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Original Investigation

Modelling potential impacts of climate change on the bioclimatic envelope and conservation of the Maned Wolf (*Chrysocyon brachyurus*)

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ABSTRACT

Forecasting the influence of climatic changes on the distribution of the Maned Wolf (*Chrysocyon brachyurus*) is important for the conservation of the species. We explored the environmental characteristics than best explain the current distribution of the species, modelled the past and present distribution, projected the niche model into the future, and identified suitable areas for conservation. Niche modelling was performed using Maxent and 21 environmental variables. For past conditions, we considered the Last Glacial Maximum (LGM) and the mid-Holocene (MH) climates. For future conditions, we used the A2a greenhouse gas emission scenario for 2050. Four General Circulation Models (FGOALS 1.0, HADCM3, IPSL-CM4 and MIROC 3.2) were used. The resulting niche model (AUC = 0.89 ± 0.02) predicts maximum probability of presence at precipitation of 106 mm during the coldest quarter, of 396 mm during the warmest quarter, and in totally flat areas. The suitable area for the Maned Wolf currently covers 4,320,364 km^2. For the LGM, there were inter-model differences in predicted areas (from 819,324 km^2 to 6,395,886 km^2) and in geographic location. The MH models showed drastic changes with respect to the present and considerable inter-model variation. Predictions for 2050 show significant (at least 33%) reductions in distribution. Only a minor fraction (39%) of the current distribution can be considered stable for the period LGM-2050. The FGOALS model was the best option for projecting species occurrence into the future because it included the three localities known for the Maned Wolf from the late Pleistocene and predicts stable areas that coincide with spatial patterns of genetic diversity. The FGOALS projection for 2050 predicts a 33% reduction in suitable habitats, indicating some stable areas (central South America) that will probably be key sites for the conservation of the species.

Introduction

Several studies have shown rapid changes in global climate conditions in the last decades and have predicted similar trends for the coming years (Cordellier and Pfenninger, 2009, and references therein). Changes on distribution patterns of biodiversity are expected as one of the major consequences from Climate Change, with important implications on conservation (Botkin et al., 2007; Svenning et al., 2009).

Evidence showing the influence of regional and global climate changes on many biological systems has increased notably in the last years (e.g., Walther et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003; Benito Garzón et al., 2008; Algar et al., 2009; Svenning et al., 2009; Willis et al., 2009). The possibility of substantial effects on many aspects of species distribution under projected future changes has also been mentioned (e.g., Berry et al., 2002; Bush, 2002; Midgley et al., 2002; Davies et al., 2008).

Among the several species potentially affected by climatic change, those taxa that are currently included in some risk category are in the most alarming situation. Most of these taxa share a group of characteristics, including a relatively large body size, slow reproduction rate and small number of offspring, highly specialized habitat requirements, a top position in trophic chains, and distributional ranges severely affected by human activities. The largest living South American canid, the Maned Wolf (*Chrysocyon brachyurus*, Illiger, 1815), meets most of these criteria. This enigmatic canid inhabits mainly the grassland savannas of central South America, and has been reported for eastern Paraguay,

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northeastern Argentina, northwestern Uruguay, southeastern Peru, central-eastern Bolivia and central-eastern Brazil (Dietz, 1985; Mones and Olazarri 1990; Nowak 1999; Rodden et al., 2004; Queirolo et al., 2011).

At present, there are no reliable global population estimates of the Maned Wolf; however, it is known to be absent from much of its former geographic range (Roig, 1991). The primary threat to the survival of the Maned Wolf is habitat loss (Roig, 1991; Myers et al., 2000; Rodden et al., 2004). The species is currently included in CITES Appendix II, and although it is included in the "Near Threatened" category of the IUCN red list, it is categorized as "Endangered" or "Vulnerable" at the national level in Argentina, Bolivia, Brazil and Peru, encompassing almost the entire distribution area of the species.

Recent works have focused on the past and present distribution of the Maned Wolf in Argentina (e.g., Prevosti et al., 2004; Miatello and Cobos, 2008) and its entire historical and present range (Prates, 2008; Queirolo et al., 2011). However, these contributions have not explored the environmental determinants of its distribution nor have they evaluated past models for the Last Glacial Maximum-Mid Holocene-Present day period. In addition, there are no studies on the influence of the different future climate change scenarios on the Maned Wolf distribution and the possible implications for its conservation in South America.

Here we attempt to identify the potential changes in the future distribution of the Maned Wolf to contribute to the development of management strategies for the conservation of the species. First, we studied the set of environmental characteristics than best explain the current distribution of the species, and modelled the spatial distribution of the ecological niche for the present day and the past (Last Glacial Maximum [LGM] and mid-Holocene [MH] periods), taking into account four General Circulation Models (GCMs). Second, assuming niche conservatism, we selected the best GCM based on its ability to predict the localities in the fossil record and their concordance with genetic diversity patterns for the species. Finally, we projected the niche model into the future using the best GCM, and identified suitable areas for conservation based on their stability over time, connectivity in space and projected future expansion or retraction.

Material and methods

Niche model

Niche modelling was performed using Maxent v3.0, a software package that implements a maximum entropy algorithm that generates a probability distribution over the pixels in a grid of the modelling area; for further specifications, refer to Phillips et al. (2006) and Elith et al. (2011). The MaxEnt algorithm has been shown to be robust for modelling presence-only occurrence data, even with very low numbers of occurrence records, outperforming many other techniques (Elith et al., 2006).

Environmental variables, occurrence records and model building

Models were fitted using the 19 bioclimatic variables available in the WorldClim database (Hijmans et al., 2005) and two topographic variables (elevation and slope) derived from the SRTM elevation model (Shuttle Radar Topographic Mission; http://srtm.usgs.gov/_/). The two sets of variables were obtained at a resolution of 30 arc-seconds and cover the entire South American continent. All variables were interpolated to a resolution of 5 arc-minutes, which seems reasonable for modelling at continental scale, since variation on bioclimatic variables is best represented at coarse resolutions.

Occurrence records of the Maned Wolf were obtained from museum collections, localities cited in the bibliography, and personal observations. Records before 1950 were not used in model fit since the current climate layers cover from 1950 to 2000 (Hijmans et al., 2005). All the current and fossil localities used in the study and their coordinates are available as Supplementary Material.

Occurrence records were found to be unevenly distributed in space, but showing a clustered pattern. Because this pattern may influence the prediction of the model, first occurrence records that were geographically too close together were removed at random, trying not to leave records in adjacent cells; as a result, not all occurrence records collected were used in model calibration. Second, with this reduced set of occurrence points, a "bias file" was created as the inverse of the Euclidian distance to all points; the Maxent interface allows the inclusion of that bias file in model fitting.

We obtained an initial set of 10 models for the species, setting Maxent to select at random 75% of the occurrence localities at each run for training, and leaving the remaining 25% for testing. This initial set was used to identify variables with minimal or no contribution to overall model. Maxent jackknife test of variable importance was used to evaluate the relative strength of each predictor variable (Yost et al., 2008). The training gain is calculated for each variable alone and the drop in training gain is calculated when the variable is omitted from the full model. Therefore, those variables that did not produce a decrease greater than 0.01 in the average training gain when they were omitted were removed. Co-variation between the remaining variables was tested by the Spearman r coefficient, considering only the cells with presence data. For the purposes of this work, only those pairs of variables with an r_s value >0.80 were considered as significantly correlated. The average training gain values of correlated variables was examined once again and the variables showing the lowest decrease in gain values when omitted from the full model were removed.

We performed 100 replicates with this reduced set of variables, again selecting at random 75% of occurrences for training and 25% for testing at each run. The values of the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) plot (Fielding and Bell, 1997; Manel et al., 2001; McPherson et al., 2004) for test points were examined, and the 10 models with the greatest AUC values were selected and averaged to obtain the final model.

Finally, to generate a binary prediction of occurrence, it was necessary to choose a threshold. Selecting a right threshold in predictive niche modelling is a difficult task, and currently there are no procedures that have no degree of arbitrariness, although some methods have been proposed as the best options (Liu et al., 2005). In the present work, we selected one of the thresholds provided by the output of Maxent, specifically one that maximizes sensitivity and specificity of the test points, since the methods recommended by Liu et al. (2005) offered an over-predicted picture of the distribution of the species analysed.

Past and future projections

Only the variables selected in the final model were used for projecting the potential distribution of the Maned Wolf into past and future climate conditions. For past conditions, we accessed the Paleoclimate Modelling Intercomparison Project Phase II database (Braconnot et al., 2007) considering the LGM (21,000 years ago) and the MH (6000 years ago) climates. Mean monthly values were obtained from the 100-year simulations in each past GCM, allowing the construction of the bioclimatic variables needed. Future climate variables were obtained from the WorldClim – IPCC 4 (CIAT) database. All the four GCMs currently available for all times periods considered: FGOALS 1.0, HADCM3, IPSL-CM4 and MIROC 3.2, were applied in this study. For future conditions, only

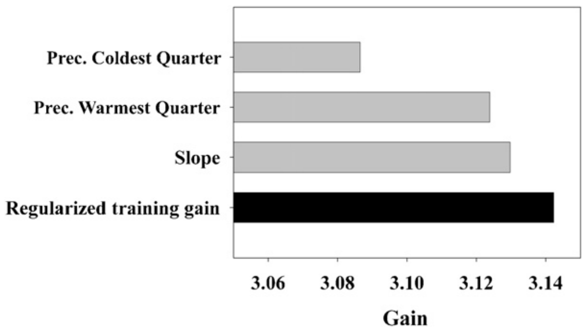

Fig. 1. Most explanatory variables for model fit, according to the jackknife test of MAXENT. Bars express the reduction in the training gain of the general model when each variable is omitted.

the A2a greenhouse gas emission scenario for 2050 was used, since it is the only scenario currently available for all cited GCMs.

For validation of past projections of niche models, an ideal approach is to make "backward-forward" projections (as in Martínez-Meyer et al., 2004 and Martínez-Meyer and Peterson, 2006), first using the current presence localities for projecting into the past, and then using the localities in the fossil record for projecting to the present time. Unfortunately, fossil remains of Maned Wolves are very scarce, with only three localities for the late Pleistocene and two for the late Holocene. Therefore, in this work we performed visual assessments of the predictive power of these models, complementing with the calculation of an AUC value for each model (Pontius and Schneider, 2001) using the ROC module of IDRISI ANDES (Eastman, 2006).

Spatial analysis

For the spatial analysis we used ARCINFO 10 (ESRI) and the extension Spatial Analysis (ESRI). The area for all past, present, and future grids was determined by projecting each grid to the corresponding UTM zones of South America. The area of the current and future distributions of the Maned Wolf included in the systems of protected areas (as delimited by World Conservation Monitoring Centre) of South America was calculated intersecting the layers with the raster calculator. For all past and future predictions, we differentiated between stable, retracted and expanded areas with respect to present-day prediction.

Results

Environmental characteristics

Only three (precipitation of the coldest quarter, precipitation of the warmest quarter, and slope) of the 21 environmental variables considered for model building had a decrease greater than 0.01 in the average training gain and were, therefore, considered relevant to model construction (Fig. 1). Considering the marginal response of each variable, the final model predicts a maximum probability of presence at precipitations of 106 mm during the coldest quarter and of 396 mm during the warmest quarter, and in completely flat areas. According to the selected threshold, the model predicts absence of the species at precipitations below 31 mm and over 237 mm in the coldest quarter and below 316 mm and over 1537 mm in the warmest quarter, and in areas with slopes greater than 1.68% (Fig. 2).

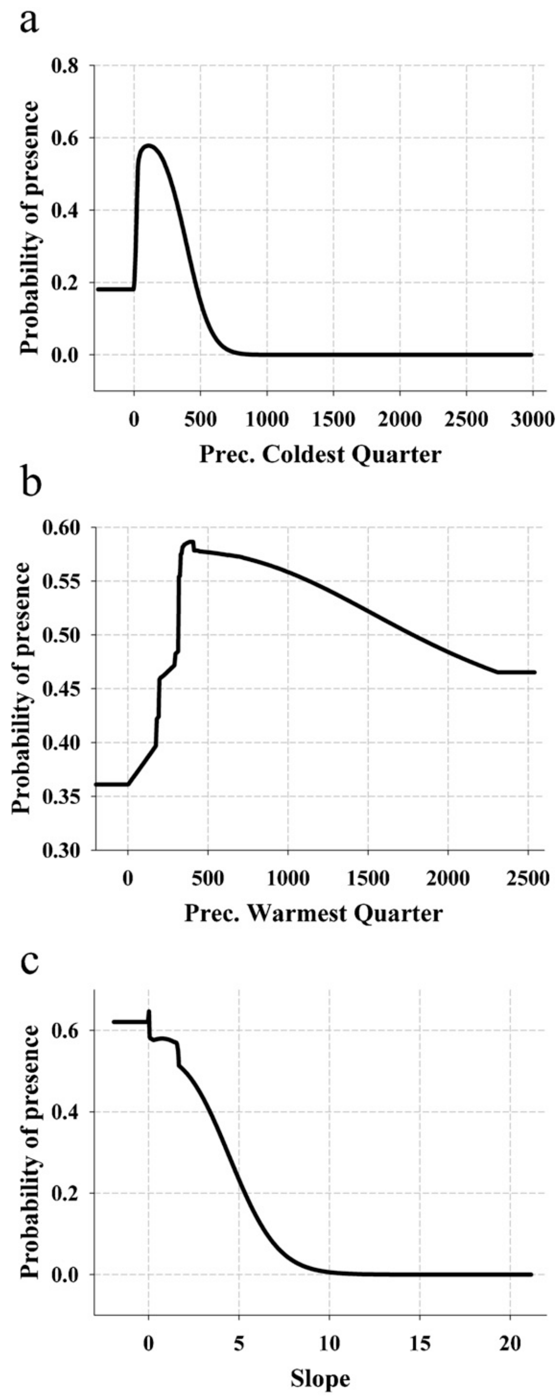

Fig. 2. Response curves of the probability of presence to relevant environmental variables. Precipitation of the Coldest Quarter and of the Warmest Quarter is expressed in mm and Slope in percentage.

Present distribution

The model obtained for the present distribution (Fig. 3) performed well, with an average AUC value of 0.89 (±0.02). According to this model, the suitable area for the Maned Wolf currently covers 4,320,364 km^2. The central region of South America, which mostly coincides with the Chacoan (Cerrado, Chaco and Pampa) Subregion and some areas of the Amazonian (Pantanal) Subregion (sensu Morrone, 2006), contains the largest and most continuous area for the species, mainly in east-central Brazil, east and north of Bolivia, northeastern Argentina and central Paraguay, reaching western

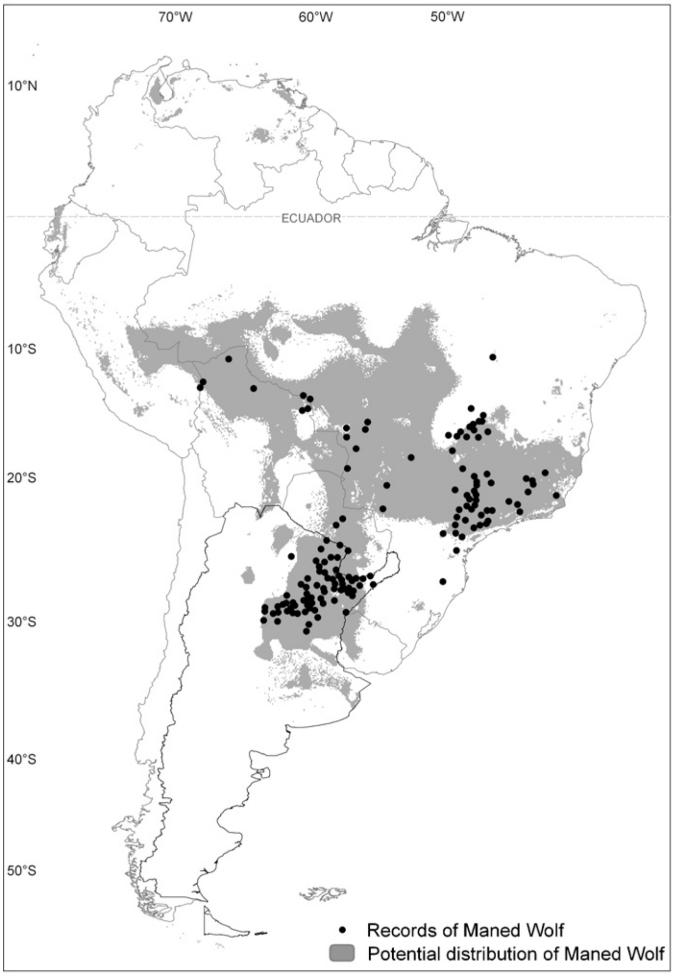

Fig. 3. Current potential distribution model for the Maned Wolf (*Chrysocyon brachyurus*, Illiger, 1815) in South America (geographic projection: South America Albers Equal Area Conic).

Uruguay and east-central Peru. Several isolated patches of varying but relatively small size occur in Venezuela, Colombia, Guyana, eastern Ecuador, central-western Peru, Brazil, Paraguay, Uruguay, and northwestern and central-eastern Argentina (including an isolated patch in Tucumán province and several small areas in Buenos Aires province) (Fig. 3).

Past projections

For the LGM, according to the selected threshold, the predicted areas were very different among GCMs, varying in size from the small 819,324 km^2 area predicted by the HACDM3 model to the large 6,395,886 km^2 area of the FGOALS model (Table 1). Projections also showed important inter-model differences in geographic location, the MIROC model projection being the most similar to the current distribution (Table 2 and Fig. 4). FGOALS projection showed a vast continuous habitable area covering most of Brazil and Paraguay, central Peru, lowlands of Bolivia, northern Argentina and Chile, and part of the Altiplano plains in the latter three countries. IPSL-CM4 model offered a very distinct projection, with a main continuous area in western Brazil, eastern Bolivia, Peru and Colombia, and southern Venezuela; minor patches in Brazil, Bolivia and northeastern South America; and isolated groups of patches in southwestern Patagonia, in Chile and Argentina. HADCM3 showed a very fragmented scenario, with the main continuous patches in northern Argentina, northeastern Brazil, and in Colombia and Venezuela (Fig. 4).

The projection of the FGOALS model included the three known localities for the Maned Wolf from the late Pleistocene, and the continuous distribution of presence probabilities yielded an AUC value of 0.92. MIROC projection included two of the three late Pleistocene presence points (AUC = 0.68), whereas HADCM3 and IPSL-CM4 projections failed to predict all these localities at the threshold selected.

The MH models showed drastic changes of the potential distribution of the Maned Wolf in comparison with the present situation (Tables 1 and 2 and Fig. 4). Predictions of the HADCM3, IPSL-CM4 and MIROC models showed a similar area that is smaller than the current distribution, whereas the FGOALS model showed a predicted area that is more than four times greater than the area predicted by the remaining MH models (Table 1). Considerable inter-model variation was observed in the geographic location of the main predicted habitable areas. FGOALS model predicted a vast continuous area, mainly in northeastern, central and southeastern Brazil, almost all Paraguay, Bolivia, and northern Argentina (south to Mendoza), and small areas in northern Chile, northwesternmost Uruguay and east-central Peru. Small patches were predicted for the Pampas and northwestern Patagonia in Argentina, central Peru and Venezuela. The IPSL-CM4 model prediction resembles an impoverished version of the prediction obtained for the LGM, with a large decrease in the extension of the continuous areas. The HADCM3 and MIROC models showed a very fragmented distribution of habitable areas, with main patches in Argentina, Brazil, Bolivia, Venezuela and Colombia.

All MH models failed to predict the two known localities for the late Holocene, although the models FGOALS, HADCM3 and MIROC predicted areas very close to one of the sites (La Bellaca, in the north of Buenos Aires province, Argentina).

Future projections

Predictions for 2050 showed a distribution of suitable habitat similar to the current situation, albeit with a smaller surface area in all cases (Table 2 and Fig. 4). In general, models show relatively large stable areas (more than 57% in all cases) but also significant reductions in the distribution (at least 33% in all the models). Stable areas were mostly located in central-South America, with retractions concentrated in the north of the distribution area, except IPSL-CM4 model, which showed an austral retraction (Fig. 4).

Stability of the species distribution range

Only a minor fraction of the projection representing the current distribution of the Maned Wolf can be considered a stable area for the LGM-2050 period (as projected by models). At best, according to the FGOALS model, only 39% of the current suitable area can be considered stable over time (Table 1 and Fig. 5). FGOALS model predicted the greatest surface area of continuous stable areas, mainly in Argentina, Bolivia and Brazil, whereas the HADMC3 model predicts stable continuous suitable habitats only in Argentina. Stable areas predicted by IPSL-CM4 and MIROC models look very fragmented (especially MIROC), with some continuous areas in Bolivia, Brazil and Peru in the former model, and in northwestern Argentina and southern Paraguay, in the latter.

Discussion

Based on overwhelming evidence of the influence of climate change on biological systems, several authors indicated the need for an integrated approach to conservation strategies, involving

Table 1
Predicted distribution area (km^2) for the Maned Wolf (*Chrysocyon brachyurus*, Illiger, 1815) in the LGM (21,000 cal. BP), the MH (6000 cal. BP), and 2050, and percentage relative to the present-day distribution area.

GCM model	Last Glacial Maximum (21,000 y)		Middle Holocene (6000 y)		2050s		Stable areas	
	Area	Percentage	Area	Percentage	Area	Percentage	Area	Percentage
FGOALS	6,395,886	148.0	6,248,269	144.6	3,112,587	72.0	1,696,463	39.3
HADCM3	819,324	19.0	1,228,059	28.4	3,073,447	71.1	277,037	6.4
IPSL-CM4	4,231,383	97.9	1,333,280	30.9	3,554,291	82.3	401,923	9.3
MIROC	3,116,670	72.1	1,213,422	28.1	3,152,573	73.0	261,447	6.0

the contributions of biogeography, ecology and applied conservation (Hannah et al., 2002a,b; Brooke, 2008; Pacheco et al., 2010; Hole et al., 2011). Here we modelled the bioclimatic envelope of the Maned Wolf for the past, the present and the next 40 years, and evaluated its potentially most suitable conservation areas, using an integrated approach.

Predicting the future distributions of species under climate change is difficult because there is no information about future ranges to evaluate model accuracy (Araújo and Rahbek, 2006; Lewis, 2006; Davies et al., 2008) and because species range adjustments are likely to be idiosyncratic (Taberlet and Cheddadi, 2002; Hampe, 2004; Thuiller et al., 2005; Heikkinen et al., 2006). Because past climate changes have left long-lasting legacies in the geographic diversity patterns (e.g., Stropp et al., 2009; Svenning et al., 2009; Willis et al., 2009), sound knowledge of the present and past distribution can be crucial to infer future tendencies (e.g., Webb, 1992 and references therein; Alsos et al., 2009; Davies et al., 2009). These investigations suggest that exploring species responses to past climate change provides the basis for projecting forward and estimating the likely effect of current climate trends on species distributions. Evaluating the effect of Quaternary climate oscillations on contemporary geographic distributions can also be helpful to understand the determinants of geographic range size. This evaluation will be of great value for effective conservation management because of the close correlation between the size of a species geographic range and the species risk of extinction (Purvis et al., 2000; Cardillo et al., 2005, 2008).

We conducted a large-scale analysis to model the Maned Wolf distribution (in temporal and geographic terms). The distribution hypotheses obtained should be further evaluated considering other sources of evidence (such as molecular and paleontological studies). We also expect that the models obtained can provide baseline information to elaborate conservation strategies.

We note that the best climatic variables for model building were not the same as those mentioned by Prevosti et al. (2004), who propose the mean annual temperature and not the precipitations as limiting factors for the distribution of the Maned Wolf in Argentina. The mean annual temperature in our analysis practically have no contribution to the average training gain; in contrast, two of the three environmental variables considered as relevant to model construction (precipitation of the coldest quarter and precipitation of the warmest quarter) are related with some of the habitat requirements frequently mentioned for this species in the literature, as its preference by treeless biomes, and seasonally flooded areas (e.g., Rumiz and Sainz, 2002; de Almeida Jácomo et al., 2004; Prevosti et al., 2004; Coelho et al., 2008; Queirolo et al., 2011). Ranges of optimal values of such variables, following our model, are characteristics of areas with seasonal rainfall (concentrated in the warmest season) satisfying the conditions for the development of humid grasslands, but not for xeric or humid forested biomes (Whittaker, 1975). The final model also predicts a maximum probability of presence in areas totally flat, which constitute a requirement previously not mentioned in the literature, but a necessary condition for the existence of flooded areas.

In general, the bioclimatic envelope obtained for the current distribution has a good fit to the occurrence localities, with an AUC value considered adequate in studies focused on management and conservation (Pearce and Ferrier, 2000). The FGOALS model also largely coincides with the current distribution of the species, as defined by Queirolo et al. (2011). However, some level of overprediction and underprediction should be considered. Overpredictions occur in Venezuela, Ecuador, east-central Peru, central-northern Brazil, northern Bolivia, northwestern Argentina, and the Pampas region of Argentina and Uruguay, where the species is currently absent (Queirolo et al., 2011). Overpredicted areas in central Brazil, northern Bolivia and central Peru correspond to areas of forest vegetation, where the Maned Wolf is unlikely to occur, despite the favourable climatic conditions. In Argentina, the FGOALS model supports historical records of the Maned Wolf for the Pampas region, but contradicts historical records for northern Patagonia and the western region (see Prevosti et al., 2004). The predicted area in the Pampas region covers Entre Ríos, southern Córdoba and Santa Fe, and northern Buenos Aires provinces in Argentina, and eastern Uruguay in Artigas, Salto, Paysandú, Río Negro, Soriano, Colonia, and Flores departments. There are historical records for southern Córdoba and northern Buenos Aires in Argentina, and for Uruguay (Prevosti et al., 2004; Chébez, 2008; Queirolo et al., 2011). The recent records of individuals in Río Negro department in Uruguay

Table 2
Stable, expanded and retracted (from LGM or MH to the present, or from the present to 2050) suitable areas for the Maned Wolf (*Chrysocyon brachyurus*, Illiger, 1815).

	Stable		Expanded		Retracted	
	km^2	%	km^2	%	km^2	%
FGOALS LGM	2,529,641	58.6	1,790,723	41.4	3,866,245	89.5
FGOALS MH	2,258,571	52.3	2,061,793	47.7	3,989,698	92.3
FGOALS 2050s	2,887,190	66.8	225,397	5.2	1,433,174	33.2
HADCM3 LGM	327,275	7.6	3,993,089	92.4	492,049	11.4
HADCM3 MH	429,202	9.9	3,891,162	90.1	798,857	18.5
HADCM3 2050s	2,514,843	58.2	558,604	12.4	1,805,521	41.8
IPSL-CM4 LGM	1,344,798	31.1	2,975,566	68.9	2,886,585	66.8
IPSL-CM4 MH	566,573	13.1	3,753,791	86.9	766,707	17.7
IPSL-CM4 2050s	2,858,303	66.1	695,988	16.1	1,462,061	33.8
MIROC LGM	2,646,645	61.3	1,673,719	38.7	470,025	10.9
MIROC MH	425,945	9.9	3,894,419	90.1	787,477	18.2
MIROC 2050s	2,501,586	57.9	650,987	15.1	1,818,778	42.1

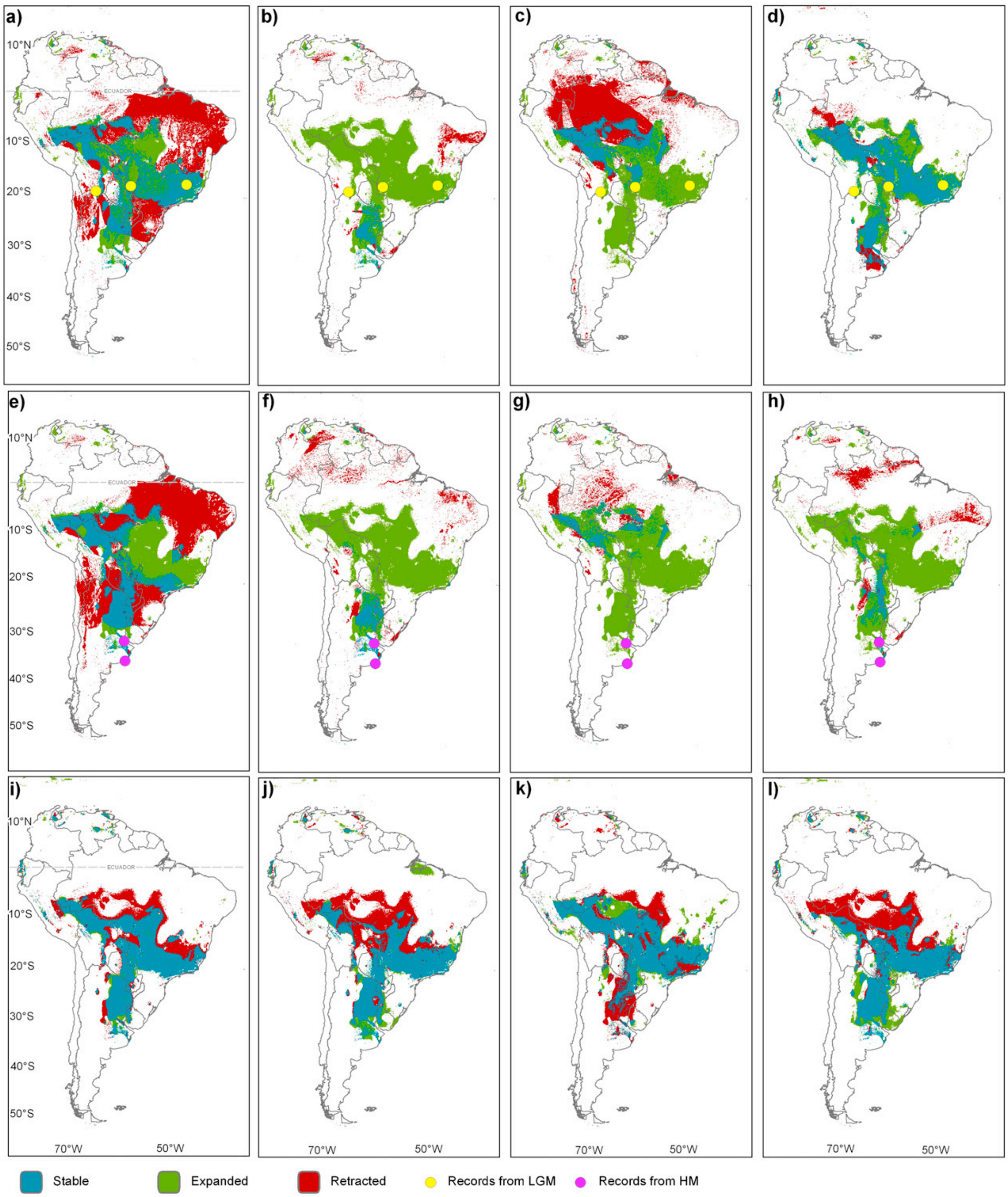

Fig. 4. Potential distribution maps for the Maned Wolf (*Chrysocyon brachyurus*, Illiger, 1815) under all the GCMs from LGM to the year 2050. (a) LGM (FGOALS); (b) LGM (HADCM3); (c) LGM (IPSL-CM4); (d) LGM (MIROC); (e) MH (FGOALS); (f) MH (HADCM3); (g) MH (IPSL-CM4); (h) MH (MIROC); (i) 2050 (FGOALS); (j) 2050 (HADCM3); (k) 2050 (IPSL-CM4); (l) 2050 (MIROC). Past projections are represented by stable (blue) plus retracted (red) areas from the past to the present condition, whereas future projections include stable (blue) plus expanded (green) areas from the present to the 2050. Fossil records from the Late Pleistocene (yellow dots) and the Late Holocene (violet dot) are also shown (geographic projection: South America Albers Equal Area Conic). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

(Chébez, 2008) indicate that the predicted areas in the Pampas region are optimal areas currently uninhabited by the Maned Wolf, which is reasonable considering that the region is the most agriculturally productive and densely populated area in Argentina and Uruguay. The model also predicts a small patch in Tucumán province, western Argentina, where there is a record from the early 20th century (Chébez, 2008), but that was not included as sample in the model formulation. Some underpredicted areas in northeastern and southeastern Brazil are shown in our model, compared with the distribution map in Queirolo et al. (2011). The observed differences may be because in the present work we excluded data gathered in interviews to local people as presence records for

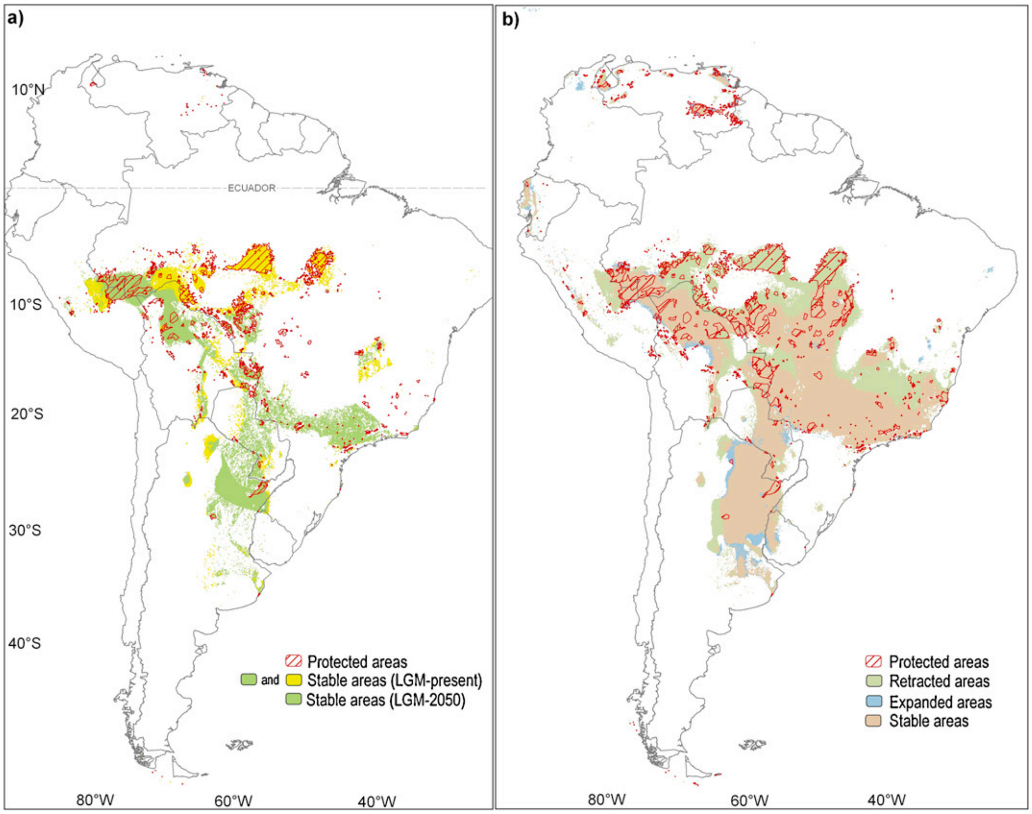

Fig. 5. Maps of the potentially stable distribution areas for the Maned Wolf (*Chrysocyon brachyurus*, Illiger, 1815). Only FGOALS scenarios are shown. (a) Stable areas from the LGM to the present, and from the LGM to 2050; (b) stable, retracted and expanded areas with respect to the present distribution (geographic projection: South America Albers Equal Area Conic).

fitting niche models, whereas Queirolo et al. (2011) included those records for drawing their distribution map. Although some areas in northwestern South America (e.g., Ecuador, Colombia, Venezuela) appear as suitable for the Maned Wolf according to our model, they are very isolated from core distributional areas (and would have never been connected in the past, with the only exception of the IPSL-CM4 model), and have no present or fossil records, suggesting that suitable habitats in these countries were never colonized. The lack of records in the Amazonian rainforest added to the fact that the Maned Wolf can be found only marginally in forested areas (e.g., Rumiz and Sainz, 2002; de Almeida Jácomo et al., 2004; Coelho et al., 2008) suggests that this biome constitute a geographic barrier to wolf dispersion.

Only FGOALS model correctly predicted the three presence localities of late Pleistocene known for the Maned Wolf, and exhibited the highest AUC value. Nevertheless, the MIROC LGM model, which predicted two of the Pleistocene points, was the most similar to current distribution. In the MH, all models failed to predict the two late Holocene presence localities, which may be due to climatic changes between the MH and the late Holocene. However, both the FGOALS and MIROC models showed suitable areas very close to the northern locality (La Bellaca; Fig. 4). Comparing the predictions for the LGM, the MH and the present day, the MIROC model showed drastic changes during MH, whereas the FGOALS model exhibited a much more gradual transition from the LGM to present-day conditions. The FGOALS models were the only ones that predicted areas in western Argentina (particularly in the MH), where there are reliable historical records (Prevosti et al., 2004), suggesting that these records correspond to relicts of a greater past distribution. A question remains about ability of wolves to colonize the plains of the Altiplano, as the FGOALS models suggest. The fact that elevation was not a relevant variable in the model fit and the existence of a fossil record in Tarija (almost 2000 m a.s.l.) suggests that the Maned Wolf may have reached the Altiplano through Tarija under favourable climatic conditions. We therefore consider the FGOALS model as the best option of the four GCMs employed in this work for projecting the bioclimatic envelope of the Maned Wolf into the future.

Results from doctoral thesis work (Prates, 2008) provided a niche model for the Maned Wolf covering the period from Last Interglacial (LIG) to the present. In that work, genetic diversity was also studied with the aim of delineating the evolutionary history of the species. The present distribution obtained in that study was somewhat smaller than that provided by our model, and underestimated relatively large areas of eastern Bolivia and northeastern Argentina, mostly because a large number of presence localities in these areas were omitted in model calibration. Prates (2008) recorded an extremely low genetic variability for the Maned Wolf and signals of a bottleneck before the LGM followed by a strong population expansion, which was in agreement with his niche models for the LIG and LGM. Genetic data also suggests a reduction and a displacement of the Maned Wolf distribution to southern South America during MH times. Our FGOALS models for the LGM and MH are in agreement with studies of Prates (2008), with a large LGM distribution and a minor and southwardly displaced area in MH times (which probably did not have any significant effect on Maned Wolf population size or any severe consequences on its genetic diversity, as argued in Prates, 2008). Furthermore, our model predicts stable areas from the LGM to the present, which coincide with spatial patterns of maximum genetic diversity for the Maned Wolf, as those recorded by Prates (2008) for Goiás and Distrito Federal states, in Brazil, and Corrientes province, in northeastern Argentina (Fig. 5).

Projecting niche models into the future is not only impossible to evaluate (since the predicted phenomenon has not yet occurred;

Table 3
Area (km^2) of the current and future predictions of the distribution of the Maned Wolf (according to the FGOALS model) covered by the system of protected areas of South America (as delimited by the World Conservation Monitoring Centre), and percentage of the predicted current and future areas.

Projection	Protected areas	
	Area (km^2)	Percentage
Present	694,575	16.1
Future	422,046	9.8
Future expansion	40,340	0.9
Future retraction	312,869	7.3
Current stable area	361,723	8.4
Future stable area	213,071	4.9

Araújo and Guisan, 2006), but also uncertain due to the use of different climatic GCMs (Buisson et al., 2010). This is a major issue because in the case of threatened species, the most accurate possible results are needed for their use in the design of mitigation measures. We attempted to avoid this problem by modelling past, present and future distributions with four GCMs, and selecting the best option. According to the FGOALS, our best model option, projections for 2050 offer a worrying picture, with a predicted reduction in suitable habitats for the Maned Wolf of approximately 33% in only 40 years. Noticeably, the other GCM models provide equally uncertain pictures. Predictions obtained with the HADCM3 and MIROC models are very similar in both area and geographic location, whereas the IPSL-CM4 is somewhat displaced toward the north but similar in total area (Tables 2 and 3).

The FGOALS model indicates some stable areas for the Maned Wolf distribution from LGM to 2050, which will probably be key areas for the conservation of the species. These areas, mainly distributed in Argentina, Bolivia, Brazil, and Paraguay, have been inhabited by Maned Wolf populations at least since the LGM and, therefore, they probably harbour the most genetically diverse populations of the species in the continent. Because of their size and continuity in space, we see the areas in north-central Bolivia, northeastern Argentina, and south-central Brazil as the most appropriate regions for the creation of protected area systems for the species. Lowland areas of central Bolivia and central Paraguay are also important in conservation terms. Central Bolivia could have been a north–south connectivity area for populations in the past, mainly in MH times, when the species distribution was possibly most fragmented. Paraguay offers this connectivity at present and in the near future (Fig. 5). Our projection, however, indicates that only a minor fraction of the future distribution will be protected by 2050, with most of the current system of protected areas relegated to retraction areas (Table 3 and Fig. 5). Protected stable areas from the LGM to the present and to the future only contain or will cover less than 9% and 5% of the Maned Wolf distribution, respectively.

Although our analysis suggests that climatic change expected for the next 40 years will be an important factor to be considered in conservation strategies of the Maned Wolf, other aspects should be taken into account. Habitat transformation and the isolation that this situation can produce over the present populations of the species are obviously among the most important factors to be considered. Accordingly, there is a great need for studies on land-use changes in the stable area determined for the Maned Wolf in this study. These areas, besides having been the most stable and continuous over the last 20,000 years, can also act as connection between suitable areas with potentially habitable environments in the future.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2012.04.008.

References

Algar, A.C., Kharouba, H.M., Young, E.R., Kerr, J.T., 2009. Predicting the future of species diversity: macroecological theory, climate change, and direct tests of alternative forecasting methods. Ecography 32, 22–33.

Alsos, I.G., Alm, T., Normand, S., Brochmann, C., 2009. Past and future range shifts and loss of diversity in dwarf willow (*Salix herbacea* L.) inferred from genetics, fossils and modeling. Global Ecol. Biogeogr. 18, 223–239.

Araújo, M.B., Guisan, A., 2006. Five (or so) challenges for species distribution modelling. J. Biogeogr. 33, 1677–1688.

Araújo, M.B., Rahbek, C., 2006. How does climate change affect biodiversity? Science 313, 1396–1397.

Benito Garzón, M., Sánchez de Dios, R., Sainz Ollero, H., 2008. The evolution of the *Pinus sylvestris* L. area in the Iberian Peninsula from the Last Glacial Maximum to 2100 under climate change. The Holocene 18, 705–714.

Berry, P.M., Dawson, T.P., Harrison, P.A., Pearson, R.G., 2002. Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. Global Ecol. Biogeogr. 11, 453–462.

Botkin, D.B., Saxe, H., Araújo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., et al., 2007. Forecasting the effects of global warming on biodiversity. Bioscience 57, 227–236.

Braconnot, P., Otto-Bliesner, B., Harrison, S., Joussaume, S., Peterschmitt, J.Y., Abe-Ouchi, A., et al., 2007. Results of PMIP2 coupled simulations of the Mid-Holocene and Last Glacial Maximum. Part 1: Experiments and large-scale features. Climate Past 3, 261–277.

Brooke, C., 2008. Conservation and adaptation to climate change. Conserv. Biol. 22, 1471–1476.

Buisson, L., Thuiller, W., Casajus, N., Lek, S., Grenouillet, G., 2010. Uncertainty in ensemble forecasting of species distribution. Global Change Biol. 16, 1145–1157.

Bush, M.B., 2002. Distributional change and conservation on the Andean flank: a palaeoecological perspective. Global Ecol. Biogeogr. 11, 463–473.

Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda- Emonds, O.R.P., Sechrest, W., et al., 2005. Multiple causes of high extinction risk in large mammal species. Science 309, 1239–1241.

Cardillo, M., Mace, G.M., Gittleman, J.L., Jones, K.E., Bielby, J., Purvis, A., 2008. The predictability of extinction: biological and external correlates of decline in mammals. Proc. R. Soc. B 275, 1441–1448.

Coelho, C.M., Bandeira De Melo, L.F., Líma Sábato, M.A., Vaz Magni, E.M., Hirsch, A., Young, R.J., 2008. Habitat use by wild maned wolves (*Chrysocyon brachyurus*) in a transition zone environment. J. Mammal. 89, 97–104.

Cordellier, M., Pfenninger, M., 2009. Inferring the past to predict the future: climate modeling predictions and phylogeography for the freshwater gastropod *Radix balthica* (Pulmonata, Basommatophora). Mol. Ecol. 18, 534–544.

Chébez, J.C., 2008. Los que se van. Fauna argentina amenazada. In: Tomo 3: Mamíferos. Albatros, Buenos Aires, Argentina.

Davies, T.J., Fritz, S.A., Grenyer, R., Orme, C.D.L., Bielby, J., Bininda-Emonds, O.R.P., et al., 2008. Phylogenetic trees and the future of mammalian biodiversity. Proc. Natl. Acad. Sci. U.S.A. 105, 11556–11563.

Davies, T.J., Purvis, A., Gittleman, J.L., 2009. Quaternary climate change and the geographic ranges of mammals. Am. Nat. 174, 297–307.

de Almeida Jácomo, A.T., Silveira, L., Felizola Diniz-Filho, J.A., 2004. Niche separation between the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Dusicyon thous*) and the hoary fox (*Dusicyon vetulus*) in central Brazil. J. Zool. Lond. 262, 99–106.

Dietz, J.M., 1985. *Chrysocyon brachyurus*. Mammalian Species 234, 1–4.

Eastman, J.R., 2006. IDRISI Andes Tutorial. Clark Labs, Clark University, Worcester, MA.

Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., et al., 2006. Novel methods improve prediction of species' distribution from occurrence data. Ecography 19, 129–151.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. Diversity Distrib. 17, 43–57.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49.
Hampe, A., 2004. Bioclimate envelope models: what they detect and what they hide. Global Ecol. Biogeogr. 13, 469–476.
Hannah, L., Midgley, G.F., Millar, D., 2002a. Climate change-integrated conservation strategies. Global Ecol. Biogeogr. 11, 485–495.
Hannah, L., Midgley, G.F., Lovejoy, T., Bond, W.J., Bush, M., Lovett, J.C., et al., 2002b. Conservation of biodiversity in a changing climate. Conserv. Biol. 16, 264–268.
Heikkinen, R.K., Luoto, M., Araújo, M.B., Virkkala, R., Thuiller, W., Sykes, M.T., 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Prog. Phys. Geogr. 30, 751–777.
Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Clim. 25, 1965–1978.
Hole, D.G., Huntley, B., Arinaitwe, J., Butchart, S.H.M., Collingham, Y.C., Fishpool, L.D.C., et al., 2011. Toward a management framework for networks of protected areas in the face of climate change. Conserv. Biol. 25, 305–315.
Lewis, O.T., 2006. Climate change, species-area curves and the extinction crisis. Philos. Trans. R. Soc. B: Biol. 361, 163–171.
Liu, C., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28, 385–393.
Manel, S., Williams, H.C., Ormerod, S.J., 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. J. Appl. Ecol. 38, 921–931.
Martínez-Meyer, E., Peterson, A.T., Hargrove, W.W., 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecol. Biogeogr. 13, 305–314.
Martínez-Meyer, E., Peterson, A.T., 2006. Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition. J. Biogeogr. 33, 1779–1789.
McPherson, J.M., Jetz, W., Rogers, D.J., 2004. The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? J. Appl. Ecol. 41, 811–823.
Miatello, R., Cobos, V., 2008. Nuevos aportes sobre la distribución del Aguará Guazú (*Chrysocyon brachyurus*, Carnivora: Canidae) en las provincias de Córdoba y Santiago del Estero, Argentina. Mastozool. Neotrop. 15, 209–213.
Midgley, G.F., Hannah, L., Millar, D., Rutherford, M.C., Powrie, L.W., 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. Global Ecol. Biogeogr. 11, 445–451.
Mones, A., Olazarri, J., 1990. Confirmación de la existencia de *Chrysocyon brachyurus* (Illiger) en el Uruguay (Mammalia: Carnivora: Canidae). Com. Zool. Mus. Hist. Nat. Montevideo 174, 1–6.
Morrone, J.J., 2006. Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. Annu. Rev. Entomol. 51, 467–494.
Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.
Nowak, R.M., 1999. Walkerĭs Mammals of the World. v.2, 6th ed. The John Hopkins University Press, Baltimore and London.
Pacheco, S., Malizia, L., Cayuela, L., 2010. Effects of climate change on subtropical forests of South America. Trop. Conserv. Sci. 3, 423–437.
Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.
Pearce, J., Ferrier, S., 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecol. Model. 133, 225–245.
Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259.
Pontius, R.G., Schneider, L.C., 2001. Land-cover change model validation by an ROC method for the Ipswich watershed, Massachusetts, USA. Agric. Ecosys. Environ. 85, 239–248.
Prates, P.H., 2008. Diversidade genetica e historia evolutiva do Lobo-Guará (*Chrysocyon brachyurus*). Unpublished Doctoral Thesis, Porto Alegre, Brazil.
Prevosti, F.J., Bonomo, M., Tonni, E.P., 2004. La distribución de *Chrysocyon brachyurus* (Illiger, 1811) (Mammalia: Carnivora: Canidae) durante el Holoceno en la Argentina: implicancias paleoambientales. Mastozool. Neotrop. 11, 27–43.
Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000. Predicting extinction risk in declining species. Proc. R. Soc. B 267, 1947–1952.
Queirolo, D., Moreira, J.R., Soler, L.A., Emmons, L.H., Rodrigues, F.H.G., Pautasso, A.A., et al., 2011. Historical and current range of the near threatened maned wolf *Chrysocyon brachyurus* in South America. Oryx 45, 296–303.
Rodden, M., Rodrigues, F., Bestelmeyer, S., 2004. Maned wolf (*Chrysocyon brachyurus*). In: Sillero-Zubiri, C., Hoffmann, M., Macdonald, D.W. (Eds.), Canids: Foxes, Wolves, Jackals and Dogs. IUCN/SSC Canid Specialist Group, Gland, Switzerland and Cambridge, U.K., pp. 38–43.
Roig, V.G., 1991. Desertification and distribution of mammals in the Southern Cone of South America. In: Mares, M.A., Schmidly, D.J. (Eds.), Latin American Mammals: Their Conservation, Ecology, and Evolution. University of Oklahoma Press, Norman, Oklahoma, pp. 239–279.
Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. Nature 421, 57–60.
Rumiz, D., Sainz, L.A., 2002. Estimación del hábitat útil y la abundancia potencial del lobo de crin o borochi (*Chrysocyon brachyurus*) en Huanchaca, Santa Cruz – Bolivia. Rev. Bol. Ecol. 11, 3–16.
Stropp, J., Ter Steege, H., Malhi, Y., ATDN, RAINFOR, 2009. Disentangling regional and local tree diversity in the Amazon. Ecography 32, 46–54.
Svenning, J., Kerr, J., Rahbek, C., 2009. Predicting future shifts in species diversity. Ecography 32, 3–4.
Taberlet, P., Cheddadi, R., 2002. Quaternary refugia and persistence of biodiversity. Science 297, 2009–2010.
Thuiller, W., Lavorel, S., Araújo, M.B., 2005. Niche properties and geographical extent as predictors of species sensitivity to climate change. Global Ecol. Biogeogr. 14, 347–357.
Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., et al., 2002. Ecological responses to recent climate change. Nature 416, 389–395.
Webb, T., 1992. Past changes in vegetation and climate: lessons for the future. In: Peters, R.L., Lovejoy, T.E. (Eds.), Global Warming and Biological Diversity. Yale University Press, New Haven and London, pp. 59–75.
Willis, S.G., Thomas, Ch.D., Hill, J.K., Collingham, Y.C., Telfer, M.G., Fox, R., et al., 2009. Dynamic distribution modelling: predicting the present from the past. Ecography 32, 5–12.
Whittaker, R.H., 1975. Communities and Ecosystems, 2nd ed. Macmillan, New York.
Yost, A.C., Petersen, S.L., Gregg, M., Miller, R., 2008. Predictive modeling and mapping Sage Grouse (*Centrocercus urophasianus*) nesting habitat using Maximum Entropy and a long-term dataset from Southern Oregon. Ecol. Inform. 3, 375–386.