

Influence of Patch Factors and Connectivity on the Avifauna of Fragmented *Polylepis* Forest in the Ecuadorian Andes

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ABSTRACT

Human-induced alteration of habitat is a major threat to biodiversity worldwide, especially in areas of high biological diversity and endemism. *Polylepis* (Rosaceae) forest, a unique forest habitat in the high Andes of South America, presently occurs as small and isolated patches in grassland dominated landscapes. We examine how the avian community is likely influenced by patch characteristics (*i.e.*, area, plant species composition) and connectivity in a landscape composed of patches of *Polylepis* forest surrounded by páramo grasslands in Cajas National Park in the Andes of southern Ecuador. We used generalized linear mixed models and an information-theoretic approach to identify the most important variables probably influencing birds inhabiting 26 forest patches. Our results indicated that species richness was associated with area of a patch and floristic composition, particularly the presence of *Gynoxys* (Asteraceae). However, connectivity of patches probably influenced the abundance of forest and generalists species. Elsewhere, it has been proposed that effective management plans for birds using *Polylepis* should promote the conservation of mature *Polylepis* patches. Our results not only suggest this but also show that there are additional factors, such as the presence of *Gynoxys* plants, which will probably play a role in conservation of birds. More generally, these findings show that while easily measured attributes of the patch and landscape may provide some insights into what influences patch use by birds, knowledge of other factors, such as plant species composition, is essential for better understanding the distribution of birds in fragmented landscapes.

Abstract in Spanish is available in the online version of this article.

Key words: bird communities; bird guilds; high Andes; forest patches; *Gynoxys*; páramo.

HABITAT LOSS AND FRAGMENTATION modify the availability, distribution, and functionality of habitats within a landscape, resulting in changes in patterns of patch use by animals (Fahrig 2003, Fischer & Lindenmayer 2007). These modifications are generally categorized into patch changes whereby factors such as habitat area, floral composition, and vegetation structure are altered, and landscape transformations, which influence the connectivity among habitat patches in a landscape (*e.g.*, Graham & Blake 2001, Ferraz *et al.* 2007, Boscolo & Metzger 2011). Understanding the relative importance of factors acting at these two scales is critical to generating effective management recommendations in human modified landscapes (Lindenmayer *et al.* 2008).

A positive association between patch area and bird species richness has been demonstrated in multiple studies (*e.g.*, Ferraz *et al.* 2007, Aubad *et al.* 2010). Birds also respond to vegetation parameters, including forest structure (*e.g.*, number and size of trees, density of the shrub layer, foliage vertical diversity; Robinson & Holmes 1982, Graham & Blake 2001), and floristic composition (Fleishman *et al.* 2003, Lee & Rotenberry 2005). Moreover, landscape characteristics influence the distribution and

abundance of species (Fahrig 2003, Fischer & Lindenmayer 2007). Landscape fragmentation usually decreases the connectivity among habitat patches affecting movement and colonization patterns by birds (Dunning *et al.* 1992, Taylor *et al.* 1993). Changes in these patch and landscape characteristics can influence the richness patterns and the composition of bird assemblages (Graham & Blake 2001, Ferraz *et al.* 2007, Devictor *et al.* 2008).

In the high Andes of South America (elevations of 3500–5000 m asl from Venezuela to Argentina), *Polylepis* (Rosaceae) forest (named after its dominant tree genus) has been extensively modified by human activities and presently exists as small and isolated patches in a landscape now dominated by grasslands (Kessler 1995, Fjeldså 2002). While the patchy distribution of *Polylepis* probably reflects a natural distribution to some extent (van der Hammen & Hooghiemstra 2003, Gosling *et al.* 2009), there is evidence that the current size and configuration of *Polylepis* are strongly influenced by human activities (Cierjacks *et al.* 2008a, Coblenz & Keating 2008). This is particularly troubling because *Polylepis* forest exhibits high endemism of species that are sensitive to human disturbance (Fjeldså 1993, Gareca *et al.* 2010).

Research evaluating how habitat degradation influences diversity in *Polylepis* forest has focused primarily on how patch characteristics influence bird communities (Cahill & Matthysen

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2007, Lloyd 2008a,b). Landscape characteristics, such as connectivity, have not been considered even though they can influence diversity in fragmented landscapes (Bierregaard *et al.* 1992, Gascon *et al.* 1999). Here, we examine how birds respond to patch characteristics and connectivity in a landscape composed of patches of *Polylepis* forest surrounded by páramo in Cajas National Park, southern Ecuador. Patch characteristics included patch area, and vegetation composition and structure. We used network analyses to quantify patch connectivity (McRae *et al.* 2008). We performed separate analyses for the bird community as a whole and for individual species. First, we hypothesized that larger patches will contain a greater number of species than smaller patches (MacArthur & Wilson 1967). Second, patches that are structurally complex and contain mature trees should have more species than patches with simple vegetation structure because the former provides greater foraging opportunities and shelter (Karr & Roth 1971). Third, floristic composition of a patch should influence bird species richness and composition because particular tree species provide different foraging opportunities (Robinson & Holmes 1982). In particular, high bird activity at plants of the genus *Gynoxys* (Asteraceae) suggests that they might influence patterns of bird diversity. Fourth, we predicted that richness of birds would be lower in isolated patches because of reduced use and colonization of such patches (Dunning *et al.* 1992, Ferraz *et al.* 2007, Wilson *et al.* 2009). Finally, given that species vary in their ability to tolerate habitat loss and fragmentation (Simberloff 1994), we explored how individual species responded to patch and landscape characteristics.

METHODS

STUDY SITE.—This study was conducted in Cajas National Park, in the high Andes of Azuay Province, south Ecuador at 2°50' S, 79°15' W (Fig. S1). The Park receives 1200–1500 mm of precipitation annually and the mean monthly temperature ranges from 5 to 12°C, although temperatures can fluctuate greatly within a day, between 0 and 20°C (IERSE 2004). *Polylepis* forest patches are embedded in the páramo and usually occupy areas at the base of cliffs (Coblentz & Keating 2008).

We used a LANDSAT 2001 image with a resolution of 30 × 30 m (Sanchez & Carbone 2009) and field explorations to locate all the *Polylepis* forest located within a single 2609 ha watershed that ranged in elevation from 3800 to 4090 m asl. We defined *Polylepis* patches as continuous areas of woodland separated from other patches by gaps of at least 150 m. This threshold was chosen because most territories of forest species are unlikely to contain open habitats of this extent (De Coster *et al.* 2009). We chose to work in a natural setting where the sizes of patches and their isolation correspond to the natural condition of the landscape. Overall, we located 26 *Polylepis* patches (Fig. S1).

BIRD SURVEYS.—We conducted five bird censuses in each patch between December 2006 and December 2007. Birds were censused within the first 4 h after sunrise (approximately 0600–1000 h) when bird activity is the greatest in these forests (B.

Tinoco, pers. obs.). Before repeating a census in a patch, we surveyed all 26 patches, rotating the time of the survey to minimize any possible bias produced by differences in bird activity related to the time of the day. All surveys were carried out by B. Tinoco on days without strong winds or rain.

In each *Polylepis* patch, we randomly placed point-counts at a distance not closer than 150 m from another point, which is a standard distance used in bird surveys to minimize the possibility of detecting the same bird in two adjacent point-counts (Bibby *et al.* 1998). We used 15 min point-counts during which all birds seen or heard within a fixed radius of 25 m were recorded (Bibby *et al.* 1998). Flyovers were excluded. The number of point-counts in each patch varied depending on the size of the patch (Table S1). Point-counts are a valid method to provide accurate estimates of richness and abundance (Bibby *et al.* 1998), and in our case, it was also chosen because the vegetation inside *Polylepis* forest is too dense to employ other methods that require active movement of the researcher.

We classified bird species based on habitat preferences. This classification was obtained from Fjeldsø (1992), Lloyd and Marsden (2008), and Tinoco and Astudillo (2007). It included *Polylepis* forest species; generalist species which use páramo, *Polylepis*, and forest borders; and páramo species. We recognize that species vary in their degree of habitat association, and that some species occupy other types of habitats elsewhere in their range, but species were assigned to habitats that occur within our study area.

VEGETATION SAMPLING.—We quantified vegetation structure and plant composition in each patch using a vegetation protocol used for bird surveys (James & Shugart 1970). We established a 20-m radius plot centered on each bird point-count. Within this plot, we established four transects in each of the four cardinal directions. To obtain a foliage height profile, we placed a 3-m pole at 4-m intervals along each transect and recorded the presence or absence of vegetation touching the pole within each 0.5 m interval from 0 to 3 m. Beyond 3 m, we visually estimated the presence or absence of vegetation at 1 m intervals until the top of canopy. We also visually estimated the canopy cover using a scale of 1–5 (1 = 0–19%, 2 = 20–39%, 3 = 40–59%, 4 = 60–79%, 5 = 80–100%). The foliage height profile and canopy cover were averaged across readings inside a vegetation plot ($N = 20$). The abundance and identity of shrubs (plants with < 3 cm diameter at breast height [dbh]) were obtained by counting the shrubs that contacted the extended arms of a person walking along each transect. At least four species of *Gynoxys* shrubs occur within *Polylepis* patches in Cajas (Minga *et al.* 2008), but their classification is highly problematic, thus we did not identify *Gynoxys* plants to species. Finally, all trees present inside the plot were counted and identified and assigned to one of four different dbh categories: 3–8 cm, 9–15 cm, 16–23 cm, 24–38 cm, and > 38 cm.

PATCH FACTORS.—Using the foliage height profiles, we calculated a Shannon diversity index to quantify vertical complexity (Hays *et al.* 1981). We also calculated a Shannon index based on species composition of shrubs and trees in each vegetation plot. We

obtained an average of vegetation features across all plots within each patch. All diversity indices were calculated with EstimateS v. 8.0 (Colwell 2006).

To obtain a composite description of the vegetation structure of the patches, we performed principal components analysis (PCA) on all the vegetation structure variables of each patch (foliage vertical complexity, number of trees of five different dbh categories, abundance of shrubs, and canopy cover). We used PC-ORD v. 5.10 to run the PCA (McCune & Mefford 2006). The resulting principal components were used as new explanatory variables to explore the influence of vegetation structure on birds (Jolliffe 2002). We also calculated the area of each patch using the LANDSAT image in the software Patch Analyst (Rempel *et al.* 2008).

LANDSCAPE CONNECTIVITY.—We used a novel class of ecological connectivity measures that are based on circuit theory and are reliable predictors of ecological connectivity (McRae *et al.* 2008). We used the software Circuitscape (v. 3.4.2, McRae & Shah 2008) to obtain connectivity of each *Polylepis* patch in our LANDSAT image. Circuitscape uses circuit theory to predict patterns of movement among individuals occupying spatially structured habitats (see McRae *et al.* 2008). The effective connectivity of a patch is calculated considering the distance to all the other patches in the landscape, the degree of resistance of the matrix, and the multiple pathways available to reach a patch (McRae *et al.* 2008). Low values of resistance indicate greater connectivity. In the connectivity analysis, we only considered two land cover types: *Polylepis* patches and non-*Polylepis* land cover. *Polylepis* patches were assigned a zero resistance value and non-*Polylepis* areas were coded with a resistance of 1. Non-*Polylepis* included páramo and small lakes (size range from 0.1 to 17 ha); because we lack information about cost of movement of birds across these different types of open areas, we combined them into a single category.

ANALYSES OF SPECIES RICHNESS AND INDIVIDUAL ABUNDANCES.—Differences in sampling effort among patches can potentially lead to biased determinations of species richness; we therefore obtained rarefied richness estimates of each patch to compare richness among patches (Gotelli & Colwell 2001). We obtained sample-based rarefaction estimates for each patch by fixing the number of samples to five, which was the minimum number of point-counts censused in a patch. Sample order was randomized 50 times for each data set. We obtained an estimate of total richness of each patch by calculating the non-parametric estimator Chao 1 (Chao 1984) using the software EstimateS v. 8.0 (Colwell 2006).

The predictor variables considered in our analysis included the first two components of the PCA, *Gynoxys* abundance, shrub diversity index, tree diversity index, patch area, and resistance. We included *Gynoxys* because during preliminary work in these study sites, we observed high bird activity by several bird species associated with these plants. We thus suspected that *Gynoxys* may be an important resource for birds in *Polylepis* forest. Moreover, *Gynoxys* is an important component of the floristic composition of *Polylepis* forests (Minga *et al.* 2008).

To avoid the inclusion of highly correlated variables in the analysis, we calculated pair-wise correlations among explanatory variables, and removed one of the pairs if they were significantly correlated (Delisle & Savidge 1997). We found a significant correlation between tree diversity and shrub diversity ($R^2 = 0.6$, $P < 0.05$). We retained shrub diversity because we considered trees to be mainly dominated by a single species, *Polylepis reticulata*, which is less informative than shrub diversity, which includes many species (Minga *et al.* 2008).

Furthermore, *Polylepis* patch ID 005 (Fig. S1) was more than three times larger than any of the other patches (Table S1). To avoid any spurious effects caused by this single large patch, we removed this patch from the dataset before all analyses. This patch was, however, included in landscape connectivity analyses because we consider that it is an important feature of the landscape with potential influence in the connectivity of patches.

We used generalized linear models (GLM) to evaluate the influence of patch connectivity and patch attributes on the estimates of bird species richness. Richness was modeled with a Gaussian distribution (Zuur *et al.* 2009). To analyze abundance data, we used generalized linear mixed models (GLMM) with a zero-inflated Poisson distribution (Hall 2004). They are appropriate models for count data when there is overdispersion caused by an excess of zeros (Martin *et al.* 2005, Zuur *et al.* 2009); the individual species modeled were absent from 55 to 80 percent of the total number of point-counts sampled. We modeled the explanatory variables as fixed effects, while the temporal replicates and the number of point-counts within a patch were treated as random effects to take into account the non-independence of successive spatial and temporal counts. Parameters were estimated by maximum likelihood using a Laplace approximation. All models were constructed with the package glmm.admb in R v. 2.10.1 (R Development core team 2009).

We used the information-theoretic approach to allow for uncertainty in the choice of the best model among a set of candidate models (Anderson 2008). We obtained AIC values corrected for small samples relative to the number of parameters (AICc) (Burnham & Anderson 2002). These AICc values were used to produce Akaike weights (w_i) following Anderson (2008), which are interpreted as the probability that a given model is the best model in the candidate set of models. We used model averaging to make inference on the whole set of models, as this is considered the best approach for selecting models when there are multiple candidate predictors (Burnham & Anderson 2002). We used the package MuMIn using the software R to perform model averaging (R Development core team 2009). Important variables are characterized by a high Akaike weight and model-averaged estimates that are higher than their standard errors (Anderson 2008).

COMMUNITY ANALYSES.—We used non-metric multidimensional scaling (NMDS) using Bray–Curtis distance to ordinate forest patches in relation to bird species composition. For this analysis, we averaged the abundance of each species per patch. Abundance values were transformed using the double square root transformation (Quinn & Keough 2002). Because NMDS does not

provide species scores, we calculated the weighted average species scores and added these to the ordination graph. The performance of the final NMDS solution was evaluated by the global minimum stress (*i.e.*, lack of fit measure) of the ordination, considering a stress value of less than 20 as adequate for interpretation (McCune & Grace 2002). Finally, Spearman rank correlations were calculated between the axis scores of sites and the explanatory environmental variables to identify the environmental variables correlated with the positions of the patches in the NMDS. The significance of the variables was then tested with a permutation test (Quinn & Keough 2002). To establish if there were statistical differences in the position in the ordination of the species grouped by habitat preferences, we employed a multi-response permutation procedure (MRPP), using Euclidean distances (McCune & Grace 2002). The NMDS and the MRPP were conducted using the package *vegan* in R v. 2.10.1 (R Development core team 2009).

RESULTS

PATCH FACTORS AND CONNECTIVITY.—The 26 *Polylepis* forest patches ranged in area from 0.14 to 21.64 ha (mean \pm SD: 2.41 ± 4.16) (Table S1), and combined, they covered 2.39 percent of the watershed. The degree of connectivity of each patch, Shannon diversity index of foliage vertical complexity, the diversity of shrubs in the Shannon diversity index, and abundance of *Gynoxys* plants varied across patches (Table S1).

The first axis of the PCA carried out on all vegetation structure variables (PC I) accounted for 32.0 percent of the variance and mainly represented canopy cover, abundance of trees with a large dbh, and vertical foliage complexity of a patch, all of which had positive loadings (Table 1). Therefore, this axis is indicative of mature *Polylepis* patches dominated by large trees with dense cover and open understory. The second axis of the PCA (PC II) accounted for 31.0 percent of the variance and was correlated with abundance of trees with low dbh, and abundance of shrubs. This was interpreted as a component representing young *Polylepis* patches dominated by small, thin trees and a high density of understory shrubs (Table 1). PC scores for each patch are shown in

TABLE 1. Eigenvectors of the principal components analysis of the vegetation structure of 26 *Polylepis* forest patches in Cajas National Park, Ecuador.

Environmental variable	PCI	PCII	PC III
Foliage vertical complexity ^a	0.39	0.00	-0.50
Abundance of shrubs	0.00	0.31	-0.66
Canopy cover	0.46	0.29	-0.24
Abundance of trees 3–8 cm DBH	-0.28	0.44	-0.25
Abundance of trees 9–15 cm DBH	-0.19	0.53	-0.23
Abundance of trees 16–23 cm DBH	-0.06	0.56	0.12
Abundance of trees 24–38 cm DBH	0.45	-0.13	0.11
Abundance of trees > 39 cm DBH	0.56	-0.11	0.25

^aFoliage Height diversity index using Shannon's formula: $-\Sigma P_i \log P_i$.

Table S1. PC III explained relatively little variation in the ordination (15.0%), and therefore was not used in further analyses.

GENERAL PATTERNS OF BIRDS.—Overall, we registered 1288 individuals of 30 species of birds in 270 point-counts performed in 26 *Polylepis* forest patches. Total species richness per patch ranged from 7 to 18 (12.85 ± 3.66). Grouping the species into habitat preferences showed that 50 percent (15 species) were *Polylepis* forest species, 27 percent (8 species) were generalists, and 23 percent (7 species) were páramo species (Table 2). The most abundant species included: *Mecocerculus leucophrys* (15.5% of records), *Xenodacnis parina* (11.3% of records), and *Metallura baroni* (9.9% records) (Table 2).

The total species richness of a patch quantified with Chao 1 estimates was positively associated with patch area (Akaike weight (w_i) = 0.942, Table 3). Models of rarefied richness identified patch area and abundance of *Gynoxys* as the most important variables (w_i = 0.821; 0.692, respectively) explaining species richness.

INDIVIDUAL SPECIES RESPONSES.—Fourteen species were abundant enough to be analyzed using GLMM (Table 4). Overall, PC I, a variable indicating mature patches conditions, together with resistance, were the variables most commonly identified as important factors probably influencing the abundance of both forest and generalist species. This indicates that species may respond to both patch and landscape factors (Table 5). Variance in the abundance of forest species was mainly positively related to mature patches and the abundance of *Gynoxys* plants. Forest species associated with mature patches included *Oreomanes fraseri*, *X. parina*, *Scytalopus latrans*, and *Anisognathus igniventris*. The abundance of *Gynoxys* plants was an important factor for forest specialists such as *Chalcostigma stanleyi*, *O. fraseri*, *X. parina*, and *Margarornis squamiger*. The resistance coefficient of a patch had a negative influence on the abundance of two forest species, *X. parina* and *A. igniventris*, suggesting that they are more abundant in more connected patches. But this same variable had a positive association with the abundance of *Asthenes griseomurina*. Patch area was an important variable for two species, *S. latrans* and *A. igniventris*, but, for *S. latrans*, its relationship with area was positive, while for *A. igniventris*, the relationship was negative. Finally, the abundance of two species classified as forest birds, *M. leucophrys* and *Sporagra magellanica*, was not associated with any of the variables included in the models (Table 4).

Mature *Polylepis* patches (PC I) and resistance were overall the most important characteristics associated with the abundance of generalist species (Table 5). The direction of the responses to these variables, however, varied among species (Table 4). Mature patch characteristics showed a positive association with the abundance of *Turdus fuscater* and *Leptasthenura andicola*, but was negatively associated with the abundance of *Ochthoeca fumicolor* and *Grallaria quitensis*. Increased patch connectivity presented a positive relationship with the abundance of *M. baroni* and *L. andicola*, but showed a negative relationship with *O. fumicolor*. Patch area presented a negative association with the abundance of *M. baroni* and *T. fuscater*. Species whose main habitat is páramo were not abundant enough to be evaluated by this modeling procedure.

TABLE 2. List of bird species registered and their mean abundances per point-count across 26 *Polylepis* forest patches in Cajas National Park, Ecuador. Scientific and English names follow the South American classification committee (Remsen et al. 2013).

Scientific name	English name	Code	Habitat affinity	Mean	SD
<i>Bubo virginianus</i>	Great Horned Owl	BUVI	Forest	0.011	0.12
<i>Glaucidium jardini</i>	Andean Pygmy-Owl	GLJA	Forest	0.004	0.06
<i>Oreotrochilus chimborazo</i>	Ecuadorian hillstar	ORCH	Páramo	0.015	0.14
<i>Chalcostigma stanleyi</i>	Blue-mantled thornbill	CHST	Forest	0.381	0.99
<i>Metallura baroni</i>	Violet-throated metaltail	MEBA	Generalist	0.470	1.06
<i>Aglaeactis cupripennis</i>	Shining sunbeam	AGCU	Generalist	0.041	0.26
<i>Cinclodes fuscus</i>	Buff-winged cinclodes	CIFU	Páramo	0.026	0.21
<i>Cinclodes excelsior</i>	Stout-billed cinclodes	CIEX	Páramo	0.004	0.06
<i>Leptasthenura andicola</i>	Andean Tit-Spintail	LEAN	Generalist	0.119	0.49
<i>Asthenes flammulata</i>	Many-striped canastero	ASFL	Páramo	0.004	0.06
<i>Asthenes griseomurina</i>	Mouse-colored thistletail	ASGR	Forest	0.211	0.69
<i>Margarornis squamiger</i>	Pearled treerunner	MASQ	Forest	0.404	1.22
<i>Grallaria quitensis</i>	Tawny antpitta	GRQU	Generalist	0.189	0.60
<i>Scytalopus latrans</i>	Blackish tapaculo	SCLA	Forest	0.126	0.56
<i>Mecocerculus leucophrys</i>	White-throated Tyrannulet	MELE	Forest	0.737	1.77
<i>Agriornis montanus</i>	Black-billed Shrike-Tyrant	AGMO	Páramo	0.004	0.06
<i>Cnemarchus erythropygius</i>	Red-rumped Bush-Tyrant	CNER	Generalist	0.033	0.21
<i>Ochthoeca fumicolor</i>	Brown-backed Chat-Tyrant	OCFU	Generalist	0.389	0.99
<i>Troglodytes solstitialis</i>	Mountain wren	TRSL	Forest	0.004	0.06
<i>Cistothorus platensis</i>	Sedge wren	CIPL	Generalist	0.004	0.06
<i>Turdus fuscater</i>	Great thrush	TUFU	Generalist	0.256	0.88
<i>Anisognathus igniventris</i>	Scarlet-bellied Mountain-Tanager	ANIG	Forest	0.115	0.53
<i>Dubusia taeniata</i>	Buff-breasted Mountain-Tanager	DUTA	Forest	0.037	0.24
<i>Oreomanes fraseri</i>	Giant conebill	ORFR	Forest	0.222	0.85
<i>Xenodacnis parina</i>	Tit-like dacnis	XEPA	Forest	0.541	1.59
<i>Diglossa humeralis</i>	Black flowerpiercer	DIHU	Forest	0.026	0.23
<i>Phrygilus unicolor</i>	Plumbeous Sierra-Finch	PHUN	Páramo	0.022	0.21
<i>Catamenia inornata</i>	Plain-colored seedeater	CAIN	Páramo	0.007	0.09
<i>Myioborus melanocephalus</i>	Spectacled redstart	MYME	Forest	0.026	0.23
<i>Sporagra magellanica</i>	Hooded siskin	SPMA	Forest	0.341	1.24

TABLE 3. Multi-model averaged weights, coefficient estimates, and standard errors of the patch variables and connectivity that explained variation in bird species richness of *Polylepis* forest patches in Cajas National Park, Ecuador. Important variables were selected based on Akaike weights (w_i) and value of the coefficient estimates.

Species	Factors	$\sum w_i$	Coefficient	SE
Total richness (Chao1)	Patch area	0.942	2.55	0.847
Rarefied richness	Patch area	0.824	0.777	0.298
	<i>Gynoxys</i>	0.692	0.700	0.320

COMMUNITY RESPONSES.—The NMDS final optimum solution in 3-D ordination explained 82.2 percent of the variance (stress = 14.3). The correlation of the environmental variables with the spatial configuration of patches in the NMDS revealed that mature patch characteristics (PC I) ($R^2 = 0.23$, $P = 0.03$) and

abundance of *Gynoxys* ($R^2 = 0.36$, $P = 0.01$) were the environmental factors associated with the differences in bird community composition among patches (Fig. 1). The ordination depicted forest species on the left of the plot, generalist species spread in a central position, and páramo species on the right of the plot (Fig. 1). The MRPP result supported the interpretation that forest, generalist, and páramo species occupied different space in the ordination ($T = -3.498$, $A = 0.052$, $P = 0.008$).

DISCUSSION

Polylepis forest is a critical habitat for high altitude Andean birds and other animals (Gareca et al. 2010). In many places, however, the remaining forest patches exhibit high fragmentation and habitat loss, which may alter the ecological processes influencing the distribution and abundance of animals dependent on *Polylepis* forest. We found that avian species richness in *Polylepis* forest was probably influenced by patch area and floral composition

TABLE 4. Multi-model averaged weights, coefficient estimates, and standard errors of the most important patch variables and connectivity that presented relationships with the abundance of different bird species in *Polylepis* forest patches in Cajas National Park, Ecuador. Important variables were selected based on Akaike weights (w_i) and coefficient estimates.

Species by groups	Factors	$\sum w_i$	Coefficient	SE
Forest				
<i>Chalcostigma stanleyi</i>	<i>Gynoxys</i>	0.860	0.273	0.113
<i>Asthenes griseomurina</i>	Resistance	0.708	0.271	0.133
<i>Margarornis squamiger</i>	<i>Gynoxys</i>	0.997	0.550	0.128
<i>Scytalopus latrans</i>	Patch area	0.834	1.032	0.197
	PC I	0.741	0.965	0.253
<i>Mecocerculus leucobryis</i>	(none)			
<i>Oreomanes fraseri</i>	<i>Gynoxys</i>	0.714	0.358	0.114
	PC I	0.469	0.170	0.098
<i>Xenodacnis parina</i>	PC I	0.999	0.929	0.206
	<i>Gynoxys</i>	0.998	0.651	0.135
	Resistance	0.651	-0.282	0.162
<i>Anisognathus igniventris</i>	Resistance	0.687	-1.229	0.545
	PC I	0.630	0.875	0.584
	Patch area	0.627	-1.162	0.845
<i>Sporagra magellanica</i>	(none)			
Generalist				
<i>Metalura baroni</i>	Patch area	0.511	-0.145	0.090
	Resistance	0.500	-0.151	0.109
<i>Leptasthenura andicola</i>	Resistance	0.687	-1.220	0.842
	PC I	0.629	0.875	0.584
<i>Ochthoeca fumicolor</i>	Resistance	0.873	0.259	0.104
	PC I	0.547	-0.187	0.012
<i>Turdus fuscater</i>	PC I	0.878	0.414	0.173
	Patch area	0.869	-0.372	0.150
	PC II	0.622	0.296	0.170
<i>Grallaria quitensis</i>	PC I	0.900	-0.360	0.141

(i.e., presence of *Gynoxys* plants). At the species level, there were multiple responses, but forest structure, connectivity, and abundance of *Gynoxys* were important predictors for the majority of species. Our results suggest that while parameters that can often be easily measured from remote-sensing imagery can provide some insights into what influences bird distributions in fragmented landscapes, field based measures, such as plant species composition, may be essential for effective management.

SPECIES RICHNESS.—In Cajas National Park, we found a positive relationship between area and species richness. The increase in species richness with area is a well-known relationship in ecology (MacArthur & Wilson 1967), and has been documented in a variety of tropical habitats including lowlands (Bierregaard *et al.* 1992, Arriaga-Weiss *et al.* 2008) and montane forest (Aubad *et al.* 2010), although a relationship between species richness and area in *Polylepis* forest has not been consistently demonstrated (Fjeldsá 1993). For example, in the Peruvian Andes, Lloyd (2008b) found

TABLE 5. Summary of the result of the multi-model averaged procedure that analyzed associations of the abundances of 14 bird species with different patch level variables and connectivity in *Polylepis* forest patches in Cajas National Park, Ecuador.

Factors	Number of species showing important responses to the factors			
	Habitat preference			
	Forest ($n = 9$)		Generalists ($n = 5$)	
	(+)	(-)	(+)	(-)
PC I	4	0	2	2
PC II	0	0	1	0
<i>Gynoxys</i>	4	0	0	0
Patch Area	1	1	0	2
Shrub diversity	0	0	0	0
Resistance	1	2	1	2

fairly similar species richness among *Polylepis* patches of different sizes. This difference is interesting, given that the avifauna of *Polylepis* forest in Peru is generally more species-rich (Fjeldsá 1992) than *Polylepis* forests at higher latitudes in other Andean countries. The contrasting result between the study by Lloyd and ours might be a consequence of the much larger patches considered in Peru; large patches in Peru ranged from 12 to 31 ha, while our largest patch included in the analysis was ~ 6 ha. More studies of species–area relationships in *Polylepis* patches in other regions may be required to clarify the relationship of species richness and area in this high-altitude vegetation type.

The models of rarefied species richness, which allow comparisons among patches with different sampling effort (Gotelli & Colwell 2001, Martensen *et al.* 2012), showed that besides area, the abundance of *Gynoxys* plants was an important predictor of species richness. In the high Andes, *Gynoxys* occurs as shrubs or trees within, and on the edge of, *Polylepis* patches (Fjeldsá 1992, Kessler 2006). *Gynoxys* hosts a large variety of arthropods, which are likely a resource for many species of birds (Fjeldsá & Krabbe 1990). *Gynoxys* also secretes sugary drops on the underside of its leaves (Fjeldsá 1992, Aguilar & Iníguez 2011), where we observed several bird species actively foraging, including *C. stanleyi*, *M. baroni*, *M. squamiger* and *X. parina*. There are few studies on the population dynamics of any plant species in *Polylepis* forest. However, according to Cierjacks *et al.* (2008b), the genus *Gynoxys* is less affected by burning than *Polylepis*, which may result in an increase in the abundance of *Gynoxys* plants in areas influenced by fires. Nevertheless, as there are no detailed reports of the frequency or distribution of fires, or any other disturbance effect in the Cajas area, we are unable to explain differences in the abundance of *Gynoxys* among patches. Future work in this habitat should focus on how high-altitude birds use the different *Gynoxys* plant species to clarify its importance for the maintenance of species diversity. Other studies have also shown that the presence of a particular plant species can explain variation in bird species richness

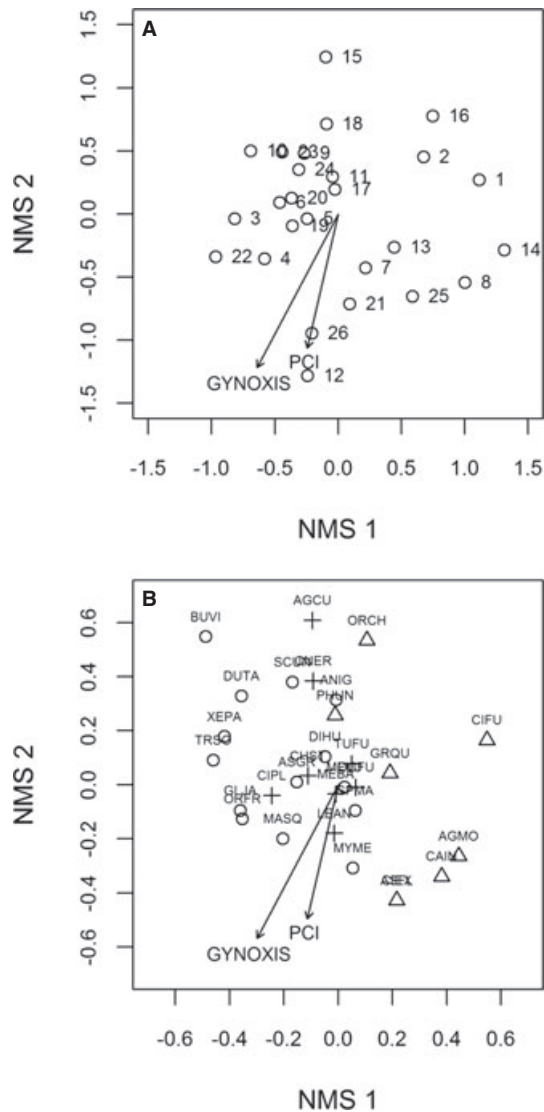


FIGURE 1. Non-metric multidimensional scaling (NMDS) of (A) 26 *Polylepis* forest patches, and (B) weighted average scores of bird species of the avian community in Cajas National Park, Ecuador. It includes significant ($P < 0.05$) correlations with environmental variables. In (B), open circles represent species associated with forest, open triangles are species associated with páramo, and crosses represent species classified as generalist. Species codes are listed in Table 2.

(Estades 1997, Hurlbert 2004, Tews *et al.* 2004). The identification of such species is particularly important for conservation and management because their presence could be a key to maintain species diversity.

SPECIES ABUNDANCES.—We found that the abundance of the majority of forest species was associated with mature patch characteristics and the abundance of *Gynoxys* plants, which probably confer more resources and shelter for birds. Lloyd (2008a) also found a positive correlation between the abundance of birds occupying *Polylepis* patches and vegetation structure. Hence,

Polylepis patches that combine a complex physical structure with the presence of *Gynoxys* may be important to maintain populations of forest birds in *Polylepis* woodlands.

In fragmented landscapes, patches that are close to each other may permit movement among patches, and as a consequence, increased resource availability (Uezu *et al.* 2005, Boscolo & Metzger 2011), and this has been also shown to be the case in *Polylepis* forests (Lloyd & Marsden 2008). We found that four species, *X. parina*, *A. igniventris*, *M. baroni* and *L. andicola*, were more abundant in more connected patches. Interestingly, although the effects of isolation are predicted to be stronger for forest specialist species (Martensen *et al.* 2008), one half of the species (*M. baroni* and *L. andicola*) that responded positively to connectedness were habitat generalists. This finding suggests that in high-altitude ecosystems, some species require resources from multiple habitats to maintain their populations (see also Tinoco *et al.* 2009, Latta *et al.* 2011).

Overall, area was only a weak predictor of the abundance of the studied species, and area was positively associated with the abundance of a single species, *S. latrans*. Lloyd (2008a) found a positive response of the abundance of several species to patch area in *Polylepis* fragmented landscapes. Among the species covered in that study were two species also analyzed here, *O. fraseri* and *X. parina*. The lack of correspondence of our results with the study by Lloyd (2008a) could be related to geographical variation in ecological requirements and the behavior of *Polylepis* bird species (Servat 2006, Lloyd 2008c). Another possible explanation, which considers the larger patches sampled by Lloyd (2008a), is that the relationship between abundance and patch area may only be detectable above a certain patch size threshold. If the latter is the case, our sampled patches may have simply been too small to detect a patch area effect on abundance. Our finding of a lack of response of species abundances to area may underscore the importance of large patches for species conservation. However, patch area will affect overall population size of species supported in a patch (Ewers & Didham 2006), and as such, large patches should be considered an important component for the long-term persistence of populations in *Polylepis* forests.

Our finding of a positive relationship between abundance of *O. fraseri* and *Gynoxys* plants is also noteworthy. *Oreomanes fraseri* is a *Polylepis* specialist that forages for insects in the bark of *Polylepis* (Servat 2006). While *O. fraseri* may be feeding on insects associated with *Gynoxys*, this has not been observed, and alternatively, our finding could be related to a condition of the forest rather than a direct response to the resources provided by *Gynoxys*. *Gynoxys* is a co-dominant plant species in some *Polylepis* forest patches (Minga *et al.* 2008), and therefore its presence may probably increase the overall heterogeneity of a patch and indirectly influence the abundance of some birds.

In general, the variables we used successfully captured the variation in bird abundances among patches. There were two species, *M. leucophrys* and *S. magellanica*, however, which did not respond to any of the variables included in the models. A possible explanation is that these species simply have broad ecological requirements (Fjeldsø & Krabbe 1990, Servat 2006). The lack of

response of these species could also be related to the influence of other environmental characteristics not included in our analysis that may influence the abundance of bird species. In Perú, Lloyd (2008a) found that the slope of the terrain and the type of ground coverage were correlated with the abundance of certain species in *Polylepis* forest. We did not quantify these variables in our patches because our landscape was relatively homogeneous. However, these variables should be considered in more heterogeneous landscapes to improve our understanding of the responses of birds to ecological characteristics of *Polylepis* forest.

CONSERVATION IMPLICATIONS.—We found that *Polylepis* patches with mature tree characteristics are particularly important for forest birds in the high Andes, as it has also been shown in Peru and Bolivia (Cahill & Matthyssen 2007, Lloyd 2008a,b). Moreover, we found that some bird species that are less common in isolated patches (e.g., *X. parina*, *M. baroni*). Conservation efforts should also focus on regulating activities such as wood extraction, grazing and fires in páramo, which can negatively affect the vegetation and spatial distribution of *Polylepis* patches (Renison *et al.* 2006, Cierjacks *et al.* 2008a).

After decades of replanting deforested highland habitats with pines and eucalyptus, restoration with *Polylepis* has recently become popular in the high Andes (Renison *et al.* 2005). However, *Polylepis* patches are not single-species forests; and other plant species probably play key roles in maintaining the ecological dynamics and diversity in *Polylepis* forest. Here, we show that the presence of *Gynoxys* plants may influence the diversity and abundance of birds in this habitat. This result exemplifies that more effort should be put into studying the ecology of *Polylepis* forest to effectively guide conservation practices for this threatened habitat.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Location of studied *Polylepis* forest patches in Cajas National Park, Ecuador.

TABLE S1. Information about the sampling effort and descriptor variables of the 26 patches of *Polylepis* forest survey in Cajas National Park, Ecuador

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