Terrestrial protected areas maintain freshwater ecosystem resilience to costly aquatic invasive species in the Panama Canal

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Terrestrial protected areas maintain freshwater ecosystem resilience to costly aquatic invasive species in the Panama Canal

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Abstract

River damming is expected to proliferate across Tropical American Rivers in the forthcoming decades with expected declines in ecosystem health to costly invasive species. Historical data and modern aquatic plant surveys of one of the largest and oldest tropical dam projects (the > 100 years old Panama Canal) reveal that modern plant communities in areas adjacent to terrestrial Natural Protected Areas (tNPAs) retain a pre-damming community structure that is apparently more resistant to invasive species. Establishing tNPAs adjacent to impounded rivers could be a cost-effective nature-based solution for tropical reservoir management.

Main text

The construction of large dam projects (> 15 m high) is predicted to accelerate across Tropical America for hydropower and water provision[1,2] (Fig. 1a). While these projects can address important socio-economic needs[3], they often have far-reaching effects on aquatic biodiversity[2,4] through the altering of biogeochemical cycles, water quality, and primary productivity[5,6], and the restriction of upstream-downstream movement of organisms, water and nutrients[4]. Less understood, however, is the impact of alien invasive species (IAS) on dam reservoirs[7,8]. The often-poor water quality of man-made reservoirs, coupled with the high variability in water levels from regulation, can stress native species while facilitating conditions for more generalist species[9] and this may explain why reservoirs have been suggested to be less resilient to IAS than natural lakes[7,9,10].

Despite considerable progress in identifying the threats of river damming to ecosystem biodiversity in the American tropics[1,2,4,8], best practices to protect aquatic biodiversity continue to be debated[11,12]. As riverine systems are primarily defined by their hydrology, conservation strategies have focused on protecting and restoring hydrological regimes to preserve the ecosystem function and biodiversity[1,4,13]. Yet, there remain substantial gaps in our understanding about the effects of land-use change, water pollution, and IAS on the ecology of dammed rivers[14]. The designation of terrestrial Natural Protected Areas (tNPAs) has been suggested as an additional solution to maintain ecosystem integrity in reservoirs[14,15,16]. Simulation of conservation strategies in the Amazon basin, has shown that the joint implementation of aquatic and tNPAs, could bring overwhelming positive effects in conserving both terrestrial and aquatic biota[12]. However, whether such an approach can be effective in heavily impacted ecosystems, such as man-made reservoirs, has yet to be demonstrated.

Lake Gatun in the Panama Canal, Panama, is one of the oldest (> 100 years) and largest (425 km^2) reservoirs in the American Tropics (Fig. 1c). It has been invaded by a suite of species including a variety of fish (e.g., the peacock bass *Cichla ocellaris*), mollusc (e.g., the red-rimmed melania snail *Melanoides (Thiara) tuberculata*, and the South American apple snail *Pomacea bridgesii*), mammals (e.g., the American manatee *Trichechus manatus*), and macrophytes (e.g., the water thyme *Hydrilla verticillata* and the water hyacinth *Eichhornia crassipes*), either accidentally or deliberately[17,18]. Furthermore, since the canal was completed in 1914, it came under the protection of the US government and extensive forest areas were safeguarded in the northern half of the lake by the creation of a nature reserve in Barro Colorado Island (BCI) in 1923[19]. The subsequent inclusion of five adjacent peninsulas in 1946 created what is currently known as the Barro Colorado Nature Monument–BCNM, whilst two more National Parks (Soberanía and the Chagres) were established later in the early 1980s on the eastern side of the lake[19] (Figure 1c). These unique long-running sanctuaries are currently characterised by the growth of mature secondary forest that positively influence in the hydrology and water quality of the associated tributary rivers[19,20,21]. They attenuate flood peaks and extreme droughts, help retain sediments, nutrients, and runoff[19,20,21]. However, the extended effects of tNPAs on the functioning and ecology of the Gatun Lake has yet to be addressed. Gatun Lake therefore presents a unique opportunity to explore the ecological effects of tNPAs on aquatic communities and their resilience to anthropogenic and natural change over a relatively long period of time; an approach that may provide a lense to help predict future dynamics of the many hundreds of dam projects that are proposed across lowland tropical areas and to offer useful insights into best practices to maintain ecosystem integrity.

In this study, we combined long-term paleoecological data from a sedimentary core with high-resolution spatial surveys of modern aquatic plant (macrophyte) communities in lake areas adjacent and not adjacent to tNPAs (Fig. 1c) to explore the role of tNPAs and the resilience of the aquatic ecosystems. To achieve this, we (1) defined a baseline, pre-dam community and ecosystem conditions, (2) surveyed the macrophyte composition of the tNPAs and other non-tNPAs, and (3) compared the macrophyte communities relative to pre-dam species (for detailed methods see[17] and supplementary material).

Our findings show that areas of Gatun Lake that are included within a tNPA sustain macrophyte communities that are more similar in their composition to baseline communities, than those from outside tNPAs (Fig. 2a). Macrophyte communities that are adjacent to tNPAs are often dominated by native macrophyte species such as *Nymphaea ampla*, *Ceratophyllum demersum, Cabomba piauhyensis,* and *Utricularia vulgaris* (Fig. 2b). These baseline taxa rarely occur in areas not adjacent to tNPAs or in the parental Chagres River (2b). In contrast, macrophyte communities in the Chagres River and areas not adjacent to tNPAs are typically dominated by the invasive *H. verticillata* and *E. crassipes.* Communities in lake areas located within transition zones of tNPAs and not protected land are characterized by a mixture of both native and IAS. In addition, macrophyte communities occurring in lake areas adjacent to tNPAs have higher beta diversity (i.e., a greater variation in species composition and abundances between sampling points) than the more homogenous, IAS-dominated lake areas not adjacent to tNPAs and in the Chagres River (Fig. 2a). Thus, tNPAs are suggested to have a striking positive effect on their adjacent aquatic ecosystems by promoting diversity, increasing community heterogeneity, and potentially enhancing the ecosystem ability to resist the establishment of IAS. While recent simulations predict a positive impact of tNPAs on lowland tropical freshwater ecosystems[12], our result is surprising because the Gatun Lake is a reservoir with a long history of human impacts and has been heavily invaded[17,18].

Reservoirs are complex hydrological systems that combine numerous features of both riverine and lacustrine environments. This river-lake continuum has proved to influence the distribution of macrophytes in other similar large, lowland, Tropical American dams such as Itaipu in Brazil, where floating plants dominate in the riverine fraction of the reservoir, submerged plant species thrive across the lake portion, and both co-exist in the riverine-lake fraction[7,22]. In Gatun Lake, physical-chemical characteristics supports such riverine-lake transition (Fig. 2c) and the studied lake areas adjacent to tNPAs are located within the river-lake portion. Thus, our results could be reflecting such river-lake gradient. However, the alike macrophyte IAS dominated communities in the Chagres River and in lake areas not adjacent to tNPAS (i.e., the lake portion of the reservoir), and modern plant communities in lake areas adjacent to tNPAs resembled those at pre-dam times. These patterns, harmoniously suggest that the aquatic flora is not necessarily following a riverine-lake gradient.

Currently the mechanisms explaining the macrophyte patterns between lake areas adjacent to tNPAs vs not tNPAS are unresolved. However, our results suggest that macrophytes may be responding to what appears to be a gradient in habitat complexity provided by land protection. Adjacent tNPAs may promote a range of light conditions in the lake littoral areas via varying canopy forest cover, retain nutrients and runoff, while promote dissolved organic matter load[19,20,21,23,24]. These various factors could encourage, varying degrees of water clarity conditions for different plants to exploit. Heterogeneous habitats sustain macrophyte diversity[25,26,27], while limit the dominance of macrophyte IAS via species coexistence[27,28]. Similarly, reductions in water quality[25] and IAS spread[29], could homogenise macrophyte communities, through the dominance of few good competitors. The observed heterogenous water clarity conditions in lake areas adjacent to tNPAs (supplementary material Fig. 1), therefore, appears to favour habitat structure for pre-dam macrophyte communities, while limiting the expansion of IAS, which have become to some extent problematic in the more human influenced areas of the Chagres River and in those lake areas with not association to tNPAs.

The economic and ecological impact of aquatic IAS on man-made lakes across Tropical America remains a critically understudied problem and long-term records are few and far between making predictions and recommendations challenging. In other, better studied (higher latitude and less-biodiverse) systems, costs can frequently exceed many hundreds of millions of US$ annually[30] and global estimates place the impact at more than US$20 billion a year[32]. And yet, invaded-prone tropical inland freshwater systems receive relatively little protection against exploitation and development compared to terrestrial and marine ecosystems. It is therefore critically important that as dam projects proliferate across developing countries in Tropical America (Fig. 1) and IAS threaten established reservoirs[7], all opportunities to curb invasions and protect native biodiversity must be explored effectively and economically[11].

Our findings illuminate a potentially overlooked role for tNPAs in maintaining aquatic native biodiversity and ecosystem integrity of tropical impounded systems. Our data is limited to macrophytes, but the implications likely extend more broadly to those invertebrates and vertebrate community members that rely on macrophyte community structure[32]. Questions remain however on the universality of the role of tNPAs and the mechanisms driving the maintenance of pre-dam species populations. Nonetheless, the inclusion of freshwater ecosystems within tNPAs is suggested to improve the protection of aquatic biodiversity without undermining terrestrial conservation goals[11,12]. Thus, to prevent river-damned ecosystem collapse across the region, we recommend: (i) other tropical protected man-made reservoirs to be similarly studied to elucidate mechanism and applications; and (ii) whenever possible, areas in the dam reservoir should be integrated within tNPAs. Such considerations are critically important given the predicted acceleration of dam projects, the ever-increasing dispersals of IAS and the fact that highly biodiverse lowland inland ecosystems are disproportionately sensitive to land use and climatic changes across the globe[33,34].

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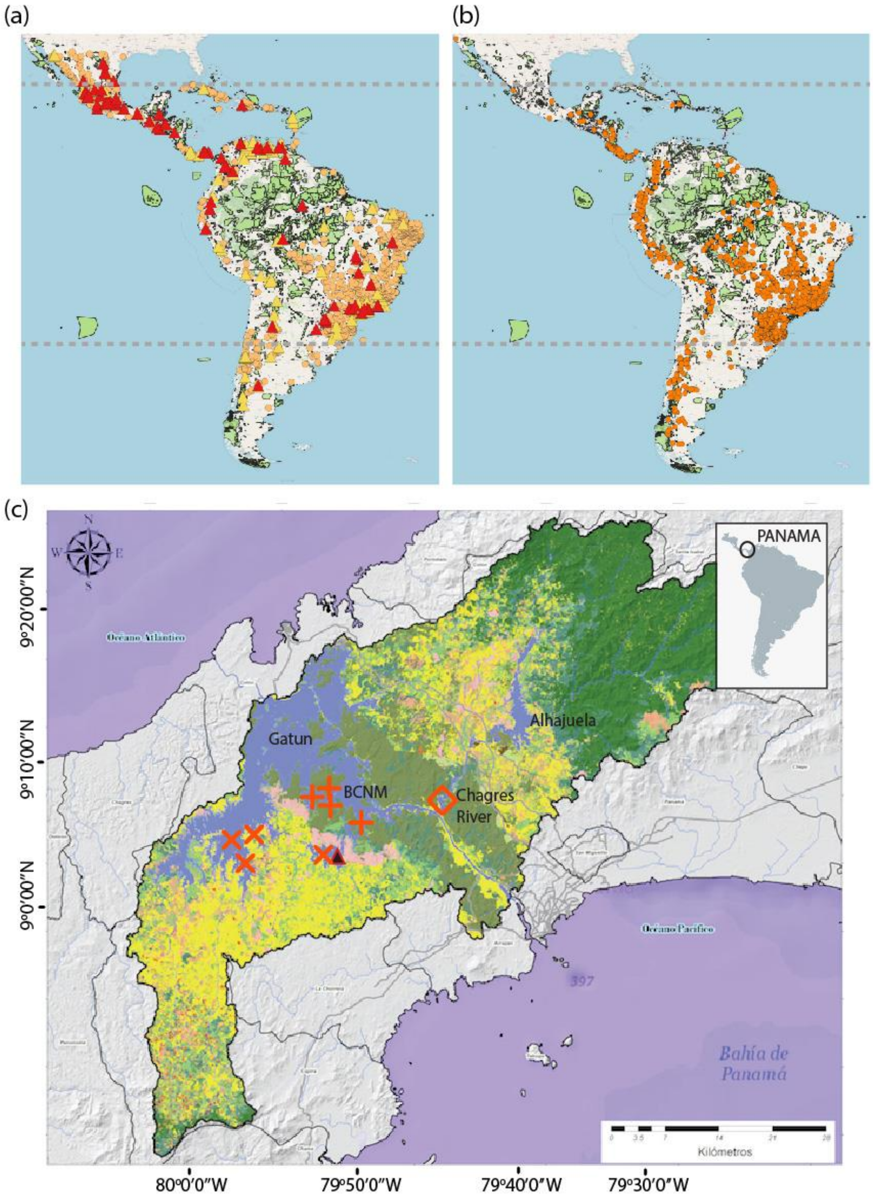

FIGURE 1 Map of Central and South America showing the geographical distribution of **(a)** terrestrial natural protected areas (tNPAs; green), documented large (> 15 m high) dams (circles), dams associated with tNPAs (yellow triangles), and dams associated with tNPAs with macrophyte invasive species records (red triangles); **(b)** proposed hydropower dams; and **(c)** map showing the location, watershed, and vegetation cover of Gatun Lake (Panama Canal). tNPAs are shown in dark-green, lake sampling areas adjacent to tNPAs in red crosses, lake sampling areas not adjacent to tNPAs in red Xs, and sampling areas in the Chagres River in a red diamond. Coring location of LGAT1[17] core is indicated by a red triangle.

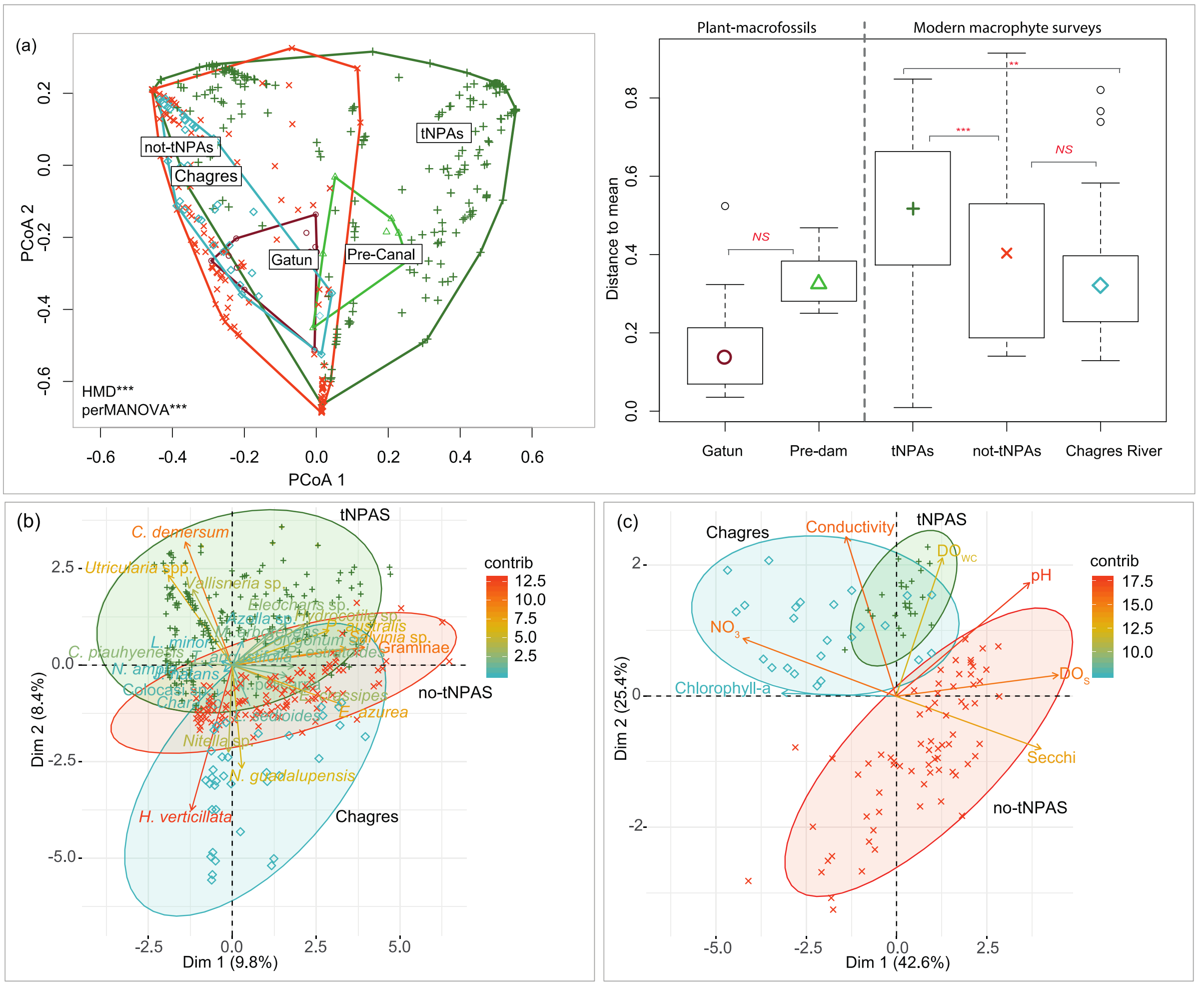

FIGURE 2 (a) Principal coordinate analysis plot (PCoA) of a homogeneity multivariate dispersion test (HMD) showing the variations of contemporary macrophyte species abundances (community heterogeneity) in three study areas of the Gatun Reservoir: the Chagres River (blue diamonds), lake areas adjacent to tNPAs (green crosses), and lake areas not adjacent to tNPAs (not-tNPAs; red Xs), and of plant macrofossils at two time periods in Gatun Lake (collected in a not-tNPAs): pre-dam times (pale green triangles) and Gatun-lake times (dark red circles). The degree of community heterogeneity of each study area is also shown as boxplots. The distance to mean of each study area is indicated in the PCoA plot by each area's label and in the boxplots by each area symbol. Compositional differences between the study areas were assessed via Permutational multivariate analysis of variance

(PERMANOVA). Differences in distance to means of each the study areas were assessed via *post hoc* pairwise comparison via Tukey Honest test under a significance level of $p \leq 0.05$. $^*p \leq 0.05$; $^{**} p \leq 0.01$; $^{***}p \leq 0.001$; NS=not significant.; **(b)** Principal component analysis (PCA) plot showing the distributions of the macrophyte species in the three study areas; (c) PCA plot showing the variation of selected physicochemical parameters in the three study areas. Dissolved oxygen (DO) in the water column (w) and the lake surface (s); Nitrates = NO_3.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Salgadoetal.Supplementarymaterial.pdf
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