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RESEARCH ARTICLE

Regime shifts in a shallow lake over 12 years: Consequences for taxonomic and functional diversities, and ecosystem multifunctionality

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Abstract

1. Under increasing nutrient loading, shallow lakes may shift from a state of clear water dominated by submerged macrophytes to a turbid state dominated by phytoplankton or a shaded state dominated by floating macrophytes. How such regime shifts mediate the relationship between taxonomic and functional diversities (FD) and lake multifunctionality is poorly understood.
2. We employed a detailed database describing a shallow lake over a 12-year period during which the lake has displayed all the three states (clear, turbid and shaded) to investigate how species richness, FD of fish and zooplankton, ecosystem multifunctionality and five individual ecosystem functions (nitrogen and phosphorus concentrations, standing fish biomass, algae production and light availability) differ among states. We also evaluated how the relationship between biodiversity (species richness and FD) and multifunctionality is affected by regime shifts.
3. We showed that species richness and the FD of fish and zooplankton were highest during the clear state. The clear state also maintained the highest values of multifunctionality as well as standing fish biomass production, algae biomass and light availability, whereas the turbid and shaded states had higher nutrient concentrations. Functional diversity was the best predictor of multifunctionality. The relationship between FD and multifunctionality was strongly positive

during the clear state, but such relationship became flatter after the shift to the turbid or shaded state.

4. Our findings illustrate that focusing on functional traits may provide a more mechanistic understanding of how regime shifts affect biodiversity and the consequences for ecosystem functioning. Regime shifts towards a turbid or shaded state negatively affect the taxonomic diversity and FD of fish and zooplankton, which in turn impairs the multifunctionality of shallow lakes.

KEYWORDS

alternative states, ecosystem multifunctionality, fish, functional diversity, shallow lakes, zooplankton

1 | INTRODUCTION

Shallow lakes are among the most common freshwater ecosystems on Earth (Verpoorter et al., 2014), and in a pristine state they are characterized by clear water and dominance of submerged macrophytes. However, increasing nutrient loading may shift shallow lakes to a turbid state dominated by phytoplankton or a shaded state dominated by small floating macrophytes (Moss, 1990; Scheffer & van Nes, 2007). Previous research has focused on factors that trigger the shift among the states or mechanisms that stabilize the different states (for review, see Hilt et al., 2017), but the impacts of regime shifts on the taxonomic diversity and functional diversity (FD) of shallow lakes remain poorly understood. Moreover, whereas previous work has shown that regime shifts can impact a wide variety of individual ecosystem functions (such as primary production or nutrient concentrations; Hilt et al., 2017), very little is known about their effect on ecosystem multifunctionality. Multifunctionality is the ability of ecosystems to simultaneously support a multitude of ecological functions and as such has become a central topic of contemporary ecology and ecosystem management (Hector & Bagchi, 2007).

During the clear, turbid and shaded states, shallow lakes exhibit different functioning and different biodiversity patterns (Moss, 1990; Scheffer et al., 1993). Ecosystems in the clear state support a high taxonomic richness of fish and zooplankton (Jeppesen et al., 1998), in part because submerged macrophytes provide effective shelters (Blindow et al., 2014; Carpenter & Lodge, 1986). During the clear state, shallow lakes have high habitat heterogeneity, favouring the development of more complex food webs with high proportions of apex piscivorous predators (Jeppesen et al., 2000; Moi, Alves, Antiqueira, et al., 2021). Conversely, lakes in the turbid and shaded states have low taxonomic richness of fish and zooplankton (Jeppesen et al., 1999). The low habitat heterogeneity during turbid and shaded states results in a simplified food web with a low proportion or absence of apex predators and dominance of benthic and planktivorous fish and small-sized zooplankton (Moi, Alves, Antiqueira, et al., 2021; Mormul et al., 2012).

It can be hypothesized that more complex food webs in the clear state (Jeppesen et al., 1999; Moi, Alves, Antiqueira, et al., 2021) have a higher FD of fish and zooplankton than lakes in the turbid and shaded states. Although this prediction has not yet been directly tested, the clear state sustains a richer combination of unique sets of functional traits, including fish (e.g. piscivores) and zooplankton (e.g. large-sized filter feeders) compared to the turbid and shaded states (Jeppesen et al., 1998; Moss, 1990; Scheffer & van Nes, 2007). Ecosystem multifunctionality is also expected to be higher in the clear state since higher taxonomic diversity and FD is required to sustain a greater range of ecosystem functions (Bagousse-Pinguet et al., 2019; Hector & Bagchi, 2007). Furthermore, the clear state often supports a great diversity of organismal traits that underlie ecosystem functioning. For example, large-sized apex predators and filter feeders control multiple ecosystem functions such as fluxes of nutrients, primary production and standing biomass (Moi, Romero, Antiqueira, Mormul, et al., 2021). The great diversity of traits related to feeding modes and habitat use during the clear state may enhance the overall resource utilization by communities, in turn increasing their ability to maintain ecosystem multifunctionality (Gross et al., 2017).

Ecological theory predicts that biodiversity (taxonomic and functional) may enhance ecosystem multifunctionality through two general mechanisms: (a) complementarity and (b) selection effect (Loreau & Hector, 2001). Complementarity enhances ecosystem multifunctionality via niche partitioning and facilitative interactions among species, or through the overall increase in resources utilization induced by species with contrasting functional traits (Bagousse-Pinguet et al., 2019). By contrast, the selection effect enhances ecosystem multifunctionality through the greater statistical probability of highly productive species being more common in more diverse ecosystems (Loreau & Hector, 2001). Recent evidence suggested that single ecosystem functions, such as nutrient retention and primary productivity, were higher in the clear state than in the turbid and shaded states (Hilt et al., 2017; Janssen et al., 2020; Su et al., 2019). However, these studies did not link their findings to taxonomic diversity and FD and did not consider multiple ecosystem functions simultaneously (i.e. multifunctionality).

Here, we used a detailed database holding data for 12 years from a shallow lake, which during this period has displayed regime shifts among three alternative states (clear, turbid and shaded). We compared the taxonomic diversity and FD of fish and zooplankton among the three states and determined their consequences for ecosystem multifunctionality. We then quantified an ecosystem multifunctionality index using a set of five ecosystem variables, including nutrient concentrations (in situ measurements of in situ measurements of total N and total P available in the water), algae production (biomass of edible algae), underwater light availability and standing animal biomass (biomass of fish community). Together, these variables provide proxies for primary production, photosynthetically active radiation, nutrient availability and standing biomass, which are important determinants of ecosystem functioning in shallow lakes (Austin et al., 2021; Moi, Romero, Antiqueira, Mormul, et al., 2021). We predicted that (a) the taxonomic diversity and FD of fish and zooplankton would be lower in the shaded and turbid states than in the clear state and that (b) ecosystem multifunctionality would be lower in the shaded and turbid states despite differences between single ecosystem functions (Hilt et al., 2017). As biodiversity–multifunctionality relationship tends to weaken with biodiversity loss (Cardinale et al., 2012), we also predicted that (c) when the taxonomic diversity and FD of fish and zooplankton decrease in the turbid and shaded state, the relationship between multifunctionality and biodiversity would weaken as well.

2 | MATERIALS AND METHODS

2.1 | Study site

Osmar is a shallow lake (60 m length, 1.1 m mean depth) located in the Upper Parana floodplain (22°46′27.53″S and 53°19′57.95″), Brazil (Figure S1). The lake is protected by a dense Atlantic Forest. The region has a tropical climate with a mean annual temperature of 22°C (mean minimum and maximum temperatures of 10.3 and 33.6°C respectively) and a mean annual precipitation of 1,500 mm (Moi, Alves, Antiqueira, et al., 2021). The data used for the analysis originate from a long-term ecological research project (PELD-Sitio PIAP) and includes 12 years (2005–2016) of data.

During the 12-year period, Lake Osmar has undergone three alternative regimes, corresponding to a clear, turbid and shaded state, as documented in two previous studies (Moi, Alves, Antiqueira, et al., 2021; Mormul et al., 2012). The presence and transitions among the states are clearly observed in the bivariate plane of light availability, total phosphorus and cover of submerged and floating macrophytes (Figure 1). Note that the sampling units were displaced from the top-right border of this plane (turbid state) to the bottom-right border (clear state), and after this to the top-left border (shaded state; Figure 1). This illustrates that as light availability, phosphorus concentrations and macrophyte cover change, the lake was pushed into distinct states. However, the regime shifts were driven by different mechanisms. The clear state was triggered by the presence of submerged macrophytes and high abundance of large piscivorous fish, which, directly and indirectly, reduced phosphorus concentrations and increased the water light availability (Moi, Alves, Antiqueira, et al., 2021; Mormul et al., 2012). The turbid state was triggered by the high abundance of migratory benthic fish, which increased the phosphorus concentration and reduced the light availability (Mormul et al., 2012). The shaded state was triggered by low water levels and the presence of small floating macrophytes, which increased the phosphorus level and reduced the light availability (Moi, Alves, Antiqueira, et al., 2021). The shifts among alternative states were not associated with seasonality because (a) each regime remained dominant for more than 2 years, and (b) the lake did not return to the previous state at the same time of the year (Figure 1).

2.2 | Characteristics of each state

The clear state occurred from June 2009 to December 2009 and from June 2012 to March 2014 and was characterized by low turbidity, intermediate abundance of phytoplankton, high coverage of submerged macrophytes and absence of small floating macrophytes (Figure S3). The turbid state occurred from June 2005 to November 2005, from March 2007 to February 2008 and from September 2008 to June 2009 and was characterized by high values of turbidity, large filamentous algae abundance and absence of macrophytes (Figure S3). The shaded state occurred from June 2014 to December 2015 and was characterized by low turbidity, low abundance of phytoplankton, absence of submerged macrophytes and high coverage of small floating macrophytes (Figure S3). We also recorded transitional states preceding the onset of the three states (clear, turbid and shaded). These transitional states occurred several times during the monitoring period and always before the lake was pushed into a more stable regime. Therefore, the transitional states were not included in the subsequent analyses.

2.3 | Fish and zooplankton sampling

The biological samplings were explicitly designed to assess the taxonomic diversity and FD of fish and zooplankton, as well as ecosystem functioning, during the three alternative states. During the 12 years, four annual standardized samples (summer, fall, winter and spring) were collected, except in 2014 when only three sampling campaigns were conducted, resulting in 47 campaigns in total. The sampling of fish, zooplankton and ecosystem variables were done using the same standardized methods throughout the whole study. The field study was properly realized with all required permissions from the Brazilian ministry of the environment [Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), National Council for the Control of Animal Experimentation (CONCEA) and Ethics Committee on Animal Use under protocol number 1420221018 (ID 001974)]. Fish were sampled with 20 m long seines with a mesh size of 0.5 cm in the littoral and middle zones of the lake for a 24-h period. As the lake is shallow, our sampling always included all lake compartments (i.e. sediment, pelagic and littoral zones). Zooplankton were sampled in the subsurface of the pelagic zone using a motorized pump and a plankton net (68 μm), filtering

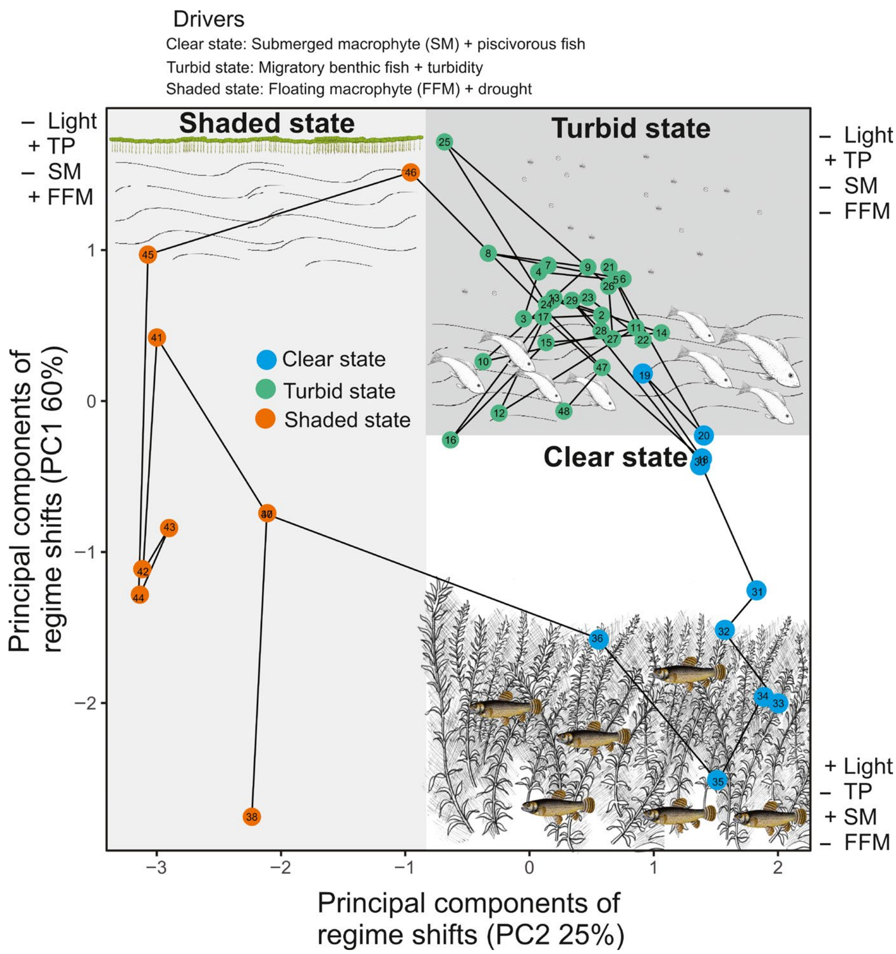

FIGURE 1 Principal component analysis (PCA) of the factors (phosphorus concentrations, light availability, submerged and floating macrophyte cover) that drive regime shifts between clear (blue circles), turbid (green circles) and shaded (orange circles) states. Each circle corresponds to a sampling unit. Note that the sampling units are displaced to different planes with the changes in phosphorus concentrations, light availability and macrophyte cover. Variables in the corners of the graph represent the drivers of the regimes [i.e. light availability, total phosphorus concentration (TP), submerged macrophytes (SMM) and free floating macrophytes (FFM)]. The images within each plane indicate the mechanisms that triggered the shift to each state; thus, the clear state was triggered by submerged macrophytes and large piscivorous fish, the turbid state was triggered by large migratory benthic fish and the shaded state was triggered by floating macrophytes and low water level. Also, only the sampling points that were not close to the borders of the bivariate plane were those that preceded the shift between the clear and turbid states corresponding to bifurcation points (points 18, 19, 20 and 30)

600 L water per sample. The samples were preserved in a 4% formaldehyde solution and buffered with calcium carbonate. To identify and enumerate (ind./m^3) all organisms, the samples were processed under an optical microscope with 100× magnification. The abundance of individuals was estimated by analysing minimum three subsamples, equivalent to 10% of the total sample, in a Sedgewick-Rafter chamber.

2.4 | Functional traits

Fish and zooplankton were identified to species and categorized into functional groups according to the traits of the species (Baumgartner et al., 2018; Braghin et al., 2018; Oliveira et al., 2017; Tables S7 and S8). We selected the most important ecological traits that best reflect the importance of fish and zooplankton for the functioning of shallow lakes (Table S1). These traits are expected to differ among states, but this remains largely unexplored in natural ecosystems (see Appendix S1 for a full explanation of the traits). For fish, we used four functional trait combinations: body size (continuous, in cm), habitat use (benthic, benthopelagic or pelagic), trophic guilds (piscivores, detritivores, omnivores, herbivores, insectivores and invertivores) and migration ability (migratory or non-migratory; Table S7). Body size was estimated by measuring the captured individuals, whereas the other traits were obtained from the literature (e.g. Baumgartner et al., 2018; Oliveira et al., 2017). For the functional categorization of zooplankton, we used five key functional traits: body size (continuous, in μm), habitat use (littoral or pelagic), feeding type (filter-feeder rotifers, sucker rotifers, predator rotifers, raptorial copepods, filter-feeder copepods, filter-feeder cladocerans and scraper cladocerans), life span (short: a life span lower than 5 days, e.g. rotifers and Cladocera, long: a life span of up to 1 month, e.g.

copepods) and predatory escape response (absent, low, medium or maximum predatory escape; Table S8; Braghin et al., 2018). Body size was estimated by measuring the captured individuals, whereas the other functional traits were obtained from the literature (Braghin et al., 2018).

2.5 | Ecosystem functions

To quantify how regime shifts affect ecosystem functioning, we scored the following five functions—nutrient concentrations, algae production, underwater light availability and standing fish biomass—for each sampling period. To assess the potential for a trade-off between individual ecosystem functions, we calculated Spearman correlation coefficients between each pair of individual standardized functions. Of the possible 10 combinations of function pairs, we found only one strong correlation (underwater light availability with algae biomass = 0.83; Figure S2). This indicates a weak trade-off between individual functions, suggesting that the multifunctionality calculation was not biased by highly correlated functions. The five functions are key properties of aquatic ecosystems (Austin et al., 2021; Moi, Romero, Antiqueira, Mormul, et al., 2021) and were measured 47 times during the study period.

2.5.1 | Nutrient concentrations

Nutrient concentrations were quantified by in situ measurements of the total phosphorous (g/L) and total nitrogen (g/L) available in the water. Total phosphorus and nitrogen reflect all fractions of these nutrients under water, and their availability often limits primary producers and, consequently, primary production (Elser et al., 2009). We took water samples and in the laboratory nitrogen was quantified using persulphate method (Bergamin et al., 1978) and determined in a spectrophotometer in the presence of cadmium using a flow-injection system (Giné et al., 1980). Total phosphorus (TP) was measured according to Golterman et al. (1978).

2.5.2 | Algae biomass

To obtain an indicator proxy for algae production, we measured the biomass of edible algae using the biovolume (individuals mm^{-1} L^{-1}) of nanoplankton: 2–60 μm and picoplankton: <2 μm (Table S9). We focused on the biomass of small algae (such as Chlorophyceae) because they are the most abundant phytoplankton group in tropical shallow lakes (Moi, Alves, Antiqueira, et al., 2021) and form the base of the food web of these ecosystems. Thus, they are the main food resource for small zooplankton that cannot feed efficiently on large algae (Lazzaro, 1997). Small edible algae were sampled in the pelagic zone using bottles and preserved in 10% acetic acid (Bicudo & Menezes, 2006). Biovolume was estimated by multiplying the abundance of each species by their mean volume. The algae volume was obtained from geometric models similar to three-dimensional shapes (Sun & Liu, 2003).

2.5.3 | Underwater light availability

We quantified the underwater light availability as the depth of the euphotic zone, which represents the depth (m) of the lake where there is sufficient light incidence for autotrophs. The euphotic zone was calculated as Secchi depth multiplied by 1.7, where 1.7 is a correction factor for estimating the light available under water (Lansac-Tôha et al., 2021). The underwater light availability is a key resource that may limit primary producers, and thereby affect the primary production in aquatic ecosystems (Scheffer, 2004).

2.5.4 | Standing fish biomass

To quantify fish biomass, all fish species were weighed using a microbalance (0.01 g precision). The standing biomass of the entire fish community (g/m^2) was then quantified by summing up the weight of all individuals and dividing it by the site area. Fish are important consumers in aquatic ecosystems, and their biomass is commonly used to reflect the ecosystem functioning (Benkwitt et al., 2020). Moreover, fish biomass is directly related to important ecosystem services such as fish production and food security (Duffy et al., 2016).

2.6 | Multifunctionality

To test the effects of regime shifts on the simultaneous performance of multiple ecosystem functions, we calculated averaging multifunctionality (Byrnes et al., 2014). We first standardized all individual ecosystem variables between 0 and 1 (rawFunction−min(rawFunction))/(max(rawFunction)−min(rawFunction)) and then calculated their average to obtain a multifunctionality index (Byrnes et al., 2014). This index reflects changes in the average level of a suite of ecosystem functions. Very high levels of the averaging index (close to 1) mean that all functions reach their maximum level of performance simultaneously. In contrast, the lowest values (close to 0) mean all functions are at their minimum level of performance. High multifunctionality index in a given state (close to 1) indicates that this state supports more functions operating at high performance levels. This implies that maintaining the lake in this state is more advantageous for maximizing their functioning. This is of key importance as ecosystems are managed and conserved to support multiple functions simultaneously (Hector & Bagchi, 2007).

2.7 | Data analysis

The taxonomic richness of fish and zooplankton was calculated using the number of species captured in each sampling campaign.

To account for possible differences in population densities between alternative states, we estimated species richness as the Chao index with abundance-based data using the iNEXT package (Hsieh et al., 2016). The Chao index is based on rarefaction and extrapolation of Hill numbers, providing an unbiased estimate of asymptotic species richness and enabling comparison among alternative states with different numbers of individuals. The FD of fish and zooplankton communities was calculated using Rao's quadratic entropy (RaoQ), which is a common measure for estimating FD (Botta-Dukát, 2005). RaoQ has the advantage that it incorporates the weighted relative abundance of each species and converts it to effective numbers. The trait matrix of fish and zooplankton had mixed variables (continuous and categorical); thus, we applied Gower's dissimilarity with Cailliez correction (Laliberté & Legendre, 2010). To further characterize the functional composition of the fish and zooplankton communities, we calculated community-weighted means (CWMs) for each functional trait (which was weighted by relative species abundances). We calculated the RaoQ and CWMs using the FD package in R (Laliberté et al., 2015).

We tested how the alternative states (fixed categorical: clear, shaded and turbid) affect (a) taxonomic richness, (b) FD and (c) CWMs of fish and zooplankton, (d) five individual ecosystem functions (nitrogen and phosphorus concentrations, underwater light availability, algae biomass and standing fish biomass) and (e) multifunctionality (averaging index) using linear mixed-effects models (LMEs) in the package NLME (Pinheiro et al., 2013). To control for seasonality effects in each state, we nested the seasons within year in each state as a random structure. This allowed the intercept to vary in each season within year independently for each state. In this floodplain ecosystem, exchange of biota in the lakes and water occurs during the flood period where the lakes may be connected with the rivers (Mormul et al., 2012). Thus, the temporal sampling performed in our study is considered independent. Moreover, we did not find temporal autocorrelation in our data using the function CAR1 in the CAR package (Fox & Weisberg, 2019). We ensured that the model assumptions of variance homogeneity, normality and outliers were met. We conducted post hoc comparisons between alternative stable states with Tukey's HSD using the *glht* function in the MULTCOMP package (Hothorn et al., 2013).

To evaluate the effects of the taxonomic diversity and FD of fish and zooplankton on ecosystem multifunctionality across the three states (clear, turbid and shaded), we also employed mixed models. We explicitly included water level to account for seasonality in the data, such as flood and drought, which also may affect ecosystem multifunctionality (Moi, Romero, Antiqueira, Mormul, et al., 2021). To determine whether the effects of the predictors on multifunctionality change among states, we added interaction terms among the predictors (taxonomic diversity and FD) and state (clear, turbid and shaded) into the models. We nested the seasons within year in each state as a random structure. We used a model selection approach to reduce the number of predictors, thereby obtaining a more parsimonious way of testing the relationships between taxonomic diversity and FD and water level versus multifunctionality. We ranked the set of candidate models consisting of every individual predictor as well as their additive combinations and interactions with state as predictor variables influencing multifunctionality. A null model was also included into the model selection process (Table S2). We checked the multicollinearity between the predictors by calculating the variance inflation factor (VIF) for each predictor. VIF >3 indicates possible collinearity, but all relationships had VIF < 2. The set of candidate models was constructed using LMEs and contrasted using sample size-corrected Akaike information criteria (AICc; Burnham & Anderson, 2002). Difference > 2 (ΔAICc < 2) was used to identify the best model using the function *ICtab* of the BBMLE package (Bolker & Development Core Team, 2020). We only show the best models (i.e. those ΔAICc ≤ 2) graphically. Finally, to analyse the relationship between the CWMs of each trait of fish and zooplankton with the individual ecosystem functions, we performed Spearman correlations in each state. All analyses were performed in R (R Core Team, 2020).

3 | RESULTS

3.1 | Taxonomic and functional diversities during regime shifts

There were marked changes in the taxonomic diversity and FD of fish and zooplankton communities over the 12-year study period. The values of both biodiversity indices increased from June 2009 to December 2009 and from June 2012 to March of 2014, coinciding with the clear state periods (Figure S4). The species richness of fish and zooplankton was higher in the clear state than in the turbid and shaded states (Table S4; Figure 2a,b). Likewise, the FD of fish and zooplankton was significantly higher in the clear state than in the shaded and turbid states (Table S4; Figure 2C,D). Neither the taxonomic diversity nor FD of fish and zooplankton differed between the turbid and shaded states (Table S4; Figure 2).

There were significant differences in the CWM of most of the functional traits of fish and zooplankton among the three alternative states (Figures S5 and S6). For fish, the CWMs of body size, pelagic habitat preference and feeding groups (apex piscivorous predators, omnivores, herbivores, insectivores and invertivores) were higher in the clear state than in the turbid and shaded states (Table S5; Figure S5). By contrast, the CWMs of detritivores and migration ability were higher in the turbid state than in the clear and shaded states (Table S5; Figure S5). For zooplankton, the CWMs of body size, littoral habitat preference, feeding groups (filter-feeding copepods and filter-feeding cladocerans), no predator escape ability and low predator escape ability were higher in the clear state than in the turbid and shaded states (Table S6; Figure S6). The CWMs of predatory rotifers and maximum predator escape ability were higher in the turbid state than in the clear and shaded states (Table S6; Figure S6). For both fish and zooplankton, all CWMs of functional traits were lowest in the shaded state (Figures S5 and S6).

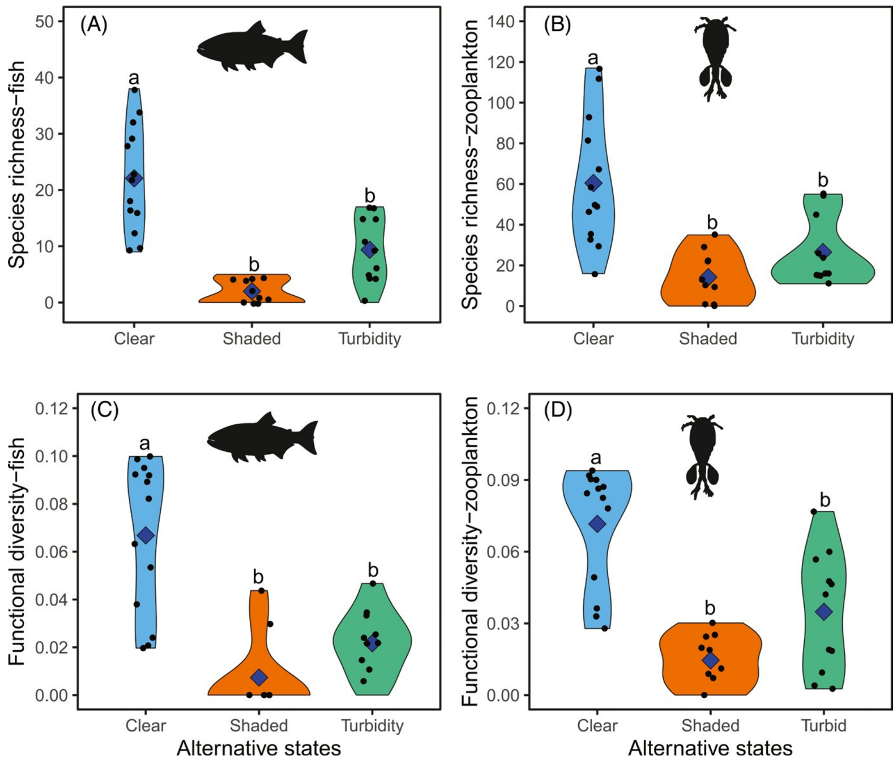

FIGURE 2 Differences in taxonomic (A, B) and functional (FD; C, D) diversity of fish and zooplankton communities among the clear, shaded and turbid states. The blue triangle in the centre of each plot denotes mean values, and the different letters indicate statistically significant differences (LME/Tukey contrasts, $\alpha = 0.05$). Jitter function was used on the data to prevent overplotting

3.2 | Multifunctionality and individual ecosystem functions during regime shifts

There were significant differences in the multifunctionality and the five individual ecosystem functions when the lake was in the three different states. Notably, the multifunctionality was significantly higher during the clear state than during the shaded and turbid states (Table S4; Figure 3A). By contrast, the nutrient concentrations, including total phosphorus and total nitrogen, were significantly higher during the shaded and turbid states (Table S4; Figure 3B,C). Finally, the standing fish biomass as well as algae biomass and underwater light availability were significantly higher during the clear state than during the shaded and turbid states (Table S4; Figure 3D–F).

3.3 | Regime shifts driving the relationship between biodiversity and multifunctionality

The AIC model selection revealed that the FD of fish and zooplankton and their interactions with states were the best predictors of the multifunctionality (Table S3). Together, FD and their interactions with states explained up to 65% of the variation in the multifunctionality. The FD of fish and zooplankton was strongly and positively associated with multifunctionality during the clear state ($p = 0.003$; Figure 4A,B). However, these relationships lost strength during the turbid and shaded states (Figure 4). Consequently, the slope of the relationship between FD and multifunctionality changed from being significantly positive during the clear state to being non-significant with negative trends during the turbid and shaded states (Figure 4C,D).

3.4 | Relationship between traits and individual ecosystem functions

In addition to changes in the relationships between FD and multifunctionality, there were also significant changes in the relationships between traits and individual ecosystem functions during the regime shifts. For example, there were many more significant correlations between traits and individual ecosystem functions during the clear state than during the turbid and shaded states (Figures 5 and 6). For fish, traits related to body size, habitat use (pelagic and benthopelagic) and feeding groups (piscivorous, omnivorous, herbivorous and insectivorous) were positively correlated with standing fish biomass, algae biomass and underwater light availability, and negatively correlated with total phosphorus during the clear state (Figure 5). In contrast, during the turbid state, large-sized detritivores with migratory ability were positively correlated with total nitrogen and total phosphorus concentration, and negatively correlated with underwater light availability (Figure 5). During the shaded state, there were only two negative correlations between feeding groups (insectivorous and invertivorous fish) and total nitrogen (Figure 5).

For zooplankton, traits related to body size, habitat use (littoral), feeding groups (filtering copepods, raptorial copepods and filtering cladocerans), life span (long) and predator escape ability (no escape, low and maximum) had strong positive correlations with the standing fish biomass, algae biomass and light availability during the clear state (Figure 6). The same traits were negatively correlated with total phosphorus during the clear state. During the turbid state, the traits related to body size, habitat use (littoral), feeding groups (sucker and filtering rotifers) and predator escape ability (low, medium and maximum) were positively correlated with total nitrogen

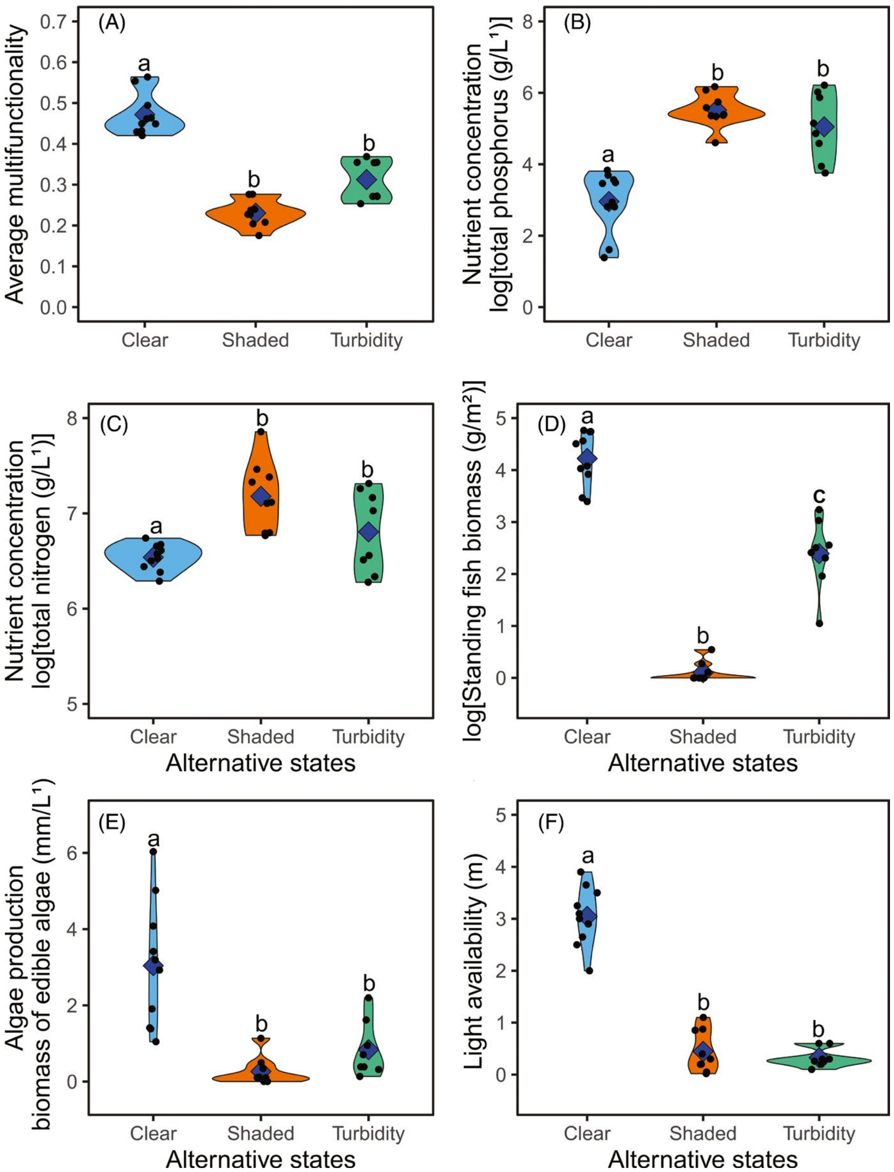

FIGURE 3 Differences in (A) multifunctionality, (B) total phosphorus, (C) total nitrogen, (D) standing fish biomass, (E) algae biomass and (F) underwater light availability among the clear, shaded and turbid states. The blue triangle in the centre of each plot denotes mean values, and the different letters indicate statistically significant differences (LME/Tukey contrasts, $\alpha = 0.05$). Jitter function was used on the data to prevent overplotting

and total phosphorus and negatively correlated with underwater light availability (Figure 6).

4 | DISCUSSION

This study revealed that species richness and the FD of fish and zooplankton were higher in the clear state than in the turbid and shaded states, indicating that the clear state sustains the highest number of species and unique sets of traits. In addition, the FD of fish and zooplankton was strongly associated with ecosystem multifunctionality during the clear state. However, this relationship weakened during the turbid and shaded states. These findings demonstrate how regime shifts alter the FD of shallow lakes, impairing the relationship between biodiversity and multifunctionality, ultimately decreasing multifunctionality. As regime shifts often occur abruptly, predicting this phenomenon for real-world ecosystems is a major challenge (Scheffer et al., 2009). Consequently, the impacts of regime shift on biodiversity and ecosystem functioning are little explored as this requires long-term and detailed ecosystem monitoring (Cooper et al., 2020). Our findings are a valuable contribution to understanding the effects of regime shifts on two facets of biodiversity (taxonomic and functional) and on ecosystem multifunctionality.

The higher taxonomic diversity and FD during the clear state was likely driven by the high coverage of submerged macrophytes. Macrophytes are known to increase habitat heterogeneity by providing space and refuge that facilitate species coexistence, thus increasing fish and zooplankton diversity (Marsh et al., 2020; Meerhoff et al., 2007). Furthermore, the trait diversity of fish and zooplankton also increases with habitat heterogeneity (Porcel et al., 2020; Stuart-Smith et al., 2013). We found that 63% (7 out of 11) and 50% (8 out of 16) of the functional traits of fish and zooplankton, respectively, were more abundant in the clear state than in the turbid and shaded states. Functional traits such as large body size, piscivorous and herbivorous feeding modes, as well as large-sized filter-feeding and low predator escape ability were abundant only during the clear water

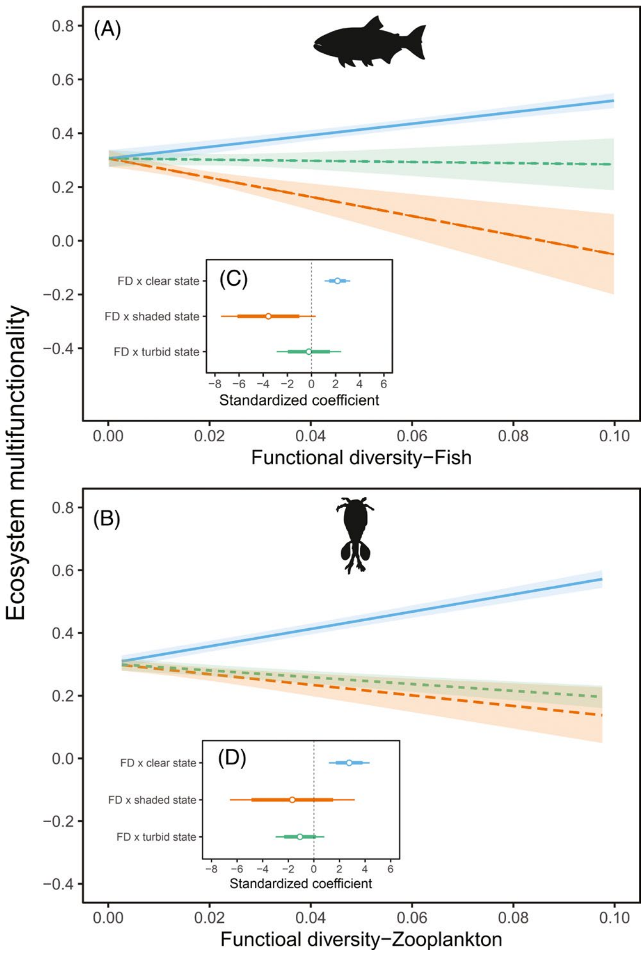

FIGURE 4 The effects of (A) fish and (B) zooplankton functional diversity on ecosystem multifunctionality during the clear, turbid and shaded states. The solid-coloured line represents the effect of a linear mixed-effects model fit, while the shaded areas represent 95% confidence intervals. The graphic was constructed using the 'interact_plot' function from the interactions R package (Long, 2019). (C, D) Estimate coefficients for the effects of the interaction term between functional diversity and each alternative state on ecosystem multifunctionality. The points represent estimates (non-scaled), thick lines represent 75% CIs and thin lines represent 95% CIs

state. These traits may be indicators of the clear state because they were absent or occurred at negligible densities during the turbid and shaded states.

We found that the taxonomic diversity and FD of fish and zooplankton decreased during the turbid and shaded states. Because few traits were abundant during these two states, this indicates that only a few species with similar sets of traits were able to persist in the ecosystem during the turbid and shaded states. During the turbid state, fish were dominated by species with a benthic habitat preference, detritivorous feeding mode and high migration ability, whereas the zooplankton were dominated by small filter-feeding rotifers with high predator escape ability. These trait combinations are common in lake ecosystems in a turbid state (Mormul et al., 2012), as these are characterized by low refuge availability, which increases the predator–prey encounter rates (Figueiredo et al., 2020) and favours small-sized prey that can evade predation or remain undetected (Špoljar et al., 2018). The turbid state also sustains simplified food webs with low densities or even absence of apex piscivorous fish (Hobbs et al., 2012). This state is also characterized by high concentrations of detritus, which favours detritivorous fish (Hobbs et al., 2012; Mormul et al., 2012). Although isolated, the studied lake may connect to an adjacent river during intense flood events, allowing the entry of migratory benthic fish and providing suitable conditions for their development during the turbid state (Mormul et al., 2012). During the shaded state, low taxonomic diversity and FD of fish and zooplankton likely reflects the high environmental stress (Janse & Van Puijenbroek, 1998; Scheffer et al., 2003). The shaded state is characterized by dominance of small floating macrophytes, low water level, poor water quality (e.g. low O_2) and low habitat heterogeneity (Moi, Alves, Antiqueira, et al., 2021). The combination of these stressors often causes high mortality of fish and zooplankton during the shaded state (Moi, Alves, Antiqueira, et al., 2021), resulting in a decline in species richness and homogenization of FD.

There was a markedly higher multifunctionality, as well as a higher standing fish biomass, edible algae biomass and underwater light availability during the clear state. Based on three lines of evidence, our findings indicate that this greater and healthier ecosystem functioning was due to higher FD during the clear state. First, the relationship between FD and multifunctionality was strongly positive during the clear state, but become flatted during the turbid and shaded states (Figure 4). Second, there were more significant links of fish and zooplankton traits with the individual ecosystem functions during the clear state (Figures 5 and 6). Third, species with key traits, such as large piscivorous fish and large filter-feeding zooplankton, were more abundant during the clear state. These findings suggest that fish and zooplankton assemblages were composed of functionally complementary species during the clear state, which allowed more ecosystem functions to be maintained by these two assemblages (Bagousse-Pinguet et al., 2019; Barry et al., 2019). Greater abundance of species with more influential traits is known to increase the efficiency of biodiversity in maintaining the ecosystem functioning (Loreau & Hector, 2001). Fish and zooplankton may increase multifunctionality in several ways, and their effects are stronger with the presence of more sets of functional traits (Moi, Romero, Antiqueira, Mormul, et al., 2021). These effects may include (a) bioturbation, (b) presence of carcasses and faeces, (c) translocation of nutrients among ecosystem compartments and (d) indirect impacts through trophic cascades. All these pathways may maximize the edible algae biomass, standing fish biomass and underwater light availability (Atkinson et al., 2017; Carpenter et al., 2001; Moi, Alves, Antiqueira, et al., 2021; Schmitz et al., 2010). Moreover, there is evidence of a positive feedback between the clear state and biodiversity. We found that the clear state increased multiple biodiversity dimensions (Figure 6). In turn, higher diversity of functional traits was beneficial to the clear state by promoting healthier functioning

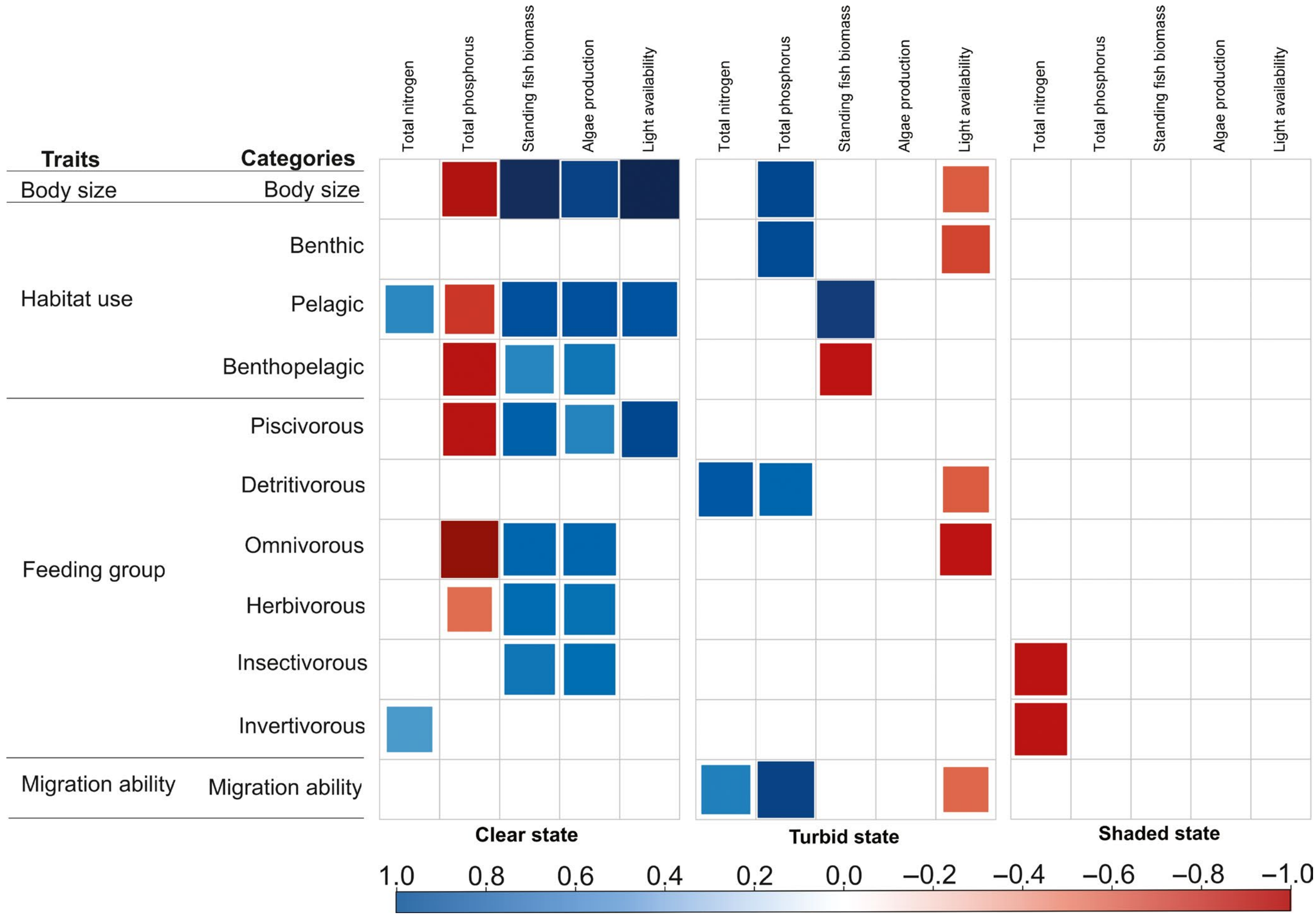

FIGURE 5 Significant correlations (Pearson; $p \le 0.05$) between the community-weighted mean traits (CWMs) of fish with the five individual ecosystem functions (total phosphorus, total nitrogen, standing fish biomass, algae biomass and underwater light availability) during each alternative stable state (clear, turbid and shaded). Colour squares illustrate significant correlations and white squares illustrate non-significant correlations

and maintaining high underwater light availability, which favours the maintenance of the clear state (Scheffer & van Nes, 2007).

Although nutrient concentrations increased during the turbid and shaded states, the standing fish biomass, edible algae biomass and underwater light availability decreased (Figure 7). There were few links between the traits and the individual ecosystem functions during these two states. Combined with the fact that the positive relationship between FD and multifunctionality become non-significant with negative trends during the turbid and shaded states, these results suggest that the loss of functional traits with regime shifts was closely accompanied by a decline in the multifunctionality. More broadly, these results highlight that regime shifts towards turbid or shaded states degrade the positive relationship between biodiversity and multifunctionality. This is because the FD needed to maintain numerous ecosystem functions is reduced (Hilt et al., 2017). Our results add to recent empirical evidence from grasslands, temperate lakes and rivers (Freitag et al., 2021; Goto et al., 2021; Zhang et al., 2020), indicating that regime shifts cause a biodiversity decline with negative consequences for important ecosystem functions. From an ecosystem management perspective, the clear state is noticeably more beneficial to human uses as it sustains a better and healthier ecosystem functioning, including higher production of fish biomass.

5 | CONCLUSIONS

Shallow lakes are the most abundant freshwater ecosystems worldwide (Verpoorter et al., 2014) and they provide multiple services to human well-being (Xu et al., 2017). Our work has shown that regime shifts alter the patterns of taxonomic and functional diversities in shallow lakes (Figure 7). Regime shifts towards turbid and shaded states weaken the relationships between biodiversity and multifunctionality by reducing the number of unique functional traits of fish and zooplankton. Our findings suggest that focusing on functional traits instead of relying only on traditional measures of species richness provides a more mechanistic understanding of regime shifts and their consequences for ecosystem functioning. We draw this conclusion because sets of traits related to the large body size, feeding mode (including piscivorous, herbivorous and insectivorous fish, and large filtering zooplankton) and habitat use (species that preferentially select shoreline habitats) were lost as the lake shifted towards turbid

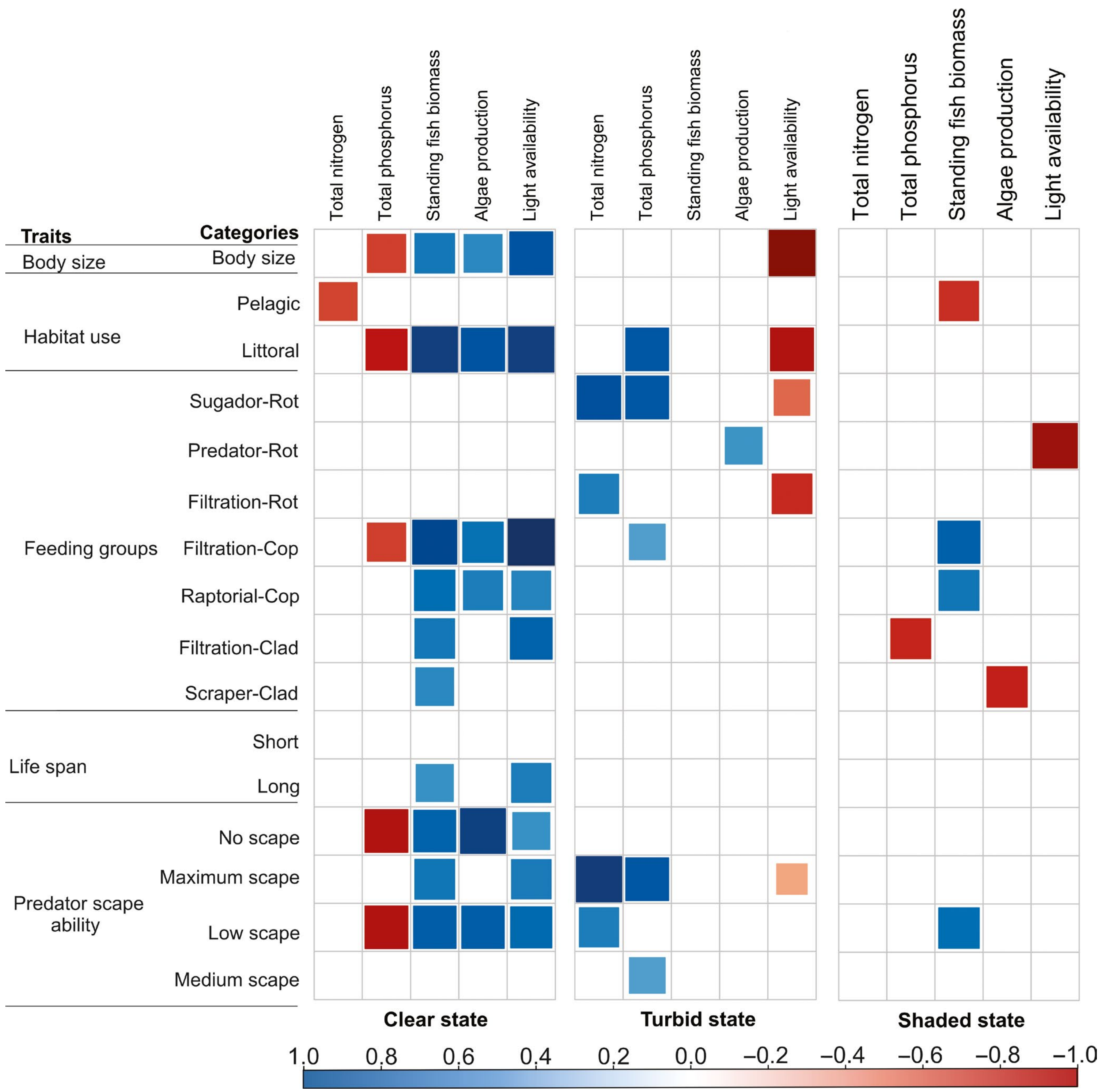

FIGURE 6 Significant correlations (Pearson; $p \leq 0.05$) between the community-weighted mean traits (CWMs) of zooplankton with the five individual ecosystem functions (total phosphorus, total nitrogen, standing fish biomass, algae biomass and underwater light availability) during each alternative stable state (clear, turbid and shaded). Coloured squares illustrate significant correlations and white squares illustrate non-significant correlations. Traits with Rot = rotifers, Clad = cladocerans and Cop = copepods

and shaded states. These groups of organisms and the associated traits tended to respond more strongly to these regime shifts. This is particularly concerning as these sets of traits were also those most strongly associated with ecosystem functions, indicating that loss of these traits will have negative consequences for the functioning of shallow lakes. In addition, the weakening of the relationship between FD and multifunctionality resulting from regime shifts indicates that biodiversity conservation alone will likely not be sufficient to sustain multifunctionality if the underlying regime shifts are not controlled. Given that regime shifts are a global issue (Hilt et al., 2017; Janssen et al., 2020; Scheffer & van Nes, 2007), our results, based on detailed monitoring data from 12 years, could assist in the management of shallow lakes world-wide that face regime shifts.

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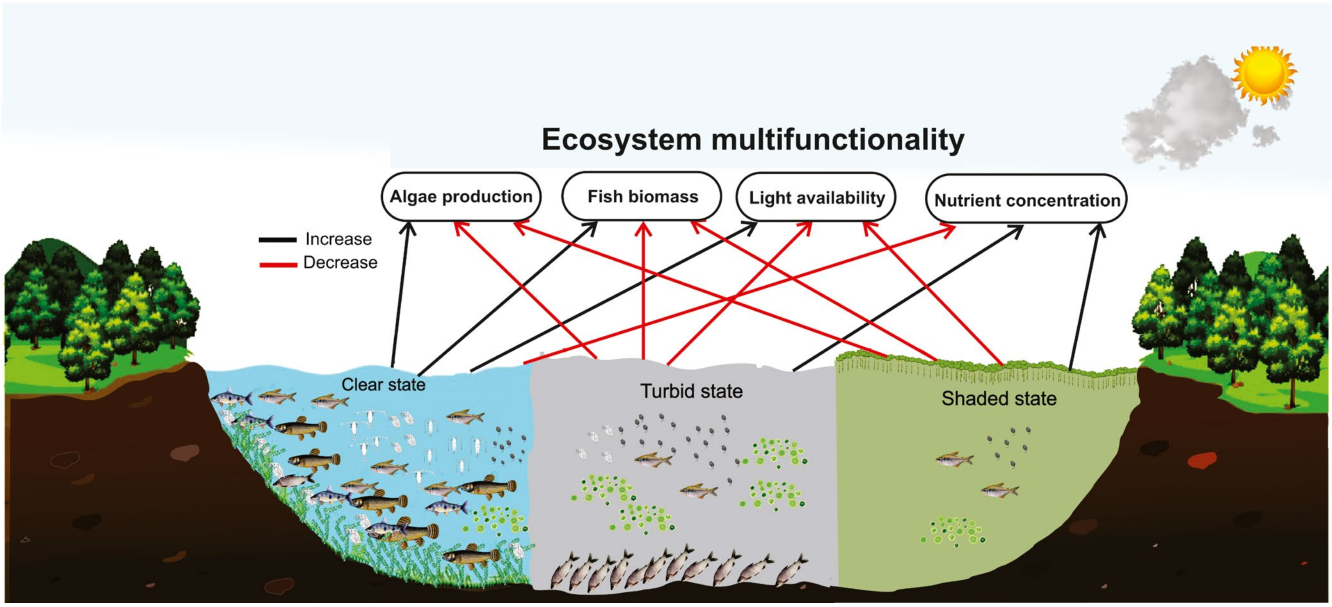

FIGURE 7 Infographic representation of the characteristics of the three alternative states in Lake Osmar: clear (left, from June 2009 to December 2009 and from June 2012 to March 2014), turbid (centre: from June 2005 to November 2005, from March 2007 to February 2008 and from September 2008 to June 2009) and shaded (right: June 2014 to December 2015). During the clear state, the lake had a high taxonomic and functional diversities of fish and zooplankton as well as the highest primary productivity and biomass stock. By contrast, in the turbid state, the lake was dominated by migratory benthic fish and small zooplankton and had a high nutrient load. During the shaded state, the taxonomic and functional diversities of both fish and zooplankton markedly decreased, and no functional trait dominated. Likewise, the primary productivity and biomass stock decreased, but nutrient availability increased in the turbid and shaded states compared to the clear state

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHORS' CONTRIBUTIONS

D.A.M., G.Q.R., E.J., P.K., D.C.A., P.A.P.A., F.T.d.M., B.R.S.F., C.C.B., A.P.F.P., L.S.M.B., R.P.M.; D.A.M. and R.P.M. developed the idea of the article; D.A.M. and D.C.A. performed the statistical analyses; D.A.M., G.Q.R., P.K., D.C.A., P.A.P.A., F.T.d.M., B.R.S.F., C.C.B., A.P.F.P., L.S.M.B. and R.P.M. wrote the original draft of the manuscript and reviewed and wrote the final version of the manuscript.

DATA AVAILABILITY STATEMENT

Data used in the article are available on the Dryad Digital Repository https://doi.org/10.5061/dryad.xd2547dgn (Moi, Romero, Jeppesen, et al., 2021).

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