



Cliff outcrops used as condor communal roosts are local hotspots of occupancy and intense use by other bird species



Sergio A. Lambertucci*, Adriana Ruggiero

Laboratorio Ecotono, INIBIOMA (CONICET-Universidad Nacional del Comahue), Quintral 1250, 8400 Bariloche, Argentina

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ABSTRACT

Cliff outcrops are structural components of the environment that can maintain a large variety of wildlife; however, they are still rather overlooked in conservation planning. We evaluate whether cliffs used by the Andean condor (*Vultur gryphus*) for communal roosting are associated with local aggregations of other bird species, and if their presence in combination with other local (vegetation cover, plant species richness, topographic heterogeneity) and regional (distance to water) environmental variables play a significant role in the structuring of local bird diversity. We selected twenty-four localities in north-western Patagonia (Argentina) to compare the abundance and richness of birds across four habitat types: a cliff used as condor roost (CC), closest cliffs to CC not used for roosting with the same (SC) or different (DC) aspect and the vegetation matrix surrounding the cliffs (MA). This led to 264 fixed 100 m-radius points spread over 96 sampling sites. We recorded more individuals and species on cliffs than on MA; however, sample-based rarefaction curves showed that the high species richness observed on cliffs was actually the consequence of the high number of individuals recorded. Habitat type, vegetation cover and the richness of dominant vascular plants were the most important variables accounting the richness and abundance of birds. We concluded that condor roosts represent suitable habitats for the aggregation of individuals of other bird species thus leading to hotspots of occupancy and high species richness. Those cliffs should be reconsidered in the mapping of important conservation areas and for the proposal of mesofilter conservation strategies.

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1. Introduction

Although cliffs had often been seen as rock outcrops without conservative value, during recent years they have increasingly been recognized as structural components of environment that could play an important role for the aggregation, foraging, breeding and resting of species (Hjort et al., 2015; Larson et al., 2000). For instance, the presence of cliffs may represent a key habitat component for mammal predators that rest on the top of these prominent landforms to get good views of the valleys (snow leopards: Chundawat, 1990), or for bird species that uses them to get refuge against bad weather conditions or predators (e.g., Andean condor: Lambertucci and Ruggiero, 2013). There is considerable evidence suggesting that the presence of conspicuous land structures (e.g., cliffs, mountains, canyons, granite outcrops) may attract large-bodied predators leading to hotspots of occupancy, high species richness or intense biological activity (for review Bouchet et al., 2014 and references therein; Mares, 1997).

Indeed, cliffs from all over the world maintain a large variety of wildlife including invertebrates, amphibians, reptiles, birds, mammals, plants and fungus (Larson et al., 2000).

The presence of cliffs influences the spatial structuring of species assemblages through a local increase in topographic complexity; the latter is often associated with local spatial variation in climatic and other environmental conditions (wind exposure, water drainage, soil hydrology, nutrient availability) that increase habitat heterogeneity thus favouring species coexistence (Burnett et al., 1998; Hjort et al., 2015; Mares, 1997; Ruggiero and Hawkins, 2008; Boyle and Martin, 2015). Actually, the presence of prominent landforms are important components of geodiversity (the variability of Earth surface materials, landforms and physical processes) that in conjunction with climatic interactions is an influential determinant of animal community dynamics, interspecific relationships, activity patterns and evolutionary histories, thus influencing biodiversity at multiple spatial and temporal scales (Bouchet et al., 2014; Hjort et al., 2015).

A positive effect of rock outcrops on species richness and occurrence has been recorded for mammals (Mares, 1997; Ward and Anderson, 1988), reptiles (Michael et al., 2008), vascular plants (Porembski et al., 1997; Speziale and Ezcurra, 2012; but see also Graham and Knight, 2004 for an exception) and birds (Martínez-Morales, 2005; Matheson

* Corresponding author at: Conservation Biology Group, ECOTONO Laboratory, Ecology Department, INIBIOMA-CONICET, Comahue National University, Quintral 1250, 8400 Bariloche, Argentina.

E-mail address: slambertucci@comahue-conicet.gob.ar (S.A. Lambertucci).

and Larson, 1998; Ward and Anderson, 1988). Nonetheless, it was still rarely studied the extent to which the presence of geosites – i.e., small (often <1 km²) geophysical features representing habitats of high importance for wildlife (Hjort et al., 2015) – interact with other environmental factors, at local and landscape scales to account for the spatial variation in species richness and abundance on a regional scale (an example is found in Michael et al., 2008). Those geosites can be considered as critical elements of the ecosystem that are important for several species in mesofilter conservation approaches to biodiversity conservation (Hunter, 2005). Here, we evaluate whether cliffs in general and, particularly, cliffs used by the Andean condor are important geosites to bird diversity that could be used in the planning of mesofilter strategies of biodiversity conservation (sensu Crous et al., 2013).

The Andean condor (*Vultur gryphus*) roosts communally on cliffs with an orientation and height that offer them refuge against bad weather conditions and predators (Donázar and Feijóo, 2002; Lambertucci and Ruggiero, 2013). Our general hypothesis was that cliffs used by the Andean condor for communal roosting are special features of environments from Patagonia (Argentina) that could be important for other bird species, thus promoting a local aggregation of individuals and species. We tested the prediction that cliffs used by the Andean condors harbour a greater number of bird species and individuals than cliffs not used by the Andean condors or the surrounding vegetation matrix. Then, we disentangled how environmental variables representing physical and biotic heterogeneity at different spatial scales of analysis interact with the presence of cliffs leading to local bird diversity hotspots.

The positive influence of rock outcrops on species diversity may be due to a multi-scale effect of landscape-level factors (e.g. geographical location, distance to water) and local-scale factors (type of landform, outcrop structural complexity, vegetation cover and local plant) (e.g., Michael et al., 2008). We assessed the relative contribution of environmental variables influencing the abundance and richness of birds at different spatial scales, as follows:

The density, diversity and reproductive success of birds have been found to be positively associated with micro-spatial heterogeneity in vegetation structure (i.e., foliage height diversity, percent of vegetation cover; MacArthur, 1972; MacArthur and MacArthur, 1961; Roth, 1976). We tested the association between the richness and abundance of birds with vegetation cover, and the richness and height of dominant vascular plants on a local plot-spatial scale of analysis. We expected high richness and abundance of birds in association with sites of high vegetation cover, height and plant species richness.

We evaluated the role of physical heterogeneity on a cliff-spatial scale of analysis. Cliff size and aspect are two factors associated with the presence of birds; in general, cliffs used by the Andean condors are large, poorly accessible outcrops, predominantly orientated towards the east-southeast and thus facing opposite to the predominant winds (Lambertucci et al., 2008; Lambertucci and Ruggiero, 2013). On the other hand, cliff size and the number and size of shelves on cliff walls are attributes that contribute to increase respectively, the area available and micro-topographic heterogeneity, which both could increase species richness and abundance (but see Rossi and Knight, 2006). We analysed the extent to which these physical attributes of the cliffs were associated with the abundance and richness of birds. We tested whether larger cliffs with greater number of shelves and a similar orientation than communal roosts support more bird species and individuals than smaller, less heterogeneous cliffs facing a different orientation.

Finally, on a landscape scale, we considered that birds need water as a vital resource (Williams and Koenig, 1980). Places with water in their proximity might be more favourable, thus supporting a higher number of individuals and species that sites located far from water. We predicted high abundance and richness of birds on cliffs close to water sources.

2. Methods

2.1. Study area

Our study was developed in an area of ca. 25,000 km² in north-western Patagonia (Argentina), approximately between 36°–41° S and 70°–71° W. Towards the west, the mountain ranges of the northern Patagonian Andes extend in a predominant north-south direction, being composed of intrusive and metamorphic rocks due to intense plutonic and volcanic activity and Tertiary folding (Coronato et al., 2008). The presence of the Andes act as a barrier to the humid westerlies causing a greater amount of and lower variability in precipitation in the Andean Cordillera compared with the eastern extra-Andean zones (Paruelo et al., 1998). Accordingly, cold temperate sub-Antarctic forests grow on the western mountain slopes, and a steady transition from open forests to scattered grass-shrub steppes occurred to the east (Paruelo et al., 1998).

Cliffs used by the Andean condor for communal roosting are mainly in the extra-Andean Patagonia zone (Lambertucci, 2010; Fig. 1). There, the landscape is composed of semiarid flat terrains, volcanic tablelands or “mesetas” and low ridges of varied geological composition, intermingled with depressions and fluvial valleys. Due to the eastward increase in continental influence and aridity there are increasing geolian erosive processes acting on drier soils or polishing volcanic rock, which lead to the presence of prominent rock outcrops (Coronato et al., 2008).

The vegetation matrix surrounding the cliffs is the typical of the Patagonian steppes, where vegetation covers ca. 50% of the soil and mean annual precipitation is about 200–500 mm; communities of vascular plants are dominated by grasses, with scarce cushion bushes

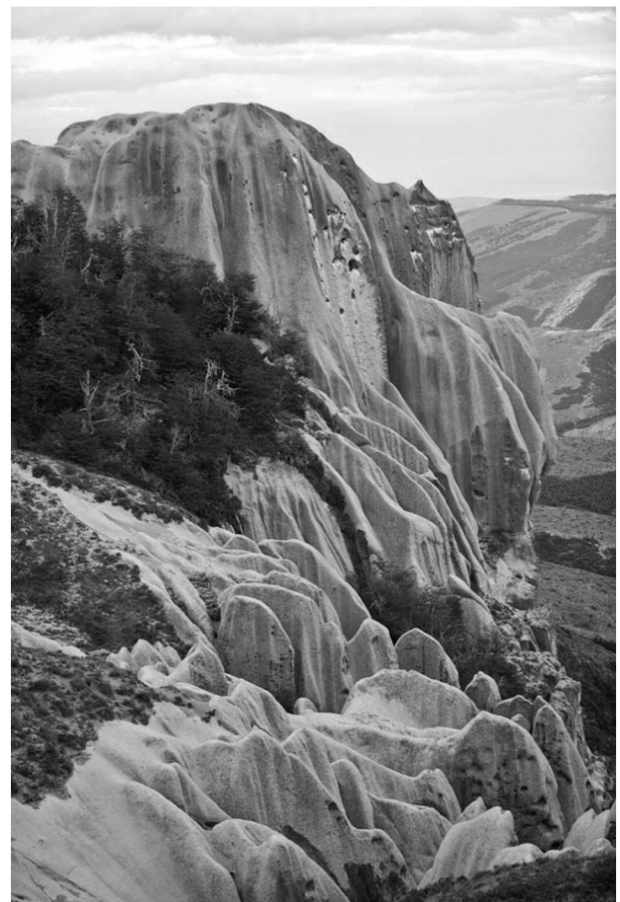


Fig. 1. Cliff used by the Andean condor (*Vultur gryphus*) as a communal roost.

(León et al., 1998). At the ecotone between the sub-Antarctic forests and the Patagonian steppes, vegetation covers ca. 60% and annual precipitation range among 500–800 mm (León et al., 1998); here vegetation consists of a mosaic of grasslands, dispersed low bushes and scattered patches of trees (see Speziale et al., 2010; Speziale and Ezcurra, 2012 for detailed floristic analyses).

2.2. Bird censuses

We selected 24 sampling localities, each one including 4 sampling habitat types (hereafter called *sampling sites*, $N = 96$, located within an area of <3 km radius): CC: a cliff used as communal roosts by condors (Fig 1); SC: a cliff not used by condors, with the same aspect than CC; DC: a cliff not used by condors, with different aspect than the communal roost; MA: vegetation matrix surrounding the cliffs. The mean distance between each particular site within a locality was ca. 1.5 km.

All the fieldwork was done by the same two observers (SAL and an assistant), in order to reduce all possible biases regarding observers detection ability. Bird counts were conducted using fixed 100 m-radius point counts established at each site (details on the number of point counts for CC, SC, DC and MA at each locality are given in Fig 2 legend). We only recorded the individuals detected within a radio of 100 m from the sampling point, except for raptors (Families

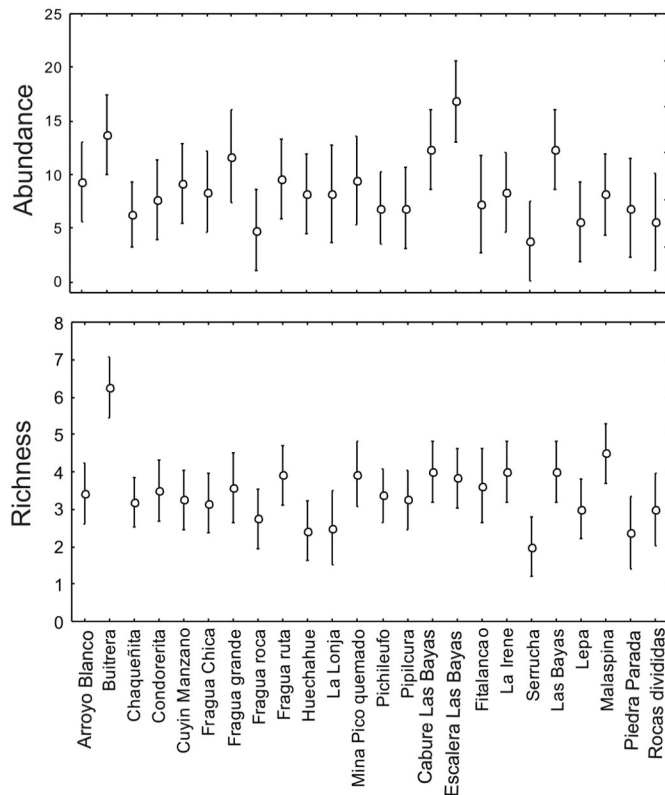


Fig. 2. Mean number of individuals of birds (abundance) and mean number of bird species (richness) and confidence interval (\pm CI) recorded at each locality studied in north-western of Patagonia. The mean richness and abundance for each locality was the total number of individuals counted at each locality divided by the total number (N) of point counts established on the four sampling sites at each locality. Localities are Arroyo Blanco: $N = 12$ (CC: $N = 3$, SC: $N = 3$, DC: $N = 3$, MA: $N = 3$), Buitrera: $N = 12$ (3,3,3,3) Chaqueñita: $N = 12$ (3, 3, 3, 3) Condorerita: $N = 12$ (3,3,3,3), Cuyin Manzano: $N = 12$ (3,3,3,3), Fragua Chica: $N = 12$ (3,3,3,3), Fragua Grande: $N = 8$ (2,2,2,2), Fragua Roca: $N = 12$ (3,3,3,3), Fragua ruta: $N = 12$ (3,3,3,3), Huechahue: $N = 12$ (3,3,3,3), La Lonja: $N = 8$ (2, 2, 2, 2), Mina Pico quemado: $N = 8$ (2,2,2,2), Pichileufo: $N = 12$ (3,3,3,3), Pipilcura: $N = 12$ (3,3,3,3), Caburé Las Bayas: $N = 12$ (3,3,3,3), Escalera Las Bayas: $N = 12$ (3,3,3,3), Fitalancao: $N = 8$ (2,2,2,2), La Irene: $N = 12$ (3,3,3,3), Serrucha: $N = 12$ (3,3,3,3), Las Bayas: $N = 12$ (3,3,3,3), Lepa: $N = 12$ (3,3,3,3), Malaspina: $N = 12$ (3,3,3,3), Piedra Parada: $N = 8$ (2,2,2,2), Rocas divididas: $N = 8$ (2,2,2,2).

Falconidae, Accipitridae, Cathartidae, Tytonidae and Strigidae) who were included up to 200 m, although we avoided recording them in more than one point count. This conservative distance and the relatively homogeneity of the regional vegetation across the sampling sites diminish the possible biases in the sampling method. Due to logistic reasons, 14 out of the 24 studied localities were censused during the southern summer (January and February) of 2008 and the remaining 10 were in the summer of 2009. Depending upon the size of the cliff, we established two or three sampling points on each communal roost 220 m apart from each other and 50 m apart from the cliff edge. Accordingly, we established the same number of sampling point counts on CC, SC, DC and MA.

At each locality all counts were done during the same morning. At each sampling period, we randomly changed the place where we started the counts and where we finished the censuses to reduce possible time biases. We used clear days without rain, from sunrise (ca. 6 am) to 11 am. At each plot, we waited 2 min before we started an 8 minute-period of counting to allow birds to recover the normal activity after the arrival of the observers (Bibby et al., 2000). All bird species heard and/or seen were recorded provided they used the plot for resting, foraging, nesting or any other behavior that demonstrate that they use it. Birds that passed flying were not recorded, unless they were foraging in the air (e.g., swallows).

Point counts do not provide unbiased estimates of the actual number of birds present at a point because only a proportion of the birds are sampled, which results in that the mean of several counts is a better (more reliable) estimation of richness and abundance at a point than single counts (Sauer et al., 1995). Thus, throughout the present study, abundance of individuals and species richness were defined, respectively, as the mean number of individuals or species counted over the total (2–3) number of point counts for CC, SC, DC and MA at each sampling locality (the number of point counts at each site is given in Fig. 2 legend).

2.3. Environmental variables

We measured ten variables to represent vegetation structure, topography, and water availability at each site, as follows:

- 1) Vegetation structure. Three 10×10 m plots (Speziale et al., 2010) were randomly placed on each site to measure a) the height of the lowest vegetation stratum, and b) height of the highest vegetation stratum by using a meter, c) the percentage of above ground vegetation cover: estimated dividing the plot in 4 subplots and calculating visually the percentage of bare ground in each subplot for then deducing this value from 100%, and d) the number of dominant vascular plant species that covered at least 10% of the plot.
- 2) The morphology of cliffs was characterized by a) maximum height (m) from the base to the top of the cliff, b) the width (m) between the lateral extremes of the cliff, c) the number of shelves as a categorical variable with four levels: (1) <30 shelves; (2) between 30 and 50, (3) between 50 and 70 and (4) >70 , d) angular aspect of the cliff measured with a compass, estimated in degrees around the middle of the outcrop in the area with greatest number of shelves, and e) elevation above sea level measured at the top of the cliff by using altimeter, or telemeter and clinometer when we were not able to reach the top of the cliff (see Lambertucci and Ruggiero, 2013).
- 3) Water availability was represented by distance to the closest water course, which was measured by telemeter or GPS for distances over 1 km.

2.4. Analyses of data

2.4.1. Differences in the abundance and richness of birds across sites and localities

We compared the mean abundance and richness of birds across CC, SC, DC and MA averaged over all localities. Then, we compared the

variation in mean abundance and richness of birds across all localities averaged over CC, SC, DC and MA (Kruskal-Wallis test). Because as more individuals are sampled more species will be recorded, the number of species recorded is not independent of the number of individuals observed (Gotelli and Colwell, 2001). We used EstimateS 8.2 (Colwell, 2009) to elaborate sample-based rarefaction curves rescaled to the number of individuals (Gotelli and Colwell, 2001). Sample-based rarefaction curves represented the means of repeated re-sampling 100 times at random from the pool of the 96 sampling sites, and subsequent plotting of the average number of species represented in the 96 sampling sites. In this way, we compare the statistical expectation of the number of species for CC, SC, DC and MA at comparative levels of sampling effort (i.e. accumulated number of individuals) (Gotelli and Colwell, 2001).

2.4.2. The association of abundance and richness of birds with environment

We analysed the relationships between the mean local abundance and richness of birds and environmental factors representing vegetation structure, cliff morphology and water availability using automated multimodel selection based on Akaike's information criterion (AIC) (Burnham and Anderson, 2002). First, we used the whole dataset to test the association of vegetation structure, habitat type and water availability with the abundance and richness of birds (hereafter referred as "whole dataset"). Then, data on MA were excluded to assess the associations of abundance and richness with attributes of cliff morphology, vegetation structure and water availability (hereafter referred as "cliffs only"). We performed an exhaustive search of minimum adequate models for abundance and species richness variation for each dataset. We considered all different combinations of environmental predictors and site (CC, SC, DC, MA) as fixed factors and "locality" and "year" as random factors with 24 and 2 levels respectively. We assumed a Gaussian error distribution and thus used the linear mixed model (lmer) routine in R3.0.3 (R Development Core Team; <http://www.r-project.org/>). We used the set of best supported models based on the $\Delta AICc < 2$ criterion for model averaging as implemented in the MuMIn package (Bartón, 2013; Grueber et al., 2011). We estimated the relative importance of each predictor variable by using the Akaike weight (w_i), which measures the relative likelihood of a model being the best supported by a dataset. The importance of a given j variable arose from the sum of w_i of all models in which the variable participated (Burnham and Anderson, 2002).

In practice, input variables that have large main effects also tend to have large interactions with other variables (Gelman and Hill, 2007). We tested the associations of richness and abundance with environmental variables in models that considered the interactions between habitat type (importance = 1 in all our analyses, see Results) and the other most important environmental variables (importance value > 0.70 based on their Akaike weights, as explained above). This allowed detecting differences in the slopes for the association of abundance and richness with the most important environmental variables (i.e. vegetation cover and richness of dominant plants, see Results) across MA, DC and SC.

3. Results

3.1. Bird abundance and richness

We performed 264 point counts where we observed 2307 individuals from 54 species, representing 19 families (see online Appendix, Supplementary File 1 Table S1). Most studied localities have similar abundance of individuals and species (Fig. 2), but as a few places (e.g., La Buitrera) have more species and individuals than the other sites some differences appeared (Kruskal-Wallis ($H_{n-1, n+1}$) species richness: $H_{23, 265} = 43.19$, $P = 0.007$; individual abundances $H_{23, 265} = 41.12$, $P = 0.012$). In general, all bird species recorded were of widespread geographical distribution at continental or subcontinental scale

and use a variety of habitats (Ferguson-Lees and Christie, 2001; online Appendix Table S2 in Supplementary File 1; cf. data on species' distributions and habitats in Fjeldsà and Krabbe, 1990).

We observed birds in all the CC point counts (66/66). On SC, we observed birds in 98.5% (65/66) of the point counts. On DC, we found birds in a 97.0% (64/66) of the point counts. We registered birds in the 89.4% (59/66) of the MA point counts. Seventeen species were observed on cliffs although not on MA, out of which thirteen were observed on CC. Species observed on cliffs were widespread raptors known to use a variety of habitats (e.g. *Circus cinereus*, *Geranoaetus melanoleucus*) or that needs cliffs for nesting and roosting (*Vultur gryphus*), widespread passerine species known to perch on rock outcrops (e.g. *Agriornis* spp., *Phrygilus unicolor*), high Andean species that uses rocky ridges (*Melanodera xanthogramma*) or use caves and crevices to avoid low night temperatures (*Oreothochilus leucopleurus*) (Ferguson-Lees and Christie, 2001; Fjeldsà and Krabbe, 1990). The Andean condor is the only threatened species and we reported the first record of a species whose geographical distribution was unknown for study region (*Catantia analis*; online Appendix Table S2 in Supplementary File 1). The four species observed exclusively on MA spend most of their time on the ground (*Lessonia rufa*, *Anthus correndera*) or in tussock grasses (*Gallinago paraguaiæ*; Table S2 in Supplementary File 1).

The mean number of individuals and species observed across habitats differed significantly (Kruskal-Wallis (H) individual abundances, $H_{3, 264} = 75.31$, $P < 0.001$; species richness: $H_{3, 264} = 86.23$, $P < 0.001$; Fig. 3). On average, we observed more individuals and species on CC, than on the other habitats, and the main difference was between those cliffs and the matrix (Fig. 3). Nonetheless, on a regional scale, and after the standardization of richness by the abundance of individuals, the expected mean richness was similar between CC and the

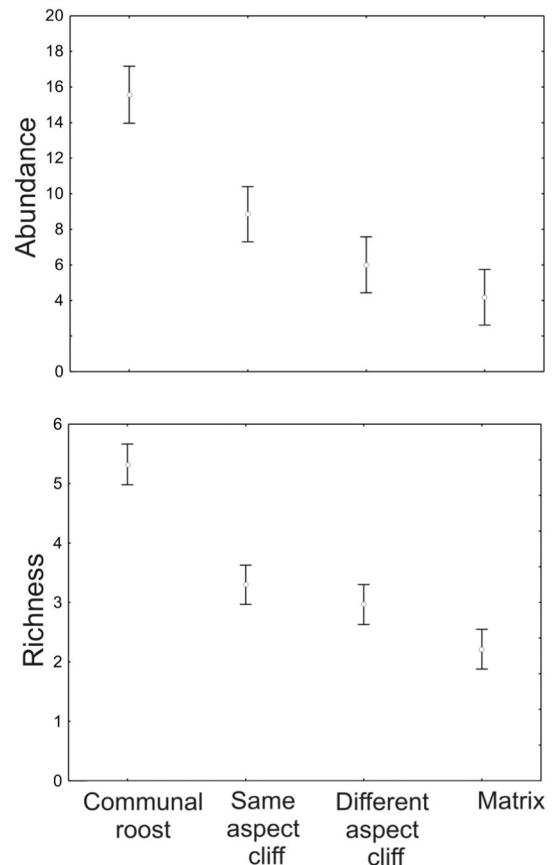


Fig. 3. Mean number of individuals (abundance) and mean number of bird species (richness) recorded plus confidence interval (\pm CI) on each type of cliff (CC, SC, DC) and in the surrounding vegetation matrix (MA) over all studied localities in north-western Patagonia. CC: N = 24, SC: N = 24, DC: N = 24, MA: N = 24.

other studied habitats (Fig. 4). Sample-based rarefaction curves confirmed that the greater total number of species observed on CC than on MA was actually the consequence of counting a greater total number of individuals on CC (Fig. 4).

3.2. The association of abundance and richness with environmental variables

We obtained 9 best supported environmental models that accounted for the mean variation in the abundance of birds and 3 best supported models that accounted for mean bird species richness across the four types of habitats (CC, SC, DC and MA; whole dataset $N = 96$; see online Appendix Table S3 in Supplementary File 2). After excluding data on MA there were 52 best supported models that accounted for the mean variation of bird abundance across cliffs (CC, SD, DC) and 3 models were best supported by bird richness data ($N = 72$; online Appendix Table S3 in Supplementary File 2).

After model averaging, the most important variables that accounted for the variation in bird abundance and richness were type of habitat (CC, SC, DC and MA) and vegetation cover (Fig. 5a–d). For the whole dataset (i.e. including MA, $N = 96$), we confirmed that the abundance

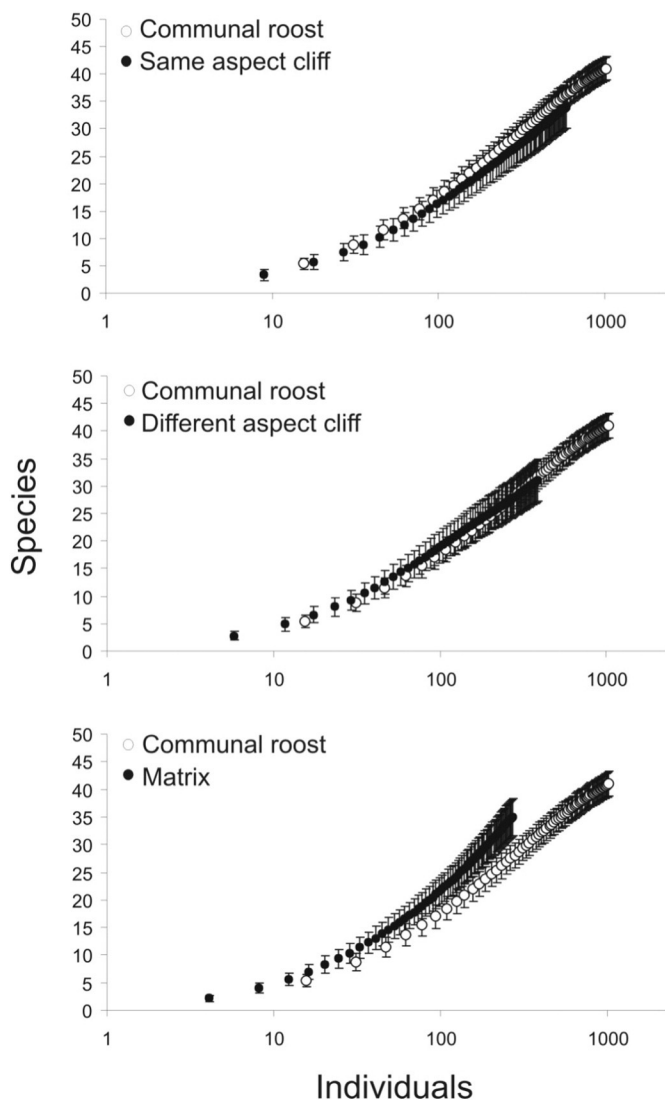


Fig. 4. Estimation of the number of species (\pm SD) in relation to the abundance of individuals obtained from a rarefaction (see Methods for more detail). In all cases we contrasted the condor communal roost and the other three study sites (same and different aspect cliffs and the matrix).

and richness of birds was low in habitats other than CC (i.e. DC, SC and MA), with the lowest abundance of birds observed in MA (Table 1). After excluding data on MA, we confirmed that the mean abundance and richness of birds was lower in SC and DC with respect to CC (Table 1).

The abundance and richness of birds also increased with the increase in the dominant plant species richness, although the association was stronger for abundance rather than for richness (Table 1). After model averaging, we confirmed that the richness of dominant plants was more important to account for the variation in abundance and richness in the whole dataset (including MA, Fig. 5a–b), and for the variation in bird abundance across different types of cliffs (Fig. 5c), rather than for bird richness on cliffs (Fig. 5d).

Statistical models that included the interactions of habitat type with vegetation cover and the richness of dominant plants predicted with greater accuracy the mean variation of abundance rather than models without the interaction terms (i.e. abundance-models that included the interaction terms showed a decrease in AIC values by >2 points compared with models without interactions, Table 2). In general, both for the whole dataset and data on cliffs only, the positive association between vegetation cover and abundance of birds increased more strongly in SC than in DC and decreased in MA; the positive association of dominant plant species richness with abundance increased in MA and decreased in SC. Nonetheless, these results are not conclusive given that the interaction terms were not statistically significant (i.e. estimated coefficients of the interaction terms in all models were lower than 2 standard errors in Table 2). In contrast, the main associations of habitat type and vegetation cover with the abundance of birds still remain significant after including the interaction terms (Table 2). On the other hand, models that did not include interaction terms predicted with greater accuracy the mean variation in species richness (i.e. showed the lowest AICs in Table 2) than models with interactions. The whole analyses indicate that the main effects of habitat type, vegetation cover and the richness of dominant plants may influence independently on the mean variation in local abundance and species richness.

The vertical structure of vegetation and cliff morphology influenced bird abundance but not bird richness. The abundance of birds decreased with the increase in the height of the highest vegetation stratum, and increased with the height of the lowest vegetation stratum (Table 1). Wide cliffs, with high number of shelves, orientated in similar direction than communal roosts (towards the northeast-east-southeast) and high elevation at the top of the cliff harboured greater abundance of birds (Table 1); however, these latter variables were of lower importance (≤ 0.5) compared with the effect of vegetation cover, type of site or number of dominant plants (Fig. 5c). In contrast, the abundance of birds decreased with cliff height (Table 1), which is possible reflecting that DC were taller than CC.

The abundance and richness of birds tended to decrease with the increase of distance to water, and the importance of water was greater (ca. 0.4) to account for abundance in the whole dataset rather than for richness (Table 1; cf. Fig. 5a–b). Distance to water was less important (<0.4) to account for differences in abundance and richness across cliffs (Fig. 5c–d).

4. Discussion

We confirmed that cliffs used as communal roosts by the Andean condor are special physical features in the Patagonian stepped environments that interact with other local components of the environment – mainly with vegetation structure and floristic richness at a local-spatial scale – to promote a high occupancy of these habitats by other bird species. We found both a greater number of individuals and species on cliffs used by the Andean condor than in other types of cliffs or the surrounding vegetation matrix. The increase in local bird species richness observed in association with cliffs used by the Andean condor was actually due to the greater number of individuals using those habitats. These results suggest that the presence of cliffs in

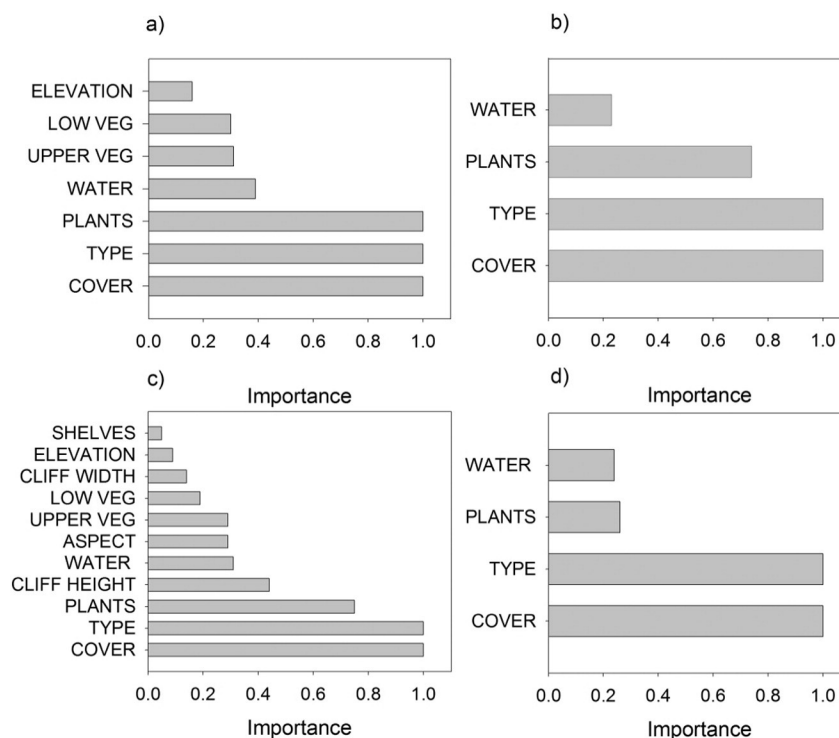


Fig. 5. Importance of variables representing habitat type, vegetation structure, topography, water availability and cliff morphology in explaining the spatial variation in abundance (a,c) and bird species richness (b,d). The first analysis used the whole dataset to test the association of habitat type and environmental variables with (a) abundance and (b) richness (whole dataset); then, data from the vegetation matrix (MA) were excluded to assess the associations of (c) abundance and (d) richness with attributes of cliff morphology, topography, and vegetation structure and water availability (cliffs only). All analyses included locality as random factor. Variables shown on each panel were those included in the best supported models based on $\Delta AICc < 2$. We obtained multi-model consensus by averaging and weighting the estimated model parameters as function of Akaike weights (w_i). The importance of each variable was the sum of w_i of all models in which the variable participated. Standardized coefficients for the average models are given in Table 1. COVER: Vegetation cover; TYPE: type of habitat (CC, SC, DC, MA); PLANTS: number of dominant vascular plants; WATER: distance to water; UPPER VEG: height of the upper vegetation stratum; LOW VEG: height of the lowest vegetation stratum; ELEVATION: altitude above sea level; CLIFF HEIGHT: height from the base to the top of the cliff; CLIFF WIDTH: the width between the lateral extremes of the cliff; ASPECT: cliff face aspect; SHELVES: number of shelves.

the open semi-desert Patagonian steppes play a significant role in the assemblage of bird species as previously shown in forested areas of other parts of the world (Ward and Anderson, 1988; Matheson and Larson, 1998; Martínez-Morales, 2005). In north-western Patagonia, cliffs used by the Andean condors can be considered local hotspots of occupancy and intense use by bird species. It is interesting to note that although bird species found on cliffs are widespread distributed in other several habitat types, they still show high abundance of individuals on cliffs suggesting their preference for those habitats. Given that cliffs can be used by a species for thousands of years (Burnham et al.,

2009), cliffs used by the Andean condors and other bird species can be indeed habitats of high conservation value.

The total richness of bird species found in our study area was in general low, which is in agreement with previous richness estimations from the same area (e.g., Ralph, 1985). The north-western Patagonia (Argentina) is well-known for their low number of threatened species, and the conservation status of almost all bird species reported in our study is of 'Least Concern'; only the Andean Condor is classified as Near Threatened (see online Appendix Table S2 in Supplementary File 1). All bird species detected throughout the present study are

Table 1

Coefficients estimations (b) for fixed effects after averaging the best supported models (i.e., models with $\Delta AICc < 2$ of the best supported model). Best supported models for each dataset are shown in online Appendix Table S2 Supplementary File 1. N = number of sites for each dataset. Locality and year were random factors in all models.

	Abundance (whole dataset) N = 96	Species richness (whole dataset) N = 96	Abundance (cliffs only) N = 72	Species richness (cliffs only) N = 72
	b	b	b	b
Intercept	15.26	5.23	15.80	5.30
MA	-10.65	-2.88		
DC	-8.91	-2.25	-9.63	-2.33
SC	-6.58	-1.94	-7.05	-1.99
Vegetation cover	2.08	0.44	2.41	0.49
Dominant plants	1.22	0.23	0.84	0.07
Water	-0.25	-0.05	-0.22	-0.07
Upper stratum	-0.19		-0.23	
Lower stratum	0.17		0.11	
Elevation	0.03		0.02	
Cliff width			0.06	
Cliff height			-0.40	
Aspect			0.17	
Shelves			0.01	

Table 2
Coefficients (*b*) and standard errors (*SE*) estimated for fixed effects from models that included the interaction term (:) between habitat type and the other most important environmental variables (importance value >0.70 after model averaging, shown in Fig. 5). AIC indicates the predictive ability of models with and without interactions; the AIC of models best supported by the data are in bold. Best supported models for each dataset are shown in Table S2 Supplementary File 1. N = number of sites for each dataset. Locality and year were random factors in all models. Coefficients in bold are more than ± 2 SE different from zero.

Variables	Abundance (whole dataset) N = 96		Species richness (whole dataset) N = 96		Abundance (cliffs only) N = 72		Species richness (cliffs only) N = 72	
	<i>b</i>	<i>SE</i>	<i>b</i>	<i>SE</i>	<i>b</i>	<i>SE</i>	<i>b</i>	<i>SE</i>
Intercept	15.33	1.08	5.26	0.25	15.51	1.21	5.32	0.26
MA	-10.77	1.50	-2.90	0.33				
DC	-8.90	1.49	-2.25	0.33	-8.86	1.70	-2.36	0.33
SC	-6.50	1.47	-1.97	0.32	-6.60	1.67	-1.99	0.33
Vegetation cover (COV)	1.83	0.89	0.27	0.20	1.89	1.03	0.32	0.21
Dominant plants (DOM)	0.85	0.96	0.19	0.22	0.90	1.12		
COV: DC	0.22	1.45	0.40	0.33	0.56	1.77	0.37	0.37
COV: SC	0.88	1.37	0.27	0.31	1.06	1.66	0.29	0.37
COV: MA	-0.45	1.74	0.09	0.39				
DOM: DC	0.99	1.47	0.22	0.33	0.98	1.73		
DOM: SC	-0.58	1.48	0.13	0.34	-0.59	1.73		
DOM: MA	1.08	1.53	0.29	0.34				
AIC	581.7		335.4		453.4		254.5	
<i>Models without interactions</i>								
Intercept	15.23	1.05	5.20	0.25	15.46	1.18	5.31	0.26
MA	-10.56	1.42	-2.84	0.31				
DC	-8.98	1.42	-2.22	0.31	-9.06	1.64	-2.36	0.32
SC	-6.47	1.40	-1.92	0.31	-6.61	1.61	-1.98	0.32
Vegetation cover (COV)	2.02	0.53	0.44	0.12	2.26	0.68	0.48	0.15
Dominant plants (DOM)	1.17	0.53	0.31	0.12	1.00	0.69		
AIC	586.6		323.3		457.8		251	

widespread generalist bird species that use a variety of habitats; some were raptors or passerine bird species previously reported as perching on cliffs and rock outcrops in other northern or southern regions within their widespread geographical distributions (see details in the Results). This reinforces the idea that cliffs used by the Andean condor in north-western Patagonia are hotspots of occupancy of widespread species. Therefore, their main role in the structuring of local species diversity may be mediated through the attraction of individuals to rest or perch, obtaining food and/or refuge against adverse weather conditions, thus leading to a local increase of abundance and species richness.

In general, the flora of the rock outcrops in north-western Patagonia shares similar dominant families and similar proportions of different phylogenetic groups with the adjacent vegetation matrix, with a low number of endemic vascular plants (Speziale and Ezcurra, 2012). Speziale and Ezcurra (2012) found that rock outcrops host a particular assemblage of native plant species that were absent from the vegetation matrix and that were 'outlier' species from their main geographical distribution (i.e., species that were widely distributed within Argentina or found in provinces either to the south or north of the country). Probably because of birds being more mobile than plants, we did not find a similar pattern of "outliers" in our bird study. Actually, *Catamenia analis* was the only species we recorded outside its previously known geographical distribution. Nonetheless, future studies that attempt to find other rare species should use other more intense sampling methods than the point-count method we used here (Bibby et al., 2000; Sutherland et al., 2004). The point-count method allows a quick and standardized assessment of bird species diversity easing site-to-site comparisons over large study areas; however, it may complicate detection of species with low abundances, which are generally rare and can be locally threatened (Bibby et al., 2000).

4.1. The association with environmental variables

Animal populations respond to the presence of topographic complexity through multiple mechanisms at multiple spatial scales (Bouchet et al., 2014). In open habitats of temperate latitudes, birds could be looking for cliffs that offer wind shelter, adequate sun

exposure, and suitable places for nesting (Lambertucci and Ruggiero, 2013; Ward and Anderson, 1988). We found the highest abundances of individuals on the two types of cliffs (CC and SC) oriented opposite to predominant wind directions, rainfall, and snowstorms. At local spatial scale, we found that the richness and abundance of birds increased in sites with high vegetation cover and high number of dominant plant species suggesting that the richness and abundance of birds responded to vegetation structure (MacArthur, 1972; MacArthur et al., 1962; Norris and Pain, 2002; Ralph, 1985; Ralph, 1985). Our results further suggests that cliffs with similar orientation than condor roosting places with high vegetation cover and embedded in a vegetation matrix with high number of dominant plant species may favour high bird occupancy, and future analyses should be conducted to confirm this trend. On the other hand, at a landscape spatial scale we found that water availability was rather important, strongly most for abundance, as we found a greater number of individuals – and hence higher species richness – in sites close to the water.

Nonetheless, the number of individuals observed on communal roosts (CC) nearly duplicate the number of individuals found on other cliffs with the same aspect (SC) suggesting the existence of other characteristics of CC that are also selected by birds. On one hand, large and tall cliffs could provide suitable space for the aggregation of birds as they provide refuge from humans and predators and favouring resource acquisition (Lambertucci and Ruggiero, 2013, Lambertucci unpubl. data; Larson et al., 2000). On the other hand, the role of biological interactions should be considered in future studies, as they may also play a role in accounting the aggregation of individuals of other species on condor communal roosts. For instance, the presence of condors on cliffs used for communal roosting could limit the presence of other predators, thus reducing the potential predation (e.g., by raptors) on birds (e.g., passerines) using the same cliffs. Moreover, cliffs used by carnivores for roosting can enrich the soil with nutrients in the surroundings improving the habitat for plants (Fedriani et al., 2015), and then for birds. Thus, these two possible and complementary biological mechanisms may also contribute to explain the main association of habitat type, and specially the presence of Andean condor communal roosts, with hotspots of occupancy and intense use for other bird species.

4.2. Conservation implications

The Andean condor is an emblematic species in all the countries located along the Andes. It has been selected as a surrogate species (Caro and O'Doherty, 1999) in different areas of its geographical distribution. Condors have large home ranges and, given their natural history and habitat requirement, they depend on large areas to maintain viable populations (Lambertucci et al., 2014; Rodríguez et al., 2004). Our results suggest that the Andean condor could also act as a surrogate species in Patagonia, mainly indicating environments with high abundances of other bird species as other top predators (Sergio et al., 2008). This species could also play a similar role throughout its entire South American distribution. Moreover, other communal roosting species (e.g., California condor and some old world vultures) might select particular cliffs for roosting that could be important for other species. This merit attention and further research.

Our results suggest that the protection of cliffs used by this species to overnight can favour other sympatric species. Nonetheless, at least in the Argentine Patagonia >90% of the cliffs used as communal roosts by the Andean condor as well as most of its large foraging area are not protected at all and are located outside reserves (Lambertucci et al., 2014; Lambertucci et al., unpubl. Data). Therefore, they are subject to different anthropogenic disturbances such as power lines, wind farms, mining, climbing, oil extraction, woodland plantations, roads, and strong livestock rising in the surroundings that could directly or indirectly affect those outcrops and the wildlife depending on them (Hjort et al., 2015; Larson et al., 2000; Lambertucci et al., 2009, 2015; Speziale et al., 2008; Walker et al., 2003). For instance, the loss of pastures, as a consequence of livestock overgrazing, prevent the migration of chinchillas (*Lagidium viscacia*) among cliffs, due to the increase in predation, isolating the entire subpopulations of this species in northern Patagonia (Walker et al., 2003). Thus, rocky cliffs in Patagonia (this study), and other geosites from all over the world (Hjort et al., 2015) are facing threats that should be considered in any sound conservation strategy.

Although the creation of protected areas is an effective coarse filter conservation strategy for ecosystems, in many cases it does not include some target species (Hunter, 2005). The mesofilter conservation has been proposed as complementary to the creation of reserves, in particular for special features of the environment that are important for some species, as the rocky cliffs (Hunter, 2005). Mesofilter conservation is based on the idea that ecosystems contain certain physical elements that are specifically associated with high diversity of species. Therefore, the identification of such mesofilters could complement existing conservation planning tools such as coarse and fine filters (Crous et al., 2013). To protect a set of small areas, including the cliffs, may be a low costs and quick strategy to implement. This kind of strategies have been proposed yet for other organisms (e.g. for snails, Fontaine et al., 2007, and other raptors Moleón et al., 2011). Moreover, the conservation of rocky outcrops and cliffs should involve the best combination of cliff-matrix places to guarantee the maximum complementarity (e.g., O'Dea and Whittaker, 2007).

The inclusion of cliffs in mesofilter conservation strategies may protect vulnerable birds as condors, and other sympatric taxa (Larson et al., 2000, this study; Matheson and Larson, 1998; Ward and Anderson, 1988). A mixed public-private conservation approach can play a key role in this strategy since cliff environments are of low productive value for farmers with livestock, which facilitate the collaboration of private owners (Roldán et al., 2010). The public interest aroused by some species (i.e., "flagship species" Caro and O'Doherty, 1999), as condors, may help in developing this kind of mixed strategies, and has the potential to be at the same time a good conservation approach for other species.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.05.013>.

References

- Bartón, K., 2013. MuMIn: multi-model inference. R Package Version. <http://www.r-forge.r-project.org/projects/mumin/1.9.13>.
- Bibby, C.J., Burgess, N.D., Hill, D.A., Mustoe, S.H., 2000. *Bird Census Techniques*. second ed. Academic Press, London.
- Bouchet, P.J., Meeuwig, J.J., Kent, S., Chandra, P., Letessier, T.B., Jenner, C.K., 2014. Topographic determinants of mobile vertebrate predator hotspots: current knowledge and future directions. *Biol. Rev.* 90, 699–728.
- Boyle, W.A., Martin, K., 2015. The conservation value of high elevation habitats to North American migrant birds. *Biol. Conserv.* 192, 461–476.
- Burnett, M.R., August, P.V., Brown, J.H., Killingbeck, K.T., 1998. The influence of geomorphological heterogeneity on biodiversity I. A patch-scale perspective. *Conserv. Biol.* 12, 363–370.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. Springer.
- Burnham, K.K., Burnham, W.A., Newton, I., 2009. Gyrfalcon *Falco rusticolus* post-glacial colonization and extreme long-term use of nest-sites in Greenland. *Ibis* 151, 514–522.
- Caro, T.M., O'Doherty, G., 1999. On the use of surrogate species in conservation biology. *Conserv. Biol.* 805–814.
- Chundawat, R.S., 1990. Habitat selection by a snow leopard in Hemis National Park, India. *Int. Pedigree Book Snow Leopards* 6, 85–92.
- Colwell, R.K., 2009. EstimateS: statistical estimation of species richness and shared species from samples. Available at: <http://viceroy.eeb.uconn.edu/estimates/>.
- Coronato, A.M., Coronato, F., Mazzoni, E., Vázquez, M., 2008. The physical geography of Patagonia and Tierra del Fuego. *Dev. Quat. Sci.* 11, 13–55.
- Crous, C.J., Samways, M.J., Pryke, J.S., 2013. Exploring the mesofilter as a novel operational scale in conservation planning. *J. Appl. Ecol.* 50, 205–214. <http://dx.doi.org/10.1111/1365-2664.12012>.
- Donazar, J.A., Feijóo, J.E., 2002. Social structure of Andean condor roosts: influence of sex, age, and season. *Condor* 104, 832–837.
- Fedriani, J.M., Garrote, P.J., Delgado, M.d.M., Penteriani, V., 2015. Subtle gardeners: inland predators enrich local topsoils and enhance plant growth. *PLoS One* 10 (9), e0138273.
- Ferguson-Lees, J., Christie, D.A., 2001. *Raptors of the World*. A&C Black, London, UK.
- Fjeldså, J., Krabbe, N., 1990. *Birds of the High Andes: A Manual to the Birds of the Temperate Zone of the Andes and Patagonia, South America*. Zoological Museum, University of Copenhagen.
- Fontaine, B., Gargominy, O., Neubert, E., 2007. Priority sites for conservation of land snails in Gabon: testing the umbrella species concept. *Divers. Distrib.* 13, 725–734.
- Gelman, A., Hill, J., 2007. *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press.
- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391.
- Graham, L., Knight, R.L., 2004. Multi-scale comparisons of cliff vegetation in Colorado. *Plant Ecol.* 170, 223–234.
- Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* 24, 699–711.
- Hjort, J., Gordon, J.E., Gray, M., Hunter, M.L., 2015. Why biodiversity matters in valuing nature's stage. *Conserv. Biol.* 29, 630–639. <http://dx.doi.org/10.1111/cobi.12510>.
- Hunter, M.L., 2005. A mesofilter conservation strategy to complement fine and coarse filters. *Conserv. Biol.* 19, 1025–1029. <http://dx.doi.org/10.1111/j.1523-1739.2005.00172.x>.
- Lambertucci, S.A., 2010. Size and spatio-temporal variations of the Andean condor *Vultur gryphus* population in north-west Patagonia, Argentina: communal roosts and conservation. *Oryx* 44, 441–447.
- Lambertucci, S.A., Ruggiero, A., 2013. Cliffs used as communal roosts by Andean condors protect the birds from weather and predators. *PLoS One* 8, e67304. <http://dx.doi.org/10.1371/journal.pone.0067304>.
- Lambertucci, S.A., Jácome, N., Trejo, A., 2008. Use of communal roosts by Andean condors in northwest Patagonia, Argentina. *J. Field Ornithol.* 79, 138–146.
- Lambertucci, S.A., Shepard, E.L.C., Wilson, R.P., 2015. Human-wildlife conflicts in a crowded airspace. *Science* 348, 502–504.

- Lambertucci, S.A., Speziale, K.L., Rogers, T.E., Morales, J.M., 2009. How do roads affect the habitat use of an assemblage of scavenging raptors? *Biodivers. Conserv.* 18, 2063–2074.
- Lambertucci, S.A., Alarcón, P.A., Hiraldo, F., Sanchez-Zapata, J.A., Blanco, G., Donazar, J.A., 2014. Apex scavenger movements call for transboundary conservation policies. *Biol. Conserv.* 170, 145–150.
- Larson, D.W., Matthes, U., Kelly, P.E., 2000. *Cliff Ecology: Pattern and Process in Cliff Ecosystems*. Cambridge University Press, Cambridge, U.K.
- León, R.J., Bran, D., Collantes, M., Paruelo, J.M., Soriano, A., 1998. Grandes unidades de vegetación de la Patagonia extra andina. *Ecología Austral* 8, 125–144.
- MacArthur, R.H., 1972. *Geographical Ecology: Patterns in the Distribution of Species*. Princeton University Press.
- MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. *Ecology* 42, 594–598.
- MacArthur, R.H., MacArthur, J.W., Preer, J., 1962. On bird species diversity. II. Prediction of bird census from habitat measurements. *Am. Nat.* 167–174.
- Mares, M.A., 1997. The geobiological interface: granitic outcrops as a selective force in mammalian evolution. *J. R. Soc. West. Aust.* 80, 131–139.
- Martínez-Morales, M.A., 2005. Landscape patterns influencing bird assemblages in a fragmented neotropical cloud forest. *Biol. Conserv.* 121, 117–126.
- Matheson, J.D., Larson, D.W., 1998. Influence of cliffs on bird community diversity. *Can. J. Zool.* 76, 278–287.
- Michael, D.R., Cunningham, R.B., Lindenmayer, D.B., 2008. A forgotten habitat? Granite inselbergs conserve reptile diversity in fragmented agricultural landscapes. *J. Appl. Ecol.* 45, 1742–1752.
- Moleón, M., Bautista, J., Madero, A., 2011. Communal roosting in young Bonelli's eagles (*Aquila fasciata*). *J. Raptor Res.* 45, 353–356.
- Norris, K., Pain, D.J., 2002. *Conserving Bird Biodiversity: General Principles and Their Application*. Cambridge University Press.
- O'Dea, N., Whittaker, R.J., 2007. How resilient are Andean montane forest bird communities to habitat degradation? *Biodivers. Conserv.* 16, 1131–1159.
- Paruelo, J.M., Beltran, A., Jobbagy, E., Sala, O.E., Golluscio, R.A., 1998. The climate of Patagonia: general patterns and controls on biotic. *Ecol. Austr.* 8, 85–101.
- Porembski, S., Seine, R., Barthlott, W., 1997. Inselberg vegetation and the biodiversity of granite outcrops. *J. R. Soc. West. Aust.* 80, 193–199.
- Ralph, C.J., 1985. Habitat association patterns of forest and steppe birds of northern Patagonia, Argentina. *Condor*, pp. 471–483.
- Rodríguez, J.P., Rojas-Suárez, F., Sharpe, C.J., 2004. Setting priorities for the conservation of Venezuela's threatened birds. *Oryx* 38, 373–382.
- Roldán, M., Carminati, A., Biganzoli, F., Paruelo, J.M., 2010. Las reservas privadas son efectivas para conservar las propiedades de los ecosistemas? *Ecol. Aust.* 20, 185–199.
- Rossi, L.G., Knight, R.L., 2006. Cliff attributes and bird communities in Jefferson County, Colorado. *Nat. Areas J.* 26, 331–338. [http://dx.doi.org/10.3375/0885-8608\(2006\)26\[331:CAABCI\]2.0.CO;2](http://dx.doi.org/10.3375/0885-8608(2006)26[331:CAABCI]2.0.CO;2).
- Roth, R.R., 1976. Spatial heterogeneity and bird species diversity. *Ecology* 773–782.
- Ruggiero, A., Hawkins, B.A., 2008. Why do mountains support so many species of birds? *Ecography* 31, 306–315. <http://dx.doi.org/10.1111/j.0906-7590.2008.05333.x>.
- Sauer, J.R., Pendleton, G.W., Orsillo, S., 1995. Mapping of bird distributions from point count surveys. USDA Forest Service Gen. Tech. Rep. PSW-GTR-149: 151–160.
- Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K., Hiraldo, F., 2008. Top predators as conservation tools: ecological rationale, assumptions, and efficacy. *Annu. Rev. Ecol. Evol. Syst.* 1–19.
- Speziale, K.L., Ezcurra, C., 2012. The role of outcrops in the diversity of Patagonian vegetation: relicts of glacial palaeofloras? *Flora Morphol. Distrib. Funct. Ecol. Plants* 207, 141–149. <http://dx.doi.org/10.1016/j.flora.2011.09.002>.
- Speziale, K.L., Lambertucci, S.A., Olsson, O., 2008. Disturbance from roads negatively affects Andean condor habitat use. *Biol. Conserv.* 141, 1765–1772.
- Speziale, K.L., Ruggiero, A., Ezcurra, C., 2010. Plant species richness–environment relationships across the Subantarctic–Patagonian transition zone. *J. Biogeogr.* 37, 449–464.
- Sutherland, W.J., Newton, I., Green, R., 2004. *Bird Ecology and Conservation: A Handbook of Techniques*. Oxford University Press, USA.
- Walker, R.S., Novaro, A.J., Branch, L.C., 2003. Effects of patch attributes, barriers, and distance between patches on the distribution of a rock-dwelling rodent (*Lagidium viscacia*). *Landsc. Ecol.* 18, 185–192.
- Ward, J.P., Anderson, S.H., 1988. Influences of cliffs on wildlife communities in southcentral Wyoming. *J. Wildl. Manag.* 673–678.
- Williams, P.L., Koenig, W.D., 1980. Water dependence of birds in a temperate oak woodland. *Auk* 339–350.