Research article

Defining Neotropical otter *Lontra longicaudis* distribution, conservation priorities and ecological frontiers

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Abstract

Understanding a species' occurrence requirements is essential for its conservation, and species distribution models (SDMs) are a powerful tool for this purpose. Here we estimated a SDM based on actual distribution information, in relation to climatic, hydrological, human population, and vegetation data sets, to understand the ecological requirements and geographic distribution of the Neotropical otter *Lontra longicaudis*, a species whose habitat requirements and conservation needs are mostly unknown. Using MaxEnt, we defined its potential distribution and most suitable areas to indicate priority areas for research and to analyze the efficiency of Protected Areas (PAs). Our findings suggest that the range of Neotropical otters could extend beyond their present estimated distribution, adding new areas in northeastern Brazil, Andean region, west Ecuador, Venezuela, Peru, Mexico, and Argentina, with higher suitability in rain forests (especially Atlantic and Amazon Forests). We also found that PAs are the most suitable areas for otter distribution. Although better than non-protected areas, PAs are close to the median of the suitability values, indicating that they still can be improved to conserve otters. Annual temperature and human population density explained most data variance in our model. We suggest the change of the actual status of Neotropical otter to Least Concern or Near Threatened categories. We recommend verifying the possible sympatry with other otters, and demonstrate that rudimentary and/or occasional recent data of occurrence can also be used in SDMs and contribute to species conservation.

Keywords: distribution range, Neotropical otter, niche modeling, reserve design, suitability

Resumo

Compreender os requisitos para a ocorrência de uma espécie é fundamental para sua conservação, e os modelos de distribuição de espécies (SDM) são uma ferramenta poderosa para essa finalidade. Aqui nós estimamos um SDM a partir de informações reais de distribuição, em relação a conjuntos de dados climáticos, hidrológicos, de população humana e de vegetação para entender as exigências ecológicas e a distribuição geográfica da lontra Neotropical *Lontra longicaudis*, espécie cujos requisitos de habitat e necessidades para a sua conservação são praticamente desconhecidos. Usando MaxEnt, definimos sua distribuição potencial e as áreas mais adequadas para a espécie a fim de indicar áreas prioritárias para pesquisa e analisar a eficácia das áreas protegidas (APs). Nossos resultados indicam que a distribuição da lontra neotropical poderia se estender além de sua distribuição atual estimada, adicionando novas áreas no nordeste do Brasil, na região andina, no oeste do Equador, na Venezuela, no Peru, no México e na Argentina, com maior adequabilidade em florestas tropicais (especialmente Mata Atlântica e Floresta Amazônica). Descobrimos também que APs são as áreas mais adequadas para a distribuição de lontra. Porém, embora sejam mais adequadas do que áreas não protegidas, as APs estão perto da mediana dos valores de adequabilidade, o que indica que elas ainda podem ser melhoradas para melhor conservar lontras. Temperatura anual e Densidade populacional humana foram as variáveis que melhor explicaram a variância dos dados em nosso modelo. Sugerimos a mudança do status real de lontra neotropical para Pouco Preocupante ou categorias Quase Ameaçada. Recomendamos verificar a eventual simpatria com outras lontras, e demonstramos que mesmo dados rudimentares e/ou ocasionais de ocorrência também podem ser usado em SDMs e contribuir para a preservação de espécies.

Palavras-chave: adequabilidade, desenho de reservas, distribuição geográfica, lontra Neotropical, modelagem de nicho

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Introduction

Understanding drivers of species distribution is essential to its conservation and determining ecological requirements[1,2]. Although field techniques can address several questions about species conservation as well as or even better than estimated distributions, experiment costs are prohibitive for large mammals. The Neotropical otter (*Lontra longicaudis)*, a solitary and elusive semiaquatic carnivore [3] with one of the largest home ranges of Lutrinae [4], is a species whose large scale dynamics cannot be addressed by traditional methods. Despite all efforts, present data are not accurate enough to determine the conservation status of the Neotropical otter based on International Union for Conservation of Nature (IUCN) criteria, and the species is now labeled as 'data deficient' [5]. In order to correct such knowledge deficiencies, the IUCN Otter Specialist Group (during the XIth IUCN OSG International Otter Colloquium in Pavia, Italy in 2011) recommended that research on this species, currently one of the least studied of the subfamily Lutrinae [5,6], should focus on defining its actual distribution, population status, and habitat requirements.

The status of Neotropical otter is important to the conservation of river ecosystems because of its role as a top-chain predator on those ecosystems, and its presence can help maintain local biodiversity [3,7]. In addition, the species requires large territory extensions to establish a viable population, as each individual requires dozens of kilometres of riparian habitats [8–10] and also depends on water physicochemical conditions and habitat structures to persist [8,9]. Modifications of those characteristics can considerably affect otter populations [9], reducing local diversity.

Despite its importance to species conservation, species distribution areas are frequently estimated using a minimum convex polygon, a method that ignores species' ecological constraints [1,2]. A more recent set of techniques, known as species distribution models (SDMs), can overcome this limitation. SDMs also provide extra information in several areas of ecology, evolution, conservation, and management [11,12]. SDMs were initially developed to predict distributions from incomplete data [13], but have been widely used in other areas related to conservation, such as the impact of biological invasions (see[14]), threatened species monitoring (see [15]), estimating distribution expansion of recovering species [16,17], and evaluating climate change impacts [17–19]. These models also identify the most suitable areas for a species, from which we can infer where it is most abundant [20,21] and which environmental characteristics are important to it.

In species with large distribution areas, such as the Neotropical otter, that knowledge can be further used to prioritize regions for species conservation while considering economic interest [22]. Large species also have more accurate representations of their distribution, as most models are based on climatic variables, which are more determinant at larger scales [23,24].

Among SDMs, Maximum entropy (MaxEnt) is a method used for predictions or inferences with presence-only data [21,25–28], and is as efficient as models with both presence and absence data [26,29]. This model tool is highly recommended for studies with the same goals as our work, since the model discriminates between appropriate and inappropriate areas fairly well when compared with other methods [26,30]. Considering all these advantages, coupled with the lack of information regarding Neotropical otter, we developed a questionnaire to collect information about *Lontra longicaudis* occurrences and sent it to researchers and environmentalists. Using their information, we modeled the species distribution using MaxEnt.

In summary, we intended to: (a) obtain an updated database with all available Neotropical otter locations in all its distribution range; (b) estimate the species distribution; (c) identify climatic, environmental and population variables that most influenced *Lontra longicaudis* habitat suitability; (d) identify recommended areas for future studies; and (e) verify if the actual network of Protected Areas is more suitable for Neotropical otter than non-protected areas.

Methods

To test the hypotheses above, we adopted the following method/work flow: first a database of known records and abiotic variables was assembled; then, we used MaxEnt Modeling to create a species distribution model; and last, specific procedures were used to address each hypothesis.

Database description

We surveyed current Neotropical otter occurrences to identify where the species is present, sampling literature and asking researchers for otter records to estimate species potential distribution.

We included all geo-referenced records published in scientific papers (search engines: Google Scholar, ISI Web of Knowledge, Scopus, Scielo) and provided by specialists working on faunal inventories, especially semiaquatic mammals (consulting 231 members of the IUCN Otter Specialist Group), and sent 331 requests directly to known scientists who work with river or mammal ecology within *Lontra longicaudis* distribution. We considered both direct (visual, captures, camera-traps), and indirect observations (including footprints, spraints and/or hair). We considered as presences only data with date information, exact geographic coordinates (converted in WGS-84 system), and collector's name. All occurrence data used in this work are listed in the supplementary material. We obtained data from Brazil, Argentina, Uruguay, Paraguay, Peru, Ecuador, Colombia, French Guiana, Suriname, Venezuela, Mexico, Bolivia, Costa Rica, and Panama, for a period covering 1991 to 2012. With this time span of 30 years we assumed that our record database accurately describes the current distribution of the Neotropical otter (Fig. 1).

We obtained abiotic data from different sources. To build the SDM, we chose *a priori* variables that we assumed to be the most significant to the species and/or were used in previous Neotropical mammal studies [28,31]: annual precipitation, precipitation of the driest month, precipitation seasonality, precipitation of the warmest quarter, annual temperature, isothermallity, and temperature standard. Other variables deemed less important were not included, as including more variables reduces model fitness [32]. One data source was the

Worldclim database, formed by 18 global raster maps representing climatic variables, averaged between years 1950-2000 [33]. We included altitude from the Shuttle Radar Topography Mission (SRTM) digital elevation raster map, human population density in 2000, obtained from GPWv3 [34], and vegetation cover in 2012, measured as the NDVI from MODIS sensors [35]. We also derived a raster map of percentage of water bodies from SRTM Water Body vector Data [36]. The value of a cell equals how many of the 100 sub-cells were covered by water body vectors. All maps had their resolution downgraded to 0.2 decimal, the minimum resolution available to all. All data, independent of source, were clipped between northern Mexico to northern Argentina, the frontiers of the species' current IUCN distribution (Fig. 1).

To test the suitability of existing Protected Areas (PAs) (see below), we used the vector map WDPA Conservation Units [37]. This global database is a joint venture by UNEP-WCMC and IUCN World Commission on Protected Areas in collaboration with governments, NGOs, academia and industry. These data are constantly updated.

Model estimation / assessment of the quality of the model

Once the database was complete, we generated a Kernel density map (0.01555 bandwidth), considering 95% of distribution use. The Kernel was used to ensure that background sampling only included areas where otter could exist (a SDM requirement) [21,25]. Within this interval, we selected 1,000 random locations to be used as background data for modeling.

MaxEnt 3.3.3k [25] estimates the probability distribution of the maximum entropy of each environmental variable within the study area. This distribution is calculated with the constraint that the expected value of each environmental variable under it matches the empirical average generated from environmental values associated with species occurrence data [25]. When MaxEnt is applied to presence-only SDM, the pixels of the study area make up the space on which the MaxEnt probability distribution is defined; pixels with known species occurrence records constitute the sample points; and the features become environmental variables. We used 75% of the records for training the model and 25% for test. The best parameter estimate was calculated using 5,000 interactions with bootstrap replication. We set the convergence threshold of 1.0×10^{-5} (i.e. increase in model fitness below which the model stops). In addition, the model was replicated 15 times to calculate confidence intervals, and model fitness was assessed based in the area under the curve [38].

Hypothesis-specific procedures

After identification of the most suitable areas for the occurrence of otters, a series of transformations were required to address each hypothesis.

To describe otter potential distribution, we first generated a consensus map from the 15 MaxEnt models using the weighted average method [39], which uses the AUC value of each model as its weight. We then considered two approaches to derive binary presence–absence maps from the continuous consensus map of suitability: one more restrictive and conservative, maximizing the sum of sensitivity and specificity (max SSS) (more details in [40]); and a second, less restrictive, with the lowest predicted value threshold (LPV) (see [25,28,41]). LPV is the lowest value of environmental suitability within an occurrence record, and Max SSS is an objective method that optimizes the discrimination between presence/absence in the same way as that between presence/random points.

Second, to test the efficiency of PAs, we compared the distribution of suitability values within and outside PAs and ran a Kolmogorov-Smirnov (KS) test to verify if these two curves differ significantly.

Last, to recommend regions for future studies and conservation initiatives, we reasoned that places with high suitability for otter and far from previous studies have a better chance to be different ecosystems/biomes and to have different environmental characteristics. Therefore, a study in those areas can explain if the otter uses different habitats in ways similar to those shown in previous studies. To accomplish this, we multiplied the suitability of a pixel by its distance to the nearest record, based on the assumption that ecological similarities decrease with distance. The index was then divided by its highest value, to ensure it varies across the more intuitive scale of 0 to 1. Note that this index implies that distance and suitability are equally important, and therefore it may recommend areas with low suitability.

All analyses were performed, and figures made, in ArcMap 9.3 [42]. The Kolmogorov-Smirnov test was conducted in the R Software [43].

Results

We obtained information on Neotropical otter in 14 of the countries that encompassed its historical distribution, including 565 occurrences (available at: *http://goo.gl/G6BaqG*). Our study included new information about Neotropical otter distribution, with new occurrences recorded outside the recognized distribution ranges (Fig. 1 and [5,44,45]). Those new occurrences included areas in northeastern Brazil [46], Venezuela, Mexico, and also in the Pacific portions of Ecuador, Peru and Colombia.

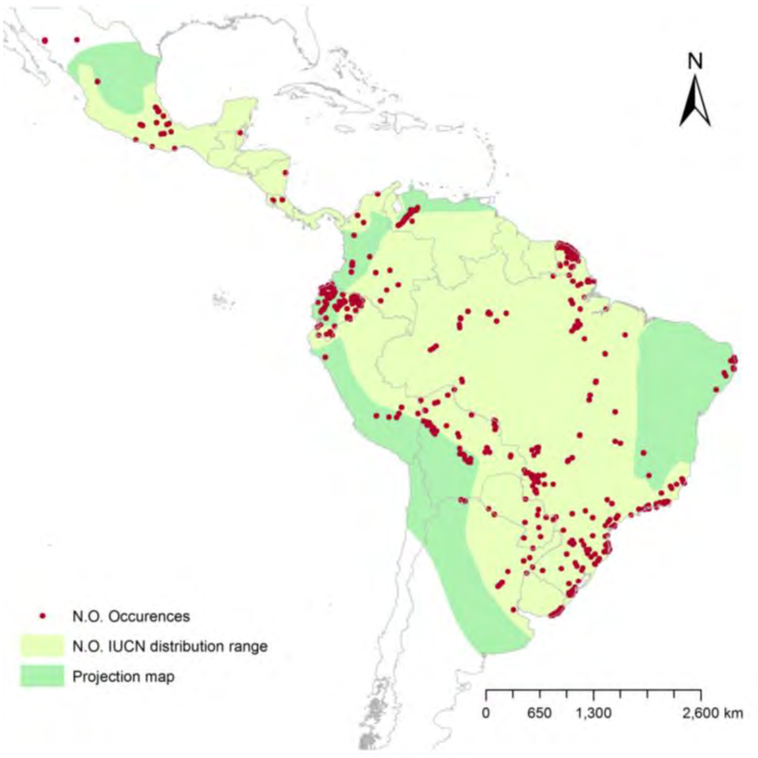

Fig. 1. Map showing Neotropical otter (*Lontra longicaudis*) unique records (n=565), in red, overlaid with IUCN distribution, in light green, and Maxent projection, in green

Neotropical otter potential distribution

We generated a map with *L. longicaudis* potential distribution, based on the two threshold criteria. With the LPV criterion we obtained a broader map than with the Max SSS criterion (Fig. 2). AUC average value was 0.809±0.016. Neotropical otter distribution range, according to the LPV, totalled 17.056.351 km^2, which represents 45.4% of North, Central and South Americas' total area and is 34% greater than IUCN's historical otter distribution. Considering Max SSS, we obtained 8.148.746 km^2, which is 21.7% of the area of the three Americas and 63.6% of IUCN's historical distribution. The consensus map, according to the LPV, contained 25.8% (4.410.023 km^2) of the distribution outside the IUCN historical range, while the Max SSS map contained 9.8% (799.728 km^2). 1.2% (163.834 km^2) of the IUCN distribution map was outside the LPV consensus map, and 42.6% (5.460.145 km^2) was outside of the Max SSS consensus map (Fig. 2).

The only regions within IUCN distribution, but absent according to LPV, were areas outside kernel regions in Central America. Distribution according to Max SSS was smaller than IUCN historical range in almost all countries (Fig. 2).

Ranges generated by both thresholds and inside the minimum convex polygon containing all locations were much wider than those indicated in B1 criteria for any IUCN endangered status (more details on [47]), where maximum value of extent of occurrence to be listed as vulnerable is less than 20,000 km^2.

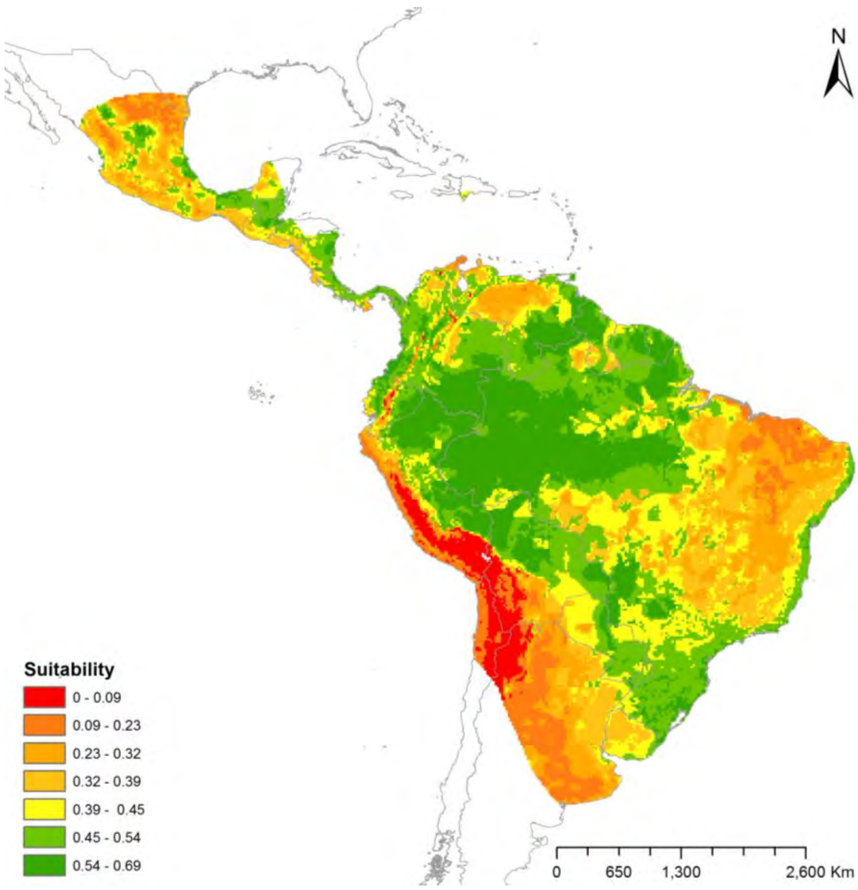

Fig. 2. Map showing potential geographical distribution and suitability values for Neotropical otter (*Lontra longicaudis*) accordingly with MAXENT. Suitability values above the lowest predicted value threshold (LPV) are shown from orange to green. Values above the maximum sum of sensitivity and specificity threshold (Max SSS) are green and values below the LPV threshold are red.

Regarding the importance of each variable, annual temperature (60.5%) was the one that most contributed to the model: highest values of suitability were associated with higher annual temperatures. Human population density was identified as the second contribution variable (29.9%), and was inversely related to otter suitability. However, higher human population densities were not completely unsuitable for otters (suitability=0.55 in low densities and 0.42 in higher population densities). Other variables had less than 2% contribution each. Vegetation, proportion of water, and altitude contributed 0%, 0.2% e 0.2% respectively.

Priority areas for future studies with Lontra longicaudis

The index proposed areas with higher values and recommended for future studies, to be the frontier between Venezuela and Guyana, other Venezuelan areas, northeastern Brazil, and regions within the Brazilian and Peruvian Amazon (Fig. 3).

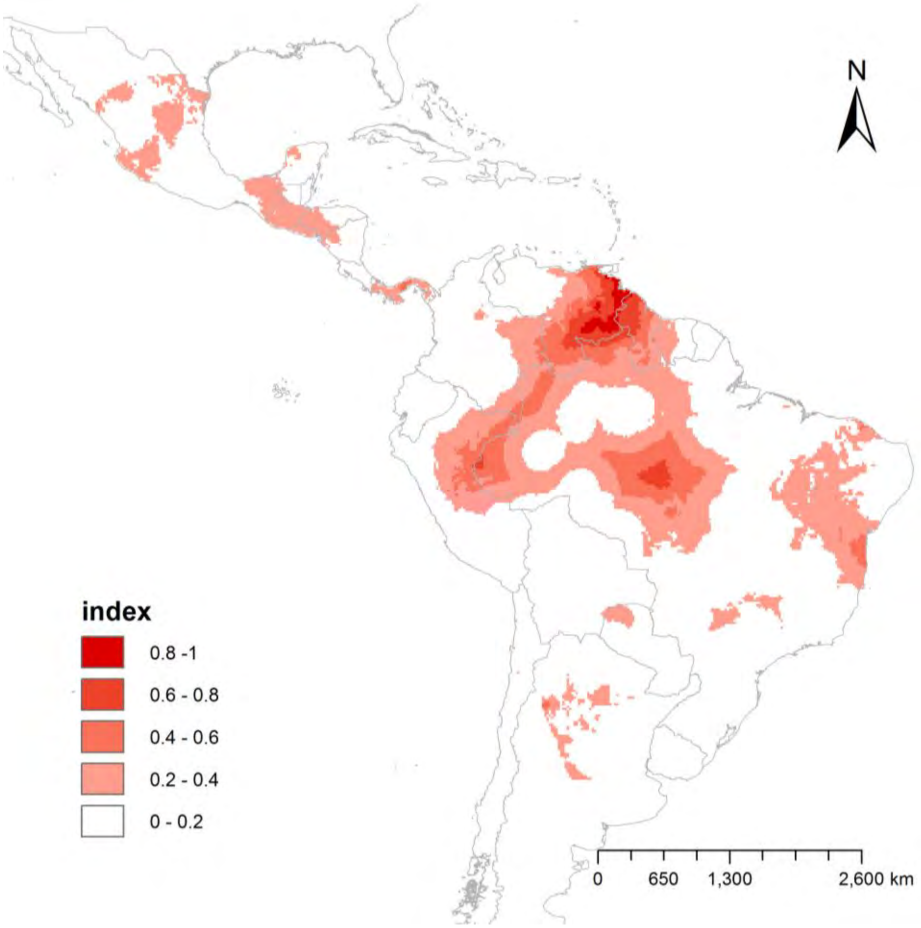

Fig. 3. Map showing values of the Index relating suitability and nearest distance of occurrence for Neotropical otter, indicating priority areas for future studies with *Lontra longicaudis*.

Suitability of Protected Areas vs Non-Protected Areas

Areas inside PAs (number of cells=7432) showed higher suitability values than areas outside them (number of cells=29,976) (KS=0.3775 p<0.0001). Kernel densities of PA were higher in higher suitabilities (0.4-0.65, with peak around 0.58) than non-protected areas (0.1-0.5, with peak around 0.4) (Fig. 4).

Beyond PAs, the higher values were observed in the Amazon region, which was the region with higher suitability cells. Other areas that had PAs with good suitability were the coastal region of the Atlantic Forest, the Guyana shield, the Pantanal, and many regions of Central America.

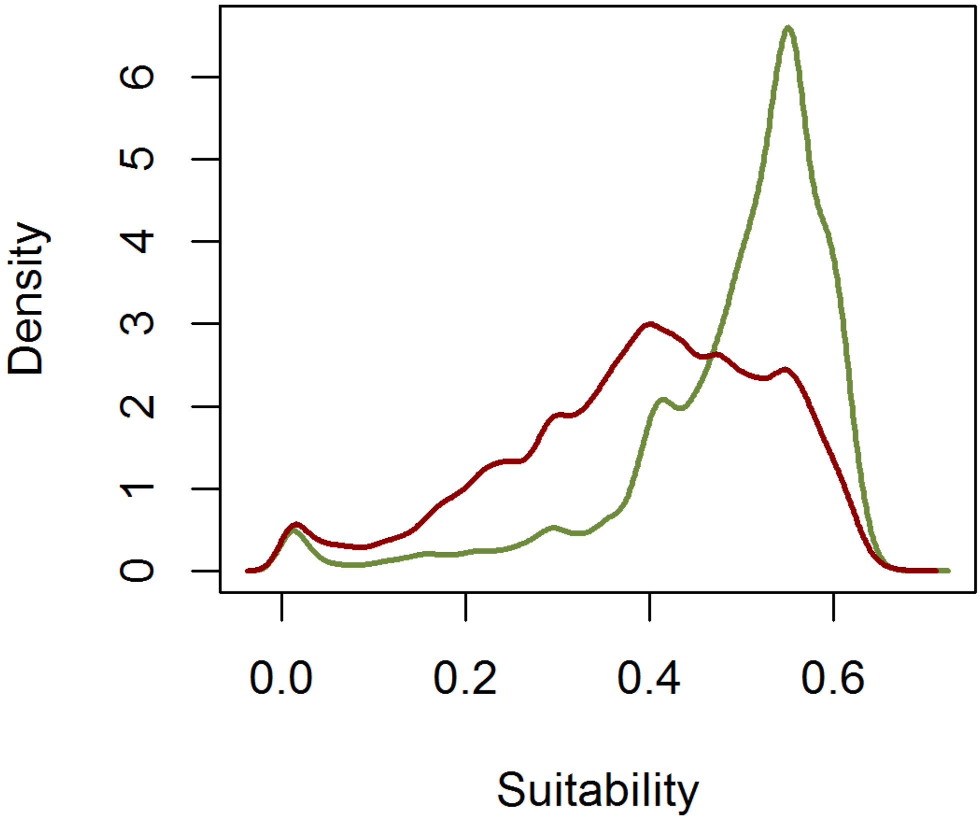

Fig. 4. Distribution of *Lontra longicaudis'* suitability estimated by kernel in protected (green line) and unprotected (red line) areas. The densities are related with the number of pixels with this value of suitability.

Discussion

In this study, we tentatively propose a model for Neotropical otter *Lontra longicaudis* (Figure 5) distribution. SDMs are powerful statistical techniques that can be used to describe species' geographic ranges [48]. There are several methods to model species distribution, but the most commonly used now is the maximum entropy approach (Maxent; [25]). The high average AUC indicates that our models had good predictive power and can be used to analyze environmental suitability. Our results showed that different variables were important to the potential distribution of this top-chain semiaquatic mammal, as shown before with another otter[49] and with another large Neotropical carnivore, the jaguar[28]. Annual temperature and human population density were the most important predictors in our model for Neotropical otter in a large scale. Our model was innovative in two aspects: we demonstrated that PAs have more suitable areas for *L. longicaudis* than non-protected areas, and we identified the Peruvian and Brazilian Amazon, the borders between Venezuela and Guyana, and Northeastern Brazil as areas for future studies.

Our model indicated that areas with high annual temperatures are the most suitable, similar to what was described in the species' revision[44]. The other important variable was human population density. Although suitability decreased with human density, its value was high even in human-dense areas. These results appear to be consistent with the biology of various otter species, as otters can occur in degraded and/or urban areas [3,50–53]. However, NDVI small contribution to the model did not support another previous hypothesis: that *L. longicaudis* requires good riparian vegetation and good den availability [54]. This difference between previous studies and our work is probably due to scaling, as we used a larger, less accurate scale (0.2 decimal degree cell size) to identify the fine scale of microhabitat selection. In microhabitat scale, there are evidences of Neotropical otter using more forested areas to select their holts [55,56]. Another environmental variable previously suggested as important, but not supported by our model, is altitude. We had locations from sea level to 4,200m high (*e.g.* Peruvian Andes), with many occurrences above 1,500m or below 300m from sea level. Despite that range, altitude did not influence most of our model replicates, in disagreement with previous studies that described Neotropical otter less abundant at high altitudes [44].

Considering the above variables, the Amazon, Atlantic Forest, and Pantanal are the most suitable environments for *L. longicaudis*, a challenge for Neotropical otter conservation. The Atlantic Forest is one of the most threatened biomes of the world[57,58], and the Amazon, although well preserved in comparison with others, has been severely degraded in recent years [59,60], with almost 20% of its Brazilian land cover (60% of total) converted to land use[61]. Despite being less suitable, regions in Central America may justify the importance of investments in them as there are well-preserved areas in several countries, and previous studies have indicated the continent as a priority for carnivore conservation [62].

Categorizing the suitability values to estimate Neotropical otter distribution also provided novel insights. Distributions categorized by both LPV and Max SSS overlap substantially with distributions described before (see [5,44]). However, even the distribution according to Max SSS, the most restrictive one, included areas absent in IUCN's map. This shows that the IUCN map needs to be updated. New regions to be added include northeastern Brazil, the Andes (in Peru, Ecuador and Colombia), northern Mexico, western Colombia, and Bolivia. These new areas may provide valuable information about the species as well as insight on what really limits the species' occurrence. The range increase beyond the IUCN northern limit seems to be related to an increase in resolution. Models based in minimum convex polygon are coarser than our distribution modeling (for comparisons with our map, see [5,44,63]). This expansion also indicates that *L. longicaudis* may expand its distribution to southern United States and thus overlap with *L. canadensis* distribution [64,65]. Further studies to identify this potential interaction or the barrier that separates both species are recommended. Another contribution of categorizing the suitability values, is to assess in which IUCN category the species should be allocated. The estimated species distribution is beyond 20,000 km^2, in spite of the threshold criteria used. Consequently, the species cannot be considered vulnerable or any other category below, according to the IUCN species extent, and we suggest the species should be moved to either Near Threatened or Least Concern.

In addition to estimating Neotropical otter distribution, we also compared the environmental suitability inside and outside PAs. In our study we showed that PAs are significantly more suitable and can help in Neotropical otter conservation, even though they have not been created specifically to protect otters. The higher suitability values inside the PAs are not surprising, as many of them were designed based on river basins or river courses [66,67].

PAs, mainly larger ones, reduce human influence and can retain populations and also assemblages [68]. PAs are especially important to conserve Amazonian ecosystems, as the majority of the remaining forests throughout the Amazon basin are within protected areas and only 1.5% of these PAs have been deforested [69]. Tropical PAs are ecologically linked to their surrounding habitats, so it's important to conserve not only the area within them, but also surrounding areas in order to maintain local biodiversity [70].

Fig. 5. Neotropical otter *Lontra longicaudis* in river margins of Brazilian Pantanal. Photo credits: Caroline Leuchtenberger/Instituto Federal Farroupilha, with permission.

Implications for conservation

Our analysis shows that spatial distribution models (SDMs) [71] can be used to evaluate whether the PAs are really conserving *L. longicaudis* within them. Such approaches increase the utility of SDMs, which were already used in PA design and management[20,72,73], to guide population surveys [74–76] even when no information about species' absences was available. Regarding future studies, we recommend focusing on northeastern Brazil, as it represents one of driest areas in Neotropical otter distribution. The Amazon regions in Brazil, Guyana, and Venezuela and the Pantanal are also identified as informative regions due to their low human density, mostly warm climate, and well-preserved areas.

As lack of knowledge about a species' distribution is one of the most important issues in mammal conservation [77], we suggest gathering and compiling otter occurrence data in Argentina, Suriname, Ecuador, Central America, Mexico, and Northeastern Brazil to corroborate our model predictions that these regions are suitable for the species. Despite Neotropical otters' wide distribution range and their being well documented in most of their distribution, our study indicates that new research is necessary to obtain Neotropical otter occurrences in areas with little information.

Despite some undocumented areas, our results suggest that we can move *L. longicaudis* from Data Deficient to Least Concern or Near Threatened Categories. We demonstrate here that rudimentary and/or occasional data of occurrence can also be used in spatial distribution models and contribute to species conservation by better describing their distribution.

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