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Eichhornia crassipes management in a eutrophic reservoir: Cover reduction, rapid recolonization, and cyanobacterial dynamics

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TITLE

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ABSTRACT

Mechanical harvesting is widely used to control *Eichhornia crassipes* in reservoirs, yet its performance is judged by biomass removed rather than the reduction and stabilization of plant cover. We integrated a 129 month Sentinel-1 time series derived using U-Net segmentation with harvesting records and water quality monitoring to evaluate harvest campaigns, recurrent expansion and phytoplankton responses in a 177 ha eutrophic tropical urban reservoir. Harvesting effort was not proportional to cover change: campaigns with comparable biomass removal produced contrasting outcomes. Cover reductions were followed by recolonization, with the two fastest episodes doubling reservoir scale cover in 19 and 20 days. Expansion was fastest after low cover phases and declined as open water surface became occupied, whereas harvesting imposed a weaker constraint on cover gain. At the reservoir outlet, higher cover was associated with lower cyanobacterial density and dominance during the dry season, while chlorophyll-a remained unrelated to cover. Station specific Random Forest models interpreted with explainable AI (SHAP) retained true color and macrophyte cover as main predictors of cyanobacterial density. These findings distinguish three dimensions often conflated in macrophyte management: operational effort, spatial outcome and ecological state. Harvested biomass should therefore be treated as an effort metric, whereas net cover change, residual cover and rebound provide direct measures of management performance. Combining deep learning satellite mapping, operational records,

explainable machine learning and in situ monitoring can support adaptive harvesting, but durable control will also require reductions in nutrient and suspended solid loads.

Keywords: *Eichhornia crassipes*; Sentinel-1; SAR; reservoir management; mechanical harvesting; cyanobacteria; eutrophication; xAI.

HIGHLIGHTS

Decadal Sentinel-1 monitoring resolved water hyacinth cover dynamics.

Rapid recolonization doubled reservoir scale cover in only 19–20 days.

Removal efficiency was campaign specific, not proportional to biomass removed.

Higher cover was linked to lower dry season cyanobacterial density downstream.

Long term control requires cover informed harvesting and nutrient load reduction.

Introduction

Recurrent invasions of floating macrophytes remain a major management challenge in eutrophic tropical and subtropical reservoirs, where persistent nutrient enrichment and favorable climatic conditions can sustain rapid re-establishment after control interventions. Among these species, *Eichhornia crassipes* forms extensive floating mats that obstruct water uses, interfere with navigation and infrastructure, restrict light penetration and gas exchange, alter dissolved oxygen dynamics, and modify aquatic habitats (Coetzee & Hill, 2012; Villamagna & Murphy, 2010). The economic burden of invasive aquatic and semi aquatic plants exceeded US$32 billion between 1975 and 2020, with most reported costs associated with freshwater systems (Macêdo et al., 2024). Long term satellite observations further indicate that floating vegetation invasions have intensified in recent decades and that their maximum cover is positively associated with urban expansion in contributing catchments, with small reservoirs being particularly vulnerable because mats can occupy much of the available water surface (Kleinschroth et al., 2021). In these spatially constrained systems, persistent watershed enrichment and the survival of residual mats can favor a rapid return to high cover conditions after control, making recurrent dominance a continuing management problem rather than a sequence of isolated invasion events.

Mechanical harvesting is commonly used to restore open water and reduce standing *Eichhornia crassipes* biomass, and its performance is frequently represented by the mass of vegetation removed. Harvested biomass quantifies operational effort and potential nutrient export, nevertheless it does not directly indicate how much floating cover was reduced, how much macrophyte remained after intervention or how rapidly residual mats recolonized the cleared water surface. Mechanical macrophyte removal can produce substantial short term reductions, yet its

ecological and operational effects vary widely among systems and depend on environmental conditions, removal intensity and the capacity of the remaining macrophyte to regenerate (Schneider et al., 2024; Thiemer et al., 2021). Incomplete removal can also leave fragments and surviving macrophyte mats that support renewed expansion, allowing macrophyte to recover even after intensive campaigns (Chala et al., 2026; Thiébaut, 2023). Therefore, the central management question is not only how much biomass was harvested, but whether the intervention produced a sustained change in the state of macrophyte cover.

Satellite remote sensing can distinguish harvesting effort from its spatial outcome by repeatedly measuring floating vegetation cover. Landsat, Sentinel-2 and other optical sensors have been used to map water hyacinth distribution and temporal changes (Janssens et al., 2022; Pádua et al., 2022), while Sentinel-1 enables monitoring despite persistent cloud cover in tropical regions and can separate infested areas from open water (Felix et al., 2024; Simpson et al., 2022). Multitemporal observations have also quantified water hyacinth expansion (Allín-Cañas et al., 2022) while longer satellite records have reconstructed invasion trajectories across multiple water bodies (Kleinschroth et al., 2021). Yet, integration of frequent satellite observations with successive operational removal campaigns remains limited. In managed reservoirs, such integration is essential to distinguish decline, rebound and near saturation and to evaluate management through growth rates, doubling times, residual cover and net cover change.The state of macrophyte cover is not only an operational outcome but also a component of reservoir ecosystem structure. Harvesting may export part of the nitrogen and phosphorus assimilated into plant tissues, but removing floating mats also changes light availability, oxygen exchange, organic matter accumulation, habitat structure and interactions between macrophytes and phytoplankton. Reviews of mechanical removal have consequently emphasized that reductions in plant abundance do not necessarily translate into uniform ecological improvement (Thiemer et al., 2021). Experimental and field studies further indicate that macrophytes can affect cyanobacterial abundance and community composition through nutrient competition, shading, habitat modification and physiological or allelopathic interactions (Cui et al., 2025; Körner & Nicklisch, 2002; Silva et al., 2025). These effects may be more evident for cyanobacterial groups than for total phytoplankton biomass, as macrophyte treatments have reduced cyanobacterial abundance without producing equivalent responses in chlorophyll-a across species and plant densities (Mowe et al., 2019).

Evaluating harvesting therefore requires considering whether the cover state produced by management is associated with changes in phytoplankton structure, rather than assuming that lower macrophyte cover necessarily represents better ecological conditions. However, long term operational studies that simultaneously link high frequency remote sensing metrics, mechanical removal records, and downstream phytoplankton dynamics remain notably absent in tropical reservoir management. To address this gap, this study proposes an outcome based evaluation framework that integrates a 129 month Sentinel-1 SAR time series, operational harvesting logs, and long term water quality monitoring from the Ibirité Reservoir, a eutrophic tropical system

under recurrent mechanical control, used as a case study. The study's main objective was to evaluate how satellite derived spatial dynamics enrich and complement conventional biomass based metrics for evaluating control efficacy and downstream ecological responses. Specifically, the research: (i) quantified the decoupling between mechanical harvesting effort and spatial cover reduction across continuous operational campaigns; (ii) parameterized macrophyte recolonization kinetics (growth rates and doubling times) as a function of antecedent cover and ongoing removal; and (iii) evaluated the associations between post harvest cover states and downstream cyanobacterial density, dominance, and chlorophyll-a across seasons.

2. Materials and Methods

2.1. Study system and monitoring data

The Ibirité Reservoir (20.0225° S, 44.1130° W), located in the municipality of Ibirité, southeastern Brazil (Figure 1a) served as the study area due previous to cyanobacterial blooms (Mozeto et al., 2014), its persistent macrophyte dominance and a 10 year history of mechanical removal efforts. The reservoir has a maximum depth of approximately 17 m (Mozeto et al., 2014), a current surface area of approximately 178 ha, and is embedded in a watershed of approximately 9,150 ha. The reservoir operates mechanically harvests of macrophyte continuously. Historical land use analysis based on the Landsat archive indicates that urban cover within the watershed increased by approximately 57% between 1991 and 2022, from ~1,930 to ~3,040 ha, while vegetated areas declined ~950 ha and the reservoir surface contracted from ~210 to ~177 ha. These long term changes provide the watershed context for interpreting recurrent macrophyte dominance under increasing urban pressure, a pattern reported for floating vegetation invasions in small urban reservoirs (Kleinschroth et al., 2021).

The regional climate is tropical with marked wet–dry seasonality, lying in the transition between humid subtropical (Cwa) and subtropical highland (Cwb) Köppen types. Approximately 87% of mean annual precipitation (1,424 mm) occurs during the wet season, from October to March, when inflow volumes, nutrient transport, and hydrodynamic conditions are likely strongest. Climate baseline data were gathered from the Ibirité conventional weather station (station code 83632)(National Institute of Meteorology, 2022).

The reservoir has a long history of aquatic macrophyte colonization, predominantly by *Eichhornia crassipes*, which forms dense floating mats capable of covering most of the reservoir surface under favorable conditions of sunlight and nutrient load. Although the satellite derived macrophyte signal is dominated by *Eichhornia* free floating mats, field campaigns revealed that other species occur mainly in nearshore zones, including *Pistia stratiotes*, *Urochloa subquadripara* and *Typha domingensis*. The combination of long term satellite observations, operational harvesting records and water quality monitoring makes the Ibirité Reservoir a suitable empirical system for evaluating recurrent management outcomes in a eutrophic tropical reservoir.

Water quality data was obtained from the monitoring programme of the Minas Gerais Water Management Institute (IGAM) for three stations associated with the reservoir (Figure 1a): BP075 and BP081, located upstream in the main tributary system, and BP085, a reservoir outlet station located a few meters downstream of the dam. The dataset covered the 2015–2025 period, with quarterly sampling from 2015 to 2023 and monthly sampling during 2024 and 2025, and comprised 233 samples distributed among the three stations. It included variables representing phytoplankton response, nutrient availability, organic loading, suspended material and general physicochemical conditions.

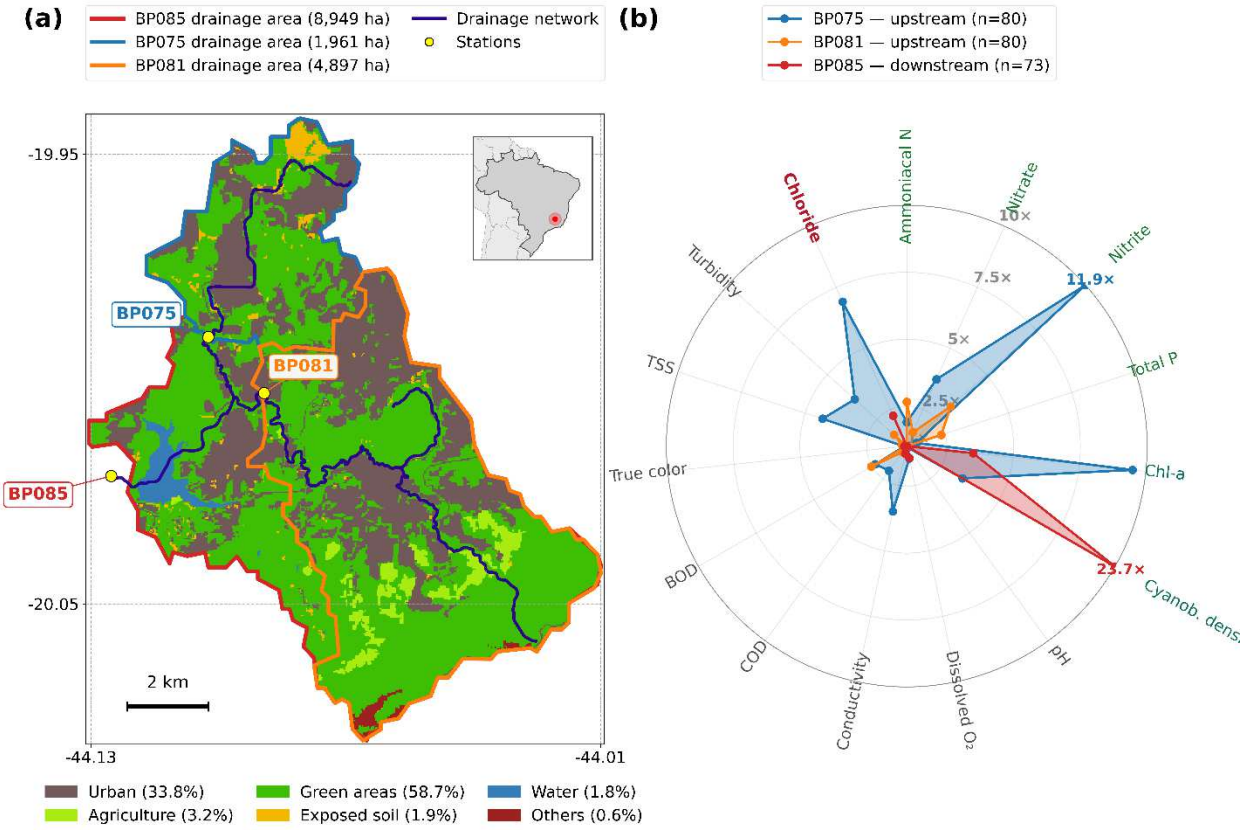

Figure 1. (a) Land use and land cover of the watershed in 2025, with the contributing drainage area of each water quality monitoring station. (b) Relative environmental signatures of the three stations (2015–2025), expressed as normalized median values.

Descriptive statistics revealed that the three stations captured distinct components of the reservoir's water quality gradient. BP081 was characterized by the highest median ammoniacal nitrogen and total phosphorus concentrations, 7.14 and 0.42 mg L^{-1}, respectively, together with the lowest median dissolved oxygen concentration, 4.28 mg L^{-1}, indicating a nutrient enriched and oxygen depleted upstream input. BP075 exhibited the highest median nitrate, nitrite, conductivity, COD, TSS and turbidity, with values of 2.69 mg L^{-1}, 0.33 mg L^{-1}, 1028 µS cm^{-1}, 62.0 mg L^{-1}, 69.0 mg L^{-1} and 33.9 NTU, respectively, suggesting a more mineralized and particle rich inflow. By contrast, BP085 had lower median nutrient concentrations than the upstream stations but showed

the highest median cyanobacterial density, 10,115 cells mL^{-1}. These descriptive patterns indicate that BP075 and BP081 represent contrasting upstream loading conditions, whereas BP085 reflects the integrated biological response downstream in the reservoir.

The biological response variables used in the analysis were cyanobacterial density ($cells.mL^{-1}$) and chlorophyll-a concentration ($\mu g.L^{-1}$). To evaluate whether changes in cyanobacteria reflected a shift in phytoplankton composition rather than only a change in total algal biomass, we calculated a cyanobacteria to chlorophyll-a ratio (RCCa) for each sample as in Equation 1. This ratio was used as a complementary, cell density to chlorophyll-a ratio, used as a proxy of relative cyanobacterial contribution. The rationale follows studies showing that chlorophyll-a alone does not describe phytoplankton composition and that cyanobacteria specific signals need to be interpreted relative to total phytoplankton biomass when assessing cyanobacterial dominance (Izydorczyk et al., 2009; Shi et al., 2015). Because phycocyanin data were unavailable, RCCa was based on cyanobacterial cell density rather than on a cyanobacteria specific pigment. It was therefore not interpreted as a standardized biomass, toxin or risk index, but as an internal proxy describing cyanobacterial cell density relative to chlorophyll-a. Because ratio based indices can be sensitive to low chlorophyll-a values and cell density does not directly represent cyanobacterial biomass, RCCa was retained for ecological interpretation only when its relationship with macrophyte cover was directionally consistent with that of cyanobacterial density.

Equation 1: $$\mathrm{RCCa} = \frac{\text{cyanobacterial density}}{\text{chlorophyll-a}}$$

2.2. Satellite derived macrophyte cover and harvesting performance assessment

Monthly macrophyte cover was derived from Sentinel-1 Synthetic Aperture Radar imagery using a U-Net deep learning segmentation model (Ronneberger et al., 2015). The training dataset comprised 26 dual polarized VV and VH Ground Range Detected (GRD) scenes acquired between 2015 and 2026, with at least one scene representing each year. Reference labels were produced through an iterative confidence guided annotation procedure, in which calibrated model confidence maps were used to prioritize scenes for manual inspection and correction. The final U-Net, implemented with a ResNet-34 encoder (He et al., 2016), was trained for binary segmentation of water and aquatic macrophyte cover. Evaluation against three independent scenes yielded a macro F1 of 94.8%, supporting the use of the resulting classifications as the macrophyte cover input for the subsequent analyses.

The trained model was then applied to the complete Sentinel-1 archive, comprising 517 GRD scenes acquired between May 2015 and January 2026. Total macrophyte area within the reservoir area of interest was calculated for each scene, and the monthly macrophyte cover series was defined by the maximum mapped extent observed within each calendar month, representing the most critical monthly macrophyte occupancy condition. Missing observations between January

and April 2022, when Sentinel-1 imagery was temporarily unavailable, were estimated by linear interpolation between the adjacent observed months.

Monthly harvested biomass (kt month^{-1}) was provided by the reservoir operator for the period from May 2015 to January 2026. This variable represents harvesting effort, expressed as the operator reported mass of macrophyte mechanically removed during each calendar month. Monthly harvesting had a median of 2.6 kt and reached a maximum of 14.6 kt.

Harvesting performance was evaluated at the scale of continuous operational campaigns by comparing recorded harvesting effort with the resulting change in macrophyte cover. Continuous operational campaigns were defined as sequences of consecutive months with recorded mechanical harvesting (>0 t month^{-1}) and were labelled R1–R10 in chronological order. For each period, we calculated initial cover, final cover, net cover change, accumulated biomass removed, mean monthly removal rate and apparent cover reduction efficiency. Apparent cover reduction efficiency (Equation 2) was defined as the difference between initial and final cover divided by accumulated harvested biomass, expressed in kilotons (ha kt^{-1}). Positive values indicate net cover reduction per unit biomass harvested, whereas negative values indicate net cover expansion during the campaign despite ongoing harvesting.

Equation 2: $$\text{Apparent cover reduction efficiency} = \frac{\text{Cover}_{\text{initial}} - \text{Cover}_{\text{final}}}{\text{Biomassa removal}_{\text{accumulated}}}$$

This period based analysis was intended to diagnose contrasts between harvesting effort and observed cover outcomes across campaigns, rather than to infer a mechanistic removal response function or an optimized harvesting threshold. The apparent cover reduction efficiency represents a surface cover outcome and should not be interpreted as mechanical, economic or nutrient removal efficiency.

2.3. Recolonization and macrophyte cover expansion analysis

Because reservoir cover oscillated through repeated cycles rather than following a single invasion trajectory, discrete macrophyte cover expansion episodes were identified and fitted independently. Candidate expansion episodes were defined as intervals beginning at a local minimum in macrophyte cover and holding at least four consecutive monthly observations with an overall net increase in cover. Cover was fitted with the logistic model (Equation 3)(Milićević, 2023), where C(t) is the macrophyte cover, K is the asymptotic maximum cover, r is the intrinsic macrophyte cover growth rate and t_0 is the inflection time. The asymptotic maximum cover K was constrained not to exceed the mapped reservoir surface area used in the analysis, 178 ha. Fitted expansion rates, initially expressed in month^{-1}, were converted to d^{-1} by dividing by 30.44 d month^{-1}. An equivalent macrophyte cover doubling time was calculated from the fitted r parameter using Equation 4. This metric stands for the exponential phase doubling time implied by the fitted logistic

curve and was interpreted as a reservoir scale descriptor of surface cover expansion, not as a physiological biomass doubling rate.

Equation 3: $$C(t) = \frac{K}{[1 + \exp(-r\,(t - t_0))]}$$

Equation 4: $$Td = \frac{\ln(2)}{r}$$

To complement the fitted expansion episodes, we used Spearman rank correlations to examine how monthly cover dynamics were associated with antecedent reservoir cover and contemporaneous harvesting effort. For months of active expansion ($\Delta C_t > 0$), we tested the associations of antecedent cover (C_{t-1}) with both absolute cover change (ΔC_t; Equation 5) and relative macrophyte cover expansion rate (Equation 6). For months with recorded harvesting, we tested the association between contemporaneous cover change and harvested biomass during the same calendar month.

Equation 5: $$\text{Absolute cover change} = C_t - C_{t-1}$$

Equation 6: $$\text{Relative growth rate } (\% \text{ month}^{-1}) \frac{C_t - C_{t-1}}{C_{t-1}} \times 100$$

2.4. Phytoplankton responses and multivariate water quality analysis

We first examined whether the macrophyte cover state was associated with phytoplankton responses at BP085, the reservoir outlet station (Figure 1). Each water quality observation was paired with the corresponding Sentinel-1 derived macrophyte cover. Spearman rank correlations were calculated between macrophyte cover and cyanobacterial density, chlorophyll-a and RCCa, both for the entire BP085 record and separately for the dry season (April–September) and wet season (October–March). Seasonal analyses were used to examine whether cover–phytoplankton associations differed between the dry and wet periods defined in Section 2.1.

To place the BP085 cover–phytoplankton relationships within the broader spatial context of the monitoring network, station specific Spearman rank correlations were then calculated between each biological response variable and the candidate water quality predictors. Spearman correlation was selected because the dataset exhibited non linear relationships, non normal distributions and extreme bloom values. Candidate predictors were selected to represent the main environmental controls and water quality conditions potentially associated with chlorophyll-a and cyanobacterial abundance. Nutrient variables (total phosphorus, ammoniacal nitrogen, nitrate and nitrite) represent resource availability for phytoplankton growth, whereas physicochemical and physicochemical variables (water temperature, pH, dissolved oxygen, turbidity, conductivity, chloride, biochemical oxygen demand, chemical oxygen demand, total suspended solids and true color) capture thermal conditions, light availability, ionic composition and organic matter

dynamics that can regulate phytoplankton biomass and favor or constrain cyanobacterial development. .Analyses were conducted separately for BP075, BP081 and BP085 to preserve the contrast between upstream water quality conditions and the integrated reservoir response observed at the outlet, following the rationale that station specific explainable models can reveal local associations that may be obscured in spatially pooled analyses (Hasani et al., 2024). Macrophyte cover was included as an additional predictor only at BP085 because this station is located immediately downstream of the dam and integrates environmental conditions generated within the reservoir. Cover was not included at BP075 or BP081 because both stations are upstream of the reservoir and are not exposed to its floating macrophyte mats.

To examine whether the pairwise associations were retained within a multivariate and non linear framework, Random Forest regression models were fitted independently for each biological response variable and for each station. Models used 400 trees, a minimum leaf size of two and median imputation of missing predictor values. Random Forests were used to establish relationships and interactions among water quality predictors, while model interpretation with explainable AI focused on ecological attribution rather than operational forecasting. This approach is consistent with water quality and cyanobacterial bloom applications in which explainable machine learning has been used to identify influential predictors while retaining ecological interpretability (Park et al., 2022; Recknagel et al., 2025). Model explanatory capacity was assessed with out-of-bag (OOB) coefficient of determination (R^2), root mean square error (RMSE) and median average error (MAE), together with the station wise Spearman correlations, in the Supplementary Material (Table S1, Figure S1).

Model behaviour was interpreted using SHapley Additive exPlanations (SHAP), a game theoretic framework that assigns each predictor a contribution to individual model estimates and supports global interpretation of complex models (Lundberg & Lee, 2017). Global predictor importance was summarized as the mean absolute SHAP value across observations.

To assess the stability of predictor rankings under sampling variability, the Random Forest model for cyanobacterial density at each station was refitted across 1000 bootstrap resamples. In each iteration, observations were sampled with replacement, the model was refitted using the same settings and predictors were ranked according to their mean absolute SHAP values (Zhang et al., 2026). Ranking stability was summarized as the percentage of resamples in which each predictor remained among the five highest ranked variables. This procedure was used to evaluate the reproducibility of the ecological attribution rather than OOB forecasting performance.

3. Results and Discussion

3.1. Harvesting effort produced contrasting cover outcomes

Across the ten operational harvesting campaigns, the amount of biomass removed and the resulting change in macrophyte cover were not proportional (Figure 2). Accumulated harvested biomass

showed a moderate negative association with net cover change, indicating a tendency toward larger cover reductions during campaigns with greater cumulative removal, although this relationship remained uncertain given the small number of campaigns evaluated ($\rho = -0.600$, $p = 0.067$; Figure 2b). Mean monthly harvesting rate was not significantly associated with apparent cover reduction efficiency ($\rho = 0.417$, $p = 0.265$; Figure 2c). Thus, harvested biomass described the magnitude of operational effort but did not consistently predict the resulting change in surface cover.

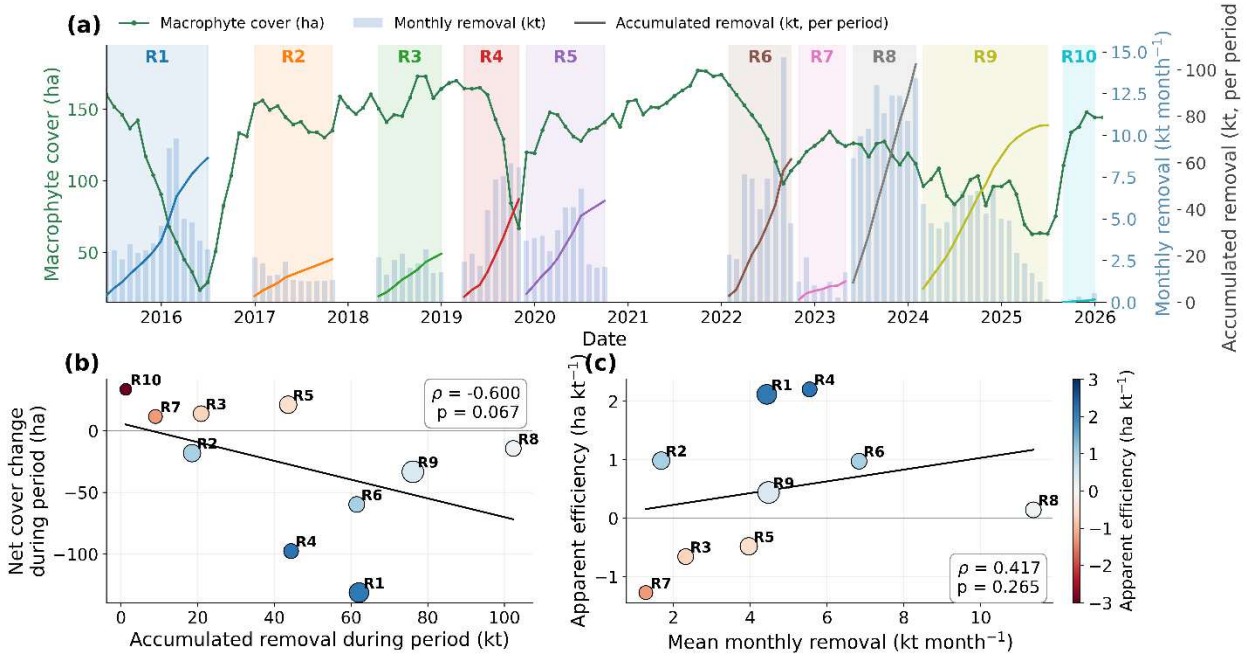

Figure 2. Ten continuous operational harvesting campaigns. (a) Macrophyte cover, monthly harvested biomass and accumulated biomass removed per campaign; (b) net cover change versus accumulated harvested biomass; and (c) apparent cover reduction efficiency versus mean monthly harvesting rate.

Contrasts among campaigns made this mismatch particularly evident. Following a cover reduction of approximately 60 ha (33% of cover) during R6, cover increased again during R7, coinciding with a sharp decline in mean monthly harvesting rate. R7 and R9 both began at cover levels close to 100 ha (56% of cover), but the two campaigns produced different trajectories: cover expanded during R7 under comparatively low harvesting effort, whereas rebound was more limited during R9, when a higher monthly harvesting rate was kept. R8 stood for the clearest mismatch between effort and outcome. More than 100 kt of biomass were removed over nine months, at the highest mean monthly harvesting rate in the record, approximately 12 kt month^{-1}, yet the campaign produced a net cover reduction of only approximately 10 ha (5% of cover).

Comparisons among the remaining campaigns reinforced the same pattern. R2 and R6 had similar apparent cover reduction efficiencies, but R6 produced a substantially larger absolute reduction in cover, coinciding with a higher monthly harvesting rate applied over a shorter operational period. R1 and R4 combined the highest apparent cover reduction efficiencies with the largest net cover reductions, showing that mechanical harvesting can substantially reduce *Eichhornia crassipes*

cover. However, the contrast with R7 and R8 shows that neither accumulated biomass nor monthly harvesting rate alone was sufficient to explain the outcome of individual campaigns.

The campaign level variability observed in Ibirité reservoir is consistent with broader evidence that mechanical removal can generate substantial short term reductions without securing a persistent low cover state. In Lake Tana, Ethiopia, a large scale campaign removed more than 75% of the standing water hyacinth cover, corresponding to approximately 1,271 ha, yet the invaded area exceeded its pre removal extent within the following year as recolonization continued under conditions favorable to invasion (Chala et al., 2026). A similar management limitation has been reported for Lake Rawa Pening, Indonesia, where continued manual and mechanical harvesting remained insufficient to maintain the target reduction in water hyacinth cover because removal did not match rapid plant proliferation under persistent nutrient inputs (Henny et al., 2026). These cases show that large removal operations can substantially alter standing macrophyte without necessarily shifting the system toward sustained control.

The Ibirité reservoir results reinforce that mechanical removal of *Eichhornia crassipes* cannot be evaluated as a fixed conversion between harvested biomass and controlled surface area. Most experimental evidence has been derived from single removal events, individual ecosystem properties and relatively short monitoring periods, while reported responses include increased post-removal growth and, under repeated removal, shifts toward communities dominated by fast-growing, removal-tolerant species; together, these findings indicate that an immediate reduction in standing macrophyte is insufficient to demonstrate persistent control or broader ecosystem recovery (Thiemer et al., 2021). Control management plans targeting *Eichhornia crassipes* have likewise produced temporary or mixed outcomes when interventions were interrupted or implemented without addressing the nutrient and hydrological conditions that sustain proliferation, highlighting the need for continuous monitoring and integrated management rather than isolated removal operations (Djihouessi et al., 2023). The ten campaigns evaluated in the Ibirité case study extended this evidence by showing that contrasting outcomes can occur repeatedly within the same reservoir, as high harvesting effort produced substantial cover reduction in some periods but only limited net change in others.

These findings support a multidimensional assessment of harvesting performance. Harvested biomass quantifies operational effort, whereas net cover change and final cover describe the immediate spatial outcome of the intervention. Apparent cover reduction efficiency provides a standardized retrospective comparison among campaigns, but it does not indicate whether the resulting cover state persists after active harvesting declines or ceases. It should therefore be interpreted together with residual cover and post intervention expansion rather than as an intrinsic property of the harvesting operation. Recurrent macrophyte cover expansion must consequently be considered when determining whether campaign level reductions stand for sustained control or only a temporary displacement of floating cover.

3.2. Rapid recolonization constrained the persistence of cover reduction

The contrasting campaign outcomes occurred within a long term sequence of cover decline, recolonization and renewed high cover dominance. Across the 129 month Sentinel-1 record from May 2015 to January 2026, *Eichhornia crassipes* cover did not follow a single invasion trajectory but repeatedly recovered after periods of reduction (Figure 3a). Five macrophyte cover expansion episodes were identified and well represented by logistic curves, with R^2 values ranging from 0.885 to 0.997 (Figure 3b–f). Fitted macrophyte cover expansion rates ranged from 0.003 to 0.045 d^{-1}, corresponding to equivalent reservoir scale doubling times of 19–224 days. The fastest episodes began after low cover phases, with doubling times of 19 days in October 2019 (G2), 20 days in July 2025 (G5) and 35 days in May 2016 (G1). Expansion was slower when the episodes began from already high cover, with doubling times of 87 days in August 2022 (G4) and 224 days in February 2021 (G3), the latter beginning at 146 ha (82% of cover), close to the available reservoir surface. Episodes G1–G5 are labelled in chronological order of onset.

Because these rates were derived from satellite mapped surface cover, they describe reservoir scale macrophyte cover expansion rather than physiological biomass growth. The fitted trajectories integrate vegetative growth, removal efforts, mat displacement, fragmentation, recolonization and the amount of open water available at the beginning of each episode. This spatial dependence was also evident at the monthly scale (Figure 4). During active expansion, the relative macrophyte cover expansion rate declined with antecedent cover (Spearman $\rho = -0.603$, $p < 0.001$; Figure 4a), while absolute monthly cover gain showed a similar negative relationship ($\rho = -0.424$, $p < 0.001$; Figure 4b). Monthly cover change also declined as harvested biomass increased, although this association was weaker than that observed for antecedent cover ($\rho = -0.333$, $p < 0.001$; Figure 4c). Together, these relationships are consistent with spatial limitation of macrophyte cover expansion: proportional and absolute gains were greatest when extensive open water remained available and progressively declined as floating mats approached reservoir scale saturation, while harvesting imposed an additional but partial constraint on monthly cover gain.

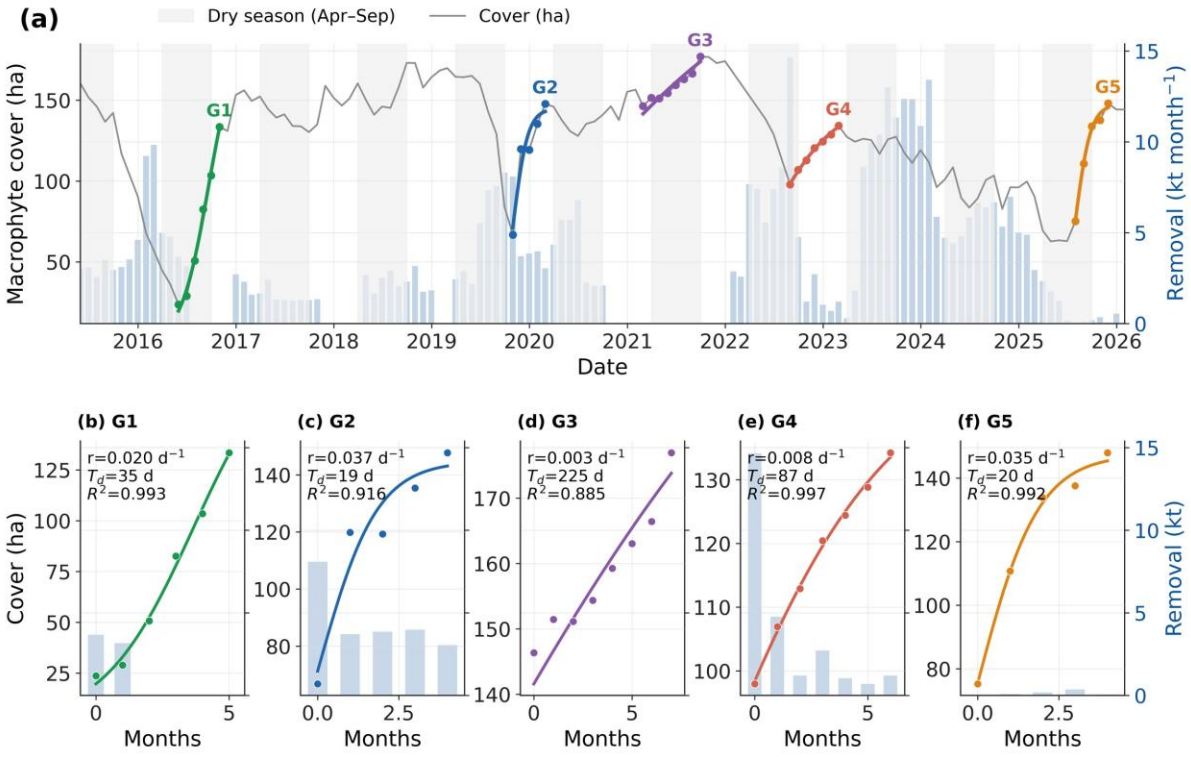

Figure 3. Recurrent macrophyte cover expansion of *Eichhornia crassipes* cover in the Ibirité Reservoir. (a) Complete monthly cover series from May 2015 to January 2026; (b–f) individual logistic fits for episodes G1–G5, annotated with fitted macrophyte cover expansion rate r, equivalent doubling time Td and fit quality R².

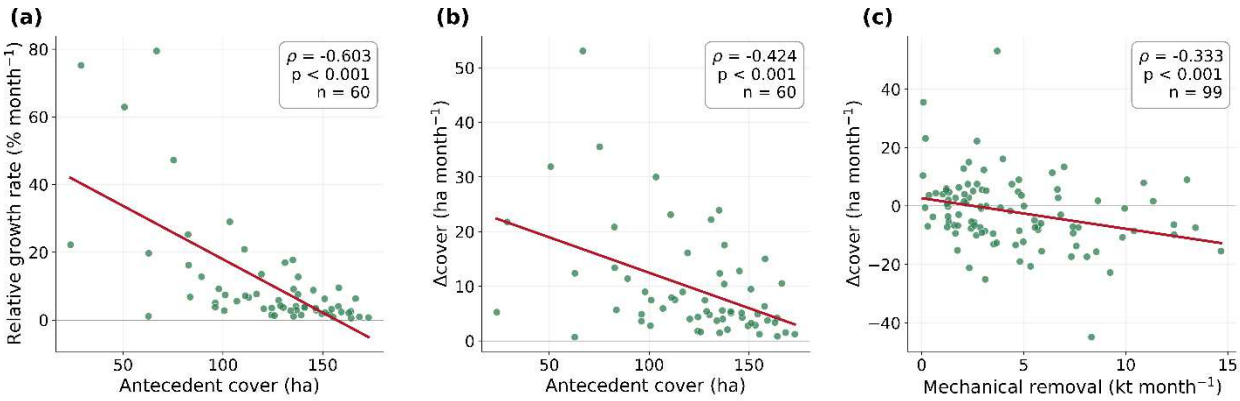

Figure 4. Relationships of antecedent cover and harvesting effort with monthly cover change at the reservoir scale. (a) Relative macrophyte cover expansion rate versus antecedent cover and (b) absolute monthly cover change versus antecedent cover during active expansion; (c) monthly cover change versus harvested biomass during months with active harvesting.

The growth episodes G2 and G5 were among the most rapid satellite observed macrophyte expansion rates reported for other invaded water bodies. In the Hydroituango Reservoir, Sentinel-2 imagery indicated that occupied area could approximately double within one month, compared with only 19–20 days in the Ibirité Reservoir (Allín-Cañas et al., 2022). Comparable rates were

observed in the Lower Mondego channels, where annual expansion trajectories corresponded to approximate doubling times of 34, 28, 23 and 50 days between 2018 and 2021 (Pádua et al., 2022). The distinctive feature of the Ibirité Reservoir was not only the speed of macrophyte expansion, but its repeated recovery after substantial declines in cover. Rapid growth resumed after multiple low cover periods, indicating a strong capacity for recolonization from residual macrophyte. This recurrent recovery is especially relevant in small reservoirs, where relatively modest absolute increases in macrophyte area can rapidly translate into a large proportion of the available water surface (Kleinschroth et al., 2021).

These expansion dynamics explain why substantial campaign level reductions may remain temporary. Harvesting creates open water areas and reduces standing cover, but residual mats can rapidly expand when favorable conditions persist, particularly after interventions leave the reservoir at low or intermediate cover. Consequently, the operational outcome of a campaign cannot be determined solely from the cover reduction achieved while harvesting is active. Residual cover and the rate of subsequent rebound are also required to determine whether the intervention produced a persistent low cover state or merely displaced the infestation temporarily. In nutrient-enriched reservoirs such as Ibirité, the same reduction that represents an immediate operational success may also create the spatial conditions for rapid recolonization.

Recurrent expansion also places mechanical harvesting within a broader nutrient management context. Actively growing *Eichhornia crassipes* mats assimilate nitrogen and phosphorus from the water column, and nutrient enrichment increases both plant productivity and nutrient uptake, allowing the vegetation to function as a temporary nutrient sink in eutrophic waters (Reddy et al., 1989, 1990). In domestic wastewater systems, nutrient removal performance was highest during active plant growth, with an optimum cultivation period of approximately 18 days before harvesting was required to maintain treatment efficiency (Rezania et al., 2015). The retained nutrients are only permanently exported from the aquatic system when plant biomass is physically removed. When vegetation instead senesces and decomposes within the water body, part of the assimilated nutrient stock can return to the water column or sediments, which is why phytoremediation and constructed wetland studies emphasize periodic harvesting to limit nutrient re-release (Kar et al., 2026; Kröger et al., 2007).

In Ibirité, mechanical harvesting can therefore simultaneously reduce surface obstruction and export part of the nitrogen and phosphorus stored in plant tissues, but neither function guarantees durable cover control. Evidence from laboratory, pilot and field scale applications indicates that the capacity of *Eichhornia crassipes* to retain nutrients and recover after removal remains closely linked to nutrient availability and local environmental conditions (Kar et al., 2026). Persistent proliferation under repeated removal has similarly been associated with continuing nitrogen and phosphorus inputs, sedimentation and sediment resuspension in eutrophic Lake Rawa Pening (Henny et al., 2026).

3.3. Managed macrophyte cover was associated with downstream phytoplankton structure

At BP085, the reservoir outlet station, the association between *Eichhornia crassipes* cover and phytoplankton structure differed substantially between seasons. During the dry season, macrophyte cover was strongly and negatively associated with cyanobacterial density ($\rho = -0.735$, $p < 0.001$, $n = 28$), whereas the relationship was weak and non significant during the wet season ($\rho = -0.180$, $p = 0.310$, $n = 34$; Figure 5a). Chlorophyll-a was unrelated to cover in both seasons (dry: $\rho = -0.111$, $p = 0.558$, $n = 30$; wet: $\rho = 0.099$, $p = 0.578$, $n = 34$; Figure 5b). The cyanobacteria-to-chlorophyll-a ratio (RCCa) followed the cyanobacterial response, with a strong dry-season association ($\rho = -0.722$, $p < 0.001$) weakening in the wet season ($\rho = -0.302$, $p = 0.083$; Figure 5c). Higher dry-season cover was thus associated with lower cyanobacterial density and dominance, while total chlorophyll-a remained unchanged — a seasonal shift in the cyanobacterial component rather than a generalized reduction in algal biomass.

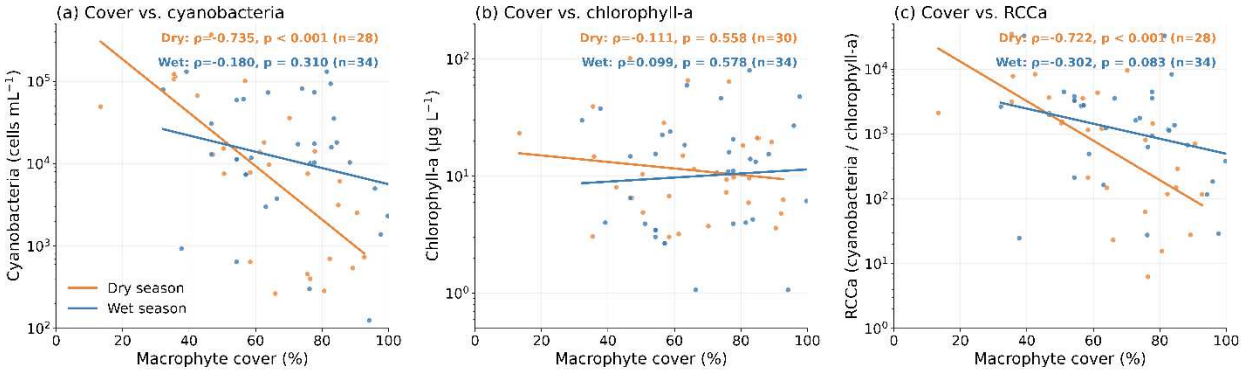

Figure 5. Seasonal relationships between *Eichhornia crassipes* cover and phytoplankton metrics at BP085: (a) cyanobacterial density, (b) chlorophyll-a and (c) the cyanobacteria to chlorophyll-a ratio (RCCa).

Because pairwise correlations may reflect shared variance among environmental predictors, station specific random forest (RF) models interpreted with SHAP values were used to determine whether the spatial pattern persisted under a multivariate and non linear framework (Figure 6). Explainable ensemble models have previously been used to identify environmental associations with chlorophyll-a and other algal response variables, while station specific implementations can reveal local controls that may be obscured when observations from different water bodies or monitoring locations are pooled (Park et al., 2022). This station specific approach was therefore retained to preserve the longitudinal differences among BP075, BP081 and BP085 (Hasani et al., 2024). The RF–SHAP models reproduced the principal pattern identified by the correlation analysis: macrophyte cover ranked among the leading predictors of cyanobacterial density and RCCa at BP085, but not of chlorophyll-a. Thus, the cover association remained detectable after accounting for non linear responses and covariance among predictors.

The stability of the cyanobacterial predictor rankings was subsequently evaluated across 1000 bootstrap resamples of each station record (Figure 7). Rankings at BP075 were moderately stable, with no variable retained among the five leading predictors in more than 62% of the resamples. At BP081, nitrate appeared in 84% of the resamples, followed by ammoniacal nitrogen and total phosphorus, reinforcing the predominance of nutrient related predictors at this station. At BP085, the ranking was more stable and compositionally distinct: true color was ranked among the five leading predictors in 99% of resamples and macrophyte cover in 73%, ahead of nitrite and water temperature. Macrophyte cover was therefore a consistently model ranked predictor of cyanobacterial density at the reservoir outlet station. These results represent model based attribution rather than prediction or causal inference, but such ecological interpretability is important for cyanobacteria bloom applications intended to support environmental monitoring and management rather than operate solely as black box predictive models (Recknagel et al., 2025).

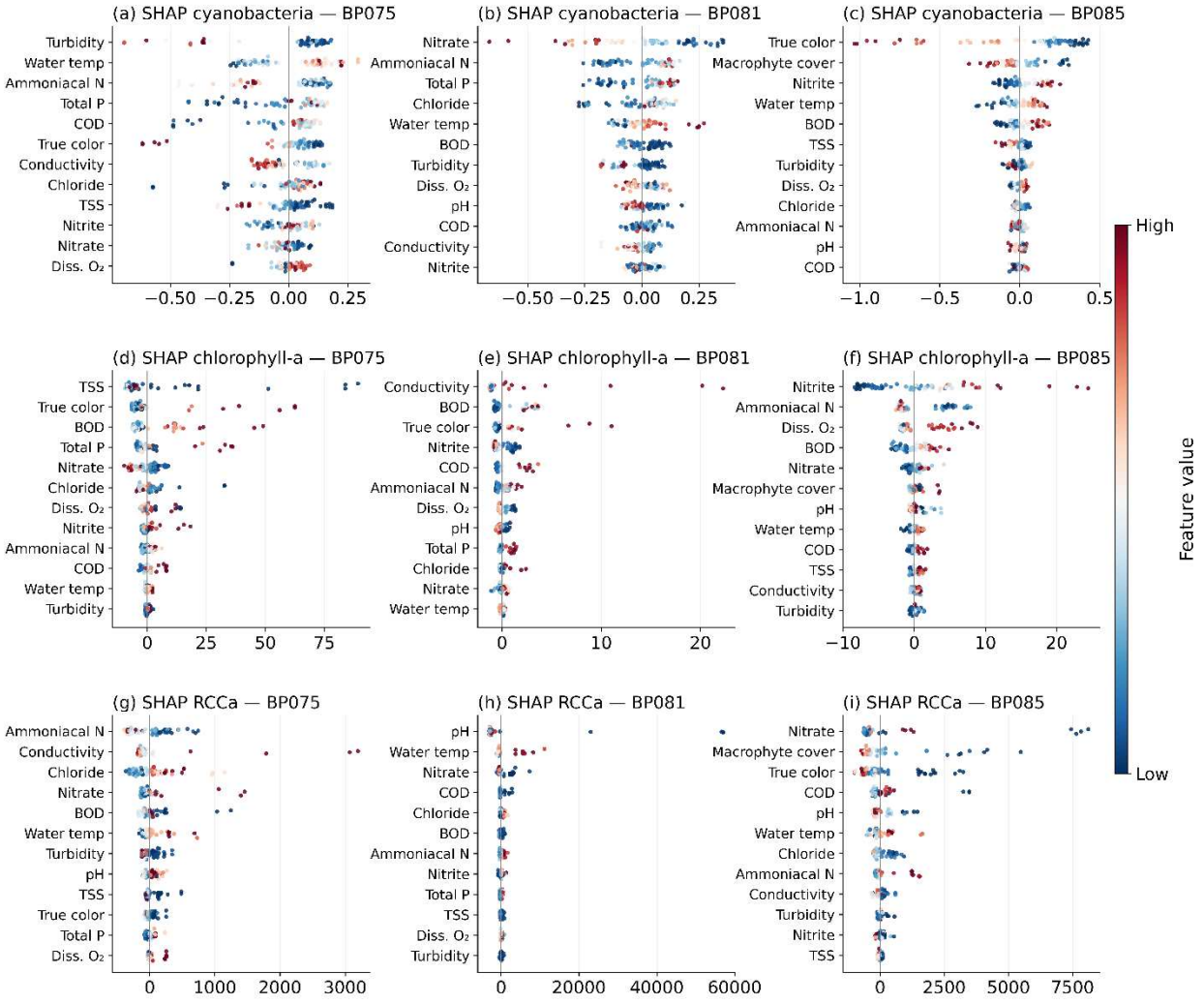

Figure 6. RF–SHAP summaries for station specific models of cyanobacterial density, chlorophyll-a and RCCa.

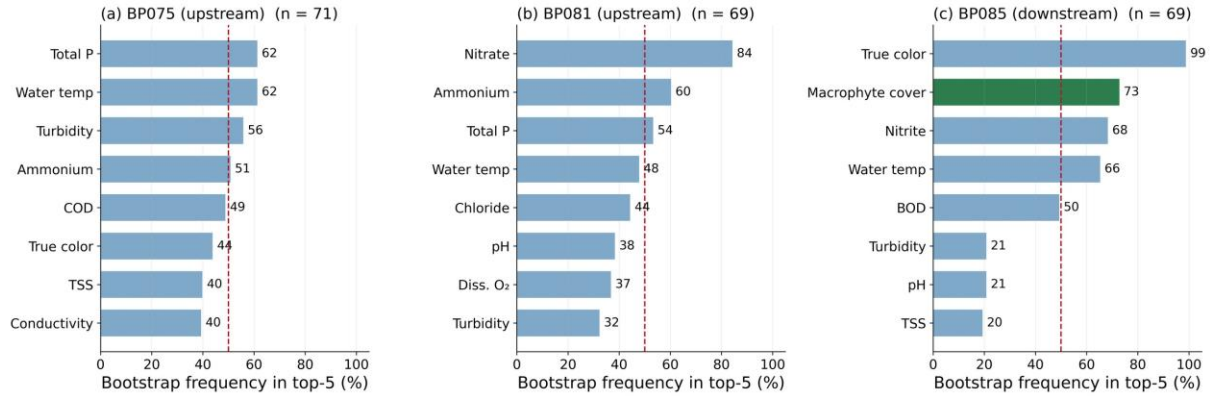

Figure 7. Stability of SHAP predictor rankings for cyanobacterial density across 1000 bootstrap resamples of each station record. The dashed line indicates a 50% retention frequency.

True color and macrophyte cover, however, did not represent independent components of the downstream environment. True color was the most stable predictor in the bootstrap analysis and was strongly associated with both cyanobacterial density ($\rho = -0.55$) and RCCa ($\rho = -0.59$), but it was also positively correlated with macrophyte cover ($\rho = +0.53$, $p < 0.001$) (Fig S1). Expanding *Eichhornia crassipes* mats can increase the accumulation of standing, trapped and decomposing organic material, and senescent tissues release dissolved and particulate carbon and nutrients during decomposition (Gamage & Asaeda, 2005). Nutrients retained in living biomass can similarly return to the water and sediments when plant tissues decay within the aquatic system (Reddy & DeBusk, 1991). True color may therefore represent an overlapping indicator of mat associated organic enrichment rather than a driver that can be separated statistically from macrophyte cover. Neither the correlation analysis nor the SHAP rankings can distinguish the individual mechanistic contribution of these two closely related variables.

The downstream specific association is consistent with evidence that aquatic macrophytes can alter phytoplankton composition without producing a uniform decline in total algal biomass. In eutrophic East Taihu Lake, areas dominated by floating leaved or submerged macrophytes supported lower *Pseudanabaena* densities and lower *2-methylisoborneol* concentrations than phytoplankton dominated areas, while experimental results indicated a stronger contribution from allelopathic processes than from nutrient competition or light limitation (Cui et al., 2025). In a tropical reservoir experiment, high density treatments of emergent macrophytes reduced the relative biovolume of filamentous cyanobacteria, including *Planktolyngbya* and *Pseudanabaena*, or increased the relative abundance of cryptomonads, while chlorophyll-a responses varied among plant species and densities (Mowe et al., 2019). Experimental evidence has also shown that macrophyte effects can be taxon specific, with photosynthetic activity and growth being more strongly inhibited in some cyanobacteria, including *Oscillatoriales* and *Microcystis aeruginosa*, than in other algal groups under conditions designed to minimize nutrient and light limitation (Körner & Nicklisch, 2002). These findings provide a plausible ecological basis for the stronger association of macrophyte cover with cyanobacterial metrics than with bulk chlorophyll-a in Ibirité.

The composition of the floating mats may further contribute to this pattern. *Eichhornia crassipes* was the dominant species, while *Pistia stratiotes* occurred in marginal areas, and experimental studies have reported inhibitory effects of both taxa on cyanobacteria. Aqueous extracts prepared from dried *P. stratiotes* and *Eichhornia crassipes* biomass inhibited the growth and altered the photosynthetic activity of *M. aeruginosa*, with the stronger response occurring under *P. stratiotes* exposure (Silva et al., 2025). Allelochemicals extracted from *P. stratiotes* also reduced *M. aeruginosa* cell density by approximately 50–90% within three to seven days without increasing extracellular microcystin release (Wu et al., 2013). These experimental findings suggest that floating mats should not be interpreted solely as a shading canopy, because canopy formation, organic matter accumulation and species specific biochemical interactions may occur simultaneously. Nevertheless, the observational design used in Ibirité cannot determine which of these mechanisms produced the field association.

The seasonal concentration of the signal provides additional ecological context. During the dry season, the lower discharge in streams, reduced hydrological disturbance and greater persistence of floating mats may strengthen the coupling between reservoir cover and the water discharged through BP085, whereas dilution, inflow pulses and mat redistribution may weaken this relationship during the wet season. In hypertrophic Hartbeespoort Dam, a cyanobacterial bloom developed within one week of the mechanical removal of *Eichhornia crassipes*, illustrating that, when the environmental conditions supporting high primary productivity persist, reducing floating cover may shift dominance from macrophytes to cyanobacteria rather than restore ecological balance (Schneider et al., 2024). The Ibirité results are consistent with this management risk, although they specifically demonstrate a dry season association between higher macrophyte cover and lower cyanobacterial density and dominance at the reservoir outlet. Harvesting should consequently be evaluated through both the reduction in floating cover and the phytoplankton state that develops afterwards, because extensive *Eichhornia crassipes* cover and major cover reductions under sustained eutrophication represent distinct ecological and operational risks.

4. Conclusions

A decade of Eichhornia crassipes management in a eutrophic tropical reservoir was assessed by integrating a 129-month Sentinel-1 cover series with harvesting records and water-quality monitoring. Harvested biomass was not proportional to cover reduction: campaigns with comparable removal produced contrasting cover outcomes, and the highest mean monthly harvesting rate yielded only a limited net reduction. Harvested biomass quantifies operational effort and potential nutrient export rather than the spatial outcome of the intervention.

Cover reductions were transient. After low-cover phases, reservoir-scale cover doubled within 19–20 days, exceeding the rate at which any campaign maintained its reduction. The minimum cover

attained during a campaign is therefore an insufficient indicator of control; persistence is defined by the duration of the reduced-cover state and the expansion rate of residual mats.

The residual cover state was ecologically relevant. During the dry season, higher macrophyte cover was associated with lower cyanobacterial density and dominance, whereas total chlorophyll-a was unrelated to cover. Under persistent nutrient enrichment, large cover reductions may therefore shift the system from macrophyte dominance toward cyanobacterial dominance, indicating that extensive cover and major cover reductions represent distinct ecological and operational risks.

Mechanical harvesting should consequently be managed as a recurrent maintenance and nutrient-export intervention rather than a definitive control measure. An adaptive framework combining satellite-derived cover, operational harvesting records and in situ phytoplankton monitoring resolves the spatial, operational and ecological dimensions that biomass metrics alone cannot. This approach is applicable to other small eutrophic tropical reservoirs subject to recurrent macrophyte proliferation; however, durable control additionally requires reducing the nutrient and suspended-solid loads that sustain high primary productivity.

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