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Giant otter populations persist and demonstrate recovery potential in suboptimal freshwater ecosystems degraded by gold mining

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ABSTRACT

In both terrestrial and aquatic ecosystems, land conversion is driving the depletion of biodiversity. Freshwater systems are especially vulnerable due to their accessibility and sensitivity to human pressures. Freshwater megafauna, which depend on suitable environmental conditions and stable prey resources, can serve as indicators of ecosystem health. We carried out visual surveys in four neotropical protected areas and the Madre de Dios gold mining corridor to examine how human pressures, particularly artisanal gold mining, influence the distribution and space use of giant otter populations. In unprotected lakes, extractive activities negatively impacted giant otter occurrence and group size, primarily through reduced water quality. Otter distribution and abundance were positively associated with water quality parameters, specifically transparency and dissolved oxygen. Protected areas maintained more stable otter populations, and otter occurrence showed seasonal variation, increasing during dry seasons. Within unprotected lakes, otters showed a tendency to occur in areas near sites with recent evidence of mining, a finding that suggests potential behavioral tolerance to lower-intensity disturbances and ability to recolonize disturbed freshwater habitats, rather than the predicted avoidance of such areas. However, this interpretation requires further investigation into long-term demographic impacts and the influence of unmeasured cumulative human pressures. Our multi-scale dataset provides unique evidence on the impacts of extractive activities on giant otter populations, underlining the need for multi-pronged conservation strategies. Our findings also emphasize the importance of protected areas in preserving neotropical freshwater biodiversity while highlighting the need to extend conservation efforts beyond current boundaries. Further research is needed on the impacts of extractive activities on otter demography and, critically, to test the hypothesis regarding the potential role of abandoned mining ponds as novel habitats for restoration of megafauna species and freshwater communities.

1. Introduction

Recent global trends of accelerated land transformation and defaunation impact freshwater ecosystems through the construction of dams, mining and land-cover change, especially in the neotropics (Castello and Macedo, 2016). These threats commonly drive the deterioration of freshwater habitat quality and the loss of hydrological connectivity (Pelicice et al., 2017). Compared to terrestrial areas, rivers and lakes, which support high levels of fish biomass, are more accessible to human populations, especially in the neotropics (Antunes et al., 2016; Azevedo-Santos et al., 2019). Larger freshwater species, some of which depend on fish resources, have low fecundity and slower life history strategies,

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which makes them particularly vulnerable to the deterioration of these ecosystems (He et al., 2020).

Human activity, which drives various types of disturbance to wildlife, can vary in type and intensity. This variation has implications for disturbance perceived by animals, which may include noise (Kunc et al., 2016), habitat modification (Wilmers et al., 2013), or the presence and movement of humans (Kays et al., 2017; Oriol-Cotterill et al., 2015). Extractive activities such as artisanal small-scale gold mining (ASGM) can represent a significant overall threat to vertebrate communities (Lamb et al., 2024). Among their specific impacts in freshwater ecosystems are bank habitat destruction, changes in hydrological processes, decreases in water quality, depletion of fish resources and loss of connectivity (Barocas et al., 2023b, 2021; Dethier et al., 2023a). In addition to their evident impacts on freshwater fish and bird biodiversity (Barocas et al., 2023a; Sonter et al., 2018), the environmental burden of ASGM is also likely to impact freshwater megafauna, which are more likely to bioaccumulate toxins (He et al., 2021, 2020).

In addition to deforestation and mercury loading, ASGM alters the landscape by creating thousands of small mining ponds, which, in turn, can drive disease transmission and land contamination. The size and connectivity of these ponds are variable, but their formation drives the establishment of novel freshwater communities (Dethier et al., 2023a; Gerson et al., 2020). Whereas a level of knowledge on the species composition of plankton, fish and invertebrates in these novel pond communities exists (Araújo-Flores et al., 2021; Timana-Mendoza et al., 2024), their functionality as ecosystems and ability to sustain species of higher trophic levels are not well understood.

The giant otter *Pteronura brasiliensis* (EN, IUCN 2021) is a top carnivore in neotropical freshwater ecosystems (Groenendijk et al., 2015; Leuchtenberger et al., 2018). Several types of human disturbance may impact giant otter distribution and abundance (Wallace et al., 2025). The construction of river dams is among the main threats to freshwater megafauna in general (He et al., 2021) and giant otters in particular, modifying their habitats (Palmeirim et al., 2014) and influencing their distribution (Calaça and de Melo, 2017; Raffo et al., 2022). An additional potential source of mortality and conflict with human populations is fishing activity. Giant otters, often perceived as competitors to fishermen, are occasionally subject to lethal control (Recharte et al., 2024). In areas with fishing activity, giant otter diet is composed of different species from those preferred by humans and has decreased nutritional value (Leuchtenberger et al., 2020).

Extractive activities, especially ASGM, can drive deterioration of giant otter habitat (Noonan et al., 2017; Wallace et al., 2025). Deforestation of suitable bank habitat can reduce the availability of dens and resting areas necessary for giant otters (Palmeirim et al., 2014). Otters in areas with gold mining can also be exposed to mercury, which accumulates in fish prey and can reach toxic levels (Barocas et al., 2023b; Martinez et al., 2018). Reduced fish availability in such areas may decrease foraging efficiency, and otters in mined areas show evidence of becoming sensitized to human presence to which they respond with increased vigilance and avoidance (Barocas et al., 2022, 2021).

Habitat selection by otters indicates a preference for areas with dense forest canopy cover on banks. In the aquatic medium, giant otters are more likely to favor open water and fallen logs, and avoid floating vegetation, preferences that appear to prioritize optimal fish habitat, cover from predators and higher quality denning locations (Abanto Valladares et al., 2022). Because giant otter populations are not well studied in areas heavily affected by mining and deforestation, little is known about their spatial responses to such disturbances and whether these extractive activities have implications for their space use, distribution and abundance. This study directly addresses this critical knowledge gap by presenting a comprehensive, multi-year, multi-region analysis of giant otter responses to extractive activities in the Amazon basin. While previous research has identified ASGM as a significant threat to vertebrate communities and freshwater megafauna, noting impacts such as mercury accumulation and behavioral sensitization, population-level impacts and detailed spatial responses of giant otters to these specific disturbances have remained largely unexplored.

Our approach builds upon existing studies on giant otter ecology, which often focus on habitat selection in pristine or less disturbed environments, by extending the investigation to human-impacted landscapes at multiple spatial scales, including the basin, freshwater body, and fine-scale locations within oxbow lakes subject to gold mining. We used occurrence data at the freshwater body and basin levels and fine-scale location data within oxbow lakes subject to gold mining to examine the multi-scale drivers of giant otter distribution and abundance in the Amazon basin. At the basin level, we analyzed distribution data from protected and unprotected areas in Peru's Madre de Dios region to understand whether giant otter occurrence was impacted by hydrological characteristics and human pressure. We compared locations of giant otter presence and absence to understand whether they differed in limnological properties and variables reflecting human activity.

In oxbow lakes, where we conducted more intense data collection, we examined whether two giant otter abundance metrics, probability of occurrence and group size, were associated with water quality, lake characteristics and human activity. We predicted that giant otter occurrence and abundance would be negatively driven by the intensity of mining and positively associated with water quality. In addition, we used a dataset collected over 17 years to examine the stability of giant otter groups by assessing temporal changes in giant otter group size within oxbow lakes.

At the finest scale, we used detailed giant otter location data in oxbow lakes subject to gold mining to examine the spatial associations of foraging giant otter groups with areas with evidence of deforestation resulting from mining. We predicted that, within oxbow lakes, giant otters would show avoidance of mined areas and preference for more pristine areas with dense forest canopy.

2. Materials and methods

2.1. Study area

We carried out field work in the Madre de Dios province of Peru, as part of two long-term studies focusing on giant otter population ecology and Amazon freshwater ecosystems. Five study areas were surveyed with different sampling intensities. At the regional scale, we conducted our research across four areas characterized by distinct protection levels: Manu National Park (11°41′ S, 71°13′ W) and Bahuaja-Sonene National Park (13°12′ S, 68°52′ W) are IUCN category II strictly protected, with control posts limiting human access; Amarakaeri Communal Reserve (12°25′ S, 70°42′ W) and Tambopata National Reserve (12°43′ S, 68°41′ W) have a lower protection level (IUCN category VI). One unprotected area is located in the gold corridor in the middle section of the Madre de Dios river (12°40′ S, 69°53′ W; Fig. 1), where significant artisanal gold mining activities have been occurring over the past three decades (Caballero-Espejo et al., 2018; Dethier et al., 2023b). The study region has a humid tropical climate with seasonal rainfall of over 2000 mm, lowest from May to September, and a mean annual temperature of 23°–24 °C. Floodplains are seasonally flooded largely due to local precipitation and poor drainage, several times between December and April for periods of 1–2 weeks. All four protected areas are sparsely populated by native communities. The Madre de Dios gold mining corridor, characterized by higher population density, contains over 15 small-sized communities with a formal population of 2500 and several more informal mining camps (Cuya et al., 2021). At the basin scale, we conducted more frequent and intensive surveys in three of the mentioned areas, including Manu NP, Amarakaeri CR, and the Madre de Dios gold mining corridor.

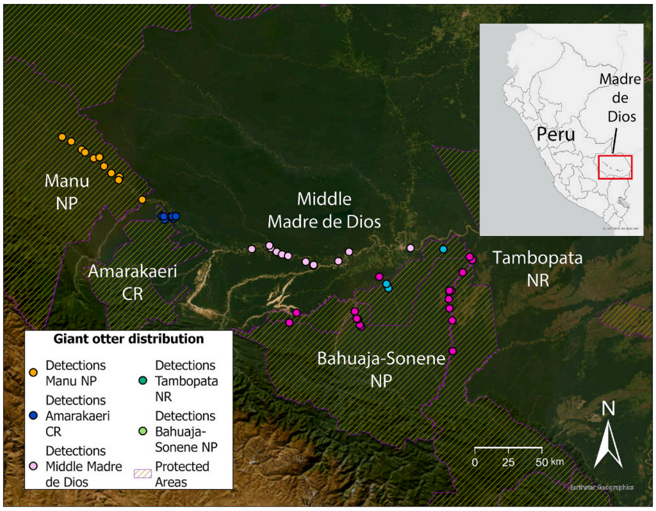

Fig. 1. Map of research area including the five sections surveyed for giant otter distribution between 2018 and 2023. Research was conducted in the Madre de Dios province of Peru.

2.2. Giant otter surveys

Surveys for visual evidence and giant otter presence signs were performed at two intensity levels. The lower intensity surveys focused on regional-scale distribution. In these, we performed transects with motorized boats along rivers and creeks and additional visits to oxbow lakes with the goal of detecting giant otter presence signs. River surveys were conducted in a 15 m aluminum boat at a standard speed to search for direct sightings of giant otters along the river stretches (Raffo et al., 2022). The principal objective was to detect giant otter presence. Thus, observations of giant otters were brief (Groenendijk et al., 2005). These were performed between 2007 and 2023 in Manu NP and between 2021 and 2023 in Amarakaeri CR, Tambopata NR and Bahuaja-Sonene NP. The higher intensity surveys involved more detailed visual observations. Between 2017 and 2023, we also conducted more intensive visual giant otter surveys in the Manu basin, spanning 12 oxbow lakes in Manu NP, and Amarakaeri CR; and 10 oxbow lakes and mining ponds in the middle Madre de Dios area. Both types of surveys consisted of teams of two or three trained researchers on an inflatable canoe, visually scanning water bodies to register giant otter observations or signs. Survey sessions lasted 2–6 h. In the case of oxbow lake surveys, each session included a scan of the entire water surface area. In case otters were observed, we registered locations and total number of individuals, and subsequently followed them for observation sessions, recording additional behavioral events (Barocas et al., 2022). As part of these more detailed surveys, group locations were recorded every 5 min, using a hand-held Garmin GPS, by estimating the distance from the kayak to the centroid of each giant otter group (Abanto Valladares et al., 2022). All sampling procedures complied with Permits 07-2017-SERNANP-PNM-JEF, 26-2023-SERNANP-JEF and D000627-2021-MIDAGRI-SERFOR-DGGSPFFS.

2.3. Regional-scale distribution and giant otter occurrence covariate analysis

To examine giant otter distribution on a regional scale, we used data from the lower intensity surveys (as described in Section 2.2) performed across oxbow lakes, river, and creek transects in consecutive years in four areas: in Manu NP between 2020 and 2023, and in Amarakaeri CR, Tambopata NR, and Bahuaja-Sonene NP between 2021 and 2023. For the Madre de Dios gold mining corridor, we used data from a preliminary area-wide survey to detect giant otters and select permanent sites surveyed in 2017 (Table S1). We considered giant otters "present" if they were observed during any of the surveys for a particular year and "absent" if none were detected during the year (acknowledging that otters may have been present at some point during the year but undetected during our surveys). To avoid replication and reduce spatial autocorrelation, we used for each study area the year with the highest number of points surveyed. This left 112 survey points in the dataset (Fig. 1, Table S2).

To associate regional distribution patterns with limnological properties and variables reflecting human activity, we used the Free Flowing Rivers dataset (Grill et al., 2019). We used the 'Near' function in ArcGIS Pro 3.1 (ESRI, 2016) to obtain the linear river feature nearest in space to each survey location. Despite some giant otter detections being within oxbow lakes, the associated linear feature reflects the position of their locations within the basin and the hydrological properties of their environment. For each feature we then obtained the values of six variables reflecting river order, hydrology, road density and connectivity in the vicinity of surveyed points (Table 1). We selected variables which reflect hydrological conditions impacting giant otter distribution and which showed variance among and within the basins in this study. We calculated area-specific means and compared the distributions of these variables between locations where giant otters were observed and locations from which they were absent. We additionally used principle components analysis (PCA; Greenacre et al., 2022) to visualize the data on a space reduced to its two main dimensions and examined possible clustering patters.

2.4. Lake and landscape metrics

To calculate lake metrics, we digitized each lake's open water body

Table 1
Limnologic and disturbance-related variables for linear features in the Free flowing Rivers dataset (Grill et al., 2019) examined for points where giant otters were observed or temporarily absent in the five research basins in Madre de Dios province, Peru.

Variable	Description	Justification
River Order	River order is defined and calculated based on the long-term average discharge in cubic meters per second using logarithmic progression: 4 = 100 – 1000 5 = 10 – 100 6 = 1—10 7 = 0.1—1 8 = 0.01—0.1	Giant otters are regularly found in oxbow lakes (Jessica Groenendijk et al., 2015), but show preference to more connected water bodies and streams (Pimenta et al., 2018).
RDD	Road construction index from GRIP database (Meijer et al., 2018). Index from 0 to 100 %	Roads may drive a decrease in freshwater body connectivity and generate runoff that decreases water quality (Castello and Macedo, 2016)
CSI	Connectivity Status. Index from 0 to 100 %; 100 % = full connectivity; 0 % = no connectivity.	Connectivity may impair giant otter movement and dispersal (Groenendijk et al., 2018)
Floodplain extent	Inundation (floodplain) extent in river reach catchment (%).	
Erosion yield in tons	Sum of erosion in tons per year per river reach. Calculated as the sum of sediment erosion within the river reach catchment (i.e., sediment erosion is not accumulated along the river network).	Giant otters show preference for well-drained soil suitable for dens and resting sites (Abanto Valladares et al., 2022; Palmeirim et al., 2014)
Volume of reach channel	Volume of the reach channel in thousand cubic meters (TCM). Calculated using width, length and depth of river channel.	Hydrological volume has implications on foraging and fish composition (Rosas et al., 1999)
Discharge volume	Average long-term (1971–2000) naturalized discharge in cubic meters per second (CMS).	Hydrological discharge variables have significance for foraging and fish composition (Rosas et al., 1999)

from a World Imagery layer. We used ArcGIS Pro (ESRI, 2016) to calculate the area and perimeter of each lake. For each lake in the mining zone, we also developed a variable that quantified the local intensity of mining. We created a buffer of 300 m around each lake's margins. We chose this distance based on the width of lakes (mean maximum width = 248.1 m), and on-ground observations suggesting that this scale captures mining operations directly associated with each lake's water body. We used published spatial mining data available as polygons (Caballero-Espejo et al., 2018) to calculate the proportion of area within the buffer where deforestation and additional signs of recent mining were evident. This proportion is subsequently referred to as 'mining intensity'.

Several aquatic organisms require minimal levels of dissolved oxygen to survive, and thus this is considered an indicator of water quality (Hauer and Lamberti, 2011). The type of vegetation, macrophyte regime and water quality in oxbow lakes may have implications on ecosystem state and species assemblages (Moi et al., 2021; Terborgh et al., 2018). We measured dissolved 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. We performed these measurements at four points within each lake, both in the wet and the dry seasons. To minimize temporal diel variation, these measurements were performed during early morning, between 6:00 and 8:00 am. Sampling locations were recorded using a Garmin© e-Trex GPS. We used the proportion of mined bank area, as well as the means of dissolved oxygen and transparency values for each census season, as explanatory variables in subsequent analyses.

2.5. Basin-scale occurrence

We were interested in the anthropogenic and environmental variables that drive pond or oxbow lake suitability to form the core of giant otter territories. For each lake surveyed during the higher intensity surveys (as described in Section 2.2) in Manu NP, Amarakaeri CR, and the Madre de Dios gold mining corridor, we specified occurrence probabilities between 2018 and 2023 as response variables in Generalized Linear Mixed Models (GLMM; Harrison et al. 2018). We selected the variable reflecting the proportion of mined bank area for the modeling procedure. From the water quality variables, we selected the season-specific means of transparency and dissolved oxygen concentration because they showed strong association with lake-specific occurrence when specified as univariate models. Because wet season occurrence was reduced compared to the dry season, we included an interaction between mining proportion and season. We included the distance from river variable in the full model but did not include lake size to avoid over-parametrization (Harrison et al., 2018), and because this variable was not strongly associated with giant otter occurrence in univariate models.

We built a full model including the interaction term between mining proportion and season (dry or wet), and fixed covariates for the multi-year seasonal means of transparency and dissolved oxygen. Lake ID was specified as a random variable in a generalized mixed model (Harrison et al., 2018) with a Poisson structure. The total number of lake and season-specific giant otter detections was specified as the response variable. We ran the full model and all additional combinations using the'*dredge*' function in the 'MUMIN' package (Barton and Barton, 2015), and assessed relative model support using AICc (Burnham and Anderson, 2002). We examined possible correlations between predictors and tested the model for overdispersion and additional assumptions (Zuur et al., 2010) using the DHARMa package (Hartig, 2020).

2.6. Temporal abundance trends

To understand whether population and group sizes were stable in our three more intensively surveyed study areas, we performed two analyses. In continuation of research by Groenendijk et al. (2014), who presented population counts and group compositions between 1990 and 2006, we compiled results of total number of adult, juvenile and cub otters observed during long-term monitoring (lower intensity surveys) in Manu NP between 2007 and 2023 and examined the consistency of population size. For each season between 2018 and 2023, when Manu NP, Amarakaeri CR and the Madre de Dios gold mining corridor were surveyed more intensively, we built a 95 % confidence interval for group sizes in each survey area and plotted them over time to visually examine whether there were temporal fluctuations.

2.7. Basin-scale abundance

The size of giant otter groups reflects the quality and carrying capacity of territories composed by oxbow lakes (Groenendijk et al., 2015). To examine the drivers of local giant otter density, we employed a similar modeling procedure with group size data collected during the higher intensity surveys (as described in Section 2.2) from each lake in Manu NP, Amarakaeri CR, and the middle Madre de Dios area, using its multi-year season-specific group size as the response variable. We built a linear mixed model including sampling season, lake size, bank mining proportion, water transparency, dissolved oxygen, size and distance from rivers as fixed factors and lake ID as a random factor. We examined the relative fit of all variable combinations to the data using the'*dredge*' function in the 'MUMIN' package (Barton and Barton, 2015). We similarly examined possible correlations between predictors. We examined the cumulative weight of each variable (i.e. the sum of the weights of all models in which this variable is included) and the best-supported model's coefficient estimates, subsequently testing it for overdispersion and additional assumptions (Zuur et al., 2010).

2.8. Habitat selection in unprotected oxbow lakes

To examine whether giant otters avoided deforested bank areas reflecting artisanal gold mining activity, we used an approach comparing used and available points (Manly et al., 2002). We restricted this analysis to group locations recorded during the higher intensity surveys (as described in Section 2.2) in nine oxbow lakes and one mining pond, all subject to gold mining. Selection for types of soil, forest canopy and floating vegetation were previously examined elsewhere (Abanto Valladares et al., 2022). We therefore restricted this analysis to locations in nine lakes and one mining pond, in which there were mining-driven deforestations scars in the banks. We considered all giant otter locations as used and generated an identical number of random ('available') points within each lake's water area. In cases with fewer than 50 observed points within a lake, we generated 50 random points to ensure that sampling captured each lake's spatial variation. We used ArcGIS (ESRI, 2016) to calculate the distance between each used and available point and the nearest spatial gold mining polygon.

We used these distances as a fixed predictor in a Generalized Linear Mixed Model (GLMM) with a binomial link function, specifying presence (for used locations) or pseudo-absence (for available locations) and the response variable. We specified lake identity as a random covariate.

We added lake-level mining intensity (the proportion of mined bank area) and lake protection (binary) as additional covariates in an interaction term with distance from mining. We built four models including these covariates and lake protection (two lakes were protected by local concessions) as fixed factors in an interaction term (Table S9). No correlation between fixed covariates exceeded $\rho = 0.64$. We additionally tested a null model, including only the random covariate (lake identity). We compared the fit of competing models using AICc (Burnham and Anderson, 2002). To examine whether possible avoidance of deforested areas was directly related to mining activity or to forest clearing and modified bank habitats left after mining, we performed this analysis with the most up-to-date mining data (between 1984 and 2019) and with data from the last decade excluded (1984–2013).

3. Results

3.1. Regional-scale distribution

Between 2017 and 2023, we performed 348 surveys on 106 sites, which included lakes, streams, and river portions in Manu National Park (NP), Amarakaeri Communal Reserve (CR), the Madre de Dios gold mining corridor, Tambopata National Reserve (NR), and Bahuaja-Sonene NP. Survey efforts and occurrence probabilities varied among years. Using data collected during the higher intensity surveys (as described in Section 2.2), overall giant otter occurrence probability (i.e. the number of giant otter detections divided by the number of surveys) was highest in the western Protected Areas (PAs): Manu NP (0.55) and Amarakaeri CR (0.83). These higher intensity surveys also demonstrated that Manu NP had relatively consistent giant otter occurrences throughout the study period, while Amarakaeri CR showed some fluctuations, including an increase in 2022 (Figs. 2a,b). The central unprotected middle Madre de Dios area (overall probability = 0.26) was less stable across seasons and years, particularly exhibiting low probabilities during wet seasons between 2019 and 2023 (Fig. 2c).

Data collected with reduced sampling intensity in Manu NP showed general agreement with results from the more intensively sampled areas, yielding similar probabilities of occurrence (Fig. 2d). In the less intensively sampled eastern PAs (Tambopata NR = 0.24; Bahuaja-Sonene NP = 0.19), where several sampling locations were rivers and creeks, giant otter occurrence values were more akin to unprotected oxbow lakes within the Madre de Dios gold mining corridor than to the more productive oxbow lakes found in the western PAs (Fig. 2 e,f). For comparisons of sites where giant otters were present versus sites where they were unobserved, using data from the regional-scale (lower intensity) surveys (the 112 survey points as described in Section 2.3), river order tended to be higher in sites of absence across all areas except Tambopata NR. Road density values were lower in unobserved sites in Manu NP but were similar in all other areas except Tambopata NR. Connectivity was close to 100 % in all areas and locations, showing no substantial variation. Reach channel volume was higher in locations where giant otters were unobserved in Manu NP, Bahuaja-Sonene NP, and Tambopata NR. Additional metrics of volume and discharge were similar among sites where giant otters were observed and unobserved in all study areas, except for Tambopata NR, where values for reach channel and discharge volume were higher in locations where giant otters were not detected (Fig. 3, Table S2). The Principal Component Analysis (PCA) plot indicated a clustering of locations in Bahuaja-Sonene NP and Tambopata NR, though no significant patterns were found in the plotted locations of giant otter presence and absence points within the two main principal component spaces (Fig. S1).

3.2. Basin-scale occurrence

Between 2018 and 2023, we conducted 712 repeated visual giant otter surveys in intensively sampled lakes of Manu NP, Amarakaeri CR and middle MdD. The overall probability of giant otter occurrence in protected oxbow lakes (0.583) was higher by a factor of 2.6 than in unprotected lakes and ponds within the Madre de Dios gold mining corridor (0.223). Giant otter occurrence was slightly higher in the dry (0.467) compared to the wet season (0.421; Fig. 4, Table S3). In all unprotected oxbow lakes, giant otters were observed at least once. Probability of occurrence in these locations ranges were 0 – 0.67 in the dry season and 0 – 0.39 in the wet season. We also documented the presence of giant otters in abandoned mining ponds on two separate occasions.

The best-supported model for giant otter occurrence (AICc weight = 0.31) included the water quality and mining proportion variables (Table S4). Otter occurrence was negatively associated with proportion of banks mined ($\beta \pm SE = -0.46 \pm 0.12$, P = 0.0001; cumulative AIC weight = 0.94), and positively associated with dissolved oxygen levels ($\beta \pm SE = 0.16 \pm 0.08$, P = 0.049; cumulative AIC weight = 0.57) and water transparency (cumulative AIC weight = 0.83; $\beta \pm SE = 0.24 \pm 0.08$, P = 0.002; Fig. 3; Table S5, S6). The fixed effects accounted for the majority of variance in giant otter occurrence (conditional $R^2 = 0.76$;

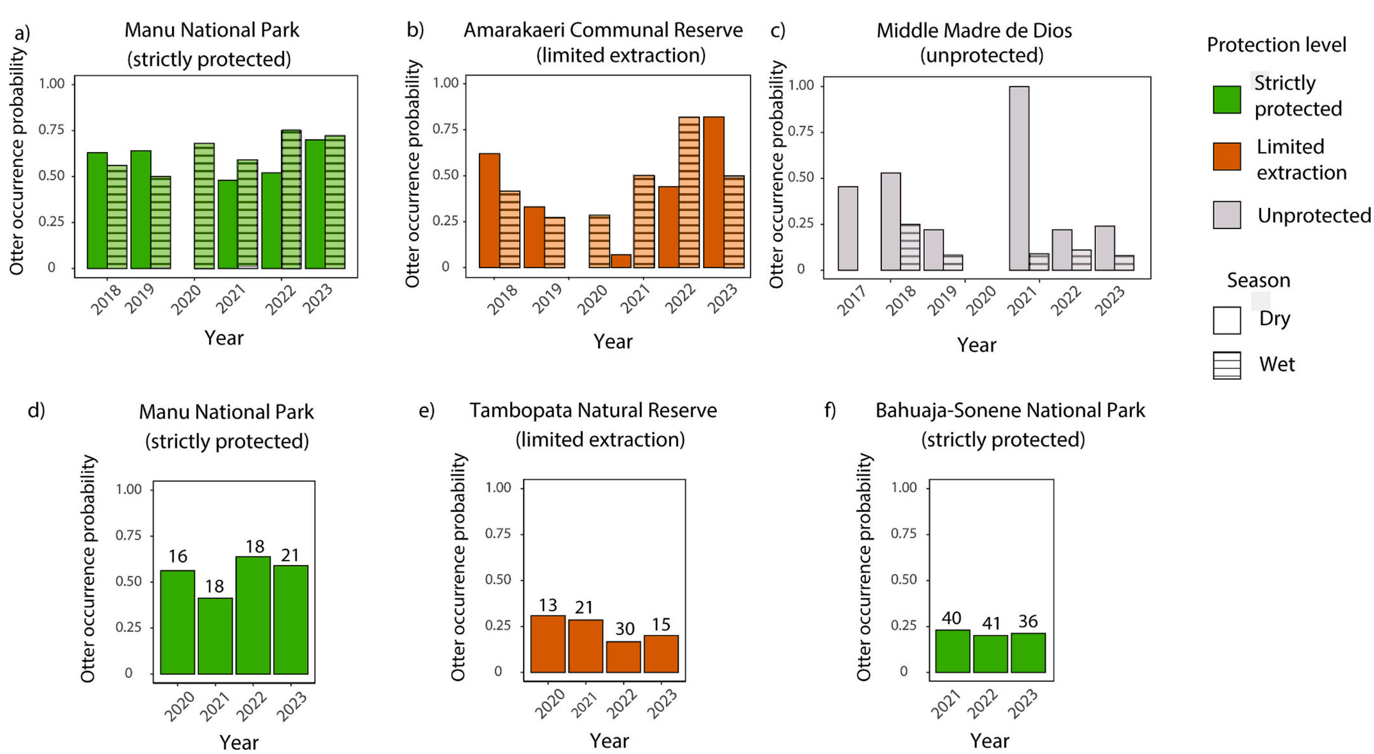

Fig. 2. Giant otter occurrence probability (the number of giant otter detections divided by the number of surveys) in oxbow lakes and river segments sampled intensively in both the wet and dry season between 2017 and 2023 (a,b,c) and with a reduced sampling effort but over more locations (d,e,f) between 2020 and 2023. Number of sites surveyed yearly appear inside bars. Research was conducted in the Madre de Dios province of Peru.

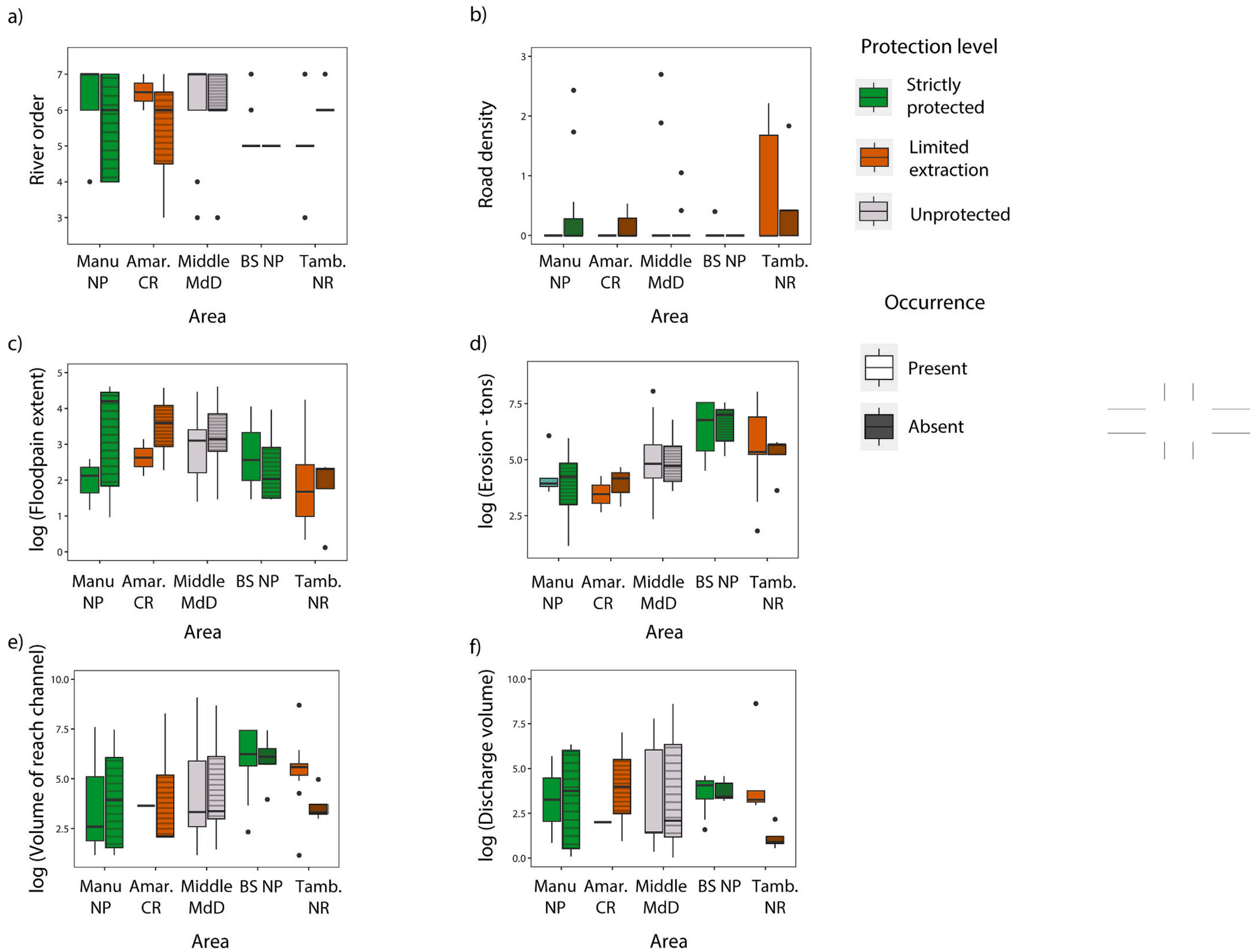

Fig. 3. Boxplots showing the distributions of six variables reflecting regional hydrological conditions and human pressure in locations (Table 1) where giant otters were observed or absent. Area codes are Manu NP (Manu National Park), Amar. CR (Amarakaeri Communal Reserve), Middle MdD (Middle Madre de Dios), BS NP (Bahuaja-Sonene National Park), and Tamb. NR (Tambopata Natural Reserve). Giant otter occurrence data were collected in four protected and one unprotected area in Peru's Madre de Dios region between 2018 and 2023.

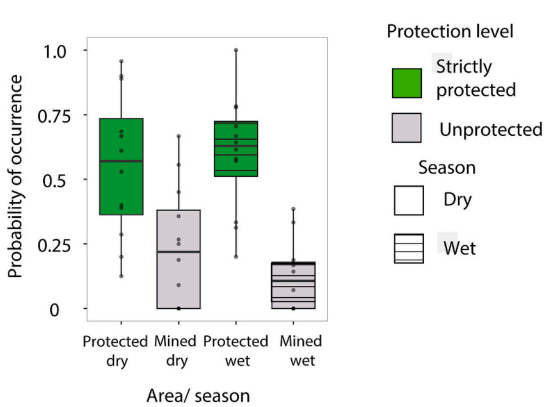

Fig. 4. Boxplots of giant otter occurrence probabilities in protected and unprotected area oxbow lakes during the dry and wet season. Giant otter occurrence data were collected in Peru's Madre de Dios region between 2018 and 2023.

marginal $R^2 = 0.62$). There were no indications of overdispersion ($P = 0.72$) or deviation from expected residual distribution ($P = 0.52$) for the best-supported model.

3.3. *Temporal abundance trends*

Total population estimates in Manu NP, surveyed with reduced sampling intensity varied between 25 and 57 (Fig. 5). Group sizes between 2018 and 2023, derived from the higher intensity surveys in Manu NP, Amarakaeri CR, and the middle Madre de Dios area, were more stable in Manu NP (mean range = 3.9, 4.6) compared to the less protected Amarakaeri RC (mean range = 1, 4.8) and the Madre de Dios gold mining corridor (mean range = 0.9, 4.2), which showed a significant decrease between 2018 and 2019, a peak in 2021 and an additional crash during the 2023 wet season (Fig. 5).

In the four oxbow lakes of the Amarakaeri CR the otter population increased from 8 to 10 individuals at 2018–2019 to 15–20 in the latter period. In the unprotected area, population sizes experienced higher fluctuation, with a decrease from the initial value of 37 to 6–12 individuals in later surveys. Mean group sizes followed similar trends. Mean group size was typically higher (~4 individuals) and stable from wet to dry seasons across years in the protected Manu NP. The pattern for the unprotected areas was substantially different, showing more differences between seasons (typically lower group size in wet season, especially for the least protected middle Madre de Dios area). Inter-annual group size was also more variable in unprotected areas (Fig. 6b).

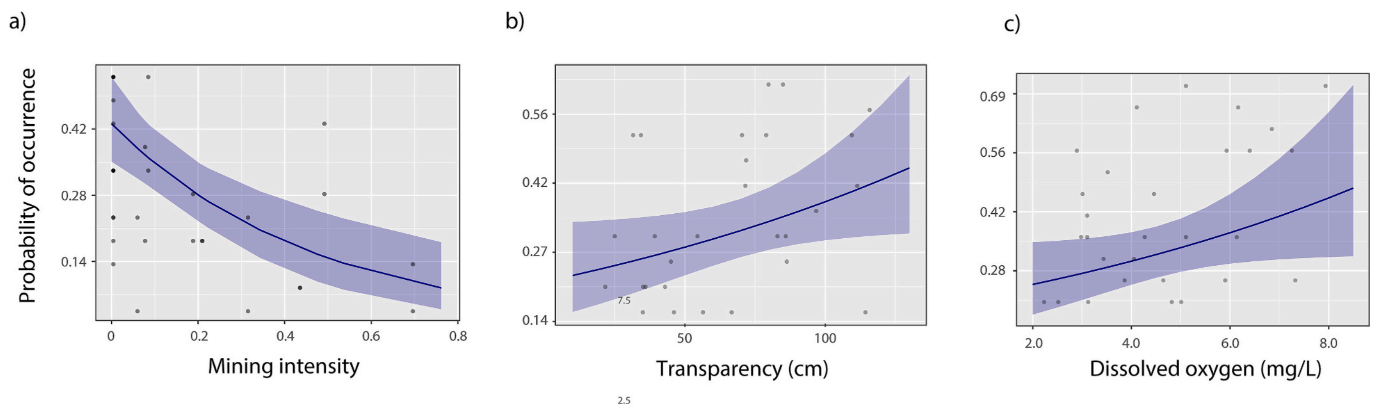

Fig. 5. Best-supported model outputs for the influences of lake mining intensity (a), water transparency (b) and dissolved oxygen concentrations (c) on giant otter occurrence probability (the number of giant otter detections divided by the number of surveys) and in protected and impacted oxbow lakes according to the best-supported model. Prediction plots were generated with the 'plot_model' function (sjPlot package; Lüdecke and Lüdecke 2015). Grey points denote observed group occurrence probabilities. Giant otter occurrence data were collected in Peru's Madre de Dios region between 2018 and 2023.

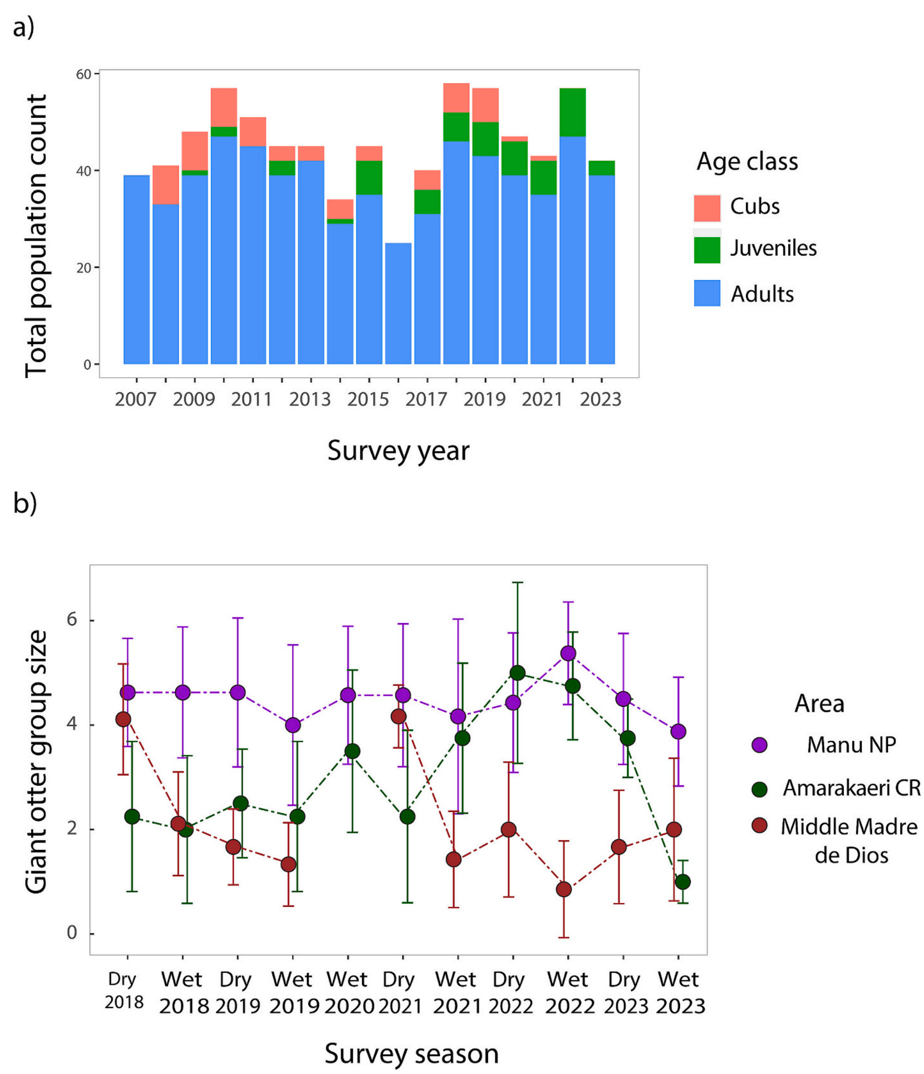

Fig. 6. Total giant otter abundance in Manu National Park over time (a) and seasonal means ± one standard error for group sizes In Manu NP (purple), Amarakaeri CR (green) and the middle Madre de Dios area (brown; b). Abundance data were collected in Peru's Madre de Dios region between 2007 and 2023. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Basin-scale abundance

For the model examining drivers of group size, utilizing data from the higher intensity surveys in Manu NP, Amarakaeri CR, and the middle Madre de Dios area, the best-supported variables were transparency (cumulative AICc weight = 0.84), dissolved oxygen (cum. weight = 0.49) and lake size (cum. weight = 0.28; Table S7, S8). Otter group size was positively associated with water dissolved oxygen levels ($\beta \pm SE = 0.41 \pm 0.21$, $P = 0.05$) and water transparency ($\beta \pm SE = 0.04 \pm 0.01$, $P < 0.001$; Fig. 7; Table S9). The fixed effects explained less than half of variance in giant otter group size (conditional $R^2 = 0.68$; marginal $R^2 = 0.32$). The model received significantly higher support compared to a null model, including only the random factor (Likelihood ratio test $x^2 = 16.0$; $P < 0.001$; $\Delta AICc = 6.6$). There were no indications of over-dispersion ($P = 0.75$) or deviation from expected residual distribution ($P = 0.85$).

3.5. Habitat selection in unprotected oxbow lakes

We collected 814 giant otter locations during the higher intensity surveys (as described in Section 2.2) from nine oxbow lakes and one pond, all subject to gold mining, and compared them with 1148 available points. The distances of used points from deforestation patches in lake banks were slightly higher compared to available points (mean ± SE used = 324.8 ± 9.3 m, median = 182.6 m; mean ± SE available = 284.8 ± 7.6 m, median = 254 m; Fig. 8). The model with a specified interaction term between the proportion of mining in lake banks and distance from mining locations was best supported (Table S10). The coefficient for distance from mining was negative ($\beta \pm SE$ distance = -0.05 ± 0.05; $P = 0.33$), suggesting that giant otter utilization of areas in proximity to mining varied with mining intensity within lakes. Used giant otter locations were negatively associated with the proportion of mined banks ($\beta \pm SE$ mined proportion = -3.18 ± 0.99; $P = 0.001$; Table S11). This relationship differed among levels of mining (Fig. 8). This model received significantly stronger support compared to the null model ($\Delta AIC = 7.7$; Likelihood ratio test $x^2 = 13.7$; $P = 0.003$). The correlation between distance from mining and lake-level mining intensity was negative and moderate (Pearson's r = -0.5). The same modeling procedure excluding mining activity from the past decade gave similar, but less significant, results: the best-supported model included an interaction between distance from mining and the lake-level mining intensity ($\Delta AIC = 4.2$; Likelihood ratio test $x^2 = 10.2$; $P = 0.02$).

4. Discussion

We conducted extensive surveys across four protected areas and one unprotected area impacted by extractive activities to investigate the influence of human pressures on the distribution and abundance of giant otters. Our results highlight reduced occurrence and increased variability in group sizes in unprotected oxbow lakes, as well as a positive association of otter occurrence and local abundance with water quality. These findings suggest that extractive activities, such as gold mining, negatively impact giant otter habitat quality and abundance. Interestingly, giant otters were more likely to occur in areas in closer proximity to deforested areas previously subject to gold mining, particularly in lakes with lower mining intensity. This finding may reflect the species' behavioral tolerance to less intensive disturbance and their ability to recolonize habitats undergoing recovery, particularly once human activity and presence diminish (Calaça and de Melo, 2017; Pimenta et al., 2018), However, inferring full adaptation from presence alone must consider potential time lags in ecosystem recovery and the influence of various unmeasured factors. This is likely not a true preference for degraded conditions, which are typically lower-quality but potentially less disturbed at certain times. Importantly, this study explicitly documents population-level impacts of extractive activities on giant otters, providing rare evidence of how disturbances at multiple spatial scales affect this top freshwater predator.

4.1. Habitat quality, water resources, and giant otter distribution

Our findings underscore the role of water quality in shaping giant otter habitat use and population dynamics. Reduced fish availability in turbid lakes – an outcome of extractive activities – can explain diminished otter occurrence and inconsistent group sizes in unprotected oxbow lakes. Water transparency, shown to be a significant driver of fish diversity, may improve giant otter foraging efficiency. Lakes with low fish availability and reduced transparency are suboptimal habitats, as demonstrated by previous studies that report lower fish capture rates in such conditions (Barocas et al., 2022, 2021). Similarly, low dissolved oxygen levels may signal impaired lake productivity, negatively affecting microorganisms and fish populations, which are crucial for sustaining giant otters (Karpowicz et al., 2020; Moi et al., 2022).

The stability of giant otter population indices was higher in protected areas like Manu NP, where seasonal and yearly fluctuations in abundance and group size were minimal. In contrast, the Madre de Dios gold mining corridor exhibited larger demographic variations. The observation that in some years unprotected lakes supported giant otter group sizes similar to those in protected areas suggests that there are no inherent differences in ecological carrying capacity of these lakes, but that the ability to support larger group sizes is periodically compromised in unprotected lakes, likely due to human disturbance such as mining. These findings indicate that the integrity of forested banks and freshwater ecosystems, ensuring stable fish resources and water quality, may provide giant otters with more predictable habitats. This line of evidence supports freshwater habitat quality as a key driver of giant otter territory stability and demographic performance.

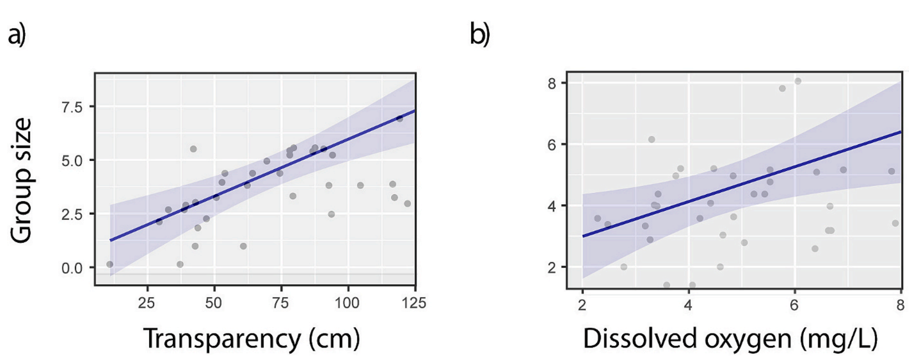

Fig. 7. Water quality variables predicting giant otter group size according to the best-supported linear mixed model. Blue lines represent coefficients and shaded areas 95% confidence intervals. Prediction plots were generated with the 'plot_model' function (sjPlot package; Lüdecke and Lüdecke 2015). Grey points denote the observed group sizes. Group data were collected in Peru's Madre de Dios region between 2018 and 2023. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

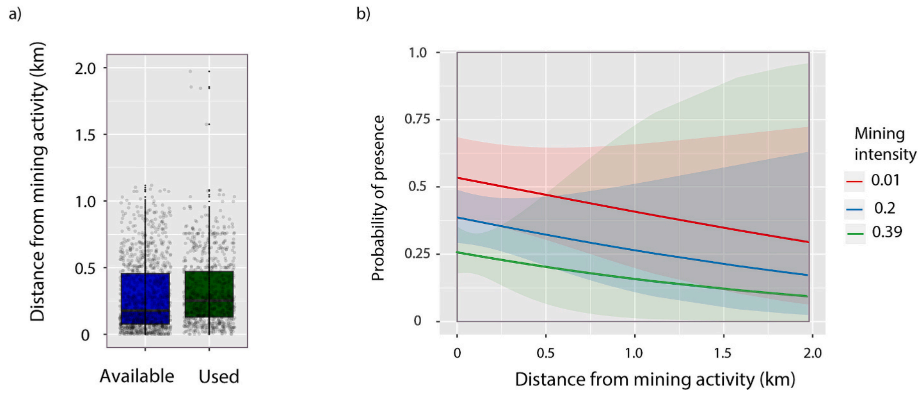

Fig. 8. Distances of used and available giant otter locations to mining activity (a) and plot of the interaction term between distance to mining and lake-specific mining intensity, reflecting different estimates of intercepts and slopes for giant otter presence probability in lakes with varying mining intensity. Shaded areas denote 95% confidence intervals Prediction plots were generated with the 'plot_model' function (sjPlot package; Lüdecke and Lüdecke 2015). Location data were collected in Peru's Madre de Dios region between 2018 and 2023.

4.2. Seasonal variations and responses to mining

Our study recorded higher giant otter occurrence during the dry season, a finding driven by seasonal differences in the least protected areas and with no notable seasonal difference in the most protected area studied (Fig. 2a). The wet season prompts territory expansions as fish resources disperse and water bodies connect, allowing otters to forage over greater distances (Leuchtenberger et al., 2015). This seasonal shift may explain the reduced otter occurrence in lakes during the wet season, particularly in mining-impacted areas with lower fish availability. Reduced densities of other piscivores, such as black caiman and piscivorous birds, further support the hypothesis that habitats impacted by extractive activities exhibit trophic downgrading due to resource depletion (Barocas et al., 2023a; Terborgh and Davenport, 2021). In contrast, in protected areas with high quality habitat, giant otters may have less need to expand their territories and leave their dry season lakes that contain sufficient resources to support the otter group throughout the year.

4.3. Adaptation to disturbed and novel ecosystems

Interestingly, despite artisanal gold mining activities for the past four decades in the Madre de Dios gold mining corridor, giant otter populations persisted and were repeatedly recorded in all this area's surveyed oxbow lakes, although they were present less frequently and in lower numbers at mined than unmined lakes. Contrary to our predictions, within mined bodies of water, giant otters were more likely to occur near areas deforested by gold mining.

While giant otters typically prefer bank areas with dense forest canopy cover, this intriguing finding might be explained by changes in the physical habitat complexity of the aquatic medium. The clearing and destruction of bank habitat associated with mining activities may inadvertently create more complex foraging areas for prey fish. Giant otters are known to favor aquatic habitats containing fallen logs, as these structures are believed to prioritize optimal fish habitat (Abanto Valladares et al. 2022). Therefore, the physical disturbance of banks (e.g., increased submerged wood or altered bank slope resulting from destruction and deforestation) could inadvertently enhance underwater structure, thereby attracting foraging otters due to a potentially more abundant or accessible prey fish base.

If, as our study suggests, the primary long-term impacts of mining are mediated by water quality, then otters may readily utilize areas where the banks have been deforested if water quality is otherwise similar to other parts of the lake. These findings indicate that the species can exhibit behavioral tolerance and recolonize disturbed habitats after human presence diminishes, reflecting their capacity to respond to lower-intensity disturbances rather than a true preference for these potentially lower-quality sites. While this demonstrates population persistence and the ability to recolonize recently mined areas where human presence is low, it is crucial to explicitly distinguish this from genuine long-term demographic viability, defined by evidence of stable reproductive success and survival rates. Our data show that giant otter populations in unprotected areas are significantly less stable and exhibit smaller, more variable group sizes compared to those in protected areas. This observed demographic instability suggests that even where recolonization occurs, habitat conditions may still be periodically compromised and unable to consistently support the stable demographic performance required for true recovery. Therefore, the observed presence patterns confirm behavioral tolerance and recolonization capacity but do not necessarily confirm long-term demographic viability or full adaptation to these altered conditions.

Extractive activities often give rise to "novel ecosystems," which, in the context of this study, refer to freshwater communities established in altered habitat structures, such as the thousands of small mining ponds created by ASGM. These ponds are characterized by modified animal and plant communities (Araújo-Flores et al., 2021; Timana-Mendoza et al., 2025). While knowledge exists regarding the species composition of plankton, fish, and invertebrates in these novel pond communities (Gerson et al., 2020), their ecological quality often remains compromised. Furthermore, their functionality as ecosystems and ability to sustain species of higher trophic levels are not well understood. Although these human-created water bodies have expanded the total lake area in heavily mined regions (Gerson et al., 2020), and we documented the presence of giant otters in abandoned mining ponds on two separate occasions, this observation is preliminary and gives rise to a critical hypothesis for future study. In combination with evidence suggesting that giant otters populations occur at lower densities in areas degraded by large hydroelectric dams (Palmeirim et al., 2014), our findings may suggest a more positive outlook for this species than previously thought in view of recent trends of neotropical freshwater ecosystem degradation (Castello and Macedo, 2016), at least with regard to enduring effects of gold mining. However, it is important to exercise caution when generalizing the adaptability of *P. brasiliensis* to other disturbed ecosystems, particularly those facing more severe or ongoing anthropogenic pressures. Further research is necessary to determine if these disturbed ecosystems are stable or merely transitional, and whether they can fully return to baseline ecological function to support populations of giant otters and sympatric species.

While this study primarily focused on the direct and indirect impacts of artisanal small-scale gold mining (ASGM), it is crucial to acknowledge that other anthropogenic factors can significantly influence giant otter distribution and behavior, potentially acting as unmeasured factors or contributing to cumulative human pressures that influence claims of adaptation. For instance, fishing pressure and the perception of otters as competitors can lead to human conflict (Leuchtenberger et al., 2018). Additionally, ecotourism activities and general boat traffic can induce disturbance-specific behavioral responses in otters, such as increased vigilance and avoidance of human presence (Barocas et al., 2022; Noonan et al., 2017).

These broader human disturbances, including the potential for direct persecution stemming from such conflicts, warrant further investigation. Such multifaceted human pressures were not fully quantified in this study, and their complex interactions could be contributing to observed patterns of occurrence or influencing perceived tolerance in ways that challenge simple interpretations of adaptation to mining. Thus, future research should aim to quantify and control for these pressures to develop a more holistic understanding of their cumulative effects on giant otter populations and to inform comprehensive conservation strategies.

4.4. Conservation implications

Human extractive activities are among the most pervasive drivers of ecosystem change, posing substantial threats to global biodiversity. For example, nearly 8 % of vertebrates on the IUCN Red List are threatened by mining (Lamb et al. 2024). Large mammals, due to their extensive spatial requirements, low reproductive rates, and position near the top of trophic networks, are often disproportionately affected by these disturbances (Martins-Oliveira et al., 2021). Our study with giant otters can serve as a model for evaluating the impacts of large mammals that play disproportionate roles in their ecosystems and can serve as an umbrella species (Caro, 2010) to facilitate the protection of ecosystem for broader biodiversity conservation and sustainable use by human communities.

Our findings reinforce the effectiveness of protected areas in mitigating human pressures and providing stable habitats for giant otters, adding to the dialogue evaluating protected area efficacy. That PAs work to conserve species is not a foregone conclusion, with barely half of studies evaluating PAs demonstrating a positive impact on biodiversity (Rodriguez-Rodriguez and Martinez-Vega, 2022). When supported by data, it is important to showcase when and how PAs contribute to biodiversity conservation to drive greater support for PAs (Watson et al., 2014). However, in regions like the Madre de Dios gold mining corridor, conservation efforts must extend beyond protected areas. Some oxbow lakes within this region are managed under local tourism and conservation concessions, effectively limiting extractive activities. Expanding such protections to additional freshwater bodies could mitigate human disturbances and safeguard these sensitive biomes.

Further studies should evaluate whether observed changes in giant otter abundance translate to differences in demographic rates, particularly reproductive success and survival – the critical components of long-term demographic viability (Groenendijk et al., 2014; Groenendijk et al., 2015). Research should also focus on testing the hypothesis that “novel habitats,” such as abandoned mining ponds, have the potential for supporting viable otter populations. This research must move beyond mere presence/absence surveys to determine the specific environmental characteristics driving their utility. Key areas of investigation include pond characteristics such as depth, hydrological connectivity (which can enhance fish biodiversity), and the robustness of their prey base (fish communities). Crucially, research must also quantify the potential risks associated with these disturbed areas, particularly the risk of toxin bioaccumulation, given that giant otters, as freshwater megafauna and top carnivores, are vulnerable to accumulating mercury from fish prey in gold mining areas. To ensure the demographic recovery and viability of giant otter populations, it is crucial that any future plans to restore degraded mining areas take the needs of species from higher trophic levels into account, including water quality, the maintenance of connectivity between water bodies, and the prioritization of suitable bank habitats.

As top predators and piscivores, giant otters may serve as indicators of freshwater ecosystem health (Bifolchi and Lodé, 2005). Their dependence on high-quality habitats and robust fish populations makes them a model umbrella species and underscores the need for continued conservation efforts. Our findings confirm concerns regarding the degradation of oxbow lakes and rivers in neotropical basins. Local communities reliant on these ecosystems for drinking water, fish protein, and recreational activities report significant declines in freshwater quality (Cuya et al., 2021), perceptions supported by evidence of reduced water quality, depauperate fish assemblages, and elevated mercury levels (Barocas et al., 2023a, 2023b, 2021). We feel that in addition to more aggressive top-down actions to protect freshwater ecosystems, long-term conservation strategies should involve empowering local communities to become stewards of these environments, fostering the combination of human activities and ecosystem health (Campos-Silva et al., 2021, 2018). Continued monitoring of the cumulative impacts of extractive activities can help secure the future of giant otters and the freshwater ecosystems they inhabit. Ultimately, given its critical vulnerability to habitat degradation via reduced water quality and subsequent trophic degradation with its surprising behavioral flexibility and ability to recolonize disturbed habitats, the giant otter presents a complex conservation challenge.

CRediT authorship contribution statement

Adi Barocas: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Johny Farfan:** Writing – review & editing, Project administration, Methodology, Investigation, Data curation. **Alejandro Alarcón Pardo:** . **Romina Camus:** Writing – review & editing, Investigation, Data curation. **Claire Marr:** Writing – review & editing, Investigation. **Leydi Auccacusi Choque:** Writing – review & editing, Investigation, Data curation. **Orquídea Otazú Loayza:** Writing – review & editing, Investigation, Data curation. **David W. Macdonald:** Writing – review & editing, Resources, Project administration, Funding acquisition, Conceptualization. **Ronald R. Swaisgood:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.114265.

Data availability

Data will be made available on request.

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