Extinctions in near time: new radiocarbon dates point to a very recent disappearance of the South American fox *Dusicyon avus* (Carnivora: Canidae)

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Almost all large carnivorans (Carnivora; > 20 kg) that inhabited South America became extinct around the Late Pleistocene–Early Holocene transition. Two exceptions were species of coyote-sized *Dusicyon*, one insular (*D. australis*) and one continental (*D. avus*). The extinction of the former is a resolved matter, but that of *D. avus*, found in the Patagonian and Pampean regions, is still poorly understood. Using the Gaussian-Resampled Inverse-Weighted McInerny method we present new radiocarbon evidence indicating that its disappearance occurred in very recent times (about 324–496 years cal BP). We found no evidence to support a role for hybridization with domestic dogs in causing the extirpation of this fox. Climatic change may have reduced its distributional range, as has happened with other mammals, although not to the extent of explaining its extinction. Climatic change, however, coupled with increased anthropogenic impacts such as hunting, domestic dogs, and/or other aspects relating to the impact of European colonization in South America's southern cone, were the probable main drivers of the recent extinction of *D. avus*. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **116**, 704–720.

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INTRODUCTION

Recent extinctions, i.e. those taking place in comparatively modern times (after AD 1500), and their study

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are important in that they may herald the onset of a sixth mass extinction (Leakey & Lewin, 1992; Mac-Phee & Flemming, 1999; Ceballos & Ehrlich, 2002; Barnosky *et al.*, 2011; Teta *et al.*, 2014). These extinctions, which have impacted a wide array of organisms, principally affected small-sized, island-dwelling species (body mass < 10 kg) in the case of mammals, and were apparently not related to climatic change (MacPhee & Flemming, 1999). Continental South American mammals showed few extinctions after the Early Holocene (MacPhee & Flemming, 1999; Turvey, 2009; Turvey & Fritz, 2011). Since the arrival of Europeans, some ten species – mostly small rodents and marsupials- are thought to have become extinct (Teta *et al.*, 2014) although taxonomic uncertainties make the true number uncertain.

South America suffered a large extinction during the Late Pleistocene–Early Holocene, mostly affecting large and mega-mammals (Barnosky *et al.*, 2004; Borrero, 2008a; Cione, Tonni & Soibelzon, 2008). Mammalian predators were also affected, and several large carnivores – including sabre-tooth cats (*Smilodon* spp.), a large jaguar (*Panthera onca mesembrina*), short faced bears (*Arctotherium* spp.), and large hypercarnivorous canids (e.g. *Canis dirus*, *Protocyon* spp.) – disappeared during the Pleistocene–Holocene transition. The surviving depauperate assemblage of large carnivorans includes only two large felids (> 50 kg; *Puma concolor*, *Panthera onca*), a large omnivorous canid (> 20 kg; *Chrysocyon brachyurus*), and a small bear (> 50 kg; *Tremarctos ornatus*; Prevosti & Rincón, 2007; Cione *et al.*, 2008; Prevosti, Ubilla & Perea, 2009; Prevosti & Soibelzon, 2012). During the late Holocene, the fox *Dusicyon avus* (10–15 kg) disappeared in the Pampean region and Patagonia (Prevosti *et al.*, 2011). The cause of the extinction of *Dusicyon australis* – the endemic Malvinas fox or Falklands wolf – in the late 19th century is a resolved matter (Cabrera & Yepes, 1940; Clutton-Brock, Corbet & Hills, 1976; Slater *et al.*, 2009; Prevosti *et al.*, 2011; Austin *et al.*, 2013), but the processes that triggered the disappearance of their continental counterpart, *D. avus*, are still controversial.

Slater *et al.* (2009) and Austin *et al.* (2013) established that *D. avus* is the sister taxon of *D. australis*, and that this clade is related to the living maned wolf (*Chrysocyon brachyurus*). *Dusicyon avus* has a rich fossil record, based on several Late Pleistocene (Lujanian) localities in Southern Brazil, Uruguay, Argentina and Chile, but there are also Holocene records from the Patagonian and Pampean regions (Argentina and Chile, Fig. 1, Supporting Information, Appendix S1; see Prevosti *et al.*, 2011; for a review). According to recent studies, the *Dusicyon* lineage became extinct in the late Holocene, first with the fading of *D. avus* around 3000 cal years BP (Prevosti *et al.*, 2011), and then in the 19th century when *D. australis* was hunted to extinction (Darwin, 1839; Clutton-Brock *et al.*, 1976; Slater *et al.*, 2009; Turvey, 2009). Hypotheses advanced to explain the extinction of *D. avus* include a change to drier climate and open vegetation or hybridization with domestic dogs, but neither are supported by published data; human expansion in South America during the late Holocene (< 3000 years BP) is gaining merit as a potential cause (Prevosti *et al.*, 2011).

Here we describe new specimens of *D. avus*, dated between 700 and 400 cal years BP, from localities in the Pampean and Patagonian regions of Argentina and southern Chile. Using the Gaussian-Resampled Inverse-Weighted McInerny (GRIWM) method (Bradshaw *et al.*, 2012), we estimated the time of extinction of this fox, and determined its occurrence in historical times. Based on this emerging evidence we revisited the potential factors that may have accounted for the extinction of *D. avus*.

MATERIAL AND METHODS

TAXONOMIC IDENTIFICATION

Taxonomic assignation of the specimens was based upon a combination of qualitative and quantitative approaches (Kraglievich, 1930; Berman & Tonni, 1987; Trejo & Jackson, 1998; Amorosi & Prevosti, 2008; Prevosti *et al.*, 2009, 2011). A list of specimens and definition of measurements utilized are provided in Supporting Information (Appendix S2). We performed a Principal Component Analysis (PCA) from the variance–covariance matrix of the ln transformed measurements following Prevosti *et al.* (2009, 2011) to evaluate the identification of the new specimens. A biplot between the length of first and second lower molar follows Prevosti *et al.* (2009, 2011). See Supporting Information, Appendix S7 for more details of these analyses. To improve sample sizes we included a large number of unpublished archaeological/paleontological specimens of *Lycalopex culpaeus*, *L. griseus* and *Dusicyon avus* (Supporting Information, Appendix S2).

NEW TAXON DATES, EXTINCTION AGE ESTIMATION, AND STABLE ISOTOPES

New accelerator mass spectrometry (AMS) ^{14}C dates produced by the National Science Foundation (NSF) – Arizona Accelerator Mass Spectrometry Laboratory (AA; University of Arizona, Tucson, USA), Centro de Datazione e Diagnostica (LTL; Università del Salento, Brindisi, Italy), and Beta Analytic (Beta; Miami,
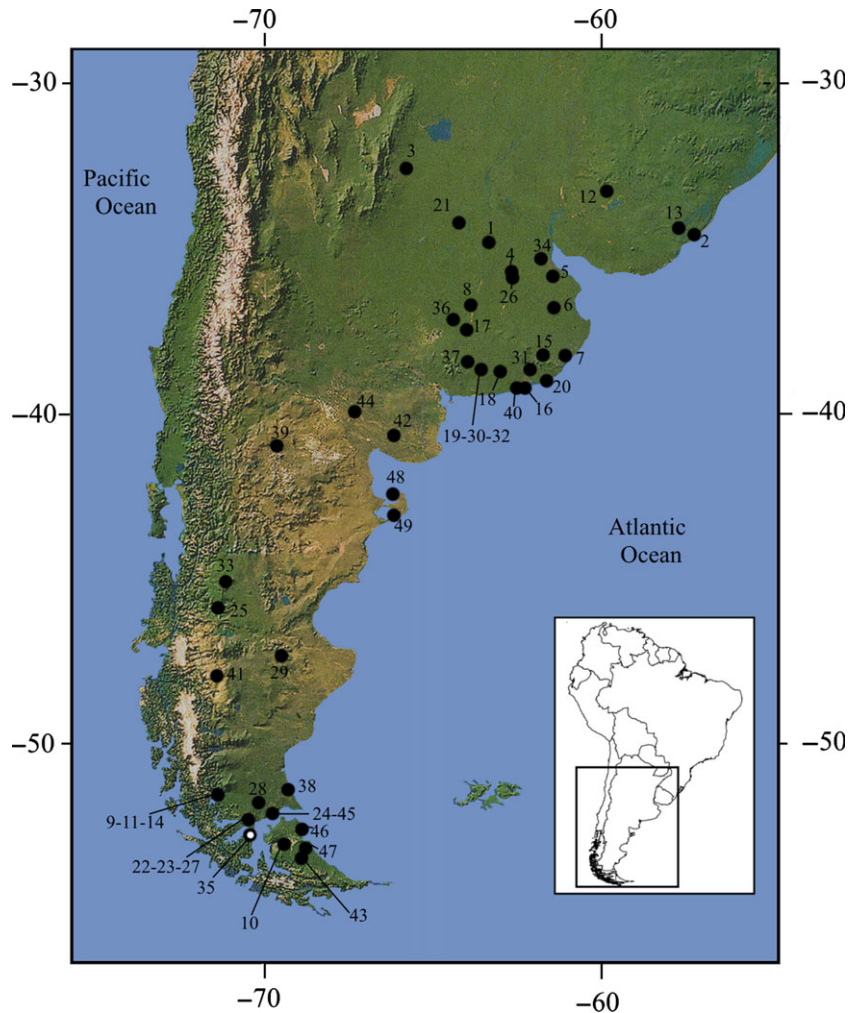
Figure 1. Map of South America's southern cone showing the distribution of the localities of *Dusicyon avus* (see Appendix S1).

USA), were obtained from five *D. avus* specimens. Calibrations of ^{14}C dates were calculated with the program CALIB 7 available at http://intcal.qub.ac.uk/calib/ (Stuiver & Reimer, 1993; Reimer *et al.*, 2009), using the SHCal13 curve (Hogg *et al.*, 2013) and two sigma ranges. To estimate the age of extinction of *D. avus* we used the GRIWM method, with an R 3.0.1 script (R Core Team, 2013) obtained from C. Bradshaw and F. Saltre, which weighs observations inversely according to the temporal distance from the last confirmed observation of a species (Bradshaw *et al.*, 2012). As some of the dates had large errors, and there were few dates between 4000 and 1000 years cal BP (Supporting Information, Appendix S3) that could bias the GRIWM results (F. Saltre, pers. comm.), we first run a model analysis reducing the error of four dates with values larger than 150 to 90 cal years. To address the second source of bias we used the younger eight dates, all of

which are <4000 cal BP (Supporting Information, Appendix S4).

Stable isotopes ($\delta^{13}C$, $\delta^{15}N$) data were obtained from the dated specimens and compared with published data for *D. avus* to determine the potential existence of dietary variability (Supporting Information, Appendix S8; for the interpretation of dietary signals with these isotopes, see Bocherens & Drucker, 2003; Fox-Dobbs *et al.*, 2007; Yeakel *et al.*, 2013).

POTENTIAL DISTRIBUTION MAPS

To explore the role that climate change may have had in affecting the distribution of *D. avus*, we performed potential distribution models using MaxEnt v.3.3.e (Elith *et al.*, 2006; Phillips, Anderson & Schapire, 2006), using specimens of different ages and two different climatic variable datasets. This software was chosen because it performs better than

alternatives with presence-only data (Elith *et al.*, 2006). We used the WorldClim database for present climatic conditions (Hijmans *et al.*, 2005), with a spatial resolution of ~ 1 km², and the CCSM4 database (Gent *et al.*, 2011) for climatic information for the middle Holocene (i.e. 6000 years), with a spatial resolution of 2.5 km². Both environmental datasets contain monthly precipitation and temperature information, and 19 bioclimatic variables. We generated two potential distribution models: one including only middle Holocene localities and the 6000 years BP database (6 ka), and the other including only late Holocene localities and the 'actual' database (0 ka). Because there is an appreciable interval between the late Holocene fossils themselves and the modern environmental conditions in the WordClim database, there was a risk that the distribution of *D. avus* in the 0 k model would be biased by greater present-day humidity. To explore this alternative we ran an analysis using the middle Holocene database and the late Holocene localities of *D. avus* (6 kaB).Ten replicates were performed for each model, with 25% of localities used as test data, random seed and 10 000 background points. We used the cumulative output and assigned predictive values of 100–51, 50–26, 25–11, 10–2 and 1–0 (Fig. 6). Variable contributions were analyzed with jackknife tests and model predictions with a threshold independent measure, the area under the receiver operator curve (AUC) (Phillips *et al.*, 2006). The AUC is interpreted as the probability that a randomly chosen present location is ranked higher that a randomly chosen background point (Merow, Smith & Silander, 2013). It varies between 0 and 1, with an AUC of 0.5 meaning that the model does not perform better than would a random model (Hernández *et al.*, 2006).

To evaluate the effects of climatic change across time, we extracted climatic information (i.e. mean annual temperature, and annual precipitation) for each recorded in *D. avus* locality from three climatic databases, the two mentioned above as well as a third for the Last Glacial Maximum database (Collins *et al.*, 2006).

ABBREVIATIONS

i/I: lower/upper incisor, respectively; c/C: lower/upper canine, respectively; p/P: lower/upper premolar, respectively; m/M: lower/upper molar, respectively; CEHA: Centro de Estudio del Hombre Austral, Instituto de la Patagonia, Universidad de Magallanes, Punta Arenas, Chile; MC: Colección Marcelo Carrera, Puerto Madryn, Chubut Argentina; MCA: Museo 'Carlos Ameghino', Mercedes, Buenos Aires, Argentina; MPEF-PV: Museo Paleontológico 'Egidio Feruglio', Trelew, Chubut, Argentina.

RESULTS

TAXONOMIC IDENTIFICATION

MCA 81-VI-1-1 is composed of an incomplete rostrum with part of the maxillary and premaxillary bones and left and right I3-M2; incomplete left and right mandibles with right c1-p1, broken p2 and p3-m1, and left c1-p2 and p4-m2 (m1 is broken; Figs 2–4, Supporting Information, Appendices S5, S6). The left p3 alveolus was reabsorbed, indicating that this tooth was lost while the animal was alive; the permanent dentition is in its final position and is moderately worn, suggesting an adult individual. CEHA 5131 is a nearly complete skull (right zygomatic arch and pterygoid bones are broken) with broken right P4, nearly complete left P4 and complete left M2 (Figs 2–4, Supporting Information, Appendices S5, S6). MC 787 and MPEF-PV 10887 are right and left mandibles, respectively. The dentition is nearly complete, but the i1-3, p1 and m3 were not preserved in the MC 787, while the m3 was missing in MPEF-PV 10887 (Figs 2–4, Supporting Information, Appendices S5, S6).

The new specimens are clearly separable from domestic dogs due to the presence of several cranial and dental traits that separate *Dusicyon* and *Canis* (see Pocock, 1913; Berta, 1989; Tedford, Taylor & Wang, 1995; Prevosti, 2010). These include: (1) the occipital forming a more rounded inion that is not so expanded posteriorly, while in *Canis* the inion is very pointed and posteriorly projecting; and (2) the jugal bone has a scar for the superficial masseter m. that is wider in *Dusicyon* than *Canis*, which instead exhibits a steeper forehead front with a more developed frontal sinus (Figs 2–4, Supporting Information, Appendices S5–S7). The dentition of *Canis familiaris* is more robust, with more bunodont teeth (e.g. molars, premolars), lower and more robust principal cusps in the premolars (especially the p4), shorter and more robust canines, and I3 with a strong mesiolingual cingulum. The M1 has a more reduced labial cingulum and a proportionally larger and more bunodont paracone, while the m1 has a stouter trigonid and a more reduced metaconid and entoconid (Figs 2–4, Supporting Information, Appendices S5–S7; Prates, Prevosti & Berón, 2010; Prevosti, 2010).

Similarly *Chrysocyon brachyurus* is easily distinguished from *D. avus* due to a larger skull, with proportionally narrower palate and rostrum, stronger sagittal crest, slender zygomatic arches, more hypocarnivorous dentition (proportionally smaller carnassials and larger M1–2 and m2–3; proportionally larger protocone in the P4, and talonid and metaconid in the m1) with taller premolars (Kraglievich, 1930; Langguth, 1970; Figs 2–4, Supporting Information, Appendices S5–S7).
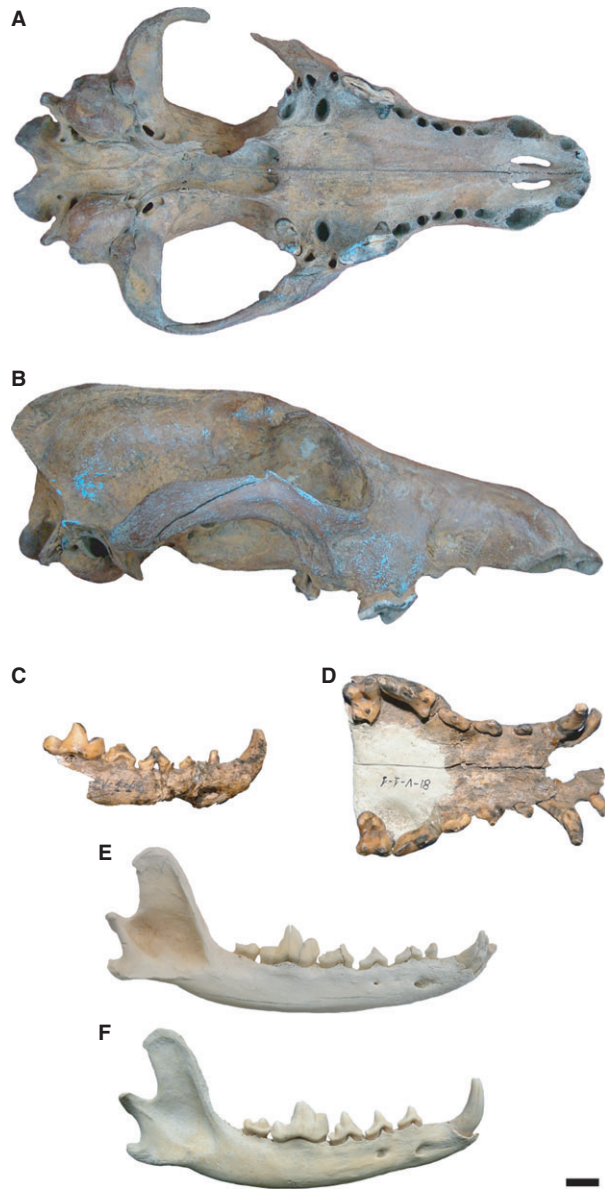
Figure 2. Specimens of *Dusicyon avus* included in this study. A, Skull in ventral view (CEHA 5131). B, Skull in lateral view (CEHA 5131). C, Right mandible in lateral view (MCA 81-VI-1-1). D, Palate in ventral view (MCA 81-VI-1-1). E, Left mandible in lateral view (MPEF-PV 10887; reflected). F, Right mandible in lateral view (MC 787). Scale bar = 10 mm.

Using size and evidence of a more carnivorous dentition, we were able to separate the new specimens from other South American living foxes (e.g. *Cerdocyon thous*, *Lycalopex gymnocercus*). We then differentially compared them with *L. culpaeus*, *Dusicyon australis* and *D. avus*. The new specimens present a set of characters that are diagnostic of *D. avus*. These include the presence of a well developed hypoconulid in the m1, a second accessory cusp and a

narrowed distal cingulum in the p4 (in *L. culpaeus* is low and wide), and a protocone placed lingually in the P4 (in *L. culpaeus* is placed mesially or mesiolingually; Prevosti *et al.*, 2011; Figs 2–4, Supporting Information, Appendices S5–S7). The new specimens have proportionally wider postorbital constrictions and processes, larger m1 in relation to m2 and a wider bulla, which are characters that are shared with *D. australis* (Prevosti *et al.*, 2011; Figs 2–4, Supporting Information, Appendices S5–S7). *D. australis* has a more reduced protocone in the P4 and smaller metaconid in the m1 than *D. avus*. The principal cusps of the premolars are taller and more acute in *D. australis* (specially the p4), the distal cingulum of the p4 is narrower and more acute in *D. australis*. In some specimens the cingulum was raised and cusp-like, but a true second accessory distal cusp is not present (Prevosti *et al.*, 2011; Figs 2–4, Supporting Information, Appendices S5–S7). The secondary palate is posteriorly extended just at the level of the distal border of the M2, while in *D. avus* it ends more anteriorly (at the level of the distal half of the M2; Figs 2–4, Supporting Information, Appendices S5–S7; Berta, 1989). The sagittal crest is more developed in several specimens of *D. avus*, while the studied *D. australis* presents a lyriform area delimited by the temporal crests (Figs 2–4, Supporting Information, Appendices S5–S7; Berta, 1989).

Morphometric analyses (i.e. Principal Component Analysis and biplot graph) were compatible with this comparison and supported the separation of *D. avus* from other similar sized South American wild canids (see Supporting Information, Appendix S7).

SITE INFORMATION, NEW TAXON DATES, ESTIMATED AGE OF EXTINCTION, AND STABLE ISOTOPES

MCA 81-VI-1-1 was discovered at the archaeological site of Río Luján 1; it was never fully described, and was initially tentatively associated with *Chrysocyon brachyurus* (Kriskautzky, 1975), later with *Canis familiaris* (Tonni & Politis, 1981). Here we conclusively refer it to *D. avus* (see also Prevosti, Bonomo & Tonni, 2004; Prevosti *et al.*, 2011). Río Luján 1 was a burial site containing six humans, one of them associated with both a jaguar (*Panthera onca*) and MCA 81-VI-1-1 (Petrocelli, 1975). The site is located in northeast Buenos Aires province (34°17′5″S, 58°52′30″W; Argentina), near the Paraná fan (Petrocelli, 1975; Salemme & Tonni, 1983; Fig. 1); the burial was dated to *c.* 600 cal years BP (Toledo, 2009; Bonaparte, Migale & Buide, 2011). This is in good agreement with the date for the *D. avus* specimen, 724 ± 52 ^{14}C year BP (AA102584; 553–718 cal years BP; Supporting Information, Appendix S3).
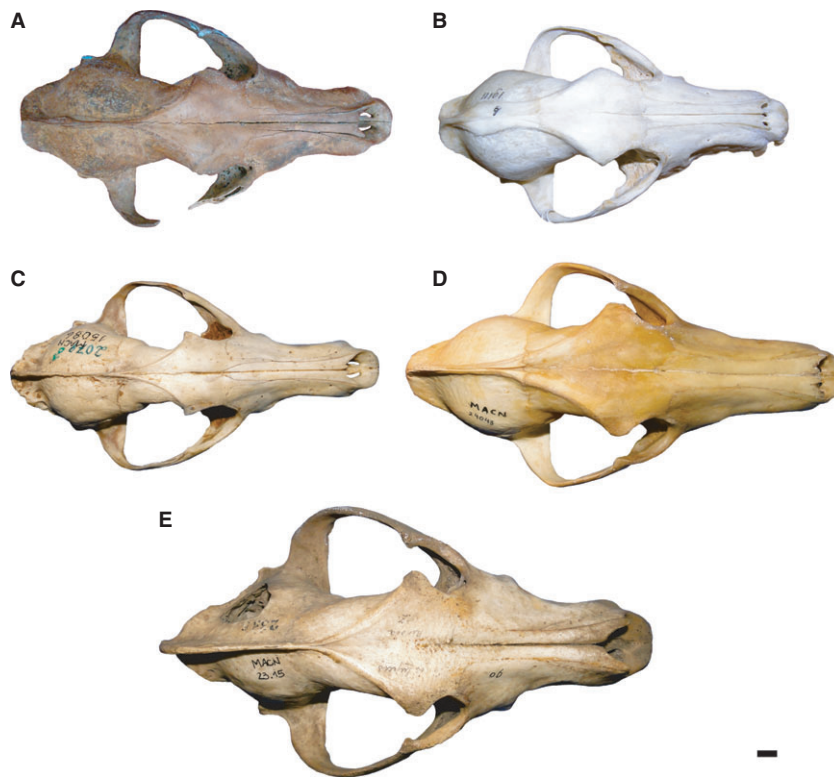
Figure 3. Dorsal view of a skull of *Dusicyon avus* compared with other canids. A, *Dusicyon avus* (CEHA 5131). B, *Dusicyon australis.* C, *Chrysocyon brachyurus.* D, *Lycalopex culpaeus.* E, *Canis familiaris.* Scale bar = 10 mm.
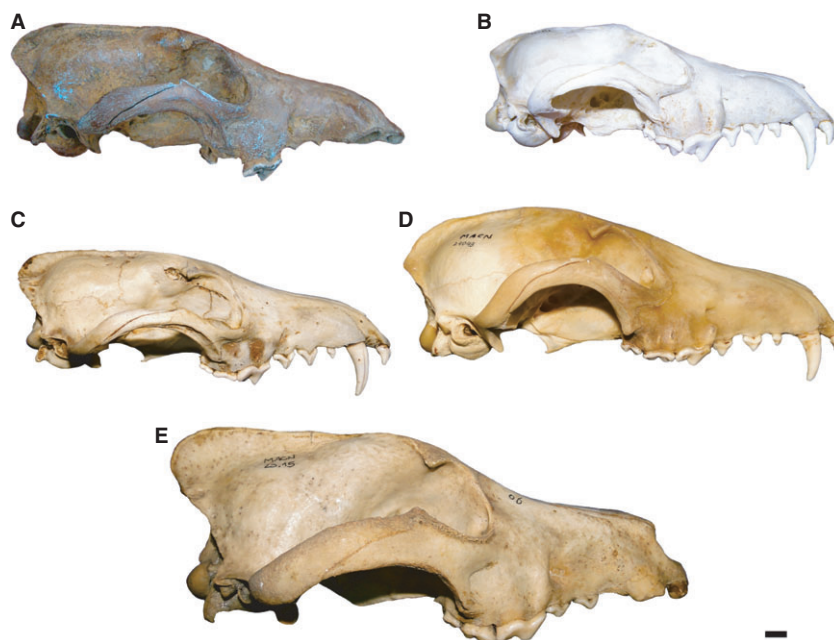

Figure 4. Lateral view of a skull of *Dusicyon avus* compared with other canids. A, *Dusicyon avus* (CEHA 5131). B, *Dusicyon australis.* C, *Chrysocyon brachyurus.* D, *Lycalopex culpaeus.* E, *Canis familiaris.* Scale bar = 10 mm.

CEHA 5131 was recovered from the historical site of Dinamarquero, situated on the northern margin of the Magellan Strait in southern Patagonia (52°24′57″ S, 70°35′02″W, Chile; Martinic & Prieto, 1986; Fig. 1). This site is an Aonikenk base camp characterized by abundant glass and metal tools, in use during the 19th century between at least 1833 and1896 (Martinic & Prieto, 1986; Martinic, 1995). Even though CEHA 5131 was found near a peat bog close to the centre of Dinamarquero, there was no evidence that it is linked with the Aonikenk occupation in any way. CEHA 5131 was dated to 400 ± 30 ^{14}C years BP (Beta365051; 324–496 cal years BP; Supporting Information, Appendix S3).

MC 787 and MPEF-PV 10887 were found in sand dune deposits in Península Valdés (Chubut, Argentina; Fig. 1), Punta Buenos Aires (42°14′3″S, 64°21′3″ W) and Playa Colombo (42°38′1″S, 64°12′1″W), all of which contain important vertebrate remains in surface assemblages (Udrizar Sauthier, 2009). MC 787 includes postcranial elements, and some ribs were used to dated it in 1112 ± 40 ^{14}C years BP (LTL13408A; 922–1060 cal years BP; Supporting Information, Appendix S3). MPEF-PV 10887 was dated to 589 ± 45 ^{14}C years BP (LTL13407A; 503–638 cal years BP; Supporting Information, Appendix S3).

A fifth *D. avus* specimen, consisting of a lower mandible with p2-m1 (CEHA CP B.B2) was found in Cueva del Puma in the Pali Aike volcanic field (52°05′37″S, 69°44′31″W; Magallanes, Chile; Martin, 2013), and was dated to 2030 ± 44 ^{14}C years BP (Beta276516; 2091–2326 cal years BP), within the previously published date range for this species (Supporting Information, Appendix S3).

GRIWM analysis using all samples indicated that *D. avus* would have become extinct during the 20th century (*c.* 1950), with a median date of 0 cal years BP. Such an analytical result theoretically implies that it might still be extant, since the upper confidence limit (2.5%) is 441 cal years after 1950. The lower confidence limit (CI; 97.5%) is 463 cal years BP. Additional GRIWM runs gave similar results (see Fig. 5; Supporting Information, Appendix S4).

Stable isotope ratios collected from Río Luján 1 δ^{13}C: −12.8, δ^{15}N: 9.6, and Dinamarquero specimens exhibit values of δ^{13}C: −20.2 and δ^{15}N: 9.6. The δ^{13}C values for MC 787 and MPEF-PV 10,887 were −18.9 and −19.9, respectively. These values were within the previously published data range (see Supporting Information, Appendix S8), with the exception of the Río Luján specimen which was more positive (δ^{13}C value, −16.8; Supporting Information, Appendix S8).

DISTRIBUTION AND POTENTIAL DISTRIBUTION MODELS

A potential distribution model 6 ka was performed with eight middle Holocene localities (Fig. 6, Supporting Information, Appendix S9). High predictive values were attained for southern and central Patagonia and western Argentina at 29°S, and mean predictive values along northern Patagonia and the Argentine Pampas (Fig. 6). Model 0 ka was performed with 13 late Holocene localities (Supporting Information, Appendix S9), and returned a southern displacement of high predictive values for Buenos Aires province, while southern Patagonia remained with high predictive values (Fig. 6). Model 6 kaB showed a pattern more similar to model 6 ka than to model 0 ka.

Jackknife tests suggested that for the 6 ka model the most important environmental variables were temperature seasonality, isothermality and January maximum average temperature, whereas altitude and August minimum temperature were more relevant for models 0 ka and 6 kaB (Supporting Information,
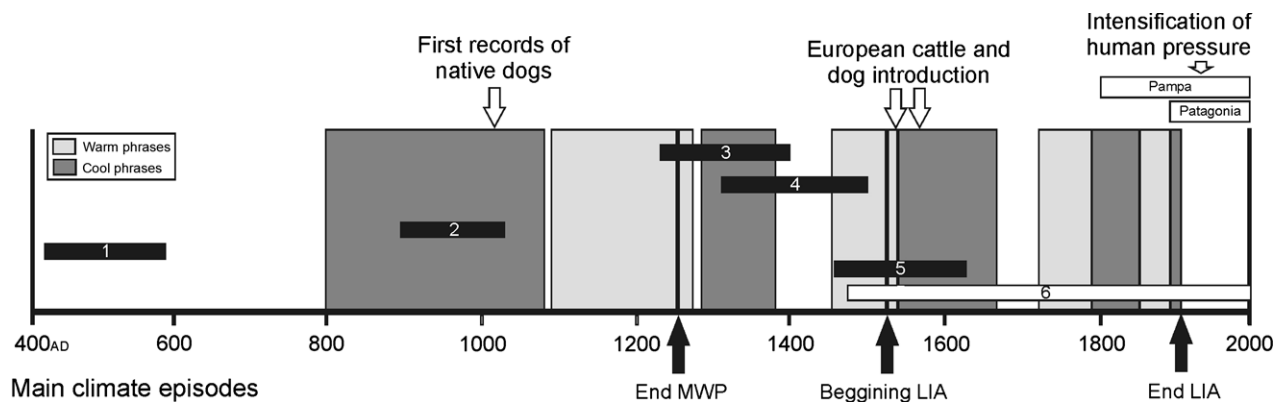

Figure 5. Records and estimated age of extinction of *Dusicyon avus*, climatic change and cultural events in Pampean and Patagonian regions during the late Holocene. (1) Cueva de los Chingues specimen. (2) Punta Buenos Aires specimen. (3) Río Luján specimen. (4) Playa Colombo specimen. (5) Dinamarquero specimen. (6) GRIWM estimation of the age of extinction. LIA, Little Ice Age; MWP, Medieval Warm Period.
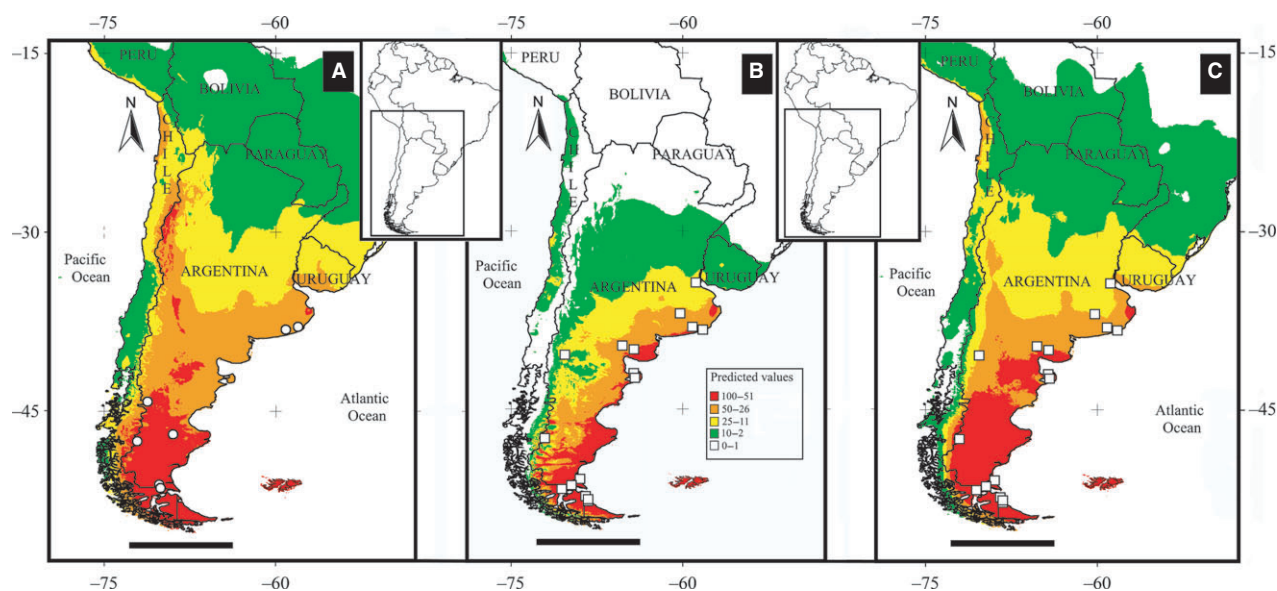
Figure 6. Potential distribution models for *Dusicyon avus*. A, Model based on the middle Holocene climatic database and middle Holocene *D. avus*. B, Model based on the present climatic database and late Holocene specimens. C, Model based on the middle Holocene climatic database and late Holocene specimens. Predictive values are 51–100 (red), 26–50 (orange), 11–25 (yellow), 2–10 (green), and 0–1 (white).

Appendix S9). All models presented better predictions that those randomly generated, with high AUC values: 6 ka, 0.997 ± 0.002; 0 ka, 0.957 ± 0.049; 6 kaB, 0.997 ± 0.002.

Considering all the Holocene localities studied, mean annual temperature during the Late Glacial Maximum (LGM) was 5.7 °C (−3.3 to 12.8 °C) and annual precipitation was 446 mm (152–1159 mm). Mean annual temperature of record localities in 6 ka was 9.8 °C (4.4–16.4 °C) and annual precipitation was 483 mm (186–977 mm; Supporting Information, Appendix S10). Mean annual temperature of record localities in the actual database was 10.5 °C (5.3–16.8 °C) and annual precipitation was 517 mm (197–1085 mm). The upper precipitation limit was smaller when only the localities used in the model 6 ka and model 0 ka were included: 765 mm for the middle Holocene, and 995 mm for the actual climatic database (Supporting Information, Appendix S10). Due to some uncertainty we excluded the Río Luján specimen, that could have been collected elsewhere and brought in by humans (see below), and the northern Pampas specimens (Laguna El Doce and Estación J. M. García), that lacked chronological data (they had a 'Holocene' age and the last one could be from the Early Holocene, see Prevosti & Pardiñas, 2001). Using this reduced sample we found a decrease of ~1 °C in the maximum of the mean annual temperature and >100 mm in the maximum annual precipitation.

DISCUSSION

AGE OF EXTINCTION

Based on an archaeological context a late Holocene extinction of *Dusicyon avus* was proposed in the 1970s and 1980s, (Caviglia, 1978, 1986; Berman & Tonni, 1987; Berman, 1994; Mansur, 2006, 2007), but was only recently confirmed by direct taxon dates using [14]C. Absolute chronology places *D. avus* last occurrence at *c*. 3000 years ^{14}C BP (Prevosti *et al.*, 2011). Martin (2013) published a taxon date of 1600 ± 40 years ^{14}C BP (1361–1536 cal years BP) based on remains found in Cueva de los Chingue, near the Magellan Strait in Chile. Similarly, Prates & Di Prado (2013) obtained a date of 2057 ± 38 years ^{14}C BP (1885–2081 cal years BP) from material recovered in Negro Muerto 2 in northern Patagonia, Argentina (Fig. 1). Our new data extend *D. avus* biochron to <1000 years ^{14}C BP, with the last record in the Pampean region at *c*. 700 ^{14}C years BP (AD 1232–1397 years), and the most recent record in southernmost Patagonia with an age of *c*. 400 years ^{14}C BP (AD 1454–1626 years). These dates would suggest that *D. avus* extinction could have occurred after the arrival of Europeans to South America (Fig. 5; Supporting Information, Appendix S3). The extinction estimate using GRIWM overlaps with the younger ^{14}C, suggesting that the extinction could have happened since 463 cal years BP (AD 1482 years). Indeed, the species could even be living

today, since the estimated age of extinction lays in the future, with a median value that falls in the middle of the 20th century (Fig. 5; Supporting Information, Appendix S3), supporting the idea that *D. avus* disappearance might have happened after the European arrival. If this is correct, *D. avus* might have been living in historical times, and even observed by naturalists and explorers travelling the southern portion of the subcontinent during the last few centuries. Unfortunately, there is no solid evidence reported from diaries and notes written during the 18th to 20th centuries to support the occurrence of a large canid attributable to *D. avus* then. The most intriguing observation was noted by George Musters who, inspired by Charles Darwin's diary, crossed 3000 km of Patagonian territory between 1869 and 1870 (Rey Balmaceda, 1976). Musters (1871) wrote 'On another occasion, when hunting, we made a circle, finishing off in the wooded district near the banks of the river [= Tecka river]. On our return we hunted over a park-like country, with alternate open glades and woods. Here we killed a doe red deer and a large description of fox, apparently identical with the Falkland Island species – *Lupus antarcticus* [= *D. australis*]'. This observation was made about 43°S, in the western portion of Chubut province near the Andean forest piedmont (Rey Balmaceda, 1976) and might have been one of the last observations of *D. avus*. An unusual large fox was also mentioned for Tierra del Fuego (Lothrop, 1928). Together with 'Aguaras' reported in the 19th century in northern Patagonia and the Pampean region (and uncritically assigned to *Chrysocyon brachyurus*; Prevosti *et al.*, 2004), these could have been in fact *D. avus* specimens. However attractive this interpretation is, and bearing the support of the GRIWM results, the available information is not enough to corroborate this hypothesis (Prevosti *et al.*, 2004, 2011).

DISCLOSING THE CAUSE FOR *D. AVUS* EXTINCTION

Three hypotheses have been advanced to explain the extinction of D. *avus* (Berman & Tonni, 1987), namely either (a) change toward a more humid climate, (b) hybridization with domestic dogs, or (c) the impact of native human population. Prevosti *et al.* (2011) showed that between the Late Pleistocene and late Holocene, *D. avus* occupied a large area (estimated at 762 351 km²) that encompassed the Pampean region and Patagonia (including Tierra del Fuego) that experienced significant climatic and environmental changes, particularly in the Holocene (Clapperton, 1993; Markgraf, 1993; Prieto & Stutz, 1996; Tonni, Cione & Figini, 1999, 2001; Mancini, 2003; Schäbitz, 2003; Grill *et al.*, 2007; Mancini *et al.*, 2008; Borromei *et al.*, 2010; Pardiñas & Teta,

2013; Tammone *et al.*, 2014). Climatic variations recorded in the last 1000 cal years, including the Medieval Warm Period and the Little Ice Age 'events' impacted the southern cone of South America (Politis, 1984; Tonni *et al.*, 1999, 2001; Deschamps, Otero & Tonni, 2003; Favier-Dubois, 2007; Borromei & Quattrocchio, 2008; Waldmann, 2008; Tonello & Prieto, 2010; Ponce *et al.*, 2011; Pardiñas, Udrizar Sauthier & Teta, 2012; Del Puerto *et al.*, 2013; Mancini & Graham, 2014; Teta *et al.*, 2014), but there is no evidence to suggest that these climatic anomalies were more deleterious than those which characterized the Late Pleistocene–Holocene, the middle Holocene, or even the Neoglacial advance (Mancini *et al.*, 2008; Tonello & Prieto, 2010; Mancini & Graham, 2014). In conclusion, there is no compelling linkage between climatic changes and the extinction of this hitherto widespread fox species (Prevosti *et al.*, 2011; Fig. 5).

The climatic parameters obtained from the climatic databases and the distribution models are congruent with the interpretation that *D. avus* inhabited open areas (e.g. grass steppe, shrub steppes) under a wide range of climatic conditions (Fig. 5). The models also show that most recorded localities experienced arid to semiarid conditions (i.e. annual precipitation < 800 mm), with variable temperature and precipitation, and high seasonality and isothermality (Supporting Information, Appendix S9). This would support the hypothesis that at least in Buenos Aires province the distribution of *D. avus* was related to more arid conditions, as has been suggested for the middle and late Holocene (e.g. Tonni *et al.*, 1999; Mancini *et al.*, 2005). Several mammal species presently associated with dry environments disappeared from their Pampean ranges during the late Holocene, including ungulates (e.g. *Lama guanicoe*; Tonni & Politis, 1980; Politis & Pedrotta, 2006; Politis *et al.*, 2011), mustelids (*Lyncodon patagonicus*; Prevosti & Pardiñas, 2001; Schiaffini *et al.*, 2013), and marsupials (*Lestodelphys halli*; Prado, Goin & Tonni, 1985; Goin, 1995, 2001). A plausible explanation would be that these range retractions were triggered by a regional change to more humid conditions (Tonni *et al.*, 1999; Stutz, Prieto & Isla, 2006; Tonello & Prieto, 2010; Del Puerto *et al.*, 2011). We verified an additional regional extirpation of *D. avus* during the late Holocene for the northeastern portion of Chubut province, probably connected with the southward advance of the Monte shrubland during warmer and drier conditions (Medieval Warm Period and present). A similar situation involving small marsupials and rodents (e.g. *Abrothrix olivacea*, *Lestodelphys halli*) has been documented for eastern Patagonia (Pardiñas *et al.*, 2012; Udrizar Sauthier & Pardiñas, 2014). However, although these climatic changes

could be linked with local retractions, they were arguably not enough to trigger the extinction of a widespread fox species.

The presence of *D. avus* in a burial site in Río Luján 1 around 700 ^{14}C years BP contravenes the climate hypothesis, as warmer and wetter conditions related to the Medieval Warm Period were prevalent in the Pampean region at this time. This specimen might have been transported for ritual purposes from elsewhere, or might have been a tame animal (Prates, 2014). A similar explanation has been invoked for a late Holocene *Lama guanicoe* record in northeast Buenos Aires province (Politis & Pedrotta, 2006; Politis *et al.*, 2011).

The second hypothesis advanced to explain the extinction of *D. avus* by Berman & Tonni (1987) – through hybridization with domestic dogs – was also discarded, as there is no evidence of hybridization in the morphology of the skull and dentition of *D. avus* nor in its mitochondrial DNA (Prevosti *et al.*, 2011; Austin *et al.*, 2013). We also failed to find any evidence of hybridization in the morphology of the new specimens, but this hypothesis remains unlikely, as hybridization with domestic dogs seems to be restricted only to the genus *Canis* (e.g. *Canis lupus*, *C. simensis*; Gottelli *et al.*, 1994; Vilà & Wayne, 1999; Macdonald & Sillero-Zubiri, 2004; Sillero-Zubiri, Hoffmann & Macdonald, 2004), and there are no records of such hybridization in living South American canids. More ancient DNA sequencing (including nuclear DNA) will be needed to further test this hypothesis.

Dusicyon avus were used by humans during the Holocene for ritual purposes, as suggested by its inclusion in burials, and its teeth were probably utilized in necklaces (Messineo & Politis, 2007; Prates *et al.*, 2010; Prevosti *et al.*, 2011; Laporte, 2014; Politis, Barrientos & Scabuzzo, 2014; Prates, 2014). Based on the frequency and the skeletal elements (mostly teeth) found in archaeological sites, Bonomo (2006) surmised that the species had a high symbolic value for aboriginal peoples. Prates (2014) inferred that a specimen from Loma de los Muertos was intentionally buried, and may have been tamed, a practice recorded for other fox species in historical times (Stahl, 2013). The increase of human populations during the late Holocene (since 3000 cal years BP; Borrero, 2008b; Martínez & Gutiérrez, 2008; Salemme & Miotti, 2008; Morales *et al.*, 2009) may have intensified the use of this species with a consequent impact on its populations (cf. Prevosti *et al.*, 2011). The new radiocarbon dates indicate that *D. avus* extinction happened very recently, perhaps as recently as the period following the arrival of Europeans. This opens the possibility that environmental modifications generated by European colonization could have caused the disappearance of this fox. Yet, the impact of pre-European populations cannot be discarded, and in fact both could be involved, as the introduction of cattle and horses changed the habits of hunter–gatherer societies in the Pampean and Patagonian regions (Huber & Markgraft, 2003; Garavaglia, 2012). Similarly, the new dates overlapped with the introduction of domestic dogs in these regions (first by early settlers around 1000 years BP, and later by Europeans; Cabrera, 1934; Prates *et al.*, 2010; Fig. 5). Large packs of feral dogs were recorded in the Pampean region in the 18th and 19th centuries (Cabrera, 1934), and the influx of European dogs may have led to an extensive replacement of the native American dogs (Castroviejo-Fisher *et al.*, 2011; but see Van Asch *et al.*, 2013). Domestic dogs could have a negative impact on *D. avus*, as vectors of canid-related diseases such as rabies or canine distemper virus, and as competitors for similar prey species as it happens in extant wild canids (Sillero-Zubiri *et al.*, 2004), or through direct predation using dogs as hunting aids (see below).

Since the Europeans settled in the Pampean and Patagonian regions important environmental changes have taken place, triggering the local extinction or population decline of several large mammals, including primary consumers and predators. Well known cases include the regional extinction of *Panthera onca*, and dramatic populational reductions of *Puma concolor* and Pampas deer *Ozotoceros bezoarticus* (Galliari, Berman & Goin, 1991). In addition, important changes in micromammal assemblages have been recorded since the 19th century in the Pampean region and since the late 19th and early 20th centuries in Patagonia (Williams, 1975; Galliari *et al.*, 1991; Aagesen, 2000; Martinic, 2002; Huber & Markgraft, 2003; Prieto *et al.*, 2004; Haberzettl *et al.*, 2006; Chebez, 2008; Medan *et al.*, 2011; Garavaglia, 2012; Lattes & Andrada, 2012; Masse, 2012; Reboratti, 2012; Belardi & Espinosa, 2013; Teta *et al.*, 2014). The introduction of cattle and horses in 1536–1580 (Cardiel, 1930; Rapoport, 1996; Garavaglia, 2012) may have brought about changes in vegetation – particularly plant extinctions and the introduction of alien species – and impacted the native communities; such changes may have also affected fire patterns in Patagonia (Huber & Markgraft, 2003; Fig. 5).

Mid-sized canids are typically generalist and therefore it is intriguing to speculate as to why *D. avus* would have been so heavily affected by these potential threats, especially taking into account that it was a medium-sized canid with a generalized dentition and diet (Prevosti & Vizcaíno, 2006; Prevosti *et al.*, 2011; Prevosti & Martin, 2013). Some living canids, especially the larger, more carnivorous species (e.g. *Canis lupus*, *Lycaon pictus*) or those limited

to small geographic areas (e.g. *C. simensis*), are more likely to be heavily affected by burgeoning human populations, and to suffer range and population reductions, but they still manage to subsist in more remote, wilderness areas (Mech & Boitani, 2003; Macdonald & Sillero-Zubiri, 2004; Sillero-Zubiri *et al.*, 2004). In contrast, other more generalist canids (e.g. *Canis latrans*, *C. aureus*, *Lycalopex culpaeus*) have experienced recent population or distribution expansions (Novaro, 1997; Sillero-Zubiri *et al.*, 2004). Thus, it is difficult to understand why these threats could be the cause of the extinction of *D. avus*.

Stable isotopes suggest that *D. avus* in the Late Pleistocene of southern Patagonia had a more carnivorous diet than living foxes, and could scavenge large and mega- mammals (Prevosti & Martin, 2013). The $\delta^{13}C$ and $\delta^{15}N$ values are consistent with a carnivorous diet (Supporting Information, Appendix S8), but display some variability (especially in $\delta^{13}C$ values). Río Luján 1 specimen has a much higher $\delta^{13}C$ values which indicate the consumption of C4 rather than C3 plant feeders). This could be a valid interpretation because C4 plant feeders (i.e. cervids) were present in the northeast of Buenos Aires province around the time of the *D. avus* burial (Loponte & Corriale, 2013), although we cannot discard an alternative explanation that this fox was kept as a pet by native peoples (Prates, 2014). More stable isotopic data are needed to test this hypothesis, but the variability observed in the limited isotopic data currently available is congruent with some degree of generalization in the fox's diet and large areal distribution (see above).

A COMBINATION OF CAUSAL FACTORS?

Changes in population densities and the behavior of early settlers in the southern cone of South America, followed by the impact of the European colonization and a climatic trend to more humid conditions, could have come together during the late Holocene in such a manner that there was a strong impact upon *D. avus* populations that had probably already suffered some reduction, as has been proposed for the Pleistocene-Holocene megafauna extinction (Cione *et al.*, 2008). In this scenario *D. avus* would have been more heavily affected because it was more carnivorous and larger than other South American foxes (Prevosti & Vizcaíno, 2006; Prevosti *et al.*, 2011; Prevosti & Martin, 2013). Furthermore, the few genetic data available would indicate that the species had low genetic variability (Austin *et al.*, 2013), something that could be related to low population densities or a population bottleneck (Chan *et al.*, 2005; Chan, Anderson & Hadly, 2006). If this inference is correct, *D. avus* would have been more sensitive to external threats (e.g. human impact, climatic change, or in combination; Frankham, 2005; Jansson *et al.*, 2012; Frankham, Bradshaw & Brook, 2014; Marris, 2014; but see Rodríguez *et al.*, 2011) than other canids. Conversely, *D. avus* had a wide distribution, apparently restricted to open environments (e.g. Patagonian steppe, Pampas), while *Lycalopex culpaeus* is also present in forested region in Patagonia and widely distributed along the Andes to northern South America (Macdonald & Sillero-Zubiri, 2004; Sillero-Zubiri *et al.*, 2004). Other living southern cone canids are also restricted to open environments and their distributions are not necessarily larger, but also occur in more closed environments such as the Monte or Chaco (e.g. *Lycalopex gymnocercus*; Macdonald & Sillero-Zubiri, 2004; Sillero-Zubiri *et al.*, 2004). The more open and nonforested environments would have had fewer areas offering refuges for this species, exposing it to human impact.

Summing up, the new data and the available information clearly support a 'multi-causal' process, in which environmental change and human impact interacted causing the recent extinction of *D. avus*.

REFERENCES

Aagesen D. 2000. Crisis and conservation at the end of the world: sheep ranching in Argentine Patagonia. *Environmental Conservation* **27:** 208–215.

Amorosi T, Prevosti FJ. 2008. A preliminary review of the canid remains from Junius Birds excavations at Fell's and Pali Aike caves, Magallanes, Chile. *Current Research in the Pleistocene* **25:** 25–27.

Austin JJ, Soubrier J, Prevosti FJ, Prates L, Trejo V, Mena F, Cooper A. 2013. The origins of the enigmatic Falkland Islands wolf. *Nature Communications* **4:** 1552.

Barnosky AD, Koch PL, Feranec RS, Wing SL, Shabel AB. 2004. Assessing the causes of Late Pleistocene extinctions on the continents. *Science* **306:** 70–75.

Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB, Charles Marshall C, McGuire JL, Lindsey EL, Maguire KC, Mersey B, Ferrer EA. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* **471:** 51–57.

Belardi B, Espinosa S. 2013. Inferencias paleoambientales a partir del análisis polínico de sitios arqueológicos del área del lago San Martín (Santa Cruz, Argentina). *Magallania* **41:** 155–169.

Berman WD. 1994. Los carnívoros continentales (Mammalia, Carnivora) del Cenozoico en la provincia de Buenos Aires. PhD Thesis, La Plata: Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.

Berman WD, Tonni EP. 1987. Canis (Dusicyon) avus Burmeister, 1864 (Carnivora, Canidae) en el Pleistoceno Tardío y Holoceno de la provincia de Buenos Aires. Aspectos sistemáticos y bioestratigráficos relacionados. *Ameghiniana* **24:** 245–250.

Berta A. 1989. Quaternary evolution and biogeography of the large South American Canidae (Mammalia: Carnivora). *University of California Publications in Geological Sciences* **132:** 1–149.

Bocherens H, Drucker D. 2003. Trophic level isotopic enrichment of carbon and nitrogen in bone collagen: case studies from recent and ancient terrestrial ecosystems. *International Journal of Osteoarchaeology* **13:** 46–53.

Bonaparte JF, Migale LA, Buide VE. 2011. *Arqueología del Río Luján. Serie Didáctica III*. Mercedes: Fondo Editorial.

Bonomo M. 2006. Un acercamiento a la dimensión simbólica de la cultura material en la Región Pampeana. *Relaciones de la Sociedad Argentina de Antropología* **31:** 89–115.

Borrero LA. 2008a. The elusive evidence: the archaeological record of the South American extinct megafauna. In: Haynes G, ed. *American megafaunal extinctions at the end of the Pleistocene*. Amsterdam: Springer, 145–168.

Borrero LA. 2008b. Early Occupations in the Southern Cone. In: Silverman H, Isbell WH, eds. *Handbook of Southern American Archaeology*. Amsterdam: Springer, 59–77.

Borromei AM, Quattrocchio M. 2008. Late and Postglacial Paleoenvironments of Tierra del Fuego: terrestrial and marine palynological evidence. In: Rabassa J, ed. *The Late Cenozoic of Patagonia and Tierra del Fuego*. Amsterdam: Elsevier, 369–381.

Borromei AM, Coronato A, Franzén L, Ponce JF, López Sáez JA, Maidana N, Rabassa J, Candel MS. 2010. Multiproxy record of Holocene paleoenvironmental change, Tierra del Fuego, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* **286:** 1–16.

Bradshaw CJA, Cooper A, Turney CSM, Brook BW. 2012. Robust estimates of extinction time in the geological record. *Quaternary Science Reviews* **33:** 14–19.

Cabrera A. 1934. El Perro Cimarrón de la Pampa Argentina. *Publicaciones del Museo Antropológico y Etnográfico de la Facultad de Filosofía y Letras, Serie A* **2:** 7–29.

Cabrera A, Yepes J. 1940. *Los mamíferos sudamericanos*. Buenos Aires, Argentina: Editorial Ediar.

Cardiel J. 1930. *Diario del viaje y misión al Río del Sauce realizado en 1748 por el R. P. José Cardiel S.J. Publicaciones del Instituto de Investigaciones Geográficas de la facultad de Filosofía y Letras*. Buenos Aires: Imprenta y Casa Editora Coni, Serie A.

Castroviejo-Fisher S, Skoglund P, Valadez R, Vila C, Leonard JA. 2011. Vanishing native American dog lineages. *BMC Evolutionary Biology* **11:** 73.

Caviglia SE. 1978. La presencia de Dusicyon avus (Burmeister 1864 en la Capa VIII de la Cueva las Buitreras (Patagonia, Argentina): su relación con otros hallazgos en Patagonia Meridional. *Abstracts of the VI Congreso Nacional de Arqueología del Uruguay* **1:** 1–16.

Caviglia SE. 1986. Nuevos restos de cánidos tempranos en sitios arqueológicos de Fuego-Patagonia. Anales del Instituto de la Patagonia. *Ser Ciencias Sociales* **16:** 85–93.

Ceballos G, Ehrlich PR. 2002. Mammal population losses and the extinction crisis. *Science* **296:** 904–907.

Chan YL, Lacey EA, Pearson OP, Hadly EA. 2005. Ancient DNA reveals Holocene loss of genetic diversity in a South American rodent. *Biology Letters* **1:** 423–426.

Chan YL, Anderson CNK, Hadly EA. 2006. Bayesian estimation of the timing and severity of a population bottleneck from ancient DNA. *Plos Genetics* **2:** e59.

Chebez JC. 2008. *Los que se van: Mamíferos Tomo 3*. Buenos Aires: Editorial Albatros.

Cione AL, Tonni EP, Soibelzon LH. 2008. Did humans cause the late Pleistocene early Holocene mammalian extinctions in South America in a context of shrinking open areas? In: Haynes G, ed. *American megafaunal extinctions at the end of the Pleistocene*. Amsterdam: Springer, 125–144.

Clapperton CH. 1993. *Quaternary geology and geomorphology of South America*. Amsterdam: Elsevier.

Clutton-Brock J, Corbet GB, Hills M. 1976. A review of the family Canidae, with a classification by numerical methods. *Bulletin of the British Museum (Natural History) Zoology* **29:** 119–199.

Collins WD, Bitz C, Blackmon M, Bonan G, Bretherton CS, Carton JA, Chang P, Doney SC, Hack JJ, Henderson TB, Kiehl JT, Large WG, McKenna DS, Santer BD, Smith RD. 2006. The community climate system model: CCSM3. *Journal of Climatology* **19:** 2122–2143.

Darwin C. 1839. *Narrative of the surveying voyages of His Majesty's Ships Adventure and Beagle between the years 1826 and 1836, describing their examination of the southern shores of South America, and the Beagle's circumnavigation of the globe, Vol. III.* London: Colburn.

Del Puerto L, García RF, Bracco R, Castiñeira C, Blasi A, Inda H, Mazzeo N, Rodruíguez A. 2011. La evolución climática holocénica para el Sudeste de Uruguay. Análisis multiproxy en testigos de lagunas costeras. In: García Rodríguez F, ed. *El Holoceno en la zona costera de Uruguay.* Montevideo, MN: Universidad de la República, 117–147.

Del Puerto L, Bracco R, Inda H, Gutiérrez O, Panario D, García Rodríguez F. 2013. Assessing links between late Holocene climate change and paleolimnological development of Peña Lagoon using opal phytoliths, physical, and geochemical proxies. *Quaternary International* **287:** 89–100.

Deschamps J, Otero O, Tonni EP. 2003. Cambio climático en la pampa bonaerense: las precipitaciones desde los siglos XVIII al XX. *Documento de Trabajo de la Universidad de Belgrano* **109:** 1–18.

Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Townsend Peterson A, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29:** 129–151.

Favier-Dubois C. 2007. Soil genesis related to medieval climatic fluctuations in southern Patagonia and Tierra del Fuego (Argentina): chronological and paleoclimatic considerations. *Quaternary International* **162–163:** 158–165.

Fox-Dobbs K, Bump JK, Peterson RO, Fox DL, Koch PL. 2007. Carnivore-specific stable isotope variables and variation in the foraging ecology of modern and ancient wolf populations: case studies from Isle Royale, Minnesota, and La Brea. *Canadian Journal of Zoology* **85:** 458–471.

Frankham R. 2005. Genetics and extinction. *Biological Conservation* **126:** 131–140.

Frankham R, Bradshaw CJA, Brook BW. 2014. Genetics in conservation management: revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. *Biological Conservation* **170:** 56–63.

Galliari CA, Berman WD, Goin FJ. 1991. Mamíferos. Situación Ambiental de la provincia de Buenos Aires. Recursos y rasgos naturales en la evaluación ambiental. *Comisión Investigaciones Científicas* **1:** 1–35.

Garavaglia JC. 2012. La pampa como ecosistema, siglos XVI–XIX. In: Otero H, ed. *Historia de la Provincia de Buenos Aires. Tomo 1 'Población, ambiente y territorio'.* Buenos Aires: Edhasa, 79–112.

Gent PR, Danabasoglu G, Donner LJ, Holland MM, Hunke EC, Jayne SR, Lawrence DM, Neale RB, Rasch PJ, Vertenstein M, Worley PH, Yang ZL, Zhang M. 2011. The community climate system model version 4. *Journal of Climatology* **24:** 4973–4991.

Goin FJ. 1995. Los Marsupiales. In: Alberdi MA, Leone G, Tonni EP, eds. *Evolución biológica y climática de la Región Pampeana durante los últimos cinco millones de años.* Madrid: Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, 165–179.

Goin FJ. 2001. Marsupiales (Didelphidae: Marmosinae y Didelphinae). In: Mazzanti DL, Quintana CA, eds. *Cueva Tixi: cazadores y recolectores de las sierras de Tandilia oriental. 1. Geología, paleontología y zooarqueología.* Mar del Plata: Laboratorio de Arqueología. UNMdP, publicación especial, 75–113.

Gottelli D, Sillero-Zubiri C, Applebaum GD, Girman D, Roy M, Garcia-Moreno J, Ostrander E, Wayne RK. 1994. Molecular genetics of the most endangered canid: the Ethiopian wolf, *Canis simensis. Molecular Ecology* **3:** 301–312.

Grill S, Borromei A, Martínez G, Gutiérrez MA, Cornou ME, Olivera D. 2007. Palynofacial analysis in alkaline soils and paleoenvironmental implications: the Paso Otero 5 archaeological site (Necochea district, Buenos Aires province, Argentina). *Journal South American Earth Sciences* **24:** 34–47.

Haberzettl T, Wille M, Fey M, Janssen S, Lu A, Mayr C, Ohlendorf C, Schäbitz F, Gerhard H, Schleser GH, Zolitschka B. 2006. Environmental change and fire history of southern Patagonia (Argentina) during the last five centuries. *Quaternary International* **158:** 72–82.

Hernández PA, Graham CH, Master LL, Albert DL. 2006. The effect of sample size and species characteristics on performance on different species distribution modeling methods. *Ecography* **29:** 773–785.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25:** 1965–1978.

Hogg AG, Hua Q, Blackwell PG, Niu M, Buck CE, Guilderson TP, Heaton TJ, Palmer JG, Reimer PJ, Reimer RW, Turney CSM, Zimmerman SRH. 2013. SHCal13 Southern Hemisphere calibration, 0–50,000 years cal BP. *Radiocarbon* **55:** 1889–1903.

Huber UM, Markgraf V. 2003. European impact on fire regimes and vegetation dynamics at the steppe-forest ecotone of southern Patagonia. *The Holocene* **13:** 567–579.

Jansson E, Ruokonen M, Kojola I, Aspi J. 2012. Rise and fall of a wolf population: genetic diversity and structure during recovery, rapid expansion and drastic decline. *Molecular Ecology* **21:** 5178–5193.

Kraglievich L. 1930. Craneometría y clasificación de los cánidos sudamericanos, especialmente los argentinos actuales y fósiles. *Physis* **10:** 35–73.

Kriskautzky N. 1975. Nuevos aportes para el conocimiento de los materiales arqueológicos obtenidos en la excavación del sitio Río Luján en la llanura aluvial de dicho curso. *Arqueología* **1:** 9–13.

Langguth A. 1970. Una nueva clasificación de los cánidos sudamericanos. *Actas IV Congreso Latinoamericano de Zoología* **1:** 129–143.

Laporte L. 2014. Estudio del ajuar funerario de los entierros humanos. In: Politis G, Gutiérrez MA, Scabuzzo C, eds. *Estado actual de las investigaciones en el sitio arqueológico Arroyo Seco 2, Partido de Tres Arroyos, Provincia de Buenos Aires, Argentina*. Buenos Aires, Argentina: Universidad Nacional del Centro de la Provincia de Buenos Aires, Facultad Ciencias Sociales, Tandil, 393–415.

Lattes AE, Andrada GE. 2012. La población entre 1870 y 2000: una dinámica demográfica diferente. In: Otero H, ed. *Historia de la Provincia de Buenos Aires. Tomo 1 'Población, ambiente y territorio'*. Buenos Aires: Edhasa, 173–212.

Leakey R, Lewin R. 1992. *The sixth extinction: patterns of life and the future of humankind*. New York: Doubleday.

Loponte DM, Corriale MJ. 2013. 2. Isotopic values of diet of *Blastoceros dichotomus* (marsh deer) in Paraná Basin, South America. *Journal of Archaeological Science* **40:** 1382–1388.

Lothrop SK. 1928. *The Indians of Tierra del Fuego. Museum of the American Indian*. New York: Haye Foundation.

Macdonald DW, Sillero-Zubiri C. 2004. *Biology and conservation of wild canids*. Oxford: Oxford University Press.

MacPhee RDE, Flemming C. 1999. Requiem Aeternam. The last five hundred years of mammalian species extinctions. In: MacPhee RDE, ed. *Extinctions in near time*. New York: Kluwer Academic/Plenum Publisher, 333–371.

Mancini MV. 2003. Paleoecología del Cuaternario tardío en el sur de la Patagonia (46_-52_ S). Argentina. *Revista del Museo Argentino de Ciencias Naturales* **5:** 273–283.

Mancini MV, Graham M. 2014. Registros polínicos de depósitos del Holoceno en el sudeste de Patagonia, Argentina: su aplicación en la reconstrucción paleoambiental. *Ameghiniana* **51:** 184–193.

Mancini MV, Paez MM, Prieto AR, Stutz S, Tonello M, Vilanova I. 2005. Mid-Holocene climatic variability reconstruction from pollen records (32–52°S, Argentina). *Quaternary International* **132:** 47–59.

Mancini MV, Prieto AR, Páez MM, Schabitz F. 2008. Late Quaternary vegetation and climate of Patagonia. In: Rabassa J, ed. *The Late Cenozoic of Patagonia and Tierra del Fuego*. Amsterdam: Elsevier, 351–367.

Mansur ME. 2006. Arqueología de la zona de Punta Bustamante (prov. de Santa Cruz, Argentina). In: Cruz I, C S, eds. *Arqueología de la costa patagónica. Perspectivas para la conservación*. Río Gallegos: Universidad Nacional de la Patagonia Austral, 173–193.

Mansur ME. 2007. Confección y uso de artefactos discoides en contextos de Cazadores-recolectores de Patagonia meridional: pesas para redes en el sitio HS01AM (prov. Santa Cruz, Argentina). In: Morello F, Martinic M, Prieto A, Bahamonde G, eds. *Arqueología de Fuego-Patagonia. Levantando piedras, desenterrando huesos y develando arcanos*. Punta Arenas: Ediciones CEQUA, 701–708.

Markgraft MV. 1993. Paleoenvironments and paleoclimates in Tierra del Fuego and Southernmost Patagonia, South America. *Palaeogeography, Palaeoclimatology, Palaeoecology* **102:** 53–68.

Marris E. 2014. Iconic island study on its last legs. *Nature* **506:** 140–141.

Martin FM. 2013. *Tafonomía de la Transición Pleistoceno-Holoceno en Fuego-Patagonia. Interacción entre humanos y carnívoros y su importancia como agentes en la formación del registro fósil*. Punta Arenas: Ediciones de la Universidad de Magallanes.

Martínez G, Gutiérrez MA. 2008. Trends in the faunal human exploitation during the Late Pleistocene and Early Holocene in the Pampean region (Argentina). *Quaternary International* **191:** 53–68.

Martinic BM. 1995. *Los Aónikenk. Historia y cultura*. Punta Arenas: Ediciones de la Universidad de Magallanes.

Martinic BM. 2002. *Breve Historia de Magallanes*. Punta Arenas: La Prensa Austral.

Martinic BM, Prieto AI. 1986. Dinamarquero, encrucijada de rutas indígenas. *Anales del Instituto de la Patagonia* **16:** 53–83.

Masse G. 2012. El tamaño y el crecimiento de la población desde la Conquista hasta 1870. In: Otero H, ed. *Historia de la Provincia de Buenos Aires. Tomo 1 'Población, ambiente y territorio'*. Buenos Aires: Edhasa, 143–172.

Mech LD, Boitani L. 2003. *Wolves: behavior, ecology, and conservation*. Chicago: University of Chicago Press.

Medan D, Torretta JP, Hodara K, De La Fuente EB, Montaldo NH. 2011. Effects of agriculture expansion and intensification on the vertebrate and invertebrate diversity in the Pampas of Argentina. *Biodiversity and Conservation* **20:** 3077–3100.

Merow C, Smith MJ, Silander JA Jr. 2013. A practical guide to MaxEnt for modeling species' distribution: what it does, and why inputs and setting matter. *Ecography* **36:** 1058–1069.

Messineo PG, Politis G. 2007. El sitio Calera. Un depósito ritual en las Sierras Bayas (Sector Noroccidental de Tandilia). In: Bayón C, Pupio A, Gonzalez de Bonaveri MI, Flegenheimer N, Frére M, eds. *Arqueología en las pampas II*. Buenos Aires: Sociedad Argentina de Antropología, 697–720.

Morales M, Barberena R, Belardi JB, Borrero L, Cortegoso V, Durán V, Guerci A, Goñi R, Gil A, Neme G, Yacobaccio H, Zárate M. 2009. Reviewing human environment interactions in arid regions of southern South America during the past 3000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology* **281:** 283–295.

Musters GC. 1871. *At home with the Patagonians (a year's wanderings over untrodden ground from the Straits of Magellan to the Rio Negro)*. London: John Murray, Albemarle Street.

Novaro AJ. 1997. Source-sink dynamics induced by hunting: case study of culpeo foxes on rangelands in Patagonia, Argentina. PhD Thesis, University of Florida, USA.

Pardiñas UFJ, Teta P. 2013. Holocene stability and recent dramatic changes in micromammalian communities of northwestern Patagonia. *Quaternary International* **305:** 127–140.

Pardiñas UFJ, Udrizar Sauthier DE, Teta P. 2012. Micromammal diversity loss in central-eastern Patagonia over

the last 400 years. *Journal of Arid Environments* **85:** 71–75.

Petrocelli JL. 1975. Nota preliminar sobre los hallazgos arqueológicos en el Valle del Río Luján (población Río Luján, Campana, Provincia de Buenos Aires). *Actas del Primer Congreso de Arqueología Argentina* **1:** 251–270.

Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190:** 231–259.

Pocock RI. 1913. The affinities of the Antarctic wolf (*Canis antarcticus*). *Proceedings of the Zoological Society of London* **83:** 382–393.

Politis G. 1984. Climatic variations during historical times in Eastern Buenos Aires Pampas, Argentina. *Quaternary of South America and Antarctic Peninsula* **2:** 133–161.

Politis G, Pedrotta V. 2006. Recursos faunísticos y estrategias de subsistencia en el Este de la región Pampeana durante el Holoceno Tardío: el caso del guanaco (*Lama guanicoe*). *Relaciones de la Sociedad Argentina de Antropología* **31:** 301–336.

Politis GG, Prates L, Merino ML, Tognelli MF. 2011. Distribution parameters of guanaco (*Lama guanicoe*), pampas deer (*Ozotoceros bezoarticus*) and marsh deer (*Blastocerus dichotomus*) in Central Argentina: archaeological and paleoenvironmental implications. *Journal of Archaeological Science* **38:** 1405–1416.

Politis G, Barrientos G, Scabuzzo C. 2014. Los entierros humanos de Arroyo Seco 2. In: Politis G, Gutiérrez MA, Scabuzzo C, eds. *Estado actual de las investigaciones en el sitio arqueológico Arroyo Seco 2, Partido de Tres Arroyos, Provincia de Buenos Aires, Argentina*. Buenos Aires: Universidad Nacional del Centro de la Provincia de Buenos Aires, Facultad Ciencias Sociales, 329–392.

Ponce JF, Borromei AM, Rabassa J, Martínez O. 2011. Late Quaternary palaeoenvironmental change in western Isla de los Estados (54.5_S, 64_W), Fuegian Archipelago. *Quaternary International* **233:** 89–100.

Prado JL, Goin F, Tonni EP. 1985. *Lestodelphys halli* (Mammalia, Didelphidae) in Holocene sediments of Southern Buenos Aires province (Argentina): morphological and paleoenvironmental considerations. In: Rabassa J, ed. *Quaternary of South America and Antarctic Peninsula*. Leiden: Balkema, 93–107.

Prates L. 2014. Crossing the boundary between humans and animals: the extinct fox *Dusicyon avus* from a hunter-gatherer mortuary context in Patagonia (Argentina). *Antiquity* **88:** 1–13.

Prates L, Di Prado V. 2013. Sitios con entierros humanos y ocupaciones residenciales en la cuenca del rio Negro (Norpatagonia, Argentina). Diacronia y multicausalidad. *Latin American Antiquity* **24:** 451–466.

Prates L, Prevosti FJ, Berón M. 2010. First records of prehispanic dogs in southern South America (Pampa-Patagonia, Argentina). *Current Anthropolology* **51:** 273–280.

Prevosti FJ. 2010. Phylogeny of the large extinct South American canids (Mammalia, Carnivora, Canidae) using a 'total evidence' approach. *Cladistics* **26:** 456–481.

Prevosti FJ, Martin FM. 2013. Paleoecology of the mammalian predator guild of the southern patagonia during the latest pleistocene: ecomorphology, stable isotopes, and taphonomy. *Quaternary International* **305:** 74–84.

Prevosti FJ, Pardiñas UFJ. 2001. Variaciones corologicas de *Lyncodon patagonicus* (Carnivora, Mustelidae) durante el cuaternario. *Mastozoología Neotropical* **8:** 21–39.

Prevosti FJ, Rincón AD. 2007. A new fossil canid assemblage from the late Pleistocene of northern South America: the canids of the Inciarte asphalt pit (Zulia, Venezuela), fossil record and biogeography. *Journal of Paleontology* **81:** 1053–1065.

Prevosti FJ, Soibelzon LH. 2012. The evolution of South American carnivore fauna: a paleontological perspective. In: Paterson B, Costa LP, eds. *Bones, clones and biomes: the history and geography of recent neotropical mammals*. Chicago: University Chicago Press, 102–122.

Prevosti FJ, Vizcaíno S. 2006. The carnivore guild of the late pleistocene of Argentina: paleoecology and carnivore richness. *Acta Paleontologica Polonica* **51:** 407–422.

Prevosti FJ, Bonomo M, Tonni EP. 2004. La distribución de *Chrysocyon brachyurus* (Illiger, 1811) (Mammalia: Carnivora: Canidae) durante el Holoceno en la Argentina: implicancias paleoambientales. *Mastozoologia Neotropical* **11:** 27–43.

Prevosti FJ, Ubilla M, Perea D. 2009. Large extinct canids from the Pleistocene of Uruguay: systematic, biogeographic and palaeoecological remarks. *Historical Biology* **21:** 79–89.

Prevosti FJ, Santiago F, Prates L, Salemme M. 2011. Constraining the time of extinction of the South American fox *Dusicyon avus* (Carnivora, Canidae) during the late Holocene. *Quaternary International* **245:** 209–217.

Prieto AR, Stutz S. 1996. Vegetación del Holoceno en el norte de la estepa patagónica: Palinología de la Cueva Epullán Grande. *Praehistoria* **2:** 267–277.

Prieto AR, Blasi A, De Francesco CG, Fernández C. 2004. Environmental history since 11,000 yr B.P. of the northeastern Pampas, Argentina from alluvial sequences of Luján River. *Quaternary Research* **62:** 146–161.

R Core Team. 2013. *R: a language and environment for statistical computing*. Available at: http://www.R-project.org/.

Rapoport EH. 1996. The flora of Buenos Aires: low richness or mass extinction? *International Journal of Ecology and Environmental Sciences* **22:** 217–242.

Reboratti C. 2012. La dinámica ambiental desde fines del siglo XIX. In: Otero H, ed. *Historia de la Provincia de Buenos Aires. Tomo 1 'Población, ambiente y territorio'*. Buenos Aires: Edhasa, 113–142.

Reimer PJ, Baillie MGL, Bard E, Bayliss A, Beck JW, Blackwell PG, Ramsey CB, Buck CE, Burr GS, Edwards RL, Friedrich M, Grootes PM, Guilderson TP, Hajdas I, Heaton TJ, Hogg AG, Hughen KA, Kaiser KF, Kromer B, McCormac FG, Manning SW, Reimer RW, Richards DA, Southon JR, Talamo S, Turney CS, van der Plicht J, Weyhenmeyer CE. 2009. IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP. *Radiocarbon* **51:** 1111–1150.

Rey Balmaceda RC. 1976. *Geografía Histórica de la Patagonia (1870–1960)*. Buenos Aires: Ediciones Cervantes.

Rodríguez R, Ramírez O, Valdiosera CE, García N, Alda F, Madurell-Malapeira J, Marmi J, Doadrio I, Willerslev E, Götherström A, Arsuaga JL, Thomas MG, Lalueza-Fox C, Dalén L. 2011. 50,000 years of genetic uniformity in the critically endangered Iberian lynx. *Molecular Ecology* 20: 3785–3795.

Salemme M, Miotti L. 2008. Archeological hunter-gatherer landscapes since the latest Pleistocene in Fuego Patagonia. In: Rabassa J, ed. *The Late Cenozoic of Patagonia and Tierra del Fuego*. Amsterdam: Elsevier, 437–483.

Salemme MC, Tonni EP. 1983. Paleoetnozoología de un sitio arqueológico en la Pampa Ondulada: Sitio Río Luján (Partido de Campana, pcia. de Buenos Aires). *Relaciones de la Sociedad Argentina de Antropología* 15: 77–90.

Schäbitz F. 2003. Estudios polínicos del Cuaternario en las regiones áridas del sur de Argentina. *Revista del Museo Argentino de Ciencias Naturales* 5: 291–299.

Schiaffini MI, Martin GM, Giménez AL, Prevosti FJ. 2013. Distribution of *Lyncodon patagonicus* (Carnivora, Mustelidae): changes from the Last Glacial Maximum to the present. *Journal of Mammalogy* 94: 339–350.

Sillero-Zubiri C, Hoffmann M, Macdonald DW. 2004. *Canids: foxes, wolves, jackals and dogs. Status survey and conservation action plan*. Switzerland and Cambridge: IUCN Species Programme.

Slater GJ, Thalmann O, Leonard J, Schweizer RM, Koepfli K-P, Pollinger JP, Rawlence NJ, Austin JJ, Cooper A, Wayne RK. 2009. Evolutionary history of the Falklands wolf. *Current Biology* 19: 937–938.

Stahl PW. 2013. Early dogs and endemic South American canids of the Spanish main. *Journal of Anthropological Research* 69: 515–533.

Stuiver M, Reimer PJ. 1993. Extended 14C database and revised CALIB radiocarbon calibration program. *Radiocarbon* 35: 215–230.

Stutz S, Prieto AR, Isla FI. 2006. Holocene evolution of the Mar Chiquita coastal lagoon area (Argentina) indicated by pollen analysis. *Journal of Quaternary Science* 21: 17–28.

Tammone MN, Hajduk A, Arias P, Teta P, Lacey EA, Pardiñas UFJ. 2014. Last glacial maximum environments in northwestern Patagonia revealed by fossil small mammals. *Quaternary Research* 82: 198–208.

Tedford R, Taylor BE, Wang X. 1995. Phylogeny of the Caninae (Carnivora: Canidae): the living taxa. *American Museum Novitates* 3146: 1–37.

Teta P, Formoso A, Tammone M, De Tommaso DC, Fernández FJ, Torres J, Pardiñas UFJ. 2014. Micromamíferos, cambio climático e impacto antrópico: Cuánto han cambiado las comunidades del sur de América del sur en los últimos 500 años? *Therya* 5: 7–38.

Toledo MJ. 2009. Geoarchaeologie de la transition Pleistocene-Holocene dans le nord-est pampeen (Buenos Aires, Argentine). Revision historique, stratigraphique et taphonomique. Perspectives pour le premier peuplement. Doctoral Thesis, París: Museum National de Histoire Naturelle.

Tonello MS, Prieto AR. 2010. Tendencias climáticas para los pastizales pampeanos durante el Pleistoceno tardío-Holoceno: estimaciones cuantitativas basadas en secuencias polínicas fósiles. *Ameghiniana* 47: 501–514.

Tonni EP, Politis G. 1980. La distribución del guanaco (Mammalia, Camelidae amelidae) en la provincia de Buenos Aires durante el Pleistoceno Tardío y Holoceno. Los factores climáticos como causas de su retracción. *Ameghiniana* 17: 53–66.

Tonni EP, Politis G. 1981. Un gran cánido del Holoceno de la provincia de Buenos Aires y el registro prehispánico de *Canis (Canis) familiaris* en las áreas Pampeana y patagónica. *Ameghiniana* 18: 251–265.

Tonni EP, Cione A, Figini A. 1999. Predominance of arid climates indicated by mammals in the pampas of Argentina during the Late Pleistocene and Holocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 147: 257–281.

Tonni EP, Cione AL, Figini A. 2001. Chronology of Holocene pedogenetic events in the Pampean area of Argentina. *Current Research in the Pleistocene* 18: 124–127.

Trejo V, Jackson D. 1998. Cánidos patagónicos: identificación taxonómica de mandíbulas y molares del sitio arqueológico Cueva Baño Nuevo 1. *Anales del Instituto de la Patagonia. Serie Ciencias Humanas* 26: 181–194.

Turvey S. 2009. In the shadow of megafauna: prehistoric mammal and bird extinctions across the Holocene. In: Turvey ST, ed. *Holocene extinctions*. Oxford: Oxford University Press, 17–40.

Turvey ST, Fritz SA. 2011. The ghosts of mammals past: biological and geographical patterns of global mammalian extinction across the Holocene. *Philosophical Transactions of the Royal Society of London* 366: 2564–2576.

Udrizar Sauthier D. 2009. Los micromamíferos y la evolución ambiental en el río Chubut (Chubut, R. Argentina). PhD Thesis, La Plata: Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.

Udrizar Sauthier D, Pardiñas UFJ. 2014. Estableciendo límites: distribución geográfica de los micromamíferos (Rodentia y Didelphimorphia) de Patagonia centro-oriental. *Mastozoología Neotropical* 21: 79–99.

Van Asch B, Zhang A, Oskarsson MCR, Klutsch CFC, Amorim A, Savolainen P. 2013. Pre-Columbian origins of Native American dog breeds, with only limited replacement by European dogs, confirmed by mtDNA analysis. *Proceedings of the Royal Society B: Biological Sciences* 280: 1142. doi:10.1098/rspb.2013.1142.

Vilà C, Wayne RK. 1999. Hybridization between wolves and dogs. *Conservation Biology* 13: 195–198.

Waldmann N. 2008. Late Quaternary environmental changes in Lago Fagnano, Tierra del Fuego (54_S): Reconstructing Sedimentary Processes, Natural Hazards and Paleoclimate. Ms. Thesis, Genève, Suisse: Faculté des sciences de l'Université de Genève, Universite de Genève.

Williams G. 1975. *The desert and the dream: a study of welsh colonization in Chubut 1865–1915*. Wales: University of Wales Press.

Yeakel JD, Guimarães PR, Bocherens H, Koch PL. 2013. The impact of climate change on the structure of Pleistocene food webs across the mammoth steppe. *Proceedings of the Royal Society B: Biological Sciences* 280: 20130239.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. List of localities of *Dusicyon avus* used in this study.

Appendix S2. List of studied canids with their respective locality, age, collection number, and measurements (in mm), collection names and measurement definitions.

Appendix S3. New and published ^{14}C taxon dates for *Dusicyon avus*. New taxon dates in bold.

Appendix S4. Estimation of extinction age of *Dusicyon avus* using the GRIWM method. (1) Analysis of the whole sample with the original data; (2) analysis of the whole sample but artificially reducing the error of four dates with values larger than 150 to 90 cal years BP; (3) analysis including only the unmodified data of late Holocene age.

Appendix S5. Ventral view of a skull of *Dusicyon avus* compared with other canids. A, *Dusicyon avus* (MCA 81-VI-1-1). B, *Dusicyon avus* (CEHA 5131). C, *Dusicyon australis*. D, *Lycalopex culpaeus*. E, *Chrysocyon brachyurus*. F, *Canis familiaris*. Scale = 10 mm.

Appendix S6. Lateral view of mandible of *Dusicyon avus* compared with other canids. A, *Dusicyon avus* (MCA 81-VI-1-1). B, *Dusicyon avus* (MPEF-PV 10887). C, *Dusicyon avus* (MC 787). D, *Dusicyon australis*. E, *Lycalopex culpaeus*. F, *Chrysocyon brachyurus*. G, *Canis familiaris*. The MPEF-PV 10887 was reflected. Scale = 10 mm.

Appendix S7. Morphometric analysis (Principal Component Analysis and biplots) comparing *Dusicyon avus* remains with other canids.

Appendix S8. Stable isotope values (δ^{13}C, δ^{15}N) of *Dusicyon avus*. New data in bold.

Appendix S9. Contribution of each variable to the potential distribution models for *Dusicyon avus*. Value of the variables with the highest contribution for each model are in bold.

Appendix S10. Value of some climatic variables for the *Dusicyon avus* localities used in each potential distribution model.