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ORIGINAL ARTICLE

Ecosystem Synchrony Among Small Shallow Lakes is Driven Differently by Their Biotic and Abiotic Similarities

Chloé Vagnon,[1,2]* Mathieu Chevalier,[3] Stéphanie Boulêtreau,[1]
Flavien Garcia,[1] Julian D. Olden,[4] and Julien Cucherousset[1]

[1]*Centre de Recherche sur la Biodiversité et l'Environnement (CRBE), Université de Toulouse, CNRS, IRD, Toulouse INP, Université Toulouse 3 – Paul Sabatier (UT3), Toulouse, France;* [2]*FRB—CESAB, Montpellier, France;* [3]*Centre de Bretagne, IFREMER-DYNECO-LEBCO, 10070 Plouzané, CS, France;* [4]*School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98105, USA*

ABSTRACT

Identifying the coordinated responses and the biotic and abiotic drivers of aquatic ecosystem dynamics across space and time is the key to understanding and predicting ecosystem trajectories under global change. Here, we applied the concept of ecosystem synchrony (that is, similarities in temporal fluctuations of ecosystem functions across space) to evaluate: (1) the coordinated dynamics of 16 French gravel pit lakes and (2) how geographic proximity, abiotic and biotic similarities explain their level of synchrony. We quantified both multi-year (two-year period) and seasonal (warm vs. cold seasons) levels of synchrony in dissolved oxygen saturation using high-frequency (10 min) measurements. We showed that the two-year ecosystem synchrony was driven by the environmental similarities in abiotic (for example, nutrient levels, hydromorphology) and biotic (for example, fish biomass) conditions between lakes yet the relative influence of these two processes varied seasonally. Indeed, ecosystem synchrony during warm seasons was primarily driven by abiotic environmental conditions, likely reflecting the stronger control of physical and chemical conditions on ecosystem functioning. Conversely, biotic similarity was more influential on ecosystem synchrony during cold seasons, suggesting a greater influence of biological structure under reduced ecosystem productivity. Geographic distance had a negligible effect, likely due to the relatively limited spatial extent of the lake network. These findings highlight the value of ecosystem synchrony as a spatiotemporal integrator of ecosystem dynamics and emphasize the need to account for both the temporal scale and local biotic and abiotic context dependencies when assessing the ecological trajectories of ecosystems.

Key words: spatial synchrony; ecosystem functioning; coordinated dynamics; dissolved oxygen saturation; high-frequency monitoring; gravel pit lakes.

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Author contributions All authors conceptualized this work. CV performed analyses. CV, MC and JC drafted the first version of the manuscript. All authors have contributed to discussions on article content and contributed to its editing and reviewing.

**Corresponding author; e-mail:* chloe.vagnon@gmail.com

HIGHLIGHTS

- Ecosystem synchrony revealed coordinated oxygen dynamics across small shallow lakes.
- The synchrony level and its drivers differ across lake pairs and seasons.
- Synchrony integrates spatiotemporal ecosystem dynamics beyond geographic proximity.

INTRODUCTION

Understanding the temporal dynamic of ecosystem processes under environmental changes is contingent on the identification of the mechanisms operating over space and time in ecosystem alterations (Brose and Hillebrand 2016). Yet, ecosystem dynamics are challenging to forecast because they are conditioned by the complex interplay between abiotic and biotic factors (Ochoa-Hueso and others, 2021). This interplay is well reflected in ecosystem functions that are emergent and measurable properties (for example, oxygen dynamics, primary production) integrative of changes in both biotic and abiotic processes that shape how ecosystems operate over time (Lovett and others, 2006). However, the spatial heterogeneity in ecosystem function dynamics is often neglected (Donohue and others, 2016) despite evidence that studying their coordinated responses across space may significantly advance our understanding of ecosystem trajectories (Loreau and others, 2003; Wang and Loreau 2014; Song and others, 2026). In this perspective, the concept of ecosystem synchrony has been recently introduced (Vagnon and others, 2024). Ecosystem synchrony is the similarity in the temporal fluctuations of an ecosystem function (for example, primary production, nutrient cycling) among multiple ecosystems. Quantifying ecosystem synchrony and identifying its drivers in natural systems hold promise for advancing our understanding of how ecosystems collectively respond to environmental perturbations (Huang and others, 2026).

From a population-level perspective, spatial synchrony usually decreases as geographic distance increases (Anderson and others, 2019; Hansen and others, 2020), and this process is defined as the Moran effect (Moran 1953). This distance-decay can arise because the likelihood of dispersal between populations decreases with distance, reducing the potential for demographic or genetic connectivity; and because environmental conditions tend to become more dissimilar as distance increases. The extent of population synchrony is, however, shaped differently depending on intrinsic local biotic and abiotic environmental conditions such as species-specific traits mediating population responses to environmental variations (Chevalier and others, 2014) or dispersal limitations such as physical barriers (Walter and others, 2017). Ecosystem synchrony may similarly be influenced by variations in abiotic (for example, ecosystem size) and biotic (for example, community composition) factors (Vagnon and others, 2024, 2025) as these parameters jointly shape the variability and characteristics of ecosystem functions from which synchrony is derived (Lottig and others, 2017; Puts and others, 2022). Therefore, ecosystems facing similar biotic and abiotic environmental conditions should exhibit similar dynamics. In addition, ecosystem synchrony can be quantified at different temporal scales (for example, seasonal, multi-year), allowing for a finer analysis of how local abiotic and biotic environmental conditions shape ecosystem synchrony and offering a more nuanced understanding (spatially and temporally) of ecosystem dynamics and their drivers than previous approaches (Lottig and others, 2017; Reuman and others, 2025). Studies on the drivers of ecosystem synchrony are rare and have mainly focused on abiotic drivers such as watershed characteristics, land cover (Lottig and others, 2017) or dam constructions (Chalise and others, 2023). Yet, the relative importance of abiotic drivers compared to biotic drivers and the variations in their effects on ecosystem synchrony throughout the year remain unknown.

Gravel pit lakes are artificial lakes widely distributed across the globe (Mollema and Antonellini 2016) that offer a particularly valuable system for studying ecosystem synchrony and its drivers to better understand ecosystem responses to perturbations. These artificial lakes, formed by sand and gravel extraction and later filled by groundwater and precipitation (Mollema and Antonellini 2016), are usually clustered and exhibit relatively high environmental heterogeneity within a relatively small geographic area. Due to their artificial nature and their socioeconomic history, they differ in age, depth, surface, nutrient status, and biotic communities, generating a mosaic of ecosystems with divergent trajectories under similar climate conditions and hosting multiple types of human activities (Santoul and others, 2009; Emmrich and others, 2014; Blanchette and Lund 2016). Anthropogenic pressures (for example, fish stocking, angling, recreational activities) further modulate environmental conditions (Gimenez and others, 2023), which can either synchronize ecosystem functions across lakes (for example, through similar dynamics of nutrient inputs: Imbert and others, 2024) or induce divergent dynamics (for example, direct impacts of invasive species of ecosystem processes: Alp and others, 2016). Additionally, gravel pit lakes undergo predictable successional changes from oligotrophic trophic status at their earlier stages toward more productive and mesotrophic trophic status as they get older (Colas and others, 2021), providing a unique opportunity to assess how ecosystem synchrony evolves during ecosystem maturation. Gravel pit lakes respond quickly to short-term seasonal changes because their structure amplifies temperature, oxygen, and nutrient fluctuations, while their biotic communities and low buffering capacity make ecosystem functions highly dynamic across seasons (Blanchette and Lund 2016; Alp and others, 2016). Their accessibility and manageable size allow for simultaneous high-frequency monitoring of several ecosystems, and enable detection of these seasonal and interannual socioecological dynamics (Imbert and others, 2024). Studying these systems is not only ecologically informative but also practically relevant, as synchronized ecosystems may respond similarly to perturbations and management plans, highlighting potential vulnerabilities but also solutions for preserving ecosystem functions.

Here, we empirically quantified the level of ecosystem synchrony among 16 gravel pit lakes located in South-western France and disentangled the effects of geographic distance, abiotic and biotic environmental similarity between them to explain their level of synchrony. We conducted separate analyses for the two-year level of ecosystem synchrony (two-year period) and the seasonal level of ecosystem (cold vs. warm seasons) to account for differences in lake productivity intensity throughout the year and potential differences in the drivers of ecosystem synchrony. We assessed ecosystem synchrony based on the similarity between high-frequency dynamics (every 10 min) of dissolved oxygen saturation (DO saturation) measured using automatic sensors following the approach in Vagnon and others, (2025). DO dynamics are not a direct measurement of ecosystem metabolism because external factors affecting oxygen variations (for example, atmospheric pressure, physical mixing) can blur this relationship, but DO dynamics are routinely monitored and remain an integrative indicator of ecosystem functioning, ecosystem health, and changes in primary production versus respiration in lakes (Odum 1985; Istvánovics and Honti 2018; Vagnon and others, 2025). We hypothesized that lakes with similar abiotic (for example, nutrient status) and biotic (for example, community composition) environmental conditions will exhibit higher synchrony than lakes with dissimilar characteristics because they share similar ecological dynamics (Vagnon and others, 2024, 2025; Huang and others, 2026). We also predicted that biotic and abiotic environmental similarities would be stronger predictors of ecosystem synchrony than geographic distance, given both the high level of environmental heterogeneity and the relatively limited spatial extent (1250 km^2) of the studied lake network (Zhao and others, 2016; Colas and others, 2021). Finally, we predicted that the magnitude of the effect of similarities in abiotic and biotic environmental conditions would vary seasonally as lake metabolic dynamics (that is, balance between carbon fixation and biological carbon oxidation) tends to decrease during cold periods and to increase during warm periods (Laas and others, 2012), potentially leading to seasonal differences in the patterns and drivers of synchrony.

MATERIAL AND METHODS

Study Sites

The 16 studied gravel pit lakes are located in the Garonne and the Ariège floodplains (Figure 1; Table S1), within a zone of 1250 km^2 (maximum distance between two lakes: 47.6 km) in south-western France in urbanized regions with a marked agricultural activity and anthropogenic pressure. They were created over the past 50 years including five lakes under 20 years old, three lakes between 20 and 30 years old, five lakes between 30 and 40 years old and finally three lakes older than 40 years. These lakes are mainly mesotrophic (< 30 µg/L of total phosphorus) with two eutrophic lakes (< 50 µg/L). As they get older, these artificial lakes usually follow a predictable pattern and progressively shift from heterotrophy to autotrophy and become more productive (Colas and others 2021). They are characterized by a maximum depth ranging between 2 and 12 m (mean = 6 m ± 3 SD; Table S1), surface ranging between 28,600 m^2 and 213,016 m^2 (mean = 142,172 m^2 ± 50,230) and perimeters varying between 815 m and 4139 m (mean = 2083 m ± 917). Due to their limited depth, these lakes are polymictic throughout the year (Nobre and others, 2025) with persistent summer stratification, and frequent mixing (Figure S1).

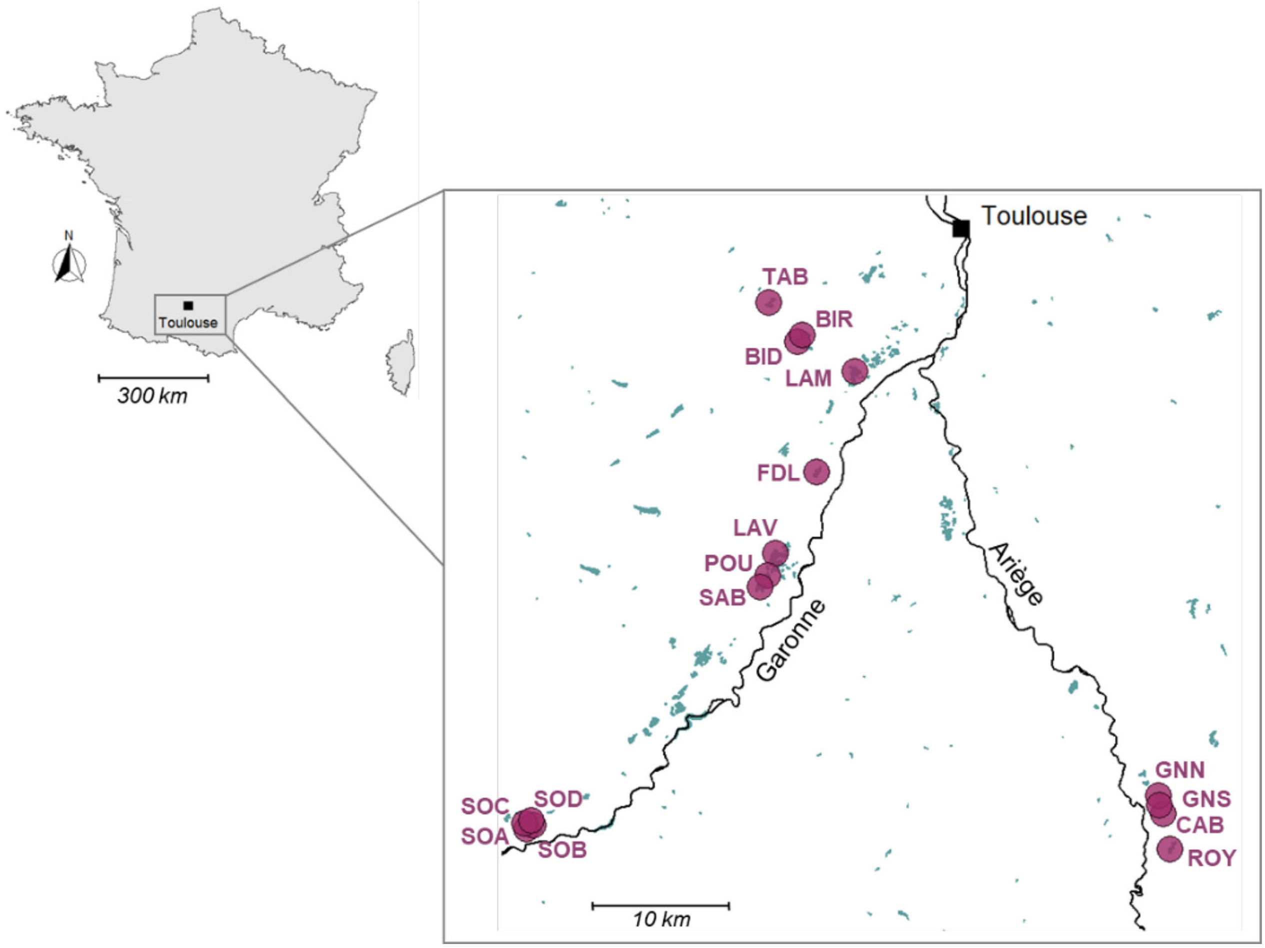

Figure 1. Map of the locations of the 16 gravel pit lakes (pink circles) along the Garonne and the Ariège floodplains (southwest of Toulouse, France). The water masses such as other gravel pit lakes and ponds around the studied area are displayed in blue (data source: BD TOPAGE® 2022).

During the last decade, multiple studies based on regular annual survey of biotic (for example, fish communities, trophic structure) and abiotic (for example, physicochemical factors) parameters on this network of lakes have highlighted varying levels of human-induced perturbations of ecosystem functioning, highly related to changes in biodiversity (for example, invasive species; Alp and others, 2016; Zhao and others, 2016; Garcia and others, 2025), biomass manipulation (for example, through stocking; Gimenez and others, 2023) and recreational activities (for example, angling practices; Imbert and others, 2024). For instance, some of these lakes have undergone different intensities of crayfish invasion that induced different decomposition rates, accelerated by up to fivefold in spring through direct detritus consumption by crayfish, which shortened the period of major detritus availability in the ecosystem (Alp and others, 2016).

Oxygen Dynamics

The 16 gravel pit lakes were equipped with high-frequency loggers (miniDOT® Clear Logger, PME, Vista, CA, accuracy 0.3 $mg.L^{-1}$) equipped with optical sensors to measure oxygen saturation and water temperature every 10 min between November 2022 and November 2024. The loggers were calibrated following the manufacturer recommendation and deployed in the deepest zone of the lakes and at 70 cm under the water surface. Specifically, a buoy was attached to a mooring using a stainless-steel cable and loggers were attached to another stainless-steel cable attached to the buoy (Nobre and others, 2025). Each logger was equipped with an automatic wiper (mini-

WIPER®, PME, Vista, CA) that cleaned the sensors every 2 h and with an anti-fouling copper plate to limit biofouling. Every three months, the data were downloaded by hands and the loggers and wipers were controlled (for example, data visualization, measurement quality, battery levels), cleaned and reinstalled. During the study period, biotic and abiotic parameters were also surveyed (see details below).

Following Vagnon and others (2025), we selected dissolved oxygen saturation to quantify ecosystem synchrony because this parameter is integrative of the balance between production and respiration in lake metabolism, which is linked with the balance between photosynthetic productivity and microbial activity and is not sensitive to temperature differences across lakes that could affect oxygen concentrations due to dilution capacity differences (Odum 1985; Istvánovics and Honti 2018). At 100% saturation, oxygen concentration is at equilibrium with atmospheric conditions (Wetzel 2001). An oxygen saturation above 100% may be more linked with an increase in autotrophic processes through photosynthesis while a saturation below 100% may be more linked with an increase in heterotrophic processes associated with a growing microbial activity and recycling of organic matter, although other factors (for example, mixing, abrupt strong temperature decrease) can participate in oxygen variations. As we regularly checked data for quality and simultaneously measured temperature with DO saturation, we ensured that oversaturation was not due to calibration issues or abrupt temperature changes. Dissolved oxygen saturation values that deviated from adjacent measurements within a daily time window were corrected using the median absolute deviation method (Pearson 2002; O'Dell and others, 2020). In the following analyses, these corrected values of oxygen saturation were averaged on a daily basis to study ecosystem functioning over years while limiting the noise from short-term fluctuations that were not of interest here. We computed summary statistics (mean, min, max, range) and the coefficient of variation of oxygen dynamics for each lake over the two years to characterize general patterns in oxygen variations before computing synchrony (Table S3).

Two-Year and Seasonal Ecosystem Synchrony

Ecosystem synchrony among all pairs of lakes was assessed by measuring the dissimilarity in their dissolved oxygen saturation dynamics. To do this, we used a dynamic time warping algorithm (DTW), which aligns time series by minimizing the distance between them across all possible temporal alignments (Müller and editor, 2007). DTW is commonly applied for comparing time series because it quantifies similarity between time series even if they differ in shape or are temporally misaligned, such as when peaks or troughs occur at slightly different times (Tormene and others, 2009). The resulting metric (the normalized distance) is calculated as the total alignment cost divided by the combined length of the two time series, providing a standardized measure of dissimilarity between temporal signals. This measure is especially valuable when comparing high-frequency time series that could include missing data due to field or material issues likely to occur when using automatic sensors in multiple ecosystems over several months or years. Applied to the concept of ecosystem synchrony, a low normalized distance indicates a high synchrony between ecosystems because it reflects a strong similarity in the dynamics of their measured functions while a high distance indicates a low synchrony. To enhance interpretability, we rescaled the DTW distance to a 0–1 scale and subtracted it from 1, so that the lowest synchrony is 0 and the highest is 1.

We first quantified ecosystem synchrony considering two-year synchrony by calculating DTW distances between the full two-year time series of oxygen saturation for each pair of lakes. To assess seasonal trends, we divided each year into a cold period and a warm period, resulting in four synchrony measurements per lake pair (that is, cold 2022–2023, warm 2022–2023, cold 2023–2024, warm 2023–2024). We discerned warm from cold periods by identifying the date at which the daily water temperature (°C) measured simultaneously with the miniDot® used to measure DO saturation remained above 18 °C for 10 consecutive days (Figure S2). The threshold of 18 °C was selected as it corresponds to the temperature at which most of the photosynthetic organisms grow after winter (Singh and Singh 2015), triggering an increase in photosynthetic activity and, therefore, in overall ecosystem productivity. This threshold was reached between April and June in all lakes, consistently coincides with observable amplitudes changes in DO saturation, which indicates a functional transition in ecosystem metabolism.

Figure 2. Daily averaged dissolved oxygen saturation (%) measured in the 16 gravel pit lakes between October 2022 and November 2024. The dashed purple lines represent an oxygen saturation at 100% above which variations usually correspond to an increase in autotrophic processes, mostly through photosynthesis, while variations below this threshold usually reflect an increase in heterotrophic processes associated with, for instance, recycling of organic matter.

Abiotic Environmental Conditions in the Lakes

We identified a set of relevant abiotic factors to discriminate the local environmental conditions in each gravel pit lake based on the physical, water chemistry and hydromorphological characteristics (Table S1) and on previous studies on the functioning of these ecosystems (Colas and others 2021). These factors included morphometric indices describing the form and the complexity of the lake were computed by integrating the perimeter (in m), surface (m^2) and maximum depth (m) of lakes. For each lake, the index *MIdx* was computed (Eq. 1) to depict hydromorphology that differentiates flatter basins (low values, that is, high surface compared to depth) from more conical basins (high values, that is, small surface compared to depth). As a complement, the shoreline index *SIdx* was computed (Eq. 2) to reflect the complexity of the lake's shoreline with high values indicating higher complexity.

$$MIdx = \frac{maximum(Depth)}{\sqrt{\frac{Surface}{10000}}} \qquad (1)$$

$$SIdx = \frac{Perimeter}{2\sqrt{\pi\, Surface}} \qquad (2)$$

Physicochemical parameters were measured every three months from October 2022 to October 2024 at the deepest part of the lake where the loggers were attached. We then used an averaged value for each year to represent the average environmental context characterizing each gravel pit lake. These parameters included specific conductivity (*Cond*, $\mu S.cm^{-1}$) and turbidity (*Turb*, NTU) measured using a multiparameter probes (YSI Pro DSS) every 1-m through the water column, water transparency based on Secchi depth (*SecD*, m) using a Secchi disk, total phosphorus concentration (*PTot*, $mg.L^{-1}$) measured on unfiltered water following the molybdate-blue method using a spectrophotometer (Uvi Light XT5, Secomam, Alès, France; absorbance measured at 880 nm) and dissolved

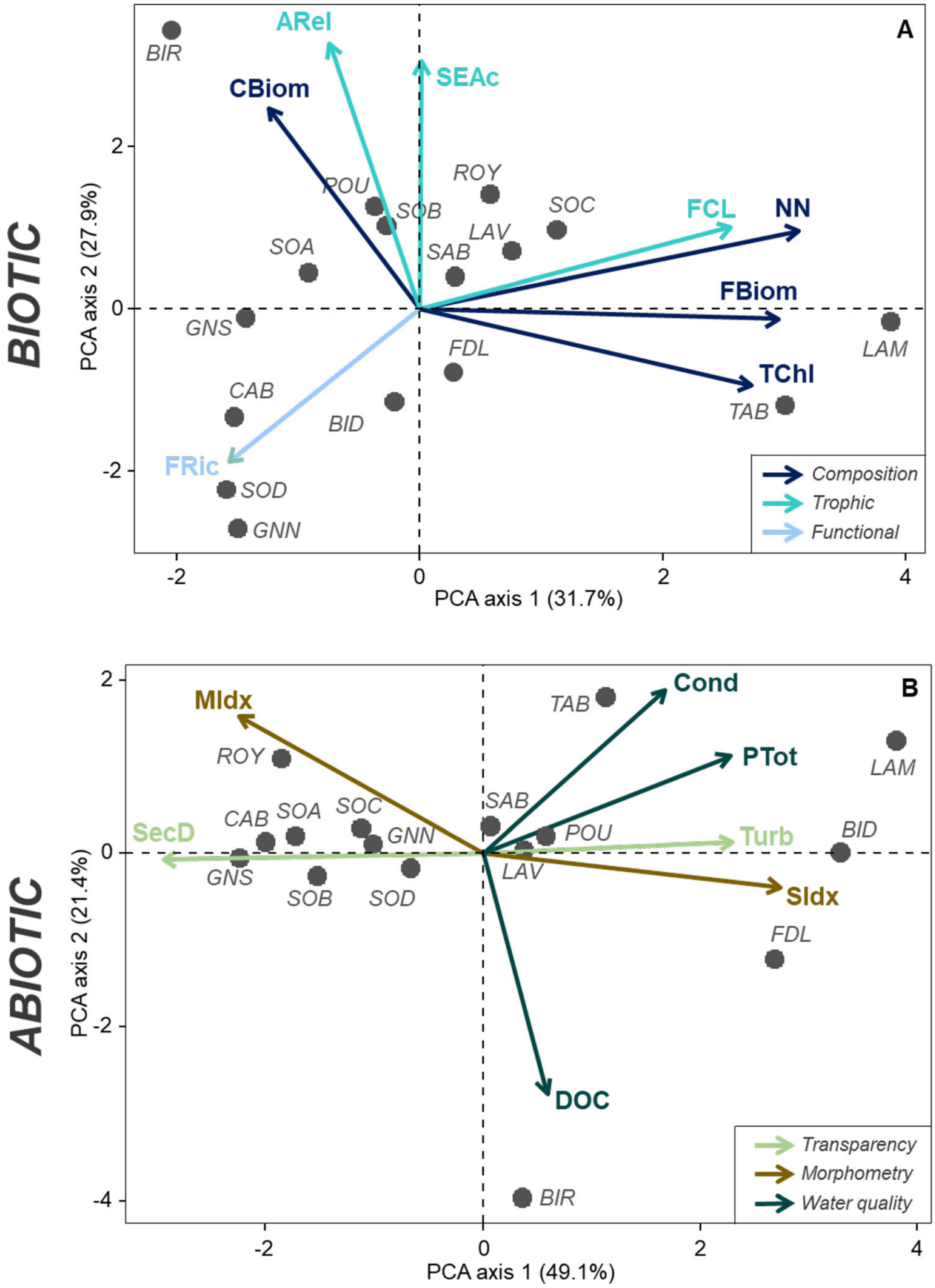

Figure 3. Biotic and abiotic dissimilarities between gravel pit lakes. (A) Represents the biplot of the two first axes of the principal component analysis (PCA) performed on biotic characteristics (arrows) of the 16 studied lakes (gray points) and (B) the biplot of the two first axes of the PCA performed on abiotic characteristics of the 16 studied lakes. Colors of both arrows and barplots code the type of variable studied. (A): ARel = autochtonous reliance, CBiom = crayfish biomass, FBiom = fish biomass, FCL = food chain length, FRic = functional richness of fish community, NN = percentage of non-native fish biomass, SEAc = Chore isotopic niche of consumers and TChl = total chlorophyll-a. (B): Cond = conductivity, DOC = dissolved organic carbon, MIdx = morphometric index, PTot = total phosphorus, SecD = Secchi depth, SIdx = shoreline development index, and Turb = turbidity.

organic carbon (*DOC,* mg.L^{-1}) measured using a Shimadzu TOC-L total organic carbon analyzer by infrared detection of CO_2 produced by catalytic oxidation at 720 °C of the organic carbon contained in water previously filtered to 0.45 µm. These variables were used as proxies for water

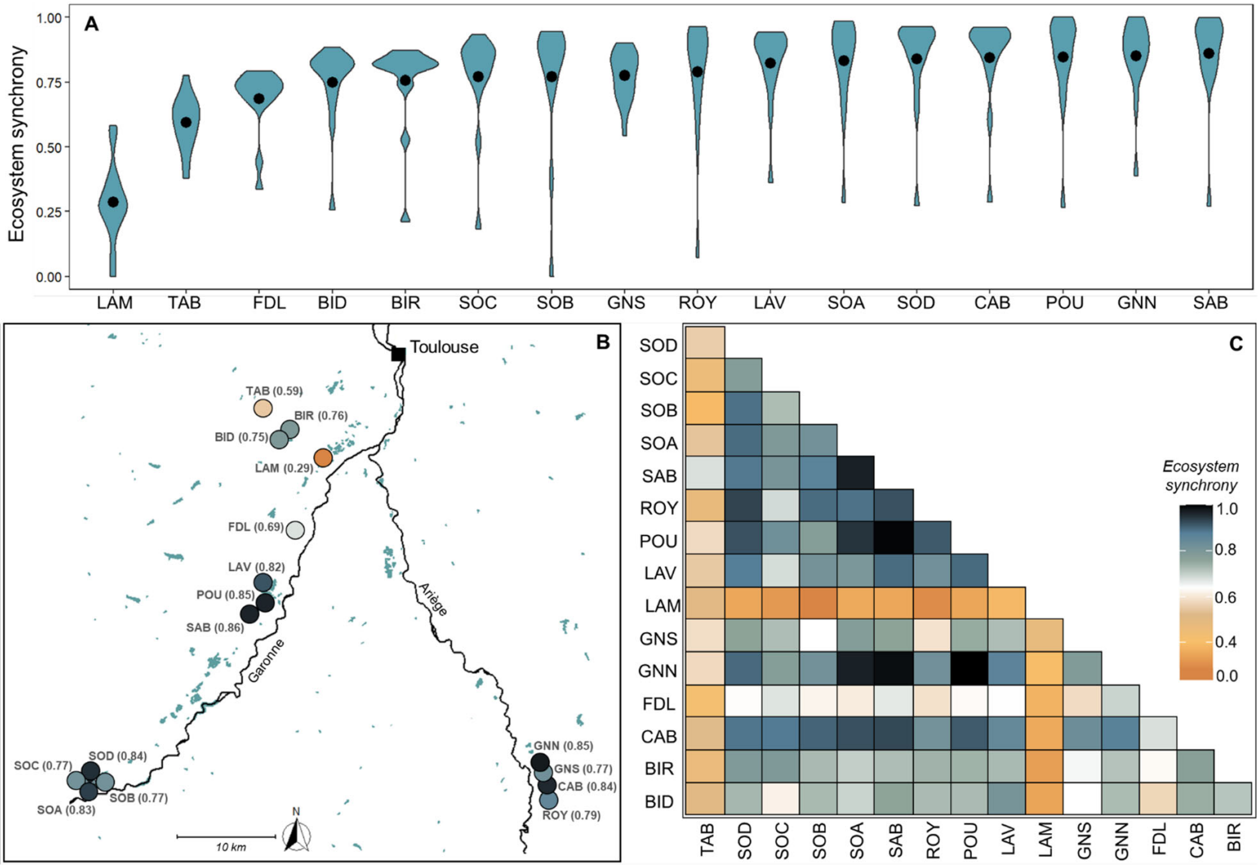

Figure 4. Two-year ecosystem synchrony between the 16 gravel pit lakes. (A) Distributions of synchrony values for each lake ordered from the least synchronized (*left*) to the most synchronized (*right*) with other lakes based on their mean synchrony value (black points). (B) Spatial distribution of the mean ecosystem synchrony per lakes (indicated in parentheses) and (C) matrix of pairwise ecosystem synchrony detailed for each pair of lakes. Two-year ecosystem synchrony quantifies the similarity between each pair of lakes during the entire time series (two years) of measurements of oxygen saturation, with the lowest ecosystem synchrony = 0 and the highest ecosystem synchrony = 1.

quality, transparency, nutrient availability for autotrophs, decomposition activity and allochthonous organic matter inputs.

Abiotic dissimilarities between lakes were then synthesized using a principal component analysis (PCA) performed on these seven factors (scaled and centered). We retained the first two axes to obtain a two-dimensional space within which we computed Euclidean distances between lakes providing the measure of dissimilarities in the local abiotic context of lakes.

Biotic Environmental Conditions in the Lakes

We identified a set of relevant factors for describing the local biotic context of gravel pit lakes (Table S2) based on the previous studies mentioned earlier. During annual surveys conducted in September for each lake, macroinvertebrates (identified at the family level) were sampled from three different littoral zones and one deep zone by combining kick-nets, Surber net and Ekman grabs. Crayfish (*Procambarus clarkii* and *Faxonius limosus*) were captured with traps. Zooplankton was sampled using Apstein limnological standard plankton nets of 200-µm mesh size while phytoplankton was sampled with 10-µm mesh size in the deepest zone of each lake (three replicates per lake) by performing vertical net tows at the deepest point of the lake, both were frozen at laboratory. Fish were sampled using a protocol that combines gill netting and electrofishing (Zhao and others, 2016). Gill netting was performed before the sunrise and lasted 1.5 h to reduce mortality. It consisted of deploying one mono-mesh net (mesh size = 50 mm) and one multi-mesh net (Pelagic EN 14757) to sample the pelagic zone in the deepest area of the lakes. The littoral zone was sampled to represent the different types of habitats using randomly deployed monomesh nets (mesh-sizes = 12, 20, 30 and 60 mm) and multi-mesh nets (Benthic EN 14757) whose number varied between 4 and 6 depending on the lake surface. Electrofishing was performed during the afternoon following the point abundance sampling approach (PASE), which is a nondestructive method to sample different fish species and life stages within lentic ecosystems (Persat and Copp 1990). An average of 26.5 ± 3.6 PASE was used depending on lake perimeter and surface (varied between 22 and 35 PASE). Each captured fish, identified to the species level, was measured for fork length (mm). Their body mass (mg) was estimated using length–weight relationships derived from a previous study conducted on each species in the study area (Zhao and others, 2019). During the study period, a total of 8156 fish belonging to 19 species (including 10 non-native species) were captured. The fish species richness in lakes varied between 1 and 15 (7 ± 4 species).

Several biotic metrics were selected to characterize the functional and structural aspects of lake communities. The total fish biomass expressed as biomass per unit of effort *(FBiom)* was used as a proxy for secondary production. To represent primary productivity, we used the annual mean concentration of chlorophyll-a measured in the water column (T*Chl*, $\mu g.L^{-1}$) in the water column (pelagic) using a portable fluorometer (AlgaeTorch, BBE Moldaenke GmbH, Schwentinental, Germany). Additionally, the proportion of the total biomass corresponding to non-native fish (*NN*) was computed to provide a proxy of invasiveness in lakes because invaded systems tend to undergo biotic homogenization, which can lead to more similar ecosystem functioning (Olden and others 2004; Petsch 2016). Invasive crayfish biomass (*CBiom*) was also included in analyses because they represent an additional entity in food webs that was shown to modify nutrient cycling in gravel pit lakes by bypassing microbial pathways by both being consumed by higher trophic levels and by accelerating organic matter decomposition (Alp and others, 2016). Functional richness (*FRic*) was computed from a multidimensional functional space computed on 16 traits (Table S4) to represent the breadth of ecological strategies in the fish communities (further details in Zhao and others, 2019; Gimenez and others, 2023).

The trophic niche of communities and overall food-web structure in the lakes were assessed through stable isotope analyses of carbon (δ^{13}C) and nitrogen (δ^{15}N) similar to Garcia and others (2025). Measurement of stable isotopes were performed on clips of pelvic fins from a subset of fish (corresponding to 46 ± 21 fish per lake between 2022 and 2024), on abdominal muscle collected on euthanized crayfish, on samples of macroinvertebrates and zooplankton. Primary consumer invertebrates sampled in the littoral areas were used as the littoral baselines while zooplankton sampled in the pelagic areas was used at the pelagic baseline in isotopic analyses to account for these two distinct carbon pathways commonly found in lakes (Post 2002). Samples were rinsed with distilled water in the field and stored in a cooler. Zooplankton, macroinvertebrates and fish fin-clips were dried at 60 °C for 72 h. All samples were analyzed at the Cornell University Stable Isotope Laboratory (COIL, USA). To capture how food-web structure and fish community resource use influence ecosystem synchrony, we included several biotic descriptors derived from stable isotope data, reflecting species interactions, energy pathways, and trophic niche breadth; factors known to shape ecosystem functioning (Vadeboncoeur and others, 2002; Borrelli and Ginzburg 2014; Poisot and others, 2015). The standard ellipse area corrected for sample size (*SEAc*) was computed on the isotopic spaces including both fish and invertebrates to characterize the extent of resource exploitation by all consumers in the food webs. We also computed the maximum trophic position to inform on the food chain length (*FCL*). In addition, the reliance of consumers at the top of the food web (trophic position > 3) on the primary productivity was computed to provide a proxy for energetic pathways (*ARel)*. Values of δ^{13}C for secondary consumers were corrected using signatures of primary consumers following Eq. 3 to make them comparable across lakes (Olsson and others 2009). The resulting corrected values for each secondary consumer i vary between 0 representing pathways only based on the decomposition of organic matter coming from allochthonous supply and 1 representing pathways only based on autochthonous primary production.

$$\delta^{13}C_i = \frac{\delta^{13}C_i - mean\left(\delta^{13}C_{primary\_consumers}\right)}{max\left(\delta^{13}C_{primary\_consumers}\right) - min\left(\delta^{13}C_{primary\_consumers}\right)} \tag{3}$$

Finally, we used the same approach as for abiotic dissimilarities to compute biotic dissimilarities by performing a PCA on the eight biotic variables previously described. We also retained the two first axes to obtain a two-dimensional space within which we computed Euclidean distances between lakes.

Statistical Analyses

We fitted a first linear mixed effect model (LMM) to test the effect of geographic distances, biotic and abiotic dissimilarities (that is, Euclidean distances on PCAs) on ecosystem synchrony. In this LMM, the two-year ecosystem synchrony was the response variable, and the three dissimilarity measures were included as fixed effects. To account for non-independence among lake pairs, the identities of the lakes in each pair were included as random effects. To investigate seasonal trends in ecosystem synchrony, we fitted two additional LMMs: one with synchrony during the warm period and the other with synchrony during the cold period as the response variables. Both models included the same set of fixed effects as in the first LMM previously described. We added the year of sampling as a random effect in addition to the lake identities in these two last models. Assumptions of linear mixed-effects models were verified by visual inspection of residual vs. fitted plots, normality of residuals, and absence of multicollinearity (with threshold $VIF < 3$; Zuur and others, 2010a, 2010b).

Statistical analyses and graphical displays 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), ‘‘IncDTW’’ for computing normalized dynamic time warping distances (Leodolter and other, 2021), ‘‘lme4’’ for fitting the linear mixed effect models (Bates and others, 2015), ‘‘sjPlot’’ (Lüdecke 2021) for analyzing and plotting model outputs and ‘‘ggplot2’’ (Wickham 2016) for creating graphics.

RESULTS

Oxygen Saturation Dynamics

Lakes exhibited different dynamics in their dissolved oxygen (DO) saturation over the study period (Figure 2; Table S3). Most of the lakes exhibited an average DO saturation close to 100% across the whole two-year time series, indicating a near-equilibrium between oxygen production and respiration. Yet, mean DO saturation ranged between 87.7% and 108.2% (Table S3). We found greater differences between lakes when considering minimum and maximum DO saturations. Minimum DO saturation was found between late summer and fall while maximum values of DO saturations were observed mainly in late spring and summer (Figure 2). The coefficients of variation of DO saturation computed across the two years varied between 7.1 and 39.5, but most of the lakes exhibited a coefficient of variation between 10 and 20 (Table S3).

Biotic and Abiotic Dissimilarities

The PCA based on biotic variables explained 59.6% of the total variance in the original variables, with the first and second axis explaining 31.7% and 27.9%, respectively (Figure 3A). The first axis is interpreted with respect to percentage of non-native fish biomass (*NN*), total fish biomass (*FBiom*) and total concentration of chlorophyll-a (*TChl*). The

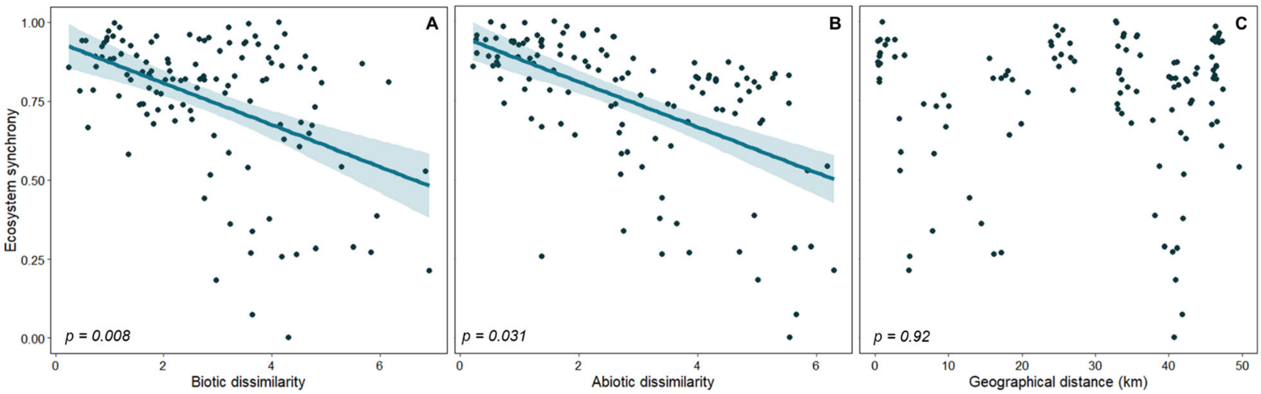

Figure 5. Relationships between two-year ecosystem synchrony and biotic (A), abiotic dissimilarities (B) and geographic distances (C) in the 16 gravel pit lakes. Each point represents a pair of lakes. Lines represent significant fitted relationships (linear mixed effect models, $p < 0.05$), and the ribbons represent the associated standard errors.

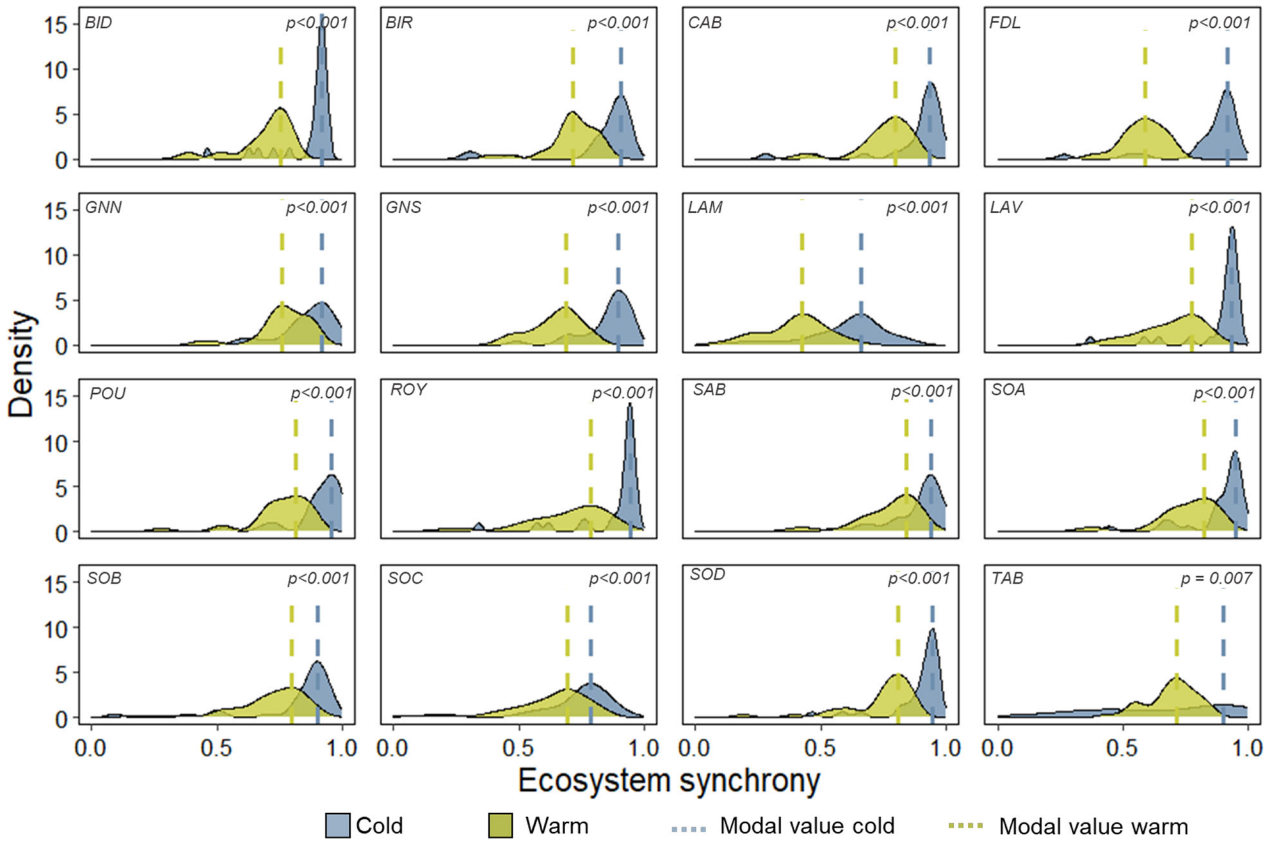

Figure 6. Seasonal ecosystem synchrony for the 16 gravel pit lakes between all the pairs of lakes. Density curves and their modal values (dashed vertical lines) are represented for the cold (blue) and warm periods (green). P values testing differences in ecosystem synchrony between cold and warm periods (Kolmogorov–Smirnoff tests) are displayed in each panel.

second axis captured aspects related to ecosystem functioning in terms of resource exploitation (wide isotopic niche represented by large *SEAc* and strong reliance on autochthonous productivity represented by high *ARel*) and high biomass of crayfish (*CBiom*), which is expected to increase organic matter recycling compared to low crayfish biomass. The average biotic dissimilarity was 2.82 (min = 0.24 between POU and SOB, and max = 6.92 between BIR and LAM).

The PCA based on abiotic variables explained 70.5% of the total variance in the original variables (Figure 3B). The majority of the variation was explained by the first axis (49.1%) describing a lake maturity gradient ranging from recently constructed lakes with high Secchi depth (high water transparency), low turbidity and simple shorelines, to more mature (and older) lakes with complex shorelines and high total phosphorus concentration and turbidity. On average, the abiotic dissimilarity was 2.77 (min = 0.22 between GNN and SOC, and max = 6.30 between BIR and LAM).

Two-Year Ecosystem Synchrony and Associated Drivers

We observed different levels of ecosystem synchrony among the 16 lakes, with SAB being overall the most synchronized with the other lakes, while the most desynchronized lake was LAM (Figure 4A). The lakes identified as the least synchronized with the other lakes tended to be the most urbanized and were also among the oldest (Figure 4B). Pairwise comparisons confirmed the wide variability in ecosystem synchrony (Figure 4C). The most synchronized pair of lakes was GNN and POU while the least synchronized pair was LAM and SOB. Even the lakes considered as the most synchronized with other lakes exhibited highly variable levels of synchrony with other lakes. For instance, ecosystem synchrony varied between

0.99 (when paired with POU) and 0.27 (when paired with LAM) for SAB.

We observed a significant decrease in ecosystem synchrony when biotic dissimilarity increased (LMM: estimate = − 0.24 ± 0.09 SE, $p = 0.008$; Figure 5A). Similar effects, though slightly weaker, were obtained with abiotic dissimilarity (est. = − 0.20 ± 0.01 SE, $p = 0.031$; Figure 5B), while geographic distance had no effect ($p = 0.92$; Figure 5C). The fixed effects explained a modest fraction of the variance in ecosystem synchrony (marginal $R^2 = 0.076$) while random effects explained most of the variance (conditional $R^2 = 0.84$).

Seasonal Ecosystem Synchrony and Associated Drivers

Importantly, lakes identified as the least synchronized over the long term remained the least synchronized in seasonal comparisons as well, reinforcing the consistency of ecosystem desynchronization patterns across temporal scales (Table S5). We found significant differences in ecosystem synchrony during the cold and the warm periods (Figure 6). On average ecosystem synchrony was higher and more consistent across all pairs of lakes during the cold period (mean = 0.83 ± 0.18 and narrow distributions) than during the warm period (mean = 0.69 ± 1.16 and wider distributions). More specifically, the distributions of ecosystem synchrony values for cold and warm periods were significantly different for all lakes (Kolmogorov–Smirnov tests: $p < 0.05$), although their modal values varied across lakes (Table S5). For instance, the modal value of ecosystem synchrony during the warm period was 1.38 times higher than during the cold period for SOC while for the warm period it was 3.85 times higher than during the cold period for FDL.

Abiotic and biotic dissimilarities affected ecosystem synchrony differently over the short term compared to the long term. During the cold period, ecosystem synchrony tended to significantly decrease with increasing biotic dissimilarity (est. = − 0.19 ± 0.01 SE; $p = 0.031$; Figure S3) but was not related to geographic distance and abiotic dissimilarity ($p = 0.906$ and 0.169, respectively). Biotic dissimilarity explained a low fraction of the variance (marginal $R^2 = 0.05$) that was mostly captured by lake identities (conditional $R^2 = 0.53$). During the warm period, ecosystem synchrony remained unrelated to geographic distance ($p = 0.46$) and was no longer affected by biotic dissimilarity ($p = 0.064$). In contrast, it significantly decreased with increasing abiotic dissimilarity (est. = − 0.17 ± 0.06 SE; $p = 0.003$), although this factor still explained a low fraction of the variance (marginal $R^2 = 0.06$), that was again mostly captured by random effects (conditional $R^2 = 0.79$).

DISCUSSION

Identifying the coordinated responses and drivers of ecosystem dynamics across space and time is key to understanding and predicting their trajectories under global change. We demonstrated that, even within a limited spatial extent, gravel pit lakes can exhibit distinct ecosystem dynamics depending on the local ecological context. While geographic distance did not influence synchrony among lakes, we demonstrated that biotic and abiotic dissimilarities played a key role in explaining the synchrony in the dynamic of dissolved oxygen saturation (a proxy for ecosystem functioning) between lakes. Crucially, these local characteristics did not exert their influence simultaneously. Instead, we observed a temporal succession of effects, with biotic factors having a prominent role during the cold season while abiotic factors were more influential during the warm season.

We offer evidence in support of our first hypothesis by demonstrating that ecosystem synchrony between gravel pit lakes varied across lake pairs, both over the whole studied period (across the two-year survey) and the short-term time scale (within years). In addition, the gradient of differences in synchrony observed among the lakes over the two years was maintained at the short-term scale. This supports the idea that ecosystems with different long-term trajectories also exhibit distinct short-term functioning, which is consistent with the notion that synergies can manifest between long-term functional trends and short-term ecosystem performance (Oliver and others, 2015). The lakes least synchronized with the others were those demonstrating the most variable seasonal oxygen dynamics, either in terms of amplitude or frequency of variation (for example, LAM, TAB or FDL). By contrast, the most synchronized lakes (for example, SOD, SAB, or GNN) were found to display low or intermediate seasonal oxygen fluctuations with buffered amplitude of variations. Because the studied lakes share similar mixing regimes and do not develop persistent summer stratification (Figure S1), synchrony analyses may not be primary driven by mixing. So, variations in synchronized oxygen dynamics among lakes likely reflect local differences in biotic and abiotic characteristics. In fact, the lakes with flat basins, complex shorelines, high turbidity, and high total phosphorus concentrations, which concurrently displayed long food chains, high invasion levels and high productivity (both primary and secondary), were the least synchronized with other lakes. This echoes previous findings that demonstrated that, as these ecosystems mature, they undergo a switch from heterotrophy to autotrophy (Colas and others, 2021), becoming increasingly influenced by fishery management and biological invasions (Zhao and others, 2016) and experiencing a decline in fish functional richness with a simultaneous stabilization of the lake trophic structure across years (Garcia and others, 2025a, 2025b). As a result, mature lakes may progressively diverge in synchrony from less mature lakes due to temporal divergence in their ecological functioning and trajectories. The landscape and vegetation surrounding lakes evolves, the balance between autochthonous and allochthonous matter changes lake turbidity, color, and the food webs can become more complex as noticed from long-term field observation. Longer-term monitoring of ecosystem metabolism will be required to confirm and further explore this emerging pattern.

Two-year ecosystem synchrony was related to geographic distance between lakes but rather to biotic and abiotic dissimilarities, confirming our second hypothesis and reinforcing the interpretations described above. This result aligns with the previous studies that found no clear evidence of spatially structured dynamics neither in the water clarity of north-eastern American lakes (Lottig and others, 2017) nor in the surface water temperature of lakes at the global scale (O'Reilly and others, 2015). Future studies focusing on the effect of geography on ecosystem synchrony in shallow lakes will necessitate comparisons between systems at larger spatial scales located in different ecoregions (Rose and others, 2017). Beyond geographic distance, our results emphasize the value of examining the role of biotic and abiotic similarities to understand ecosystem synchrony. While previous studies tended to consider separately the effect of biotic and abiotic factors on spatial populations synchrony (Wang and others, 2019; for example, Larsen and others, 2023), with a particular focus on environmental dissimilarity (that is, the Moran effect), we demonstrated that accounting for both factors is paramount to accurately explain ecosystem synchrony. Lakes with similar morphologies and physicochemical characteristics were more synchronized, which is congruent with the previous findings in north temperate lakes where long-term trends in metabolism and water clarity were closely linked to abiotic characteristics (for example, depth, mean total phosphorus, Secchi depth; Rose and others 2017; Ladwig and others, 2022). In addition, lakes with similar productivity, functional richness, community composition and trophic structure exhibited higher synchrony in oxygen dynamics, which reflects the intricate link between biodiversity characteristics and ecosystem functioning in shaping long-term ecosystem trajectories (Brose and Hillebrand 2016; Gonzalez and others, 2020). These findings suggest that studying ecosystem synchrony and its drivers across various ecosystem types could yield valuable insights into how abiotic and biotic dynamics interact to shape ecosystem synchrony in response to environmental changes. Different outcomes could indeed emerge in systems with highly dynamic physical and biological constraints such as rivers or, on the contrary, in large deep lakes where these dynamics are more stable and buffered over time (Bertoni 2011).

Ecosystem synchrony differed between cold and warm seasons and was differently correlated to biotic and abiotic factors, consistently with our third hypothesis. A common pattern across all studied lakes was the higher level of ecosystem synchrony during the cold period. This period is characterized by a low productivity and low metabolic demand, promoting more stable oxygen dynamics (Scharfenberger and others, 2019), which ultimately leads to increased synchrony between lakes. In these circumstances, abiotic factors are less likely to limit the balance between heterotrophic and autotrophic processes (Baxa and others 2021), which may explain why similarities in biotic characteristics (communities and trophic structure) are more influential during the cold period (independently of the time of sampling as biotic sampling are performed in September). In contrast, abiotic factors contributed more to explaining patterns in ecosystem synchrony during the warm period. This period coincides with the growing season, during which biological activity intensifies leading to larger variations in oxygen dynamics and promoting a stronger contrast between autotrophic and heterotrophic processes when compared to the cold period (Laas and others 2016; Ladwig and others 2022). Abiotic factors such as nutrient availability, lake size or water transparency drive the balance between these processes during the warm period and can interact in complex ways (Ladwig and others 2022; Puts and others 2022). For instance, the oxygen demand from the sediment plays a smaller role in the metabolic balance of highly productive lakes compared to less productive ones (Baxa and others

2021). Thus, during the warm period, abiotic characteristics become the primary limiting factors, and differences in their similarity between lakes are closely associated with differences in synchrony measured by oxygen saturation. Future studies based on ecosystem functions exhibiting different phenological patterns may offer complementary insights into the drivers of short-term ecosystem synchrony. For instance, synchrony in the dynamics of litter decomposition during the warm period could be less driven by abiotic characteristics than biotic characteristics such as crayfish biomasses that was demonstrated to alter the seasonal phenology of this function (Alp and others 2016). Conducting similar studies in ecosystems located in different ecoregions would bring further insights on the drivers of short-term synchrony by including different seasonal climatic patterns (for example, wet vs. dry seasons).

CONCLUSIONS

This study revealed variable levels of ecosystem synchrony between ecosystems in both short-term functioning and two-year trajectories, and demonstrated their dependence on the joint effect of abiotic and biotic similarities among ecosystems. Our findings offer a valuable foundation to explore the interplay between biotic and abiotic dynamics and ecosystem functioning. Future studies investigating synchrony in the dynamics of abiotic (for example, phosphorus concentrations) and/or biotic factors (for example, phytoplankton biomasses) across systems in different regions, and relating this pattern to synchrony in short-term ecosystem functioning, could build upon these preliminary outcomes. Here, we worked on dissolved oxygen that could be measured continuously with a reasonable accuracy and cost-effectiveness, which is not yet the case for chlorophyll-a or nutrients. We hope that future developments in low-cost environmental sensors could help to measure continuously and accurately other environmental parameters at a high-frequency and in multiple ecosystems. Such investigations would not only open avenues to test theories on the mechanisms driving ecosystem dynamics, but also offer applied perspectives on ecosystem resilience. For instance, measuring deviations from previously synchronized trajectories may serve as an early warning signal of shifts in ecological states. Accordingly, ecosystem synchrony could become a valuable addition to the suite of tools used in adaptive management frameworks, offering a novel indicator for monitoring and responding to environmental change.

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DATA AVAILABILITY

Data and scripts used to run analyses and generate figures in this manuscript are available at the Zenodo repository: https://doi.org/10.5281/zenodo.17629143.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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