Low-frequency, threatened habitats drive the large-scale distribution of Andean Condors in southern Patagonia

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The analysis of factors that determine the distribution of top-scavengers at large scales can provide clues to understanding important ecological processes and may be useful in establishing conservation and management strategies. Here, we conducted a large-scale survey to study the distribution of the threatened Andean Condor *Vultur gryphus* in relation to environmental factors in southern Patagonia. This area has undergone the settlement of livestock and the introduction of exotic wildlife, although to a lesser extent than in the distribution of Condors in northern Patagonia. The aim of this study was to determine the relevance of different factors such as the availability of food resources, the availability of suitable nesting and roosting places and the presence of humans on large-scale condor distribution. Our results show that the presence of meadows was the primary factor shaping Andean Condor distribution, despite the fact that this habitat occupies only 4% of the Patagonian landscapes. However, this habitat has a high probability of herbivore presence, so Condors seem to optimize their searching. The availability of nesting and roosting cliffs also contributed to explaining the observed distributions. Our results suggest that Condor distribution in southern Patagonia is a compromise between the spatial locations of two low-frequency habitats – meadows and cliffs. A successful Condor conservation strategy in southern Patagonia should include the protection of these habitats and the regulation of farming expansion, including the recovery of meadows.

Keywords: deviance partitioning, herbivores, *Lama guanicoe*, livestock, meadows, *Vultur gryphus*.

Disentangling the drivers of species distributions at large geographical scales can provide clues to understanding ecological processes such as habitat use, competition or behaviour (Turner 1989, Flather & Sauer 1996, Sánchez-Zapata & Calvo 1999). Moreover, it may be useful to establish conservation and management strategies, particularly in endangered species (Rushton *et al.* 2004, Guisan *et al.* 2013). Additionally, understanding broader patterns of ecological processes can be

essential because they are usually considered good surrogates of ecosystem processes (Sergio *et al.* 2008), they may have significant effects in structuring terrestrial ecosystems (e.g. Pace *et al.* 1999, Schmitz & Suttle 2001, Ripple & Beschta 2004, Beschta & Ripple 2009) and they provide valuable ecosystem services (e.g. Morales-Reyes *et al.* 2015, Donázar *et al.* 2016).

Patagonia is a large wilderness territory in South America. It has suffered important ecological changes during the last century, such as the settlement of high numbers of domestic livestock and the introduction of exotic wildlife (Vásquez

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2002). The replacement of large wild herbivores by domestic ungulates began in the Neolithic (≈ 11 000 years ago), and spread across the globe in parallel with the expansion of humans and their livestock industry (Zeder 2008). In the Americas, this process was not triggered until the arrival of Europeans in the 16th century, and in certain parts of the continent, such as in Patagonia, this substitution did not begin until the end of the 19th century (Barba 2007). Subsequently, persecution by humans has decimated the native herbivore populations (Lesser Rhea *Rhea pennata* and Guanaco *Lama guanicoe*), which were replaced by livestock, mainly sheep and cattle (Novaro *et al.* 2000, Baldi *et al.* 2001, 2004).

Currently, Patagonia supports a population of 5.7 million livestock head plus other herbivores, which exert a much more intense grazing pressure than that of native species, as the livestock populations are concentrated and sometimes supplemented (INE 2007, INDEC 2008). Erosion, loss of vegetation cover and changes in floristic communities (e.g. Beeskow *et al.* 1995, Bisigato & Bertiller 1997) are added to the virtual extinction of predators and large scavengers due to conflicts with humans as a result of predation or competition (Vásquez 2002). Top predators and scavengers, such as the Puma *Puma concolor* and the Andean Condor *Vultur gryphus*, have completely shifted their diet to include new invaders (Novaro *et al.* 2000, Lambertucci *et al.* 2009), so native herbivore communities are considered functionally extinct in some areas (Novaro *et al.* 2000, Lambertucci *et al.* 2009). However, the consequences of livestock presence on the distribution of large vertebrate consumers (carnivores and scavengers) are not well known.

In Patagonia, the so-called *mallines*, natural upwellings of water such as wet meadows and watersheds, are highly productive areas that have large concentrations of livestock (Ayesa *et al.* 1999, Buono *et al.* 2010). These areas were formerly occupied by native herbivores (León *et al.* 1998, Bellis *et al.* 2006). In this context, it is expected that consumers (predators and scavengers) concentrate their foraging activities and change their distribution patterns on a large scale following the concentration of these new predictable resources. Moreover, this concentration of resources may have facilitated human persecution of potential competitors (native herbivores) and predators, such that they may have been excluded from areas of strong competition with humans (Ceballos & Ehrlich 2002, Morrison *et al.* 2007).

The Andean Condor is a long-lived obligate scavenger inhabiting the Andes Mountain ranges in South America (Lambertucci 2007). During the last century the Andean Condor has suffered important retractions in its distribution range, which has led it to be classified as Near Threatened worldwide and vulnerable for Argentina (Birdlife International 2015). In Patagonia, human persecution may be responsible for Condor rarefaction. In fact, Condors were traditionally considered lamb predators and their persecution was rewarded by the authorities (Lambertucci 2007). In addition, indirect poisoning from baits aimed at killing carnivores, as well as lead contamination have had a profound impact on the Condor populations (Lambertucci *et al.* 2011, BirdLife International 2015, Wiemeyer *et al.* 2017). In recent years, researchers have gained important knowledge about dietary choices, movement ecology and foraging behaviour of Andean Condors (e.g. Donázar & Feijóo 2002, Kusch 2004, Lambertucci *et al.* 2008, 2009, Lambertucci & Ruggiero 2013, Alarcón *et al.* 2016, Alarcón 2016), but how habitat and food availability shape their large-scale distributions remains poorly studied.

Our aim was to disentangle how environmental factors determine the large-scale distribution of this top scavenger. For this purpose, we took advantage of a large-scale survey in southern Patagonia, Argentina, and in Tierra del Fuego, Chile. We predicted that Andean Condor habitat use was determined by the two important factors of food sources and resting–breeding places. Therefore, we expected to find more Condors where herbivore (livestock and wild species) abundance was high or in highly productive areas that may harbour greater abundances of herbivores. Additionally, we expected more Condors in areas where the presence of cliffs, which are needed for roosting and breeding, was high. We also considered the effect of human presence on the abundance of Condors, as this factor may play a role (Speziale *et al.* 2008, Barbar *et al.* 2015).

MATERIAL AND METHODS

Study area

The study was carried out in southern Patagonia, in the Santa Cruz and Tierra del Fuego provinces (Argentina) and the Magallanes, Tierra del Fuego

and Última Esperanza provinces (Chile) (47°–57°S; 65°–72°W; Fig. 1). The climate is dry and cold, with strong predominantly westerly winds, and a marked west-to-east gradient in precipitation and temperature, decreasing from north-east to south-west (Paruelo *et al.* 1998). The topography is dominated by the Andes Mountains crossing from north to south in the western edge of the study area. From west to east, the roughness of the Andean Mountains gradually smooths down to a large central plateau that reaches the Atlantic Ocean. The Patagonian plateau is occupied by Magellan shrub steppe and sub-Andean grasslands (León *et al.* 1998). The Andean foothills and slopes are mainly occupied by sub-Antarctic deciduous forests of *Nothophagus pumillio* and *Nothophagus antarctica*. In the drainage lines between hills and plateaus or where the groundwater level rises above the land surface, azonal wet meadows and watersheds appear (Marcolín *et al.* 1978). Austral peat moss and tundra cover the most southern part of the Tierra del Fuego region (Movia *et al.* 1987).

Human population density is very low (< 1.0 inhabitants/km^2) and is restricted to a few cities (INDEC 2012). Marine fisheries, oil extraction and sheep ranching are the most important economic activities in the study area (Brown *et al.* 2006). Sheep, but also cattle, goats and horses, were introduced into Patagonia as early as the 1500s; in southern Patagonia, there are about 5.4 million sheep, 0.25 million cows and 22 000 horses (INE 2007, INDEC 2008).

Field procedures

A total of 58 systematic 30-min point counts were conducted during November–December 2013 following established methodologies (Sánchez-Zapata *et al.* 2007, Fig. 1). Points were distributed along the Andean Condor distribution range and covering the east–west gradient according to the difference in landscape structure. Point counts were separated by a mean distance of 21.5 km (range 91.5–6.9 km) to avoid recounting birds. Observations were conducted by three experienced observers with the help of binoculars (10×) and field scopes (20–60×), always in places with high visibility and under good weather conditions. All Andean Condors observed either flying overhead or standing on the ground were recorded. The sex and age of each Andean Condor were recorded

when possible on the basis of plumage characteristics and the presence of combs (see Ferguson-Lees & Christie 2001). For each point, we recorded the following information: coordinates and hour of observation, the number of wild herbivores (Guanacos and Lesser Rheas) and livestock (sheep, cattle and horses), and the number of houses in the visual range. To characterize potential foraging areas, we conducted two additional roadside car transects of 10 km around all point counts to determine the number of livestock, native herbivores and houses (Fig. 1).

Environmental variables

For each point count we characterized 26 environmental variables, which included principal land coverages, a productivity index, topography, potential cliffs, human disturbances and trophic resources (a description of all variables is included in Table 1). Given the high mobility of the species, up to 350 km in a day (Lambertucci *et al.* 2014), for all variables (except for potential cliffs and spatial coordinates) we used a multi-scale analysis of variables, using four buffer distances: 1, 2, 5 and 10 km. These distances were selected to encompass potential landscape effects at different scales for a species with wide-ranging movements.

Trophic resources included the number of each livestock category (sheep, cattle and horse) and native species (Guanaco and Lesser Rhea), counted in each point count and during the roadside tracks in buffers of 1, 2, 5 and 10 km. Three additional variables were calculated for each spatial scale: the sum of all native herbivores, the sum of all domestic livestock and the sum of domestic livestock standardized to livestock units using Chilonda and Otte (2006). Productivity indexes are frequently used as a surrogate of primary productivity and vegetative growth in terrestrial ecosystems (Box *et al.* 1989). We employed the average of the normalized difference vegetation index (NDVI) values during the 15-day period in which fieldwork was carried out, and the annual average net primary productivity (NPP) values for 2012. Cliffs potentially used as breeding places and communal roosts were identified using digital slope maps in those areas with a mean slope above 80% and size > 100 m^2. We calculated the distance from each point count to the nearest potential cliffs and total surface of potential cliffs in the
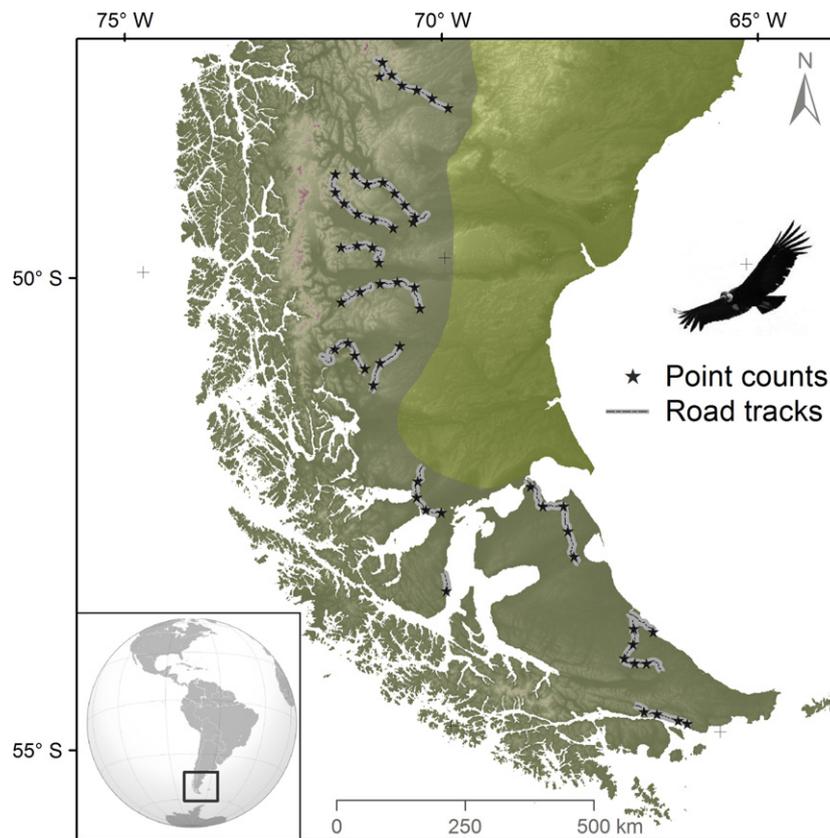
Figure 1. Location of point counts conducted in southern Patagonia. We also included the road-tracks associated with each point count. Shadow layer shows Andean Condor distribution (modified from Lambertucci 2007).

150-km buffer around each point count. This radius was selected because it is the mean daily flight distance of the species (Lambertucci *et al.* 2014). The time of day of each point count was also included because it is related to the distance between resting and foraging areas (Alarcón 2016). We calculated the number of buildings (towns, houses and farms) counted during roadside tracks in 1-, 2-, 5- and 10-km buffers around each point count and the distance from each point count to the nearest urban area. All landscape and spatial variables were calculated using ArcGIS 9.3 (ESRI Inc., USA).

Data analysis

We used generalized linear models (GLMs; McCulloch & Searle 2000) to relate environmental factors to the number of Andean Condors per point count. We built multivariate models with ecological meaning to establish response relationships between the dependent variables and the independent variables for each prediction. Prior to constructing each multivariate model, we tested for collinearity. High collinearity among variables can lead to high standard errors and difficulties in interpreting parameter estimates in the GLMs (Graham 2003). To evaluate potential collinearity problems we calculated the variance inflation factors (VIFs) for each predictor with all others in a model (Neter *et al.* 1990). Variables with VIF > 5 are a cause for concern and VIF > 10 indicates severe collinearity and therefore these variables were excluded from the models (Neter *et al.* 1990). In our case, two trophic resource variables, cattle and sheep abundance at the point count scale, presented a high VIF (> 12). Thus, we only included sheep abundance as a variable in point count scale models. Also, a high collinearity was detected for two productivity variables, NPP and NDVI (> 14), and for a land uses variable, the Patagonian steppe (> 8.9), at all scales studied. All of them were removed from the models.

Table 1. Description of all environmental variables used in this study and their source from which the data were obtained. Variables in italics were excluded based on high collinearity.

		Source*
Trophic resources		
Sheep	Number of sheep	Field data
Cattle	Number of cattle	Field data
Horse	Number of horses	Field data
Livestock	Total of sheep, cattle and horses	Field data
Livestock Stnd.	Total of livestock units (standardized)	Field data
Guanac.	Number of Guanacos	Field data
Rhea	Number of Lesser Rheas	Field data
Native prey	Total of Guanacos and Lesser Rheas	Field data
Productivity		
NDVI mean	Mean of normalized difference vegetation index	LAADS
NDVI sd	Standard deviation of normalized difference vegetation index	LAADS
NPP mean	Mean of net primary production	LAADS
NPP sd	Standard deviation of net primary production	LAADS
Land uses		
Steppe	Percentage of Magellan shrub steppe (%)	GLC2000
Meadows	Percentage of meadows (%)	GLC2000
Forest low	Percentage of low dense sub-Antarctic deciduous forest (%)	GLC2000
Forest high	Percentage of high dense sub-Antarctic deciduous forest (%)	GLC2000
Bare ground	Percentage of bare ground (%)	GLC2000
Crop	Percentage of crop (%)	GLC2000
Water	Percentage of water surface (%)	DCW
Dist. Water	Distance to nearest water surface (km)	DCW
Potential cliffs		
Dist. Cliff	Distance to potential breeding/roosting cliffs (km)	CGIAR – CSI
Cliff Area $_{150}$	Surface of potential breeding/roosting cliffs (km^2)	CGIAR – CSI
Time	Hour of the day	Field data
Human presence		
Houses	Number of human buildings in 1- and 5-km buffer counted during road-transects.	Field data
Dist. Urb.	Distance to nearest urban area (km)	GLC2000
Spatial coordinates		
Y	Latitude	Field data
X	Longitude	Field data

*GLC2000: Global Land Cover 2000. http://www.glcn.org/. DCW: Digital Chart of the World. http://worldmap.harvard.edu/data/geon ode:Digital_Chart_of_the_World. LAADS: Level-1 and Atmosphere Archive & Distribution System. http://ladsweb.nascom.nasa.gov/. CGIAR – CSI Consortium for Spatial Information. http://srtm.csi.cgiar.org/.

We used a negative binomial error distribution in the GLM to solve the overdispersion detected in Andean Condor abundance. We used the corrected Akaike information criterion (AICc; Burnham & Anderson 2003) for ranking models, and computed delta AICc to determine the strength of evidence and AICc weights to represent the relative likelihood of each model (Burnham & Anderson 2003). All models that showed a higher AICc value than the null model (intercept) were discarded. To assess specifically the differences between livestock and native prey models to explain the variation of Andean Condor abundance, we used a log-likelihood chi-square test of deviance, comparing each model respectively with the null model. The effect of spatial scales on Andean Condor abundance models was assessed by comparing the percentage of explained deviance (D^2) of the best environmental models (trophic, land uses, NDVI and topography) across the four selected scales (1-, 2-, 5- and 10-km buffers).

To disentangle the effect of factors, we performed deviance partitioning using a partial regression analysis (Anderson & Gribble 1998). We joined previous models in these groups: trophic resources (livestock and native prey) and landscape configuration (land uses + productivity + topography + potential cliffs + human presence). Statistical models of environment–abundance relationships

may be influenced by spatial autocorrelation in abundance, environmental variables or both. Failure to account for spatial autocorrelation can lead to incorrect conclusions and invalidate abundance models (Keitt *et al.* 2002). To assess the spatial autocorrelation of Andean Condor abundance, we included an additional group integrated by a combination of linear, quadratic and cubic distributions of the spatial coordinates of each point count (x, y, x^2, y^2, x^3, y^3, xy, x^2y, xy^2). Previously, spatial coordinates were centred and standardized (Legendre & Legendre 1998). We selected the best model of each group (lowest ΔAICc) and built the multivariate model for the group. Each multivariate model was reduced by stepwise backward selection, and the percentage of deviance explained (D^2) was calculated for each of the most parsimonious models. We then calculated the proportion of the deviance explained by the combination of all three reduced models and obtained the percentage of pure deviances for each group. We used R statistical software (R Development Core Team 2005) with the MASS package for the GLM analysis, and AICcmodavg for model ranking (Mazerolle 2012).

RESULTS

Condors were detected in 32 of 58 point counts surveyed (55.2%), in which a total of 212 birds (range 0–31; mean ± sd 3.7 ± 6.4) were recorded (Fig. S1). Mean sex ratio (F/M) per point count was 0.43 ± 0.38 ($n = 114$) and the mean juvenile ratio (Jv/Ad) per point count was clearly skewed to adult birds, 0.17 ± 0.24 ($n = 157$). Mean abundance by sex and age class recorded per point count was adult male 1.04 ± 1.92, adult female 0.37 ± 0.86, subadult male 0.09 ± 0.39, subadult female 0.09 ± 0.34, juvenile male 0.16 ± 0.53 and juvenile female 0.26 ± 0.97.

Abundance models

Land cover models used as indirect food resource surrogates best explained the spatial pattern of Andean Condor abundance in southern Patagonia. The presence of suitable nesting and roosting places also provided a good fit. Finally, human disturbances and local abundance of food resources were the worst factors in explaining Andean Condor abundance (ΔAICc < 1.5; see Table 2). Across all models, environmental variables performed better at a large than at a fine scale (see below, Table 2).

Within land cover, the percentage of meadow cover at the large scale was included in all land cover models that improved the null model, showing a positive relationship with Andean Condor abundance. Only one other variable, the presence of sub-Antarctic deciduous forest at the large scale, was also included in these models, but always together with meadow cover.

Table 2. Competing generalized linear models for Andean Condor abundance in southern Patagonia.

Models	Variables	K	AICc	ΔAICc	W
Land uses and productivity	Meadow$_{10}$	2	135.30	0.00	0.33
	Meadow$_{10}$ + Forest high$_5$	3	136.39	1.09	0.19
	Meadow$_{10}$ + Forest high$_{10}$	3	137.07	1.77	0.14
	Meadow$_{10}$ + Forest low$_{10}$	3	137.80	2.49	0.09
	Meadow$_{10}$ + Forest low$_5$	3	138.03	2.73	0.08
Nesting and roosting sites	Cliff area$_{150}$ + Time	3	245.68	0.00	0.49
	Dist. Cliff + Cliff area$_{150}$	3	246.32	0.65	0.35
	Dist. Cliff + Cliff area$_{150}$ + Time	4	247.96	2.28	0.15
Human disturbances	Dist. Urb + Dist. Urb^2 + Houses$_5$	3	252.80	0.00	0.56
	Dist. Urb + Dist. Urb^2 + Houses$_{10}$	4	255.11	2.30	0.18
	Dist. Urb + Dist. Urb^2	4	255.12	2.32	0.18
Direct trophic resources	Sheep$_{10}$ + Guanac$_{10}$ + Cattle$_{10}$ + Rhea$_{10}$	6	254.03	0.00	0.26
	Sheep$_{10}$ + Guanac$_{10}$ + Cattle$_{10}$	5	254.1	0.07	0.25
	Sheep$_{10}$ + Guanac$_{10}$ + Cattle$_{10}$ + Rhea$_{10}$ + Horse$_{10}$	7	255.46	1.43	0.13
	Sheep$_5$ + Guanac$_5$ + Cattle$_5$ + Rhea$_5$	6	255.8	1.77	0.11

Null model AICc = 257.85. K = total number of parameters, AICc = corrected Akaike's information criterion, ΔAICc = difference between the AICc value for that model and the best model, and W = Akaike's weights. We only show models where ΔAICc < 3. The subscripts indicate the scale used in kilometres (e.g. 1 = 1 km, 10 = 10 km, or PC = Point Count).

For the second best set of models, those of suitable nesting and roosting places, the area of potential cliffs was in all models, and the day-hour when the point count was conducted were in two models. The distance to the nearest potential cliff was also in two models, showing a negative relationship with Andean Condor abundance (Table 2).

The best human disturbance model included the distance to urban areas and number of houses at the large scale; both variables showed a negative relationship with Condor abundance. The best models of direct food resources included livestock and native species abundance variables at the large scale (see Table 2). To specifically analyse the effect of different prey classes, we evaluated the fit of potential prey models individually vs. the null model. The models that only included native prey abundances failed to improve the null model at any scale studied (likelihood ratio tests; $P = 0.43$), but livestock models achieved this at the 10-km scale (likelihood ratio tests; $P = 0.02$).

Spatial scale effect and deviance partitioning

Specific analysis of the percentage of deviance explained changes at all spatial scales between Andean Condor abundance models and showed that trophic resources and land uses increased their deviance at larger scales. Topography did not show a relationship with scale and NDVI showed a slight decline at the larger scale (Fig. 2).

The total percentage of deviance explained by models of Andean Condor abundance was 63.4%. Most of this was retained by the landscape configuration (pure effect 10.6% of the total deviance) and its interactions with the other groups (41.7%). This percentage was distributed as follows: 18.1% shared with spatial autocorrelation, 9.1% shared with trophic resources and the remaining 14.5% in the interaction of the three groups. Trophic resource pure effects retained only 2.9% of the total variance, while the pure effects of spatial-correlation explained 7.8% (Fig. 3).

DISCUSSION

We found that Andean Condor abundance in the south of its distribution range was driven by the configuration of habitat cover, mainly meadows, and the presence of rocky cliffs used as suitable
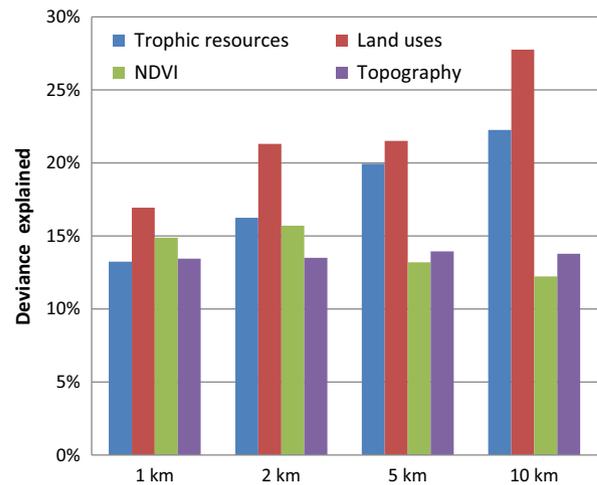

Figure 2. Percentage of explained deviance of Andean Condor abundance models by four environmental group variables across different spatial scales in southern Patagonia.
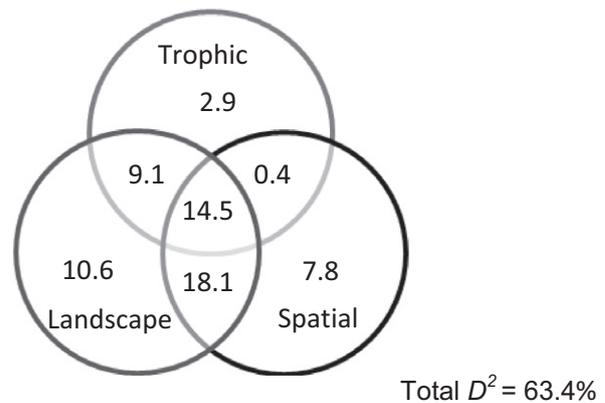

Total D^2 = 63.4%

Figure 3. Deviance partition using a partial regression analysis of Andean Condor abundance in southern Patagonia. We show the percentages of explained deviance of Andean Condor abundance accounted for by each one of three selected groups: (1) 'Trophic' (livestock abundance and wildlife prey abundance), (2) 'Landscape' (land uses, productivity, topography and potential cliffs) and (3) 'Spatial' (spatial autocorrelation) and by the interactions among them. We also included the total explained deviance of the model (total D^2). For each group we selected the best model ranked by AICc and reduced by stepwise backward selection (Table 2).

nesting and roosting places. These findings agree with our hypothesis that Condors were distributed in highly productive areas that may harbour greater abundances of herbivores and in areas where the presence of cliffs, which are needed for roosting and breeding, was high. In contrast, direct distribution of food resources and human presence

explained little of the variance in Andean Condor abundance. These results suggest that the Andean Condor distribution pattern observed is a compromise between the spatial distribution of nesting and communal roosting sites and habitats used as surrogates of potential trophic food resources. Interestingly, both meadows and cliffs are scarce and spatially aggregated in southern Patagonia, reinforcing the idea that these drivers must play an important role in the distribution of this scavenger. Similarly, the better performance of large-scale variables for all the models tested suggests that Andean Condors may perceive the landscape patterns at large scales, consistent with their wide-ranging movements.

Although meadows appear to be an important driver for Andean Condor distribution, they occupy just 1–4% of the Patagonian central plain and 5–7% of the Andean Cordillera and pre-Cordillera (Mazzoni & Vázquez 2004, Fig. S1). However, this habitat is 5–10 times more productive than the surrounding steppes (Ayesa *et al.* 1999, Buono *et al.* 2010). This was the main reason that led farmers to preferentially occupy these areas during the process of livestock range expansion in Patagonia (León *et al.* 1998). Although the abundance of herbivores should be a good indicator of the occurrence of carrion, Andean Condors seem to optimize their search in areas where the probability of presence of herbivores is usually high. This fact agrees with previous work in African vultures, which showed that in certain seasons the movements of these scavengers did not always overlap with the distribution of live ungulates (Kendall *et al.* 2014). Thus, scavengers would select areas not because of the abundance of live prey but because of the probability of mortality. In this sense, areas with higher risk of predation would have lower livestock abundance but a higher likelihood of carrion. These results are in accordance with the foraging theory, which predicts that mobile predators such as raptors or scavengers should hunt or roam more frequently in habitat patches yielding the greatest probability of energy gains (Pyke 1984, Stephens & Krebs 1986).

We did not control for livestock management practices, such as seasonal movements occurring prior to our census. Therefore, the Condor distribution pattern may reflect a previous distribution of livestock in suitable habitats. However, despite the fact that abundance of livestock and native wildlife provided a limited explanation of the distribution of Andean Condors, an interesting conclusion may be drawn. Andean Condors were more abundant in areas where domestic livestock and wild herbivores were both present. This could indicate that the two resources are complementary and therefore native herbivores are not yet functionally extinct in this area.

The particular landscape configuration that occurs in Patagonia and Tierra del Fuego may have conditioned our results. The north–south axis formed by the Andean Cordillera triggers the spatial correlation of landscape variables and trophic resources. In Patagonia, food resources are located mainly in sub-Cordilleran hills and in the central plain, while safe and large cliffs are available closer to the central Andean Cordillera. The mobility of this species enables them to decouple the location of the nesting or resting sites from the feeding grounds (Lambertucci & Ruggiero 2013, Alarcón *et al.* 2017). However, this strategy is constrained, as Andean Condor, as a large soaring bird, depends on wind for long-distance movements. The presence and strength of uplifts depend on geographical and atmospheric factors as well as the season and time of day, which constrains the movement and exploratory capacity of the Condor (Shepard *et al.* 2011, 2013, Shepard & Lambertucci 2013, Alarcón *et al.* 2017). This could explain why eastward of our study area, a cold-flat area where flying conditions are not good but where there is high livestock abundance, we could not detect any foraging Condors (Figs S2 and S3). Condors must take advantage of wind resources that peak in the afternoon but find a sparsely distributed food resource that peaks early in the morning (Alarcón *et al.* 2017). Therefore, the distribution in foraging areas is a trade-off between the locations of particular features of the land (used as surrogates of prey distribution), the presence of cliffs and wind resources (Shepard *et al.* 2013, Alarcón *et al.* 2017, and our results).

This work is a starting point for improving the understanding of the factors controlling the large-scale distribution patterns of Andean Condors. However, some methodological considerations must be taken into account for the development of future work. Point counts have been widely used to study large-scale distribution patterns in birds because they are a quick, inexpensive and effective method and allow the collection of data in moderately large areas (Bibby *et al.* 2000, Travaini *et al.* 2004), and thus seems highly justified in our study

system. However, the use of this method has been questioned because it only provides a fixed picture of the species distribution pattern (Fuller & Mosher 1981). In our case, this potential weakness should be minimized, as recent movement ecology studies of the Andean Condor have found no strong seasonal differences in home-range size and fidelity (Alarcón 2016). The sampling design tried to minimize double counting by maximizing the distance between point counts, using a large number of observers, and by reducing the time of travel between point counts to avoid double counts. Additionally, we drove the car in either the same direction or contrary to the direction Condors move (from the mountain to the steppe, or vice versa), so we counted Condors passing (flying from the roosting to the foraging area). According to tagged Condors in a similar area, the probability that a bird moved between those areas more than once a day is almost zero (e.g. Lambertucci *et al.* 2014, Alarcón *et al.* 2016, 2017). We are therefore confident that double counts were rare or non-existent, and so should not strongly influence our results. Finally, we are aware that the limited geographical and temporal scope of the fieldwork may also have constrained our conclusions. For this reason, future studies should address possible spatial and temporal variability by sampling in different seasons and over larger areas.

Conservation implications

Much of southern Patagonia is in a good conservation state and is still considered one of the main strongholds for species such as the Guanaco and the Puma, as well as the Andean Condor (Lambertucci 2007, Pedrana *et al.* 2010, 2011, Moraga *et al.* 2015, Travaini *et al.* 2015), which represents an invaluable biological and cultural heritage in South America. This study supports the idea that the conservation of wide-ranging species such as the Andean Condor requires a landscape approach. Essential key habitats need to be correctly identified, as they may be far apart or in different countries (Lambertucci *et al.* 2014), leading to varying protection needs.

Cliffs are considered an essential resource for nesting and communal roosting because they provide refuge from adverse weather and from threats posed by predation or anthropogenic disturbances, and may be used as information transfer centres (Lambertucci *et al.* 2008, Lambertucci & Speziale 2009, Lambertucci & Ruggiero 2013, Harel *et al.* 2017). However, Condor communal roosts are also used intensively by other bird species, and could be useful for the identification of local high biodiversity areas (Lambertucci & Ruggiero 2016). More than 90% of these key areas for Andean Condor survival are not included inside protected areas (Lambertucci *et al.* 2014). Future conservation actions should include cliffs, and particularly communal roosts, in mesofilter conservation strategies. This would benefit not only the vulnerable Andean Condor but also other sympatric taxa (Lambertucci & Ruggiero 2016).

Wet meadows, or *mallines*, are also very important areas for the conservation of many native species including water beetles, amphibians and fishes (Perotti *et al.* 2005, Bellis *et al.* 2006, Epele & Archangelsky 2012). These areas are one of the most productive habitats in Patagonia (Ayesa *et al.* 1999, Mazzoni & Vázquez 2004) and are considered key elements in Patagonian livestock production systems (Golluscio *et al.* 1998). In this work, we found that meadows are key habitats not only for native herbivores and livestock but also for scavengers with large home-ranges. This implies that Patagonian herbivores and carnivores depend on these environments, which only cover a small percentage (< 4%) of southern Patagonia and Tierra del Fuego.

Farmer management practices may threaten the long-term permanence and sustainability of Patagonian wet meadows by the increase of desertification due to livestock overgrazing (Golluscio *et al.* 1998, León *et al.* 1998, Perotti *et al.* 2005) or by the use of groundwater (Perotti *et al.* 2005). Additionally, climate change will probably result in increased temperatures and modifications of rainfall patterns (Paruelo *et al.* 1998, Sala *et al.* 2000, Crego *et al.* 2014). Changes in the spatial distribution and abundance of these key habitats may have unexpected effects on a top scavenger already facing conservation threats. Finally, we must continue to improve our knowledge of the ecology of vultures in South America and in the establishment of effective conservation areas. This process will favour not only this target species but also other native species that use these endangered habitats, and will allow the conservation of the ecosystem services that they provide.

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SUPPORTING INFORMATION

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

Figure S1. Distribution of Andean Condor abundance per point count and presence of wet meadows in southern Patagonia.

Figure S2. Longitudinal (W-E) and latitudinal (N-S) distribution of Andean Condor abundance and total domestic livestock (in 10-km buffer) in southern Patagonia.

Figure S3. Longitudinal (W-E) and latitudinal (N-S) distribution of Andean Condor abundance and potential cliffs (in 150 km) in southern Patagonia.