Seeking alternative stable states in a deep lake

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Abstract

1. Hysteresis linked to alternative stable states may explain delays in water quality recovery despite reduced nutrient loadings in shallow lakes. Because deep lakes are assumed to be less prone to critical transitions, similar delays are attributed to the confounding effects of additional environmental disturbances, such as climate warming. Herein, we hypothesised that the lack of evidence of nutrient-driven alternative stable states in a deep lake arises from the fact that the nutrient threshold that causes the critical transition is lower than the nutrient threshold in shallow lakes. Thereby, it might have been crossed much earlier in the lake history.

2. To test this hypothesis, we focused on the palaeo-ecological trajectory of Lake Varese, which is a deep, hypereutrophicated peri-alpine lake undergoing restoration. Proxies for drivers of ecological state (i.e. total phosphorus—TP—through diatoms and pigments) and ecological responses (Cladocera), as well as a repeatable analysis, were used to identify transitions and to distinguish hysteretic delays from those of the ecosystems responding to additional constraints over the past century.

3. Our results suggest spatial heterogeneity in the ecological response. The littoral habitats changed abruptly and prematurely for a low TP threshold, causing a shift that met many criteria of a flickering-type critical transition. Soon after the littoral shift, a striking increase in the lake phosphorous concentration was recorded and drove the pelagic assemblage towards a new state. This transition was abrupt, and the pelagic communities exhibited limited evidence of recovery; however, we found no evidence of hysteresis. Therefore, the modern ecological trajectory of the pelagic communities is currently driven by climate warming.

4. This detailed analysis allowed us to go beyond the general pattern that links ecological responses to drivers and suggest that a nonlinear transition following eutrophication can take place in a deep lake synchronously with linear transitions. Instead of triggering a new regime shift, climate warming, to which pelagic habitats are more sensitive than littoral ones, has driven the lake further from its safe operating space.

KEYWORDS
alternative stable state, early warnings, eutrophication, palaeo-ecology, spatial heterogeneity
INTRODUCTION

Because man-made eutrophication has been held up as the most important threat on lake water quality over the last 60 years (Schindler, 2006), primary management actions have consisted of controlling and reducing external nutrient loadings into lakes (Jeppesen, Søndergaard, & Liu, 2017). These initiatives have been successful in some cases (Edmondson, 1991), but most of the time, result in incomplete recovery (Sas, 1989) and decades-long delays in lake response (Jeppesen et al., 2005). Delays are manifested either as a weak response of lake nutrient concentrations to decreased nutrient loadings (Larsen, Schults, & Malaeug, 1981) or as limited reinstatement of water transparency despite decreases in lake nutrient concentrations (Anneville, Souissi, Molinero, & Gerdeaux, 2009). When the latter situation is observed in shallow and unstratified lakes, one hypothesis is related to the hysteretic response of primary producers following a nutrient-driven critical transition (Scheffer, Carpenter, Foley, Folke, & Walker, 2001; Scheffer & van Nes, 2007).

Shallow lakes have long been archetypal systems for testing regime shift theories (Jackson, 2003; Scheffer & van Nes, 2007; Scheffer et al., 2001), in which the specific feedback mechanisms responsible for alternative turbid and clear-water stable states are mostly tied to water mixing, sediment resuspension and macrophyte interaction with water clarity (reviewed in Hilt, 2015). Because the relative magnitude of all three processes decreases with lake size and depth (Janssen et al., 2014), the stabilising mechanisms responsible for alternative stable states are generally assumed to be limited in larger, deeper and thermally stratified lakes (Capon et al., 2015; Scheffer & van Nes, 2007). In fact, for lakes, which have a maximum depth that exceeds 10 m (Genkai-Kato & Carpenter, 2005; Hilt, 2015; Hilt, Henschke, Rücker, & Nixdorf, 2010), linear or continuous, rather than discontinuous responses to nutrient concentrations are expected (Janssen et al., 2014; van Nes & Scheffer, 2005).

Generally, in deep lakes, the delayed and incomplete recovery of water transparency is regarded as an outcome of additional human disturbances (including climate warming, Alric et al., 2013; Jeppesen et al., 2005; Perga et al., 2015) driving the system to a new ecological trajectory (Battarbee, John Anderson, Jeppesen, & Leavitt, 2005; Bennion, Simpson, & Goldsmith, 2015). Indeed, climate change can impact lake ecosystems through several direct and indirect pathways, including a lengthening of the stratification period and enhancement of hypoxia, both promoting P release from the sediment, changes in water level or nutrient loadings, or temperature-induced changes in biotic interactions (Jeppesen et al., 2017).

However, recent studies provided evidence for alternative stable states in relatively deep lakes, with stabilising mechanisms that varied substantially as compared to shallow lakes. The deep (20 m) Lake Erhai, in China, has undergone a nutrient-driven regime shift in the early 21st century (Wang et al., 2012). Nutrient loadings from agriculture on Lake Erhai catchment increased continuously from 1960 up to 2000, resulting at first in a trend change in primary producers as long as the lake bottom was oxygenated. Twenty years of short-lived changes in the lake level (due to both human and climatic effects) acted as a trigger for bottom hypoxia and recycling of biologically available phosphorus from the upper sediment. Hypolimnetic oxygen depletion has created a positive feedback mechanism from which eutrophication boomed, and the lake shifted to an alternate attractor in 2001. Alternative stable states could also be experimentally triggered in the water column of deep lakes, manipulating top-down pressure (Seekell, Cline, Carpenter, & Pace, 2013). This fish-manipulation experiment suggests that in pelagic-dominated lakes, trophic cascades can shift a system from a stable planktivore-dominated state to an alternate piscivore-dominated state (Seekell et al., 2013). Hence, not only regime shifts might be possible in deep lakes, but due to the difference in the mechanisms in play, they could occur also at a much lower nutrient threshold than the one observed in shallow and small lakes (Janse et al., 2008; Scheffer & van Nes, 2007), whereas the range of nutrient concentrations for which two stable states coexist could be narrower (van Nes, Scheffer, van den Berg, & Coops, 2002).

Since the critical transition might have been crossed very early in the lake history, at rather low human disturbance levels and before any historical monitoring, potential hysteresis might be difficult to demonstrate with instrumental data in deep stratified lakes. Instead, because deep lakes are an ideal context for measuring sequential sedimentation, they provide an opportunity for high-resolution palaeo-ecological reconstruction (Perga et al., 2015) allowing to test for early nutrient-driven regime shifts triggering alternative stable states (Bunting et al., 2016; Randsalu-Wendrup, Conley, Carstensen, & Fritz, 2016; Wang et al., 2012).

We explored the long-term ecological dynamics of Lake Varese (northern Italy), which is a relatively large and deep lake that underwent drastic changes over the course of the 20th century. This lake became hypereutrophic in the 1950s. Phosphorus abatement measures efficiently cut lake nutrient concentrations by a factor 3 at first, reducing them to values more typical of eutrophic status (100 µg P L⁻¹), after which the lake has stabilised despite further management actions (Zaccara, Canziani, Roella, & Crosa, 2007). Rare monitoring data provide little observational evidence of ecological recovery of Lake Varese, despite 40 years of nutrient remediation (Zaccara et al., 2007). We aimed at testing whether the delay in the ecological recovery of this deep lake, under a reduction in phosphorus concentrations after hypereutrophication, arose from a hysteretic process (the hypothesis of alternative stable states due to an early nutrient-driven regime shift) or to the confounding effect of climate warming that has countered remediation measures (climate-warming hypothesis). To this end, the ecological state (sensu Mac Nally, Albano, & Fleishman, 2014) of the lake over the last 170 years has been reconstructed using subfossil cladoceran remains, along with the temporal dynamics of dominant environmental forces (Alric et al., 2013; Sayer, Davidson, Jones, & Langdon, 2010).

A sudden change in an ecosystem state variable is a necessary, albeit insufficient, condition of regime shift (Andersen, Carstensen, Hernández-García, & Duarte, 2009; Dakos, Carpenter, van Nes, & Scheffer, 2015; Spears et al., 2017). Indeed, an ecosystem state variable responding through a smooth and continuous pressure-status
relationship to a strong stepwise change of this driver over time (as, e.g., a sudden increase in phosphorus concentrations or the sudden atmospheric warming observed over Europe in the late 1980s, Woolway et al., 2017) would itself exhibit an abrupt change (Andersen et al., 2009) in the absence of any bistability (Dakos et al., 2015). Therefore, we used a multistep process aimed at testing all three necessary properties of a regime shift (sudden change, threshold-response and bistability, Andersen et al., 2009; Bunting et al., 2016). We also tested whether major abrupt breaks were preceded by a loss of resilience, manifested through increased variance and autocorrelation, that is expected signals for critical slowdowns (the recovery rate from small perturbations becomes very slow) and flickering (the system starts jumping back and forth between alternative basins of attraction) preceding a regime shift (Dakos et al., 2012; Scheffer et al., 2009). Finally, the settlement of a new stable regime shall be followed by a lower variability of state variables (Dakos et al., 2015; Scheffer & van Nes, 2007).

2 METHODS

2.1 Study site and climate

Lake Varese (45°48 N, 08°45 E) is a warm monomictic lake (14.8 km², z_max = 26 m) that is located 238 m above sea level in the subalpine region of north-western Italy (Figure 1). The two main tributaries, the Brabbia channel and the Tinella stream, have annual average discharges of 23 × 10⁶ and 10 × 10⁶ m³ year⁻¹, respectively. The water flows out through one effluent, the Bardello stream, whose annual average discharge is 80.4 × 10⁶ m³ year⁻¹. Lake Varese has a water renewal time of approximately 2 years (Provini, Marchetti, & Tartari, 1992). It qualifies as a hollow lake according to the basin shape index (Bi = 2.8; Meybeck, 1995) and, compared to lakes where regime shift studies were tested (Scheffer, Hosper, Meijer, Moss, & Jeppesen, 1993; Seekell et al., 2013; Van Donk, Gulati, Iedema, & Meulemans, 1993), we qualified it as a deep lake. Increased consumerism following the end of World War II (Scrivano, 2005) as well as the mass immigration of Italians to Milan and the north-western part of Italy in the 1950s and the 1960s (Foot, 1999) generated important demographic pressure on the region surrounding Lake Varese. Uncontrolled inputs of domestic phosphorus have led to lake hypereutrophication since the 1950s (>400 µg PL⁻¹ in 1975) (Istituto di Ricerca Sulle Acque, 1980), with negative consequences for the local fish populations that have been exploited since 1900. Remediation actions were conducted nationwide to reduce the P load in fresh water based on the first water quality law in 1976 (with successive regulations of a maximal allowed percentage of P in detergent). Subsequent local P abatement measures (a new wastewater treatment plant in

![Figure 1](image1.png)
1994) led to a 68% reduction in the external load, and the lake reached eutrophic status in the late 1990s (117–130 μg P L⁻¹) (Crosta, 1999) but stabilised thereafter, despite further reductions of inputs. Complementary measures to limit P release from sediment (hypolimnetic water withdrawal and oxygen injection) from 2000 to 2003 had no better success at reducing TP concentrations. The internal P loads, inherited from the past hypereutrophication phase and remobilised from the sediment through bottom hypoxia, might be responsible for maintaining TP concentrations at levels typical of eutrophic status. Again, it is yet unclear whether this resistance to remediation is the result of hysteresis (Genkai-Kato & Carpenter, 2005) or climate warming fostering bottom hypoxia (Jenny et al., 2014).

The climate of the region is subcontinental and temperate, with warm and dry summers and cool and wet winters. The data sets of annual, winter and summer air temperatures, as well as precipitation, were extracted from the gridded HISTALP data set (Auer et al., 2007) according to lake geographical coordinates for the time period covered by the sedimentary records (1837–2010). The data show a significant trend in atmospheric temperature over the last 100 years (Mann–Kendall = 0.50, p < 2.66 × 10⁻¹⁶), with an initial slow increase from 1900 to 1980 (+0.1°C/decade), which was reinforced by a significant shift in the mid-1980s (+1°C in 5 years). Such a trend is common to the overall European region (Woolway et al., 2017). A weak, yet significant, decreasing trend in local annual precipitation has been detected (Mann–Kendall = −0.15, p < .004).

2.2 | Coring & dating

A sediment core (VAR 10.10 74 cm long) was collected in 2010 using a gravity corer with a PVC tube from the lake’s deepest zone (45°49’51” N, 8°43’08” E). Half of VAR 10.10 was sliced at a 1-cm interval and was used to count diatoms and cladoceran, as well as to measure pigments. The chronology was based on 210Pb, 226Ra, 137Cs and 241Am activities measurement using gamma spectrometry, carried out in September 2010 on a reference core (VAR 10.4 89 cm long). In every 1 cm of the first 28 cm of core VAR 10.4, the (210Pb unsupported) excess activities were calculated by subtracting the (226Ra-supported) activity from the total (210Pb) activity. Lake Varese sediment presents a laminated facies, characteristic of deep water anoxic conditions (Jenny et al., 2013) in their topmost portion. The number of laminae compared with the age model (on VAR 10.4, the dated core) allowed us to confirm that the sediment was annually varved. Varve counting could then be used to validate the age model and to correlate the dates between the VAR 10.4 and VAR 10.10 cores.

2.3 | Inferred water [TP]

Only sporadic TP measurements were available. The mean total phosphorous (TP) concentrations were reconstructed using diatom and pigment-based inference models. The two proxies were combined because both methods present well-known limitations. On the one hand, the diatom responses to perturbation may be delayed (Davidson et al., 2011) and could give seasonally biased results, as diatoms are often most abundant in the spring and autumn (Reynolds, 1984). Therefore, diatom-inferred TP does not necessarily capture changes in TP at low concentrations (Berthon, Alric, Rimet, & Perga, 2014). On the other hand, pigments are known to be sensitive to early changes in pressure (Bunting et al., 2016; McGowan et al., 2005), but they do not reflect TP concentrations when P is no longer a limiting factor, which is the case at very high TP levels. To compensate for the limitations of each of these inference methods, we compiled a composite inferred-TP (I-TP), in which Carl-TP was used until 1946 and DI-TP thereafter, as an independent driver for ecological changes in the analysis. The individuals DI-TP and Carl-TP, such as the validation for I-TP, are presented extensively in Appendix S1.

2.4 | Subfossil cladocerans

The cladoceran remains were analysed according to Frey (1986). More than 400 cladoceran remains were counted and identified per sample (headshields, shells, post-abdomens, post-abdominal claws, mandibles and others) using the Szeroczyńska and Samaja-Korjonen keys (2007) and an Olympus BX41 microscope at 100–200 magnification. Bosmina were determined to the species level (B. longirostris, E. longispina and E. coregoni), as well as chydorids, whenever possible. Given their taxonomic complexity, Daphnia spp. were identified to the genus level.

2.5 | Statistical analysis

Data aggregation and statistical analyses were performed using R version 3.1.2 (2014-10-31) (R Core Team, 2014), as well as the packages cited below. The main changes in the cladoceran community over time were summarised using a multivariate ordination method, comparing a principal component analysis (PCA) and detrended correspondence analysis (DCA) ordinations performances (package “vegan,” Oksanen et al., 2016). The DCA explained more variance in the data set than the PCA and was thereafter selected. We used information summarised in the orthogonal principal components and the known taxa ecological preferences (Bjerring et al., 2009; Hann, 1989) to describe the main changes in the community structure. Change-point analysis (package “changepoints,” Killick, Haynes, Eckley, Fearnhead, & Lee, 2016) was used to estimate the changes in the series mean. Because DCA can spread long or dominant gradients over several ordination axes (Simpson & Birks, 2012), we tested the analysis on several ordination axes. Changes in the mean DCA axes were assessed using the pruned exact linear time method and constrained with a penalty. Lower penalty values occurred when more change points were identified. The penalty was determined with Akaiake’s information criterion (AIC) and was verified manually by conducting an elbow plot. Bootstrapped series (1,000 iterations) were generated from ordination axes using the
The relative contribution of changes in TP (assessed from I-TP) and climate (air temperature and mean annual precipitation records) to the dynamics of DCA scores was assessed using the generalised additive models (GAMs) as in Alric et al. (2013). The final GAMs were chosen by computing models using various forcings as covariates, and the best models were chosen following the AIC. Then, the choice of whether to include a correlation structure was made using the log likelihood of each model (package “mgcv,” Wood, 2016). The competing forcing variables and their effects were separated based on the computed contribution that each covariate makes to the fitted model (Simpson & Anderson, 2009).

Finally, the DCA scores were plotted against the identified dominant drivers to detect threshold pressure-status relationships and potential bistability (state phase and F-density plots as in Wang et al., 2012).

Theoretical early warning signals (EWS) were sought for the identified transitions, and among the indicators that have been previously proposed, autocorrelation (AR(1)) and variance (SD) were chosen because these two are the most robust for time aggregation, which is typical of palaeo-ecological records (Frossard, Sausserau, Perasso, & Gillet, 2015). The theory behind rising AR(1) is that before an abrupt ecological change, feedbacks will progressively fail to maintain the ecosystem in its current state. When approaching a tipping point, the system will take more time to recover (i.e. return to the centre of the basin of attraction) from disturbances. As a result, wider fluctuations should be mirrored into an increase in SD. EWS were computed (package “earlywarnings,” Dakos et al., 2012) using a bandwidth of 5%–45% of the data set length (i.e. 8–70 years) to assess the robustness of the output (Spear et al., 2017). The analysis was also performed on a time series of the residuals (the observed values minus the local polynomial regression fitting through weighted least squares) and standardised to the square root of the corresponding period (to account for the irregular time resolution), as suggested by Carstensen, Telford, and Birks (2013), for varying time windows. Significant monotonic trends in AR(1) and SD (on the DCA scores and residuals) preceding the catastrophic transition were tested using Mann–Kendall’s rank correlation tests on various window sizes (6–15 data points, i.e. ca. 13–33 years) to test the robustness of the results. Finally, if an ecosystem entered a new alternative stable state, SD is expected to be low again because the return rates to the new stable state are high again. To test this hypothesis, the average SDs were compared before and after the transitions using a t test (10 sample windows, i.e. 22 years).

3 RESULTS

3.1 Age model

The oldest sediment in the core (from 74 to 20 cm) presented a homogeneous deposit that was lighter below 29 cm and darker above. The most recent 20 cm of the core was silty-clay finely laminated sediment (1 mm thick), with alternatively yellow to dark grey layers, and the thickness of the laminae decreased upward. The $^{210}$Pb$\text{ex}$ ($^{210}$Pb unsupported excess) activity decreased logarithmically with two distinct linear trends before/after the 8 cm depth (Figure 2). The constant flux from the constant sedimentation rate (CFCS) model (Krishnaswamy, Lal, Martin, & Meybeck, 1971) was applied to the two parts of the profile. The levels of $^{210}$Pb$\text{ex}$ represented mean accumulation rates of 0.48 $\pm$ 0.06 cm year$^{-1}$ ($r^2 = 0.837$) between depths of 28 and 8 cm and 0.29 $\pm$ 0.04 cm year$^{-1}$ ($r^2 = 0.927$) in the upper 8 cm of the core (Figure 2), that is approximately 40% lower than in the rest of the core. Caesium peaks (typical for the 1986 Chernobyl disaster and 1963 maximum radionuclide fallout from atmospheric nuclear tests) were detected at 7.5 cm and between 19.5 and 21.5 cm, with a maximum at 19.5 cm, whereas the $^{241}$Am maximum (a tracer of the 1963 maximum radionuclide fallout) was only detected at the 19.5 cm depth and was thus associated with the deepest of the two $^{137}$Cs peaks (Appleby, Richardson, & Nolan, 1991). Artificial radionuclide data thereby confirmed the sedimentation rates computed from the CFCS $^{210}$Pb$\text{ex}$ age model. Varve counting over the first 20 cm (dated at 1960) further confirmed this age model and allowed date correlation of the two cores. Unfortunately, short-lived radionuclides were not measured over the whole sediment core, and the deepest dated layer corresponded to 1941 $\pm$ 10 years AD at 29 cm. Below 28 cm, the dating was based on extrapolation of the lower part of the CFCS age model. Sedimentary data (LOI, water content) did not present any significant variations below 20 cm depth, supporting a rather constant mean sedimentation rate over the lower part of this core. Under this postulate, the VAR10.4 core covers the 1816 ($\pm$26)—2010 time period, and VAR 10.10, used for the biological analysis, covers the 1837 ($\pm$22)—2010 time period. However, throughout the manuscript, the age model below 1940 was taken with caution and the main changes highlighted in this study occurred after 1940.

3.2 Inferred total phosphorus

I-TP (Figure 3) represents the status before eutrophication corresponded to a mesotrophic lake (I-TP < 15 $\mu$g TP L$^{-1}$). I-TP exhibited a slight increase as early as the 1870s and reached 25 $\mu$g TP L$^{-1}$ just before World War II. Between 1946 and 1948, I-TP increased abruptly from ca. 25 $\mu$g TP L$^{-1}$ to >200 $\mu$g P L$^{-1}$. This abrupt change was consistent for both pigment-inferred and diatom-inferred TP. I-TP remained high, oscillating between 200 and 300 $\mu$g TP L$^{-1}$ until the early 1980s. Thereafter, I-TP decreased continually from >300 $\mu$g TP L$^{-1}$ down to 75–100 $\mu$g TP L$^{-1}$ in the most recent samples, which is consistent with currently monitored values.
3.3 | Major dynamics within the ecological proxy

The length of DCA axis 1 was greater than the length of axis 3 (1.98 versus 1.30 SD), which indicates that DCA adequately summarised the information in the data set. Because the first axis was still short and two-dimensional plots are often necessary to convey most of the complex data structure (Wartenberg, Ferson, & Rohlf, 1987), the second axis was included in the analysis. The two-first axes accounted for 73% of the total variance in the cladoceran community (Figure 3). DCA1 (46%) essentially accounted for the dominant changes in pelagic species, with the low scores on axis 1 indicating an important contribution of *Chydorus sphaericus* (loadings < 0.4) and *Eubosmina* sp. (loadings < 1.0) to the assemblage, whereas high scores were correlated with an important contribution of *Daphnia* spp. (loadings > 1). DCA2 (27%) accounted for the changes in the littoral communities, such as for the littoral to pelagic ratios; the low values on axis 2 were correlated with the macrophyte-associated species *Rynchotalona falcata*, *Phyllostachys nigra* and *Prostephanus truncatus* and *Eurycerca* (loadings < 0.5), and the highest values were correlated with greater abundance of *Eubosmina* sp.

3.4 | Nature, drivers and EWS for the breaks detected on cladoceran assemblages

The change-point analysis revealed three dates of significant breaks in DCA1 scores: 1926/1928, 1946/1948 and 1983/1988. There was only one break in the DCA2 that was dated in 1944/1946 (Figure 3). The same change-point analysis was conducted on the bootstrapped series of DCA1 and DCA2 with 1,000 iterations, indicating an average of 0.165 and 0.006 change points, respectively, indicating that the number of transitions detected was not the result of chance but, instead, of a specific ordination in time.

On DCA1 (Figure 4a), the first transition of the total cladoceran community in 1926/1928 corresponded to a smooth increase in the DCA1 scores as I-TP went from < 20 to > 20 $\log PL/C_0$ during a transient warming period. This gradual transition was driven by a progressively higher contribution of *Daphnia* spp. to the total assemblage (from 1% to 18%) to the detriment of *Bosmina* sp. and a relatively higher representation of littoral habitats within the total cladoceran assemblage. The second transition (1946/1948) signalled a deep reorganisation of the cladoceran pelagic community structure. The sudden increase of I-TP between 25 and > 200 $\log PL/C_0$ coincided with the disappearance of *Daphnia* spp., replacement by *Eubosmina* sp. and overall dominance by *C. sphaericus*, with DCA1 scores close to 0. The latest transition on DCA1 was dated between 1983 and 1988. It marked the unprecedented dominance by *Daphnia* spp. within a few years (68% of the total assemblage) and the appearance of littoral yet ubiquitous cladoceran species (*Alona* spp., mainly *Alona rectangula*, *Alona affinis* and *Alona intermedia*) that differed from pre-eutrophication assemblages. The probability density functions (Figure 4b) indicated that the distribution of DCA1 scores between the pre-1946 and post-1948 time periods overlapped until the 1983/1988 break, after which the scores were very distinctive. The final GAM for DCA1 (Table 1, Figure 4c, deviance explained 71.2%), chosen according to the AIC computation, included a significant smooth term for I-TP.

![Figure 2](https://example.com/figure2.png)
and the mean annual air temperature (MAAT, \(p < 2 \times 10^{-16}\)). A correlation structure for the model errors was not supported by a likelihood ratio test, and the two models (with and without the correlation structure) provided effectively the same fit for the observed data. Therefore, the simplest model was retained. Both fitted relationships between DCA1 scores and covariates were nonlinear (EDF = 4.09 and 3.92 for I-TP and MAAT, respectively), with threshold values for which contributions changed signs. I-TP contributed to pushing the DCA1 scores from positive to negative values for inferred concentrations ranging between 50 and 100 µg PL\(^{-1}\), whereas MAAT essentially contributed to increasing DCA1 above MAAT >13.7°C. The 1926/1928 smooth transition corresponded to a transient positive contribution of MAAT, whereas the 1946/1948 transition matched an important shift in s(I-TP) from positive to strongly negative values, supporting the theory that nutrients were by far the dominant trigger of such the abrupt mid-20th century transition (Figure 4c). The GAM run for the 1,000 bootstrapped values of I-TP indicated that the contribution of I-TP was significant for the 5%–95% confidence interval for all I-TP (Appendix S1). In turn, MAAT was the clear driver of the 1983/1988 transition, and Lake Varese clearly exhibited a strong response to the climatic regime shift characterised in Europe in the 1980s by Woolway et al. (2017) (+1°C in 5 years). Interestingly, over the period depicted by the sediments, I-TP and MAAT exhibited antagonistic effects on the DCA1 scores.

The DCA1 scores over the most recent period were significantly different from those observed 50 years ago for similar I-TP values (Figure 4c), but these differences in the reversal trajectory were attributed to the significant contribution of MAAT over the last 30 years. The phase-space plot between DCA1 scores and MAAT also suggested a threshold relationship linking forcing to the response (Figure 4d). The values of EWS were linked to the window chosen for the computation (Appendix S2) as well as to the window of calculation for the Mann–Kendall trend test. However, whatever the computation method, the variance and autocorrelation of DCA1 scores decreased along all of the records. Therefore, even though the 1946/1948 transition was preceded by a rise in SD and AR(1), no stabilisation or decreased variance occurred after the transition (Table 2, Figure 4f).

Detrended records of cladoceran composition (DCA2, Figure 5a) before and after the 1944/1946 transition are clustered within two different groups. Until 1944, the scores jumped above 0.8, highlighting the loss of the littoral diversity and thriving Eubosmina sp. The final GAM on DCA2 (Table 1, Figure 5b, deviance explained = 62.8%) selected a nonlinear smooth term only for I-TP (\(p < 2 \times 10^{-16}\)), and the likelihood ratio test rejected a correlation structure. The fitted relationship with I-TP in DCA2 was nonlinear (EDF = 2.41), with 24–25 µg PL\(^{-1}\) threshold values for

### Figure 3
Palaeostratigraphy of Lake Varese cladoceran communities from 1837 to 2008 with the core descriptor (LOI), environmental parameters (MAAT: mean annual air temperature (Auer et al., 2007) and I-TP: inferred total phosphorus), selected cladoceran taxa/groups (units: fluxes [remains cm\(^2\) year\(^{-1}\)]) and selected axes of DCAs for the total cladoceran assemblage. The horizontal grey areas correspond to the detected transitions.
which the contributions switched from negative to positive. DCA2 captured the nutrient-driven changes in the cladoceran community composition, one data point earlier than the actual sudden shift in I-TP (and thereby DCA1), through the loss of macrophyte-associated species. Because all sedimentary analyses were conducted on the same half core, this delay is meaningful and independent from potential inaccuracies in the age model. Altogether, the results strengthened the information from DCA1, namely that the mid-1940s transition was nutrient-driven and favoured *Eubosmina* sp. over littoral diversity. The probability density functions (Figure 5b) pointed to a segregated distribution of DCA2 scores before and after the mid-1940s transition. The phase-space plot between DCA2 scores (Figure 4c) showed a clear separation of data points before and after the transition, indicating a significant change in the cladoceran community composition. The probability density functions (Figure 5b) demonstrated a significant shift in DCA2 scores, suggesting a change in the nutrient regime. The early warning signal (EWS) indicators (Figure 4e and f) showed a decrease in autocorrelation (AR(1)) and variance (SD) before the transition, indicating a change in the system's dynamics.
and I-TP (Figure 5d) outlined two clusters for a I-TP threshold of approximately 24–25 μg P L⁻¹. Because I-TP has not crossed the initial threshold (25 μg P L⁻¹), we do not have evidence of the existence of two alternative cladoceran states for an overlapping range of I-TP. SD and AR(1) of the DCA2 scores significantly increased over the 10–20 years preceding the 1944/1946 critical transition (Table 2). Furthermore, the variance in the following state was significantly lower SD (t < 0 and p < .05), tested through t tests and identified with two asterisks in the table.

4 | DISCUSSION

Lake Varese underwent three ecological transitions over the past 170 years. While the first one in the 1920s was gradual, the two following ones entirely restructured the cladoceran assemblage: once in the mid-1940s, and, most recently, in the 1980s. DCA allowed decomposition of the changes in communities into pelagic and littoral components. The timing, drivers and dynamics of the transitions were different between these two components, further suggesting the possibility of spatial heterogeneity in the susceptibility of regime shift in this stratified lake (Scheffer & van Nes, 2007). The results on DCA1 underlined the necessity to consider the possibility of multiforcings acting on ecological dynamics when evaluating restoration trajectories (e.g. Bennion et al., 2015). DCA2 instead gave a more precise picture of the nutrient-driven changes.

4.1 | Changes in the pelagic community

Unsurprisingly for a rather deep lake, the subfossil records archived in the deep sediment core essentially reflected the changes in the pelagic (Daphnia spp., Eubosmina sp. and Bosmina sp.) and opportunist pelagic (C. sphaericus, de Bernardi, Giussani, Manca, & Ruggiu, 1990; Manca & Comoli, 1995) cladoceran species (95% of the total assemblage). Therefore, the temporal variability in the ecological state of the pelagic, dominant habitat of Lake Varese was well captured in DCA1, and the per cent of explained variability accounted for by the GAM supports the hypothesis that changes in lake phosphorus concentrations and atmospheric temperatures were the dominant drivers of its dynamics.

### TABLE 1
Summary for the final GAMs fitted to variables scores for DCA axes (performed on the cladoceran assemblage). GAM: general additive models, without correlation structure, as selected by log-likelihood ratio test; I-TP: inferred total phosphorus; MAAT: mean annual air temperature; EDF: effective degrees of freedom for the regression spline; Ref.df: reference degrees of freedom used to compute the p-value; F: F-statistics; p-value: associated probabilities; Res.dev (% explained): deviance is a measure of residual variation around the final GAM models analogous to the sum of square in linear regression.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Model</th>
<th>Covariate</th>
<th>EDF</th>
<th>Ref.df</th>
<th>F</th>
<th>p-Value</th>
<th>Res.dev (% explained)</th>
<th>Threshold</th>
</tr>
</thead>
<tbody>
<tr>
<td>DCA1 (46%)</td>
<td>GAM</td>
<td>s(I-TP)</td>
<td>4.087</td>
<td>5.020</td>
<td>7.671</td>
<td>6.93 × 10⁻⁶</td>
<td>50–100 μg P L⁻¹</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>s(MAAT)</td>
<td>3.918</td>
<td>4.836</td>
<td>26.060</td>
<td>&lt;2 × 10⁻¹⁶</td>
<td>13.1–13.7°C</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>9.000</td>
<td></td>
<td></td>
<td></td>
<td>71.2</td>
<td></td>
</tr>
<tr>
<td>DCA2 (27%)</td>
<td>GAM</td>
<td>s(I-TP)</td>
<td>2.414</td>
<td>2.961</td>
<td>39.760</td>
<td>&lt;2 × 10⁻¹⁶</td>
<td>24–25 μg P L⁻¹</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>3.410</td>
<td></td>
<td></td>
<td></td>
<td>62.8</td>
<td></td>
</tr>
</tbody>
</table>

### TABLE 2
Summary of the Kendall rank correlation coefficients (τ, calculated for a sample of 10 values before the break) and t tests for comparisons of means (calculated for 10 points before and after the breaks—only six points after the 1983/1988 transition) with corresponding p-values obtained from the tests on autocorrelation at the first lag (AR(1)) and standard deviation (SD) calculated for DCA1 and DCA2 scores and their residuals for each break, identified using the change-point analysis method. Significant p-values are in bold. Significant increases of AR(1) and SD before the break (t > 0 and p < .05) were considered as EWS and are identified with asterisks in the table. New alternative stable states following transitions implied lower SD (t < 0 and p < .05), tested through t tests and identified with two asterisks in the table.

<table>
<thead>
<tr>
<th>Axis</th>
<th>Breaks</th>
<th>Test parameter</th>
<th>DCA scores</th>
<th>Standardised residuals of DCA scores</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>AR(1)</td>
<td>SD</td>
</tr>
<tr>
<td>DCA1</td>
<td>1946/1948</td>
<td>Test</td>
<td>0.590</td>
<td>0.974</td>
</tr>
<tr>
<td></td>
<td></td>
<td>p-Value</td>
<td>0.006*</td>
<td>&lt;0.001*</td>
</tr>
<tr>
<td></td>
<td>1983/1988</td>
<td>Test</td>
<td>0.538</td>
<td>–0.718</td>
</tr>
<tr>
<td></td>
<td></td>
<td>p-Value</td>
<td>0.012*</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>DCA2</td>
<td>1944/1946</td>
<td>Test</td>
<td>0.462</td>
<td>0.769</td>
</tr>
<tr>
<td></td>
<td></td>
<td>p-Value</td>
<td>0.033*</td>
<td>&lt;0.001*</td>
</tr>
</tbody>
</table>

Unsurprisingly for a rather deep lake, the subfossil records archived in the deep sediment core essentially reflected the changes in the pelagic (Daphnia spp., Eubosmina sp. and Bosmina sp.) and opportunist pelagic (C. sphaericus, de Bernardi, Giussani, Manca, & Ruggiu, 1990; Manca & Comoli, 1995) cladoceran species (95% of the total assemblage). Therefore, the temporal variability in the ecological state of the pelagic, dominant habitat of Lake Varese was well captured in DCA1, and the per cent of explained variability accounted for by the GAM supports the hypothesis that changes in lake phosphorus concentrations and atmospheric temperatures were the dominant drivers of its dynamics.
The sudden mid-1940s shift in DCA1 scores coincided with the rapid increase in lake phosphorus concentrations, which, according to I-TP, jumped from 25 to >200 µg P L⁻¹ within a couple of years. Consistently, GAM identified I-TP as the trigger of this sudden change. Yet, this strong, stepwise change occurred after 20 years of gradual rearrangements of the cladoceran community structure. Before 1926, *Bosmina longirostris* was the dominant pelagic species, but it was progressively supplanted by *Daphnia* spp. between 1926 and 1946. During this time period, the sediment content in the carotenoid pigments had already started to increase, suggesting an early and slow eutrophication phase. Furthermore, this time period also coincided with a transient overall global warming phase, between 1920 and 1945 (Jenny et al., 2016). The GAM attributed this early and gradual rearrangement in the pelagic cladoceran community to...
atmospheric warming rather than to the earlier increase in I-TP. It is actually more plausible that both factors occurred simultaneously and interacted in this substitution of Bosmina sp. by Daphnia spp. The mechanisms by which increased TP could foster such a transition are rather direct and relate to Daphnia stoichiometric requirements. Daphnia spp. is more susceptible to phosphorus limitations than Bosmina species (Schulz & Sterner, 1999), making them highly sensitive to increasing TP concentrations in lake waters (Alric et al., 2013). The outcome of the competition between Daphnia and Bosmina species becomes beneficial to the former when P limitation is released (Alric et al., 2013; Schulz & Sterner, 1999). If the community effects of warming were consistent between this transient warming phase and the most recent warming period (post-1988), that is, favouring Daphnia spp. over small-bodied cladoceran species, they are somewhat in contradiction with those more traditionally expected species. The direct and indirect consequences of a warmer climate, such as warming water, potentially higher abundance of filamentous algae and subsequent increased fish predation pressure, are all expected to favour Bosmina or Eubosmina sp. over Daphnia spp. (Alric et al., 2013; Jeppesen et al., 2007). However, there are alternative mechanisms that would favour Daphnia spp. over small-bodied cladocerans in a warmer climate. For instance, a longer stratification of the lake, promoted by warmer air temperatures, would extend the period when Daphniidae can seek refuge from fish predators in the hypolimnion (Manca, Torretta, Comoli, Amsinck, & Jeppesen, 2007). Furthermore, Daphniidae can benefit from accentuated growth at the onset of the season when predation pressure is still low (Boersma, van Tongeren, & Mooij, 1996). TP concentrations in pelagic waters could also indirectly depend on atmospheric temperatures if P transport from the catchment, and remobilisation from the sediment or evapotranspiration and inflow are modified due to climate variability (Jeppesen et al., 2009). However, beyond these speculations, the meaningful message is that the ecological outcome of a warmer climate on species assemblages is highly idiosyncratic. Depending on the geomorphology, exposure or trophic level, climate warming can be detrimental to a species in one lake, but beneficial to the same one in a neighbouring system (Alric et al., 2013; Li et al., 2016).

While Daphnia spp. thrived during the earlier eutrophication phases, they became rare within a couple of years as the lake turned hypereutrophic. At these high concentrations, P does not favour Daphnia spp. anymore, as the presence of filamentous algae or cyanobacteria typical of hypereutrophic conditions interferes with their feeding apparatus and therefore their ability to feed (DeMott, Gulati, & Van Donk, 2001; Gliwicz, 1990). Alternatively, the C. sphaericus that dominated the hypereutrophic assemblage is one of the only cladoceran species able to cope with algal filaments (Tönno et al., 2016). The growth of this species has been related to important cyanobacterial blooms on which opportunistic C. sphaericus attach (de Bernardi et al., 1990) and feed (Manca & Comoli, 1995). The substitution of Bosmina by Eubosmina sp. shall instead be explained as a top-down mediated secondary consequence of hypereutrophication (Perga, Desmet, Enters, & Reyss, 2010). Lake bottom anoxia, which appeared during this phase, has triggered massive fish mortality since the 1960s (Ceccuzzi, 2003, 2008; Provincia di Varese, 2010), benefitting Eubosmina sp. because they are better competitors than B. longirostris when fish are absent (Brooks & Dodson, 1965).

Therefore, the succession in cladoceran pelagic assemblages during Lake Varese hypereutrophication is in line with nutrient-driven changes that have already been documented in literature (Alric et al., 2013; Li et al., 2016); however, the speed at which this shift occurred is stunning, especially for a large lake. There was considerable interest in testing whether such a dramatic shift evidenced a critical transition between alternative stable states. The relationship between I-TP and pelagic cladoceran changes might not be linear, but the exact shape of the relationship was actually difficult to accurately define, due to the steep and synchronous change in both the response and the driver. However, a threshold effect is quite likely, since the DCA1 scores remained quite stable until the mid-1980s, despite substantial variability in I-TP between 200 and 300 µg P L$^{-1}$. Yet, beyond 200 µg P L$^{-1}$, nitrogen instead of phosphorus is the limiting nutrient of phytoplankton growth (Seip, 1994), thereby explaining why the amount of pelagic cladoceran changes above this threshold did not scale to I-TP. If re-oligotrophication did not take the reciprocal path, this apparent bistability could be firmly attributed to the additional impact of climate warming on the cladoceran pelagic communities. Consequently, the suddenness of the 1946 shift in the pelagic community structure arose from both a strong stepwise change in I-TP and a threshold-type pressure-response relationship that tied cladoceran community structure to I-TP. The criteria for loss of resilience and true bistability were not met, as the variance kept increasing after the transition as it did over the preceding three decades. Altogether, our analysis did not provide any evidence of a nutrient-driven regime shift generating a hysteretic response in pelagic ecological communities causing decreased nutrient concentrations.

The mid-1980s transition observed for the pelagic assemblages has been clearly driven by warming, although a return of decreasing nutrient concentrations below the 150 µg P L$^{-1}$ threshold could potentially interact in the responses. The F-density plot highlighted that the recent most ecological status of the pelagic communities does not compare to any situation observed over the last century and suggested that pelagic communities in a still-nutrient-rich deep lake are highly sensitive to climate warming (Alric et al., 2013; Berthon et al., 2014; Savichtcheva et al., 2015). A study conducted on the large but shallow Lake Winnipeg, using an overall reasoning similar to ours, indicated that even if atmospheric warming had been quite pronounced in that region, the nutrient effects override the climate effect in controlling the lake planktonic trajectory. As such, lake depth, along with nutrient concentrations, appears to be an important regulator of the sensitivity of planktonic communities to climate warming. Warming reinforces the strength and duration of thermal stratification in deep and stratified lakes (Adrian et al., 2009; Kraemer et al., 2015). In P-rich lakes, these hydrodynamic changes increasingly cause vertical heterogeneity of P and inflating changes in plankton communities (Pomati, Matthews, Seehausen, & Ibelings,
2017) when the lake is sufficiently rich. However, and contrary to previous observations of eutrophicated lakes, warming did not reinforce hypereutrophication symptoms in Lake Varese (Moss et al., 2011). The re-emergence of *Daphnia* spp. and rarefaction of *C. sphaericus* suggested a lower contribution of filamentous algae to phytoplankton populations. A bottom-up scenario that was favourable to *Eubosmina* sp. was replaced by climate as a driving factor favouring *Leptodora kindtii* and *Daphnia* spp. These two species are now the principal components of the pelagic community, and *B. longirostris* does not have a competitive advantage in recovering its prior-eutrophication habitat. This new balance in the pelagic community suggests a currently low fish fauna pressure from predation (Ceccuzzi, Terova, Brambilla, Antonini, & Saroglia, 2011). Altogether, the climate-warming hypothesis explained the delay in recovery of the pelagic habitat, which is dominant in the deep Lake Varese.

If the warming-driven reorganisation of the pelagic cladoceran communities in the 1980s occurred suddenly, its dynamic was consistent with the observed shift in atmospheric temperature over Europe (a 1°C increase within 5 years, between 1983 and 1988). Although climate might have triggered a regime shift, this situation, of a strong stepwise change in the driver, was not expected to generate EWS (Dakos et al., 2015). In fact, no sign of resilience loss was observed (Table 2). The results also suggest that the driver-response relationship was nonlinear, with a threshold value at 13.7°C, but the paucity of data points after the transition limited the confidence of the fit. Lastly, atmospheric temperatures obeyed a monotonic increasing trend, offering no opportunity to test for bistability. Although climate warming has been shown to trigger diatom regime shifts in lakes (Smol et al., 2005), other examples are rare. The time resolution of palaeo-ecological studies might limit our ability to evaluate whether recent climate warming is prompt in triggering regime shifts in deep lakes, and we ended up in conjectures either confirming or disproving this hypothesis. Interestingly, the variance of DCA1 scores increased throughout the record, independently from the potential bias due to uneven time resolution (the same trend was observed on the calculated residuals, accounting for the change in time resolution). Increased variance can be interpreted as a loss of resilience in the ecosystem under pressure (Dakos et al., 2015), but this also comes with a weakened predictability of the further evolution of the lake (Bunting et al., 2016; Cottingham, Rusak, & Leavitt, 2000). Therefore, even though the lake’s main pelagic habitat might not be undergoing hysteresis, its management could face some “surprise effects.”

### 4.2 Changes in the littoral community

The question of alternative states in lakes is usually dealt with from a spatially averaged perspective, under the tacit assumption that changes occur synchronously lakewide. However, instead, regime shift could be restricted to certain habitats or could occur at different paces, depending on habitats (Janssen et al., 2017; Scheffer & van Nes, 2007; van Nes & Scheffer, 2005). Herein, the littoral assemblages were well recorded in the sediment archives despite the lake shape, depth and location of the coring site, thereby allowing to separately consider the dynamics of littoral versus pelagic habitats. DCA2 mirrored both the temporal changes in the littoral species, along with the ratio of benthic versus planktonic species. These changes contributed significantly to the lakewide modifications of cladoceran assemblages (27% of the total variability explained on DCA2). DCA2 suffered only one transition in 1944/1946, during which a diverse littoral community, made of species indicative of a productive and macrophyte-rich littoral zone, such as *Graptoleberis testudinaria*, *Alonella excisa*, *Alonella nana* and *R. falcata* (Bjerring et al., 2009; Hann, 1989), became extinct. Although this transition was unequivocally attributed to increased I-TP, it occurred several years earlier than in the pelagic habitat and anticipated the sudden increase in TP. The I-TP threshold value of the shift was estimated at <25 μg P L⁻¹, a value that was, of course, subjected to the uncertainty in I-TP reconstruction, but that was undoubtedly lower than the threshold that triggered the drastic change in pelagic communities, revealing a higher sensitivity of littoral habitats to nutrient enrichment. The compared temporal dynamics of the littoral and pelagic communities suggested that the macrophyte belts might have also played a role in buffering the response of the lake TP facing increasing loads; at some points, they even benefitted from it, limiting sediment resuspension and phosphorus release and favouring nutrient retention (Hilt, 2015; Scheffer & Jeppesen, 1998; van Donk et al., 1993) until a nutrient threshold was met. Therefore, the sudden loss of the macrophyte stabilising nutrient effect fostered a direct response of lake nutrient concentrations to loadings from the catchment within the following years (Genkai-Kato & Carpenter, 2005), leading to fast and hasty hypereutrophication. Because this transition also occurred during a transient warmer period, potential changes in lake water levels or runoff could have contributed to the sudden reduction in macrophyte coverage, although experimental and observational results indicated submerged macrophyte resilience to warming (Kosten et al., 2011; Mckee et al., 2002), even in situations of synchronous nutrient enrichment. Despite the baby boom high birth rates, the demography during the 1940s follows the same increasing trend as the one in the previous decades, that is on average +588 inhabitants year⁻¹ in 1931–1936 as compared to +552 inhabitants year⁻¹ in 1936–1951 (Appendix S1, Figure S1.4). Then, under the assumption that P loadings to the lake scale to the population in the catchment through domestic sewage, nutrient inputs to the lake shall not have suddenly peaked in the 1940s. Therefore, the sudden loss in macrophytic belts would have been triggered by a gradual increase in nutrient inputs to the lake, a dynamic expected for a regime shift. Yet, the changes in the nutrient loads to the lake have not been documented for this time period. The indirect evidences we rely on cannot fully decipher whether the sudden loss of macrophytes in the 1940s indeed pinpointed a regime shift or instead an abrupt ecological transition mirroring a sudden environmental upheaval. Nevertheless, the littoral of Lake Varese seemed to have buffered the increasing nutrient loads of the first half of the 20th century arising from the increased human activity on its catchment, until macrophyte disappearance.

Littoral species were rare during the hypereutrophication phase, and even though their contribution to the total assemblage increased in the most recent period, those are essentially ubiquitous or
sediment-associated species (*Monoplis dispar* and *Leydigia acanthocercoides*, *Alona* sp.), rather than those representing the restoration of vegetated littoral areas (*A. nana*, *A. excisa* and *Camptocercus rectirostris*) (Bjerring et al., 2009). As a matter of fact, most recent assemblages fall within a density distribution of those observed right after hypereutrophication (Figure 5b). The lake phosphorous concentration has significantly decreased but is no longer responding to further reductions in nutrient loads, suggesting a hysteretic response of I-TP itself (Genkai-Kato & Carpenter, 2005). Because the initial critical transition occurred at low I-TP values, which is far below the current one, we had no opportunity to fully test for bistability. Nevertheless, the re-oligotrophication trajectory of littoral habitats has not occurred along the reciprocal pathway; this time, this phenomenon cannot be attributed to climate warming. Bearing in mind that EWS are not diagnostic tools for regime shifts, since they sometimes fail to predict nonlinear changes (Burthe et al., 2015) and that regime shifts may also occur without any early warnings (Hastings & Wysham, 2010), the dynamics of EWS are consistent with a loss of resilience. Overall, the transition observed on DCA2 met several requirements to qualify as nutrient-induced shift from one stable state to another, even though the lack of direct data for nutrient loads during this time period precludes any definitive conclusion. As hypothesised, a critical transition was crossed early in the lake history, at a nutrient threshold that would be difficult to reverse. Transient outbreaks in *Eubosmina* sp. in the late 19th and early 20th century (1856, 1874 and 1918) could even be interpreted as an early flickering process; that is, the system started jumping back and forth between the different basins of attraction, which is more likely than a critical slowing down under these circumstances (Wang et al., 2012). Although the shift in the littoral area followed the theory of a shallow lakes regime shift, the absence of recovery may now be tied to internal P loadings creating a new positive feedback loop.

5 | CONCLUSION

Our analysis revealed that continuous and abrupt responses to environmental drivers can occur within a single lake and that critical transitions can be habitat dependent. The increasing nutrient load in the early 20th century in Lake Varese triggered spatially and timely segregated ecological responses acting in destabilising chain reactions. Because large and deep lakes are spatially heterogeneous, and their pelagic-benthic habitats are less connected than in shallow lakes (Tunney, McCann, Lester, & Shutler, 2012; Vander Zanden & Vadeboncoeur, 2002), the littoral habitats can endure alternative stable states that are desynchronised in timing and dynamics, with the pelagic areas (van Nes & Scheffer, 2005). Our results suggest that monitoring littoral areas could indicate the signals of abrupt changes, even in deep lakes, as a littoral shift is preceded by a recorded loss of resilience. Today, the nutrient-rich, pelagic ecosystem is highly sensitive to climate warming. This means that in the case of Lake Varese, the combination of new factors are counteracting restoration efforts, further reducing the ecosystem potential for returning to its pre-disturbance functional state as it is driven further from its safe operating space (Scheffer et al., 2015).

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