

# Avifaunal changes as a consequence of large-scale livestock exclusion in the mountains of Central Argentina

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## Summary

1. In the high Mountains of Córdoba (Central Argentina) large native herbivores were replaced completely by domestic livestock early in the 20th century. Recently, livestock were excluded in a large portion of the mountains to reduce alarming soil erosion rates, leading to an unnatural situation as the area has a long evolutionary history of large herbivore grazing. Many of the birds living in this area are endemic subspecies. Lack of large herbivore grazing can reduce plant diversity, but the response of birds is unknown.

2. We surveyed birds in 46 1·8-ha transects distributed across eight vegetation units under (a) traditional livestock rearing and (b) 4 years of livestock exclusion. We described bird communities per transect using density and richness. The effects of grazing situation and vegetation units on these parameters were analysed by two-way analysis of variance (ANOVA). Additionally, we analysed bird composition through detrended correspondence analysis (DCA).

3. Livestock exclusion caused, in all vegetation units, significant reductions in observed bird density and richness when all species were included in the analysis, and when the 12 endemic subspecies were considered separately. An analysis for each guild showed a similar pattern but differences were significant only for richness of insectivorous and granivorous birds. Vegetation units always showed significant differences in bird density and richness, with no significant interactions between vegetation and grazing situations. Community composition described through DCA was different between vegetation units but not between grazing situations. Endemic birds were associated mainly with rocky areas.

4. *Synthesis and applications.* In areas where large native herbivores are locally extinct, extensive exclusion of domestic livestock is not recommended where bird conservation is also a priority. Where possible, we suggest reintroducing native large herbivores. Where reintroductions are not feasible, livestock must be excluded only from those sites where it is most necessary, and maintained elsewhere at reduced stocking rates. To mimic past natural grazing regimes more effectively, livestock grazing regimes should incorporate temporal fluctuations at seasonal, yearly and decade scales.

**Key-words:** Córdoba Mountains, endemic birds, large herbivores, livestock abandonment, *Polylepis* woodlands

## Introduction

Lands devoted to domestic livestock production occupy around 25% of the world's terrestrial surface (Asner *et al.* 2004). However, the effect of livestock on ecosystem integrity is still controversial, partly because domestic livestock grazing has variable effects on ecosystems (Milchunas &

Lauenroth 1993; Holechek, Pieper & Herbel 1998; Cingolani, Noy-Meir & Díaz 2005). In systems with a long evolutionary history of grazing vegetation is adapted to large herbivores, and current domestic livestock do not seem to cause serious damage to ecosystem structure and functioning (Milchunas, Sala & Lauenroth 1988; Perevolotsky & Seligman 1998; Adler *et al.* 2004, 2005). Indeed, livestock grazing is often recommended for conservation purposes (e.g. Dolek & Geyer 2002; Laiolo *et al.* 2004; Rook *et al.* 2004). However, there is

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also evidence of irreversible land degradation in systems which have been subjected to high grazing pressure, such as African deserts and savannas (Milton *et al.* 1994; Fynn & O'Connor 2000; Tobler, Cochard & Edwards 2003), and many South American high mountain areas (Ellenberg 1979; Fjeldså & Kessler 1996; Cingolani *et al.* 2004; Renison *et al.* 2006), which are well known for their richness of endemic bird species (Fjeldså 1993; Nores 1995). Although the effects of grazing and grazing exclusion have been well studied in plant communities varying in historic grazing regimes, less is known regarding other taxa, particularly birds (Loe *et al.* 2007).

Recently, lower prices for beef and other products of small-scale mountain farming have made it difficult to compete with large-scale farming in fertile lowlands. These factors, together with the cultural and economic attraction of urban centres, have led to the abandonment of many marginal South American mountain lands, thus reducing land degradation and creating interesting opportunities for the recovery of biodiversity and ecosystem processes (Aide & Grau 2004). However, there is controversy as to whether livestock grazing should be excluded totally from these areas. In particular, if large native herbivores which modulated the vegetation dynamics in evolutionary times are extinct, livestock could replace their function (Fuhlendorf & Engle 2001).

One such area is the high mountains of Córdoba (central Argentina), a series of geographically isolated ridges more than 1000 m above the surrounding flat area, where grazing by large herbivores has a long evolutionary history. Before the massive extinctions of the Pleistocene, several herbivores inhabited this area: the gliptodon *Glyptodon* sp., milodon *Scelidotherium* sp., the camelids *Lama*, *Palaeolama* sp. and *Macrauchenia* sp., horse predecessors *Equus* sp. and the toxodon *Toxodon* sp. (Pucheta *et al.* 1998). Later, the mountains were grazed by guanacos *Lama guanicoe*, rheas *Rhea americana* or *Pterocnemia pennata* and an unknown kind of deer, all of which were observed in the region until the 1920s, when they became locally extinct (Díaz, Acosta & Cabido 1994; Miatello *et al.* 1999). Around 400 years ago, domestic livestock (cattle, goats, sheep, mules and horses) were introduced, and since the 1920s they have been the only large herbivores in the area. In the mountains of Córdoba livestock grazing, along with associated ranching activities, has influenced plant communities substantially and greatly increased soil erosion. Today, almost 20% of the area is composed of rock exposed by soil erosion, mainly of anthropogenic origin (Cingolani *et al.* 2003, 2004). In 1998 livestock were excluded in a large area to reduce erosion rates as a result of the implementation of a National Park (Teich *et al.* 2005).

Effects of livestock exclusion on plant diversity and vegetation structure have been well studied in the Córdoba Mountains. Exclusion has both positive and negative effects for conservation, depending on time-scale and the underlying conservation objective. Short-term (< 4 years) livestock exclusion has several positive effects: it reduces soil erosion rates (A. M. Cingolani & D. Renison, unpublished data) and also produces a substantial increase in vegetation height and production of shoots, leaves and seeds without changing substantially

the composition of plant communities (Pucheta *et al.* 1998; Cingolani *et al.* 2003). Medium-term (4–20 years) livestock exclusion is detrimental for plant diversity: it causes an increase in the cover of tussocks and a reduction in plant diversity due to the higher competitive ability of few species, normally controlled by grazing (Pucheta *et al.* 1998; Cingolani *et al.* 2003, 2004). Studies of long-term (> 20 years) livestock exclusion do not exist, but it is likely that this would benefit forest recovery, a highly desirable conservation objective which seems to be difficult to achieve without long-term livestock exclusion (Renison *et al.* 2005, 2006; Teich *et al.* 2005). The only study in the Córdoba Mountains which included taxa other than plants involved insect abundance and richness, which was shown to increase with grazing exclusion (Cagnolo, Molina & Valladares 2002). Thus, we do not yet have a clear picture of whether or not livestock exclusion is good for wider biodiversity conservation, and at what temporal and spatial scales it should be applied.

World-wide, birds are considered good bio-indicators, and analysing bird communities could provide insights into which could be the best management scenarios to adopt. However, the prediction of the changes in bird communities caused by short- and long-term livestock exclusion would be difficult due to the lack of general models and the contrasting results found in studies from different continents (Fuller & Gough 1999; Laiolo *et al.* 2004; Loe *et al.* 2007). For example, in North America it has been shown that traditional livestock management produces a decrease in bird biodiversity because of a lack of variability in management regimes (e.g. Fuhlendorf & Engle 2001). In contrast, European countries have implemented different agri-environment schemes, assuming that agricultural abandonment will be detrimental for biodiversity, but the effects of these programmes on bird diversity are not well understood (e.g. Kleijn & Sutherland 2003). Comparatively little is known about the effects of grazing in other regions of the world, particularly in the mountains of South America. Therefore, assessing the effects of livestock on native bird communities in the high Córdoba Mountains is of foremost importance for local and regional conservation efforts. This is particularly relevant because the high Córdoba Mountains and other similar mountains in central Argentina have high levels of bird endemism (Nores 1995).

In this study, our goals were to: (1) compare bird communities between areas under traditional livestock management and areas with 4 years of grazing exclusion, (2) determine the association between bird communities and vegetation units, which are in part the result of long-term livestock pressure (Cingolani *et al.* 2004), and (3) discuss the management implication of this research for bird conservation.

## Materials and methods

### STUDY AREA

This study was conducted in the upper portion of the Córdoba Mountains (1800–2400 m a.s.l., 31°34' S, 64°50' W; 145 000 ha), in central Argentina. The area constitutes a biogeographical island

**Table 1.** Vegetation units in the study area, proportion of the landscape they occupy, brief description of where each is found and the habitat type according to Cingolani *et al.* (2004)

Vegetation units	Proportion (%)	Found on	Habitats
1. Dense <i>Polylepis</i> woodlands	2.9	Pronounced rocky slopes and gorges	Woodlands
2. <i>Polylepis</i> woodlands and outcrops	9.0	Pronounced rocky slopes and gorges	Woodlands
3. Thick tussocks and hydromorphic lawns	3.8	Flat landscapes with different degrees of dissection	Grasslands
4. Thin tussocks grasslands	18.4	Flat landscapes with different degrees of dissection	Grasslands
5. Grazing lawns	3.7	Flat landscapes with different degrees of dissection	Grasslands
6. Outcrops and tussocks	30.3	Landscape of hills and rocky slopes	Rock
7. Outcrops and erosion	26.5	Landscape of hills and rocky slopes	Rock
8. Erosion pavements	5.4	Landscape of hills and rocky slopes	Rock

with more than 40 endemic plant and animal taxa, including 12 endemic subspecies of birds (Nores 1995; Miatello *et al.* 1999). Because of its small area it harbours small bird populations considered susceptible to human influence (Bucher & Nores 1988; Heil *et al.* 2007). The vegetation was classified into eight vegetation units that belong to three habitat types: woodlands, grasslands and rock habitats (Table 1; Cingolani *et al.* 2004). Vegetation units are mainly the product of a combination of physiographic characteristics and long-term ranching activities (Cingolani *et al.* 2003, 2004; Renison *et al.* 2006). In some cases, a vegetation unit may be transformed into another through different long-term management practices, such as livestock rearing, livestock exclusion and the common practice of burning grasslands and woodlands (Cingolani *et al.* 2004; Teich *et al.* 2005; Renison *et al.* 2006).

Two basic grazing situations existed in the study area when our survey was performed: (1) traditional grazing: livestock management within privately owned lands (129 000 ha), where livestock activities have been fairly intense during the last 400 years and effective stocking rate ranges generally from 0.4 to more than 1.5 cattle equivalents ha<sup>-1</sup> with paddocks usually stocked all year round (Cingolani *et al.* 2003; Teich *et al.* 2005), and (2) grazing exclusion: traditional grazing until 1998, when the National Park administration took over 26 000 ha of land and livestock was excluded completely 4 years before our field surveys.

## STUDY DESIGN AND BIRD SURVEYS

We conducted a study with a factorial design with eight vegetation units and two grazing situations. We selected 46 sampling transects using a geographical information system (GIS) of the area, which included a vegetation map obtained from a 2001 TM satellite image (Cingolani *et al.* 2004). Transects (300 m long and 60 m wide, 1.8 ha) were selected in homogeneous patches of each vegetation unit, and were always located at least 220 m away from roads or houses. We sampled six transects per vegetation unit (three under traditional livestock management and three under livestock exclusion), with two exceptions due to the lack of large enough areas within the unit to conduct the surveys. One exception was the 'outcrops and erosion' vegetation unit, where we sampled four transects under traditional grazing and two under livestock exclusion, and the other was the 'dense *Polylepis* woodland' vegetation unit, where we had one transect under traditional grazing and three under livestock exclusion. Distance between two transects of the same vegetation unit ranged from 2 to 40 km.

Surveys were conducted from December 2002 to March 2003, when bird richness was highest because of the arrival of summer resident species that use this area for breeding. Additionally, during the

summer, differences in bird communities are easier to detect due to their territorial behaviour compared to their aggregated distribution in the winter, when mixed flocks of up to 200 individuals can be seen (Ordano 1996). We recorded all birds observed or heard within the transect and each transect was surveyed three times in cycles which lasted approximately 19 days, separated by intervals of 10 days. Thus, each transect was visited approximately every 29 days. We surveyed birds between 0800–1200 h and 1530–1930 h because those were the periods with the highest bird activity. Visiting schedules were arranged to obtain an even distribution of visiting hours between transects. Adult and fledgling individuals were counted during surveys. Surveys were conducted during favourable weather conditions and by only one person (C. G.) to avoid interobserver bias. The observer was trained to estimate visually the 30 m at each side of the line transect with < 10% error prior to beginning the surveys.

Nomenclature follows Miatello *et al.* (1999). The number of transects, their length and the number of times that they required sampling were determined during a preliminary study using species accumulation curves. The width was determined as the maximum distance that would allow similar detection probabilities in all vegetation units, including woodlands. For each transect, we recorded the altitude a.s.l. and the slope inclination from the GIS.

## DATA ANALYSIS

Distance sampling procedures (Buckland *et al.* 2001) could not be used to estimate bird density because of violation of the assumptions due to the low abundances of the target species. Instead, we developed a relative index of density by averaging the numbers of individuals detected on each transect. This index was expressed as number of individuals per transect, and can be used only for comparisons between the conditions studied, but not to make inferences about absolute densities (see also Heil *et al.* 2007). We then calculated, for each transect, the overall bird density as the sum of the observed density of all species, the species richness as the overall number of observed species and the density and richness of guilds classified into insectivorous, granivorous and omnivores (as in Ordano 1996; details in Table S1, see Supplementary material). As the National Park was created to protect endemic and endangered taxa we also included density and richness of endemic subspecies according to Miatello *et al.* (1999). Carnivorous (including carrion eaters) and endangered taxa were not considered in separate categories due to their low abundances. In all cases, Shannon diversity indices were also calculated, but results were always similar to those of species richness; therefore, for simplicity we reported only the latter.

Initially, to determine differences in bird community structure between the vegetation units, livestock conditions and altitude above

sea level, we performed two-way analyses of covariance (ANCOVA) for the following variables: density and richness of all recorded species together, of endemics and of each guild. We included as independent factors vegetation units (eight levels, Table 1), grazing situations (two levels, traditional livestock management and livestock exclusion), the interaction of vegetation unit  $\times$  livestock condition and altitude above sea level as a covariate. Only significant terms were left in the final models (Underwood 1997); as the covariate and the interaction term were never significant (see Results), in practice we performed analyses of variance (ANOVAs). We used Type III sums of squares, which can handle unbalanced designs better than Types I and II (Milliken & Johnson 1984). When differences were found between vegetation units, we used Duncan's *post-hoc* test to assess significant differences between vegetation units. Slope was not included as a covariate, as vegetation units differed in slope steepness and thus slope and vegetation units were not independent (Table 1).

To determine the main directions of variation in bird composition across transects, a data matrix of 44 transects  $\times$  39 species (eliminating two transects where no birds were observed and nine species which were observed in only one transect) was subjected to detrended correspondence analysis (DCA, ter Braak 1987). In this way, each transect was positioned along two main axes (synthetic variables) that summarized their composition.

## Results

We found a total of 48 species and an average of 10.6 individuals per transect (Supplementary material, Table S1). All species were native to the area, and all 12 endemic subspecies were recorded. The most frequently detected species was the grass wren *Cistothorus platensis*, with an average of 2.01 observations per transect. The two species that followed were the rufous-collared sparrow *Zonotrichia capensis* and the plumeous sierra-finch *P. unicolor cyaneus*, which were observed at an average of 0.81 and 0.80 individuals per transect, respectively. At the other extreme, nine species were found in only one transect, and no birds were observed in two transects corresponding to the erosion pavements unit.

### BIRD DENSITY AND RICHNESS

Overall, bird density and species richness were significantly higher under traditional grazing than under grazing exclusion, and also showed significant differences among vegetation

units (Table 2, Fig. 1). Bird density in erosion pavements was around one order of magnitude lower than in all the remaining units, which had similar density (Fig. 1b). Bird richness was lowest in erosion pavements; intermediate in the three grassland units and in dense *Polylepis* woodlands; and highest in the three units containing rock outcrops, which were *Polylepis* woodlands and outcrops, outcrops and tussocks and outcrops and erosion (Fig. 1d). For both overall density and richness, no significant interactions were detected between grazing situation and vegetation units, nor was there a significant effect of altitude above sea level.

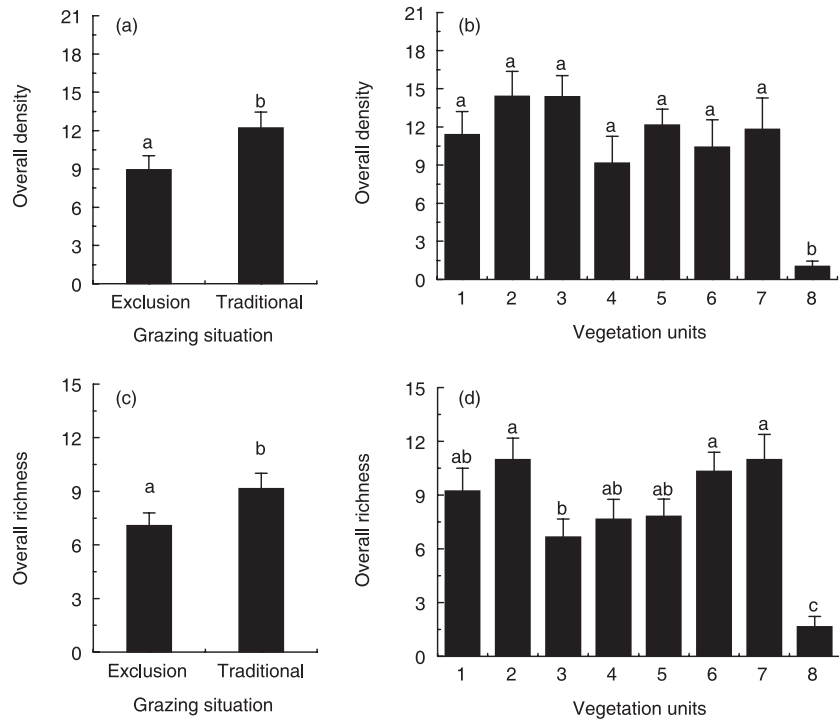
Endemic subspecies density and richness followed a similar pattern to that of overall bird richness, being significantly higher under traditional grazing than under grazing exclusion, with significant differences among vegetation units (Table 2; Fig. 2). No significant interactions were detected between grazing situation and vegetation units, nor was altitude above sea level significant.

When analysing guilds separately, differences in grazing situation never reached significance for bird density, while species richness per guild was significantly higher under traditional grazing than under grazing exclusion for insectivorous and granivorous birds only (species richness per transect of 1.8 ha: insectivorous with grazing,  $5.00 \pm 0.53$ , exclusion,  $3.87 \pm 0.39$ ; granivorous with grazing,  $1.83 \pm 0.35$ , exclusion,  $1.26 \pm 0.26$ ; Table 2).

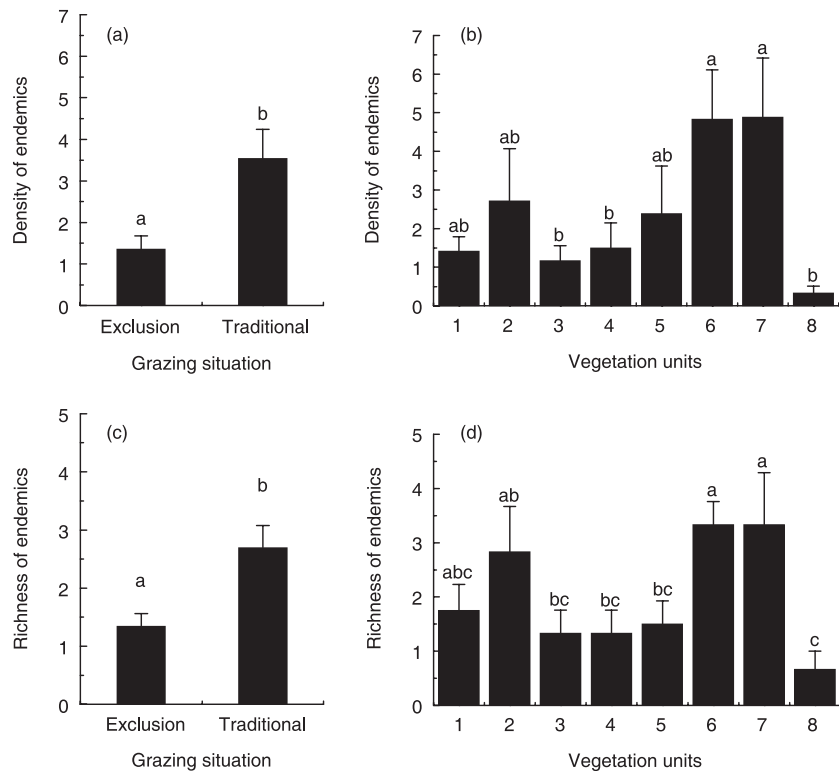
Density and richness of the three guilds were significantly different between some of the vegetation units (Table 2, Fig. 3). Insectivorous bird density and species richness was lowest in erosion pavements but did not vary significantly among the other units, except for the thick tussocks and hydromorphic lawns unit where insectivorous density was higher (Fig. 3a,b). Granivorous bird density and species richness was lowest in erosion pavements and the three grassland units, and highest in the other units (the two units with woodlands and the two remaining units with rock outcrops, Fig. 3c,d). Omnivore bird density was higher in the two units with woodland; intermediate in three units with grasslands; and lower in the three units of the rock habitat (Fig. 3e). Omnivore bird species richness was highest in *Polylepis* woodlands with outcrops; lowest in rock pavements; and intermediate in the other units (Fig. 3f). In testing guild effects, no significant interactions were detected between grazing

	Grazing situation d.f. = 1	Vegetation units d.f. = 7
Overall bird density	$F = 7.686$ ; $P = 0.009$	$F = 6.686$ ; $P < 0.001$
Overall bird richness	$F = 7.936$ ; $P = 0.008$	$F = 9.972$ ; $P < 0.001$
Endemics density	$F = 7.832$ ; $P = 0.008$	$F = 2.787$ ; $P = 0.020$
Endemics richness	$F = 11.095$ ; $P = 0.002$	$F = 3.611$ ; $P = 0.005$
Insectivorous density	NS	$F = 9.123$ ; $P < 0.001$
Insectivorous richness	$F = 4.174$ ; $P = 0.048$	$F = 3.923$ ; $P = 0.003$
Granivorous density	NS	$F = 8.718$ ; $P < 0.001$
Granivorous richness	$F = 4.383$ ; $P = 0.043$	$F = 11.626$ ; $P < 0.001$
Omnivorous density	NS	$F = 3.269$ ; $P = 0.008$
Omnivorous richness	NS	$F = 4.591$ ; $P = 0.001$

**Table 2.** ANOVA tests ( $F$ - and  $P$ -values), where the response variable was bird density and richness, considered for all birds, endemics and by guild; and the factors were grazing situations and vegetation units. Interaction terms and the covariate altitude were not included in the table because they were never significant, and only significant terms were left in the final models (Underwood 1997). Other non-selected terms are shown as NS (not significant)



**Fig. 1.** Overall observed bird density (above) and richness (below) per 1.8 ha transect for grazing situation (a, c) and vegetation units (b, d). Vegetation unit 1 = dense *Polylepis* woodlands, 2 = *Polylepis* woodlands and outcrops, 3 = thick tussocks and hydromorphic lawns, 4 = thin tussock grasslands, 5 = grazing lawns, 6 = outcrops and tussocks, 7 = outcrops and erosion, 8 = erosion pavements. Different letters indicate significant differences ( $P < 0.05$ ).



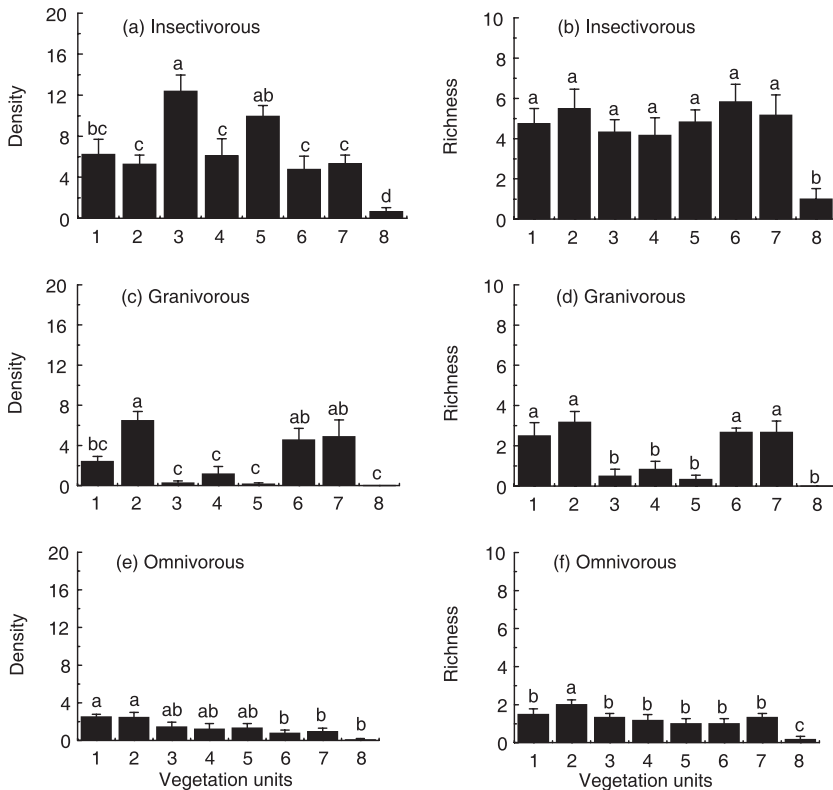
**Fig. 2.** Observed density (above) and richness (below) of endemics per 1.8 ha transect for (a) grazing situation and (b) vegetation units. Vegetation units as in Fig. 1. Different letters indicate significant differences ( $P < 0.05$ ).

situation and vegetation units, nor was the covariate altitude above sea level significant.

#### BIRD COMMUNITY STRUCTURE

The ordination analysis (DCA) showed a considerable variability in bird species composition across transects. Transects

of the three main habitat types (woodlands, grassland and rock, Fig. 4) were separated according to bird composition in the space defined by the first two DCA axes. However, transects within the same habitat type but in different vegetation units or grazing situations were not discriminated in the space defined by the two first DCA axes, nor by the third axis (not shown). Both grazing situations showed a similar



**Fig. 3.** Density (left graphs) and richness (right graphs) for insectivorous, granivorous and omnivorous birds observed in 1.8 ha transects for eight vegetation units (labels as in Fig. 1). Different letters indicate significant differences ( $P < 0.05$ ).

variability along both axes, indicating no substantial difference in  $\beta$  diversity between traditional livestock management and grazing exclusion. DCA axis 1 (eigenvalue 0.70) separated transects in woodland and rock habitats, located in the sector with low scores, from transects in grasslands habitats (Table 1), which had higher scores along the axis (Fig. 4a). DCA axis 2 (eigenvalue 0.35) separated transects found in woodland habitats (Table 1) from transects found in rock habitats (Table 1, Fig. 4b).

Grasslands habitats were dominated by the grass wren, the southern lapwing *Vanellus chilensis*, the spectacled tyrant *Hymenops perspicillata* and the long-tailed meadowlark *Sturnella loica obscura*. Of these, the most characteristic was the southern lapwing, which was not recorded in any of the other two main habitat types. The spectacled tyrant and the long-tailed meadowlark were recorded in other habitats but at lower abundance, while the grass wren was abundant everywhere. Other characteristic species of grasslands, little represented in other habitat types, were Hellmayr's pipit *Anthus hellmeyri* and the South American snipe *Gallinago paraguayensis* (see Supplementary material, Table S1).

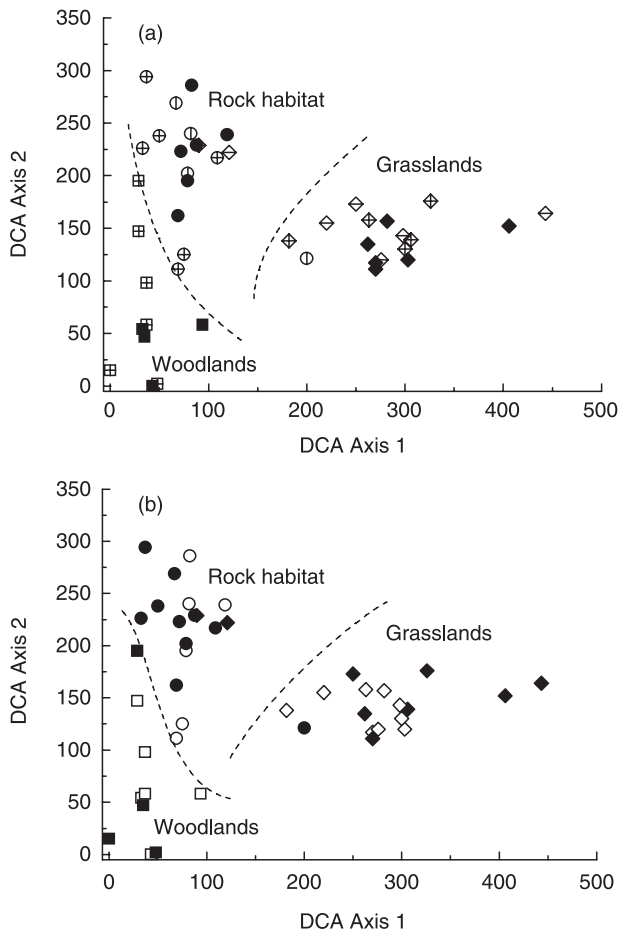
Woodlands habitats were dominated by the grey-hooded parakeet *Bolborhynchus aymara*, the chiguanco thrush *Turdus chiguanco*, the rufous-collared sparrow and the grass wren. The first two species were the most characteristic, with little representation in other habitats. Other species found in woodlands were the brown-capped tit-spinetail *Leptasthenura fuliginiceps*, the tufted tit-tyrant *Anairetes parulus*, the plain-coloured seed-eater *Catanemia inornata cordobensis* and the Andean swift *Aeronautes andecolus* (see Supplementary material Table 1).

Rock habitats were dominated mainly by the plumeous sierra-finch, followed by the rufous-collared sparrow. Typical species of rocky habitats were the Córdoba canastero *Asthenes sclateri sclateri*, the rufous-naped ground tyrant *Muscisaxicola rufivertex achalensis* and the blue-and-white swallow *Notiochelidon cyanoleuca*, although the last one was also common in grasslands (see Supplementary material, Table S1).

## Discussion

### GRAZING SITUATION

Large herbivores alter ecosystems leading to a range of responses which can have negative or positive effects on biodiversity, depending on factors such as grazing timing and intensity, evolutionary history of grazing and resource availability for plants (Cingolani, Noy-Meir & Díaz 2005). The Córdoba Mountains have a long evolutionary history of grazing by wild large herbivores which are now extinct, and the large-scale lack of grazing due to domestic livestock exclusion in the National Park represented a novel situation for the system. This measure was necessary to reduce soil erosion and augment forest cover. However, in the medium term (4–20 years), livestock exclusion produces loss of plant diversity (Díaz *et al.* 1994; Pucheta *et al.* 1998), and our results show that exclusion also produces short-term loss of bird abundance and richness, presumably because many bird species inhabiting the grazed landscape are not adapted to the non-grazed situation. Given the sensitivity of the mountains of Córdoba to grazing, in these mountains large herbivores could be considered keystone species.



**Fig. 4.** Transect ordination along DCA axes 1 and 2, indicating vegetation units and grazing situations. (a) Different symbol shapes represent the three main habitat types and symbol fills represent the vegetation units within main habitats: woodlands: ■, dense woodlands (1), ▨, woodlands and outcrops (2); grasslands: ◆, thick tussocks grasslands (3), ◇, thin tussock grasslands (4), ◇, grazing lawns (5); rock habitats: ●, outcrops and tussocks (6), ⊕, outcrops and erosion (7), ⊙, erosion pavements (8). (b) As in the previous plot, the shape of the symbols represent the three main habitat types (squares: woody habitats, diamonds: grassland habitats, circles: rocky habitats), and the symbol fill the grazing situation. Open symbols: grazing exclusion, filled symbols: traditional grazing.

The mechanisms underlying the loss of bird density and richness after livestock exclusion are probably related to small-scale loss of habitat heterogeneity, which is a well-known driver of species richness (Fuhlendorf & Engle 2001; Moreira *et al.* 2003; Laiolo, Rolando & Valsania 2004; Fuhlendorf *et al.* 2006). In most vegetation units of the mountains of Córdoba, small-scale habitat heterogeneity is higher in grazed than ungrazed areas because livestock creates patches of short grasses and forbs intermingled with tussocks and other taller vegetation, while in ungrazed areas some of the short grasses grow as tall as the tussocks. This tendency to vegetation structure homogenization with exclusion should extend to larger spatial scales with longer exclusion periods (< 4 years), as those species which do not grow in height are replaced eventually by tall tussocks and the land-

scape becomes more homogeneous, with patches of tall tussock grasslands dominating grasslands and woodland understorey (Pucheta *et al.* 1998; Cingolani *et al.* 2003, 2004).

Tall grasses and dense tussocks may interfere with birds finding food on the ground or within their leaves, and in detecting or escaping from predators (Devereux *et al.* 2004, 2005; Whittingham & Evans 2004; Whittingham *et al.* 2006). A similar decline in bird (and especially in insectivorous birds) density and diversity was also found in Norway's mountains with reduced or total exclusion of grazing, which was attributed to grazing producing gaps in the vegetation that made insect larvae more available (Loe *et al.* 2007). This food-release process in vegetation gaps could be occurring in our study area. In addition to the loss of heterogeneity, the growing cover of tussocks in ungrazed areas increases dramatically the abundance of rodents (Polop 1989). Competition with rodents for seeds available on the ground surface could be an explanation for the decline in most of the granivorous species of our study areas, including some of the endemics such as the ash-breasted sierra-finch *Phrygilus plebejus naroskyi* and the plumbeous sierra-finch *P. unicolor cyaneus*. Little is known about the natural history of endemics, but long-tailed meadowlark forages by looking for insects under dung, and the rufous-naped ground-tyrant *Muscisaxicola rufivertex achalensis* catches insects which fly over grazing lawns (C. G., personal observation), which shows that many species are dependent partially on livestock activity.

Less clear are the mechanisms involved in density and richness reduction with exclusion in rocky habitats, especially the rock and erosion unit and the rock pavements. We expected to find significant interactions between vegetation units and short-term grazing exclusion, as grassland structure changes faster than eroded areas which hardly change with livestock exclusion, and a large proportion of the rock outcrop habitat is not affected by livestock grazing at all. However, our analysis had little power to detect interactions (range 0.20–0.45), so the lack of significant interactions may be an artefact of small sample sizes.

Studies in North American prairies generally show a negative effect of livestock on birds (Fondell & Ball 2004), but this is due probably to the intensive livestock management that tends to homogenize the landscape (Fuhlendorf & Engle 2001), while in South America and especially in the Córdoba Mountains, livestock mainly roams freely in large paddocks and fire is used to promote regrowth of different vegetation types (Renison, Cingolani & Suarez 2002; Cingolani *et al.* 2004). In Australia, grazing by large herbivores has a short evolutionary history and livestock reduces the abundance of bird species (Martin & Possingham 2005).

In the mountains of Europe, domestic grazing has a history of over 6000 years; thus, we would expect livestock exclusion to have negative effects on bird communities. However, we are aware of three relevant studies with apparently contrasting results. In England, increasing sheep populations leading to very high grazing pressure are considered detrimental for bird conservation (Fuller & Gough 1999). In Italy, livestock exclusion/reduction promotes shrub and tree encroachment of

grasslands maintained by livestock and overall bird richness and density are generally favoured, but not grassland birds of conservation concern (Laiolo *et al.* 2004). In Norway, bird diversity and density is favoured by moderate sheep densities (Loe *et al.* 2007). The differences and similarities among studies could be explained by the different temporal scales involved and relative stocking rates, which in England could be too high for bird persistence, whereas in Norway and in the Córdoba Mountains stocking densities could be compatible with short-term bird persistence (but we emphasize not with soil conservation in the Córdoba Mountains: see next section).

We compared only traditional (high) livestock stocking rates with short-term livestock exclusion, but not moderate stocking rates or long-term exclusion. Given that intermediate frequencies of disturbances and intermediate disturbance intensities are expected to increase biodiversity (Gordon *et al.* 2004), we emphasize the need for further studies involving long-term monitoring. Of particular importance are studies that also include the role played by fire in the modification of habitat suitable for birds.

#### VEGETATION UNITS

Each of the three main habitats of our study area (woodlands, grasslands and rock) comprised several vegetation units that differed in bird density, richness and composition. This is not a surprising result, as bird communities are well known to respond to habitat structure (Hunter 1990; Moreira *et al.* 2003; Fuhlendorf *et al.* 2006). Most birds of conservation concern in our study areas belong to the woodland habitat (Miatello *et al.* 1999), which has been reduced greatly in the last centuries (Renison *et al.* 2006). Given that woodlands harbour unique bird communities the area must be managed to increase woodland area, which may be achieved by reducing fires, by excluding livestock to avoid browsing and by active reforestation (Renison *et al.* 2005, 2006; Teich *et al.* 2005). Some of these measures may, in the short term, reduce overall bird diversity, even within woodlands, so they must be implemented carefully and in small areas, leaving other woodland areas with moderate grazing pressure.

Most endemic species were associated with rock outcrops, where they seek refuge, nest and search for food around the abundant lichens and plants that grow on the rocks due to the high humidity levels. In contrast to forests and grasslands that extend to lower altitudes, most rock outcrop habitats are found only above 1800 m a.s.l. The flora and fauna communities above this altitude are isolated from other mountains with similar climate by hundreds of kilometres (Nores 1995), and rock outcrops have possibly provided a stable habitat where several subspecies of birds evolved. Because of the rugged terrain, rock outcrops have been less affected by human activities and will probably remain this way, although special attention must be paid to tourist activities, as rock climbing is gaining popularity in the area and human presence is known to affect bird communities negatively in these mountains (Heil *et al.* 2007).

Soil erosion has been prominent in the Córdoba Mountains and must be reduced for several reasons, such as increasing the water-holding capacity of the mountains, reducing loss of productivity, loss of plant biodiversity and loss in woodland restoration potential (Cingolani *et al.* 2004; Renison, Hensen & Cingolani 2004). Bird conservation adds another reason, as vegetation units with erosion were less valuable for birds than units without erosion and the erosion pavement unit was the poorest habitat for all types of birds. Additionally, heavy grazing and associated activities such as vegetation burning produced a trend of transformation from woodlands to grasslands to eroded rocky surfaces (Cingolani *et al.* unpublished), which in the long term can reduce habitat heterogeneity by eliminating little-represented habitats (woodlands), hence reducing  $\beta$  bird diversity. Grasslands seem to be of importance for several insectivorous species, which perch on rocks or tall tussocks and hunt prey in the air, and ground foragers, which search on the surface or probe into the ground.

#### APPLICATIONS

Given the sensitivity of the Córdoba Mountains to grazing, and that livestock favours short- and medium-term  $\alpha$  diversity of plants and birds but at a long-term cost in  $\beta$  diversity, soil erosion and woodland reduction, careful consideration must be given to the management of these mountains. Grazing exclusion must be implemented where it is most needed (e.g. areas with soil erosion or where woodlands are under-represented), but taking into account the different conservation and livestock production needs. Woodland cover must be enhanced to augment the representation of woodland bird specialists.

In the National Park, livestock was reintroduced experimentally at moderate stocking rates in paddocks with tussock accumulation (after this study took place in 2002 and 2003; Teich *et al.* 2005), and native guanacos have been reintroduced recently (in 2007). Presumably native guanacos will not cause the same levels of erosion as domestic livestock (Tavarone 2004), and according to our studies should promote the persistence of plants and birds. Efforts should be directed to reintroducing native guanacos in privately owned lands outside the National Park that are subject to pastoral abandonment. In other areas, traditional livestock rearing cannot be excluded due to economic or cultural reasons, so alternative livestock management practices must be developed to minimize soil erosion and increase woodlands. Economic incentives to locals are an alternative that may enhance the success of these strategies. Ideally, livestock stocking rates should be reduced, and the grazing regimes should incorporate temporal fluctuations at seasonal, yearly and decadal scales to imitate more effectively the densities and fluctuations of extinct native large herbivores under which the vegetation in the natural grazing system evolved (Cingolani, Noy-Meir & Diaz 2005).

Because our study area has a long history of human degradation, it is still unknown if reintroducing guanacos and imitating past natural disturbance rates would, alone, restore



its ecosystem services and reduce erosion rates. For example, erosion gullies may have to be revegetated manually and in certain areas woodland restoration may need to be accelerated by planting (Renison *et al.* 2005). In all cases, careful monitoring and adaptive management strategies will be required (Goldsmith 1996).

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## Supplementary material

The following supplementary material is available for this article.

**Table S1.** Average observed bird abundance and proportion of transects where the species was observed for 46 transects in the mountains of Central Argentina.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2007.01388.x>.

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