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

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Abstract Regime shifts are major reorganization of ecological processes, creating new sets of mechanisms that drive the new ecological regime. Such rearrangements can affect how and how much the system responds to pressures other than those that created the shift (interactive carryover). Lake Geneva still exhibits high levels of productivity despite reductions in phosphorus to its reference baseline; the continued high productivity is likely due to the synergistic effects of climate change. We tested whether the contemporary Lake Geneva plankton community response to air temperature, one symptom of climate change, differed from the responses to past changes in air temperature. We used paleoecology to quantify the changes in plankton communities, as a proxy of general ecological changes, over the past 1500 years. Our results show that from 563 AD (beginning of the record) to the twentieth century, the cladoceran assemblage remained stable, despite climate variability of 3°C in air temperature. The plankton community of Lake Geneva appeared to shift for the first time in the 1500 year record in 1946, and dynamic linear models suggested that 1958–1961 was a critical

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transition period when the ecosystem changed state. Littoral species were lost, and the assemblage became dominated by pelagic species. The shift took place around the beginning of the current long-term monitoring program, when local perturbations (eutrophication) were escalating. Our results suggest that eutrophication acted as a switch towards a lake more vulnerable to climate change.

**Keywords** Resilience · Climate warming · Eutrophication · Temporal ecology · Paleoecology · Interactive carryover

**Introduction**

Communities and ecosystems are shaped by multiple environmental pressures acting at different spatial and temporal scales (Wolkovich et al. 2014). Pressures are mechanisms of natural or anthropogenic origin causing an effect on a given ecosystem, whether it is at small or large scale, and may alter ecosystems state. An ecosystem state is the condition of the ecosystem that can be described quantitatively and qualitatively by its physical, chemical, and biological characteristics (Oesterwind et al. 2016). Multiple concurrent pressures, from local to global origins, may (1) complicate the identification of pressures responsible for changes (Simpson and Anderson 2009), (2) hide the effects of restoration measures by changing the baseline conditions (Battarbee et al. 2005), and (3) increase the risk of regime shifts (Rocha et al. 2015). A regime shift is a change between stable ecosystem state, typically when a pressure reaches a threshold in intensity; the change from one state to the other is referred to as tipping point. As local and global issues have become intimately linked, one popular view suggests that alleviating local human pressures on ecosystems should foster ecosystem resilience to global pressures, such as climate change (Scheffer et al. 2015a; Rocha et al. 2015), because 62% of identified pressures responsible for regime shifts in aquatic, terrestrial and subcontinental systems may be managed locally or regionally (Rocha et al. 2015).

The complexities and number of pressures on ecosystems yet hamper our ability to demonstrate how reducing local pressures may increase ecosystem resilience to climate change. In fact, some empirical observations on coral reefs show that their resistance to climate change symptoms (ocean acidification, higher water temperature) is higher (not lower) where local pressures already excluded disturbance-sensitive taxa, or when the two pressures mitigate each other (Côté and Darling 2010). Indeed, the idea that reducing one pressure will benefit the ecosystem only holds if this pressure and climate change have additive or synergetic effect, i.e., their combined impact is greater than, or the sum of, their impacts taken separately. However, in an assessment for marine systems, 43% of interactions between pressures had an antagonist effect, i.e., their combined effect is lesser on the studied organization level (population, community) than the sum of each stress taken separately (Piggott et al. 2015). In such a situation, the two pressures mitigate one another, and reducing only one pressure can either have little effect or worsen the impacts of the second pressure.

Additive, synergetic, and antagonistic effects continue to be studied when both pressures act simultaneously, but we suspect these effects can also be relevant when pressures act asynchronously. A number of studies acknowledge that the impact of the same pressure can have different consequences depending on the antecedent state of the ecosystem and its previous exposure to the same or other pressure (Perga et al. 2018; Ryo et al. 2019). Frequent exposure to the same pressure can result in accumulative carryover, if a system responds differently to the same level of perturbation due to a short-term memory. For example, the stratification pattern of high altitude lake during summer following a rainfall can remain relatively unchanged or be disrupted over several days depending on the frequency of previous rainfalls that whipped out or not the watershed from its sediment (Perga et al. 2018). Ecosystems can furthermore show long-term memory of being exposed to a pressure; interactive carryover describes a situation

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where a system will respond differently to a pressure depending on its prior exposure or absence of exposure to another pressure. In fact, any system that underwent a regime shift is likely to respond differently to other pressures too, because the characteristics of the ecosystem (the ecosystem state) changed. To our knowledge, the concept of interactive carryover has only been discussed at short time scales (Ryo et al. 2019).

Lake Geneva (CH, FR) is a large peri-alpine lake in Central Europe. A long-term monitoring program initiated in 1957 captured the onset of the eutrophication, when total phosphorus (TP) went from 10 µg L\(^{-1}\) (close to background levels, inferred at 6–8 µg L\(^{-1}\) from diatoms, Berthon et al. 2013) to 50 µg L\(^{-1}\) in the early 1960s, and up to 90 µg L\(^{-1}\) in the late 1970s (Rimet et al. 2020). Initial evaluations, using correlation between TP and phytoplankton biomass, established that levels around 20 µg L\(^{-1}\) would allow restoration of Lake Geneva. Eutrophication was tackled by the effort of Swiss (first) and French (later) politics from the late 1970s. The 20 µg L\(^{-1}\) target was reached a decade ago without any quantifiable decline in algal biomass or production (Tadonlélé et al. 2009). However, other anthropogenic pressures may have promoted algal growth during this time (Tadonlélé et al. 2009; Alric et al. 2013). Thereafter, the restoration goal was adjusted to 10–15 µg L\(^{-1}\) 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). Inter-annual plankton community is not responding to further nutrient concentrations reduction and is instead responding to climate change (Perga et al. 2015). While the extent of the 1970s eutrophication has likely no antecedent in Lake Geneva, summer air temperature (SAT) anomalies fluctuated within a range of 3 °C (Büntgen et al. 2006) over the period of 800–1800 AD. These fluctuations have a similar amplitude to variations observed over the twentieth and twenty-first centuries, but it is unknown how the lake ecology responded to these previous fluctuations.

We hypothesized that eutrophication was the main driver of ecosystem changes (Carpenter 2005; Dong et al. 2012), and tested the hypothesis that Lake Geneva underwent a regime shift as a result of the twentieth century eutrophication. We also tested the hypothesis that critical transitions can 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). If so, we tested whether its plankton community responded to previous warming episodes differently from its current response to similar warming as a result of interactive carryover. We use paleoecology to characterize the planktonic communities over the last 1.5 millennia. 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 and evaluate whether there had been any previous eutrophication episode (Wunsam and Schmidt 1995), while sub-fossil cladocerans were regarded as a proxy for ecological responses. Cladocerans are sensitive to changes in the environment, and their temporal patterns record bottom-up changes in resources, alterations in habitat structure, and diversity and top-down impacts of predation (Davidson et al. 2011). To test our hypotheses, we first used multivariate analyses to visualize the trajectory of Lake Geneva cladoceran assemblage. Then, we applied dynamic linear models to assess whether any transition period was critical (Taranu et al. 2018). Finally, we used General Additive Models to identify the contribution of local versus climate pressures (Wood 2016).

Study site

Lake Geneva is the largest lake of Western Europe, with a maximum depth of 309 m (Fig. 1). The human population in its watershed has increased threefold since the late nineteenth century, directly initiating the well documented eutrophication. Restoration efforts successfully reduced nutrients concentration such as observed phosphorus concentration in Lake Geneva has been below 20 µg L\(^{-1}\) since the 2010s. Although Lake Geneva’s hydrological function had been impacted since the first dam was built in the late nineteenth 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 twentieth 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).

Materials and methods

Sediment record and dating

A paleo-record dataset was built using two sediment cores (KK8 and Ku-IV) 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 14C measurements (Kremer et al. 2012), and new paleomagnetic secular variations measurements for the deeper section (Fig. 2). Details are given in Electronic Supplementary Materials 1 (ESM1).

Selection of climate data

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 1500 years in central Europe. A notably cold period was likely triggered by a volcanic eruption in the “Dark Age”, 536–660 AD (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, 1850-present) (Abram et al. 2016), mainly attributed to human impact.

Climate fluctuations over the past millennia are marked by significant regional offsets (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 established from tree-rings width time series for 180 larch (Larix decidua Mill.). Recent and historic trees come from the Rhône valley, directly linked to Lake Geneva (Büntgen et al. 2006). The record goes back to
755 AD, corresponding to the last 1250 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 (ESM2). 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 Szeroczyńska and Sarmaja-Korjonen (2007) and an Olympus BX41 microscope at 100–200 magnification.

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 dynamic linear models (DLMs) (Pole et al. 1994) to evaluate whether any transition had the characteristics of critical transitions (Taranu et al. 2018). Briefly, 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) (Taranu et al. 2018). The method accounts for differences in compaction and mixing, which are frequent in paleorecords but can impact detection of changepoint by traditional methods. 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 (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. The relative contribution of changes in I-TP and climate (SAT anomalies) to the dynamics of PCA scores were assessed by using the Generalized Additive Models (GAM). The final GAM were chosen by computing models using I-TP and SAT as covariates, and the best models were chosen following the AIC. Then, the choice to include or not a correlation structure (AR (1) or CAR (1) to account for uneven sampling) was made using the log-likelihood of each model (Wood 2016). The
competing forcing variables and their effects were separated based on the computed contribution of each covariate to the fitted model (Simpson and Anderson 2009). Computational work and visualization was using R version 3.6.3 (R Core Team 2020).

Results

Age model

The excess $^{210}\text{Pb}$ profile measured on core KK8 showed a regular decrease punctuated by two drops in $^{210}\text{Pb}$ on the profile (Fig. 2a). Following the lithology and Arnaud et al. (2002), these low values of $^{210}\text{Pb}$ refer to instantaneous deposits and thus were excluded from the construction of the event-free sedimentary record. $^{210}\text{Pb}$ activities plotted on a logarithmic scale revealed two different mean sedimentation rates (SR), respectively of $0.23 \pm 0.04$ cm year$^{-1}$ above 12.1 cm (event-free sequence) and $0.83 \pm 0.23$ cm year$^{-1}$ 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 AD for the event layer t2 (turbidite). The $^{137}\text{Cs}$ activity profile reveals two peaks at $5.5 \pm 0.5$ cm and $15.5 \pm 0.5$ cm, corresponding respectively to 1986 (Chernobyl accident) and 1963 (atmospheric atomic tests) (Appleby et al. 1991). Below 23.5 $\pm$ 0.5 cm, the recorded $^{137}\text{Cs}$ activities are close to zero, pointing to a sequence deposited before 1955 (first $^{137}\text{Cs}$ fallout) (Appleby et al. 1991). These three $^{137}\text{Cs}$ markers are in good agreement with the CFCS age model over the last century which confirms its reliability (Fig. 2a).

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 (ESM1, Table S1.2): (i) the coring year, (ii) three time-markers from $^{137}\text{Cs}$ activity, (iii) the age of turbidite t2 dated from $^{210}\text{Pb}$ 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 563–1940 period (Fig. 2a). Our results show that the “recent” cladoceran assemblage is radically different from the one characteristic of the 563–1940 period (Fig. 3e, f). Major ecological changes were summarized by two principal components of the cladoceran assemblages (Principal Component 1 (PC1) and PC2, Fig. 4) 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. 4a). For clarity purposes, we grouped the remaining species in a group “others”. These species are mainly littoral (macrophyte and/or sediment associated, Fig. 4b).
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 *E. longispina*, the earliest postglacial colonist in alpine lakes (Nauwerck 1991), and *Sida crystallina* var. *limnetica* (O.F. Müller 1776) (Fig. 3e, 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 twentieth century. From the 1940s, the absolute abundance of both *Daphnia* spp. and *S. crystallina* increased (Fig. 3d). This period likely marks a period during which the food elemental quality improved, benefiting to *Daphnia* spp. that has high stoichiometric thickness and sedimentation rate.
Levels of phosphorus increased, but under a threshold that prevented any restructuring in the phytoplankton assemblage (ESM2) (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 $< 10 \mu g \text{l}^{-1}$ TP-range, since the resulting light limitation would have compromised the maintenance of the macrophyte-associated specie. From the early 1960s, when concentration went beyond $10–20 \mu g \text{l}^{-1}$ TP, 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 scores on cladoceran assemblage, including a significant smooth term for I-TP, Dev. Expl. = 79.4%, df = 4.077, $F = 55.99, p < 0.001$, Fig. 5) (Alric et al. 2013), and occurred at a relatively low I-TP threshold of $10–20 \mu g \text{l}^{-1}$ TP.

Between 1946 and 1961 AD, the pristine Lake Geneva, hosting both littoral and planktonic habitats, shifted to an anthropogenic impacted, plankton-dominated state. Since the late 1980s, abundance of the predator Leptodora kindtii (Focke 1844) increased, concomitant with air temperature warming in the alpine region (Alric et al. 2013; Woolway et al. 2017).

The best DLM was obtained for a lag of 1 and a delta of 0.84, and gave a $R^2$ of 0.80, and indicates a transition in 1958/1961 (Fig. 6c). 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 ($R^2 = 0.79$ 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 $R^2$ and delta. The DLM suggests that the change in cladoceran assemblage in 1958/1961 is a critical transition (Fig. 6c).
Discussion

Large lakes are not typically considered as vulnerable to critical transitions between stable states, because most feedbacks associated with stable states in lakes are linked to the littoral zone, which represents a relatively small amount of habitat in large lakes (Hilt 2015). However, our case study on Lake Geneva suggests that critical transitions can occur in large lakes, and they would occur at a lower nutrient level than levels considered critical for shallow lakes (Hilt et al. 2010; Bruel et al. 2018). After 1200 years of ecological stability despite changes in air temperature, seemingly low levels of phosphorus triggered a critical transition in Lake Geneva. The timing of the critical transition caused by eutrophication matches the loss of the littoral zone and the strengthening of top-down control.

Fig. 5  

**a** Fitted smooth function for I-TP from the final GAM for the cladoceran assemblage PC1 scores with approximate 95% pointwise confidence intervals on the fitted functions (grey bands). The tick marks inside the panels on the x-axis show the distribution of observed values for the two covariates. The number in brackets on the y-axis (4.08) is the effective degrees of freedom for the smooth function. When the smooth function as positive scores, the function predicts levels of I-TP (I-TP > 10–16 µg l⁻¹) are favoring cladoceran species with horizontal diversity) and gained a predator, *Leptodora kindtii*, increasing its vertical diversity. *Leptodora kindtii* was a consistent component of the assemblage but its relative numerical abundance was < 1% until the 1980s, while it now represents > 10% of the assemblage (Alric et al. 2013). High horizontal and vertical diversity respectively increase and decrease stability to large perturbations (Zhao et al. 2019). Littoral areas could thus be functionally crucial components of habitat heterogeneity, biodiversity, and resilience, even in a large and deep lake for which their representability is always minor (Vander Zanden and Vadeboncoeur 2002).

Before the 1950s, the ecological status of Lake Geneva, as mirrored by cladoceran and diatoms communities, appeared invulnerable 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 twentieth and twenty-first centuries. 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 may have 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 samples disproportionately represent the period of resistance (pre-twentieth century), and thus the decoupling between climatic signal and ecological response.

Ryo et al. (2019) conceptualized and reviewed examples of such interactive carryover, i.e., when a prior pressure changes an internal parameter or mechanism of a system, which leads the system to respond to a posterior pressure differently (more, or less, depending whether pressures act synergistically or antagonistically) from how it would have responded without the experience of the first pressure (Fig. 7). 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, further supports that the recent vulnerability to climate is an example of interactive carryover. 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 but nutrient levels that remained low. Lake Annecy surface water temperature increased by 4 °C between the 1970s and the 2000s (+2.5 °C in Lake Geneva) but the cladoceran assemblage did not
change, exhibiting greater resistance (Perga et al. 2015).

The idea that, in the face of multiple pressures, managers could build resilience to continued global change through actions that address local or regional pressures, is often presented (Rockström et al. 2009; Scheffer et al. 2015a; Rocha et al. 2015). More specifically, if two pressures have similar impacts on the ecosystem, then the level of pressure 2 allowing the system to operate in its safe operating state under low levels of pressure 1, may be too high if the level of pressure 1 increases (Scheffer et al. 2015a). Our findings expand this idea by showing that there is a legacy of pressure 1 in the response to pressure 2 (Fig. 7, Battarbee et al. 2005). In Lake Geneva, eutrophication acted as a switch from a regime of resistance to a regime of frequent restructuring, and a more vertical food web structure. As a consequence, if

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**Fig. 7 a** Idealized diagram illustrating temporal ecological response of Lake Geneva to increasing and decreasing pressures, 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 pressures. **b** Our findings suggest the baseline may have changed at a tipping point. As a perspective, we question whether vulnerability to pressure 2 (e.g., climate) is true only after pressure 1 (e.g., eutrophication) decreased the resilience of the system.
local pressures must be reduced to build resilience, reduction needs to be done before the ecosystem has been pushed beyond its limits (Fig. 7b).

Detailed observations by the pioneer limnologist FA Forel at the beginning of the twentieth century reported thriving macrophytic, charophytic belts around Lake Geneva 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). Macrophyte surveys in 1975, 1997, and 2009 indicate a much more depauperate littoral zone (Perfetta 2011). If the littoral zone is key to the resistance of Lake Geneva to past climatic variability, then efforts to restore the littoral areas should be sustained. Lake Geneva charophytic vegetation shows sign of recovery, and are faster to recover than macrophytic beds because they depend solely on water to absorb nutrients (Perfetta 2011). Macrophytic beds would also require reducing the encroachment of urban infrastructures on the littoral zone (rockfill, seawalls, channelling of small tributary streams, harbours).

While the loss of the littoral macrophytic habitat coincides with the loss of resistance towards climate variability, it remains unclear whether macrophytic habitat and resistance towards climate variability are linked by a causal relationship or whether both are the results of the same disturbance (eutrophication). If macrophytic habitat reduced vulnerability to climate change, there would be mechanisms in the littoral habitat acting as a buffer for fluctuating temperatures. Most of the research available on the role of littoral habitats was conducted on shallow lakes or streams (Kosten et al. 2009; Scrine et al. 2017). Littoral areas only occupy a few percentages of large lakes surface; whether this small share hold mechanisms sufficient to confer resilience to large lakes remains to be demonstrated. Future research should investigate the functional role of littoral areas in large lakes.

Ecosystems evolve over timescales that are impossible to experience by a human eye (Wolkovich et al. 2014), yet humans are the ones responsible for their management (Vitousek et al. 1997). Managers have the difficult job of making decisions of which they may never see the results. The short (at the scale of Lake Geneva history) eutrophication episode triggered long-lasting effects in the ecological state of the system (interactive carryover, Ryo et al. 2019). Long-term ecological research networks undoubtedly provide invaluable knowledge on ecosystems specificities and frameworks for ecological theories (Maberly et al. 2018), and restoration goals. Yet, our result raises the vexing observation that the historical dataset for Lake Geneva initiated in 1957, despite being one of the longest series in the world, may not provide an adequate reference for the Lake Geneva ecological baseline condition. The newest generation of managers may only know Lake Geneva as an ecosystem undergoing re-oligotrophication. Could this lead to an example of “shifting baseline syndrome” (Pauly 1995)? The syndrome 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 re-oligotrophication as the contemporary process and the eutrophication period as its history. We must acknowledge that Lake Geneva (and most systems) were highly different for millennia before the Anthropocene (Steffen et al. 2015). To prevent increased tolerance for environmental degradation, we must set appropriate baselines for conservation, restoration, and management (Soga and Gaston 2018).
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