Distribution of *Lyncodon patagonicus* (Carnivora, Mustelidae): changes from the Last Glacial Maximum to the present

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The Patagonian weasel (*Lyncodon patagonicus*) is one of the least known carnivores from South America, and excluding some contributions, knowledge of it seems anecdotal. It is supposed to inhabit herbaceous and arid environments of Argentina and Chile. Here we assess the potential distribution of the Patagonian weasel both during the present and the Last Glacial Maximum (LGM). We also integrate some of this information, providing a historical and geographic analysis (both through ecological niche modeling and biogeographic schemes) of the distribution of *L. patagonicus*. We found 2 major core areas of distribution, 1 in northwestern Argentina and another in southern Argentina (i.e., Patagonia). Patagonian weasel distribution seems to be primarily related to cold areas with marked temperature seasonality and elevations below 2,000 m above sea level. From LGM to the present, we observed a major retraction in potential distribution areas that might indicate the existence of a vicariance process affecting Patagonian weasel distribution.

Key words: biogeography, distribution records, Last Glacial Maximum, MaxEnt, Mustelidae

The small-sized carnivore fauna of South America, and Argentina in particular, have been poorly studied, especially in their distributional aspects. Despite the contributions of Sielfeld and Castilla (1999) and Vianna et al. (2011) on the river otter *Lontra provocax*, the distribution of most mustelid species remains poorly known. Introduced species, such as the American mink (*Mustela vison*), despite their impact on native ecosystems, have not been properly assessed. The Patagonian weasel *Lyncodon patagonicus* (de Blainville 1842) is one of the least known carnivores from South America (Prevosti and Pardiñas 2001; Prevosti et al. 2009; Redford and Eisenberg 1992) and is supposed to inhabit herbaceous and shrub steppes in arid or semiarid woodlands in Argentina and Chile (Osgood 1943; Prevosti and Pardiñas 2001; Prevosti et al. 2009). According to Díaz and Lucherini (2006) it is a rare species occurring in several ecoregions (i.e., Dry Chaco, Espinal, Patagonian Steppe, and Monte), and its distribution in Argentina includes most provinces from Salta in the north to Santa Cruz in the south. This enigmatic small carnivore has been catalogued as "Near Threatened" in the Red Book of Argentine Mammals (Díaz and Ojeda 2000) and "Data Deficient" by the International Union for Conservation of Nature (Kelt and Pardiñas 2008).

Analyzing the distribution patterns of a given species allows us to understand its relationship with the environment, including biotic and abiotic factors (Franklin 2009). However, the area that a species occupies is not invariant throughout time, but it is highly affected by climatic and/or geomorphological processes (Ruzzante et al. 2011). In this context, the area in which *L. patagonicus* lives has been affected by several geological processes (e.g., glacial and interglacial periods) during the last 25,000 years, processes that modified both the topography and climatic conditions of vast areas of southern South America (Rabassa et al. 2011). These include the Last Glacial Maximum (LGM), which occurred between 25 and 16 thousand years ago (ka) (Rabassa et al. 2005), and which has been considered among the most important factors influencing species distribution and diversity patterns worldwide (Ruzzante et al. 2011).

The chorological history of *L. patagonicus* might have been heavily affected by these glacial cycles, and the inclusion of novel techniques like predictive distribution modeling can help us reveal some of these changes. The basic goal of these techniques is to predict geographic areas that satisfy the species' environmental requirements through an ecological niche model (Phillips et al. 2004). The models aim to predict the occurrence of suitable habitat that might be occupied by a certain species (Franklin 2009) on the basis of the species' occurrence and recorded localities.

In this study, we aim to assess the potential distribution of the Patagonian weasel *L. patagonicus* both during the present and the LGM, linking the common factors between them and evaluating the principal features that might affect its geographical distribution. We also analyzed the species' distribution in a biogeographic context, from a regional to an ecoregional scale.

Materials and Methods

The study region represents the southern portion of South America, particularly Argentina and Chile, although the potential distribution of the species was evaluated at a continental scale (i.e., South America). We visited the main mammal collections of Argentina: Fundación Félix de Azara, Ciudad Autónoma de Buenos Aires; Instituto Miguel Lillo, San Miguel de Tucumán; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciudad Autónoma de Buenos Aires; and Museo de La Plata, La Plata; to search for materials assignable to *L. patagonicus*. Specimens from Chilean collections were not analyzed and only their geographical coordinates were used. Apart from this, no other individuals from *L. patagonicus* are known to exist in Chilean collections and an internet search through MaNIS (http://manisnet.org/manis/) yielded no specimens from the country. In addition, we searched the literature to obtain presence of actual and Pleistocene/Holocene localities of the species (see Prevosti et al. 2009). Localities without associated geographical coordinates were georeferenced with Global Gazetteer (http://www.fallingrain.com) maps, and plotted into a geographic information system (GIS).

The potential distribution of *L. patagonicus* was evaluated using the software MaxEnt version 3.3.3e (Phillips et al. 2004). This software was chosen because it performs better than other alternatives with <100 records and presence-only data (Elith et al. 2006; Peterson et al. 2007), and provides response curves for each environmental variable, representing how the MaxEnt prediction is affected by each variable (Moratelli et al. 2011). Recent examples of the use of this software can be seen in Martin (2010, 2011), Torres and Jayat (2010), and Moratelli et al. (2011).

We used 2 sets of environmental variables: one for the LGM (i.e., ~20,000 years before present) on the basis of the community climate system model (Collins et al. 2004) with a spatial resolution of 2.5 arc-min or ~20 km², and the other with climatic conditions from 1950 to 2000 and 30 arc-s of spatial resolution or ~1 km2 (Hijmans et al. 2005a, www.

worldclim.org). The 1st data set contains 19 bioclimatic variables derived from the Paleoclimate Modelling Intercomparison Project Phase II (see Collins et al. 2004). The 2nd data set contains elevation data; average monthly minimum, medium, and maximum temperatures; monthly precipitation; and 19 bioclimatic variables (Hijmans et al. 2005a). We generated 4 basic models: including all Pleistocene/Holocene (fossil) records (model A); including only Holocene (fossil) localities (model B); including all recent (not fossil) localities (including "historical" records, model C); and including localities since 1950 (model D). The first 2 models (A and B) were generated with the LGM climate data, and the other two (C and D) with the actual/current environmental data set 1950–2000.

Ten replicates were performed for each model, with 25% of the localities used as training data, 1,000 iterations, random seed, and 10,000 background points. The cumulative output was selected and we assigned probability values of 51–100 (black), 26–50 (dark gray), 11–25 (gray), 2–10 (light gray), and 0–1 (white). Variable contributions were analyzed through MaxEnt's jackknife tests. We evaluated model predictions both with threshold-dependent and threshold-independent tests, using *P*-values of 1, 5, and 10; area under the curve (AUC), and the receiver operating characteristics, respectively (Phillips et al. 2004, 2006). Finally, we integrated all the data in a GIS using DIVA-GIS version 5.4 (Hijmans et al. 2005b).

A further analysis was performed to somehow validate the generated models. For this, we extracted values of bioclimatic variables from the historical localities (not fossil) using the latest climatic database (Hijmans et al. 2005a), and also extracted bioclimatic values from the LGM database using fossil localities. We then calculated the average for all points (i.e., localities) and plotted them together in Fig. 1 and Fig. 2 (see bioclimatic variable names in Appendix I). We observed the same pattern in both actual and fossil variables, indicating that the same variables affect the distribution of *L. patagonicus*, and thus, validate the models.
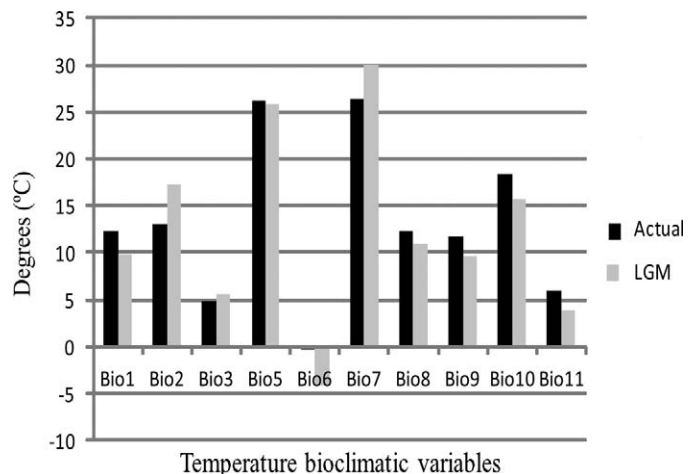

Fig. 1.—Temperature bioclimatic variables in both actual and Last Glacial Maximum models. For a better representation of scale, BIO4 has been eliminated.
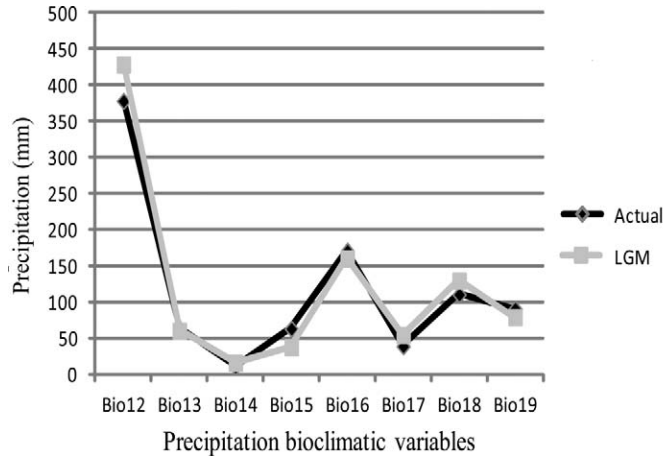
Fig. 2.—Precipitation bioclimatic variables in both actual and Last Glacial Maximum models.

Because the models containing fossil localities include a broad temporal sample (i.e., some are clearly younger, whereas others may be older than the LGM), we generated a 5th model in which the climatic parameters were changed according to climatic variation (of the modeled variables) between LGM and the present. This 5th model (E) was generated by projecting all historical records over a new actual data set that was modified according to parameters extracted from the LGM in the following way: we generated 1,000 random points with Arcview 3.3 (ESRI 2002) across South America to extract climate values from the 19 bioclimatic variables of the LGM data set; we then calculated the average of the 1,000 points for each variable and added or subtracted that value to the corresponding variable in the 1950–2000 data set. In this way, we obtained a new set of modified environmental variables that reflects changes between present day and LGM times. Last, each actual (not fossil) locality was assigned on a geographic basis to a particular ecoregion following Olson et al. (2001).

RESULTS

Localities recorded for *L. patagonicus* are presented in Table 1 and Fig. 3. Although 73 localities were listed, we were not able to assign an age (i.e., actual or fossil) to record 38 (2,000 m E of Puerto Pirámides, Table 1), therefore excluding it from ecological niche modeling (ENM) analysis. Of these, 20 correspond to specimens recovered from Pleistocene and Holocene deposits and 52 to extant records (Table 1, Fig. 3). Fossil records are scattered in an area that extends from 28°10′ to 52°05′37″S, and from 57°33′ to 70°40′W (Table 1, Fig. 3). The species' current (extant) geographic distribution extends from 25°38′ to 50°01′S, and from 62°15′ to 72°38′W. Marginal localities are Azul to the east, Alemanía to the north, and Puerto Prat to the south and west (**boldface** in Table 1). Of all the records, 94% (*n* = 70) are from Argentina and only 4 are from Chile: 2 extant and 2 fossils (Table 1). Interestingly, the southermost and westernmost record for the species is represented by 1 locality in southern Chile (Puerto Prat,

locality 8, Fig. 3). Taken in equal periods of 35 years, 50% of the extant records for *L. patagonicus* are concentrated in the period from 1977 to 2012 (Table 1).

Potential distribution models are presented in Fig. 4. Models A (*n* = 15) and B (*n* = 20) generated with fossil records and LGM environmental data show an area of high prediction (black shading, Fig. 4A) that covers most of La Pampa, Neuquén, Río Negro, and Chubut provinces, southern and western Mendoza Province, and eastern Santa Cruz Province. This area extends into northern Chile through the western portions of San Juan, La Rioja, and Catamarca provinces in Argentina, and also includes much of the continental platform that is now under water, but was probably emerged in its majority during the LGM (Rabassa et al. 2005; Figs. 4A and 4B). From model A to model B (Pleistocene/Holocene to Holocene) a major reduction in levels of prediction in central and southern Buenos Aires Province and western Córdoba Province is shown (black arrows in Fig. 4B).

Both models with extant records (C and D) show a similar pattern, with a reduction in total area from the model with all records (*n* = 52) to the one with records after 1950 (*n* = 35), at all levels of prediction (Figs. 4C and 4D, respectively). A large area of high (>50%) prediction values appears concentrated in western Patagonia and the Somuncurá Plateau in Chubut and Río Negro provinces, surrounded by an area of medium (25–50%) prediction values that extends over most of Patagonia (Figs. 4C and 4D). Separated from this area are several other smaller high-prediction areas in southern and western Mendoza, southern Buenos Aires Province (area A, Fig. 4C), central Chile (area B, Fig. 4D), and a somewhat continuous area from central San Juan to central Salta provinces (Figs. 4C and 4D)

Percent contribution of each variable to the 4 models (A–D) are presented in Table 2. Ten variables contributed most to both LGM models, with 98.1% in model A and 97.8% in model B. Nineteen and 17 environmental variables contributed the most to the models with extant records, 91.9% in C and 89.1% in D. One variable (mean temperature of the coldest quarter) contributed >60% in both LGM models (64.1% in A and 60.3% in B), whereas 2 variables (temperature seasonality and October precipitation) contributed >50% to the models with extant data (61.7% in C, 57.9% in D). The other variables, with smaller contributions, were related to minimum temperature of coldest month and precipitation taken by quarters in the LGM models (A and B), and elevation and winter/late fall minimum temperature and precipitation in the models with extant data (C and D, Table 2). Variables containing information not present in the remainder were mean temperature of coldest quarter in model A, precipitation seasonality in model B, and altitude in models C and D. Other jackknife tests (i.e., using test gain instead of training gain, and that using AUC) show only one variable (minimum temperature of the coldest month) as the most important in LGM models, and temperature seasonality, November precipitation, and annual precipitation as the most important variables in C and D models, whereas altitude was the variable containing information not present in the remainder (Table 2).

TABLE 1.—Record localities for *Lyncodon patagonicus*. Abbreviations are as follows: Argentine localities: BA, Buenos Aires; Ca, Catamarca; Ch, Chubut; Co, Córdoba; LP, La Pampa; LR, La Rioja; M, Mendoza; N, Neuquén; RN, Río Negro; S, Salta; SC, Santa Cruz; SE, Santiago del Estero; SJ, San Juan; SL, San Luis; T, Tucumán. Chilean localities (denoted by asterisks): Ar, Araucanía; Mg, Magallanes. Ecoregions: 1) Dry Chaco, 2) Espinal, 3) High Monte, 4) Humid Pampas, 5) Low Monte, 6) Magellanic Subpolar Forest, 7) Patagonian Steppe, 8) Southern Andean Steppe, 9) Southern Andean Yungas, 10) Valdivian Temperate Forest. Ea = Estancia.

Locality number	Locality	Latitude	Longitude	Model	Reference
1	**Azul** (BA, 4)	36°47′	59°51′	C	Burmeister 1879
2	Rincón Grande (BA, 2)	39°42′	63°13′	C	Doering 1881
3	Carmen de Patagones (BA, 2)	40°48′	63°00′	C	Doering 1881
4	Arroyo Quichaure (Ch, 7)	43°50′	70°50′	C	Burmeister 1888
5	Lago Blanco (Ch, 7)	45°56′	71°16′	C	Koslowsky 1904
6	Río Guenguel (Ch, 7)	46°00′	71°32′	C	Koslowsky 1904
7	Near Puerto Santa Cruz (SC, 7)	50°01′	68°32′	C	Allen 1905
8	**Puerto Prat*** (Mg, 6)	51°37′	72°38′	C	Wolffsohn 1923
9	Bonifacio (BA, 4)	36°49′	62°15′	C	Pocock 1926
10	La Rioja (LR, 1)	29°25′	66°51′	C	Cabrera 1929
11	Patquia (LR, 1)	30°03′	66°53′	C	Yepes 1935
12	Aguada Grande (SC, 7)	47°20′	67°35′	C	Yepes 1935
13	Tupungato (M, 8)	33°21′55″	69°08′03″	C	Roig 1965
14	Tunuyán (M, 5)	33°34′24″	69°01′19″	C	Roig 1965
15	San Carlos (M, 5)	33°45′57″	69°02′04″	C	Roig 1965
16	San Rafael (M, 5)	34°36′35″	68°21′12″	C	Roig 1965
17	Marimenuco* (Ar, 10)	38°42′	71°06′	C, D	Peña 1966
18	**Alemanía** (S, 1)	25°38′	65°37′	C, D	Olrog 1976
19	Cafayate (S, 3)	26°06′	65°57′	C, D	Olrog 1976
20	Santa María (Ca, 3)	26°42′	66°02′	C, D	Olrog 1976
21	Andalgalá (Ca, 3)	27°36′	66°20′	C, D	Olrog 1958
22	El Timbó (T, 1)	26°14′	65°23′	C, D	Olrog 1958
23	Colalao del Valle (T, 3)	26°22′	65°56′	C, D	Olrog 1976
24	Amaicha del Valle (T, 3)	26°23′	65°55′	C, D	Olrog 1976
25	Banda del río Salí (T, 9)	26°51′	65°10′	C, D	Olrog 1976
26	Sol de Julio (SE, 1)	29°33′	63°27′	C, D	Olrog 1976
27	Uspallata (M, 3)	32°41′	69°22′	C, D	Castro and Cicchino 1986
28	Cueva del Tigre (M, 7)	35°45′49″	69°13′	C, D	Trajano 1991
29	San Carlos de Bariloche (RN, 10)	41°08′	71°17′	C, D	Massoia 1992
30	Guampacha (SE, 1)	28°03′	64°48′	C, D	Massoia and Latorraca 1992
31	Salinas Grande (LP, 2)	37°09′	63°39′	C, D	Prevosti and Pardiñas 2001
32	Macachín (LP, 2)	37°09′	63°40′	C, D	Prevosti and Pardiñas 2001
33	Ea. Cerro de los Pinos (N, 7)	39°57′	71°05′	C, D	Prevosti and Pardiñas 2001
34	9 km SE Los Menucos (RN, 7)	40°53′24″	68°02′59″	C, D	Prevosti and Pardiñas 2001
35	Aeropuerto Bariloche (RN, 7)	41°9′	71°9′	C, D	Prevosti and Pardiñas 2001
36	Puerto Pirámide (Ch, 7)	42°34′	64°18′	C, D	Prevosti and Pardiñas 2001
37	Río Senguerr (Ch, 7)	45°2′	70°50′	C	Prevosti and Pardiñas 2001
38	2,000 m al E de Puerto Pirámides	42°34′	64°16′	–	Prevosti and Pardiñas 2001
39	Pampa de Gualilán (SJ, 8)	30°80′	68°90′	C, D	Sanabria and Quiroga 2003
40	Cabo Dos Bahías (Ch, 7)	44°54′	65°39′	C, D	Harris 2008
41	Ea. San Pedro (RN, 7)	40°54′	70°42′	C, D	Teta et al. 2008
42	Ea. El Desafío (RN, 7)	41°18′	71°06′	C, D	Teta et al. 2008
43	Puesto Horno, Ea. Maquinchao (RN, 7)	41°42′	68°39′	C, D	Teta et al. 2008
44	Cañadón Angostura de Cides, Ea. Calcatreo (RN, 7)	41°43′	69°22′	C, D	Teta et al. 2008
45	Ea. Calcatreo (RN, 7)	41°42′	69°24′	C, D	Prevosti et al. 2009
46	Piedra Parada (Ch, 7)	42°39′	70°06′	C, D	Prevosti et al. 2009
47	Puerto Madryn (Ch, 5)	42°45′	65°02′	C, D	Prevosti et al. 2009
48	Puesto El Chango, Ea. Santa María (Ch, 7)	45°27′51″	69°25′54″	C, D	Prevosti et al. 2009
49	10 km S Perito Moreno, RN 40 (SC, 7)	46°41′	70°52′	C, D	Prevosti et al. 2009
50	Extremo NE Lago Cardiel, RN 40 (SC, 7)	48°54′	71°01′	C, D	Prevosti et al. 2009
51	Ea. Yuquiche (RN, 7)	41°39′	69°32′	C, D	This work
52	Costa del Chubut (Ch, 7)	42°36′9.7″	70°22′19.4″	C, D	This work
53	Río Chalía Ea. La Ensenada, Ruta 288. 110 km al Oeste de Piedrabuena (SC, 7)	49°35′	69°34′	C, D	This work
54	Luján (BA)	34°34′	59°06′	A	Ameghino 1888
55	Córdoba (Co)	31°25′	64°12′	A	Ameghino 1889
56	Las Represas de las Indias (SE)	28°10′	63°00′	A, B	Kraglievich and Rusconi 1931
57	Cortaderas (BA)	38°21′	61°06′	A, B	Politis et al. 1983
58	Chenque Haichol (N)	38°35′	70°40′	A, B	Massoia 1992

TABLE 1.—Continued.

Locality number	Locality	Latitude	Longitude	Model	Reference
59	Tres Arroyos 1* (Mg)	53°23′	68°47′	A, B	Latorre 1998
60	Estación Manuel J. García (BA)	34°40′	59°26′	A	Prevosti and Pardiñas 2001
61	Camet Norte (BA)	38°00′	57°33′	A	Prevosti and Pardiñas 2001
62	Las Lagunitas (SL)	33°41′	65°28′	A	Prevosti and Pardiñas 2001
63	Cueva y Paredón Loncomán (RN)	40°47′	70°10′	A, B	Andrade et al. 2005
64	Alero Santo Rosario (RN)	41°43′	68°40′	A, B	Andrade et al. 2007
65	Ea. El Centenario (SL)	34°12′27″	65°51′59″	A, B	Prevosti et al. 2009
66	Punta Buenos Aires (Ch)	42°12′	64°11′	A, B	Prevosti et al. 2009
67	El Riacho (Ch)	42°25′	64°36′	A, B	Prevosti et al. 2009
68	Playa Pardelas (Ch)	42°38′	64°12′	A, B	Prevosti et al. 2009
69	Establecimiento San Pablo (Ch)	42°39′55″	64°12′54″	A, B	Prevosti et al. 2009
70	Punta Este (Ch)	42°47′	64°57′	A, B	Prevosti et al. 2009
71	Cerro Avanzado (Ch)	42°50′	64°52′	A, B	Prevosti et al. 2009
72	El Pedral (Ch)	42°57′	64°22′	A, B	Prevosti et al. 2009
73	Cueva de los Chingues, PN Pali-Aike* (Mg)	52°05′37″	69°44′31″	A, B	Prevosti et al. 2009

All 4 models showed better predictions than those randomly generated at cumulative values of 1, 5, and 10, with high AUC values: $A = 0.948 \pm 0.055$ (*SD*), $B = 0.973 \pm 0.013$ (*SD*), $C = 0.949 \pm 0.009$ (*SD*), $D = 0.959 \pm 0.018$ (*SD*), Table 3.

Model E shows a similar pattern to model C (Fig. 5). Patagonia and northwestern Argentina show extended areas at all levels of prediction; the same is true for a small area in southern Buenos Aires. Major changes are observed in temperature-related variables, indicating that cooler conditions might allow a broader distribution of *L. patagonicus*. With an AUC value of 0.935 ± 0.015 (*SD*), and as with models C and D, temperature seasonality contributed the most to the model (65.9%), followed by precipitation of warmest quarter with 7.7%.
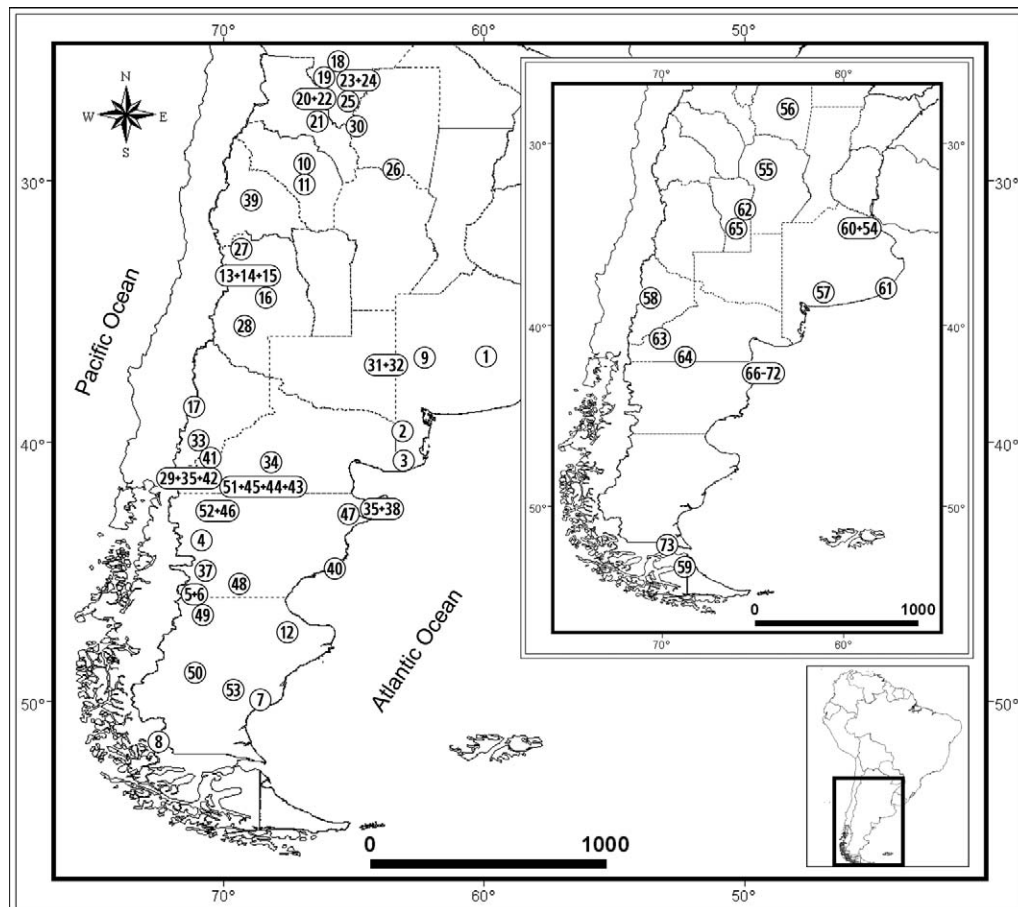

Fig. 3.—Record localities for *Lyncodon patagonicus* for Argentina and Chile organized by date (see Table 1). Inset represents fossil localities. Each number belongs to "locality number" in Table 1.
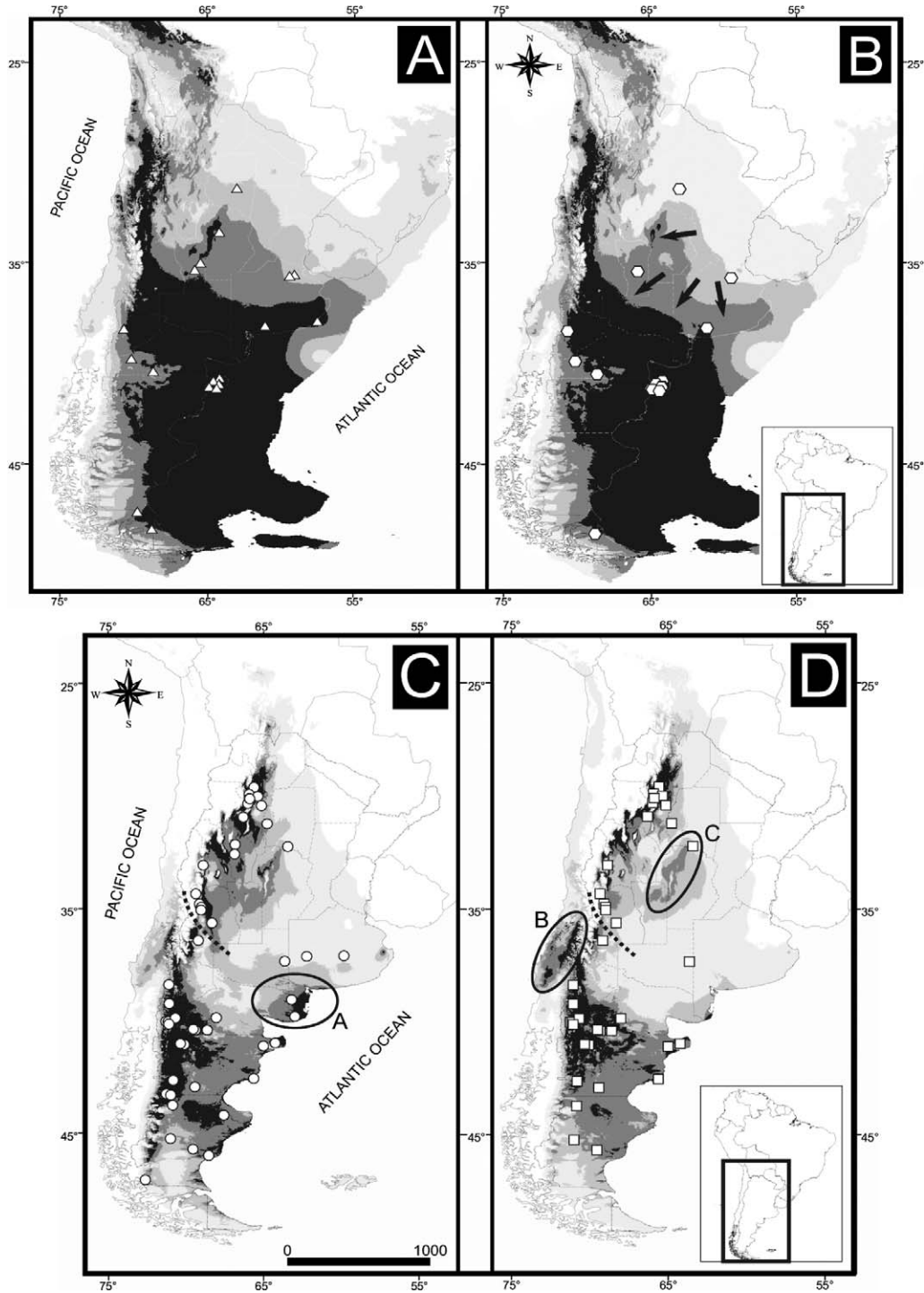
FIG. 4.—A) Potential distribution models for *Lyncodon patagonicus* using Pleistocene/Holocene (fossil) localities (white triangles), B) using only Holocene (fossil) localities (white hexagons), C) using all actual (not fossil) localities (white circles), and D) using those (actual) recorded after 1950 (white squares). Probability values are 51–100 (black), 26–50 (dark gray), 11–25 (gray), 2–10 (light gray), and 0–1 (white). Important changes are marked as selected areas (see "Results").

In a biogeographic context, extant records of *L. patagonicus* are mostly concentrated in the Andean region ($n = 28$), Patagonian subregion ($n = 25$) sensu Morrone (2001), and Patagonian Steppe ecoregion ($n = 25$) sensu Olson et al. (2001; Table 1, Fig. 6).

DISCUSSION

The Patagonian weasel is distributed from Salta (Argentina) to the southern portion of continental South America, with most localities being found along western Argentina (Fig. 3). Several records from eastern localities throughout its central

TABLE 2.—Percent contribution of each variable for the 4 models (A–D) generated (see "Results") for *Lyncodon patagonicus*. In bold, variables with major contribution.

Variable	A Contribution	A Permutation	B Contribution	B Permutation	C Contribution	C Permutation	D Contribution	D Permutation
Mean temperature of coldest quarter	**64.1**	45.5	**60.3**	58.1	3.8	1.6	3.6	5.8
Minimum temperature of coldest month	**9.1**	27.9	**13.8**	24	2	14.3	2.9	0.5
Precipitation seasonality	7	2.4	7.7	0.7	2.5	1.3	3.2	1.4
Temperature seasonality	4.9	9.6	4.8	11.9	**55.1**	1.1	**48.3**	1.2
Precipitation of driest quarter	2.7	6.5	2.3	1.2	0.6	7.9	0.3	0.1
Precipitation of wettest quarter	2.6	0.1	2.8	0.3	1.2	0.7		
Isothermality	2.4	0	1.6	0	0.4	3.8	0.9	8.3
Precipitation of driest month	2.3	5.7			0.4	0.7	1.4	13.4
Annual precipitation	1.5	0	0.7	0	0.3	0		
Mean diurnal range	1.5	0.1	1.6	0	0.6	0.3	1	0
Mean temperature of warmest quarter	0.9	0	0.8	0				
Mean temperature of driest quarter	0.3	1	0.6	0.1	0.8	2.1	2.2	1.4
Precipitation of coldest quarter	0.2	0.4	2.3	1.7				
October precipitation					**6.6**	8.9	**9.6**	19.2
Elevation					5.9	6.1	6.6	15.1
November precipitation					3.8	1.6	3.6	5.8
July minimum temperature					2.8	5.1	2	16.5
June minimum temperature					2.1	12.1	1	4
September minimum temperature					1.9	0	1.4	0
August minimum temperature					1.4	3.8		
July precipitation					1.1	1.4	1.1	0.1
February maximum temperature					1	1.9	2.9	4.9
March precipitation					0.9	0.6	1.1	0.3
February precipitation					0.9	4.7	0.9	1.6
Total	99.5		99.3		96.1		94	
Total of the 2 most important variables	73.2		74.1		61,7		57.9	

Jackknife test of variable importance

	A	B	C	D
Variable with highest explanatory power	Minimum temperature of coldest month	Minimum temperature of coldest month	July minimum temperature	July minimum temperature
Variable with most "unique" information	Mean temperature of coldest quarter	Precipitation Seasonality	Elevation	Elevation

Jackknife test of variable importance using test gain

	A	B	C	D
Variable with highest explanatory power	Minimum temperature of coldest month	Minimum temperature of coldest month	Temperature seasonality	Temperature seasonality
Variable with most "unique" information	Precipitation seasonality	Minimum temperature of coldest month	Elevation	Elevation

Jackknife test of variable importance using area under the curve

	A	B	C	D
Variable with highest explanatory power	Minimum temperature of coldest month	Minimum temperature of coldest month	Annual precipitation	November precipitation
Variable with most "unique" information	Precipitation seasonality	Minimum temperature of coldest month	Elevation	Elevation

distribution (e.g., Buenos Aires Province) are from the late 1800s or early 1900s and the species is likely to be absent from the area today (see ENMs, and also Prevosti and Pardiñas 2001). Some areas have a concentration of records (e.g., Chubut and Tucumán provinces), which might reflect the work of different scientists/research groups (e.g., Olrog 1976).

From a historical perspective, an increase of 50% in the species' known localities occurred in the last 35 years (1977–2012). In contrast, for over 70 years the species was known from fewer than 15 localities scattered mostly throughout its current known range (Table 1, Fig. 3). Following a similar pattern, fossil records were scant and concentrated in the north of the species distribution, with a 70% increase ($n = 14$) since 2001 (Table 1), reflecting an increase in paleontological work in eastern Chubut and Buenos Aires provinces. Fossil records of *L. patagonicus* with good stratigraphic data come from the Lujanian (125–4.5 ka), one of them close to the LGM (Camet Norte), whereas a specimen from Lujan (Buenos Aires Province) was collected in the "Pampeano Lacustre" of Ameghino and its age could be assigned to a broad period between 73 and 12 ka (Prevosti and Pardiñas 2001; Toledo 2011). Other Pleistocene specimens lack enough chronological information, something that occurs with some Holocene specimens as well (see Prevosti and Pardiñas 2001). The presence of *L. patagonicus* during the late Pleistocene in the east of Buenos Aires Province, beyond the historical range of

TABLE 3.—Results of predicted areas for cumulative threshold values of 1, 5, and 10 for the 4 models (A–D) generated.

	A		B		C		D	
Cumulative threshold	Fractional predicted area	*P*-value	Fractional predicted area	*P*-value	Fractional predicted area	*P*-value	Fractional predicted area	*P*-value
1	0.1575	0.0203	0.1745	0.0010	0.1614	0.0000	0.1687	0.0000
5	0.0994	0.0337	0.1121	0.0009	0.1173	0.0000	0.1082	0.0000
10	0.0721	0.0379	0.0821	0.0006	0.0930	0.0000	0.0786	0.0067

this species, was associated with the existence of colder and drier climates on the basis of the evidence revealed by other mammals and other biotic proxies (see Prevosti and Pardiñas 2001; Prevosti et al. 2009). The same could be said for the Holocene records from northeastern and southern Buenos Aires Province, which are also associated with a fauna that represents evidence of drier weather (Prevosti and Pardiñas 2001; Quattrocchio et al. 2008). In sum, fossil evidence indicates that the presence of *L. patagonicus* during the Late Pleistocene–Holocene in eastern Buenos Aires Province, where it has been absent since historical times, is related to the

presence of drier climates, in agreement with the models presented herein.

The 4 models generated represent the 1st attempt to analyze the potential distribution of a rare "Southern Cone" endemic carnivore, and is also the first for a South American carnivore using fossil records. Although potential distribution in models A and B might have some bias due to some differences between ages between localities and the temporal database (i.e., LGM), we believe that these models are a reasonable representation of the distribution of *L. patagonicus*, both extant and fossil. In this respect, variable contributions of the models show that the same variables influence the distribution of the Patagonian weasel at continental scale. A general trend can be observed when analyzing the models in a historical
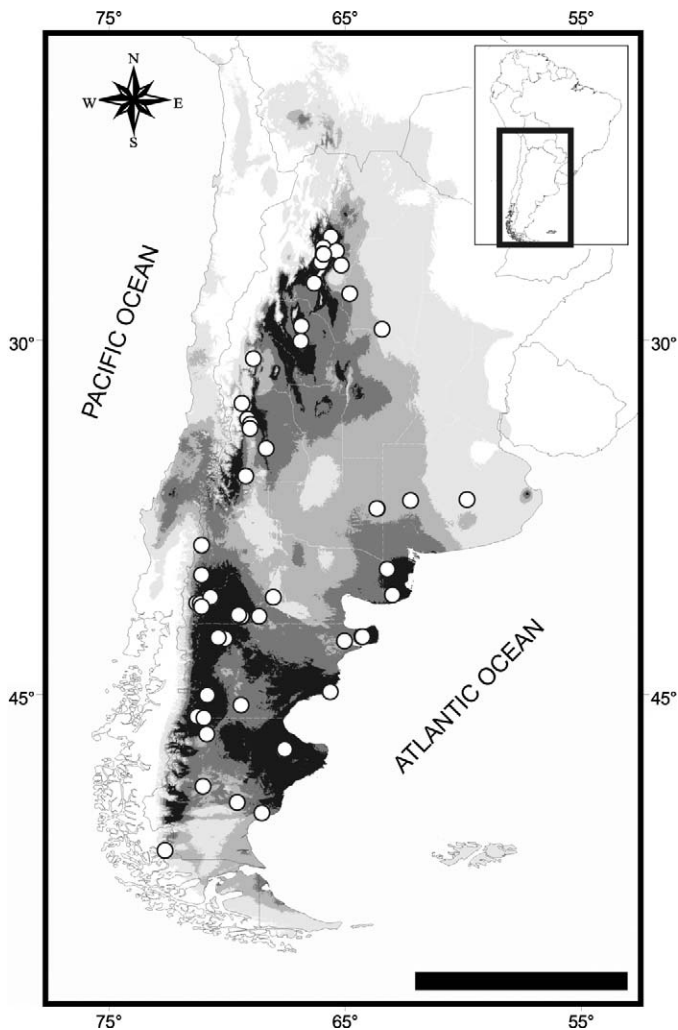

FIG. 5.—Potential distribution model E, using all actual (not fossil) localities (white circles) and a modified climate data set (see "Materials and Methods").
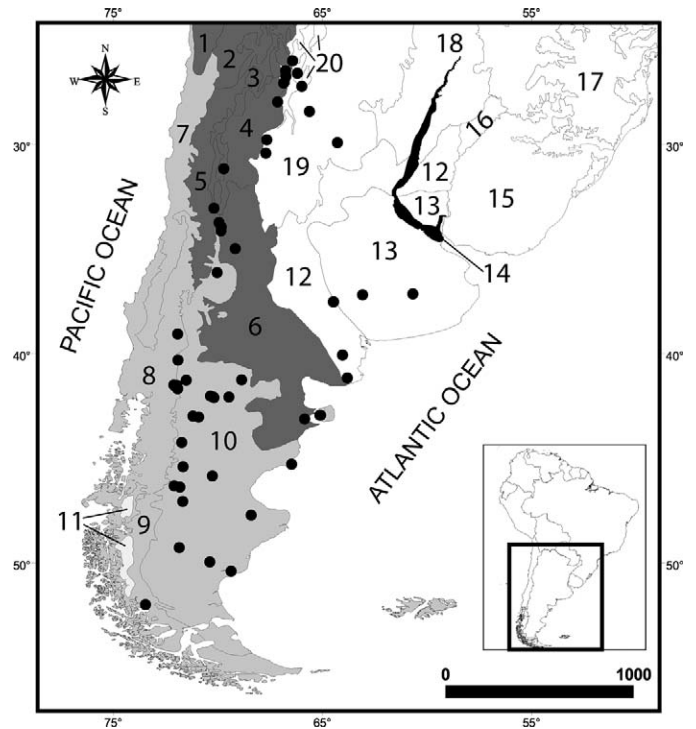

FIG. 6.—Record localities (black circles) in a biogeographic context. Ecoregions follow Olson et al. (2001): 1 = Atacama Desert; 2 = Central Andean Dry Puna; 3 = Central Andean Puna; 4 = High Monte, 5 = Southern Andean Steppe; 6 = Low Monte; 7 = Chilean Matorral; 8 = Valdivian Temperate Forest; 9 = Magellanic Subpolar Forest; 10 = Patagonian Steppe; 11 = Rock and Ice; 12 = Espinal; 13 = Humid Pampas; 14 = Paraná Flooded Savanna; 15 = Uruguayan Savanna; 16 = Southern Cone Mesopotamian; 17 = Araucaria Moist Forest; 18 = Humid Chaco; 19 = Dry Chaco; 20 = Southern Andean Yungas.

perspective, from LGM to 1950 (Fig. 4): a shift from an eastern, highly continuous distribution (Fig. 4A) to a western, highly patched distribution (Fig. 4D). This is true for high- (black shading) and medium-prediction areas (dark gray shading), and to a lesser extent to the areas with low prediction values (light shading) (Fig. 4). These patterns could be indicating a retraction in the distribution of *L. patagonicus* from times of the LGM (i.e., vicariance), a process that has increased in the past century as shown when data from 1950 are used to generate the model (Fig. 4D).

Although potential distribution in models A and B seems to be overpredicting large areas (especially for high prediction values), many of the observed patterns can be explained by climatic conditions of that time. The shift from west to east, far from the Andes Mountains, might be explained by vast glacial extensions covering such areas, and the presence of extreme climatic conditions typical of periglacial environments (Rabassa et al. 2011). Also, a drop in sea level of 100–140 m during glaciations exposed much of the continental platform, adding substantial surfaces that were occupied (or susceptible of being so) by the biota, including *L. patagonicus* (Rabassa et al. 2005). Even more important, during glaciations a displacement in oceanic anticyclones might also have occurred (Rabassa et al. 2005). So, the Pacific anticyclone moved northward, and (recent) La Pampa and Buenos Aires provinces were affected by the influence of "westerlies" (cold and dry winds—Rabassa et al. 2005). In other words, the limits of climatic conditions typical of Patagonia (cool and dry, westerly winds, and moderate temperature) extended toward the northeast, covering the entire Pampa region (Iriondo and García 1993). Due to the sea level drop, areas of what today is Buenos Aires and eastern La Pampa provinces would have experienced a more extreme continental-like climate (i.e., with higher thermal amplitude), away from the oceanic influences of modern climate. In the context of the distribution of *L. patagonicus*, this is corroborated by the presence of fossils of this species in the area (inset in Fig. 3).

The 2 models with recent (i.e., not fossil) data show a large high-prediction area in west-central Patagonia (Figs. 4C and 4D), and other minor high-prediction areas that appear scattered in western Argentina from ∼27° to 36°S, and another small area in Chile from approximately 35° to 38°S. As pointed out above, these areas are reduced in model D (Fig. 4D), appear discontinuous, or have shifted from high (black shading) to medium (dark gray) prediction values (e.g., area C, Fig. 4D). Contrary to this, the area of central Chile (area B, Fig. 4D) with medium prediction values has shifted to high prediction values in model D, and a medium-/medium-low-prediction area appears north of this one, reaching the border between Chile and Perú at approximately 25°S (Fig. 2D). This shift in potential distribution is consistent with projections of climate change for central Chile, which shows an increasing aridity in the area (Watson et al. 1998).

Both models with extant data (Figs. 4C and 4D) show the same geographic areas with high probability of occurrence, although model C seems to overpredict some geographical

areas by the inclusion of "historical" localities, such as those present in Buenos Aires and La Pampa provinces (Fig. 3, Table 1). Following this, a high-probability area is shown in southern Buenos Aires Province, though the intense human-driven modifications and an increase of precipitation in this region during the last 100 years makes the occurrence of *L. patagonicus* in the area quite unlikely (see Prevosti and Pardiñas 2001).

The models generated with extant localities show 2 areas diffusely connected (or separated) at 35–36°S (dashed lines, Figs. 4C and 4D). These are coincident with the supposed distribution of the 2 subspecies that have been recognized for *L. patagonicus*: *L. p. thomasi* Cabrera 1929 and *L. p. patagonicus* (de Blainville 1842) for northwestern and southern subspecies, respectively. Clearly, a detailed morphological and taxonomic study is needed to clarify the status of the named subspecies.

The environmental variables that appear to have the greatest influence on the potential distribution models are mostly related to minimum temperatures of the coldest months and, with smaller contributions, precipitation and elevation (Table 2). When environmental variables are compared between the models, a trend in which temperature-related variables represent a smaller percentage of the total predictions can be observed, from 82% in model A to 55.2% in model D. Contrary to this, a small increase in the contribution of precipitation-related values can be observed, with a maximum of 18.6% in model D. Birney and Monjeau (2003) and Monjeau et al. (2009) indicate minimum temperatures as the highest determinant of species distribution in a South American context. The latter reference also relates minimum temperatures with energy availability per area. Although the distribution of *L. patagonicus* seems to be primarily related to minimum temperatures, elevation and precipitation also play an important role. Jackknife tests show temperature and precipitation variables as the most important, with altitude as the most important variable containing information not present in the others. In this way, cold areas with marked temperature seasonality, spring precipitations, and altitudes below 2,000 m above sea level (asl) appear to be the best suited for the distribution of *L. patagonicus* (Table 2).

Recent localities are not distributed evenly, with only two of them from Chile and the rest from Argentina, mostly in Patagonian Steppe environments, followed by High Monte and Dry Chaco (sensu Olson et al. 2001). These 3 ecoregions receive less than 700 mm of annual precipitation and are structurally composed of shrubby steppes or dry forests (Burkart et al. 1999), which mostly agrees with previous works that depict the Patagonian weasel as an inhabitant of cold and dry areas (Prevosti and Pardiñas 2001). Both high-prediction areas in models C and D (Figs. 4C and 4D) are partially coincident with the extension of 2 ecoregions (sensu Olson et al. 2001). The 1st area is mostly coincident with the High Monte and, on a lower prediction level, with western parts of the Dry Chaco ecoregions. The 2nd area extends throughout the southern provinces of Argentina, from southern

Neuquén, west and central Río Negro and Chubut provinces, to central Santa Cruz, all along the Patagonian Steppe ecoregion. This area is strongly affected by dry winds from the South Pacific anticyclone and low mean annual temperatures of 5–10°C (Manzini et al. 2008), in coincidence with the environmental variables shown to be the most important determinants of the ENMs (see above). It is important to point out that areas with high probability of presence in southern Argentina seem restricted to this biome (i.e., Patagonian Steppe), avoiding areas of the Low Monte ecoregion (Fig. 6). However, the absence from this ecosystem might be due to a lack of shrubby steppes and the predominant sagebrush (jarillal) dominated by *Larrea* spp. (Roig-Juñent et al. 2001).

Areas above 2,000 m asl show very low prediction values, probably representing real natural barriers to the dispersal of *L. patagonicus*.

In our study, we aimed to predict areas that satisfy the species' environmental requirements through ENM (Phillips et al. 2004). However, animal distribution is also affected by interspecific processes such as competition and predation (Krebs 1985; Palomares and Caro 1999). According to published information, *L. patagonicus* appears to be sympatric with the lesser Grison (*Galictis cuja*), at least at a regional scale (Yensen and Tarifa, 2003). During our study, we found both species to be partially sympatric throughout their range and syntopic in only 1 locality (sensu Rivas 1964); the latter term seems to be more appropriate for describing interactions at a smaller scale (i.e., those that should influence the distribution of *L. patagonicus* at a habitat level). Unfortunately, no information on species density or other ecological aspects that might affect populations at this scale is available, which makes any analysis on the relationships between *G. cuja* and *L. patagonicus* highly speculative. Ongoing work on skull shape morphometrics shows partial overlap of skull and mandible shape of these species (M. I. Schiaffini, pers. obs.). However, niche overlap might be avoided by size differences (see Yensen and Tarifa 2003, Prevosti et al. 2009). Field studies should provide complementary information to test for niche overlap and other ecological aspects of these poorly studied species. Until then, very little can be said in relation to how these small carnivores interact.

Although records of *L. patagonicus* extend from northwestern to southern Argentina along more than 2,500 km, potential distribution models show that the species distribution is concentrated in 2 areas, one in northwestern Argentina between approximately 23°30′ and 35°S, and another in Patagonia between approximately 37° and 46°S. Further analyses using other approaches (e.g., molecular) could shed some light on the structure (if any) of the species population throughout its range. Temperature seasonality and minimum winter temperatures, together with elevation and spring precipitation, seem to be the greatest determinants of the species geographical distribution. The inclusion of LGM models allowed us to infer its past distribution, and strengthens the idea that *L. patagonicus* inhabits cold and dry areas, such as those that were during the Pleistocene and parts of the Holocene in what today is considered Pampas sensu lato. The extension of Patagonian climate during glacial periods is supported by loess deposits in the Pampas region (see Rabassa et al. 2005); fossils of the species studied herein, which are actually absent from this area, support this shift. The novel techniques implemented in this work allow us to infer that *L. patagonicus* is experiencing a retraction in distribution area. This can be related (at least broadly) to the species being affected by glacial cycles that occurred in Patagonia during the Late Quaternary, spreading during these periods to eastern areas, and retracting during interglacial periods to western portions of South America. This has direct implications on the conservation of this rare carnivore.

RESUMEN

El Huroncito Patagónico (*Lyncodon patagonicus*) es uno de los carnívoros menos conocidos de Sudamérica, y excluyendo algunas contribuciones, su conocimiento parece anecdótico. Se supone que habita ambientes áridos con vegetación herbácea de Argentina y Chile. En el presente estudio evaluamos la distribución potencial del Huroncito Patagónico durante el presente y el Último Máximo Glacial (UMG). Para ello integramos información proveniente de análisis históricos y geográficos (Modelado de Nicho Ecológico y esquemas biogeográficos) de la distribución de *L. patagonicus*. De esta manera obtuvimos dos grandes áreas núcleo de distribución para la especie, una en el noroeste de Argentina y otra hacia el sur de Argentina (i.e., Patagonia). La distribución del Huroncito Patagónico parece estar relacionada en primer lugar con áreas frías de marcada estacionalidad térmica y altitudes por debajo de los 2000 m.s.n.m. El modelo generado indica que desde el UMG hasta el presente, hubo una mayor retracción en las áreas de distribución potencial, lo cual podría indicar la existencia de un proceso de vicarianza que afectó la distribución del Huroncito Patagónico.

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APPENDIX I

BIO1 = annual mean temperature

BIO2 = mean diurnal range (mean of monthly [max. temp.–min temp])

BIO3 = isothermality (BIO2/BIO7)(100)

BIO4 = temperature seasonality ($SD \times 100$)

BIO5 = maximum temperature of warmest month

BIO6 = minimum temperature of coldest month

BIO7 = temperature annual range (BIO5–BIO6)

BIO8 = mean temperature of wettest quarter

BIO9 = mean temperature of driest quarter

BIO10 = mean temperature of warmest quarter

BIO11 = mean temperature of coldest quarter

BIO12 = annual precipitation

BIO13 = precipitation of wettest month

BIO14 = precipitation of driest month

BIO15 = precipitation seasonality (coefficient of variation)

BIO16 = precipitation of wettest quarter

BIO17 = precipitation of driest quarter

BIO18 = precipitation of warmest quarter

BIO19 = precipitation of coldest quarter