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RESEARCH ARTICLE

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Protected land enhances the survival of native aquatic macrophytes and limits invasive species spread in the Panama Canal

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Abstract

1. This study examined whether protected land in a tropical reservoir's catchment can promote the survival of native aquatic plants (macrophytes) and limit the spread of invasive alien plant species (macrophyte IAS), which can threaten native wildlife and require expensive remediation. As the number of tropical river dams is expected to increase in the coming decades to meet societal demands, it is crucial to explore solutions for preserving aquatic biodiversity.
2. The study used a before–after–control–intervention design, based on monitoring data and long-term sedimentological, climatic and ecological records from both lake and river zones adjacent to protected and unprotected lands around the 100-year-old Gatun Lake in the Panama Canal, Panama. The research examined the impact of impoundment and the invasion of *Pontederia crassipes* (water hyacinth) and *Hydrilla verticillata* (water thyme) on native macrophyte communities and environmental variables.
3. Lake zones adjacent to protected lands had lower nutrient concentrations, greater variations in water depth profiles and reduced fluctuations in water chemistry than lake zones outside areas of land protection. In addition, the results showed that whereas zones adjacent to unprotected land became dominated by macrophyte IAS, lake zones adjacent to protected areas were more resilient to the spread of macrophyte IAS and were able to maintain viable populations of native pre-dam species for >100 years.
4. This study indicates that protecting land adjacent to tropical reservoirs could be a cost-effective solution for preserving aquatic macrophyte biodiversity by retaining nutrients, stabilizing water chemistry, providing habitat heterogeneity and protecting native vegetation, while still supporting terrestrial conservation goals. These findings could aid in planning measures for the hundreds of proposed dam projects across lowland tropical areas and provide new insights into best practices for enhancing river ecosystem resilience.

KEYWORDS
invasive aquatic species, palaeolimnology, Panama Canal, protected areas, reservoirs, tropical rivers

1 | INTRODUCTION

The construction of tropical dams is expected to increase in the coming years to address water and hydropower needs (Zarfl et al., 2015), but dams provide an opportunity for the spread of aquatic invasive alien species (IAS; Johnson et al., 2008), particularly aquatic plants (macrophyte IAS; Thomaz et al., 2015). Macrophyte IAS, defined here as non-indigenous species that cause economic and/or ecological harm to the aquatic system (IUCN, 2000), can have a range of adverse effects, including the loss of native species, the homogenization of macrophyte communities and shifts in limnological conditions (Boylen et al., 1999; Scheffer et al., 2003; Muthukrishnan & Larkin, 2020).

Protecting land can help to maintain ecosystem structure and functioning by limiting the spread of invasive plants (Foxcroft et al., 2011). Although this idea has received limited empirical support for freshwater ecosystems, protecting riparian land may benefit native aquatic sessile plants by reducing nutrient loads, stabilizing water conditions and promoting habitat variation (heterogeneity) (Naiman et al., 2010). In addition, preserving a dense native macrophyte cover may limit the spread of invasive species through resource competition (Capers et al., 2007; Salgado et al., 2022). Although there are mixed effects on motile organisms such as fish (Marchetti et al., 2004), this approach may offer a cost-effective solution for enhancing river macrophyte resilience.

To estimate the benefits of land protection on preserving native macrophytes while shielding reservoir areas from macrophyte IAS, it is necessary to have an understanding of the ecological conditions before damming occurred, and before land was protected and species invaded. A before–after–control–intervention (BACI) framework is therefore desirable (Wauchope et al., 2022). In this approach, populations of aquatic macrophytes (native and IAS) occurring in the lake adjacent to protected and unprotected land (CI) and before and after (BA) dam/protection/invasion are independently and simultaneously (BACI) compared to assess causality. This then offers an opportunity to discern whether the spatial structure of native vs. macrophyte IAS is a result of land protection or parallel changes in environmental factors (e.g. dam implementation or water quality change), or because the location of protected land coincides with lake sectors where native species were already overperforming (Wauchope et al., 2022). Ecological time-series data are needed for BACI impact evaluations (Wauchope et al., 2021), but such long-term records are rare in the tropics where pre-dam and early invasion phases can take decades to manifest fully (Salgado et al., 2019). Contemporary surveys, historical records and palaeolimnology offer a solution by providing reliable spatial–temporal assessments of native and invasive macrophyte dynamics, including records of potentially confounding factors spanning decades to centuries (Salgado et al., 2020).

This study uses a BACI approach to explore whether land protection limits the spread of macrophyte IAS and benefits native species and pre-dam communities in the artificial Gatun Lake, Panama Canal (Figure 1). Long-term climatic, environmental and palaeolimnological data are used to characterize biotic and abiotic conditions before and after dam implementation. Spatial surveys of contemporary macrophyte species and water chemistry are conducted in lake zones adjacent to protected and unprotected land. The following four hypothesises were constructed and tested:

1. Native macrophyte cover in lake zones adjacent to protected land is significantly higher than in lake zones adjacent to unprotected land.
2. Macrophyte IAS cover in lake zones adjacent to unprotected land is significantly higher than in lake zones adjacent to protected land.
3. Macrophyte composition was less spatially variable in pre-dam times.
4. Since dam implementation, rates of macrophyte community change in lake zones adjacent to protected land have been substantially lower than in those lake zones adjacent to unprotected land.

In addition, this study explored how land protection can safeguard native macrophytes, including mechanisms that potentially promote more stable physical and chemical conditions, increased nutrient retention and greater habitat heterogeneity.

2 | MATERIALS AND METHODS

2.1 | Study system

Gatun Lake is the main lake of the Panama Canal, Panama (9°11′N, 79°53′W) (Figure 1). It is one of the largest man-made lakes in the world with a surface area of 425 km^2 and a maximum water depth of 30 m, and is bound by extensive shallow lake waters (<8 m). The lake facilitates global interoceanic shipping while also acting as a freshwater reservoir supplying water and hydropower to Panama City and surrounding towns (Condit et al., 2001). The water quality and nutrient concentrations (nitrates ($N\text{-}NO_3$), nitrites ($N\text{-}NO_2$) and phosphates ($P\text{-}PO_4$) all <0.1 mg L^{-1}) in the lake are considered excellent to good according to the quality standards of the United States Environmental Protection Agency (EPA, 1986). Water retention times in the lake are relatively short, as approximately 90%

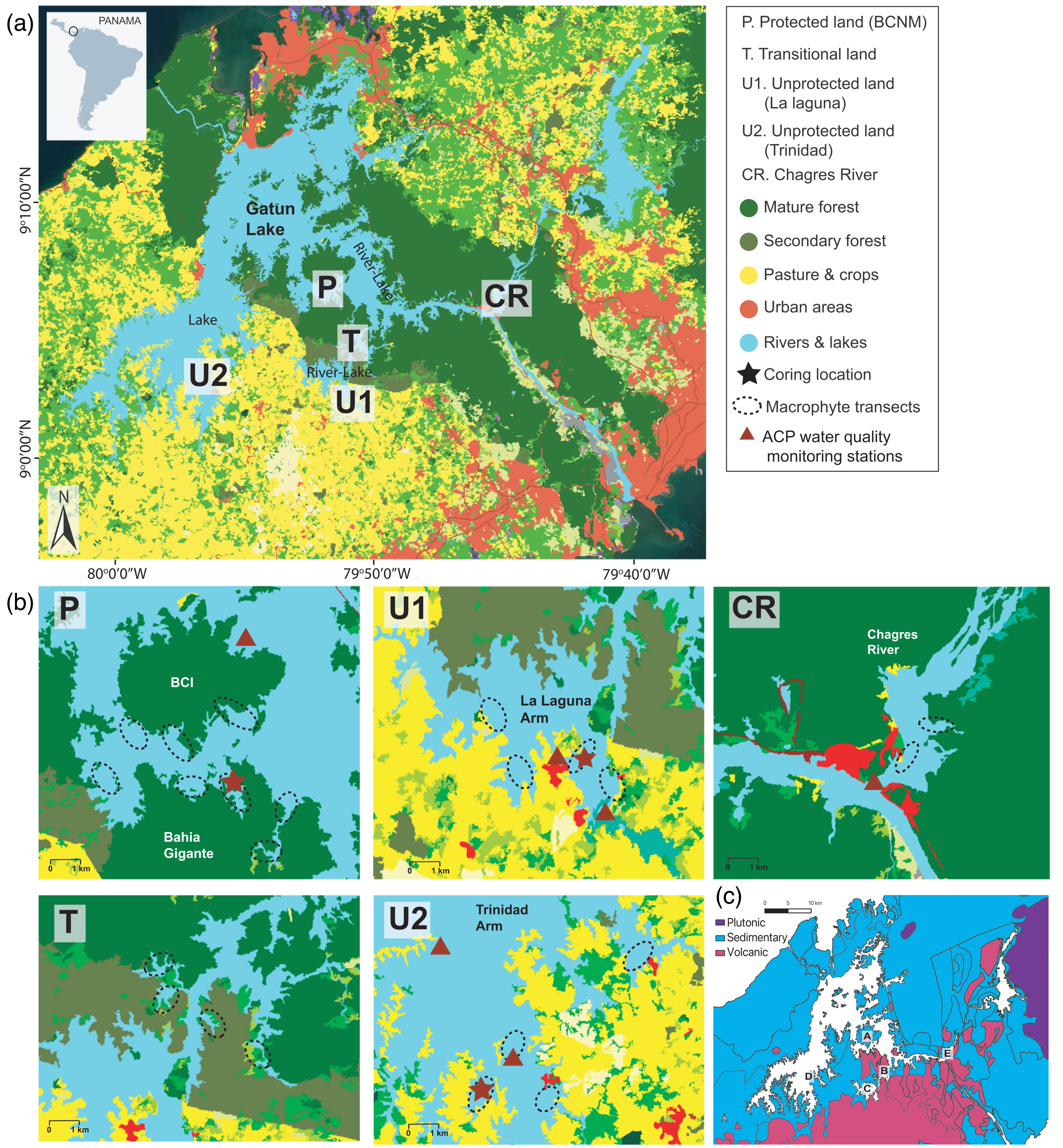

FIGURE 1 (a) Map of Gatun Lake (Panama Canal) showing the different land-use types, the Panama canal zone and the locations of the lake and river zones sampled for this study. The reservoir river–lake hydrology gradient is also indicated. (b) Details of the sampling lake and river zones including sediment coring locations, transects surveyed for macrophytes and water chemistry sampling stations. (c) Geology of Gatun Lake.

of the total daily freshwater runoff (approximately 1.06 $\times$ 10^7 m^3) is discharged through the locks in the operation of the Panama Canal and for hydropower production (Salgado et al., 2020).

Gatun Lake has experienced recurring aquatic invasions over a century, as documented by Salgado et al. (2020) and Castellanos-Galindo et al. (2020). The present study focused on the Asian water thyme (*Hydrilla verticillata*) and the South American water hyacinth (*Pontederia crassipes*), which invaded shortly after infilling. The northern half of the lake has forested areas exceeding 1500 ha, protected by the Barro Colorado Nature Monument created between 1920 and 1950 after the completion of the Panama Canal in 1913 (Figure 1a; Condit et al., 2001). Unprotected land has been deforested for fruit plantations, grasslands and urban and canal-related infrastructure (Condit et al., 2001).

2.2 | Contemporary control–intervention estimates

2.2.1 | Land-use types

Three land-use type areas on the central and western sides of Gatun Lake were chosen to study the effects of land protection schemes (i.e. protected, transitional and unprotected) on aquatic vegetation, while avoiding extrinsic influences from the daily operations of the canal zone (e.g. shipping, dredging and mechanical controls of macrophyte cover). To account for potential co-influences with the reservoir river–lake hydrological gradient (Figure 1a), the mouth of the Chagres River was also included. All areas share a similar catchment geology (volcanic – mostly andesites and sedimentary rocks; Figure 1c), making them comparable. Soil characteristics vary depending on land use; protected lands are richer in organic matter, calcium and nitrogen, whereas unprotected lands have lower nitrogen but higher bulk densities and silt content (Appendix S1).

2.2.2 | Macrophyte surveys

Aquatic macrophyte cover (submerged and floating charophytes and angiosperms) of invasive (*H. verticillata* and *P. crassipes*) and native species was surveyed from a boat using the UK Standard Joint Nature Conservation Committee protocols for site monitoring (JNCC, 2009) across lake and river zones adjacent to the selected land-use areas. Specifically, two unprotected lake zones (La Laguna and Trinidad arms), two protected zones (BCI and Bahia Gigante) and two transitional zones in the south west of Bahia Gigante were sampled (Figure 1a,b). The JNCC methodology characterizes macrophyte communities within each of the selected lake/river zones, based on 100 m transects in both littoral and open waters (Gunn et al., 2010). Along each 100 m transect, the macrophyte cover (%) of each species occurring within 1 m^2 was surveyed using a grapnel, at depths of 25, 50, 75 and >75 cm. Sampling occurred every 20 m along each transect to avoid pseudo-replications. Cover of emergent sedges (graminoids) was also recorded. Macrophytes in deeper water (>100 cm) were surveyed starting at the midpoint of each transect towards the centre of the lake or river basin until a maximum of 10 sampling points had been sampled. The water depth at each sampling point was also recorded.

The area of the selected lake zones sampled was relatively similar, with unprotected zones at ~820 ha, protected zones at ~857 ha, and transitional zones at ~767 ha (Table 1). The mean water depths sampled were also similar, with protected zones at 1.42 ± 1.25 m, unprotected zones at 1.29 ± 0.93 m and transitional zones at 1.63 ± 0.95 m. The area of the Chagres River sampling zone was ~117 ha and had a mean water depth of 0.94 ± 0.76 m. The macrophyte surveys were conducted in March–April 2013 in the Chagres River and in the protected, unprotected (La Laguna) and transitional lake zones (Figure 1b). The survey of the other unprotected lake zone (Trinidad) was conducted during the

TABLE 1 Average and standard deviation of selected physical and chemical parameters monitored in the studied lake and river zones during the dry (January–April 2013) and wet (May–July 2019) seasons by the Autoridad del Canal de Panamá (ACP) water quality monitoring division (Paton & Panama Canal Authority, 2020a).

		Area (ha)	TA (mg L-1)	Chl-a (mg L-1)	Conductivity (µS cm-1)	DO (mg L-1)	N-NO2 (mg L-1)	N-NO3 (mg L-1)	P-PO4 (mg L-1)	pH	Depth (cm)	Secchi (cm)
Chagres River	Average	117	47.8	2.7	107.0	7.0	0.002	0.046	0.010	7.2	139	130
	Standard deviation		4.6	0.9	15.7	0.4	0.001	0.004	0.000	0.1	106	0
Protected	Average	857	38.0	3.9	91.5	7.9	0.001	0.037	0.010	7.5	157	91
	Standard deviation		2.6	2.0	9.0	0.1	0.001	0.001	0.000	0.1	142	0
Unprotected	Average	767	21.3	2.9	165.1	6.7	0.003	0.051	0.012	6.9	152	197
	Standard deviation		4.7	1.3	135.9	0.4	0.001	0.009	0.003	0.3	113	58
Transitional [a]												

Abbreviations: Chl-a, chlorophyll-a; DO, dissolved oxygen; N-NO_2, nitrites; N-NO_3, nitrates; P-PO_4, phosphates; TA, total alkalinity.

[a]Values for the transitional lake zone were derived by averaging the values for Chagres River and the protected lake zones (for details see the Methods section).

sedimentary coring campaign in July 2019 (see Section 2.2.4). To ensure independence in the data, the transects were set apart in the field by a distance of > 2 km, and four transects per lake zone were surveyed, and two for the Chagres River. The JNCC macrophyte sampling approach may not identify all species present. However, previous studies have shown its suitability to provide reliable relative data on the spatial variation and abundances of the most characteristic macrophyte species (Salgado et al., 2018a; Salgado et al., 2019).

2.2.3 | Contemporary water quality sampling

Data on phytoplankton biomass (chlorophyll-a, mg L^{-1}), dissolved oxygen (DO mg L^{-1}), conductivity (μsm), pH, P-PO_4 (mg L^{-1}), N-NO_3 (mg L^{-1}), N-NO_2 (mg L^{-1}), total alkalinity (TA mg L^{-1}) and Secchi depth (cm) from the surveyed lake or river basin were obtained from the monthly monitoring programme of the Autoridad del Canal de Panama (Paton & Panama Canal Authority, 2020a). The locations of the sampling stations are indicated in Figure 1b and details of analytical methods are presented in Appendix S2. Variables other than DO are typically considered as the main structural drivers of macrophyte communities in tropical rivers and reservoirs (Sousa et al., 2009; Mormul et al., 2010; Salgado et al., 2020). Dissolved oxygen was measured in mg L^{-1} to compare it with available historical records and better characterize water quality conditions in the lake and river zones. Prior to analysis, the data for DO in mg L^{-1} were compared against percentage DO to check for potential variation resulting from differences in temperature across the sampling sites. The patterns did not differ, supporting the use of mg L^{-1}. As submerged species such as *H. verticillata* can improve water transparency by competing with phytoplankton, Secchi depth data were also used to explore potential effects of IAS on lake limnology. The summer average (January–April 2013) and early rainy season average (May–July 2019; for Trinidad Arm) of each parameter from the Autoridad del Canal de Panamá (ACP) monitoring data were used to compare against the macrophyte surveyed data.

2.3 | Before–after and before–after–control–intervention estimates

2.3.1 | Palaeolimnological data

Plant macrofossils were used to determine macrophyte cover before and after dam construction. The information was derived from three, short (<1 m), littoral sediment cores collected in the two unprotected lake zones (La Laguna arm – 9°2′49.58″N, 79°50′6.33″W, core code LGAT1; Trinidad arm – 9°2′0.38″N, 79°57′44.45″W, LGAT2) and in the protected lake zone of BCI (9° 7′8.09″ N, 79°50′2.41″W; BCI1; Figure 1b). The LGAT1 core was collected in 2013 using a Livingstone piston sampler and the BCI1 and LGAT2 cores using a large-bore corer in 2019. Sheltered basins with higher macrofossil accumulation that were previously ancient river or swamp areas were selected for coring. All three cores were dated using radionuclide measurements of ^{210}Pb, ^{137}Cs, and ^{241}Am under the CRC model (Appleby, 2001). Ages below the top dated sediment samples were fitted in the 'scam' package (Pya, 2022) using a monotonic decreasing shape-constrained generalized additive model (GAM; Simpson, 2018).

The number of sediment samples analysed for plant macrofossils differed among the cores: 23 samples were analysed from LGAT1, 15 from LGAT2 and 12 from BCI1. This difference in the number of sediment samples analysed per core was dictated by varying sedimentation rates over similar temporal time periods (Appendix S3). For LGAT1, between 2 and 4 g of dried sediment per sample were used, while 20 mL of wet sediment was used for LGAT2 and BCI1. Plant macrofossils were retrieved from the residues of sieved core material following standard methods (Birks, 2001) and its relative abundances were standardized as the number of fossils per 100 cm^3. Owing to poor fossil preservation of *H. verticillata*, a semiquantitative abundance scale was created, where 0 represents its absence and 3 represents high abundance. The abundance scale was implemented according to its well-documented history in the lake (Salgado et al., 2020) and to the current distribution patterns depicted by the contemporary surveys.

2.3.2 | Historical environmental data

Annual means of the selected contemporary physical and chemical parameters were calculated for the period 2003–2019. The data were obtained from the monthly monitoring programme of the ACP (Paton & Panama Canal Authority, 2020a). Available historical records of DO, Secchi and nutrients for 1970, 1972 and 1995 were retrieved from Salgado et al. (2020). In addition, precipitation records (5 year average) from BCI from 1930 to 2019 were obtained from STRI's Physical Monitoring Program (Paton & Panama Canal Authority, 2020b).

2.4 | Data analysis

2.4.1 | Testing CI estimates

The Tukey honest test was used to determine whether there were significant pairwise variations between the contemporary cover of native and macrophyte IAS in the different study lake or river zones. A p-value of <0.05 was used to indicate that the differences observed between the groups were probably not due to chance.

2.4.2 | Potential mechanisms

Habitat heterogeneity for macrophytes was determined following Salgado et al. (2018b) as the variations in water depth derived from the survey points in each lake or river zone. To estimate whether there are consistent differences in habitat heterogeneity between the zones, homogeneity analysis of multivariate dispersions (HMD; Anderson et al., 2006) was used. The HMD was run in the 'vegan' package (Oksanen et al., 2022) using Euclidean dissimilarities. Owing to unequal numbers of water depth samples among the groups, a correction of square-root ($n/(n-1)$) was applied in the HMD. *Post hoc* comparisons between the lake and river zones were again assessed using the Tukey honest test.

To assess macrophyte compositional gradients associated with the lake and river zones, multiple factor analysis (MFA; 'FactoMiner' R package; Le et al., 2008) was used. By clustering the different macrophyte growing forms (native floating, native submerged, floating IAS and submerged IAS) together with categorical variables (land-use type), the MFA identifies the groups that explain the most variation in the data. The macrophyte cover data were scale-transformed in the MFA to reduce skewness and rescale the data into comparable units (Le et al., 2008). In addition, a second MFA was performed by including the scale-transformed physical and chemical variables as an additional group to characterize the limnological conditions of the lake and river zones and explore drivers of macrophyte community change.

2.4.3 | Testing BA and BACI estimations

To detect macrophyte community temporal rates resulting from dam/land protection implementation, GAM models were used with the 'mgcv' package in R (Wood, 2017). Plant macrofossil variation gradients were derived from a principal curve (PrC) using the 'analogue' package in R (Simpson, 2007). The resulting PrC scores were fitted in independent GAMs against time using smooth functions based on Simpson (2018). To avoid overfitting trends, the residual maximum likelihood method was used, and a Gaussian distribution with an identity link was used to model the time-series data. A base function (k) of 15 and 10 was used for LGAT1 core data and LGAT2 and BCI1 cores, respectively, to achieve the best model fit. The 'gratia' package in R (Simpson, 2022) was used to determine significant compositional thresholds in the time-series data by identifying the first derivative function of each GAM, with trends deviating from 0 indicating significant periods of change (Simpson, 2018).

2.4.4 | Potential mechanisms (BACI estimates)

To assess macrophyte response to dam and land protection implementation over space and time, a third MFA was applied. The plant macrofossil data from all three cores were grouped into macrophyte growth type (native floating, native submerged, floating IAS and submerged IAS) together with precipitation records and annual physical and chemical data. Two categorical variables were included: before and after dam implementation, and lake zone (core code). All quantitative group variables were scale-transformed in the MFA for analysis.

To test whether protected lake zones have greater temporal stability in physical and chemical conditions than unprotected lake or river zones, a second HMD analysis was applied to the selected monthly ACP data (2003–2019). To standardize the data into comparable units and to allow comparison with the MFA results, the chi-square distances were used in the HMD.

3 | RESULTS

3.1 | CI estimates

3.1.1 | Macrophyte cover at protected and unprotected lake and river zones

Twenty-two macrophyte taxa were recorded during the modern surveys (Table 2). Native floating species included *Ludwigia sedoides*, *Nymphaea ampla*, *Pistia stratiotes*, *Pontederia azurea* and *Salvinia auriculata*; native submerged species included *Ceratophyllum demersum*, *Vallisneria americana*, *Najas arguta*, *Chara* cf. *kenoyeri* and *Cabomba furcata*. The two invasive species studied, *H. verticillata*, and *P. crassipes*, were also commonly recorded.

Cover of *H. verticillata* (44.3 ± 38.8%) was significantly ($p < 0.05$) and substantially higher in the unprotected lake zones and in the Chagres River (36.9 ± 30.5%) than in the protected (2.5 ± 14.39%) and transitional lake zones (32.6 ± 32.5%; Figure 2a, Appendix S4). Floating cover of *P. crassippes* was also significantly higher in the Chagres River (6.7 ± 12.9%) than in the protected lake zones (0.7 ± 4.8%). In turn, native cover of *C. demersum* (41.8 ± 38.3%), *Utricularia* cf. *foliosa* (7.5 ± 12.2%) and *Hydrocotyle umbellata* (4.4% ± 12.9%), was significantly higher in the protected lake zones than in the unprotected zones (*C. demersum*, 0.8% ± 6.0%; *H. umbellata*, 0.3% ± 2.5%: *Utricularia foliosa*, not recorded) and in the Chagres River (*C. demersum*, not recorded; *H. umbellata*, 3.5 ± 9.4%; *U. foliosa*, not recorded) (Figure 2b). Native cover of *C. furcata* (41.8 ± 38.3%) was significantly higher in the transitional lake zones (18.2 ± 21.0%) than across the other lake and river zones, whereas those of *N. arguta* (10.6 ± 11.5%) and *Nitella* sp. (4.0 ± 10.0%) were only recorded in the Chagres River. Native cover of *P. azurea* (0.7 ± 4.8%) was significantly ($p < 0.05$) and substantially lower in the protected and transitional lake zones (0.2 ± 1.4%) than in the unprotected lake (11.7 ± 21.3%) and river zones (9.2 ± 14.9%).

3.1.2 | Mechanisms of change

Mean values of the water chemistry and physical parameters are presented in Table 1. The HMD analysis detected a significant ($p = 0.007$) variation in habitat heterogeneity between the lake and river zones. Protected lake zones had the greatest complexity (mean

TABLE 2 Macrophyte taxa recorded during the monitoring surveys of 2013 and 2019 in selected lake zones adjacent to protected (P), transitional (T) and unprotected (UP) land and in the Chagres River (CR) mouth. The native or introduced status of each species was determined through the Kew Botanical Gardens Plants of the World Online platform (https://powo.science.kew.org/).

Taxa	Growth type	Native	Introduced	Basin
Graminoids	Emergent			P, T, UP, CR
Polygonum spp.	Emergent			P, UP
Montrichardia arborescens	Emergent	Yes		UP
Azolla filiculoides	Free-floating	Yes		P
Hydrocotyle umbellata	Rooted/floating	Yes		P, T, UP, CR
Lemna minor	Free-floating			T
Ludwigia sedoides	Rooted-floating	Yes		UP
Ludwigia helminthorrhiza	Rooted-floating	Yes		P, UP
Marsilea polycarpa	Submerged/floating	Yes		T, UP
Nymphaea ampla	Rooted-floating	Yes		P, T, UP, CR
Pistia stratiotes	Free-floating	Yes		P, T, UP, CR
Pontederia azurea	Rooted-floating	Yes		P, T, UP, CR
Pontederia crassipes	Free-floating		Yes	P, T, UP, CR
Salvinia auriculata	Free-floating	Yes		P, T, UP, CR
Cabomba furcata	Submerged/floating	Yes		TA
Chara cf. *kenoyeri*	Submerged	Yes		P, T, UP, CR
Ceratophyllum demersum	Submerged	Yes		P, T, UP
Hydrilla verticillata	Submerged		Yes	P, T, UP, CR
Najas arguta	Submerged	Yes		T, CR
Nitella sp.	Submerged			CR
Utricularia cf. *foliosa*	Submerged	Yes		P, T
Vallisneria americana	Submerged	Yes		P, T

distance to median (mdm) = 88.6) followed by transitional zones (mdm = 74.6), unprotected zones (mdm = 62.7) and the Chagres River (mdm = 46.9) (Figure 2c).

The MFA explained 19% of the total macrophyte variation and clearly separated the data by lake and river zones (Figure 3a). Dimension 1 contributed to 11% of the explained variation and dimension 2–9%. Submerged cover of native species and *H. verticillata* contributed the most to dimensions 1 and 2, while graminoid cover also significantly contributed to dimension 2 (Appendix S5). Sampling points in protected lake zones clustered in the top-left-hand side of the plot and were associated with *C. demersum*, *U. foliosa*, *H. umbellata* and *V. americana* cover. Sampling points in unprotected lake and river zones clustered on the right-hand side of the plot. These zones were associated with plant cover of *H. verticillata*, *N. arguta*, *P. stratiotes*, *P. azurea*, *P. crassipes* and graminoids. Macrophyte cover of *C.* cf. *kenoyeri* and *L. sedoides* was further related to the unprotected lake zone in the Trinidad arm. Sampling points in transitional lake zones distinctively clustered on the lower left side of the plot and related to cover of *C. furcata* and *U.* cf. *foliosa*.

When contemporary physical and chemical parameters were included in the MFA, the analysis explained 24% of the total variation in both biotic and abiotic factors (Figure 3b). Lake and river zones, and native and invasive submerged macrophyte cover, contributed the most to dimension 1, whereas lake and river zones alone contributed to dimension 2 (Appendix S5). Protected lake zones were positively associated with TA, DO, pH and phytoplankton biomass, and unprotected lake zones with nutrient content ($N\text{-}NO_3$ and $P\text{-}PO_4$), conductivity and Secchi depth. Transitional lake zones and the Chagres River were positively related to $N\text{-}NO_2$.

3.2 | BA and BACI estimates

Age models of the three cores are presented in Appendix S3. Fifteen macrophyte taxa were recorded by plant macrofossil analysis including *P. azurea* (seeds), *P. crassipes* (rootcaps), *C. demersum* (seeds, stems, leaves and leaf spines), *S. auriculata* (leaves, trichomes and rhizoids), *Nitella* sp. and *Chara* sp. (oospores), *P. stratiotes* (rhizoids), *N. arguta* (seeds) and graminoids (a wide range of seeds) (Figure 4a). Seeds from *Cecropia* spp. trees and terrestrial woody debris were also retrieved.

A significant compositional threshold associated with dam construction was identified by GAMs across the three cores (Figure 4b). In the protected lake zone (BCI1 core), the rate of compositional change stabilized relatively quickly after lake infilling, whereas in both unprotected lake zones (LGAT1 and LGAT2 cores), plant communities gradually shifted towards novel associations.

The MFA explained 35% of the variance in historical biotic and abiotic data, with contributions of 20 and 15% for dimensions 1 and 2, respectively (Figure 5a). Categorical variables of lake zones and dam implementation contributed to the distinct spatial structure in the data (Appendix S6). Native and invasive submerged plant cover groups made the greatest contribution to the variation. Pre-dam times

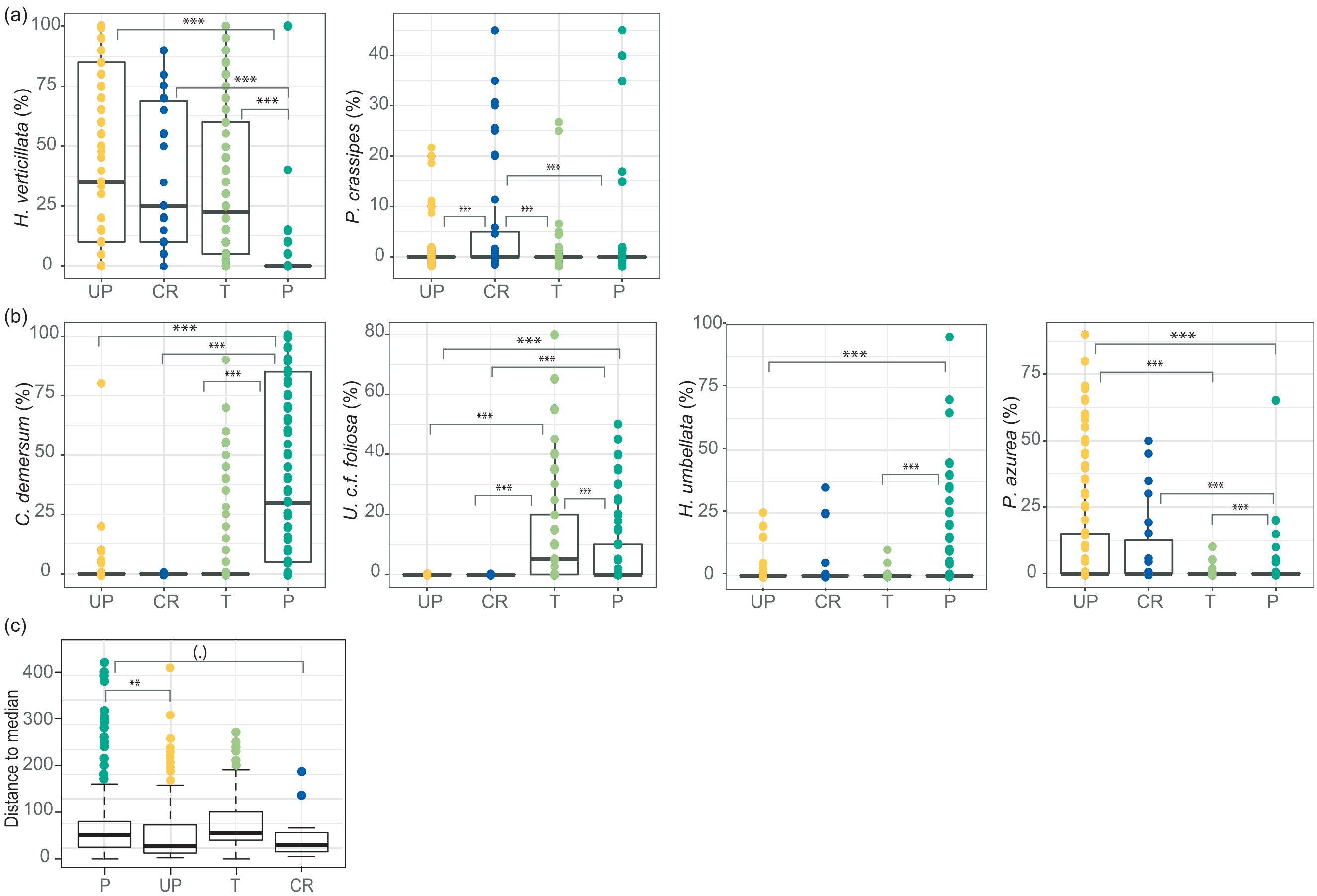

FIGURE 2 Boxplots showing significant pairwise comparisons (horizontal brackets) of (a) macrophyte invasive alien plant species (IAS) cover, (b) macrophyte native species cover, (c) habitat heterogeneity (measured as the variation in water depths) across protected (P), unprotected (UP), transitional (T) and Chagres River (CR) zones. (.) $p \leq 0.1$; *$p \leq 0.05$; **$p \leq 0.01$; ***$p \leq 0.001$.

grouped all three core sediment data in the top left of the multivariate space with baseline taxa and abundant woody debris and riparian *Cecropia* trees. The BCI1 core showed little change in macrophyte communities post-dam and was positively associated with DO and TA. The LGAT2 core shifted towards an association of *Chara* sp., *H. verticillate* and graminoids positively related to N-NO_3 and conductivity, while LGAT1 moved towards a *P. azurea*, *Nitella* sp., *H. verticillata*, *P. stratiotes* and *S. auriculata* assemblage positively related to N-NO2 and precipitation.

The HMD analysis of historical physical and chemical data (2003–2019) found significantly greater stability over time in the protected lake zones (mdm = 0.086, $p < 0.001$) compared with the unprotected lake and river zones (mdm = 0.14 and 0.91 respectively) (Figure 5b). The analysis also confirmed that the spatial structure in physical and chemical conditions observed during contemporary macrophyte surveys (Figure 3b) remained consistent over a 17-year period (Figure 5c).

4 | DISCUSSION

This study found that the protected lands formed just after construction of Gatun Dam have helped maintain native macrophyte species and resist the spread of IAS in Gatun Lake for more than 100 years, corroborating a previous study in European water bodies (Gallardo et al., 2017). The present study found a higher occurrence of native macrophytes in lake zones adjacent to protected land compared with unprotected land (prediction 1), a greater occurrence of macrophyte IAS in unprotected lake zones than in protected ones (prediction 2), a similar macrophyte community composition across the river landscape pre-damming (prediction 3), and a lower rate of native macrophyte change in lake zones adjacent to protected land post-impoundment (prediction 4).

4.1 | Potential mechanisms and processes

A healthy riparian forest positively affects aquatic ecosystem functioning and water quality (Naiman et al., 2010). Land protection mechanisms promote lower-nutrient waters, stable water chemistry, greater habitat heterogeneity and dense native cover, all of which are suggested to support native macrophyte species and protect lake zones from macrophyte IAS. Terrestrial soils in protected lands retain more nutrients than those in unprotected lands, consistent with the water chemistry monitoring data in the present study. In the Panama

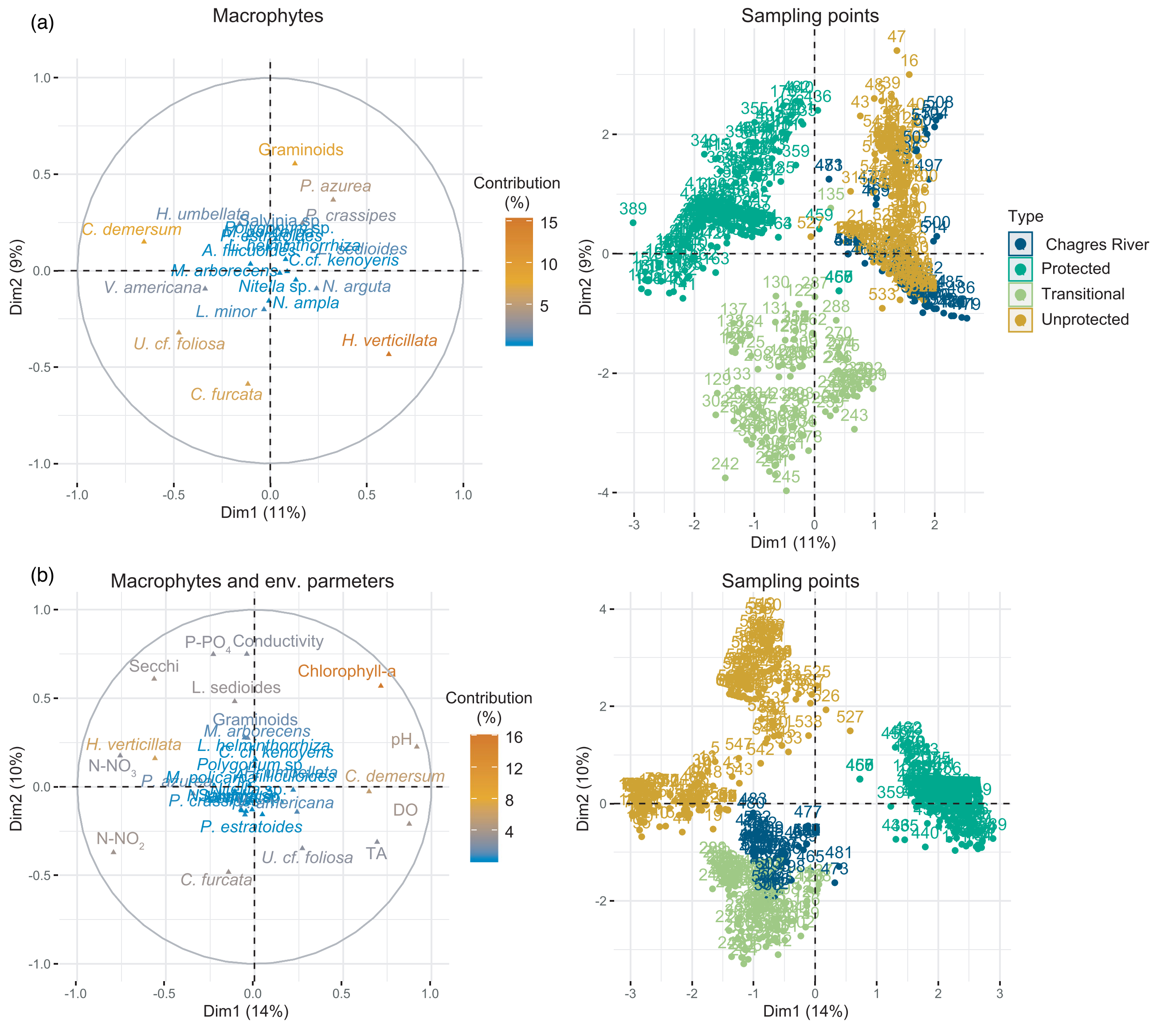

FIGURE 3 Multiple factor analysis (MFA) plot showing (a) the variation of contemporary native and IAS macrophyte cover, and (b) the variation of (a) in conjunction with water physical and chemical parameters (dissolved oxygen (DO), total alkalinity (TA); nitrates ($N\text{-}NO_3$), nitrites ($N\text{-}NO_2$), electrical conductivity and water transparency (Secchi depth)) and phytoplankton biomass (chlorophyll-a). The associated distribution of the sampling points according to land-cover type is also presented in (a) and (b).

Canal, protected forests also reduce runoff, flow peaks and extreme droughts in tributary rivers (Ogden et al., 2013). These characteristics of protected land are likely to be important because the results of the study indicate that increasing water nutrient content and fluctuating water chemistry conditions can hinder native plant growth and result in the dominance of more generalist invasive species (Scheffer et al., 2003; Salgado et al., 2019).

Habitat heterogeneity can promote the co-existence of aquatic species (Meerhoff & de los Ángeles González-Sagrario, 2021). In Gatun Lake, riparian forests probably enhance habitat heterogeneity for macrophytes by providing gradients of shade and depth and shoreline entanglements (Naiman et al., 2010). Protected lake zones may thus enhance niche availability for native macrophyte species to co-exist compared with unprotected zones (Salgado et al., 2018b). The riparian canopy probably contributes to this complexity by providing diverse shading conditions, which could have also helped limit the spread of macrophyte IAS (Ali et al., 2011), as *H. verticillata* and *P. crassipes* often benefit from less shaded conditions (Van et al., 1976; Sousa et al., 2009).

The invasive *H. verticillata* can rapidly replace native submerged species such as *C. demersum* owing to factors such as better carbon use in alkaline waters, low light requirements and competitive strategies (Van et al., 1976; Hofstra et al., 1999). The prevalence of *C. demersum* in Gatun Lake, however, indicates species co-existence. This suggests that variations in TA between the lake zones may be less important, whereas habitat heterogeneity and a more dense resident submerged

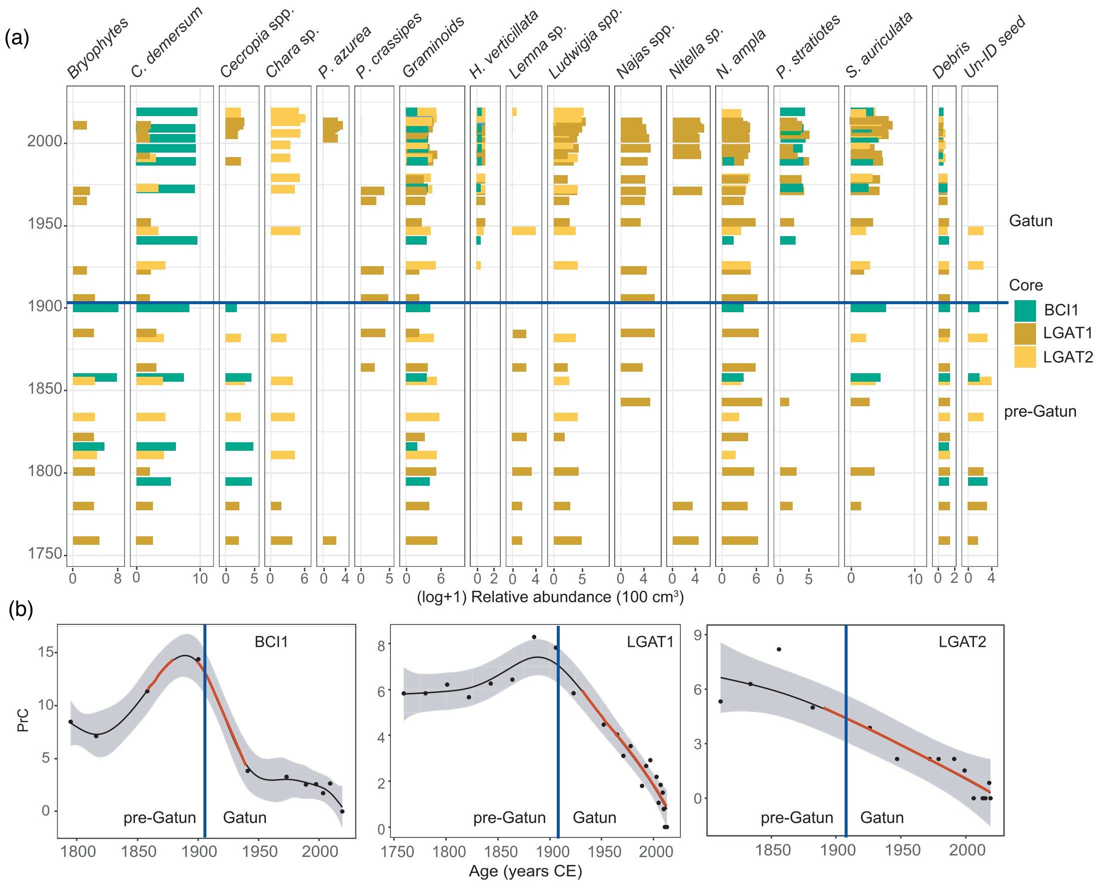

FIGURE 4 (a) Stratigraphy of plant macrofossils in the cores BCI1 (protected zone), LGAT1 (unprotected zone, La Laguna) and LGAT2 (unprotected zone, Trinidad); (b) generalized additive model (GAM) plots of temporal changes in plant macrofossils found in the three cores. Significant compositional changes at each core are indicated with a red line. Gatun Dam implementation is indicated by a dark blue vertical line in (a) and (b). CE, Common Era.

canopy in the protected lake zones may be of greater relevance (Capers et al., 2007; Salgado et al., 2022). As canopy competition between *C. demersum* and *H. verticillata* can be determined by periods of pre-emption or establishment (Hofstra et al., 1999; Bianchini et al., 2010), the increased abundance of *C. demersum* with the dam is likely to have provided a competitive advantage over *H. verticillata* in the protected lake zones. However, in more human-influenced zones with greater space pre-emption, *H. verticillata* may have had a competitive advantage (Sousa et al., 2009).

4.2 | Confounding factors and caveats

Other factors, such as wind and wave exposure, may also contribute to the observed spatial variation of macrophytes in Gatun Lake. Wind and wave forces are known to influence macrophyte and chemical distribution in large lakes such as Gatun (Van Zuidam & Peeters, 2015). In protected lake zones, wind-driven currents are likely to have less influence than in unprotected zones, but the presence of large shipping vessels crossing the canal zone increases exposure to large waves, which can increase sediment transport, propagule movement, and the fragmentation and uprooting of submerged plant stands (Van Zuidam & Peeters, 2015). Although exposure to these stressors may play a role, the prominent cover of submerged macrophytes in both protected and unprotected lake zones suggests that they may not be critical in explaining the observed patterns.

Propagule pressure – the number of propagules arriving in the lake – is a key mechanism for explaining the success of macrophyte invasion in tropical reservoirs (Thomaz et al., 2015). This study did not quantify the propagule flux from the two macrophyte IAS, but their floating structures are commonly observed moving across the lake. Indeed, the passage of high propagules into the canal zone from river tributaries was reported as the main invasion mechanism of *P. crassipes* (Hearne, 1966), and in response a weed control programme has been implemented since the dam's construction (Hearne, 1966). The programme has achieved moderate success in controlling macrophyte growth (Von Chong, 1986), particularly that of *P. crassipes*, and therefore has probably helped mitigate some of the impact of macrophyte IAS.

Large reservoirs also have a hydrological gradient in river–lake conditions that affects macrophyte distribution (Winton et al., 2019).

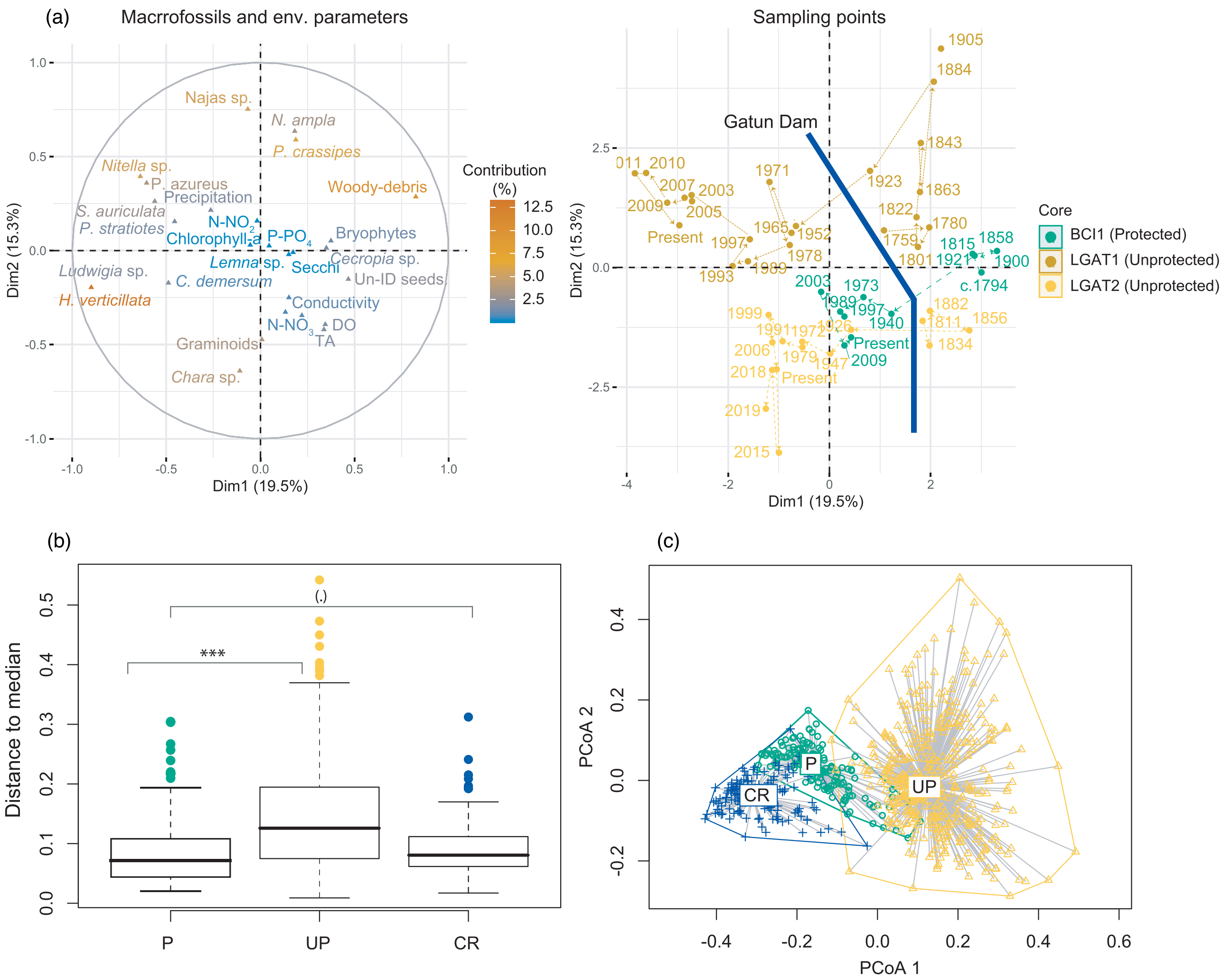

FIGURE 5 Multiple factor analysis plot showing (a) the variation of plant macrofossils and physical and chemical parameters (DO, TA, $N\text{-}NO_3$, $N\text{-}NO_2$, electrical conductivity and water transparency (Secchi depth)), phytoplankton biomass (chlorophyll-a) and annual precipitation (5 year average). The trajectory of compositional change in the cores BCI1, LGAT1 and LGAT2 is also indicated. Boxplots (b) and plot (c) of homogeneity multivariate dispersion results for the historical (2003–2019) physical and chemical quality parameters in the lake and river zones. The implementation of Gatun dam is indicated in (a) by a thick blue line. (.) $p \le 0.1$; *$p \le 0.05$; **$p \le 0.01$; ***$p \le 0.001$; and (c) principal coordinate analysis (PCoA) plot of HMD results.

Floating plants are often found near the reservoir mouth, submerged plants near the dam and both types in the intermediate river–lake fraction (Mormul et al., 2010). In Gatun Lake, macrophytes follow this gradient to some degree, with *P. crassipes* and *P. azurea* prevalent near the reservoir mouth and in the river–lake fraction, and submerged plants dominating in the river–lake and lake sections. However, the distribution of macrophytes is not entirely determined by the reservoir hydrology, as suggested by the similar floristic composition between the river and two unprotected lake zones, whereas the protected zones (river–lake fraction) are uniquely dominated by *C. demersum*.

Consideration should also be given to the constraints of the palaeolimnology data and radiometric analyses, including poor preservation of *H. verticillata* in the sediments and uncertainties in the age model, sedimentation rates and historical physical and chemical records. However, the relative abundances of the main plant species over space and time in the same lake zones were accurately characterized, suggesting that the constraints are unlikely to have a significant impact on the inferences made in this study.

4.3 | Implications for conservation

Limiting aquatic invasions is crucial to preserve global biodiversity and protecting land is an effective tool to do so (Foxcroft et al., 2017), but no studies have investigated the role of protected land in limiting macrophyte IAS in tropical man-made reservoirs, where native biodiversity is high but prevention and management options are limited (Pyšek et al., 2020). The annual cost of managing *P. crassipes* in fresh waters, especially reservoirs, in tropical Central and South

Americas is estimated at US$179.9 million (Heringer et al., 2021), highlighting the need to explore solutions to curb invasions and protect native aquatic biodiversity as dam projects accelerate across the region (Pereira et al., 2018).

This study combined monitoring data with palaeoecological techniques to propose that protected land can maintain aquatic macrophyte biodiversity in tropical reservoirs by retaining nutrients, stabilizing water chemistry, providing habitat heterogeneity and protecting native vegetation, while still supporting terrestrial conservation goals (Leal et al., 2020). To ensure environmentally sustainable river damming projects and protect native macrophyte species from the spread of IAS, the following recommendations are proposed:

1. Implement land protection schemes along the reservoir's littoral areas, starting from the dam's design stages, to provide native species with a competitive advantage over macrophyte IAS.
2. Land protection should be located outside the main operational areas of the reservoir to avoid any other human interference.
3. Use a variety of invasion management schemes, such as mechanical removal or biocontrol, in addition to land protection.
4. Maintain water quality by addressing eutrophication, a growing problem in tropical reservoirs that can eventually erode the positive effects of land protection against the spread of alien species.
5. Identify the native species that need protection and the necessary habitat conditions for their survival, as each species has unique requirements for protection.

These recommendations are particularly crucial as multi-dam landscape projects are expected to accelerate and macrophyte invasions continue to spread.

AUTHOR CONTRIBUTIONS

Jorge Salgado conceived the ideas and designed the methodology; Jorge Salgado collected and analysed the data; Aaron O'Dea provided funding; Jorge Salgado led the writing of the manuscript and all authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare (10.6084/m9.figshare.22795997).

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REFERENCES

Ali, M.M., Hassan, S.A. & Shaheen, A.S.M. (2011). Impact of riparian trees shade on aquatic plant abundance in conservation islands. *Acta Botanica Croatica*, 70(2), 245–258. https://doi.org/10.2478/v10184-010-0012-7

Anderson, M.J., Ellingsen, K.E. & McArdle, B.H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9(6), 683–693. https://doi.org/10.1111/j.1461-0248.2006.00926.x

Appleby, P.G. (2001). Chronostratigraphic techniques in recent sediments. In: Smol, J.P. (Ed.) *Tracking environmental change using lake sediments. Vol. 1: basin analysis, coring, and chronological techniques*. Dordrecht: Kluwer Academic Publishers, pp. 171–203.

Bianchini, I., Cunha-Santino, M.B.D., Milan, J.A.M., Rodrigues, C.J. & Dias, J.H.P. (2010). Growth of *Hydrilla verticillata* (Lf) Royle under controlled conditions. *Hydrobiologia*, 644(1), 301–312. https://doi.org/10.1007/s10750-010-0191-1

Birks, H.H. (2001). Plant macrofossils. In: Smol, J.P. & Birks, H.J.B. (Eds.) *Tracking environmental change using lake sediments, Vol. 3: Terrestrial, algal and siliceous indicators*. Dordrecht: Kluwer Academic Publishers, pp. 49–74.

Boylen, C.W., Eichler, L.W. & Madsen, J.D. (1999). Loss of native aquatic plant species in a community dominated by Eurasian watermilfoil. *Hydrobiologia*, 415, 207–211. https://doi.org/10.1023/A:1003804612998

Capers, R.S., Selsky, R., Bugbee, G.J. & White, J.C. (2007). Aquatic plant community invasibility and scale-dependent patterns in native and invasive species richness. *Ecology*, 88(12), 3135–3143. https://doi.org/10.1890/06-1911.1

Castellanos-Galindo, G.A., Robertson, D.R., Sharpe, D.M. & Torchin, M.E. (2020). A new wave of marine fish invasions through the Panama and Suez canals. *Nature Ecology & Evolution*, 4(11), 1444–1446. https://doi.org/10.1038/s41559-020-01301-2

Condit, R., Robinson, W.D., Ibáñez, R., Aguilar, S., Sanjur, A., Martínez, R. et al. (2001). The status of the Panama Canal watershed and its biodiversity at the beginning of the 21st Century: long-term ecological studies reveal a diverse flora and fauna near the Panama Canal, harbored within a corridor of forest stretching from the Caribbean to the Pacific, but deforestation, land degradation, erosion, and overhunting remain threats. *Bioscience*, 51(5), 389–398. https://doi.org/10.1641/0006-3568(2001)051[0389:TSOTPC]2.0.CO;2

EPA - United States Environmental Protection Agency. (1986). *Quality criteria for water*. Washington DC: Office of Water Regulation and Standards.

Foxcroft, L.C., Jarošík, V., Pyšek, P., Richardson, D.M. & Rouget, M. (2011). Protected-area boundaries as filters of plant invasions. *Conservation Biology*, 25(2), 400–405. https://doi.org/10.1111/j.1523-1739.2010.01617.x

Foxcroft, L.C., Pyšek, P., Richardson, D.M., Genovesi, P. & MacFadyen, S. (2017). Plant invasion science in protected areas: progress and priorities. *Biological Invasions*, 19(5), 1353–1378. https://doi.org/10.1007/s10530-016-1367-z

Gallardo, B., Aldridge, D.C., González-Moreno, P., Pergl, J., Pizarro, M., Pyšek, P. et al. (2017). Protected areas offer refuge from invasive species spreading under climate change. *Global Change Biology*, 23(12), 5331–5343. https://doi.org/10.1111/gcb.13798

Gunn, I.D., O'Hare, M., Carvalho, L., Roy, D.B., Rothery, P. & Darwell, A.M. (2010). Assessing the condition of lake habitats: a test of methods for surveying aquatic macrophyte communities. *Hydrobiologia*, 656(1), 87–97. https://doi.org/10.1007/s10750-010-0437-y

Hearne, J.S. (1966). The Panama Canal's aquatic weed problem. *Hyacinth Control Journal*, 5, 1–5.

Heringer, G., Angulo, E., Ballesteros-Mejia, L., Capinha, C., Courchamp, F., Diagne, C. et al. (2021). The economic costs of biological invasions in Central and South America: a first regional assessment. *NeoBiota*, 67, 401–426. https://doi.org/10.3897/neobiota.67.59193

Hofstra, D.E., Clayton, J., Green, J.D. & Auger, M. (1999). Competitive performance of *Hydrilla verticillata* in New Zealand. *Aquatic Botany*, 63(3–4), 305–324. https://doi.org/10.1016/S0304-3770(98)00125-9

IUCN—International Union for Conservation of Nature. (2000). *Guidelines for the prevention of biodiversity loss caused by alien invasive species*. Gland: IUCN.

JNCC - Joint Nature Conservation Committee. (2009). *Draft common standards monitoring guidance for standing waters*. Peterborough, UK: Joint Nature Conservation Committee.

Johnson, P.T., Olden, J.D. & Vander Zanden, M.J. (2008). Dam invaders: impoundments facilitate biological invasions into freshwaters. *Frontiers in Ecology and the Environment*, 6(7), 357–363. https://doi.org/10.1890/070156

Le, S., Josse, J. & Husson, F. (2008). FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software*, 25(1), 1–18. https://doi.org/10.18637/jss.v025.i01

Leal, C.G., Lennox, G.D., Ferraz, S.F., Ferreira, J., Gardner, T.A., Thomson, J.R. et al. (2020). Integrated terrestrial–freshwater planning doubles conservation of tropical aquatic species. *Science*, 370(6512), 117–121. https://doi.org/10.1126/science.aba7580

Marchetti, M.P., Moyle, P.B. & Levine, R. (2004). Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. *Freshwater Biology*, 49(5), 646–661. https://doi.org/10.1111/j.1365-2427.2004.01202.x

Meerhoff, M. & de los Ángeles González-Sagrario, M. (2021). Habitat heterogeneity in shallow lakes and ponds: importance, threats, and potential for restoration. *Hydrobiologia*, 849(17-18), 3737–3760. https://doi.org/10.1007/s10750-021-04771-y

Mormul, R.P., Alves Ferreira, F., Sala Michelan, T., Carvalho, P., Silveira, M.J. & Thomaz, S.M. (2010). Aquatic macrophytes in the large, subtropical Itaipu Reservoir, Brazil. *Revista de Biología Tropical*, 58(4), 1437–1451.

Muthukrishnan, R. & Larkin, D.J. (2020). Invasive species and biotic homogenization in temperate aquatic plant communities. *Global Ecology and Biogeography*, 29(4), 656–667. https://doi.org/10.1111/geb.13053

Naiman, R.J., Decamps, H. & McClain, M.E. (2010). *Riparia: ecology, conservation, and management of streamside communities*. New York: Elsevier.

Ogden, F.L., Crouch, T.D., Stallard, R.F. & Hall, J.S. (2013). Effect of land cover and use on dry season river runoff, runoff efficiency, and peak storm runoff in the seasonal tropics of Central Panama. *Water Resources Research*, 49(12), 8443–8462. https://doi.org/10.1002/2013WR013956

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., et al. (2022). vegan: Community Ecology Package. R package version 2.6–2. https://CRAN.R-project.org/package=vegan

Paton, S. & Panama Canal Authority. (2020a). Panama Canal Authority Data. Smithsonian Tropical Research Institute. Collection. https://doi.org/10.25573/data.11793768.v1

Paton, S. & Panama Canal Authority. (2020b). Panama Canal Precipitation (R to Z). Smithsonian Tropical Research Institute. Dataset. https://doi.org/10.25573/data.11791872.v4

Pereira, L.S., Neves, R.D.A.F., Miyahira, I.C., Kozlowsky-Suzuki, B., Branco, C.W.C., de Paula, J.C. et al. (2018). Non-native species in reservoirs: how are we doing in Brazil? *Hydrobiologia*, 817(1), 71–84. https://doi.org/10.1007/s10750-017-3446-2

Pya, N. (2022). scam: Shape Constrained Additive Models. R package version 1.2–13. https://CRAN.R-project.org/package=scam

Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T. et al. (2020). Scientists' warning on invasive alien species. *Biological Reviews*, 95(6), 1511–1534. https://doi.org/10.1111/brv.12627

Salgado, J., Sayer, C.D., Brooks, S.J., Davidson, T.A., Goldsmith, B., Baker, A.G. et al. (2018a). Eutrophication homogenizes shallow lake macrophyte assemblages over space and time. *Ecosphere*, 9, e02406. https://doi.org/10.1002/ecs2.2406

Salgado, J., Sayer, C.D., Brooks, S.J., Davidson, T.A. & Okamura, B. (2018b). Eutrophication erodes inter-basin variation in macrophytes and co-occurring invertebrates in a shallow lake: combining ecology and palaeoecology. *Journal of Paleolimnology*, 60, 311–328. https://doi.org/10.1007/s10933-017-9950-6

Salgado, J., Sayer, C.D., Willby, N., Baker, A.G., Goldsmith, B., McGowan, S. et al. (2022). Habitat heterogeneity enables spatial and temporal coexistence of native and invasive macrophytes in shallow lake landscapes. *River Research and Applications*, 38(8), 1387–1399. https://doi.org/10.1002/rra.3839

Salgado, J., Vélez, M.I., Caceres-Torres, L.C., Villegas-Ibagon, J.A., Bernal-Gonzalez, L.C., Lopera-Congote, L. et al. (2019). Long-term habitat degradation drives neotropical macrophyte species loss while assisting the spread of invasive plant species. *Frontiers in Ecology and Evolution*, 7, 140. https://doi.org/10.3389/fevo.2019.00140

Salgado, J., Vélez, M.I., González-Arango, C., Rose, N.L., Yang, H., Huguet, C. et al. (2020). A century of limnological evolution and interactive threats in the Panama Canal: long-term assessments from a shallow basin. *Science of the Total Environment*, 729, 138444. https://doi.org/10.1016/j.scitotenv.2020.138444

Scheffer, M., Szabo, S., Gragnani, A., van Nes, E.H., Rinaldi, S., Kautsky, N. et al. (2003). Floating plant dominance as a stable state. *Proceedings of the National Academy of Sciences*, 100(7), 4040–4045. https://doi.org/10.1073/pnas.0737918100

Simpson, G. (2022). gratia: graceful ggplot-based graphics and other functions for GAMs fitted using mgcv. R package version 0.7.3. https://gavinsimpson.github.io/gratia/

Simpson, G.L. (2007). Analogue methods in palaeoecology: using the analogue package. *Journal of Statistical Software*, 22(2), 1–29.

Simpson, G.L. (2018). Modelling palaeoecological time series using generalised additive models. *Frontiers in Ecology and Evolution*, 6, 149. https://doi.org/10.3389/fevo.2018.00149

Sousa, W.T.Z., Thomaz, S.M., Murphy, K.J., Silveira, M.J. & Mormul, R.P. (2009). Environmental predictors of the occurrence of exotic *Hydrilla verticillata* (Lf) Royle and native *Egeria najas* Planch. in a sub-tropical river floodplain: the Upper River Paraná, Brazil. *Hydrobiologia*, 632(1), 65–78. https://doi.org/10.1007/s10750-009-9828-3

Thomaz, S.M., Mormul, R.P. & Michelan, T.S. (2015). Propagule pressure, invasibility of freshwater ecosystems by macrophytes and their ecological impacts: a review of tropical freshwater ecosystems. *Hydrobiologia*, 746(1), 39–59. https://doi.org/10.1007/s10750-014-2044-9

Van, T.K., Haller, W.T. & Bowes, G. (1976). Comparison of the photosynthetic characteristics of three submersed aquatic plants. *Plant Physiology*, 58(6), 761–768.

Van Zuidam, B.G. & Peeters, E.T. (2015). Wave forces limit the establishment of submerged macrophytes in large shallow lakes. *Limnology and Oceanography*, 60(5), 1536–1549. https://doi.org/10.1002/lno.10115

Von Chong, C. (1986). Manejo de la vegetación acuática en el canal de Panamá. *Revista Lotería*, 372, 108–121. https://doi.org/10.1002/lno.10115

Wauchope, H.S., Amano, T., Geldmann, J., Johnston, A., Simmons, B.I., Sutherland, W.J. et al. (2021). Evaluating impact using time-series data. *Trends in Ecology & Evolution*, 36(3), 196–205. https://doi.org/10.1016/j.tree.2020.11.001

Wauchope, H.S., Jones, J.P., Geldmann, J., Simmons, B.I., Amano, T., Blanco, D.E. et al. (2022). Protected areas have a mixed impact on waterbirds, but management helps. *Nature*, 605(7908), 103–107. https://doi.org/10.1038/s41586-022-04617-0

Winton, R.S., Calamita, E. & Wehrli, B. (2019). Reviews and syntheses: dams, water quality and tropical reservoir stratification. *Biogeosciences*, 16(8), 1657–1671. https://doi.org/10.5194/bg-16-1657-2019

Wood, S.N. (2017). *Generalized additive models: an introduction with R*, 2nd edition, New York: Chapman and Hall/CRC.

Zarfl, C., Lumsdon, A.E., Berlekamp, J., Tydecks, L. & Tockner, K. (2015). A global boom in hydropower dam construction. *Aquatic Sciences*, 77, 161–170. https://doi.org/10.1007/s00027-014-0377-0

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