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High extinction risk and limited habitat connectivity of Muñoa's pampas cat, an endemic felid of the Uruguayan Savanna ecoregion

Flávia P. Tirelli[a,b,c,d,*], Tatiane C. Trigo[d,e], Diego Queirolo[f], Carlos Benhur Kasper[g], Nadia Bou[h], Felipe Peters[d], Fábio D. Mazim[d], Juan Andrés Martínez-Lanfranco[i,j], Enrique M. González[j], Caroline Espinosa[c], Marina Favarini[d], Lucas Gonçalves da Silva[k], David W. Macdonald[b], Mauro Lucherini[l,m], Eduardo Eizirik[a,d]

[a] PUCRS, School of Health and Life Sciences, Laboratory of Genomics and Molecular Biology, 6681 Ipiranga Av., Building-12, Porto Alegre, 90619-900, Brazil
[b] Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, OX13 5QL, UK
[c] Graduate Program in Animal Biology, Universidade Federal do Rio Grande do Sul, Bird and Mammal Evolution, Systematics and Ecology Lab, 9500 Bento Gonçalves Av., Block-IV, Building-43435, Room106, Porto Alegre, 91501-970, Brazil
[d] Instituto Pró-Carnívoros, 1030 Horácio Neto Av., Atibaia, 12945-010, Brazil
[e] Mammalogy Sector, Museum of Natural Sciences, Department of Biodiversity, Secretariat of Environment and Infrastructure (SEMA), 1427 Dr. Salvador França St., Porto Alegre, 90.690-000 Brazil
[f] Centro Universitario Regional Noreste, Universidad de la República, Rivera, Uruguay
[g] Graduate Program in Biological Sciences, Mammals and Bird Biology Lab (LABIMAVE), Universidade Federal do Pampa (UNIPAMPA), 1847 Antònio Trilha Av., São Gabriel, 97300-000, Brazil
[h] Departamento de Biodiversidad y Genética, Instituto de Investigaciones Biológicas Clemente Estable (IIBCE), 3318, Italia Av., Montevideo, 11600, Uruguay
[i] Department of Biological Sciences, University of Alberta, CW 405 Biological Sciences Bldg, Edmonton, T6G 2E9, Canada
[j] Mammalogy Section, National Museum of Natural History (MNHN), 1825 Miguelete Str., Montevideo, 11800, Uruguay
[k] UnB Cerrado Research Centre, University of Brasília, Campus Universitário Darcy Ribeiro SN Asa Norte, 70910-900, Brazil
[l] Mammal of Behavioral Ecology Group(GECM), INBIOSUR, CONICET-UNS, San Juan 671, Bahía Blanca, 8000, Argentina
[m] Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur (UNS), San Juan 670, Bahía Blanca, 8000, Argentina

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ABSTRACT

Muñoa's pampas cat (recently proposed to be a distinct species, *Leopardus munoai*) is a small felid that is endemic to the Uruguayan Savanna ecoregion (encompassing southern Brazil, north-eastern Argentina and Uruguay). Previous studies have suggested that it is threatened, but its conservation assessment has been hampered by the scarcity of data on its ecology, including spatial distribution, population size, and connectivity. To address these issues, we developed current spatial distribution models and used them to: (i) identify the environmental variables affecting *L. munoai* habitat suitability; (ii) generate estimates of population size to assess its conservation status based on IUCN criteria; (iii) estimate habitat suitability in protected areas; (iv) identify potential paths of connectivity among protected areas and sites of confirmed occurrence; and (v) assess the proportion of the estimated connectivity paths that overlap with threatened areas (based on future threat projections). Our results indicated higher habitat suitability in the central area of the species' distribution. All estimates (based on different demographic assumptions) indicated that *L. munoai* should be categorized in one of the IUCN threatened categories. Worryingly, several estimates indicated that it may be Critically Endangered. Only 0.73 % of its high-suitability landscape is presently protected, and connectivity among most protected areas and occurrence records was low. Additionally, areas with estimated connectivity among occurrence records mostly overlapped with regions with a high level of future habitat loss threat (92.46 %), highlighting the urgent need for an international approach to ensure the long-term survival of this elusive felid.

* Corresponding author. Present address: Graduate Program in Animal Biology, Universidade Federal do Rio Grande do Sul, Bird and Mammal Evolution, Systematics and Ecology Lab, 9500 Bento Gonçalves Av., Block-IV, Building-43435, room 106, Porto Alegre, 91501-970, Brazil.
E-mail address: flavia.tirelli@gmail.com (F.P. Tirelli).

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1. Introduction

The increasing loss of natural habitats is leading to severe declines in geographic range and population size for several wild species on a global scale (Butchart et al., 2010; Li et al., 2016). A frequent consequence of habitat loss is habitat fragmentation, which creates a matrix of human-transformed land cover containing isolated patches of natural habitats (Rands et al., 2010). By reducing the amount and connectivity of suitable habitat, human disturbances tend to have negative impacts on wildlife, even inducing local extirpation (Fahrig, 2003). This is especially problematic for endemic taxa with restricted geographic distributions (McKinney, 2002).

Muñoa's pampas cat, also known as Uruguayan pampas cat, is a small wild cat inhabiting open areas of the Uruguayan Savanna, a subtropical grassland ecoregion (Olson et al., 2001) located in Uruguay, southernmost Brazil, and a small area of north-eastern Argentina. This felid seems to have been historically isolated in this region due to geographic barriers such as the La Plata river on the south, the Paraná/Paraguay rivers on the west and the Atlantic Forest on the north (Johnson et al., 1999; Nascimento, Cheng, & Feijó, 2020; Santos, Trigo, de Oliveira, Silveira, & Eizirik, 2018; Sartor, 2016). Based on its genetic and morphological uniqueness, the IUCN Cat Specialist Group (Kitchener et al., 2017) has recognized it as a distinct pampas cat subspecies (*L. colocola munoai*). More recently, a taxonomic revision of the pampas cat complex (Nascimento et al., 2020), including a large morphological database, mitochondrial DNA (mtDNA) data and ecological niche models, indicated that it should be recognized as a species-level taxon (*Leopardus munoai*). Overall, these analyses have demonstrated that this felid presents unique morphological, genetic and ecological features, and should be considered a distinct unit for conservation assessment and management actions. There is urgency in conducting such conservation planning on behalf of this endemic felid, since the natural grasslands of the Uruguayan Savanna have been largely transformed by agriculture (especially rice and soybean), cattle ranching, and forest plantations (*Eucalyptus* spp. and *Pinus* spp.) (Martino, 2004; Overbeck et al., 2015). These human activities have led to the extinction of several local mammal species (Queirolo, 2016). Moreover, this ecoregion is presently considered one of the most critical conservation priorities for terrestrial vertebrates in the Neotropics (Loyola, Kubota, da Fonseca, & Lewinsohn, 2009). Given this scenario, Muñoa's pampas cat has been categorized as 'Endangered' (EN) in the regional listing for Rio Grande do Sul state, in southernmost Brazil (FZB (Fundação Zoobotância do Rio Grande do Sul), 2014), and as a threatened species with conservation priority in Uruguay (González et al., 2013). These categorizations, as well as a global assessment of the pampas cat complex (Lucherini, Eizirik, de Oliveira, Pereira, & Williams, 2016), had been conducted before this endemic felid was formally recognized as a distinct taxon (Kitchener et al., 2017; Nascimento et al., 2020), and based on scarcer ecological data than is currently available. Given the current understanding of its distinctiveness, improved ecological data, novel analytical approaches and a constantly worsening threat scenario, we consider it timely to perform an in-depth assessment of its conservation status.

The few surveys performed so far on Muñoa's pampas cat suggest that it occurs at very low population densities (0.01 to 0.05 individuals/km^2) (Queirolo, Almeida, Beisiegel, & Oliveira, 2013). Two recent studies have estimated its potential distribution, one focusing on Uruguay (Bou, Cuyckens, González, & Meneghel, 2019), and another more broadly on the Uruguayan Savanna ecoregion (Nascimento et al., 2020). Both studies (which used the Maxent algorithm and records since 1958) observed that suitable habitats for this species are associated with grassland areas. More specifically, these studies found an association with wetlands in Uruguay (Bou et al., 2019) and identified precipitation as an important predictor (Nascimento et al., 2020). In spite of these advances, several additional questions of conservation relevance need to be answered, such as: (i) How do environmental variables influence its habitat suitability? (ii) Is this species in risk of extinction? (iii) What is the proportion of suitable areas that are protected across the *L. munoai* range? (iv) Is there connectivity of suitable habitats among protected areas within its distribution, and among documented sites of occurrence? (v) Will this connectivity be threatened in the future?

In the present study, we aimed to answer these questions by developing spatial distribution models (SDMs) using biotic and abiotic variables and recent occurrences records, and applying five different algorithms to characterize current habitat suitability for this species. We then used these results to estimate the number of mature individuals remaining in the wild under different demographic scenarios, and to assess its conservation status based on IUCN criteria. We also calculated the extent of suitable areas for Muñoa's pampas cat that is currently protected. In addition, we assessed potential population connectivity for this cat throughout its distribution, to identify paths between suitable protected areas, as well as between confirmed records. Finally, we compared estimated connectivity among current areas of occurrence in the face of future habitat conversion (Oakleaf et al., 2015, 2019), aiming to observe the effects of land use changes on the prospects of persistence for this endemic felid.

2. Material and methods

2.1. Species occurrence data

We collected geographic coordinates for all recorded *L. munoai* occurrences from 2000 to 2018 (Fig. 1). Records included photographs (including camera-trap images), individuals found dead in the field (e.g., road-killed, killed by domestic dogs), museum specimens, personal observations from the authors and other field biologists, and scientific publications (Appendix A).

The locations of all records were converted into decimal degree coordinates using the WGS84 reference system. These presence data were checked for duplicate records, by cross-checking the coordinates and then cleaning them using the 'dismo' package (Hijmans, Phillips, Leathwick, & Elith, 2017) in *R v.3.5.1* (R Core Team, 2018). Using the same package, we created a sampling bias file to reduce the spatial correlation among records. Because there is no study with this type of information for Muñoa's pampas cat, we conducted our filtering by using the information on the home range size (Espinosa et al., 2017) of other species from Pampas cat complex and used only presence points located > 10 km apart from each other in our analyses. This is a conservative procedure, since 5 km is the radius of a circle encompassing 78.5 km^2, which is more than four times the average home range size for this taxonomic complex (*Leopardus braccatus*19.47±3.64 km^2 (Silveira, Jácomo, & Malzoni Furtado, 2005) and *L. garleppi* - 14.86±14 km^2 (Tellaeche, 2015)). After we created the sampling bias file, we tested data points for spatial autocorrelation (Moran's I) in ArcGIS 10.4.1 (Environmental Systems Research Institute, 2016). As we only had presence data, we substituted absence points with background data and randomly generated 500 "pseudo-absences" (Hijmans et al., 2017).

2.2. Selection of variables

We constructed models of the potential distribution of Muñoa's pampas cat using variables that are (i) likely to be of biological importance for the species, (ii) related to characteristics of the ecoregion to which it is endemic and (iii) biologically interpretable (Barstow & Leslie, 2012; Bou et al., 2019; Fitzpatrick, Gotelli, & Ellison, 2013; Nascimento et al., 2020; Tirelli, 2017). In a previous work (Tirelli, 2017), we had tested eight bioclimatic variables, five of which were related to temperature (Tirelli, 2017), and observed that Precipitation Seasonality had the largest contribution to our SDMs (61.6 %). Because of that and following Fitzpatrick et al. (2013) suggestion that it is important to choose biologically interpretable variables in SDM studies, we then chose to include two bioclimatic variables, BIO1 (Annual Mean Temperature) and BIO15 (Precipitation Seasonality) (Karger et al., 2017a,

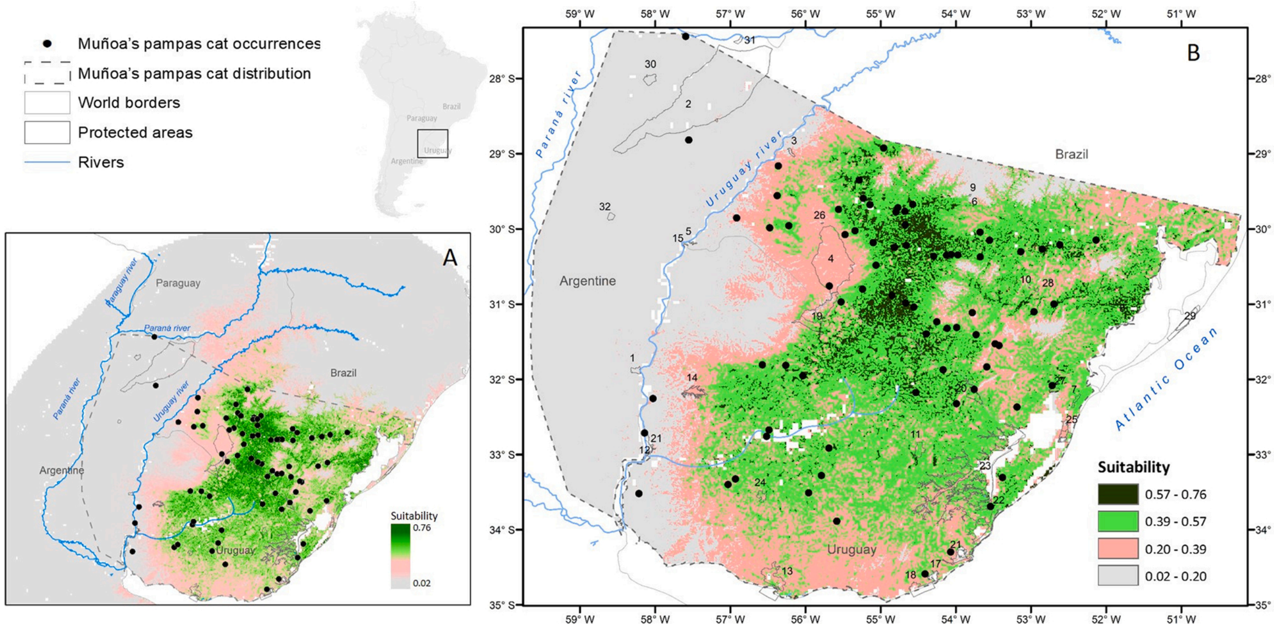

Fig. 1. Ensemble Spatial distribution model (SDM) of Muñoa's pampas cat (*Leopardus munoai*). A) General ensemble SDM showing medium (pink) and low (grey) suitability pixels outside this felid's distribution range. B) Map showing the ensemble SDM exclusively inside Muñoa's pampas cat geographic distribution (Nascimento et al., 2020) and categorized by levels of suitability (from low [0.02 – 0.20] to high [0.57 – 0.76]). This map overlaid on the World Database on Protected Areas layer (http://www.wdpa.org/) (1=El Palmar (ARG); 2=Iberá (ARG); 3=Reserva Biológica do São Donato (BRA); 4=Área de Proteção Ambiental Ibirapuitã (BRA); 5=Parque Estadual do Espinilho (BRA); 6=Parque Natural Municipal dos Morros (BRA); 7=Refúgio de Vida Silvestre Banhado do Maçarico (BRA); 8=Parque Estadual do Camaquã (BRA); 9=Reserva Biológica do Ibicuí Mirim (BRA); 10=Reserva Particular do Patrimônio Natural Boa Vista (BRA); 11=Quebrada de los Cuervos y Sierras del Yerbal (URU); 12=Esteros de Farrapos e Islas del Río Uruguay (URU); 13=Humedales del Santa Lucia (URU); 14=Montes del Queguay (URU);15=Rincón de Franquía (URU); 16=Esteros y Algarrobales del Río Uruguay (URU); 17=Laguna de Rocha (URU); 18=Laguna Garzón (URU); 19=Reserva de Biosfera Bioma Pampa (Valle del Lunarejo/Laureles-Cañas) (URU); 20=Paso Centurión y Sierra de Ríos (URU); 21=Laguna de Castillos (URU); 22=San Miguel (URU); 23=Bañados del Este (URU); 24=Localidad Rupestre Chamanga (URU); 25=Estação Ecológica do Taim (BRA); 26=Reserva Biológica do Ibirapuitã (BRA); 27=Reserva Biológica do Mato Grande (BRA); 28=Parque Estadual do Podocarpus (BRA); 29=Parque Nacional da Lagoa do Peixe (BRA); 30=Mburucuyá (ARG); 31=Apipé Grande (ARG); 32=Rincón de Santa María (ARG)).

2017b). Since some studies have emphasised the relationship of this species with open grassland areas (Barstow & Leslie, 2012; Bou et al., 2019; Nascimento et al., 2020), we decided to use land use and a vegetation index to test it. For land use, we chose a landscape index that includes anthropogenic land use, from the ESA GlobCover Project (http://due.esrin.esa.int/page_globcover.php). In this variable, we included the categories occurring in the ecoregion (categories: 14, 20, 30, 40, 50, 130, 180, 210, from ESA GlobCover Project, [http://due.esrin.esa.int/page_globcover.php]). In addition, we used the Normalized Difference Vegetation Index (NDVI) (data from 2016, in the Time Series Database from the Global Agriculture Monitoring Project; GLAM [http://pekko.geog.umd.edu/usda/beta]). The ecoregion can be considered an arid environment at different times of the year (Olson et al., 2001), and we therefore also included distance to rivers (estimated with the Euclidean Distance tool in ArcGIS 10.4.1, based on http://hydrosheds.cr.usgs.gov (Lehner, Verdin, & Jarvis, 2006)) and Seasonal Precipitation (already cited). Additionally, as there is reasonable variation in altitude and temperature in the ecoregion (Olson et al., 2001, Hackensack et al. 2020), we included, respectively, elevation (Shuttle Radar Topographic Mission [http://www2.jpl.nasa.gov/srtm]) and Annual Mean Temperature (already cited). We modified the global environmental layers using the Spatial Analyst and Conversion tool in ArcMap within ArcGIS 10.4.1 to equalize their geographic boundaries, cell size, and coordinate system. To do so, we extracted them as a mask layer with a buffer of 500 km around the Uruguayan Savanna and resampled each of them to the same resolution (each pixel with ~0.74km^2) (Young, Carter, & Evangelista, 2011).

To avoid collinearity of variables in the modelling process, we applied the variance inflation factor (VIF) (Marquardt, 1970; Naimi & Araújo, 2016). We excluded the variables with the highest VIF (>5) (Naimi & Araújo, 2016). These analyses were perform with the package 'usdm' (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014) in R. The 'Landscape information' layer was not tested with respect to its collinearity, since it is a categorical variable.

2.3. Building SDMs

The ensemble modelling approach allows more robust analyses than a single algorithm model, because it circumvents the bias of each single model (Ahmad et al., 2020). (i) Generalized Linear Models (GLM) and (ii) Generalized Additive Models (GAM); and three machine-learning methods: (iii) Random Forests (RF), (iv) Boosted Regression Trees (BRT), also known as Gradient Boosting Machine (GBM), and (v) Maximum Entropy (MaxEnt). The GLM is a generalization of ordinary least squares regression (McCullagh & Nelder, 1989), and GAMs are an extension to GLM with a smoothing function (Hastie & Tibshirani, 1990). The RF is a machine-learning method that is an extension of classification and regression trees (Breiman, 2001). BRT or GBM are a combination of two techniques, decision tree algorithms and boosting methods (Friedman, 2001). Finally, MaxEnt is based on the maximum entropy approach, and it is one of the most popular tools for modelling species ecological niches and its results indicate habitat suitability (Phillips, Anderson, & Schapire, 2006).

We used presence and pseudo-absence data (random points) that represent the background context for the models. The data were randomly divided into training and testing datasets to allow *post hoc* validation of the results, in which each model was evaluated against the training data. We used 70 % of the included points for training and 30 % for testing all the models. We generated 30 replicates of the same model with each algorithm through partitioning using cross-validation (Naimi

& Araújo, 2016). Therefore, a total of 150 models were generated from the five different algorithms. The performance of each independent model was evaluated by calculating the area under the receiver operating characteristic (ROC) curve, abbreviated to Area Under the Curve of the test dataset (AUC_{test}) (Pearson, 2007), by the AUC difference (AUC_{diff}) between the training and test data to quantify overfitting (Warren & Seifert, 2011), and by true skill statistics (TSS) (Allouche, Tsoar, & Kadmon, 2006). The best models were identified based on the AUC values, which range from 0 to 1; values close to 1 indicate a good performance, while AUC values <0.5 suggest a random prediction. The AUC_{diff} value is expected to be close to zero in models with low over-fitting (Warren & Seifert, 2011). Finally, TSS values range from -1 to +1, where 1 indicates perfect agreement and TSS<0 indicates a performance no better than random (Fletcher & Fortin, 2018). We generated an ensemble of predictions by individual SDMs using weighted averaging based on the highest TSS values. We used "Max (spe+sen)" (Naimi & Araújo, 2016) as the optimum threshold criterion, since it is a minimization of the sum of false negative and false positive misclassification likelihoods; it is also formally equivalent to a maximization of Youden's index, one of the commonly used cut-point value methods (Freeman & Moisen, 2008; Unal, 2017).

We also computed an estimate of variable importance (VI) for all predictor variables, using a mean variable importance for multiple models; the VI was based on training dataset of all models. We then calculated the response of species suitability to the range of values in each variable based on the fitted models. We performed all these analyses with the package 'sdm'version 1.0–89 (Naimi & Araújo, 2016) in R software.

We used the currently proposed distribution of this taxon (Nascimento et al., 2020) as a mask for the ensemble SDM, and classified values of suitability estimated by the model into four different categorized levels of suitability (very low, low, medium, and high). For this approach, we considered our minimum value to be the minimum value of suitability extracted from real occurrences, and our maximum value to be the highest suitability value estimated in the ensemble SDM. Therefore, we divided this suitability range into four equal interval categories, each interval increases 0.19 of suitability from each other.

As an additional post-evaluation exercise for model performance, we assessed the percentage of additional records of this species that were located in areas of varying suitability levels. To do so, we used records had not included in the SDM analyses, and we looked for additional records of the species, obtained in 2019 and 2020. Then we plotted these records onto the final SDM and extracted the values of suitability. These analyses were performed with ArcMap from ArcGIS 10.4.1.

2.4. Status assessment of Muñoa's pampas cat

According to the IUCN Standards and Petitions Committee (2019) guidelines, we estimated of the number of mature individuals (MI) of Muñoa's pampas cat using the equation $d * A * p$ (IUCN Standards & Petitions Committee, 2019). In this equation, d is an average estimated population density (individuals/km^2) available (Oliveira et al., 2010; Queirolo et al., 2013); A is our predicted area resulting for different levels of suitability of our ensemble SDM (total area predicted, low-to-high, medium-to-high, and high); and p is the estimated proportion of mature individuals. We assumed six different proportions of mature individuals (p), based on knowledge from related taxa (see Appendix B).

According to Queirolo et al. (2013), habitat loss and population decline are expected to be 14 % in the next 21 years or three generations. As a complement to that, the majority of the species' distribution overlaps with the highest category of global future threats of conservation (Oakleaf et al., 2015, 2019). This should be considered as a conservative approach, because the species is also threatened by roadkills, killing by dogs (see Appendix A), and hunting by humans (Peters, Mazim, Favarini, Soares, & Oliveira, 2016). Assuming that the species is in population decline, we used the estimated number of mature individuals to assess if it belongs to a threatened category, based on criterion C ("Small population size and decline") of the IUCN Red List. We did not use other criteria due to the scarcity of data available to apply them. Threatened categories in this item were considered as follows: Vulnerable (VU) when MI < 10,000 individuals; Endangered (EN) < 2, 500 individuals; or Critically Endangered (CR) < 250 individuals (IUCN Standards & Petitions Committee, 2019).

2.5. Protected areas and ecological systems

To assess the degree of protection of the habitats where Muñoa's pampas cat are expected to occur in this region, we downloaded the World Database on Protected Areas from 2020 (http://www.wdpa.org/), which includes nationally protected areas, areas designated under regional and international conventions, and privately protected areas. We overlaid the protected areas onto our ensemble SDM and extracted suitable areas of the species that are officially protected. We then calculated the percentage of these suitable areas that are protected relative to the total size of the area of suitability, and that of high suitability areas.

To increase the knowledge on ecological aspects related to Muñoa's pampas cat, we downloaded the Ecological Systems (ES) found within the Uruguayan Savanna (https://www.ufrgs.br/labgeo/index.php/50-dados-espaciais/249-sistemas-ecologicos-das-savanas-uruguaias), and we extracted the highest suitably values of the species ensemble SDM for each of the 13 categories of ES. These ES were developed by Hasenack, Weber, Boldrini, & Trevisan (2010) using supervised classification maps, with locally a detailed classification based on geographical relief, soil type (including anthropogenic activities) and especially the dominant vegetation. Subsequently, we calculated which ES had the largest percentage of higher suitably values for the species.

2.6. Muñoa's pampas cat connectivity and future threats

For the connectivity analyses, we inverted the ensemble SDM surface, using the "Raster Calculator" tool from ArcGIS 10.4.1 and we used it as an input file of resistance to the movement of Muñoa's pampas cat among protected areas and sites where individuals were recorded (McRae, Shah, & Mohapatra, 2013). We used *Circuitscape v. 4.0.5* (McRae et al., 2013) with two input files for each analysis: (i) inverted SDM of Muñoa's pampas cat specifying per-cell resistances; and (ii) a focal node location file (a vector layer with the [1] protected areas or with [2] occurrence records). We then used the "pairwise" mode in the program to compare resistance values across pairs of protected areas or occurrence records. This software creates output maps with levels of connectivity among chosen focal nodes (values range from 0 to 100, where 100 indicates the highest connectivity, and values below 10 indicate very low or no connectivity); and a pairwise table with resistance values for each pair of chosen focal nodes (the lowest values denoting the highest facilitation of movement). In the pairwise table, each analysis generates a different range of resistance values. Therefore, here we selected the 10 lowest resistance values (i.e., the highest connectivity values) within the range of each analysis ([1] protected areas and [2] occurrence points) to identify the pairwise comparison with the highest connectivity.

Finally, we compared the resulting maps of connectivity among this cat's occurrence records with the future global development threat map (Oakleaf et al., 2015, 2019 [https://doi.org/10.7927/61jv-th84]). This is a dataset of development trends that forecasts global habitat conversion based on a combination of a variety of threats (agricultural expansion, urban expansion, etc.) and identifies categories ranging from negligible to high threat of conversion (Oakleaf et al., 2015, 2019). Here, we overlaid the connectivity map of sites of current occurrence with this dataset. Subsequently, we counted the number of pixels with low-to-high connectivity values (more specifically values >10, range

0–100) for each of the threat categories. We did not compare future global development threat maps with protected area connectivity since the protected areas are correlated with this threat map (Oakleaf et al., 2015, 2019).

3. Results

We collected 93 location records of Muñoa's pampas cat from 2000 to 2018 (Appendix A). As we subsampled the data, the final dataset resulted in 75 records (Fig. 1). We found no evidence of significant spatial autocorrelation among data points ($I=-0.02$, Z-score$=-0.52$, $P=0.60$). We also did not observe any collinearity among our environmental variables (Appendix C).

3.1. SDM analyses

The ensemble SDM indicated higher suitability for the Muñoa's pampas cat in the central area of the species distribution in Uruguayan Savanna (Fig. 1). We also observed some level of suitability for the Muñoa's pampas cat outside species distribution, in northwestern Rio Grande do Sul state (Brazil), in the provinces of Misiones, Corrientes, and Entre Ríos, (Argentina), and in Itapúa (Paraguay) (Fig. 1A).

The predicted results of each algorithm provided a good fit to the data considering that all values had $AUC \geq 0.85$, $AUC_{diff} \leq 0.13$, and $TSS \geq 0.67$ (Appendix D). As an additional exercise for the post-evaluation of model performance, we used 22 location records of Muñoa's pampas cat, which were different from the ones used in the SDM (including four new records from 2019 and 2020) (Appendix A). From this, we also observed good results for the model, with 90.91 % of the additional records falling in areas of medium to high suitability, and no record being found in an area of very low suitability (Appendix E).

BIO15 (Precipitation Seasonality) was the variable with the highest importance, followed by elevation and annual temperature (BIO1) (Fig. 2A). BIO15 influenced negatively the predicted presence of Muñoa's pampas cat; the highest values of suitability for the species were associated with the lowest levels of precipitation seasonality (~16 %). Regarding annual temperature, the highest suitability values occurred around 19 °C, while higher temperatures were negatively correlated with habitat suitability. Additionally, we found that elevations around 270 m were the most suitable for the taxon. Other variables influencing suitability, in order of importance (Fig. 2A), were NDVI (with a negative effect), distance to rivers (with higher values of suitability associated with areas farther than 0.05 km from rivers), and land use, indicating greater suitability in areas with a mosaic vegetation of natural and modified habitats ([grassland/shrubland/forest] [50–70 %] / cropland [20–50 %]) (category 30 of ESA GlobeCover) (Fig. 2B).

3.2. Status assessment, protected areas and ecological systems

All the assessed combinations of parameters indicated that Muñoa's pampas cat currently comprises <10,000 mature individuals. Therefore, based on IUCN's criterion C, it should be included in some threatened category (Table 1). Further, this felid was classified as Endangered or Critically Endangered in 13 of the 24 demographic scenarios that we assessed, which were based on varying thresholds of habitat suitability, and different proportions of mature individuals in its populations (Table 1). We also estimated that only 3.9 % of its distribution is presently protected, and that only 0.73 % of high-suitability areas are contained within protected areas (Fig. 1B, Appendix F). Of the 32 protected areas occurring within its range, only 11 (see 8, 10, 11, 13, 19, 20, 23, 24, 25, 27, 28 in Fig. 1B) presented at least one pixel assigned to a high category of suitability.

Finally, we observed that the ecological systems that presented the highest percentages of high suitability values were 'Mixed field with Andropogoneae and Asteraceae' (39.16 %) and 'Grassy field' (27.08 %) (Appendix G).

3.3. Muñoa's pampas cat connectivity and future development threat

For analyses of protected areas, connectivity maps values ranged from 0 to 37.5 (Fig. 3A), which last value indicated highest connectivity (Fig. 3A), a low level of connectivity, since general values range from 0 to 100 (see Material and methods). Pairwise resistances values (prv) ranged from 0.01 (highest connectivity) to 2.5 (lowest). Because, according to our definition (see Material and methods), prv < 0.11 were considered indicative of high connectivity, only 2.02 % (n=20) of 992 pairs of protected areas were highly connectivity (Appendix H). When considering occurrence points, connectivity maps values ranged from 0 to 83.7 (highest connectivity) (Fig. 3B). The values of the pairwise resistance analysis ranged from 0.09 (highest connectivity) to 1.06 (lowest connectivity), and prv < 0.19 were consider the ones with greater connectivity to movement (according to our definition [see Material and methods]). Pairs among occurrence points presenting higher connectivity were 4.93 % (n=252) of the 5,112 pairs (Appendix I). In addition, 92.46 % of connectivity areas (values from 10 to 83.7) were assigned to greater levels of threat than current ones in the future development threat map (Fig. 4).

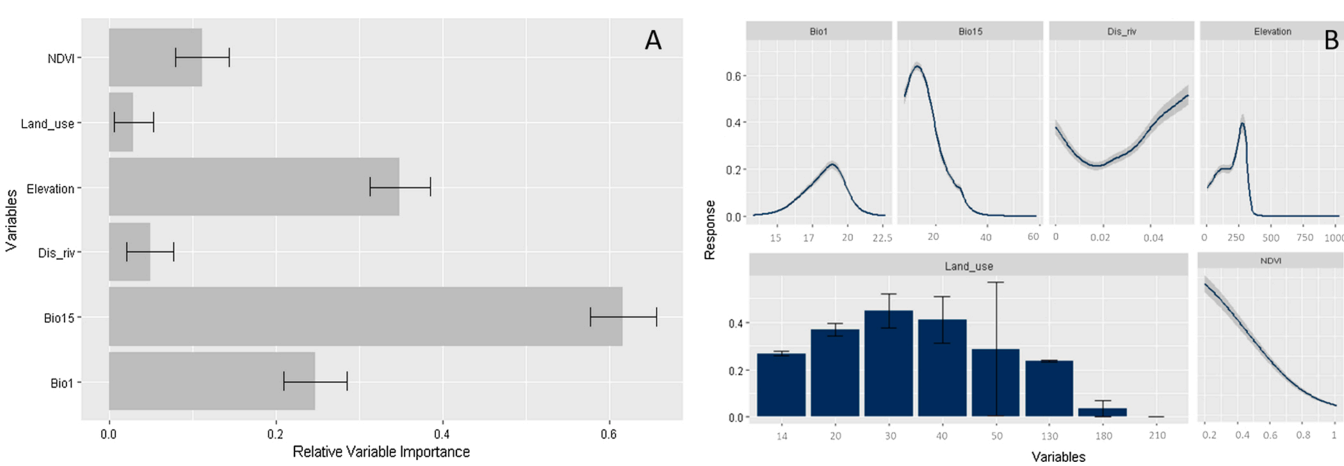

Fig. 2. Environmental variables affecting Muñoa's pampas cat (*Leopardus munoai*) occurrence in distribution models. A) Relative mean variable importance (VI) for multiple models; VI was based on the training dataset of all models; and error bars show the standard deviation. B) Response of species habitat suitability to the range of values for each variable based on the fitted models. Error bars show the standard deviation.

Table 1
Population size estimates and corresponding conservation status (according to the IUCN Red List of Endangered Species categories, using criterion C1) of Muñoa's pampas cat (*Leopardus munoai*) based on increasingly stringent thresholds of habitat suitability (this work), an average density estimate ($d = 0.03$ individuals/km^2) (Oliveira et al., 2010; Queirolo et al., 2013 [0.01-0.05 individuals/km^2]), and different assumed proportions of mature individuals (*p*, Appendix B). For each suitability level, the estimated area of occurrence (*A*) was estimated, and used to calculate to total number of individuals (N), and the number of mature individuals (MI) based on different assumed proportions (*p*). For every combination, the conservation status was assessed based on MI: Vulnerable [VU]: < 10,000 mature individuals; Endangered [EN]: < 2,500 mature individuals; Critically Endangered [CR]: < 250 mature individuals (IUCN Standards & Petitions Committee, 2019).

Suitability	*A* (km^2)	N	0.1 (*p*)		0.2 (*p*)		0.3 (*p*)		0.4 (*p*)		0.5 (*p*)		0.6 (*p*)	
			MI	Status	MI	Status	MI	Status	MI	Status	MI	Status	MI	Status
0.02 – 0.76	492579	14777	1478	EN	2955	VU	4433	VU	5911	VU	7389	VU	8866	VU
0.20 – 0.76	298590	8958	896	EN	1792	EN	2687	VU	3583	VU	4479	VU	5375	VU
0.39 – 0.76	174438	5233	523	CR	1047	EN	1570	EN	2093	EN	2617	VU	3140	VU
0.57 – 0.76	20789	624	62	CR	125	CR	187	CR	249	CR	312	EN	374	EN

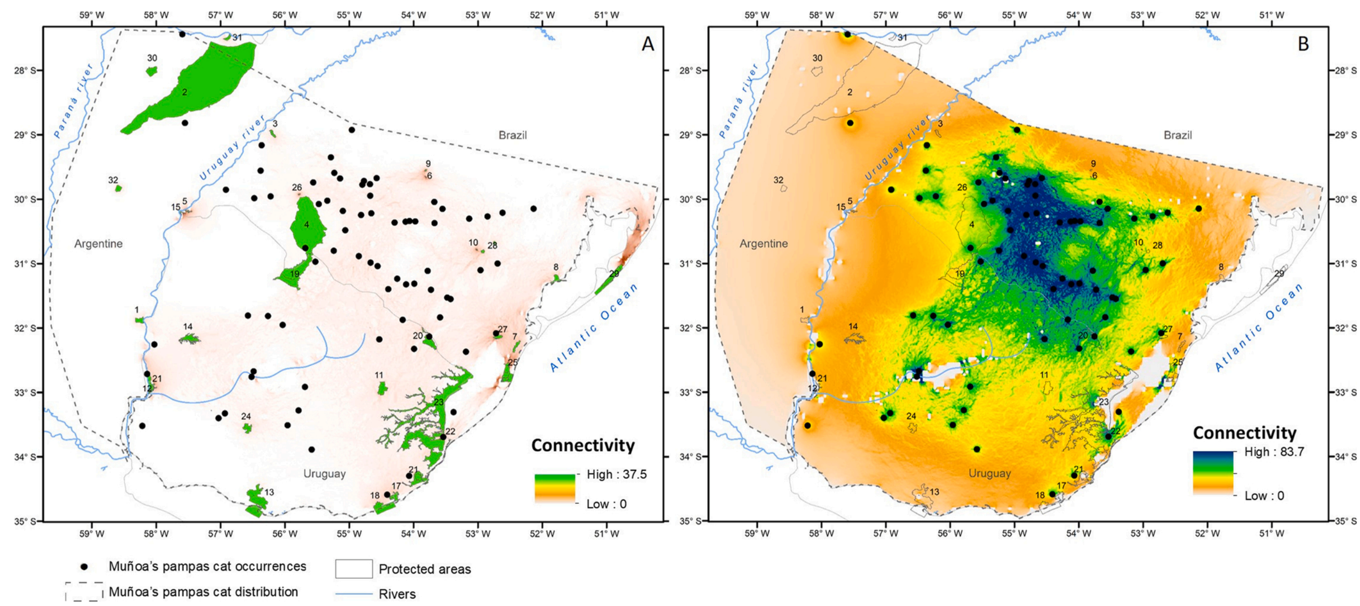

Fig. 3. Maps of connectivity for the Muñoa's pampas cat. A) Connectivity among protected areas (1=El Palmar (ARG); 2=Iberá (ARG); 3=Reserva Biológica do São Donato (BRA); 4=Área de Proteção Ambiental Ibirapuitã (BRA); 5=Parque Estadual do Espinilho (BRA); 6=Parque Natural Municipal dos Morros (BRA); 7=Refúgio de Vida Silvestre Banhado do Maçarico (BRA); 8=Parque Estadual do Camaquã (BRA); 9=Reserva Biológica do Ibicuí Mirim (BRA); 10=Reserva Particular do Patrimônio Natural Boa Vista (BRA); 11=Quebrada de los Cuervos y Sierras del Yerbal (URU); 12=Esteros de Farrapos e Islas del Río Uruguay (URU); 13=Humedales del Santa Lucia (URU); 14=Montes del Queguay (URU);15=Rincón de Franquia (URU); 16=Esteros y Algarrobales del Río Uruguay (URU); 17=Laguna de Rocha (URU); 18=Laguna Garzón (URU); 19=Reserva de Biosfera Bioma Pampa (Valle Del Lunarejo/Laureles-Cañas) (URU); 20=Paso Centurión y Sierra de Ríos (URU); 21=Laguna de Castillos (URU); 22=San Miguel (URU); 23=Bañados del Este (URU); 24=Localidad Rupestre Chamanga (URU); 25=Estação Ecológica do Taim (BRA); 26=Reserva Biológica do Ibirapuitã (BRA); 27=Reserva Biológica do Mato Grande (BRA); 28=Parque Estadual do Podocarpus (BRA); 29=Parque Nacional da Lagoa do Peixe (BRA); 30=Mburucuyá (ARG); 31=Apipé Grande (ARG); 32=Rincón de Santa María (ARG)). B) Connectivity among occurrence points.

4. Discussion

Our results provide novel information on spatial patterns of habitat suitability and connectivity of *L. munoai* across its entire distribution. Based on a reliable and up-to date SDM, we found that the highest suitability areas for Muñoa's pampas cat were located in the centre of the species' distribution, between southern Brazil and Uruguay, with medium-to-very low suitability values in Argentina. This follows a general idea in ecology, postulating that central areas of a species' distribution are more favourable than the limits of its range (Ricklefs, 2010). Nevertheless, the highest value of suitability was 0.76, suggesting that even the best habitats remaining in this threatened ecoregion may not present excellent conditions for this endemic species. As a result of the overall low suitability and the limited size of this cat's distribution, we estimated that its population size is considerably small, irrespective of the different demographic scenarios that we assessed. Furthermore, we found reduced connectivity among suitable habitats, suggesting that areas that are crucial for the movement of Muñoa's pampas cats across the landscape (i.e., corridors) are scarcely available. Finally, our results indicate that remaining areas with low-to-high connectivity levels largely overlap with habitats that are highly likely to be converted into human-dominated landscapes in the near future. These results lead us to conclude that this species is severely threatened and in urgent need of cross-border conservation plans. In the following sections, we discuss our results in the light of our main questions.

4.1. How environmental variables influence Muñoa's pampas cat habitat suitability?

Our results indicated that precipitation seasonality (BIO15) had a strong negative influence on Muñoa's pampas cat habitat suitability. Usually, seasonal precipitation is positively correlated with tree growth stages of forested habitats, and then with their maintenance (Brienen & Zuidema, 2005). Because we found that this variable was negatively correlated with Muñoa's pampas cat suitability, we infer that there is a negative association between this felid and the climatic conditions that favour the growth of forest in these regions. In agreement with this hypothesis, our analysis related to vegetation cover (NDVI) suggested

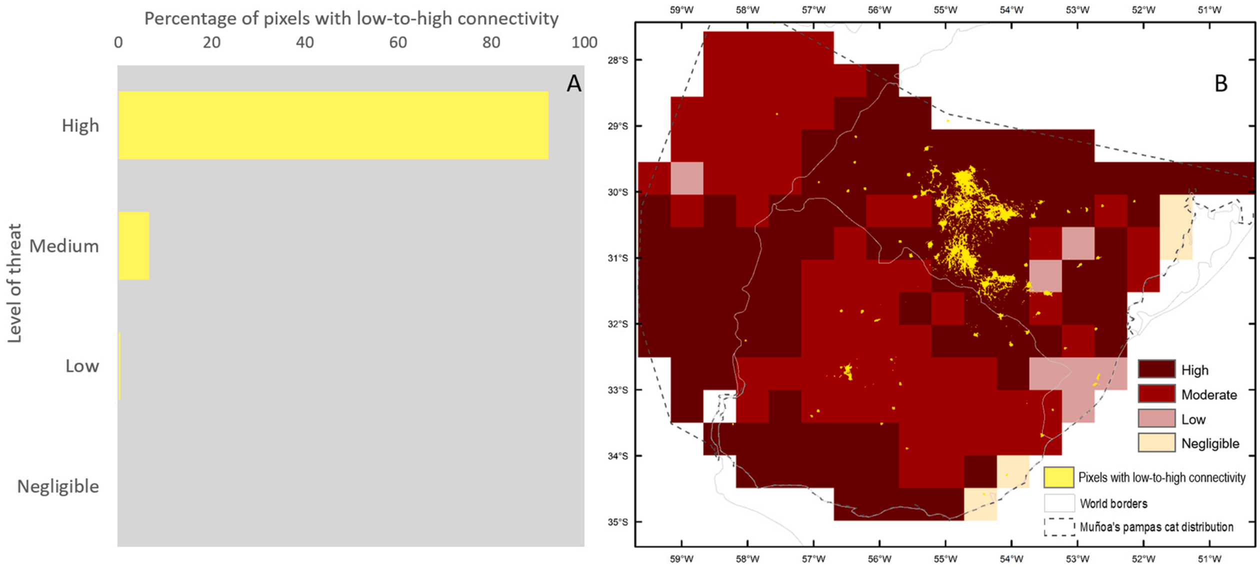

Fig. 4. Results of main connectivity values of occurrence records of Muñoa's pampas cat compared with different categories of the future global development threat map (Oakleaf et al., 2015, 2019 [https://doi.org/10.7927/61jv-th84]). A) Percentage of connectivity in each threat level category. B) Map showing connectivity areas (values of connectivity ranging from 10 to 83.7) overlapped in each different categories of theat.

low or no suitability for the species in areas with the highest vegetation cover. We also found that higher temperatures and elevations were negatively correlated with habitat suitability. We agree with Nascimento et al. (2020) who pointed out that this set of conditions that are associated with Muñoa's pampas cat differs from those associated to other species of the Pampas cat complex, whose habitat suitability is positively related to warmer temperatures and more seasonal precipitation (such as in the Brazilian Cerrado), or cooler and highly seasonal climates (e.g., in the high Andes of western Argentina). Thus, Muñoa's pampas cat seems adapted to a specific set of environmental conditions, which are distinct from those present in the rest of the complex's distribution (Nascimento et al., 2020).

Some areas of medium suitability (~0.45) for Muñoa's pampas cat occurred in regions with intermediate levels of anthropogenic activity, such as mosaics of natural vegetation (grassland/shrubland/forest) and croplands. Additionally, the largest percentage of high suitability values overlapped with the ecological system called 'Mixed field with Andropogoneae and Asteraceae' (Hasenack et al., 2010) which, according to Hasenack et al. (2010), is a mixture of natural grassland (54.6 %), anthropogenic areas (37.9 %), forest (6.2 %), and water (1.3 %). Most of this area has deep soils with low fertility. These findings indicate that natural grasslands are very important for this species (as observed by Bou et al. (2019) and Nascimento et al. (2020)), but that the same areas that can be suitable for *L. munoai* are potentially important for human activities, and consequently the populations of this cat could be negatively affected by ongoing and future modifications of these areas. While these same results suggest that Pampas cats might be able to adapt to a certain degree to habitat modification, it is crucial to emphasize that most of the Uruguayan Savanna ecoregion is categorized as having the highest future threat of conversion (Oakleaf et al., 2015, 2019), and that the entire ecoregion has already been severely altered by cattle ranching and agriculture (main economic activities in Brazil and Uruguay) during the past 400 years (Martino, 2004). These anthropogenic alterations of natural habitats have led to the classification of the ecoregion as 'Critical/endangered' (Loyola et al., 2009) and to the local extinctions of several species, including the jaguar *Panthera onca* (Linnaeus, 1758), lowland tapir *Tapirus terrestris* Linnaeus, 1758, collared peccary *Pecari tajacu* (Linnaeus, 1758), and white-lipped peccary *Tayassu pecari* (Link, 1795) (Queirolo, 2016).

4.2. Is this species at risk of extinction?

All 24 demographic scenarios that we assessed generated an estimated population size that would place Muñoa's pampas cat in one of the IUCN categories of extinction threat. Furthermore, eight scenarios placed it in the EN category, and five scenarios in the CR category, highlighting the conclusion that it may be severely threatened. This felid is already categorized as EN in Rio Grande do Sul state, Brazil (FZB (Fundação Zoobotância do Rio Grande do Sul), 2014). In Uruguay, it is considered threatened and a conservation priority (González et al., 2013). These regional categorizations will likely be revised in the near future to indicate increased level of concern, given the update in this group's taxonomy (highlighting the distinctiveness of Muñoa's pampas cat), improved modelling of ecological aspects, such as reported here, and updated information on threats, e.g., massive recent expansion of cropland areas in Rio Grande do Sul (Brazil) (Overbeck et al., 2015) subsidized by the Brazilian government (Brasil, 1991).

4.3. What proportion of L. Munoai suitable habitat is protected?

We observed that most of Muñoa's pampas cat's suitable range is located outside of protected areas and that only a small proportion (28.2 %) of protected areas in the region presented any pixels in the highest category of habitat suitability. These findings reveal a critical conservation problem for this species. While the majority of the 39 protected areas within Muñoa's pampas cat range are located in Brazil (21), the protected areas with the largest amount of high-suitability habitat were in Uruguay: Bañados del Este, Paso Centurión y Sierra de Ríos, and Bioma Pampa Biosphere Reserve (Valle Del Lunarejo/Laureles-Cañas). Overall, it is clear that, to conserve this species, it is crucial: (i) to increase the existing protected areas; (ii) to create new ones, and (iii) in private areas, to promote land-sharing practices to balance the goals of food production and biodiversity conservation (Fischer et al., 2008). All of these proposed actions should prioritize high-suitability habitat for Muñoa's pampas cat.

4.4. How connected are the protected areas within its distribution? And how connected are sites of recorded occurrence?

The very limited landscape-scale connectivity for this felid among protected areas and among confirmed occurrence records is an additional reason for conservation concern, because it can decrease gene flow and effective population sizes, preclude recolonization and even induce local extirpations (Fahrig, 2003). In this context, our results can support conservation planning, since we mapped areas that are important for Muñoa's pampas cat movement across its range. The most connected protected areas were Ibirapuitã Protected Area (Brazil) and Valle del Lunarejo/Laureles-Cañas (Uruguay). The most connected pairs of core areas were São Valentim and São Gabriel, and Dom Pedrito and Bagé municipalities in Brazil. The latter areas also showed high connectivity with Rivera and Cerro Largo departments in Uruguay, which in turn, may connect with other departments of the country, such as Tacuarembó and Durazno. Such findings open up direct avenues to plan and implement corridor initiatives focused on the conservation of this felid.

4.5. Will the remaining habitat connectivity be threatened in the future?

The high risk of future habitat conversion projected for areas that are critical for Muñoa's pampas cat connectivity indicates that, if prompt actions are not taken to conserve these regions, the range of this felid will become highly fragmented soon, accelerating its population declines. A cross-border conservation strategy involving institutions of Brazil and Uruguay and favouring sustainable farming systems combined with strict nature reserves (IUCN category Ia) is therefore advisable (Dudley, 2013).

5. Conclusion

Our results reveal that this endemic felid is severely threatened with extinction due to a combination of small population size, limited availability and scarce protection of suitable habitat, and imminent perspective of losing population connectivity because of projected habitat conversion. The current monoculture-based agriculture expansion, along with other human-related threats (e.g., road kills, persecution by domestic dogs, retaliatory hunting for predation on poultry, etc.), can lead to the extinction of this species in the coming decades. Although our findings provide baseline information that may inform immediate conservation actions, there is an urgent need for more detailed assessments of population densities and reproductive rates, as well as studies that define more precisely what type and degree of disturbance can be tolerated by Muñoa's pampas cats. This is particularly relevant because probably, the landscapes outside protected areas, especially those with land-sharing approaches and sustainable cattle ranching, will be increasingly essential for the long-term persistence of this elusive and poorly known felid.

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Ethical standards

Not applicable.

CRediT authorship contribution statement

Flávia P. Tirelli: Conceptualization, Formal analysis, Investigation, Writing - original draft, Visualization, Project administration, Funding acquisition. **Tatiane C. Trigo:** Conceptualization, Investigation, Writing - review & editing. **Diego Queirolo:** Conceptualization, Investigation, Writing - review & editing. **Carlos Benhur Kasper:** Investigation, Writing - review & editing. **Nadia Bou:** Investigation, Writing - review & editing. **Felipe Peters:** Investigation, Writing - review & editing. **Fábio D. Mazim:** Investigation. **Juan Andrés Martínez-Lanfranco:** Investigation, Writing - review & editing. **Enrique M. González:** Investigation. **Caroline Espinosa:** Investigation. **Marina Favarini:** Investigation. **Lucas Gonçalves da Silva:** Conceptualization, Writing - review & editing. **David W. Macdonald:** Writing - review & editing, Supervision. **Mauro Lucherini:** Conceptualization, Writing - review & editing, Supervision. **Eduardo Eizirik:** Conceptualization, Writing - review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.jnc.2021.126009.

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