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The return of giant otter to the Baniwa Landscape: A multi-scale approach to species recovery in the middle Içana River, Northwest Amazonia, Brazil

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ABSTRACT

Commercial hunting for the 20th century international fur trade was responsible for the collapse of giant otter populations throughout Amazonia. Some thirty years after the wildlife trade was outlawed, giant otter populations have begun to show signs of recovery. The Baniwa indigenous people from the Upper Rio Negro region of Brazil have witnessed the recovery of otter populations in areas where they had been wiped out by hunting. To evaluate the giant otter recovery process, we identified local and landscape variables contributing to the re-establishment of the species throughout Baniwa territory. We conducted transect sampling in lakes and streams in search of direct and indirect signs of giant otter occurrence. During surveys, we recorded three local variables, and through radar and satellite image, obtained six landscape variables in buffers of 250 m, 500 m and 1000 m. Using generalized linear models we identified the 250 m buffer as the most suitable scale within which to study giant otter habitat use. Connectivity between shallow and elongated waterbodies were the most reliable landscape indicators of otter population presence on the middle Içana River. Our results highlight the importance of small and connected water bodies to species recovery, a fact that should be taken into consideration in the creation of protected areas and local resource management plans. With this study we hope to contribute to the advancement of giant otter conservation strategies, as well as to an increased role for indigenous people in managing their territory and resources towards more effective biodiversity conservation.

1. Introduction

The giant otter (*Pteronura brasiliensis*) was the species most impacted by commercial hunting for the international fur trade during the mid-20th century in Amazonia (Antunes et al., 2016). High prices for their pelts (Antunes et al., 2014) as well as intrinsic biological and ecological characteristics, such as low reproductive rate and strong social organization (Pimenta et al., 2018), contributed to a low resilience which drove giant otter populations to collapse throughout the Central Amazon (Antunes et al., 2016). The species has long been considered locally extinct in many areas within its historical range (Carter and Rosas, 1997; Duplaix et al., 2015; Pimenta et al., 2018). Some thirty years after the prohibition of hunting and trade in wild animal products by national and international law, giant otter populations began to show signs of recovery in Colombia (Díaz and Sánchez, 2002), Peru (Recharte and Bodmer, 2009; Groenendijk et al., 2014) and Brazil (Rosas et al., 2007; Leuchtenberger and Mourão, 2008; Ribas et al., 2012; Leuchtenberger et al., 2013; Lima et al., 2014).

Reoccupation of hunted-out areas after local extinction occurs via the migration of individuals from metapopulations resident in refuge areas through source-sink dynamics (Joshi and Gadgil, 1991). Such refuge areas need to be sufficiently remote to be mostly free of human pressure, and contain populations close to carrying capacity (Novaro et al., 2000). The dispersal of individuals from an established population to a new area, via migration, depends on the capacity of the species for movement between habitats through the landscape (Metzger and Décamps, 1997; Schenck et al., 2003). Consequently, the way in which habitats are distributed within a landscape has implications for connectivity, and therefore, for its suitability for a given species (Lyra-Jorge et al., 2010).

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Variations in population patterns (e.g. abundance, density, encounter rate) in particular habitats may provide a way to assess species response to different landscape structures and configurations (Lyra-Jorge et al., 2010). These different conformations define the habitat requirements necessary for species establishment, and reflect a population's demographic potential, as well as the individuals' ability to move through the landscape (Metzger and Décamps, 1997; Uezu et al., 2005). High quality habitats tend to be used more than degraded ones (Garshelis, 2000). This reflects matrix permeability, and is directly related to the maintenance of the flow of individual animals (Taylor et al., 1993) - a factor essential to species persistence (Metzger and Décamps, 1997; Uezu et al., 2005; Umetsu and Pardini, 2007).

Habitat selection by a species can vary at both spatial and temporal scales. However, an erroneous or arbitrary choice of scale can result in false inferences concerning the influence of the landscape on habitat selection by a species (Chambers et al., 2016). A multiple-scale approach can help avoid such errors when analyzing the strength of the relationship between species and habitat use (Thompson and McGarigal, 2002; Grand et al., 2004; Gaillard et al., 2010; Mateo-Sánchez et al., 2013), and provide a better understanding of the role of landscape in ecological relations and processes (Neel et al., 2004; Cushman et al., 2008). In this context, variations in local characteristics of habitats occupied by giant otters (Duplaix et al., 2015) suggest some flexibility in relation to microhabitat aspects. Moreover, variations in the reported sizes of giant otter home ranges (Duplaix et al., 2015) makes it difficult to assess the appropriate scale at which to study landscape requirements for the species.

On the other hand, there is a consensus concerning giant otter dependence on healthy riverine ecosystems, such that the species is recognized as a strong indicator of environmental quality (Barnett et al., 2000). As an apex predator, the giant otter regulates its prey populations (Treves and Karanth, 2003). In consequence, their disappearance may have impacts at several trophic levels (Gittleman, 2001), which makes the giant otter a key species for the conservation of wetlands. Floodplains comprise some 30% of Amazonia, and are among the world's most threatened ecosystems (Darwall et al., 2008; Junk et al., 2014). Expansion of human occupation and exploitation of forest resources has long contributed to the degradation of these environments (Agostinho et al., 2005), representing major threats to giant otter population recovery. For this reason, the species remains classified as “Endangered” on the IUCN Red List (Groenendijk et al., 2015a). A knowledge of giant otter habitat requirements, from local to landscape scale, is crucial for maintaining viable populations and for making conservation decisions that are appropriate to both the species and the habitats it occupies.

The Upper Rio Negro remains the most well-preserved region in the Amazon, and as part of the northern Rio Negro basin, may harbor one of the largest populations of giant otters in South America (Duplaix et al., 2015). The region is also home to over twenty distinctive indigenous groups, some 10% of Brazil's indigenous cultural and linguistic diversity, who, through their political organizations and partnerships with Nongovernmental Organizations (NGOs) have developed innovative strategies for social development and sustainable management of their territories (Cabalzar and Ricardo, 2006). However, the Rio Negro basin has been targeted for large-scale development projects, including mining operations and hydroelectric dams. Laws currently under debate in the Brazilian congress such as PL 3729/2004, and the proposed constitutional amendment 215 (PEC 215/2010), would deregulate the process of environmental licensing for such projects, weaken indigenous peoples' constitutionally guaranteed land rights, and loosen the rules restricting the exploitation of resources in different categories of protected areas (Ferreira et al., 2014; Fearnside, 2016). Such policy changes would threaten both the biological and cultural diversity of the region.

The Baniwa indigenous people, who inhabit the Içana River in São Gabriel da Cachoeira municipality, Upper Rio Negro, Amazonas, Brazil, persuaded by outsiders, hunted otters and other commercially valuable species from the mid-1950s until the late 1970s, leading to a collapse of otter populations near their settlements (Pimenta, 2016; Pimenta et al., 2018). In recent decades, the Baniwa have witnessed the recovery of otter populations in areas where these animals had been wiped out by hunting. The Baniwa welcome the recovery of otter populations as a sign of general ecological health, especially with regard to fish stocks. The return of the giant otters was partly responsible for awakening within the Baniwa people an awareness of the need for a fishing management plan for the region: the use of lakes and streams need to be regulated in a way that guarantees the Baniwa's fish stocks, while avoiding damage to the giant otter's recovery process. Using the giant otter as an indicator of fish stock resources, we seek to generate information to support the Baniwa people's fishing management plan by identifying, at multiple scales, the essential environmental elements necessary for the reestablishment of giant otter populations. We hope this contribution will advance conservation strategies for otter species and Amazonian wetlands more generally, while also supporting indigenous peoples in their community-based management and conservation strategies.

2. Methods

2.1. Study area

The upper Rio Negro is located in the northwest Amazon within the Brazilian municipalities of Barcelos, Santa Isabel do Rio Negro and São Gabriel da Cachoeira, along the border with Colombia and Venezuela. The region is home to a tremendous diversity of indigenous peoples, including some twenty ethnic groups speaking languages belonging to five distinctive cultural-linguistic families (Cabalzar and Ricardo, 2006). The Baniwa people belong to the Arawakan language family and have inhabited the Içana River Basin for centuries (Wright, 2005). The Içana River Basin originates in Colombia, but most of its 696 km length occurs in Brazilian territory. Here, the Içana River runs through the Indigenous Land of the Upper Rio Negro receiving water from several tributaries (including the Aiari, Cuiari, Piraiauara and Cubate rivers), until it joins the Rio Negro (Cabalzar and Ricardo, 2006).

At its source, the Içana is a white water river, but changes color to reddish and black after receiving waters from its tributaries. This variation in the composition of its waters, soil type and human habitation history creates a diverse mosaic of landscapes and vegetation types (Shepard et al., 2004). The region has many micro-ecosystems with diverse ecological characteristics, including areas of savannah-like open forest, known in Portuguese as *campinarana* or *caatinga* (in Baniwa, *hamáliani*), upland *terra-firme* (*éedzawa*), seasonally flooded blackwater forests (*igapó* in Portuguese; *álape* in Baniwa), and secondary forests (*capoeira*; *heñame*) (Abraão et al., 2010). Our study area on the middle Içana consisted mostly of nutrient-poor sandy soils with seasonally flooded igapó forests interspersed with numerous lakes and small streams relatively abundant in fish (Shepard et al., 2004). Within the so-called “lakes region” there are some 65 km of river, along which ten Baniwa communities are currently distributed. We visited nine of these communities during the research period in 2015.

2.2. Survey of giant otter occurrence

We surveyed a total of 150 km of waterways, including 19 lakes (97.3 km) and 16 small streams (52.6 km), once each, during 22 consecutive days at the beginning of the low-water period, which is when giant otters are restricted to such permanent watercourses. Because the species is diurnal, we conducted field sampling between 6 am and 6 pm (Groenendjik et al., 2005). We traveled along the whole margin of the water body in search of direct (e.g. sightings of groups or individuals) and indirect (e.g. footprints, latrines, burrows and lay-up sites) signs of otter presence at a maximum speed of 10 km/h (Yoccoz et al., 2001;

Pollock et al., 2002; Groenendjik et al., 2005). We performed GPS tracking (using Garmin eTrex 10) along the entire route and georeferenced all detected signs. To increase probability of direct and indirect detection, the field team was composed of one boatman and two binocular-using observers.

2.3. Local and landscape variables

Given the importance of habitat suitability and accessibility to the process of reoccupation, we measured the following landscape variables: perimeter, area, habitat availability, shape, isolation of the water body and distance to Baniwa communities. Considering the requirements for successful establishment in a new area, we measured the following local variables: margin slope, water transparency and depth. Local variables were measured in situ in a 300 m continuous transect (Palmeirim et al., 2014). We measured slope margins with a clinometer at the water-surface interface, water transparency with a Secchi Disk, and depth with a 20 m cord marked every 50 cm, carrying a 5 kg weight. The last two variables were always measured in the middle of the watercourse.

We analyzed landscape variables with ALOS-Palsar radar images (L-band, mode *Fine Bean Dual*, polarization HH and HV, 12.5 m spatial resolution, path/frame: 136/10; date: 11-2008) and Landsat 8 OLI and TIRS satellite images (15 m panchromatic spatial resolution, path/row: 004/59; date: 09-2015). Using ArcGis version 10.4.1 software (ESRI, Redlands, CA), we calculated the perimeter and area of each sampled water body, and obtained the shape based on two previous measurements following the calculation of the shape index suggested by Cintra et al. (2007): $SI = P/200(\pi A)^{0.5}$. Where, SI = shape index; P = perimeter in kilometers; $\pi = 3.14$; A = area in square kilometers. When $SI = 1$ we are referring to circular water bodies, $SI > 1$ to elongated water bodies, and $SI \geq 6$ to rectilinear water bodies.

To assess habitat availability and degree of isolation, we established a buffer around each water body to delimit the spatial scale at which the landscape would be analyzed. To test the most suitable scale for the study of habitat use by giant otter, we opted for a multi-scale approach (Thompson and McGarigal, 2002; Grand et al., 2004; Mateo-Sánchez et al., 2013; Shirk et al., 2014; Chambers et al., 2016), which covered the limit suggested by otter specialists (F. Rosas and F. Michalski, personal communications), and created buffers of three different sizes around the sampled water bodies: 250 m, 500 m and 1000 m.

Because giant otters move mostly through aquatic environments (Duplaix, 1980; Carter and Rosas, 1997), we measured habitat availability and isolation based on the floodable area of each sample unit. First, we did a supervised classification of the satellite image, cross-referencing the ALOS/PALSAR radar image, Google Earth TM images and the Baniwa-defined landscape categories described by Abraão et al. (2008), resulting in 90 validation points, which matched our classification with an accuracy of 85% across samples (Congalton, 1991). We distinguished nine landscape classes (Fig. 1): *terra-firme* forest, four different types of open-canopy *campinarana*, *igapó* flooded forest, herbaceous vegetation, sand bank and exposed water body. We checked and manually refined all these classes via filters in order to exclude class noise. Then, we added the proportion of buffer occupied by exposed water area to the area of flooded forest and herbaceous vegetation to obtain the percentage of habitat effectively available to otters in each sampled water body at different spatial scales. To evaluate the degree of isolation, we created a center point in each sampled water body, and then calculated the Euclidean distance from this centroid to the edge of each exposed adjacent water body identified within the respective buffer. Finally, we used the average Euclidean distance between water bodies for each buffer scale (Metzger, 2004). We disregarded the distance from the centroid to the main river, since all the water bodies sampled were connected to the Içana River.

Since negative interactions with people can cause giant otter avoidance (Oliveira et al., 2015), we used the distance from communities to evaluate possible effects of human activities on giant otter sightings in the middle Içana. Using satellite images, we calculated the distance of each giant otter encounter and sign to the nearest community distance along waterways rather than straight-line Euclidean distance, since that is how both the Baniwa and the otters move throughout the landscape.

2.4. Data analysis

First, we calculated the occurrence of giant otters in each sample unit through the sum of direct and indirect signs detected in all transects from each water body. Due to the low number of detections of direct signs of giant otter in the landscape, we carried out the subsequent analyzes with the total number of signs detected in each lake or stream. Then we compiled the microhabitat data for each transect and calculated the median variables to obtain a single value that represented the water body's environmental variations. We performed a Shapiro-Wilk test to assay whether data had a normal distribution. As it did not, we used generalized linear models (GLM) that meet this premise, while considering other types of data distribution (Zuur et al., 2009; McCullough, 2013).

Before modeling, we evaluated the colinearity between the set of variables at the local and landscape scale with a Spearman correlation test (Zuur et al., 2009). At the local scale, we considered variables as correlated when they had a value of $rho > 0.50$, and considered in subsequent models only those variables that were biologically representative. At the landscape scale, we retained all variables in the subsequent analysis, even if measurements had high colinearity, because the purpose is to evaluate only the strength of the correlations. Subsequently, we used GLM to determine which sets of variables would best represent the variation between the giant otter occurrence and the predictive variables for the species. During the exploratory analysis we also checked the data set to evaluate the presence of possible outliers (Zuur et al., 2009).

Since over-dispersion was not detected in the set of variables, we chose GLM models with a Poisson error distribution family. However, as the number of transects varied according to waterbody size, we applied an *offset* parameter to standardize the effort between units samples (Zuur et al., 2009). To avoid overly complex models (total degrees of freedom in species GLMs = 35 water bodies), we used a preliminary model selection to filter the variables that showed higher weight of importance in the GLMs (Kindt and Coe, 2005). We initially created three sets of models, one with scale-dependent landscape variables, one with scale-independent landscape variables, and a third with local variables. Before fitting each of these models, the explanatory variables were standardized to Z scores (Zuur et al., 2009). In the final model we added only those variables that showed significance $p < 0.05$, or a near-term trend to this value (up to $p < 0.09$) (Zuur et al., 2010). We generated 27 models, including a full model, a null model and 25 combinations. We evaluated the significance of each variable based on the homogeneity of the residues, and later plotted these against the adjusted values and the explanatory variables.

Finally, we selected the best combination of variables to describe the giant otter occurrence based on the multimodel approach using the Akaike Information Criterion (AIC), Akaike weight (AIC ω) and delta AIC (Δ AIC) (Burnham and Anderson, 2004). We considered best-fit models to predict the giant otter occurrence to be only those with $\Delta AIC \leq 2$. We used AIC ω to determine the relative importance of each variable in the final model. Unless a single model had $AIC\omega i \geq 0.90$, we made inferences about other models of the analyzed data by summing the ωi weights of all the models that included that variable (Burnham and Anderson, 2004). We obtained model averaged estimates of parameters when more than one model had $\Delta AIC \leq 2$. To develop these analyzes we used *vegan*, *lme4*, *visreg* and *MuMIn* packages on R software 3.2.1.

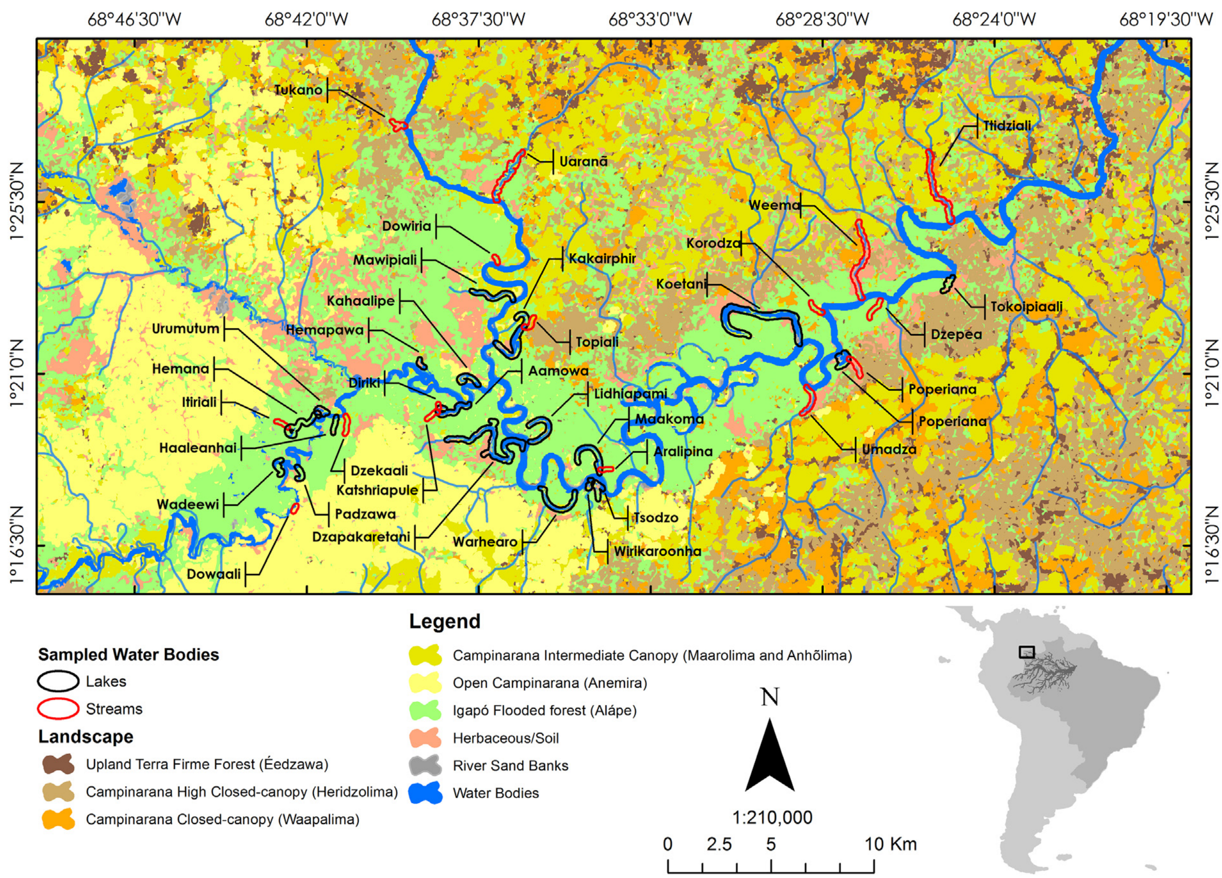

Fig. 1. Middle Içana region. Location of the lakes and streams sampled during this study, and of the different landscape classes detected with Landsat 8 OLI and TIRS satellite imagery, and ALOS/PALSAR radar image, and aligned with Abraão et al. (2008).

3. Results

Of 35 water bodies sampled, 21 (10 lakes, 11 streams) showed signs of giant otter occurrence. According to Baniwa oral histories, before the onset of commercial hunting, large groups of giant otters used to be found in most of the lakes and streams in the Içana River system (Pimenta et al., 2018). The apparent absence of otters from one third of the sampled water bodies indicates that the recovery process is not yet complete in the region. For details on giant otter occurrence signs and characteristics of lakes and streams, see Tables A1 and A2 in Supplementary material.

Collinearity analysis indicated that only the variables *area* and *perimeter* were correlated (rho = 0.891, $p < 0.001$). We chose to exclude the variable *area* from the subsequent analyses, considering that *perimeter*, which refers to the extension of the interface between the terrestrial and aquatic environment, would be more representative of the essential environment for giant otters (Palmeirim et al., 2014). A collinearity test of the variables *habitat availability* and *isolation* indicated a significant correlation between the three buffer scales (rho values ranged from 0.557 to 0.994, all with values of $p < 0.05$), confirming that although measurements were made at different scales, they were correlated.

Water body isolation in the 250 m buffer was the unique landscape variable with significant value in the scale-dependent model. Meanwhile, the model for scale-independent landscape variables has shown *perimeter* and *shape* of the water body as landscape variables with some degree of significance to explain the occurrence of giant otter in the middle Içana River (see Tables A3 and A4 in Supplementary material for details on landscape variables models). These landscape variables were included in the final model, along with the variables *margin slope* and *depth* of the water body, both local variables with significant values in the microhabitat model (see Table A5 in Supplementary material). As *hydrography* is linked with several local and landscape variables, it was also added to the final model.

From the combinations of these variables, we generated 25 models (Table A6 in Supplementary material). Six of which presented Δ AIC ≤ 2 (Table 1). In relation to landscape variables, we found that *Water body isolation in the 250 m buffer* [$\beta = -0.305$; IC 95% (-0.104, -0.651)], *perimeter* [$\beta = -0.254$; IC 95% (0.018, -0.623)] and *hydrography* [$\beta = -0.789$; IC 95% (0.109, -1.789)] were the variables that best explained the occurrence of giant otters on the middle Içana River. In relation to local variables, only *margin slope* [$\beta = 0.302$; IC 95% (0.012, 0.735)] had sufficiently high explanatory value to explain giant otter occurrence on the middle Içana River. *Isolation* showed a negative relationship with otters (Fig. 2A), indicating that the farther the sampled water body was located in relation to adjacent water bodies, the lower the occurrence of giant otters. Affected by the misaligned extension of the lakes *Koetani* and *Dzapakaretani*, the perimeter had a negative relation with giant otter occurrence, indicating that the larger the perimeter of the water body, the smaller the occurrence of the species (Fig. 2B). Margin slope showed a positive relation, indicating that the presence of steep river banks favors the occurrence of otters (Fig. 2C).

Although *shape* and the *depth* of the water body showed low explanatory power for giant otter occurrence, their summed AICωi indicated that these parameters were responsible for, respectively, 28% and 10% of giant otter occurrence, alongside the others parameters of the best-fit models. The positive relation of *shape*, and the negative relation with *depth*, indicates that the occurrence of giant otter in the middle Içana River may also be influenced by the presence of shallow and elongated water bodies. Finally, the presence of *hydrography* in all fitted models (AICωi = 1), and the association between giant otter with

Table 1
Top-ranked models (ΔAIC ≤ 2) showing the most important parameters (slope) of explanatory variables (Untransformed coefficients of covariates) from the GLMs on giant otter occurrence on the middle Içana River, Amazonas, Brazil. Significance values were *p < 0.05, **p < 0.001 and §indicates a weak effect. Standard errors are in parentheses.

Models	Isolation 250 m	Shape	Perimeter	Slope	Depth	Hidrography	K	AICc	Δ AIC	AICω
M 13			−0.312§ (0.170)	0.363* (0.183)		−0.550 (0.440)	4	92.4	0.00	0.19
M 12	−0.314* (0.170)			0.170 (0.181)		−0.871§ (0.453)	4	92.7	0.27	0.17
M 16	−0.321* (0.172)	0.121 (0.141)				−1.058** (0.363)	4	92.9	0.49	0.15
M 15	−0.310§ (0.169)		−0.118 (0.150)			−1.064** (0.358)	4	93.0	0.52	0.15
M 24		0.225 (0.150)	−0.344* (0.172)	0.392* (0.184)		−0.357 (0.471)	5	93.3	0.83	0.13
M 22	−0.234 (0.179)		−0.235 (0.172)	0.297 (0.196)		−6.600 (0.467)	5	93.5	1.04	0.11
M 09	−0.336* (0.170)				−0.054 (0.238)	−1.040* (0.521)	4	93.5	1.10	0.10
Model averaged	−0.305* (0.176)	0.168 (0.154)	−0.254§ (0.188)	0.302* (0.186)	−0.054 (0.238)	−0.789§ (0.510)	–	–	–	–
Summed AICω	0.69	0.28	0.58	0.60	0.10	1.00	–	–	–	–

Note: Only models with AIC weight (ω) > 0.1 and Δ AIC < 2 are shown. *K*: number of parameters; *AICc*: Akaike Information Criterion (AIC) corrected for small sample sizes; Δ *AIC*: difference in Akaike Information Criterion values between each model and the best model; AICω: model weight. Model averaged: Model-averages the estimate of a parameter of interest among a set of candidate models; Summed AICω: Relative importance of variables based on the sum of AICω of the models that include the variable.

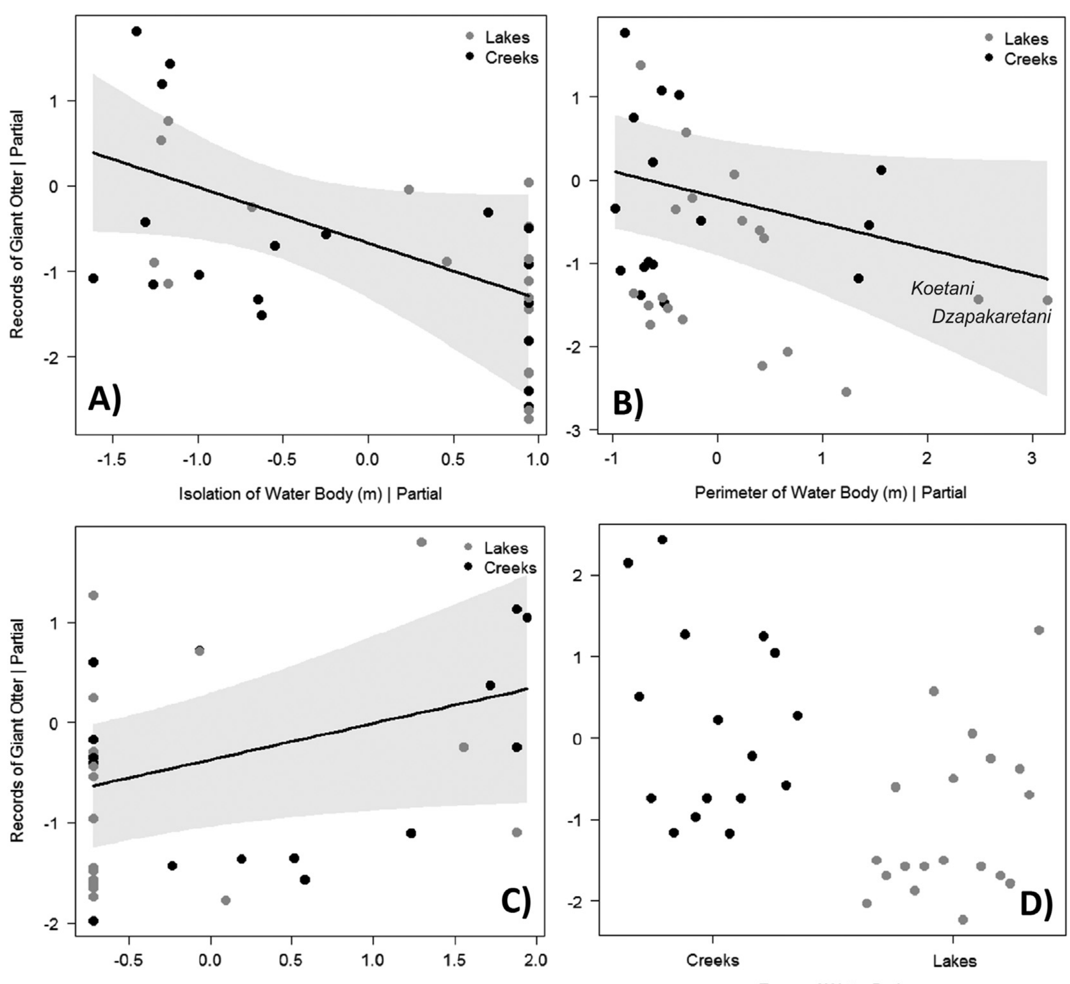

Fig. 2. Local and landscape variables influencing giant otter occurrence on the middle Içana River, Amazonas, Brazil. Occurrence of giant otters in relation to water body isolation in a 250 m buffer zone (A); in relation to extent of water body perimeter (B); otters in relation to slope of the river (C) and between types of water body (D). In our generalized linear models all these landscape and local variables had significant values (p < 0.05) in explaining the occurrence of otters in the lakes and streams on the middle Içana River.

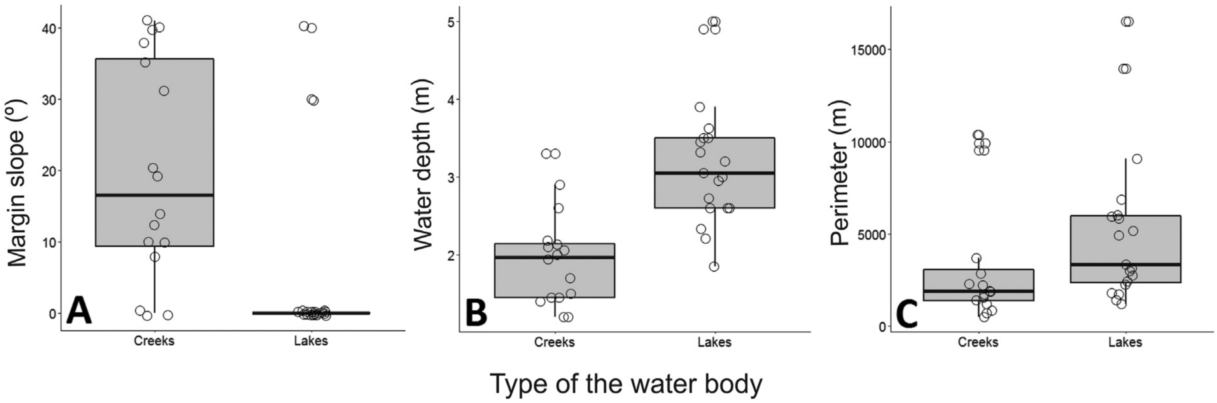

Fig. 3. Local and landscape variables which presented significant correlation with type of the water body.

creeks, suggests that small water bodies are more suitable environments for the occurrence of the species (Fig. 2D). Furthermore, the strong correlation of *hydrography* with *margin slope* (Wilcox test, W = 254.5, p = 0.0001), *perimeter* (Wilcox test, W = 91, p = 0.044) and *water depth* (Wilcox test, W = 28.5 p = 4.56×10^{-5}) (Fig. 3) highlights the importance of landscape relief as a structure responsible for promoting species establishment.

4. Discussion

The response of giant otters to isolation at a fine spatial scale reinforces the notion that connectivity between habitats is a crucial factor in enabling the process of recolonization of the historical hunting areas, and so allowing movement of individual giant otter through the matrix from the source areas. Our results also indicate that the establishment of giant otter in formerly hunted-out regions of the Içana River during the dry season depends on the presence of shallow elongated water bodies with high availability of areas for building shelter. The remote headwaters of such elongated streams were also identified by Baniwa research collaborators as the refuge areas where otter populations survived during the period of intense commercial hunting (Pimenta et al., 2018), indicating that these were probably source areas for the species recovery in the middle Içana river after commercial hunting was banned.

The multi scale approach to habitat use analysis has been deployed for studies on several types of carnivores, and has generally suggested that the response to landscape variables at fine spatial scales represent the effects of landscape on foraging area, while the response at larger scales represents the influence of landscape on home range (Chambers et al., 2016; Mateo-Sánchez et al., 2013; Shirk et al., 2014; Wasserman et al., 2012; Wilkinson et al., 2013). Generally, population size interacts with landscape according to the potential home range size and species-specific patterns of movement, which are themselves directly related to body size and regional productivity (Tucker et al., 2014).

The recorded size of giant otter home ranges varies greatly according to the ecosystem, flooding and methods used for its estimation (Leuchtenberger et al., 2013; Duplaix et al., 2015). Though it may attain 7.9 km^2 during flood season in the Brazilian Pantanal mashy habitats (Leuchtenberger et al., 2013), during the dry season in natural lagoons in the Amazon, the home range of *P. brasiliensis* was estimated between 0.5 and 2.8 km^2 (Utreras et al., 2005; Staib, 2005) - which is quite small when compared to other large Amazonian carnivorous mammals (Eisenberg and Redford, 2000). The small size of giant otter home ranges highlights the species's limited capacity for movement and hence persistence in areas distant from adjacent water bodies (Duplaix, 1980; Carter and Rosas, 1997; Michalski and Peres, 2005). Despite the strong swimming ability of giant otters, our results for habitat isolation at the 250 m scale indicate that movement of giant otter individuals is restricted to the social group's territory, an area that varies from 0.1 to 1 km^2 in natural lakes in Amazonia (Staib, 2005; Groenendijk et al., 2015b).

Similarly, the association of giant otter occurrence with sites of smaller perimeters could also be a reflection of the limitation of the species to small territories. However, a study conducted before and after the filling of the Balbina Dam (Amazonas, Brazil) found that the increase in lake perimeter due to the appearance of numerous islands in the flooded area did not result in a proportional increase in giant otter populations (Palmeirim et al., 2014). According to the authors, the giant otter population did not follow the increase in available perimeter due to the low quality of the newly-formed habitats that comprised the flooded area. Although the Içana River is an extremely preserved area and has a landscape quite different from that of a hydroelectric power reservoir, it is possible that the negative relationship recorded between giant otter and perimeter is also related to an absence of high-quality habitats into which new populations of the species could establish.

The pattern of geographical relief in the middle Içana landscape mosaic may also be responsible for influencing otter occurrence. A refined analysis of the perimeter variable made it clear that this relation is influenced by the two largest lakes of the middle Içana, *Dzapakaretani* (16.5 km) and *Koetani* (13.9 km). Both lakes were completely flooded during the sampling period (margin slope average = 0°) preventing the detection of any evidence of the species's presence in periods of extreme drought. Another 16 (84.2%) of sampled lakes were flooded during sampling, while only 3 (18.7%) of the streams had submerged margins at this time (*Dzekaali*, *Korodza* and *Umadza*). Analysis of the location of these water bodies revealed that all the flooded lakes and streams occurred in *igapó* areas, while most lakes and streams that retained at least some exposed margin occurred in *campinarana* areas, which give access to the headwaters formed in the *terra-firme* (Fig. 1). Thus, it is possible that the apparent selection of giant otter for steeply inclined banks (up to 40°) is associated with the greater availability of areas for the construction of shelter on such areas because they are less flood-prone. This finding reinforces the fact noted previously by Lima et al. (2012) that river margins are a key habitat for giant otter conservation.

Shallow lakes may not be capable of supporting giant otter groups for extended periods, since such lakes quickly become isolated in the dry season (Ribas et al., 2012). This has also been backed by studies of Groenendijk et al. (2015b) and Leuchtenberger et al. (2015) who both found that small (and shallow) lakes provided poor habitats for giant otters and negatively impacted the reproductive success of groups using them. However, the high rates of giant otter encounters in shallow and elongated water bodies underscores the importance of small streams and forest creeks for the species in the Içana River. Elongated water bodies generally have greater areas covered by vegetation and are considered more complex than circular ones, because they harbor a greater diversity of microhabitats, thus favoring a high diversity of aquatic fauna (Patton, 1975; Gorman and Karr, 1978; Bojsen and Barriga, 2002). Additionally, the preference for shallow water bodies by giant otters may be related to the ease of visually encountering and successfully capturing fish for food (Lima et al., 2012; Staib, 2005). Because of its strongly territorial nature, piscivorous habit (Duplaix, 1980; Rosas et al., 1999; Groenendijk et al., 2014; Groenendijk et al., 2015b), and high energetic demands (the giant otter can consume 10% of its own body weight in fish per day: Carter et al., 1999), the giant otter seems to favor small creeks where food resources are more easily available. Although they forage opportunistically during the flooded period, feeding on other small vertebrates and arthropods, fish comprise the greater part of the giant otter diet (Rosas et al., 1999; Cabral et al., 2010). For this reason, studies of the diversity and productivity of ichthyofauna in areas occupied by the giant otter are essential (e.g. Silva et al., 2013).

Fishing is also the main source of animal protein for human riverine populations of the Amazon. Many local human populations consider giant otters as competitors to their own fishing activities, and sometimes animals are killed punitively for this reason (Gómez and Jorgenson, 1999; Recharte et al., 2008; Rosas-Ribeiro et al., 2012). Such conflicts with human fishermen currently represent a significant threat to the conservation of the species (Groenendijk et al., 2015a). For the Baniwa, however, the giant otter plays an important role in the mythology of the origins of the first shamans. The giant otter is considered the “Shaman of the Waters”, responsible for the regulation and health of aquatic environments (Pimenta, 2016). Nonetheless, such traditional beliefs were not enough to stop the Baniwa from hunting otters to local extinction when the price for their pelts was high. Yet Baniwa do associate the local extinction of giant otters with a concomitant decline in fish populations, a kind of “revenge of the shaman of the waters.” Now the Baniwa welcome the return of the species to the Içana River as a harbinger of increasing fish stocks. Such a positive view of the species by the Baniwa people bodes well for the development of community-based fishery and territorial management plans that value the conservation of the giant otter within the broader human-occupied landscape.

Furthermore, a preliminary survey (Pimenta, unpublished data) indicates that there is currently no overlap in habitat use by Baniwa fishermen and giant otters: the ten sites most used by Baniwa for fishing are large lakes, while otters prefer shallower water bodies, especially small streams. Our data also suggests that giant otters tend to shy away from human presence, being somewhat more apparent in environments farther from Baniwa communities. This scenario has the potential to reduce the kind of direct conflicts that threaten otter populations elsewhere. However, the continued growth and territorial expansion of giant otter populations could lead to increasing frequency of encounters and conflicts with Baniwa fishermen, changing the status of the current relationship (see Lima et al., 2014). Understanding indigenous people's evolving attitudes towards otters and other endangered predators is essential for developing measures to mitigate conflicts, thus contributing to species recovery and to the maintenance of fish stocks, an essential activity for the Baniwa people.

5. Conclusion

Habitat selection and home range size by giant otters may change in seasonal landscapes, due to fish dispersion and the availability of banks for resting sites (Duplaix, 1980; Leuchtenberger et al., 2013). Our study suggests that landscape-scale level characteristics may have a greater influence on the occurrence of giant otters than local habitat characteristics during the dry season. However, we need further studies to evaluate the influence of different landscape metrics, including the effect of matrix diversity on displacement and dispersion processes (e.g. Verbeylen et al., 2003; Larue and Nielsen, 2008) in different ecosystems. Such studies will help us understand habitat selection by giant otters and evaluate the recolonization potential of the species within its historical range. We found evidence that well-drained rainforest creeks should be considered as preservation areas for giant otters in management plans for Baniwa territory, thus avoiding direct conflicts that might interfere with the species recovery process. The success of any management plan requires a thorough understanding of the relationships between local human populations, vulnerable species and the environments they both occupy. Protected areas, including indigenous and extractive reserves inhabited by human populations, can act as refuge areas for threatened and endangered species, and are thus a critical part of the recovery process after periods of extreme historical overexploitation. In this specific case, we found that the local Baniwa people maintain a positive attitude towards the giant otter as a protective “shaman” for aquatic environments, thus facilitating conservation strategies for the species within broader community-based management plans. More generally, we argue for the importance of local community participation in wildlife research and management of the Amazonian floodplains.

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Appendix A. Supplementary data

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