



Are protected areas working for endangered frogs in the Peruvian Andes?

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Received: 11 April 2021 / Revised: 2 March 2022 / Accepted: 1 April 2022 / Published online: 6 June 2022
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Abstract

Assessments of the performance of protected-area (PA) networks for aquatic biodiversity conservation are rare yet essential for successful conservation of species. This is especially crucial in highly biodiverse, developing tropical countries where biodiversity loss is most pronounced. We assessed a PA network in the central Andes of Peru that encompasses parts of the geographical distribution of two endangered, endemic, high-elevation *Telmatobius* frogs. Sites within and beyond PA boundaries were classified into three different PA types: (a) strict-use (prohibits use by local inhabitants), (b) multi-use (allows some use by local inhabitants), and (c) unprotected (no restrictions). We conducted spatial analysis of species distributions, quantified species abundances and population trends, and measured potential threats and ecological integrity in each PA type. Spatial analysis indicated range contractions of 57.7% (*T. macrostomus*) and 69.0% (*T. brachydactylus*). Defaunation rates and species abundances in PAs were similar to those outside PAs. Poaching, livestock, and solid waste were the predominant threats. Analysis of ecological integrity indicated that strict-use sites had greater biotic index and habitat assessment scores compared to multi-use sites. These results suggest that despite benefits of greater ecological integrity in strict-use PAs, protection type has little effect on the conservation of aquatic species by itself. Protected areas are unlikely to be effective without better management of the trade-offs between cultural activities and biodiversity conservation. For PA networks to be of better conservation value for aquatic biodiversity in the developing world, they should be community-oriented and connect high-quality habitats, with their borders defined by catchments.

Keywords Amphibians · Aquatic biodiversity conservation · Endangered species · Protected areas · *Telmatobius macrostomus* · *Telmatobius brachydactylus*

Resumen

Las evaluaciones del desempeño de las redes de áreas protegidas (AP) para la conservación de la biodiversidad acuática son raras pero esenciales para la conservación exitosa de

Communicated by Clinton Jenkins.

This article belongs to the Topical Collection: Biodiversity protection and reserves.

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especies. Esto es especialmente crucial en los países tropicales en desarrollo con alta biodiversidad donde su pérdida es más pronunciada. Evaluamos una red de AP en los Andes centrales de Perú que abarca partes de la distribución geográfica de dos ranas altoandinas del género *Telmatobius*, endémicas y en peligro de extinción. Los sitios dentro y fuera de los límites de la AP se clasificaron en tres tipos diferentes de AP: (a) uso estricto (prohíbe el uso de recursos naturales por parte de los habitantes locales), (b) usos múltiples (permite algún uso por parte de los habitantes locales) y (c) desprotegidos (sin restricciones). Realizamos un análisis espacial de la distribución de especies, cuantificamos la abundancia de especies, las tendencias poblacionales, medimos las amenazas potenciales y la integridad ecológica en cada tipo de AP. El análisis espacial indicó un rango de contracciones de 57,7% (*T. macrostomus*) y 69,0% (*T. brachydactylus*). Las tasas de defaunación y abundancia de especies en las AP fueron similares a las de fuera de las AP. La caza furtiva, el ganado y los desechos sólidos fueron las amenazas predominantes. El análisis de la integridad ecológica indicó que los sitios de uso estricto tenían un índice biótico y puntajes de evaluación de hábitat más altos en comparación con los sitios de usos múltiples. Estos resultados sugieren que a pesar de los beneficios de una mayor integridad ecológica en las AP de uso estricto, el tipo de protección tiene poco efecto en la conservación de las especies acuáticas por sí mismo. Es poco probable que las áreas protegidas sean efectivas sin una buena gestión de las compensaciones entre las actividades culturales y la conservación de la biodiversidad. Para que las redes de AP tengan un mejor valor de conservación para la biodiversidad acuática en el mundo desarrollado, deben estar orientadas a la comunidad y conectar hábitats de alta calidad con sus fronteras definidas por cuencas.

Introduction

Since the late 19th century, the establishment of protected areas (PAs) has been a global cornerstone for modern conservation efforts (Watson et al. 2014). Unfortunately, many PAs only exist on paper, and despite their legal status, conservation efforts within them are minimal or non-existent (Tranquilli et al. 2014). These “paper parks” are often magnified in the developing world where thousands of PAs suffer significant funding deficits (James et al. 1999; Wilkie et al. 2001). Among many other factors (e.g., logging, hunting, fire, and grazing), insufficient funding limits effective management and coverage of PA networks (Bruner et al. 2001; 2004). This is troubling, considering that biodiversity loss is pronounced in tropical and developing countries (Ceballos 2007). Of particular concern are megadiverse countries such as Peru, which is a global hotspot for amphibians with 655 described species (AmphibiaWeb 2021). Currently, Peru has 241 PAs, covering >226,000 km² (17.6% of the country’s surface; SERNANP 2020). Of these, 75 are protected by the federal government and categorized into national parks, sanctuaries, reserves, reserved zones, protection forests, wildlife refuges, and communal and hunting reserves, which entail different levels of protection (Aguilar et al. 2012). As elsewhere, PAs in Peru were created to preserve iconic landscapes (e.g., Machu Picchu Historic Sanctuary) and protect habitat for biodiversity conservation (e.g., Manu National Park). However, PAs can also be created to sustain the livelihood of local communities, support national economies, enhance fisheries, and alleviate pressures associated with climate change, which present multiple conflicting aims (Watson et al. 2014).

The Junín National Reserve, Historic Sanctuary of Chacamarca and National Sanctuary of Huayllay are three PAs in the high-Andes of central Peru. This PA network denotes two levels of protection: strict and multi-use. Strict-use PAs prioritize biodiversity conservation generally without people (nature for itself), while multi-use PAs also focus on providing sustainable benefits for people (nature for people; Mace 2014). The movement away from species conservation towards conservation of ecosystem services in the latter, allows local inhabitants to ‘rationally’ use the protected natural resources to sustain their livelihoods. This PA network also encompasses part of the geographical distribution of two endemic, high-elevation *Telmatobius* amphibians, the fully-aquatic Junín giant frog (*T. macrostomus*) and the semi-aquatic Junín riparian frog (*T. brachydactylus*).

Twenty-eight of the 63 described species of *Telmatobius* frogs are distributed in Peru (AmphibiaWeb 2021). Unlike most other frogs, adult *Telmatobius* are highly or strictly aquatic, showing their greatest diversity at high elevations, above the tree line (Barrionuevo 2017). *Telmatobius macrostomus* and *T. brachydactylus* have elevational ranges of 3200–4600 and 4000–4600 m above sea level, respectively. *Telmatobius macrostomus* is the world’s largest aquatic frog (Sinsch and Aguilar-Puntriano 2021), and *T. brachydactylus*, like most *Telmatobius* species, is smaller. Geographically and phylogenetically they are closest to one another (Castillo and Aguilar 2019), with adults occupying the benthos. *Telmatobius brachydactylus* is typically found inhabiting lotic environments whereas *T. macrostomus* is more commonly associated with lentic environments (Sinsch 1986), however, they have been found to live in sympatry (Castillo and Aguilar 2019). Although little is known about the ecology of *T. brachydactylus*, adult and larval *T. macrostomus* are generalists, feeding entirely on aquatic prey (Castillo and Elias 2021; Watson et al. 2017a).

Amphibians play a key role in aquatic food webs. They can reach high densities and biomass, exhibit high per-capita consumption rates, serve as important prey resources, and are often used as bioindicators as their populations are influenced by numerous environmental factors (Schiesari et al. 2009; Dixon et al. 2011). In addition to their importance in nutrient cycling, food web dynamics and indicators of ecosystem health, *T. macrostomus* and *T. brachydactylus* were historically a culturally important resource for human consumption (Angulo 2008). Currently, they are categorized as Endangered by Peruvian and International legislation due to declining population trends (IUCN SSC Amphibian Specialist Group 2018a; b). Unfortunately, the current status of these species in terms of presence/absence, measures of abundances, and the identification of potential threats is poorly documented. This is concerning, especially considering that *Telmatobius* frogs have undergone severe population declines across much of their geographic range (Angulo 2008). Besides the threat of unsustainable harvest, species of *Telmatobius* are threatened by habitat loss, fragmentation and water pollution from urban, agricultural, and mining expansion, invasive species, climate change, and emerging infectious diseases (Catenazzi and von May 2014; Petermann Razetto 2021).

The purpose of this paper is to assess the conservation value of a PA network for aquatic species in a data-poor region of the developing world. We adapted the approach of Parrish et al. (2003) by measuring threat status and ecological integrity in different PA types and conducted a survey of two frog populations at 46 locations with historic records for one or both *Telmatobius* species. Our specific research goals were to: (1) identify the current geographical distributions of *T. macrostomus* and *T. brachydactylus*; (2) quantify *Telmatobius* abundances and population trends; and (3) measure potential threats and ecological integrity

at sites in different PA types. Our study area offers a unique opportunity to evaluate the effectiveness of PAs for aquatic species conservation in the face of extreme funding deficits, inadequate management, and surrounding resource extraction. This effort to address the conservation impact of PA type for endangered and endemic frogs is the first we know of and aims to provide critical information for biodiversity conservation and PA management.

Methods

Study area and sampling

The Junín National Reserve, Historic Sanctuary of Chacamarca, and National Sanctuary of Huayllay were designated as national PAs in 1974. The Junín National Reserve, which includes Lake Junín, a wetland of international importance under the Ramsar convention (site no. 882), is an historically important habitat for *Telmatobius macrostomus*, covering 530 km². It was created for biodiversity conservation, and also under the auspices of contributing to the social and economic development of the area through the sustainable use of natural resources. Therefore, local inhabitants are allowed to use the area's natural resources to sustain their livelihoods, and commercial use is allowed under management plans. In 1932, a dam was constructed at the outflow of Lake Junín, immediately downstream of the San Juan River and the uppermost reach of the Mantaro River, to generate hydroelectricity for Cerro de Pasco's silver mining operations (Rodbell et al. 2014). Numerous populated areas exist within the Junín National Reserve and its associated buffer zone (e.g., Carhuamayo, Ondores, Ninacaca, and Huayre), including the capital of the Junín province (Junín), with a population of >10,000 people. In contrast, the Historic Sanctuary of Chacamarca and National Sanctuary of Huayllay cover areas of 25 km² and 68.2 km², respectively, and are designated as areas of strict protection. Therefore, the extraction of resources, as well as modifications and transformations of the natural environment, is prohibited. These PAs are far less populated and have only a few local inhabitants whose livestock (mostly sheep, cows and camelids) graze the areas.

We compiled a bibliographic search of historic and recent records from 1948 to 2017 (Department of Herpetology, San Marcos Natural History Museum, theses and reports) of the presence of *T. macrostomus* and *T. brachydactylus*, along with recent sightings from park rangers and local residents throughout the study area. Large bodies of water (e.g., Lake Junín) were not surveyed due to logistical constraints involving the use of a boat, accessibility to sites, extreme environmental conditions, and health and safety requirements of participants. As a result, a total of 46 locations were identified and 109 stream transects within the locations were searched (Fig. 1). We classified locations into three types (hereafter 'PA types'): (a) strict-use (5 locations within the Historic Sanctuary of Chacamarca and National Sanctuary of Huayllay), (b) multi-use (33 locations within the Junín National Reserve), and (c) unprotected (8 locations outside of the PA network). The surveys took place from October to December 2018 and consisted of a standardized method in which 100 m transects were searched thoroughly, with an effort of 4 person-hours per transect, moving in the upstream direction using dip-nets (net dimensions 0.4×0.4 m with 4.8 mm mesh). Surveyors performed dip-net sweeps in all types of microhabitats: pools, riffles, backwaters, beneath overhanging banks, along the substrate, and within floating and emerged vegetation

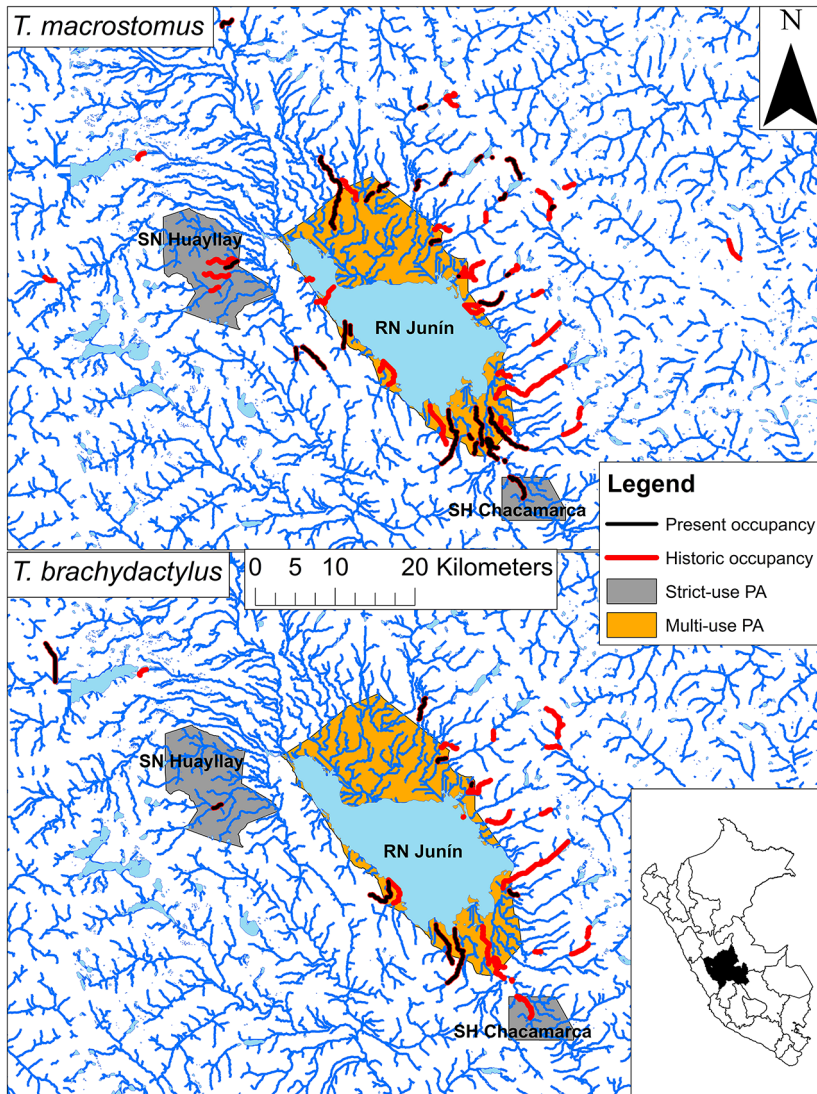


Fig. 1 Historic (1948–2017) and present (2018) occupancy of *Telmatobius macrostomus* and *T. brachydactylus* at stream segments throughout their known historic range. Insert: Peru with the regions Junín and Pasco shown in black

checking the contents of their nets after each pass through the water. To increase confidence that *T. macrostomus* or *T. brachydactylus* were absent from a site, we performed each survey twice. Watson et al. (2017b) found that two frog surveys on a particular transect are enough to be 95% certain that *T. macrostomus* is absent from a site. Captured individuals were

identified to species using Peters (1873) and Sinsch (1986), and grouped in general stages as either tadpoles, metamorphs or adults following Gosner (1960).

Geographical distribution

To analyze the geographical distribution of *T. macrostomus* and *T. brachydactylus*, we delineated stream segment-level watersheds throughout the study area (*sensu* Strager et al. 2009). Specifically, we generated a high-quality drainage map of the study area using digital elevation (DEM) data from the Shuttle Radar Topography Mission (United States Geological Survey Earth Resources Observation and Science Center 2020; *sensu* Thieme et al. 2007) with a resolution of 1 arc-second (30-meter) in ArcMap Version 10.6.1. Using a hydrologically corrected (fill) DEM we created flow direction and flow accumulation datasets to delineate stream segment-level watersheds from the raster data. All transects surveyed were assigned to their appropriate segment-level watersheds. We assumed frog presence/absence within a transect (100 m) to be equivalent to their presence/absence within a segment-level watershed. Finally, we compared historic occupancy (1948–2017) to present occupancy (2018) by calculating the area of the segment-level watersheds occupied by each species at each time interval (i.e., the percent area occupied within and outside of PA type boundaries), and the percent area lost compared to the known historic area.

Abundance and population trends

To test the effect of PA type on the abundance of each species, we used analysis of variance (ANOVA) with type-III sums-of-squares (unbalanced design) and statistical significance ($p < 0.05$). To investigate population trends, we compared abundances of *T. macrostomus* at ‘long-term’ sites. We used abundance data collected at eight sites (transects) from the current study (October – December 2018) and during a research trip in June – July 2019 and compared them to abundance data collected at the same sites in October 2015 and April 2016. Detection probability was assumed constant across surveys because tadpoles, metamorphs, juveniles and adults are known to coexist at all times of the year, due to their extensive larval development and constant reproductive activity, possibly linked to stable water temperatures (Vellard 1951; Sinsch 1986; Watson et al. 2017b; Castillo and Elias 2021). Regardless, we searched each transect twice to account for human error in capture. However, it should be noted that detection probabilities of amphibians have the potential to vary for a variety of environmental and physiological reasons. We used a two-way ANOVA to investigate the fixed main effects of PA type (three levels: strict-use, multi-use, and unprotected) and year (two levels: 2015–2016 and 2018–2019) on total abundance. Prior to analyses, we standardized abundance to catch per unit effort (CPUE; number of individuals captured per person-hour), and tested variance heterogeneity with Levene’s test.

Threat status and ecological integrity

To measure threat status at each site (transect) we recorded the presence or absence of 11 potential threats (Table 1). Threats included: the presence of solid waste, rainbow trout (*Oncorhynchus mykiss*; introduced species), livestock (< 1 m), railway line (< 50 m), sewage, road (< 50 m), laundry washing, high sedimentation (due to its relationship as a cause

Table 1 List of the potential threats identified at each transect, the rationale for their inclusion in the assessment, and their percent presence at each of the protected-area types

Potential threat	Reason	Presence (%)		
		Strict-use	Multi-use	Unprotected
Poaching	Biodiversity loss	100.0	100.0	100.0
Livestock (<1 m)	Habitat degradation	100.0	94.3	92.9
Solid waste	Contaminant	85.7	89.7	71.4
Rainbow trout (<i>O. mykiss</i>)	Introduced species	42.9	11.5	64.3
Laundry washing	Contaminant	28.6	24.1	35.7
High sedimentation	Habitat degradation	0.0	56.3	35.7
Sewage	Contaminant	14.3	10.3	7.1
Road (<50 m)	Habitat fragmentation	14.3	8.0	7.1
Mining	Habitat degradation	0.0	8.0	14.3
Chuño	Habitat alteration	0.0	5.7	7.1
Railway line (<50 m)	Habitat fragmentation	0.0	10.3	0.0

for cleaning canals), chuño (a traditional Andean food where potatoes are buried in a stream bed and left to ferment before they are excavated and dried), poaching, and mining within the catchment. These potential threats were identified during the 2nd Workshop to Establish a Conservation Strategy for the Frogs of Junin (Watson et al. 2016). To visualize if threats were driving differences in PA types, we applied principal coordinates analysis (PCO; Jacard dissimilarity coefficient). Vector overlays (Pearson's correlation) were used to visualize which threats were strongly correlated (absolute value > 0.5) to a PCO. Separation of sites, with PA type overlays, in ordination space was used to interpret the degree of difference between sites in different PA types. To determine if there were differences between PA type and cumulative threats, we used the non-parametric Kruskal Wallis test, with statistical significance ($p < 0.05$).

To measure the ecological integrity of PA types, we used aquatic invertebrate communities, as well as a variety of physical and chemical conditions at 20 sites throughout the study area. Sites were classified as above into PA type: strict-use (seven sites within the Historic Sanctuary of Chacamarca and National Sanctuary of Huayllay), multi-use (seven sites within the Junin National Reserve), and unprotected (six sites outside of the PA network). Aquatic invertebrate communities were sampled in October 2015 and April 2016 following a modified version of the multi-habitat approach for low gradient streams (Watson et al. 2017b). At each site, we obtained 11 dip/kick-net samples using a D-frame net (net dimensions 0.3×0.3 m with $500 \mu\text{m}$ mesh) to sample a total of 1.0 m^2 (WVDEP 2014). We filtered all 11 samples through a $250 \mu\text{m}$ sieve and preserved the composite sample in 95% ethanol. A random sub-sample of 200 invertebrates ($\pm 10\%$) from each site were identified to family or the lowest possible taxonomic level, and eight aquatic invertebrate community metrics were calculated. These included taxa richness, Ephemeroptera/Plecoptera/Trichoptera (EPT) richness, % EPT abundance, % E abundance, % Chironomidae, % 2 dominant families, Modified Hilsenhoff Index (MHI), and the Andean Biotic Index (ABI; *sensu* Rios-Touma et al. 2014). To assess habitat quality, we used a rapid bioassessment protocol (Barbour et al. 1999). Additionally, we recorded descriptions of stream substrate, mean stream width, and mean stream depth at evenly spaced points along the 100 m transects. Instream water quality measurements (pH, temperature, and specific conductance) were obtained instantaneously with an ExStik EC500 meter prior to each survey.

To investigate if differences existed between aquatic invertebrate communities and PA type, we used a combination of multivariate statistics and ordination procedures. Prior to analyses, invertebrate abundance data were fourth-root transformed to reduce the influence of dominant species to allow less abundant species to contribute to differences in community composition. Then, we used non-metric multidimensional scaling (NMDS; Bray-Curtis distance coefficient) to visualize differences in aquatic invertebrate assemblages among different PA types. We labeled samples (sites) in ordination space by PA type and added to the ordination weighted mean positions of selected taxa. Additionally, we correlated significant aquatic invertebrate community metrics and instream parameters to the ordination. Correlations were considered significant when $p < 0.05$ (for 999 permutations of the data). Next, ADONIS (ANOVA using distance matrices) was used to test for differences. Finally, we used Similarity Percentage (SIMPER) to identify which aquatic invertebrates contributed most to the average dissimilarity between PA types. ANOVA and Tukey's HSD post-tests were used to identify which community metrics and instream parameters were statistically different among PA types. All statistical analyses were performed in the R statistical environment Version 3.6.1 (R Development Core Team 2020). NMDS, ADONIS and SIMPER were performed with the package *vegan* (Oksanen et al. 2019). PCO was performed in Primer 6 (PRIMER-E, Ivybridge, UK).

Results

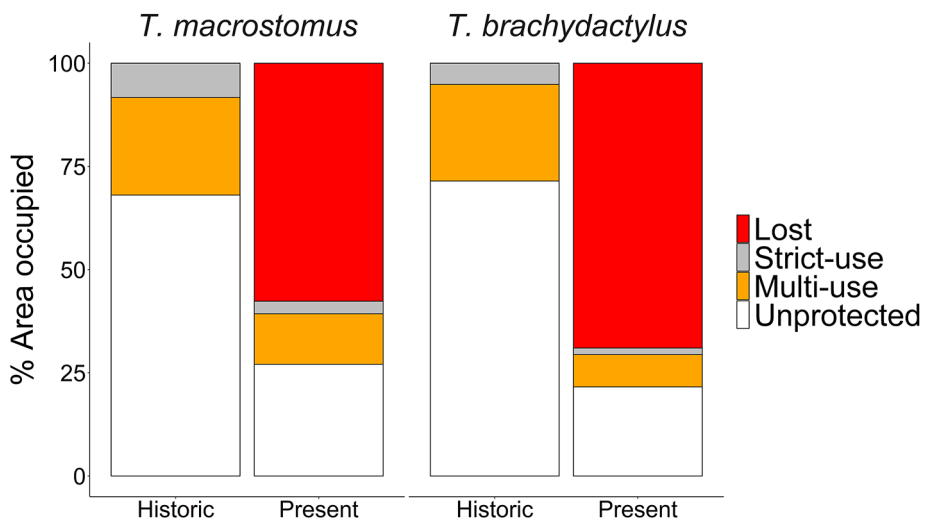


Fig. 2 Historic (1948–2017) and present (2018) percent area of occupancy for *Telmatobius macrostomus* and *T. brachydactylus* by protected-area type and percent area lost compared to known historic segment-level watersheds

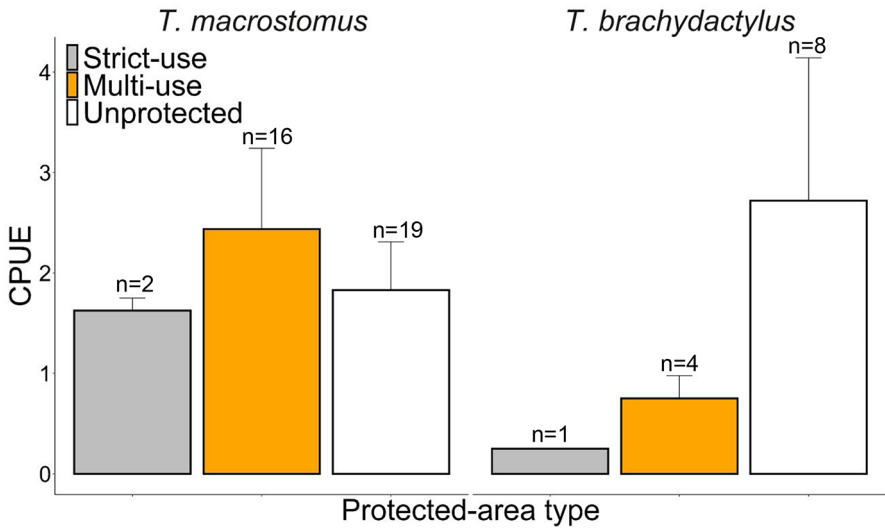


Fig. 3 Mean (+SE) CPUE (Catch Per Unit Effort; individuals captured per person-hour) of *Telmatobius macrostomus* and *T. brachydactylus* at occupied transects in 2018. Transects are grouped by protected-area type (strict-use, multi-use, and unprotected). Sample sizes are shown above bars

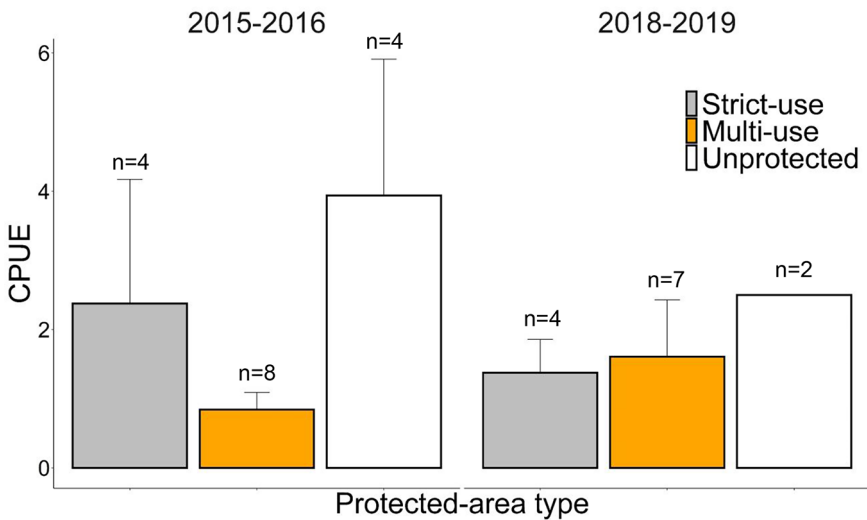


Fig. 4 Mean (+SE) CPUE (Catch Per Unit Effort; individuals captured per person-hour) of *Telmatobius macrostomus* in long-term transects. Transects are grouped by protected-area type (strict-use, multi-use, and unprotected) and years. Sample sizes are shown above bars

Geographical distribution, abundance, and population trend

We delineated a total of 8,455 segment-level watersheds throughout the study area which averaged 2.35 km² in size (Fig. 1). Spatial analysis indicated range contractions of 57.7% (*T. macrostomus*) and 69.0% (*T. brachydactylus*) from known historic locations (Fig. 2). Of the current known areas identified to be occupied by *T. macrostomus*, 12.3% are in the Junín National Reserve (multi-use PA), and 3.0% are in the Historic Sanctuary of Chacamarca and National Sanctuary of Huayllay (strict-use PAs). While for *T. brachydactylus*, 7.8% are in the Junín National Reserve and 1.6% in the National Sanctuary of Huayllay.

There was no difference between catch per unit effort in transects grouped by PA type for *T. macrostomus* ($F_{2,34} = 0.265$, $P = 0.769$) or *T. brachydactylus* ($F_{2,10} = 0.586$, $P = 0.575$) during the 2018 surveys (Fig. 3). There was also no significant difference between catch per unit effort and PA type ($F_{2,28} = 2.520$, $P = 0.102$) and year ($F_{1,28} = 0.417$, $P = 0.525$) for *T. macrostomus* at ‘long-term’ transects (Fig. 4), and no interaction ($F_{2,28} = 0.649$, $P = 0.532$).

Threat status

Two PCO axes accounted for 51.8% of the variation between transects in the threat variables (Fig. 5). The presence of high sedimentation (-0.96) was correlated with PCO 1; while PCO 2 was strongly correlated with the presence of solid waste (0.73), trout (-0.73), and

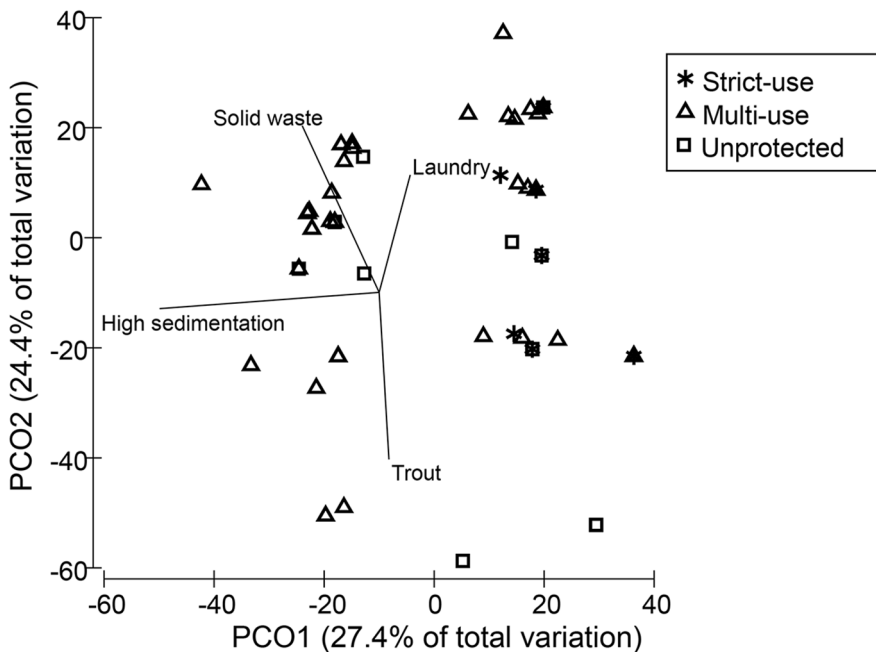


Fig. 5 Bivariate scatter plot of principal coordinate (PCO) 1 and 2 scores for each transect overlaid with protected-area type. Threats with high (>|0.5|) correlation are shown

laundry washing (0.51; Fig. 5). There was no separation in ordination space between multi-use sites and unprotected sites, however, strict-use sites grouped together in the positive direction of PCO 1. Overall, the predominant threats identified at the strict-use sites (transects) were livestock (100%) and solid waste (85.7%; Table 1). For multi-use sites, the most prevalent threats identified were livestock (94.3%), solid waste (89.7%), and high sedimentation (56.3%), and for unprotected sites livestock (92.9%), solid waste (71.4%) and trout (64.3%) were the main threats (Table 1). Illegal harvesting was assumed equal (100%) across all sites because poaching occurs throughout the study area (personal communications with SERNANP staff). There was no significant difference between PA type and cumulative threats (Kruskal-Wallis, $\chi^2=0.451$, $df=2$, $P=0.798$).

Ecological integrity

A total of 8,205 aquatic invertebrates were identified from the 20 sites sampled in 2015 and 2016. There were significant differences in aquatic invertebrate communities between PA types ($F_{2,37} = 4.539$, $P < 0.001$, $R^2 = 0.20$; Fig. 6). Subsequent pairwise comparisons found that aquatic invertebrate communities from strict-use sites were statistically different to

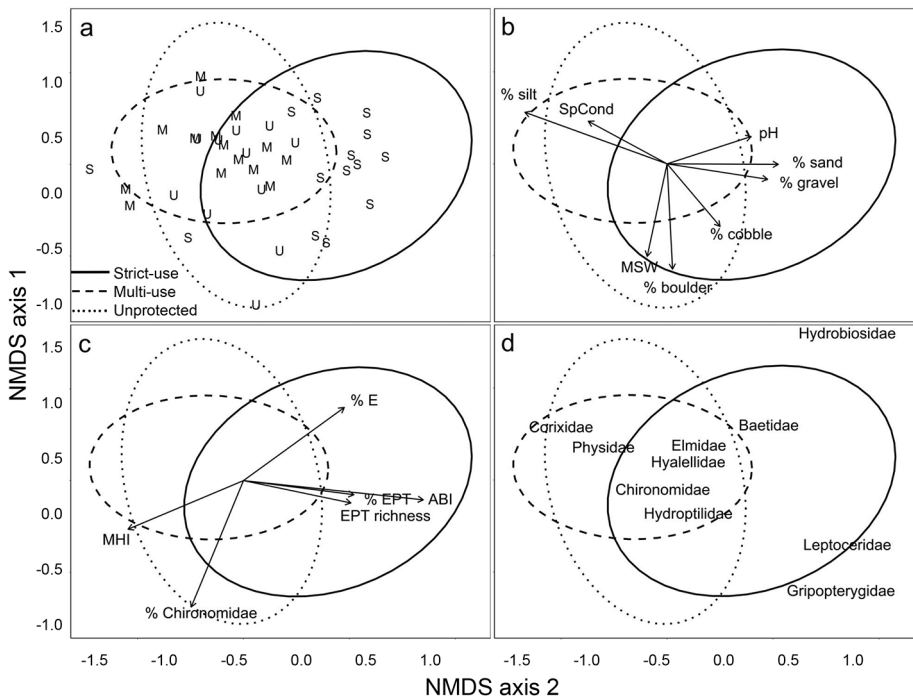


Fig. 6 Nonmetric multidimensional scaling (NMDS) ordination of aquatic invertebrate samples from 2015–2016 (Bray-Curtis distance coefficient) in two dimensions showing (a) sites labeled by protected-area type (S=strict-use, M=multi-use and U=unprotected), (b) in-stream parameters, (c) invertebrate metrics, and (d) weighted mean positions of selected taxa. Stress=0.14 in the three-dimensional solution. SpCond: specific conductance; MSW: mean stream width; ABI: Andean Biotic Index; EPT: Ephemeroptera Plecoptera Trichoptera; E: Ephemeroptera; MHI: Modified Hilsenhoff Index. ADONIS p value=0.001

those in multi-use sites ($F_{1,26} = 7.121$, $P < 0.001$, $R^2 = 0.22$), and unprotected sites ($F_{1,24} = 4.817$, $P < 0.001$, $R^2 = 0.17$), but the multi-use sites were not statistically different to those in unprotected sites ($F_{1,24} = 1.094$, $P = 0.39$, $R^2 = 0.04$). SIMPER analysis indicated that 80.5% of the dissimilarity between multi-use and strict-use sites was explained by the invertebrate families Hyalellidae (19.5%), Baetidae (17.1%), Chironomidae (11.0%), Corixidae (11.0%), Physidae (11.0%), and Elmidae (10.9%). Multi-use and unprotected sites had 82.0% of their dissimilarity explained by Hyalellidae (20.1%), Chironomidae (18.1%), Physidae (11.4%), Elmidae (11.4%), Hydroptilidae (10.7%), and Baetidae (10.3%). Strict-use and unprotected sites had 82.8% of their dissimilarity explained by Hyalellidae (21.3%), Baetidae (17.1%), Chironomidae (14.9%), Elmidae (13.1%), Hydroptilidae (9.2%), and Corixidae (7.2%). ANOVA tests showed that strict-use sites had greater EPT richness than multi-use and unprotected sites ($F_{2,37} = 12.33$, $P < 0.001$; Table 2), and % E was greater at strict-use sites than unprotected sites ($F_{2,37} = 3.94$, $P = 0.028$; Table 2). The Andean Biotic Index (ABI score) was greater at strict-use sites than at multi-use sites ($F_{2,37} = 4.19$, $P = 0.023$; Table 2).

In terms of physical habitat and water quality, strict-use sites had lower conductivity compared to multi-use and unprotected sites ($F_{2,37} = 10.90$, $P < 0.001$; Table 2), and mean stream depth was lower at strict-use sites than multi-use sites ($F_{2,37} = 3.45$, $P = 0.042$; Table 2). The

Table 2 Means and standard deviations (SD) of physical habitat, instream parameters, and aquatic invertebrate metrics for each protected-area type

	Protected-area type						F-value	df
	Strict-use (n=7)		Multi-use (n=7)		Unprotected (n=6)			
	Mean	SD	Mean	SD	Mean	SD		
pH	8.27	0.61	7.99	0.48	8.15	0.48	0.96	2,37
Temperature (°C)	12.71	2.08	13.25	2.31	13.01	3.40	0.15	2,37
Conductivity ($\mu\text{S cm}^{-2}$)	256.90 ^a	136.74	417.07 ^b	69.71	405.75 ^b	77.39	10.90	2,37
Mean stream width (m)	2.66	2.31	5.08	3.50	9.84	12.80	3.10	2,37
Mean stream depth (m)	0.50 ^a	0.16	0.98 ^b	0.79	0.61 ^{ab}	0.31	3.45	2,37
% RVHA score	67.39 ^a	11.90	48.61 ^b	13.80	58.13 ^{ab}	14.36	6.94	2,37
% Bedrock	0.00	0.01	0.00	0.00	0.00	0.00	0.93	2,37
% Boulder	0.00	0.00	0.00	0.00	0.06	0.14	2.97	2,37
% Cobble	0.09 ^{ab}	0.16	0.01 ^a	0.03	0.15 ^b	0.16	3.62	2,37
% Gravel	0.24 ^a	0.22	0.03 ^b	0.06	0.17 ^{ab}	0.21	7.18	2,37
% Sand	0.22 ^a	0.21	0.06 ^b	0.12	0.04 ^b	0.09	7.80	2,37
% Silt	0.29 ^a	0.36	0.77 ^b	0.31	0.45 ^{ab}	0.39	6.62	2,37
% Clay	0.15	0.18	0.14	0.20	0.12	0.16	0.10	2,37
Taxa richness	8.64	2.06	8.43	2.24	8.58	1.83	0.04	2,37
% EPT	33.80	20.70	18.78	25.94	17.37	15.73	2.44	2,37
EPT richness	3.00 ^a	1.36	1.21 ^b	0.80	1.33 ^b	0.89	12.33	2,37
MHI	5.33	0.55	5.82	0.86	5.72	0.63	1.95	2,37
% Chironomidae	15.55	9.78	17.83	19.78	24.58	20.79	0.93	2,37
% 2 Dominant	74.21	10.99	68.74	12.64	71.74	16.45	0.59	2,37
% E	23.30 ^a	21.24	9.29 ^{ab}	14.28	6.96 ^b	11.22	3.94	2,37
ABI score	42.93 ^a	12.44	33.07 ^b	7.67	34.50 ^{ab}	7.86	4.19	2,37

Means with different letters among protected-area types are statistically different ($p < 0.05$; analysis of variance, Tukey post-test). RVHA: Rapid Visual Habitat Assessment; EPT: Ephemeroptera, Plecoptera, Trichoptera; MHI: Modified Hilsenhoff Index; E: Ephemeroptera; ABI: Andean Biotic Index

percent Rapid Visual Habitat Assessment (RVHA) score was greater at strict-use sites than multi-use sites ($F_{2,37} = 6.94$, $P=0.003$; Table 2). For stream substrate, strict-use sites had a greater percentage of gravel than multi-use and unprotected sites ($F_{2,37} = 7.18$, $P=0.002$; Table 2), and a greater percentage of sand than multi-use sites ($F_{2,37} = 7.80$, $P=0.001$; Table 2). Multi-use sites had a greater percentage of silt than strict-use sites ($F_{2,37} = 6.62$, $P=0.003$; Table 2), and unprotected sites had a greater proportion of cobble than multi-use sites ($F_{2,37} = 3.62$, $P=0.037$; Table 2).

Discussion

In general, the effectiveness of PAs is compromised by explicitly aiming to meet diverse human expectations other than biodiversity conservation and supporting recreational or agricultural activities (Acreman et al. 2020). In the high-Andes of central Peru, local inhabitants primarily use the protected natural resources for agricultural purposes (e.g., grazing of livestock), but also extract sod to dry and use as fuel, and clear reeds for thatching. Such land-use practices are detrimental to aquatic systems and, therefore, if PAs are to be more effective, management of the trade-offs between culturally important practices and biodiversity conservation is required. Furthermore, our results show that PA status alone is not adequate for aquatic species conservation. Although strict-use PAs had greater ecological integrity, defaunation rates and species abundances of endangered and endemic frogs in PAs are similar to those outside PAs. Our analysis demonstrates that PAs are unlikely to be effective for aquatic biodiversity conservation unless management can reduce threats from external pressures. The threats quantified throughout our study area identified poaching, livestock grazing, and solid waste as the most prevalent. Although some of the threats quantified are quite localized to the study area (e.g., chuño harvest), all of the threats measured are proxies of global change that have been well documented as detrimental to biodiversity conservation (e.g., Cohen et al. 1993; Davis 2003). For example, introduced rainbow trout, a predator/competitor, as a proxy of invasive species and high sedimentation or chuño harvest as a proxy of land-use development. In addition to these ubiquitous threats, other ecological processes also explain why PA status, by itself, does not guarantee aquatic biodiversity conservation.

For PAs to be of value for conservation of aquatic biodiversity, they must account for hydrologic connectivity (Roux et al. 2008). Here, we refer to hydrologic connectivity in an ecological sense relating to the water-mediated transfer of inorganic and organic matter, and dispersal of aquatic organisms (Pringle 2001). This is of primary importance to the value of PAs for aquatic species conservation. Protected areas are geographically fixed, and pervasive land use development can have profound effects on their ecological integrity (Pringle 2001; Hannah et al. 2007). Consequently, disturbances well outside PA boundaries (e.g., deforestation and mining) can result in the direct transmission of pollutants (e.g., sedimentation, nutrients, and mine drainage) to recipient ecosystems. Unfortunately for Lake Junín, the Upamayo Dam has resulted in decades of mine drainage from the Cerro de Pasco region entering the lake, making the sediments among the most polluted in Peru (Rodbell et al. 2014). Therefore, PAs are only effective if root causes to ecological impairment are identified and prevented, allowing the integrity and maintenance of communities, populations, and endangered species to persist (Parrish et al. 2003; Francozo et al. 2015).

With regard to connectivity as a means of aquatic organism dispersal and population viability, the metacommunity concept (Leibold et al. 2004) also explains why PAs, by themselves, cannot guarantee aquatic biodiversity conservation. For example, Merriam and Petty (2016) demonstrated that even aquatic communities within the most pristine streams are at risk of extirpation when isolated within an intensively mined region. Metacommunity and metapopulation processes, such as rescue and mass effects, can become easily altered, and aquatic biodiversity will not be sustained by simply protecting un-impacted streams (Merriam and Petty 2016). This has serious implications for PAs in heavily impacted regions like Junín and Pasco, Peru, increasing their vulnerability to becoming population sinks for the wildlife that they were designated to conserve and protect.

The use of aquatic invertebrate communities as a proxy for ecological integrity in our study showed that strict-use sites had greater biotic index and habitat assessment scores than multi-use and unprotected sites. As expected, the strict-use PAs (Historic Sanctuary of Chacamarca and National Sanctuary of Huayllay) have fewer human settlements within their boundaries in comparison to the multi-use PA (Junín National Reserve) and unprotected sites. Since most human activities include the modification and use of resources it is not surprising that aquatic invertebrate communities in more anthropogenically altered landscapes/riverscapes are more degraded than communities in more pristine habitats (i.e., strict-use PAs). This result is consistent with numerous studies (e.g., Lammert and Allan 1999; Mancini et al. 2005). Similarly, Françoso et al. (2015) found that strict-use PAs have significantly less deforestation rates than multi-use PAs. In addition, Ferreira et al. (2020) observed higher mammal diversity within strict-use PAs compared to multi-use PAs and attribute this difference to the level of protection. Currently, the strict-use PAs here comprise <20% of the area of the multi-use PA (Fig. 1).

Although we did not investigate the role of PA size as a variable that could influence their effectiveness as management tools for the conservation of these endangered and endemic frogs, other studies have found that a key contrast between Freshwater Protected Areas (FPAs) and Marine Protected Areas (MPAs) is that size matters (Watson et al. 2022). When resources become limited in an MPA, highly mobile species emigrate in search of more suitable habitats and resources outside of the PA. However, strictly aquatic species in FPAs may not be able to ‘spill-over’ or migrate between waterways, so the number of juveniles and adults that an FPA can accommodate is ultimately regulated by the quality and extent of target species’ habitat (Watson et al. 2022). Debate over PA size dates back almost a century, when Wright et al. (1933) recognized that PAs in the United States were too small for wide-ranging species. This scale mismatch continues today (e.g., Chundawat et al. 2016), and is exemplified by migratory species that depend on the quality and connectivity of disparate habitats. On the other hand, non-migratory species have very different spatial-scale requirements. For range-limited, endangered species, the most urgent conservation action is the establishment of new PAs for target species in good quality habitat. Undoubtedly, the persistence of endangered aquatic species in heavily impacted regions is grim, and although not ideal, smaller PAs are especially important for conserving endemic species (Shafer 1995; von May et al. 2008). Furthermore, smaller PAs have the potential to be managed more intensively, focusing on reducing local-level threats (e.g., poaching, livestock grazing, and solid waste).

It is evident that a key factor for conserving biodiversity is the appropriate design of PAs, however, it is likely that no single design will provide benefits for all, and species-

specific responses to protection will occur (Halpern 2003). Therefore, for PAs to succeed in the conservation of individual species, their establishment should be linked with programs designed to provide information on their effectiveness as management tools (Watson et al. 2021), and to direct *a posteriori* adaptive management actions (Halpern and Warner 2003). While highly and strictly aquatic species require core aquatic habitats, most amphibians have a dual reliance on terrestrial and freshwater ecosystems to complete their life-histories. For *T. macrostomus* and *T. brachydactylus* basic ecological information, such as movement or habitat requirements for reproduction, is lacking. Therefore, restricting our attention to amphibian population dynamics and community ecology in freshwater systems alone, as has been the tradition, is guaranteed to lead to incomplete understanding of the basic ecology and management requirements of these and other aquatic species (Lowe 2009). Terrestrial zones around aquatic environments are important for protecting aquatic species and may be more important than previously thought (Semlitsch and Bodie 2003). It is evident that most species are of conservation concern because certain aspects of their life history bring them into conflict with land development (Steen et al. 2012), and *Telmatobius* frogs of the high Andes are probably no exception.

In addition to habitat loss, the principal threat to 9 out of every 10 threatened amphibian species (Baillie et al. 2004), poaching is known to be one of the greatest threats to wildlife conservation worldwide (Moore et al. 2018). In fact, the harvesting of wild *Telmatobius* spp. for human consumption is the predominant threat affecting amphibians in the Peruvian Andes (Angulo 2008; Aguilar et al. 2010). Furthermore, the live trade of frogs harvested from wild populations facilitates the spread of chytrid fungus *Batrachochytrium dendrobatidis*, which has had its greatest effects in large-bodied, range-restricted anurans (Scheele et al. 2019), and has been responsible for the collapse of anuran species richness and abundance in Manu National Park, Southeastern Peru (Catenazzi et al. 2010). A recent study by Peterman Razetto (2021) confirms that chytrid fungus is found in the Junín National Reserve and that both species have been infected. To reduce poaching-related threats, and consequently the risk of spreading disease through live trade, Moore et al. (2018) suggests increasing the number of anti-poaching patrols to sites where the probability of poaching is high, and/or expanding the number of park ranger posts. However, these recommendations are not cost-effective avenues for PAs with funding limitations. Recently, a regional ordinance (N°331-GRJ/CR) was passed declaring the conservation and protection of both *Telmatobius* species a priority. Although the ordinance does not restrict the harvesting and sale of these endangered amphibians in local markets, it still marks a significant step towards the ultimate goal of conservation. Unfortunately, due to financial resource constraints, effective legislation in the developing world relies on voluntary compliance (Rowcliffe et al. 2004). Given that poachers will not comply voluntarily, we believe that the protection of these species will depend on community-based environmental education initiatives.

Aguilar et al. (2010) considers the importance of local inhabitants in Andean amphibian conservation, and although somewhat controversial, demonstrates how in the absence of resources (e.g., national herpetologists to carry out long-term monitoring), local inhabitants are the only source of information available. Furthermore, locally-lead projects will eventually facilitate the behavior changes needed to make sustainable, long-term conservation gains. This also highlights the importance of local PAs (versus national PAs), such as private and municipal reserves. In addition to requiring fewer economic resources, local PAs can have better monitoring practices, better relations with surrounding communities, and can

provide better protection for endangered, endemic species than national PAs (von May et al. 2008; Aguilar et al. 2010; Shanee et al. 2017).

In conclusion, many PAs are becoming progressively more isolated as surrounding land-use and resource extraction intensifies to meet ever-increasing global demand. Additionally, human activity within PA boundaries is prevalent worldwide. In fact, one-third of protected land is under intense human pressure (Jones et al. 2018) and, therefore, the analogy of PAs as oceanic islands surrounded by inhospitable seas of anthropogenically impacted environments seems even more relevant today (Haila 2002). For PAs to be of more value to aquatic species, we recommend the strict protection and connection of unprotected high-quality habitats to the existing PA network with borders defined by watershed boundaries. For this to happen, freshwater focal areas and critical management zones must first be identified and embedded within catchment management zones (Abell et al. 2007; Esselman and Allan 2010). However, adopting such a protection strategy must be done in a hierarchical framework that builds upon existing high-quality habitats, and that prioritizes poorer habitats for future restoration (Merovich et al. 2013). It is also recommended that more effort is needed to ensure that any socioeconomic objective of a PA is consistent with maintenance or restoration of ecosystem resilience and conservation of aquatic biodiversity (Acreman et al. 2020). Therefore, a community-based approach to PA management such as local PAs could provide strategic management solutions tailored to specific (local-level) threats and needs. This is especially important to meet conservation targets and provide financially feasible solutions for the expansion of PA networks in resource limited regions of the developing world (Le Saout et al. 2013; Shanee et al. 2017). These results further highlight the need for a more holistic approach to environmental management that approaches conservation and sustainability issues by incorporating life histories, species' requirements, habitat protection and restoration as unified goals.

Acknowledgements We thank Oscar Damián Baldeón, Winy Arias Lopez, Austin Fitzgerald, and numerous volunteers for their help with field sampling; Roberto Elias and Rogger Angel Moreno Lino for logistical support; Cesar Aguilar for providing access to the Scientific collection and providing suggestions that improved the project; David Schiel, Mike Hickford, and Jon Harding for helpful comments; three anonymous referees and editor Clinton Jenkins for comments that improved the manuscript; and the local communities and municipalities in the Junín and Pasco provinces.

Authors' contributions ASW and LC equally conceived the research idea; designed the methodology; collected field data; performed statistical analyses and wrote the manuscript.

Funding This project was funded in part by the National Geographic Society (grant number EC-352 C-18).

Open Access funding enabled and organized by CAUL and its Member Institutions

Availability of data and material The geographical distribution data analysed are not publicly available due sensitive information regarding endangered species locations but are available from the corresponding author on reasonable request. All non-sensitive data are available on figshare: <https://doi.org/10.6084/m9.figshare.19294451>.

Code Availability All code used for analyses are available on figshare: <https://doi.org/10.6084/m9.figshare.19294451>.

Declarations

Conflict of 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.

Ethics approval All work conforms to the legal requirements of the country in which it was carried out, including those relating to conservation and welfare, and to the Journal's policy on these matters. All sampling was approved by the Junín National Reserve (Resolución Jefatural N°006-2018-SERNANP-RNJ-JEF) and the Denver Zoological Foundation's Animal Welfare Committee (DZIR 2018-024).

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References

- Abell R, Allan JD, Lehner B (2007) Unlocking the potential of protected areas for freshwaters. *Biol Conserv* 134:48–63
- Acreman M, Hughes KA, Arthington AH, Tickner D, Duenas M-A (2020) Protected areas and freshwater biodiversity: a novel systematic review distils eight lessons for effective conservation. *Conserv Lett* 13:1–14
- Aguilar C, Ramírez C, Rivera D, Siu-Ting K, Suarez J, Torres C (2010) Anfibios andinos del Perú fuera de Áreas Naturales Protegidas: amenazas y estado de conservación. *Revista Peruana de Biología* 17:5–28
- Aguilar C, Gamarra R, Ramirez C, Suarez J, Torres C, Siu-Ting K (2012) Anfibios andinos y estudios de impacto ambiental en concesiones mineras de Perú. *Alytes* 29:88–102
- Aguilar-Puntriano C, Sinsch U (2021) Growth trajectory of the world's largest aquatic frog (*Telmatobius macrostomus*): skeletochronological analysis of digit growth marks. *Salamandra* 57:291–294
- AmphibiaWeb (2021) University of California, Berkeley, CA, USA. Accessed 29 Oct 2021.
- Angulo A (2008) Conservation needs of *Batrachophrynus* and *Telmatobius* frogs of the Andes of Peru. *Conserv Soc* 6:328–333
- Baillie JEM, Hilton-Taylor C, Stuart SN (eds) (Editors). 2004. 2004 IUCN Red List of Threatened Species. A global species assessment. IUCN, Gland, Switzerland and Cambridge, UK
- Barbour MT, Gerritsen J, Snyder BD, Stribling JB (1999) Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish. US Environmental Protection Agency, Office of Water Washington, DC
- Barrionuevo JS (2017) Frogs at the summits: phylogeny of the Andean frogs of the genus *Telmatobius* (Anura, Telmatobiidae) based on phenotypic characters. *Cladistics* 33:41–68
- Bruner AG, Gullison RE, Balmford A (2004) Financial costs and shortfalls of managing and expanding protected-area systems in developing countries. *Bioscience* 54:1119–1126
- Bruner AG, Gullison RE, Rice RE, de Fonseca GAB (2001) Effectiveness of parks in protecting tropical biodiversity. *Science* 291:125–128
- Castillo L, Aguilar C (2019) Description of *Telmatobius brachydactylus* tadpole (Anura: Telmatobiidae). *Rivista peruana de biología* 26:469–474
- Castillo L, Elias R (2021) Descripción en época seca del microhábitat del renacuajo de *Telmatobius macrostomus* (Peters, 1873) “rana gigante del Lago Junín” en los afluentes del lago Chinchaycocha / Perú. *Ecología Aplicada* 20:25–34
- Catenazzi A, von May R (2014) Conservation status of amphibians in Peru. *Herpetological Monogr* 28:1–23
- Catenazzi A, Vredenburg VT, Lehr E (2010) *Batrachochytrium dendrobatidis* in the live frog trade of *Telmatobius* (Anura: Ceratophryidae) in the tropical Andes. *Dis Aquat Organ* 92:187–191
- Ceballos G (2007) Conservation priorities for mammals in megadiverse Mexico: the efficiency of reserve networks. *Ecol Appl* 17:569–578

- Chundawat RS, Sharma K, Gogate N, Malik PK, Vanak AT (2016) Size matters: Scale mismatch between space use patterns of tigers and protected area size in a Tropical Dry Forest. *Biol Conserv* 197:146–153
- Cohen AS, Bills R, Cocquyt CZ, Caljon AG (1993) The impact of sediment pollution on biodiversity in Lake Tanganyika. *Conserv Biol* 7:667–677
- Davis MA (2003) Biotic globalization: does competition from introduced species threaten biodiversity? *Bio-science* 53:481–489
- Dixon AD, Cox WR, Everham EM, Cielley DW (2011) Anurans as biological indicators of restoration success in the greater Everglades ecosystem. *Southeast Nat* 10:629–646
- Esselman PC, Allan JD (2010) Application of species distribution models and conservation planning software to the design of a reserve network for the riverine fishes of northeastern Mesoamerica. *Freshw Biol* 56:71–88
- Ferreira GB, Collen B, Newbold T, Oliveira MJR, Pinheiro MS, de Pinho FF, Rowcliffe M, Carbone C (2020) Strict protected areas are essential for the conservation of larger mammals in a priority region of the Brazilian Cerrado. *Biol Conserv* 251:108762
- Françoso RD, Brandão R, Nogueira CC, Salmons YB, Machado RB, Colli GR (2015) Habitat loss and the effectiveness of protected areas in the Cerrado Biodiversity Hotspot. *Natureza & Conservação* 13:35–40
- Gosner KL (1960) A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183–190
- Haila Y (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecol Appl* 12:321–334
- Halpern BS (2003) The impact of marine reserves: do reserves work and does reserve size matter? *Ecol Appl* 13:S117–S137
- Halpern BS, Warner RR (2003) Matching marine reserve design to reserve objectives. *Proc. R. Soc. Lond. B* 270:1871–1878
- Hannah L, Midgley G, Andelman S, Araújo M, Hughes G, Martinez-Meyer E, Pearson R, Williams P (2007) Protected area needs in a changing climate. *Front Ecol Environ* 5:131–138
- IUCN SSC Amphibian Specialist Group (2018a) *Telmatobius macrostomus*. *The IUCN Red List of Threatened Species* 2018: e.T2645A89195689. <https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T2645A89195689.en>. Downloaded on 28 September 2020
- IUCN SSC Amphibian Specialist Group (2018b) *Telmatobius brachydactylus*. *The IUCN Red List of Threatened Species* 2018: e.T56329A89204767. <https://dx.doi.org/10.2305/IUCN.UK.20181.RLTS.T56329A89204767.en>. Downloaded on 28 September 2020
- James AN, Gaston KJ, Balmford A (1999) Balancing the Earth's accounts. *Nature* 401:323–324
- Jones KR, Venter O, Fuller RA, Allan JR, Maxwell SL, Negret PJ, Watson JEM (2018) One-third of global protected land is under intense human pressure. *Science* 360:788–791
- Lammert M, Allan JD (1999) Assessing biotic integrity of streams: effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. *Environ Manage* 23:257–270
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7:601–613
- Le Saout S, Hoffmann M, Shi Y, Hughes A, Bernard C, Brooks TM, Bertzky B, Butchart SHM, Stuart SN, Badman T, Rodrigues AS (2013) Protected areas and effective biodiversity conservation. *Science* 342:803–805
- Lowe WH (2009) Amphibians. In: Likens GE (ed) *Encyclopedia of Inland Waters*. Oxford Academic Press, pp 439–445
- Mace GM (2014) Whose conservation? *Science* 345:1558–1560
- Mancini L, Formichetti P, Anselmo A, Tancioni L, Marchini S, Sorace A (2005) Biological quality of running waters in protected areas: the influence of size and land use. *Biodivers Conserv* 14:351–364
- Merovich GT, Petty JT, Strager MP, Fulton JB (2013) Hierarchical classification of stream condition: a house-neighborhood framework for establishing conservation priorities in complex riverscapes. *Freshw Sci* 32:874–891
- Merriam ER, Petty JT (2016) Under siege: isolated tributaries are threatened by regionally impaired meta-communities. *Sci Total Environ* 560:170–178
- Moore JF, Mulindahabi F, Masozera MK, Nichols JD, Hines JE, Turikunkiko E, Oli MK (2018) Are ranger patrols effective in reducing poaching-related threats within protected areas? *J Appl Ecol* 55:99–107
- Oksanen J, Guillaume Blanchet F, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Szoecs E, Wagner H (2019) *Vegan: community ecology package*, R package version 2.5-6. R Foundation for Statistical Computing, Vienna
- Parrish JD, Braun DP, Unnasch RS (2003) Are we conserving what we say we are? Measuring ecological integrity within protected areas. *BioScience* 53:851–860

- Petermann Razetto AK (2021) Determinación de la presencia de *Batrachochytrium dendrobatidis* en las ranas altoandinas: *Telmatobius macrostomus* y *Telmatobius brachydactylus*, en la Reserva Nacional de Junín, Perú. Universidad Peruana Cayetano Heredia, Lima, Peru
- Peters W (1873) Über die von Dr. JJ v. Tschudi beschriebenen Batrachier aus Perú. Monatsbericht der königlich preussischen Akademie der Wissenschaften zu Berlin 1873:622–624
- Pringle CM (2001) Hydrologic connectivity and the management of biological reserves: a global perspective. *Ecol Appl* 11:981–998
- Ríos-Touma B, Acosta R, Prat N (2014) The Andean Biotic Index (ABI): revised tolerance to pollution values for macroinvertebrate families and index performance evaluation. *Revista de Biología Tropical* 62:249–273
- Rodbell DT, Delman EM, Abbott MB, Besonen MT, Tapia PM (2014) The heavy metal contamination of Lake Junín National Reserve, Peru: An unintended consequence of the juxtaposition of hydroelectricity and mining. *GSA today* 24:4–10
- Roux DJ, Nel JL, Ashton PJ, Deacon AR, de Moor FC, Hardwick D, Hill L, Kleynhans CJ, Maree GA, Moolman J, Scholes RJ (2008) Designing protected areas to conserve riverine biodiversity: Lessons from a hypothetical redesign of the Kruger National Park. *Biol Conserv* 141:100–117
- Rowcliffe JM, de Merode E, Cowlshaw G (2004) Do wildlife laws work? Species protection and the application of a prey choice model to poaching decisions. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271:2631–2636
- Schiesari L, Werner EE, Kling GW (2009) Carnivory and resource-based niche differentiation in anuran larvae: implications for food web and experimental ecology. *Freshw Biol* 54:572–586
- Semlitsch RD, Bodie JR (2003) Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conserv Biol* 17:1219–1228
- SERNANP (2020) Listado oficial de ANP. <https://www.gob.pe/sernanp>
- Shafer CL (1995) Values and shortcomings of small reserves. *Bioscience* 45:80–88
- Shanee S, Shanee N, Monteferrri B, Allgas N, Pardo AA, Horwich RH (2017) Protected area coverage of threatened vertebrates and ecoregions in Peru: comparison of communal, private and state reserves. *J Environ Manage* 202:12–20
- Sinsch U (1986) Anfibios de la sierra central del Perú, una clave de identificación para adultos y larvas. *Bol de Lima* 45:23–33
- Steen DA, Gibbs JP, Buhlmann KA, Carr JL, Compton BW, Congdon JD, Doody JS, Godwin JC, Holcomb KL, Jackson DR, Janzen FJ, Johnson G, Jones MT, Lamer JT, Langen TA, Plummer MV, Rowe JW, Saumure RA, Tucker JK, Wilson DS (2012) Terrestrial habitat requirements for nesting freshwater turtles. *Biol Conserv* 150:121–128
- Strager MP, Petty JT, Strager JM, Barker-Fulton J (2009) A spatially explicit framework for quantifying downstream hydrologic conditions. *J Environ Manage* 90:1854–1861
- Thieme M, Lehner B, Abell R, Hamilton SK, Kellndorfer J, Powell G, Riveros JC (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
- Tranquilli S, Abedi-Lartey M, Abernethy K, Amsini F, Asamoah A, Balangtaa C et al (2014) Protected Areas in Tropical Africa: Assessing Threats and Conservation Activities. *PLoS ONE* 9:e114154
- Vellard J (1951) Estudios sobre batracios andinos. I. El grupo *Telmatobius* y formas afines. *Memorias del Museo de Historia Natural Javier Prado* 1:1–89
- von May R, Catenazzi A, Angulo et al (2008) Current state of conservation knowledge on threatened amphibian species in Peru. *Trop Conserv Sci* 1:376–396
- Watson AS, Hickford MJH, Schiel DR (2021) Freshwater reserves for fisheries conservation and enhancement of a widespread migratory fish. *J Appl Ecol* 58:2135–2145
- Watson AS, Hickford MJH, Schiel DR (2022) Interacting effects of density and temperature on fish growth rates in freshwater protected populations. *Proceedings of the Royal Society B* 289:20211982
- Watson AS, Fitzgerald AL, Baldeon OJD (2017a) Diet composition and prey selection of *Telmatobius macrostomus*, the Junín giant frog. *Endanger Species Res* 32:117–121
- Watson AS, Fitzgerald AL, Baldeon OJD, Elias RK (2017b) Habitat characterization, occupancy and detection probability of the Endangered and endemic Junín giant frog *Telmatobius macrostomus*. *Endanger Species Res* 32:429–436
- Watson AS, Fitzgerald AL, Damián-Baldeón OJ, Chamorro Cuestas A, Castillo Roque L (2016) Ranas altoandinas en la región de Junín: estado actual y plan estratégico de conservación. Junín, Perú
- Watson JE, Dudley N, Segan DB, Hockings M (2014) The performance and potential of protected areas. *Nature* 515:67–73
- Wilkie DS, Carpenter JF, Zhang Q (2001) The under-financing of protected areas in the Congo Basin: so many parks and so little willingness-to-pay. *Biodivers Conserv* 10:691–709

Wright GM, Dixon JS, Thompson BH (1933) Fauna of the National Parks of the United States: a preliminary survey of faunal relations in National Parks. US Government Printing Office

WVDEP (West Virginia Department of Environmental Protection) (2014) Benthic invertebrate sampling, processing, and analysis: standard operating procedures. WVDEP, Charleston, WV

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