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Factors affecting the seasonal succession of phytoplankton functional groups in a tropical floodplain reservoir in Vietnam

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ABSTRACT

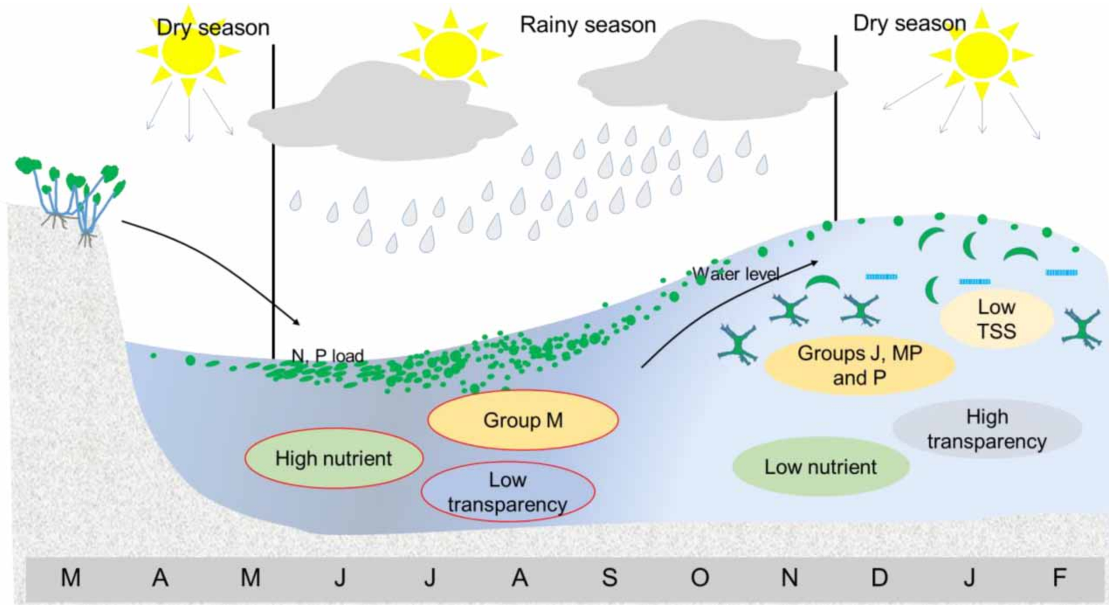
Phytoplankton communities can be classified into different groups based on physiological, morphological, and ecological functions. In this study, the responses of phytoplankton functional groups (PFGs) to physicochemical variables and hydraulic regimes were investigated and used as ecological indicators in the Tri An Reservoir (TAR), a eutrophic tropical floodplain reservoir located in southern Vietnam. Altogether, 148 phytoplankton taxa were identified and assigned to 16 PFGs; the four predominant PFG groups were M (*Microcystis* spp.), MP (filamentous cyanobacteria: *Oscillatoria* spp., and some other diatoms: *Gomphonema angustatum*, *Navicula* sp.), J (green algae: *Coelastrum* spp., *Cosmarium* spp., *Pediastrum* spp., *Scenedesmus* spp., *Staurastrum* spp., *Tetradesmus* spp., *Tetraëdron* spp., and *Xanthidium* spp.), and P (*Closterium* spp., *Aulacoseira granulata*, *Fragilaria* spp., *Pinnularia* spp., and *Desmidium baileyi*). The average PFG biovolume ranged from 79.6 $\pm$ 20.2 to 230.1 $\pm$ 69.1 mg/L with M being the dominant group. The trophic state index (TSI) indicated that the water condition was light-eutrophic to hyper-eutrophic. It was found that the large water level fluctuation resulted in seasonal nutrient dynamics, with higher nutrient concentrations and higher turbidity during the low water level period and vice versa. The redundancy analysis (RDA) indicated that the nutrient concentrations, water level fluctuation, and mixing regimes were critical factors in the PFG selection in the TAR. Therefore, we assumed that water level fluctuation management coupled with biological competition have the potential to control toxic cyanobacteria in the TAR. In conclusion, the PFGs are suitable for examining the effects of environmental conditions on phytoplankton dynamics in tropical floodplain reservoirs, but their sensitivity to long-term changes in water quality and eutrophication requires further investigation.

Key words: environmental variables, floodplain reservoir, functional groups, hydrological conditions, water level fluctuation

HIGHLIGHTS

- Phytoplankton functional groups (PFGs) in relation to the ecological conditions in a tropical floodplain reservoir were investigated.
- The trophic state index (TSI) ranged from light-eutrophic to hyper-eutrophic conditions.
- Sixteen PFGs were found with the dominant group being M (*Microcystis* spp.).
- Nutrient concentrations, water level fluctuation, and mixing regimes are critical factors in selecting PFGs in the TAR.

GRAPHICAL ABSTRACT



INTRODUCTION

Phytoplankton communities are the primary producers in lake ecosystems and play an important role in the food chain (Reynolds *et al.* 2002; Salmaso *et al.* 2015). They contribute approximately 50% of global primary production (Reynolds *et al.* 2002). Phytoplankton are photosynthetic and suspended in the water column; thus, their community composition and structure are affected by geographical location and multiple environmental variables (Amengual-Morro *et al.* 2012). The main environmental variables that affect the phytoplankton structure include light, turbidity, salinity, grazing, temperature, and nutrient availability (Becker *et al.* 2010). Because the presence of phytoplankton reflects the pollution status of an aquatic ecosystem, they have long been used in water quality monitoring (Amengual-Morro *et al.* 2012).

Physicochemical variables play an important role in determining phytoplankton dynamics in lakes and reservoirs (Huang *et al.* 2014; Yang *et al.* 2019; Nan *et al.* 2020). Previous studies have reported that light intensity, water temperature, and available phosphorus and nitrogen are among the top variables that regulate phytoplankton composition and biomass (Reynolds 1999; Wang *et al.* 2011; Nan *et al.* 2020). A reservoir's hydrodynamics also contribute to its water quality and bio-productivity by impacting the reservoir's self-purification, ecosystem conditions, the movement of suspended and dissolved particles, sediment distribution, and the transport of associated contaminants (Dubnyak & Timchenko 2000; Wang *et al.* 2011). In addition, some studies have reported that water level fluctuations strongly influence the phytoplankton development in inland waters (Naselli-Flores & Barone 2003; Wang *et al.* 2011; Liu *et al.* 2015). In man-made reservoirs characterized by large water level fluctuations, hydraulic regimes such as water flow and dynamic pressure have been shown to have a greater influence on annual and interannual variations in phytoplankton biomass and vegetation than physicochemical variables (Naselli-Flores & Barone 2003; Liu *et al.* 2015; Ahmad *et al.* 2020; Yamini *et al.* 2020; Chau *et al.* 2021).

Many studies have examined the driving factors of phytoplankton growth in different freshwater systems (de Figueiredo *et al.* 2006; Zhu *et al.* 2013; Pham *et al.* 2017; Cao *et al.* 2018; Yao *et al.* 2020). In temperate or subtropical lakes and reservoirs, a high phytoplankton biomass or even the formation of surface water blooms often occurs during the summer months because of sufficient solar radiation and a high water temperature (de Figueiredo *et al.* 2006; Cao *et al.* 2018; Yao *et al.* 2020). Hence, temperature and light irradiance are the two most important factors influencing the phytoplankton composition in these regions. However, the responses of phytoplankton to environmental variables and hydraulic regimes in tropical systems have not been investigated to the same extent. In tropical areas with sustained high temperatures and solar radiation, phytoplankton may thrive throughout the year (Pham *et al.* 2017). Therefore, other factors, such as turbidity, precipitation (Pre), nutrient availability, and hydrodynamic regimes, may play vital roles and need to be examined.

Morphological methods have traditionally been used to monitor and characterize phytoplankton community structures. However, phytoplankton species have short generation times and large population sizes, so they can develop morphological and physiological adaptive strategies to survive in different aquatic environments (Izaguirre *et al.* 2012). By dividing phytoplankton into subdivisions according to their adaptive strategies, Reynolds proposed 31 phytoplankton functional groups (PFGs) or assemblage codons that may potentially dominate or co-dominate in a given environment (Reynolds 1997; Reynolds *et al.* 2002). Recently, Padisák *et al.* (2009) revised and updated the list to 39 PFGs identified by alphanumeric labels according to their sensitivity and tolerance. Because PFGs are distinguished in terms of trophic state, habitat properties, and environmental tolerance, they have been widely used to classify phytoplankton and study their relationships in aquatic ecosystems (Zhu *et al.* 2013; Salmaso *et al.* 2015; Latinopoulos *et al.* 2020). The PFG approach has also been used to better understand the functional redundancy within the phytoplankton taxa and the algal biomass–diversity relationship in different freshwater ecosystems worldwide (Török *et al.* 2016; Görgényi *et al.* 2019; Wang *et al.* 2021). However, studies on PFGs in tropical floodplain ecosystems were relatively scarce compared with those in temperate or subtropical regions.

The Tri An Reservoir (TAR) in Vietnam is a semi-fluvial environment with a water level fluctuation of about 10 m, which is between a river and a lake on an aquatic ecosystem continuum (Nguyen *et al.* 2020). Characteristics of TAR phytoplankton have been addressed in previous studies, especially the cyanobacterial composition, the mechanism of cyanobacterial bloom formation, and the relationships of limnological and environmental variables to cyanobacterial toxicity (Dao *et al.* 2010; Nguyen *et al.* 2020; Pham *et al.* 2020). However, to our knowledge, there have been no studies on PFGs and their relationships with the environmental conditions in the TAR.

In the present study, we investigated PFG dynamics in the TAR, a tropical eutrophic floodplain reservoir in southern Vietnam. We then analyzed the main limnological factors regulating the phytoplankton community structure and PFGs. We hypothesized that different PFGs were present and that their seasonal variation could be used as a bioindicator. Nutrient availability and hydrodynamic regimes may play important roles in PFG dynamics in the TAR. To test our hypothesis, we investigated phytoplankton dynamics using the Reynolds PFGs approach sensu (Reynolds *et al.* 2002), and identified the driving forces affecting the succession of PFGs in the TAR.

MATERIALS AND METHODS

Study area

Phytoplankton assemblages were studied in the largest eutrophic reservoir in Vietnam (Figure 1). Located in the middle of the Dong Nai River basin, the TAR has a tropical climate with two distinct seasons: a dry season from November to April and a rainy season from May to October (Nguyen *et al.* 2020). The annual rainfall, air temperature, and wind speed are roughly estimated to be 2,200 ± 200 mm, 33 ± 2 °C, and 9 ± 2 m/s, respectively. The TAR has a surface area and volume of 320 km^2 and 2.7 billion m^3, respectively.

Samples collection and analysis

Water samples for environmental variable analyses were collected monthly between March 2019 and February 2020 at six stations (TA1–TA6) in the TAR (Figure 1). The water samples were packed in an ice box, transported to the laboratory, and analyzed immediately. The concentration of dissolved oxygen (DO), water temperature, and water pH were measured on-site at a depth of 0.3 m using a multiparameter meter (WTW 3320, Weilheim, Germany). The transparency (Trans) was measured using a Secchi disk. The water depth (WD) was measured using a rope connected to a plummet.

To measure the chlorophyll-a (Chl-a) concentration, the sub-sample was filtered through glass fiber filters (Whatman GF/F, England) and extracted in 90% acetone overnight in the dark. After centrifugation, the samples were measured at 630–750 nm using a spectrophotometer (UV-VIS, Harch, 500). The Chl-a concentration was calculated using the trichromatic equations (APHA 2005). Water parameters, namely nitrate (NO_3^-–N), phosphate (PO_4^{3-}–P), total nitrogen (TN), and total phosphorous (TP), were measured colorimetrically in triplicate with a spectrophotometer (Hach DR/2010) following the APHA (2005) methods: nitrate 4500NO_3^- (B), phosphate 4500PO_4^{3-} (B), TN Kjeldahl, 4500N (C), and TP 4500P (D), respectively. The concentration of total suspended solid (TSS) was determined using the weight difference method (2540D) (APHA 2005). The concentration of dissolved inorganic nitrogen (DIN) was determined as the sum of NH_4^+–N, NO_2–N, and NO_3^-–N. The concentration of dissolved inorganic phosphorus (DIP) was calculated as PO_4^{3-}–P. The monthly TAR precipitation data for the sampling period were obtained from the Meteorological Center.

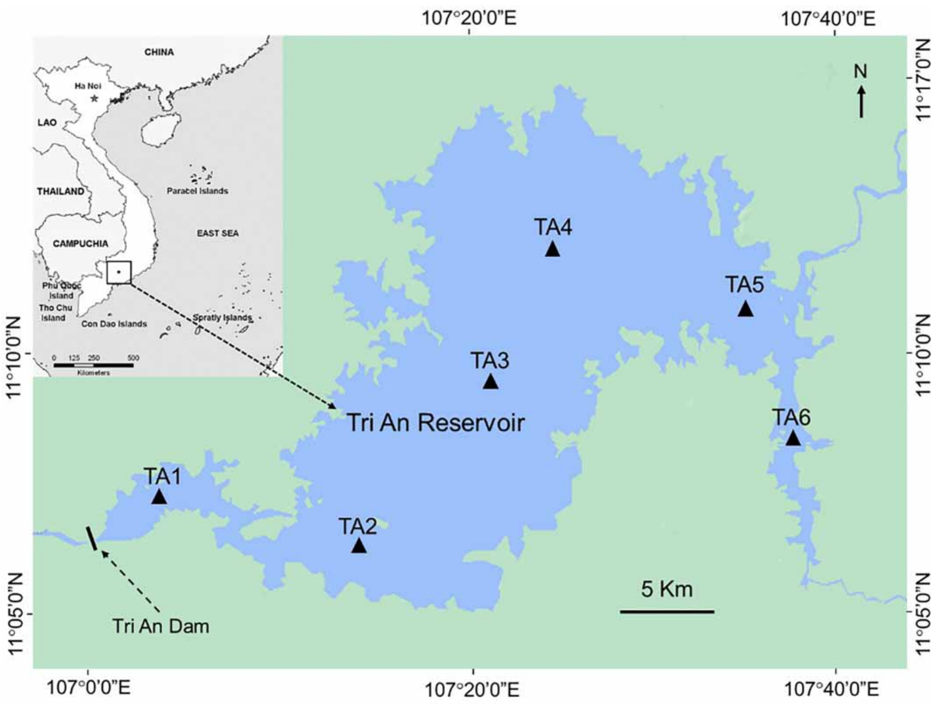


Figure 1 | Map of the TAR with sampling stations.

Phytoplankton were collected by towing 25 μm plankton nets just below the water surface. Quantitative samples of phytoplankton were collected from 1 L raw water samples. All samples were preserved in the field with acidic Lugol's solution (1% final concentration). The quantitative samples were then concentrated to 5 mL and kept at room temperature before analysis. Phytoplankton were identified to the species level as far as possible using the standard works of Komárek & Anagnostidis (1989, 1999, 2005) and Edward & David (2015). Cell numbers were enumerated using a 1 mL counting chamber under 400× magnification. For each sample, at least 100 random transects for over 400 cells were applied.

Assignment to functional groups

All species contributing ≥5% to the total biomass were assigned to one of the PFGs according to the methods of Reynolds *et al.* (2002) and Padisák *et al.* (2009). In this study, PFGs with more than 10% relative biomass at each sampling were defined as the dominant PFGs.

Trophic status

The euphotic zone (z_{eu}) was determined by the Secchi disk depth (Cole 1994). Tropical lakes are fundamentally monomictic; therefore, the mixing depth (Z_{mix}) was taken as equal to the average depth (De Crop & Verschuren 2019). The ratio between Z_{eu} and Z_{mix} (Z_{eu}/Z_{mix}) was used as an indicator of light availability in the mixing zone (Yang *et al.* 2019). Phytoplankton biovolume was calculated based on geometric shapes according to Hillebrand *et al.* (1999), and subsequently expressed as fresh weight, where 1 $mm^3/L = 1$ mg/L (Wetzel & Likens 2000).

The trophic state index (TSI) was calculated according to Carlson (1977) using a logarithmic transformation (Ln) of Chl-a concentration, transparency, and TP following the equation:

$$\mathrm{TSI} = 0.54 \times \mathrm{TSI(Chl-a)} + 0.297 \times \mathrm{TSI(Tran)} + 0.163 \times \mathrm{TSI(TP)}$$

where

$$\mathrm{TSI(Chl-a)} = 9.81 \times \mathrm{Ln(Chl-a)} + 30.6\ (\mu g/L)$$
$$\mathrm{TSI(SD)} = 60 - 14.41 \times \mathrm{Ln(SD)}\ (m)$$
$$\mathrm{TSI(TP)} = 14.42 \times \mathrm{Ln(TP)} + 4.15\ (\mu g/L)$$

The TSI value was used to classify the trophic status of the reservoir, as indicated in Table 1 (Carlson 1977).

Data analysis

One-way analysis of variance (ANOVA) was used to examine the differences in environmental variables between seasons. The redundancy analysis (RDA), a multivariate ordination method, was used to determine how much variance in the biomass of the selected PFGs was attributed to environmental factors in the dry and rainy seasons. Data were log-transformed by $\log(X + 1)$ to normalize their distributions before analysis. Only PFGs with a contribution of more than 3% of the total biomass were selected for this analysis to reduce the influence of rare groups. All analyses was performed using the STATISTICA7, and *p*-values less than 0.05 were considered statistically significant. The RDA analysis was analyzed using CANOCO version 4.5 for Windows (Leps & Smilauer 2003).

RESULTS

Variations of euphotic depth and mixing depth

The mean Z_{eu}, Z_{eu}/Z_{mix}, precipitation, and water depth in the TAR during the study period are shown in Figure 2. The Z_{eu} values were low all year round; they varied from 0.65 to 5.21 m (average 2.51 ± 1.66 m), with the highest value recorded in December and the lowest value in June. The Z_{eu} values were higher than 2 m in October to April, but less than 2 m in other months. Z_{eu}/Z_{mix} ratio values were low and ranged from 0.06 to 0.27 m (average 0.16 ± 0.07 m). The mean annual precipitation in the TAR is about 2,200 ± 200 mm, with monthly precipitation ranging from 0 to 390 mm, peaking in October. The water depth of the TAR changed seasonally, and varied from 10.4 to 19.6 m (average 14.9 ± 3.5 m). Water depth was within the median range and then rapidly decreased to the lowest level from March to July, reaching the minimum value during the May to July period. As the rainy season arrived, with high precipitation during May to October in combination with Tri An dam operation, the water level rose gradually from July to November and often peaked in November. It fell gradually from November to March (Figure 2).

Physical and chemical variables

The mean, minimum, and maximum values of the water quality variables in the TAR during the study period are shown in Table 2. The water temperature of the reservoir ranged from 26.7 to 36.6 °C (mean 29.9 ± 3.4 °C) and from 27.3 to 32.7 °C (mean 29.7 ± 1.8 °C C) in the dry and rainy seasons, respectively. The water temperature was not significantly different between the dry and rainy seasons. The water pH was weakly alkaline, ranging from 6.5 to 8.6 (mean 7.1 ± 0.74) and

Table 1 | Trophic status classification based on the TSI value

TSI	≤30	30–40	40–50	50–60	60–70	>70
Trophic status	Oligotrophic	Oligo-mesotrophic	Mesotrophic	Light-eutrophic	Medium-eutrophic	Hyper-eutrophic

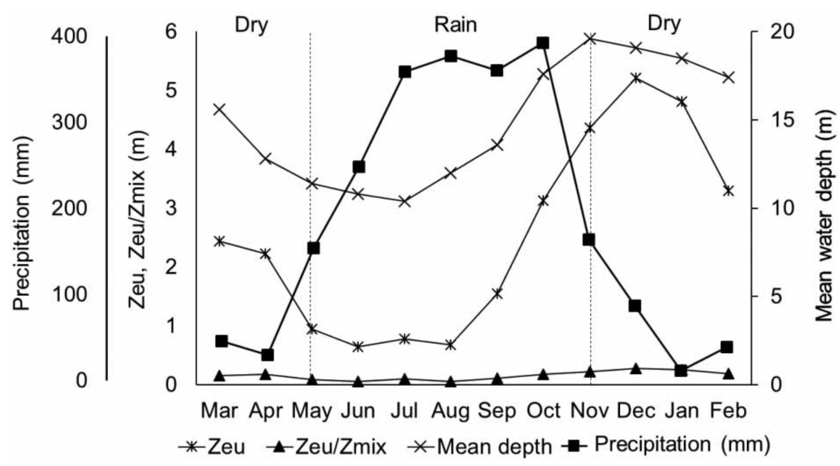


Figure 2 | Mean variations Z_{eu}, Z_{eu}/Z_{mix}, precipitation, and water depth in the TAR during the study period.

Table 2 | Mean values and ranges (min–max) of water quality variables in the TAR during the study period

Water variables	Dry season (November–April) Mean	Min	Max	Rainy season (May–October) Mean	Min	Max	*p* value
Tem (C)	29.9	26.7	36.6	29.1	27.3	32.7	0.58
pH	7.1	6.5	8.6	7.2	6.6	8.9	<0.05
Trans (cm)	116	30	230	44	5	220	<0.001
DO (mg/L)	5.9	3.5	7.4	5.7	3.3	7.6	0.27
TSS (mg/L)	12.7	2.0	45.0	62.8	3.5	285.0	<0.001
DIN (mg/L)	0.59	0.2	1.51	0.43	0.31	1.96	<0.05
DIP (mg/L)	0.04	0.02	0.08	0.07	0.04	0.15	<0.05
TN (mg/L)	1.22	0.4	3.6	2.35	0.5	13.8	<0.01
TP (mg/L)	0.07	0.04	0.16	0.19	0.06	0.85	<0.001
Chl-a (mg/L)	17.3	2.8	114.6	44.6	4.2	369.4	<0.05

Tem, temperature; Trans, transparency; DO, dissolved oxygen; TSS, total suspended solids; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; TN, total nitrogen; TP, total phosphorus; Chl, chlorophyll-a.

from 6.6 to 8.9 (mean 7.2 ± 0.77) in the dry and rainy seasons, respectively. The pH was higher in the rainy season than in the dry season ($p < 0.05$). There was a wide variation in transparency, which ranged from 30 to 230 cm (mean 116 ± 54 cm) and from 5 to 220 cm (mean 44 ± 37 cm) in the dry and rainy seasons, respectively. The TSS also exhibited wide variation, ranging from 2.0 to 45.0 mg/L (mean 12.7 ± 10.4 mg/L) and from 3.5 to 285.0 mg/L (mean 62.8 ± 44.3 mg/L) in the dry and rainy seasons, respectively. Transparency was significantly higher in the dry season than in the rainy season, while the TSS was higher in the rainy season than in the dry season ($p < 0.001$). DO largely changed from 3.5 to 7.4 mg/L (mean 5.9 ± 0.87 mg/L) and from 3.3 to 7.6 mg/L (mean 5.7 ± 0.72 mg/L) in the dry and rainy seasons, respectively. DO was not significantly different between the dry and rainy seasons. DIN ranged from 0.2 to 1.51 mg/L (mean 0.59 ± 0.19 mg/L) and from 0.31 to 1.96 mg/L (mean 0.63 ± 0.27 mg/L) in the dry and rainy seasons, respectively. DIP ranged from 0.02 to 0.08 mg/L (mean 0.04 ± 0.01 mg/L) and from 0.04 to 0.15 mg/L (mean 0.07 ± 0.02 mg/L) in the dry and rainy seasons, respectively. Both DIN and DIP were higher in the rainy season than in the dry season ($p < 0.05$). TN ranged from 0.4 to 3.6 mg/L (mean 1.22 ± 0.63 mg/L) and from 0.5 to 13.8 mg/L (mean 2.35 ± 2.1 mg/L) in the dry and rainy seasons, respectively. TP ranged from 0.04 to 0.16 mg/L (mean 0.07 ± 0.03 mg/L) and from 0.06 to 0.85 mg/L (mean 0.19 ± 0.04 mg/L) in the dry and rainy seasons, respectively. Both TN and TP exhibited the same patterns as DIN and DIP, with higher values in the rainy season than in the dry season ($p < 0.01$). Chl-a ranged from 2.8 to 114.6 μg/L (mean 17.3 ± 8.6 μg/L) and from 4.2 to 369.4 μg/L (mean 44.6 ± 33.5 μg/L) in the dry and rainy seasons, respectively. Chl-a levels were also higher in the rainy season than in the dry season ($p < 0.05$).

Trophic state index

Figure 3 shows the mean TSI values and trophic status of the reservoir. The TSI values in the TAR varied from 56 to 81.2, implying that the reservoir shifted from light-eutrophic to hyper-eutrophic conditions. The TSI values were especially high from March to October, indicating that eutrophication in the water was often high.

Phytoplankton functional group

In total, 148 phytoplankton taxa were identified from the TAR during the study period. These taxa included cyanobacteria, diatoms, chlorophytes, dinoflagellates, and euglenophytes. Phytoplankton taxa in the reservoir were classified into the following 16 PFGs: C, D, F, G, H1, J, L_O, L_M, M, MP, P, S1, S2, S_N, W1, and X1 (Table 3). Of these PFGs, the J, M, MP, and P PFGs were dominant, with their respective proportions higher than 10% of the phytoplankton biomass.

The functional groups M (*Microcystis aeruginosa*, *Microcystis botrys*, *Microcystis panniformis*, *Microcystis flosaquae*, *Microcystis wesenbergii*) and P (*Closterium gracile, Closterium aciculare, Closterium moniliferum, Aulacoseira granulata, Fragilaria* sp., *Fragilaria intermedia, Pinnularia nobilis, Pinnularia viridis, Desmidium baileyi*) were dominant at all studied sites. In the dry season, the proportions of groups M and P ranged from 8.3 to 78.4% and from 10.4 to 48.6% of the total biomass,

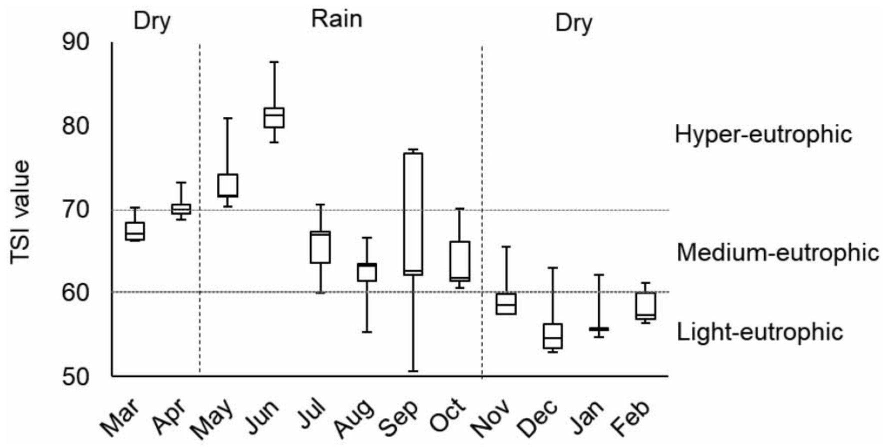


Figure 3 | Trophic status of the TAR during the study period based on the TSI.

Table 3 | Phytoplankton functional groups with the main representatives species recorded in the TAR

No.	FG	Phytoplankton species
1	C	*Stephanodiscus* sp., *Cyclotella meneghiniana*, *Cyclotella comta*, *Aulacoseira ambigua*, *Aulacoseira granulata var. angustissima*
2	D	*Nitzschia acicularis*, *Nitzschia filiformis*, *Nitzschia longissima*, *Nitzschia recta*, *Synedra acus*, *Synedra ulna*, *Cymbella cistula*, *Surirella robusta*, *Surirella splendida*, *Surirella* sp.
3	F	*Kirchneriella lunaris*, *Oocystis borgei*, *Oocystis elliptica*, *Oocystis pusilla*
4	G	*Eudorina elegans*, *Volvox* sp., *Pleodorina californica*, *Sphaerocystis schroeteri*
5	H1	*Dolichospermum cylindrica*, *Dolichospermum affine*, *Dolichospermum circinale*, *Dolichospermum flosaquae*, *Dolichospermum planctonicum*, *Dolichospermum spiroides*, *Dolichospermum smithii*, *Dolichospermum viguieri*
6	J	*Coelastrum microporum*, *Cosmarium contractum*, *Cosmarium granatum*, *Cosmarium* sp., *Pediastrum duplex*, *Pediastrum simplex*, *Scenedesmus acuminatus*, *Scenedesmus quadricauda*, *Scenedesmus bijugus*, *Staurastrum arachne*, *Staurastrum archeri*, *Staurastrum arctiscon*, *Staurastrum bigibbum*, *Staurastrum brachiatum*, *Staurastrum cerastes*, *Staurastrum dorsidentiferum*, *Staurastrum freemanii*, *Staurastrum gracile*, *Staurastrum limneticum*, *Staurastrum manfeldtii*, *Staurastrum natator*, *Staurastrum pinnatum*, *Staurastrum sebaldi*, *Staurastrum smithii*, *Staurastrum stauphorum*, *Staurastrum sexangulare*, *Staurodesmus convergens*, *Staurodesmus cuspidicurvatus*, *Staurodesmus dejectus*, *Staurodesmus megacanthus*, *Tetradesmus dimorphus*, *Tetradesmus lagerheimii*, *Tetraëdron gracile*, *Tetradesmus obliquus*, *Xanthidium acanthophorum*, *Xanthidium sansibarense*
7	L_O	*Peridinium* sp., *Chroococcus limneticus*, *Merismoperia glauca*
8	L_M	*Ceratium hirundinella*
9	M	*Microcystis aeruginosa*, *Microcystis botrys*, *Microcystis panniformis*, *Microcystis flosaquae*, *Microcystis wesenbergii*
10	MP	*Oscillatoria limosa*, *Oscillatoria princeps*, *Oscillatoria tenuis*, *Oscillatoria peronata*, *Gomphonema angustatum*, *Navicula* sp.
11	P	*Closterium gracile*, *Closterium aciculare*, *Closterium moniliferum*, *Aulacoseira granulata*, *Fragilaria* sp., *Fragilaria intermedia*, *Pinnularia nobilis*, *Pinnularia viridis*, *Desmidium baileyi*
12	S1	*Planktothrix agardhii*, *Pseudanabaena mucicola*, *Pseudanabaena limnetica*, *Phormidium* sp.,
13	S2	*Arthrospira platensis*
14	SN	*Cylindrospermopsis raciborskii*
15	W1	*Euglena deses*, *Euglena oxyuris*, *Euglena acus*, *Phacus acuminatus*, *Phacus longicauda*, *Phacus ovalis*
16	X1	*Ankistrodesmus fasciculatus, Ankistrodesmus falcatus, Ankistrodesmus fusiformis, Ankistrodesmus spiralis, Chlorella* sp.

respectively. In the rainy season, group M was strongly dominant at sites TA1–TA4, comprising up to 81.6% of the total biomass (at TA2), whereas group P comprised up to 27.1% of the total biomass (Figure 4).

The monthly variation in the biomasses of the TAR PFGs is shown in Figure 5. The biomass of group M was dominant from May to November, with the highest value in September (295.8 mg/L) associated with a *Microcystis* spp. bloom (Figure 6).

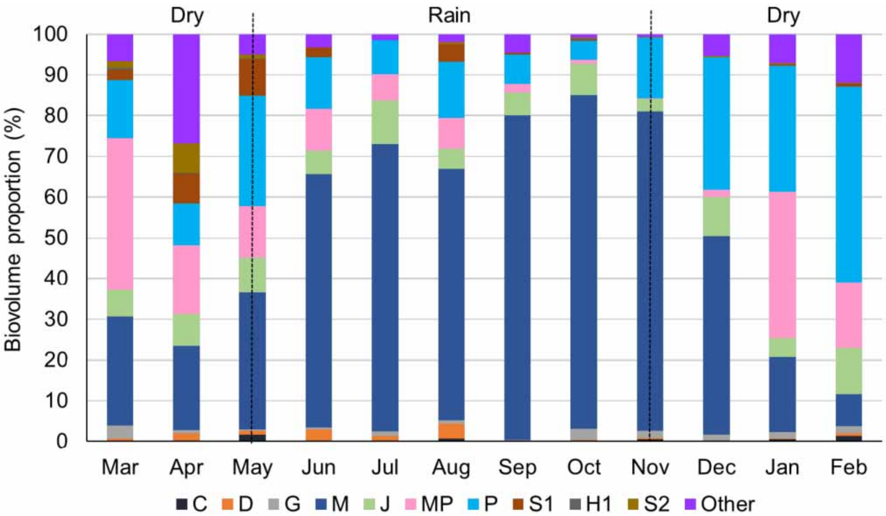


Figure 4 | Seasonal variation of the relative proportion of the functional groups of phytoplankton in the TAR.

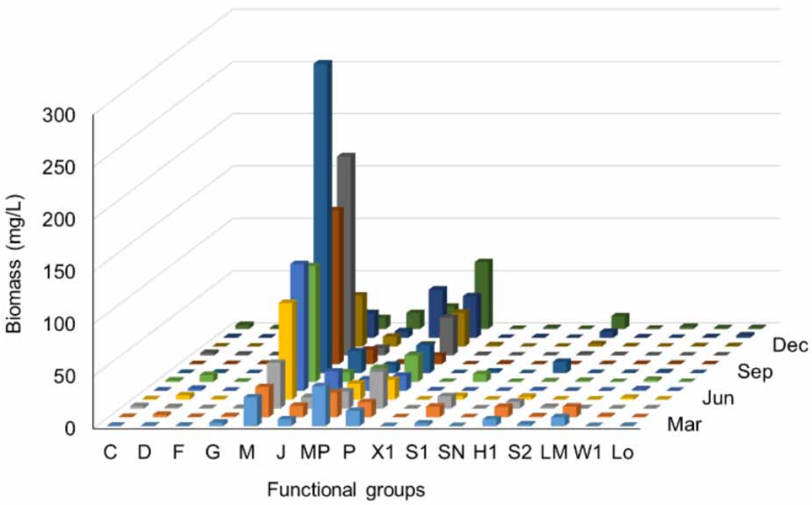


Figure 5 | Monthly variation of biomass of the functional groups of phytoplankton in the TAR.

Figure 6 | Cyanobacterial bloom dominated by *Microcystis* spp. in the TAR in September, 2019.

Other PFGs made prominent contributions to the algal biomass in the TAR, including groups J (green algae: *Coelastrum* spp., *Cosmarium* spp., *Pediastrum* spp., *Scenedesmus* spp., *Staurastrum* spp., *Tetradesmus* spp., *Tetraëdron* spp., *Xanthidium* spp.), MP (filamentous cyanobacteria: *Oscillatoria limosa*, *Oscillatoria princeps*, *Oscillatoria tenuis*, *Oscillatoria perornata*, and some other diatom: *Gomphonema angustatum*, *Navicula* sp.), and P (*Closterium* spp., *Aulacoseira granulata*, *Fragilaria* spp., *Pinnularia* spp., and *Desmidium baileyi*). In contrast to the biomass of group M, the biomasses of groups MP and P were high in the dry months (November to March).

The spatial and seasonal variations in phytoplankton abundance (mean $\pm$ SD) in the TAR are shown in Figure 7. The density of algal cells was highest in the rainy season, especially at sites TA1–TA3 (lower sites of the reservoir). The mean algal cell densities at TA2 and TA3 reached maxima of 4.52×10^7 and 4.48×10^7 cells/L, respectively. The algal cell densities tended to decrease from the lower sites to the upper sites in both seasons (Figure 7). In September 2019, a heavy bloom of cyanobacteria occurred at TA2 and TA3, and the bloom-forming species was Microcystis spp. (Figure 6).

Redundancy analysis

Biplots of the RDA generated using 13 abiotic variables and 10 PFGs in the TAR in the dry and rainy seasons are shown in Figure 8. Z_{eu}/Z_{mix}, Z_{eu}, TSS, transparency, Pre, WD, nitrogen, and phosphorus were found to be among the most important environmental factors that affect PFGs in the TAR. However, different influences were observed in different seasons. In the dry season, the first two axes explained 85% of the total variance (first axis accounted for 67.9% and second axis accounted for 17.1%). The first axis was mainly correlated with Z_{eu}/Z_{mix}, Z_{eu}, transparency, WD, Tem, and Pre. The second axis was mainly determined by pH, DIP, TSS, TN, TP, DO, and DIN (Figure 8(a)). The first RDA species axis was positively correlated with Tem (0.071) and pH (0.47), and negatively correlated with Z_{eu}/Z_{mix} (–0.83), Z_{eu} (–0.82), WD (–0.80), transparency (–0.79), Pre (–0.79), DO (–0.42), and DIN (–0.37). The second RDA axis was mainly positively correlated with DIN (0.51), DO (0.37), transparency (0.48), WD (0.46), and negatively correlated with DIP (–0.91), TSS (–0.75), TN (–0.58), pH (–0.8), Pre (–0.43), TP (–0.40), and Tem (–0.68). In the rainy season, the first two axes explained 78% of the total variance (first axis accounted for 50.4% and second axis accounted for 27.6%). The first axis was mainly correlated with Z_{eu}/Z_{mix}, Z_{eu}, transparency, Pre, WD, and DO, and the second axis was mainly defined by TN, DIN, DIP, TSS, and TP (Figure 8(b)). The first axis was slightly positively correlated with pH (0.24), and negatively correlated with Pre (–0.69), Z_{eu} (–0.59), Z_{eu}/Z_{mix} (–0.58), transparency (–0.56), WD (–0.51), DO (–0.45), and TN (–0.33). The second RDA axis was mainly positively correlated with TN (0.55), DIN (0.42), TSS (0.41), TP (0.29), and DIP (0.22), and negatively correlated with DO (–0.34) and Z_{eu}/Z_{mix} (–0.11).

DISCUSSION

The TAR is the largest man-made reservoir in Vietnam; and it was established in 1986 by the damming of the Dong Nai River (Nguyen *et al.* 2020). The TAR has two inflows: Dong River in the northeast and Nga River in the southeast (Figure 1). This

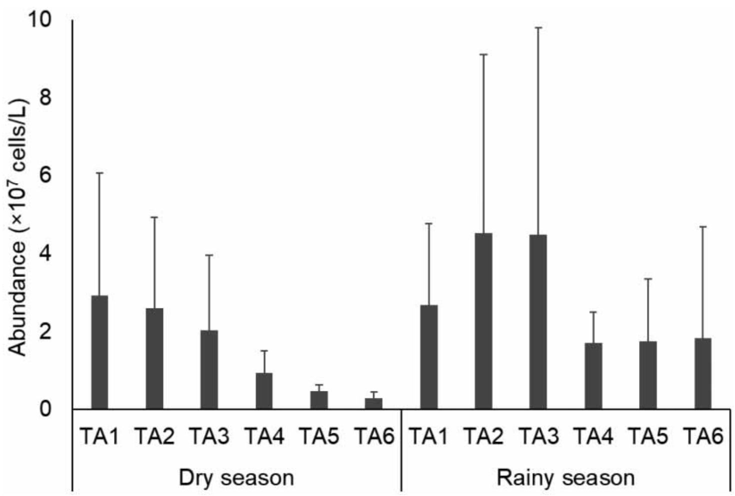


Figure 7 | Seasonal abundance of phytoplankton in the TAR.

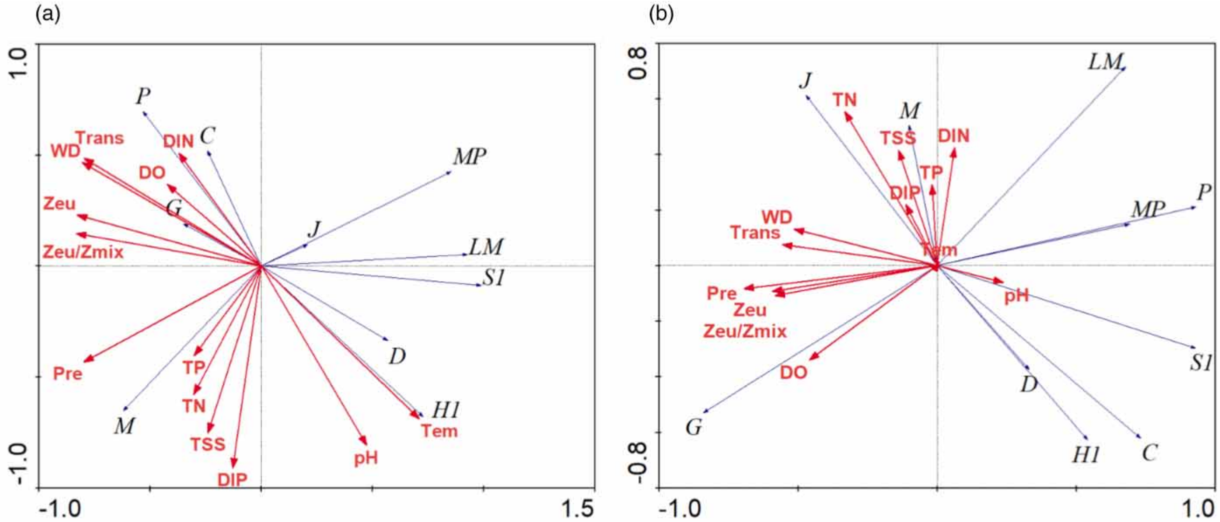


Figure 8 | Biplots of the RDA based on the biomass of the representative functional groups of phytoplankton and the environmental variables in the TAR in (a) dry season and (b) rainy season.

large shallow basin exhibits considerable annual water level fluctuation, depending on precipitation, dam operation, and land use and land cover changes (Truong *et al.* 2018). The reservoir displays some natural river features, particularly during low water level periods, and shows a limnophase character during high water level periods. Thus, the TAR is naturally flooded during the high water season (Nguyen *et al.* 2020; Pham *et al.* 2020). At that time, the reservoir's dimensions can be enhanced by orders of magnitude in volume and surface area, similar to a floodplain reservoir. In the TAR, the mean water level changes seasonally, in accordance with precipitation and the operation of the Tri An dam. During the study period, the TAR mean water level ranged approximately from 10.4 to 19.6 m (Figure 2). This large water level fluctuation resulted in nutrient dynamics in this ecosystem. Generally, high water level in rainy season increases nutrient concentrations, turbidity, and consequently enhances phytoplankton biomass (Nõges *et al.* 2003; Bakker & Hilt 2016). In the TAR, an increase in nutrient concentrations and high turbidity during the low water period (early rainy season) was also observed. This characterization has been reported in several floodplain lentic water bodies, such as the Paraguay River and floodplain, the Parana River floodplain in Brazil, the Changjiang River floodplain lake (Poyang Lake) in China, and the Danube River floodplain in Austria (Train & Rodrigues 1998; Tockner *et al.* 1999; De Oliveira & Calheiros 2000; Liu *et al.* 2015).

Rainfall and operation of the Tri An dam not only impacted the water level but also influenced the water's Z_{eu} zone. More than 80% of southern Vietnam's annual precipitation falls during the rainy season (May to October) (Nguyen *et al.* 2014; Truong *et al.* 2018), bringing external materials and nutrients from the terrestrial ecosystem into the reservoir via surface runoff (Pham *et al.* 2020). This resulted in higher dissolved nutrient concentrations in the rainy season and decreased water transparency, or a decreased Z_{eu} zone, from May to August in the study period. The reduction in nutrient concentrations during the dry season may be due to the lack of runoff events and absorption by phytoplankton. Our results agree with previous studies that show decreases in TN and TP in eutrophic rivers/reservoirs were mainly due to the reduction of non-point pollution sources and increase in biological activity (Huang *et al.* 2014; Braga *et al.* 2015; Yang *et al.* 2019; Akagha *et al.* 2020). The Z_{eu} zone in the TAR increased sharply from September to December and peaked in December when water was stored for later use. Despite the high solar radiation (with a mean monthly total of sun hours ranging from 145 to 263 h) at the TAR (Pham *et al.* 2020), the Z_{eu}/Z_{mix} ratio in the reservoir was very low. This indicated that the light availability in the water column was low.

Although many studies have been conducted on the effect of environmental factors on phytoplankton dynamics, the mechanisms regulating the succession of phytoplankton communities are complex, and there are case-by-case differences (Xiao *et al.* 2011; Lenard *et al.* 2019; Yao *et al.* 2020). In temperate eutrophic lakes, air temperature has been identified as the principal factor regulating the total phytoplankton biomass and Chl-a (Lenard *et al.* 2019). Light availability and the hydrologic regime were key factors determining the longitudinal differences in PFGs in the subtropical Gorges Reservoir, China (Zhu *et al.* 2013). Similar patterns were observed in two tributaries of Gorges Reservoir: the Daning River and the Xiangxi

River (Wang *et al.* 2011; Zhu *et al.* 2013). A study of a deep, monomictic, oligo-mesotrophic canyon-reservoir showed that external factors, such as monsoonal hydrology and artificial drawdown, were the driving factors of PFGs (Xiao *et al.* 2011). In another deep, monomictic, meso-eutrophic reservoir in subtropical southern Brazil, the mixing regime was found to be the main determining factor for the seasonal dynamics of the phytoplankton community (Becker *et al.* 2009). In Lake Catemaco, a tropical lake in Mexico, grazing by filter-feeding fish, permanent mixing, low transparency, and nitrogen limitation are the key factors in selecting the dominance of cyanobacteria Cylindrospermopsis spp. (S_N group) (Komárková & Tavera 2003).

Previous studies conducted at the TAR reported that water temperature and light availability were not driving factors for phytoplankton and cyanobacteria. Rather, high TN, phosphate, and TP concentrations in the rainy season in combination with a high TSS concentration, low or medium transparency, and low water level have reportedly led to a shift in TAR cyanobacterial blooms (Nguyen *et al.* 2020; Pham *et al.* 2020). In this study, the seasonal succession of the PFGs was regulated not only by environmental variables but also hydrodynamics, such as water level, euphotic depth, and the mixing regime. In general, the four predominant PFGs identified in the TAR were groups M, J, MP, and P. These PFGs are typical of eutrophic environments (Liu *et al.* 2015). Therefore, they could be used to identify the spatial and seasonal variations of aquatic environments. However, this study is limited to the short-term changes. Their sensitivity to long-term variation in water quality and eutrophication requires further investigation.

Group M was dominant during the rainy season when nutrient availability was high in the water and euphotic depth and mixing depth were low in the water column. Our results also suggest that increased turbidity in the TAR during the early months of the rainy season reduces light penetration in the water column. Furthermore, the dominance of group M species during this period may be due to their buoyancy and depth regulation (Reynolds *et al.* 1987). During the dry season, it was found that there is higher water transparency, euphotic depth, and mixing depth in the water column; however, the lower nutrient concentration could lead to the succession of other PFGs, such as J, MP, and P. Our results are consistent with previous observations indicating that water level fluctuations have a complex influence on environmental changes and PFG succession (Naselli-Flores & Barone 2003; Wang *et al.* 2011; Liu *et al.* 2015).

It has been reported that in Poyang Lake, China, the potamophase condition during the low water level period supported diatom development, and that the limnophase condition during the high water level period selected a cyanobacteria biomass, groups M, MP, and H1 (Liu *et al.* 2015). This is a little different from our case in the TAR. We found that the potamophase condition supported the growth of cyanobacteria, group M, and prolonged its dominance in the total phytoplankton biomass until the early stage of the limnophase (high water level condition). The stable environment during the limnophase led to a high biomass of other PFGs, such as J, MP, and P. Given that *Microcystis* spp. are more sensitive to mixing conditions in the water column (Reynolds *et al.* 2002), the reduction of *Microcystis* spp. biomass during the high water level period could be explained by the unfavorable conditions of the mixture regime in the water column and competition with other phytoplankton (e.g., groups J and P). *Microcystis* spp. have been reported to be dominant and bloom-forming in many water bodies around the world, including in the TAR (Harke *et al.* 2016; Pham *et al.* 2020). Numerous studies have been conducted to mitigate their excessive growth and adverse effects. Our results suggest that water level fluctuations coupled with biological competition are potential factors that can be used to control *Microcystis* biomass in the TAR.

CONCLUSIONS

This is the first study to investigate the influence of environmental factors on the seasonal succession of PFGs in a tropical floodplain reservoir in Vietnam, and further examined the effect of hydraulic regimes on these groups. It was found that the reservoir's considerable water level fluctuation resulted in seasonal nutrient dynamics, with a higher nutrient concentration and a higher turbidity during the low water level period, and vice versa. PFGs were driven by both physicochemical variables and hydraulic regimes. The physicochemical variables regulated the seasonal succession of the PFGs, and mixing regimes and water level determined the environmental conditions. Nutrient availability and water level were found to be the key factors responsible for the selection of phytoplankton species in the TAR. Our results confirm the potential of PFGs as tools for examining environmental effects on phytoplankton assemblages in tropical floodplain reservoirs. However, their sensitivity to long-term changes in water quality and eutrophication of the TAR requires further investigation.

AUTHOR CONTRIBUTIONS

T.L.P. conceptualized the manuscript and outlined the draft; T.L.P., T.H.Y.T., and T.T.T. were involved in field sampling; T.H.Y.T. and T.T.T. were involved in laboratory analysis and data curation; T.L.P. and T.H.Y.T. wrote the original draft; T.L.P., T.H.Y.T., and T.T.T. revised and edited the manuscript. All authors have read and agreed to the published version of the manuscript.

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CONFLICTS OF INTEREST

The authors declare they have no conflict of interest.

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DATA AVAILABILITY STATEMENT

All relevant data are included in the paper or its Supplementary Information.

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