Reduced dry season fish biomass and depleted carnivorous fish assemblages in unprotected tropical oxbow lakes

Abstract

The effectiveness of protected areas in maintaining biodiversity is increasingly under debate. Specifically, the responses of animal populations in freshwater ecosystems to disturbances outside protected areas are not well understood. Fish assemblages can serve as an indicator of such responses. We used dry season oxbow lake fish occurrence data implemented within a Measurement of Biodiversity framework to examine the influence of extractive activities on the richness, structure and abundance of fish assemblages. We compared oxbow lakes in protected areas with lakes subject to artisanal small-scale gold mining (ASGM) and other human activities. The main components of fish biodiversity maintained by lake protection were abundance and biomass. The strongest predictors of community structure were fishing intensity and water transparency. As variation in these factors are likely a consequence of ASGM, our results may indicate indirect impacts of ASGM on freshwater ecosystems. Our analysis of fish trophic guilds also suggested that carnivores dominated fish assemblages in protected lakes, whereas in disturbed lakes detritivores were more frequent, suggesting a trophic downgrading of freshwater ecosystems subject to ASGM. Taken together, our results indicate responses of fish assemblages to human activity associated with ASGM. In the western Amazon, protected and isolated areas appear to be successful at maintaining the integrity of fish assemblages. Given the vulnerability of freshwater habitats and their high value for ecosystem services, we recommend local community engagement and resource allocation to prevent the degradation of oxbow lake habitats and the depletion of local aquatic biodiversity in unprotected areas.

Keywords: Environmental variables, Fish community, Habitat structure, Human disturbance, Ichthyofauna, Neotropical fishes, Protected areas, Riparian zone, Spatial environmental variables, Species richness, Wetlands

1. Introduction

Aquatic ecosystems in the neotropics are particularly vulnerable to the effects of human activities, especially through land transformation and the resulting loss of hydrological connectivity (Castello and Macedo, 2016; Pelicice et al., 2017). Some of the environmental damages of land transformation can be mitigated by land protection and enhancement of connectivity among fluvial basins, as well as localized community-driven management (Barlow et al., 2018; Campos-Silva and Peres, 2016). Evaluating the effectiveness of protected areas in conserving the integrity of wildlife habitats and populations is important to inform protected area management and determine the value of this approach to conservation (Pringle, 2017; Watson et al., 2014). The unique dynamics of freshwater ecosystems has largely been neglected in the planning of protected area systems (Abell et al., 2007). Given their elevated vulnerability compared to other habitat types (Collen et al., 2014), spatial analyses highlight the need to prioritize freshwater ecosystem protection (Azevedo-Santos et al., 2019; Leal et al., 2020).

Extractive mining activities pose a threat to biodiversity on multiple levels and spatial scales, impacting both environmental parameters and aquatic species assemblages (Sonter et al., 2018). One of the most widespread forms of habitat alteration in the Amazon is the extraction of alluvial gold (Asner et al., 2013). While taking place with varying intensity in several areas of the Amazon during the second half of the 20th century, Artisanal Small-scale Gold Mining (ASGM) activities have surged in neotropical biomes over the last two decades, promoting substantial increases in deforestation rates (Caballero-Espejo et al., 2018). ASGM, occurring in rivers, lakes and accessible terrestrial land patches, causes hydroscape transformation through a number of ecological processes. These include soil washing with high pressure water causing erosion and bank habitat loss, habitat fragmentation through deforestation (Sonter et al., 2017), and the modification of aquatic hydrogeological processes as a result of increased sediments suspended in the body of water (Dethier et al., 2019). In addition, ASGM drives significant environmental contamination through the release of large quantities of toxic substances, especially mercury and cyanide (Malm, 1998; Veiga et al., 2014). In remote areas, the economy formed around ASGM may expose natural ecosystems to additional pressures. Mining-associated infrastructure development can attract human populations, causing new threats (Sonter et al., 2017) or exacerbating pre-existing threats, such as the introduction of invasive species and habitat loss from other land uses (Edwards et al., 2014). Also, improved accessibility as a result of mining infrastructure can increase fishing and hunting (de Carvalho Freitas et al., 2012). Evidence for such effects, however, is scarce, likely because they are cryptic and difficult to directly quantify (Raiter et al., 2014). One observable effect of ASGM at the landscape level is an increase in deforestation (Asner and Tupayachi, 2017).

Freshwater habitats in the Amazon basin contain high functional and taxonomic diversity of fishes, representing over 15% of fish species worldwide, with high rates of endemism (Dagosta and De Pinna, 2019). ASGM can have severe impacts on such biodiversity. Specifically, in tropical streams, ASGM has negative effects on fish taxonomic diversity and the occurrence of larger sized habitat specialists, favoring smaller, more ubiquitous species, without detectable effects on overall fish species richness and biomass (Allard et al., 2016; Brosse et al., 2011). Studies focused on habitat structure and hydrological processes suggest that rivers and streams subject to ASGM show decreased transparency and microhabitat diversity due to sedimentation (Dedieu et al., 2014; Dethier et al., 2019; Mol and Ouboter, 2004). Similar effects have been documented in lakes and reservoirs (Maia et al., 2018). Human-driven alteration of such ecosystems can make them more vulnerable to invasion and promote homogenization and trophic downgrading of fish and invertebrates (Petsch, 2016). Such alteration in the abundance of feeding guilds can ignite trophic cascades and have consequences for various ecosystem-level processes such as carbon sequestration and biogeochemical cycles (Estes et al., 2011).

Here, we examined the effectiveness of protected areas by quantifying the relative influences of fishing, ASGM and bottom-up environmental processes on medium-sized and large fish assemblages in a series of tropical oxbow lakes of a western Amazon biodiversity hotspot, the Madre de Dios province in Peru (Thieme et al., 2007), during the dry season. Our design included 'control' locations within protected areas and 'treatment' locations in unprotected areas with significant ASGM activity. We conducted our research in and around one of South America's premier protected areas, the Manu National Park. Manu is part of a UNESCO biosphere reserve, a World Heritage Site, and is considered one of the most biodiverse areas on Earth, making it a suitable case study to assess protected area effectiveness.

Our research incorporated several bottom-up covariates with variables reflecting top-down forcing from humans to allow us to examine the relative importance of a range of ecological and anthropogenic processes in determining fish abundance and diversity. We first investigated whether a number of components of biodiversity, such as species richness, fish abundance and fish biomass, are similar among protected and perturbed area oxbow lakes. Second, we examined whether spatial (i.e. how individuals are distributed among locations) or non-spatial (variation in occurrence among location types) components of oxbow lake perturbation had the largest influence on fish accumulation curves using the approach developed by McGlinn et al. (2019). Third, we tested the relative effects of bottom-up factors, ASGM pressure and associated fishing activities as drivers of the fish assemblage β diversity and species composition dissimilarity. Fourth, because human activities often result in losses of apex consumers (Estes et al., 2011), we compared the relative abundance of fish feeding guilds. We tested whether the proportions of carnivorous, detritivorous and omnivorous fish species differed in oxbow lakes outside protected areas. Taken together, our research questions allow the evaluation of the efficacy of protected areas in the region, promising to inform management decisions within and outside protected areas.

2. Materials and Methods

2.1 Study area

We carried out field work in the Madre de Dios province of Peru, as part of a study focusing on freshwater Amazon ecosystems. We focused on oxbow lakes, a type of shallow, elongated body of water commonly found in proximity of rivers of Amazon floodplains, that is created when a meander of a river gets cut off from the main channel due to erosion (Terborgh et al., 2018). Our study included 12 oxbow lakes in the protected areas of Manu National Park (11º41' S, 71º13' W) and the Amarakaeri Communal Reserve (12º25' S, 70º42' W), and 10 unprotected oxbow lakes in the lower part of the Madre de Dios river (12º40' S, 69º53' W; Figure 1), where significant mining activities have been occurring over the last three decades (Caballero-Espejo et al., 2018; Dethier et al., 2019). Disturbed lakes were located downstream from protected lakes. During the sampling period, all lakes were separated from the main river by land, with distances between their centroid and the river varying between 0.68 and 1.52 km for protected lakes and 0.94 and 2.76 km for unprotected lakes (Table S1). Thus, in both protected and unprotected areas there was considerable variation in lake-river dry season connectivity (Terborgh and Davenport, 2021). The study region has a humid tropical climate with a seasonal rainfall, lowest from May to September and varying from about 1700-3300 mm per year depending on proximity to the base of the Andes. Floodplains are seasonally flooded largely due to local precipitation and poor drainage, several times between December and April for brief periods (often <1–2 weeks). Large areas of slightly more elevated floodplain may infrequently or never receive floodwaters from the river. Because of wet season flooding and hydrogeological processes, both protected area and lower Madre de Dios oxbow lakes may be exposed to the effects of upstream human activities, although these impacts should be minimal, limited to indigenous communities, due to protected status of the entire watershed.

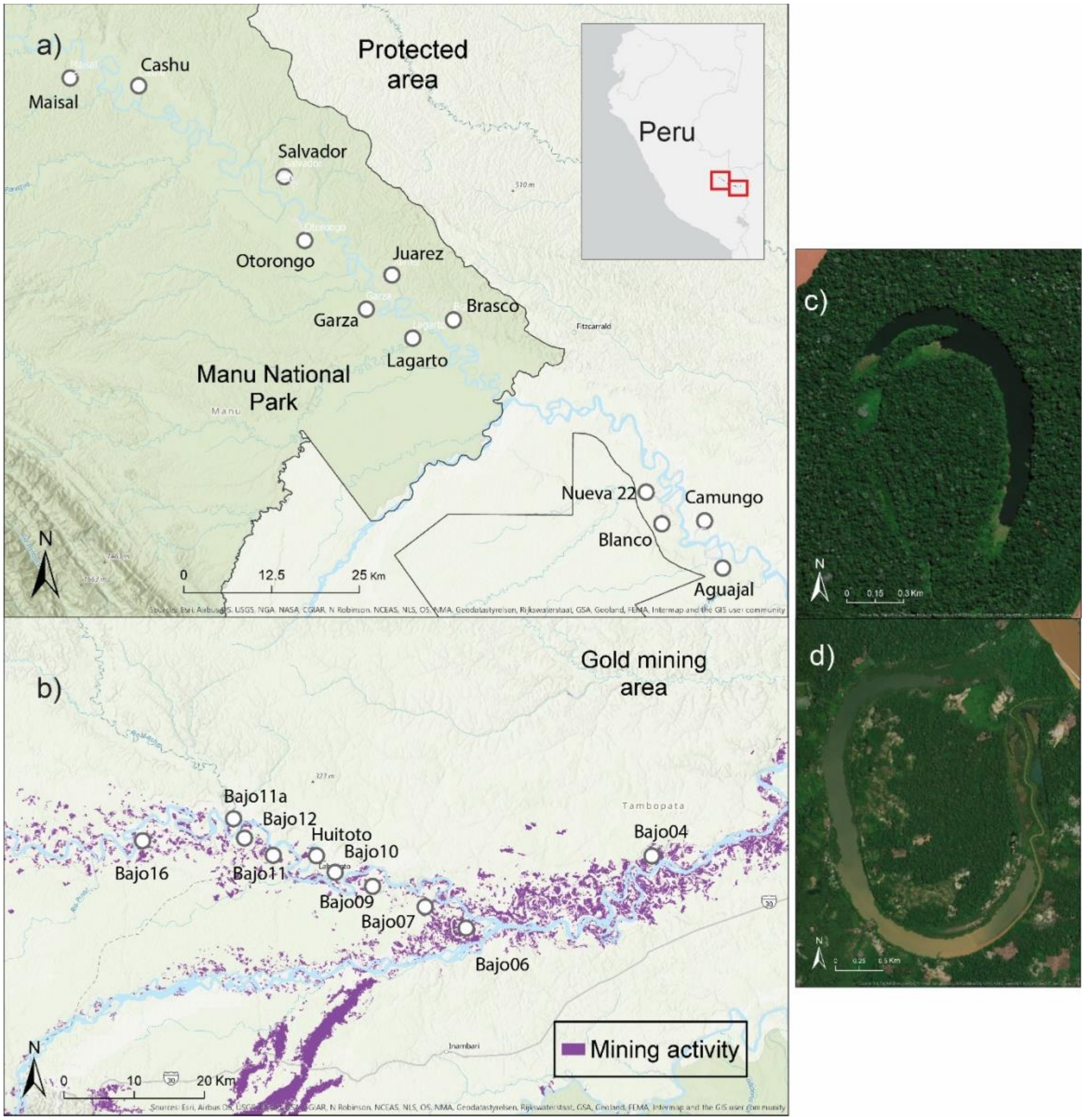

Figure 1. Map of research area in southeastern Peru with locations of fish surveys, including oxbow lakes in the protected areas of Manu National Park and Amarakaeri Communal Reserve (a), and oxbow lakes in the gold mining zone, with mining activity (Caballero-Espejo et al., 2018; b) and satellite images illustrating a protected (c) and a mined oxbow lake (d).

Manu National Park, a category II protected area (designated to protect large-scale ecological processes and biodiversity), has a number of local indigenous Matsiguenga communities, one of which overlaps the research area (Shepard et al., 2010). Members of this community have a short fishing season in the nearby Maizal oxbow lake (J. Kapechi, personal communication). The lower Madre de Dios mining area contains 11 small-sized communities with a formal population of 2,500. However, the true population is likely much higher, as there are several hundred smaller, informal camp sites, mostly formed around ASGM activities. During the last three decades, ASGM has increasingly become the area's main economic activity (Caballero-Espejo et al., 2018; Swenson et al., 2011). The area's communities and oxbow lakes can only be accessed through the Madre de Dios river.

2.2 Lake and landscape metrics

We developed a suite of abiotic and top-down covariates, including variables reflecting human activity, as predictors of fish abundance and diversity (Table 1). The type of vegetation and water quality in oxbow lakes may have important implications on its productivity and species assemblages. Neotropical oxbow lakes typically alternate between phytoplankton and macrophyte-dominated regimes reflected in the water surface Normalized Differential Vegetation Index (NDVI; Terborgh et al., 2018). We used the relevant bands on Landsat 8 satellite images (Roy et al., 2014) to calculate NDVI of the water body. In each lake, we averaged all point values within the area of continuous water to obtain a mean NDVI value (Terborgh et al., 2018). Because NDVI did not significantly differ between the sampling years (

$t_{21} = -1.06$; $P = 0.29$) we used as covariates values from the month of fish sampling. Several aquatic organisms require minimal levels of dissolved oxygen to survive and thus it is considered an indicator of water quality (Röpke et al., 2016). We assessed water quality parameters in each lake by measuring oxygen levels using a colorimetric Dissolved Oxygen Test Kit (LaMotte Company, Chestertown, MD, USA). We also used a Secchi disk (Test Assured©, Jupiter, FL, USA) to measure water transparency. To account for spatial variation, we performed both types of measurements at four points within each lake.

We developed variables that quantified the local and regional intensity of mining. For the local scale, we created a buffer of 300 m around each lake's margins. We chose this distance based on the width of sampled lakes (mean maximum width = 248.1 m). We used spatial data quantifying mining activities over the last three decades (Caballero-Espejo et al., 2018) to calculate the proportion of area from the buffer where deforestation and additional signs of recent mining were evident. The regional variable included the area surrounding each lake using a buffer of 5 kilometers around its centroid. Similarly, we calculated the proportion of mined area from the total buffer area. We also developed a variable quantifying the intensity of fishing within lakes. Fishing in the area is performed either by leaving gillnets tied to poles for several hours and posterior collection or the use of drag nets from small, motorized boats. We used the number of fishing poles observed within lakes and the presence and number of motorized boats to quantify fishing activity. Fishing index varied from no fishing (score 0) to consistent commercial fishing using motorized boats (score 3; Table 1). In addition to black caiman (*Melanosuchus niger*), giant otters (*Pteronura barsiliensis*) are one of the significant piscivorous species in tropical oxbow lakes and their presence may affect fish abundance. We calculated giant otter probability of occurrence in each lake by dividing the number of lake surveys in which otters were observed by the total number of visits. Each lake was surveyed at least 12 times for a mean of 3 hours per visit.

2.3 Fish sampling

We carried out a standardized fish sampling effort across sites. Each lake was sampled either during 2018 or 2019. To control for seasonal variation (Campos-Silva et al., 2020), we performed all fish sampling between May and July (months which belong to a similar stage of the dry season), except three sessions (7.1%), which took place in September for logistic reasons. We conducted 44 sampling sessions representing over 195.3 hours in 22 oxbow lakes (mean ± SE = 8.9 ± 0.6 hours per lake; Table S1, S2). We used gillnets of 0.4 mm nylon (40m long, 2m high), composed of three nets of mesh sizes 5, 7.5 and 10 mm between adjacent knots. The gillnet was set perpendicular to the lake shore, near the middle section of each lake and deployed for two to four sampling sessions, during the period before and after sunset (mean start time: 15:13, mean finish time = 19:15; mean ± SE 4.03 ± 0.12 hours per session). All fish captured were weighed, measured for length and photographed. Fish were subsequently identified based on specialized literature and taxonomic classification following Fricke et al.(2018) . Fish were then released in a different part of the lake after processing to avoid recapture. All sampling procedures complied with San Diego Zoo Global IACUC permit #17-012, Directorial Resolution Nº 126-2017 – GOREMAD/GRDE – DIREPRO and Permit 07-2017-SERNANP-PNM-JEF.

2.4 Fish assemblage analyses

The goal of our sampling protocol was to quantify species richness, abundance and biomass of medium and large-sized fish in oxbow lakes. Thus, our sampling did not cover the entire fish community in lakes sampled, which includes smaller species (e.g. da Silva et al., 2013). Nonetheless, to ensure that our sampling effort was adequate, we calculated abundance-based sampling completeness (Chao & Jost, 2012), using the “iNEXT” package (Hsieh et al., 2016). In addition to species richness (i.e. counting the total number of species per site), we calculated the first-order Jackknife estimator (Gotelli and Colwell, 2011) using the VEGAN package (Oksanen et al., 2016).

Table 1. Description, scale and justification of variables predicting fish species richness and abundance in oxbow lakes of the Madre de Dios province, Peru.

Variable	**Description**	**Scale (units)**	**Justification**
Size	Area of the open body of water	0 - 2 (km^2)	Larger lakes may support higher fish biomass
Elevation	Altitude of the lake centroid	206 - 483 (m)	Species abundance and distribution can vary with altitude
Dissolved oxygen	Oxygen level in water using a colorimetric Dissolved Oxygen Test Kit	0 - 9 (mg/L)	Dissolved oxygen is considered an indicator of water quality
Transparency	Depth of visibility with a Secchi disk	0 - 127 (cm)	Transparency can indicate the visibility and amount of organic matter in the water
NDVI	Normalized Differential Vegetation Index calculated from Landsat 8 images	-1 - 1	NDVI can indicate an oxbow lake ecological state and productivity (Terborgh et al., 2018)
Mining intensity	Proportion of mined area around lake bank	0 - 1	Mining can destroy bank habitat and promote the spill of toxic substances into water
Fishing intensity	Category of fishing observed during lake visits (0 =no fishing; 1= fewer than 10 net poles; 2 = more than 10 net poles /recent fishing signs; 3 = Fishing observed with motorized boats)	0 - 3	High fishing intensity may deplete local abundances and not permit population recovery
Otter occurrence	The proportion of surveys in which giant otters were detected out of total surveys	0 -1	Giant otters can impact fish communities through direct predation and indirect fear effects

Because our dataset included richness and abundance data on both the lake level and the area level, we performed a multi-scale analysis of the components of species richness (i.e. total number of species), using the Measurement of Biodiversity approach developed by McGlinn et al., (2019). We directly quantified contributions of changes in the total number of individuals (N), relative abundance (i.e. the Species Abundance Distribution - SAD) and aggregation of species, each represented by a distinct accumulation curve, to richness gains or losses due to ASGM across scales. Differences in accumulation curves of the same type from mined and protected areas represent the contributions of the three aforementioned components on the respective curve and can be used to quantify these contributions to change in species richness. The spatial plot-based accumulation curve contains all three components, combining the non-spatial approach of Gotelli and Colwell (2011) and the spatially constrained approach of Chiarucci et al. (2009). The spatial plot accumulation curve accumulates sites in a spatially explicit manner within each treatment. Each site is used as a starting site, and the resulting set of curves are averaged to produce a smoother curve. The difference between the spatial curves from protected and mined sites, calculated by subtracting the expected richness in mined areas from protected areas for a given number of sites, quantifies the effect of protection on all three components of richness (McGlinn et al., 2019).

Next, we constructed non-spatial, lake-specific species accumulation curves to estimate the effects of within-species aggregation on differences in species richness. In this case, because individuals are shuffled between sites within the mined and protected area, the difference between the non-spatial curves from the mined versus protected sites is the effect of protection on N and the SAD only. Subtracting the difference between the two non-spatial curves (representing the N and SAD effects) from the difference between the spatial curves provides the isolated effect of aggregation (McGlinn et al., 2019). We additionally removed the effects of protection on aggregation and N by constructing individual-based rarefaction curves (Gotelli and

Colwell, 2011). The difference between the individual-based rarefaction curves from the mined versus protected sites represents the protection effect on the SAD only. The contribution of changes in N was calculated by subtracting the difference between the individual-based rarefaction curves (SAD effect only) from the difference between the two non-spatial curves (McGlinn et al., 2019). Finally, to determine whether the observed treatment effects on each component differed from a random expectation, we examined departures for all effects (aggregation, N, and the SAD) from the null expectation across all sites by comparing empirical curves to the 95% quantiles of curves generated by the null models.

2.5 Lake covariates and fish assemblage patterns

To test for the influence of different covariates on the dissimilarity of fish assemblages among lakes, we used the non-parametric PERMANOVA test (Anderson, 2001). Fish assemblages were represented by species-by site matrices. The significance of the test was given by F-tests based on sequential sums of squares from 10,000 permutations of the raw data. We considered physical and chemical lake properties (lake altitude, size, dissolved oxygen, NDVI and transparency levels) as environmental variables and covariates reflecting additional top-down forces (mining intensity, fishing intensity and giant otter occurrence; Table 1). We built five different models: 1) A model including only environmental variables; 2) A model including only top-down variables with mining; 2) A model including only top-down variables with fishing; 4) A model including both top-down and environmental variables with mining and 5) a model including both top-down and environmental variables with fishing. We performed this analysis with two indices of dissimilarity: 1) the Bray-Curtis distance, which performs well with relative abundance data (Anderson et al., 2006), and 2) the Chao dissimilarity metric, a probabilistic extension of Bray-

Curtis which better accounts for rare and unseen species (Chao et al., 2005). We assessed model performance by examining the total of variance explained by the PERMANOVA test.

To further test the relative influence of environment and human activity, we dissected oxbow lake fish β-diversity into its environmental and biotic components, using distance-based Redundancy Analysis (RDA; Peres-Neto et al. 2006). This involves partitioning community variance into the fractions explained by environmental and top-down variables, using the model

$$Y = f[E + S] + R,$$

where Y is the community response matrix, E and S are matrices of environmental and top-down covariates, respectively, and R is a matrix of residuals (adapted from Dray et al., 2012). We tested for significant differences in the variation explained using a bootstrap procedure (Peres-Neto et al., 2006). RDA models were fitted to a Hellinger-transformed fish assemblage matrix. The Hellinger transformation divides by the total abundance at a site and then takes the square root (therefore dampening the effect of extremely abundant species), and has previously been shown to have desirable properties in the context of RDA (Legendre and Gallagher, 2001). PERMANOVA was performed with the *adonis* function and RDA analyses were performed with the *varpart* function, both from the VEGAN package in R (Oksanen et al., 2016).

2.6 Fish feeding guilds

We used two approaches to examine the effects of lake protection on fish feeding trophic structure. First, we divided the fish into three feeding guilds, carnivores, omnivores and detritivores, using collected data for local species and FishBase (Froese and Pauly 2017; Table S3). We calculated the relative abundance within guilds per lake sampled and compared them using 95% confidence intervals. We also compared the proportions of each feeding guild among areas using a chi-square test for proportions. Second, for the 10 most abundant species, we calculated the catch per unit effort for each sampled lake. We subsequently compared these between mined and protected lakes using a one-way Anova test (McDonald, 2009) .

3. Results

3.1 Fish biodiversity

We captured 1,922 fish representing 50 species from 20 families (Table S3). Sampling completeness did not differ among areas (protected range: 89.3% - 100%; unprotected range: 73.5% - 99.4%; Table S2). Protected lakes had slightly higher (but nonsignificant) species richness compared to unprotected lakes, with fish abundance and fish biomass significantly higher in protected lakes (Figure 2). This pattern was not detected using the first order jackknife estimator (mean ± SE: protected = 15.3 ± 2.0; unprotected = 14.4 ± 1.7).

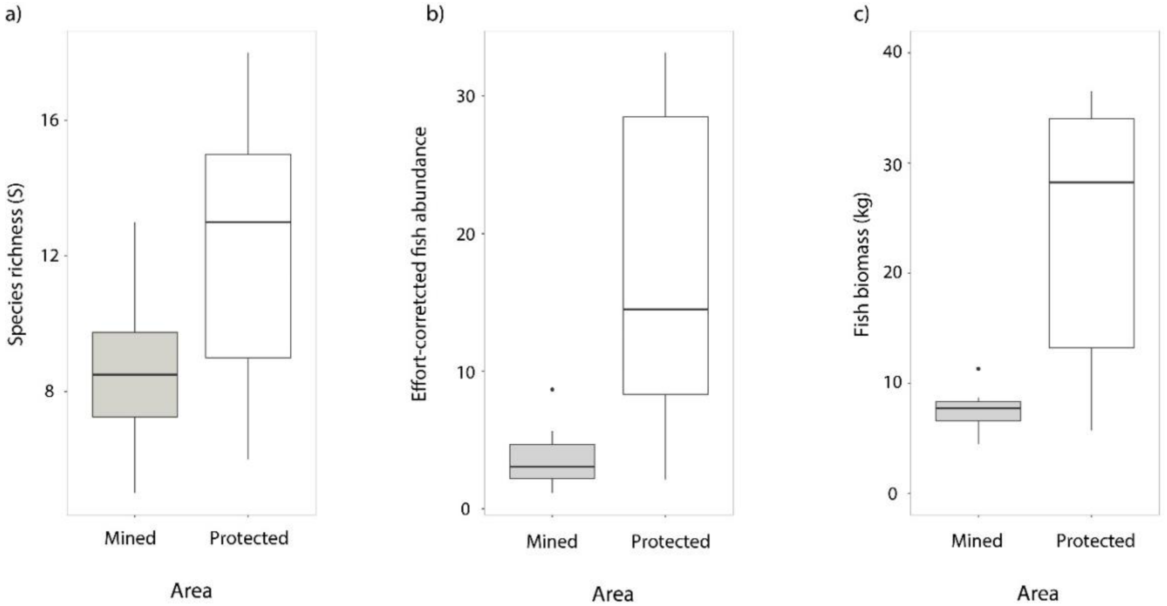

Figure 2. Box plots comparing fish species richness (a), effort-corrected fish abundance (b) and total fish biomass (c) in protected oxbow lakes and oxbow lakes with gold mining and fishing activity. Data were collected during 2018-2019 in the Madre de Dios province, Peru.

Results from the multi-scale Method of Biodiversity analysis show that species accumulation curves of mined lakes were below protected lake curves at all scales (Figure 3a-c). Separating the effect into the three components, we found that ASGM actually had a positive effect on species richness through its impact on the shape of the SAD (Figure 3f). This result suggests that ASGM has made the local community more balanced across species, meaning that dominant species were most significantly influenced by the habitat shifts. However, the negative effect of ASGM on species richness through reductions in the density of individuals was more dominant (Figure 3h,i) and made a much larger contribution to the effect of mining on richness. The effect of aggregation (Figure 3g) is much smaller compared with the other two components and was most important at small spatial scales.

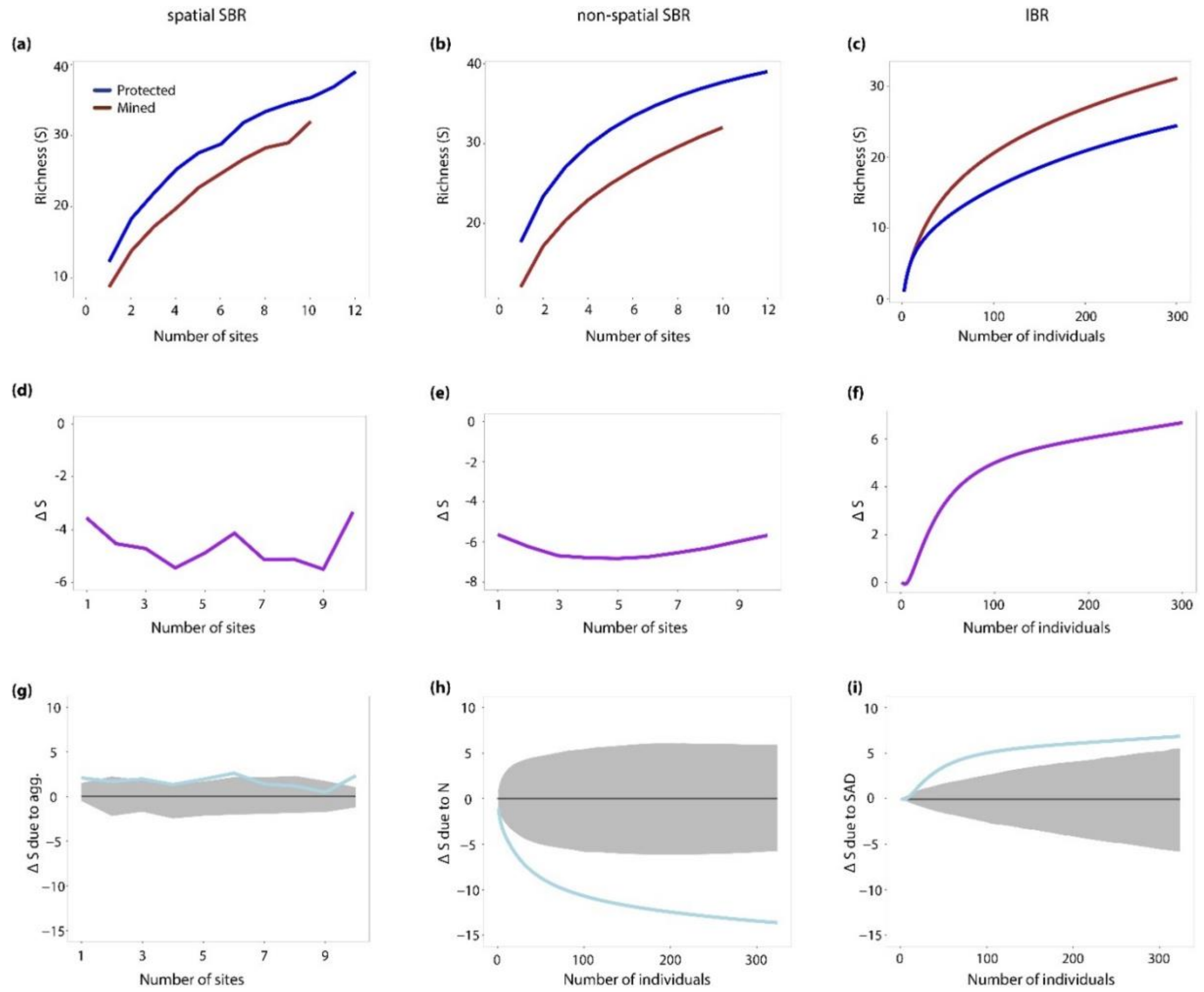

Figure 3. Plot of the Measurement of Biodiversity (McGlinn et al. 2019) multiscale analysis applied to the fish assemblage dataset. Panels a–c, show the mined (brown) and protected (blue) in the three types of rarefaction curves. The difference (i.e., treatment effect) for each set of curves is plotted in panels d–f. By taking the difference we can obtain the treatment effect on richness through a single component (g–i). The grey shaded area in g–i shows the 95% acceptance interval for each null model. See text for details.

3.2 Lake covariates and fish assemblage patterns

Mining intensities at local and regional scales were highly correlated (Spearman ρ = 0.96). Thus, we only used the local mining variables in subsequent analyses. Further, we did not include both the local mining and fishing variables in the same model because they were highly correlated (Spearman ρ = 0.81). Elevation was removed from top-down PERMANOVA models for a similar reason. We present the results of two models including top-down covariates separately, both of which explained more than half of the variation. The model including the fishing covariate performed best ($R^2 = 0.55$). In addition to fishing intensity, other significant predictors of fish assemblage dissimilarity were transparency and otter occurrence (Table 2). Models with the Bray distance matrix did not perform as well in explaining variance in dissimilarity but showed similar results (Table S4). RDA results suggested that both sets of variables were significant predictors of assemblage structure (environmental $F_{(5,15)} = 2.71$; $P = 0.009$; top-down $F_{(3,17)} = 2.25$; $P = 0.04$). The proportion of variation explained by environmental variables was higher (environmental adj. $R^2 = 0.17$; top-down adj. $R^2 = 0.12$) with considerable overlap in variation among sets (Figure 4). The proportion of unexplained variation was 0.76.

Table 2. Permutational MANOVA results of two models assessing the effects of abiotic and biotic variables on fish assemblage dissimilarity, using the Chao distance metric, in oxbow lakes of the Madre de Dios province, Peru.

Variable	*Df*	*MS*	R^2	*F*	*P*
Fishing activity model					
Size	1	0.037	0.013	0.38	0.74
Dissolved oxygen	1	0.194	0.066	2.08	0.13
Transparency	1	0.554	0.189	5.88	0.001*
NDVI	1	0.122	0.041	1.30	0.33
Otter occurrence	1	0.271	0.093	2.71	0.05*
Fishing intensity	1	0.428	0.147	4.59	0.01*
Residual	14	1.33	0.449		
Mining activity model					
Size	1	0.037	0.013	0.38	0.71
Dissolved oxygen	1	0.194	0.067	1.62	0.24
Transparency	1	0.549	0.189	4.57	0.06*
NDVI	1	0.254	0.087	2.11	0.13
Otter occurrence	1	0.139	0.048	1.15	0.40
Mining intensity	1	0.052	0.018	0.44	0.73
Residual	14	1.682	0.578		

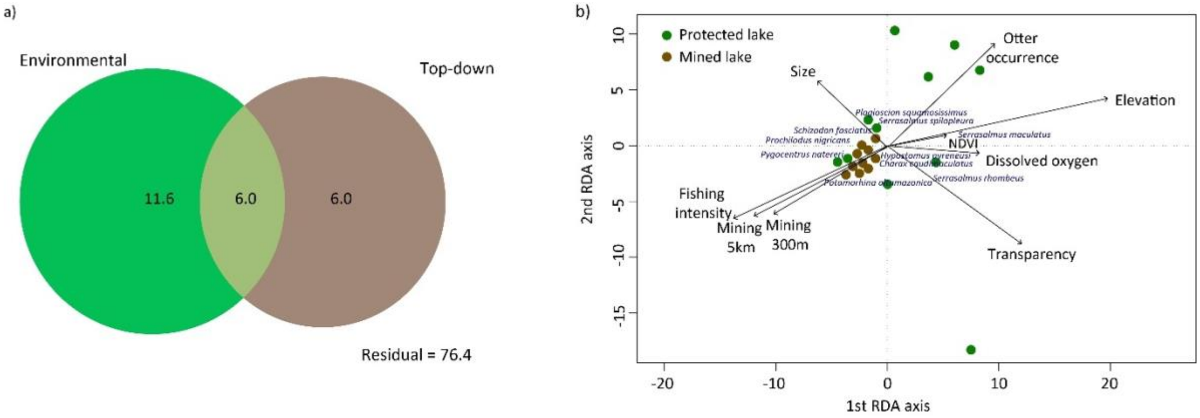

Figure 4. Variation partitioning of fish assemblage data represented across a Euler diagram (a). Community variation was partitioned using redundancy analyses (RDA) according to two sets of environmental and top-down covariates. Percentage values represent the adjusted coefficient of multiple determination (R^2 adj) and the value lying outside the area of the Euler diagram represents the percentage variation left unexplained. (b) Ordination tri-plot depicting the position of sampling points (colored circles), most abundant species (blue labels) and environmental and top-down variables (black arrows) along the first two axes of a redundancy analysis (RDA) of fish assemblage composition data. Fish were sampled during 2018-2019 in the Madre de Dios province, Peru.

3.3 Feeding guild analysis

Feeding guild was known for 99.6% of sampled fish, including 17 carnivorous, 19 omnivorous and nine detritivorous species (Table S3). Carnivorous species dominated protected lake assemblages ($\chi^2 = 612$, $P < 0.001$; Figure 5), whereas detritivores were the dominant guild in mined lakes ($\chi^2 = 39.5$, $P < 0.0001$). For both, there was a slight overlap in 95% CIs. Omnivore proportions were similar among areas ($\chi^2 = 0$, $P = 0.97$). Five of the ten most abundant species were carnivorous. Effort-corrected abundance of three piranha species of the genus *Serrasalmus* were 9.5 to 22.8 times higher in protected lakes compared to mined lakes. One-way Anova results confirmed that these abundances were higher in protected lakes (*S. maculatus*: $F_{(2,20)} = 135.1$, $P < 0.001$; *S. rhombeus*: $F_{(2,20)} = 78.5$, $P < 0.001$; *S. spilopleura*: $F_{(2,20)} = 98.3$, $P < 0.001$; Table S95). Of the four examined detritivores, *Potamorhina amazonica,* the most dominant in the mined area (39% of captured fish), had slightly lower abundances in mined compared to protected lakes ($F_{(2,20)} = 280.7$, $P < 0.001$). Abundances of all other detritivores were higher in protected lakes, except *Hypostomus pyreneusi* (Table S5).

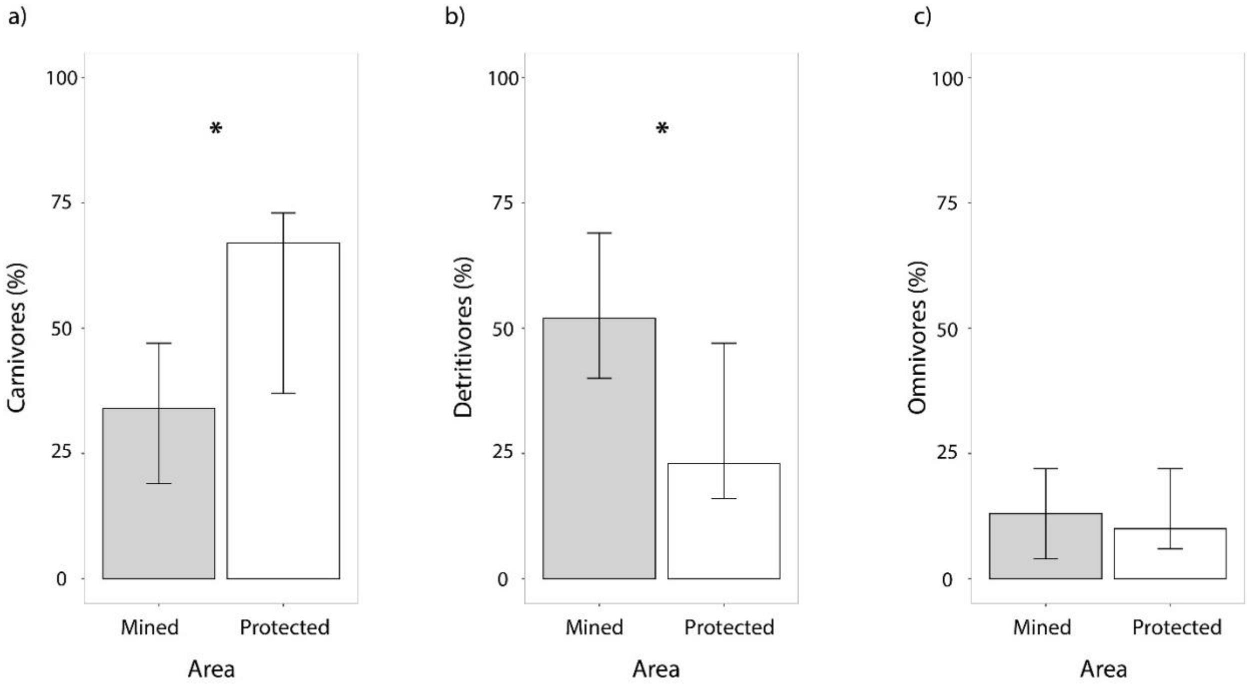

Figure 5. Bar plots comparing the percentages of carnivorous (a), detritivorous (b) and omnivorous fish (c) in protected oxbow lakes and oxbow lakes with gold mining and fishing activity. Error bars show 95% confidence intervals. Data were collected during 2018-2019 in the Madre de Dios province, Peru.

4. Discussion

We sampled disturbed and protected oxbow lakes to examine whether land protection is effective at maintaining local dry season fish assemblage biodiversity in the face of human activity. Our multi-scale analysis indicated that the pattern of apparent decrease in species richness in disturbed lakes was a consequence of differences in the most abundant species. Furthermore, the intensity of fishing activities and the level of transparency (indicating water quality and suspended matter) were the strongest predictors of fish species assemblage composition. Overall, decreases in abundance and biomass in disturbed lake fish assemblages were driven by declines in carnivorous species and were characterized by an increase in the proportion of detritivores.

This may indicate trophic downgrading of fish assemblages. While similar fish responses to disturbances driven by human activities, including ASGM, have been found in streams (Allard et al., 2016; Brosse et al., 2011), our findings provide novel evidence of such patterns in tropical oxbow lakes.

Whereas fish species richness in the mined area and within specific lakes was only mildly reduced, fish assemblages in lakes subject to ASGM showed significant reductions in total abundance and biomass. This conclusion was supported both by direct comparisons of treatment and control sites (Figure 2) and by the Measurement of Biodiversity analysis, which suggested that the most significant contribution to the difference in richness was due to reduced densities of individuals in the mining area (Figure 3). That a significant portion of this response was driven by differences in abundance of the five most frequently sampled carnivorous fish species—three from the *Serrasalmus* piranha genus—suggests that this feeding guild was the most sensitive to human activities, and that these species may have disproportionate impacts on community structure. Similar human-mediated declines of ecologically equivalent species have been documented in various disturbed aquatic and terrestrial ecosystems, including freshwater lakes (Estes et al., 2011; Folke et al., 2004). Our findings indicate that decreased abundance of carnivorous fish and altered fish assemblage structures could be a driven by ASGM.

Several lines of evidence demonstrated that the intensity of fishing in oxbow lakes had influence on fish assemblages. Such findings of indirect harvest-related consequences of extractive mining on wildlife populations are rare in the literature. Demand for bushmeat by mine workers can increase harvest both in mining locations and adjacent areas and drive decreases in biodiversity (Owusu et al., 2019). In addition, infrastructure developed for mining may bring new threats to biodiversity by enabling access to areas previously minimally exploited (Deikumah et al., 2014;

Sonter et al., 2017). As the majority of human settlements in the lower Madre de Dios gold mining area is composed of immigrants for economic purposes (Wyatt et al., 2017), it is likely that immigration has increased local demand for fish. Thus, increased fishing pressure is likely an indirect effect of ASGM. In this system, indirect influences of ASGM on oxbow lakes were more detectable compared to direct ones.

Further findings suggested that in addition to fishing pressure, water transparency was an important environmental driver of fish assemblage structure and that a larger proportion of the variation in β diversity among lakes was explained by environmental covariates. Decreased levels of transparency were documented in freshwater streams affected by gold mining, as a result of bank soil erosion and increases in suspended matter (Dedieu et al., 2014). Such patterns have also been shown in riverine sites of the Madre de Dios area basins (Dethier et al., 2019). Decreased transparency can influence assemblages of invertivores and surface fishes, including neotropical fish where several species are associated with water clarity (Merigoux et al., 1999). An increase in quantities of suspended matter may explain the higher frequency of detritivores in gold mining area oxbow lakes and may negatively impact carnivorous species by reducing prey detection distance and impairing prey capture rates (Utne-Palm, 2002).

Our results reflect fish assemblages during the dry season, when lakes are disconnected or maintain loose connection with rivers through swamps and creeks (da Silva et al., 2013). However, in the Manu basin and to a lower degree in the lower Madre de Dios, flood pulses, which have a role in transporting fish species and nutrients between rivers and adjacent oxbow lakes, occur during the wet season (Osorio et al., 2011). Significant changes in fish and invertebrate communities may occur in oxbow lakes (Röpke et al., 2016) and abandoned mining pools (Araújo-Flores et al., 2021). Increased lateral connectivity and distinct hydrological conditions allow larger species to be present mainly during the wet season (Röpke et al., 2016) and species turnover to behave in a predictable manner (Fernandes et al., 2014). Although we considered environmental factors such as lake size and elevation, due to logistic constraints, we were not able to account for seasonal variability. It is plausible that these pulse dynamics mitigate human-driven perturbations to unprotected oxbow lake fish communities and increase fish abundance in protected oxbow lakes. Thus, it is possible that our findings would have yielded even more pronounced differences between protected and disturbed lakes if fish populations were not partially replenished during seasonal flooding. Quantifying how ASGM and fishing activities interact with seasonality to influence fish assemblage structure and abundance in this system could be a promising research direction. In addition, although our relative abundance and richness estimates are comparable for our study system, they do not constitute comprehensive fish species surveys and comparisons with other work should be done cautiously. Smaller fish species, which are not targeted for subsistence and commercial fishing, may not be as sensitive to human disturbance and lake habitat modification and thus may not show numerical responses in unprotected areas, as observed with larger fish.

Consistent with findings of high Amazon-wide coverage of biodiversity (Jézéquel et al., 2020), within protected areas we found high integrity of fish assemblages, suggesting that regionally, current regulations within protected areas, which mostly limit access to protected freshwater ecosystems, are effective. Specifically, the sustainability of fishing and hunting within Manu National Park is under debate. Local Matsiguenga communities mostly hunt in the proximity of settlements and fish in adjacent rivers and streams (Shepard et al., 2010). Thus, oxbow lakes could function as refugia to maintain healthy fish populations during the dry season, with more significant interchange during floods in the wet season (Osorio et al., 2011). Our finding that fishing may impact fish abundance should provide guidance to managers regarding specific lakes that are more vulnerable. In the lower Madre de Dios ASGM area, local fishing for subsistence or commercial purposes was documented in 9 of 10 oxbow lakes. Thus, the lack of consistent regulation on fishing in the mining zone may contribute to a decrease in local fish numbers and the depletion of fish assemblages. Since fish constitute a significant part of local diets, especially for people involved in ASGM (Diringer et al., 2015), our results question the sustainability of current practices. Evidence of high mercury levels in fish (Yard et al., 2012) and human communities of Madre de Dios especially those living in mining zones (Ashe, 2012) should also deter local communities from reliance on fish for their diets. Targeting these communities with education and training, however, may be difficult because their temporary residence means they have less of a vested interest in the long-term sustainability of their actions. These mining communities contrast with local indigenous communities, which rely on the sustainability of fishing to support nutritional needs (Campos-Silva and Peres, 2016). We recommend the development of tailored approaches with a different mix of regulation/enforcement and educational support.

Similar to several other types of vulnerable freshwater ecosystems, tropical oxbow lakes have unique biodiversity and provide significant ecosystems services to local communities, among which are freshwater and fishing resources (Quirino et al., 2019). Preventing the degradation of bank habitats and the depletion of local biodiversity should be prioritized as a goal of stake holders and conservationists both on local and Amazon-wide scales (Laurance et al., 2012). Our findings also inform the broader debate on protected areas. As the backbone shouldering much of the burden to protect Earth’s biodiversity, protected area efficacy is sometimes questioned, particularly in the absence of data demonstrating a positive impact on biodiversity (Pringle, 2017). Here we demonstrate that during the dry season the Manu protected area is effective in its efforts to protect freshwater fish populations, even while allowing some harvest by indigenous communities. The effectiveness of this area at conserving biodiversity may provide justification for financial support for this and other protected areas (Watson et al., 2014). Further regulation and/or educational efforts may mitigate the impacts of human use of oxbow lakes outside of protected areas, allowing some activities to continue while ensuring a healthy aquatic ecosystem supporting human and wildlife communities.

Data Availability Statement

Fish occurrence data will be deposited at the Dryad repository.

Conflict of Interest

The authors declare no conflict of interest

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