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Bioclimatic constraints to Andean cat distribution: a modelling application for rare species

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ABSTRACT

Aim To identify the bioclimatic niche of the endangered Andean cat (*Leopardus jacobita*), one of the rarest and least known felids in the world, by developing a species distribution model.

Location South America, High Andes and Patagonian steppe. Peru, Bolivia, Chile, Argentina.

Methods We used 108 Andean cat records to build the models, and 27 to test them, applying the Maxent algorithm to sets of uncorrelated bioclimatic variables from global databases, including elevation. We based our biogeographical interpretations on the examination of the predicted geographic range, the modelled response curves and latitudinal variations in climatic variables associated with the locality data.

Results Simple bioclimatic models for Andean cats were highly predictive with only 3–4 explanatory variables. The climatic niche of the species was defined by extreme diurnal variations in temperature, cold minimum and moderate maximum temperatures, and aridity, characteristic not only of the Andean highlands but also of the Patagonian steppe. Argentina had the highest representation of suitable climates, and Chile the lowest. The most favourable conditions were centrally located and spanned across international boundaries. Discontinuities in suitable climatic conditions coincided with three biogeographical barriers associated with climatic or topographic transitions.

Main conclusions Simple bioclimatic models can produce useful predictions of suitable climatic conditions for rare species, including major biogeographical constraints. In our study case, these constraints are also known to affect the distribution of other Andean species and the genetic structure of Andean cat populations. We recommend surveys of areas with suitable climates and no Andean cat records, including the corridor connecting two core populations. The inclusion of landscape variables at finer scales, crucially the distribution of Andean cat prey, would contribute to refine our predictions for conservation applications.

Keywords

Andes, biogeographical barriers, biogeography, climatic niche, species distribution models.

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INTRODUCTION

A central postulate in biogeography is that climate exerts a dominant control over the distribution of species, as evidenced by fossil records (Davis & Shaw, 2001) and recent observed trends (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003). Founded in the ecological niche theory (Hutchinson, 1957), climatic envelope models provide a suitable tool

to test and advance the ecological and evolutionary theories underpinning the fields of biogeography and biological conservation (Araújo *et al.*, 2004; Munguía *et al.*, 2008; Makowsky *et al.*, 2010). Indeed, various modelling techniques developed over the last decades to study species' responses to the environment are now prominent in modern ecological theory (Heegaard, 2002; Guisan & Thuiller, 2005; Sagarin *et al.*, 2006; Austin, 2007; Elith & Leathwick, 2009).

Models based on bioclimatic variables at macro-scales are producing successful simulations of current distributions, and refined algorithms perform well with presence-only data and limited number of localities (Elith & Leathwick, 2009; Franklin *et al.*, 2009). These advances are particularly relevant for poorly known, rare and endangered species, and cryptic or nocturnal animals for which absence is difficult to define (Engler *et al.*, 2004; Papeş & Gaubert, 2007; Pearson *et al.*, 2007; Brito *et al.*, 2009; Thorn *et al.*, 2009; Wilting *et al.*, 2010). The Maxent algorithm, based on maximum entropy theory (Phillips *et al.*, 2006), is known to outperform alternative presence-only models when sample sizes are small (Hernandez *et al.*, 2006; Wisz *et al.*, 2008); it is also less sensible to the choice of calibration area for pseudo-absences (Giovanelli *et al.*, 2010) and performs particularly well for range-restricted or specialized organisms (Elith *et al.*, 2006; Phillips *et al.*, 2006).

We used Maxent to model the climatic niche of Andean cats (*Leopardus jacobita*) at the continental scale of South America. Andean cats are listed as endangered (Acosta *et al.*, 2008) and are considered one of the rarest and least known felids in the world (Villalba *et al.*, 2004; Brodie, 2009). Our poor understanding of the biology of Andean cats stems from their elusive behaviour and seemingly low population densities (Lucherini *et al.*, 2008; Marino *et al.*, 2010); and until recently there was only a small set of confirmed locations for the species (Yensen & Seymour, 2000; Villalba *et al.*, 2004). Thanks to the coordinated effort of members of the Andean Cat Alliance over the last decade, the number of confirmed localities has now increased to more than 200. The database compiled for this study includes published and unpublished records from Argentina, Bolivia, Chile and Peru (Sanderson, 1999; Perovic *et al.*, 2003; Barbry & Gallardo, 2006; Sorli *et al.*, 2006; Cossios *et al.*, 2007; Napolitano *et al.*, 2008; Viscarra, 2008; Torrico, 2009). Most records are confined to the Central Andes above 4000 m, but several recent findings also locate them at much lower elevation in arid regions of west Argentina (Di Martino *et al.*, 2008).

The newly extended database opens up the possibility of using statistical models with the following objectives: a) to explore the key dimensions of the climatic component of the Andean cat ecological niche (Pearson & Dawson, 2003), and b) to identify regions with environmental conditions similar to where the species is known to occur (Pearson *et al.*, 2007). While elevation clearly is a strong, albeit indirect, predictor of habitat suitability for Andean cats, the barrier effect of the Andes also creates asymmetric climatic conditions on each side of the cordillera (Garreaud, 2009), known to affect the

distribution of species and their genetic variability (Chesser, 2000; Weigend, 2002; Marin *et al.*, 2007; Cossios *et al.*, 2009). To include these complex climatic patterns, we considered multiple climatic predictor variables at the level of South America, benefiting from Maxent's ability to handle complex functions and to produce easily interpretable response curves (Phillips *et al.*, 2006). In this paper, we also describe the process of variable selection, aimed at minimizing redundancy and to include factors related to the physiology of animals in harsh environments such as those of the High Andes. We discuss the scope for improvements and applications of these niche models, and elaborate on the implications of the species' dietary specialization upon Chinchillidae rodents - the chinchillas and viscachas of South America (Walker *et al.*, 2007; Napolitano *et al.*, 2008; Viscarra, 2008; Torrico, 2009).

METHODS

Location data

The authors compiled the Andean Cat Alliance database with reliable records spanning the period 1988–2009. These comprise the localities of 39 skins, three skulls, 19 sightings, 25 camera-trap captures, 99 DNA identifications (94 faecal samples, four hair samples and one skin sample), and 52 radio-tracking fixes from the only specimen ever trapped, an adult female captured in Bolivia (Delgado *et al.*, 2004).

To minimize the spatial dependences attributed to true biological origin or differential searching intensities across regions (Segurado *et al.*, 2006), we subsampled the data at a distance sufficient to reduce spatial autocorrelation. The spatial autocorrelation detected among some pairs of variables of the location data was dropped to levels depicted as insignificant by the Moran's I Test (Moran, 1950) after randomly selecting just one locality point per each 3×3 km cell of an over-imposed grid. As a result, the dataset was reduced from 237 to 135, of which 108 were used to run the models and 27 (20%) to test them.

Selection of variables

We selected predictor variables from the following: the WorldClim database of bioclimatic interpolated climate surfaces at 1-km resolution (derived from monthly temperature and rainfall values)(Hijmans *et al.*, 2005); the Global Land Cover GLC2000 at 1-km resolution (land cover types) (Bartholome & Belward, 2005); Shuttle Radar Topographic Mission (SRTM) at a resolution of 90 m (elevation, orientation and topography index) (Rabus *et al.*, 2003); and the Global Inventory Modelling and Mapping Studies (NDVI = Normalized Difference Vegetation Index at 250 m) (Tucker *et al.*, 2004). The latter two were resampled in ArcGIS 9.2 to a 1-km resolution. For area measurements, the layers were projected into UTM coordinates with the original datum WGS84.

We first summarized the climatic information associated with the locality data using principal component analysis

(PCA). The PCA helped to identify the sets of variables more strongly associated with the first and second axes of the ordination (with highest positive or negative loading scores), which together accounted for 79% of the variation among localities (Table 1). Between any two redundant variables (i.e. with Pearson correlation values > 0.70), those considered as surrogates for cold tolerance and moisture stress were preferred, because of the cold and dry climate of the High Andes (for example, minimum temperature of the coldest month rather than mean temperature of the cold quarter to represent absolute minimum temperatures). Because of redundancy in the climatic data, a few variables satisfied our correlation threshold. For this study, we ran models with all combinations of minimally correlated variables, both with and without elevation (Table 2).

Statistical model and validation

Maxent is a machine learning algorithm that estimates the most uniform distribution (maximum entropy) across the study area given the constraint that the expected value of each

environmental predictor variable under this estimated distribution matches its empirical average (Phillips *et al.*, 2006). The modelled probability is a 'Gibbs' distribution (i.e. exponential in a weighted sum of the features) and the model logistic outputs have a natural probabilistic interpretation representing degrees of habitat suitability (0 = unsuitable to 0.99 = best habitat) (Pearson *et al.*, 2007). For a detailed explanation of modelling methodology using Maxent, refer the studies by Phillips *et al.* (2006) and Phillips & Dudik (2008). We applied version 3.2.19 of the Maxent software with default values, up to 1000 iterations and implementing linear, quadratic and product features types (Phillips & Dudik, 2008).

We partitioned the occurrence locations randomly into two subsamples, using 80% of the locations as the training dataset and the remaining 20% for testing the resulting (partitioned) models. The measure of fit implemented by Maxent is the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (ranging from 0.5 = random to 1 = perfect discrimination). Some studies have pointed to some limitations in the use of AUC as a measure of performance in presence-only models (Lobo *et al.*, 2010), but this is often used as a single threshold-independent measure of choice for model performance; it has been shown to be independent of prevalence and a highly effective measure of the performance of ordinal score models (Manel *et al.*, 2001; McPherson *et al.*, 2004; Thuiller *et al.*, 2005).

Variable contribution and response curves

We considered Maxent's heuristic estimates of the relative contribution of environmental variables to the models and the results of jackknife analyses for each environmental layer (Phillips & Dudik, 2008). For the variables with highest predictive value, we examined the response curves showing how each of these environmental variables affects the Maxent prediction (Phillips & Dudik, 2008). The curves illustrate how the logistic prediction changes as each environmental variable is varied, while keeping all other environmental variables at their average sample value. The curves thus represent the marginal effect of changing exactly one variable.

RESULTS

Explanatory variables and model performance

The exploratory analyses of bioclimatic variables led to four combinations of minimally correlated variables, including elevation and various measures of temperature and precipitation (Table 2). Two combinations retained elevation as an explanatory variable plus measures of temperature variation, either the annual range (model A) or the mean diurnal range (model B) (themselves highly inter-correlated); all other temperature descriptors were closely correlated with elevation. The two other combinations were formed by the minimum and maximum temperatures of the coldest and warmest months (models C and D) as explanatory variables, or the

Table 1 Results of a principal component analysis (PCA) of bioclimatic and elevation variables associated with the Andean cat presence localities (*n* = 135).

Variables	PCA loadings			
	PC1	PC2	PC3	PC4
Elevation	**0.28**	0.17	0.05	0.01
Precipitation seasonality	**0.28**	−0.06	0.21	0.01
Temperature mean diurnal range	**0.24**	−0.13	0.02	0.64
Temperature annual range	0.13	**−0.31**	−0.15	0.42
Temperature seasonality	0.06	**−0.35**	−0.22	0.04
Precipitation of wettest month	0.04	**0.34**	0.24	0.12
Precipitation of warmest quarter	−0.10	**0.32**	0.14	0.29
Mean temperature of wettest quarter	−0.12	**−0.25**	0.38	0.06
Precipitation of wettest quarter	−0.16	**0.31**	0.11	0.31
Maximum temperature of warmest month	−0.18	**−0.31**	0.06	0.22
Annual precipitation	−0.20	**0.29**	0.04	0.26
Mean temperature of warmest quarter	−0.22	**−0.29**	0.10	0.06
Temperature annual mean	**−0.26**	−0.22	0.25	0.10
Precipitation of coldest quarter	**−0.26**	0.04	−0.43	0.08
Precipitation of driest month	**−0.28**	0.07	−0.37	0.10
Precipitation of driest quarter	**−0.28**	0.12	−0.30	0.12
Mean temperature of driest quarter	**−0.29**	−0.13	0.01	−0.12
Mean temperature of coldest quarter	**−0.31**	−0.01	0.33	0.06
Minimum temperature of coldest month	**−0.33**	−0.02	0.21	−0.19
Proportion of variance	0.43	0.36	0.10	0.05
Cumulative proportion	0.43	0.79	0.88	0.93

The columns show loading factors associated with the first four principal component factors or axes (PC), with the percentage of the variance explained by each of these factors at the bottom. In bold are highlighted the highest loading scores showing the two groups of variables associated with the first and second principal components.

Variables	Complementary models				Table 2 Four complementary models of Andean cat habitat suitability, with and without elevation as explanatory variable.
	Percentage contribution of variables				
	Model A	Model B	Model C	Model D	
Elevation	49.7	47.4			
Temperature					
Annual mean temperature				62.4	
Mean diurnal range temperature		50.0		35.8	
Temperature annual range	49.4				
Minimum temperature of coldest month			57.3		
Maximum temperature of warmest month			37.1		
Precipitation					
Annual precipitation		1.2		0.8	
Precipitation of driest quarter	0.8		5.6		
Precipitation of coldest quarter		1.5		1.8	
Models' performance					
Training AUC	0.988	0.989	0.988	**0.990**	
Test AUC	0.984	0.989	0.985	**0.993**	

The values are Maxent's heuristic estimates of the relative contribution of environmental variables to the models (Phillips & Dudik, 2008). In grey are highlighted the variable/s in each model that contained the most useful information alone, and/or the most information that is not present in other variables (according to Jackknife tests of each environmental layer, not shown).
AUC, area under the curve.

annual mean temperature and mean diurnal range (models C and D). Minimally correlated variables describing precipitation contributed little to the models; among them, the amount of rainfall during the dry season was the more useful variable. The other environmental layers depicting productivity (NDVI), topography, orientation and land use type showed no predictive value (results not shown).

All four models based on these sets of uncorrelated variables provided good fit to the data and were successfully validated by the test dataset (Table 2). Model D provided the best fit, combining as predictor variables the annual mean and mean diurnal range temperature, with the amount of rainfall in the dry season (winter) and throughout the year. The variables that contributed the most information not present in other variables (from jackknife tests of each environmental layer, not shown) were elevation and a measure of temperature: mean diurnal range of temperature in model B; minimum temperature of the coldest month in model C; and mean annual and mean diurnal range temperature in model D.

Predicted range of suitable climates for Andean cats

We focused on model D - that with the highest AUC - to describe the geography of the areas climatically suitable for Andean cats (Fig. 1). All four models provided similar geographic predictions, with the main difference being the amount of area climatically suitable, albeit of low probability value, in Argentine Patagonia - the prediction from model D was intermediate in this regard. We chose the lowest predicted value associated with any one of the presence records to distinguish suitable from unsuitable conditions; this 'lowest presence threshold' identifies pixels predicted as being at least as suitable as those where a species' presence has been recorded (Hernandez *et al.*, 2006; Pearson *et al.*, 2007; Raxworthy *et al.*, 2007). The lowest predicted probability associated with a record was 0.028, corresponding to the southernmost locality (38.3° S, 69.9° W) and lowest elevation (650 m) (Di Martino *et al.*, 2008).

The areas predicted as suitable by the model covered 1,172,320 km^2, including: 326,720 km^2 (28%) in Perú, 233,270 km^2 (20%) in Bolivia, 127,560 km^2 (11%) in Chile, and 466, 260 km^2 (40%) in Argentina. Suitable climatic conditions for Andean cats were found along the High Andes and at lower elevations in the eastern slopes of the cordillera, towards the Argentine Patagonian steppes (Fig. 1). The most favourable climatic conditions were in the central portion of the predicted latitudinal range. The pixels with highest probabilities are concentrated around the region of the triple frontiers between Bolivia, Chile and Peru (18° S 69° W) and Argentina, Bolivia and Chile (23° S 67° W). These are connected by a band of highly suitable climates along the highest peaks. This bottleneck in optimal climatic conditions coincides with a climatic boundary at around 20° S in Bolivia, known as the 'Andean Knee', where the cordillera takes a sharp bend south (Fig. 1). The northern extreme of the climatically suitable range was predicted to be around 6.5° S and coincided with a climatic and biogeographic feature known as the 'Peruvian Low' or Huancabamba Depression; further north only small patches with suitable climatic conditions were predicted, in the highest peaks of the Ecuadorian Andes.
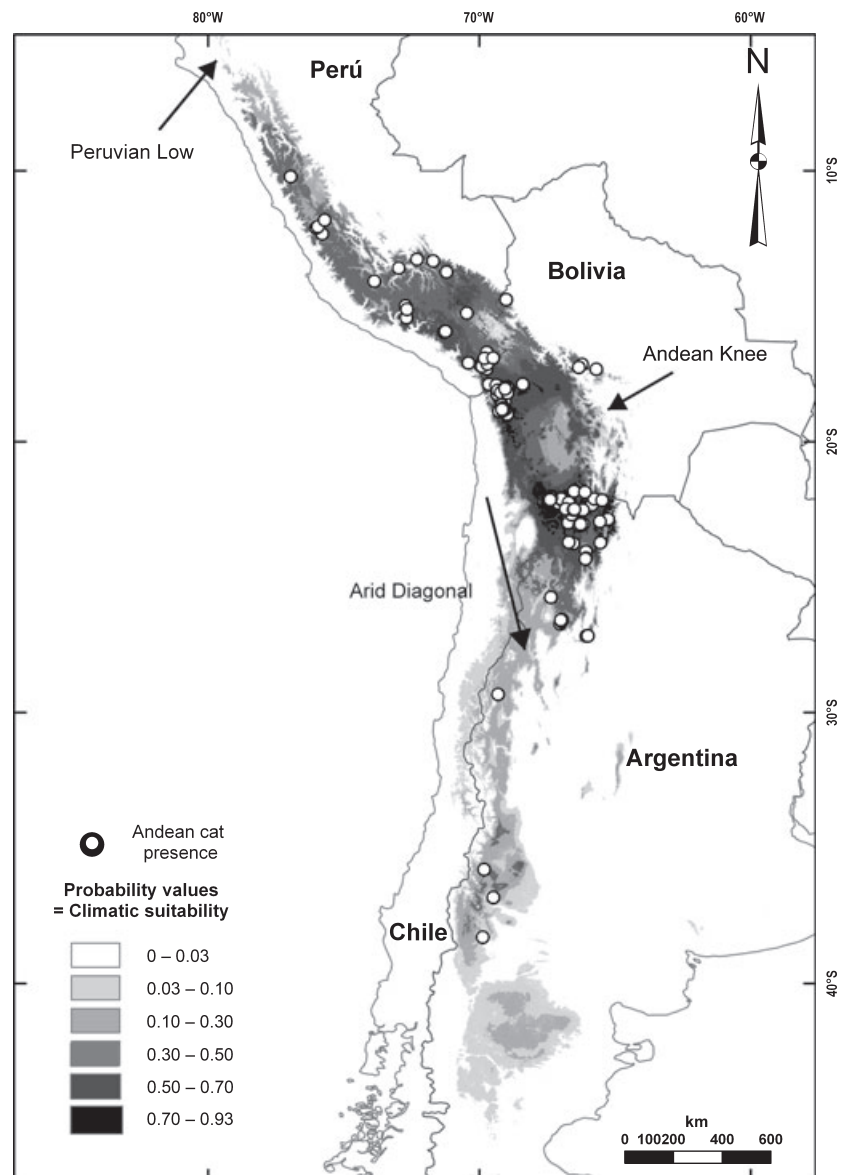
Figure 1 Andean cat suitability map (model D in Table 2). The lowest threshold for suitability (0.028) corresponds to the lowest probability of a known location and 0.93 to the highest.

Southwards, climatically suitable conditions narrowed markedly between 24° and 29° S along the Andes, where the 'Arid Diagonal' traverses the cordillera between Chile and Argentina (Fig. 1). While conditions improved further south, as latitude decreases below around 40° S the greater humidity and colder climate result in wet forests and glaciers seemingly unsuitable for Andean cats. A 'tail' of climatically suitable area, albeit of low suitability, descends into the Argentine Patagonia at the southern extreme of the predicted range, from where only a few records exist.

Climatic niche and response curves

The response curves in Fig. 2 illustrate how Maxent predictions of climatic suitability vary with elevation and key climatic variables across South America (only shown for those variables with highest predictive value, as shown in Table 2). Climatic

suitability peaked around 4 °C of mean annual temperature, decreasing rapidly towards warmer climates (Fig. 2a); the empirical average from location data was 5.4 °C (SD 2.5, $n = 135$). With regard to the maximum temperature of the hottest month, the best climatic conditions were predicted around 20 °C, with an empirical average of 17.3 °C (SD 3.3) (Fig. 2b). All other curves showed more skewed responses, with optimal climatic conditions close to environmental extremes: around −13 °C of minimum temperature of the coldest month, and decreasing rapidly towards values just above zero (empirical average −9.0 °C, SD 3.2) (Fig. 2c); and around 12–20 °C of mean difference between the daily maximum and minimum temperatures (empirical average 17.6 °C, SD 1.6) (Fig. 2d). Most temperature-related aspects of the climatic niche of Andean cats were associated with variations in elevation. Suitable climatic conditions were mostly restricted to areas above 2000–3000 m, and incrementing
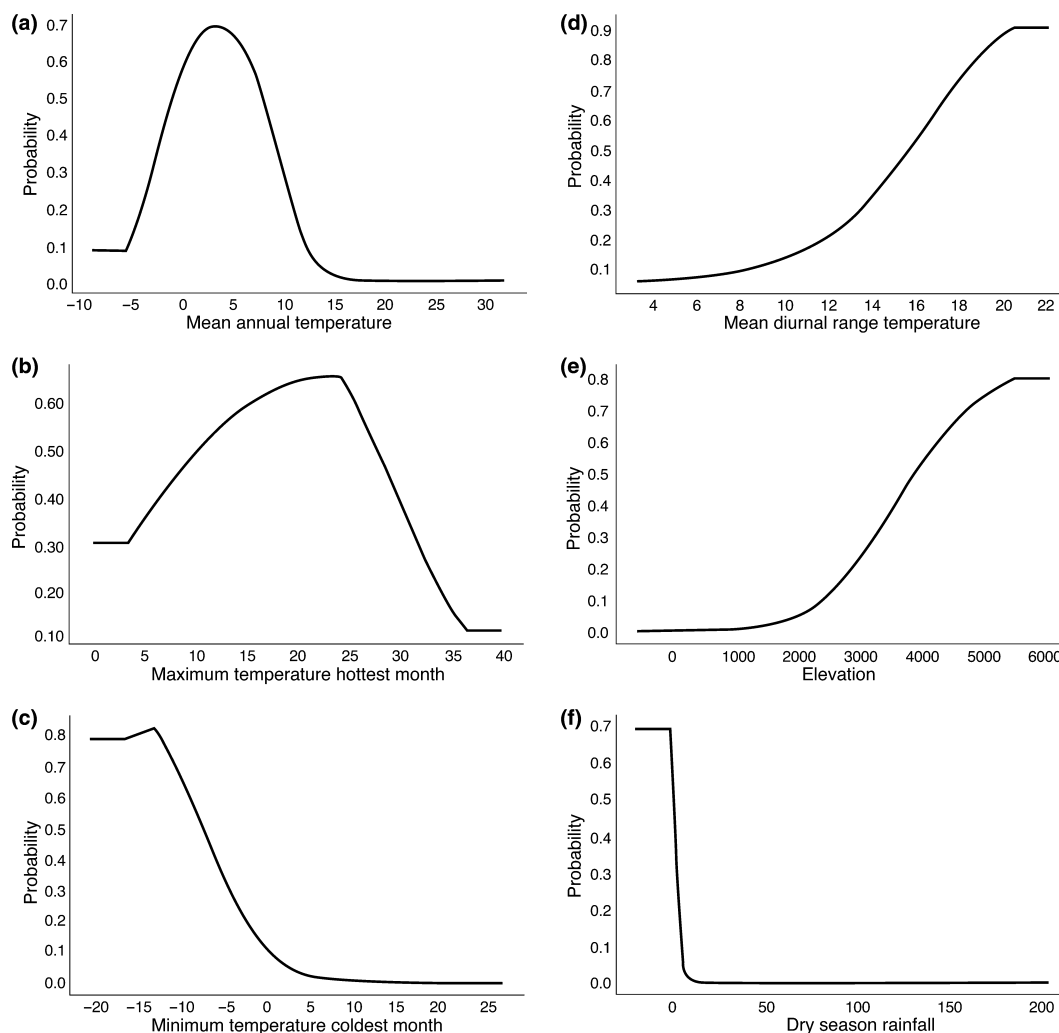
Figure 2 Marginal response curves showing how environmental variables affected the Maxent prediction of suitability (i.e. how the logistic prediction changes as each environmental predictor is varied, while keeping all others at their average sample value).

rapidly up to elevations above the empirical average of 4160 m (SD 620) (Fig. 2e). All Andean cat locations were in arid lands, with an empirical average of 268 mm of rainfall per year (SD 242), of which on average 185 mm (SD 139) fall in a relatively wet summer, and very little during winter. Climatic suitability decreased abruptly from areas with little or no rainfall during the dry season, towards areas with 50 mm or more (dry season empirical average 6.7 mm, SD 13.1) (Fig. 2f).

Three climatic variables were used to represent the environmental space of the Andean cat records along a north–south axis (Fig. 3). These environmental relationships notably change direction at around the latitude of the Andean Knee (20° S), where the Maxent model predicted a discontinuity in highly suitable climates. This is a region of extreme aridity, with cold weather and large diurnal temperature fluctuations (Fig. 3), conditions that become less harsh south and northwards, and seemingly less suitable for Andean cats towards the edges of the range. There is an apparent climatic gap that coincides with the latitudinal range of the Arid Diagonal, and

the climatic conditions further south in the much lower lying Patagonian steppe tend to resemble those of the High Andes at the northern edge of the species range.

DISCUSSION

This study contributes relatively simple bioclimatic models for a rare species, which, despite a considerable increase in research and conservation efforts over the last 10 years, is still considered among 14 threatened and severely understudied felid species requiring more attention by conservation biologists (Brodie, 2009). The models provide valuable information on the climatic dimension of the Andean cat niche and on the effect of biogeographic barriers on its distribution, evidence of some bioclimatic constraints. We also discuss this fundamental source of uncertainty in climatic niche models, which is the assumption that climate limits species distributions (Parmesan & Yohe, 2003). Factors other than climate can prevent species from occupying areas that would otherwise be climatically
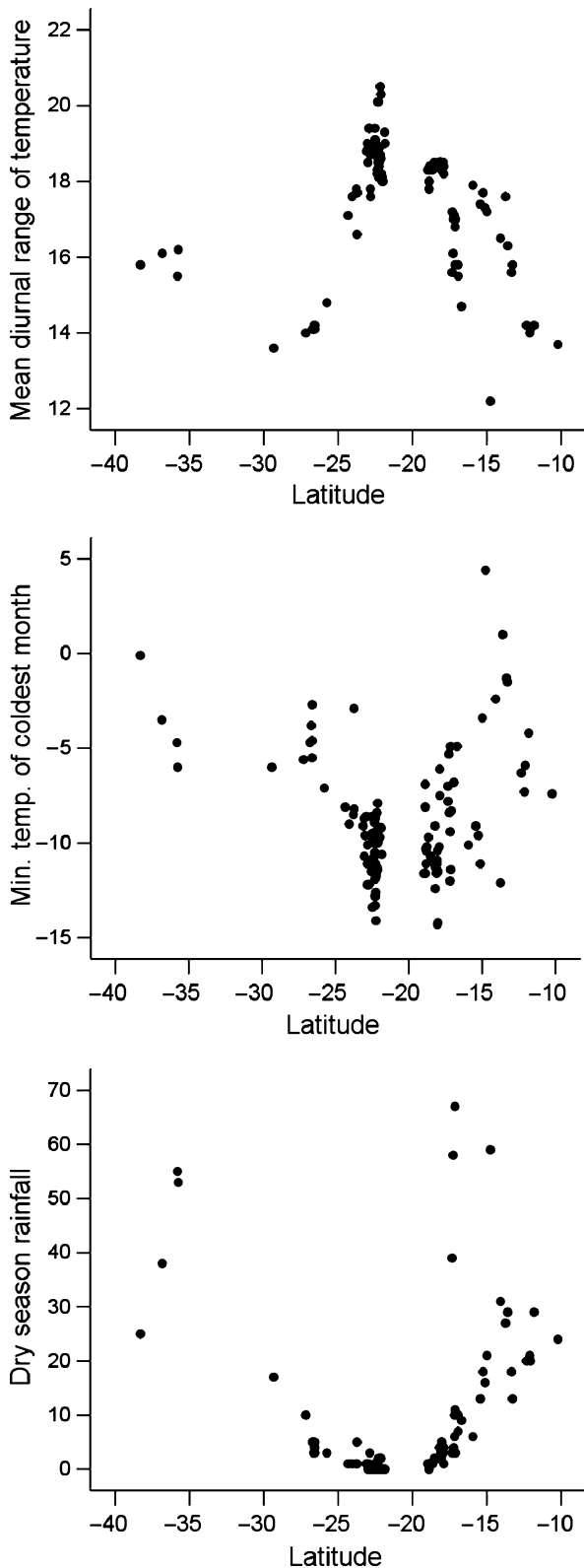
Figure 3 Variations in the climatic space determined by climatic variables associated with Andean cat records, along the latitudinal axis of its range. Notably, climatic relationships change direction in areas of climatic inversions along the Andes such as the Andean Knee around 20° S and the Arid Diagonal around 30° S, where the Maxent models predict lower climatic suitability.

suitable (Gaston, 2003) and in this case study these include the following: biotic interactions such as competition for prey and refuge with the Pampas cat and other carnivores; dispersal limitations created by geographic barriers (which the model successfully identified); and the distribution of the rodent prey.

The climatic characteristic associated with known Andean cat records – cold, dry, and with extreme diurnal variations in temperature – were present along the Andes in areas of montane grasslands, shrublands and steppes. These formations range from the Wet Puna ecoregion in Peru – with extensions into the Cordillera Central Paramo, through the Central Andean and Dry Punas, and descending into the Patagonian Steppe (Olson et al., 2001). One of the strengths of the model was its ability to identify areas with environmental conditions similar to those where the species is known to occur. We acknowledge that caution should be exerted in the interpretation of these results, because of the possibility of models 'overpredicting'. On the one hand, the choice of the South American continent as calibration area for the pseudo-absences could lead to over-predictions (Lobo et al., 2010); on the other, the Maxent algorithm tends to over-fit to the data and it performs well in species with restricted distributions (Phillips & Dudik, 2008). We therefore suggest prioritizing surveys of regions with suitable climatic conditions and no records of Andean cats to explore a highly suitable corridor connecting the two core areas, the possibility of unrecorded populations (for example in Patagonia), and to refine the models. It is possible that new records influence the shape of these predictions as more field studies are undertaken, particularly if data are provided from areas with environmental conditions poorly represented in this dataset such as the Patagonian steppe.

Within the predicted geographical range of the species, areas of relatively low suitability coincided with absences of, or few, Andean cat records, and major biogeographical barriers. The same climatic barriers are well-recognized boundaries for other plants and animals in South America (Chesser, 2000; Weigend, 2002; Marin et al., 2007; Cossios et al., 2009; Rex et al., 2009), supporting our hypothesis of bioclimatic constraints on the distribution of Andean cats in present or past climatic conditions. These biogeographical barriers were: (1) marking the northern limit of the range, the *Peruvian Low* or *Huancabamba Depression*, an arid east–west valley dropping to about 500 m where the Marañón river, source of the Amazon River, originates (Weigend, 2002; Weigend et al., 2010); (2) the *Andean Knee* in Bolivia, an hyper-arid transition zone between the Wet Puna with summer precipitations and the Dry Puna of extreme aridity (Cossios et al., 2009), where suitable climates narrow at the core of the species' range – no Andean cat records exist for this region; and (3) the *South American Arid Diagonal*, another hyper-arid zone where precipitation patterns change on each side of the cordillera between Chile and Argentina (Garreaud, 2009), predicted as suboptimal for Andean cats and with a single record. The study by Cossios (2009) found out that these same biogeographic

barriers explain the observed genetic structure of Andean cat populations, with two northern haplotype groups separated at the location of the climatic transition in the Andean Knee, and the two main lineages separated at the Arid Diagonal some 200,000–300,000 years ago. It is apparent that limiting climatic conditions may have existed at least since then and that dispersal by Andean cats still is strongly constrained by post-glacial expansion (Cossios, 2009).

The bioclimatic envelope describing the Andean cat niche is amenable to interpretations of physiological limits to the species' climatic tolerance, although biotic interactions should also be considered (discussed further below). The shape of the relationship between predicted suitability and temperature is characteristic of species with a single optimum, where the species is most likely to occur, and decreasing likelihood of occurrence with distance from this optimum (Mueller-Dombois & Ellenberg, 1974). In contrast, the skewed relationships

with minimum temperature and diurnal thermal amplitude indicate that the optimum for the species is near the extreme of a gradient (Oksanen & Minchin, 2002; Austin, 2007). The narrow environmental ranges of the Andean cat climatic niche indicate a stress-tolerant species (Thuiller *et al.*, 2004). Morphological and physiological adaptations to the extreme aridity, increased wind speeds, severe cold temperatures and decreased partial pressures of oxygen, that characterize the High Andes climate, could give Andean cats an adaptive advantage over their potential competitors. Examples are the Andean cat's large auditory bullae (a distinctive taxonomic character (Garcia-Perea, 2002; also apparent in sand cats *Felis margarita;* Huang *et al.*, 2002), and short legs and long hair with dense woolly under fur (as in snow leopards *Panthera uncial*) (McCarthy & Chapron, 2003). Physiological adaptations to life at high altitudes such as high blood oxygen affinities in chinchillas *Chinchilla brevicaudata* (Ostojic *et al.*,
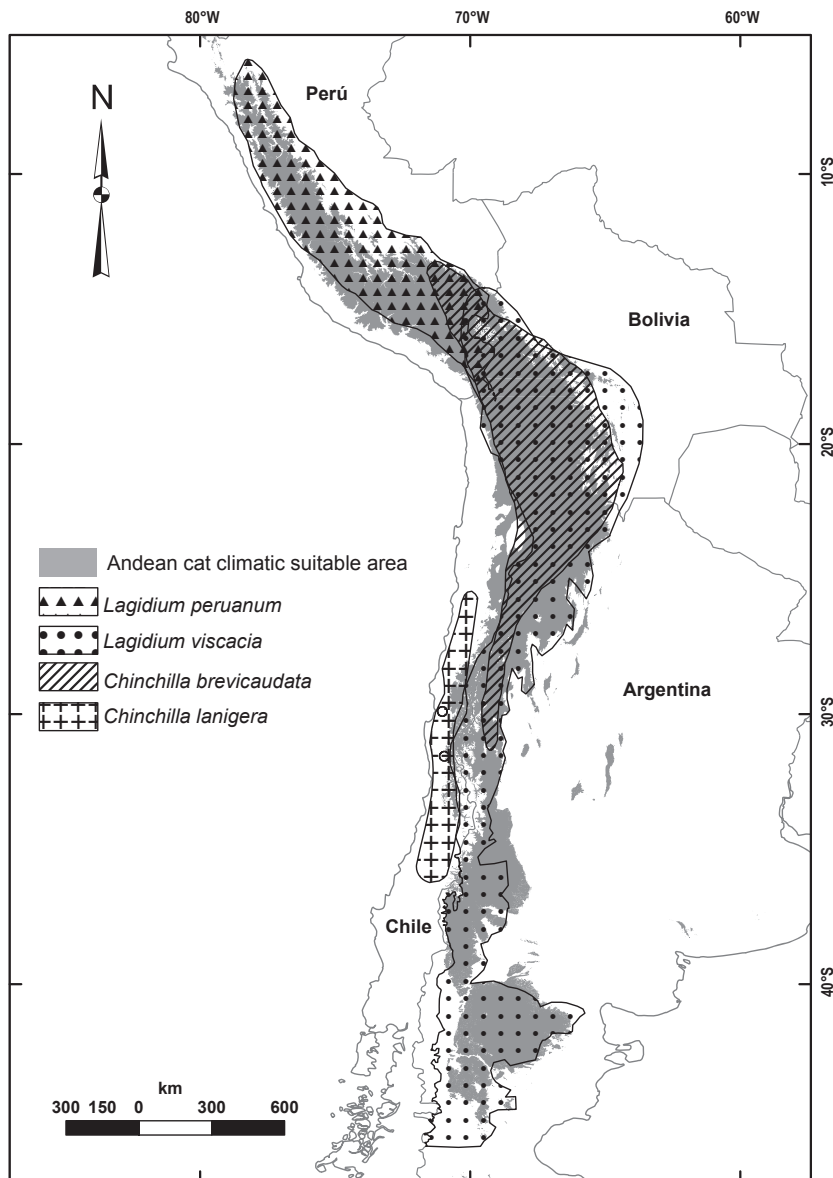
Figure 4 Map showing the overlying distributions of four Chinchillidae species (Patterson *et al.*, 2003; and updated from Parera, 2002 with unpublished data) and of suitable climates for Andean cats, as predicted by this paper's model. *Chinchilla lanigera* and *C. brevicaudata* are extinct and nearly extinct in the wild respectively (Iriarte & Jaksic, 1986 and Jiménez, 1996).

2002) and vicuñas *Vicugna vicugna* (Chiodi, 1970) have not been studied in Andean cats.

The habitat specificity of Andean cats also contrasts markedly with the generalized habits and ample distributions of sympatric carnivores in the Andes, such as, pumas (*Puma concolor*), culpeo foxes (*Pseudolopex culpaeus*) and Pampas cats (*Leopardus colocolo*) (Redford & Einsenberg, 1992; Nowell & Jackson, 1996; Rau *et al.*, 1998). Where they coexist in the High Andes, however, they share a limited pool of rodent prey (Marino *et al.*, 2010) and Andean cats depend more heavily on the mountain viscacha (Walker *et al.*, 2007; Napolitano *et al.*, 2008; Marino *et al.*, 2010). A likely explanation is that Andean cats are more efficient exploiters of the rock-specialist viscachas and chinchillas, conferring them a competitive advantage over sympatric carnivores. Notably, the areas predicted as suitable for Andean cats overlap closely with the approximate distributions of these Chinchillidae species (Fig. 4). These matching distributions, both present and historical, indicate similar climatic niches and potentially linked evolutionary histories. These Chinchillidae are large, rock-dwelling rodents, weighing 0.8–3 kg, and highly adapted to an extreme climate. The *Chinchilla* spp. have been driven to the edge of extinction owing to the demand for their thick, soft fur (Iriarte & Jaksic, 1986), and it is particularly important to explore the impacts of this extirpation of wild chinchillas *Chinchilla lanigera* and *C. brevicaudata* (Jiménez, 1996) on the current distribution of Andean cats.

Our recommendations to further improve the fit of Andean cat distribution models (Heikkinen *et al.*, 2006; Araújo & Luoto, 2007) are as follows: including landscape variables at finer spatial scales to account for more directly explanatory variables and resources (Hirzel & Le Lay, 2008) - crucially, the distribution of rocky outcrops used by the cat and its prey for refuge (Walker *et al.*, 2003) - and taking into account the spatial variations in the abundance of other carnivores. Very detailed data are also required to capture the characteristically patchy distribution of strong anthropogenic effects (Sagarin *et al.*, 2006), in our study case mining operations, hunting of prey species by people and killing of Andean cats for traditional ceremonies or by domestic dogs (Villalba *et al.*, 2004; Cossios *et al.*, 2007; Lucherini & Merino, 2008). Nevertheless, given serious concerns about species' responses to climate warming, the difficulty in detecting rare species and the speed of degradation of natural habitats, simple, large-scale bioclimatic models can be used to evaluate potential impacts of climate change on distribution, and identify populations, habitats and regions most at risk from climate change (Hannah *et al.*, 2007; Heller & Zavaleta, 2009; Mawdsley *et al.*, 2009).

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