

# Extreme Climatic Event Triggers a Lake Regime Shift that Propagates Across Multiple Trophic Levels

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## ABSTRACT

Extreme climatic events, such as heatwaves and droughts, are occurring more frequently in many regions of the world. Lakes may be especially vulnerable to climatic perturbations, which can trigger sudden ecosystem changes through alterations in the hydrologic regime. However, the nature of lake response to climatic extremes, and associated long-term ecosystem-level implications are difficult to predict, due to the paucity of time series allowing exploration of ecosystem behavior before, during, and after extreme events. We investigated the impacts of the 2003 European heatwave on a small, stratifying lake by analyzing available limnological data between 1986 and 2012. In summer 2003, a shift from an unvegetated to a macrophyte-dominated regime occurred, due to the rapid spread of a benthic charophyte. We explored candidate mechanisms driving the shift by comparing empirical observations with the outcome of a model on lake alternative states parameterized for our study lake. Our results support the hypothesis

that enhanced light availability due to a heatwave-induced decrease in water level drove the switch in dominant primary producers. The spread of the charophyte was associated with strong depletion of inorganic nutrients and suppression of the typical summer phytoplankton peak. These bottom-up interactions triggered cascading effects at higher trophic levels, inducing a decline in herbivorous zooplankters with high food requirements and in predatory taxa. Some of the changes in the lake food web persist through the available time series. If incidence of heatwaves increases, as projected across temperate regions, our findings suggest that abrupt and long-lasting ecosystem-level reorganizations may occur in small, stratifying lakes.

**Key words:** heatwave; alternative states; submerged macrophytes; cascading effects; ecological interactions; LTER network; time series; chronological clustering.

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## INTRODUCTION

Ecosystems may exhibit abrupt shifts to a contrasting regime triggered by environmental change (Scheffer and Carpenter 2003; DeYoung and others 2008). These regime shifts may cause considerable socio-economic losses through deterioration of ecosystem functions and services (Folke and others 2004), and they pose serious management issues with respect to

their reversibility, costs and feasibility of restoration measures, and the adoption of effective policies to enhance ecosystem resilience (Carpenter and others 1999; Groffman and others 2006; IPCC 2012). Climate change is a major trigger of ecosystem-level regime shifts, as it can gradually impair the resilience of a system and increase the probability of catastrophic transitions driven by stochastic perturbations (Scheffer and others 2001). In aquatic systems, sudden and persistent community reorganizations are increasingly reported as a consequence of changes in large-scale climatic patterns (Hare and Mantua 2000; Smol and others 2005; Kortsch and others 2012; Boucek and Rehage 2014). In particular, lakes are sensitive ecosystems to environmental change (Parker and others 2008; Williamson and others 2009). Recent global warming is expected to alter physico-chemical and biological processes in lakes by affecting water temperature and heat balance, duration and stability of thermal stratification, water level, length of the growing season, and ice phenology in systems that are ice-covered in winter (Adrian and others 2009). These impacts derive from a combination of changes in average climatic conditions and extreme climatic events. Climatic extremes, especially heatwaves and droughts, have increased in frequency, duration, and magnitude in many regions of the world, and this trend is predicted to continue (Jentsch and others 2007; IPCC 2012), thereby raising urgent questions regarding their ecosystem-scale consequences on freshwater systems (Jones 2013).

Fluctuations in lake depth are prominent impacts of heatwaves and droughts, due to alterations in the balance between precipitation and evaporation (Jones 2013). A reduction in water level enhances the amount of light reaching lake bottom and increases the critical turbidity at which benthic vegetation is able to grow, giving submerged macrophytes a potential competitive advantage over phytoplankton (Scheffer 1998). If a lake lies within a range of conditions for which multiple equilibria exist, or if the underwater light regime is close to the critical threshold for macrophyte growth, a small change in water level due to a climatic perturbation might trigger a steep response of primary producers and tip the system to a contrasting regime (Scheffer and others 1993, 2001). Such swift transitions have largely been documented in shallow, eutrophic lakes, where modest decreases in water level can induce switches in dominance from phytoplankton to submerged macrophytes (Blindow 1992; Van Geest and others 2007; Zhao and others 2012). However, the magnitude and abruptness of vegetation responses to water level fluctuations strongly depend on lake

morphometry (Scheffer 1990), and few studies examined the potential for nonlinear responses of relatively deeper, stratifying lakes to climatic extremes affecting their water balance (Van Geest and others 2007; Hansen and others 2013).

The primary aim of this work is to investigate ecological processes governing lake ecosystem responses to extreme climatic events. Specifically, we explored the impacts of the 2003 European heatwave (Luterbacher and others 2004; Schär and others 2004) on a stratifying lake, and we looked for evidence of abrupt ecosystem-level changes that might be indicative of a regime shift. The study lake is an ideal model system to investigate ecological implications of climatic events. Being a remote and pristine mountain lake, local anthropogenic pressures that might confound the influence of climatic patterns are minimized (Hazeu and others 2010). Its simple food web, with few trophic levels, facilitates the detection of changes in community structure and the associated driving mechanisms (Primicerio and others 2007). The lake's surface area falls within the range estimated to include the highest number of lakes globally (Downing and others 2006). Finally, long-term limnological time series are available for this site, including several years before and after the heatwave, thus providing a unique opportunity to investigate long-term ecosystem consequences of a climatic extreme.

A sudden transition from a phytoplankton- to a macrophyte-dominated regime occurred during the heatwave. We hypothesized that a heatwave-induced decrease in water level acted as the key factor promoting macrophyte growth across the lake bottom. We used a model by Scheffer (1998) to investigate whether our candidate hypothesis could plausibly explain the observed switch from pelagic to benthic control of primary production. We further expected that consequences of the phase shift would propagate across multiple trophic levels. Specifically, we built a conceptual model mapping the main ecological interactions and ecosystem engineering processes hypothesized to induce higher-order effects along the lake food web, and we analyzed physico-chemical and biological time series to verify the occurrence of the major mechanisms predicted by our conceptual model.

## MATERIALS AND METHODS

### Study Site and Long-Term Time Series

Lake Scuro Parmense is an oligotrophic dimictic lake located in the Northern Apennines (Italy) at an altitude of 1527 m a.s.l. (Lon: 10.046 E; Lat:

44.382 N; Figure S9). It has a surface of 1.2 ha, maximum depth of 9.4 m, and the drainage basin covers an area of 17.1 ha. Ice cover usually lasts from November to May. The lake is naturally fishless, and although fish have occasionally been released, no self-sustaining population is present. Lake Scuro is part of the Long-Term Ecosystem Research Network (LTER) site IT09 Mountain Lakes. Limnological surveys were carried out in the open water season (May–October) of the following years: 1986, 1989–1994, 1998, 2003, 2007–2009, and 2012. Samples were collected at weekly to monthly intervals from the point of maximum lake depth. Maximum depth, Secchi disk transparency, and water temperature profiles at 1-m intervals were recorded in each occasion. Water samples were collected at different depths and the following hydrochemical variables were analyzed: pH, electrical conductivity, total alkalinity, dissolved oxygen, nitrate, nitrite, ammonium, soluble reactive phosphorus, dissolved reactive silica, and chlorophyll-*a*. One qualitative and two quantitative zooplankton samples were taken by means of vertical hauls using a 50- $\mu$ m net. Details on hydrochemical analytical methods can be found in Viaroli and others (1994). Zooplankton identification and counting were performed following Bottrell and others (1976). Field and lab methods did not change over time. In 2012, attenuation of photosynthetic active radiation (PAR) in the water column was measured at 1-m intervals with an underwater quantum sensor (LI-192, Li-Cor Inc.). Until the summer of 2003, no benthic vegetation had ever been observed. After the sudden and massive development of a charophyte in 2003 (see Results), we qualitatively estimated depth distribution of benthic vegetation in each year by dragging the lake bottom along a transect from the maximum depth point to the shore. We also collected macrophyte samples for taxonomic identification.

Results of surveys conducted between 1986 and 1998 were described in previous publications (Antonietti and others 1988; Rossetti and others 1996; Rossetti and Viglioli 2001), whereas data recorded from 2003 to 2012 are unpublished. Zooplankton data collected in 2012 were not available at the time this study was completed. Metadata on all physico-chemical and biological datasets are accessible through the Drupal Ecological Information Management System created within the Life + Project EnvEurope (<http://data.lter-europe.net/deims/>) (Oggioni and others 2012; Kliment and others 2013). Monthly average air temperatures recorded from 1978 to 2012 at a station 30 km far

from the lake (Lon: 9.933 E; Lat: 44.433 N; 1040 m a.s.l.) were downloaded from the National Oceanic and Atmospheric Administration website ([www.climate.gov](http://www.climate.gov)).

## Heatwave Impacts on Physical Lake Characteristics

We compared average summer water level and temperature in 2003 with the respective long-term means (1986–2012). To verify whether the heatwave affected underwater light regime, we downloaded satellite-based total monthly irradiation values at the study area from the HelioClim solar radiation database ([www.soda-is.com](http://www.soda-is.com)). We calculated total irradiation reaching different lake depths in each month with the Lambert-Beer law, using values of average monthly vertical light attenuation coefficient ( $E_0$ ) estimated according to the following equation:

$$E_0 = 0.016 \times Chla + \frac{1.3}{\sqrt{SDT}}, \quad (1)$$

where Chla is chlorophyll-*a* concentration ( $\mu\text{g l}^{-1}$ ) and SDT is Secchi disk transparency (m) (Scheffer 1998). Our  $E_0$  estimates are in close agreement with values reported for oligotrophic lakes (Koenings and Edmundson 1991). However, to further validate our results, we used the Lambert-Beer law to calculate the vertical attenuation coefficient from *in-situ* irradiance profiles measured in 2012. We compared these values with those obtained using equation (1) and percentage error ranged between 1.7 and 13.4%. We assumed a lake surface reflectance of 5% (Middelboe and Markager 1997) and we calculated PAR as 47% of total irradiation (Chambers and Kalff 1985). We summed monthly PAR values at each depth over summer months (Jun–Aug), to estimate the total amount of PAR available during the macrophyte growing season in each year. We compared the summer 2003 PAR depth profile with the corresponding long-term average.

## Modeling Ecosystem Response to a Climatic Extreme

To explore whether a heatwave-associated drop in water level could plausibly trigger the observed shift from an unvegetated to a macrophyte-dominated lake bottom, we applied a model by Scheffer (1998) that can give rise to two alternative stable states in shallow lakes: one with abundant benthic vegetation and clear water, and one characterized by the absence of macrophytes and higher turbidity

(Scheffer and others 1993, 2001). The effect of turbidity on equilibrium vegetation abundance  $V$  is described by a Hill function (2), whereas equilibrium turbidity  $E$  varies with vegetation as a Monod function (3) (Scheffer 1998):

$$V = \frac{h_E^p}{E^p + h_E^p} \quad (2)$$

$$E = E_0 \times \frac{h_v}{h_v + V}. \quad (3)$$

These curves represent the nullclines of the vegetation-turbidity interaction system. Points on the phase plane where nullclines intersect are system equilibria.

To investigate whether, and under which conditions, the model predicts a sudden change in dominant primary producers similar to that observed in 2003, we parameterized the model by defining plausible ranges of parameter values based on long-term data from the lake or according to literature data and our knowledge of the system. We estimated  $E_0$  (vertical light attenuation coefficient in absence of macrophytes) for each sampling date using equation (1), and we set it to vary between the minimum ( $0.4 \text{ m}^{-1}$ ) and maximum ( $0.8 \text{ m}^{-1}$ ) values calculated in June–July for the period 1986–1998, when no benthic vegetation was observed (Figure S1). We focused on light attenuation conditions during June–July because that was the critical time of the season for charophyte establishment in 2003. Vegetation percentage cover necessary to cause a 50% decrease in vertical light attenuation ( $h_v$ ) may vary between 0 and 1, and it is commonly approximated to 0.2 in shallow lakes (Van Nes and Scheffer 2005; Van Geest and others 2007). Because this value increases with lake depth, and our study lake is relatively deeper than most shallow lakes to which the model has been applied (Scheffer and Van Nes 2007; Van Geest and others 2007), we varied this parameter between 0.2 and 1. The power  $p$  defines the shape of vegetation response to changes in turbidity or water level (Scheffer 1998). It depends on lake morphometry, being higher for flat lakes than for v-shaped ones (Scheffer 1990). Most of the literature sets  $p = 4$  for lakes that have a somewhat flatter morphometry than Lake Scuro (Van Nes and Scheffer 2005; Van Geest and others 2007; Van Nes and others 2007). We therefore varied  $p$  between 2 and 4 to account for the more heterogeneous depth profile of our study lake. The critical light attenuation at which vegetation colonizes the lake bottom ( $h_E$ ) is inversely related to water level (Scheffer

1998). Under water levels recorded before and after 2003, macrophytes were either absent (pre-2003) or unable to colonize the whole lake bottom (post-2003) at light attenuation values down to about  $0.4 \text{ m}^{-1}$ , suggesting that  $h_E$  is lower than  $0.4 \text{ m}^{-1}$  at average lake depth. In 2003, when water level reached an historical minimum (see Results) and macrophytes spread across the lake, the attenuation coefficient ranged between  $0.5$ – $0.6 \text{ m}^{-1}$ . Because  $h_E$  varies with lake depth, we simulated equilibrium vegetation percentage cover as a function of  $h_E$  to investigate the nature of the system's response to a decrease in water level (that is, an increase in  $h_E$ ) similar to that observed in 2003 (from  $<0.4 \text{ m}^{-1}$  to  $0.5$ – $0.6 \text{ m}^{-1}$ ). Model sensitivity to changes in other parameter values ( $E_0$ ,  $h_v$ , and  $p$ ) was assessed by varying each parameter within the range of plausible values defined for the study lake and exploring changes in model behavior associated with different combinations of parameter values.

## Ecosystem-Level Implications of Macrophyte Take-Over

To test whether the 2003 heatwave and macrophyte establishment were associated with significant changes in abiotic and biotic lake features, we carried out chronological clustering of physico-chemical and biological time series. This technique identifies breakpoints in multivariate time series, without requiring homogenous sampling frequency (Legendre and others 1985). We divided time series in two sets, one with physico-chemical variables, including chlorophyll-*a*, and one with zooplankton species abundances. Because we were interested in detecting years of marked ecological change, we set the time step of our analysis to year and calculated annual means of each variable (Hare and Mantua 2000; Weijerman and others 2005). We carried out chronological clustering by performing a multivariate regression tree analysis on each set of time series, with year as the explanatory variable (Borcard and others 2011). We analyzed the two sets separately to verify whether environmental and community data would lead to the identification of the same change point year(s). Values of physico-chemical variables collected at different depths were averaged across the whole water column. All physico-chemical variables were standardized prior to analysis by subtracting their mean and dividing by their standard deviation (Borcard and others 2011). We included Secchi depth, maximum lake depth, water temperature, % saturation of dissolved oxygen, pH, total alka-



linity, electric conductivity, nitrate, ammonium, dissolved reactive silica, and chlorophyll-*a*. We excluded soluble reactive phosphorus and nitrite as they fell below analytical detection limits in most of the sampling dates. Species abundances were  $\log(x + 1)$  transformed to reduce the influence of highly abundant species (Ruppert and others 2010; Borcard and others 2011). To exclude extremely rare taxa, we only included rotifer and crustacean species reaching in at least one sampling date 1000 ind  $m^{-3}$  and 500 ind  $m^{-3}$ , respectively. Implications of the phase shift on physico-chemical features and zooplankton community structure over time were further analyzed by means of principal component analysis (PCA) and nonmetric multidimensional scaling (NMDS) (Legendre and Legendre 1998; Kortsch and others 2012).

All analyses were performed with the software R (version 3.0.2) using packages deSolve (version 1.10-8) to solve equations of the Scheffer's model, mvpart (version 1.6-1) for multivariate regression tree analysis, and vegan (version 2.0-10) for PCA and NMDS.

## RESULTS

### Heatwave and Physical Lake Characteristics

Average summer air temperature in 2003 was 2.7°C higher than the maximum value recorded since 1978 (Figure 1), and it was 2.6 standard deviations above the long-term mean for the study period (Figure 2). Correspondingly, mean summer water temperature in 2003 ( $15 \pm 3.1^\circ\text{C}$ ) exceeded that in all other years (Figure 2), whereas summer

water level was the lowest ever recorded, down to a minimum of 6.8 m in August 2003 (Figures 3, S7).

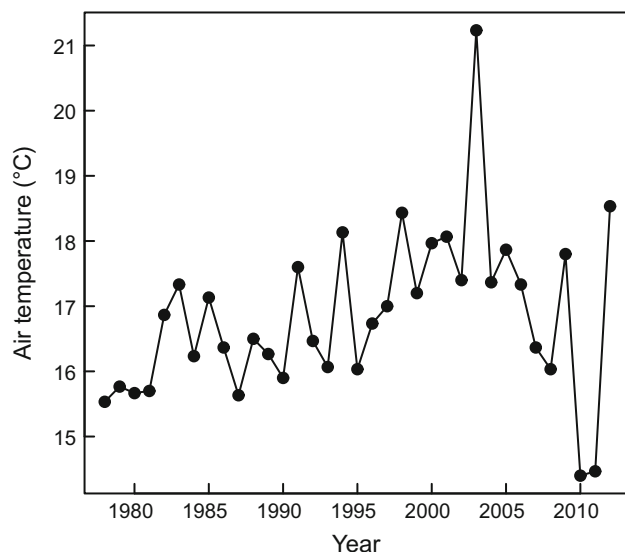
Estimated total PAR reaching the lake bottom in summer 2003 was  $72.26 \text{ mol m}^{-2}$ , more than twice as high as the long-term mean of  $31.25 \pm 19.09 \text{ mol m}^{-2}$  (Figure S2).

In June 2003, the charophyte *Nitella gracilis* was observed for the first time. *Nitella* rapidly colonized the whole lake bottom, forming a dense, uniform mat which started to decline in September. In the following years, the charophyte was always present in summer (Figure S8), although its depth distribution was confined between  $-2$  and  $-7$  m.

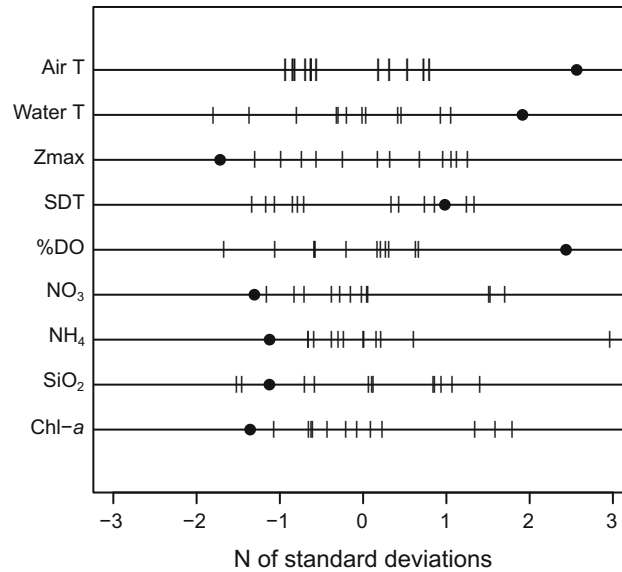
### Modeling Vegetation Response to Changes in Water Level

Chlorophyll-*a* concentration varied extensively over the time series, and was negatively associated with Secchi disk transparency (Pearson  $r = -0.48$ ,  $P < 0.01$ ; Figure 4a). Under the corresponding values of light attenuation coefficient ( $E_0$ ), irradiation reaching depths deeper than seven meters was low and just below the minimum threshold reported to allow charophyte growth (Figure 4b).

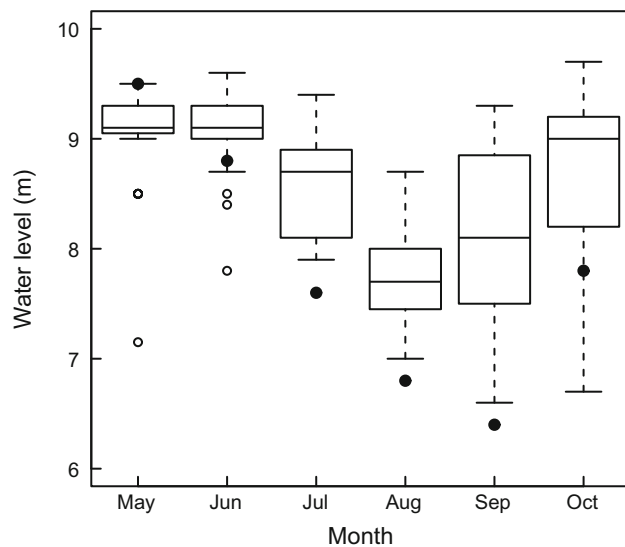
Over the range of parameter values considered for Lake Scuro, simulations of equilibrium vegetation as a function of  $h_E$  indicate a potential for the lake to exhibit multiple equilibria only for  $h_V$  less than 0.4 and  $p$  greater than 3 (Figures 5, S4). For  $h_V$  greater than 0.4 the model shows only one possible equilibrium, although it still predicts discontinuous responses to changes in  $h_E$  when  $p$  is at least 3. Specifically, for  $E_0$  approximately  $0.5\text{--}0.6 \text{ m}^{-1}$  (summer 2003 values, dashed curves in Figure 5a-b), the model predicts that an increase in  $h_E$  from



**Figure 1.** Average summer (Jun–Aug) air temperature recorded from 1978 to 2012 at a weather station 30 km from the study lake.



**Figure 2.** Summer (Jun–Aug) averages of physico-chemical variables measured at Lake Scuro in each year. Averages were standardized by subtracting the long-term (1986–2012) summer mean and dividing by the long-term standard deviation. Black circles: 2003; Vertical segments: other years. *Air T* air temperature, *Water T* water temperature, *Zmax* maximum depth, *SDT* Secchi depth; *%DO* % dissolved oxygen, *Chl-a* chlorophyll-*a*. Long-term means (*m*) and standard deviations (*sd*): *Air T*: *m* = 17.3°C, *sd* = 1.5°C; *Water T*: *m* = 12.5°C, *sd* = 1.3°C; *Zmax*: *m* = 8.4 m, *sd* = 0.4 m; *SDT*: *m* = 5.2 m, *sd* = 1.1 m; *DO*: *m* = 86.4%, *sd* = 11.9%; *NO<sub>3</sub>*: *m* = 85.4  $\mu\text{g l}^{-1}$ , *sd* = 40.4  $\mu\text{g l}^{-1}$ ; *NH<sub>4</sub>*: *m* = 51.6  $\mu\text{g l}^{-1}$ , *sd* = 42.8  $\mu\text{g l}^{-1}$ ; *SiO<sub>2</sub>*: *m* = 0.2 mg  $\text{l}^{-1}$ , *sd* = 0.1 mg  $\text{l}^{-1}$ ; *Chl-a*: *m* = 2.5  $\mu\text{g l}^{-1}$ , *sd* = 1.3  $\mu\text{g l}^{-1}$ .

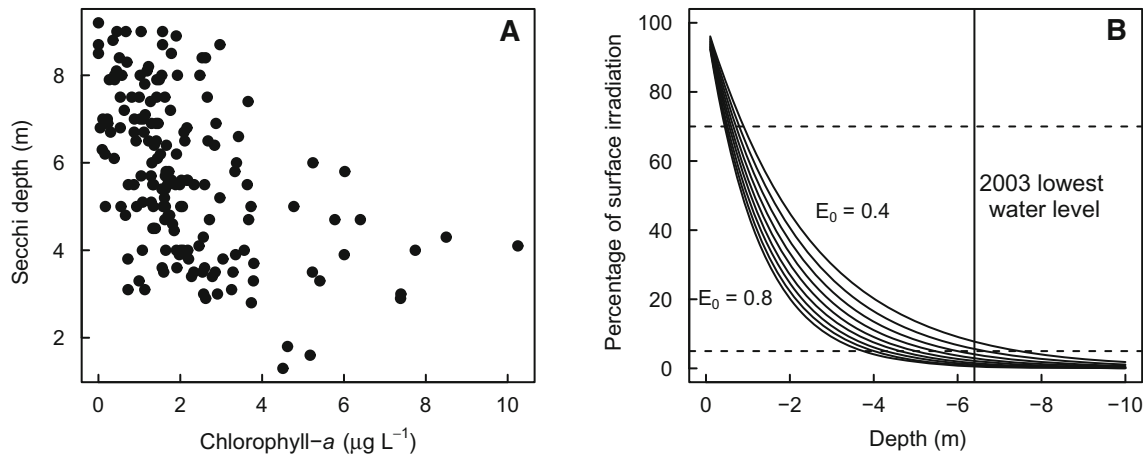


**Figure 3.** Boxplots of monthly water levels recorded between 1986 and 2012, with values measured in 2003 shown as filled circles. Boxes indicate the first and third quartiles, whereas the horizontal thick line shows the median. Whiskers indicate the most extreme values less than 1.5 times the interquartile range, and open circles represent values outside 1.5 times the interquartile range.

less than 0.4 to 0.5–0.6  $\text{m}^{-1}$ , estimated as a consequence of the 2003 drop in water level, determines a shift of the equilibrium from an unvegetated to a macrophyte-dominated condition. As expected, for *p* less than 3 the model predicts a gradual rather than discontinuous response to changes in water level (Figure 5c), which contrasts with the rapid spread of the macrophyte observed in 2003.

### Ecosystem Implications of Macrophyte Take-Over

Chronological clustering on environmental and biological data identified 2003 as the major breakpoint in the time series, indicating the occurrence of marked changes in both hydrochemical features (Figures 6, S5a) and zooplankton community structure (Figures 7, S5b–c, S6).



**Figure 4.** (A) Secchi depth transparency as a function of chlorophyll-*a* concentration averaged over the water column. Each point represents a sampling date. (B) % decrease in irradiation with depth calculated with the Lambert-Beer law for different  $E_0$  values within the range (0.4–0.8  $\text{m}^{-1}$ ) estimated in June–July at Lake Scuro between 1986 and 2012. Horizontal dashed lines: minimum and maximum percentage of surface irradiation allowing charophyte growth based on literature data (see Supplementary Material). Vertical solid line: lowest water level measured in 2003.

Percentage saturation of dissolved oxygen near lake bottom usually drops significantly over summer, with minima down to 0% and a long-term mean of  $51 \pm 35\%$  in August. In summer 2003, hypolimnetic oxygen never went below 90%, and it reached a peak of 130% in August. Nitrate and dissolved reactive silica normally exhibit a clear seasonal pattern: their concentrations decrease over summer, with minima in July–August and regeneration in Autumn. Conversely, a peak in ammonium is generally observed near the sediment in late summer, when hypolimnetic hypoxia occurs. In 2003, summer concentrations of these nutrients were the lowest ever recorded (Figure 6b). Nitrate and ammonium remained below the detection limit in August and September, whereas the respective long-term summer averages equal  $85.4 \pm 40.4 \mu\text{g l}^{-1}$  and  $51.6 \pm 42.8 \mu\text{g l}^{-1}$  (Figure 2). In the years before 2003, average summer concentration of dissolved reactive silica was  $0.32 \pm 0.14 \text{ mg l}^{-1}$ . In 2003, a mean value of  $0.06 \pm 0.04 \text{ mg l}^{-1}$  was recorded. After 2003, reactive silica remained relatively low, with summer levels often below detection limit.

The seasonal inorganic nutrient depletion is generally paralleled by an increase in chlorophyll-*a*, which peaks in July–August. In 2003 summer chlorophyll-*a* levels were 1.36 standard deviations below the long-term mean (Figure 2). An unprecedented delayed maximum of  $6.9 \mu\text{g l}^{-1}$  was observed in September 2003.

Rotifers with a raptorial feeding behavior, that is, *Ascomorpha* spp. (sum of *A. ecaudis* and *A. saltans*),

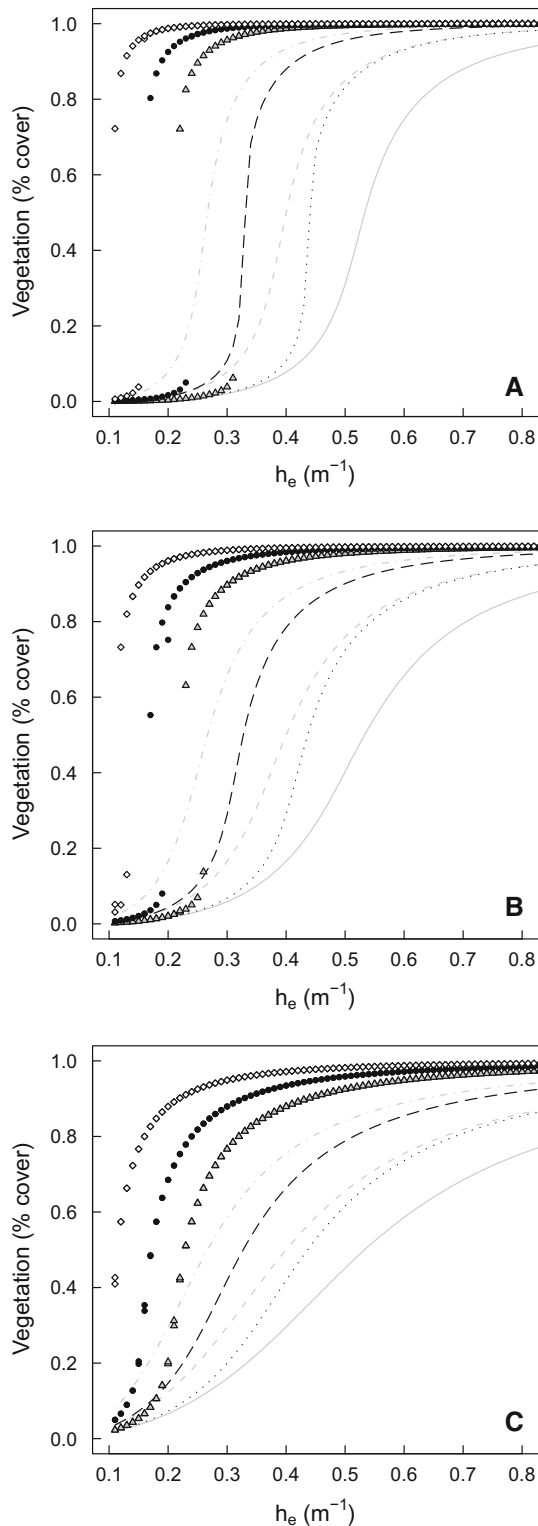
*Polyarthra* sp., and *Synchaeta pectinata* (Obertegger and others 2011), declined permanently after 2003 (Figure 7b). *Synchaeta pectinata* used to peak in summer, with maxima ranging between 4884 ind  $\text{m}^{-3}$  and 43,957 ind  $\text{m}^{-3}$ . In 2003, it did not exceed 65 ind  $\text{m}^{-3}$ , and afterwards it was never found again in the lake. Maximum densities of *Polyarthra* sp. reached on average  $38,220 \pm 15,731$  ind  $\text{m}^{-3}$  in the pre-2003 period. In 2003, summer abundance dropped to 13,866 ind  $\text{m}^{-3}$ , and in the following years it remained below 340 ind  $\text{m}^{-3}$ . Densities of *Ascomorpha* spp. never exceeded 3500 ind  $\text{m}^{-3}$  after 2003, whereas pre-2003 values ranged between 8891 ind  $\text{m}^{-3}$  and 67,744 ind  $\text{m}^{-3}$ .

Similarly, the polyphagous rotifers *Asplanchna priodonta* and *Ploesoma hudsoni* showed the lowest abundances of the whole time series in 2003, although they recovered to pre-2003 densities in the following years.

Filter-feeding rotifers underwent a marked shift in dominance. *Conochilus* gr. *unicornis-hippocrepis* exhibited a record-setting peak of 549,415 ind  $\text{m}^{-3}$  in September 2003, thus reaching higher densities than *Keratella cochlearis* for the first time since the beginning of surveys (Figure S6).

The warm stenothermal cladoceran *Diaphanosoma brachyurum*, which had disappeared from the lake since 1992, re-appeared in 2003 and its population is now well established (Figure S5b).

*Eudiaptomus intermedius* is the only calanoid in the lake. It is univoltine and reproduction occurs between May and June. The highest population densities are



◀ **Figure 5.** Results of Scheffer's model (Scheffer 1998) parameterized for Lake Scuro illustrating equilibrium benthic vegetation percentage cover as a function of  $h_E$ , a parameter that is inversely related to water level (a decrease in water level corresponds to an increase in  $h_E$ ). Changes in model results obtained by setting the parameter  $p$  to three different values are reported, namely (A)  $p = 4$ , (B)  $p = 3$ , and (C)  $p = 2$ . Within each plot, the effect of select combinations of the remaining model parameters ( $E_0$  and  $h_v$ ), encompassing the whole range of values defined for each parameter, is illustrated by different curves: black dashed:  $h_v = 0.6$ ,  $E_0 = 0.6$ ; black dotted:  $h_v = 0.6$ ,  $E_0 = 0.8$ ; gray dot-dashed:  $h_v = 1$ ,  $E_0 = 0.4$ ; gray dashed:  $h_v = 1$ ,  $E_0 = 0.6$ ; gray solid:  $h_v = 1$ ,  $E_0 = 0.8$ ; Curves represented by symbols indicate parameter combinations that give rise to alternative equilibria when  $p \geq 3$ : white diamond:  $h_v = 0.2$ ,  $E_0 = 0.4$ ; black circle:  $h_v = 0.2$ ,  $E_0 = 0.6$ ; gray triangle:  $h_v = 0.2$ ,  $E_0 = 0.8$ . 3D plots illustrating changes in model behavior associated with the full range of values considered for each parameter are reported in the Supplementary Material (Figure S4).

females ( $171 \text{ ind m}^{-3}$ ) and mean number of eggs per female ( $14.17 \pm 3.76$ ) in May–June 2003 were comparable to the corresponding long-term means ( $169 \pm 161 \text{ ind m}^{-3}$  and  $11.1 \pm 3.3$ , respectively). However, the subsequent peak in nauplii was the lowest ever recorded ( $6500 \text{ ind m}^{-3}$ , against a pre-2003 average of  $16,816 \pm 7793 \text{ ind m}^{-3}$ ). Similarly, copepodid abundances in summer 2003 were lower than in any other year. For instance, copepodids II and III did not exceed  $967 \text{ ind m}^{-3}$  and  $276 \text{ ind m}^{-3}$ , respectively, whereas their corresponding long-term averages equal  $7093 \pm 5021 \text{ ind m}^{-3}$  and  $8606 \pm 4463 \text{ ind m}^{-3}$ . An unusual second peak in *Eudiaptomus* nauplii was recorded in September 2003 ( $26,727 \text{ ind m}^{-3}$ ; Figure S5c).

## DISCUSSION

Our findings provide evidence of an abrupt regime shift triggered by an extreme climatic event in a stratifying, oligotrophic lake. We show that ecological implications of the shift affect multiple trophic levels and determine marked changes in community structure that persist long after the climatic anomaly. We propose a conceptual model illustrating potential drivers and mechanisms underlying lake ecosystem response to a climatic extreme (Figure 8).

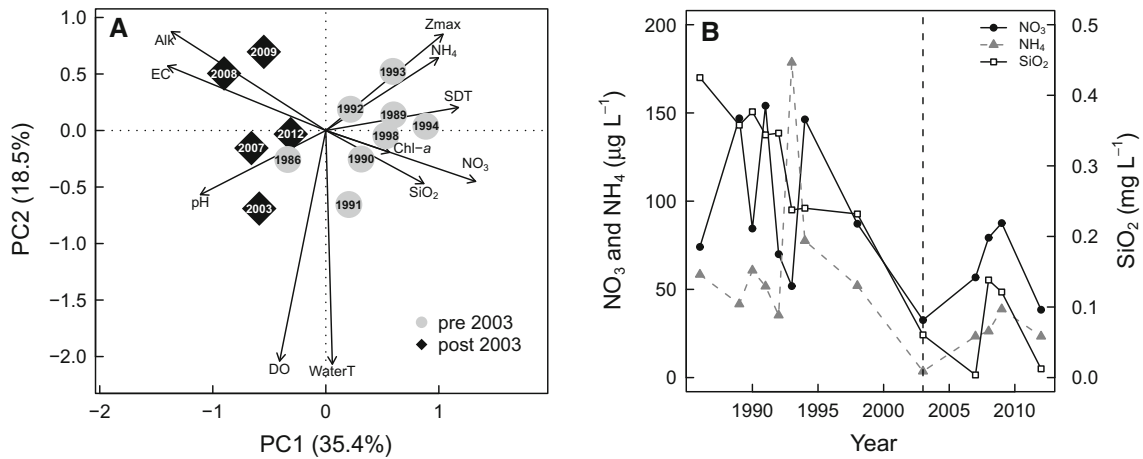
### Mechanisms Underlying Macrophyte Take-Over

During the 2003 European heatwave, air temperatures exceeded long-term averages by 2–3°C over most of central and southwestern Europe (Luter-

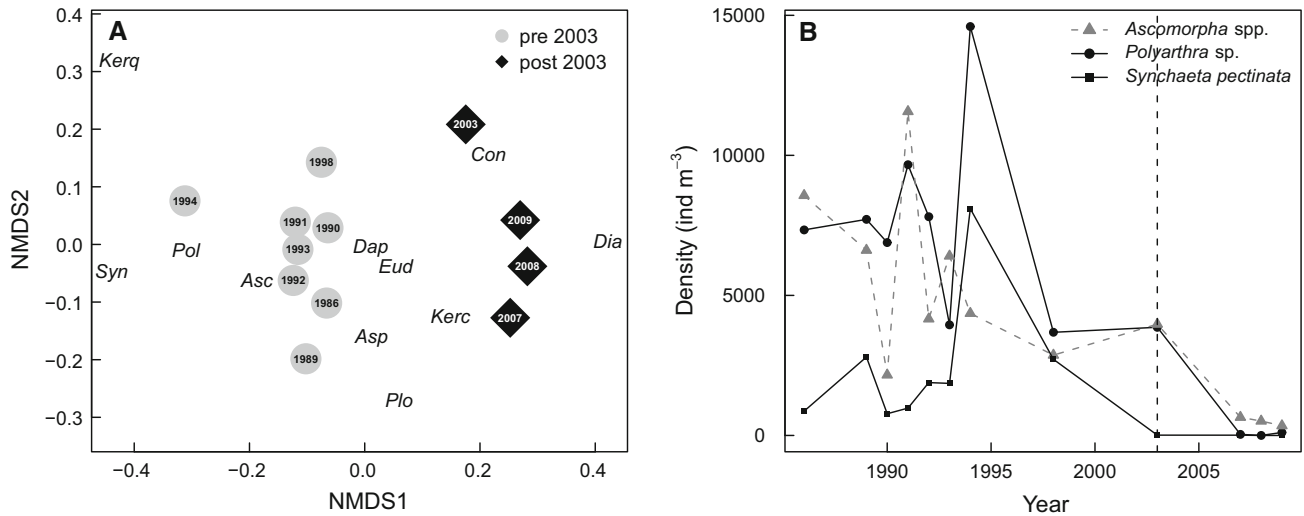
usually observed in June–July, with an average maximum of  $27,027 \pm 7401 \text{ ind m}^{-3}$ .

Between May and July 2003 *Eudiaptomus* did not exceed  $9541 \text{ ind m}^{-3}$ , which is the lowest value of the time series (Figure S5c). Density of ovigerous





**Figure 6.** (A) PCA biplot of physico-chemical variables over the years. *Gray circles and black diamonds* illustrate the partition of the time series into two groups of years as obtained by chronological clustering. *Alk* total alkalinity, *EC* electric conductivity; other abbreviations as in Figure 2. (B) Time series of summer (Jun–Aug) averages of selected hydrochemical variables. The vertical dashed line indicates the year 2003.

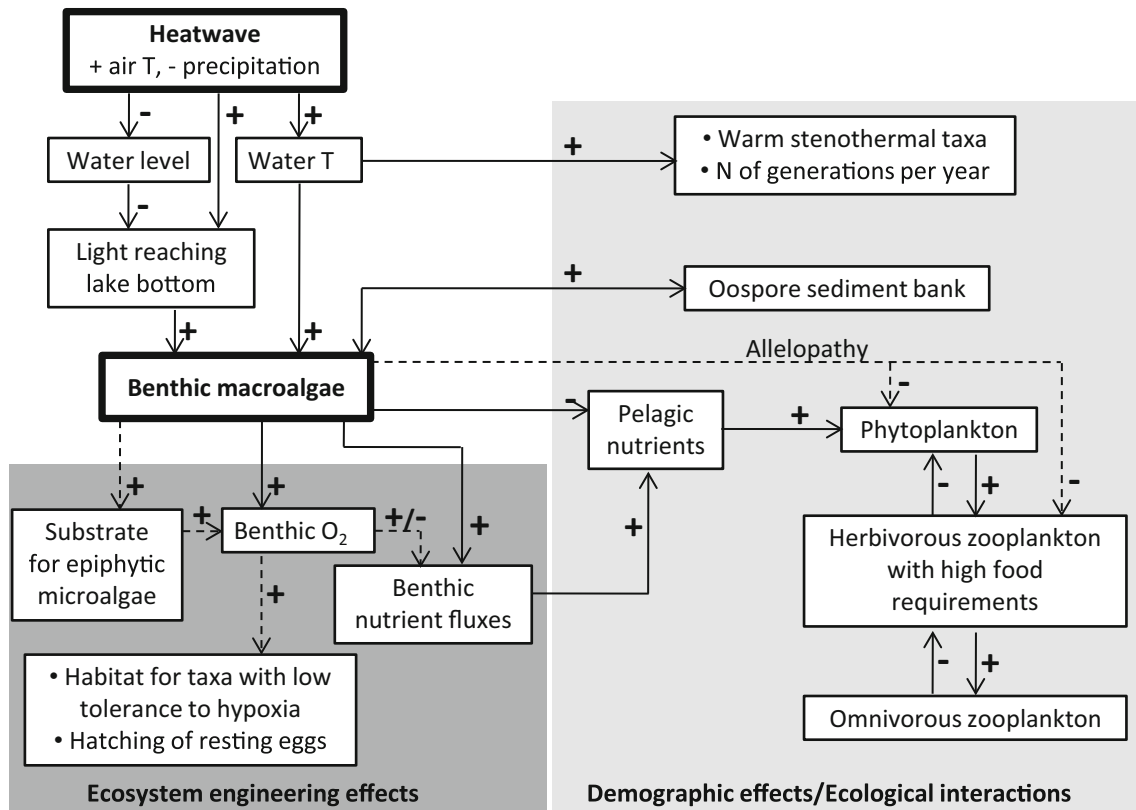


**Figure 7.** (A) NMDS biplot showing changes in zooplankton community structure over the years. *Gray circles and black diamonds* as in Figure 6. Only the most abundant rotifer and crustacean species are shown. *Taxa abbreviations* Asc, *Ascormorpha* spp.; Asp, *Asplanchna priodonta*; Con, *Conochilus* gr. *unicornis-hippocrepis*; Kerc, *Keratella cochlearis*; Kerq, *Keratella quadrata*; Plo, *Ploesoma hudsoni*; Pol, *Polyarthra* sp.; Syn, *Synchaeta pectinata*; Dap, *Daphnia* gr. *longispina*; Dia, *Diaphanosoma brachyurum*; Eud, *Eudiaptomus intermedius*. Stress = 0.096. (B) Time series of annual average abundances of the main raptorial rotifer taxa. The vertical dashed line indicates the year 2003.

bacher and others 2004; Schär and others 2004), whereas precipitation was markedly lower than the long-term mean (Rebetez and others 2006). Increases in water temperature represent a major impact of heatwaves on relatively large lakes. Accordingly, in summer 2003, exceptionally high water temperatures were recorded in several large European lakes, which also exhibited longer and stronger stratification of the water column, enhanced hypolimnetic oxygen depletion, increased

internal nutrient loading, and blooms of cyanobacteria (Jankowski and others 2006; Jöhnk and others 2008; Wilhelm and Adrian 2008).

We observed a comparable increase in water temperature in Lake Scuro (Figure 2), especially in the epilimnion. However, the relatively small size of the lake and associated watershed make the system particularly susceptible to fluctuations in water level, so that the extremely hot and dry conditions in 2003 caused a drop in lake depth



**Figure 8.** Conceptual model illustrating the main ecological mechanisms regulating the response of a small, stratifying lake to an extreme climatic event (heatwave). *Solid lines* indicate processes that we observed in Lake Scuro, whereas *dashed lines* represent mechanisms derived from the literature (see “Discussion” section). *Signs* represent positive (+) and negative (–) effects, respectively.

(Figures 3, S7). Reduced water depth, together with an increase in solar irradiance due to lower cloud cover (Jöhnk and others 2008; Maazouzi and others 2008), is expected to increase the amount of light reaching lake bottom (Figure 8). This was confirmed by the unprecedented high bottom PAR values in summer 2003 in Lake Scuro (Figure S2). Enhanced light availability due to water level decrease most likely created favorable conditions for the rapid spread of benthic vegetation (Blindow 1992; Van Geest and others 2007; Zhao and others 2012).

Water temperature probably had a minor influence, as temperature near the bottom was not significantly higher in June–July 2003 compared to other years (Figure S3). Confounding factors affecting macrophyte growth, such as water color, alkalinity, grazing pressure, nutrient input, and substrate type, did not change over the years.

No benthic vegetation was observed before 2003 (Rossetti, pers. comm.), further corroborating the extraordinary and abrupt nature of the massive growth recorded in 2003. The lack of any sign of

macrophyte vegetative growth before 2003 leads to two alternative hypotheses on the arrival of *Nitella* in the lake. The macrophyte might have been introduced in the lake for the first time in 2003 as a result of a dispersal event coincident with the heatwave. Conversely, the charophyte might have already been present in the lake as sediment oospores due to a previous colonization event. We cannot rule out any of these hypotheses. However, even if the arrival of the macrophyte was the result of a coincident dispersal event, the confinement of *Nitella* to depths less than 7 m after 2003 supports the hypothesis that under average lake depth the light regime is not suitable for extensive charophyte growth, and the extreme hydrological conditions recorded in 2003 most likely played a crucial role in triggering the spread of the macrophyte across the whole lake bottom.

The hypothesis of the key role of light availability is further supported by the Scheffer’s model parameterized for Lake Scuro (Figure 5). Conclusive evidence that makes it possible to distinguish between alternative equilibria and simple nonlin-

ear behavior requires, among others, accurate estimates of model parameter values for the study lake (Hansen and others 2013), which is beyond the scope of this application. However, the model's output allows for exploration of the regions of parameter space where the system is likely to show a certain type of discontinuous response.

Alternative equilibria typically arise in shallow, eutrophic lakes, where vegetation-turbidity feedbacks are strong (Van Nes and others 2002). In relatively deeper, oligotrophic lakes, macrophytes influence a smaller portion of the water column and turbidity is less of a limiting factor to their growth (Scheffer 1998). As a result, the slopes of the vegetation-turbidity nullclines are expected to decrease, to a point where they only intersect once and no hysteresis occurs (Scheffer 1990). Accordingly, the model indicates the potential for Lake Scuro to exhibit alternative equilibria only for unrealistically low values of  $h_v$ , which are typical of shallower, more productive lakes (Van Nes and Scheffer 2005; Van Geest and others 2007). In fact, although the presence of the charophyte was associated with extremely low chlorophyll-*a* levels, we did not detect a marked increase in water transparency, which is relatively high in the lake even without benthic vegetation (Figure 2). This suggests that a very high vegetation percentage cover is needed to impact water clarity in Lake Scuro—that is,  $h_v$  is most likely closer to the higher end of the 0.2–1 range—and that the increase in bottom light availability was more likely a result of lower water level rather than a positive feedback of vegetation on transparency.

Over the range of parameters applicable to Lake Scuro ( $h_v > 0.6$  and  $E_0$  close to the long-term summer average of  $0.6 \pm 0.1 \text{ m}^{-1}$ ) the system may exhibit an abrupt, nonlinear response, although not involving alternative equilibria, and the model confirms that an increase in critical light attenuation ( $h_E$ ) due to a drop in water level comparable to that occurred in 2003 may induce a shift to a vegetation cover close to 100% (Figure 5a–b). Although the gradual response predicted by the model for  $p$  less than 3 (Figure 5c) is in contrast with the rapid phase shift that took place in summer 2003, the agreement between our field observations and model predictions when  $p$  is at least 3 suggests that the heatwave-induced decrease in lake depth is a plausible explanation for the observed concurrent ecosystem changes.

Because the lake does not seem to lie within a range of parameter values for which alternative equilibria exist, it is expected to switch back to an unvegetated regime once average water levels are restored and bottom light availability is reduced. The

persistence of *Nitella* at depths less than 7 m up to nine years after the extreme event suggests that the new regime, although probably not truly stable, might behave like a “ghost” of a stable state by slowing down the lake dynamics through positive feedbacks that prevent the system from quickly settling back to its previous regime (Scheffer and Carpenter 2003; Van Geest and others 2007). We observed the production of oospores by the charophyte, a phenomenon that probably acts as a positive feedback by creating a seed bank that increases chances of population maintenance over time (Figure 8). Even if the lake will tend to shift back to an unvegetated regime, the long transient phase and the establishment of a seed bank are likely to facilitate future re-colonizations, thus lowering the threshold to be crossed to trigger a new phase shift.

### Consequences of the Shift Across Lake Food Web

The massive development of benthic vegetation is predicted to generate ecosystem-level cascading effects triggered by ecosystem engineering and ecological interactions (Figure 8).

One of the most striking consequences of the charophyte take-over was the alteration of the oxygen seasonal pattern. Despite strong stratification of the water column, the persistence of oxygen oversaturation throughout the summer was likely due to high photosynthetic activity within the macrophyte bed (Carpenter and Lodge 1986; Frodge and others 1990). The oxygenation of deep hypoxic/anoxic water layers has been shown to cause substantial changes in lake food webs, for example, by increasing habitat quality and quantity for hypoxia-intolerant taxa (Field and Prepas 1997; Arend and others 2011) and by improving conditions for the hatching of resting eggs (Gilbert and Schroeder 2004; Brown 2008).

Macrophytes also provide a structural function by supplying surface area for epiphytic microalgae, which contribute to oxygen production and represent a food source for plant-associated herbivores (Kairesalo and others 1989; Jaschinski and others 2010; Blindow and others 2014). Such epiphytic assemblages are often dominated by diatoms (Kairesalo and others 1992; Hawes and Schwarz 1996). This might explain the marked decrease in dissolved reactive silica observed in Lake Scuro, despite the reduction in pelagic chlorophyll-*a* associated with the spread of the charophyte (Figure 2).

Low chlorophyll-*a* levels in summer 2003 suggest the occurrence of strong bottom-up interactions involving resource competition between

benthic macroalgae and phytoplankton (Søndergaard and Moss 1998) (Figure 8), as confirmed by the exceptionally low concentrations of inorganic nutrients (Figures 2, 6b). Macrophytes modulate the availability of resources to phytoplankton by taking up nutrients from the water column and by regulating nutrient fluxes from the sediment through several mechanisms, including preventing re-suspension of nutrient-rich sediment particles and modifying the sediment redox potential as a result of oxygen production (Kufel and Kufel 2002). High oxygen concentrations at the sediment–water interface, such as those recorded in the summer of 2003, may prevent release of iron-bound phosphorus from the sediment and may enhance losses of nitrogen from the system by promoting coupled nitrification/denitrification (Risgaard-Petersen and Jensen 1997; Søndergaard and others 2003). Nutrients are then released through decomposition upon plant senescence (Landers 1982; Shilla and others 2006), which is in agreement with the atypically delayed peak in chlorophyll-*a* occurred during the *Nitella* decline phase in September 2003. Macrophytes can also inhibit microalgal growth through allelopathy, although the relative importance of this mechanism is debated (Van Donk and Van de Bund 2002; Mulderij and others 2007; Rojo and others 2013).

The switch from pelagic to benthic control of primary production induced structural and functional changes at higher trophic levels (Figures 7, S5b–c).

Nutrient depletion is expected to cause a shift in phytoplankton size structure toward smaller size classes, as smaller cells generally have higher scaled nutrient affinity and thus competitive advantage over larger cells under limiting resources (Kamenir and Morabito 2009; Edwards and others 2012; Barton and others 2013). Macrophyte-induced decrease in phytoplankton quantity and quality may have thus selectively impaired herbivore raptorial rotifers (Figure 7b), which feed on larger particles and have higher food requirements than microphagous ones (Pourriot 1977; Obertegger and others 2011), with negative cascading effects on the abundance of their rotifer predators.

Lower resource availability probably also exacerbated competitive interactions among filter-feeding taxa, leading to changes in their seasonal dynamics. *Conochilus* shifted its typical summer peak to September (Figure S6), when the delayed phytoplankton bloom and release from competition with summer herbivorous taxa allowed the rotifer to become dominant. A similar pattern was observed in Lake Washington, where a longer growing season due to climate warming and sum-

mer resource depletion determined a shift of *Conochilus* peaks toward autumn (Hampton 2005).

The lack of the typical phytoplankton summer maximum could also explain the low abundances of *Eudiaptomus* juveniles. Calanoid early ontogenetic stages have higher food requirements than adults and represent a bottleneck for population development (Hart 1996; Seebens and others 2007). Potential confounding factors can be excluded, as egg production after spring thaw was similar to previous years, predatory pressure is absent, and water temperature in 2003 was not sufficiently high to negatively affect *Eudiaptomus* mortality (Herzig 1983; Jimenez-Melero 2005). The development of an additional generation in autumn (Figure S5c) was an exceptional event which has been reported for other copepods as a result of lake warming and prolongation of the growing season (Gerten and Adrian 2002).

Increased water temperature is also expected to have a positive effect on warm stenothermal taxa (Figure 8). The re-appearance of the warm-water cladoceran *Diaphanosoma brachyurum* in 2003 (Figure S5b) supports this hypothesis. The persistence of its population years after the triggering event further confirms the long-lasting nature of the observed changes.

Previous work on macrophyte-phytoplankton regime shifts in lakes mainly focused on shallow, nonstratifying eutrophic systems. Our results indicate that relatively deeper, oligotrophic lakes may also exhibit abrupt and persistent ecosystem-level reorganizations in response to an extreme climatic event. Although the shift does not seem to involve alternative stable states, the new regime appears to possess feedback mechanisms that ensure the persistence of some functional and structural changes at multiple trophic levels long after the perturbation.

A few caveats need to be taken into consideration when interpreting these findings. Our observations are based on a single extreme event, because no other comparable heatwaves occurred in the area during the survey period. A similarly intense heatwave hit Europe in July 2006, but that event was centered at higher latitudes than the 2003 heatwave (Rebetez and others 2009), and summer air temperatures in our study area did not show marked anomalies in 2006 (Figure 1).

Extreme climatic events include highly diverse phenomena, such as heatwaves, droughts, heavy rainfall, storms, and floods (IPCC 2012). The nature and magnitude of ecosystem responses can substantially vary according to the type of triggering event and its timing, duration, abruptness, and



spatial extent. For example, relatively rapid and short-lived events, such as flood pulses and storms, are hypothesized to affect ecosystem resistance and resilience in a different way than events acting on a comparatively longer and more gradual time scale, such as heatwaves and droughts (Scheffer and others 2001; Scheffer and Carpenter 2003; Jones 2013). Lake responses may also differ depending on the relative strength of the impacts that distinct climatic extremes exert on water quality, water quantity, and/or the physical habitat (Jones 2013). As a result of this large variability in the nature of potential impacts, predicting lake ecosystem responses to different types of extreme climatic events remains a critical scientific and management challenge (Jentsch and Beierkuhnlein 2008; Smith 2011).

Finally, it is important to stress that the observational nature of our study prevents us from conclusively discerning univocal causal relationships among the observed dynamics. The coupling of empirical data with a modeling approach helps in exploring the most likely mechanisms underlying the observed patterns. However, more research is needed that combines long-term surveys with controlled experimental approaches to confirm the causal nature of the key processes emerging from field observations and to improve the parameterization and calibration of explanatory and predictive models.

Despite these limitations, our findings are corroborated by other studies recording similarly abrupt ecological shifts in multiple aquatic ecosystems in the area affected by the 2003 European heatwave. For example, Van Geest and others (2007) reported a significant increase in the occurrence of shifts to a macrophyte-dominated state among 70 Dutch floodplain lakes after a widespread decrease in water level in summer 2003. Abrupt shifts in the benthic communities of aquatic systems have also been reported as a result of the 2003 heatwave (Mouthon and Daufresne 2006; Daufresne and others 2007; Munari 2011).

Climatic extremes comparable to the 2003 European heatwave are predicted to increase in frequency and intensity in several geographic regions (IPCC 2012; Jones 2013), suggesting that abrupt shifts similar to that reported in this and other studies may become more common in the near future.

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## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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