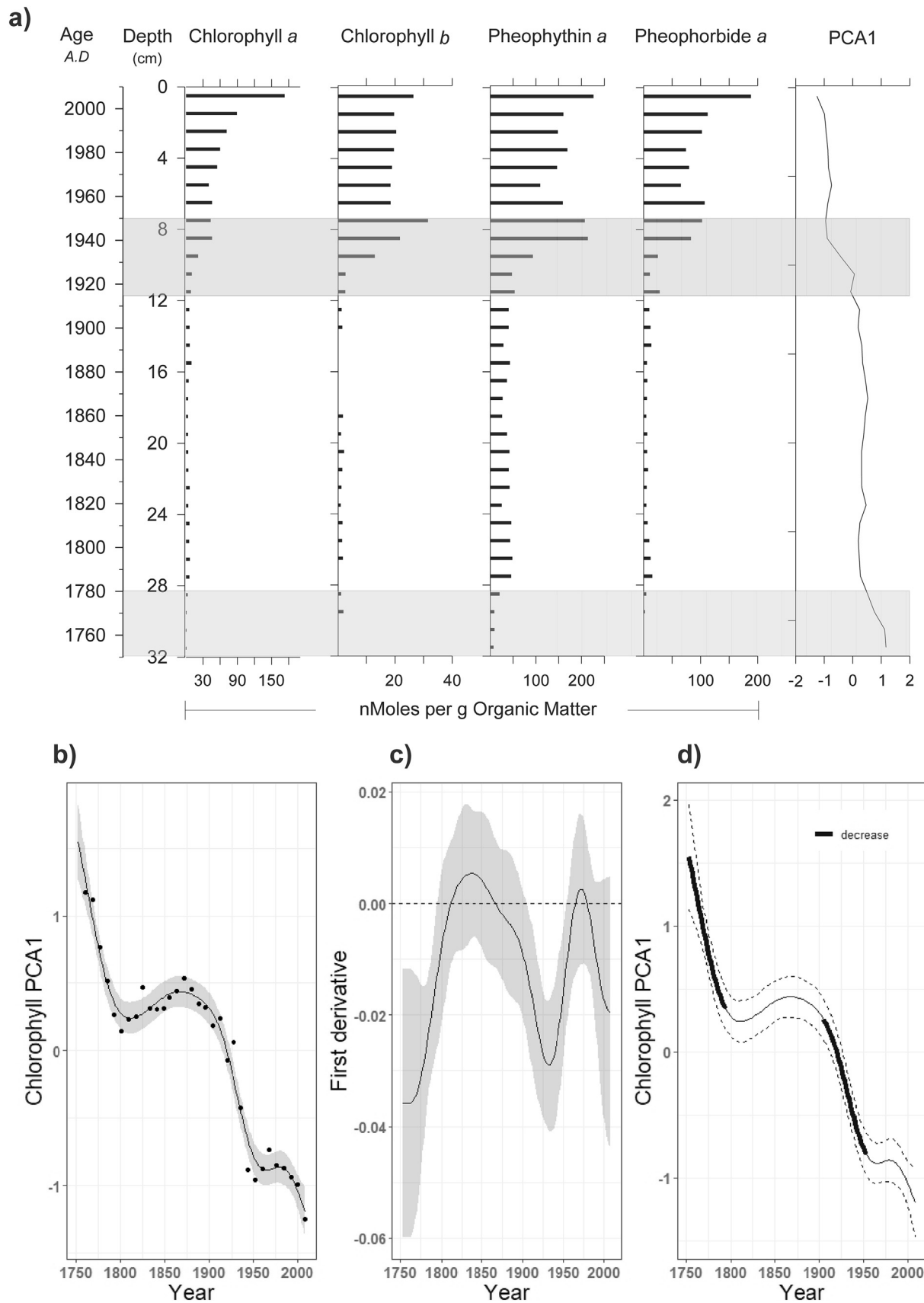
Fig. 5. a Chlorophyll and derivatives stratigraphy of Blanca Chica Lake and the scores of principal component analysis. The shaded area corresponds to the transition. **b** GAM-based trend fitted in the time series of scores of PCA. **c** Estimated first derivative of the GAM fitted trend and 95% simultaneous confidence interval. **d** Periods of transition, highlighting the decreasing trend. For further details, see Fig. 3.
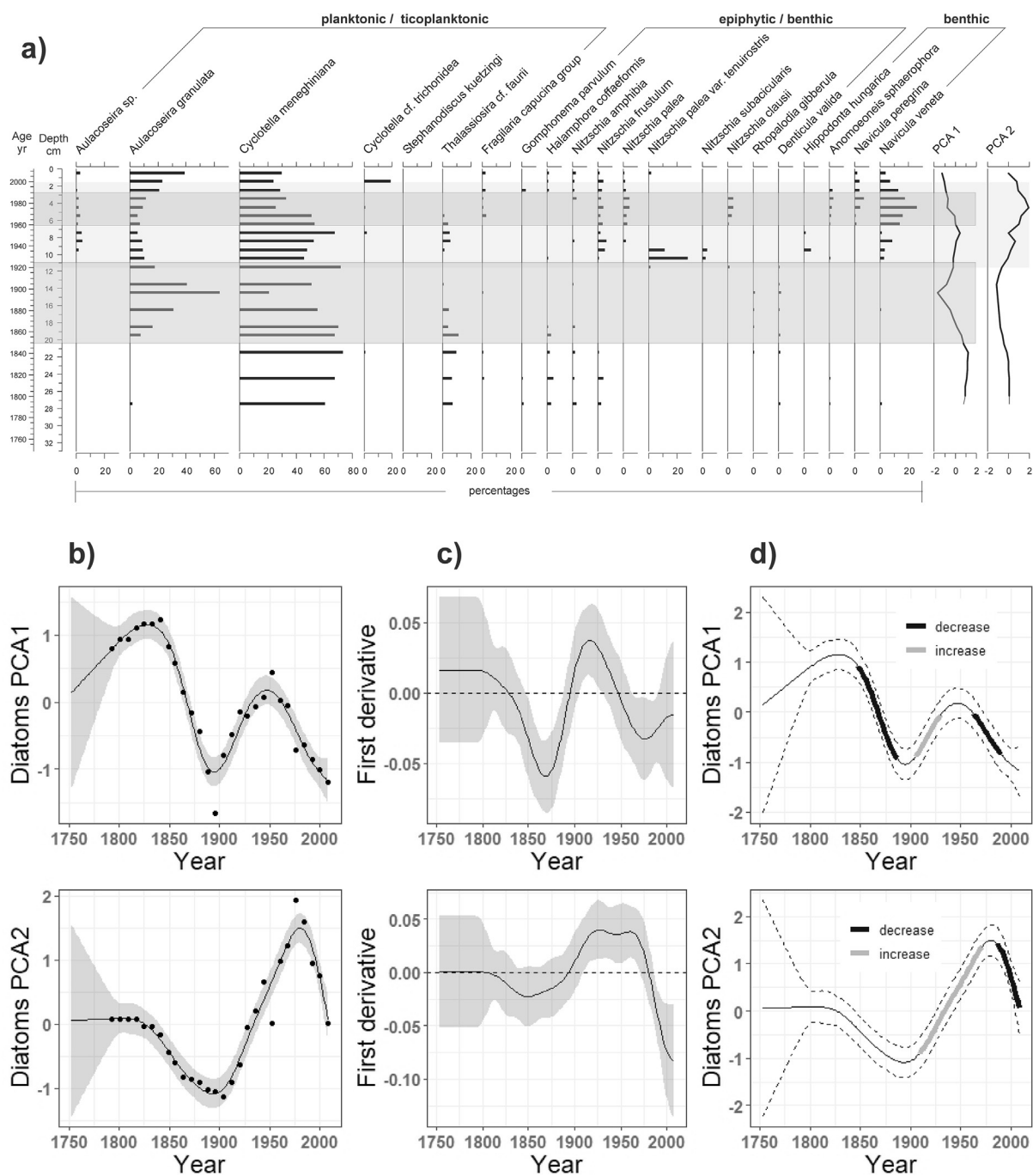
Fig. 6. a Stratigraphy of the most abundant (higher than 3%) diatoms taxa in Blanca Chica Lake and the scores of principal component analysis. The shaded area corresponds to the transition to the time series of PCA1 (dark grey) and PCA2 (light grey). **b** GAM-based trend and confidence intervals fitted in the time series of scores of PCA1 (b, upper panel) and PCA2 (b, lower panel). **c** Estimated first derivative of the GAM fitted trend and 95% simultaneous confidence interval. **d** Periods of transition. For further details, see Fig. 3.

increase of *A. granulata* (Fig. 6a,c,d).

Cladocera assemblage was represented by sub-fossil chitinous remains of planktonic, littoral and benthic species (Fig. 7a). Total sum of remains increased from 1750 to the top of the sedimentary record. The transition detected was characterized by a shift in species composition. The fist axis of the correspondence analysis (CA1) explained 80% of the variance. *Chydorus sphaericus* group and *Pleuroxus varidentatus* had the highest scores along CA1, whereas *Bosmina Leiderobosmina huaronensis* and *Coronatella monocantha* had the lowest (Fig. 6a). The fitted GAM on CA1 scores accounted for a large percent of the deviance in the time series (Table 1, Fig. 7b). A transition was detected between ca. 1860 to

1880 (Fig. 7b,c,d). The assemblage composition shifted from being composed of littoral, *C. sphaericus* group and *P. varidentatus* and benthic *Leydigia louisi cf*, species to being dominated by the pelagic *B. huaronensis* after the transition (Fig. 7a). Moreover, a rising trend in the ratio Bosmina:Chydorids occurred and benthic species richness increased (*L. luoisi cf*, *Ovalona glabra*, *C. monocantha*) after the transition.

Rotifera remains were represented by resting eggs, being *Filinia* the species that dominated the assemblage (Fig. 8a). CA explained 67% of the variance of the time series (axes 1 and 2). CA1 captured the dynamic of *Filinia* sp. which contributed the highest score while the other rotifer species contributed with negative values (*Brachionus* sp. and
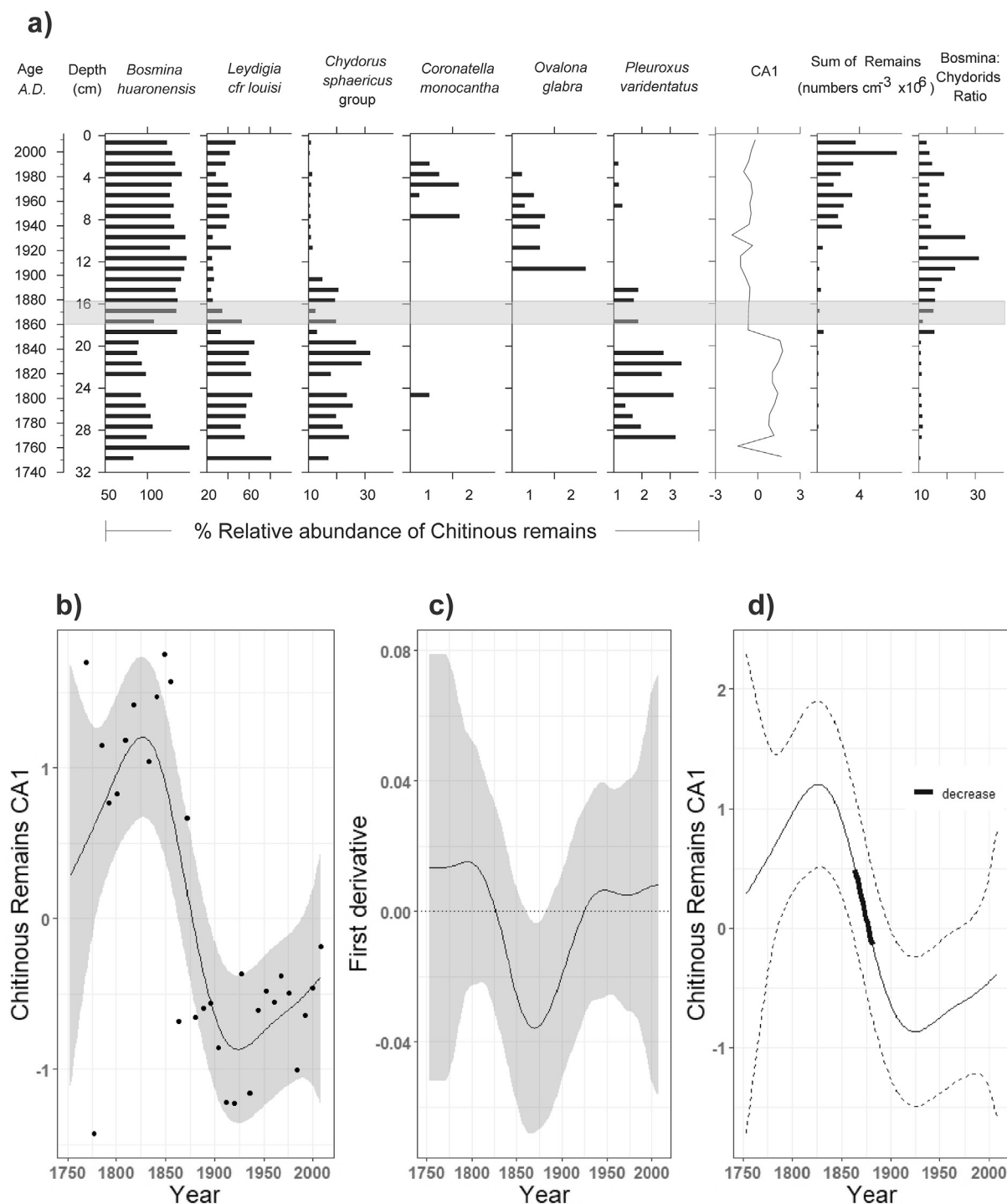
Fig. 7. a Cladocera stratigraphy (chitinous remains) of Blanca Chica Lake and the scores of Correspondence Analysis (CA). The shaded area corresponds to the transition. **b** GAM-based trend fitted in the time series of scores of CA. **c** Estimated first derivative of the GAM fitted trend and 95% simultaneous confidence interval. **d** Periods of transition, highlighting the decreasing trend. For further details, see Fig. 3.

Hexarthra sp.). CA2 represented mainly the profile of *Keratella* sp., which had the highest score along this axis. GAM-based trend in CA1-scores explained a large percent of the deviance (Table 1, Fig. 8b). The detected transition (ca. 1920–1990) (Fig. 8b,c) involved a shift in the species composition from *Filinia* sp. (up to 75% contribution) to *Brachionus* sp. dominance. After the transition rotifer richness increased. GAM results in CA2 were not significant (smooth term: p > 0.05, deviance explained = 3.7%).

Further, we found evidence of a response in other trophic levels, like secondary and tertiary consumers (gasteropods, fish). Plant seeds and

macrophyte-associated gastropod disappeared after ca. 1910; while fish scales increased towards the top of the core after ca. 1980 (Supplemental Information, Fig. S3).

3.3. Indicators of ecosystem-scale processes

We found multiple evidences of non-linear dynamics, bimodality, community structure changes at different trophic levels (nutrient, producers, consumers) and/or increase variance prior to the shift for the transitional periods identified: ca. 1860–1900 and 1915/20–1990.
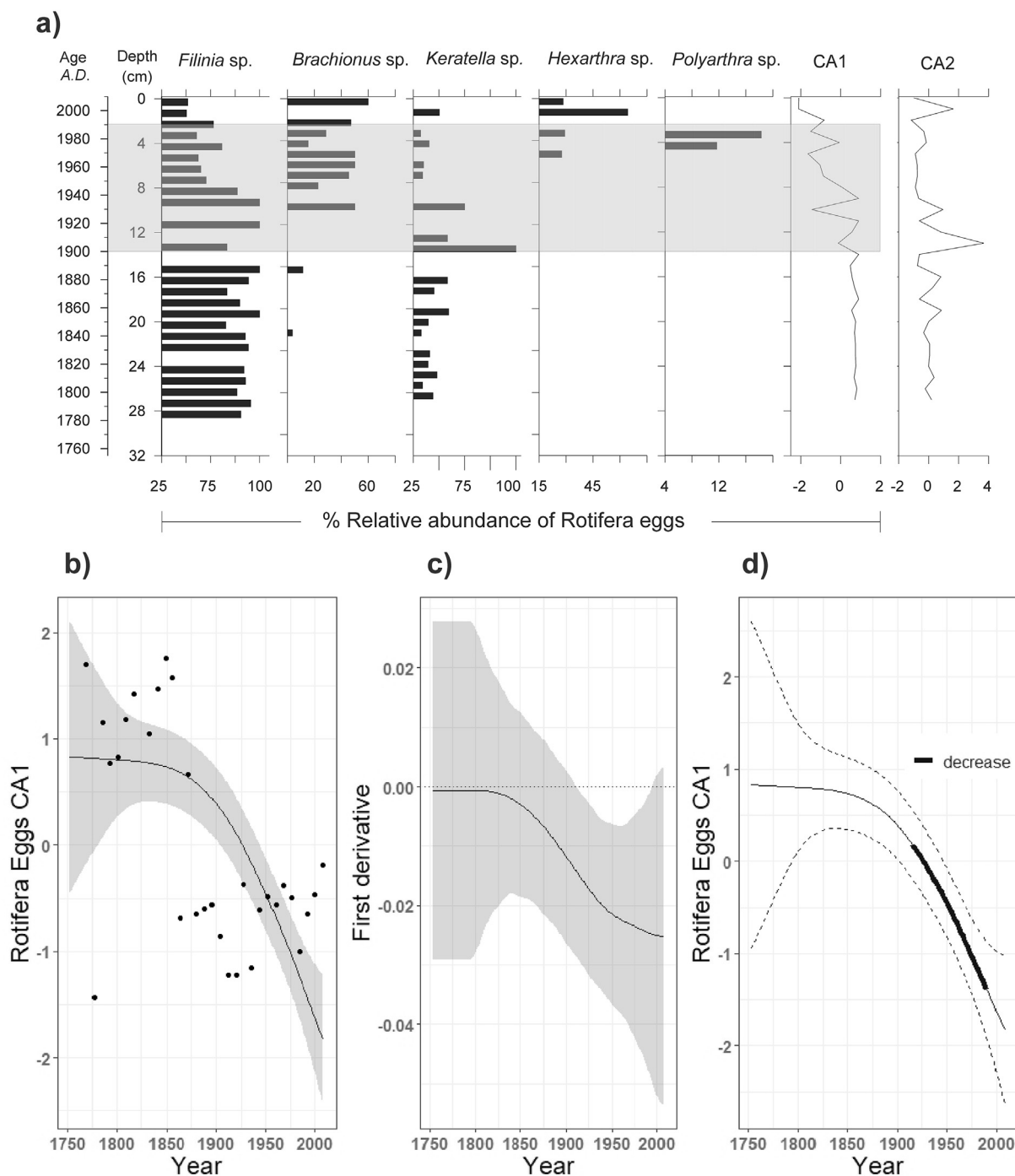
a)

b) **c)** **d)**

Fig. 8. a Rotifera stratigraphy (resting eggs) of Blanca Chica Lake and the scores of Correspondence Analysis (CA). The shaded area corresponds to the transition detected by fitting GAM to ordination scores. **b** GAM-based trend fitted in the time series of scores of CA. **c** Estimated first derivative of the fitted trend and 95% simultaneous confidence interval in the GAM trends fitted. **d** Periods of transition, highlighting the decreasing trend. For further details, see Fig. 3.

Multiple-level responses occurred at the first lake transition (ca. 1860–1900). The change in diatom (dominance of *A. granulata*) and cladoceran composition (from benthic-littoral to pelagic species dominance) and reduction in vegetation and in the gastropod *Biomphalaria*, point out a change in lake compartment contribution (from littoral to pelagic dominance). The transition corresponds to non-linear or critical dynamics as cladocerans and diatoms showed a bimodal distribution for post- and transitional periods (Fig. 9). For these indicators, no EWI (standard deviation or autocorrelation) were detected (Supplemental Information Table S1); but, a change in the scores of multivariate analysis comparing post- and transitional periods was identified

(Table 2).

The second lake transition (ca. 1915/20–1990) is supported by multiple-level responses of nutrients, primary producers (chlorophylls, carotenoids and diatoms) and consumers (rotifers and fish). During this transitional period, nutrient level raised, cyanobacteria and turbid diatom species dominated the primary producer assemblage, rotifer species richness and fish scales increased. The probability density functions of chlorophylls and carotenoids for post- and transitional periods showed a bimodal pattern (Fig. 9). Also, EWI were detected over multiple trophic levels and along a span of rolling windows (10, 20, 30, 40, 50 and 60). Significant positive trends (i.e., increase) for
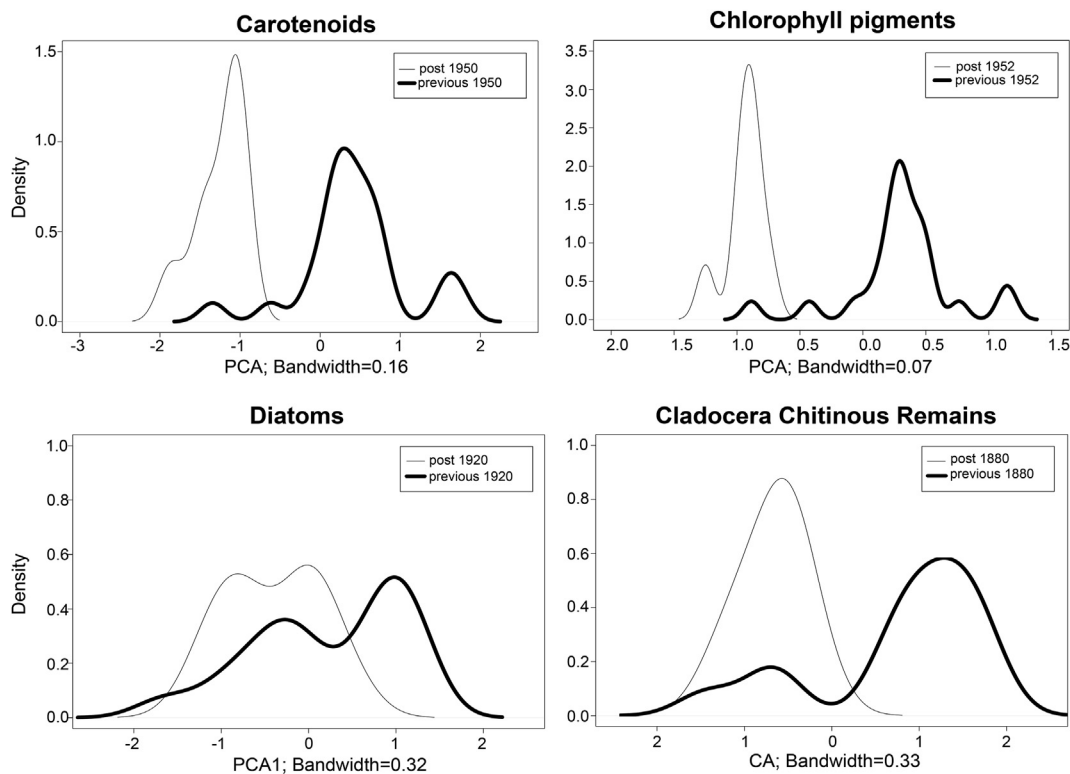
Fig. 9. Probability density functions (Gaussian kernel density estimation) in the scores of ordination analyses for the transition and post-transition periods, indicating bimodality for cladoceran, diatoms, carotenoid and chlorophyll pigments.

Table 2

Results from t-tests analyses in the scores of the ordination analyses and in the standard deviation (SD) comparing post- and transitional periods. SD was calculated as a leading indicator of a regime shift using a rolling window of 20 percent of the data length. The statistic t, the associated degrees of freedom and the p-values are presented (ns: non-significant, *: < 0.05, **: < 0.01, ***: < 0.001). nd: the analysis cannot be determined as no SD data was available for the period. Acronyms: Cladocera CR: cladocerans chitinous remains.

Indicators	Transition	PCA/CA	Scores			Standard	Deviation	
			Mean Post Transition	Mean Transition	t, (df), p-values	Mean Post Transition	Mean Transition	t, (df), p-values
Chlorophylls	1915–1952	−0.93		−0.265	3.36, (7.25), *	0.010	0.010	0.009, (10.6), ns
	1760–1780	0.768		0.288	2.67, (4.8), *	nd	nd	nd
Carotenoids	1920–1950	−1.219		−0.463	−2.6, (8.43),*	0.05	0.031	−4.12, (6.9),* *
	1760–1780	0.288		1.203	3.2, (4.5), *	nd	nd	nd
Diatoms PCA1	1850–1930	−0.220		−0.441	−0.84, (13.7), ns	0.156	0.103	−1.64, (15.2), ns
Cladocera CR	1860–1880	−0.855		0.740	3.88,(7.4), **	0.315	0.4	0.94, (13.5), ns

standard deviation occurred in geochemical indicators, carotenoid pigments, diatoms (PCA2) and rotifers (CA1) (Fig. 10; Supplemental Information, Table S1). The period of increased variance coincided in most of the cases with the transitional period detected by GAM-based trends. No trend in autocorrelation was detected for any indicators. Finally, ordination scores (carotenoids) and standard deviation differed between post- and transitional periods (Table 2). Data length did not allow the comparison for the rest of the indicators.

4. Discussion

The ^{210}Pb-derived age model allowed the development a chronology over the past ca. 250 years in Blanca Chica Lake. During this timeframe, three transitions were detected ca.1760–1800, 1860–1900 and 1915–1990. Only the latter two transitions involved drastic changes in the lake, implying the reconfiguration of the ecosystem. We found shifts in state variables belonging to different trophic levels and lake communities. In addition, the dynamic of these abrupt changes were non-linear and multimodality and increased variance (only in the

last transition 1915–1990) were detected in the time series of the different biological and geochemical proxies (Table 3). All these features, combined with the low frequency of these events allow to consider them consistent with regime shifts, possibly of different nature and dynamics.

4.1. Indicators of regime shifts

Regime shifts are an ecosystem-scale phenomena (Spears et al., 2017). The reorganization that produce a new and stable ecosystem must be detected across multiple physical and biological components (Lees et al., 2006). Our results show that the transition that occurred ca.1860–1900 involved major changes in the structure of the ecosystem and at least two trophic levels were implicated: primary producers and primary/secondary consumers (cladocerans and gastropod), belonging to the pelagic, littoral and benthic compartments of the lake (Table 3). The assemblage of sub-fossil Cladocera shifted from the dominance of littoral-benthic to pelagic (*Bosmina huaronensis*) species. In addition, the macrophyte associated gastropods and plant seeds disappeared from
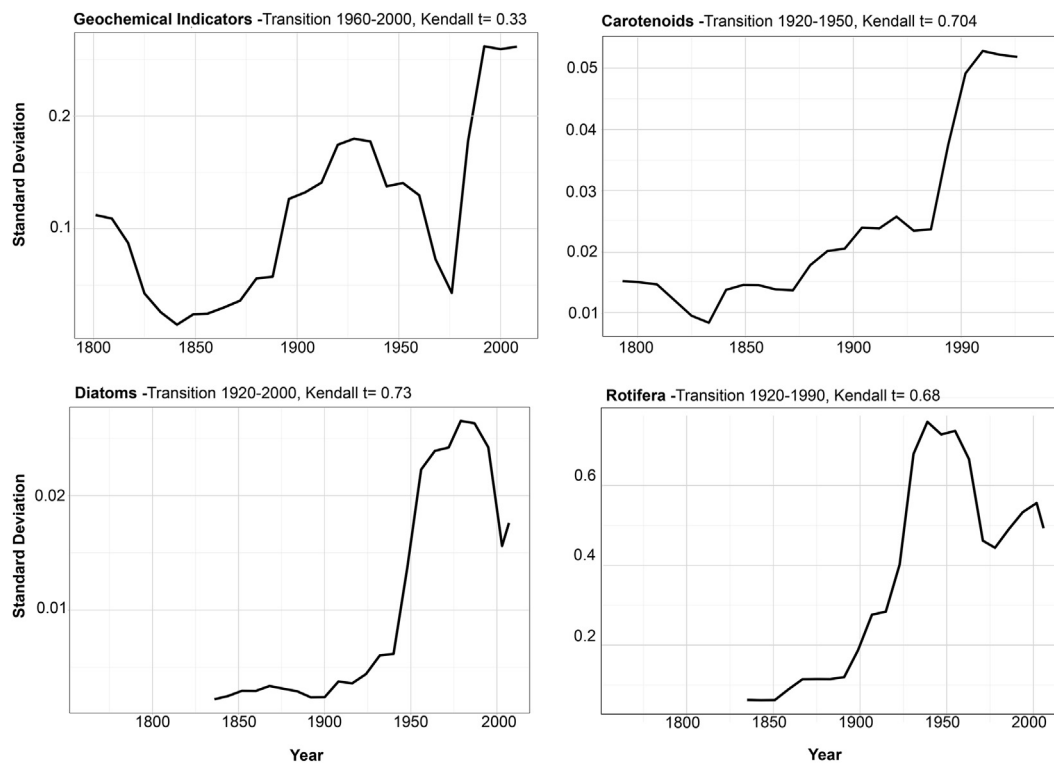
Fig. 10. Standard deviation estimated in the scores of the first and second axis (if selected) of the PCA or CA as an early warning indicator of a regime shift. Results for a rolling window of 20% are presented. Trends were calculated relying on Mann-Kendall rank correlation test (Kendall τ).

Table 3
Summary of major changes and regime shifts detected in Blanca Chica Lake during the last 250 years based on multiple-trophic level responses from biological and geochemical proxies and ecological indicators of regime shifts. EWI: Early Warning Indicators (SD: standard deviation or AR: autocorrelation (not detected)). ↑: increasing trend, -: trend not detected.

Type of Regime Shift	Changes in the Lake	Indicator	Timing of Transition	Multimodality	Reversion	EWI
Threshold State Response	• Increase water level. • Shift in the diatom assemblage from *C. meneghiniana* + diatoms indicating clear condition to *A. granulata*, forward to *C. meneghiniana*.	Diatoms	1850–1920	✓	✓	–
(1860–1900)	• Shift from littoral benthic cladoceran species to the dominance of pelagic *Bosmina*. • Macrophytes associated gastropod disappeared.	Cladocera	1880	✓	no	–
Critical Transition	• Shift to eutrophication phase ca.1950–1990. • Increase in primary productivity. • Cyanobacteria dominance. • Dominance of diatoms of turbid conditions. • Increase in zooplankton richness.	Geochemical	1960–2000	✓	no	↑SD
		Chlorophyll pigments	1915–1952	✓	no	–
		Carotenoid pigments	1920–1950	✓	no	↑SD
(1915/20–1990)	• Change in lake metabolism.	Diatoms	1915–2008	✓	no	↑SD
		Rotifers	1910–1990	✓	no	↑SD

the system after 1860, concomitant with a change in the diatom assemblage. During the transition, diatoms of clear conditions like pelagic *Thalassiosira* (Padisák et al., 2009) and the littoral epiphytic/benthic diatoms (e.g., *Gomphonema*) diminished their contribution and finally disappeared while *A. granulata* (associated to turbid and turbulent conditions (Padisák et al., 2009)) increased its contribution (Fig. 6). By the end of the transition, *C. meneghiniana* dominated the assemblage of diatoms, whereas littoral and benthic species that had disappeared during the transition reappeared in the lake, indicating a reversion to a clear water condition. Together, the shift in the diatom assemblage, the dominance of *Bosmina* and the high ratio of *Bosmina*: chydorids after ca. 1880 suggest an increase in the lake water level. Several studies have pointed out a change towards pelagic cladoceran species with higher water levels (Sarmaja-Korjonen and Alhonen, 1999; Çakıroğlu et al., 2016; Levi et al., 2016). Therefore, these changes suggest a major physical reorganization of the ecosystem structure towards a lake

characterized by a pelagic dominance and a higher water column. The high variance explained by the GAM fitted to the cladoceran and diatom scores and the bimodal distribution of the scores (Fig. 9, Table 3) confirmed the non-linear nature of the shift. Multimodal distribution can account for critical transitions (multiple stable states), but also for non-linear ones (threshold state response) (Scheffer and Carpenter, 2003). The lack of EWI detection in chitinous Cladocera remains or diatoms (Table 3) is not conclusive as supportive evidence of any type of regime shifts. EWI tend to emerge when the system is approaching smoothly a bifurcation point (critical transitions) or a non-catastrophic threshold (Scheffer et al., 2009). False negatives represent situation when sudden transitions occur, but no early warning signal could be detected (Scheffer et al., 2009). Possible causes include changes over time of the external perturbations, the statistical difficulty of picking up EWI because long time series are required or variability is not captured (Carpenter and Brock, 2006; Scheffer et al., 2009) or

simply because abrupt perturbations lead to regime shifts without any forewarning leading indicator (Hastings and Wysham, 2010). In our study, it is difficult to ascribe the absence of leading indicators to a specific type of regime shift (critical transitions or threshold state response). However, the shift and reversion in the diatom assemblage (from *C. meneghiniana* plus benthic epiphytic diatoms to *A. granulata* and back forward to *C. meneghiniana*) could support a threshold state response. Reversibility of regime shifts can be considered as an evidence for linear or non-linear regime shifts (threshold state response) (Andersen et al., 2009) as the threshold is set by external conditions (Boettiger et al., 2013). Interestingly, cladocera assemblage did not show a reversion, meaning that each state variable was responding to different thresholds (water transparency for diatoms and water level for cladocerans). Therefore, the abrupt change that occurred in the system from a littoral to a pelagic dominance involving the decline of vegetation and associated species, the dominance of higher water level indicators, the change in diatom assemblage and its reversion, plus the multimodality and non-linear dynamics detected suggest that this change is consistent with a non-linear regime shift, probably a "threshold state response" (Table 3).

The ca. 1915–1990 transition, involved multiple-level responses of different biological and geological variables (Table 3). The lake switched towards a system of higher nutrient levels, algal production and fish contribution, concomitant with an abrupt change in community composition of primary producers and zooplankton. Primary producers shifted towards the dominance of species with high nutrient demands adapted to turbid environments like cyanobacteria and diatoms of mixed and turbid waters (*A. granulata*). Zooplankton, represented by Rotifera eggs, increased species richness. In addition, C:N ratio shifted to values ~11, suggesting a change in lake metabolism towards an autotrophic condition. Thus, four trophic levels belonging to different components of the food web (pelagic, benthic and littoral) were implicated in this transition (nutrients, primary producers, primary and secondary/tertiary consumers), indicating a change in lake structure and function. Ordination scores from geochemical variables, chlorophyll, carotenoids, diatoms and Rotifera showed a non-linear dynamics, revealed by the fitted GAMs and multimodality. In addition, variance increase occurred during the transitional period, i. e. preceded the ecosystem shift, in ordination scores of geochemical variables, carotenoids, diatoms (PCA axis 2) and rotifera eggs. The multiple responses of different indicators, multimodality in the time series and increased variance are consistent with a critical transition (Table 3). Also, the shift in community composition, as well as in lake metabolism, are a clear sign of eutrophication. Cyanobacteria increment has been identified as an indicator of eutrophication in paleoecological studies (Battarbee et al., 2011; Taranu et al., 2015). In our study, cyanobacteria carotenoids increased disproportionally, doubling its contribution and incrementing up to 8–10 times its concentration after the transition. Eutrophication has been recognized as a cause for the occurrence of critical transitions (Vermaire et al., 2017; Taranu et al., 2018). In this study, the detection of multiple ecological indicators at different trophic levels and the signs of eutrophication support the occurrence of a regime shift in Blanca Chica; particularly, a critical transition shifting to an eutrophic stable state ca. 1950–1990.

4.2. Drivers of transitions

The sedimentary record of Blanca Chica spans two climatologically distinct periods: the end of the Little Ice Age (LIA) (Piovano et al., 2009) and the Current Warm Period (Bird et al., 2011). Paleohydrological and paleolimnological reconstructions based on Pampean lacustrine sedimentary sequences indicate that arid conditions prevailed since the end of the LIA (CE 1750) until CE 1870/1880 and that lakes were ephemeral systems with low water depth (Piovano et al., 2009; Córdoba et al., 2014). Accordingly, all biological indicators were consistently recorded in Blanca Chica sedimentary archive since ca. 1760–1780, a time at

which the lake became a permanent lacustrine system. Before AD 1760 diatoms or cladoceran remains were absent or only few remains were found at some levels, indicating the existence of an ephemeral aquatic system for short time intervals. From ca. 1870/1880 to 1977 a progressive increase in effective moisture occurred along the region, reflected by intermediate lake levels (Córdoba et al., 2014). Instrumental data for Blanca Chica Lake show a rise in precipitation since earliest 1900 (time for which first records are available) (Supplemental Information, Fig. S4). This suggests that the first abrupt change in cladoceran, littoral vegetation and diatoms (ca. 1870/80), indicative of high water levels, was triggered by an external climatic factor: the precipitation increase.

We detected a drastic change in the lake water quality, leading to a shift towards an eutrophic state around 1950. The exact cause of this inferred critical transition is difficult to pinpoint without historical data on the lake catchment. However, the abrupt change in land use that occurred in the Pampa during the twenty century can be proposed as the main driver. In the Southern Pampas (where the lake is located), the landscape was a natural grassland with little human intervention until 1880s; by 1930, 30% of the area was dedicated to annual crops, implying a drastic change in land use and a major ecological disruption in the landscape (Viglizzo et al., 2001). The carotenoid record transitioned between 1920 and 1950, shifting to cyanobacteria dominance, coinciding with the abrupt change in land use. Meta-analyses based on paleolimnological records have indicated that during the Anthropocene, cyanobacteria contribution to lake production was low or minimal before 1800 (Battarbee et al., 2011; Taranu et al., 2015) and that the expansion of cyanobacteria has been non-linear, disproportionate relative to other algae groups and induced mainly by fertilization (Taranu et al., 2015). We cannot dismiss the role of other potential factors, like temperature. Nonetheless, the synchronicity of the timing for the shift with the introduction of intensive agricultural activities in the region suggests that nutrient input derived from human activities was the main driver of this ecological shift.

4.3. Study implications

This multiple-indicators paleolimnological study revealed that resilience indicators can be detected at different trophic levels, implying that regime shifts can be upscale to the whole aquatic ecosystem. Our study stresses the relevance of combining different statistical indicators applied to multiple proxies from different trophic levels, to detect different types of regime shifts and understand their dynamics. Although regime shifts are ecosystem phenomena, many studies have based their findings on the response of one state variable (Capon et al., 2015; Spears et al., 2017), which might lead to misinterpretations. The inclusion of different indicators sums evidence that provides a better diagnosis of lake dynamics and processes and the type of regime shift that occurred.

In our study, we combined different statistical tools to test transitions, absence of linearity, multimodality and the trend of resilience indicators. The combination of GAMs analysis applied to paleoecological data (Simpson, 2018) and EWI (Dakos et al., 2012) allowed to test the occurrence of a transitional period, its non-linear dynamics and to explore anomalous variance. The utility and scope of EWI have been debated, rendering different outcomes (Frossard et al., 2015; Litzow and Hunsicker, 2016; Bruel et al., 2018; Taranu et al., 2018). For this reason, we decided to explore standard deviation (SD) and autocorrelation (AR) over a span of rolling window sizes and considered the occurrence of an EWI trend if was detected over the entire range of rolling window sizes analyzed. Managers should consider this criterion as well as search EWI at different trophic levels. Frossard et al. (2015), have tested the robustness of EWI detection to temporal aggregation, concluding that SD is robust to data aggregation up to 10 and 5 years under a critical slowing down and flickering scenario, respectively; but, autocorrelation trends could be detected if time resolution was lower

than 2 years (only for a critical slowing down). In our study, increase SD was detected under a time resolution of 8 years, thus we suggest that critical slowing down might be the process implicated in this critical transition (ca. 1950–70). Sediment compaction and mixing erode AR signal (Taranu et al., 2018), but core compression did not occur in this study. In line with Frossard et al. (2015), we found that the time aggregation of 8 years precluded the detection of AR. Recently, inconsistence in the detection of AR trends lead to propose new techniques (time-varying autoregressions) to detect regime shifts on lake sediment archives (Taranu et al., 2018).

We could identified a transitional period for each regime shifts, but we have to conclude that indicators showed different responses (reversion or not) and timing for the transition (Table 3). Even when a driver is the same, communities or species can display different responses, transitional timing, resilience and thresholds. For example, we observed that a transition occurred around 1880 both in diatoms and cladocerans, but the former showed a reversion whereas cladocerans did not. The timing for the transition must be associated with the resilience of each indicator and the threshold; thus, abrupt changes in the assemblages occurred at different moments (e.g., carotenoid pigments 1920–1950 versus rotifers 1920–1990, Table 3). Therefore, manager should use the most sensitive indicators to track the first responses of the lake to a specific driver, but then they have to search for ecological indicators of regime shifts at multiple-trophic levels to corroborate the interpretation of the phenomena observed.

5. Conclusions

Shallow lakes have been quoted as archetype ecosystems displaying critical transitions; nonetheless, we have tested and found evidence consistent with two different regime shifts: threshold-state and critical transitions. We showed how resilient indicators and thus critical transitions, scale up the whole lake food web: from nutrients to higher trophic levels. The detection of regime shifts is a complex and defiant task, difficult to prove using observational data (Petraitis, 2013). Thus, several state variables belonging to multiple levels are necessary to search for indicators of regime shifts as responses can vary depending on functional levels (community, populations, species), the type of driver, the parameters that affect each threshold, the resilience of each indicator. If not, misinterpretation of lake dynamics could occur. We found that GAMs applied to paleoecological studies is a useful tool to detect transitions (Simpson, 2018) and should be complemented with other auxiliary techniques to reveal the nature of the transitions. Nonetheless, new statistical tools are necessary to develop for searching indicators of regime shifts (Taranu, et al., 2018). Despite the sediment record biases, we show that multiple-indicators paleolimnological studies can became fruitful case studies to examine regime shift dynamics, allowing to analyze ecological indicators over several state variables along an extended time period.

CRediT authorship contribution statement

María de los Ángeles González Sagrario: Conceptualization, Methodology, Investigation, Resources, Writing - original draft, Writing - review & editing, Visualization, Funding acquisition, Project administration. **Simona Musazzi:** Methodology, Investigation, Resources, Writing - review & editing, Visualization. **Francisco Elizalde Córdoba:** Methodology, Writing - review & editing, Visualization. **Manuela Mendiolar:** Software. **Andrea Lami:** Conceptualization, Methodology, Investigation, Resources, Writing - review & editing, Visualization, Funding acquisition, Project administration.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106536.

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