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# Experimental Evidence for the Desynchronization of Ecosystem Dynamics by Global Change

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## ABSTRACT

Anticipating ecosystem responses to global change requires identifying the isolated and combined effects of environmental disturbance across both space and time. Examining the coordinated responses of ecosystems has recently emerged as a powerful approach to advance this understanding. We conducted two complementary experiments to identify whether, and if so how, warming temperatures, nutrient enrichment, predator overexploitation (i.e., reduced apex predator abundance) and their combination drive coordinated responses of freshwater ecosystems by evaluating the dynamics of synchrony between control and disturbed mesocosms using high-frequency dissolved oxygen saturation measurements, an integrative parameter of the metabolic balance of ecosystems. Nutrient enrichment desynchronized the oxygen dynamics and their component cycles between treatments, likely arising from elevated primary production. Warming and overexploitation tended to desynchronize oxygen cycles from the control, particularly at short time scales. Nutrient enrichment combined with warming dampened desynchronization between control (ambient) and treatment mesocosms, whereas desynchronization was enhanced when simultaneously subject to predator overexploitation. As one of the first experimental demonstrations of global change impacts on ecosystem synchrony, this study highlights the need—and opens new avenues—to detect alterations in ecosystem functioning across previously unexplored spatial and temporal scales.

## 1 | Introduction

The last century was marked by unprecedented environmental change, leading to the loss of biodiversity and degradation of ecosystem functioning globally (Díaz et al. 2019). A fundamental challenge to anticipating these impacts is a stronger scientific basis to our understanding of ecosystem response to biotic and abiotic alterations that are highly dynamic and

often interact in non-linear ways (Fei et al. 2018; Garcia et al. 2014; Oliver et al. 2015). Investigating global change threats to ecological processes requires careful consideration of the multiple temporal facets (i.e., duration and frequency) of perturbations (Burthe et al. 2016) and how they manifest across spatial scales, from local to global (Soranno et al. 2019). Advancing this understanding is challenged by the fact that global change factors rarely occur in isolation, causing

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ecosystems to experience disturbances that may act collectively in antagonistic, additive or synergistic ways (Jackson et al. 2021), resulting in uncertain outcomes for ecosystem functioning over time. Identifying the spatial and temporal extent of global change impacts and disentangling their isolated and combined effects on ecosystem functioning are thus a research priority to reach a better apprehension of future ecosystem trajectories.

Ecosystem functioning results from a suite of multiple ecological processes operating at different scales. Previous investigations have primarily focused on either the changes in ecological processes of a given ecosystem over time (temporal changes) or differences in ecological processes across different ecosystems at a given time (spatial changes; Donohue et al. 2016). Yet, perturbations can alter ecosystem functioning at multiple spatial and temporal scales through mechanisms (e.g., changes in diel natural metabolic cycles) that are inherently challenging to understand without considering the coordinated responses of multiple ecosystems (Reuman et al. 2025). In this context, ecosystem synchrony, defined as the similarity in the temporal fluctuations of a given ecosystem function among multiple ecosystems, offers a useful concept to study coordinated ecosystem dynamics and help elucidate the effect of global change factors on ecosystem functioning (Vagnon et al. 2024). As disturbed ecosystems are expected to display altered dynamics, studying their correlated responses compared to undisturbed ecosystems is key to revealing changes in functioning and helping disentangle the impacts of co-occurring global change factors (Burthe et al. 2016). Ecosystem synchrony can deliver novel insights on the spatio-temporal extent of global change impacts as it is assessed from emergent properties whose altered dynamics can be interpreted directly across space in time. In addition, it offers new perspectives to examine changes in the overall dynamics of ecosystem functioning and to capture finer-scale temporal patterns of the natural cycles within those dynamics (e.g., diel metabolic cycles, seasonal deoxygenation within lakes; Xu et al. 2022) which have historically been difficult to characterize in ecology. Nevertheless, the study of ecosystem synchrony is still in its infancy and empirical investigations on the coordinated responses of ecosystems to isolated and combined effects of global change factors are needed.

The present study experimentally addressed this emerging question by investigating ecosystem synchrony under multiple global change factors in freshwater ecosystems. We used two independent mesocosm experiments to measure the effects of warming waters, nutrient enrichment and predator overexploitation in different ecological contexts. Mesocosm experiments offer a valuable intermediate between highly controlled microcosm experiments and complex natural ecosystems where testing new theories and disentangling the effects of multiple perturbations can be challenging (Richard et al. 2025; Stewart et al. 2013). We used freshwater ecosystems because they are both sentinels of environmental changes and integrators of the effects of multiple human-induced stressors on biodiversity (Reid et al. 2019). We quantified the differences in the level of ecosystem synchrony measured between pairs of undisturbed (control treatments) and disturbed mesocosms (global change factor treatments) based on the high-frequency monitoring of dissolved oxygen

saturation, an integrative parameter of the metabolic balance of ecosystems (Diamond et al. 2021; Odum 1956). Because both the overall dynamics of oxygen saturation and the natural cycles within these dynamics can be differentially influenced by environmental changes, we assessed the effects of perturbations relative to control on (i) the average oxygen saturation time series and their variability, (ii) the synchrony of entire oxygen saturation time series and (iii) the synchrony of the cyclicity of oxygen saturation time series to obtain a complementary assessment of the impacts of global change factors (both isolated and combined). We predicted that the general level of synchrony of the entire oxygen saturation time series would vary among treatments depending on the extent to which each treatment alters the average oxygen saturation values and their variability. We also anticipated that oxygen cyclicity would be more desynchronized at subdaily and daily time scales because this frequency of variation reflects alterations of short-term oxygen cycles (e.g., daily metabolism), which are more likely to occur than longer-term alterations (e.g., shifts in seasonal rhythm). In the three-step analyses, we expected combined factors to cause antagonistic effects when they caused similar changes—such as increased oxygen from either nutrient enrichment or trophic downgrading—due to stressor redundancy (Orr et al. 2022). By contrast, we expected the effects to be synergistic when the factors caused opposite changes—like nutrient enrichment boosting primary production while warming increased respiration.

We present the first experimental evidence that global change factors can disrupt ecosystem synchrony compared to undisturbed systems through alterations of oxygen dynamics. These factors affect synchrony differently depending on whether they act alone or together, and their impacts vary across time scales. Our findings highlight the value of incorporating ecosystem synchrony into studies of spatio-temporal changes in ecosystem functioning, enhancing our ability to anticipate shifts in ecosystem dynamics. Compared to previous studies on multiple stressors, which have typically focused on single time points, ecosystem synchrony offers the key advantage of integrating ecosystem dynamics across multiple temporal scales.

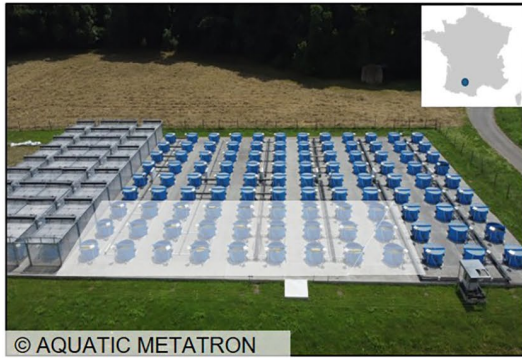
## 2 | Material and Methods

### 2.1 | Experiment 1

The first experiment (Experiment 1) was performed at the Aquatic Metatron based at the CNRS experimental platform of Moulis (France, 42°57' N, 1°05' E; Figure 1a; Richard et al. 2025) using 24 mesocosms, each with a volume of 1.8 m<sup>3</sup> (170 cm diameter and 100 cm high). Mesocosms were inoculated in October 2020 with sediment, periphyton, phytoplankton and zooplankton sourced from two local gravel pit lakes (43°36'16.747" N, 1°26'39.152" E). Several benthic macroinvertebrates (e.g., Aselidae, Chironomidae, Coenagrionidae, Lymneidae, Planariidae) were collected from gravel pit lakes, the Garonne, the Ariège and the Lèze rivers and were introduced twice between April and early July 2021. In addition, *Populus nigra* leaves (20 g) were added monthly from March to September 2021 to each mesocosm (mimicking allochthonous subsidies) while mesocosms received *Elodea canadensis* (5 g) in early July representing primary producers. During the experiment, mesocosms

## (a) Experimental designs

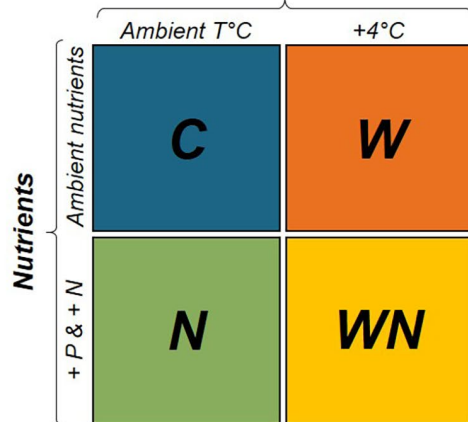
*Experiment 1*



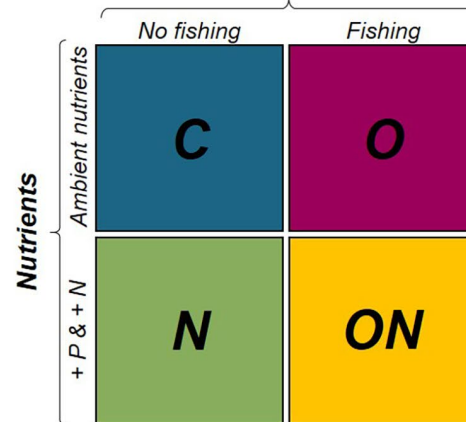
*Experiment 2*



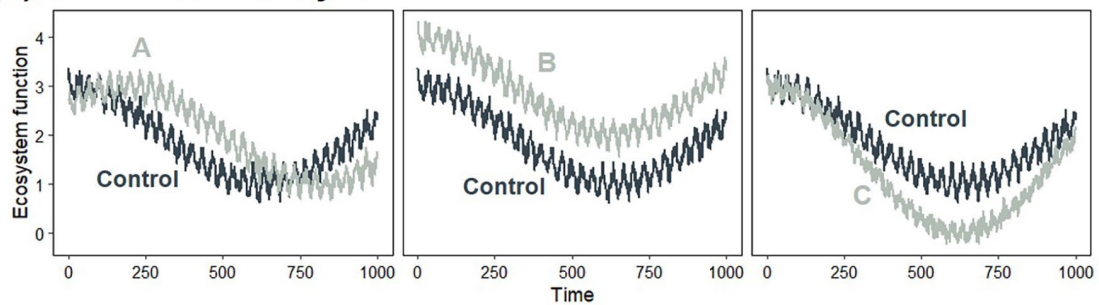
### Warming



### Overexploitation of top predators



## (b) Time-series analyses



	A vs. Control	B vs. Control	C vs. Control
<b>Statistical comparison between treatments including time-dependencies</b>	non-significant differences (on average no difference)	significant differences (on average higher B than control)	significant differences (on average lower C than control)
<b>Synchrony of the whole time-series</b>	low ccf0, high ccfmax, time-lag > 0	high ccf0, high ccfmax, time-lag = 0	medium ccf0, medium ccfmax, time-lag = 0
<b>Synchrony of the cyclicity</b>	AWP ratio = 1 for both small and large time scales	AWP ratio = 1 for both small and large time scales	AWP ratio > 1 for small time scale, AWP ratio = 1 for large time scale

**FIGURE 1** | Study framework. (a) Experimental facilities with the full-factorial designs used in Experiment 1 (*left*) and Experiment 2 (*right*). Each letter represents a treatment: Control (C, no global change factor), Warming (W, +4°C), Nutrients (N, phosphorus and nitrogen addition) and Overexploitation (O, intensive fishing of the apex predator). (b) Illustrations and analyses of time series to identify and interpret the effect of treatments on average dissolved oxygen saturation (ARIMA models), the synchrony of the entire oxygen saturation time series (cross-correlation analyses) and the synchrony of oxygen saturation cyclicity (wavelet analyses). A, B, C represent three different time series that are compared with the Control in the example.

remained uncovered to allow natural aerial colonisation by insects (further details in Marin et al. 2025). The food webs in these mesocosms were typical of fresh waters with three trophic levels.

The experiment consisted of a full-factorial design with two types of global change factors (warming and nutrient enrichment); it started on July 21, 2021 and ended on September 21, 2021. Water temperature had two modalities: ambient temperature (no warming) and continuous elevated water temperature by +4°C (Warming) to match the IPCC predictions that global average temperature will increase by 4°C by the end of the 21st century if greenhouse gas levels continue to rise at present levels (IPCC 2023). Temperature warming was possible using three 600 W titanium heaters placed at the center of the water column of each mesocosm. Nutrient enrichment had two modalities: ambient nutrients (no nutrient addition) and nutrient addition. This treatment consisted of weekly nutrient additions of 0.15 g of  $\text{KH}_2\text{-PO}_4$  and 1.9 g of  $\text{NH}_4\text{-NO}_3$  in each mesocosm (with a N:P ratio of 20:1), resulting in a total of 0.3 g of phosphorus and 6 g of nitrogen added to each mesocosm during the entire experiment. These inputs were designed to supply nutrients in excess, thereby ensuring that the system exceeded eutrophic thresholds and reached an enriched, eutrophic state (i.e., total phosphorus > 30  $\mu\text{g L}^{-1}$ ; Carlson 1977). Additions of nitrogen and phosphorus corresponded to the range used in other experimental studies investigating the effects of eutrophication on pond functioning—for example, 3.0  $\text{mg N L}^{-1}$  and 500  $\mu\text{g P L}^{-1}$  (Bakker and Nolet 2014), or ~0.013  $\text{mg N L}^{-1}$  and 0.5  $\text{mg P L}^{-1}$  (Hambright et al. 2007). Each treatment—Control (no warming and ambient nutrient), Warming, Nutrients and Warming+Nutrients—was replicated six times, totaling 24 mesocosms.

## 2.2 | Experiment 2

The second experiment (Experiment 2) was conducted at the experimental lake platform PLAN AQUA located on the CNRS-ENS field station near Paris (France, 48°17' N, 2°40' E; Figure 1a). It included 16 artificial ponds of 750  $\text{m}^3$  (15 × 30 m) with shallow littoral zones (30 cm of water) and a deep central zone (3-m deep; <https://www.aquacosm.eu/mesocosms/national-experimental-platform-in-aquatic-ecology-planaqua>). Each pond was inoculated between Spring and Summer 2014 with sand from the Loire River containing microorganisms, plant propagules and animal resting stages. Ponds were not covered to favour the rapid development of macrophyte communities (*Typha* spp. and *Juncus* spp.) and to allow for the natural colonisation of invertebrates. Fish were added in 2016 to reconstruct communities including roach (*Rutilus rutilus*), sunbleak (*Leucaspius delineatus*), gudgeon (*Gobio gobio*), ninespine stickleback (*Pungitius pungitius*) and European perch (*Perca fluviatilis*) as the apex predator. The food webs in these ponds were typical with four trophic levels.

This experiment consisted of a full-factorial design with two global change factors (overexploitation and nutrient enrichment) and started in October 2018. Overexploitation had two modalities: no exploitation (presence of apex predator) and overexploitation (intensively fishing the apex predator using small trawl nets and fish traps in November 2019). The European

perch was selected as the apex predator because it is a ubiquitous freshwater predator usually occupying high trophic positions in food webs (Linzmaier et al. 2018). It is also relatively easy to maintain in experimental ponds and is native and smaller than other common predators such as the Northern pike (*Esox lucius*). Nutrient enrichment had two modalities: ambient nutrients and nutrient addition. This treatment consisted of 20 successive nutrient additions twice a week, resulting in a total of 294.36 g of phosphorus ( $\text{KH}_2\text{-PO}_4$  form) and 1914.46 g of nitrogen ( $\text{NH}_4\text{-NO}_3$  form) added to each mesocosm during the entire experiment. These inputs were designed for the same reasons as previously mentioned in Experiment 1. To ensure consistency with Experiment 1, we analyzed here a similar duration from May 8, 2020 to July 10, 2020. Each treatment (i.e., Control, Overexploitation, Nutrients and Overexploitation+Nutrients) was replicated four times, totaling 16 mesocosms.

## 2.3 | Dissolved Oxygen Dynamics

The dynamic of dissolved oxygen concentration is expected to be affected by multiple global change factors such as warming, eutrophication or biodiversity alteration because autotrophic and heterotrophic processes are dependent on both abiotic (e.g., temperature, nutrient availability) and biotic characteristics (e.g., population biomass or community composition) (Appling et al. 2018; Diamond et al. 2021). Dissolved oxygen concentration ( $\text{mg L}^{-1}$ ) and water temperature (°C) were measured every 10 min using dissolved oxygen sensors (Ponsel, acc. 0.2  $\text{mg L}^{-1}$ ) linked to a centralised supervising system and using autonomous dissolved oxygen sensors (HOBO U26-001, acc. 0.2  $\text{mg L}^{-1}$ ) in Experiment 1 and 2, respectively. Calculated dissolved oxygen saturation (hourly average; Figures S1 and S2) was used in the analyses to ensure that time series were comparable among treatments independently of the influence of temperature on oxygen solubility. Values of dissolved oxygen saturation that were unusual relative to neighbouring measurements were corrected using the method of the median absolute deviation using a daily time window (O'Dell et al. 2020; Pearson 2002).

## 2.4 | Synchrony of Entire Oxygen Saturation Time Series

To test the effect of global change factors on ecosystem synchrony, we assessed pairwise comparisons of oxygen saturation dynamics between each undisturbed mesocosm (Control) and disturbed mesocosms subject to a global change factor (Warming, Nutrients, Overexploitation or their combination depending on the experiment). Synchrony was quantified among those subject to global change treatments and among control (ambient) mesocosms that represented a reference level of synchrony for undisturbed conditions (Figure 1b, Figure S3). The level of synchrony between the whole time series of oxygen saturation was estimated using a cross-correlation approach as commonly employed to quantify population synchrony (e.g., Hopson and Fox 2019). This method is particularly adapted to compare high-frequency time series because it quantifies the similarity between time series (i.e., here the level of synchrony) while accounting for temporal lags, thereby capturing shifts in the timing of covariations between two signals (Tahmasebi et al. 2012).

In our study, we used three complementary metrics to characterise ecosystem synchrony: *ccf0* which is a measure of the correlation between two time series calculated regardless of potential time-lags between them (i.e., synchrony without temporal realignments); *ccfmax* which is a measure of the maximum correlation between two time series calculated across a given range of possible time-lags (i.e., maximum synchrony); and *Time-lag* which is the lag for which the maximum correlation is found (i.e., time-lag effect of treatments on synchrony). Correlation values close to  $-1$  indicate strong negative synchrony and values close to  $1$  reflect strong positive synchrony. In our study, the time-lags were evaluated in hourly steps across a range from  $-24$  to  $+24$  h. In addition, we used a dynamic time warping approach, which complements cross-correlation analyses by accounting for both time-lags and differences in the amplitude of changes in oxygen saturation (Figure S4).

## 2.5 | Synchrony of Oxygen Saturation Cyclicity

The impact of global change factors on the synchrony of oxygen cyclicity was explored by decomposing the dynamics of oxygen saturation into the frequency of oxygen variations at subdaily, daily, weekly and monthly time scales using a wavelet analysis (Xu et al. 2022). Time series are often composed of a combination of cyclic patterns occurring with different frequencies that wavelet analysis decomposes into amplitude and frequency of variations along different time scales depending on the cycle of interest. For instance, seasonal fluctuations in air temperature would appear as a strong signal at the annual scale while daily transition between night and day would be reflected by variations at the daily time scale.

We computed the wavelet power spectrum (WPS) of each oxygen saturation time series by applying the Morlet wavelet function. This function makes it possible to obtain a time-frequency decomposition of time series that helps identify the dominant frequencies, amplitudes, and phases in the dynamics of oxygen saturation (Torrence and Compo 1998). First, the continuous wavelet of each time series was computed as:

$$W_n(s) = \sum_{n'=0}^{N-1} x_{n'} \psi^* \left[ \frac{(n' - n)\delta t}{s} \right] \quad (1)$$

with the wavelet coefficient  $W_n(s)$ , the wavelet time scale  $s$  (subdaily, daily, weekly or monthly), the time step  $n'$ , the localised time index  $n$ , the length of time series  $N$ , the discrete time series  $W_n$  ( $n=0, \dots, N-1$ ), the time interval of sampling  $\delta t$ .  $\psi^*$  is the complex conjugate of the wavelet function  $\psi$  normalised by the Morlet function.

Second, the wavelet power spectrum (WPS) at time  $n$  and time scale  $s$ , was calculated for each oxygen time series as:

$$\text{WPS}_n(s) = |W_n(s)|^2 \quad (2)$$

Following this equation, WPS reflects the strength of cyclic patterns and increases with the frequency and consistency of repeated oxygen fluctuations at a given time scale (Torrence and

Compo 1998). WPS was then averaged (AWP) along each time scale  $s$  to represent a global measure of the intensity of oxygen variations at a given time scale. This makes it possible to identify when the frequency of oxygen variations (i.e., the number of times oxygen cyclic patterns were repeated) is the highest along the different time scales.

Third, the effect of global change factors on the synchrony of oxygen cyclicity was measured by computing the ratio of AWP (Equation 3) between disturbed and control mesocosms in each experiment (Chalise et al. 2023).

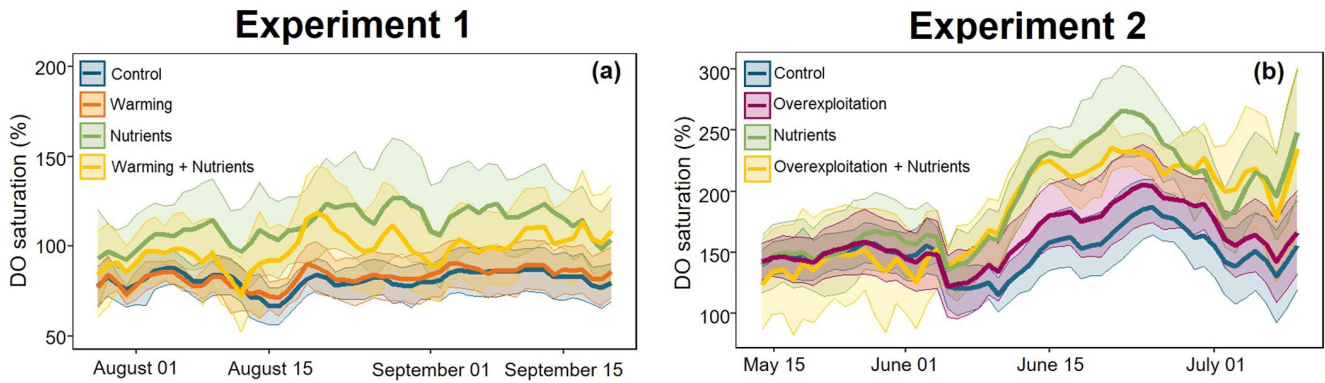
$$\text{AWP Ratio}_{ji}(s) = \frac{\text{AWP}(s) \text{ of Control}_i}{\text{AWP}(s) \text{ of global change factor}_j} \quad (3)$$

where  $s$  represents the subdaily, daily, weekly or monthly time scale,  $i$  is the replicate identity of the Control and  $j$  is the replicate identity submitted to the global change factor (i.e., Warming, Nutrients and Warming + Nutrients in Experiment 1; Overexploitation, Nutrients and Overexploitation + Nutrients in Experiment 2). This ratio is used as an indicator of changes in oxygen cyclicity to determine if the frequency of oxygen variations is higher or lower under global change factors. A ratio close to  $1$  reflects similar oxygen cyclicity between undisturbed and disturbed mesocosms at the time scales, thus reflecting a strong synchrony. Values  $> 1$  indicates an increase in the frequency of oxygen variations in disturbed mesocosms (i.e., acceleration in oxygen production and assimilation in the metabolic balance) while values  $< 1$  indicates a decrease in the frequency of oxygen variations in disturbed mesocosms (i.e., deceleration in oxygen production and assimilation in the metabolic balance), both indicating a decrease in synchrony between control and disturbed mesocosms through an alteration of oxygen cyclicity.

## 2.6 | Statistical Analyses

For each experiment, we first fitted linear mixed effect models to test the effect of treatments (Control, Warming, Nutrients and Warming + Nutrients in Experiment 1 and Control, Overexploitation, Nutrients and Overexploitation + Nutrients in Experiment 2) on differences in the average value of oxygen saturation and on its variability (Figure 1b). We considered mesocosm identity as a random effect and we accounted for time-driven autocorrelations between oxygen saturation measurements in the models by including a First order autocorrelation-moving average as a correlation structure. The response variable was the daily average oxygen saturation in the first model, the weekly average oxygen saturation in the second model, and the coefficient of variation of daily oxygen saturation (computed from hourly oxygen saturation values each day) in the third model.

Second, we tested significant differences in synchrony of time series between treatments using Kruskal-Wallis tests followed by Dunn's post hoc comparisons (Figure 1b). In Experiment 1, we tested the isolated effect of Warming and Nutrient treatments by comparing *ccf0*, *ccfmax* and *Time-lag* values computed for all pairwise combinations of Control replicates with Warming replicates (hereafter *Control\_Warming*) and Control replicates with



**FIGURE 2** | Daily dynamics of dissolved oxygen saturation averaged from each mesocosm for each treatment in Experiment 1 (left) and Experiment 2 (right). Full lines represent the average values and ribbons are the standard deviations.

the Nutrient replicates (*Control\_Nutrients*). The same analysis was performed to test the isolated effects of Overexploitation (*Control\_Overexploitation*) and Nutrients (*Control\_Nutrients*) in Experiment 2. To test the combined effect of treatments, we compared synchrony metrics between *Control\_Warming*, *Control\_Nutrients* and those computed from the pairwise comparison between Control and combined treatments (hereafter *Control\_Warming+Nutrients*) in Experiment 1. Similarly, we tested the differences between *Control\_Overexploitation*, *Control\_Nutrients* and *Control\_Overexploitation+Nutrients* in Experiment 2.

Third, we tested the effect of treatment on oxygen saturation cyclicity (Figure 1b). The response variable  $\log_{10}(\text{AWP Ratio})$  was analysed using linear mixed-effect models (LMM, one per experiment). The fixed effects included the treatment, the time scale at which oxygen cyclicity was studied (subdaily, daily, weekly, monthly) and their interaction. Mesocosm identity was included as a random effect. Tukey post hoc tests were performed on the estimated marginal means derived from LMMs to identify the significant differences from a ratio of 1 (corresponding to the comparison between *Control\_Control* and global change factors at each time scale) and the significant pairwise differences in the effects of global change factors at each time scale.

All statistical analyses were performed with R version 4.3.2 (R Core Team 2023) using the packages ‘pracma’ for correcting the oxygen saturation time series (Borschers 2023), ‘WaveletComp’ for conducting wavelet analyses (Roesch and Schmidbauer 2018), ‘lme4’ for fitting the linear mixed effect models (Bates et al. 2015), ‘emmeans’ (Lenth 2023) for estimated marginal means comparisons and ‘ggplot2’ (Wickham 2016) for graphical displays.

### 3 | Results

#### 3.1 | Oxygen Time-Series Under Global Change Factors

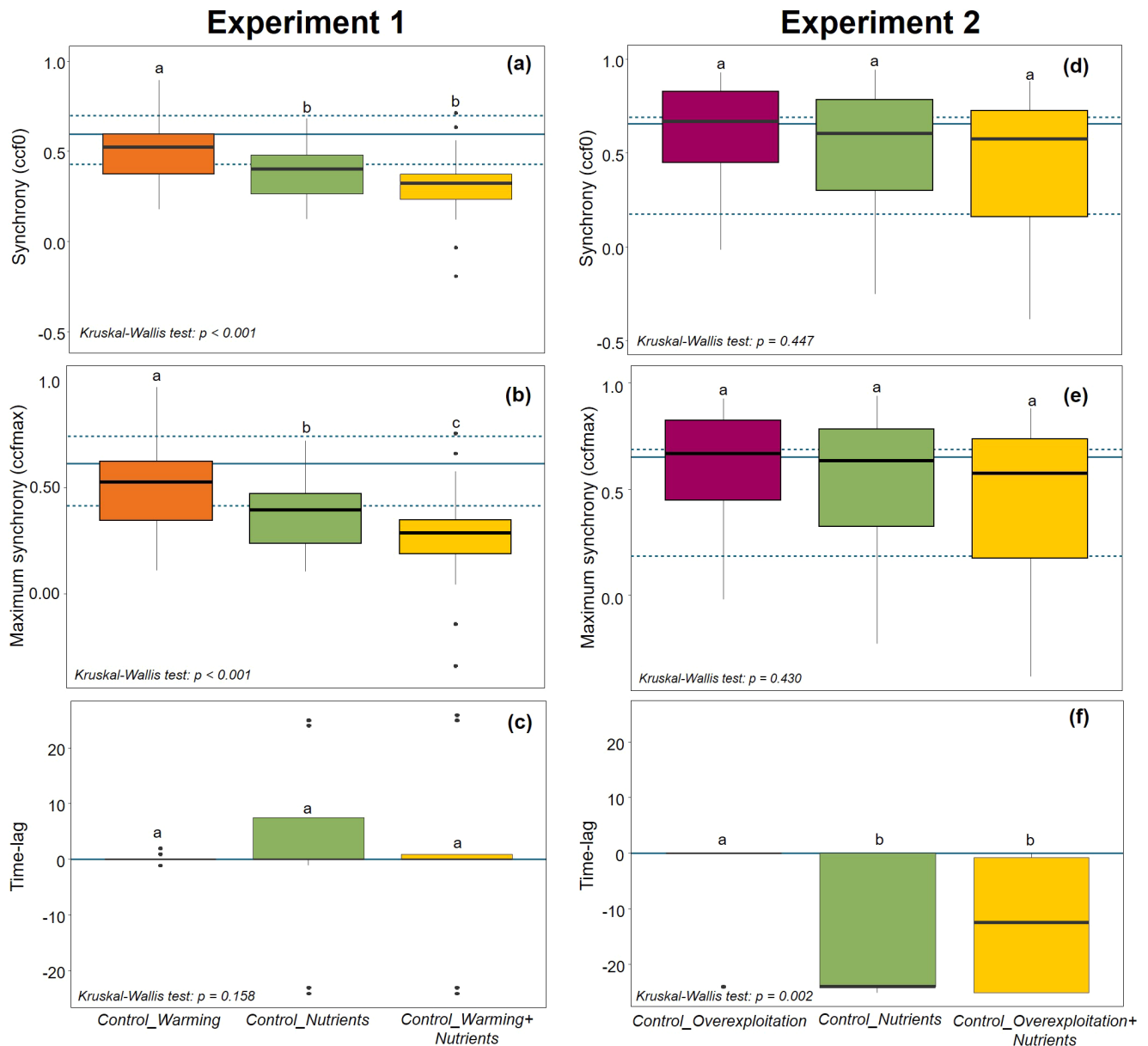
In Experiment 1, dissolved oxygen saturation significantly increased in the Nutrients and Warming+Nutrients treatments when compared with the Control, both in terms of daily oxygen dynamics (Figure 2a; Table S1:  $p=0.001$  and  $0.025$ , respectively)

and weekly oxygen dynamics ( $p=0.003$  and  $0.19$ , respectively), but also induced higher variations in oxygen dynamics ( $p=0.001$  and  $<0.001$ , respectively). By contrast, there was no significant effect of the Warming treatment on oxygen saturation in any models ( $p>0.05$ ).

In Experiment 2, results differed depending on the response variable considered. There was no significant effect of treatment on the daily average oxygen saturation (Figure 2b; Table S1:  $p>0.05$ ). The weekly average oxygen saturation only increased in the Nutrient treatment ( $p=0.03$ ). The Overexploitation + Nutrients treatment was the only treatment that induced significantly higher daily oxygen variations based on the coefficient of variations ( $p=0.02$ ).

#### 3.2 | Synchrony of Entire Oxygen Saturation Time Series

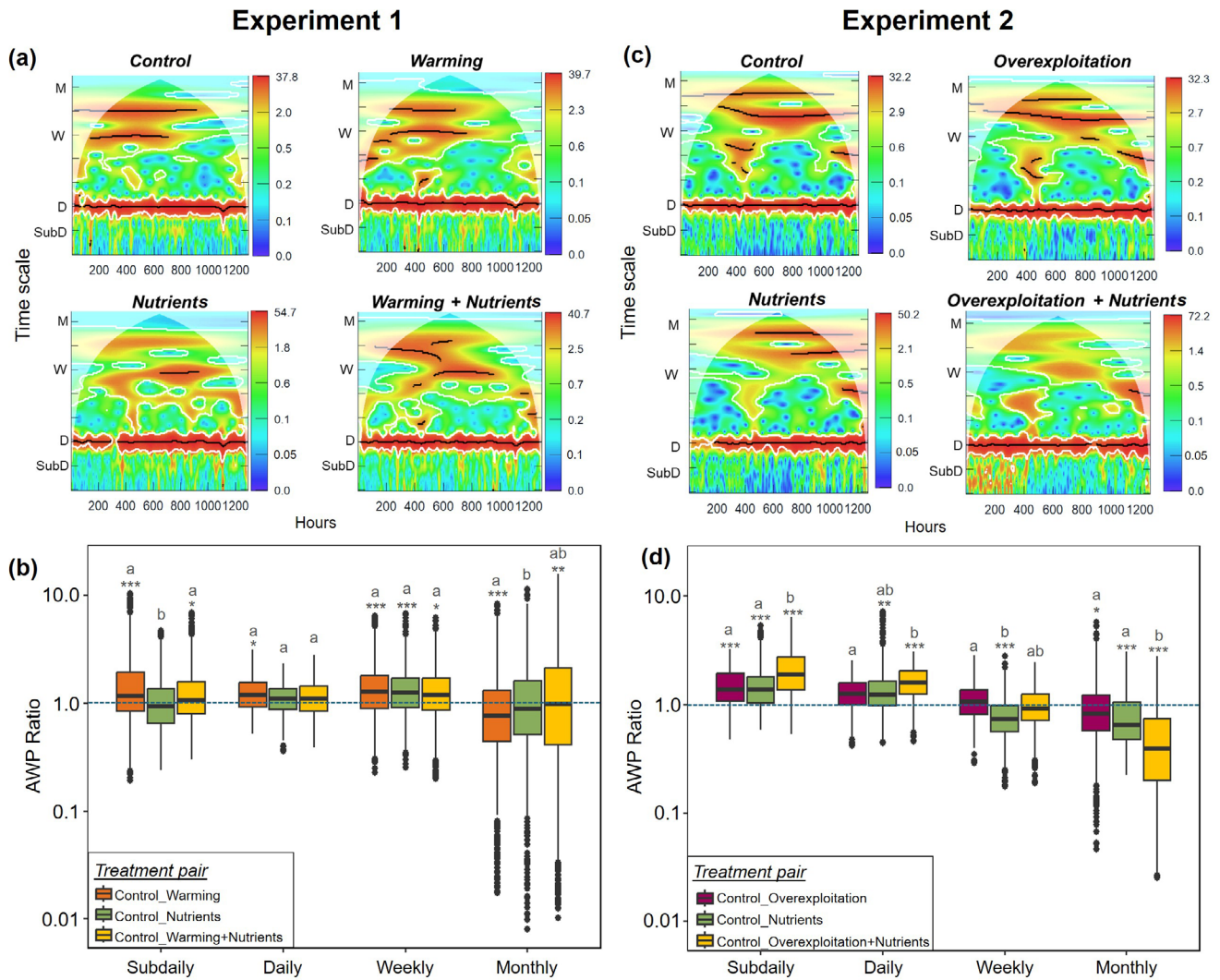
In Experiment 1, the Warming treatment alone did not alter ecosystem synchrony as indicated by positive high cross-correlation values both without (mean  $ccf0$  *Control\_Warming* =  $0.50 \pm 0.17$  SD; Figure 3a) and with (mean  $ccfmax$  =  $0.51 \pm 0.17$ ; Figure 3b) temporal realignment. These cross-correlation values were comparable to those observed in the comparisons among control mesocosms (*Control\_Control*; Figure S3). By contrast, the Nutrients treatment induced a significant decrease in ecosystem synchrony, as reflected by both  $ccf0$  (mean  $ccf0$  *Control\_Nutrients* =  $0.38 \pm 0.15$ ; Dunn post hoc test:  $p=0.003$ ; Figure 3a) and  $ccfmax$  (mean  $ccfmax$  *Control\_Nutrients* =  $0.40 \pm 0.14$ ;  $p=0.005$ ; Figure 3b). The Warming+Nutrients treatment caused the strongest alteration of synchrony (mean  $ccf0$  *Control\_Warming+Nutrients* =  $0.31 \pm 0.17$  and mean  $ccfmax$  *Control\_Warming+Nutrients* =  $0.32 \pm 0.17$ ), with a level of synchrony significantly lower than the Warming treatment for both  $ccf0$  and  $ccfmax$  ( $p<0.001$ ) and significantly lower than the Nutrient treatment for  $ccfmax$  ( $p=0.002$ ) but not for  $ccf0$  ( $p=0.130$ ). Although maximum cross-correlation values were occasionally observed when accounting for time lags, these lags were not significantly different between treatments ( $p=0.158$ ; Figure 3c), that is, there was no temporal delay in oxygen dynamics in these treatments. Results with dynamic time warping supported the desynchronization effects of nutrient addition in both experiments (Figure S4).



**FIGURE 3** | Effect of each treatment on the ecosystem synchrony in Experiment 1 (left) and Experiment 2 (right) measured using cross-correlation analyses. (a and d) represent levels of ecosystem synchrony (i.e., cross-correlation values) without considering time-lag between each pair of oxygen time series analysed ( $ccf_0$ ). (b and e) represent the maximum synchrony (i.e., maximum cross-correlation values,  $ccf_{max}$ ) computed by accounting for potential time-lags between the pairs of oxygen saturation time series and (c and f) are the time-lags at which maximum ecosystem synchrony is found. The full and dashed lines in blue represent the median values and the quantile regressions at 5% and 75%, respectively, of  $ccf_0$  in the Control treatment. Different letters correspond to significant differences between each global change factor treatment tested with Kruskal–Wallis tests and Dunn post hoc tests ( $p = 0.05$ ).

In experiment 2, similar levels of synchrony were observed in the Overexploitation and the Nutrients treatments as indicated by  $ccf_0$  (mean  $ccf_0$   $Control\_Overexploitation = 0.58 \pm 0.30$  and mean  $ccf_0$   $Control\_Nutrients = 0.51 \pm 0.38$ ; Dunn post hoc test:  $p = 0.338$ ; Figure 3d) and  $ccf_{max}$  (mean  $ccf_{max}$   $Control\_Overexploitation = 0.59 \pm 0.30$  and mean  $ccf_{max}$   $Control\_Nutrients = 0.53 \pm 0.37$ ;  $p = 0.391$ ; Figure 3e) values. The Overexploitation+Nutrients treatments did not significantly alter synchrony (mean  $ccf_0$   $Control\_Overexploitation + Nutrients = 0.42 \pm 0.39$ , mean  $ccf_{max}$   $Control\_Overexploitation + Nutrients = 0.43 \pm 0.39$ ) compared to the isolated effects of

the Overexploitation ( $p = 0.106$  for  $ccf_0$  and  $0.108$  for  $ccf_{max}$ ) and Nutrients ( $p = 0.202$  for  $ccf_0$  and  $0.169$  for  $ccf_{max}$ ) treatments. However, we identified significant differences in time lags for which maximum synchrony was found between the Overexploitation treatments and both the Nutrients treatment ( $p = 0.004$ ) and the Overexploitation+Nutrients treatments ( $p < 0.001$ ; Figure 3f). Specifically, maximum synchrony ( $ccf_{max}$ ) was observed when realigning the oxygen time series from disturbed mesocosms by  $-10$  to  $-24$  h compared to undisturbed mesocosms, suggesting that variations in oxygen dynamics occurred earlier in these treatments. Such time lag effects of



**FIGURE 4** | Wavelet Power Spectrum (WPS) diagrams averaged by treatments are provided as illustration frequency of oxygen variations for Experiment 1 (a) and Experiment 2 (c). Colours represent the normalised wavelet power (red is the highest power that corresponds to the highest frequency of oxygen variations, scale is plot-specific) and ‘SubD’, ‘D’, ‘W’ and ‘M’ are subdaily, daily, weekly and monthly time scales. The synchrony of oxygen cyclicity measured from the Average Wavelet Power Ratios (AWP Ratio) between oxygen pairs of each control replicate (undisturbed mesocosms) and global change factors (disturbed) are represented for Experiment 1 (b) and Experiment 2 (d). Dashed lines are the ratio of 1 for which global change factors do not alter synchrony while ratio significantly > 1 or < 1 indicates increased or decreased frequency of cyclicity, respectively. Letters represent significant differences in AWP Ratio across treatments within each time scale (Tukey post hoc test,  $p$  threshold = 0.05) and stars represent the sufficient differences from a ratio of 1 (Tukey post hoc test,  $p$  thresholds: \* = 0.05, \*\* = 0.01, \*\*\* = 0.001). Note that the boxplots are represented on a  $\log_{10}$  scale, but the y labels have been back-transformed from the  $\log_{10}$  values for better readability.

nutrient enrichment might explain the desynchronizing effects of nutrient enrichment also revealed by dynamic time warping in Experiment 2 (Figure S4).

### 3.3 | Synchrony of Oxygen Saturation Cyclicity

In Experiment 1, the Warming treatment desynchronized oxygen cyclicity at every timescale (subdaily, daily, weekly and monthly; Table S2, LMM:  $p < 0.001$ ), although not in the same way. At subdaily, daily and weekly time scales, desynchronization resulted from a significant increase in the frequency of oxygen variations compared to the control as illustrated by higher wavelet power spectra (i.e., more numerous red zones in the Warming treatment wavelet diagrams; Figure 4a) and

AWP Ratio significantly > 1 (Figure 4b,  $p$  subdaily < 0.001,  $p$  daily = 0.04 and  $p$  weekly < 0.001). By contrast, at the monthly time scale, synchrony decreased due to a significant reduction in the frequency of oxygen variations in warmed mesocosms (more numerous green to blue zones in the wavelet diagrams and AWP Ratio significantly < 1;  $p < 0.001$ ). The effects of the Nutrients treatment were much more contrasted and globally did not desynchronize oxygen cyclicity (LMM:  $p = 0.31$  and AWP Ratio not significantly different from 1) except at the weekly time scale (ratio significantly > 1; Figure 4b,  $p < 0.001$ ). The frequency of oxygen variations at the sub-daily time scale in the Nutrients treatment was significantly lower than in the Warming and the Warming+Nutrients treatments (Figure 4b: both  $p < 0.001$ ), was similar at the daily ( $p = 0.39$  and 0.98, respectively) and weekly time scales ( $p = 0.99$  and

0.71, respectively) and was significantly higher than in the Warming treatment at the monthly time scale ( $p=0.01$ ). Finally, the Warming+Nutrients treatment globally altered the synchrony of oxygen cyclicity (LMM:  $p=0.008$ ) by significantly increasing the frequency of variations at sub-daily and weekly time scales (AWP Ratio  $>1$ ; Figure 4b:  $p=0.04$  and  $0.03$ , respectively) and decreasing it at the monthly time scale ( $p=0.009$ ). Its intermediate effect compared to the isolated effects of the Nutrients and the Warming treatments suggested potential non-additive or compensatory interactions.

In Experiment 2, the overexploitation treatment globally desynchronized oxygen cyclicity (Table S2, LMM:  $p<0.001$ ). This desynchronization was reflected by a significant increase in the frequency of oxygen variation as illustrated by higher wavelet power spectra (i.e., more numerous red zones in the Overexploitation treatment wavelet diagrams; Figure 4c), especially at the subdaily time scale (Figure 4d, AWP Ratio significantly  $>1$ ;  $p<0.001$ ) and a significant decrease at the monthly time scale (AWP Ratio  $<1$ ;  $p=0.04$ ) but not at other time scales. By contrast, the Nutrients treatment desynchronized oxygen cyclicity at every time scale by inducing significant increases in the frequency of oxygen variations at sub-daily, daily and weekly scales (AWP Ratio  $>1$ ,  $p$  sub-daily  $<0.001$ ,  $p$  daily  $=0.003$  and  $p$  weekly  $<0.001$ ), but a significant decrease at the monthly scale ( $p<0.001$ ). Nutrients desynchronized oxygen cyclicity to a similar extent as the Overexploitation treatment at the subdaily, daily and monthly time scales and as Overexploitation+Nutrients at daily and weekly time scales. Finally, the Overexploitation+Nutrients treatment also desynchronized oxygen cyclicity (Table S2, LMM:  $p<0.001$ ) and caused the highest increases in frequency of oxygen variation at subdaily and daily time scales and the strongest decreases at monthly time scales compared with other treatments, suggesting that the two factors in combination additively affected ecosystem synchrony at the different studied time scales.

## 4 | Discussion

Understanding the spatial and temporal scales at which global change drivers operate—and teasing apart their individual and combined effects on ecosystem functioning—remains a core challenge in ecology. This study offers two empirical insights into how ecosystems respond to isolated and combined disturbances. First, we found that nutrient addition (in isolation or in combination with other global change factors) tended to increase mean oxygen saturation and variations compared to the other factors. This result was associated with a generally lower ecosystem synchrony, either through lower overall synchrony levels (Experiment 1) or through time lags in oxygen variations (Experiment 2) while no significant effects were detected for the other global change factors, supporting our first hypothesis. Second, we found that nutrient enrichment, warming and overexploitation all influenced oxygen cyclicity across time scales ranging from sub-daily to monthly with most effects found on short-term time scales, validating our second hypothesis. Finally, comparing isolated and combined global change factors showed that combined disturbances can have additive effects on ecosystem synchrony, but may also dampen each other's impact as initially expected.

Using ecosystem synchrony as a novel currency to assess the effects of global change factors on ecosystems, we detected the significant effect of nutrient enrichment on oxygen dynamics and on the cycles constituting these dynamics. Nutrient inputs can lead to various metabolic responses, including increased respiration that often decreases oxygen saturation (Cross et al. 2022; Gutiérrez-Cánovas et al. 2024) or by increasing net primary productivity (Brauns et al. 2022) leading to increased oxygen saturation (Jeppesen et al. 2021; Pendleton et al. 2015; Seabloom et al. 2021). This latter mechanism is consistent with the increases in oxygen levels and its variability in experiments and is supported by preliminary observations of increased primary production in the water column in both experiments (Figure S5). Yet, the effects in Experiment 2 were weaker and may have been buffered by additional mechanisms. In fact, our results revealed that nutrient enrichment affected ecosystem synchrony through different ways across experiments with a stronger effect on the synchrony of the overall oxygen time series in Experiment 1 (although time lags in oxygen dynamics were detected in Experiment 2) and a stronger effect on the synchrony of oxygen cyclicity in Experiment 2. Mesocosms in Experiment 2 were structurally and ecologically more complex than in Experiment 1, allowing potentially stronger variations among replicates, which ultimately might weaken statistical power to detect significant effects of treatments on the overall synchrony based on entire oxygen time series. Mesocosms in Experiment 2 were also installed for a longer period and would potentially explain better detection of stronger divergences in functioning of both short-term and long-term cycles across treatments as systems had more time to settle. Overall, our study demonstrates that nutrient enrichment is a key driver affecting multiple dimensions of ecosystem synchrony but whose effects might be context-dependent. It thus emphasizes the need for future studies assessing how varying nutrient concentrations, frequencies of addition, and ecosystem's buffering capacities may modulate these effects in natural ecosystems.

This study also revealed different temporal extents in the observed effects of global change factors on ecosystem dynamics by bringing complementary insights into the effects on the cyclicity of oxygen. Specifically, we identified that the impacts of warming and overexploitation were undetectable in the entire oxygen dynamics but were much more apparent when decomposing the oxygen dynamics across multiple time scales. Warming affected the synchrony of oxygen cyclicity at subdaily and daily time scales by increasing the frequency of oxygen variations. This effect ultimately manifested in desynchronization of oxygen cyclicity but not in the desynchronization of the whole dynamic of oxygen saturation (also validated by the absence of the effect of warming on oxygen saturation values and coefficient of variations). This may reflect changes in the balance between autotrophic and heterotrophic processes, potentially driven by hourly fluctuations in water temperatures (Jeppesen et al. 2021; Moore et al. 2021; Zhi et al. 2023). However, to confirm this mechanism, additional investigations considering changes in the biomass and structure of autotrophic and heterotrophic communities are needed. Similar desynchronization patterns of oxygen cyclicity were induced by overexploitation. The removal of apex predators through overexploitation can cause trophic downgrading, leading to marked changes in ecosystem functioning (Estes et al. 2011). Trophic cascades that can induce a change in the

biomass of primary producers are a common mechanism leading to these effects (Pendleton et al. 2015; Seabloom et al. 2021). In the present study, increased primary productivity (Figure S5) could have contributed to changes in the metabolic balance of oxygen by enhancing oxygen production and assimilation likely supported by the four trophic level structure of the food webs in these mesocosms, expected to cause a positive top-down effect on the first trophic level (Su et al. 2021). Another potential mechanism that remains to be explored is the modification of the diel behavioural rhythms of primary consumers associated with the removal of the apex predator (McIntosh and Townsend 1996; Meutter et al. 2005) which could modify the patterns of primary production and could ultimately induce changes in daily oxygen dynamics.

Multiple human-induced stressors act simultaneously in nature and their interacting effects can have profound consequences on ecosystems (Jackson et al. 2021). We found that multiple global change factors in combination influenced ecosystem synchrony in ways that differed from their isolated effects, and that the nature of these interactions varied depending on the factor involved. Specifically, nutrient enrichment combined with warming dampened desynchronization of oxygen dynamics while nutrients combined with overexploitation acted additively to elevate desynchronization. These findings highlight the importance of focusing future research on the mechanistic underpinnings of ecosystem desynchronization, particularly those related to changes in primary productivity driven by nutrient availability, and how these interact with trophic alterations caused by overexploitation or with temperature-driven metabolic shifts. For instance, nutrient enrichment can increase primary productivity, shifting the metabolic balance toward greater oxygen production compared to respiration (Seabloom et al. 2021). However, this effect may be weakened by warming because it stimulates the activity of heterotrophic organisms and increases respiration (Moore et al. 2021). By contrast, the overexploitation of an apex predator can induce an increase in the biomass of primary producers (Pendleton et al. 2015; Seabloom et al. 2021) that may reinforce the increase in primary productivity caused by nutrient enrichment (Östman et al. 2016). These findings challenge the assumption that similar perturbations tend to dampen each other, suggesting instead that some combinations may accelerate ecological change (Orr et al. 2022). However, as our experiments were conducted in simplified, semi-controlled systems, natural ecosystems may be more buffered against such effects (Stewart et al. 2013). The dynamics of natural ecosystems (and their synchrony) submitted to multiple perturbations could be affected to a weaker extent by global change factors than in experiments because they exhibit a higher level of complexity in terms of size, habitat diversity or biodiversity that may provide them a greater buffering capacity to face perturbations (Donohue et al. 2016; Jackson et al. 2021). Upscaling our experimental observations to natural ecosystems is critical.

In conclusion, this study provides the first experimental evidence that ecosystem synchrony can be profoundly altered by global change and that this alteration can occur both on the overall dynamic of oxygen saturation and on the cycles constituting this dynamic. By identifying and decoupling the isolated and combined effects of different global change factors, we reveal the complex and context-dependent nature of their

influence on different facets of ecosystem synchrony. This supports the importance of considering complementary approaches to fully appreciate ecosystem synchrony, its underlying mechanisms and their alteration. Additional empirical studies on ecosystem synchrony are now needed in different types of ecosystems and in various geographical areas using measurements of different and multiple ecosystem functions (multifunctionality) to expand these first experimental evidences. We argue that the use of ecosystem synchrony could ultimately help in identifying the mechanisms destabilising ecosystem dynamics at finer time scales than hitherto investigated and improve our ability to anticipate ecosystem trajectories and identify early warning signals preceding transitions in the ecological state of ecosystems facing perturbations.

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### Author Contributions

All authors conceptualised this work. Chloé Vagnon performed analyses. Chloé Vagnon and Julien Cucherousset drafted the first version of the manuscript. All authors have contributed to discussions on article content and have contributed to its editing and reviewing.

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### Data Availability Statement

Data and Rcodes are available in a Dryad repository associated with the DOI: [http://datadryad.org/share/LINK\\_NOT\\_FOR\\_PUBLICATION/wmUNbIk7NwXcVsCwrQ69Z-plUKD8gQpI4bBla88U6QY](http://datadryad.org/share/LINK_NOT_FOR_PUBLICATION/wmUNbIk7NwXcVsCwrQ69Z-plUKD8gQpI4bBla88U6QY).

### Peer Review

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### Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ele70271-sup-0001-Supinfo.docx.