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Refined assessment of the geographic distribution of Geoffroy's cat (*Leopardus geoffroyi*) (Mammalia: Felidae) in the Neotropics

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Abstract

Understanding the fine-scale geographic distribution of a species has applications in biogeography, ecology, evolution and conservation. Species distribution models (SDM) have been widely used to predict geographic and climatic ranges of species. Geoffroy's cat *Leopardus geoffroyi* is a small felid of least concern that occupies a wide variety of habitat types in Argentina, Bolivia, Brazil, Chile, Paraguay and Uruguay. We evaluated the fine-scale distribution of Geoffroy's cat at the sub-continental level, estimated its current extent and area of occurrence and discussed the current and potential ranges developed with SDM. On the basis of species occurrences (n = 1502) and large-scale environmental data, two model types ('environmental' and 'land cover') were developed using MaxEnt. The estimated extent of occurrence of Geoffroy's cat was 3 180 664 km^2, but the potential area of occurrence predicted by our environmental model was 70% larger due to areas with high suitability (i.e. >0.5) compared to the species' current range. The most important bioclimatic factors affecting Geoffroy's cat presence were temperature seasonality, mean temperature of the coldest quarter and annual precipitation. Two recent records obtained outside the known distribution of the species fell within the high-suitability area (i.e. >0.5) predicted by our model. Our SDM suggest that this habitat-generalist felid is probably expanding its distribution range by taking advantage of changes in human land use.

Introduction

Defining geographic distribution is crucial for any species and has applications in biogeography, ecology, evolution and conservation. Species distribution models (SDM) have been widely used to infer the ecological requirements of species and to predict their geographic and climatic ranges (DeMatteo & Loiselle, 2008; Marino *et al.*, 2010; Abba *et al.*, 2012). SDM can be applied to conservation prioritization, discovery of new populations of known species or predicting the expansion of exotic species (Araújo & Guisan, 2006; Phillips, Anderson & Schapire, 2006). Combined with Geographic Information Systems (GIS), SDM have also facilitated spatial analysis of species representation in protected areas, the understanding of geographic relations with other species and the estimation of habitat loss due to land-use changes (Elith & Leathwick, 2009; Ferraz *et al.*, 2012; Dawe, Bayne & Boutin, 2014; Cuyckens, Morales & Tognelli, 2015).

Geoffroy's cat *Leopardus geoffroyi* is a small felid (*c*. 4 kg) considered of least concern (The IUCN Red List of Threatened Species, 2015), ranging in Argentina, Bolivia, Brazil, Chile, Paraguay and Uruguay. The species occupies a wide variety of habitat types in the sub-tropical and temperate Neotropics, including shrubby woodlands, dry forests and savannas of the

Chaco, Patagonian shrub, Monte desert/semi-desert, Pampas grasslands and wetlands in both pristine and disturbed areas (Pereira & Aprile, 2012). Although it is considered a relatively common carnivore throughout its range (The IUCN Red List of Threatened Species, 2015), its presence is still controversial in several areas, and an accurate fine-scale distribution map is not available for this species.

New records outside the known range of Geoffroy's cat distribution (Saavedra *et al.*, 2011; Bertrand & Newman, 2014; Rinas *et al.*, 2014) could be due to increased surveying efforts and improvement in detection techniques (camera trapping). Another possibility is the expansion of its range into previously unoccupied areas, as is currently occurring with other species such as the maned wolf *Chrysocyon brachyurus* (Queirolo *et al.*, 2011), the crab-eating fox *Cerdocyon thous* (Fracassi *et al.*, 2010) and the coyote *Canis latrans* (Gompper, 2002).

Here, we evaluate the fine-scale distribution of Geoffroy's cat at the sub-continental level, modeling its potential range on the basis of climatic, topographic and human-related (i.e. land cover) variables. We also estimate its current extent of occurrence, that is the area contained within the shortest continuous imaginary boundary that can be drawn to encompass all records, and the area of occurrence, that is the area within the extent of occurrence that is actually occupied by the species (IUCN Standards and Petitions Subcommittee, 2011). Finally, we discuss the current and potential ranges obtained for the species considering habitat modification in the Neotropics and Geoffroy's cat ecology.

Materials and methods

Predictive distribution models for Geoffroy's cat were developed based on an extensive set of presence records and selected environmental variables. We gathered records of Geoffroy's cats from January 2000 to January 2014 based on geographic positions (lat/long coordinates) and dates from: (1) field surveys (i.e. live sighting, live trapping or roadkill) and (2) perusal of skins and skulls (i.e. specimens preserved by rural people or deposited in museum and private collections). In addition, from 2010 to 2012 we distributed an email survey requesting Geoffroy's cat records to qualified informants (e.g. field researchers, park rangers and naturalists) living in six countries included within the species distribution range. We identified people with extensive knowledge or experience in identifying wild carnivores; thus, their reports were considered accurate for species identification. Also, we conducted an exhaustive bibliographic revision to obtain published records of the species. The reliability of all obtained records was thoroughly evaluated, mainly those records of melanistic Geoffroy's cats, due to the possible misidentification with black domestic cats *Felis catus*, jaguarundis *Puma yagouaroundi* or melanistic southern tigrinas *Leopardus guttulus* (Trigo *et al.*, 2013). Only those records that were free of any doubt (through pictures, detailed descriptions or reference material) were included in our database.

To minimize spatial autocorrelation attributed to unequal sampling effort across regions (Segurado, Araujo & Kunin, 2006), the data were sub-sampled at a distance that was sufficient to reduce spatial autocorrelation. After randomly selecting only one locality point per 1 × 1 km cell, the spatial autocorrelation was not significant according to the Moran's I test (Moran, 1950). As Geoffroy's cat records were not uniformly distributed throughout the species range, a kernel density layer was used as bias layer in the modeling process to avoid influence of record density (Kramer-Schadt *et al.*, 2013).

To calculate the extent of occurrence, we used all presence records and generated the extent using the 'Aggregate points' tool, with four decimal degrees as the aggregation distance to avoid leaving gaps in Geoffroy's cat distribution. To calculate the area of occurrence, we used the environmental model converted to binary (absence/presence) and extracted the area inside the extent of occurrence according to the IUCN definition (IUCN Standards and Petitions Subcommittee, 2011).

An 'environmental model' and a 'land-cover model' were developed employing maximum entropy algorithm as implemented in MaxEnt Software version 3.3.3k (Phillips *et al.*, 2006). This algorithm is considered robust for modeling presence-only occurrence data (Elith *et al.*, 2006). To consider a possible northward expansion of the species' potential distribution, models were based on the entire South American subcontinent. There is no consensus about the selection process of environmental variables that best explain the range of species, but the use of many environmental layers may tend to overfit the model (Phillips *et al.*, 2006). On the other hand, it is not clear which environmental variables have the most biological meaning for Geoffroy's cat. To determine the pre-candidate environmental variables, preliminary models were performed including 19 bioclimatic (obtained from the WorldClim database version 1.4, http://www.worldclim.org; Hijmans *et al.*, 2005) and three topographic variables, successfully used for the flat headed cat *Prionailurus planiceps* (Wilting *et al.*, 2010), Andean cat *Leopardus jacobita* (Marino *et al.*, 2011) and jaguar *Panthera onca* (Tôrres *et al.*, 2008). The Worldclim variables represent annual and seasonal trends as well as temperature and precipitation extreme values for the 1950–2000 period and have a resolution of 30 arc-seconds (Supporting Information Fig. S1), that is *c.* 1 km^2; (Hijmans *et al.*, 2005). Topographic information included altitude (derived from a digital elevation model produced by the NASA – Shuttle Radar Topographic mission), from which we derived aspect and slope.

Candidate environmental models were validated by using 75% of the data for training and 25% for testing the models, with 100 repetitions (Araújo & Guisan, 2006). Data were sampled by bootstrapping with 10 random partitions with replacements and run settings included a convergence threshold of 0.00001 and 10 000 background points. We tested for correlation between variables using Pearson (Supporting Information Fig. S2). Based on these results, three candidate models of non-correlated (Pearson <0.7) variables with high (>7%) contribution to each model were selected to avoid collinearity and minimize redundancy. To measure general performance we used the area under the receiver operating characteristic curve (AUC). The AUC measures discrimination, that is the ability of the model to correctly classify records, as presence/absence. AUC goes from 0 to 1, where 1 is perfect classification and 0.5 means it classifies as random. We selected the best model using the Akaike's information criterion (AIC) which is a measure of the relative quality of statistical models (Burnham & Anderson, 2002) using ENM Tools (Warren, Glor & Turelli, 2008).

For the most accurate final model, we examined the response curves showing how each of these environmental variables affects the MaxEnt prediction (Phillips & Dudík, 2008). We projected this model geographically to represent the area of occurrence. Although continuous results convey more information than binary outputs (Vaughan & Ormerod, 2005), for many applications (as to assess representation in protected areas) the continuous prediction afforded by species distribution modeling must be converted to a map of presence or absence, so a threshold indicative of species presence must be fixed. The selection of thresholds to transform probabilities of occurrence into binary predictions is one of the most controversial issues in SDM (Papeş & Gaubert, 2007; Rebelo & Jones, 2010). To convert the continuous suitability model in a binary map we used expert criteria to define the lowest threshold that included all known presence areas which was 0.17.

Only to test for the importance of land use on Geoffroy's distribution, we generated a 'land-cover model' in an analogous way as the environmental model, but using those variables selected in the environmental model plus 'land cover', obtained from Globcover (ESA & UCLouvain, 2010). Since this data layer was last updated in 2009, those records obtained after this year or before 2000 were excluded from this analysis. In that way, the proper assignment of each location to a land-cover category was ensured, minimizing mistakes due to changes.

Results

Overall, 2393 records of Geoffroy's cat were obtained. After excluding uncertain data and records at <1 km, only 1502 records (Supporting Information Fig. S3) were considered for modeling; of those, 574 records were used for the land-cover model. The extent of occurrence of this felid is 3 415 550 km^2 and encompasses Argentina, Uruguay, southern Brazil, western and southern Paraguay, southern-central Bolivia and small areas of southeastern Chile (Fig. 1).

The exploratory analyses of bioclimatic variables led to three combinations of non-correlated variables with different relative contributions to each environmental model (Table 1). According to values in Phillips & Dudík (2008), some models (B, C and land cover) slightly underperform (i.e. AUC values under 0.75). Although as we used a lot of presence records, it is logical to obtain a lower AUC value and models were useful in terms of predicting the Geoffroy's cat distribution. All three models provided similar geographic predictions (not represented here), but the most accurate model according to AIC criterion was model C (Table 1), which involves substantial contributions of three predictive variables (annual precipitation, mean temperature of coldest quarter and temperature seasonality; Table 1).

The response curves based on model C illustrate how MaxEnt predictions of climatic suitability varied with environmental variables across South America. At low annual precipitation levels (i.e. <121 mm) suitability was low (0.35), whereas an increase in precipitations triggered an increase in suitability. Maximum (0.55) probability of presence is at 151 mm; increasing precipitation does not increase the suitability any further (Supporting Information Fig. S4a). Regarding the mean temperature of the coldest quarter, the highest probabilities (i.e. >0.5) of Geoffroy's cats presence occurred within a range of 3–22°C (mean value = 11.5°C) (Supporting Information Fig. S4b). Suitability gradually increased with increasing temperature seasonality (Supporting Information Fig. S4c).

By using an *ad hoc* threshold, most (99.4%) of the extent of occurrence polygon estimated for Geoffroy's cats was classified as suitable (i.e. suitability >0.17) by our environmental model (Fig. 1). But, in addition, this model predicted three highly suitable areas (i.e. suitability >0.5) out of the species current range: (1) toward the northeast of, but contiguous with, the extent of occurrence (Paraguay and Brazil); (2) a small area in southwestern Bolivia, adjacent to sites with confirmed Geoffroy's cat presence and (3) an isolated large area in central Chile, on the opposite side of the Andean Mountains. As a result, potential area of occurrence predicted by our model is 5 397 463 km^2, remarkably higher than the actual extent of occurrence of this felid. The 'land-cover model' depicted land cover as the variable contributing the most (39.7%; Table 1) and showed a good general performance (AUC = 0.731). In general, the geographic projection of the land-cover model was similar to the environmental model and both models predicted presence in Valdivian forests. Some differences were the predicted absence of the species in the Paranaen forest of Misiones (Argentina) and the southern region of Brazil. In the Patagonia, some areas were of low suitability in the environmental model and absence in the land-cover model (Fig. 2).

Discussion

Geoffroy's cat is one of the most common and studied small felid in southern region of South America. However, this is the first study thoroughly describing its current and potential distribution based on the largest set of presence records (>1500) and large-scale environmental data. The extent of occurrence map obtained for Geoffroy's cats is similar to the 3 180 664 km^2 range map generated by experts of IUCN (The IUCN Red List of Threatened Species, 2015) with two important expansions based on new field data. On one hand, recent efforts have been carried out to systematically survey felids in central and western Bolivia, which resulted in new Geoffroy's cat records outside its previously known distribution area and the expansion of its altitudinal range to almost 3740 m a.s.l. in Bolivia (M. Da Silva, unpubl. data). On the other hand, new surveys in southern Brazil have slightly expanded northward the distribution limit of the species.

According to the environmental model, the most important bioclimatic features affecting Geoffroy's cat presence appears to be temperature seasonality, mean temperature of the coldest quarter and annual precipitation. Mean temperatures of the coldest quarter lower than 1.4°C greatly reduces the suitability, indicating that very cold winters are important constraints to Geoffroy's cat distribution. However, some degree of

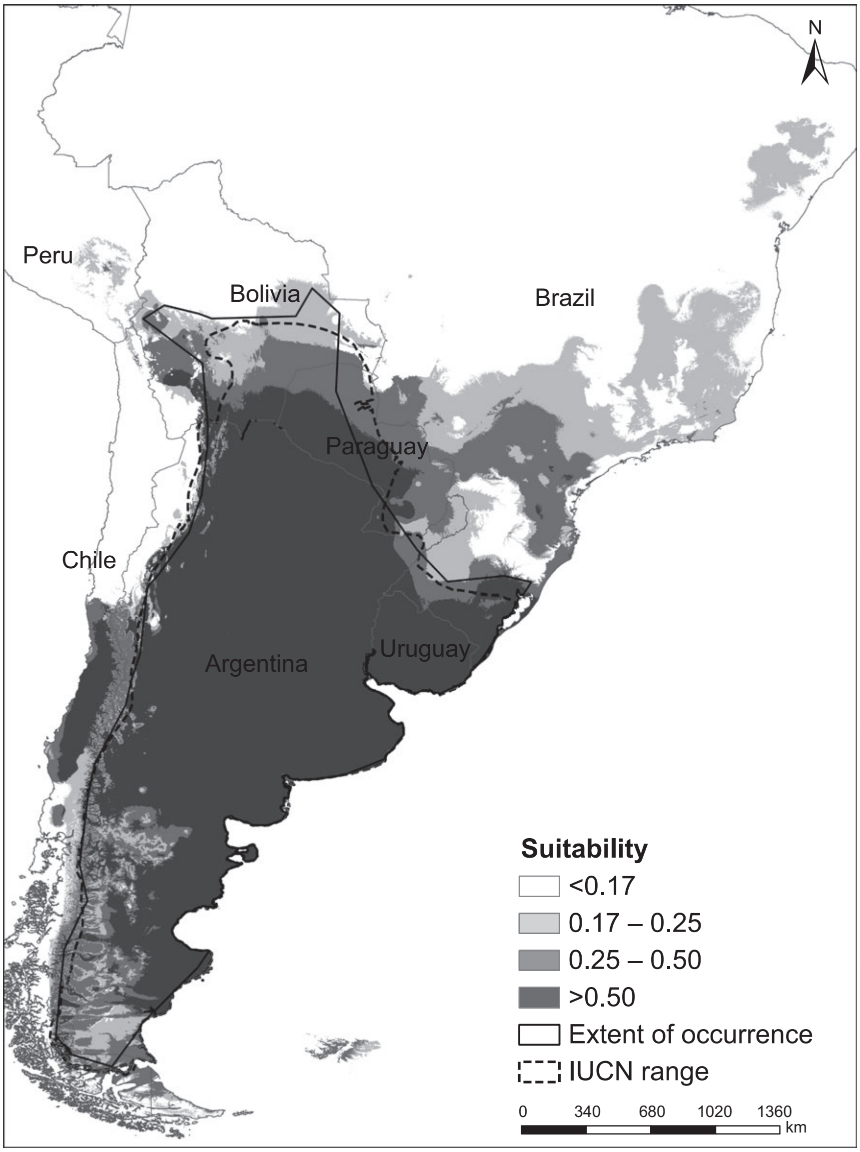

Figure 1 Extent of occurrence and geographic projection of Geoffroy's cat *Leopardus geoffroyi* distribution model with different environmental suitabilities (scale of gray), based on 1502 presence records, MaxEnt logistic output and 'Model C' (see text for details). The 'expert map' contour of IUCN (The IUCN Red List of Threatened Species M, 2015) is also shown.

Table 1 Relative contribution (%) of land cover, elevation and bioclimatic variables, Akaike's information criteria and difference and number of parameters used for candidate environmental models for Geoffroy's cat *Leopardus geoffroyi* geographic distribution

	Model A	Model B	Model C	Land-cover model
Land cover				39.7
Elevation		9.9		
Precipitation of the warmest quarter		16.6		
Annual precipitation	19.6	21.7	25.3	11.7
Mean temperature of the coldest quarter	52.8		53.7	19.6
Mean temperature of the wettest quarter		12.9		
Temperature seasonality	22.5	38.8	21.0	29.0
Annual mean temperature		5.1		
AUC values	0.908	0.729	0.721	0.731
Parameters	4.0	5.0	3.0	
AICc	4383.0	4363.0	4348.0	
ΔAICc	35.0	15.0	0.0	

AUC, area under the curve; AIC, Akaike's information criterion.

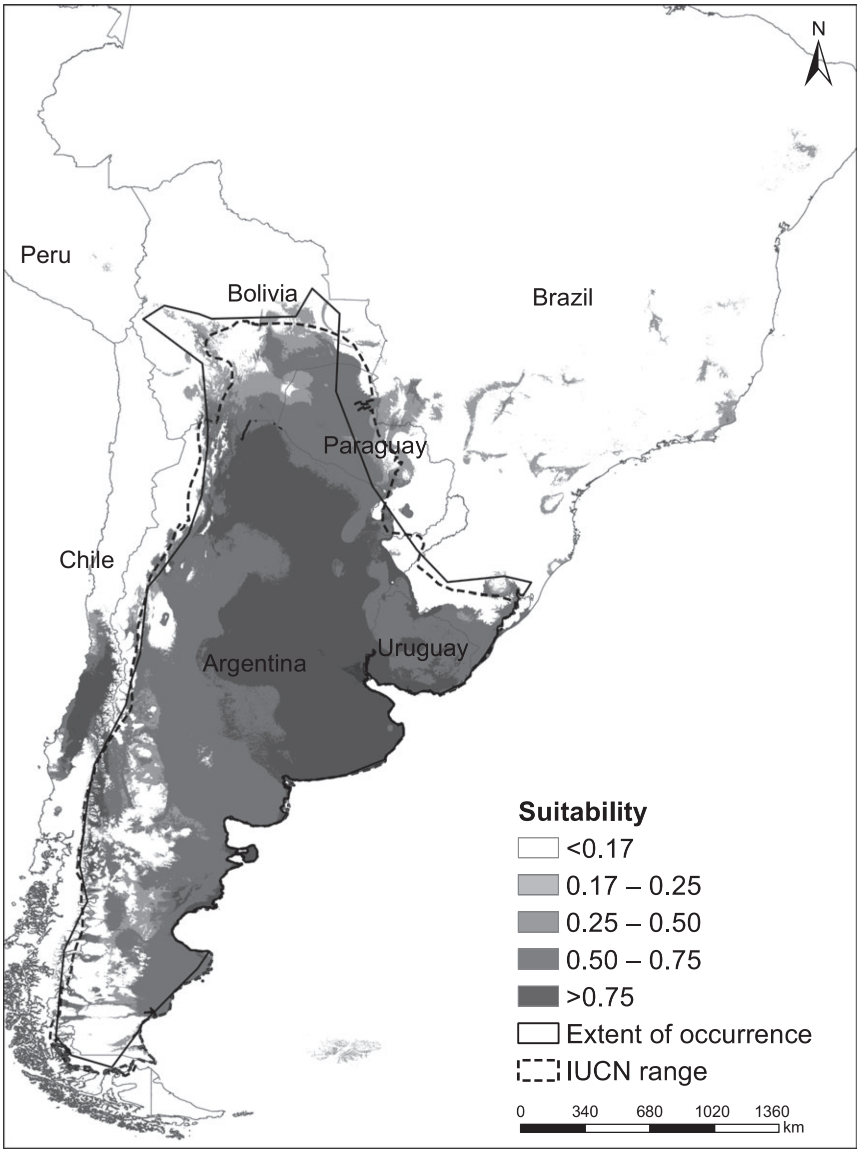

Figure 2 Geographic projection of the Geoffroy's cat *Leopardus geoffroyi* land-cover distribution model with different suitabilities (scale of gray), based on 574 presence records, MaxEnt logistic output and four variables (annual precipitation, mean temperature of coldest quarter and temperature seasonality and land cover). The 'expert map' contour of IUCN (The IUCN Red List of Threatened Species M, 2015) is also shown.

temperature seasonality is present over its whole range, characteristic of temperate climates. Suitability greatly increases above 151 mm of annual precipitation; areas with lower values are less suitable. The negative effects of drought years on the ecology and demography of this cat has been demonstrated (Pereira, Fracassi & Uhart, 2006; Pereira & Novaro, 2014), supporting the predictive ability of our model.

In the land-cover model, the 'land-cover' variable reduced markedly the importance of variables that are affecting the cat presence less directly (i.e. climatic variables). Therefore, the environmental model could not be predicting the distribution of this species in a completely reliable way. The land-cover model adjusts better in the area of the Paranaen forest in northeast Argentina and Brazil, but this could be an artifact of the threshold, nevertheless this model has in general higher values of suitability (i.e. reaching 0.75 vs. 0.5 in the environmental model), which suggests that it adjusts better. Distribution of Geoffroy's cat is more determined by land-cover than by environmental variables.

The environmental model, but not the land-cover model predicts Geoffroy's cat in Paranaen forests (northeast of Argentina and southern Brazil). Geoffroy's cat was never recorded in the Atlantic rainforest (Nowell & Jackson, 1996), but new solid evidence confirmed its presence in this eco-region, close to Iguaçu National Park, in Brazil (Bertrand & Newman, 2014). Another recent record of this felid was obtained in Misiones province, Argentina, in an area composed by shrubs, farms and grasslands (Rinas *et al.*, 2014) toward the northeast of the known distribution of this cat, very close to the southern limit of the Atlantic rainforest eco-region (Burkart *et al.*, 1999). Although these two new records are surprising (e.g. the Iguaçu record is located *c.* 300 km from the closest confirmed occurrence sites in Argentina and Paraguay), both of them are included within the high-suitability area (i.e. >0.5) predicted by our environmental model. This suggests that climate is suitable in this area, but the land-cover category is not. These areas are suffering from deforestation and land cover could have changed since 2009, so those areas could be occupied by Geoffroy's cat in the future.

The Geoffroy's cat distribution in Brazil, in spite of the high probabilities of occurrence detected by the environmental model in areas further from the southern region, seems to be really limited to Rio Grande do Sul state in its southern portion as predicted by the land-cover model. In fact, no reliable record is available in the literature about the occurrence of this cat in other Brazilian regions even in face of several surveys existing in these areas. The only record known outside of this range is from Paraná state in southeastern Brazil (Margarido & Braga, 2004), however, this is really unreliable because no documentation of the specimen is available in the literature, which could indicate a misidentification. Nevertheless, on a local scale, new surveys seem to slightly expanded northward the distribution limit of this species in Rio Grande do Sul state. But also in this case, this pattern might be attributed to the occurrence of hybridization events between *Leopardus geoffroyi* and *L. guttulus* that could be hampering the accurate identification of pure individuals and leading to a misperception of a geographic expansion (Trigo *et al.*, 2014). In this case, additional studies focusing on the geographic and ecological patterns of pure and hybrid specimens distribution are still needed to specifically characterize the exact limits of this species occurrence in southern Brazil.

Based on broad potentially suitable climatic and topographic areas toward the northeast of the current extent of occurrence of this cat, it is likely that Geoffroy's cat can expand its distribution farther northeast. However, since this species does not inhabit rainforests, its northeast expansion should only be possible by taking advantage of human modifications of land. At least two lines of evidence support this hypothesis: (1) Geoffroy's cats are behaviorally flexible and commonly found in agroecosystems and rural areas (Castillo *et al.*, 2008; Di Bitetti *et al.*, 2011; Pereira, Walker & Novaro, 2012) and (2) Geoffroy's cat has a remarkable dispersal capacity (Pereira & Novaro, 2014), allowing the species to reach disconnected areas from its main distribution. In that way, Geoffroy's cats may be able to colonize new areas when forest cover is lost, following human land changes and expanding its range. Those patches of transformed land in a matrix of natural Atlantic rainforest are gradually being connected and in that way offering sufficient new habitat suitable for Geoffroy's cat and this felid could occupy another 'island' following human land transformations. A similar process was observed already for canids in that area (F. Garcez and E. Eizirik, unpubl. data).

Both models predict a potential area of occurrence in the Valdivian forest, a tempered forest located in the Chile–Argentina border region. The suitable habitat in Chile predicted by our model with high suitability (i.e. >0.5) also includes the Matorral, where no records of this species exist. Geoffroy's cat is recorded in Valdvian forest in Argentine side, but not in Chile, where only kodkod *L. guigna* occurs. The Andes Mountains could act as topographic barrier impeding Geoffroy's cats' ability to colonize this region. Andes Mountains act as biogeographical barrier for several species (Vuilleumier & Monasterio, 1986; Brumfield & Edwards, 2007). The kodkod is a species highly specialized to the ecoregion of Valdivian Forests, only occurring here and in Chilean Matorral (Cuyckens *et al.*, 2015). Geoffroy's cat could be excluded by this species. Although kodkod is of a smaller size (1.4–2.8 kg vs. 2.5–8 kg for Geoffroy's cat; Pereira & Aprile, 2012), restricted species that have specialized diets (as kodkod) are often more efficient resource exploiters than are generalized widespread species (Walker *et al.*, 2007). Our work supports the idea of Geoffroy's cat showing habitat plasticity and being an opportunistic species (De Oliveira *et al.*, 2010).

A particular situation arises with our model in Bolivia, where the suitability for this felid is surprisingly low in both models in spite of its confirmed occurrence. In general, areas where Geoffroy's cats records occur and that receive a lower suitability may indicate that *L. geoffroyi* is less strictly associated to the habitats typical of these areas. The Patagonia receives also low probabilities of occurrence; this area could be less suitable because of extreme dry climate, also more fieldwork in this area could increase the number of records to represent its presence in these areas better.

The MaxEnt Software accounts for some pitfalls, for example, it assumes that sample is random (Royle *et al.*, 2012), but when gathering records from different sources (as in our case), this is violated. Also, it does not estimate the probability of occurrence directly, but rather the environmental suitability for the species (Royle *et al.*, 2012), so for most species there is a need for more robust species range maps, perhaps those based on occupancy models that account for imperfect detections (e.g. Karanth *et al.*, 2009). Nevertheless, by accounting for sampling bias, collinearity among bioclimatic variables, incorporating a land-use layer, using multimodel selection based on AIC we improved the scientific rigor of MaxEnt analysis.

The fine-scale distribution map and the habitat model here presented for Geoffroy's cats are based on an objective methodology and an international effort. The knowledge of the distribution range of elusive carnivores is a very valuable tool to understand their ecology as well as for conservation planning. We gathered an extremely large sample size of unpublished data in South America. Our study also showed that SDM could be useful tools to predict the expansion of a native species under changing land use.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Map of land cover, superimposed with extent of occurrence and presence records of Geoffroy's cat *Leopardus geoffroyi*.
Figure S2. List of the 19 bioclimatic variables of Worldclim.
Figure S3. Table of correlation of Pearson (*r*) between each pair of 22 environmental (19 bioclimatic and three topographic) variables for selection of modeling.
Figure S4. Graphics of relationships between bioclimatic features and probability for Geoffroy's cats presence derived from the 'environmental' model: (a) temperature seasonality, (b) mean temperature of the coldest quarter and (c) annual precipitation.