Influences of succession and erosion on bird communities in a South American highland wooded landscape

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ABSTRACT

In South American highland forests, domestic grazing can cause major changes in forest structure and soil quality thereby altering resources available to avian communities. However, the consequences of changes in variability in plant growth forms after disturbance are little known. Understanding forest succession effects on avifauna is critical though, given that area in secondary forests is expected to increase in the future. We sampled bird communities at 172 sample points in *Polylepis* shrublands and forests patches in Argentina. For each of these points, we calculated vegetation variables (NDVI, NDVI texture indices), landscape pattern variables (patch area and connectivity), and human disturbance variables (erosion, distances to settlements and roads), based on a Landsat 5 TM image, a local land cover map, and topography (slope and altitude) from a Digital Elevation Model. Bird communities in *Polylepis* forests included approximately twice as many species and double the abundance than those in shrublands. Species composition strongly differed between the two growth forms as well, birds that use the ground vegetation to nest and forage were less abundant in shrubland patches, air foragers were also less abundant in shrubland patches. Soil erosion, proximity to human settlements and forest isolation were the best predictors of bird richness and abundance in *Polylepis* vegetation patches. Abundance of birds that use the ground for nesting and foraging were negatively related to soil erosion. We concluded that *Polylepis* avifauna communities are primarily influenced by human impact on soils rather than by vegetation structural characteristics. *Polylepis* vegetation restoration and reduction of livestock grazing would likely reduce soil erosion rates, promote natural regeneration, increase patch connectivity and enhance microhabitat conditions for avifauna in high-altitude *Polylepis* forests and shrublands.

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1. Introduction

Livestock grazing plays an important role in the dynamics of mountainous forest ecosystems in South America (Vera, 2000; Cingolani et al., 2005, 2008). Livestock grazing may be necessary to maintain ecosystem structure and function if the native wild herbivore populations are decimated or extinct or if herbivores presence is ancient in the ecosystem (Cingolani et al., 2005, 2008, 2014). However, if the ecosystem is maintained at commercially optimal stocking rates (i.e. high grazing pressure), it may be seriously affected (Cingolani et al., 2013, 2014). Large herbivore grazing alters tree survival and growth form, prevents shrublands from succeeding to forest, and may maintain grasslands in sites where

forests could grow (Vera, 2000; Renison et al., 2006; Giorgis et al., 2010; Marcora et al., 2013). Overgrazing also induces soil erosion and with it loss of litter cover, seed banks, soil nutrients, water infiltration, and soil chemical properties (Renison et al., 2010; Hiltbrunner et al., 2012). This ultimately changes landscape configuration and functionality, thereby affecting available resources for native fauna and consequently faunal abundance and richness (Waltert et al., 2004).

Birds have been used as bio-indicators of land cover integrity in many ecosystems; because they provide services (e.g. seed dispersal, pest control, pollinitation) that are essential for ecosystem functioning and sustainability (Ogada et al., 2008). When distinct ecosystems, such as forests, are lost or altered, the ecological roles of birds change (Sekercioglu et al., 2004). Soil erosion adversely affects forests by modifying soil organic content, water penetrability, and vegetation cover. These changes in turn, strongly affect presence and abundance of different plant species, and aerial and

soil invertebrates. As a result, both food availability for insectivorous birds (Molina et al., 1999; Gilroy et al., 2008; Bellis and Muriel, in press) and nesting substrates (e.g. Neave et al., 1996; Wilson et al., 2005) are reduced. This makes it important to understand the relative roles of grazing and soil erosion as causal factors of changes in bird communities in highland forest systems that are grazed, in order to inform conservation strategies (Quesada et al., 2009).

The highland forests in central Argentina is a site of international importance for bird conservation (Fjeldså, 1993; Herzog et al., 2003; Cahill and Matthysen, 2007; Lloyd and Marsden, 2008). The forest is an Important Bird Area (IBA – AR 161, *sensu* Birdlife International, 2014a) and located within an Endemic Bird Area (EBA 058, *sensu* Birdlife International, 2014b). In this region, wooded highlands (~1700–2800 m asl) are dominated by *Polylepis australis* forests. The genus *Polylepis* is endemic to South America, where it forms almost all tropical tree lines. Unfortunately, *Polylepis* forest is considered to be among the most endangered tropical and subtropical mountain ecosystems in the world (Fjeldså and Kessler, 1996; Gareca et al., 2010) and the majority of the ca. 30 species of the genus are classified as vulnerable (Toivonen et al., 2011). Currently, *Polylepis* forest remain only as scattered remnant patches of a once more continuous distribution, and are largely restricted to ravines and rocky outcrops where the impact of livestock grazing and anthropogenic burning is low (Fjeldså and Kessler, 1996; Kessler, 2002; Renison et al., 2006; Cingolani et al., 2008; Gareca et al., 2010). Mature *P. australis* forests typically are characterized by considerable volumes of standing and dead wood, a dense fern understory and presence of the *Maytenus boaria*, a shade tolerant tree species (Renison et al., 2011), but such forests are increasingly rare.

Polylepis shrubland is an early stage on the successional path to *Polylepis* forests. *Polylepis* shrubland is maintained in shrub form by browsing and by frequent anthropogenic fires in the majority of the species' range (Cabido and Acosta, 1985; Fjeldså and Kessler, 1996; Renison et al., 2006; Cingolani et al., 2008; Giorgis et al., 2010; Marcora et al., 2013) and is often accompanied by widespread soil erosion (Renison et al., 2006; Cingolani et al., 2008; Gareca et al., 2010; Toivonen et al., 2011). The structure of shrub and tree forms of *Polylepis*, and resources available for avifauna, differ considerably (Teich et al., 2005; Cingolani et al., 2008). In *Polylepis* shrublands, grazing pressure is higher and erosion is more active (Cingolani et al., 2004). Moreover, lower overstory, tree basal area and vertical complexity (Renison et al., 2011), combined with the reduction of associated vines, ferns and other understory plants, affects nesting and foraging resources available to avian *Polylepis* specialists (Fjeldså, 1993). However there is no information about the conservation value of *Polylepis* shrubland for native birds. Conversion of *Polylepis* forest to shrubland has, to date, been linked with changes in avifauna distribution and habitat availability only at the scale of individual patches of forests (e.g. Fjeldså and Kessler, 1996; Kessler et al., 2001; Herzog et al., 2003; Cahill and Matthysen, 2007; Lloyd and Marsden, 2008, 2011; Bellis et al., 2009, 2014; Tinoco et al., 2013), and no studies have addressed the combined influence of changes in vegetation structure (defined as variability in plant growth forms) and extensive soil erosion on the bird community.

Our goal was to evaluate relationships between vegetation structure (measured as variability of above-ground biomass), soil erosion, and spatial arrangement of *Polylepis* patches and characteristics of bird communities. Unlike previous studies on *Polylepis* birds that used only vegetation data at the local or point scale, we considered information at broad and fine scales simultaneously using texture measures, an effective tool for characterizing vegetation from remotely sensed data. Texture variables are indexes related to both between-vegetation patches and within-vegetation

patches structures (Bellis et al., 2008; St Louis et al., 2009), and have been successfully used to model birds in different environments such as savannas (Wood et al., 2013), forests (Culbert et al., 2012; Wood et al., 2013), grasslands (Bellis et al., 2008), and desert scrub ecosystems (St-Louis et al., 2009). Recent studies showed that image textures were better predictors of avian richness than field-measured vegetation structure (Wood et al., 2013), and could be used to map species richness over larger areas, such as *Polylepis* forests, where limited access make it difficult to measure traditional forest variables in the field.

In this study we addressed the following questions: (1) Are there differences in bird species richness and assemblage structure between *Polylepis* forests and shrublands? (2) What are the main vegetation attributes associated with these bird communities? (3) Does bird assemblage structure within *Polylepis* forest and shrubland have implications for vegetation management and conservation strategies?

2. Methods

2.1. Study area

Our study was conducted in the upper vegetation belt of the Sierras Grandes of Córdoba (Central Argentina, 1,700–2,800 masl, 31°34′S, 64°50′W; 124,700 ha), in "Quebrada del Condorito" National Park (26,000 ha) and two adjacent designated water reserves (National 12,000 and Provincial 117,000 ha). Vegetation consisted of a mosaic of tussock grasslands, *P. australis* woodlands and shrublands, grazing lawns, granite outcrops and eroded areas with exposed rock surfaces (Cingolani et al., 2004). The first humans settled in the area about 8000 years ago and altered the environment by using fire for hunting (Berberián, 1999; Pastor, 2000). Since early European settlements (~400 years ago) *Polylepis* forests have been affected by logging and fire to create grazing grounds for horses, sheep, goats, and cattle (Díaz et al., 1994). In 1997, "Quebrada del Condorito" National Park and the water reserves were created to reduce soil erosion and protect vegetation in order to maintain water-holding capacity. However, the water reserves are under private ownership, traditional livestock practices continue, and soil erosion remains a severe problem in most of the area (Cingolani et al., 2008; Renison et al., 2010).

Forests (characterized by tree-form *Polylepis*) currently occupy 2.5% (3157 ha) of our study area (Cingolani et al., 2008). In Sierras Grandes of Córdoba, *P. australis* attains a height of up to 14 m and lives up to 120 years (Suárez et al., 2008; Renison et al., 2011). The rare patches of mature *P. australis* possess several attributes found nowhere else in these mountain ecosystems, such as a relatively high volume of standing and down dead wood (19.5 m³/ha on average), a dense fern understory (up to 30% cover), many fungus species, overstory of approximately 72%, and presence of many *Maytenus boaria*, a rare shade-tolerant tree species (Renison et al., 2011).

Shrublands dominated by *Polylepis* occupy 9.4% (11,674 ha) of the area and are mixed with grasslands and rocky outcrops, both natural and resulting from erosion. Shrublands show different degrees of disturbance, and usually have overstory of ⩽23%, little standing or down dead wood (<3 m³/ha), low fern cover (<7%), few *Maytenus boaria* trees (<6 individuals/ha), an average shrub height of ⩽5 m, and an average age ~47 years (Renison et al., 2011).

2.2. Bird Surveys

Bird data were collected during two breeding seasons (January 18 to March 19 2006, and October 20 2007 to March 30 2008) when bird species richness peaks due to presence of both migrant

and resident breeding species. Bird species richness was estimated using standard point count techniques. One observer (SD) recorded all birds seen and heard within a 50-m radius for 10 min (Bibby et al., 1992). At each point, the observer waited 5 min before starting the count to minimize the observer impact on bird behavior (Bibby et al., 1992). A total of 172 sample point-count stations were located randomly (105 in forests and 67 in shrublands), at least 150 m apart, to avoid double counting the same bird at neighboring points. Sampling points were located as close to the center of each *Polylepis* patch (shrubland or forest) as possible. In the majority of *Polylepis* patches, there was one sampling point per patch. In a few extensive patches in ravines, we were able to count at two points that were surrounded by approximately 150 m of *Polylepis*. The difference in the number of sampling points between forest and shrubland patches was due to differences in availability of large patches. Heterogeneity of *Polylepis* shrublands, which are intermingled with grasslands and rocky outcrops (see above), results in considerable variation in overstory cover among patch sizes. Thus, patch was reclassified based on% of overstory cover, which differed from the original size classification. Based on the classification of Renison et al. (2011) we considered a single shrubland patch to be an area of distinguishable borders with overstory cover of ⩾23%. In the case of forests, we considered a single forest patch as an area with distinguishable borders and overstory cover ⩾60%. This method of overstory cover approximation correlates well with above-ground biomass (Peek, 1970) and has been used to describe effects of patch size on avian foraging behavior in tropical forests (Morrison et al., 2010).

Birds counts were conducted twice at each point in each breeding season, always during favorable weather conditions (minimal wind and no rain), and usually between dawn and 11 am or 3 pm to 5 pm local time, for a total of 4 counts at each point over the course of the study. Nocturnal species and species that flew over the *Polylepis* patch without landing (e.g., *Vultur gryphus*) were not considered. We varied the order of counts, so that at least one of the four point counts was conducted during early morning hours and one during the afternoon. Bird taxonomic names follow Remsen et al. (2011).

2.3. Independent variables

We calculated independent variables (i.e. human disturbance indicators and vegetation variables) for the entire study area, using ENVI GIS (ENVI, 2004). The specific techniques used to calculate each independent variable is explained below. All independent variables (texture indexes, slope, altitude, connectivity, etc.) were available in raster format with 30-m resolution. For each bird sampling points, we had global positioning system locations. We thus extracted the pixel value for each independent variable at the location of each bird surveys points.

2.3.1. Polylepis structure and heterogeneity

For vegetation analysis we used a cloud-free spring Landsat 5 TM image (November 20 2005, Path 229; Row 082; covering the entire 364,000 ha study area), provided by CONAE (Comisión Nacional de Actividades Espaciales). Geo-referencing (to UTM 20 South projection, WGS-84 datum) was carried out by matching the CONAE satellite image to an already rectified 2010 Landsat 5 TM L1T image (obtained from the United States Geological Survey Earth Resources Observation and Science data center; USGS EROS; http://edc.usgs.gov), and resampling with the nearest neighbor algorithm. Georeferencing error was 0.26 pixels (7.8 m), which we deemed acceptable given that the data analysis was performed in moving windows of 7×7 pixels (see below for details).

As a proxy for above-ground biomass, we calculated the Normalized Difference Vegetation Index (NDVI, Paruelo et al.,

1997). Based on the NDVI image, we then calculated NDVI texture values to characterize the distribution of plant biomass. Specifically, we calculated three texture measures of NDVI that predict bird species richness well in open overstory patches: mean, contrast and homogeneity (St-Louis et al., 2009). Mean texture represents the average distribution of image elements (Dong-Chen and Wang, 1990), high mean values indicate greater plant productivity, and we used this measure as a proxy for resource availability. Texture contrast is a measure of pixel value variation and is an indicator of spatial heterogeneity of green plant biomass. Textural homogeneity takes into account the spatial arrangement of pixels (Baraldi and Parmiggiani, 1995; Tuttle et al., 2006), and we employed it as an estimate of the dispersion of green plant biomass. Homogeneity provided a measure of resource concentration (Table 1). NDVI texture was calculated at several scales ranging from 3×3 pixels (0.81 ha), to 7×7 pixels (4.41 ha), and ultimately 11×11 pixels (10.89 ha), in order to determine the scale at which plant biomass distribution pattern was most strongly related to avian community metrics. For our multivariate models we ultimately used the 7×7 pixel (4.41 ha) NDVI measures because univariate models indicated the strongest relationship with overall species richness at this scale. NDVI texture at this scale also explained occurrence of seven forest bird species in Maine (Hepinstall and Sader, 1997) as well as birds of the Chihuahuan Desert (St Louis et al., 2009).

2.3.2. Topography

We estimated altitude (meters above sea level), and slope (degrees), at the same resolution as texture variables, i.e. 7×7 pixels of 30-m resolution (4.41 ha), based on a Digital Elevation Model (DEM; provided by CONAE) (Table 1).

2.3.3. Polylepis patch configuration

Based on an existing vegetation classification of Sierras Grandes land cover, which has 87% post-classification accuracy (Cingolani et al., 2004). We created two maps: one for *Polylepis* forests and

Table 1
Independent variables calculated in *Polylepis* forests and shrublands of central Argentina (See text for details).

Independent Variables	N pixel resolution/areal analyses extent (ha)	Description
Human disturbance indicators		
Soil erosion	$7 \times 7/4.41$	% eroded areas and bare rock erosion pavements
Distance to human settlements	1/0.09	Distance to nearest house (m)
Distance to roads	1/0.09	Distance to nearest road (m)
Vegetation patches configuration		
Area density	$33 \times 33/98$	% pixels dominated by *Polylepis*
Connectivity	$79 \times 79/562$	% probability of pixel to be *Polylepis*
Vegetation patches productivity and heterogeneity		
NDVI	1/0.09	Proxy for plant productivity
Index of Texture_mean	$7 \times 7/4.41$	Proxy for resource availability in the study area
Index of Texture_homogeneity	$7 \times 7/4.41$	Measures of resource concentration
Index of Texture_contrast	$7 \times 7/4.41$	Indicator of biomass diversity
Topography		
Elevation	1/0.09	Estimated from DEM (m)
Slope	$7 \times 7/4.41$	Estimated from DEM (degrees)

one for *Polylepis* shrublands. For each map we calculated patch sizes and frequency, and two measures of landscape configuration: area density and connectivity (Riitters et al., 2002). Area density of *Polylepis* is defined as the proportion of pixels dominated by *Polylepis.* Connectivity measures the conditional probability that a pixel adjacent to a *Polylepis* pixel is also *Polylepis*. Larger values of area density and connectivity indicate larger patch area and closer proximity to *Polylepis*, respectively (Riitters et al., 2002; Table 1). These metrics facilitated tailoring the interpretation of landscape configuration according to functional group by explicitly incorporating spatial scale (Riitters et al., 2002). We measured density and connectivity within 6 different moving window sizes ranging from 33 × 33 pixels to 79 × 79 pixels. Smaller window sizes are more sensitive to finer-scale (or higher spatial frequency) patterns; larger window sizes are more sensitive to coarser-scale (or lower spatial frequency, Riitters et al., 2002). After inspecting a correlation matrix to determine the scale most strongly associated with avian patterns, we retained the scale of 33 × 33 pixels (98 ha) for area density and of 79 × 79 pixels (561.7 ha) for connectivity.

2.3.4. Human disturbance

As proxy measures for long-term livestock impact, and historical human impact on soils, we estimated percentage of eroded areas and distance to roads and human settlements (Cingolani et al., 2008; Renison et al., 2011). As a proxy for the current livestock stocking rate we used three categories of grazing: high, moderate, and none (in the National Park) following Renison et al. (2006). These measures approximate factors ultimately affecting vegetation structure, but unfortunately more precise information related to livestock management was lacking (Cingolani et al., 2008).

Based on the Sierras Grandes land cover map (Cingolani et al., 2004), we also measured erosion by combining two erosion classes from the map: a) erosion and outcrops (30,572 ha; 24.5% of the total area), defined as a mosaic of rocky outcrops and eroded stony grasslands and rock pavements, with small fully vegetated patches, and b) erosion pavements (6,426 ha; 5.2% of the total area), defined as areas with more than 80% of the surface covered by flat, bare rock erosion pavements (Cingolani et al., 2004). Eroded areas are easily differentiated from natural outcrops due to surrounding erosion gullies and sparse lichen cover (Cingolani et al., 2004). The proportion of eroded land was summarized for each 7 × 7 pixel (4.41 ha) moving window and assigned to the central pixel (Table 1). Lastly, we estimated the distance to roads and distance to settlements as two continuous variables (Table 1) from Sierras Grandes roads and settlements maps.

3. Data analysis

In order to characterize the bird community we calculated species richness, total abundance (N), and the proportional abundance of each bird species expressed as abundance of the species divided by total abundance (ni/N). We were not able to adjust abundance of each species according to its detectability because we had low abundances across all species sampled and this precluded the use of procedures like Distance sampling (Buckland et al., 2001). Instead, we used relative abundances at point counts, which have good performance when used with high number of replicates (Newell et al., 2013), although we acknowledge it can only be used for comparisons between the conditions studied and not to make inferences about the absolute density of the species. To adjust for differences in species detectability we compared species richness between *Polylepis* growth forms using rarefaction curves. Rarefaction analysis calculates species richness after standardizing differences in abundance among samples by estimating the

expected number of species of each sample if all samples were reduced to a standard size (Magurran, 2004). We used the coverage estimator suggested by Chao and Jost (2012), to develop comparable estimates of the number of species. We used the Mann Whitney U test (Quinn and Keough, 2002) to compare specific richness and abundances between bird communities and forest and shrubland patch attributes (Table 1).

We fitted multiple regression models to evaluate the contribution of selected vegetation variables in predicting species richness. Although species richness is an incomplete indicator of biodiversity, it is one straightforward way to describe community and regional diversity (Magurran, 2004) and widely used in ecological models of community structure (MacArthur and Wilson, 1967; Gotelli and Colwell, 2001; Magurran, 2004).

First, we conducted an exploratory analysis to verify that the assumptions of linear regressions were met, and tested for collinearity among vegetation variables (defined as Spearman's $r \geqslant 0.75$; Appendix B). In the case of the response variable, we log-transformed species richness (measured as the maximum number of species recorded per point count) to meet linearity assumptions. Because our main focus was to understand vegetation cover variables related to bird richness, rather than identify the single best explanatory model we used best subsets regression and hierarchical partitioning analysis to assess the importance of variables included in the models (Quinn and Keough, 2002).

Best subsets regression performs an exhaustive search of all possible models where the maximum number of predictors allowed is specified *a priori,* and ranks the models based on their Bayesian Information Criterion (BIC) values to obtain a subset of models that best explains response. Hierarchical partitioning examines all possible models and averages the improvement in fit for each predictor variable, both independently and jointly, across all models (Quinn and Keough, 2002).

We used 12 variables to run the models and considered the 20 best models explaining bird species richness obtained in each best subsets analysis. The best subset analysis indicated which variables were most commonly included in bird richness models and the hierarchical partitioning analysis indicated the proportion of variance explained by each variable relative to the total variance explained by the full model (Quinn and Keough, 2002). We checked for spatial autocorrelation of the model residuals using a semivariogram randomization analysis (Legendre et al., 2002) and did not detect spatial correlation in the models that we estimated.

Bird species were grouped into guilds by foraging strata and nest type (Appendix A) according to the literature (Parker et al., 1996; López de Casenave et al., 1998; Blendinger, 2005; Dardanelli et al., 2006). Foraging strata guilds included birds feeding in three strata: ground, foliage, and air (composed by flycatchers and other birds that catch their prey in the air). Nesting guilds included: open-nesting birds (open nest above the ground), closed-nesting birds (cavities and domed nests above the ground) and ground-nesting birds (any type of nest on the ground). We used Friedman test (Quinn and Keough, 2002) to check for differences in abundance of bird species per group between *Polylepis* forests and shrublands.

4. Results

4.1. Birds

We recorded a total of 28 bird species in *Polylepis* patches, eight of them were endemisms, two represented by full endemic species and six represented by local endemic subspecies (Appendix A). All birds recorded were native. Fourteen species were found exclusively in forest patches and 5 exclusively in shrublands

(Appendix A). *Polylepis* shrublands had lower bird species richness and abundance relative to forests (U = 4363, P = 0.01; Appendix A). We recorded about double the number of bird species and also double the individual abundance in forests than in shrublands. Only 34.5% of birds (10 species) were shared in both communities (Appendix A). Coverage-based rarefaction (Chao and Jost, 2012) showed very high and equivalent completeness for forest (98.3%) and shrubland (95.1%) sampling. Rarefaction analysis confirmed that our results were not an artifact of differences in the number of collected individuals (Fig. 1). Both *Polylepis* shrubland and forest were adequately and comparatively sampled.

4.2. Study area and patch characteristics

P. australis forests and shrublands exhibited significant differences in terms of their above-ground biomass, soil erosion and spatial pattern (Table 2). Forests had higher mean texture, texture contrast, and patch connectivity than shrublands, and less area of eroded soil and less texture homogeneity (Table 2).

Forest patches ranged from 0.32 to 263.6 ha with 92% of patches <10 ha. Most patches occurred below 2000 m a.s.l, and had a long narrow shape that followed the profile of ravines, but we also found some patches on flat sites at the bottom of ravines or on gentle slopes. Shrubland patch sizes ranged from 0.09 to 724 ha with 95% of patches <10 ha. Shrubland patches occurred on sites that were topographically similar to those of forests, and did not differ from forest patches in terms of their average distance to settlements and roads, area, NDVI, or elevation (Table 2).

4.3. Bird richness and relationship with Polylepis forms

Best subset and hierarchical partitioning analysis indicated that erosion (with negative effects), and distance to settlements and woodland connectivity (with positive effects) had the greatest predictive power to explain bird richness (Fig. 2). Local characteristics of forest and shrubland *Polylepis* growth-forms such as variation in structure and heterogeneity measured as spatial distribution of biomass (contrast and mean textures with positive effects) had the second highest predictive power. The remaining variables captured substantially less variance (Fig. 2).

Bird abundance in some guilds differed between *Polylepis* shrublands and forests. For example, ground foraging, air foraging, and ground nesting birds were significantly more abundant in forest (Table 3).
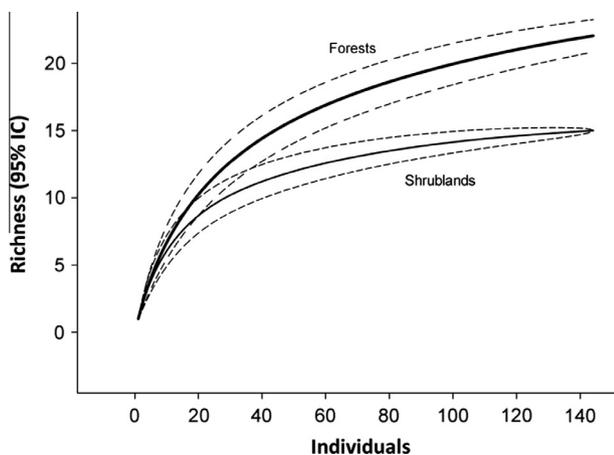

Fig. 1. Rarefaction curves for bird species richness in *Polylepis* forests and shrublands of central Argentina. Curves represent the expected species richness for different sample sizes.

Table 2
Independent variables used to characterize patches of *Polylepis* shrublands (n = 67) and forests (n = 105) of central Argentina.

Variable	Forests		Shrublands		P-value
	Mean	S. E.	Mean	S. E.	
Distance to human settlements (m)	2810	55.62	2302.98	167.7	0.5
Distance to roads (m)	386.35	46.87	613.38	71.71	0.07
Area density (%)	18	1	18	1	0.43
Patch connectivity (%)	85	35	77	1	<0.0001
Texture_mean index	41.94	0.24	36.48	0.31	<0.0001
Texture_homogeneity index	0.3	0.01	0.33	0.01	0.02
Texture_contrast index	21.62	1.23	13.85	0.91	<0.0001
NDVI index	0.31	0.02	0.30	0.01	0.69
Elevation (m)	1943.97	12.86	1936.61	17.03	0.43
Slope (degrees)	17.47	0.74	14.99	0.82	0.07
Erosion (%)	3	1	7	1	<0.0001

5. Discussion

Our results showed that shrublands, an early successional stage of forests, had lower bird richness and abundance relative to forests. However, the lower richness and abundance was largely attributable to human-caused erosion rather than differences in structural characteristics between forest and shrubland patches. Erosion, forest isolation, and nearness to human settlements were the main factors explaining lower bird species richness. Erosion can affect avifauna directly by reducing invertebrates and seeds for ground foraging birds (Woinarski et al., 1999; Wilson et al., 2005; Gilroy et al., 2008) and nesting resources for ground nesting birds (Hutto, 1985; Albanesi et al., 2014). Indirectly, lower vegetation cover may increase predation risk by interfering with birds detecting or escaping from predators (Whittingham and Evans, 2004; Whittingham et al., 2006). In the study area, soil erosion may have affected feeding and reproduction of birds thereby contributing to lower abundances of ground nesting and ground and air foragers such as the endemics *Catamenia inornata cordobensis, Cinclodes comechingonus, Phrygilus unicolor cyaneus,* and *Asthenes modesta cordobae* and potentially the absence of others bird species (Appendix A), as these species depend on ground level vegetation to nest and forage (del Hoyo et al., 2014). These results are consistent with those of García et al. (2008), who studied avifaunal changes in different vegetation units of the mountains of central Argentina under different grazing regimes. According these authors, endemic birds and overall bird richness and density were significantly lower in vegetation units with erosion than in those without. Other recent studies in the same region showed that habitat with a combination of higher soil penetrability, deeper litter stratum, and greater soil cover are preferred by the endemic long-tailed meadowlark (*Sturnella loyca obscura;* Bellis and Muriel, in press). However, worldwide, literature linking soil degradation and avian diversity loss is mainly restricted to farmland birds (e.g., Waltert et al., 2004; Donald and Evans, 2006; Gilroy et al., 2008) where soil quality loss due to agricultural intensification can be severe. Studies that quantify effects of erosion on bird communities in semi-wild environments are lacking. To the best of our knowledge, our study is unique in linking differences in bird richness and abundance to soil erosion and accumulated livestock pressure on *Polylepis* forests.

In the study region, the lack of a strong relationship between soil loss and topographic features is somewhat counterintuitive, but this may be the case because livestock avoids very steep slopes where most remaining *Polylepis* woodlands persist (Renison et al., 2010). In Southwest China mountains, long-term human disturbances also influenced soil degradation more than slope position did (Fu et al., 2004).
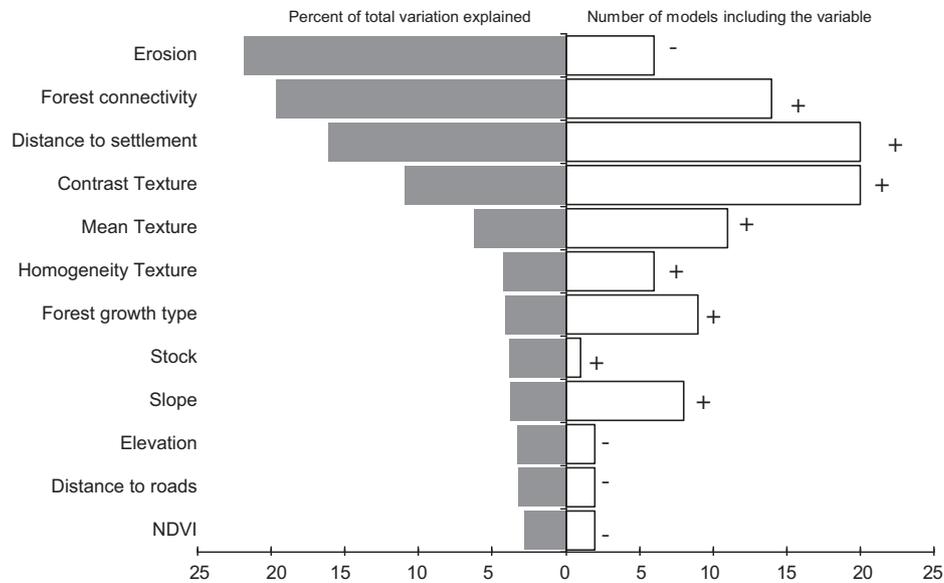
Fig. 2. Summary of regression analysis of bird species richness. White bars show results from the best subset analysis (number of times a variable entered the 10 best models). Grey bars represent the variability explained by each variable when all variables are included in the model, i.e., the results from the hierarchical partitioning analysis. Positive (+) and negative (−) indicate the direction of the relationship with bird species richness.

Table 3
Comparison of the mean abundance in each of the different bird groups between *Polylepis* shrublands and forests of central Argentina.

Guilds	Mean (± S. E.)		*P*-value
	Forest patches	Shurbland patches	
Foraging strata			
Air	5.41 (2.95)	1.94 (1.62)	<0.0001
Foliage	6.35 (2.68)	7.50 (2.96)	0.76
Ground	2.04 (0.65)	1.17 (0.56)	0.0031
Nest type			
Open nest	6.10 (2.62)	4.86 (2.80)	0.051
Closed nest	2.94 (0.78)	3.20 (1.20)	0.5554
Ground nest	2.89 (2.02)	1.21 (0.52)	<0.0001

Connectivity and patch size are key variables affecting biodiversity in many landscapes (Metzger, 2000; Dardanelli, 2006; Lindenmayer and Fischer, 2006; Lloyd and Mardsen, 2008; Martensen et al., 2008). Both theoretical and empirical evidence suggest that the spatial patterns of habitat for populations of some species are particularly important when the area in suitable patches (e.g., forest) occupies <30% of an area (Turner et al., 2001). Below this threshold, the effect of vegetation cover loss can be exacerbated and rapid losses of some species can occur (Turner et al., 2001; Radford et al., 2005). In the Sierras Grandes of Argentina, *P. australis* forests represented only 2.5% (3157 ha) of our study area and our models indicate that connectivity among forest patches is important. Given that *Polylepis* birds reduce flight frequencies with increasing patch isolation and regulate their movement patterns based on how they perceive the *Polylepis* shrublands and forests (Lloyd and Marsden, 2011), we speculate that there may be a compensatory effect between connectivity and area of *Polylepis* patches with similar structural characteristics.

As a result, forest patch aggregation could be a way to maintain larger forest bird richness, even if the overall proportion of *Polylepis* remains small. In *Polylepis* forests of Ecuador, greater patch size and connectivity benefited forest bird richness and species abundance (Tinoco et al., 2013), and a similar pattern was observed in the case of Brazilian Atlantic Forest avifauna (Martensen et al., 2008).

Proximity to human settlements also could have contributed to differences in bird communities. From a behavioral perspective, human presence is a source of disturbance of birds at the individual, population, and community levels. Animals trade off avoiding disturbance against activities that may increase fitness, such as foraging, mating, and parental care (Fernández-Juricic and Schroeder, 2003; Fernández-Juricic et al., 2004, 2005). Thus, the relationships between *Polylepis* growth form (forests versus shrublands) and tolerance of disturbance by humans may be related to the protective and obstructive properties of vegetation for different bird species. Studies in the mountains of central Argentina have shown that bird tolerance of human disturbance varies among bird species and depends on vertical vegetation structure. For example, tree height increased tolerance of *Z. capensis* and *C. maculosa* to human disturbance, most likely because taller trees provided more refuge from disturbance (Fernández-Juricic et al., 2004). Similarly, perch height, an important aspect of the vertical structure of vegetation, increased tolerance of the endemic birds *P. unicolor cyaneus* and *S. loyca obscura* to human disturbance (Fernández-Juricic et al., 2005). The proportions of shrublands often is high near settlements because *Polylepis* patches are frequently burned by humans and heavily browsed by livestock close to houses (Teich et al., 2005; Renison et al., 2006) increasing the soil impedance and salinity and reducing soil organic matter content (Renison et al., 2010).

Contrary to our expectations, differences in bird communities between forest and shrubland patches were not well explained by vegetation structure (as measured by NDVI texture measures). However, vegetation structure did contribute to the overall models of bird species richness and abundance. Bird species richness increased with vegetation structural heterogeneity and aboveground biomass (i.e. NDVI contrast and NDVI mean textures). Theory predicts that vegetation patches with a complex architecture provide more resources and opportunities for microhabitat segregation (MacArthur and MacArthur, 1961; MacNally et al., 2001; St Louis et al., 2009) resulting in a positive correlation between species diversity and structural diversity (MacNally et al., 2001). In *Polylepis* forests, a variety of elements contribute to vegetation structure including high plant species richness, a

structurally complex understory, a high density of large trees, ample ground cover, and high litter depth (Fjeldså and Kessler, 1996; Cahill and Matthysen, 2007; Lloyd, 2008; Lloyd and Mardsen, 2008, 2011). In *Polylepis* shrublands, the lack of structural features, such as high overstory, large tree basal area and tall trees (Renison et al., 2011), combined with a reduction in associated vines, ferns and other understory plants, affects nesting and foraging resources available to *Polylepis* birds (Fjeldså, 1993; Bellis et al., 2009, 2014). Similar to our study, Culbert et al. (2012) found that landscape composition were slightly superior to vegetation structure measures for explaining avian species richness. This supports the premise that vegetation structure is more effective in explaining bird species richness patterns over small to medium extents (Hutto, 1985; St Louis et al., 2009; Culbert et al., 2012; Wood et al., 2013) whereas landscape arrangement and productivity are more important at broad extents. Indeed, Rogers et al. (2009) demonstrated that in areas with long-lasting human disturbance, such as the Sierras Grandes of Central Argentina, landscape structure is a better predictor of biodiversity than local site conditions.

The importance of forest patches as reservoirs of avian biodiversity is well documented (e.g. Lindenmayer and Fischer, 2006; Dardanelli et al., 2006; Martensen et al., 2008; Tinoco et al., 2013) indicating that conservation of even small forest patches can help maintain a relatively high proportion of avian diversity associated with this structural class. *Polylepis* shrublands had lower avian species richness than forest patches, however, shrublands did provide habitat for some species not found in forest patches. Shrubland patches thus have value in its own right for bird species adapted for early successional vegetation (King and Schlossberg, 2014). However, given that *Polylepis* in both growth forms occupies such a tiny proportion of its former distribution, it is clear that increasing both extent and connectivity among patches would benefit both *Polylepis* forest and shrubland-associated bird species.

6. Management Implications

The area of *Polylepis* forests and shrubland in the mountains of central Argentina and in other highland mountains in South America has declined substantially relative to the times prior to European settlement (Kessler, 2002; Purcell and Brelsford, 2004). The vegetation of the Sierras Grandes is "consumer controlled" and *Polylepis* forests could be more extensive if livestock grazing pressure was lower (Renison et al., 2006; Cingolani et al., 2008; Marcora et al., 2013). This is why we suggest that reduction or partial suppression of livestock grazing may be necessary to promote natural successional processes, and allow *Polylepis* shrublands and forests to recover. Soil degradation also must be considered in decision-making about alternative management practices, especially on private lands. Grazing exclusion or reduction of livestock stocking densities could be an effective mechanism to reduce soil erosion. Although this does not imply that the soil profile with all its properties would be restored rapidly, erosion rates could be reduced, and this would favor sediment accumulation and soil formation (Cingolani et al., 2013). In the National Park itself, livestock exclusion in the most degraded areas combined with rotational grazing and the recent reintroduction of the native grazer *Lama guanicoe* (Cabido, 2008) is expected to maintain or even increase native plant diversity thereby reducing soil erosion. However, to increase representation and diversity of forests and shrubland birds, restoration should aim also to expand *Polylepis* forest and shrubland area and increase landscape heterogeneity by providing a mix of regenerating, young, and mature stands (Renison et al., 2010).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.03.047.

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