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Avian community structure and habitat use of *Polylepis* forests along an elevation gradient

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Background. As one of the highest and most unique systems in the world, *Polylepis* forests are recognized both as center of endemism and diversity along the Andes and as a system under serious threat from human activities, fragmentation, and climate change. Effective conservation efforts are limited, in part, by our poor understanding of the habitat needs of the system’s flora and fauna.

Methods. In 2014-2015, we studied bird communities and 19 associated local and landscape attributes within five forested glacial valleys within the Cordillera Blanca and Huascaran National Park, Peru. Birds were surveyed in dry (May-August) and wet (January-April) seasons at 130 points distributed along an elevational gradient (3,300-4,700 masl) and analyzed using Canonical Correspondence Analysis (CCA).

Results. A total of 50 species of birds, including 13 species of high conservation concern, were associated with four basic habitat types: (1) *Polylepis sericea* forests at low elevations, (2) *P. weberbaueri* forests at high elevations, (3) Puna grassland and (4) shrublands. Four species of conservation priority (e.g., *Poospiza alticola*) were strongly associated with large forest patches (~10-ha) dominated by *P. sericea* at lower elevations (<3,800 masl), whereas another four (e.g., *Anairetes alpinus*) were associated with less disturbed forests of *P. weberbaueri* at upper elevations (>4,200 masl).

Discussion. Results suggest that, in addition to conserving large (>10-ha) *P. sericea* forests at lower elevations as the cornerstone for maintaining bird diversity, any high elevation (>4,200 masl) relicts of *P. weberbaueri*, irrespective of size, should be prioritized for conservation.
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Abstract

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Results. A total of 50 species of birds, including 13 species of high conservation concern, were associated with four basic habitat types: (1) Polylepis sericea forests at low elevations, (2) P. weberbaueri forests at high elevations, (3) Puna grassland and (4) shrublands. Four species of conservation priority (e.g., Poospiza alticola) were strongly associated with large forest patches (~10-ha) dominated by P. sericea at lower elevations (<3,800 masl), whereas another four (e.g., Anairetes alpinus) were associated with less disturbed forests of P. weberbaueri at upper elevations (>4,200 masl).
Discussion. Results suggest that, in addition to conserving large (>10-ha) *P. sericea* forests at lower elevations as the cornerstone for maintaining bird diversity, any high elevation (>4,200 masl) relicts of *P. weberbaueri*, irrespective of size, should be prioritized for conservation.

Key words  Andean birds, Climate change, Conservation, Endemics, Mountain systems, Threatened species
INTRODUCTION

Tropical mountains are well known to support impressively high species diversity and endemism (Körner, Nakhutsrishvili & Spehn, 2006; Spehn et al., 2012), and the tropical Andes, in particular, stand out as a biodiversity hotspot (Myers et al., 2000; Antonelli & Sanmartín 2001). One unique Andean system, nestled in the humid and dry Puna along the Andes, is the Polylepis forest (Simpson, 1979; Simpson, 1986; Kessler, 2006). Considered as one of the world’s highest elevation forests (Gareca et al., 2010), they represent a center of avian diversity (Fjeldså et al., 1996; Fjeldså, 2002) and endemism (Fjeldså, Lambin & Mertens, 1999; Fjeldså, 1993), with several birds restricted to this specific ecosystem (Fjeldså & Kessler 2004; Gareca et al., 2010; Lloyd, 2008a; Lloyd, 2008b; Lloyd, 2008c; Lloyd & Marsden, 2008). According to Fjeldså (2002), 214 bird species use Polylepis forest along the entire range of the Andes, 51 of which are these species strongly associated and 14 of which are highly specialized. Unfortunately, Polylepis forests continue to be threatened by habitat loss, fragmentation, and degradation (Renison, Hensen & Cingolani, 2004; Jameson & Ramsay, 2007; WCMC-IUCN, 1998) while facing future threats from climate change (Şekercioğlu, Primack & Wormworth, 2012). The IUCN Red List of Threatened Species recognized 12 bird species associated with Polylepis forest as globally threatened (Birdlife Conservation 2016). These species are thought to be particularly sensitive to human activities and habitat degradation, given their limited dispersal abilities (Lloyd & Marsden, 2011), high degrees of ecological specialization (Fjeldså, 1993; Servat, 2006), and small population sizes (Lloyd, 2008a). The Royal Cinclodes (Cinclodes aricomae) for example, is critically endangered with an estimated population of 250 individuals restricted to the Polylepis woodlands of southeast Peru (Cuzco, Apurimac, Ayacucho, and Junin) (BirdLife International, 2016; Aucca et al, 2015). Other species include the Ash-breasted Tit-
tyrant (*Anairetes alpinus*), the Plain-tailed Warbling-finch (*Poospiza alticola*) and the White-browed Tit-spinetail (*Leptasthenura xenothorax*) among others.

Although several studies have described bird communities associated with *Polylepis* woodlands in general terms (Fjeldsa, 1987; Frimer & Moller, 1989; Fjeldsa, 1992; Fjeldså & Kessler, 2004), few have identified specific habitat characteristics associated with different species (Herzog, Soria & Matthysen, 2003; Matthysen, Collet & Cahill, 2008; Lloyd, 2008a; Lloyd & Marsden, 2008; Tinoco et al., 2013) and even fewer, have systematically surveyed species across an entire elevation gradient covered by the *Polylepis* ecosystem (Kessler et al., 2001). Recent studies show that many *Polylepis* specialist birds are closely associated both with the physical characteristics of the landscape (e.g., patch size, connectivity) (Lloyd & Marsden, 2008; Tinoco et al., 2013) and local habitat attributes (Lloyd, 2008c). Because *Polylepis* forests show high variation in plant composition and structure throughout their elevational range (3,400 masl to 4,700 masl), birds may specialize on particular microhabitats or even plant species. For example, elevational ranges of several *Polylepis* trees and shrubs are highly variable, going as low as 900 masl in the case of *P. australis* (Márcora, 2013) or as high as 5,200 m in the case of *P. tarapacana* (Troll, 1973; Simpson, 1979; Kessler, 2005).

In this study, we (1) described shifts in the floristics and structure of *Polylepis* forests along an elevational gradient, (2) examined how bird communities changed with elevation, habitat attributes, and landscape characteristics, and (3) identified specific habitat and landscape attributes associated with threatened and endemic birds in the Cordillera Blanca of Peru. A deeper understanding of bird-habitat relationships along the elevational gradient will provide essential information to guide conservation of specialized *Polylepis* communities and endangered
species, especially under the threat of climate change (Şekercioğlu, Primack & Wormworth, 2012).

**METHODS**

**Study area**

The research was conducted in Cordillera Blanca, the highest tropical mountain range in the world, located in Ancash Department in Peru (9°06’19" S, 77°36 ’21" W) (Figure S1). Study sites were located within Huascaran National Park and Huascaran Biosphere Reserve, both protected since 1975 and declared a world heritage site by UNESCO in 1985 (SERNANP, 2010). The complex topography of the study area includes 44 deep glacial valleys spanning extensive elevational gradients that, in only a few kilometers, ascend from 2,400 masl to mountains reaching 5,000 masl to 6,768 masl at the peak of Huascaran, the world’s highest tropical mountain (Byers, 2000). Each valley included several patches of *Polylepis* forest surrounded by a matrix of bushes, grasslands, wetlands, lagoons and other plant communities. These forests represent the largest extents of protected *Polylepis* woodland in the world (Zutta, 2009; Zutta et al. 2012). Mean annual rainfall is ~844 mm and is most plentiful at high elevations (Schauwecker et al., 2014). There is also a strong seasonality, with the year partitioned into dry (May to August) and wet (September through April) seasons, with precipitation peaking during January through March (~130 mm per month). Mean annual temperature is 13.5°C, but daily temperatures can plummet to -15°C at night and soar to 23°C at noon during the dry season.

Five glacial valleys on the Pacific slope were selected for study based on accessibility, the presence of broad elevational gradients, and spatial distribution along the Cordillera Blanca. Three parallel valleys ranging from 3,300 masl to 4,700 masl were located in the north of...
Cordillera Blanca (Parón, Llanganuco and Ulta), and two valleys (Llaca and Rajucolta) were located more centrally within the Cordillera, covering an elevational gradient from 3,800 m to 4,700 masl. Data were collected from mid-May to mid-August 2014, corresponding to the dry season, and from mid-January to mid-April 2015, corresponding to the wet season.

Habitat surveys

During each season, field teams measured 19 habitat and landscape variables within 130 circulars plots with a 10-m radius (only one was measured in a 50-m radius), centered on each point and divided into four quadrants by the intersection of North-South and East-West axes at the plot center. Percentage of mosses, Puna grass, rocks and bare ground were estimated in each quadrant and later averaged for use in analysis. In addition, the height and diameter at breast height (DBH) of the nearest tree (woody vegetation with individual main stems >10 cm DBH) within each quadrant were measured and the tree was identified to the species level. When we encountered multi-stemmed trees, all stems were measured in the field but the average DBH of individual stems was used for analysis. Biomass was calculated using the allometric equation (Eq. 1) developed for Polylepis trees by Espinoza and Quispe (2005) after their study in HNP.

\[
\text{Biomass} = 0.0694 \times DBH^{2.35996} \quad (\text{Eq. 1})
\]

The total number of trees >10 cm DBH was counted by quadrant, as was the number of shrubs (multi-stemmed woody vegetation ≤ 10 cm DBH; typically Lupinus, Senecio, Berberis, Baccharis, Gynoxys and small Polylepis), to calculate tree and shrub density in the circular plot, adjusted for an area of 100 m². As an indicator of vertical forest structure, canopy depth, defined
as canopy height minus the height of the canopy base, and groundcover height (groundcover: vegetation ≤ 50 cm) also were measured at each quadrant. We used the mean of these variables for the subsequent analysis. A spherical densiometer was used to estimate canopy cover at the center of every point. For the landscape measurements, I estimated the percentage of forest within a 50-m circular plot, the patch size of forest in ha (points outside forest were 0 ha), and the distance from the point center to the nearest forest edge (positive values indicated inside the forest and negative outside). All metrics were calculated using Quantum GIS Geographic Information System (QGIS Development Team, 2009) and the OpenLayers Plugin 1.3.6 based on CNES/Astrium satellite images from Google Earth 2015 with 1-m resolution.

Bird surveys

I used a robust sampling design for multiple species to survey the bird community (Jolly, 1965; Kendall, Nichols & Hines, 1997; Kendall, 2001). Points were separated by >150 m and stratified by elevation so as to span the entire elevational gradient of each valley (3,300 masl to 4,700 masl). GPS coordinates and elevation (±10 m) were recorded at every point, and adjusted with a Digital Elevation Model (DEM) of 10 m resolution. A total of 30 points were located in each of the three larger valleys of Parón, Llanganuco and Ulta and 20 points in the smaller valleys of Llaca and Rajucolta. A total of 70 points were located inside woodlands dominated by Polylepis trees, 46 in areas dominated by shrubs and short-statured trees, such as Gynoxys/Buddleja, 6 within Eucalyptus forest, and 8 in Puna grassland (Figure S2).

All 130 points were surveyed for 3 consecutive days during the dry and again in the wet season. Each point was visited three times during the dry season by a single observer, and five times during the wet season by two observers. At each point, the observer recorded all birds seen
or heard within 50 m over a 10-min period. Surveys were conducted from sunrise (~0500-0600 h) to ~1200 h, and the order of surveys was reversed each visit to avoid bias related to bird activity, time of day, and/or observer experience (Lloyd, 2008a; Lloyd, 2008b). For each bird detection, we recorded time, species, number of individuals, linear distance from the point count center, and habitat type. Individuals detected multiple times were only counted once. The Cornell Lab of Ornithology and the Institutional Animal Care and Use Committee (IACUC) of Cornell University provided full approval for this observational research. The entire field study was approved by Servicio Nacional de Areas Naturales Protegidas del Peru (SERNANP), under the Resolution PNH-N. 014 – 2014.

Data analysis

Because habitat variables did not differ statistically between seasons, we used the mean of the two seasons in all analyses. Habitat variables were tested for normality and independence using Shapiro-Wilk W test ($p<0.01$) and Spearman’s D correlation test ($r<0.75$), respectively. We compared habitat attributes among the 5 valleys using the non-parametric Kruskal-Wallis test. Changes in habitat along the elevation gradient were examined using a non-metric multidimensional scaling (NMMS) and Bray-Curtis similarity index on Past 3.08 (Hammer, Harper & Ryan, 2001).

Changes in forest composition (i.e., Polylepis spp.) with elevation were examined using an occupancy model with elevation as the single covariate in program MARK (White & Burnham 1999). We used detection/no-detection data of the different Polylepis species at each point count with a detection probability equal to one ($p = 1$). Bird-habitat associations were examined using a Canonical Correspondence Analysis (CCA) (Braak, 1986), which illustrates the habitat – bird
178 relationships in a biplot of the two vectors with the highest eigenvalues and have been used in
179 other *Polylepis* studies (Lloyd, 2008c). The analysis was restricted to those bird species that were
180 observed in at least 20 independent times over both seasons and over the 130 point count
181 locations. Peruvian endemics and threatened birds species were defined according to the
182 International IUCN Red List of threatened species (Birdlife Conservancy, 2016).
183
184 **RESULTS**
185
186 **Habitat characteristics**
187 Valleys differed significantly height and composition (e.g., moss, Puna grass, rock) of ground
188 cover, as well as in forest patch sizes and amount of forest within 50 m (Table 1). Interestingly,
189 most structural attributes of the forest, such as DBH, tree height, canopy cover, and tree and
190 shrub density, were similar among valleys.
191 Both occupancy models and the NMMS indicated that habitat changed with elevation (Table
192 2; Figure 1; Table S1; Figure S3). Elevation was a significant predictor of occupancy for the two
193 *Polylepis* species within the study area (Likelihood ratio test: *P. sericea*: $x^2=18.58$, df=1,
194 $p=0.0001$; *P. weberbaueri*: $x^2=36.98$, df=1, $p=0.0001$) (Table 2); with *P. sericea* being replaced
195 by *P. weberbaueri* as elevation increased. *P. sericea* was most common in the study area, at 33%
196 occupancy ($Psi$-hat: 0.33; SE: 0.044; 95% CI: 0.25-0.43) compared to 17 % for *P. weberbaueri
197 ($Psi$-hat: 0.17; SE: 0.042; 95% CI: 0.10-0.27). Occupancy probability for *P. sericea* decreased
198 monotonically with increasing elevation, from 0.8 at 3,300 m, 0.5 at 3,870 masl and only 0.1 at
199 4,680 masl; whereas *P. weberbaueri* increased more rapidly from 0.1 at 3980 masl, to 0.5 at
200 4,390 masl and to 0.8 at 4,680 (Figure 1). A coexistence zone for the two species was observed
201 between 4,060 to 4,350 masl (Figure S4).
For other habitat variables, the first NMMS axis was positively associated with elevation, DBH, *P. weberbaueri*, and biomass and negatively associated with groundcover height and shrub density (Table S1; Figure S3). The second NMMS axis was negatively associated with elevation and positively associated with structural characteristics typical of *P. sericea* forest (e.g., tree height, canopy cover, canopy depth), and landscape characteristics, including amount of forest, patch size and internal distance to the edge. Collectively these axes showed that landscapes at lower elevations had larger patches of forest (~>10 ha) dominated by *P. sericea*, with smaller and fewer trees and shrubs, resulting in lower biomass overall, than upper elevations. Sampling points at higher elevations, on the other hand, were dominated by smaller patches of *P. weberbaueri* with taller and larger trees, high canopy cover, and comparatively less understory height.

**Habitat and bird community ordination**

In total, 8,839 records of 101 bird species were recorded at the point counts – with 2,853 observations of 77 species recorded during the dry season compared to 5,986 observations of 88 species in the wet season. Fifty bird species were recorded in at least 20 independent detection events, including 13 species of conservation concern (Table 3) representing 6 Peruvian endemics and 6 IUCN Red List - threatened species and two *Polylepis* specialists (*Grallaria andicolus* and *Xenodacnis parina*).

Nearly half of the variation in bird communities (48.3 %) with respect to habitat and landscape attributes was explained by the first two CCA vectors, with a sum of all eigenvalues of 0.74. The first vector, which explained 28.7 percent of the variation, was associated with low elevations, large patches of *P. sericea*, high tree densities, dense canopy cover, and tall
understory vegetation. The second vector, explaining 19.6% of the variance, was positively associated with small patches of *P. weberbaueri* at high elevation and with tall trees, high canopy cover, abundant mosses, and sparse grass and shrubs (Figure 2; Table 4).

Birds were associated with four main habitat clusters (Figure 3): (1) habitat structure associated with *P. sericea* dominated forest (e.g., canopy cover, patch size, forest interior (distance to the edge), tree density and height) (Cluster I), (2) habitat structure associated with *P. weberbaueri*, such as higher levels of mosses, rocks, biomass, DBH and slope (Cluster II), (3) grassland associated with Puna or other open habitats (Cluster III), and (4) dense areas with tall herbaceous groundcover and high shrub density (Cluster IV).

Seventeen bird species were strongly associated with *Polylepis* forest. Of these, 9 species were associated with *P. sericea* habitat (Cluster I), including four threatened/endemic species the Rufous-Eared Brush-Finch (*Atlapetes rufigenis*), Plain-tailed Warbling-finch (*Poospiza alticola*), Giant Conebill (*Oreomanes fraseri*) and the Baron’s Spinetail (*Cranioleuca antisiensis baroni*); three widely distributed insectivores: Black-crested Warbler (*Myiothlypis nigrocristata*); Rufous-Breasted Chat-tyrant (*Ochtoeca rufipectoralis*), Brown-Bellied Swallow (*Notiochelidon murina*); and two hummingbirds: Shining Sunbeam (*Aglaeactis cupripennis*) and Tyrian Metaltail (*Metallura tyrianthina*). The other eight species were associated with *P. weberbaueri* habitat (Cluster II). These included the endangered Ash-breasted Tit-tyrant (*Anairetes alpinus*), the near-threatened Tawny Tit-spinetail (*Leptasthenura yanacensis*), the endemic and vulnerable White-cheeked Cotinga (*Zaratornis stresemanni*), the endemic Ancash Tapaculo (*Scytalopus affinis*), and the widespread Stripe-headed Antpitta (*Grallaria andicolus*), White-Throated Tyrannulet (*Mecocerculus leucophrys*), Thick-billed Siskin (*Spinus crassirostris*), and Tit-like Dacnis (*Xenodacnis parina*) (Table 3).
Interestingly, many species were associated with grasslands and shrublands (Cluster III and IV). Seventeen species were associated with grasslands and open habitats (e.g., flycatchers, canastersos, finches, ground-tyrants, earth creepers, and hummingbirds), although only one of these was an endemic species - Striated Earthcreeper (Geocerthia serrana). Another sixteen species were associated with shrublands (Cluster IV), including two endemic species - Black Metaltail Hummingbird (Metallura phoebe) and Rusty-Crowned Tit-Spinetail (Leptasthenura pileata).

**DISCUSSION**

Polylepis forests in Huascaran National Park and Biosphere supported unique bird communities, including several threatened and endemic bird species (Fjeldså & Kessler, 2004; Gareca et al., 2010). Bird communities changed markedly along elevational gradients in response to shifts in habitat structure and floristics within each of the valleys. Birds generally were associated with four types of habitat within the valleys – (1) lower elevation $P. \text{sericea}$ forests, (2) higher elevation $P. \text{weberbaueri}$ forests, (3) grasslands and Puna habitat, and (4) successional shrublands. Although each of these habitats supported at least one endemic or declining species, the Polylepis forests supported the greatest number of threatened and endemics. That said, forests varied in terms of their suitability for any given bird species, which were associated with different characteristics of each of the two types of Polylepis habitat defined here.

At lower elevations (3,300 – 4,000 m); four birds of concern were strongly associated with large patches of mature $P. \text{sericea}$ forests. These include the near-threatened Giant Conebill ($Oreomanes fraseri$), a bird that specializes in nesting (Cahill, Matthysen & Huanca, 2008) and foraging on Polylepis bark (Fjeldså & Krabbe, 1990; Servat, 2006; Lloyd, 2008b), that in our
analysis was mainly associated with the interior of the forest and large diameter trees. Our finding is consistent with previous studies showing that the Giant Conebill favored large trees in mature forests (Lloyd, 2008a) and avoided edges (Cahill & Matthysen, 2007). The other three species, the Plain-tailed Warbling-finch (*Poospiza alticola*), the Banon’s Spinetail (*Cranioleuca baroni*) and the Rufous-eared Brush-finch (*Atlapetes rufigenis*), are recognized as endemics and threatened species but otherwise their ecology is poorly known (Huffstater, 2012; Schulenberg & Jaramillo, 2015). In my system, the Plain-tailed Warbling-finch and the Banon’s Spinetail were associated with the interior of large patches of dense and mature *Polylepis* forest at relatively much lower elevations than the Giant Conebill. The Rufous-eared Brush-finch, on the other hand, seemed better able to persist in smaller patches and near edges. The Plain-tailed Warbling-Finch, which is listed as endangered (EN) by Birdlife International, was relatively common in our study area and was often seen foraging in pairs, familiar groups and/or mixed flocks in *Polylepis sericea* mixed forest with *Gynoxys* and *Alnus*. Further population studies are needed to better understand its status and the extent to which my observations might signal population recovery. Three other species widely distributed along the Andes, the Rufous-breasted Chat-tyrant (*Ochthoeca rufispectoralis*), the Black-crested Warbler (*Myiothlypis nigrocristata*) and the Shining Sunbeam (*Aglaeactis cupripennis*) were associated with the interior of *P. sericea* forest. At upper elevations (>4, 000 masl), some of the most endangered species were associated with what are seemed to be less-disturbed *P. weberbaueri* forests (more natural or pristine), based on their remoteness, inaccessibility, in very steep and rocky terrain with high abundance of mosses. Surprising, though, these endangered birds were not associated with the amount of forest or patch size. Among these bird species was one of most highly threatened of the Andes, the Ash-breasted Tit-tyrant (*Anairetes alpinus*), which has a global population estimated in 780
293 individuals that declined by 10 - 19 percent between 2002-2012 in Peru and Bolivia (U.S. Fish
294 and Wildlife Service 2012). Another two birds of concern, the endemic and vulnerable White-
295 cheeked Cotinga (*Zaratornis stresemanii*) and the neared threatened Tawny Tit-spinetail
296 (*Leptasthenura yanacensis*), were also *Polylepis* specialists and were strongly associated with
297 mosses and rocks inside remote *P. weberbaueri* stands, suggesting that they require more natural
298 or pristine characteristics found in the less accessible high elevations, regardless of patch size.
299 These findings are consistent with previous studies that report high abundance of these species in
300 small high elevation *Polylepis* woodlands (Lloyd, 2008a; Lloyd, 2008b; Sevillano-Ríos, Lloyd &
301 Valdés-Velásquez, 2011) and the high variability in edge-avoidance by the Tawny Tit-spinetail
302 in Bolivia (Cahill & Matthysen, 2007).
303 Thus, conservation of high-elevation patches, regardless of size, will likely prove essential to
304 maintaining populations of these threatened species. For example, previous studies of *Polylepis*
305 forest in Cordillera Blanca registered none or very few Ash-breasted Tit-tyrants, despite covering
306 a large number and area of *Polylepis* woodlands (Fjeldså, 1987; Frimer & Nielsen, 1989; Servat,
307 2006; Sevillano-Ríos, Lloyd & Valdés-Velásquez, 2011). However, these studies mainly
308 surveyed forest below 4,300 masl. This suggests that even large *Polylepis* forests at low
309 elevations will not be sufficient to maintain populations of some threatened species like the Ash-
310 breasted Tit-tyrant. Therefore, the conservation of high elevation *Polylepis* patches, regardless of
311 their size would be a priority for the conservation of these bird species.
312 In the other hand, a surprising number of birds were associated with Puna grasslands and
313 shrublands. Although these environments are typically considered hostile (Lloyd & Marsden,
314 2008), they were heavily used by several hummingbirds, including the endemic *Metallura*
315 *phoebe*, tyrants, flycatchers, canasteros and finches. One possible explanation for the relatively
high diversity in grasslands and shrublands is that they offer a higher diversity of resources that complement those available in *Polylepis* woodlands. A recent study suggested that *Gynoxys*, a common woody tree/shrub that occurs within several *Polylepis* forests along the Andes, plays an important role in the composition and structure of the *Polylepis* bird community in Ecuador (Tinoco et al., 2013). Not only does *Gynoxys* produce sugary secretions and host a high variety of arthropods, it also provides structure that improves connectivity among *Polylepis* patches (Fjeldså & Krabbe, 1990; Kessler, 2006; Tinoco et al., 2013). Importantly, our field observations suggest that the value of open habitats may depend, in part, on the proximity to *Polylepis* forest, because we observed many of the grassland/shrubland-associated birds roosting in forests at night, when air temperatures drop to freezing in open areas, but remain warmer inside the forest. From a conservation perspective, then, *Polylepis* forest may support the broader bird community in the valleys and not only *Polylepis* specialists.

One unexpected finding of our study was the floristic shift along the elevational gradient, whereby larger patches of *P. sericea* forests (typically below 3,800 masl) were gradually replaced by smaller patches of larger and taller *P. weberbaueri* trees at higher elevations (Figure S2). The greater height and larger DBH of *Polylepis* trees at upper elevations is counter-intuitive (Figure 4), given the harsh environment, but could result from lower levels of human activity and resource extraction at the higher and more inaccessible areas. Kessler et al., (2014), found a marginally significant negative relationship between tree height and human disturbance, across a range of *Polylepis* species in disturbed areas, being marginally smaller than those in undisturbed areas in Cusco. For this reason, high elevation remnants in inaccessible areas may be the only remaining examples of the more “natural” vegetation conditions of *Polylepis* forest, similarly to what was suggested for other plants communities of the high Andes (Sylvester, Sylvester &
Kessler, 2014). However, another explanation could be simply differences in the climatic niche optima between species and their different physiological/genetic characteristics. The replacement pattern of *Polylepis sericea* with *P. weberbaueri* at higher elevations suggests that the species have different tolerances (e.g., physical, edaphic, climatic and ecological), which has important implications for the growing number of *Polylepis* reforestation, afforestation and general restoration projects. For example, many projects may not select the most suitable species, but instead often elect to use other *Polylepis* species (e.g., *P. incana* and *P. racemosa*) that respond well initially but suffer high mortality after 15-20 years (C. Aucca, 2009, pers. comm.), and may even compete with native species.

**Implications for conservation**

Our research has three main implications for conservation: (1) large patches (>10 ha) of mature *Polylepis* at low elevations should be a cornerstone for Andean bird conservation given their ability to support diverse bird communities, including several endemic and specialist species; (2) small *Polylepis* patches (< 2 ha) at high elevations provide unique habitat to severely threatened species and, thus, are critical refuges that also warrant protection; and (3) habitats that are usually less recognized for their conservation value, such as grasslands and shrublands, support surprisingly large numbers of species and even several endemics. However, the degree to which the suitability of grassland and shrubland habitats is related to proximity of *Polylepis* forest for roosting warrants further study. An important caveat of our findings is that we focused on habitat use and associations and, therefore, cannot speak to the quality of the habitat nor the extent to which it affected condition, reproduction, or survival. Given the paucity of
demographic information on birds using *Polylepis* forest, additional work is required to evaluate habitat quality and identify the key features required to support populations.

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Table 1

Habitat and landscape attributes (Mean ± SD, Min – Max) at five glacial valleys in Huascaran National Park, Peru, 2014-2015.

Number of survey points are indicated below valley names. Numbers of trees measured are indicated below tree height and dbh. Statistical differences are in bold p<0.05.
Table 1.

|                        | Total n=130 | Llanganuco n=30 | Llaca n=20 | Ulta n=30 | Rajucolta n=20 | Parón n=30 | Between-localities differences |
|------------------------|-------------|-----------------|------------|-----------|----------------|-----------|-------------------------------|
| Elevation (m)          | 4080 ± 327.8 | 3999 ± 322.6    | 4274 ± 225.1 | 4030 ± 331.9 | 4249 ± 240.4    | 3971 ± 67 | \( \chi^2:14.96, p<0.005 \) |
|                        | 3302 - 4678 | 3468 - 4513     | 4007 - 4610 | 3515 - 4495 | 3965 – 4678    | 3302 - 4591 |                                |
| DBH (cm)               | 29.7 ± 33.84 | 28.9 ± 26.87    | 28.5 ± 22.52 | 23.4 ± 34.86 | 41.2 ± 33.91   | 30.9 ± 43.82 | \( \chi^2:6.12, p=0.191 \) |
|                        | n=274       | n=69            | n=49       | n=33       | n=70           | n=70      |                               |
| Tree height (m)        | 6.4 ± 2.96  | 6.2 ± 2.58      | 5.2 ± 2.84 | 8.6 ± 3.97 | 7.0 ± 2.30     | 5.3 ± 1.72 | \( \chi^2:1.44, p=0.838 \) |
|                        | n=274       | n=69            | n=49       | n=33       | n=70           | n=70      |                               |
| Ground cover height (cm)| 0.8 ± 0.34  | 1.0 ± 0.35      | 0.8 ± 0.22 | 0.8 ± 0.42 | 0.7 ± 0.19     | 0.9 ± 0.27 | \( \chi^2:21.17, p=0.001 \) |
|                        | 0.0 - 1.68  | 0.4 - 1.68      | 0.5 - 1.25 | 0.0 - 1.63 | 0.2 - 1.03     | 0.6 - 1.38 |                                |
| Canopy depth (m)       | 1.4 ± 1.42  | 1.5 ± 1.12      | 1.3 ± 0.79 | 1.8 ± 2.39 | 1.00 ± 1.04    | 1.3 ± 0.77 | \( \chi^2:2.57, p=6.33 \)   |
|                        | 0.00 - 11   | 0.00 - 4.33     | 0.00 - 2.63 | 0.00 - 11  | 0.00 - 3.5     | 0.00 - 2.75 |                                |
| Tree Density (Ind/100 m²) | 3.2 ± 3.82  | 4.5 ± 4.96      | 4.0 ± 6.13 | 2.8 ± 3.83 | 2.6 ± 3.57     | 2.4 ± 2.22 | \( \chi^2:4.70, p=0.320 \)  |
|                        | 0.00 - 17.19 | 0.00 - 17.19   | 0.00 - 14.01 | -10.50    | -5.41         | 0.00 - 11.78 |                                |
| Bushes Density (Ind/100 m²) | 14.5 ± 12.08 | 24.1 ± 13.18   | 10.2 ± 6.03 | 17.5 ± 14.69 | 9.6 ± 7.63     | 10.5 ± 7.21 | \( \chi^2:8.59, p=0.072 \)  |
|                        | 0.00 - 111.41 | 0.00 - 111.41  | 2.55 - 23.87 | 0.32 - 33.1 | -46.15         | 2.55 - 27.37 |                                |
| Moss cover percent     | 0.3 ± 0.25  | 0.3 ± 0.29      | 0.6 ± 0.25 | 0.2 ± 0.21 | 0.2 ± 0.18     | 0.2 ± 0.15 | \( \chi^2:24.48, p=0.001 \) |
|                        | 0.00 - 0.94 | 0.00 - 0.94     | 0.11 - 0.89 | -0.75      | -0.79         | 0.00 - 0.74 |                                |
| Puna grass cover percent | 0.3 ± 0.32  | 0.4 ± 0.32      | 0.2 ± 0.33 | 0.4 ± 0.31 | 0.3 ± 0.37     | 0.1 ± 0.14 | \( \chi^2:29.88, p=0.001 \) |
|                        | 0.0 - 0.95  | -0.95            | -0.91      | 0.95       | 0.94          | 0.0 - 0.73 |                                |
| Rock cover percent     | 0.4 ± 0.26  | 0.3 ± 0.21      | 0.7 ± 0.22 | 0.3 ± 0.22 | 0.3 ± 0.37     | 0.3 ± 0.18 | \( \chi^2:38.75, p=0.001 \)  |
|                        | 0.00 - 0.95 | 0.00 - 0.94     | 0.29 - 0.94 | -0.70      | 0.02 - 0.95   | 0.03 - 0.78 |                                |
| Bare ground percent    | 0.4 ± 0.26  | 0.1 ± 0.18      | 0.0 ± 0.02 | 0.1 ± 0.10 | 0.1 ± 0.06    | 0.1 ± 0.10 | \( \chi^2:9.95, p=0.041 \)   |
|                        | 0.00 - 0.95 | 0.00 - 0.75     | 0.00 - 0.06 | -0.50      | -0.23         | 0.00 - 0.36 |                                |
| Cover percent          | 0.5 ± 0.38  | 0.5 ± 0.40      | 0.6 ± 0.39 | 0.5 ± 0.44 | 0.4 ± 0.34    | 0.5 ± 0.41 | \( \chi^2:1.12, p=0.892 \)   |
|                        | 0.00 - 1.00 | 0.00 - 1.00     | 0.00 - 1.00 | -1.00      | -1.00         | 0.00 - 1.00 |                                |
| Slope                  | 23.2 ± 9.89 | 18.7 ± 9.17     | 25.2 ± 10.80 | 23.8 ± 11.00 | 24.6 ± 8.30   | 25.0 ± 8.9 | \( \chi^2:8.18, p=0.085 \)   |
| Feature                  | 0 - 0.79 | 0 - 0.79 | 0 - 0.79 | 0 - 0.79 | 0 - 0.79 | 0 - 0.79 | 0 - 0.79 | 0 - 0.79 | 0 - 0.79 | 0 - 0.79 |
|-------------------------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
| Forest on 50 m-r plot   | 0.35 ± 0.26 | 0.39 ± 0.26 | 0.47 ± 0.23 | 0.24 ± 0.25 | 0.27 ± 0.27 | 0.39 ± 0.25 | 2 \( \chi^2 \): 13.53, \( p = 0.009 \) |
| Patch size (ha)         | 31.2 ± 50.68 | 62.4 ± 85.02 | 31.9 ± 29.94 | 3.9 ± 7.03 | 39.4 ± 43.19 | 21.7 ± 20.65 | 2 \( \chi^2 \): 13.94, \( p = 0.007 \) |
| Distance to the edge (m) | -41.5 ± 186.56 | -7.1 ± 72.79 | 31.7 ± 78.83 | -60.2 ± 111.05 | -192.8 ± 403.29 | -5.2 ± 64.31 | 2 \( \chi^2 \): 16.24, \( p = 0.003 \) |
Table 2 (on next page)

Occupancy estimates (Psi) of Polylepis sericea and P. weberbaweri within five valleys in Huascaran National Park, Peru.

$p=$ encounter probability and Elev = Elevation in m.
Table 2.

|            | P. sericea | Psi - hat | SE   | 95% CI | AICc  |
|------------|------------|-----------|------|--------|-------|
| p (1) Psi (Elev) | 0.335      | 0.045     | 0.25 – 0.43 | 154.5 |
| p(.) Psi (Elev)  | 0.335      | 0.045     | 0.25 – 0.43 | 154.5 |
| p(.) Psi(.)      | 0.354      | 0.041     | 0.27 – 0.44 | 170.98|

|            | P. weberbaueri |              |      |        |       |
|------------|----------------|--------------|------|--------|-------|
| p (1) Psi (Elev) | 0.168      | 0.043       | 0.10 – 0.27 | 116.52|
| p(.) Psi (Elev)  | 0.168      | 0.043       | 0.10 – 0.27 | 116.52|
| p(.) Psi(.)      | 0.262      | 0.039       | 0.19 – 0.34 | 149.41|
**Table 3**(on next page)

Ordination of the 13 bird species of conservation concern for the first four canonical factors from the CCA.

Higher values are shown in bold.
Table 3.

| Species                        | Axis 1 | Axis 2 | Axis 3 | Axis 4 |
|-------------------------------|--------|--------|--------|--------|
| Anairetes alpinus EN          | -1.310 | 3.243  | -2.454 | 0.970  |
| Atlapetes rufigenis NT E      | 0.208  | 0.612  | 1.003  | -0.802 |
| Cranioleuca baroni E          | 0.877  | 1.054  | 0.923  | 0.256  |
| Grallaria andicolus φ         | -0.521 | 0.276  | 0.518  | 0.354  |
| Leptasthenura pileta E        | 1.109  | -0.709 | 0.151  | 1.768  |
| Leptasthenura yanacensis NT φ | -2.130 | 2.734  | -2.341 | 0.206  |
| Metallura phoebe E            | 0.880  | -0.499 | 0.447  | 0.355  |
| Oreomanes fraseri NT φ        | 0.332  | 1.571  | -0.090 | 1.142  |
| Poospiza alticola EN E φ      | 1.790  | 0.843  | 0.408  | 0.279  |
| Scytalopus affinis E φ        | -0.525 | 0.518  | 0.232  | 0.777  |
| Geocerthia serrana E          | -0.947 | -0.364 | -0.455 | -0.999 |
| Xenodacnis parina φ           | -0.327 | 0.408  | 0.584  | -0.752 |
| Zaratornis stresemanni VU E φ | -0.218 | 2.608  | -3.645 | 1.363  |

NT = Near Threatened; VU = Vulnerable; EN = Endangered (IUCN 3.1 2016)

φ = Polylepis specialist; E = Endemic
Table 4 (on next page)

Ordination of 19 habitat variables on the first four canonical factors from the CANOCO analysis.
|                                | Factor 1 | Factor 2 | Factor 3 | Factor 4 |
|--------------------------------|----------|----------|----------|----------|
| Patch size ha                 | 0.536    | 0.273    | -0.040   | 0.051    |
| P. sericea presence           | 0.459    | -0.010   | 0.249    | 0.184    |
| Forest in 50 m-r plot %       | 0.429    | 0.514    | 0.262    | -0.119   |
| Tree density                  | 0.356    | 0.316    | 0.211    | -0.106   |
| Groundcover height m          | 0.354    | -0.172   | 0.073    | -0.138   |
| Canopy depth m                | 0.319    | 0.423    | 0.137    | -0.217   |
| Canopy cover                  | 0.318    | 0.439    | 0.156    | -0.216   |
| Tree height m                 | 0.289    | 0.435    | 0.109    | -0.200   |
| Shrub density                 | 0.162    | -0.248   | 0.034    | -0.108   |
| Distance to the edge m        | 0.158    | 0.443    | 0.317    | -0.019   |
| DBH cm                        | -0.001   | 0.381    | 0.090    | -0.022   |
| Slope                         | -0.026   | 0.287    | -0.125   | -0.068   |
| Moss %                        | -0.081   | 0.522    | 0.230    | -0.208   |
| Grass %                       | -0.082   | -0.431   | -0.242   | -0.334   |
| Bare ground %                 | -0.120   | -0.002   | 0.228    | 0.103    |
| Biomass                       | -0.158   | 0.189    | 0.076    | 0.022    |
| Rocks %                       | -0.284   | 0.392    | -0.082   | -0.036   |
| P. weberbaueri presence       | -0.302   | 0.601    | -0.033   | -0.103   |
| Elevation m                   | -0.848   | 0.473    | 0.095    | 0.173    |
Figure 1

Occupancy estimates $\psi$ for *P. sericea* and *P. weberbaueri* along an elevational gradient.

Fine lines represent the 95% CI.
Figure 2

Ordination plot of 19 habitat variables across an elevational gradient of *Polylepis* woodlands along the first two canonical axes from the CANOCO analysis.
Figure 3

Ordination of 50 bird species points within 19 environmental variables upper case for the first two canonical factors from the CCA x and y axes.

For cluster descriptions: see text. Bird species of conservation concern are in bold type.

Agcu: *Aglaeactis cupripennis*; Analp: **Anairetes alpinus**; Anni: *Anairetes nigrocristatus*; Anre: *Anairetes reguloides*; Asfl: *Asthenes flamulata*; Ashu: *Asthenes humilis*; Atru: **Atlapetes rufigenis**; Cain: *Catamenia inornata*; Chol: *Chalcostigma olivaceum*; Chst: *Chalcostigma stanleyii*; Cifu: *Cinclodes fuscus*; Coru: *Colaptes rupicula*; Coco: *Colibri coruscans*; Coci: *Conirostrum cinereum*; Crba: **Cranioleuca baroni**; Dibr: *Diglossa bruneiventris*; Gran: *Grallaria andicolus*; Lepi: *Leptasthenura pileata*; Leya: *Leptasthenura yanacensis*; Levi: *Lesbia victoridae*; Mele: *Mecocerculus leucophrys*; Meph: **Metallura phoebe**; Mety: *Metallura tyriantina*; Muci: *Muxisacsicola cinerea*; Myni: *Myiothlypis nigrocristatus*; Myst: *Myioteretes striaticollis*; Ocle: *Octhoeca leucophrys*; Ocoe: *Octhoeca oenantoides*; Ocru: *Octhoeca rufipectoralis*; Ormu: *Orochelidon murina*; Orfr: **Oreomanes fraseri**; Ores: *Oreotrochilus stella*; Pafa: *Patagioenas faciata*; Pagi: *Patagonas gigas*; Phme: *Phalcoboenus melanopterus*; Phpl: *Phrygilus plebejus*; Phpu: *Phrygilus punensis*; Phun: *Phrygilus unicolor*; Poru: *Polioxolmis rufipennis*; Poal: **Poospiza alticola**; Saau: *Saltator aurantirostris*; Scaf: **Scytalopus affinis**; Spcr: *Spinus crassirostris*; Spma: *Spinus magellanicus*; Trae: *Troglodites aedon*; Tuch: *Turdus chiguano*; Tufu: *Turdus fuscater*; Geje: *Geocerthia jelski*; Gese: **Geocerthia serrana**; Xepa: *Xenodacnis parina*; Zast: **Zaratornis stresemanni**
