

# Latitudinal patterns of bird richness, diversity and abundance in *Polylepis australis* mountain forest of Argentina

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## Summary

Many South American hotspots of bird endemism are found in *Polylepis* dominated forests. Although the avifauna of *Polylepis* forests has been relatively well studied in the tropical Andes, little is known in Argentina. In this study, we characterize the Argentine avifauna of *Polylepis australis* forests along their entire latitudinal gradient of distribution and provide a first systematic bird list and their conservation status. Fieldwork was carried out from 1,500 to 2,800 m a.s.l. in three study sites: North (Jujuy province), Centre (Tucumán province) and South (Córdoba province); we surveyed 30 point counts per site. We recorded 543 individuals belonging to 50 bird species; two subspecies are endemic to the South site and four species are typical *Polylepis* forest birds of the North and Centre sites. We identified four species of conservation concern; one globally threatened and three declining at regional level. Bird richness and abundance decreased with latitude; and equitability showed an inverse pattern. Sorenson's similarity index ranged from 12% to 40% showing a large latitudinal turnover in avian communities. Disturbance-sensitive species were the most diverse group in the North site. Variations in species richness, evenness and guild composition may be a response to latitude, but also to differences in habitat complexity and food availability, which appear to be a consequence of forest degradation at the South site. We recommend: (1) the enlargement of Calilegua National Park to include the *Polylepis australis* belt to assure the conservation of many disturbance-sensitive species which could decline or disappear in degraded areas; (2) management of Quebrada del Condorito National Park to increase the forest structure complexity and therefore provide habitat for disturbance-sensitive species.

## Resumen

Muchas áreas de especiación de aves endémicas de Sudamérica se encuentran en bosques dominados por *Polylepis*. Aunque la avifauna de estos bosques ha sido relativamente bien estudiada en los Andes tropicales, en Argentina su conocimiento es escaso. En este estudio, caracterizamos la avifauna de los bosques de *Polylepis australis* de Argentina a lo largo de su gradiente latitudinal de distribución y confeccionamos la primer lista sistemática de aves y su estado de conservación. El trabajo de campo se realizó en una faja altitudinal de 1,500 a 2,800 m snm en tres sitios de estudio: Norte (provincia de Jujuy), Centro (provincia de Tucumán) y Sur (provincia de Córdoba) donde se relevaron 30 puntos de conteo por sitio. Registramos 543 individuos pertenecientes a 50 especies de aves; dos subspecies son endémicas del sitio Sur y cuatro especies son aves típicas de los bosques de *Polylepis* de los sitios Norte y Centro. Identificamos cuatro especies de interés para la conservación, una globalmente amenazada y tres disminuyendo a nivel regional. La riqueza y la abundancia de aves decreció con la latitud; la

equitatividad mostró un patrón inverso. El índice de similitud de Sorenson osciló entre 12% al 40% mostrando un gran recambio latitudinal en las comunidades de aves. Las variaciones en la riqueza, equitatividad y en la composición de gremios responderían a la latitud pero también a las diferencias en la complejidad del hábitat y en la disponibilidad de alimento como consecuencia de la degradación del bosque en el sitio Sur. Recomendamos: (1) ampliar el Parque Nacional Calilegua para incluir un área de *Polylepis australis* y asegurar la conservación de muchas especies sensibles al disturbio que podrían disminuir o desaparecer en áreas degradadas; (2) manejar el Parque Nacional Quebrada del Condorito para incrementar la complejidad estructural del bosque y proveer hábitats para especies sensibles al disturbio.

## Introduction

Forests dominated by the genus *Polylepis* characterize the higher mountain regions of South America and are distributed in small patches primarily restricted to ravines and rock outcrops. Recent studies suggest that the peculiar distribution of *Polylepis* trees may be the result of thousands of years of human activities (Kessler 2002, Renison *et al.* 2006). A long history of logging (Fjeldså and Kessler 1996, Renison *et al.* 2006), fire management (e.g. Renison *et al.* 2002, Cingolani *et al.* 2008), overgrazing (e.g. Teich *et al.* 2005, Cingolani *et al.* 2008), and soil degradation (Renison *et al.* 2006, Torres *et al.* 2008) has reduced these forests to small isolated patches restricted to rocky outcrops where the impact of livestock and burning is low (Fjeldså and Kessler 1996; Renison *et al.* 2006, Cingolani *et al.* 2008; Coblenz and Keating 2008). Consequently, *Polylepis* forests are now considered one of the most threatened Neotropical vegetation types (Jameson and Ramsay 2007). Despite the limited extent and patchy distribution of *Polylepis* forest, they still harbour a high bird species richness including many endemics that have been relatively well studied in the tropical Andes (Fjeldså 1993, Kessler *et al.* 2001, Herzog *et al.* 2003, Fjeldså and Kessler 1996, Cahill and Matthysen 2007, Lloyd and Marsden 2008, Lloyd 2008a,b). However, in Argentina quantitative data for *Polylepis* forest bird communities are scarce.

In Argentina, several Important Bird Areas (IBAs) include *Polylepis* forests with globally threatened bird species (Di Giacomo 2005) and restricted-range bird species belonging to three Endemic Bird Areas (EBA): EBA 056 'High Andes of Bolivia and Argentina', EBA 057 'Argentina and south Bolivian yungas', and EBA 058 'Mountains of central Argentina' (Stattersfield *et al.* 1998). However, very few attempts have been made to study avian communities of *Polylepis* forests. To our knowledge, there is only one study that compares avian composition among forests of *P. australis*, *P. tomentella* and *P. hieronymi* (Renison *et al.* in press) and two non-specific studies that included, but were not exclusive to, *Polylepis* forests in the mountains of central Argentina (Heil *et al.* 2007, García *et al.* 2008).

To initiate the study of *Polylepis* forest birds in Argentina, our goal is to perform a first characterization of *Polylepis australis* bird assemblages along their latitudinal gradient of distribution. Specifically we determined: a) richness, equitability, diversity and abundance of avian communities; b) bird species composition turnover; and c) bird conservation status. These data may be useful to direct future studies and conservation priorities and serve as a baseline for monitoring avifaunal changes over time.

## Methods

### *Study areas*

Fieldwork was carried out in *P. australis* forest fragments located in the eastern slopes of the Andes in northern Argentina and in Sierras Grandes of Argentina. We selected three sampling sites along the *P. australis* latitudinal gradient (Figure 1). The North site corresponds to Alto

Calilegua, Jujuy province ( $23^{\circ} 37' S$ ,  $64^{\circ} 54' W$ ; 2,714 m) and Centre site corresponds to La Ovejera, Tucumán province ( $26^{\circ} 50' S$ ,  $65^{\circ} 45' W$ ; 2,400 m). These two sites belong to the upper cloud forest of the southern Yungas (or subtropical montane forests) where *P. australis* and *Alnus acuminata* forests are followed by alpine Andean grasslands and meadows (Cabrera 1976). Annual vertical precipitation reaches 1,500 mm and is mainly concentrated in the austral summer (December–March). Fog and horizontal precipitation can be equivalent to the vertical precipitation or even exceed this volume (Hunzinger 1995). The South site corresponds to Sierras Grandes, Córdoba province ( $31^{\circ} 58' S$ ,  $64^{\circ} 56' W$ ; 1,950 m) which is located in a small chain of mountains 400 km east of the Andean Mountains. In the South site, *P. australis*

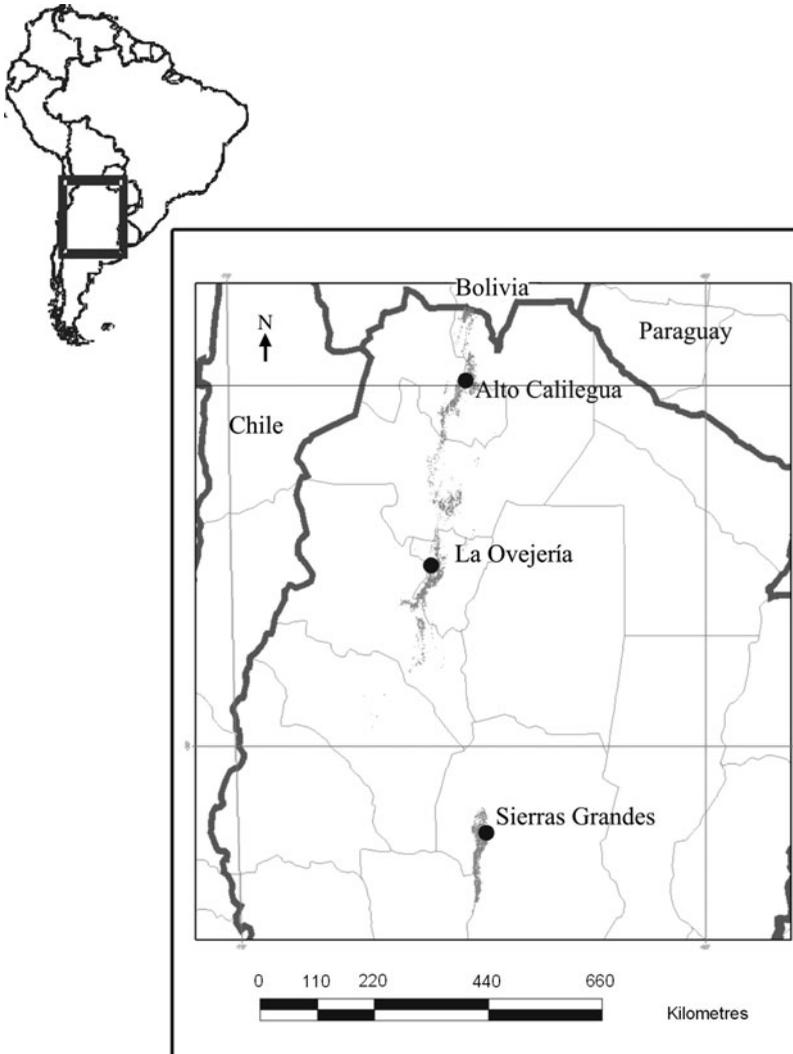


Figure 1. Distribution range of *Polylepis australis* forest to Argentina. Filled circles represent the different study sites. North site: Alto Calilegua (Jujuy province) and Centre site: La Ovejera (Tucuman province) are located on the Andean slopes of the Yungas, and South site: Sierras Grandes in the mountains of central Argentina.

dominates the upper strata of woodlands and shrublands with other less abundant woody species, such as: *Maytenus boaria*, *Escallonia cordobensis*, *Berberis hieronimii*, *Satureja spp.*, and *Gaultheria poeppigii* (Cabido and Acosta 1985, Cingolani *et al.* 2004). Mean annual precipitation is 840 mm, with 83% of rainfall concentrated in the warmer months (October to April, Renison *et al.* 2002).

### *Bird survey*

Bird data were collected during the summer season (January to March 2006) when bird richness is highest due to 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 large mixed flocks can be seen (Ordano 1996, García *et al.* 2008). Bird species and abundance were quantified using 10-minute point counts randomly distributed in each *P. australis* study site. This count period maximized probability of bird detection in cryptic species (Bibby *et al.* 1992, Ralph *et al.* 1995, Lee and Marsden 2008). We located an average of 30 survey points separated by at least 150 m (or 10 min travelling distance) to avoid double-counts between neighbouring points. At each point, the surveyor waited 5 min as a settling down period before starting the counts (Bibby *et al.* 1992, Ralph *et al.* 1995). Birds occurring within 50-m fixed-radius of each point were recorded visually or acoustically. Point counts were surveyed twice in favourable weather conditions. Daily counts included 3-hour periods after sunrise. To reduce biases, experienced observers conducted all bird surveys (LR and EM with 10 and four years of experience, respectively). Nocturnal species and species that only overflow the forest (e.g. Andean Condor *Vultur gryphus*) were not considered. Taxonomic identification of birds was determined following Mazar-Barnett and Pearman (2001).

### *Data analysis*

As a measure of relative density we calculated encounter rates per bird species (ER) recorded in each point count. ER was expressed as number of detections per point (10 min and 0.78 ha) for each species recorded. Richness and diversity of bird communities were calculated using EstimateS v.8.0 software (Colwell 2006). Sample species richness was estimated from the sample-based rarefaction curves (Mau Tau; Sobs; Mao *et al.* 2005). Sample was randomised 50 times for each dataset. To examine changes in species composition along the latitudinal gradient, the robust bootstrap estimator ( $S_{boot}$ ; Colwell and Coddington 1994) was used as a richness measure and Simpson's index ( $1/D$ ) as a diversity measure. This index better reflects the entire species abundance distribution than other indices of the same general form (Magurran 1988). We also calculated the Simpson Equitability index ( $S_E$ ; Magurran 1988) to compare along the gradient the evenness with which individuals were distributed among the different species. Changes in composition of avian communities along the gradient (beta diversity) were tested with the Sorenson qualitative index (Magurran 1988).

We also analyzed the contribution to the *Polylepis* bird assemblage from birds of surrounding habitat types: (1) subtropical montane forests of the Andes (i.e., selva Tucumano-Boliviano), (2) shrublands/grasslands, or (3) not restricted to a single habitat, here defined as generalists (Fjeldså and Krabbe 1990, Stotz *et al.* 1996, Narosky and Yruzieta 2003). Functional groups were established according to habitat use of species as determined from the literature (Fjeldså and Kessler 1996, Dardanelli *et al.* 2006). Groups were classified as: disturbance-sensitive species (DS, species that use mainly the forest: understorey, ground, medium stratum or canopy), disturbance-tolerant species (DT, species that primarily use forest edges, shrublands and open areas) and neutral species (N, habitat generalists). Here we defined habitat in the narrow sense of vegetation structure rather than as the full array of biotic and abiotic factors in the environment.

We tested changes on bird communities among sites with a Kruskal-Wallis test and differences in the number of species of functional groups within and among sites with  $\chi^2$  goodness of fit test (Zar 1984).

## Results

We recorded a total of 543 birds belonging to 50 species (Table 1). The most commonly recorded species were: Rufous-collared Sparrow *Zonotrichia capensis* with 27.6% ( $n = 150$ ) of all detected individuals, followed by Chiguanco Thrush *Turdus chiguanco* 11.9% ( $n = 65$ ), Red-tailed Comet *Sappho sparganura* 5.9% ( $n = 32$ ) and Brown-capped Tit-spinetail *Leptasthenura fuliginiceps* 2.8% ( $n = 15$ ). Bird richness ( $S_{boot}$ ) decreased with latitude (Kruskall-Wallis  $S_{boot} = 14.42$ ,  $P = 0.0007$ ) with more species recorded at North and Centre sites than at the South site. Bird diversity followed a different pattern (Kruskall-Wallis  $1/D = 21.88$ ;  $P < 0.0001$ ), with the highest diversity at the Centre site, intermediate at the South site and the lowest at the North site. The difference in richness - diversity patterns were due to a strong North - South increment in equitability index (Table 2).

Sorenson's similarity index was low, showing a species turnover along the latitudinal gradient. North and Centre sites shared 11 species (40%), North and South shared five species (12%) and Centre and South sites shared seven species (34%). Approximately half of the species in each site occurred only in that site; in the North and Centre sites species richness was determined by species associated with subtropical montane forest, while the number of species of shrublands and grassland was similar in the three sites (Figure 2).

In terms of habitat use groups (Table 2), there was a significantly higher number of disturbance-sensitive species (DS) detected in the North site ( $\chi^2 = 8.81$ ,  $P = 0.01$ ). The Centre and South sites did not show significant differences in the richness of sensitive, tolerant or neutral species ( $\chi^2 = 1.51$   $P = 0.46$ ;  $\chi^2 = 0.86$ ,  $P = 0.65$ , respectively). Comparing the number of species per habitat group along the gradient, only DS of the North site showed significant differences ( $\chi^2 = 6.93$ ,  $P = 0.03$ ) in respect to the other sites.

## Discussion

Our results show a general pattern of decrease in bird richness and number of disturbance-sensitive species of *Polylepis* bird communities with latitude, coupled with an increment in the evenness of the species distribution. The lower equitability index at the North site resulted from the higher dominance of forest-dependent birds which caused a reduction of diversity index at this site. Many studies show that diversity can change with changes in evenness independently of species richness. That is, a community with evenly distributed species appears more diverse than a community that is dominated by a few species (Magurran 1988, Stirling and Wilsey 2001).

Besides this latitudinal avifaunal pattern, we found a high species turnover among sites. The species turnover could be influenced by vegetation types within and surrounding *P. australis* forest patches. North and Centre sites are structurally rich and their associations with other plant species such as vines, ferns and bromeliads makes them favourable feeding habitats for many birds (Fjeldså 1993). On the contrary, in the South site *P. australis* usually produces lateral basal ramifications forming shrublands and only occasionally forms dense forest stands (Enrico *et al.* 2004, Cingolani *et al.* 2004, 2008, Renison *et al.* 2006). These differences in the growth habit of *P. australis* change the forest structure (Kessler 2000) and availability, so could be inducing a reduction in bird richness (Bellis *et al.* unpubl. data). The positive response of bird species richness to habitat complexity has been well documented in tropical forests (Bennett *et al.* 2004, Watson *et al.* 2004, Barlow *et al.* 2006). Specifically in *Polylepis* forests, habitat complexity and quality are important determinants of avian diversity (Terborgh 1977, Kessler *et al.* 2001, Lloyd and Marsden 2008). Habitat features such as density of large trees, vegetation cover, and patch size are very important for many forest-dependent birds (Lloyd 2008a,b, Lloyd and Marsden

Table 1. List of bird species and encounter rates expressed as number of detections per point (10-min. sampled period) recorded in *Polylepis australis* forest of Argentina. North (Jujuy province), Centre (Tucumán province) and South (Córdoba province) sites. DS: disturbance-sensitive species, DT: disturbance-tolerant species and N: neutral species. (\*) Endemic subspecies. (+) Species closely associated with *P. australis* forests.

Species Names	Sites			Functional Group
	North	Centre	South	
<i>Nothoprocta pentlandii</i>	0	0.07	0	DS
<i>Falco sparverius</i>	0	0.07	0	DT
<i>Penelope dabbeni</i>	0.10	0	0	DS
<i>Columba maculosa</i>	0	0	0.10	N
<i>Leptotila verreauxi</i>	0	0.03	0.03	DS
<i>Zenaida auriculata</i>	0	0	0.03	N
<i>Aratinga mitrata</i>	0.93	0	0	DT
<i>Bolborhynchus aymara</i>	0	0.30	0.27	DT
<i>Bolborhynchus aurifrons</i>	0.4	0	0	DT
<i>Aeronautes andecolus</i>	0	0	0.20	DT
<i>Amazilia chionogaster</i>	0	0.07	0	DS
<i>Colibri coruscans</i>	0.13	0.03	0	DT
<i>Sappho sparganura</i>	0.90	0.13	0.03	N
<i>Colaptes melanochloros</i>	0	0	0.13	DS
<i>Cinclodes atacamensis</i>	0	0.07	0	DT
<i>Cinclodes fuscus</i>	0.10	0	0.03	DT
<i>Cinclodes oustaleti olrogii*</i>	0	0	0.03	DT
<i>Craniolaema pyrrhophia</i>	0.10	0	0	DS
<i>Leptasthenura fuliginiceps</i>	0.20	0.20	0.10	DS
<i>Leptasthenura platensis</i>	0	0	0.03	DT
<i>Phacellodomus maculipectus</i>	0.07	0	0	DT
<i>Phacellodomus striaticeps</i> <sup>+</sup>	0.10	0	0	DS
<i>Scytalopus superciliosus</i>	0	0.17	0	DS
<i>Anairetes parulus</i>	0	0	0.33	DT
<i>Knipolegus signatus</i>	0.03	0	0	DS
<i>Mecocerculus leucophrys</i>	0.17	0.17	0	DS
<i>Myiotheretes striaticollis</i>	0.20	0.10	0	DS
<i>Ochthoeca leucophrys</i>	0.07	0	0	DT
<i>Sayornis nigricans</i>	0	0.03	0	DT
<i>Tyrannus melancholicus</i>	0	0.03	0	N
<i>Haplochelidon andecola</i>	0	0.60	0	DT
<i>Troglodytes aedon</i>	0	0.33	0.13	N
<i>Turdus chiguanco</i>	0.53	1.17	0.47	N
<i>Turdus nigricaps</i>	0	0.33	0	DT
<i>Aimophila strigiceps</i>	0	0.07	0	DS
<i>Atlapetes fulviceps</i>	0.23	0	0	DS
<i>Catamenia analis</i>	0	0.13	0	DT
<i>Catamenia inornata cordobensis*</i>	0	0	0.03	DT
<i>Myioborus brunnicaps</i>	0	0	0.17	DT
<i>Phrygilus unicolor</i> <sup>+</sup>	0.37	0	0	DS
<i>Poospiza baeri</i> <sup>+</sup>	0.07	0.17	0	DS
<i>Poospiza erythrocephala</i>	0.07	0	0	DS
<i>Saltator aurantiirostris</i>	0.03	0	0	DS
<i>Thlypopsis sordida</i>	0.07	0	0	DS
<i>Thraupis bonariensis</i>	0.20	0.20	0	DS
<i>Zonotrichia capensis</i>	3.2	1.73	0.07	N
<i>Carduelis atrata</i> <sup>+</sup>	0.20	0.10	0	DS
<i>Carduelis magellanica</i>	0.07	0.83	0	DT
<i>Carduelis uropygialis</i>	0.10	0	0	DT
<i>Molothrus bonariensis</i>	0	0.13	0	N

Table 2. Species richness, diversity and functional group composition estimated for bird communities of North, Centre and South sites of *Polylepis australis* forest of Argentina. ER: encounter rates expressed as the number of detections per 10-minute survey period.  $S_{\text{obs Mau Tau}}$ : sample species richness from sample-based rarefaction curves.  $S_{\text{boot}}$ : bootstrap estimator;  $1/D$ : Simpson's index. Different letter shows significant differences ( $P < 0.05$ ).

	Sites		
	North ( $\pm$ SE)	Centre ( $\pm$ SE)	South ( $\pm$ SE)
Mean ER	0.32 (0.13)	0.28 (0.08)	0.13 (0.03)
Number of individuals (N)	259	218	67
Species richness ( $S_{\text{obs Mau Tau}}$ )	19.71 (1.13)a	18.87 (1.11)a	17.16 (0.27)b
Species richness ( $S_{\text{boot}}$ )	22.86 (1.27)a	22.24 (1.24)a	19.60 (0.28)b
Species diversity ( $1/D$ )	6.02 (0.03)a	8.88 (0.31)b	8.69 (0.13)c
Equitability ( $E_s$ )	0.23 (0.001)a	0.31 (0.01)b	0.51 (0.01)c
Number of disturbance-sensitive Species (DS)	15a	11b	4b
Number of disturbance-tolerant Species (DT)	8	9	7
Number of disturbance-neutral Species (N)	3	6	6

2008). Besides forest quality, the surrounding vegetation may also be an important driver of bird communities; we found that the birds that use *Polylepis* forests are mainly species of neighbouring vegetation types (i.e., subtropical montane forest; shrubland/grassland). Thus, in agreement with observations of Lloyd (2008a,b) in Peruvian *Polylepis* forest, the matrix exerts a significant influence on avifauna composition.

In South America, the southern range distribution of avian species highly associated with *Polylepis* forests (e.g., Tawny Tit-spinetail *Leptasthenura yanacensis*, Thick-billed Siskin *Carduelis crassirostris*, Giant Conebill *Oreomanes fraseri*) only reached the Northern site, with no records at Centre or South sites. Therefore, we were unable to find bird specialists of *P. australis* forests, in contrast to Herzog *et al.* (2003) and Lloyd (2008a,b) who detected many highly associated bird species in tropical *Polylepis* forests of Bolivia and Peru.

We found four species, broadly distributed in other vegetation types, which were present in the three sites surveyed: *Leptasthenura fuliginiceps*, *Sappho sparganura*, *Turdus chiguanco*, and *Zonotrichia capensis*. The *Polylepis* forest assemblage has a mixed origin of species associated with subtropical montane forest and species associated with shrublands and grasslands.

Regarding the habitat sensitive species group, the North site harboured significantly more disturbance-sensitive species than tolerant or neutral species. The low similarity in composition of bird communities along the gradient, beta diversity, showed a species turnover from disturbance-sensitive species to species relatively resilient to human disturbance. Generalist and dispersive species such as House Wren *Troglodytes aedon*, *Zonotrichia capensis*, and Eared Dove *Zenaida auriculata*, became abundant towards the South to the detriment of forest species. Two possible factors that can compound the absence of habitat disturbance-sensitive species in the South site are the structural simplification of the vegetation and the high degradation of *Polylepis* forest. Most *Polylepis* specialists are insectivorous and therefore both vegetation structure and habitat disturbance (mainly fire) may reduce food resources for them (J. Cahill *in litt.*). Similar patterns of beta bird diversity changes were detected in a gradient of disturbed forest of central Argentina where increasing fire pressure caused an important structural simplification of the habitat (Albanesi *et al.* 2008), in forests of the tropical Andes (O'Dea and Whittaker 2007) and, in logged versus unlogged forest of Bolivia (Felton *et al.* 2008).

Of the total species recorded, two (Olrog's Grey-flanked Cinclodes *Cinclodes oustaleti olrogi* and Plain-coloured Seedeater *Catamenia inornata cordobensis*) are endemic subspecies that we recorded in the South site (EBA 058) and four (Black Siskin *Carduelis atratus*, Plumbeous Sierra-finch *Phrygilus unicolor*, Streak-fronted Thornbird *Phacellodomus striaticeps*, and

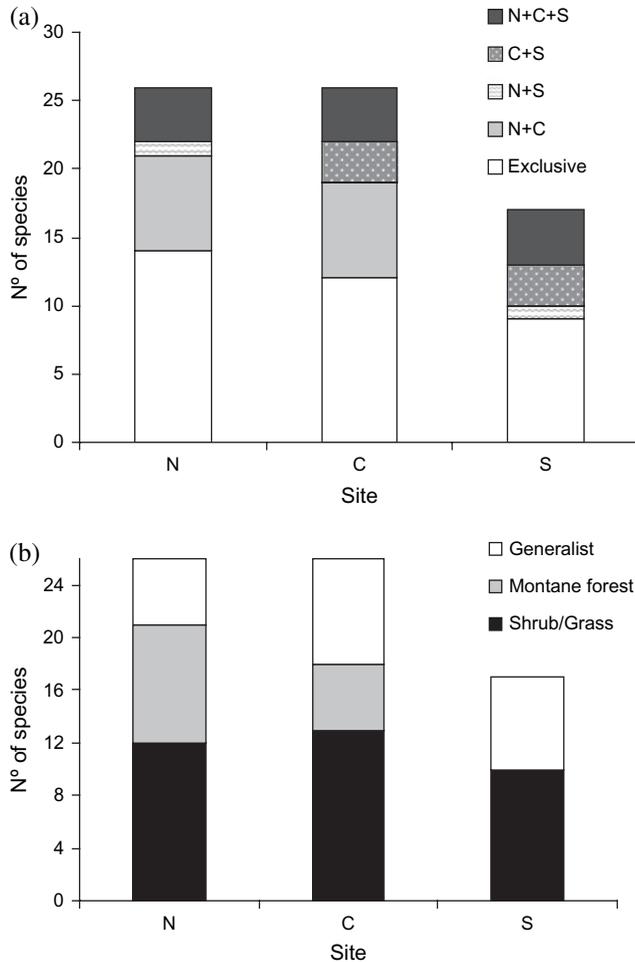


Figure 2. Bird species richness in North (N), Centre (C), and South (S) sites along the latitudinal range of *Polylepis australis* in Argentina. (a) Number of species recorded in the three sites (N+C+S), shared by two sites, or exclusive to one site and (b) number of species associated to subtropical montane forest, shrubland or grasslands, or not associated to a particular habitat (generalist).

Tucuman Mountain Finch *Poospiza baeri* are typical *Polylepis* forests birds (Fjelds  2002) that we recorded in the North and Centre sites (EBA 057). We also recorded four species of conservation concern: *Poospiza baeri*, a globally threatened species categorized as ‘Vulnerable’ by Birdlife International (2007) due to its restricted range and the loss of its natural habitat as a consequence of land conversion and use of pesticides (Peris 1997, Di Gi acomo 2005). Grey-hooded Parakeet *Bolborhynchus aymara*, *Leptasthenura fuliginiceps*, and *Turdus chiguanco* are declining at regional level in the South site (Miatello *et al.* 1999), as a consequence of habitat loss caused primarily by fires and overgrazing. Livestock overgrazing in the South site is responsible of transformation of woodlands into grasslands and eroded rock surfaces (Cingolani *et al.* 2008). This degradation process has negatively affected bird diversity at the landscape level (Garc a *et al.* 2008).

### Implications for conservation

This work is a first approach to understanding the assemblage and status of the avifauna in *Polylepis australis* forest along its distribution range in Argentina and it constitutes a starting point for more comprehensive studies. Initial management recommendations can be formulated on the basis of our study. We recommend the expansion of Calilegua National Park to include the *P. australis* belt in its northern ranges – a project that is being considered by the present National Parks Administration. This is especially important as these *Polylepis* forest sites harbour many disturbance-sensitive species, which will disappear if these areas are degraded. We also recommend managing Quebrada del Condorito National Park in the southern ranges to augment the complexity of forest structure and thus provide suitable habitat for disturbance-sensitive species.

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