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Protected areas maintain neotropical freshwater bird biodiversity in the face of human activity

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ABSTRACT

Because of their accessibility, freshwater ecosystems are particularly sensitive to deforestation and bank habitat fragmentation. Their responses to human activities in general, and specifically to small-scale extractive activities, are not well understood. Protected Areas (PAs) can be an effective tool to secure the conservation of freshwater animal assemblages. Given their ability to respond to changes in site quality and local resources, waterbirds could be suitable wetland ecosystem indicators. To examine the effectiveness of PAs in protecting neotropical biodiversity, we used repeated visual count surveys of freshwater and forest-associated birds, comparing species richness and abundance in protected oxbow lakes with lakes subject to gold mining and fishing activities. Bird community structure was predicted by the proportion of mined area in lake banks and water quality. Bird richness was reduced in unprotected oxbow lakes, and this pattern was stronger for aquatic species. Land protection was the most important predictor of bird abundance. Over half the species (53%) showed markedly reduced abundance in the unprotected sites. Our results provide evidence for the effectiveness of PAs in maintaining freshwater biodiversity and for the impacts of human activities on neotropical wetland bird assemblages. Our findings also suggest that water-associated species may be sensitive to the deterioration in hydrological processes promoted by these activities. By documenting the maintenance of elevated freshwater bird biodiversity within two PAs, our results inform the debate on their effectiveness. We recommend the extension of legal protections for freshwater ecosystems and their banks to prevent further degradation of essential habitats and animal communities, driven by expanding informal and illegal mining activities.

1. Introduction

Freshwater environments in the neotropics are increasingly accessible through roads and waterways and thus face threats from anthropogenic extractive activities, which can promote land transformation and compromise hydrological connectivity (Antunes et al., 2016; Castello and Macedo, 2016). These processes can have major impacts on the structure and function of animal freshwater communities. Several studies have found that species living in freshwater habitats are faring worse than terrestrial species and their extinction risks are generally higher than those of their terrestrial counterparts. Such evidence is mounting for mammals, reptiles, amphibians, fish and invertebrates (Collen et al., 2014; McRae et al., 2016; Tickner et al., 2020). Bird assemblages associated with wetland areas can also respond to land transformation and subsequent changes in the terrestrial and aquatic medium (Jia et al., 2018; Kingsford et al., 2017).

Whereas the designation and maintenance of protected areas (PAs) has long been considered one of the main strategies to protect biodiversity levels in the face of global anthropogenic change and defaunation, their effectiveness in achieving this goal remains under debate (Gaston et al., 2008; Watson et al., 2014). A recent analysis, focused on freshwater birds, suggests that PAs have a mixed impact on these species, with a strong indication that areas managed for waterbirds or their habitat are more likely to benefit populations, and a weak signal that larger PAs are more beneficial than smaller ones (Wauchope et al., 2022).

Given their broad distribution and ability to respond rapidly to changes in site quality and local resources, waterbirds could be suitable

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indicators of the state of wetland ecosystems. In the tropics, there is evidence suggesting that bird assemblages respond to forest loss, habitat fragmentation (Moura et al., 2016; Saldanha Bueno et al., 2018), and road construction (Ahmed et al., 2014). Bird biodiversity, especially in the tropics, typically decreases in heavily disturbed areas, responses which can be influenced by species-specific ecological traits (Newbold et al., 2014; Saldanha Bueno et al., 2018).

Extractive activities in general, and mining in particular, can have significant impacts on biodiversity (Sonter et al., 2018). Increasingly common in both accessible PAs and unprotected watersheds in the Amazon (Asner et al., 2013), Artisanal Small-scale Gold Mining (ASGM) can drive freshwater ecosystem degradation through three main processes: bank and freshwater habitat loss, habitat fragmentation through deforestation (Sonter et al., 2017), and the modification of hydrogeological processes in the aquatic medium (Sonter et al., 2018). In addition, the informal practice of ASGM can entail major ecological consequences through the release of mercury to air and water and its subsequent accumulation in species of diverse trophic levels (Malm, 1998).

In this study, we evaluated the effectiveness of PAs in maintaining the richness and abundance of bird assemblages by combining an assessment of habitat modification driven by extractive activities with extensive surveys of bird assemblages and water quality in neotropical freshwater ecosystems in the Peruvian Amazon. We focused our surveys on oxbow lakes, highly productive bodies of water in proximity of river floodplains, commonly impacted by ASGM. Oxbow lakes were surveyed both in protected and disturbed areas in Peru's Madre de Dios region, where gold mining has increasingly taken place in the last three decades (Caballero-Espejo et al., 2018; Swenson et al., 2011). Based on evidence demonstrating the effects of habitat destruction on freshwater ecosystems (Castello and Macedo, 2016), we hypothesized that unprotected lakes subject to human activities would show reduced bird biodiversity as reflected by species richness and abundance.

Accordingly, we predicted that there would be an identifiable difference in the composition of species between protected and unprotected bodies of water, and that this dissimilarity among lakes would be proportional to the degradation of surrounding bank habitat and to differences in water quality associated with anthropogenic activities. We additionally evaluated the relative effects of lake conditions and factors reflecting human activity on bird populations at the species level. Using N-mixture models that estimate abundance based on spatially replicated counts (Royle, 2004), we compared the abundance of bird species that vary in their degree of association with freshwater environments. We predicted that, in the face of anthropogenic activities, PA effectiveness would be increased for freshwater specialists, which are more dependent on the aquatic portion of the oxbow lake habitat, compared to forest-

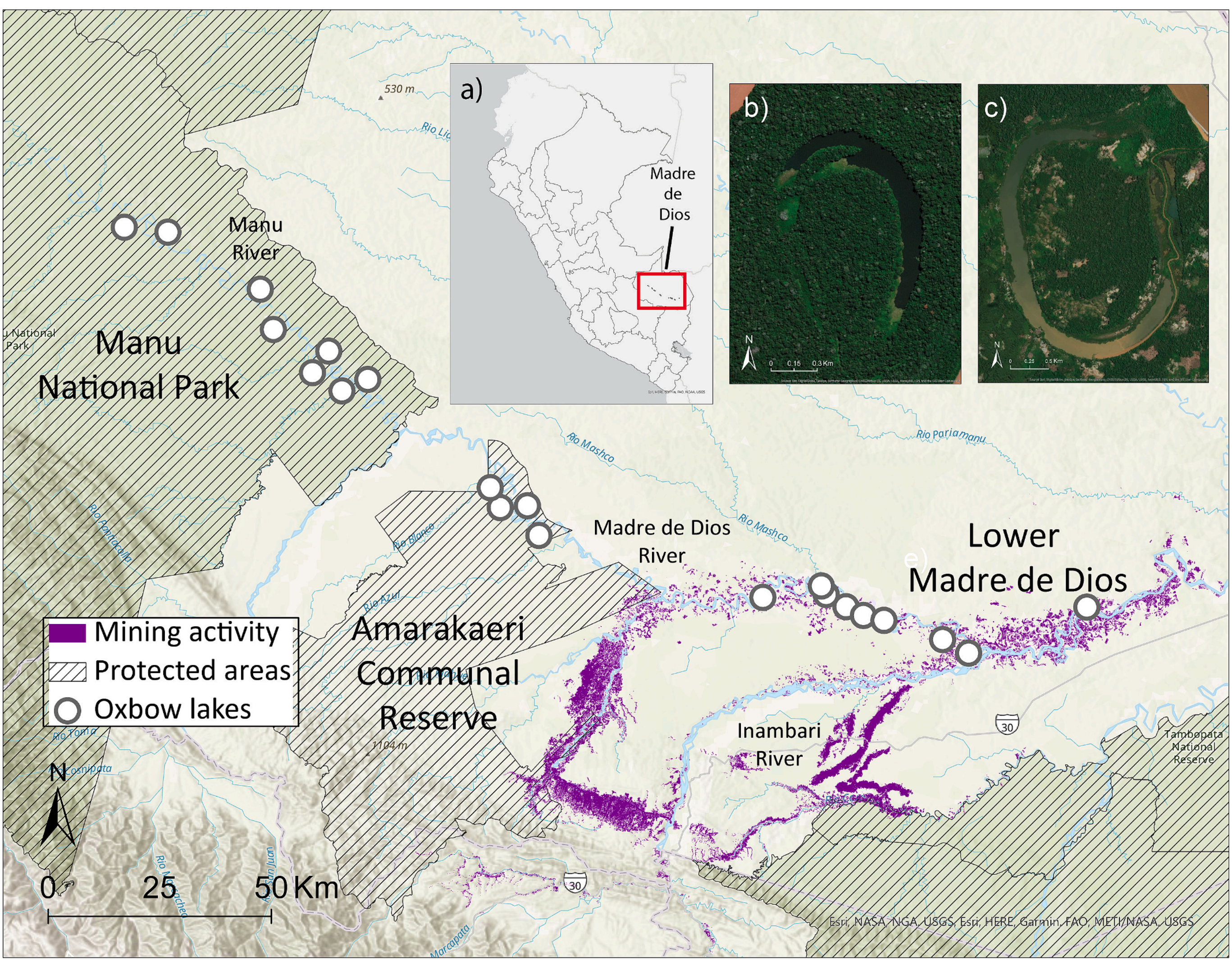

Fig. 1. Map of research area in southeastern Peru (a) with locations of bird surveys, including oxbow lakes in the protected areas of Manu National Park and Amarakaeri Communal Reserve, and oxbow lakes in the gold mining zone, including spatial data of mining activity (Caballero-Espejo et al., 2018)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

associated species and habitat generalists.

2. Materials and methods

2.1. Study area

We carried out field work in the department of Madre de Dios in south-eastern Peru, as part of a study examining the state of Amazon freshwater ecosystems (Barocas et al., 2022). We focused on oxbow lakes, a type of shallow, elongated body of water commonly found in proximity of Amazon floodplain rivers, created when a meander of a river becomes disconnected from the main channel due to erosion and deposition (Terborgh et al., 2018). Our study included eight oxbow lakes in Manu National Park (11°41′ S, 71°13′ W), four in the Amarakaeri Communal Reserve (12°25′ S, 70°42′ W), and nine unprotected oxbow lakes in the lower part of the Madre de Dios river (12°40′ S, 69°53′ W; Fig. 1, Table S1), subject to significant ASGM (Caballero-Espejo et al., 2018; Scullion et al., 2014). The maximal aerial distance between the most upstream and downstream lakes was 220 km. On average, protected oxbow lakes were found at higher elevations (mean ± SE 349.7 ± 20.1 m) compared to lakes in the gold mining area (mean ± SE 234.7 ± 4.2 m). However, they did not show significant differences in mean temperature (protected mean ± SE = 25.03 ± 0.01°C; unprotected = 25.09 ± 0.03°C) or annual precipitation (protected mean ± SE = 3075.6 ± 116.4 mm; unprotected = 3292.2 ± 96.3 mm). Manu oxbow lakes are part of the Madre de Dios river basin, same as Amarakaeri and lower Madre de Dios oxbow lakes, located downstream from them. The Manu river is a tributary of the Madre de Dios river, belonging to the same floodplain and characterized by similar vegetation types, landcover categories and hydrological conditions (Lehner and Grill, 2013; Thieme et al., 2007). 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.

The lower Madre de Dios mining area contains 11 small-sized communities with a formal population of 2500 and several more informal mining camps (Cuya et al., 2021). During the last three decades, ASGM has become the area's main economic activity (Caballero-Espejo et al., 2018; Swenson et al., 2011). Lake bank vegetation is characterized by strips of marsh, shrubs, isolated trees and vines. Oxbow lakes are highly productive and contain suitable bird nesting and foraging sites that are relatively protected from predators (Terborgh & Davenport, 2021). One detailed study of an oxbow lake suggested that bird communities are composed of forest species and aquatic species that may also inhabit other bodies of water such as wetland and riverine systems (Robinson, 1997).

2.2. Lake conditions

We used satellite images and field data to quantify the ecological conditions and water quality of oxbow lakes. We determined the status of lakes based on visual surveys and data on ASGM, based on classification of satellite images of the research area between 1985 and 2017, resulting in a raster layer of mined areas with a 30 × 30 m pixel size (Caballero-Espejo et al., 2018). Because over this period deforestation was still visible in recent satellite images, we did not differentiate between recent and older signs of mining. Lakes were classified as 'protected' if they were located within a protected area and did not show deforestation signs after repeated drone flights including its banks and the body of water (Abanto Valladares et al., 2022), and 'unprotected' in case there was evidence of bank deforestation. For unprotected lakes, we quantified the local intensity of mining by creating a buffer of 300 m around each lake's margins. We chose this value based on the width of lakes (mean maximum width = 248.1 m). For each lake, we calculated the proportion of area from the buffer showing signs of deforestation and recent mining. We developed an index of bank deforestation intensity by dividing the deforestation area in the bank by the total 300 m buffer area. For following analyses, the protection covariate was binary (i.e protected = 1; unprotected = 0, whereas the bank deforestation covariate was continuous (values between 0, meaning no deforestation, and 50%; Table S1).

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 (pixel resolution = 30 × 30 m; Roy et al. 2014) taken in the same season of bird surveys to calculate NDVI of the water body. In each lake, we averaged all pixel values within the water body to obtain a mean NDVI value (Terborgh et al., 2018). Several aquatic organisms require minimal levels of dissolved oxygen to survive (Röpke et al., 2016) and therefore dissolved oxygen is considered an indicator for water quality. We measured oxygen levels with a LaMotte Dissolved Oxygen Test Kit (LaMotte ©, Chestertown, MD, USA). We also used a Secchi disk (Test Assured©, Jupiter, FL, USA) to measure water transparency, reflecting the concentration of suspended sediments (Dethier et al., 2019). To account for spatial variation, we performed these measurements four times within each lake during the dry season. We examined whether ecological variables reflecting lake conditions differed among protected and unprotected oxbow lakes using an unpaired *t*-test.

Land protection can have positive impacts for biodiversity (Watson et al., 2014), whereas deforestation as a result of anthropogenic activity could drive declines in species richness and abundance (Castello and Macedo, 2016). Thus, we used lake protection status and mined area proportion as predictors in subsequent analyses. We also chose as covariates NDVI, which may reflect the ecological state of an oxbow lake (Terborgh et al., 2018), dissolved oxygen and transparency, which are indicators of water quality and nutrients availability.

2.3. Avian surveys

Between August 2017 and September 2019, we performed repeated censuses of oxbow lake bird assemblages. Each lake was surveyed at least three times in consecutive days, during the dry season (May-September). We chose the dry season to minimize variation as a result of seasonal flooding and migrations, and for logistic reasons. Each survey included two trained observers equipped with binoculars, notebooks and bird guides. Teams were led by the same two persons (AB and NAV). Surveys were conducted at peak bird activity times, during early morning (5:30 to 10:00) and late afternoon (15:00 to 18:00). Using a Grabner XR Trekking inflatable rubber boat (Grabner©, Vienna, Austria), surveyors moved along lake banks and registered bird species, the location, and the number of individuals. We restricted analyses to all individuals seen within an estimated 30-m radius from the observer position, avoided repeated counts and discarded all flyovers. All field activities were performed under Permits 07-2017-SERNANP-PNM-JEF and MINAGRI/SERFOR permit number 0084-2018.

2.4. Bird assemblage analyses

We assessed sampling completeness per oxbow lake by individual-based rarefaction curves produced with 1,000 bootstrap replications in the INEXT R package (Hsieh et al., 2016). Sampling completeness per lake was quantified as a percentage between the recorded and the estimated number of species based on the first-order Jackknife estimator (Gotelli and Colwell, 2011), calculated using the VEGAN package (Oksanen et al., 2016).

We subsequently examined β-diversity for three different datasets: 1) all species observed; 2) species associated with aquatic ecosystems; 3) species that rely completely on aquatic ecosystems (specialists). We extracted these data from two main sources (Stotz et al., 1996; Wilman et al., 2014). Water specialists were defined as either species that spend at least 80% of foraging time in water or in the vicinity of water bodies, or species whose diet is composed of at least 90% fish. Water-associated generalists were defined as either species that spend at least 10% of foraging time in the body of water, or species whose diet is composed by at least 10% fish. The remaining species were considered forest-associated generalists since, according to Stotz et al., (1996), their habitats included at least one forest type and they were detected on the forested banks of freshwater bodies.

We examined whether proportion of bank mining and additional variables influenced community structure. First, to establish whether there is spatial structure in the data, we used distance-based Moran's Eigenvector Maps (implemented with the quickMEM function, v1.0.0, provided in Borcard et al. (2011) and adjusted for distance-based RDA). The latitude and longitude of each lake's centroid were used to represent its geographic location. Because the global spatial structure statistic was not significant ($p = 0.48$), we proceeded to test for the influence of covariates on the dissimilarity of bird assemblage among lakes, using the non-parametric Permanova test (Anderson, 2001) implemented in the *adonis* function of the VEGAN package (Oksanen et al., 2016). Bird assemblages were represented by species-by-site matrices. The significance of the test was determined by F-tests based on sequential sums of squares from 10,000 permutations of the raw data. Correlation tests among variables revealed that the protection covariate, the proportion of bank deforestation and elevation were correlated (correlation coefficient > 0.7; Table S2). Thus, we did not include them in the same model. We considered the proportion of mined area around lakes, dissolved oxygen level, transparency and NDVI as predictors of the variance shown in non-metric multidimensional scaling analyses (Anderson, 2001). We also built competing models including the protection and elevation covariates. We used an additive model including all four lake-specific covariates and examined the proportion of variation explained with the Bray-Curtis and Chao distance metrics. The Bray-Curtis distance performs well with relative abundance data (Anderson et al., 2006) and the Chao dissimilarity metric better accounts for rare and unseen species (Chao et al., 2005). To further test whether elevation was a significant driver of community structure, we also performed these analyses with datasets of only protected oxbow lakes and only unprotected oxbow lakes. The additive models tested with these datasets included elevation, dissolved oxygen, transparency and NDVI.

2.5. Species abundance models

We modeled species abundance in each oxbow lake using an N-mixture model (Royle, 2004). N-mixture models use count data with spatial and temporal replication (multiple sites with multiple surveys per site) to estimate abundance while accounting for imperfect detection (Royle, 2004). To meet model assumptions of constant abundance across surveys, we removed from the dataset species not associated with freshwater or distributed along oxbow lake banks and probable transients, such as parrots (Psittaciformes), woodpeckers (Piciformes) and vultures (Cathartiformes). To avoid sampling bias and uncertainty related to species with low detection probability (Banks-Leite et al., 2014), we also removed all species for which there were 10 detections or less. This left us with 55 species for the analysis. For the remaining dataset, we implemented a Bayesian multi-species (or community) version of the N-mixture model in which covariates are modeled hierarchically with community level hyper-parameters (Yamaura et al., 2012). We included the following lake-specific covariates for abundance: protection (yes/no), mining intensity (the proportion of mined lake banks), transparency, mean dissolved oxygen level, and NDVI. Despite the correlation between the protection and mining intensity covariates, we felt that they reflect different metrics and thus chose to include them in the same models. We were specifically interested in their influence on bird abundance. To account for differences in the size of oxbow lakes, we modeled the abundance as the number of individuals per km of shoreline by including length of shoreline as an offset in the abundance model. No covariates were included for the detection probability, but detection probability was species-specific and modeled hierarchically with a normal hyper-prior.

To examine whether species ecological traits can predict their response to mining, we extracted the following traits for each species: body mass, trophic level, and geographic range size (Table S3). We modeled the regression coefficient for the land protection covariate (i.e. whether lakes were protected or not) for each species as a function of these traits and water specialization or water association, specified as a categorical variable with 'forest associated generalists' as the reference category. The model was implemented in JAGS 4.3 (Plummer, 2003) through R 3.6 (R Development Core Team, 2019). We ran three chains with a length of 500,000 and burn-in of 200,000.

3. Results

In 128 surveys of 21 oxbow lakes (Mean ± SD = 6.1 ± 1.6 surveys per lake), we recorded 9,687 detections of 179 species, representing 143 genera and 48 families (Table S4). The number of detections per lake ranged from 182 to 894 (Mean ± SD = 461.3 ± 164.8) and the number of species observed per lake ranged from 40 to 86 (Mean ± SD = 61.6 ± 10.4). Despite our sampling effort, individual-based rarefaction curves indicated total species richness metrics would need additional sampling efforts to reach asymptotic values for all lakes (Fig. S1), as expected for communities where there is a large proportion of rare, difficult-to-detect species (Banks-Leite et al., 2014). Completeness of the species inventory per lake ranged from 67% to 84.4% (Table S1). These metrics indicate that the number of species found should be regarded as conservative. Observed species geographic ranges included both PAs and unprotected areas (Birdlife International, 2017). It is possible that differences in observations were a consequence of climatic or large-scale geographic factors that influence bird distributions.

Lake conditions differed among oxbow lakes. The difference was most significant for dissolved oxygen ($t_{18} = 2.80$, $P = 0.01$), whereas means of transparency and NDVI were different but not significant (transparency $t_{18} = 0.37$, $P = 0.71$; NDVI $t_{18} = 0.84$, $P = 0.41$; Fig. 2). Unprotected lake sizes were on average larger than protected lakes (protected: Mean ± SE = 41.8 ± 8.5 ha; mined: Mean ± SE = 80.4 ± 17.8; Fig. 1). Permanova results suggested that the proportion of mined area explained the largest amount of variance in species composition (Adonis r^2 statistic: 0.28; $F_{20} = 9.43$; $P = 0.001$), followed by water transparency ($r^2 = 0.12$; $F_{20} = 3.98$; $P = 0.003$) and dissolved oxygen ($r^2 = 0.1$; $F_{20} = 3.49$; $P = 0.03$; Table 1). The full model using the Chao distance explained a larger proportion of the variance ($r^2 = 0.53$) compared to the Bray-Curtis distance ($r^2 = 0.34$; Table S5). This model also performed better compared to models including land protection (Chao $r^2 = 0.44$; Bray-Curtis $r^2 = 0.28$) and elevation (Chao $r^2 = 0.40$; Bray-Curtis $r^2 = 0.27$). These results indicate that the proportion of mined area in lake banks was better supported than elevation as a driver of variation in community structure. Using the reduced datasets, the elevation covariate did not significantly explain community structure within unprotected oxbow lakes (Chao partial $r^2 = 0.34$; $P = 0.1$), or within protected oxbow lakes (Chao partial $r^2 = 0.04$; $P = 0.69$).

3.1. Abundance models

We modeled the abundance of 55 bird species as a function of various covariates using an N-mixture model. Mean estimated species richness for the 55 species included in the analysis was higher in protected lakes compared to lakes outside PAs for all species observed, aquatic species, and species specialized in aquatic ecosystems, where this pattern was stronger (Fig. 3). Nonmetric multidimensional scaling based on estimated abundances for each species showed a clear separation in the community structure for mined and non-mined lakes (Fig. 3).

Detection probabilities varied between 0.2 and 0.54 (Table S6). Of

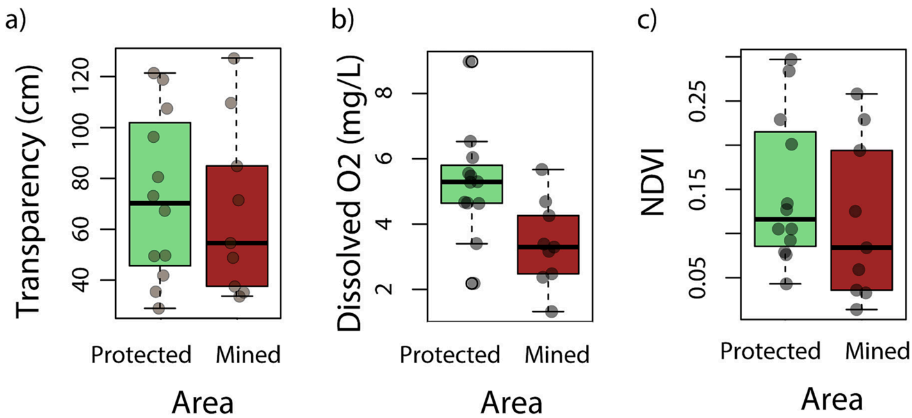

Fig. 2. Boxplots of ecological and water quality variables for oxbow lakes where avian surveys were conducted in Madre de Dios, Peru.

Table 1
Permutational MANOVA results of a modeal examining the effects of abiotic and biotic variables on bird assemblage dissimilarity, using the Chao distance metric, in oxbow lakes of the Madre de Dios province, Peru.

Variable	*Df*	*MS*	R^2	*F*	*P*
Mining proportion	1	0.09	0.28	9.43	>0.001
Dissolved oxygen	1	0.03	0.11	3.49	0.01
Transparency	1	0.04	0.12	3.98	0.03
NDVI	1	0.01	0.03	0.93	0.52
Residual	16	0.15	0.47		

the examined lake-specific covariates, lake protection had the strongest effect: in 31 of 55 species the credible intervals for the regression coefficient did not overlap 0 (Table S6; Fig. 4). Of the remaining covariates, transparency (29 species), dissolved oxygen (23), NDVI (21) and mining intensity (14 species; Table S5) predicted abundance. 53% of all species showed higher abundance in protected areas, whereas 43% of species had similar abundance and for 6% abundance increased (Table 2; Fig. 4). Decline patterns were more evident in water specialists (58% of 15 species showing significant decline; Fig. 4). Forest-associated species also showed responses to land protection, with 35% with similar abundance and 55% declining (Fig. 4). The sensitivity of water-associated generalists to anthropogenic activities was confirmed by the linear model examining ecological traits. Water-associated species were more likely to be positively influenced by land protection ($\beta \pm SE = -2.93 \pm 1.04$); 95% CI = (−5.01, −0.89)) when compared to forest species. Responses to land protection were also associated with geographic range ($\beta \pm SE = 1.18 \pm 0.45$); 95% CI = (0.3, 2.07)).

4. Discussion

Our results indicate reduced bird species richness and abundance in lakes outside PAs. This pattern was more accentuated for water-associated species and freshwater specialists. Outside PAs, oxbow lake water quality was reduced, with lower dissolved oxygen and transparency levels. Further, the degree of bank deforestation and covariates reflecting water quality predicted the composition of bird assemblages. The main human activities documented in unprotected oxbow lakes were fishing and ASGM (Barocas et al., 2021), suggesting that these may be driving bird numerical responses. Responses of tropical birds to forest habitat fragmentation are well documented (Newbold et al., 2014). Our findings are in line with these patterns, indicating that land protection, geographic isolation and limited access may mitigate bird species and community-level responses by avoiding human-driven degradation of neotropical freshwater ecosystems.

The bird biodiversity patterns documented could also be a consequence of geographic and climatic processes. Variation in elevation and local temperature can have implications for bird species richness and abundance (Hawkins et al., 2007; McCain, 2009). Because of the spatial arrangement of lakes within the research area, we were unable to completely tease apart the influences of land protection and natural environmental and climatic factors. However, we feel that in this case climatic and biogeographic influences are less likely because of the relative spatial proximity among groups of lakes, the similar hydrologic conditions of the floodplain where lakes are found (Thieme et al., 2007), the modest differences in elevation (mean = 115 m) and because these areas have similar mean temperatures and annual precipitation. In addition, analyses with the reduced datasets indicate that elevation, the geo-climatic variable with the highest variation among study areas, is not a significant driver of community structure. Thus, we can identify no plausible ecological drivers of our findings, including factors associated with elevation.

The majority of species demonstrating increased abundance inside PAs were water-associated, likely a result of their greater dependence on aquatic resources depleted by human activities (Barocas et al., 2021). However, we also observed declines in several forest-associated species (Fig. 4). Thus, if protection of lakes from human activity is indeed the driver of bird biodiversity patterns, the value of land protection is likely to extend beyond the immediate spatial proximity of lake banks into forest edges surrounding lakes. These results confirm concerns for water-associated species in the face of land transformation and habitat fragmentation (Saldanha Bueno et al., 2018; Zurita et al., 2017). Forest patches cleared by human activity outside PAs commonly create further fragmentation and reduce the availability of continuous habitat, promoting edge effects (Ahmed et al., 2014). While responses to fragmentation are not as strong and conclusive as the effects of habitat loss (Fahrig, 2003), both processes may act in synergy (Brook et al., 2008), especially at the water-forest interface, where forest edges already exist.

For water specialists, land protection and limitation of human access to oxbow lakes can prevent the deterioration of foraging microhabitats, bank habitat homogenization and decline in water quality, as evidenced by lower levels of dissolved oxygen and reduced transparency found in oxbow lakes outside PAs. Land transformation by deforestation tends to promote local water runoff and stream discharge, whereas ASGM activities may increase water sediment load, resulting in a murkier, more polluted water body (Dethier et al., 2019). The pollution, water contamination and modification of hydrogeological processes avoided in oxbow lakes, possibly as a result of land protection, can percolate to higher trophic levels. Extractive activities may impact avifauna which depend on freshwater bodies through the reduction of prey available to species that forage on fish (Terborgh and Davenport, 2021).

Besides reduced water quality and shoreline habitat degradation, in areas subject to extractive activities and especially ASGM, high levels of mercury pollution may be an additional driver of bird demographic responses (Whitney and Cristol, 2017). Artisanal miners extract gold by

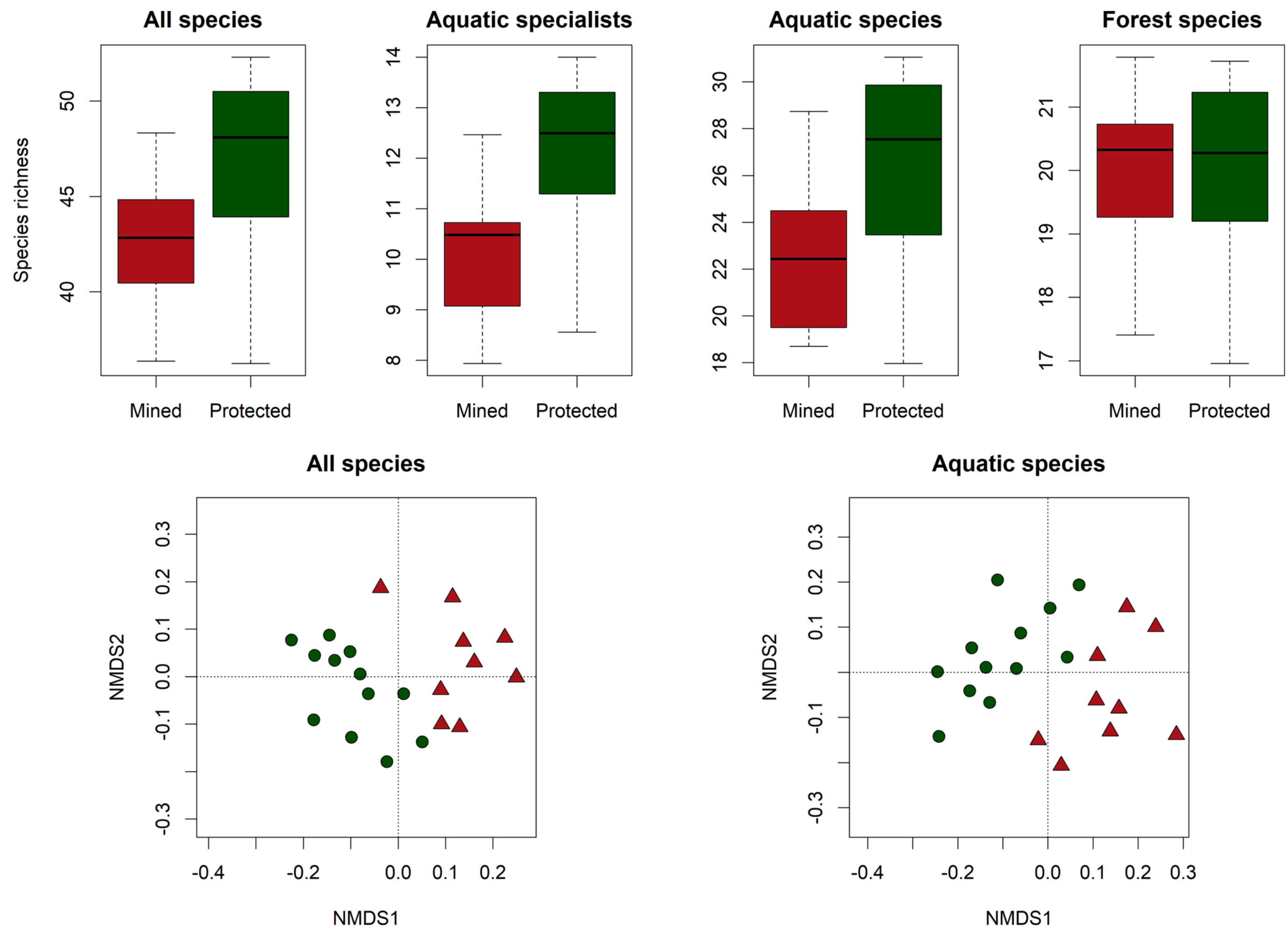

Fig. 3. Top: Bird species richness (out of 55 total species included in the analysis) in mined and protected oxbow lakes in the Peruvian Amazon, estimated with an N-mixture model. Bottom: Ordination of oxbow lakes using nonmetric multidimensional scaling based on the estimated abundance of 55 bird species. Brown triangles indicate mined lakes, while green circles indicate protected lakes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

dredging sediments from the bottom of lakes and rivers and using mercury (Hg), thereby polluting waters via its release (Malm, 1998). In neotropical areas subject to ASGM, high quantities of Hg were found across several taxa and trophic levels, including fish (Barocas et al., in revision; Martinez et al., 2018), birds (Gerson et al., 2022) and humans (Ashe, 2012). To understand the long-term effects of extractive activities on bird population, assessing mercury levels and their effects on bird genetics, behavior and demographics in mined areas can be a promising research direction.

4.1. Conservation implications

Our results add to findings on recent worldwide decreases in freshwater animal populations (McRae et al., 2016) and to evidence that the disruption of multiple ecological processes promoted by habitat modification have negative effects on freshwater ecosystems in the tropics (Castello and Macedo, 2016; Sonter et al., 2018). One of the main obstacles to securing the conservation of Amazon freshwater ecosystems is the inconsistency in protective legislation (Castello and Macedo, 2016). In Manu National Park, the protection of oxbow lakes is achieved by restriction of human access. It remains to be seen whether this strategy is practical in more accessible areas with significant human pressure for extractive activities. Our findings also indicate that, similar to fish assemblages (Barocas et al., 2021), protective measures in place in Manu National Park have been effectively sustaining oxbow lake bird populations. Extending these protections outside PAs may also help provide ecosystem services to neighboring human communities (Azevedo-Santos et al., 2019).

One of the big questions facing conservation science is whether PAs are effective in maintaining biodiversity levels. In fact, some PAs have been shown to be ineffective at conserving species inside their boundaries (Pringle, 2017; Watson et al., 2014). Without documentation of effectiveness, PAs are vulnerable to criticism and eroding support (Geldmann et al., 2018; Parrish et al., 2003). Our findings inform the debate, underscoring how well Manu National Park and its buffer zones are protecting the oxbow lake-associated avifauna. To date, Manu has remained relatively immune to expanding human activities outside the Park, vulnerable only to a relatively small, but growing and changing indigenous population living within and around the Park (Altamirano, 2021; Shepard et al., 2010). Maintaining these protections and extending them outside PAs will help secure the maintenance of freshwater biodiversity. One additional outcome of our research is to underscore the need to formulate regional, watershed-wide conservation management plans in the western Peruvian Amazon, as previously suggested (Thieme et al., 2007).

Author contributions

AB and RRS designed research. AB, NAV and AAP collected data. AB and MWT analyzed data. AB drafted the manuscript. All authors

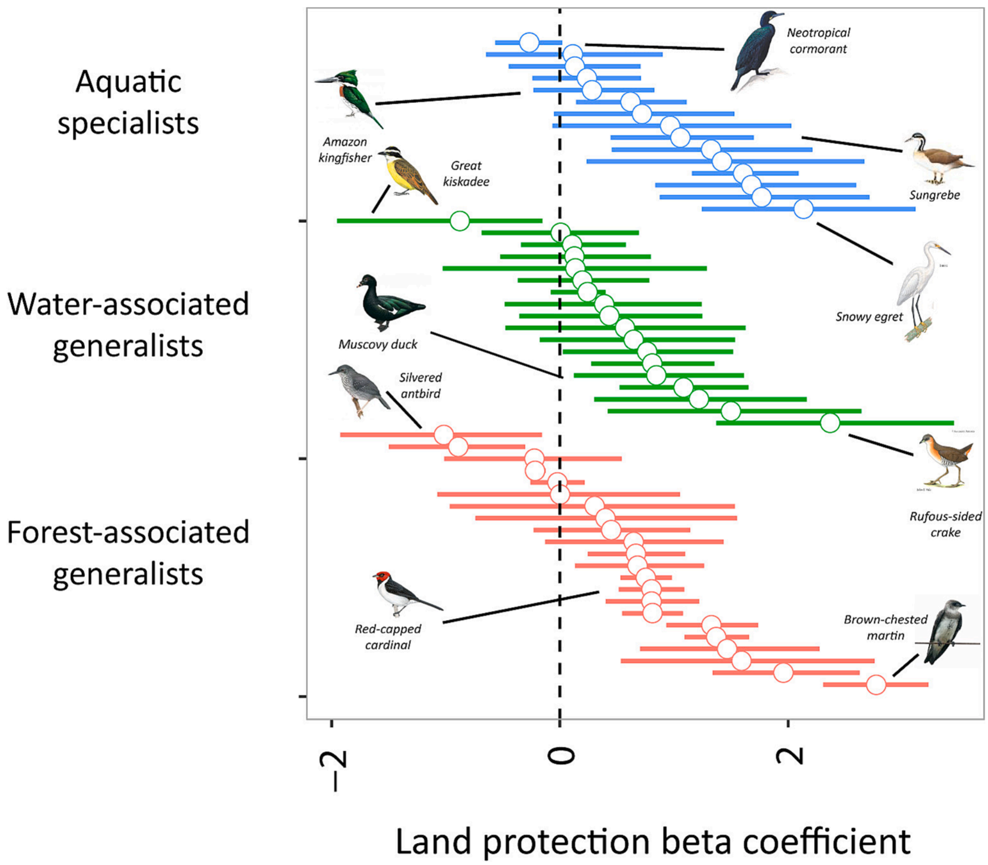

Fig. 4. Mean and 95% credible intervals of coefficients of land protection as a binary variable used to estimate oxbow lake bird abundance with N-mixture models. A positive coefficient denotes increased density in protected oxbow lakes. Bird species are sorted by three classes of habitat specialization with aquatic specialists on top and forest specialist at the bottom, and ascending coefficient estimates within each class. The figure shows model estimates for 55 species. Table S6 has the full model outputs.

Table 2
Proportions of bird species showing increased abundance in protected oxbow lakes, measured by overlap of the βcoefficient of land protection with 0. Abundances calculated from surveys during 2017–2019 across 21 oxbow lakes in the Madre de Dios province, Peru.

Species category	Total	Higher abundance in PAs	Similar abundance	Lower abundance in PAs
All species	55	28	24	3
Aquatic species	35	18	17	0
Aquatic specialists	15	8	7	0

reviewed and contributed to the latest version of the manuscript.

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.

Data availability

Data will be made available on request.

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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.2023.110256.

References

Abanto Valladares, N., Alarcon Pardo, A., Chiaverini, L., Groenendijk, J., Harrington, L. A., Macdonald, D.W., Swaisgood, R.R., Barocas, A., 2022. High-resolution drone imagery reveals drivers of fine-scale giant otter habitat selection in the land-water interface. Conserv. Sci. Pract. e12786.

Ahmed, S.E., Lees, A.C., Moura, N.G., Gardner, T.A., Barlow, J., Ferreira, J., Ewers, R.M., 2014. Road networks predict human influence on Amazonian bird communities. Proc. R. Soc. B Biol. Sci. 281, 20141742–20141742. https://doi.org/10.1098/rspb.2014.1742.

Altamirano, A.G., 2021. El Parque Nacional del Manu, los pueblos indigenas y sus derechos: situación actual y tendencias. Rev. Antropol. 37–60.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46.

Anderson, M.J., Ellingsen, K.E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. Ecol. Lett. 9, 683–693.

Antunes, A.P., Fewster, R.M., Venticinque, E.M., Peres, C.A., Levi, T., Rohe, F., Shepard, G.H., 2016. Empty forest or empty rivers? A century of commercial hunting in Amazonia. Sci. Adv. 2, e1600936–e. https://doi.org/10.1126/sciadv.1600936.

Ashe, K., 2012. Elevated mercury concentrations in humans of madre de dios, Peru. PLoS One 7, 1–6. https://doi.org/10.1371/journal.pone.0033305.

Asner, G.P., Llactayo, W., Tupayachi, R., Luna, E.R., 2013. Elevated rates of gold mining in the Amazon revealed through high-resolution monitoring. Proc. Natl. Acad. Sci. 110, 18454–18459. https://doi.org/10.1073/pnas.1318271110.

Azevedo-Santos, V.M., Frederico, R.G., Fagundes, C.K., Pompeu, P.S., Pelicice, F.M., Padial, A.A., Nogueira, M.G., Fearnside, P.M., Lima, L.B., Daga, V.S., et al., 2019. Protected areas: A focus on Brazilian freshwater biodiversity. Divers. Distrib. 25, 442–448.

Banks-Leite, C., Pardini, R., Boscolo, D., Cassano, C.R., Püttker, T., Barros, C.S., Barlow, J., 2014. Assessing the utility of statistical adjustments for imperfect detection in tropical conservation science. J. Appl. Ecol. 51, 849–859. https://doi.org/10.1111/1365-2664.12272.

Barocas, A., Vega, C.M., Alarcon Pardo, A., Araujo Flores, J., Fernandez, L.E., Groenendijk, J., Pisconte, J., Macdonald, D.W., Swaisgood, R.R., In revision. Local intensity of artisanal gold mining drives mercury accumulation in neotropical oxbow lake fishes. Sci. Tot. Env.

Barocas, A., Araújo Flores, J.M., Alarcon Pardo, A., Macdonald, D.W., Swaisgood, R.R., 2021. Reduced dry season fish biomass and depleted carnivorous fish assemblages in unprotected tropical oxbow lakes. Biol. Conserv. 257, 109090.

Barocas, A., Farfan, J., Groenendijk, J., Mendoza, J., Silva, J., Mujica, O., Ochoa, J.A., Macdonald, D.W., Swaisgood, R.R., 2022. Disturbance-specific behavioral responses of giant otters exposed to ecotourism and extractive activities. Anim. Conserv. 25, 15–26.

Birdlife International, 2017. IUCN Red List for birds.

Borcard, D., Gillet, F., Legendre, P., et al., 2011. Numerical ecology with R. Springer.

Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. Trends Ecol. Evol. 23, 453–460. https://doi.org/10.1016/j.tree.2008.03.011.

Caballero-Espejo, J., Messinger, M., Román-Dañobeytia, F., Ascorra, C., Fernandez, L.E., Silman, M., 2018. Deforestation and forest degradation due to gold mining in the Peruvian Amazon: A 34-year perspective. Remote Sens. 10, 1–17. https://doi.org/10.3390/rs10121903.

Castello, L., Macedo, M.N., 2016. Large-scale degradation of Amazonian freshwater ecosystems. Glob. Chang. Biol. 22, 990–1007. https://doi.org/10.1111/gcb.13173.

Chao, A., Chadzon, R., Colwell, R.K., Shen, T.-J., 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecol. Lett. 148–159 https://doi.org/10.1111/j.1461-0248.2004.00707.x.

Collen, B., Whitton, F., Dyer, E.E., Baillie, J.E.M., Cumberlidge, N., Darwall, W.R.T., Pollock, C., Richman, N.I., Soulsby, A.M., Böhm, M., 2014. Global patterns of freshwater species diversity, threat and endemism. Glob. Ecol. Biogeogr. 23, 40–51. https://doi.org/10.1111/geb.12096.

Cuya, A., Glikman, J.A., Groenendijk, J., Macdonald, D.W., Swaisgood, R.R., Barocas, A., 2021. Environmental perceptions and barriers for conservation among artisanal small-scale gold mining communities in southeastern Peru. Glob. Ecol. Conserv. 31, e01816.

Dethier, E.N., Sartain, S.L., Lutz, D.A., 2019. Heightened levels and seasonal inversion of riverine suspended sediment in a tropical biodiversity hot spot due to artisanal gold mining. Proc. Natl. Acad. Sci. USA 116. https://doi.org/10.1073/pnas.1907842116.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515. https://doi.org/10.1146/132419.

Gaston, K.J., Jackson, S.F., Cant, L., Cruz-pi, G., 2008. The ecological performance of protected areas. Annu. Rev. Ecol. Evol. Syst. 39, 93–113. https://doi.org/10.1146/annurev.ecolsys.39.110707.173529.

Geldmann, J., Coad, L., Barnes, M.D., Craigie, I.D., Woodley, S., Balmford, A., Brooks, T. M., Hockings, M., Knights, K., Mascia, M.B., et al., 2018. A global analysis of management capacity and ecological outcomes in terrestrial protected areas. Conserv. Lett. 11, e12434.

Gerson, J.R., Szponar, N., Zambrano, A.A., Bergquist, B., Broadbent, E., Driscoll, C.T., Erkenswick, G., Evers, D.C., Fernandez, L.E., Hsu-Kim, H., et al., 2022. Amazon forests capture high levels of atmospheric mercury pollution from artisanal gold mining. Nat. Commun. 13, 1–10.

Gotelli, N.J., Colwell, R.K., 2011. Estimating species richness. Biol. Divers. Front. Meas. Assess. 12, 39–54.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A., Soeller, S.A., 2007. Climate, niche conservatism, and the global bird diversity gradient. Am. Nat. 170, S16–S27.

Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol. Evol. 1451–1456 https://doi.org/10.1111/2041-210X.12613.

Jia, Q., Wang, X., Zhang, Y., Cao, L., Fox, A.D., 2018. Drivers of waterbird communities and their declines on Yangtze River floodplain lakes. Biol. Conserv. 218, 240–246.

Kingsford, R.T., Bino, G., Porter, J.L., 2017. Continental impacts of water development on waterbirds, contrasting two Australian river basins: Global implications for sustainable water use. Glob. Chang. Biol. 23, 4958–4969.

Lehner, B., Grill, G., 2013. Global river hydrography and network routing: baseline data and new approaches to study the world's large river systems. Hydrol. Process. 27, 2171–2186.

Malm, O., 1998. Gold mining as a source of mercury exposure in the Brazilian Amazon. Environ. Res. 77, 73–78. https://doi.org/10.1006/enrs.1998.3828.

Martinez, G., McCord, S.A., Driscoll, C.T., Todorova, S., Wu, S., Araújo, J.F., Vega, C.M., Fernandez, L.E., 2018. Mercury contamination in riverine sediments and fish associated with artisanal and small-scale gold mining in Madre de Dios, Peru. Int. J. Environ. Res. Public Health 15, 1–15. https://doi.org/10.3390/ijerph15081584.

McCain, C.M., 2009. Global analysis of bird elevational diversity. Glob. Ecol. Biogeogr. 18, 346–360.

McRae, L., Freeman, R., Marconi, V., 2016. Living Planet Report 2016 : Risk and Resilience in a New Era.

Moura, N.G., Lees, A.C., Aleixo, A., Barlow, J., Berenguer, E., Ferreira, J., Mac Nally, R., Thomson, J.R., Gardner, T.A., 2016. Idiosyncratic responses of Amazonian birds to primary forest disturbance. Oecologia 180, 903–916. https://doi.org/10.1007/s00442-015-3495-z.

Newbold, T., Scharlemann, J., Butchart, S., Sekercioglu, C., Alkemade, R., Booth, H., Purves, D., 2014. Ecological traits affect the response of tropical forest bird species to land-use intensity. Proc. R. Soc. B Biol. Sci. 280, 20122131–20122131. https://doi.org/10.1098/rspb.2012.2131.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., et al., 2016. Vegan: community ecology package. R Foundation, Vienna, Austria. R package version 2.3-5.

Parrish, J.D., Braun, D.P., Unnasch, R.S., 2003. Are we conserving what we say we are? Measuring ecological integrity within protected areas. Bioscience 53, 851–860.

Plummer, M., 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling, in: Proceedings of the 3rd International Workshop on Distributed Statistical Computing. pp. 1–10.

Pringle, R.M., 2017. Upgrading protected areas to conserve wild biodiversity. Nature 546, 91–99. https://doi.org/10.1038/nature22902.

Robinson, S.K., 1997. Birds of a Peruvian oxbow lake: populations, resources, predation, and social behavior. Ornithol. Monogr. 613–639.

Röpke, C.P., Amadio, S.A., Winemiller, K.O., Zuanon, J., 2016. Seasonal dynamics of the fish assemblage in a floodplain lake at the confluence of the Negro and Amazon Rivers. J. Fish Biol. 89, 194–212.

Roy, D.P., Wulder, M.A., Loveland, T.R., Woodcock, C.E., Allen, R.G., Anderson, M.C., Helder, D., Irons, J.R., Johnson, D.M., Kennedy, R., et al., 2014. Landsat-8: Science and product vision for terrestrial global change research. Remote Sens. Environ. 145, 154–172.

Royle, J.A., 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60, 108–115. https://doi.org/10.1111/j.0006-341X.2004.00142.x.

Saldanha Bueno, A., Dantas, S.M., Henriques, L.M.P., Peres, C.A., 2018. Ecological traits modulate bird species responses to forest fragmentation in an Amazonian anthropogenic archipelago. Divers. Distrib. 24, 387–402. https://doi.org/10.1111/ddi.12689.

Scullion, J.J., Vogt, K.A., Sienkiewicz, A., Gmur, S.J., Trujillo, C., 2014. Assessing the influence of land-cover change and conflicting land-use authorizations on ecosystem conversion on the forest frontier of Madre de Dios. Peru. Biol. Conserv. 171, 247–258.

Shepard, G.H., Rummenhoeller, K., Ohl-Schacherer, J., Yu, D.W., 2010. Trouble in paradise: indigenous populations, anthropological policies, and biodiversity conservation in Manu National Park. Peru. J. Sustain. For. 29, 252–301.

Sonter, L.J., Ali, S.H., Watson, J.E.M., 2018. Mining and biodiversity: key issues and research needs in conservation science. Proc. R. Soc. B - Biol. Sci. 285, 20181926. https://doi.org/https://doi.org/10.1098/rspb.2018.1926.

Sonter, L.J., Herrera, D., Barrett, D.J., Galford, G.L., Moran, C.J., Soares-Filho, B.S., 2017. Mining drives extensive deforestation in the Brazilian Amazon. Nat. Commun. 8, 1–7. https://doi.org/10.1038/s41467-017-00557-w.

Stotz, D.F., Fitzpatrick, J.W., Parker III, T.A., Moskovits, D.K., 1996. Neotropical birds: ecology and conservation. University of Chicago Press.

Swenson, J.J., Carter, C.E., Domec, J.C., Delgado, C.I., 2011. Gold mining in the Peruvian amazon: Global prices, deforestation, and mercury imports. PLoS One 6. https://doi.org/10.1371/journal.pone.0018875.

Terborgh, J.W., Davenport, L.C., Belcon, A.U., Katul, G., Swenson, J.J., Fritz, S.C., Baker, P.A., 2018. Twenty-three-year timeline of ecological stable states and regime shifts in upper Amazon oxbow lakes. Hydrobiologia 807, 99–111. https://doi.org/10.1007/s10750-017-3384-z.

Terborgh, J., Davenport, L., 2021. Mobile piscivores and the nature of top-down forcing in Upper Amazonian floodplain lakes. Hydrobiologia 848, 431–443.

Thieme, M., Lehner, B., Abell, R., Hamilton, S.K., Kellndorfer, J., Powell, G., Riveros, J. C., 2007. Freshwater conservation planning in data-poor areas: An example from a remote Amazonian basin (Madre de Dios River, Peru and Bolivia). Biol. Conserv. 135, 484–501. https://doi.org/10.1016/j.biocon.2006.10.054.

Tickner, D., Opperman, J.J., Abell, R., Acreman, M., Arthington, A.H., Bunn, S.E., Cooke, S.J., Dalton, J., Darwall, W., Edwards, G., et al., 2020. Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. Bioscience 70, 330–342.

Watson, J.E.M., Dudley, N., Segan, D.B., Hockings, M., 2014. The performance and potential of protected areas. Nature 515, 67.

Wauchope, H.S., Jones, J.P.G., Geldmann, J., Simmons, B.I., Amano, T., Blanco, D.E., Fuller, R.A., Johnston, A., Langendoen, T., Mundkur, T., Nagy, S., Sutherland, W.J., 2022. Protected areas have a mixed impact on waterbirds, but management helps. Nature. https://doi.org/10.1038/s41586-022-04617-0.

Whitney, M.C., Cristol, D.A., 2017. Impacts of sublethal mercury exposure on birds: a detailed review, in: Reviews of Environmental Contamination and Toxicology. Springer, pp. 113–163.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M., Jetz, W., 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals: Ecological Archives E095-178. Ecology 95, 2027.

Yamaura, Y., Royle, J.A., Shimada, N., Asanuma, S., Sato, T., Taki, H., Makino, S., 2012. Biodiversity of man-made open habitats in an underused country: a class of multispecies abundance models for count data. Biodivers. Conserv. 21, 1365–1380.

Zurita, G.A., Pe'er, G., Bellocq, M.I., 2017. Bird responses to forest loss are influenced by habitat specialization. Divers. Distrib. 23, 650–655. https://doi.org/10.1111/ddi.12559.