Avifaunal responses after two decades of *Polylepis* forest restoration in central Argentina

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**ABSTRACT**

The high Andean *Polylepis* woodlands are home to a unique biota, including an outstanding avifauna. They are one of the most threatened mountain ecosystems worldwide; accordingly, they have been the object of the first restoration initiatives in South America. Here, we evaluated the effectiveness of 20-year *Polylepis australis* woodland restoration efforts to recover the woodland bird communities. We recorded bird diversity and abundance in an ongoing restoration site (with a high proportion of woodland) and in a control site, where no active restoration efforts were made (with a high proportion of grasslands and bare soil), 15 and 20 years after the start of the restoration project. We compared the avifauna of these sites with that of reference mature woodlands, using published records of the study region. At the ongoing restoration site, bird diversity increased over time, as well as abundances of species associated with *P. australis*, whereas those parameters remained stable at the control site. Our results are the first evidence that active restoration of *P. australis* entails passive restoration of the avifauna occurring in these unique upland forests.

**Introduction**

Woodlands of the genus *Polylepis* occur across broad altitudinal, latitudinal and precipitation ranges. They are present along the Andes and nearby mountain ranges, from Venezuela to central Argentina, being one of the forest communities with the greatest latitudinal extension in the world [1]. These woodlands also form the highest tree lines in the world [2]. They are characterized by their high level of endemism [3,4], and are currently regarded as one of the most threatened ecosystems in the Tropical Andes [5].

These particular upland woodlands retain soils and nutrients [6,7], capture large amounts of atmospheric carbon, regulate run-off, and improve water capture in regions with many foggy days [8]. Birds are essential for woodland ecosystem functioning (e.g. seed dispersal, pest control, pollination); thus, when the abundance of different plant species is reduced, birds are strongly affected due to decreases in food availability and nesting substrates. For this reason, the number of bird species and their abundances are approximately twofold in *Polylepis* forests compared with the surrounding degraded areas [9]. Hence, the conservation and restoration of these highland forests have a critically important dual role: protecting a rich biodiversity while providing valuable environmental and socioeconomic services [10,11].

The main factors controlling pre-human *Polylepis* woodland dynamics were precipitation and landscape heterogeneity [12]. A review by Renison et al. [13] found that, at present, *Polylepis* woodland distribution is strongly associated with sites of low anthropogenic impact, indicating that human-ignited fires and browsing by domestic livestock would be the main causes for the decline of these forests. This finding partly explains that these woodlands occur mainly in topographic areas characterized by very steep and inaccessible escarpments [14]. In particular, *Polylepis australis* (hereafter *Polylepis*) woodlands in the mountains of central Argentina have been drastically reduced due to overgrazing by introduced livestock for over 400 years [15]; grazing caused an alarming soil erosion process that resulted in 20% loss of soil surface above 1500 m asl [16]. These forests currently cover only 12% of the landscape [17], and the remnant patches are severely degraded, showing a significant loss of structural complexity [18].

*Polylepis* woodlands hold a unique biota, particularly of habitat specialist birds [19]. Most of these birds have undergone a continuous population decline, which is likely linked to the loss of habitat and fragmentation [20]; for this reason, avian communities are one of the conservation priorities [21]. Of the bird species recorded throughout the distribution of the genus *Polylepis*, two are categorized as critically endangered, eight are endangered, eight are vulnerable, and...
nine are near threatened (http://www.iucnredlist.org/). In addition, 70% of these species have restricted distribution ranges, whereas 52% have a high degree of association with Polylepis woodlands [22]. At the landscape level, birds associated with Polylepis are present mainly in remnant woodland patches of different sizes and shapes, often of complex topography, surrounded by a grassland or shrubland matrix [9,23]. At the patch level, resource availability, the characteristics of the edge vegetation, growth mode, and degree of disturbance have a marked influence on Polylepis bird assemblages [24–26].

Due to the alarming conservation status of Polylepis woodlands, one of the first restoration projects was implemented in 1997 in Córdoba province, Argentina. After more than 20 years of restoration activities, soil loss was largely reduced and more than 30% of the forest cover was restored [27]. However, even though plantation of trees in degraded areas favors forest cover, it does not necessarily imply the recovery of the associated wildlife [28]; indeed, restoring habitat for wildlife depends on multiple factors and spatial scales [29]. For this reason, this study evaluated, for the first time, if the Polylepis restoration project also contributed to the recovery of the native avifauna associated with these woodlands. We hypothesized that the active restoration of a Polylepis forest would increase bird diversity, since vegetation patches with a complex architecture provide more resources and opportunities for microhabitat segregation. In this study, we provide field data of the avifauna in an ongoing restoration site (hereafter, restoration site) and in a control site, and compare them with avifauna data of mature Polylepis woodlands located in protected or inaccessible areas in the study region, using published records [9,30,31].

Methods

**Study area description**

The study was conducted in the mountains of central Argentina, known locally as “Sierras Grandes de Córdoba”; it is characterized by a heterogeneous landscape of hills and plateaus with gentle valleys and deep ravines [14]. Mean temperature is 5°C in winter and 11.4°C in summer, and mean annual precipitation is 900 mm, concentrated in the warmest months, between October and April [11]. The site under restoration, located in Los Gigantes massif, encompasses a 22-ha area characterized by a heterogeneous combination of open valleys, rocky outcrops, deep ravines, ridges, and slopes at altitudes ranging from 2,200 to 2,300 m asl. Restoration activities consisted of excluding livestock using wire fences and planting about 35,000 native tree saplings mainly of Polylepis (86%), with Maytenus boaria (9%) and Escallonia cordobensis (5%) from 1997 to 2007 [27]. Ongoing activities include planting of native grasses and forbs in gullies showing active soil erosion and the systematic control of the existing non-native grasses and trees (https://www.ecosistemasarg.org.ar/proyectos).

**Site physiognomy**

Two sampling areas were selected (Figure 1): the site where the first project for the ecological restoration of Polylepis woodlands was implemented and a control site (30 ha) of similar topographic characteristics and elevation, adjacent to the restoration site, where no restoration activities had been conducted (Figure 2). The landscape of both selected sites (restoration and control) was very similar in 1997 according to the vegetation map reported in Cingolani et al. [32]. We classified the landscape into five physiognomic types, following Flores et al. [15]: Woodlands, Grasslands, Short-grass terrains or Lawns, Rocky outcrops, and Erosion pavement. We used 2017 satellite images obtained from Google Earth version 7.3 for the study period (https://www.google.com/earth/index.html, accessed 6 April 2019). We visually differentiated the physiognomic units based on color and texture, and on previous experience and field surveys in the study area. The proportion of each physiognomic unit was calculated by dividing the area covered by each type into the total area, using Qgis version 3.0.

**Bird sampling**

Bird sampling was conducted during the bird reproductive season (austral summer), in January 2012 and 2017, 15 and 20 years after the start of the forest restoration project, respectively. During each survey, diversity, abundance and composition of bird community were estimated using the point count method [33]. In each study site, 30 count points were randomly located in accessible areas, and an intensive systematic sampling was performed to avoid double-counts between neighboring points [34]. At each point, after waiting for 5 minutes, the same observer (an ornithologist specialized in bird identification in the study area) recorded all the bird species seen or heard within a 20-m radius for 10 min. Surveys started 30 min after sunrise and lasted 3 to 4 h; each point was sampled 10 times each year, at a minimum of one-day interval.

**Data analysis**

Bird communities were characterized in terms of species richness, bird abundance and Shannon diversity index [35]. Differences in species diversity were calculated using a Test-t. To adjust for differences in species detectability, we compared species richness between sites and seasons using rarefaction curves. Rarefaction
analysis calculates species richness after standardizing differences in abundance among samples by estimating the expected number of species of each sample if all samples were reduced to a standard size [35]. All analyses were performed using the software PAST v 3.25 [36]. We also compared the species recorded in this study with avifauna data of mature Polylepis woodlands located in protected or inaccessible areas in the study region, using published records [9,30,31].

To identify patterns of bird community variation across the control and restoration sites, we used a Detrended correspondence analysis (DCA) [37]. Moreover, to understand the importance of Polylepis restoration on avifauna, two additional DCAs were carried out focusing on the abundance of Anairetes parulus and Leptasthenura fuliginiceps, two characteristic species of these forests in the study area [31].

Finally, to evaluate the species associated with a particular forest site (i.e. control and restoration sites), we performed an Indicator Species Analysis (ISA), following the method of Dufrêne and Legendre [38]. This approach selects the characteristic species of each site based on the abundance and fidelity of occurrence of each species in a particular habitat type (group). We calculated $A_{ij}$, i.e. the mean of abundance of species $i$ in the group $j$, compared with all the study groups, and $B_{ij}$, i.e. the relative frequency of occurrence of species $i$ in the group $j$. Then, the indicator value (IV) was obtained as follows: $IV = A_{ij}B_{ij}100$. This IV value was statistically tested using the Monte Carlo method [39]. A perfect characteristic species of a site will be that showing an IV of a significance level <0.05, i.e. one that is always present and is exclusive to the restoration site or to the control site. We
also evaluated the percentage of these species that belonged to each of the trophic guilds in birds.

**Results**

**Site physiognomy**

In the restoration site, woodlands had the largest cover, whereas in the control site, the dominant covers were grasslands and lawns, with a high percentage of bare soil (Figure 2).

**Bird sampling**

A total of 30 bird species were recorded; specifically in the restoration site, 17 species were recorded in 2012 and 25 species in 2017 (Supplementary information 1). Bird abundance also showed variation between study years at the *Polylepis* restoration site, with 1005 individuals recorded in 2012 and 869 individuals in 2017. Between 15 and 20 years after the start of the restoration project in 1997, species diversity increased ($H_{2012} = 2.39$, $H_{2017} = 2.74$, $t = 9.12$, $P < 0.0001$) in the restoration site with respect to the control site ($H_{2012} = 2.60$ and $H_{2017} = 2.55$), whereas the control site showed no differences between study years ($t = 1.47$, $P = 0.14$). Rarefaction analysis confirmed that our results were not an artifact of differences in the number of collected individuals (Supplementary information 2).

Differences in physiognomy between *Polylepis* forests restoration and control sites separated the bird species into two groups. The first and second axes of the DCA explained 41% of the total variability and clearly split the

![Figure 2. Proportion of each physiognomic unit in the control (left) and restoration (right) sites, 20 years after the start of the restoration project in 1997.](image-url)
restoration site from the control site (Figure 3(a)). *A. parulus* (Figure 3(b)) and *L. fuliginiceps* (Figure 3(c)) were recorded mainly in the restoration site.

**Representative species analysis**

Four species (Monte Carlo test based on 1000 permutations; $P < 0.05$) resulted significant and closely

![Figure 3](image_url)

**Figure 3.** (a) Detrended correspondence analysis (DCA) showing the ordination of bird species. The restoration and control sites are indicated with a green and red circle, respectively. (b) and (c) *Airetus parulus* and *Leptasthenura fuliginiceps* abundances, respectively, in both sites; the point size indicates the abundance of the species at each survey points. RF: restoration site; C: control site.
associated with the restoration site; three of them (75%) were insectivores; in turn, six species were selected in the control sites, three of which (50%) were granivores (Table 1).

Discussion

We hypothesized that bird diversity at the *Polylepis* restoration site increased with increasing forest cover and complexity. Our results indicate that at least 20 years of active restoration of this woodland were necessary for the passive recovery of the native avifauna. Thus, this study shows the importance and effectiveness of restoration actions in sites like our study area, since they contribute to the persistence of viable populations of the different bird species associated with these mountain woodlands [23,40].

A review including 39 studies revealed that during secondary forest regeneration, the avifauna takes longer to recover than other taxa; thus, it can be predicted that bird species richness and composition will increase approximately 20 to 40 years after the start of forest restoration [41]. In addition, bird species richness in High-Andean forest fragments was found to increase with increasing habitat quality and topography complexity [42]. In our study, the abundance of birds associated with *Polylepis*, such as *Anairetes parulus* and *Leptasthenura fuliginiceps* [43], markedly increased in the restoration site between 15 and 20 years after the start of the restoration project, suggesting that these birds bred there. In addition, 20 years after the start of the restoration activities, practically all the species recorded in well-preserved *Polylepis* woodland sites [9,30,31], with the only exception to *Catamenia analis* and *Knipoles aterrimus*, were observed.

Most of the bird species closely associated with the restoration site are insectivores and woodland habitat specialists. This result can be explained by the increased structural complexity of the *Polylepis* woodland over time after planting [44], and the consequent availability of resources for the woodland avifauna, allowing the establishment of new species and the increased abundance of the species already present. Moreover, the occurrence of species with different life habits in the restoration site (such as *Turdus chiguango*, *Bubo magellanicus*, *Elaria albiceps*, *Sappho sparganura* and *Psilopogon aymara*) also suggests that the restoration process generated the ecological conditions for the development of new resources; in turn, these resources allow the development of other trophic guilds of birds (i.e. carnivores, omnivores, frugivores, nectarivores). Conversely, the bird species closely associated with the control site were mainly granivores associated with grasslands or rocky outcrops (such as *Geospizopsis unicolor* and *Zonotrichia capensis*), the predominant physiogony of the upper belt mountains in central Argentina after the last century’s retraction of the *Polylepis* forests [18].

Most of the bird species associated with *Polylepis* have small population sizes and restricted distribution ranges [20]. Therefore, in the restoration site, the presence of species categorized as of conservation priority, such as *Cinclodes olrogi* [22], reinforces the importance of projects like the present one to promote the recovery of specialist birds of this particular ecosystem [45–47], whose bird richness depends on patch connectivity and conservation [9]. In turn, a recent study found no evidence that *Polylepis* specialist bird species were sensitive to patch size, and indicated the high ecological value of small patches for their conservation [48].

The evidence presented in this study shows that the active ecological restoration of *Polylepis* can be effective not only in regenerating these upland woodlands but also in the gradual recovery of its native avifauna. At least in this particular case, the presence and abundance of bird species associated with forest habitat were notably increased at the restoration site. Even though our study area was near the southern distribution of *Polylepis* genus, our results may encourage *Polylepis* forest restoration projects in other sites, in particular in the central area of their distribution, where most bird endemics are found [3,24].

Due to the increasing number of *Polylepis* restoration projects (https://www.globalforestgeneration.org/Accin-Andina), we also suggest that in future evaluations, baseline studies should be conducted with the aim of determining not only the initial extent of *Polylepis* forest but also the initial bird biodiversity. In addition, species detectability and seasonality should be considered possible sources of bias [49]. Further research in the study area is necessary to determine if other taxa present in reference *Polylepis* forests have also been recovered or, rather, if it will be necessary to apply active restoration measures until ecological restoration of the whole biota and ecosystem services of this montane forest is achieved. The results obtained

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**Table 1.** Bird species and trophic guilds significantly associated with the restoration and control sites.

| Site     | Species           | Indicator value (%) | Trophic guilds |
|----------|-------------------|---------------------|----------------|
| Restoration | *Turdus chiguango* | 39                  | Omnivores      |
|          | *Anairetes parulus* | 33                  | Insectivores   |
|          | *Leptasthenura fuliginiceps* | 18              | Insectivores   |
|          | *Troglydytes aedon*  | 19                  | Insectivores   |
|          | *Geospizopsis unicolor* | 70              | Granivores     |
|          | *Cinclodes cunechipingon* | 55              | Insectivores   |
|          | *Zonotrichia capensis* | 49              | Granivores     |
|          | *Muscisaxicola rufigen* | 25              | Insectivores   |
|          | *achalensis*       |                     |                |
|          | *Leistes loya obscurus* | 19              | Omnivores      |
|          | *Geospizopsis plebeja* | 14              | Granivores     |

*P < 0.05
after 20 years of the project implementation are very encouraging.

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