

Reframing Lake Geneva ecological trajectory in a context of multiple but asynchronous drivers

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Abstract

There are no doubts long-term observatories provide unique insight on ecosystems trajectories. Can we use earliest data to set restoration goals? We take the example of Lake Geneva, for which descriptions of the ecosystem are available for as soon as the late 19th and early 20th century. Forel writes about how the luxuriant growth of plant communities provided important habitat for aquatic animals, as well as trapping nutrients and affecting water currents. It can be hard to believe Forel is referring to the same lake as present-day Lake Geneva; however, without continuous monitoring, this qualitative description can hardly be compared to recent observations. We resorted to paleolimnology to quantify the changes in plankton communities, as a proxy of general ecological changes, over the past 1,500 years. Our results show that from 563 AD (beginning of the record) to the 20th century, the cladoceran assemblage remained stable, despite important amplitude of climate variability (3°C). Trajectory of Lake Geneva shifted for the first time in 1946. Online dynamic linear models revealed the following transition, in 1958-1961, transition was critical, i.e., the ecosystem changed state. Littoral associated species were totally lost, and the assemblage is now dominated by pelagic species. The shift took place around the beginning of the long-term monitoring program, when local perturbations (eutrophication) were escalating. Our result raises the vexing observation that the historical dataset, one of the longest records in the world, may not provide a baseline for Lake Geneva's condition.

Introduction

There is no specific data crisis for Lake Geneva (CH, FR). It is one of the lakes in the world with the largest amount of data, going back to the end of the 19th century (Forel 1892), and with a regular monitoring since 1957 (SOERE OLA-IS). In the early stages of the monitoring, managers recorded the increase of total phosphorus (TP) going from 10 $\mu\text{g P.l}^{-1}$ (i.e., close to background levels, inferred at 6-8 $\mu\text{g.l}^{-1}$ from diatoms, Berthon et al. 2013) to 50 $\mu\text{g P.l}^{-1}$ in the early 1960s, and up to 90 $\mu\text{g P.l}^{-1}$ in the late 1970s.

The long-term monitoring is expected to have captured the major and dominant modifications in Lake Geneva ecology because the record began at the heel of the “hockey stick curve” of human pressures on Lake Geneva (Alric et al. 2013; Jenny et al. 2014). Both old records and recent findings yet cast doubts on this assumption. Detailed observations by the pioneer limnologist FA Forel at the very beginning of the 20th century reported thriving macrophytic, charophytic belts around the lake in 1904, forming “true underwater forests, as picturesque, mysterious and attractive as the most beautiful forests of your mountains” (translation by Vincent and Bertola 2014), a feature which let no traces in the 1975, 1997, and 2009 macrophyte surveys (Perfetta 2011).

Initial evaluations, using correlation between TP and phytoplankton biomass, established that levels around 20 $\mu\text{g P.l}^{-1}$ would allow restoration of Lake Geneva (CIPEL 2007). Eutrophication was tackled by the effort of Swiss (first) and French (later) politics from the late 1970s. The 20 $\mu\text{g P.l}^{-1}$ were reached, a decade ago, without any quantifiable decline in algal biomass or production. In the meanwhile, evidence that other anthropogenic drivers were at play in promoting algal growth had been produced (Tadonl  k   et al. 2009; Alric et al. 2013). Thereafter, the restoration goal was reviewed to target 10-15 $\mu\text{g P.l}^{-1}$ (CIPEL 2010), to account for potential additive or synergistic effect of nutrient enrichment with other human pressures. This concentration range actually corresponds to the earliest phosphorous concentrations ever measured in the lake, at the beginning of the monitoring survey in the late 1950s (Berthon et al. 2013). Although phosphorus levels are asymptotically reaching this second target, both primary production and algal biomass are still comparable to those of maximum eutrophication (CIPEL 2018, pp. 106–112).

Explaining the decoupling between initial driver and symptom of eutrophication requires to remember that ecosystems are the complex output of both space and time constraints (Wolkovich et al. 2014). Relative stability is guaranteed by feedback mechanisms (endogenous processes), conferring them resilience towards exogenous perturbation (Hodgson et al. 2015). When exogenous

drivers exceed endogenous feedbacks, systems can shift to an alternative state (Scheffer and Carpenter 2003). The presence of multiple drivers is rather the norm, but the increase of anthropogenic pressure since the 19th century is pushing many ecosystems close to their limits of resistance, to an alternative state (Rocha et al. 2015). The possibility for critical transitions even in large lakes is now being reconsidered under the hypothesis that they may occur at even lower nutrient thresholds in large and deep lakes than in shallow lakes (Hilt et al. 2010; Hilt 2015; Bruel et al. 2018). Regime shifts come along with major reorganization of ecological processes, creating a whole new set of mechanisms ruling the new ecological regime (Carpenter 2005). Such rearrangements then affect how and how much the system respond to the initial driver (accumulative carryover), but also to external drivers other than the one that created the shift (interactive carryover, Ryo et al. 2019). An ecosystem that shifted can be vulnerable to further shifts through dominos effect or hidden feedback mechanisms (Rocha et al. 2018).

If Lake Geneva actually shifted early to an alternative state, not only the lake we currently monitor would be different in biological composition to the one that fascinated Forel, but it would also differ in the way its biology responds to other drivers, such as climate variability. So, was Forel's Lake Geneva the same lake that we have been monitoring so far? Or in contrast, had the lake already significantly changed in ecological state before the monitoring started? Did Lake Geneva actually experience a regime shift already before being under surveillance? The questions of patterns and scales are crucial in ecology (Levin 1992); our primary objective is to reframe the long-term monitoring data in a longer perspective. Our second objective is to formulate hypotheses on implications of an alternative new state when it comes to establish restoration goals.

We resort to paleoecology, to extend beyond the instrumental monitoring records and cover for the last 1.5 millennia. Paleoecology gives the possibility to cover long period of times on a single system, allowing to get rid of the variations linked to geographical area and different local settings. Biological proxies (diatoms and cladocerans) were retrieved and analyzed from an accurately dated composite sediment core. Sub-fossil diatom records were used to infer past concentrations in total phosphorous (Wunsam and Schmidt 1995), while sub-fossil cladocerans were regarded as the proxy for ecological responses, as they show high sensitivity to changes in the environment, recording bottom-up changes in resources, alterations in habitat structure, and diversity and top-down impacts of predation (Davidson et al. 2011). First, we used multivariate analyses to visualize the trajectory of Lake Geneva cladoceran assemblage. Paleorecords can be characterized by differences in compaction and mixing, that can impact detection of changepoint by traditional methods (Taranu et al. 2018). As a result, we turned to online dynamic linear models to assess whether any transition

was critical (Taranu et al. 2018). We used General Additive Models to identify the contribution of local versus climate drivers (Wood 2016). We resort to paleoecology, to extend beyond the instrumental monitoring records and cover for the last 1.5 millennium. Paleoecology gives the possibility to cover long period of times on a single system, allowing to get rid of the variations linked to geographical area and different local settings. Biological proxies (diatoms and cladocerans) were retrieved and analyzed from an accurately dated composite sediment core. Sub-fossil diatom records were used to infer past concentrations in total phosphorous (Wunsam and Schmidt 1995), while sub-fossil cladocerans were regarded as the proxy for ecological responses, as they show high sensitivity to changes in the environment, recording bottom-up changes in resources, alterations in habitat structure, and diversity and top-down impacts of predation (Davidson et al. 2011). First, we used multivariate analyses to visualize the trajectory of Lake Geneva cladoceran assemblage. Paleorecords can be characterized by differences in compaction and mixing, that can impact detection of changepoint by traditional methods (Taranu et al. 2018). As a result, we turned to online dynamic linear models to assess whether any transition was critical (Taranu et al. 2018). We used General Additive Models to identify the contribution of local versus climate drivers (Wood 2016).

Materials and methods

Study site

Lake Geneva is the largest lake of Western Europe, with a maximum depth of 309 meters (Fig. 1_MAP). The human population in its watershed has increased threefold since the late 19th century, directly initiating the well documented eutrophication. Observed concentration in Lake Geneva has been below 20 $\mu\text{g P.l}^{-1}$ since the 2010s. Although Lake Geneva's hydrological function had been impacted since the first dam was built in the late 19th century at the lake outflow, it is the changes in TP that have triggered the onset of deep water hypoxia (Jenny et al. 2014) as well as quantitative and qualitative changes in planktonic (Anneville and Pelletier 2000; Alric et al. 2013; Berthon et al. 2014) and fish (Anneville et al. 2017) populations since the 1950s. At the same time, the regional atmospheric warming has reached +2°C over the 20th century, i.e., twice the global average, with a first warming phase starting in the 1930s and 1940s. Evidence suggests that the most recent atmospheric warming (since the 1980s), superimposed on fluctuations in TP, has altered the

physical, biogeochemical, and ecological structure of Lake Geneva (Alric et al. 2013; Perga et al. 2015; Anneville et al. 2017).

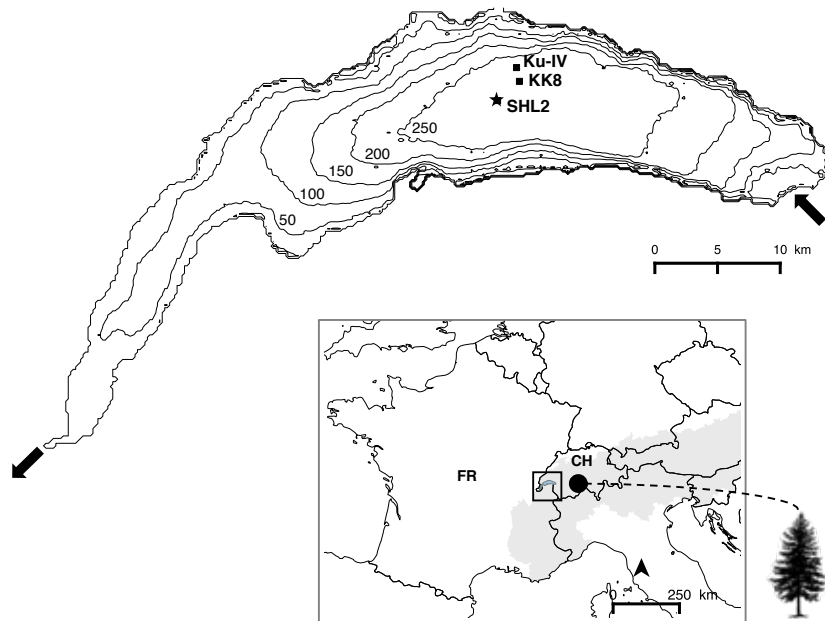


Figure 1_MAP. Lake Geneva lies at the border between France (FR) and Switzerland (CH) in the peri-alpine domain (Alps as grey surface on the bottom-right insert map). The bathymetry (in meters), sediment core localization (black squares), and monitoring point (star) are indicated. Arrows indicate the Rhône river inflow and outflow. The black circle on the bottom insert map shows the location of the four trees-ring sites used by Büntgen et al. (2006) to reconstruct SAT anomalies.

Sediment record and dating

A paleo-record dataset was built using two sediment cores collected in 2010 in the deepest basin of Lake Geneva. The two closely spaced sediment records were merged into one composite record LEM10-CC using the stratigraphic level of turbidite t2 as identified by Kremer et al. (2015). Dating relied on radionuclide measurements for the upper part of the core, previous ^{14}C measurements (Kremer et al. 2012), and new paleomagnetic secular variations measurements for the deeper section (Fig. 2_AGEModel). Details are given in Supplementary Materials S1.

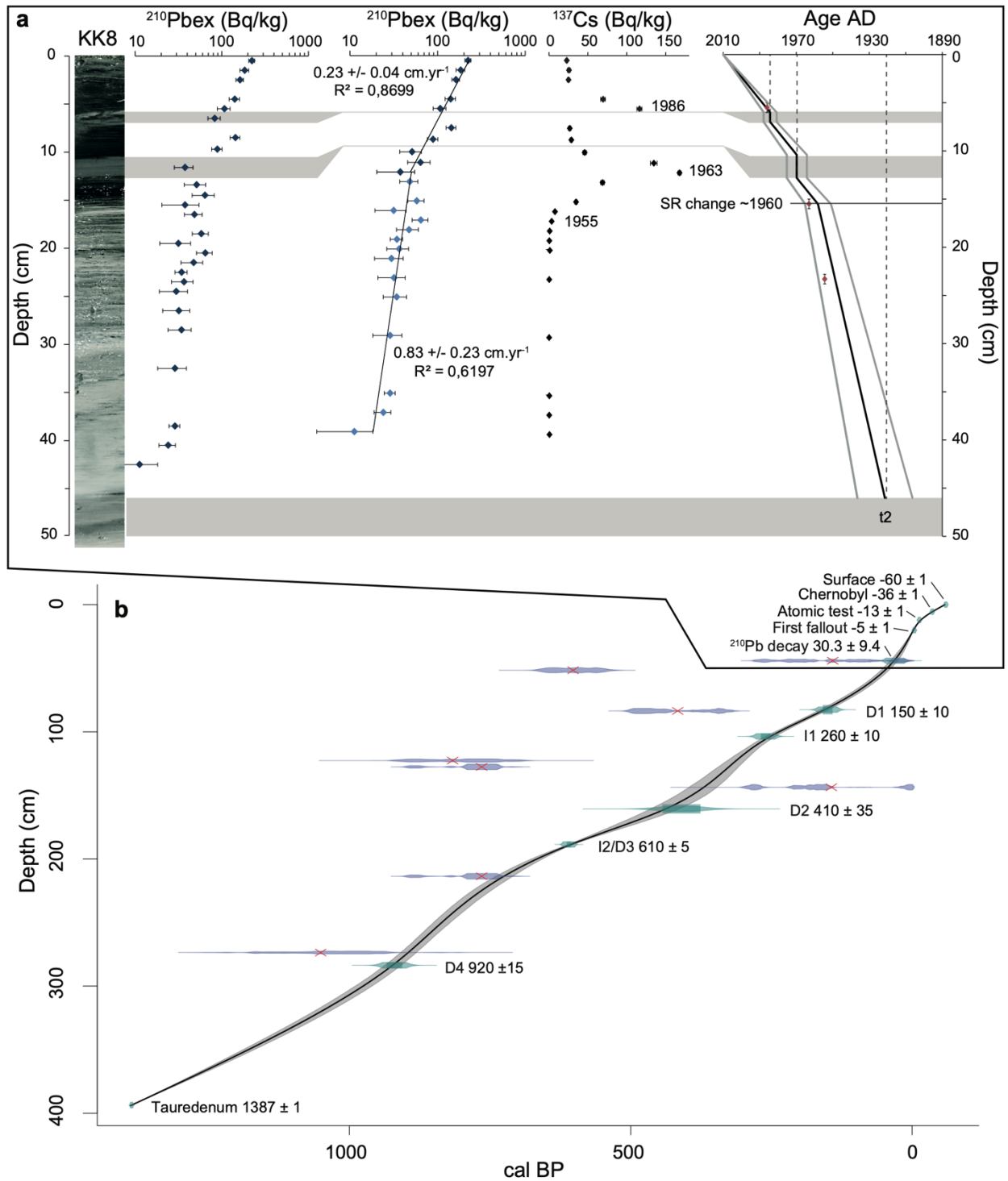


Figure 2_AGEMODEL. a) Chronology (with 1σ uncertainties) of the uppermost part of core KK8 based on activity of short-lived radionuclides ($^{210}\text{Pb}_{\text{ex}}$ and ^{137}Cs) and the application of a CFCS model to the event-free sedimentary profile of $^{210}\text{Pb}_{\text{ex}}$ (right panel). Uncertainties of ^{137}Cs activities are included as dots size. A main sedimentation rate (SR) change appears around 1960 AD. Grey bands correspond to event layers / turbidite intervals, interpreted as instantaneous deposits (relatively to the rest of the chronology). **b)** Age-depth model of composite record LEM10-CC built

with Clam R-code package (Blaauw 2010a) from 11 stratigraphic horizons. Event layers with thickness above 1 cm were interpreted as instantaneous events (Kremer et al. 2015) and removed before the age model computation. The envelope (grey area) represents the 2-sigma probability interval. Data not used to fit the age model (^{14}C dating) are marked with a red cross. See Supplementary Materials S1 for details.

Selection of climate data

Lack of restoration in Lake Geneva could be explained by recent climate change (Alric et al. 2013). We seek long-term air temperature records to establish whether similar warming episodes took place. A substantial climatic variability has been reported for the past 1,500 years in central Europe. A notably cold period was likely triggered by a volcanic eruption in the “Dark Age”, 536–660 AD (Larsen et al. 2008; Büntgen et al. 2016), followed by a prolonged period of relative climate stability (Medieval Quiet Period, ~725–1025 AD, Bradley et al. 2016). The ensuing Medieval Warm Period (MWP, ca. 900–1300 AD) showed average summer air temperatures (SAT) similar to those observed between the 1950s and 1970s (0°C SAT anomaly, Ljungqvist 2010). There then followed a new cold period, the LIA (ca. 1300–1850 AD; -3°C SAT anomaly, Ljungqvist 2010) before the recent warming (recent Climate Change rCC, 1850-present, Abram et al. 2016), mainly attributed to human impact.

Climate fluctuations over the past millennia are marked by significant regional offsets (Crowley and Lowery 2000; Mann and Jones 2003). It was thus essential to choose a relevant reconstruction of the climatic forcing, but also to understand the region it accounts for, as some climatic signals are more regional than others. We selected a local reconstruction of SAT anomalies from the Rhône valley, directly linked to Lake Geneva (Büntgen et al. 2006). The record goes back to 755 AD, corresponding to the last 1,250 years of our sediment record. When cladoceran sample covered several years, an average SAT anomaly was calculated for the same period and used to provide the climatic context for Lake Geneva.

Reconstruction of TP levels

In Lake Geneva, a long-term monitoring program, initiated in 1958, spans most of the eutrophication and the re-oligotrophication phases. Changes in total phosphorus concentrations were inferred from

diatom sub-fossil remains for the previous period when there was no monitoring data (Supplementary Materials S2). We used a composite TP record (DI-TP until 1957, monitoring data from 1958), thereafter referred to as I-TP. The confidence in I-TP is very high as the first changes in diatoms communities took place after the onset of the monitoring program.

Ecological dynamic

Cladocera were regarded as the main proxy for ecosystem state. Continuous sub-sampling of LEM10-CC was carried out, and one out of three samples were selected for cladoceran remains counting. Remains were analyzed according to Frey (1986): a minimum number of 400 cladoceran remains per sample (headshields, shells, post-abdomens, post-abdominal claws, mandibles and others) were counted and identified using the determination keys of Szeroczynska and Sarmaja-Korjonen (2007) and an Olympus BX41 microscope at 100-200 magnification. *Bosmina* sp. were determined to the species level (*B. longirostris*, *E. longispina*, and *E. coregoni*), as well as chydorids, whenever possible. Regarding the complexity of the taxa (Alric et al. 2016), *Daphnia* spp. were identified to the genus level.

Statistical analysis

The main dynamics of the cladoceran community over time were summarized using Principal Component Analysis (PCA, an indirect gradient analysis method, Jolliffe 1986), after Hellinger transformation of the percent data. We then turned to online dynamic linear models (DLMs, Pole et al. 1994) to evaluate whether any transition had the characteristics of critical transitions (method in Taranu et al. 2018). Shortly, DLMs are used to model and forecast in time-series analysis. The modelling part of DLMs strongly borrows from the regression model family, while the forecasting resembles the ARIMA models logic. While in a linear regression model, parameters are statics, in DLMs, parameters are treated as time-varying. DLMs will proceed to estimate state at time t , using all observations since the beginning of the time-series up to $t-1$, and tolerating lags (p in $AR(p)$). The method we used is well suited to long-term paleo-reconstructions because it handles missing values in the time series (Copyright 2017, Stephen R. Carpenter, method published in Taranu et al. 2018). A critical transition is characterized by eigenvalues of the Jacobian matrix crossing 1 from below, indicating the system lost its capacity of returning toward the mean (i.e., its previous state:

the system goes into a new state. Scheffer et al. 2015b). Best lag and delta (discount factor, accounting for variance) were chosen by computing AIC scores.

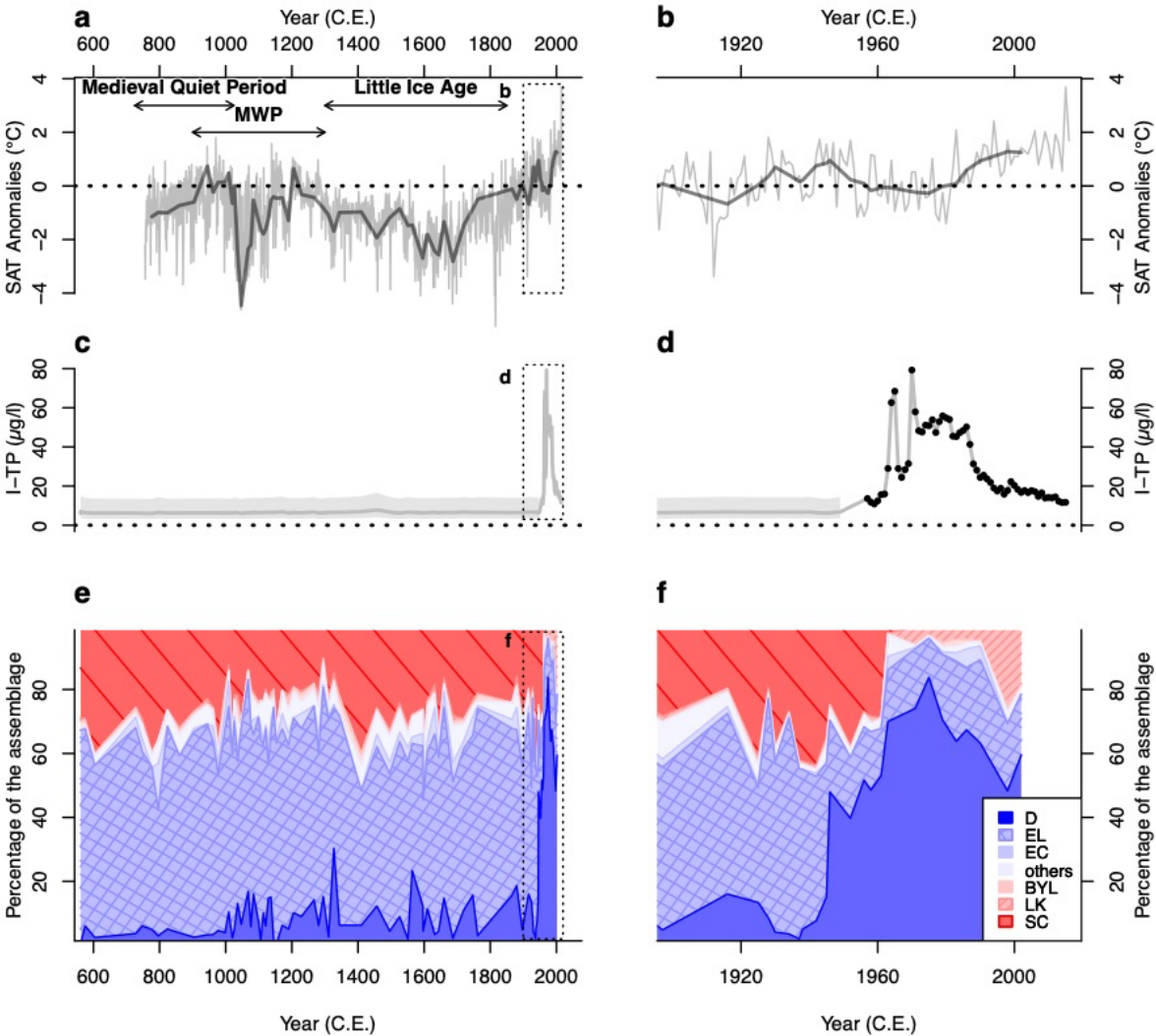


Figure 3 **DESCRIPTIF**. Changes in temperature, lake phosphorus concentrations, and cladocera assemblage since 563 AD. (a, b) Reconstructed summer (June to August) air temperature anomaly (SAT anomaly) from the Rhone valley (Switzerland) for the 755–1960 time period. Measured SAT converted into SAT anomaly at the Cointrin weather station (Switzerland) for the 563–2016 (a) and 1900–2016 (b) time-interval. Light grey line represents annual data; dark grey line represents the selected temperature for each sample, accounting for changes in sample thickness and sedimentation rate. (c, d) Diatom-inferred total phosphorus (DI-TP) concentration (thick grey line, with confidence interval) compared to the monitoring data for the 563–2016 (c) and 1900–2016 (d) time-interval (SOERE SI-OLA, Thonon-les-bains, France). (e, f) Changes in cladoceran assemblage for the 563–

2016 (e) and 1900–2016 (f) time-interval. D: *Daphnia* spp., EL: *Eubosmina longispina*, EC: *Eubosmina coregoni*, BYL: *Bythotrephes longimanus*, LK: *Leptodora kindtii*, SC: *Sida crystallina*, others: other taxa.

Results

Age model

The excess ^{210}Pb profile measured on core KK8 showed a regular decrease punctuated by two drops in $^{210}\text{Pb}_{\text{ex}}$ on the profile (Fig. 2_AGEMODEL_a). Following the lithology and Arnaud et al. (2002), these low values of $^{210}\text{Pb}_{\text{ex}}$ refer to instantaneous deposits and thus were excluded from the construction of the event-free sedimentary record. $^{210}\text{Pb}_{\text{ex}}$ activities plotted on a logarithmic scale revealed two different mean sedimentation rates (SR), respectively of $0.23 \pm 0.04 \text{ cm.yr}^{-1}$ above 12.1 cm (event-free sequence) and $0.83 \pm 0.23 \text{ mm.yr}^{-1}$ below this depth. Ages of the original sediment sequence provide a continuous age-depth relationship with a main sedimentation change dated around 1960 AD and $1919.7 \pm 9.4 \text{ AD}$ for the event layer t2 (turbidite). The ^{137}Cs activity profile reveals two peaks at $5.5 \text{ cm} \pm 5 \text{ mm}$ and $15.5 \text{ cm} \pm 5 \text{ mm}$, corresponding respectively to 1986 (Chernobyl accident) and 1963 (atmospheric atomic tests) (Appleby et al. 1991). Below $23.5 \text{ cm} \pm 5 \text{ mm}$, the recorded ^{137}Cs activities are close to zero, pointing to a sequence deposited before 1955 (first ^{137}Cs fallout). These three ^{137}Cs markers are in good agreement with the CFCS age model over the last century which confirms its reliability (Fig. 2_AGEMODEL_a).

From the event free composite core LEM10-CC, we calculated a continuous age-depth relationship with the R-code package ‘Clam’ version 2.2 (Blaauw 2010b). This age model integrates 11 stratigraphic horizons (Supplementary Materials S1, Table S1.2): i) the coring year, ii) three time-markers from ^{137}Cs activity, iii) the age of turbidite t2 dated from ^{210}Pb profile, iv) five dated points from the new paleomagnetic study (Crouzet et al. 2019), together with v) the 563 AD historical time marker. The chronology of the composite record LEM10-CC was already constrained on the 563–2010 time-period by the Tauredunum deposit event and the coring year. The new chronology adds data from short-lived radionuclide activities and paleomagnetic secular variations allowing a rare dating precision in regard to the length of the core. The best Clam model was obtained using a smooth spline interpolation with a smoothing term of 0.32 which avoids sudden change in

sedimentation rates (Fig. 2_AGEModelb). We also tested the age-depth model using the Bayesian model Bacon (Blaauw and Christen 2011) with the same input data (Supplementary Materials S1). This independent Bacon model allows a comparison with Clam model and shows that both curves have the same trend. The Clam model was favored because it better fits the original time markers of radionuclides markers that are important for a precise 20th century chronology.

Total phosphorus levels as a proxy for local human impact

The diatom fossil assemblage was dominated by *Pantocsekiella comensis*, a species typical of oligotrophic lakes (Harris 1987; Willen 1991; Hall and Smol 2010), over the whole period preceding the onset of the monitoring (Supplementary Materials S2). TP concentrations inferred from diatom assemblages confirm that no significant changes in I-TP were recorded for the period 563–1957 AD (Fig. 3_DESCRIPTIFc&d) despite a long history of human presence in Alpine Europe (Kaplan et al. 2009).

Ecological changes inferred from cladoceran assemblages

Our results show that the “recent” cladoceran assemblage is radically different from the one characteristic of the 563–1940 period (Fig. 3_DESCRIPTIFe&f). Major ecological changes were summarized by two primary principal components of the cladoceran assemblages (PC1 and PC2, Fig. 4_PCA) of the ordination analysis that accounted for 80% of the total variability within the dataset.

The excellent coherence of the signal recorded on the partial overlapping zones of the two cores with the previously published record of Alric *et al.* (2013) attests for the reproducibility of our results for the pelagic zone of Lake Geneva. The species distribution was largely unbalanced, with 6 species being dominant in the record (Fig. 4_PCaa). For clarity purposes, we grouped the remaining species in a group “others”. These species are mainly littoral (macrophyte and/or sediment associated, Fig. 4_PCAb).

From the beginning of the record and for twelve centuries, the cladoceran community of Lake Geneva was dominated by the same two species, the pelagic *Eubosmina longispina*, the earliest postglacial colonist in alpine lakes (Nauwerck 1991), and *Sida crystallina* var. *limnetica* (Fig.

3_ DESCRIPTIFe&f). The latter species occupies both pelagic and littoral habitats (Forel 1892), which supports the likely presence of macrophytic belts around the lake before the 20th century. From the 1940s, the absolute abundance of both *Daphnia* spp. and *S. crystallina* increased (Fig. 3_ DESCRIPTIFd). This period likely marks a period during which the food elemental quality improved, benefiting to *Daphnia* spp. that has high stoichiometric requirements (Urabe et al. 1997; Elser et al. 2001; Hessen et al. 2002). Levels of phosphorus increased, but under a threshold that prevented any restructuration in the phytoplankton assemblage (Supplementary Materials S2, DeMott and Gulati 1999). Furthermore, the maintenance of *S. crystallina* followed by its decline hint that no changes in algal biomass took place in the <10 µgTP.L⁻¹ range, since the resulting light limitation would have compromised the maintenance of the macrophyte-associated specie. From the early 1960s, when concentration went beyond 10-20 µgTP.L⁻¹, *Daphnia* spp. eliminated *E. longispina*, while the habitat-demanding *S. crystallina*, that had been continuously present since 563 AD, almost vanished in Lake Geneva in 1961 AD. *Daphnia* spp. made the most of the nutrient driven changes in the phytoplankton community structure while the herbivorous *E. longispina* suffer from their lower feeding efficiency compared to the larger phytoplankters. Such successive transitions have been confidently attributed to eutrophication (GAM for PC1 including a significant smooth term for I-TP, Dev. Expl.= 79.4%, df= 4.077, F= 55.99, p = 2.78·10⁻³⁷, Fig. 5_ GAM) (Alric et al. 2013), and occurred at a relatively low I-TP threshold of 10–20 µgP.L⁻¹. Between 1946 and 1961 AD, the pristine Lake Geneva, hosting both littoral and planktonic habitats, shifted to an anthropogenic impacted, plankton-dominated state.

The best DLM was obtained for a *lag* of 1 and a *delta* of 0.84, and gave a R² of 0.80, and indicates a transition in 1958/1961 (Fig. 6_ DLMc). Note that S. Carpenter (who coded the script) recommends *deltas* ranging from 0.9 to 0.99. Constraining DLM to that window resulted in a slightly lower fit (R²= 0.79 for *delta*= 0.9), but no change in critical transition (1958/1961). *Delta* accounts for potential variability in the time-series being tested for critical transition. Lower *delta* is smoothing the signal, which explains the inverse relationship between R² and *delta*. The DLM suggests that the change in cladoceran assemblage in 1958/1961 is a critical transition (Fig. 6_ DLM c).

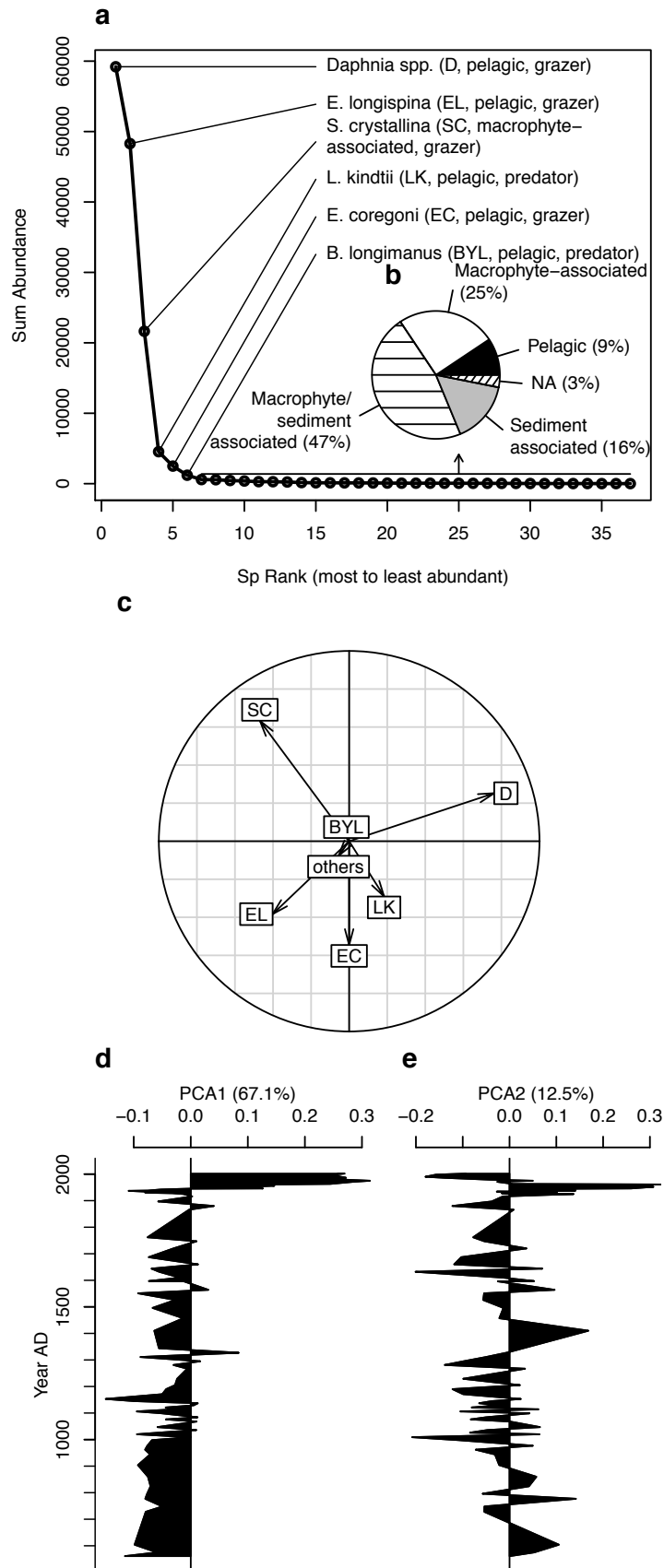
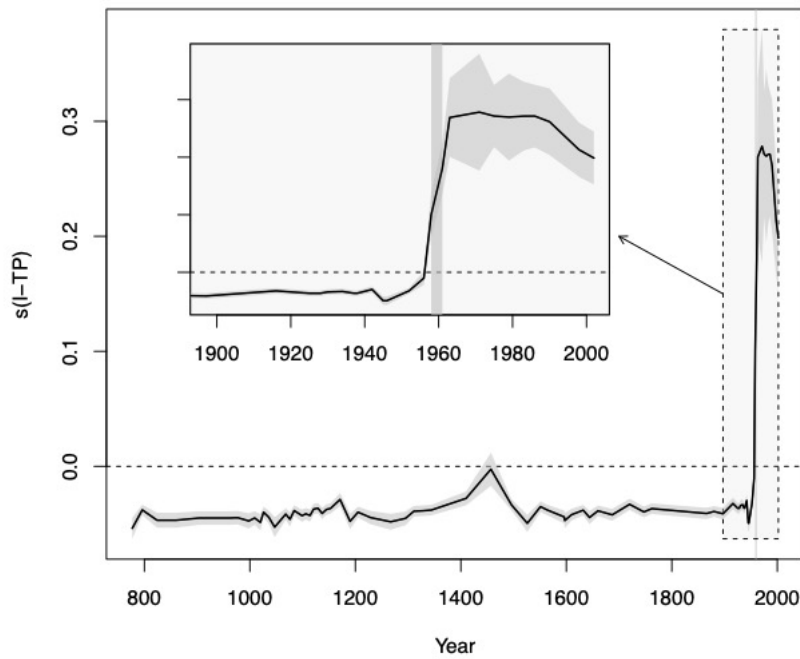


Figure 4_PCA. (a) Ranking of species by abundances; (b) frequency of habitat for species that rank 7 to 37 in abundance; these low abundant species are grouped as “others” in the PCA. (c-e) Results from the PCA. (c) cocircle showing contribution of species to the first factorial plan. (d) PC1 and (e) PC2 scores over the years. Species code: SC: *Sida crystallina* var. *limnetica*, CH: *Chydorus* sp., EL: *Eubosmina longispina*, EC: *Eubosmina coregoni*, BYL: *Bythotrephes longimanus*, LK: *Leptodora kindtii*, BL: *Bosmina longirostris*, D: *Daphnia* spp.



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Figure 5_GAM. Temporal contribution of I-TP ($s(I-TP)$) to PC1 with approximately 95% pointwise confidence intervals to the contribution. Where the band includes the dashed zero line, the contribution of the covariate is not statistically significantly different from the intercept.

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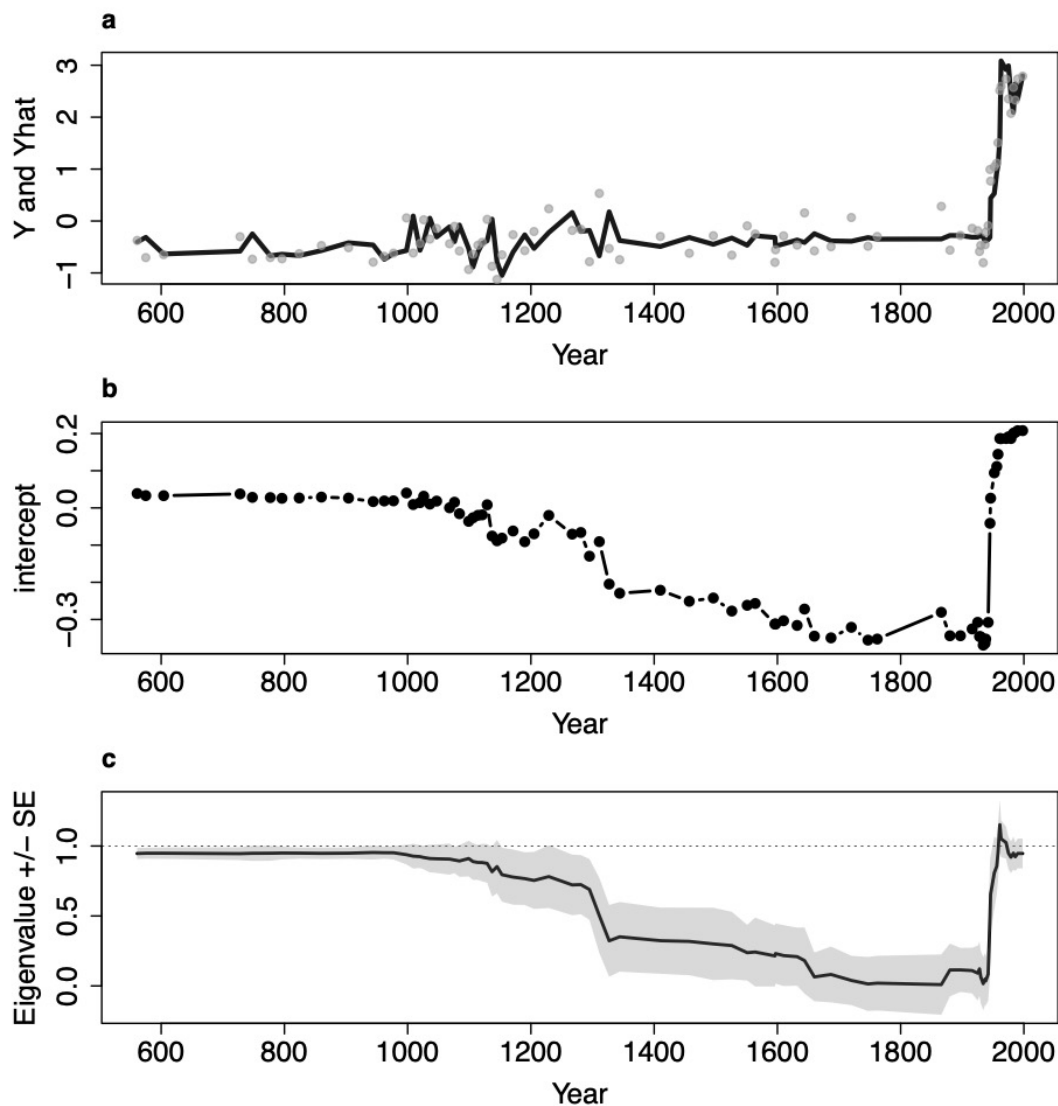


Figure 6_DLM. Summary of online dynamic linear model (DLM) results for Lake Geneva ($n = 81$). (a) The time series (grey points), goodness of fit (black line), (b) intercept, and (c) eigenvalue (black line) with standard error (shaded area) are shown.

Discussion

We show that from 563 AD until the beginning of the 20th century, the ecological state of Lake Geneva as depicted by cladoceran assemblages remained stable despite the climate variability of 3°C evidenced by local reconstructions (Fig. 3_DESCRIPTIFa) (Büntgen et al. 2006). TP levels remained low indicating a good buffering capacity of the system in regards to the land occupation in the Alpine area over this period (Kaplan et al. 2009). The sediment archive mirrored the well-documented eutrophication phase in Lake Geneva, that started at low levels of TP ($< 10 \mu\text{g P.l}^{-1}$)

and led to the dominance of pelagic taxa. As TP concentrations are decreasing since the 1980s, the macrophytic-associated specie *S. crystallina* is not recovering and instead, the predatorous *L. kindtii* represent now a larger proportion of the assemblage (Fig. 3_DESCRIPTIF). DLM revealed a critical transition in 1958-1961, for I-TP levels around 12-16 $\mu\text{g.l}^{-1}$. It happened ca. 9 years before the critical transition identified for the oxygen level by Taranu *et al.* (2018). Lake Geneva hypoxic volume regime is one of the case study in the paper presenting the method. The driver for the critical transition in oxygen level was also attributed to eutrophication (Jenny *et al.* 2014; Taranu *et al.* 2018). The “recent” cladoceran assemblage is radically different from the one characteristic of the 563–1940 period, underlying the relevance of paleolimnological tools even for lakes that have been continuously surveyed as early as the late 1950s such as Lake Geneva. We show that from 563 AD until the beginning of the 20th century, the ecological state of Lake Geneva as depicted by cladoceran assemblages remained stable despite the climate variability of 3°C evidenced by local reconstructions (Büntgen *et al.* 2006). TP levels remained low indicating a good buffering capacity of the system in regards to the land occupation in the Alpine area over this period (Kaplan *et al.* 2009). The sediment archive mirrored the well-documented eutrophication phase in Lake Geneva, that started at low levels of TP ($< 10 \mu\text{g P.l}^{-1}$) and led to the dominance of pelagic taxa. As TP concentrations are decreasing since the 1980s, the macrophytic-associated specie *S. crystallina* is not recovering and instead, the predatorous *L. kindtii* represent now a larger proportion of the assemblage (Fig. 3_DESCRIPTIF). DLM revealed a critical transition in 1958-1961, for I-TP levels around 12-16 $\mu\text{g.l}^{-1}$. It happened ca. 9 years before the critical transition identified for the oxygen level by Taranu *et al.* (2018). Lake Geneva hypoxic volume regime is one of the case studies in the paper presenting the method. The driver for the critical transition in oxygen level was also attributed to eutrophication (Jenny *et al.* 2014; Taranu *et al.* 2018). The “recent” cladoceran assemblage is radically different from the one characteristic of the 563–1940 period, underlying the relevance of paleolimnological tools even for lakes that have been continuously surveyed as early as the late 1950s such as Lake Geneva.

Potential processes lost with the critical transition

Large lakes are not typically considered as vulnerable to critical transitions between stable states, because most feedbacks associated with stable states are linked to some extent to the littoral zone (e.g., connection with sediment that includes resuspension of particles and remobilization of phosphorus, Hilt 2015). Other research suggests the threshold may be lower (Hilt *et al.* 2010), and

that the focus on the pelagic zone in deep lakes may overlook the role of the benthic and littoral zone (Vander Zanden and Vadeboncoeur 2002). The timing of eutrophication matches the loss of the littoral zone and the strengthening of the top-down control. Littoral areas could be functionally crucial components of habitat heterogeneity, biodiversity, and resilience, even in a large and deep lake for which their representability is always minor. The almost complete disappearance of *S. crystallina* remains after 1961 AD is consistent across pelagic cores (see Alric et al. 2013 Fig. 4_PCA), but also across lakes sharing the same timing of eutrophication (Lake Maggiore, Manca et al. 2007; Lake Bourget, Alric et al. 2013; Lake Lugano, unpublished data). *S. crystallina*, *Daphnia* spp., and *Eubosmina* sp. all graze on phytoplankton. The community lost the former of these grazers (reduced horizontal diversity) and gained a predator, *L. kindtii*, increasing its vertical diversity. *L. kindtii* was a consistent component of the assemblage but its relative abundance was <1% until the 1980s (>10% of the assemblage). High horizontal and vertical diversity respectively increase and decrease stability to large perturbations (Zhao et al. 2019). The new planktonic food web structure of Lake Geneva makes it in theory less resilient to future large perturbations. Species interactions (and specifically, predation), were also found to mediate community response to large perturbation (drought); these responses were amplified at lower elevations, representing warmer climate in the space-for-time approach used by the authors (Amundrud and Srivastava 2019).

If the littoral zone is key to the resistance of Lake Geneva to past climatic variability, then the effort to restore the littoral areas should be sustained. Lake Geneva charophytic vegetation shows sign of recovery (Perfetta 2011). Charophytic vegetation is recovering faster than macrophytic beds because they depend solely on water to absorb nutrients (Perfetta 2011). However, restoration of the littoral vegetation is not solely a function of the nutrient concentration, but also urban infrastructure (rockfill, seawalls, channelling of small tributary streams, ...) and harbours.

Multiple yet asynchronous drivers: interactive carryover

Eutrophication drove the major habitat and species change in Lake Geneva, as in the overwhelming number of cases for lakes (Carpenter 2005). More generally, land use is responsible for most of the negative impacts across terrestrial and freshwater ecosystem (e.g., Bajard et al. 2018). However climate change is increasingly exacerbating the impact of other drives on nature and human well-being (IPBES 2019). Our study shows that Lake Geneva is no exception to the trend. After 1,200 years of ecological stability despites changes in air temperature, relatively low levels of phosphorus

triggered a critical transition in the system. It seems that before the 1950s, the ecological status of Lake Geneva, as mirrored by cladoceran (and diatoms, see Supplementary Materials S2) communities, was not vulnerable to changes of 3°C in air temperature and its consequent effects on lake water temperature. Indeed, SAT anomalies fluctuated within a range of 3°C over the period 800-1800 AD alone in Central Europe (Büntgen et al. 2006), which falls into the same amplitude as the variations observed over the 20th and 21st centuries (Fig. 4_PCAa&b). However, at the scale of the past 150 years, the same method (sediment remain analysis, ordination, GAM) revealed that climate warming was a significant driver of cladoceran (Alric et al. 2013) and diatoms (Berthon et al. 2014) assemblages. Our conjecture is that vulnerability to climate variability has changed following the critical transitions. Alric *et al.* (2013) and Berthon *et al.* (2014), working at the scale of the past 150 years, were able to quantify vulnerability to climate, while our sample disproportionately represent the period of resistance (pre-20th century), and thus the decoupling between climatic signal and ecological response.

Ryo et al. (2019) conceptualize and review examples of such interactive carryover, i.e., when a prior driver changes an internal parameter or mechanism of a system, which lead the system to respond to a posterior driver differently (more, or less, depending whether drivers act synergistically or antagonistically) from how it would have responded without the experience of the first driver (Fig. 7_CONCEPT). The fact that air temperature increased to the same rate (+0.4°C per decade) and amplitude of anomalies (+2°C) in the 1930-1950s, without triggering the same responses, supports that hypothesis. Ecological vulnerability to climate change would not only be tied to the rate at which water is warming but also to inherited local human alterations of the lake food web. This conclusion is corroborated by a recent diachronic approach conducted at the neighboring, oligotrophic Lake Annecy under the same climatic context, where the lake surface water temperature has increased by 4°C between the 1970s and the 2000s (+2.5°C in Lake Geneva) but the cladoceran assemblage has barely responded to the change (Perga et al. 2015).

The idea that in the face of multiple stressors, addressing local or regional drivers could build resilience to continued global change, is often presented (Rockström et al. 2009; Scheffer et al. 2015a; Rocha et al. 2015). If two drivers have similar impacts on the ecosystem, then the level of driver 1 that allows the systems to operate in its safe operate state under low levels of driver 2, may be too much if driver 2 increases (Scheffer et al. 2015a). Conversely, if local stressors already modified the ecosystem, its response to decreasing driver may not result in a return to the exact same baseline, because climate change (or another driver) may have changed these boundary conditions (Fig. 7_CONCEPTa, Battarbee et al. 2005). Our findings expand this idea. In here, we

show that eutrophication actually acted as a switch from a regime of resistance to a new regime of frequent restructuration, and a different, more vertical, food web structure. If local drivers have to be reduced to build resilience, it needs to be done before the ecosystem has been pushed beyond its limits (Fig. 7_CONCEPTb). The idea that in the face of multiple stressors, addressing local or regional drivers could build resilience to continued global change, is often presented (Rockström et al. 2009; Scheffer et al. 2015a; Rocha et al. 2015). If two drivers have similar impacts on the ecosystem, then the level of driver 1 that allows the systems to operate in its safe operate state under low levels of driver 2, may be too much if driver 2 increases (Scheffer et al. 2015a). Conversely, if local stressors already modified the ecosystem, its response to decreasing driver may not result in a return to the exact same baseline, because climate change (or another driver) may have changed these boundary conditions (Fig. 7_CONCEPTa, Battarbee et al. 2005). Our findings expand this idea. In here, we show that eutrophication acted in fact as a switch from a regime of resistance to a new regime of frequent restructuration, and a different, more vertical, food web structure. As a consequence, if local drivers must be reduced to build resilience, it needs to be done before the ecosystem has been pushed beyond its limits (Fig. 7_CONCEPTb).

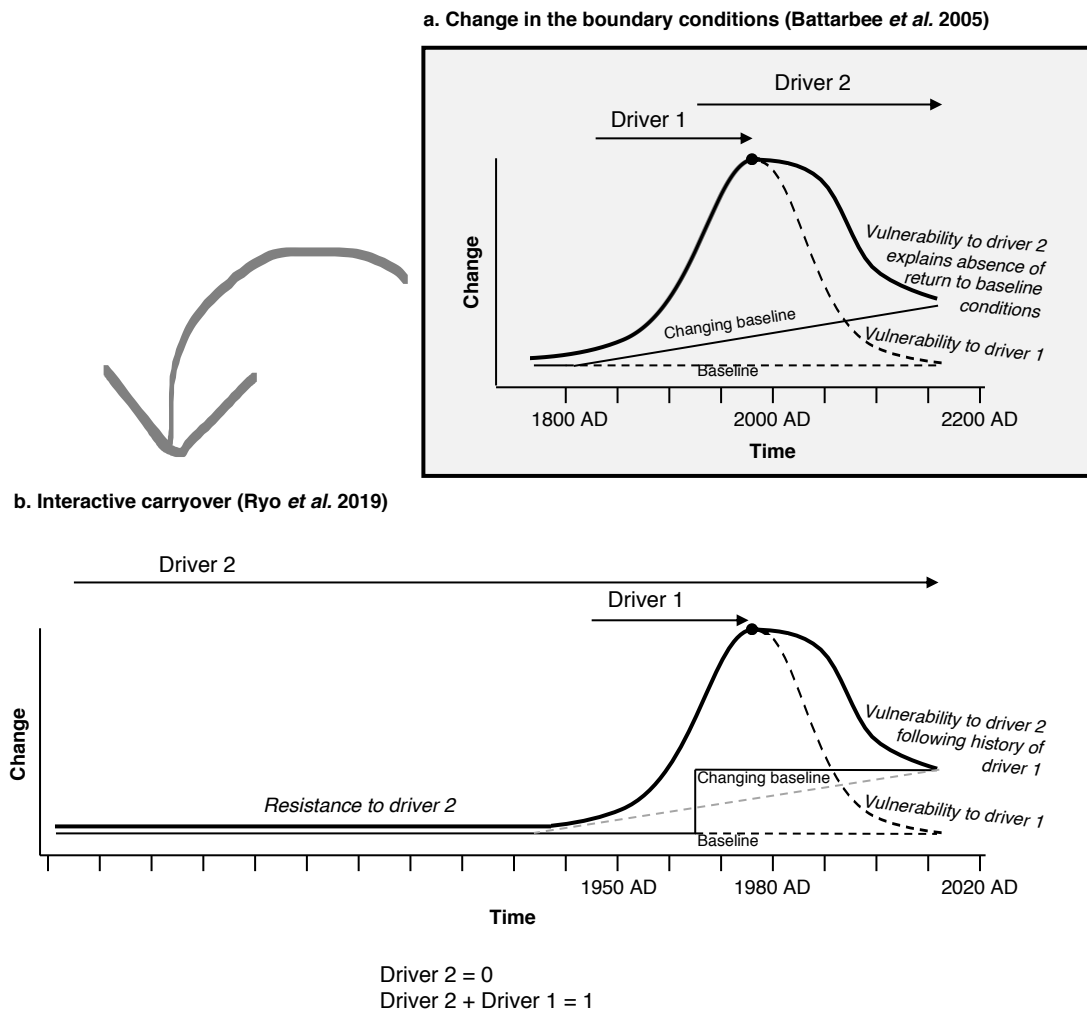


Figure 7_CONCEPT. (a) Idealized diagram illustrating temporal ecological response of Lake Geneva to increasing and decreasing drivers, freely adapted from Battarbee *et al.* (2005). They concluded that new baseline conditions should be targeted in restoration programs because of the juxtaposition of several forcings. (b) Our findings suggest the baseline may have changed as a tipping point. As a perspective, we question whether vulnerability to driver 2 (e.g., climate) is true only after driver 1 (e.g., eutrophication) decreased the resilience of the system.

Time perspective and implication for managers

Ecosystems evolve over timescales that are impossible to experience by a human eye, yet humans are the ones responsible for their management (Vitousek *et al.* 1997). Ecologists acknowledge this and there is no doubt long-term observatories provide invaluable knowledge on ecosystems specificities and framework for ecological theories (Maberly *et al.* 2018). Our results show that Lake

Geneva long-term monitoring database, despite being one of the longest series in the world, may not be documenting the baseline condition. Further research should aim at deciphering whether the beginning of the monitoring captured a transient equilibrium (sensu Hastings et al. 2018), preceding the ecosystem crucial transition. Ecosystems evolve over timescales that are impossible to experience by a human eye, yet humans are the ones responsible for their management (Vitousek et al. 1997). Ecologists acknowledge this and there is no doubt long-term observatories provide invaluable knowledge on ecosystems specificities and framework for ecological theories (Maberly et al. 2018). Our results show that Lake Geneva long-term monitoring database, despite being one of the longest series in the world, may not be documenting the ecological baseline condition. Further research should aim at deciphering whether the beginning of the monitoring captured a transient equilibrium (sensu Hastings et al. 2018), preceding the ecosystem crucial transition.

The newest generation of managers may only know Lake Geneva as an ecosystem undergoing re-oligotrophication. Could this study lead to an example of “shifting baseline syndrome” (Pauly 1995)? The syndrome, as first described in fisheries, arises when each generation of fisheries scientists accepts as a baseline the stock characteristics that occurred at the beginning of their career (Pauly 1995). In this case, the new generation of lake managers could accept as contemporary process the re-oligotrophication, and as history the eutrophication period. While Lake Geneva has now shifted long before the newest generation of lake managers was born, we should keep in mind the lake was once different. It is important to acknowledge this long history, to prevent increased tolerance for environmental degradation, and set appropriate baselines for conservation, restoration, and management (Soga and Gaston 2018). As a more general note, we realize that managers have the difficult job of making decisions that will trigger results they won’t see the total extent of within their lifetime. The short (at the scale of Lake Geneva history) eutrophication episode triggered long lasting effect in the ecological state of the system (interactive carryover, Ryo et al. 2019). The newest generation of managers only know Lake Geneva as a meso-oligotrophic system. Our results show the importance of accounting for longer ecosystem and lake trajectories (Wolkovich et al. 2014).

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Authors contribution

RB, SG, MEP conceived the study and interpreted the results. RB, SG, KK, PS, CC, JLR conceived the age model. RB and AM analyzed the core sub-fossil samples. All authors contributed to the writing.

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Reframing Lake Geneva ecological trajectory in a context of multiple but asynchronous drivers

Bruel et al.

Supplementary Material S1 – Lake Geneva sediment record

1. Sediment core sampling and approach

We built a paleo-record dataset using two sediment cores collected in 2010 in the deepest basin of Lake Geneva. This Supplementary Material details the dating of the composite LEM10-CC from two cores (Ku-IV and KK8).

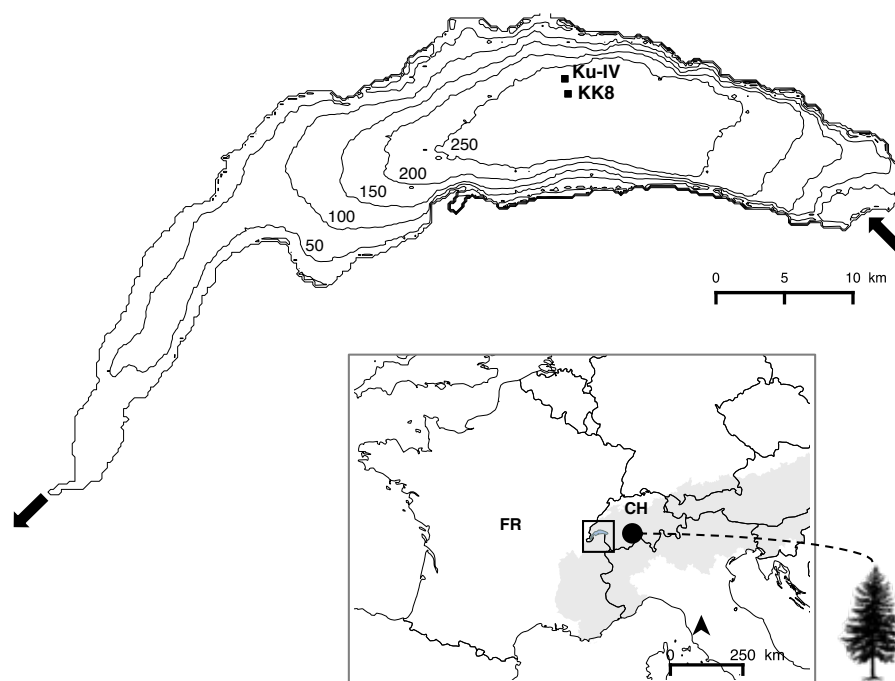


Figure S1.1. Lake Geneva lies at the border between France (FR) and Switzerland (CH) in the peri-alpine domain (Alps as grey surface on the bottom-right insert map). The bathymetry (in meters) and sediment core localization (black squares) are indicated. Arrows indicate the Rhône river inflow and outflow. The black circle on the bottom insert map shows the location of the four trees-ring sites used by Büntgen *et al.* (2006) to reconstruct SAT anomalies.

2. Methods

2.1 Construction of the composite core LEM10-CC

A paleo-record dataset was built using two sediment cores collected in 2010 in the deepest basin of Lake Geneva (Fig. 1). The main sediment archive is a long core covering the past 4,000 years (Ku-IV, 12 m, Long. E 6.60810/ Lat. N 46.47652, sampled on 02/09/2010) published by Kremer *et al.* (2012, 2015c). From this previously dated and studied core, only the 4.31 upper meters of the sediment sequence situated above the Tauredunum deposit of 563 AD documented by Kremer *et al.* (2012) were analyzed. As the top of Ku-IV was neither complete nor well preserved, the last ~100 years of the record could not be considered for this core. Thus, we used a short surface sediment cores as complementary archives to fill this gap. The short core, very similar to Ku-IV and located only 1.1 km southward, was used to solve the chronology issue of the past ca.100 years (KK8, 1.31 m, Long. E 6.61124/ Lat. N 46.46665, sampled on 19/04/2010). To build a coherent chronology, the two closely spaced sediment records were merged into one composite record LEM10-CC using the stratigraphic level of turbidite t2 (47.5-51.5 cm on KK8, 54.5-61.5 cm on Ku-IV) as identified by Kremer *et al.* (2015a) in both records.

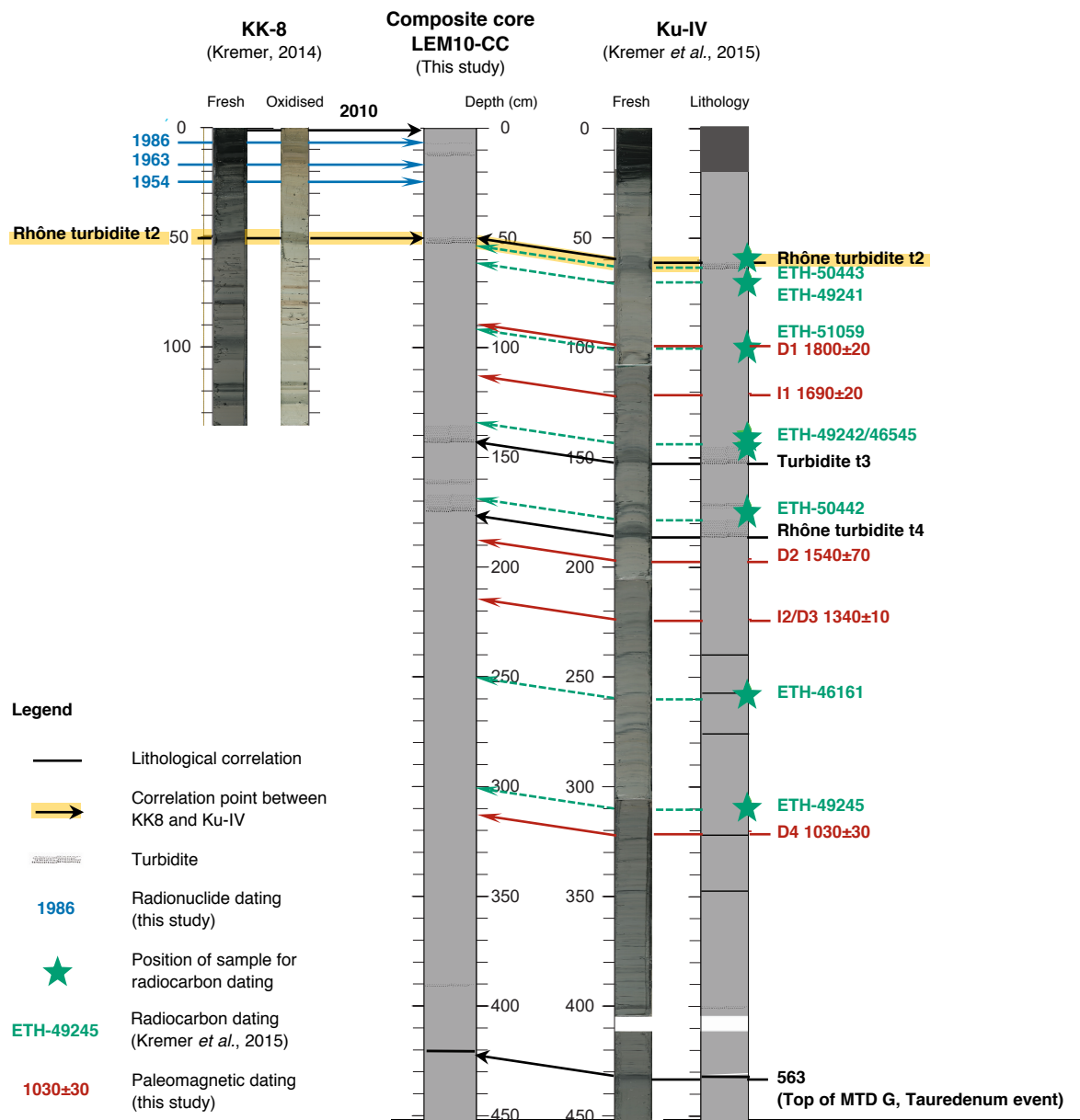


Figure S1.2. Construction of the composite LEM10-CC sediment record with core photographs and lithology description used in this study. From left to right, KK-8 (fresh sediment), KK8 (oxidized sediment), LEM10-CC composite record (lithology), Ku-IV (fresh sediment), Ku-IV (lithology). The lithological correlations are represented with black lines and arrows. Dated horizons are represented by blue (^{137}Cs activity peaks), red (paleomagnetism) and green (radiocarbon) lines and arrows, and stars, respectively (see legend); the corresponding ages are written next to the horizons.

2.2 Age model of LEM10-C

From the event free composite record LEM10-CC (see below), we calculated a continuous age-depth relationship with the R-code package ‘Clam’ version 2.2 (Blaauw 2010a) and compared the output with the Bayesian model ‘Bacon’ (Blaauw and Christen 2011).

2.2.1 Removal of event layers

The chronology of the composite core LEM10-CC is based on short-lived radionuclide activities, paleomagnetic secular variations, the coring year and a historical event. From the original 4.21-m-long composite core LEM10-CC, seven event layers with thickness above 1 cm were interpreted as instantaneous events (Kremer et al. 2015a). They were thus removed from the raw sequence to construct a 3.93-m-long event-free composite core (Wilhelm et al. 2012). The depth and thickness of these events, and details on the dating methods, are listed in Table S1.1.

Table S1.1. Core depth of event layers in original and composite sediment records along layer thickness. Last column include reference to identified instantaneous events in Kremer *et al.* (2015a) or radiocarbon dated material (Kremer et al. 2012).

Core where event layer was originally observed	Projected depth (cm) in composite LEM10-CC	Thickness of the event layer (cm)	Correlation with Kremer et al. ^{5,7}
KK8	6 – 7	1	
KK8	10.4 – 12.8	2.4	
KK8	47.5 – 51.5	4	t2, Rhône turbidite ⁸
Ku-IV	135.5 – 142.5	7	
Ku-IV	162.5 – 166.5	4	
Ku-IV	170.5 – 179.5	7	¹⁴ C age ETH-50442, t4 (Kremer et al. 2015a)
Ku-IV	391 – 393	2	¹⁴ C age ETH-49245 (Kremer et al. 2015a)

2.3.2 Dating from radionuclide activity

The activity of short-lived radionuclides (^{210}Pb , ^{226}Ra and ^{137}Cs) was measured in the uppermost 43 cm of core KK8, following a non-regular sampling step of 1 to 2 cm, in order to match facies boundaries, and using 0.3–2.4 g samples of dried sediment. Measurements were made by gamma spectrometry, using high-efficiency, very low background, well-type Ge detectors in the Modane underground laboratory (Reyss et al. 1995). The ^{210}Pb *unsupported* excess activity ($^{210}\text{Pb}_{\text{ex}}$) were calculated by subtracting the ^{226}Ra -supported activity from the total ^{210}Pb activity. We then used the Constant Flux/Constant Sedimentation (CFCS) model applied to the decrease of $^{210}\text{Pb}_{\text{ex}}$ to calculate a mean sedimentation rate (Goldberg 1963). The sedimentation rate uncertainties derived from the standard error of the linear regression of the CFCS model.

2.2.2 Dating from paleomagnetic secular variations

The natural remanent magnetization (NRM) versus depth was measured in order to compare with known paleomagnetic secular variations such as Arch3k model (Donadini et al. 2009). Paleomagnetic investigations were performed on U-channel sub-samples of core Ku-IV, using a 3-axis, 2-G enterprise cryogenic magnetometer at the CEREGE laboratory (Aix-Marseille University, France). The NRM was progressively demagnetized using alternating field (AF) in 10, 20, 30, 40 and 60 mT steps. The demagnetization diagrams (Zijderveld 1967) showed that behaviour was mainly unidirectional. Principal component analyses and calculation have been performed using puffin plot software (Lurcock and Wilson 2012) to calculate the Characteristic Remanent Magnetization (ChRM). Measurements affected by side effects (close to U-channel extremities) were removed. We also imparted and demagnetized the samples' anhysteretic and isothermal remanent magnetizations (ARM and IRM respectively) in order to ensure there is no change in magnetic mineralogy (see procedure in Wilhelm et al. 2016). Because the magnetic carrier properties were very stable along the entire studied section, we could be confident in the resulting ChRM direction.

2.3.3 Historical event as stratigraphic marker

The base of the studied sediment sequence is the top of a large basin-wide mass movement deposit that has been related to the historical rockfall of 563 AD (“Tauredunum event”, Kremer et al. 2012).

2.3.4 Radiocarbon dating

Samples of organic macro-remains were analyzed for radiocarbon dating (Kremer et al. 2012).

3. Results

3.1 Chronology from radionuclides activity (1919-2010)

The excess ^{210}Pb profile measured on core KK8 showed a regular decrease punctuated by two drops in $^{210}\text{Pb}_{\text{ex}}$ on the profile (Fig. S1.3). Following the lithology and Arnaud *et al.* (2002), these low values of $^{210}\text{Pb}_{\text{ex}}$ refer to instantaneous deposits (first two layers listed in Table S1.1) and thus were excluded from the construction of the event-free sedimentary record. $^{210}\text{Pb}_{\text{ex}}$ activities plotted on a logarithmic scale revealed two different mean sedimentation rates (SR), respectively of $0.23 \pm 0.04 \text{ cm.yr}^{-1}$ above 12.1 cm (event-free sequence) and $0.83 \pm 0.23 \text{ mm.yr}^{-1}$ below this depth. Ages of the original sediment sequence provide a continuous age-depth relationship with a main sedimentation change dated around 1960 AD. With this result, the age of the event layer t2 (turbidite), initially determined from ^{14}C dating as 1785 ± 115 (Kremer *et al.* 2015a) is now much better constrained to 1919.7 ± 9.4 .

The ^{137}Cs activity profile of core KK8 reveals two peaks at $5.5 \text{ cm} \pm 5 \text{ mm}$ and $15.5 \text{ cm} \pm 5 \text{ mm}$, corresponding respectively to 1986 (Chernobyl accident) and 1963 (atmospheric atomic tests, Appleby *et al.* 1991). Below $23.5 \text{ cm} \pm 5 \text{ mm}$, the recorded ^{137}Cs activities are close to zero, pointing to a sequence deposited before 1955 (first ^{137}Cs fallout). These three ^{137}Cs markers are in good agreement with the CFCS age model over the last century, which confirms its reliability (Fig. S1.3).

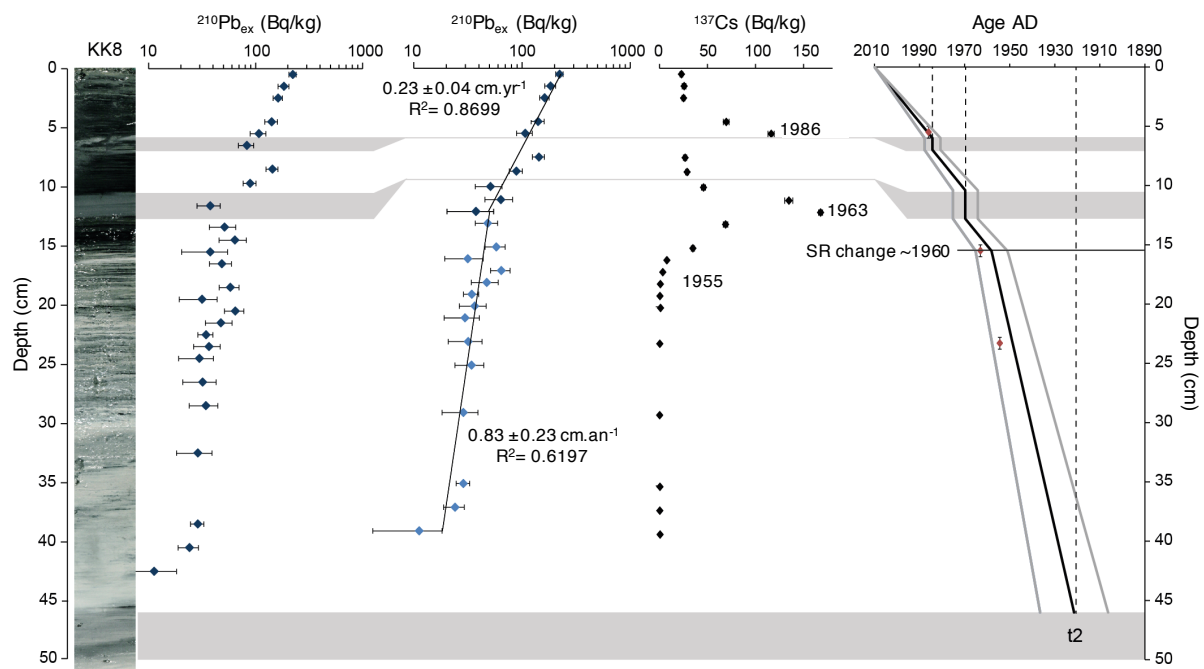


Figure S1.3. Chronology (with 1σ uncertainties) of the uppermost part of core KK8 based on activity of short-lived radionuclides ($^{210}\text{Pb}_{\text{ex}}$ and ^{137}Cs) and the application of a CFCS model to the event-free sedimentary profile of $^{210}\text{Pb}_{\text{ex}}$ (right panel). Uncertainties of ^{137}Cs activities are included as dots size. A main sedimentation rate (SR) change appears around 1960 AD.

Grey bands correspond to event layers / turbidite intervals, interpreted as instantaneous deposits (relatively to the rest of the chronology).

3.2 Record of paleomagnetic secular variations

The declination and inclination of the ChRM measured on Ku-IV were compared with those issue for Arch 3k model (Donadini et al. 2009) in order to provide additional and independent age depth coordinates. Assuming NRM is acquired during or immediately after deposition, this comparison with reference curves allowed the identification of two inclination points and four declination points (Table S1.2). Inclination points I1 (1690 ± 20) and I2 (1300 ± 50) were respectively observed at 121 ± 10 cm and 221 ± 15 cm (Fig. S1.4) and declination points D1 (1800 ± 20), D2 (1540 ± 70), D3 (1370 ± 40) and D4 (1030 ± 30) were respectively observed at 100 ± 15 cm, 196 ± 15 cm, 224 ± 10 cm and 322 ± 10 cm (Fig. S1.5). I2 and D3 were observed for the same depth, thus allowing narrowing the confidence interval of the $224 \text{ cm} \pm 10 \text{ cm}$ depth to an age of 1340 ± 10 cm.

Table S1.2. The name of the stratigraphic horizons (ID), the dating method, the age and error (cal. BP) are given along of the original core name, the respective projected depth in raw and corrected composite record LEM10-CC. (ChRM = Characteristic Remanent Magnetization)

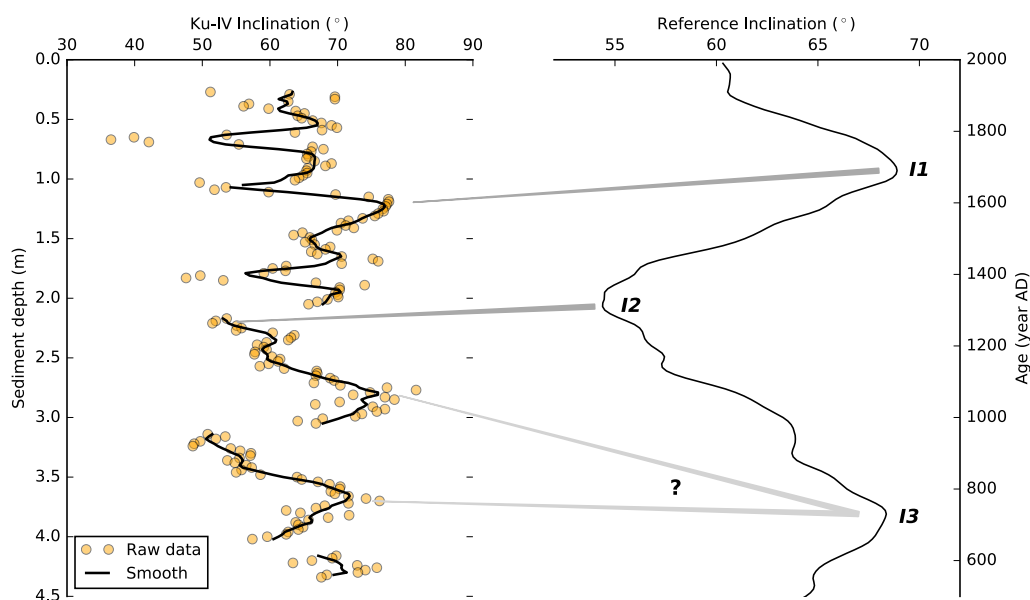
* ^{14}C ages rejected by Kremer et al.(2012).

** ^{14}C ages used to build the age-depth model by Kremer et al.(2012) but rejected in this study in the light of new dated horizons.

ID	Dating Method	Age cal. BP (yr)	Original sediment core	Projected depth (cm) in LEM10-CC	Event corrected depth (cm) in LEM10-CC
Surface sediment	Coring year	-60 ± 1	KK8	0	0
Chernobyl	^{137}Cs	-36 ± 1	KK8	5.5 ± 0.5	5.5 ± 0.5
Atomic test	^{137}Cs	-13 ± 1	KK8	15.5 ± 0.5	12.1 ± 0.5
Before test	^{137}Cs	-5 ± 1	KK8	23.5 ± 0.5	20.1 ± 0.5
Rhône turbidite t2 (Kremer et al. 2015a)	^{210}Pb decay	30.3 ± 9.4	KK8	47.5 ± 0.5	44.1 ± 0.5

ETH-50443*	¹⁴ C yr BP	143 ± 30	Ku-IV	52 ± 1	44.6 ± 1
ETH-49241*	¹⁴ C yr BP	614 ± 51	Ku-IV	60 ± 1	51.6 ± 1
D1	ChRM	150 ± 10	Ku-IV	90 ± 7.5	82.6 ± 7.5
ETH-51059*	¹⁴ C yr BP	382 ± 35	Ku-IV	90 ± 10	82.6 ± 10
I1	ChRM	260 ± 10	Ku-IV	111 ± 5	103.6 ± 5
ETH-49242*	¹⁴ C yr BP	877 ± 59	Ku-IV	130 ± 1	122.6 ± 1
ETH-46545*	¹⁴ C yr BP	870 ± 25	Ku-IV	135 ± 1	127.6 ± 1
ETH-50442**	¹⁴ C yr BP	198 ± 30	Ku-IV	167 ± 1	144.6 ± 1
D2	ChRM	410 ± 35	Ku-IV	186 ± 7.5	160.6 ± 7.5
I2/D3	ChRM	610 ± 5	Ku-IV	214 ± 5	188.6 ± 5
ETH-46161**	¹⁴ C yr BP	870 ± 25	Ku-IV	250 ± 10	224.6 ± 10
ETH-49245**	¹⁴ C yr BP	1102 ± 72	Ku-IV	300.9 ± 3	273.6 ± 3
D4	ChRM	920 ± 15	Ku-IV	312 ± 5	286.6 ± 5
Tauredenum	Historical time marker (Kremer et al. 2012)	1387 ± 1	Ku-IV	421 ± 1	393.6 ± 1

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Figure S1.4. Inclination curve of Ku-IV averaged over a 12-cm-window (left panel) and comparison with the reference inclination calculated from Arch3k model (Donadini et al. 2009)

for Lake Geneva (right panel). The I1 and I2 inclination points are used in the age-depth model (Figure S1.9).

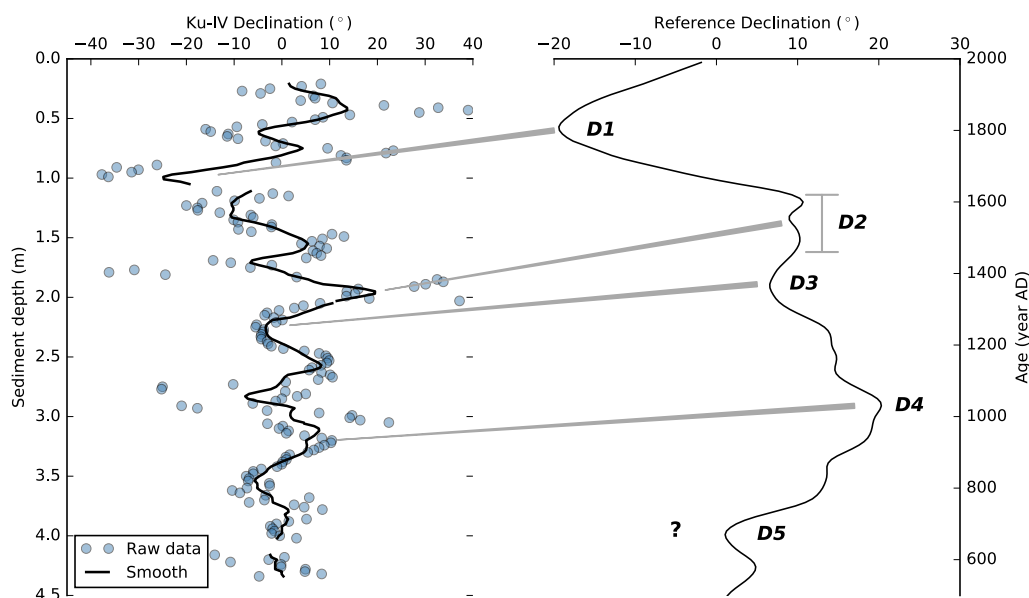


Figure S1.5. Declination curve of Ku-IV averaged over a 12-cm-window (left panel) and comparison with the reference declination calculated from Arch3k model (Donadini et al. 2009) for Lake Geneva (right panel). The D1 to D4 declination points are used in the age-depth model (Figure S1.9).

3.3 Age-depth model

From the event free composite core LEM10-CC, we calculated a continuous age-depth relationship with the R-code package ‘Clam’ version 2.2 (Blaauw 2010a). This age model integrates 11 stratigraphic horizons (Table S1.2): i) the coring year, ii) three time-markers from ^{137}Cs activity, iii) the age of turbidite t2 from ^{210}Pb activity, iv) five dated points from the new paleomagnetic study, together with v) the 563 AD historical time marker. The chronology of the composite record LEM10-CC was already constrained on the 563-2010 time-period by the Tauredunum deposit event and the coring year. The new chronology add data from short-lived radionuclide activities and paleomagnetic secular variations allowing a rare dating precision in regards to the length of the core. The best Clam model was obtained using a smooth spline interpolation with a smoothing term of 0.32 which avoids sudden change in sedimentation rates (Fig S1.6). We also tested the age-depth model using the Bayesian model Bacon (Blaauw and

Christen 2011) with the same input data (Fig. S1.7). This independent Bacon model allows a comparison with Clam model and shows that both curves have the same trend. The Clam model was favored because it better fits the original time markers of radionuclides activity that are important for a precise 20th century chronology.

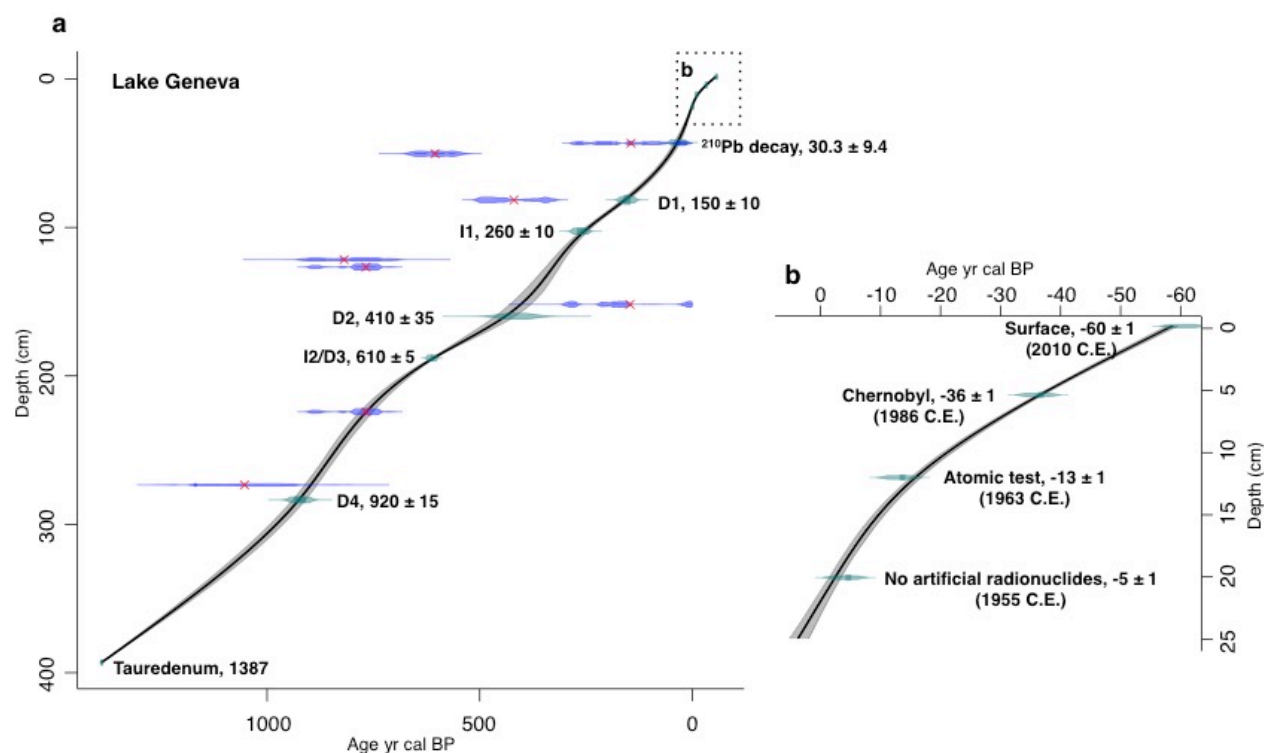


Figure S1.6. Age-depth model of composite record LEM10-CC built with Clam R-code package (Blaauw 2010b) from 11 stratigraphic horizons. **(a)** Total record and **(b)** zoom on the three ¹³⁷Cs dates. Event layers with thickness above 1 cm were interpreted as instantaneous events (Kremer et al. 2015a) and removed before the age model computation. The envelope (grey area) represents the 2-sigma probability interval. Data not used to fit the age model are marked with a red cross. See Supplementary Materials S1 for details.

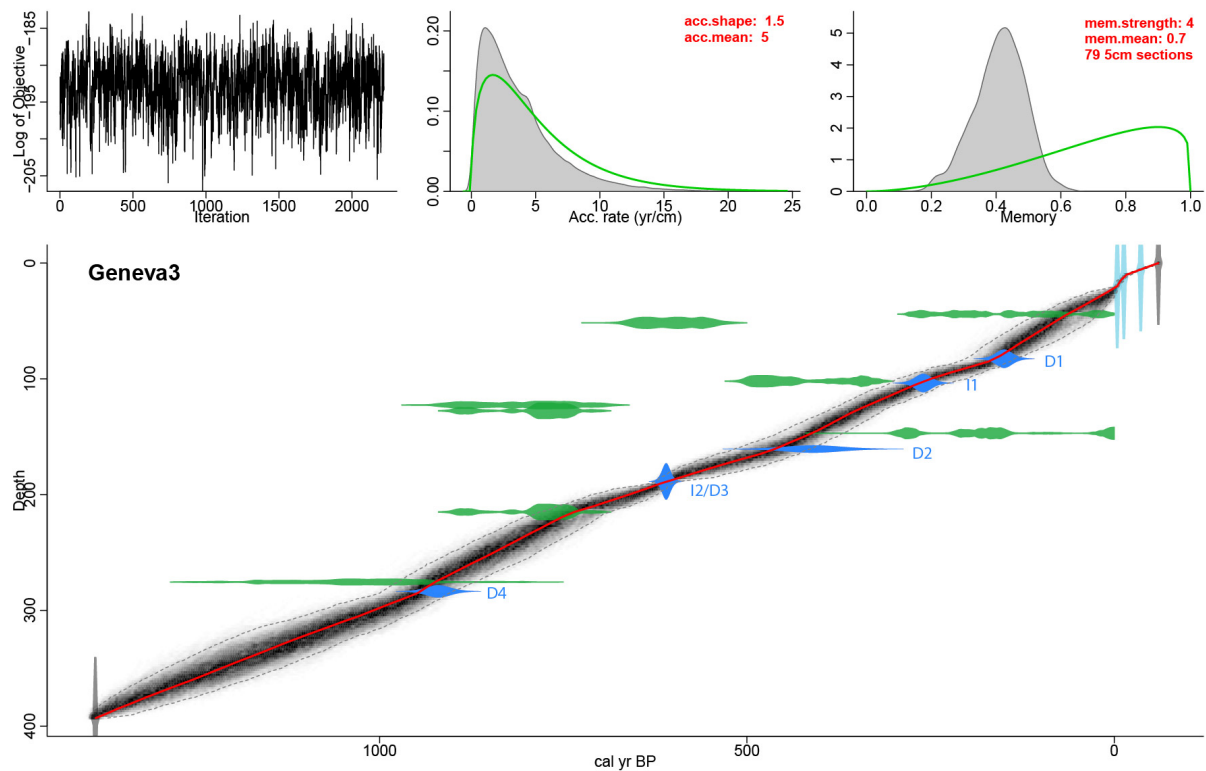


Figure S1.7. Age-depth model of composite core LEM10-CC built with Bacon (Blaauw and Christen 2011) (Tab. S.1). The upper left panel shows the iteration history, the upper middle panel shows the prior (green line) and posterior (grey area) of the sediment accumulation rate (yr/cm), and the upper right panel shows the prior (green line) and posterior (grey area) of the memory (1 cm autocorrelation strength). The bottom panel indicates the age-depth model. The solid red line represents the single ‘best’ model based on the weighted mean age for each depth. Associated uncertainties are represented by the grayscale (the darker grey dots are indicative for more likely ages and the dashed black lines indicate the model’s 95% probability intervals). The age-depth model is built on the age of the surface sediments (grey) and individual ages obtained from radionuclides (light blue), radiocarbon dating (green) and paleomagnetism (blue).

4. Discussion

4.1 Validity of the age model

The LEM10-CC age model reveals younger ages than previously estimated (Kremer et al. 2015a). ^{14}C dates are typically older due to the classical effect of terrestrial organic macroremain reworking in the catchment. On the other hand, paleomagnetic chronology may be affected by the lock-in depth (i.e. the delay in acquisition of the primary magnetization), that

implies that sediments are systematically older than the geomagnetic feature they preserve (Sagnotti et al. 2005; Mellström et al. 2015). We chose the paleomagnetism dating over the ^{14}C dates because their uncertainties ranges at the centimeter scale (Katari et al. 2000), i.e. decadal scale in Lake Geneva, instead of century scale errors in the case of ^{14}C . Besides, this paleomagnetism based model intercepts the age error of the four ^{14}C retained by Kremer *et al.* (2012), confirming their realism (Fig. S1.6). The final age model does not show any large change in the sedimentation rates along the 1450 year-record, and does not call for any more hypotheses. The comparison between the Clam- and Bacon-modelled age-depth curves points to the same chronological trend but the Clam model provide a better fit of the radionuclides activity markers. The 20th century chronology is essential in this study, hence Clam-model was chosen.

4.2 Sedimentation rates

The resulting sedimentation rates obtained with the Clam age-depth model are of 0.2 cm.yr⁻¹ to 0.3 cm.yr⁻¹ from 563 to 1913. From 1913 to 1968, sedimentation rate increases as and varies between 0.5 and 1 cm.yr⁻¹, corresponding to the change of core, which is interpreted as a difference in compaction due to both different coring methods and porosity. However a drastic -and unexpected for a top core interval- decrease towards smaller values around 0.3 cm.yr⁻¹ is observed since the 1960's. Although coring locations of KK-8 and Ku-IV are located distally from the Dranse and Rhone River deltas (Kremer et al. 2015a, b), sedimentation rates follows a general trend also observed in seven cores located more proximally to the Rhone River delta (Silva et al. 2016). Indeed, deep Lake Geneva sediment is mainly driven by changes in the sedimentary load of the rivers (Loizeau and Dominik 2000). The recent decrease in sedimentation rate observed in this study but also in Silva *et al.* (2016), is certainly related to the decrease in the sediment load of the Rhone River system since the 1960s (Loizeau and Dominik 2000). This change in sediment load is explained by the strong modifications in the hydrology and sediment routing of the Rhône catchment (Bakker et al. 2017) that happened after the building of several major hydropower systems in Wallis (Loizeau and Dominik 2000).

217 The combination of different dating methods crossed with a good knowledge of Lake Geneva
218 sedimentation dynamics (Loizeau and Dominik 2000) and hydrological historic events (Kremer
219 et al. 2015a, b) allowed to build an age model for the sediment record with relatively low age
220 error. This was crucial as we later compared the plankton dynamics reconstructed from the
221 sediment to an independent climatic record (see main text).

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Reframing Lake Geneva ecological trajectory in a context of multiple but asynchronous drivers

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Supplementary Material S2 – Total Phosphorus in Lake Geneva: long-term monitoring data and inference from diatoms assemblages

Lake Geneva total phosphorus concentrations (TP) have been measured once or twice a month at the deepest point of the lake since 1958 (Système d’Observation et d’Expérimentation au long terme pour la Recherche en Environnement – Observatoire des LAcs alpins – <http://www6.dijon.inra.fr/thonon/L-observatoire-OLA>). In the first years of available monitoring data i.e. from 1958 (first full year), TP concentrations in the epilimnion were around 12 $\mu\text{g TP.L}^{-1}$ but already within an increasing trend confirming that eutrophication had already started. TP reached 79 $\mu\text{g TP.L}^{-1}$ in 1970, stabilized transiently around 50 $\mu\text{g TP.L}^{-1}$ in the 1972–1986 period, and has been decreasing since then. Current TP concentrations are similar to those measured during the beginning of the monitoring (close to 15 $\mu\text{g TP.L}^{-1}$) (Fig. S2.1). In order to extend the TP record beyond 1958, total phosphorus concentrations (0-20 m) were inferred from the composition of subfossil diatoms in LEM10-CC. Previous works on short cores, covering 1880-2010, had confirmed that diatom-inferred TP provide reliable estimates in Lake Geneva (Berthon et al. 2013) and capture changes in epilimnetic (0-20m) TP concentrations above 8 $\mu\text{g.L}^{-1}$.

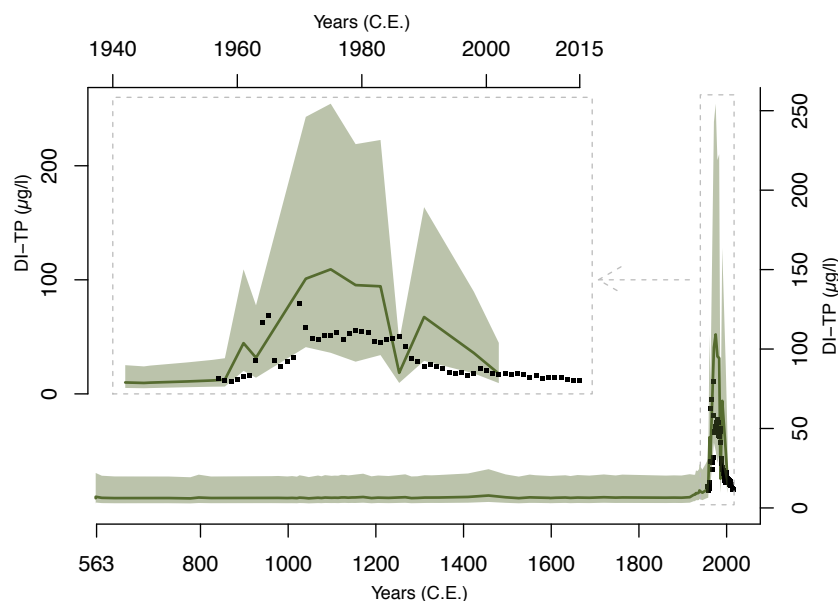


Figure S2.1. Total phosphorus (TP) in Lake Geneva. Solid green line corresponds to diatom inferred TP (DI-TP) from LEM10-CC core. Green envelop depict the interval of confidence (95%) of the DI-TP, calculated by bootstrap with 1000 iterations. Black squares are epilimnetic TP from long-term monitoring (1958–2015, SOERE OLA). The top-left graph shows the detail for the 1940-2015 period.

Diatoms counting were carried out on sub-samples of LEM10-CC. Sub-samples for diatom analysis were cleaned with H_2O_2 and HCl following Renberg (1990). Diatom frustules were mounted in Naphrax. On each slide, at least 300 valves were counted and identified by light microscopy, using phase contrast with $1000\times$ magnification, following Krammer and Lange-Bertalot (1986, 1988, 1991a, b). Description of changes in the diatom assemblage was done resorting to stratigraphically constrained hierarchical clustering (CONISS), using R version 3.1.2 (R Core Team 2014), as well as the *rioja* package (Juggins 2015). Mean total phosphorous concentrations were reconstructed from a diatom-based inference model based on 345 surface sediment samples collected in lakes in Europe along a trophic gradient (<http://craticula.ncl.ac.uk/Eddi>, Battarbee et al. 2001). The calibration dataset covered a large trophic gradient, with mean annual TP ranging from 2 to $1189 \mu\text{gP.L}^{-1}$. Reconstruction was performed, using weighted averaging with inverse deshrinking (ter Braak and van Dame 1989). The root mean squared error of prediction (RMSEP) was calculated for each sample set using bootstrapping with 1000 cycle. Diatom profiles and lake DI-TP reconstruction were performed using program C2 (version 1.7.2, Juggins 2007).

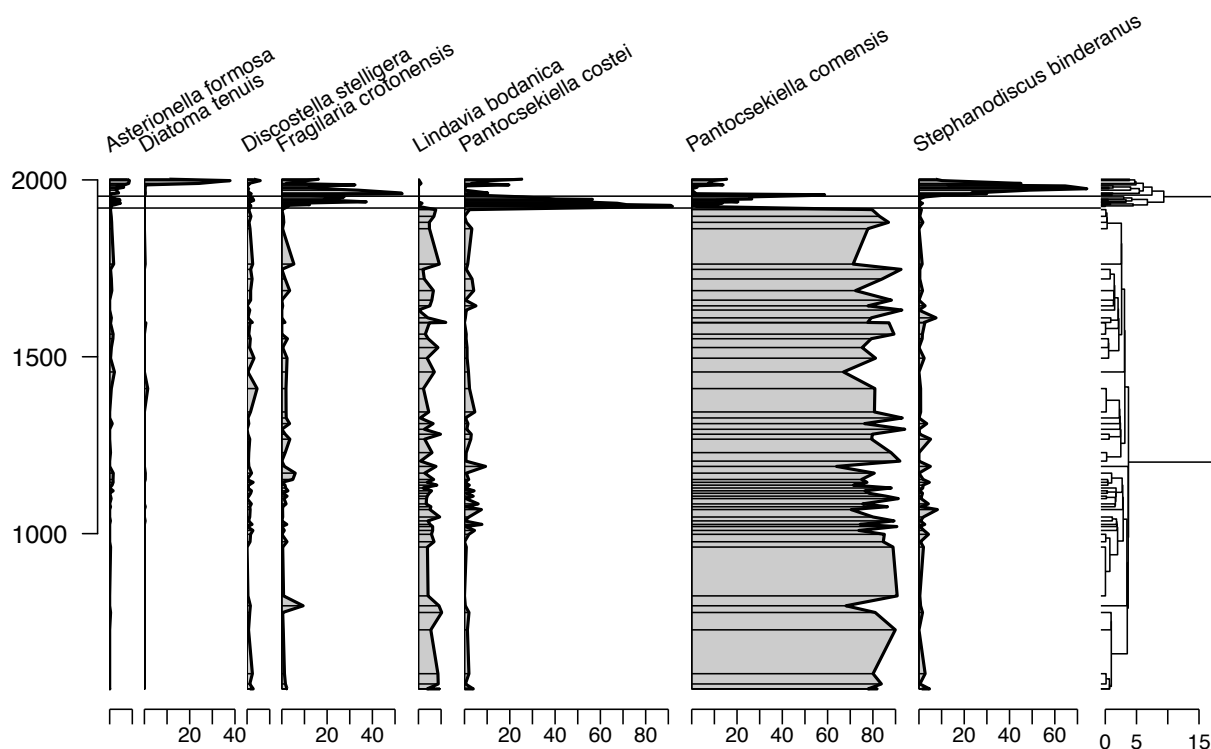


Figure S2.2. Summary diatom stratigraphy of the most common taxa in Lake Geneva LEM10-CC sequence. The horizontal lines mark the two significant changes in diatom assemblage at the scale of the study.

The paleo-record, on which a hierarchical CONISS analysis was performed, revealed two significant changes in the subfossil diatom assemblage of Lake Geneva between 563 and 2010, and both took place in the 20th century (1916 / 1925 and 1952 / 1956) (Fig. S2.2). Before 1916, the assemblage was largely dominated by the centric species *Pantocsekiella comensis* (70-80 %), seconded by *Lindavia bodanica* (5-10 %), both species typical of oligotrophic waters. The subfossil diatom record had been stable for the whole 1400 year-long record (Fig. S2.2). Only a slight 8% increase of *Pantocsekiella costei* during the 11th century was worth noticing. Inferred-TP were thereby stable and low ($< 14 \mu\text{g.L}^{-1}$) before the 20th century, typical for an oligo/oligomesotrophic lake. From 1925 and up to 1952, *P. comensis* got substituted by *Pantocsekiella costei*, another species affiliated to nutrient poor waters. *Fragilaria crotonensis* made up to 50% of the assemblage. *F. crotonensis* is somewhat distinctive of waters with higher nutrient levels. The increased contribution of *F. crotonensis* could thereby illustrate a slow and slight increase in TP as soon as the 1920s. Thereby inferred TP remained below $14 \mu\text{g.L}^{-1}$ for this time-period, excluding any important human driven change in TP in the lake before the 1950s. The second transition in 1952 / 1956 marked the loss of *Pantocsekiella* sp., while *F.*

crotonensis declined in favor of *Stephanodiscus binderanus* that represented up to 74% of the assemblage in 1971. This specific succession is typical for eutrophication and not surprisingly, inferred TP increased up to 109 $\mu\text{g.L}^{-1}$ in 1979, mirroring measured trends in total phosphorus concentrations. Not significant at the time-scale of the study, was the recent reorganisation (in the four-top-most samples of LEM10-CC i.e. reflecting a change in the interval of 1983 / 1986) with a return of *Pantocsekiella* sp. (< 20% vs. > 70% before 1916), and new species i.e. *Asterionella formosa* and *Diatoma tenuis*. The most recent part of the record thereby reflected the recent abatement in water TP. The good coherence between DI-TP and measured TP, as well as the confidence in the age models, allowed the creation of a composite TP record (thereafter referred as to inferred TP, I-TP). DI-TP was used up to 1958 and monitoring data thereafter, avoiding any uncertainties linked to reconstructions.

Changes in diatom inferred-TP are considered as representative and indicative of the local human activities in the lake watershed (Battarbee et al. 2005). Juggins *et al.* (2013) noted that a number of calibration data sets for diatoms infer secondary gradients and not the major gradient affecting diatom species composition. Indeed, weighted averaging calibration assumes that the species respond to an environmental gradient (e.g. [TP]) according to a Gaussian distribution and that the taxa with an ecological optimal TP close to that of the lake will occur with greater abundance. However, the calibration used (Battarbee 2000) was mainly based on the classic trophic sequence from *Pantocsekiella comensis* to *Asterionella/Fragilaria crotonensis* to *Stephanodiscus* (Harris 1987), which reflects the known ecology of the main planktonic diatoms (Willen 1991; Hall and Smol 2010) and was, therefore, considered reliable (Juggins 2013, p384). The reliability of the diatom inferences based on this sequence has been shown in the present study and elsewhere by comparing the DI-TP with historical TP values (e.g. Marchetto and Bettinetti 1995). However, because a small lag in diatoms responses in Lake Geneva has been documented, we used a composite TP record (DI-TP until 1957, monitoring data from 1958), thereafter referred to as I-TP. The confidence in I-TP is very high as the first changes in diatoms communities took place at the beginning of the monitoring program.

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