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Abundance and patterns of rarity of *Polylepis* birds in the Cordillera Vilcanota, southern Perú: implications for habitat management strategies

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Summary

Point count distance sampling surveys were conducted at three sites in the Cordillera Vilcanota to determine whether variation in high-Andean species richness, diversity and abundance was a reflection of *Polylepis* habitat quantity. Bird community and abundance measures revealed that there was considerably variation in bird species richness, diversity and mean encounter rates between large, medium, and small forest patches. Densities of *Polylepis*-dependent bird species (including five globally-threatened and eight restricted-range species) were greater in larger forest patches and differed significantly between different patch size categories. Density estimates for matrix-dependent species were higher in smaller *Polylepis* patches indicating that the matrix exerts an influence on bird species composition and abundance in remnant *Polylepis* forests, particularly smaller patches. Comparison of lowland forest habitat specialists using three categories of rarity revealed that between 19–22% of all *Polylepis*-dependent species were intrinsically rare within larger forest patches, and a greater number (34–74%) were rare in smaller forest patches. Population estimates for all species, in particular for all threatened species, were extremely low, numbering $\leqslant$ 10 individuals at nine of the ten sites examined. The results suggest that declines in the densities of certain *Polylepis* birds may be predictable following habitat loss and that these patterns of rarity should govern population recovery goals through appropriate habitat restoration strategies. Such strategies are urgently required and must be designed to prevent further habitat loss, and to increase *Polylepis* habitat quantity to boost threatened bird populations in the Cordillera Vilcanota.

Resumen

Evaluaciones de distancias de puntos de conteo fueron conducidas en tres lugares en la Cordillera Vilcanota para determinar si la variación en la riqueza, diversidad y abundancia de las especies de los Andes altos, era un reflejo de la cantidad de hábitats de *Polylepis*. La comunidad de aves y su abundancia revelaron que hubo una considerable variación en la riqueza de especies, diversidad y la media encontrada en rangos parches de bosque comprendidos entre grandes, medios y pequeños. La densidad de especies de aves dependientes de *Polylepis* (incluyendo cinco amenazados globalmente y ocho especies con rango restringido) fueron mayores en parches grandes de bosque y difirieron significativamente entre diferentes categorías de tamaños de parche. La densidad estimada para especies matriz-dependientes fue mayor en pequeños parches de *Polylepis* indicando que la matriz ejerce una influencia en la composición de especies de aves y abundancia en vestigios de bosques de *Polylepis*, particularmente parches pequeños. En comparación con especialistas de hábitat de bosque bajo, empleando tres categorías de rareza revelaron que entre 19–22% de todos las especies dependientes de *Polylepis* fueron intrínsicamente raras dentro de parches grandes de bosque, y un número mayor (34–74%)

fueron raras en los parches pequeños de bosque. La población estimada para todas las especies, en particular para todas las especies amenazadas, fue extremadamente baja, contando $\leqslant$ 10 individuos en nueve de los 10 sitios examinados. El resultado sugiere que la disminución en la densidad de ciertas aves de *Polylepis* se podría predecir después de la pérdida de hábitat y que esos patrones de rareza podrían servir como objetivos para la recuperación de la población a través de estrategias de restauración de hábitats apropiados. Este tipo de estrategias son requeridas con urgencia y deberían estar diseñadas para prevenir futuras pérdidas de hábitats, incrementar la cantidad de hábitat de *Polylepis* para aumentar la población de aves amenazadas en la Cordillera Vilcanota.

Introduction

The number and type of bird species that inhabit isolated forest patches is largely dependent on the area of the patch (Ambuel and Temple 1983, Blake and Karr 1987). Forest patches are often surrounded by an 'inhospitable' matrix of disturbed habitat e.g. agricultural land, with significantly different habitat structure, floral and faunal composition (e.g. Stouffer and Bierregaard 1995, Gascon *et al.* 1999, Driscoll 2005). This concept is central to many conservation strategies (Diamond 1975, Fischer *et al.* 2005) because forest-dependent species are often restricted to only the largest remnant forest patches (Blake and Karr 1984, 1987). This is often a result of the smaller forest patches being dominated by ecological generalists that are able to forage in the surrounding matrix habitat (Ambuel and Temple 1983, Laurance 1994, Antongiovanni and Metzger 2005).

Many threatened Neotropical forest-dependent bird species are habitat specialists with narrow geographical distributions (BirdLife International 2004). Conservation of these forest habitat specialists may best be approached by identifying and conserving key areas of forest habitat, in conjunction with the strategy of conserving the largest forest areas (Kratter 1995). High-Andean *Polylepis* forests are one of the most threatened forest habitats in Latin America (Fjeldså and Kessler 1996, Stotz *et al.* 1996, Kessler 2002). As a consequence of ongoing habitat loss and degradation (e.g. Lægaard 1992, Renison *et al.* 2004, Teich *et al.* 2005) many of the constituent habitat specialist bird species are restricted to remnant forest patches surrounded by a matrix of either disturbed puna (non-forest) habitat above 3,800 m elevation, or evergreen shrubs and other woody plant species (depending on the level of burning) below this elevation. Furthermore, many of these bird species are presumed to have extremely small populations in the tiny forest patches that remain (Fjeldså 1988, 1993, 2002). In the Cordillera Vilcanota, southern Perú, six globally-threatened high-Andean bird species, and seven other restricted-range species, are dependent to a degree, on *Polylepis* woodland and intolerant of the surrounding puna matrix habitat (Lloyd and Marsden *in press*). For these threatened species intolerant of the matrix habitat, the maintenance of viable populations inside remaining forest patches is the only realistic conservation option. An important consideration is therefore whether these bird species occur in reasonable numbers in forest patches of different sizes.

Density is one of the most important operational terms in ecology (Peters 1991) and is often used to express both the distribution and abundance of species within an ecological community or landscape, and for habitat management recommendations (Smallwood 2001). Density estimates can provide a strong foundation for the conservation of *Polylepis* forest bird species in Peru, particularly as the current IUCN criteria for ranking the degree of threat to any bird species are highly quantitative (BirdLife International 2004, Lloyd 2004; 2007). Reliable density estimates could allow conservation biologists to make a number of predictions regarding the numbers of birds in unsurveyed highly fragmented areas (Buckland *et al.* 1993, Jones *et al.* 1995, Marsden 1999). Furthermore, determining whether or not *Polylepis* birds are intrinsically low-density species in different patch size categories links habitat restoration efforts in areas where *Polylepis* habitat once existed, to meaningful quantitative ecological units (numbers of individuals per unit area of habitat) that are critical for setting realistic population recovery goals and maintaining viable populations (e.g. Tear *et al.* 1995, Rivera-Milan *et al.* 2003).

The objective of this paper is to examine *Polylepis* bird species richness, diversity, and densities in different forest patch size categories and ask whether variation in these factors is a reflection of habitat quantity. Are *Polylepis* bird species intrinsically rare species? Do patterns of rarity within the *Polylepis* bird community have significant implications for high Andean habitat management strategies?

Methods

Study sites

Polylepis bird communities were surveyed in three valleys in the Cordillera Vilcanota mountain range, Dept. of Cusco, southern Perú (Fig 1). Mantanay (13°12′S, 72°09′W) is one of the largest areas of *Polylepis racemosa* woodland in the Cordillera Vilcanota, located at *c.* 3,400–4,500 m elevation, above the village of Yanahuara. The site was surveyed during 67 field days in July 2003, October 2004, and September 2005. Yanacocha (13°17′S, 72°02′W) is another area of *P. racemosa* woodland, located at *c.* 3,700–4,500 m elevation, above the village of Huaocari, and was surveyed for 28 days in October 2003 and June 2004. Laguna Queuñacocha (13°12′S, 72°10′W) is a small area of *P. pepei* woodland, located at *c.* 4,200–4,500 m elevation above the village of Huilloc (hereafter referred to as Huilloc), and was surveyed during 22 field days in December 2003 and July 2004.

Habitat measurements

Polylepis forest patches were assigned to one of three size categories: small (0.1 – 0.8 ha), medium (4.5–9.0 ha), and large (12.0–31.5 ha) patches. I consider whole patches as potentially containing both forest-interior and forest-edge habitat because of the size and shape of the forest patches. Deforestation throughout the Cordillera Vilcanota has not followed a regular pattern mainly because of the topographical complexity of the region, with only a few high Andean areas still having patches of mature *Polylepis* forest (closed canopy, large trees etc). Some areas

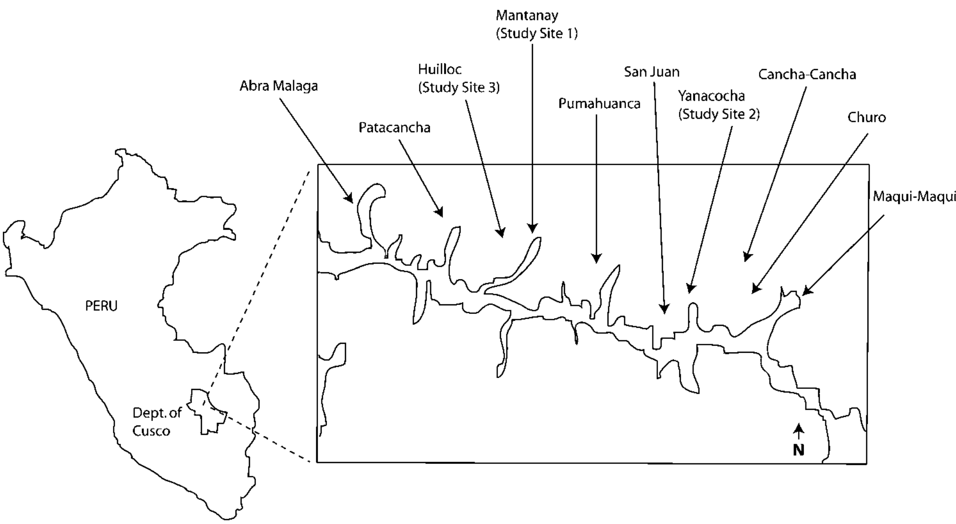

Figure 1. Map showing location of ten areas of *Polylepis* woodland (including three study sites) situated in the Urubamba valley, Cordillera Vilcanota.

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in the Cordillera Vilcanota have been cut more extensively than others and the amount of regeneration may be very variable. Consequently, most of the forest patches are irregular in shape and habitat quality. Data on estimated forest cover for ten sites in the Cordillera Vilcanota (Fig 1), including the three study sites, refer to land surface cover in Aucca *et al.* (2001) and are shown in Table 4.

Bird surveys

Birds were surveyed at plots within *Polylepis* using a variable circular plot method (Reynolds *et al.* 1980) adapted by Jones *et al.* (1995). This distance sampling method allows for differences in detectability between different species, and within a species between different habitats (Buckland *et al.* 1993, 2001). The method also allows for some unidentified bird contacts, so long as all bird contacts encountered at, and very close to, the recorder are identified (Buckland *et al.* 1993, 2001). Bird surveys were conducted between 05h30 and 16h30 and only during hours of suitable weather (i.e. in the absence of snow, rain or strong wind). Between June–September in the Cordillera Vilcanota, bird vocal activity begins around 06h30 and around 05h30 between October and December and there is no conspicuous peak in high-Andean bird vocal activity at either the pre-dawn or dawn period (pers. obs.) as observed in the Amazonian lowlands (e.g. Terborgh *et al.* 1990, Lloyd 2004).

I was the only recorder for all bird surveys; with over two years experience of surveying birds using similar methods in Perú, and over four years of experience in high Andean landscapes as a naturalist and bird tour leader, I was familiar with the vocalizations of all of the region's bird species. Following arrival at each plot, I sat quietly for a five minute 'settling down' period (Bibby *et al.* 2000) before spending twenty minutes recording all bird contacts. Each contact was assigned to one of three categories; seen; heard; or seen and heard, and species and the number of individuals in each group recorded. I then estimated horizontal distance from the centre of the census plot to each contact. Two repeats of each transect were made at each site making a total of 266 point counts. The direction of the surveys along transects was rotated to counter the bias of bird activity and the time of day.

Data analysis

Bird species richness and diversity

Bird species richness and diversity were calculated using rarefaction analysis (Simberloff 1972). Rarefaction estimates the number of species from a given sample of point transects based on multiple random sampling (James and Rathburn 1981) and was implemented using EstimateS v.7.5 (Colwell 2005). Sample order was randomised 50 times for each dataset (Lee 2005). Sample species richness was estimated from the sample-based rarefaction curves (Mau Tau; S_{obs}). The bootstrap estimator (S_{boot}: Smith and van Belle 1984, Colwell and Coddington 1994) a widely used and easily understood robust estimator (Borgella and Gavin 2005, Lee 2005) was used as a measure of estimated species richness. Bird species diversity was measured using the Shannon-Wiener index (H'), which takes into account both species richness and the relative abundance of each species (Magurran 2004, Lee 2005).

Density estimates

Distance data were analyzed using the program DISTANCE v. 4.1 (Thomas *et al.* 2004). Only bird species with $\geqslant$ 20 records were considered for the calculation of density estimates, with the majority of species fulfilling the minimum of 40 records required to estimate densities (Buckland *et al.* 1993). Four key functions (uniform, half-normal hazard rate and negative exponential all with cosine series adjustment) were considered for each analysis. Key function selection was evaluated using Akaike's Information Criteria (AIC) and a chi-square statistic was used to assess the 'goodness of fit' of each function (Buckland *et al.* 1993). Calculation of % CV was done empirically (e.g. Lloyd 2000, 2004). Repeated point transects increased species sample sizes, providing a more precise estimate of variance and increasing the reliability of the detection function (Buckland *et al.* 2001, Lee 2005). Distance data were pooled across all sites and patch size categories to produce a single species-specific detection function from which species-specific density estimates were calculated in each forest patch size category (Marsden 1999, Marsden *et al.* 2001). Pooling records generated a more precise modelling of detectability because the combined AIC values of the separate patch size detection functions were greater than the AIC value for the pooled detection function (Buckland *et al.* 2001). The shape criteria were examined for heaping or cluster bias and any outliers were right-hand truncated where necessary (Buckland *et al.* 1993). Determination of actual values for truncation and subsequent grouping of records into distance bands followed visual inspection of detection histograms and checking of % SE for density estimates under different analysis conditions (Buckland *et al.* 2001). Encounter rates (number of individuals per point) as an estimate of relative abundance, were calculated for species that did not fulfil the minimum sample size criterion (Lee 2005).

Population estimates

Forest area data from all the locations were used together with the combined species density estimates to calculate total population estimates, where possible, for each species, using the formula: total population estimate = density estimate x area (Marsden *et al.* 2005). Minimum and maximum population sizes were based on the lower- and upper confidence intervals obtained from the density estimates (Jacobs and Walker 1999).

Results

Bird species richness and diversity

Both measures of species richness (S_{obs}) and the Shannon-Wiener index (*H′*) were fairly similar across all three forest patch size categories (Table 2). Identical numbers of globally-threatened and restricted-range species were recorded in large and medium patches at Mantanay and Yanacocha, and large patches at Huilloc but fewer species in both categories were recorded in medium and small patches at Huilloc. Species richness (S_{obs} and S_{boot}) was greater in large and small forest patches at Mantanay and greater in medium forest patches at Yanacocha. The Shannon-Wiener index of species diversity (*H′*) was greater in large patches at Mantanay and Huilloc, and in medium forest patches at Yanacocha. Fewer threatened and restricted-range species were recorded in medium and small patches at Huilloc.

Encounter rates and density estimates

Generally, the mean encounter rate was higher in large patches, than in medium or small patches (Table 2). Mean encounter rate of birds in large and small forest patches across all three sites was highest at Huilloc, and higher in medium forest patches at Yanacocha.

When sample sizes were pooled across all three sites and all three forest patch size categories, I was able to calculate total *Polylepis* density estimate for all 36 species (Table 3). Most species (22) had density estimates < 10 individuals km^{-2}; eight species had density estimates ranging between 10–20 individuals km^{-2}; five species had density estimates > 20 individuals km^{-2}; and only one species had a density estimate > 30 individuals km^{-2}. The most abundant species was *A. castelnaudii*, and the rarest was *O. oenanthoides*. The most abundant globally threatened species was *L. xenothorax*, and the rarest *C. aricomae*.

There was a significant difference in the density of all bird species between each patch size category (mean density estimate large patch = 7.0 ± 6.6; medium = 5.2 ± 6.2; small = $4.5 \pm$

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9.2 Kruskal-Wallis test; $\chi^2_2 = 10.8$, $P < 0.01$). *A. castelnaudii* (restricted-range) was the most abundant species in both large and medium forest patches and *G. andicola* (restricted-range) was the rarest in both large and small patches. In small forest patches the most abundant species was *P. unicolor* (matrix-dependent) and the rarest in medium patches was *C. aricomae* (*Polylepis*-dependent and globally-threatened). Generally, threatened and restricted-range species were more abundant in large forest patches than in medium or small forest patches, except for *A. castelnaudii* and *G. andicola* which were more abundant in medium patches.

Estimates of population sizes

Population estimates for all species at the ten locations are shown in Table 4. Estimates were higher in areas with greater forest cover (e.g. Mantanay) and smaller in areas with the least

Table 1. Bird species recorded during point count distance sampling surveys at three *Polylepis* sites in the Cordillera Vilcanota. Conservation status * follows BirdLife International (2004). Patterns of habitat occupancy † from Lloyd (2007) and refer to the three study sites.

Species	**Status ***	**Habitat Occupancy †**
Aglaeactis castelnaudii	Restricted-range	*Polylepis* forest
Oreotrochilus estella	Not threatened	*Polylepis*-matrix interface
Chalcostigma stanleyi	Not threatened	*Polylepis* forest
Colaptes rupicola	Not threatened	Matrix habitat
Cinclodes aricomae	Critical	*Polylepis* forest
Cinclodes fuscus	Not threatened	*Polylepis*-matrix interface
Leptasthenura yanacensis	Near-threatened	*Polylepis* forest
Leptasthenura xenothorax	Endangered	*Polylepis* forest
Cranioleuca albicapilla	Restricted-range	*Polylepis* forest
Asthenes ottonis	Restricted-range	*Polylepis* forest
Asthenes humilis	Not threatened	Matrix habitat
Asthenes urubambensis	Not threatened	*Polylepis* forest
Asthenes virgata	Restricted-range	*Polylepis*-matrix interface
Grallaria andicola	Restricted-range	*Polylepis* forest
Scytalopus simonsi	Restricted-range	*Polylepis* forest
Mecocerculus leucophrys	Not threatened	*Polylepis* forest
Anairetes alpinus	Endangered	*Polylepis* forest
Anairetes parulus	Not threatened	*Polylepis* forest
Ochthoeca rufipectoralis	Not threatened	*Polylepis* forest
Ochthoeca oenanthoides	Not threatened	*Polylepis*-matrix interface
Troglodytes aedon	Not threatened	*Polylepis* forest
Turdus chiguanco	Not threatened	*Polylepis* forest
Turdus fuscater	Not threatened	*Polylepis* forest
Conirostrum cinereum	Not threatened	*Polylepis* forests
Conirostrum ferrugineiventre	Restricted-range	*Polylepis* forests
Oreomanes fraseri	Near-threatened	*Polylepis* forests
Xenodacnis parina	Restricted-range	*Polylepis* forests
Diglossa brunneiventris	Not threatened	*Polylepis* forests
Zonotrichia capensis	Not threatened	Matrix habitat
Phrygilus punensis	Not threatened	*Polylepis*-matrix interface
Phrygilus unicolor	Not threatened	Matrix habitat
Phrygilus plebejus	Not threatened	Matrix habitat
Idiopsar brachyurus	Not threatened	*Polylepis*-matrix interface
Catamenia inornata	Not threatened	*Polylepis*-matrix interface
Carduelis atrata	Not threatened	*Polylepis*-matrix interface
Carduelis crassirostris	Restricted-range	*Polylepis* forest

Table 2. Bird species richness and diversity of different *Polylepis* forest patch categories in the three valleys in the Cordillera Vilcanota, southern Peru. S_{obs} = sample species richness from sample-based rarefaction curves. S_{boot} = bootstrap estimator. H′ = Shannon-Wiener index of bird diversity (see Data analysis).

	LARGE			**MEDIUM**			**SMALL**		
	Mantanay	**Yanacocha**	**Huilloc**	**Mantanay**	**Yanacocha**	**Huilloc**	**Mantanay**	**Yanacocha**	**Huilloc**
Number of point counts	44	28	28	30	20	6	40	24	26
Mean encounter rate	1.67	1.58	2.03	1.11	1.15	1.08	1.79	1.37	2.15
Species richness (S_{obs})	35 ± 1.66	26 ± 2.07	27 ± 0.67	27 ± 1.32	29 ± 2.62	19 ± 3.37	29 ± 1.83	21 ± 0.89	23 ± 2.13
Species richness (S_{boot})	37 ± 0.61	27 ± 0.57	28 ± 0.48	30 ± 0.97	33 ± 1.21	24 ± 4.36	33 ± 0.99	23 ± 0.49	26 ± 0.99
Species diversity (*H′*)	2.98 ± 0.01	2.76 ± 0.01	2.90 ± 0.03	2.84 ± 0.04	2.93 ± 0.03	2.46 ± 0.06	2.63 ± 0.03	2.77 ± 0.03	2.79 ± 0.04
Number of threatened species (restricted-range)	6 (9)	6 (8)	6 (6)	6 (9)	6 (9)	4 (5)	6 (9)	6 (9)	3 (5)

Table 3. Encounter rates and density estimates ± % CV, with 95% confidence intervals for 36 commonly encountered bird species in different forest patch size categories, at the three sites. Density estimates (DE) are expressed as number of individuals km^{-2} *Polylepis* forest. Encounter rates * expressed as total number of individuals recorded per point count (± SD).

Species	Total *Polylepis* DE ± % CV (95 % CI)	Large patch DE ± % CV (95 % CI)	Medium patch DE ± % CV (95 % CI)	Small patch DE ± % CV (95 % CI)
Aglaeactis castelnaudii	47.8 ± 17.9 (33.6 – 68.0)	23.6 ± 28.0 (12.4 – 45.0)	25.6 ± 30.3 (13.3 – 49.3)	0.20 ± 0.40 *
Oreotrochilus estella	10.8 ± 39.6 (5.0 – 23.5)	0.09 ± 0.29 *	0.04 ± 0.19 *	0.16 ± 0.36 *
Chalcostigma stanleyi	12.3 ± 36.5 (6.0 – 25.1)	6.4 ± 60.5 (2.0 – 21.1)	5.7 ± 45.6 (2.1 – 15.4)	0.08 ± 0.27 *
Colaptes rupicola	8.2 ± 156.8 (0.8 – 84.6)	0.04 ± 0.20 *	0.07 ± 0.26 *	0.19 ± 0.39 *
Cinclodes aricomae	1.0 ± 43.0 (0.4 – 2.1)	2.5 ± 73.7 (0.6 – 10.8)	0.5 ± 40.5 (0.2 – 1.1)	0.01 ± 0.11 *
Cinclodes fuscus	6.3 ± 43.0 (2.8 – 14.2)	2.1 ± 29.5 (1.0 – 4.1)	0.6 ± 43.1 (0.2 – 1.9)	10.9 ± 51.3 (4.1 – 28.8)
Leptasthenura yanacensis	11.9 ± 28.6 (6.8 – 20.8)	11.6 ± 43.3 (4.6 – 29.4)	8.9 ± 45.5 (3.3 – 24.3)	5.1 ± 21.4 (3.0 – 8.5)
Leptasthenura xenothorax	15.9 ± 23.0 (10.2 – 24.9)	25.3 ± 15.1 (18.8 – 34.1)	9.6 ± 21.7 (5.9 – 15.7)	0.07 ± 0.25 *
Cranioleuca albicapilla	13.9 ± 28.4 (8.0 – 24.2)	20.1 ± 55.0 (7.1 – 57.2)	13.1 ± 36.6 (6.4 – 27.1)	0.08 ± 0.27 *
Asthenes ottonis	8.5 ± 62.5 (2.4 – 29.8)	16.3 ± 39.0 (7.7 – 34.4)	5.2 ± 51.2 (1.5 – 17.9)	0
Asthenes humilis	1.7 ± 31.3 (1.3 – 2.4)	0	0.04 ± 0.19 *	2.4 ± 36.8 (1.1 – 4.9)
Asthenes urubambensis	1.4 ± 59.3 (0.4 – 4.3)	0.09 ± 0.29 *	0.07 ± 0.35 *	0.08 ± 0.27 *
Asthenes virgata	3.4 ± 42.0 (1.5 – 7.7)	0.11 ± 0.31 *	0.07 ± 0.26 *	0.07 ± 0.25 *
Grallaria andicola	2.0 ± 40.8 (0.9 – 4.4)	1.3 ± 25.8 (0.5 – 3.9)	3.3 ± 70.7 (0.8 – 12.8)	1.2 ± 70.4 (0.3 – 4.8)
Scytalopus simonsi	3.9 ± 35.4 (2.0 – 7.9)	6.1 ± 30.2 (3.2 – 11.4)	2.2 ± 40.6 (0.9 – 5.1)	0.07 ± 0.25 *
Mecocerculus leucophrys	8.6 ± 41.3 (3.8 – 19.3)	11.8 ± 43.8 (4.9 – 28.3)	1.0 ± 57.7 (0.2 – 5.5)	0
Anairetes alpinus	4.9 ± 31.7 (2.6 – 9.2)	4.3 ± 41.8 (1.8 – 10.1)	2.6 ± 48.2 (0.9 – 7.4)	0.04 ± 0.21 *
Anairetes parulus	14.8 ± 24.2 (9.2 – 24.0)	13.8 ± 31.6 (7.1 – 26.6)	6.6 ± 64.1 (1.1 – 41.3)	0.06 ± 0.23 *
Ochthoeca rufipectoralis	11.1 ± 21.9 (7.2 – 17.1)	5.1 ± 21.0 (3.3 – 8.0)	5.3 ± 36.2 (2.5 – 11.2)	0.07 ± 0.25 *
Ochthoeca oenanthoides	0.5 ± 38.0 (0.2 – 1.0)	0.14 ± 0.35 *	0.23 ± 0.43 *	0.08 ± 0.27 *
Troglodytes aedon	5.3 ± 19.0 (3.6 – 7.7)	8.1 ± 22.4 (5.2 – 12.9)	3.0 ± 19.8 (1.9 – 4.5)	2.4 ± 24.6 (1.5 – 3.9)
Turdus chiguanco	1.0 ± 47.1 (0.4 – 2.2)	0.5 ± 73.4 (0.1 – 1.9)	2.3 ± 53.1 (0.7 – 7.8)	0.01 ± 0.11 *
Turdus fuscater	1.9 ± 48.6 (0.7 – 5.1)	3.7 ± 34.4 (1.9 – 7.2)	1.5 ± 31.2 (0.8 – 2.8)	0.01 ± 0.11 *
Conirostrum cinereum	28.3 ± 38.8 (14.8 – 54.2)	15.1 ± 45.6 (5.1 – 45.1)	8.4 ± 30.8 (4.5 – 15.6)	13.4 ± 50.5 (4.7 – 38.0)
Conirostrum ferrugineiventre	14.1 ± 30.5 (7.5 – 26.4)	14.9 ± 32.5 (7.5 – 29.4)	8.5 ± 27.0 (4.8 – 15.1)	0
Oreomanes fraseri	16.6 ± 13.6 (12.2 – 22.5)	22.1 ± 14.8 (16.5 – 29.6)	12.9 ± 30.0 (6.7 – 24.9)	5.5 ± 22.5 (3.5 – 8.6)
Xenodacnis parina	17.9 ± 41.1 (7.2 – 44.5)	23.5 ± 24.6 (14.4 – 38.6)	10.5 ± 52.6 (2.4 – 46.5)	0.19 ± 0.39 *
Diglossa brunneiventris	3.3 ± 36.8 (1.6 – 6.8)	3.9 ± 61.1 (1.0 – 15.2)	1.0 ± 48.4 (0.1 – 4.6)	0.04 ± 0.21 *
Zonotrichia capensis	9.6 ± 31.1 (5.2 – 17.7)	4.3 ± 49.9 (1.5 – 11.9)	19.9 ± 37.8 (9.1 – 43.7)	6.3 ± 34.6 (3.1 – 12.8)

Table 3. Continued.

Species	**Total *Polylepis* DE ± % CV (95 % CI)**	**Large patch DE ± % CV (95 % CI)**	**Medium patch DE ± % CV (95 % CI)**	**Small patch DE ± % CV (95 % CI)**
Phrygilus punensis	5.9 ± 19.4 (4.0 – 8.7)	5.3 ± 27.0 (2.9 – 9.5)	15.3 ± 65.6 (3.0 – 79.2)	11.3 ± 45.7 (4.4 – 28.9)
Phrygilus unicolor	21.3 ± 33.4 (11.1 – 41.2)	5.4 ± 52.2 (1.9 – 15.7)	0.02 ± 0.13 *	41.3 ± 25.2 (25.1 – 68.1)
Phrygilus plebejus	8.7 ± 50.0 (3.1 – 24.3)	6.8 ± 91.0 (0.4 – 122.0)	0	16.8 ± 46.6 (6.1 – 45.9)
Idiopsar brachyurus	4.5 ± 75.6 (1.0 – 19.1)	0.01 ± 0.10 *	0.07 ± 0.26 *	0.19 ± 0.39 *
Catamenia inornata	4.3 ± 21.3 (2.8 – 6.5)	3.9 ± 25.1 (2.3 – 6.5)	2.2 ± 58.8 (0.0 – 239.2)	13.7 ± 65.3 (3.5 – 52.6)
Carduelis atrata	8.8 ± 24.3 (5.4 – 14.6)	5.4 ± 46.8 (1.8 – 16.4)	1.5 ± 42.2 (0.5 – 4.1)	31.4 ± 45.8 (12.6 – 78.3)
Carduelis crassirostris	9.9 ± 22.9 (6.2 – 15.7)	11.4 ± 39.7 (5.0 – 25.8)	9.1 ± 33.3 (4.4 – 18.7)	0.04 ± 0.21 *

Table 4. Population estimates of 36 species of *Polylepis* birds in ten locations in the Cordillera Vilcanota. Estimates of forest cover from Aucca *et al.* (2001). Figures in parentheses represent minimum and maximum population sizes based on confidence intervals calculated for density estimates by DISTANCE. NR = not recorded.

Species	**Abra Malaga 0.13 km²**	**Patacancha 0.07 km²**	**Huilloc 0.09 km²**	**Mantanay 1.71 km²**	**Pumahuanca 0.39 km²**	**San Juan 0.13 km²**	**Yanacocha 0.13 km²**	**Cancha-Cancha 0.27 km²**	**Churo 0.03 km²**	**Maqui-Maqui 0.08 km²**
Aglaeactis castelnaudii	6 (5 – 9)	3 (2 – 5)	4 (3 – 6)	82 (57 – 116)	19 (13 – 27)	6 (4 – 9)	6 (5 – 9)	13 (9 – 18)	1 (1 – 2)	4 (3 – 5)
Oreotrochilus estella	1 (1 – 3)	1 (0 – 2)	1 (1 – 2)	18 (9 – 40)	NR	NR	1 (1 – 3)	NR	0 (0 – 1)	1 (0 – 2)
Chalcostigma stanleyi	2 (1 – 3)	NR	1 (1 – 2)	21 (10 – 43)	5 (2 – 10)	NR	2 (1 – 3)	3 (2 – 7)	0 (0 – 1)	1 (1 – 2)
Colaptes rupicola	1 (0 – 11)	1 (0 – 6)	1 (0 – 8)	14 (1 – 144)	3 (0 – 33)	1 (0 – 11)	1 (0 – 11)	2 (2– 3)	0 (0– 2)	1 (0– 7)
Cinclodes aricomae	0 (0 – 0)	NR	0 (0 – 0)	2 (1 – 4)	0 (0 – 1)	NR	0 (0 – 0)	0 (0 – 1)	0 (0 – 0)	0 (0 – 0)
Cinclodes fuscus	1 (0 – 2)	0 (0 – 1)	1 (0 – 1)	11 (5 – 24)	3 (1 – 6)	1 (0 – 2)	1 (0 – 2)	2 (1 – 4)	0 (0 – 0)	1 (0 – 1)
Leptasthenura yanacensis	2 (1 – 3)	1 (1 – 1)	1 (1 – 2)	20 (12 – 36)	5 (3 – 8)	NR	2 (1 – 3)	3 (2 – 6)	0 (0 – 1)	1 (1 – 2)
Leptasthenura xenothorax	3 (3 – 5)	2 (1 – 2)	2 (2 – 3)	43 (32 – 58)	10 (7 – 13)	NR	3 (3 – 5)	7 (5 – 9)	1 (1 – 1)	2 (2 – 3)
Cranioleuca albicapilla	NR	NR	1 (1 – 2)	24 (14 – 41)	5 (3 – 9)	2 (1 – 3)	2 (1 – 3)	4 (2 – 7)	0 (0 – 1)	1 (1 – 2)
Asthenes ottonis	2 (1 – 5)	1 (1 – 2)	2 (1 – 3)	28 (13 – 59)	6 (3 – 13)	2 (1 – 4)	2 (1 – 5)	4 (2 – 9)	0 (0 – 1)	1 (1 – 3)
Asthenes humilis	0 (0 – 0)	0 (0 – 0)	0 (0 – 0)	3 (2 – 4)	NR	NR	0 (0 – 0)	NR	NR	NR
Asthenes urubambensis	0 (0 – 1)	NR	0 (0 – 0)	2 (1 – 7)	1 (0 – 2)	0 (0 – 1)	0 (0 – 1)	0 (0 – 1)	0 (0 – 0)	0 (0 – 0)
Asthenes virgata	1 (0 – 1)	0 (0 – 1)	0 (0 – 1)	6 (3 – 13)	NR	0 (0 – 1)	1 (0 – 1)	NR	NR	0 (0 – 1)
Grallaria andicola	0 (0 – 1)	0 (0 – 0)	0 (0 – 0)	3 (2 – 8)	1 (0 – 2)	1 (0 – 1)	0 (0 – 1)	1 (0 – 1)	0 (0 – 0)	0 (0 – 0)
Scytalopus simonsi	1 (0 – 2)	1 (0 – 1)	1 (0 – 1)	10 (6 – 19)	2 (1 – 5)	NR	1 (0 – 2)	2 (1 – 3)	0 (0 – 0)	1 (0 – 1)
Mecocerculus leucophrys	NR	NR	1 (0 – 2)	15 (7 – 33)	3 (2 – 8)	NR	1 (1 – 3)	2 (1 – 5)	0 (0 – 1)	NR
Anairetes alpinus	1 (0 – 1)	NR	1 (0 – 1)	8 (4 – 16)	2 (1 – 4)	NR	1 (0 – 1)	1 (1 – 3)	0 (0 – 0)	0 (0 – 1)
Anairetes parulus	2 (1 – 3)	1 (1 – 2)	1 (1 – 2)	25 (16 – 41)	6 (4 – 9)	2 (1 – 3)	2 (1 – 3)	4 (3 – 6)	0 (0 – 1)	NR
Ochthoeca rufipectoralis	2 (1 – 2)	2 (1 – 1)	1 (1 – 2)	19 (12 – 29)	4 (3 – 7)	1 (1 – 2)	2 (1 – 2)	3 (2 – 5)	0 (0 – 1)	1 (1 – 1)
Ochthoeca oenanthoides	0 (0 – 0)	NR	0 (0 – 0)	1 (0 – 2)	0 (0 – 0)	0 (0 – 0)	0 (0 – 0)	0 (0 – 0)	0 (0 – 0)	NR

Table 4. Continued.

Species	Abra Malaga 0.13 km²	Patacancha 0.07 km²	Huilloc 0.09 km²	Mantanay 1.71 km²	Pumahuanca 0.39 km²	San Juan 0.13 km²	Yanacocha 0.13 km²	Cancha-Cancha 0.27 km²	Churo 0.03 km²	Maqui-Maqui 0.08 km²
Troglodytes aedon	1 (1 – 1)	0 (0 – 1)	1 (0 – 1)	9 (6 – 13)	2 (1 – 3)	1 (1 – 1)	1 (1 – 1)	1 (1 – 2)	0 (0 – 0)	0 (0 – 1)
Turdus chiguanco	0 (0 – 0)	0 (0 – 0)	0 (0 – 0)	2 (1 – 4)	0 (0 – 1)	0 (0 – 0)	0 (0 – 0)	0 (0 – 1)	0 (0 – 0)	0 (0 – 0)
Turdus fuscater	NR	0 (0 – 1)	0 (0 – 1)	6 (3 – 12)	1 (1 – 3)	1 (0 – 1)	1 (0 – 1)	1 (1 – 2)	0 (0 – 0)	0 (0 – 1)
Conirostrum cinereum	4 (2 – 7)	2 (1 – 4)	3 (1 – 5)	48 (25 – 93)	11 (6 – 21)	NR	4 (2 – 7)	8 (4 – 15)	1 (0 – 2)	2 (1 – 4)
Conirostrum ferrugineiventre	2 (1 – 4)	1 (1 – 2)	1 (1 – 2)	24 (13 – 45)	6 (3 – 10)	NR	2 (1 – 4)	4 (2 – 7)	0 (0 – 1)	1 (1 – 2)
Oreomanes fraseri	3 (2 – 4)	2 (1 – 2)	2 (2 – 3)	38 (28 – 51)	9 (6 – 12)	NR	3 (2 – 4)	6 (4 – 8)	1 (0 – 1)	2 (1 – 2)
Xenodacnis parina	3 (2 – 5)	NR	2 (1 – 4)	40 (25 – 66)	9 (6 – 15)	3 (2 – 5)	3 (2 – 5)	6 (4 – 10)	1 (0 – 1)	2 (1 – 3)
Diglossa brunneiventris	0 (0 – 1)	NR	0 (0 – 1)	6 (3 – 12)	1 (1 – 3)	NR	0 (0 – 1)	1 (0 – 2)	0 (0 – 0)	0(0 – 1)
Zonotrichia capensis	1 (1 – 2)	1 (0 – 1)	1 (1 – 2)	16 (9 – 30)	4 (2 – 7)	1 (1 – 2)	1 (1 – 2)	3 (1 – 5)	0 (0 – 1)	1 (0 – 1)
Phrygilus punensis	1 (1 – 1)	0 (0 – 1)	1 (0 – 1)	10 (7 – 15)	2 (2 – 3)	NR	1 (1 – 1)	2 (1 – 2)	0 (0 – 0)	1 (0 – 1)
Phrygilus unicolor	3 (2 – 6)	1 (1 – 3)	2 (1 – 4)	36 (19 – 70)	8 (4 – 16)	3 (1 – 5)	3 (2 – 6)	6 (3 – 11)	1 (0 – 1)	2 (1 – 3)
Phrygilus plebejus	1 (0 – 3)	1 (0 – 2)	1 (0 – 2)	15 (5 – 42)	3 (1 – 10)	1 (0 – 3)	1 (0 – 3)	2 (1 – 7)	0 (0 – 1)	1 (0 – 2)
Idiopsar brachyurus	NR	NR	0 (0 – 2)	8 (2 – 33)	NR	NR	1 (0 – 3)	1 (1 – 5)	NR	NR
Catamenia inornata	1 (0 – 1)	0 (0 – 0)	0 (0 – 1)	7 (5 – 11)	2 (1 – 3)	1 (0 – 1)	1 (0 – 1)	1 (1 – 2)	0 (0 – 0)	0 (0 – 1)
Carduelis atrata	1 (1 – 2)	1 (0 – 1)	1 (1 – 1)	15 (9 – 25)	3 (2 – 6)	1 (1 – 2)	1 (1 – 2)	2 (1 – 4)	0 (0 – 0)	1 (0 – 1)
Carduelis crassirostris	1 (1 – 2)	1 (0 – 1)	1 (1 – 1)	17 (11 – 27)	4 (2 – 6)	NR	1 (1 – 2)	3 (2 – 4)	0 (0 – 0)	1 (1 – 2)

forest cover (e.g. Churo). All population estimates were extremely low, even in the areas with the greatest forest cover. No species had a population estimate greater than 82 individuals (*A. castelnaudii* at Mantanay). Of the six globally-threatened species, population estimates did not exceed 43 individuals (*L. xenothorax* at Mantanay).

Discussion

My results confirm what has become a general pattern for forest-dependent bird communities in fragmented landscapes: higher species richness and diversity in larger forest patches, and low densities of individual species. Densities of *Polylepis* bird species were greater in larger forest patches and differed significantly between different patch size categories. Similar declines in bird density with decreasing forest patch size following habitat fragmentation have been recorded in a number of studies (e.g. Willis 1979, Laurance 1991, Newmark 1991, Radford and Bennett 2004) with low density species being at greater risk (Stouffer and Bierregaard 1995, Stratford and Stouffer 1999). Applying the same criteria to the *Polylepis* bird communities of the Cordillera Vilcanota suggests that the species most at risk from future habitat loss are *C. aricomae*, *A. urubambensis*, *A. alpinus*, *G. andicola* and *S. simonsi* (Table 3).

Density estimates for the majority of matrix-dependent species were higher in smaller *Polylepis* patches (Table 3). This is an important finding, indicating that the matrix exerts a significant influence on bird species composition and abundance in *Polylepis* forests, particularly smaller patches. Matrix habitat is often the most extensive and connected element in fragmented forest landscapes (Forman 1997) and forest patches must be examined as part of a wider, dynamic landscape (Lindenmayer *et al.* 2002, Wethered and Lawes 2003). Matrix habitat management will therefore be an integral component of optimizing *Polylepis* conservation efforts in the Cordillera Vilcanota.

I was unable to calculate density estimates for both *A. urubambensis* and *A. virgata* in any of the three forest patch size categories due to insufficient sample sizes. *A. urubambensis* has often been considered as being 'common' at a number of *Polylepis* forest sites, particularly at the northern end of the Cordillera Vilcanota where the species shows a distinctive preference for bushy *P. pepei* or *P. sericea* forests on cloud-enshrouded ridges (Walker and Fjeldså 2005, Fjeldså pers. comm). Some authors have commented that populations of *A. urubambensis* are almost certainly declining due to ongoing loss of *Polylepis* and elfin forest habitats (e.g. Stotz *et al.* 1996, Birdlife International 2004, Remsen 2003) but the species can be often overlooked due to its skulking behaviour (Fjeldså pers. comm). The paucity of records for *A. urubambensis* during the survey probably reflects the genuine rarity of the species at the three study sites. This rarity and that similar numbers of the forest-matrix interface species *A. virgata* were also recorded in all forest patch size categories merit investigation.

There are limitations to this study, mainly how representative are these results of other high Andean regions, and accounting for potential sources of bias in the census methodology. Individual bird species have specific habitat requirements and I acknowledge that there may be considerable variation in densities and population estimates of individual species related to habitat quality and climate (e.g. humidity) in different high Andean areas. Consequently, densities and population estimates of some of the globally threatened species may be higher in other *Polylepis* areas.

One potential sources of bias in the census methodology is whether all individuals for all species were detected efficiently, particularly skulking species (e.g. *S. simonsi*) that may have moved from the census plots during the five minute settling period. Failure to record these species would violate one of the main assumptions of Distance Sampling (see Buckland *et al.* 1993). Another potential source of bias concerns whether the higher density estimates for the majority of matrix-dependent species in smaller *Polylepis* patches than in either large or medium patches, is simply an artefact of habitat quality i.e. is it possible that the methodology performed better in smaller forest patches because they are more open, with less dense vegetation cover, due to greater logging activity. Individual birds foraging across small forest patches are generally more mobile and this could result in higher encounter rates in small patches rather than in large or medium patches. Further analysis of settling down periods, length of counts, and influence of habitat quality on encounter rates are required to explore these possibilities.

Patterns of rarity and implications for conservation

The density estimates for *Polylepis* birds are fairly low, and are lower still in small forest patches, but are *Polylepis* bird species intrinsically low density species? There are no quantitative population surveys of other Andean habitat specialists with which to compare the *Polylepis* density estimates. Further insight may therefore be provided by comparing these densities with those of lowland habitat specialists. Kratter (1995) used spot-mapping to estimate densities of insectivorous birds restricted to patches of *Guadua* bamboo in three different lowland forest habitats. In order to create a classification compatible with Kratter's spot-mapping study, I have adapted three categories of rarity based on rarity criteria designated by Terborgh *et al.* (1990): (1) resident bird species with measured density estimates of $\leqslant$ 2 individuals but $\geqslant$ 1 individual km^{-2}; (2) resident species with densities too low to estimate ($\leqslant$ 0.5 individual km^{-2}); (3) overall rarity (category 1 + category 2).

A number of conclusions can be made from the analysis in Table 5. In general, patterns of rarity varied within each habitat specialist bird community, and between *Polylepis* and *Guadua* bamboo habitats. Within the *Guadua* bamboo community, the largest number of rare species in both category 1 and 2, were found in river-edge bamboo, than in bluff-top or floodplain bamboo habitat. Overall, the majority of bamboo specialists were not intrinsically rare, with 74–95% of species abundant (high density estimate per unit area of habitat) within this rare and patchy lowland habitat (Kratter 1995).

In the first rarity category, a greater number and percentage of *Polylepis* birds are considered rare in large and medium patches, and in all patch sizes combined, compared with both small *Polylepis* patches, and the three different *Guadua* bamboo habitats. However, this is only a relatively small number and percentage of the *Polylepis* bird community. The most noticeable patterns of rarity within the *Polylepis* community are evident in both the second and third categories. A greater number of *Polylepis* birds are considered category 2 rarities in small forest patches, than bamboo birds in all three lowland bamboo habitats. The category 3 results show

Table 5. correlates of rarity in two Neotropical habitat specialist bird communities. Data are number of species. Figures in parenthesis represent percentage of species' totals. Data on bamboo birds * from Kratter (1995) and converted to individual km^{-2}. Rarity categories adapted from Terborgh *et al.* (1990). Birds classified as dependent, to a degree, on *Polylepis* forests † from (Lloyd 2007).

	CATEGORY 1 Density $\leqslant$ 2 individuals but $\geqslant$ 1 individual km^{-2}.	**CATEGORY 2** Densities too low to estimate ($\leqslant$ 0.5 individual km^{-2})	**OVERALL RARITY**
Bamboo birds (19 species) *			
Bluff-top bamboo	1 (5%)	0	1 (5%)
Floodplain bamboo	0	2 (11%)	2 (11%)
River-edge bamboo	0	5 (26%)	5 (26%)
***Polylepis* birds (27 species) †**			
Combined estimate	5 (19%)	0	5 (19%)
Large patch estimate	3 (11%)	3 (11%)	6 (22%)
Medium patch estimate	5 (19%)	4 (15%)	9 (34%)
Small patch estimate	1 (4%)	19 (70%)	20 (74%)

that, overall, *Polylepis* birds are rarer than lowland *Guadua* bamboo birds. More importantly, it shows that between 19–22% of species are intrinsically rare species within their rare and highly fragmented habitat, and that a greater number of *Polylepis* bird species (between 34–74% of all species) become rarer in smaller forest patches. Declines in the densities of certain *Polylepis* birds may therefore be predictable following habitat loss and these patterns of rarity should govern population recovery goals through appropriate habitat restoration strategies.

Habitat restoration in the Cordillera Vilcanota

Populations of all *Polylepis* birds are extremely low in the remaining forest areas of the Cordillera Vilcanota, and are probably much lower than had been suspected by previous authors (e.g. Fjeldså 1988, 1993, Fjeldså and Kessler 1996). For some bird species, this is certainly not a cause for concern. Many species, e.g. *C. rupicola*, *A. ottonis*, *A. parulus*, *C. cinereum*, *T. fuscater*, *T. chiguanco*, *P. punensis*, and *C. atrata*, are found in a variety of widespread, and less threatened Andean habitats (see Fjeldså and Kessler 1996 and Parker *et al.* 1996). What is of great concern, are the extremely low population estimates for all six globally-threatened species (Table 4). This analysis of abundance and rarity shows that there is no substitute for the quantity of habitat needed to support viable populations of threatened, low-density, *Polylepis* bird species throughout the Cordillera Vilcanota. Habitat restoration strategies designed to prevent further forest habitat loss and increase forest habitat quantity in areas where *Polylepis* forest previously existed are urgently required to boost populations of these threatened species. The Peruvian organisation Asociación Ecosistemas Andinos (ECOAN) is currently pioneering such an approach, and as a result of their efforts, *Polylepis* habitat restoration efforts are currently underway at a small number of locations in the Cordillera Vilcanota.

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