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ORIGINAL PAPER

Bird community variation across *Polylepis* woodland fragments and matrix habitats: implications for biodiversity conservation within a high Andean landscape

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Abstract The scattered and dwindling *Polylepis* woodlands of the high Andean global hotspot have been identified as being of particular importance to biodiversity conservation, and yet little is known of the make-up of their faunal communities, how these vary across landscapes, and how well species might tolerate matrix/edge habitats. We examined the bird communities and vegetation characteristics of *Polylepis* woodlands and the surrounding matrix habitats at three sites in the Cordillera Vilcanota, southern Perú (3,400–4,500 m). The vegetation structure of woodlands varied significantly across the three sites but all were dominated by two *Polylepis* tree species, with mossy ground cover. Matrix habitats were treeless and dominated by ground-level *puna* grass-steppe or boulder scree vegetation. Bird species richness and diversity, encounter rates and the number of globally-threatened and restricted-range bird species were consistently higher in the *Polylepis* forests, than in matrix habitat. We used canonical correspondence analysis (CCA) to identify habitat gradients across the landscape, and to classify bird species according to their association with *Polylepis*, the matrix or *Polylepis*-matrix interface. There were few matrix-restricted bird species, but around half the bird community, including fourteen threatened or restricted-range species, were *Polylepis*-dependant. Many of these species had very narrow niches. The *Polylepis*-matrix interface was dominated by species traditionally considered invasive ecological generalists. Our study illustrates the overriding importance of *Polylepis* interior habitats, indicating that conservation strategies for high Andean birds must focus on patch size maintenance/enlargement, enhancement of within-patch habitat quality, and efforts to safeguard connectivity of suitable habitat across what is essentially an inhospitable *puna*/scree matrix.

Keywords Biodiversity conservation · Bird communities · Forest fragmentation · High Andes · Matrix · *Polylepis* · Threatened species

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Introduction

The Tropical Andes has been described as the richest and most diverse of the world's 34 biodiversity hotspots (Myers 1988; Myers et al. 2000), with around 15,000 endemic plants, and nearly 500 threatened species of amphibian, bird and mammal species (Mittermeier et al. 1998). Anthropogenic impacts have been particularly severe in the hotspot's montane forests (e.g., Cornelius et al. 2000; Watson 2003) and the loss and degradation of *Polylepis*- dominated woodland is of particular international concern because of its limited extent, fragmented distribution, the high levels of endemism amongst its flora and fauna, and the inadequacy of its protection within national reserved areas (Fjeldså 1993, 2002b).

There is little doubt that the present-day localized distribution of *Polylepis* forests in Perú and elsewhere within the hotspot is a direct result of human activity (Ellenberg 1958; Fjeldså and Kessler 1996; Kessler 2002). *Polylepis* woodlands are impacted by humans in several ways (Renison et al. 2006), including firewood collection (Fjeldså 1993), farming practices (Etter and Villa 2000) e.g., fire management (Lægaard 1992; Renison et al. 2002) or browsing by livestock (Teich et al. 2005), and soil degradation (Renison et al. 2004) that combine to prevent *Polylepis* regeneration, and restrict *Polylepis* woodland to localized and highly fragmented habitats (Fjeldså 2002a; Kessler 2002). Additionally, high altitude or treeline woodlands may be sensitive to natural or anthropogenic changes in climatic conditions (e.g., MacDonald et al. 1998), while pressures on high altitude woodlands may be further affected by changes in rural lifestyles and land use (Chepstow-Lusty and Winfield 2000), themselves brought about by climate change (Young and Lipton 2006).

While there is a consensus that the high Andean landscapes are very seriously threatened, we know surprisingly little of their faunal make-up and the ecological sensitivities of individual taxa that inhabit them. Recent work has identified regional differences in plant communities of *Polylepis*-dominated woodlands (Terrazas and Ståhl 2002; Navarro et al. 2005). However, very little has been published on any animal taxon of *Polylepis* woodlands (Yensen and Tarifa 2002). The situation is further complicated since non-*Polylepis* habitats within the high Andes, such as *puna* grass-steppe and boulder scree also hold restricted-range animal species, and although these species tend to be more dispersive and widespread (Stotz et al. 1996; Kessler 2002), contraction of one habitat may have knock-on effects on taxa due to replacement by other habitats.

With such a lack of quantitative data, it is impossible to predict the consequences for important taxa of continued habitat change within the region, to start to address any potential problems associated with global climate change, or indeed even to properly frame the broad agenda for habitat management strategies in the region because we do not know the biodiversity value of each habitat component with the landscape mosaic.

The goal of this paper is to identify habitat-wise patterns of community composition and species occupancy across a high Andean landscape, to help guide strategies for biodiversity conservation in the region. To achieve this goal, we have the following objectives:

1. To compare bird species richness, diversity and abundance across the three sites and between *Polylepis* woodland patches and matrix habitats.
2. To identify bird species which are largely restricted to individual components of the landscape (*Polylepis*, matrix and interface) and to determine the importance of each of these habitats for species of high conservation importance (threatened and restricted-range species).

Methods

Study sites and study design

Polylepis bird communities and the surrounding habitats were surveyed in three valleys in the Cordillera Vilcanota mountain range, Dept. of Cusco, southern Peru (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, and was surveyed during 22 field days in December 2003 and July 2004.

Our sampling design was centred on plots, randomly placed within *Polylepis* woodland (123 plots) and the non-wooded matrix (45 plots). *Polylepis* patches were defined as continuous areas of woodland separated from surrounding patches by gaps of at least 30 m (Villard et al. 1995; Bentley and Catterall 1997). Patch area was determined by calculating the area from measuring the length of boundaries around each fragment. At the study sites, patches ranged from 0.1 to 31.5 ha. In the surrounding matrix habitat but within the immediate valleys holding *Polylepis* patches, plots were established in randomly-placed locations, although at least 150 m from each other (Blake and Karr 1987).

Habitat surveys

At each plot, we recorded the elevation and degree of slope and estimated percentage vegetation cover and percentage ground cover using a sighting tube (Bibby et al. 2000). Ground cover was classified according to three habitat categories: moss, grass-steppe, and boulder-scree. We recorded presence/absence of fire damage and the presence/absence of livestock (tracks and faeces). Within a ten-metre radius of each plot all live and dead (i.e., cut-down/

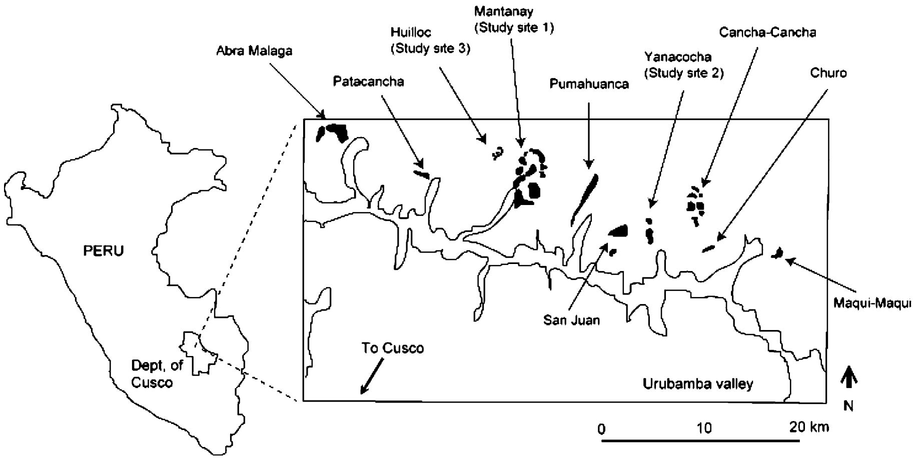

Fig. 1 Location of *Polylepis* woodlands, including the three study sites, in the Urubamba Valley, Cordillera Vilcanota, Peru

logged) trees with a diameter at breast height (DBH) >0.1 m was selected. For each live tree we recorded the following: tree species/genus; DBH; overall tree height; height of lowest foliage; height of upper foliage; and the distance from the tree to the plot's central point. For dead trees we recorded tree species/genus; DBH at the point of cutting; the height of the dead tree; and the distance of the tree to the survey plot.

Bird surveys

Birds were surveyed at plots within *Polylepis* and the matrix using a point count distance sampling method (Reynolds et al. 1980; adapted by Jones et al. 1995), although in this study, we did not calculate density estimates but instead used encounter rates of birds recorded within 50 m of the plot's central point. Bird surveys were conducted between 05 h30 and 16 h30 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 06 h30 and around 05 h30 between October and December (HL pers. obs.) and there is no conspicuous peak in high-Andean bird vocal activity at either the pre-dawn or dawn period (HL pers. obs.) as observed in the Amazonian lowlands (Terborgh et al. 1990; Lloyd 2004). HL was the only recorder for all bird surveys, with over two years experience of surveying birds using similar methods in Peru, and, following over four years of experience in high Andean landscapes as a naturalist and bird tour leader, was familiar with the vocalizations of all of the region's bird species. Following arrival at each plot, the surveyor sat quietly for a 5 min 'settling down' period (Bibby et al. 2000) before spending 20 min recording all bird contacts. For each contact, we recorded species and the number of individuals in each group. Two repeats of each forest transect and one of each matrix transect were made at each site making a total of 291 point counts. The direction of the surveys along transects in both the matrix and forest habitat was rotated in an attempt to minimise any bias associated with variable bird activity at different time of day.

Data analysis

Conservation status of threatened bird species follows BirdLife International (2004). Species were classified as restricted-range species following Stattersfield et al. (1998). Habitat variables were examined for normality using Kolmogorov–Smirnov tests. Across-site differences in vegetation measures were examined using non-parametric Kruskal–Wallis tests. 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.750 software (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 easily understood and generally robust estimator (Lee 2005), was used as a measure of estimated species richness. Bird species diversity was represented by the Shannon–Wiener index (H') which takes into account both species richness and the relative abundance of each species (Magurran 2004).

To identify patterns of bird community variation across sites and to relate these to the main habitat gradients, we used Canonical Correspondence Analysis (CCA—ter Braak 1986). This multivariate technique has previously proven effective in describing the relationship between avian community structure and environmental variability (Gregory and Gaston 2000; Pearman 2002). CCA creates a linear combination of habitat variables in

Table 1 Gross habitat characteristics (mean ± SD) of *Polylepis*-dominated woodland patches and matrix at three sites in the Cordillera Vilcanota, Peru

Habitat variable	Forest ($n = 123$)			Matrix ($n = 45$)		
	Mantanay	Yanacocha	Huilloc	Mantanay	Yanacocha	Huilloc
Elevation (m)	4,012 ± 110.7	3,885 ± 89.7	4,281 ± 63.1	4,021 ± 94.4	3,957 ± 99.6	4,276 ± 69
Degree of slope (°)	33 ± 9.3	33 ± 11	38 ± 9.9	21 ± 13.2	37 ± 12	34 ± 8.3
% Canopy vegetation	57.1 ± 23.0	65.6 ± 18.4	37.8 ± 18.2	0	0	0
% Ground cover grass-steppe	31.7 ± 31.2	6.3 ± 16.6	18.7 ± 21.7	86.0 ± 19.9	77.0 ± 33.9	0
% Ground cover moss	52.3 ± 41	71.6 ± 41.1	64 ± 39.8	0	0	0
% Ground cover boulder-scree	18.0 ± 31.5	22.1 ± 41	17.3 ± 34	14 ± 19.9	14 ± 19.9	100 ± 0.0

which the differences between species ecological profiles are simultaneously maximised on each of the habitat variables (Jullien and Thiollay 1996). We used biplots to illustrate the relationship between the habitat variables and the ordination axes derived from the species data (the number of birds of each species per survey plot). This provided a more detailed interpretation of which variables most influenced the structure of the bird community, how habitat variables were interrelated, and where each species ordinate along each habitat axis (ter Braak 1986; Julian and Thiollay 1996; Grand and Cushman 2003). We used only species with 20 or more observations for this analyses of habitat use. Thirteen habitat variables from a total of 168 plots were entered into the analyses. The ordination of habitat variables on the first two axes of the CCA was plotted along with the species scores of those 39 species included in the analysis.

To identify patterns of habitat occupancy (niche position and breadth) by high-Andean birds within the landscape, mean scores ± standard deviation (SD) were plotted along the main habitat ordination axis for each bird species. The ‘position’ of *Polylepis* and matrix habitat along this axis was plotted using the mean scores ± SD for each survey plot. Species whose mean score lay to the left of, or within the SD of the mean score of *Polylepis* survey plots were classified as ‘*Polylepis*-dependent’. Species whose mean score lay within, or to the right of, the SD of the mean score for matrix survey plots were classified as ‘matrix-dependent’. Species located between the two ranges were considered to have a preference for the forest-matrix interface.

Results

Habitat characteristics

The matrix habitat at both Mantanay and Yanacocha was dominated by grazed/burned grass-steppe, and by boulder-scree at Huilloc. No trees were recorded from any of the matrix plots (Table 1). Mosses were the dominant ground cover at survey plots located in *Polylepis* habitat (Table 1).

There were significant across-site differences in all *Polylepis* patches vegetation characteristics except densities of live and dead trees (Table 2). Mantanay contained largest girthed trees but the tallest live trees were recorded at Yanacocha. At Huilloc, 31.5% of trees were dead (either cut down/logged), compared with 17.5% at Mantanay, and only 6.3% at Yanacocha. A greater proportion of trees at Mantanay (9.3%, $n = 66$) showed evidence of

Table 2 Mean values ± SD and results of Kruskal–Wallis tests of *Polylepis* woodland structure variables across three study sites in the Cordillera Vilcanota, Peru

Habitat variable (m)	Mantanay ($n = 859$ trees)	Yanacocha ($n = 239$ trees)	Huilloc ($n = 165$ trees)	Across-site difference
Density live trees	6.42 ± 0.33	6.02 ± 0.34	5.84 ± 0.54	$\chi^2_2 = 3.2$ $P = 0.198$
DBH live trees	0.25 ± 0.17 ($n = 709$)	0.19 ± 0.16 ($n = 224$)	0.12 ± 0.54 ($n = 113$)	$\chi^2_2 = 15.9$ $P < 0.001$
Height of live trees	4.88 ± 0.19	7.24 ± 0.25	4.28 ± 0.18	$\chi^2_2 = 12.2$ $P < 0.01$
Height of lowest foliage	2.14 ± 0.14	3.67 ± 0.25	0.96 ± 0.10	$\chi^2_2 = 28.2$ $P < 0.01$
Density dead trees	6.02 ± 0.20	5.96 ± 0.53	6.09 ± 0.38	$\chi^2_2 = 0.1$ $P = 0.95$
DBH dead trees	0.31 ± 0.18 ($n = 150$)	0.15 ± 0.10 ($n = 15$)	0.19 ± 0.02 ($n = 52$)	$\chi^2_2 = 22.1$ $P < 0.001$

DBH = diameter at breast height (m). Density of live and dead trees is mean distance from trees to plot's central point

recent burning than at Yanacocha (2.7%, $n = 6$) while no trees at Huilloc showed sign of recent burning. The presence of livestock (their faeces or tracks) was recorded at all 168 plots across all three sites.

Bird species richness and diversity in *Polylepis* and matrix habitat

A total of 2,453 bird encounters was recorded during the bird surveys. Only 1.3% ($n = 52$) of all bird contacts were unidentified. Bird species richness (S_{obs} and S_{boot}) and the Shannon–Wiener index of species diversity (H') were greater in forest habitat than in the matrix (Table 3). Both bird species richness and species diversity at each locality was greater in forest habitat than in the matrix. For *Polylepis* forest, species richness was greater at Yanacocha, than at Mantanay and Huilloc respectively and the Shannon–Wiener index of species diversity was greater at Huilloc, than at Mantanay and Yanacocha (Table 3). Across the three sites, six threatened species and nine restricted-range species were recorded in *Polylepis* plots, with all of these species recorded at both Mantanay and Yanacocha (two restricted-range species were not recorded from Huilloc). Only one threatened and four restricted-range species were recorded in the matrix.

Vegetation and bird community ordination

The vectors for habitat variables in Fig. 2 accounted for 65.6% of the variation of the 39 bird species with respect to the 14 habitat variables, the sum of all eigenvalues being 0.82. Two clusters of survey plots are apparent in Fig. 3, with one cluster of *Polylepis* habitat at variable elevations positioned on the left-hand side, and a second cluster of matrix plots at lower elevations positioned in the right-hand section. There were relatively few plots ordinated between these two clusters, these being either plots in *Polylepis* edge habitats or those located in very small *Polylepis* patches with highly disturbed (grazed) ground cover habitat.

Most bird species centroids were projected on the left-hand side of the bird community ordination plot (Fig. 4), indicating a preponderance of birds associated with *Polylepis* woodlands. Bird centroids on the right-hand side of Fig. 4 (those found mainly in matrix

Table 3 Bird community measures of *Polylepis* woodland and matrix habitat from three valleys in the Cordillera Vilcanota, Peru

	Forest				Matrix			
	Mantanay	Yanacocha	Huilloc	All *Polylepis* sites	Mantanay	Yanacocha	Huilloc	All matrix sites
Number of survey repeats	114	72	60	246	20	15	10	45
Identified contacts	966	679	391	2036	184	112	69	365
Unidentified contacts	21	13	14	48	4	0	0	4
Mean encounter rate (groups per plot)	2.87 ± 2.10	2.94 ± 2.40	2.47 ± 1.57	4.04 ± 3.50	1.53 ± 1.25	1.38 ± 1.10	1.30 ± 0.92	3.22 ± 2.47
Species richness (S_{obs})	41 ± 2.31	40 ± 1.64	37 ± 1.18	52 ± 1.13	24 ± 1.61	25 ± 2.43	9 ± 1.67	40 ± 1.85
Species richness (S_{boot})	43.2 ± 0.45	43.1 ± 0.76	38.7 ± 0.56	54.4 ± 0.19	27.5 ± 0.55	29.4 ± 1.64	10.2 ± 0.59	45.6 ± 0.99
Species diversity (H')	3.16 ± 0.01	3.02 ± 0.01	3.17 ± 0.01	3.35 ± 0.01	2.36 ± 0.02	2.35 ± 0.07	1.86 ± 0.03	2.73 ± 0.01
Number of threatened/ Restricted range species	6/9	6/9	6/7	6/9	1/2	0/2	0/0	1/4

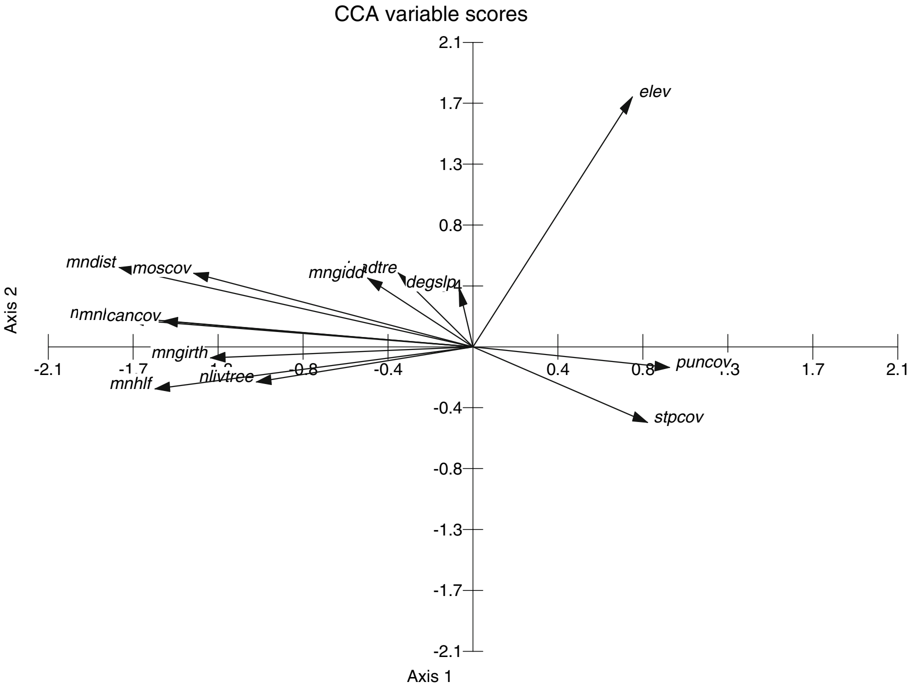

Fig. 2 Ordination of 14 habitat variables on the first two canonical axes from CANOCO analysis. Habitat variables are described in the methods section and are labelled as follows: *nlivtree* number of live trees, *mngirth* mean girth live trees, *mnheight* mean height live trees, *mnhlf* mean height lowest foliage, *mnhuf* mean height upper foliage, *mndist* tree density, *ndeadtre* number of dead trees, *mngidd* mean girth dead trees, *degslp* degree of slope, *elev* elevation, *cancov* percentage canopy vegetation cover, *puncov* percentage puna grass ground cover, *stpcov* percentage steppe/boulder scree ground cover, *moscov* percentage moss ground cover

habitat and at the higher elevation woodland-matrix interface) are both more scattered and quite distinct from the cluster of *Polylepis* birds. Abundances of six species were 'correlated' with elevation, and generally, these species were associated with *Polylepis* woodland-matrix interface (those positioned along the upper right-hand quadrant of Fig. 4).

Niche position and breadth within the bird community

Niche position and width for all 37 bird species are shown in Fig. 5 and summarised in Table 4. Mean scores for seven species, including five restricted-range species were positioned to the left of the mean score SD for *Polylepis* plots (highest negative scores). The niche breadth for these species did not extend beyond the range of mean *Polylepis* survey plot scores. All six globally-threatened species, and three other restricted-range species were located within the mean score SD of all *Polylepis* survey plots (negative scores). The niche breadth of all globally-threatened and eight of the nine restricted-range species did not extend into the mean score SD of the matrix habitat.

Eight species were classified as *Polylepis* dependent and the niche breadth of these species, which included 'ecological generalists' such as *Troglodytes aedon* and *Zonotrichia capensis*, extended into the *Polylepis*-matrix interface, but not into the mean score SD of matrix habitat. Mean scores of nine species, including one restricted-range species (*Asthenes*

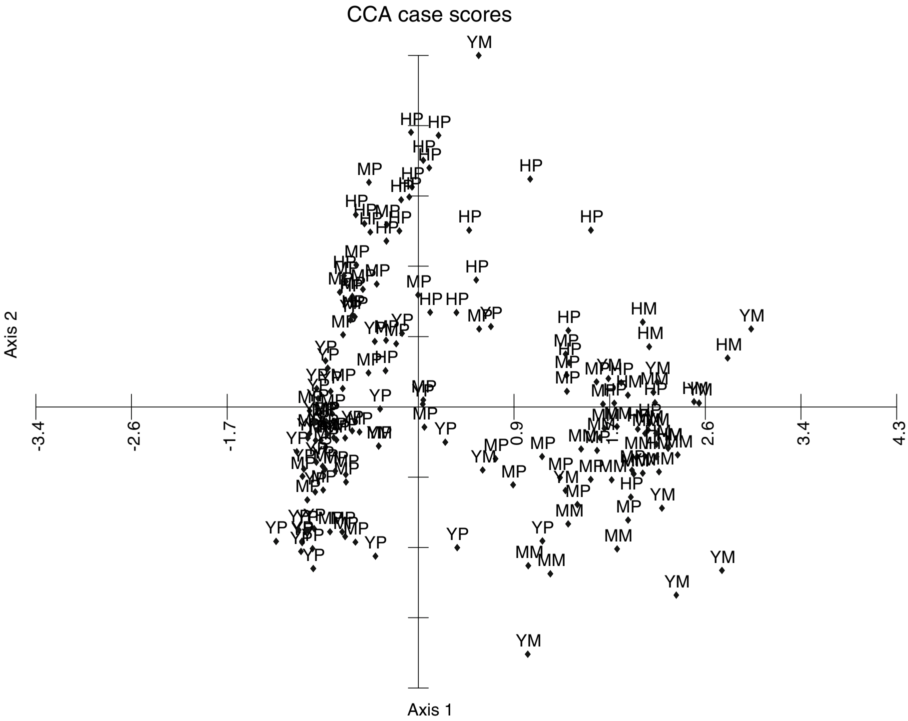

Fig. 3 Ordination of census plots in each habitat type at each of the three sites on the first two canonical axes of the CANOCO analysis. Census plots with high scores in *Polylepis* or matrix habitat are labelled for each site: MP = Mantanay *Polylepis*; YP = Yanacocha *Polylepis*; HP = Huilloc *Polylepis*; MM = Mantanay matrix; YM = Yanacocha matrix; HM = Huilloc matrix

virgata), were associated with the forest-matrix interface. These species had the largest niche breadths within the bird community. Four species with axis scores positioned within the mean score SD of matrix habitat, and with niche breadth not extending into the mean score SD of *Polylepis* habitat were considered matrix dependent.

Discussion

Our vegetation analyses and ordination illustrate the binary nature of the *Polylepis*-matrix landscape within the study area. Of course, there were differences in the nature of *Polylepis* woodland (in terms of elevation and habitat ‘quality’) and across two matrix types (*puna* grass-steppe or boulder scree) but there were very few intermediate plots sharing characteristics of both *Polylepis* and matrix. In turn this indicates a relatively sharp border between *Polylepis* and matrix which may be natural but is more likely to be a product of anthropogenic activities such as grazing and/or fire (Ellenberg 1958; Fjeldså and Kessler 1996; Kessler 2002).

The within-patch habitat characteristics of the three sites were different, again reflecting both natural conditions and exposure to different levels of anthropogenic disturbance. Logging disturbance was common at Mantanay and especially Huilloc while there was no logging activity recorded at Yanacocha. At this last site, grazing pressure was the main

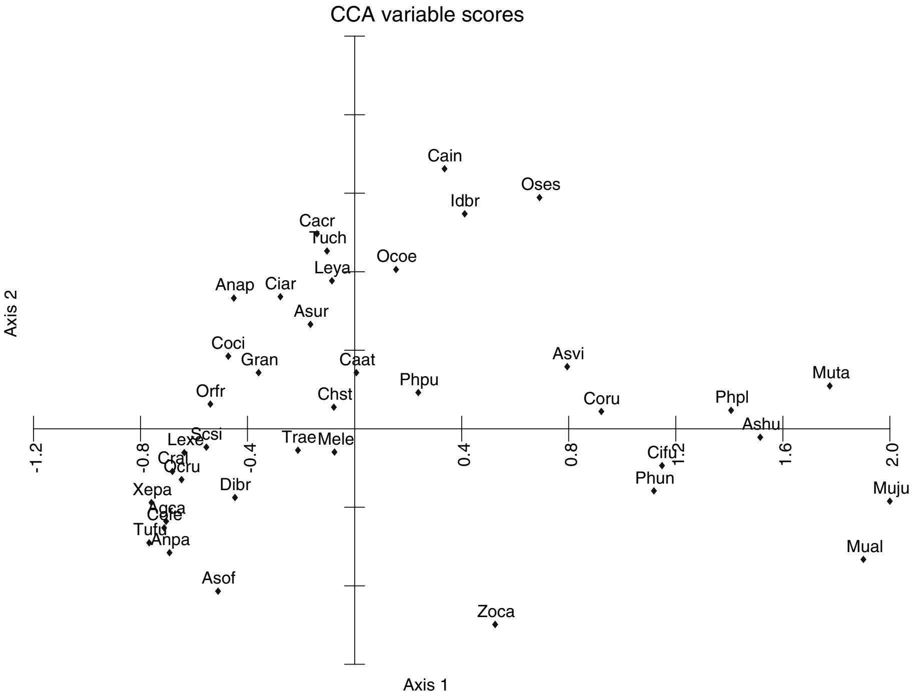

Fig. 4 Ordination of 39 bird species on the first two canonical axes from the CANOCO analysis. Bird species with high scores on either/both axis are labelled as follows: Agca *Aglaectis castelnaudii*, Anap *Anarites alpinus*, Anpa *Anarites parulus*, Ashu *Asthenes humilis*, Asot *Asthenes ottonis*, Asur *Asthenes urubambensis*, Asvi *Asthenes virgata*, Cain *Catamenia inornata*, Caat *Carduelis atrata*, Cacr *Carduelis crassirostris*, Chst *Chacostigma stanleyi*, Ciar *Cinclodes aricomae*, Cifu *Cinclodes fuscus*, Coci *Conirostrum cinereum*, Cofe *Conirostrum ferrugineiventre*, Coru *Colaptes rupicola*, Cral *Cranioleuca albicapilla*, Dibr *Diglossa brunneiventris*, Gran *Grallaria andicola*, Idbr *Idiopsar brachyurus*, Leya *Leptasthenura yanacensis*, Lexe *Leptasthenura xenothorax*, Mele *Mecocerculus leucophrys*, Mual *Muscisaxicola albilora*, Muju *Muscisaxicola juninensis*, Muta *Muscisaxicola taczanowski*, Oceo *Ochthoeca oeanthoides*, Ocru *Ochthoeca rufipectoralis*, Orfr *Oreomanes fraseri*, Oses *Oreotrochilus estella*, Phpl *Phrygilus plebejus*, Phpu *Phrygilus punensis*, Phun *Phrygilus unicolor*, Scsi *Scytalopus simonsi*, Trae *Troglodytes aedon*, Tuch *Turdus chiguanco*, Tufu *Turdus fuscater*, Xepa *Xenodacnis parina*, Zoca *Zonotrichia capensis*

form of habitat disturbance. The matrix habitat at all sites consisted of largely disturbed grass-steppe habitat with smaller areas of dense *puna* tussock grass and boulder scree. The principal cause of anthropogenic disturbance in the matrix across the landscape was grazing with some smaller areas of burning for pasture.

Patterns of habitat occupancy and niche breadth

The niche breadth analysis illustrates the binary nature of the high-Andean landscape for the majority (22 of the 39) bird species studied, including all globally threatened, and for all but one of the restricted-range species. The remaining 17 species (including one restricted-range species) had broad niches extending into either or both *Polylepis* and matrix habitats. Niche breadth for all globally-threatened and eight restricted-range species were narrow and did not extend into either the forest-matrix interface or the matrix habitat. This inability to use the matrix may be an important factor in population declines and localised extinctions of

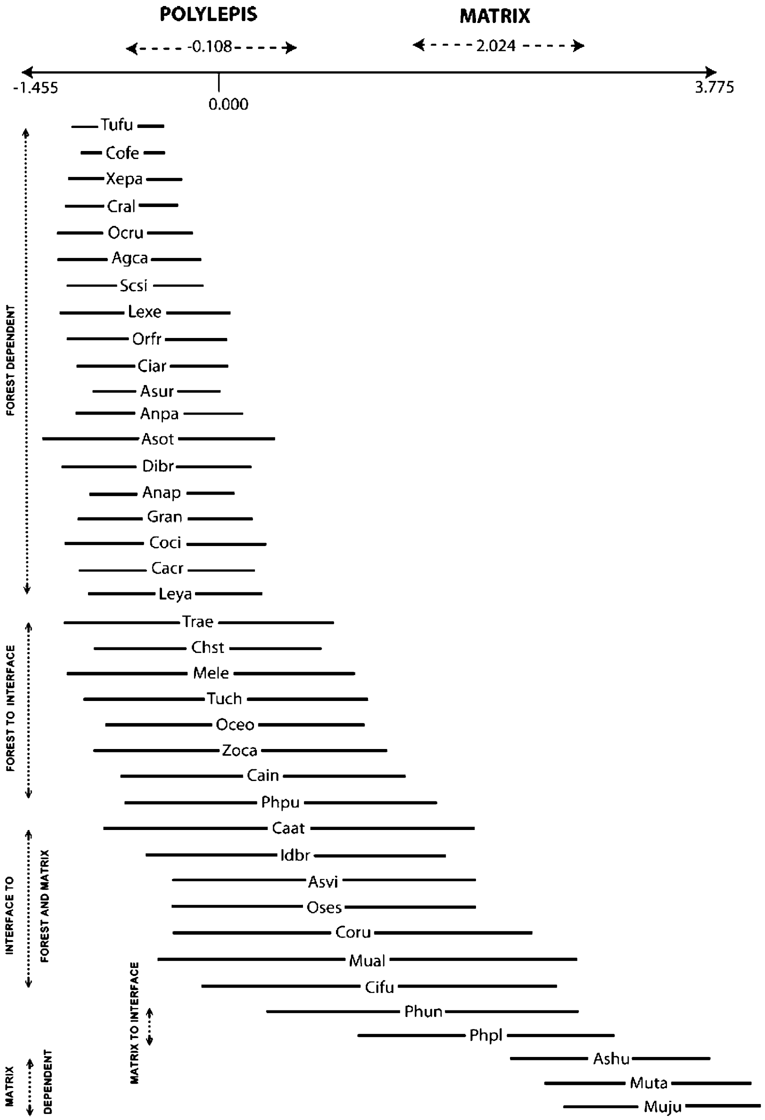

Fig. 5 showing position of *Polylepis* and matrix census plots with niche breadth of 39 high Andean bird species across a fragmented *Polylepis* landscape in the Cordillera Vilcanota, Peru. Bird species are labelled as follows: Agca *Aglaectis castelnaudii*, Anap *Anarites alpinus*, Anpa *Anarites parulus*, Ashu *Asthenes humilis*, Asot *Asthenes ottonis*, Asur *Asthenes urubambensis*, Asvi *Asthenes virgata*, Cain *Catamenia inornata*, Caat *Carduelis atrata*, Cacr *Carduelis crassirostris*, Chst *Chacostigma stanleyi*, Ciar *Cinclodes aricomae*, Cifu *Cinclodes fuscus*, Coci *Conirostrum cinereum*, Cofe *Conirostrum ferrugineiventre*, Coru *Colaptes rupicola*, Cral *Cranioleuca albicapilla*, Dibr *Diglossa brunneiventris*, Gran *Grallaria andicola*, Idbr *Idiopsar brachyurus*, Leya *Leptasthenura yanacensis*, Lexe *Leptasthenura xenothorax*, Mele *Mecocerculus leucophrys*, Mual *Muscisaxicola albilora*, Muju *Muscisaxicola juninensis*, Muta *Muscisaxicola taczanowski*, Oceo *Ochthoeca oeanthoides*, Ocru *Ochthoeca rufipectoralis*, Orfr *Oreomanes fraseri*, Oses *Oreotrochilus estella*, Phpl *Phrygilus plebejus*, Phpu *Phrygilus punensis*, Phun *Phrygilus unicolor*, Scsi *Scytalopus simonsi*, Trae *Troglodytes aedon*, Tuch *Turdus chiguanco*, Tufu *Turdus fuscater*, Xepa *Xenodacnis parina*, Zoca *Zonotrichia capensis*

Table 4 Summary of niche position and niche breadth of 39 high-Andean bird species in the Cordillera Vilcanota, Peru

Forest-dependent	Forest but extending to interface	Interface but extending into both forest and matrix	Matrix but extending to interface	Matrix-dependent
Aglaeactis castelnaudii	*Chalcostigma stanleyi*	*Oreotrochilus estella*	*Phrygilus plebejus*	*Asthenes humilis*
Cinclodes aricomae[a]	*Mecocerculus leucophrys*	*Colaptes rupicola*	*Phrygilus unicolor*	*Muscisaxicola juninensis*
Leptasthenura xenothorax[a]	*Ocththoeca oeanthoides*	*Cinclodes fuscus*		*Muscisaxicola taczanowski*
Leptasthenura yanacensis[a]	*Turdus chiguanco*	*Asthenes virgata*		
Cranioleuca albicapilla	*Troglodytes aedon*	*Muscisaxicola albilora*		
Asthenes ottonis	*Zonotrichia capensis*	*Idiopsar brachyurus*		
Asthenes urubambensis[a]	*Phrygilus punensis*	*Carduelis atrata*		
Grallaria andicola	*Catamenia inornata*			
Scytalopus simonsi				
Anairetes alpinus[a]				
Anairetes parulus				
Ocththoeca rufipectoralis				
Turdus fuscater				
Conirostrum cinereum				
Conirostrum ferrugineiventre				
Oreomanes fraseri[a]				
Xenodacnis parina				
Diglossa brunneiventris				
Carduelis crassirostris				

[a] Denotes globally threatened species

Polylepis patch specialists, as is often the case for populations of forest patch specialists in fragmented landscapes (e.g., Diamond et al. 1987; Laurance 1991; Bierregaard and Stouffer 1997; Gascon et al. 1999; Antonigiovanni and Metzger 2005).

Perhaps counter-intuitively, most of the species that appear to be *Polylepis* specialists (those with niche positions at the leftmost end of Fig. 5) with narrowest niche breadth were not globally-threatened. These include both widespread (e.g., *Turdus fuscater*, *Ochthoeca rufipectoralis*) and restricted-range (e.g., *Conirostrum ferrugineiventre*, *Xenodacnis parina*) species, but key is that they also occur in elfin forest and humid montane scrub habitats (Fjeldså and Krabbe 1990, Stotz et al. 1996) as well as *Polylepis*. It was the species whose niche position most closely matched the mean score for *Polylepis* woodlands, and those with relatively narrow niche breadth not extending into the forest-matrix interface that were most likely to be globally-threatened (e.g., *Asthenes urubambensis*, *Anairetes alpinus*).

We cannot be sure how representative our results are of other high-Andean regions, or for other taxa in *Polylepis*-matrix landscapes. Few quantitative data exist, but *Polylepis* patches, rather than matrix habitats, have been found to be most important for threatened and/or restricted-range bird species in Bolivia and in other areas of Perú (Fjeldså and Kessler 1996; Herzog et al. 2003). Elsewhere in the Andes, open agricultural matrix habitats are considered hostile environments for threatened restricted-range bird species dependent on lower elevation cloud forest (O'Dea and Whittaker 2007). Collectively, these results indicate that forest-dependent birds respond to habitat fragmentation in the Andes as they do elsewhere in tropical lowland forests (Renjifo 1999; O'Dea and Whittaker 2007).

Similarly, patterns of niche position and habitat occupancy of some species often considered invasive ecological generalists (e.g., *Z. capensis*, *T. aedon*, *Turdus chiguanco*) may not hold true for other Andean regions. For example, the results demonstrate that *Z. capensis*, *T. aedon*, and *Turdus chiguanco* were in fact, largely woodland dependent (Fig. 5). Their niche position lay within the mean score SD for *Polylepis* survey plots, and all species had relatively broad niches, extending into the forest-matrix interface. At first glance, this would suggest that the traditional perception of these species being invasive species from forest-edge (Estades and Temple 1999) or disturbed *puna* matrix habitat (Fjeldså 1993) needs to be re-evaluated. However, these species appear to be reasonably flexible in their habitat choice across their ranges (Stotz et al. 1996), and only a tiny fraction of their populations occurs in *Polylepis* areas.

It is not known whether the patterns we found are also representative for other taxa, due to a lack of biodiversity assessments of high-Andean landscapes (Fjeldså 2002a). Research from Bolivia has shown that there are fewer *Polylepis*-dependent mammals and most species also occur in elfin forests and *puna* matrix (Tarifa and Yensen 2001; Yensen and Tarifa 2002). Identification of habitat occupancy patterns for high Andean plants is complicated by the presence/absence of specific soil types, and sites with early stages of vegetation succession (e.g., Kessler 1999; Terrazas and Ståhl 2002). More comprehensive sampling may reveal similar patterns of habitat occupancy in high Andean landscapes: a recent study of lower elevation Andean cloud forest amphibians did identify a sharp contrast between species found in forest and open agricultural habitats (Toral et al. 2002).

Implications for biodiversity conservation

Most landscape ecology models assume a patch-hostile matrix binary habitat mosaic (Wiens 1997; Murphy and Lovett-Doust 2004), and this was what we found in this high-Andean landscape, at least for most globally threatened and restricted-range species. In turn we suggest that management of within-patch habitat quality (i.e., maintenance of particular forest structural characteristics and patch size) should be the cornerstone of biodiversity conservation efforts within the landscape. However, to focus on habitat patches alone will not always achieve desired conservation outcomes (Fischer et al. 2005). Whilst the conservation value of matrix habitats such as agricultural land, boulder scree and *puna* grassland is generally low across much of the high Andes (Stotz et al. 1996), its widely acknowledged that the management of matrices in fragmented forest landscapes merits a significantly higher conservation priority (Lindenmayer and Franklin 2002; Watson et al. 2005; Yamaura et al. 2006). Widespread forest- and matrix-dependent species with broad niches extending into the forest-matrix interface (e.g., *T. aedon, Z. capensis*, *P. unicolor*) and the sizable niche breadth of species dependent on the forest-matrix interface (e.g., *C. fuscus*, *A. virgata*, *C. atrata*) indicate that the matrix exerts an influence of bird community composition in *Polylepis* patches. We conclude therefore that more quantitative evidence on the role of the surrounding matrix and the *Polylepis*-matrix interface will be crucial in bringing about sympathetic changes to matrix land-use patterns. The integration of such changes with forest patch management will facilitate *Polylepis* landscape connectivity, and produce the most effective biodiversity conservation strategies within the high Andean landscape.

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