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Research article

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Bird species richness in High-Andean forest fragments: habitat quality and topography matter

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Abstract. Montane forests worldwide are known centers of endemism and biodiversity but are highly threatened by fragmentation processes. Using data collected in 15 Polylepis forest remnants covering 2000 hectares, we investigated how bird species richness and bird community composition, particularly for species of conservation concern, are influenced by habitat quality and topography in the Tunari National Park in the High Andes of Bolivia. Bird species richness was highest in topographically complex, low-elevation *Polylepis* patches located in areas with a high potential to retain rainwater. Bird communities differed strongly between Polylepis lanata and P. subtusalbida remnants, each supporting different threatened and endemic species. Within the P. subtusalbida forest, high-elevation fragments characterized by high amounts of sunlight and low anthropogenic disturbance were more likely to contain threatened species. Surprisingly, we found no effect of fragment size on the diversity or composition of bird communities or the presence of bird species of conservation concern. The presence of exotic plantations (Pinus and/or Eucalyptus spp.) in or outside forest remnants was negatively associated with the number of bird species as well as with occurrence of the endangered Cochabamba-mountain finch (Compsospiza garleppi). To support the different communities found in Polylepis forests, these results suggest that conservation efforts should be directed towards both forest types (P. subtusalbida and *P. lanata*) present in the area. For an efficient management of avian diversity, exotic plantations should be established away from native remnants while existing patches should be managed to maintain or increase habitat quality. Finally, the importance of local topography in determining avian species richness and community composition in forest fragments, mainly through topographic controls on moisture distribution and the amount of sunlight received by the fragments, should be considered when planning conservation and reforestation schemes.

Keywords. Bird communities, conservation, exotic plantations, Polylepis, Tunari NP.

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Introduction

Montane forests worldwide are important centers of biodiversity and endemism and provide numerous ecosystem services as they help to retain water, stabilize soils, store carbon and increase soil fertility (AUBAD et al. 2010). Unfortunately, montane forests, located in topographically complex areas, are heavily affected and threatened by fragmentation processes, mainly caused by anthropogenic activities such as land conversion for agriculture (DOUMENGE et al. 1995; CAYUELA et al. 2006). To protect and restore these habitats and their biodiversity, it is important to understand factors and processes influencing species persistence (FLASPOHLER et al. 2010; TINOCO et al. 2013). Such information is especially urgent for the management of *Polylepis* woodlands, a unique ecosystem with large numbers of endemic and threatened species occurring in the South American High Andes up to 5200 m (FJELDSÅ 1993; NAVARRO et al. 2005). Due to extensive historical and ongoing anthropogenic activities, less than 10% of the original *Polylepis* forest cover is estimated to remain, making it one of the most endangered forested ecosystems in the world (WCMC 2004). This degradation is mainly caused by slash-and-burn agriculture techniques, cattle overgrazing, firewood collection and the replacement of native forests by exotic plantations (FJELDSÅ & KESSLER 1996; HENSEN 2002; BALDERRAMA 2006; GARECA et al. 2007, 2010; HENSEN et al. 2012). Today, Polylepis forests mostly remain as small patches restricted to highly inaccessible areas like ravines, ledges and steep slopes (RENISON et al. 2011; SYLVESTER et al. 2014; ALINARI et al. 2015). There is a strong debate as to what extent their patchy distribution is natural (GOSLING et al. 2009; WILLIAMS et al. 2011) or caused by anthropogenic activities, but evidence points to human-induced pressures leading to extensive habitat loss and increased isolation over time (FJELDSÅ & KESSLER 1996; CIERJACKS et al. 2007; TORRES et al. 2008; TOIVONEN et al. 2011; ALINARI et al. 2015).

While little is known of the characteristics of *Polylepis* forest patches influencing biodiversity within Bolivia, the area, elevation and habitat quality of forest fragments all have been found to influence *Polylepis* bird communities in forests of Argentina, Peru and Ecuador (FJELDSÅ 1993; LLOYD 2008a; BELLIS *et al.* 2009, 2015; SEVILLANO RÍOS *et al.* 2011; TINOCO *et al.* 2013; SEVILLANO-RÍOS & RODEWALD 2017). Although these studies showed that small forest fragments may constitute important habitats for many species, including threatened and endemic ones (LLOYD & MARSDEN 2011), larger and/or higher quality forest remnants were often found to support larger and more diverse communities (FJELDSÅ 1993; BELLIS *et al.* 2009, 2015). Predictors such as soil erosion, humidity, habitat complexity, *Polylepis* tree species and plant composition can also affect *Polylepis* bird communities (FJELDSÅ 1993; LLOYD & MARSDEN 2008; BELLIS *et al.* 2009, 2015; TINOCO *et al.* 2013; SEVILLANO-RÍOS & RODEWALD 2017). However, few fine-scale topographical features, beside elevation and slope angle, have been included in such analyses (LLOYD & MARSDEN 2008; SEVILLANO RÍOS *et al.* 2011; BELLIS *et al.* 2015) despite their role in increasing habitat diversity locally (HOMEIER *et al.* 2010).

Here, we assessed which factors correlate with bird species richness and community composition in a fragmented *Polylepis* forest area in the Tunari National Park (TNP), one of the most important areas for the conservation of *Polylepis* and its associated avifauna in Bolivia and South America in general (FJELDSÅ 2002; BALDERRAMA 2006; FAUNAGUA 2015). The park was created in 1962 to protect the native vegetation, to improve water resource management and to prevent erosion, landslides and floods. It should also limit the expansion of the city of Cochabamba and function as a recreational area for its residents, yet urban encroachment and land conversion to agriculture have taken a heavy toll, particularly on its Cochabamba-facing southern slope (SERNAP 2016). Nevertheless, the TNP still represents the last main stronghold of two vulnerable tree species endemic to Bolivia, namely *Polylepis subtusalbida* (distributed on the southern slope) and *P. lanata* (mainly present on the more humid northern and eastern slopes). Both forest types are important to support endemic and threatened animal and plant species (FJELDSÅ 2002; GARECA *et al.* 2010). The southern slope area is specifically important for the conservation of the endangered Cochabamba-mountain finch (*Compsospiza garleppi*, IUCN 2018) and several High-Andean species and has consequently been designated an Important Bird and Biodiversity Area by BirdLife International (2017).

Because in the TNP, *Polylepis* patches are strongly clustered in different watersheds, we investigated factors driving bird species richness patterns and community composition across different watersheds ('watershed-level analysis') before focusing on individual patches ('patch-level analysis'). In addition, we studied which factors affect the presence of endemic and/or threatened bird species at both watershed and patch levels. We hypothesize that factors related to fragmented or poor habitat quality patches, such as smaller fragment size, isolated and small *Polylepis* trees and the presence of exotic plantations, will negatively affect bird species richness and bird community composition, in particular the presence of threatened and specialized species. Inversely, topographical complexity of fragments with large small-scale terrain heterogeneity and (topography-driven) soil moisture is hypothesized to allow for more diverse bird communities.

Material and methods

Study area

The Tunari National Park (TNP, 16°55′–17°34′ S, 66°55′–66°44′ W), a 300000 ha area located in Bolivia, ranges from 2750 to 4400 meters a.s.l. Above 3200 meters, two endemic vegetation associations dominate in the park (NAVARRO *et al.* 2005): *Berberis commutata - Polylepis subtusalbida* and *Styloceras columnare - P. lanata* (KESSLER & SCHMIDT-LEBUHN 2006). The first woodland type is characteristic of the arid habitats found on the southern slope of the park (precipitation: 600–800 mm) and forms monospecific tree stands while the second is associated with trees of the yungas habitats on the more humid northern and eastern slopes (precipitation: 900–1000 mm, NAVARRO *et al.* 2005). Native forests are estimated to cover about 4% of the park, although the exact distribution of the remaining *Polylepis* patches remains unknown (SANABRIA SILES *et al.* 2012).

Forest mapping

Polylepis remnants were located in the TNP with a combination of available maps and a LANDSAT8 image (30 m resolution). Their exact boundaries were mapped with a GPS device during field surveys conducted between September and December in 2014 and 2015 and complemented with Google Earth for inaccessible areas. These remnants are generally strongly isolated as they are restricted to watersheds located in different valleys separated by deep ravines or high ridges. On the southern slope, remnants within watersheds are further fragmented into smaller patches which are separated from each other by agricultural fields, pastures, puna grasslands or exotic plantations (*Eucalyptus globulus* and/or *Pinus radiata*). Because of this clustered configuration of the patches, we decided to carry out the analysis at 'watershed' and at 'patch' levels, assigning each *Polylepis* patch to a specific watershed. Some watersheds only contain a single patch (Fig. 1, Table 1). We uncovered four watersheds with *Polylepis subtusalbida* (one to three patches per watershed, in total 16 different patches, which together cover about 832 ha; details in Tables 1–2). Our patch-level analysis considers all sampled individual patches of *Polylepis subtusalbida* of the southern slope.

Bird surveys

Bird surveys were carried out from September to December in 2014 and 2015. We surveyed nine out of ten watersheds where *P. subtusalbida* patches were located on the southern slope (corresponding to 15 of the 16 *P. subtusalbida* patches uncovered) and two *P. lanata* watersheds (Fig. 1). We were unable to survey the remaining three watersheds (one *P. subtusalbida* and two *P. lanata* watersheds), for which we relied on previously collected data (see below). We used an adapted version of the MacKinnon-list method, which groups observations of birds into consecutive lists of species. A species accumulation curve is generated by adding those species not recorded in any previous list to the total species number, which is then plotted as a function of the list number. This method thus relates cumulative species

TABLE 1

Polylepis forest watersheds inside the Tunari National Park with the number of patches and total size of forest cover detected and surveyed per cluster, *Polylepis* tree species, observed species richness (Sobs), estimated species richness (Chao2 and ICE), the number of species observed by José Balderrama ("Expert list", used when no other data was available) and the total survey time in minutes.

Watershed name	Number of patches	Forest size (ha)	<i>Polylepis</i> sp.	Sobs	Chao2	ICE	Expert list	Survey Time (min)
СНА	2	48.1	P. subtusalbida	43	47.8	47.8	_	2672
СНО	1	3.2	P. subtusalbida	33	33.5	34.6	_	1108
LAP	3	208.1	P. subtusalbida	59	67.9	68.2	_	3897
LIR	1	302.8	P. subtusalbida	53*	_	_	53	_
PAJ	1	11.6	P. subtusalbida	36	50.3	46.3	_	1175
PAL	1	15.1	P. subtusalbida	30	55.0	44.0	_	521
PINT	2	34.7	P. subtusalbida	32	38.0	37.8	_	1036
SAM	3	46.4	P. subtusalbida	46	60.0	57.8	_	2868
TAQ	1	100.8	P. subtusalbida	44	71.7	70.2	_	1789
THO	1	61.3	P. subtusalbida	35	35.1	35.3	_	2912
CAN	1	43.4	P. lanata	33	52.0	44.6	_	1792
ESP	1	34.5	P. lanata	53*	_	_	53	_
ICA	1	65.9	P. lanata	50*	_	_	50	_
MOR	1	1028.9	P. lanata	38	41.3	43.3	_	1140
Average	1.5	143.2	_	40.3	48.5	47.0	_	1230
Median		139.0	_					

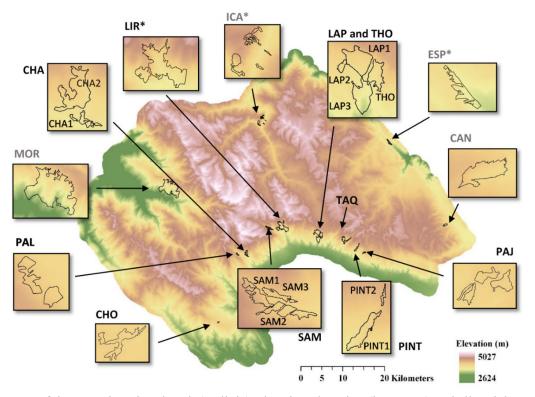


Fig. 1 – Map of the Tunari National Park (Bolivia), showing elevation (in meters) and all *Polylepis* forest fragments included in the analysis. Names of the watersheds are indicated in bold outside the frames, in black for *Polylepis subtusalbida* and in grey for *Polylepis lanata* tree species. Patches within watersheds are shown within frames. * indicates watersheds for which we obtained bird data from a local expert.

TABLE 2

Patch name	Size (ha)	Sobs	Chao2	ICE	Survey Time (min)
CHA1	6.8	38	64.7	50.8	1825
CHA2	41.3	33	35.6	34.8	847
СНО	3.2	33	33.5	34.6	1108
LAP1	104.4	45	49.0	49.9	2349
LAP2	12.7	45	42.0	41.5	711
LAP3	91	36	53.0	47.0	837
PAJ	11.6	36	50.3	46.3	1175
PAL	15.1	30	55.0	44.0	521
PINT1	30.9	24	30.9	32.0	754
PINT2	3.6	29	42.2	37.5	282
SAM1	19.3	35	39.6	39.4	946
SAM2	17.9	36	70.0	47.7	1118
SAM3	9.2	22	50.8	40.3	804
TAQ	36.8	44	71.7	70.2	1789
THO	61.3	35	35.1	35.3	2912
Average	31.0	33.8	48.2	42.8	1230
Median	17.9				

List of surveyed patches of the southern slope of the Tunari National Park with area size (ha), survey time (min), observed species richness (Sobs), and Chao2 and ICE estimates of true species richness.

richness to the number of observations, rather than time or space, and thereby accounts for moderate differences in observer qualification and field conditions (MACKINNON & PHILLIPS 1993). HERZOG *et al.* (2002) found that for tropical, species-poor habitats (such as *Polylepis* remnants), 10-species lists were more robust. Therefore, our master list of observations was later processed into such 10-species lists, each list starting with the observation following the last observation of the previous list and therefore containing the ten first different species observed (HERZOG *et al.* 2002; O'DEA *et al.* 2004; MACLEOD *et al.* 2011; CAVARZERE *et al.* 2012). In addition, following HERZOG *et al.* (2002), observations beyond 50 m from the observer were excluded as detectability of forest birds substantially declines beyond that distance.

Surveys were carried out by two skilled observers (C.F and H.L, the latter replaced by J.B for the surveys conducted in MOR, Fig. 1). Both observers walked slowly and randomly inside the patches and recorded the species (identified visually or orally) for each encounter and the time of observation. Unknown songs and calls estimated to originate within a 50 meter-radius from the observer were recorded to be later identified and incorporated into the species lists. As they are difficult to differentiate in the field, *Turdus chiguanco* and *T. fuscater* were both recorded as *Turdus* spp. (TURSP) and *Nothoprocta pentlandii* and *N. ornata* were both recorded as *Nothoprocta* spp. (NOTSP). Surveys were conducted on days without wind or rain from dawn (05h30) to midday and from late afternoon to dusk (18h30) for a total of 321.6 hours. *Polylepis* patch size ranged from 3.2 to 1028.9 ha (median: 17.9 ha, Table 2 and Figs S1–S2), and survey intensity was roughly proportional to patch size (r = 0.50, P = 0.055, Table 2). Flyovers and obvious non-target species (not specifically associated with forest habitats, e.g., water-birds, grassland specialists and raptors) were excluded. For the three watersheds that we could not survey ourselves (i.e., LIR, ICA and ESP; Fig. 1), we used bird surveys conducted in 2004 and 2005 by the local expert on birds occurring in the Cochabamba region and particularly in the *Polylepis* forests of the TNP (J.B., BALDERRAMA 2006, 2009). These data were collected during four-days systematic surveys of each of

these patches to sample all bird species present, during which J.B. walked slowly across the forest patches, actively searching any bird species previously undetected. Thus, our final dataset consists of bird surveys in ten watersheds located on the southern slope (totaling 16 *P. subtusalbida* patches), and four watersheds elsewhere in the park (each of them containing one *P. lanata* patch).

Vegetation characteristics

For the 15 *P. subtusalbida* patches where we conducted bird surveys ourselves, vegetation characteristics were obtained in 279 randomly selected 5 m diameter-sampling plots (approximate density of one plot per ha). In these, we visually estimated (1) the proportion of exotic trees within the overall tree cover ('exotic tree ratio') and (2) tree height, and we measured (3) diameter at breast height (DBH) and (4) canopy density with a convex spherical crown densimeter. We scored (5) the degradation level caused by fire, logging and grazing on a scale from 0 to 3 (none, low, medium or high) and used the median of these scores as an 'anthropogenic degradation index'. Due to difficulty of access, these measures are not available in three of the watersheds (LIR, ICA and ESP, Fig. 1) and were thus not included in the watershed analysis. Lastly, we mapped all exotic plantations (*Eucalyptus globulus* and/or *Pinus radiata* stands) located within 150 m of the *Polylepis* remnants with a GPS device. Because between-patch movements of *Polylepis*-associated birds decrease at distances of more than 200 meters (LLOYD & MARSDEN 2011), we calculated (6) the extent to which each *Polylepis* patch/watershed is surrounded by these plantations as the average proportion of the surface covered by exotics across three buffer areas at 50, 100 and 150 m distances (adapted method from DUNFORD & FREEMARK 2005).

Spatial habitat variables

Using a Digital Elevation Model (ASTER GDEM, 30 m resolution, https://lpdaac.usgs.gov/) in ArcGIS 10.1, we derived for each *Polylepis* patch (7) mean elevation, (8) (log-transformed) surface area, (9) the average number of hours of sunlight at least half a watershed or patch receives per day ('illumination time'), (10–13) four different measures of local topographic variation (percentage of depressions, ridges, steep slopes and gentle slopes of each watershed or patch) derived from the Topographic Index (TPI, see S1 for detailed technical explanation), (14) the Topographic Wetness Index, (TWI, BEVEN & KIRKBY 1979) a measure of the topographical control over hydrological processes which is related to forest productivity and soil moisture (BESNARD et al. 2013; WILSON et al. 2013; CAMPOS et al. 2015). The TWI represents the potential accumulation capacity in a given pixel and was obtained through the D-infinity flow accumulation algorithm with the TauDEM tool (TARBOTON 2009) in ArcGIS 10.1. Finally, we computed from LANDSAT8 images (15) the mean Normalized Difference Vegetation Index (NDVI), a proxy for resources available to consumers (HURLBERT & HASKELL 2003; BELLIS et al. 2015) and (16) the Tasseled Cap Wetness index (TCW), the actual soil and plant moisture content, with the Tasseled Cap function in ArcGIS 10.1. LANDSAT images (30 meters resolution, courtesy of the U.S. Geological Survey) were recorded in August 2015, the driest month of the year, when the contrast between dry puna grasses/agricultural crops and evergreen Polylepis (and other native) trees or exotic plantations is maximal. All calculations were performed at watershed and patch levels separately.

To avoid the inclusion of correlated variables, two Principal Component Analyses (PCA) were performed for the patch-level analysis. A first PCA ('TopoPCA') included all variables describing patch topography (variables (7), (9), (10–13)) while a second PCA ('VegPCA') was performed on habitat quality and vegetation-related variables ((1), (2), (3), (4), (5)) as well as (6) surrounding exotics and (15) mean NDVI. At watershed level, one PCA was applied for topographic variables while surrounding exotics and NDVI were included as separate variables due to the lack of vegetation data. PCA was carried out with the package 'ade4' in R (DRAY & DUFOUR 2007). We retained the number of PCA

TABLE 3

Association between six topographic variables and principal components (TopoPCA analysis) at watershed and patch levels with loadings of each variable and variation explained per axis.

	W	Vatershed lev	el		Patch level	
	TopoAxis1	TopoAxis2	TopoAxis3	TopoAxis1	TopoAxis2	TopoAxis3
Elevation	0.12	0.73	0.59	0.01	0.84	0.47
Illumination time	0.49	-0.12	-0.14	0.48	-0.08	0.34
Depressions	-0.16	0.66	-0.72	-0.37	0.41	-0.57
Gentle slopes	0.53	0.01	-0.14	0.52	-0.02	-0.11
Steep slopes	-0.46	0.00	0.27	-0.42	0.12	0.52
Ridges	-0.48	-0.14	-0.17	-0.43	-0.32	0.23
Variation	0.58	0.21	0.11	0.61	0.18	0.15

axes needed to capture > 80% of the variation present in the data as explanatory variables (three axes at the patch-level, two at the watershed level, Tables 3-4). As they are uncorrelated to other variables, area and both moisture-related variables (TWI and TCW) were used as separate explanatory variables. At both patch- and watershed-level, no strong correlations remained between final sets of explanatory variables (patch-level: all r < 0.48, watershed level: all r < 0.67). At patch level, the first axis of the TopoPCA (TopoAxis1) represents well illuminated patches with a smooth topography. The second axis (TopoAxis2) is associated with high elevation and rugged (i.e., high numbers of depressions in the terrain) patches, while the third axis (TopoAxis3) is correlated with high elevation, high illumination, and rugged terrain (prevalence of steep slopes and high numbers of depressions). At watershed level, we retained as explanatory variables the two first axes of the TopoPCA (TopoAxis1 and TopoAxis2), with similar interpretations as above. The first axis of the VegPCA (VegPCA1) represents forest patches strongly affected by exotic plantations, which contain and are surrounded by high amounts of exotics with sparse, small *Polylepis* trees. The second axis (VegAxis2) is indicative of high-quality patches, i.e., denser patches with tall *Polylepis* trees and limited anthropogenic degradation levels. The third axis (VegAxis3) is correlated with patches heavily affected by exotic plantations, characterized by little and small *Polylepis* trees, with many exotic plantations inside or around the patches.

Bird species richness estimates

Because our species accumulation curves show that observed species richness does not reach an asymptote in the sampled watersheds and patches (Figs S3–S4), we calculated two different samplebased, non-parametric estimates of total species richness for each watershed and patch: Chao2 and Incidence-based Coverage Estimator (ICE), using the EstimateS software (Version 9, R.K. Colwell, http://purl.oclc.org/estimates). Chao2 and ICE have been shown to outperform other types of estimators (GOTELLI & COLWELL 2001; BROSE *et al.* 2003; COLWELL *et al.* 2012), especially in similar species-poor forest remnants (HERZOG *et al.* 2002; KATTAN *et al.* 2006; TINOCO *et al.* 2013). Because species lists of J.B. for the watersheds of ICA, ESP and LIR were recorded during longer visits by an experienced ornithologist and with the specific goal to find all species present in the area, we assume that these values are close to total species richness (as estimated by Chao2 and ICE).

TABLE 4

Association between seven vegetation-related variables (with NDVI = Normalized Vegetation Index, a measure of greenness and DBH = diameter at breast height) and principal components (VegPCA analysis) at patch level with loadings of each variable and variation explained per axis.

	VegAxis1	VegAxis2	VegAxis3
Surrounding exotics	0.38	0.16	0.37
Degradation index	-0.33	-0.57	0.18
Exotics ratio	0.36	0.06	0.66
NDVI	-0.43	-0.10	-0.04
Canopy density	-0.23	0.74	-0.14
Tree height	-0.44	0.30	0.33
DBH	-0.44	0.02	0.51
Variation	0.54	0.19	0.11

Statistical analysis

To explain species richness patterns at watershed and patch level, we applied Generalized Linear (Mixed) Models (GL(M)M) in which Chao2 or ICE species richness estimates were specified as dependent variable. At the watershed-level, fixed effects included the first two axes of the watershed-level topographical PCA, (log) area, NDVI, surrounding exotics, TWI, TCW and finally *Polylepis* tree species. At the patch-level, in addition to the first three axes of the topographical and vegetation PCAs, (log) area, TWI and TCW were modelled as fixed effects while the watershed in which a patch is situated was included as a random effect. Following BURNHAM & ANDERSON (2002), model selection proceeded through a multi-model averaging framework based on the Akaike's Information Criterion corrected for small sample sizes (AIC_c), as implemented in the R package MuMin (BARTON *et al* 2018). We ran all possible combinations of predictor variables, and as no single model attained decisive support (i.e., AIC_c weight (AIC_w) > 0.95), AIC_w were calculated for all variables (Table S1). Only variables with AIC_w > 0.5 were considered informative (BURNHAM & ANDERSON 2002). We validated the models by using random subsets of the watershed/patches with a bootstrap analysis of 100 random partitions in R (R DEVELOPMENT CORE TEAM 2008). Normality of model residuals was verified and met (Shapiro-Wilk W > 0.9). All statistical analyses were performed with the software R.

A separate analysis was conducted for each of the threatened and/or endemic bird species recorded more than once in the area (based on IUCN 2018, Table S2), at both watershed and patch level. These were five threatened species (*Asthenes heterura* (near threatened, NT), *Compsospiza garleppi* (endangered, EN), *Sylviorthorhynchus yanacensis* (NT), *Conirostrum binghami* (NT), *Pseudosaltator rufiventris* (NT) and four country endemics (*Oreopsar bolivianus, Aglaeactis pamela, Coeligena violifer, Asthenes harterti*). We applied a similar modelling framework as described above, but because we focused on the presence/absence of these species in different watersheds or patches, a binomial error distribution was used. To avoid model fitting difficulties related to (quasi) separation, we applied Fisher's penalized logistic regression as implemented in the R package *logistf* (HEINZE *et al.* 2013). As above, predictors were considered as potentially relevant when their AIC_w were > 0.5.

To investigate community composition patterns at watershed and patch level, we applied non-metric multidimensional scaling (NMDS; bray distance) based on bird species presence/absence data in watersheds and patches, respectively (Table S3). Generally, ordination with stress values smaller than 0.2, 0.1 and 0.05 are considered of fair, good and excellent quality, respectively. We then identified which species most strongly underlie the ordination (p < 0.05) and which environmental factors (the same factors used to explain species richness, see above) correlate with the ordination axes (p < 0.05) for each axis of the NMDS with the *envfit* function from the R package *vegan* (OKSANEN *et al.* 2019).

Results

Bird species richness

We recorded 144 species, of which 50 were found exclusively in *Polylepis lanata* patches, and 80 only in *P. subtusalbida* (Table S3), among which the endangered and endemic *Compsospiza garleppi*. At the watershed level, Chao2 estimates of species richness vary from 33.5 (CHO) to 71.7 (TAQ), with a mean of 48.5. ICE estimates vary from 34.6 (CHO) to 70.2 (TAQ), with a mean of 47 (Table 1). At the patch level, observed species richness varies from 22 bird species (SAM3) to 44 (TAQ). Chao2 estimates ranged from 30.9 (PINT1) to 71.7 (TAQ), with an average of 48.2. ICE estimates ranged from 32.0 (PINT1) to 70.2 (TAQ) with an average of 42.8 (Table 2).

Species richness predictors

Different variables influenced overall bird species richness at the watershed versus patch level. Topography was most important at the watershed level, as watersheds with a high topographic potential to retain rainwater harbored more species (Chao2 and ICE; $AIC_w = 0.62$ and 0.52, Fig. 2a, Table S1). At the patch level, species richness was highest in productive *Polylepis* patches with few exotic plantations, regardless whether *Polylepis* trees were tall and dense (Chao2 and ICE estimators with $AIC_w = 0.60$ and 0.63, respectively) or not (Chao2 estimator with $AIC_w = 0.68$; Fig. 2b, Table S1). Species richness was also higher in rugged low-elevation patches with short illumination times and few steep slopes (Chao2 and ICE estimators with $AIC_w = 0.88$ and 0.87, respectively). Surprisingly, fragment area did not appear to be an important predictor of bird species richness at either patch or watershed level (i.e., all $AIC_w < 0.28$; Tables S1–S2).

Birds of conservation concern

Four out of the nine bird species of conservation concern were only included in the analysis at the watershed level, either because they were absent from *P. subtusalbida* patches (*Aglaeactis pamela*, *Coeligena violifer*, *Asthenes harterti*) or present in all of them (*Pseudosaltator rufiventris*). Topographyrelated variables (TopoPCA axes) influenced the presence of all species of conservation concern (Table 5), except *C. violifer*, whose distribution was mainly governed by vegetation productivity (high NDVI values). Vegetation parameters, particularly the two first axes of the VegPCA, influenced the patch-level distribution of four species (Table 5). *Compsospiza garleppi* was only observed in *P. subtusalbida* watersheds located at higher elevation and on steep slopes, where it was most likely to be observed in patches with small *Polylepis* trees but unaffected by exotic plantations. The *Polylepis*

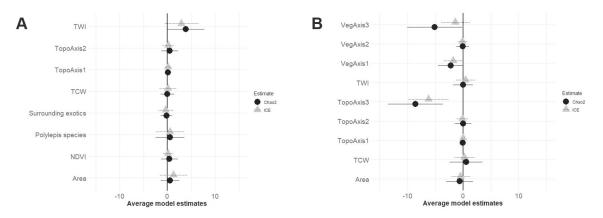


Fig. 2 – Akaike's Information Criterion weights (AIC_w) model averaged estimates and their standard deviation for all variables included in the Generalized Linear Mixed Models (GLMM) analysis at **(a)** watershed and **(b)** patch levels for Chao2 (black dots) and Incidence-based Coverage Estimator (ICE, grey triangles) total species richness estimates.

TABLE 5

Akaike's Information Criterion weights (AIC_w) , coefficient values and standard errors (SE) of important variables for Firth's regression models on presence of species of conservation concern. * indicates coefficients with a value larger than their standard errors. Country endemics are indicated in bold and IUCN status between brackets (LC = Least Concern; NT = Near-Threatened; EN=Endangered).

	Species	Variable	AIC _w	Coefficient	SE
	Aglaeactis pamela (LC)	P. lanata [*]	1.00	5.95	1.89
		TopoAxis1	0.57	0.51	0.96
	Coeligena violifer (LC)	P. lanata [*]	1.00	3.69	1.37
		NDVI	0.43	0.48	0.61
	Sylviorthorhynchus yanacensis (NT)	P. subtusalbida*	1.00	2.13	1.64
		TopoAxis1	0.63	0.50	0.64
	Asthenes harterti (LC)	P. lanata [*]	1.00	3.89	1.38
~		TopoAxis2	0.42	-0.39	0.31
Watersheds	Asthenes heterura (NT)	P. lanata	1.00	0.38	0.23
ers		TopoAxis1	0.63	0.18	0.11
vat	Oreopsar bolivianus (LC)	P. lanata	1.00	0.69	0.85
>		TopoAxis2	0.66	0.97	1.01
		Surrounding exotics	0.60	-0.34	1.53
	Compsospiza garleppi (EN)	P. subtusalbida [*]	1.00	2.46	1.89
		TopoAxis2	0.49	0.65	0.96
	Conirostrum binghami (NT)	P. subtusalbida	1.00	1.12	1.37
		TopoAxis2	0.58	0.46	0.61
	Pseudosaltator rufiventris (NT)	P. subtusalbida [*]	1.00	0.34	1.94
		TopoAxis2*	0.60	0.11	0.72
	Sylviorthorhynchus yanacensis (NT)	VegAxis2*	0.93	1.54	1.18
		Wetness	0.61	-1.11	1.40
	Asthenes heterura (NT)	TopoAxis1*	0.98	0.99	0.56
	Oreopsar bolivianus (LC)	TopoAxis1*	0.94	-1.12	0.96
S		VegAxis1*	0.81	-0.61	0.56
raucines	<i>Compsospiza garleppi</i> (EN)	TopoAxis1*	0.85	-0.54	0.46
L A		VegAxis1	0.55	-0.18	0.30
		VegAxis2	0.63	-0.56	0.67
	Conirostrum binghami (NT)	TopoAxis1	0.71	0.28	0.33
		TopoAxis2	0.56	0.56	0.76
		VegAxis2	0.51	0.35	0.55

specialist *Conirostrum binghami* occurred more often in the most elevated and rugged *P. subtusalbida* watersheds, and in the higher elevated, well illuminated and less degraded patches. The other specialist, *Sylviorthorhynchus yanacensis* was mainly present in well-lit *P. subtusalbida* stands, particularly in drier and less degraded patches. *Asthenes heterura* was most likely to be found on well-illuminated, gentle slopes while *Oreopsar bolivianus* was more observed in high-elevation and steep *P. lanata* watersheds, devoid of exotic plantations. The occurrence of *P. rufiventris* was limited to elevated *P. subtusalbida* watersheds on rugged terrain. *A. harterti* occurred exclusively in *P. lanata* stands, avoiding rugged areas at higher elevations. Finally, *A. pamela* was observed in *P. lanata* forest watersheds located on well-illuminated gentle slopes.

Community composition

Thirty-three species out of 144 contributed significantly to the NMDS ordination of the watersheds (Table S4) and two factors, *Polylepis* species and NDVI, were significantly associated with the first axis of the NMDS (p = 0.05 and p = 0.047 respectively, Fig. 3a). None of the tested factors were significantly associated with the second axis of the NMDS. The ordination was good as residual stress value equaled 0.099 (non-metric fit $R^2 = 0.979$). Nine bird species, among which the endemic *A. harterti*, *A. pamela* and *C. violifer*, significantly drove the ordination on the left of the first axis, which corresponds to *P. lanata* watersheds characterized by high NDVI values (Fig. 3a, Table S4). Eight species, among which the near-threatened *S. yanacensis* and *P. rufiventris*, significantly drove the ordination to the right of the first axis, which corresponds to less productive *P. subtusalbida* watersheds (Fig. 3a, Table S4). Fourteen species significantly drove the ordination on the second axis, a pattern which was not related

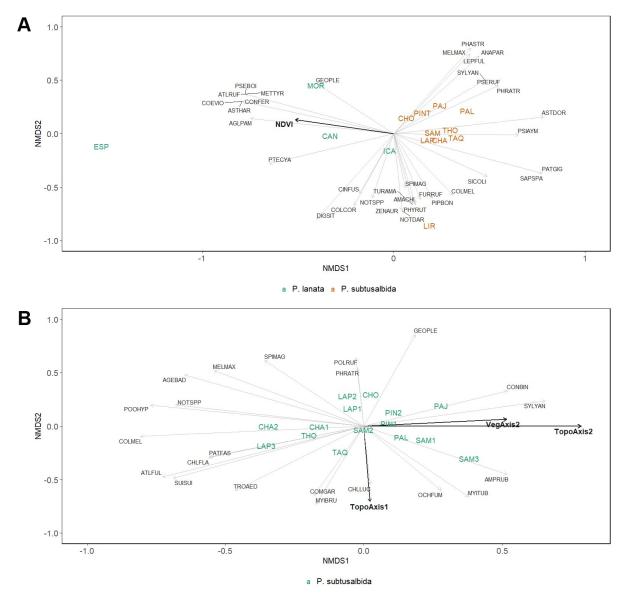


Fig. 3 – Ordinations with species (light grey vectors) significantly influencing the ordination (p < 0.05) and environmental vectors (bold black) being significantly correlated with the ordination (p < 0.05) at (a) watershed (b) patch levels. *Polylepis subtusalbida* watersheds and patches are indicated in green and *Polylepis lanata* watersheds are indicated in orange.

to any of the factors included in the analysis, but upon visual inspection appears to mainly correspond to the *P. subtusalbida* LIR watershed (Fig. 3a, Table S4).

Twenty-two bird species significantly drove the NMDS ordination of patches on at least one of the NMDS axes (Table S5). Two factors related to habitat quality and topography were significantly associated with the first axis of the NMDS (VegAxis2, p = 0.048 and TopoAxis2, p = 0.02, respectively; Fig. 3b) while one factor related to topography was significantly associated with the second axis (TopoAxis1, p = 0.002). The ordination was fair as residual stress value equaled 0.144 (non-metric fit $R^2 = 0.99$). Three species, among which the near-threatened *C. binghami* and *S. yanacensis*, significantly drove the ordination on the right of the first axis, which corresponds to denser, less degraded and more elevated patches with rugged terrains while nine species, none of them of conservation concern, significantly drove the ordination to the bottom of the second axis, which corresponds to well-illuminated patches located on smoother terrains, while four species without conservation concern significantly drove the ordination to the second axis, which corresponds to less illuminated patches located on smoother terrains, while four species without conservation concern significantly drove the ordination to the upper section of the second axis, which corresponds to less illuminated patches located on topographically complex terrain (Fig. 3b, Table S5).

Discussion

Polylepis forest remnants of the Tunari National Park constitute an important habitat for Andean bird conservation as they harbor 144 different species, including numerous endemic and/or threatened species (Table S2). We observed 18 out of the 26 bird species that were originally used to support the designation of the park as an Important Bird and Biodiversity Area, highlighting the important role of small *Polylepis* remnants for biodiversity. Overall avian species richness, the distribution of species of conservation concern and community composition across the TNP were influenced by both topography and *Polylepis* remnant habitat quality. Moister *Polylepis* remnants harbored richer bird communities, while on the southern slope, bird species richness was highest in *P. subtusalbida* patches located at lower elevations and on less steep but uneven terrains with high amounts of local depressions. The presence of exotic plantations, in- or outside the patches, negatively affected bird species richness, and rugged *Polylepis* trees were more likely to support species of conservation concern. *Polylepis lanata* and *P. subtusalbida* forest remnants generally tended to support different species, including several species of conservation concern.

The topographical position of *Polylepis* patches influences its associated avifauna through both their local water retention capacity and the amount of sunlight they receive. Across the park, we found that areas located in basins or valleys with a topology favoring rainwater retention, and therefore potentially being characterized by higher soil moisture, exhibit more diverse communities. Water availability is a major limiting factor for tree growth in the high Andes, even though *Polylepis* trees are physiologically adapted to survive in arid environments (AZOCAR *et al.* 2007). *Polylepis* tree establishment and survival is higher in moister conditions (GOSLING *et al.* 2009; ALINARI *et al.* 2015) and in areas sheltered from wind (SPARACINO *et al.* 2019). Topography-related soil moisture can therefore determine the distribution of *Polylepis* trees (BADER & RUIJTEN 2008; TOIVONEN *et al.* 2018) and humid forests have been reported to be related to higher plant and bird species richness in *Polylepis* forests of various countries (FJELDSÅ 1993; GARECA *et al.* 2010). In our study area, moister fragments located in basins or valleys, thus sheltered from the strong winds, are likely to be more suitable habitats for *Polylepis* trees and their associated avifauna.

On the southern slope, we found that bird communities of well-illuminated *P. subtudalbida* patches were less diverse but contained distinct communities characterized by the presence of several species,

among which the endangered and endemic *C. garleppi*. A positive association with exposure to sunlight was also found for several species of conservation concern, particularly insectivorous *A. heterura*, *S. yanacensis*, *C. binghami* and nectivorous *A. pamela*. The amount of sunlight reaching a forest patch characterizes its microclimate and therefore influences its insect activity and plant productivity. Though such a sun exposure effect has already been reported for *C. binghami* (DE COSTER *et al.* 2009), our results suggest that illumination is also important for other bird species in montane environments and influences the composition of communities inhabiting forest patches.

We found more species-rich, distinct bird communities in rugged forest remnants, probably because topographically diverse areas offer more suitable breeding, roosting and sheltering sites, or protection from predators (MARTÍNEZ-MORALES 2005). Uneven grounds also protect the soil against erosion caused by grazing livestock (TORRES *et al.* 2008; RENISON *et al.* 2010; ALINARI *et al.* 2015; BELLIS *et al.* 2015). Topography appears to be especially important for *C. binghami* and *P. rufiventris* which are largely restricted to forest stands located at high elevations, on steep slopes and rugged terrains.

Besides topography, we found that forest remnants surrounded by pine or eucalyptus plantations supported less diverse communities, a pattern which has been observed in other *Polylepis* patches of the Cochabamba department (HJARSEN 1998; BALDERRAMA 2006) and in other native forests elsewhere (FJELDSÅ & KESSLER 1996; ZURITA et al. 2006; DE LA HERA et al. 2013). On the southern slope, the presence of exotic trees in particular had a direct negative influence on C. garleppi and O. bolivianus. eucalyptus (Eucalyptus globulus) and pine (Pinus radiata) trees have been introduced into the TNP from the 1970s onwards for forestry purposes and to stabilize soils (GARECA et al. 2007; BRANDT et al. 2012). In 2002, documented exotic plantations officially covered 1.7% of the surface of the TNP as compared to 3.9% covered by native forests (SANABRIA SILES et al. 2012). In the TNP, like in many degraded tropical areas, exotic plantations are often established near native forest fragments to increase forest cover (ESTADES & TEMPLE 1999; WETHERED & LAWES 2003; BUSTAMANTE & SIMONETTI 2005). While they may constitute suitable habitats for many species (ESTADES & TEMPLE 1999; BARBOSA et al. 2017), exotic plantations, especially when they are near native forest fragments, can strongly affect bird communities in these fragments by favoring generalists and causing the loss of specialized species (WETHERED & LAWES 2003; ZURITA et al. 2006; MORTELLITI & LINDENMAYER 2015). Exactly why the presence of exotic plantations in and around *Polylepis* fragments negatively affects bird species richness and the presence of some species of conservation concern inside the fragments remains unclear. A first possibility is that they reduce habitat quality within forest remnants. Exotics, and eucalyptus trees especially, can indeed affect soil quality, compete with the native vegetation and become invasive (GARECA et al. 2007; BRANDT et al. 2012; BRUGGER et al. 2019). A second possibility is that these dense plantations of high trees surrounding forest remnants constitute a barrier to many bird species unable or unwilling to cross large distances in unsuitable habitats (LLOYD & MARSDEN 2011) and therefore increase the level of isolation of already heavily fragmented and scattered Polylepis fragments. Whichever processes are involved, and given our findings, we would recommend to prevent the establishment of exotic plantations in the vicinity of *Polylepis* fragments in the TNP (MORTELLITI & LINDENMAYER 2015).

It should, however, be noted that responses to *Polylepis* fragmentation and matrix composition likely are species-specific (PREVEDELLO & VIEIRA 2010). This is well illustrated by the endangered and endemic Cochabamba mountain-finch (*Compsospiza garleppi*), whose range is restricted to the mountain slopes in the departments of Cochabamba and Potosí (BALDERRAMA 2009; BIRDLIFE INTERNATIONAL 2012). Even though long considered a strict *Polylepis*-specialist, it was recently found to be rather dependent on *Polylepis*-associated shrubs and was also observed feeding on nearby crops (HUANCA *et al.* 2009). Our results show that Cochabamba mountain-finches are indeed more tolerant to anthropogenic exploitation and forest degradation than true specialists such as *C. binghami* and *S. yanacensis* (although *C. garleppi* is less likely to occur near forest fragments containing or being surrounded by exotic plantations). In

the TNP, *C. garleppi* however has a privileged relationship with the *P. subtusalbida* ecosystem as it was only observed in such fragments, particularly in well illuminated and rugged patches that were not surrounded by exotic plantations.

Finally, but importantly, our results indicate that patch surface area did not serve as an important predictor for bird species richness, nor for the presence of any of the species of conservation concern. Reported effects of fragment area on species richness inside *Polylepis* patches have been mixed so far, with some studies reporting a strong negative correlation (TINOCO et al. 2013) while others found none (LLOYD 2008a). FJELDSÅ & KESSLER (1996) also observed that the presence of Polylepis-associated bird species across the Andes was not strongly related to patch area and that many species persisted in most of the remaining patches, if they were of sufficient quality. It is thus generally assumed that Polylepis-dependent species have become adapted to the fragmentation of their habitats due to the long history of anthropogenic deforestation in the area and that they survive as metapopulations, i.e., small populations connected by dispersal, although some species have been reported to avoid tiny (< 1 ha) isolated patches (LLOYD & MARSDEN 2011). Unfortunately, little is known about the number, size and spatial configuration of the fragments necessary for the metapopulations of these species to persist (HANSKI 1998; HANSKI & OVASKAINEN 2002). More research is therefore needed to know if the small populations recorded in the small *Polylepis* patches of the TNP are viable or if they are expected to go extinct (extinction debt, PURCELL et al. 2002; HANSKI & OVASKAINEN 2002; LLOYD 2008b; SEVILLANO Ríos et al. 2011). Understanding such processes is particularly important for specialized and threatened species which occur at very low densities in the area such as C. binghami and L. vanacensis (CAHILL & MATTHYSEN 2007).

There were several logistical constraints associated with surveying the avifauna in the remote and heavily fragmented montane habitats that are Polylepis woodlands, unavoidably resulting in some limitations associated with our data. To gather the data to evaluate species richness in *Polylepis* patches, we used an adapted version of the MacKinnon list method, previously shown to be effective to survey the avifauna of species-poor and remote habitats such as Andean Polylepis forests (POULSEN et al. 1997; O'DEA et al. 2004; MACLEOD et al. 2006). While this method proved useful to survey birds in our study area, numerous visits of the patches were required to approach the asymptomatic species richness and reduce the uncertainty associated with the use of species richness estimators (MACLEOD et al. 2011). Due to the long traveling distances between watersheds, we were also unable to randomize our visits to the different sites, a condition necessary to generate independent visits among sites. Additionally, and due to difficulty of access, we could not survey three of the watersheds in the area, ESP, ICA and LIR, for which we relied on lists generated by a local expert. We found that one of these areas, LIR, appeared to contain distinct communities as compared to the other watersheds (Fig. 3b), although this difference was not explained by any of the environmental factors studied. More data would be needed to determine if this pattern is due to other environmental factors not captured by our own data or to eventual observer biases. The latter seems however unlikely as this pattern was only observed in one of the three areas surveyed by the local expert.

We conclude that *Polylepis* tree species, habitat quality, topographic complexity and water availability influence avian species communities in *Polylepis* woodlands. While responses to forest fragmentation likely are species-specific, our results show that higher quality patches characterized by older *Polylepis* trees, denser canopies and less signs of human activity, are favored by *Polylepis*-associated bird species. Our results emphasize the importance of local topography in determining the bird species richness that a forest fragment may sustain, through topographical controls on moisture distribution and illumination, and thus on forest productivity and ultimately on the resources available to the avifauna. Conservation and reforestation schemes in similarly fragmented montane forests should therefore account for the topographic characteristics of forest patches, as topography can contribute to habitat quality of patches.

This relationship may become even more important when considering the conservation of such forests and their biodiversity in the face of current climate change trends suggesting that the High Andes may become drier in the future (GARECA *et al.* 2010; CHEVALLIER *et al.* 2011; MARCORA *et al.* 2013). Furthermore, the establishment of exotic trees close or within native forest fragments should be discouraged. Finally, we suggest that conservation and management efforts should be directed towards both *Polylepis* forest types (*P. lanata* and *P. subtusalbida* fragments) as they contain different bird communities, and that small forest patches also contribute to local bird communities, as habitat quality (i.e. dense forests with tall trees) proved to be more important than fragment size itself, indicating that small fragments should also be conserved.

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Supplementary material

S1 Detailed technical information: calculation of the TPI

The Topographic Position Index (TPI, WEISS 2001), a measure of local topographic variation, was calculated as the difference between the elevation of the focal pixel and the average elevation of all surrounding pixels within a pre-determined radius (here: 25 m). Pixels with large absolute TPI values (larger than the SD value of the TPI layer, following WEISS 2001) were categorized as being positioned in a depression (negative values) or on a ridge (positive values) while pixels with small absolute TPI values were categorized as belonging to slopes. We used slope values to distinguish between pixels located on a steep slope when their slope angle exceeded 34 degrees, as this corresponds to the maximum inclination where agriculture is practiced within the TNP (SANABRIA SILES *et al.* 2012) or on a gentle slope if otherwise. The proportion of pixels in a patch belonging to each of these four categories (i.e., depression, ridge, steep slope, gentle slope) was used as indicator for local topographic variation.

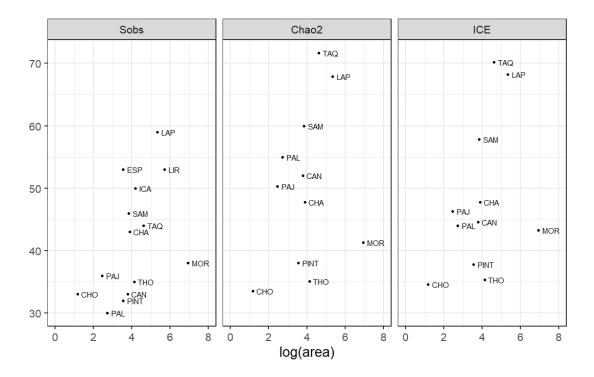
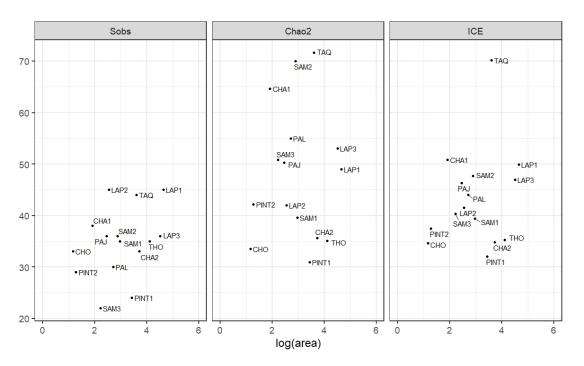


Fig. S1 – Observed (Sobs), Chao2 and Incidence-based Coverage Estimator (ICE) species richness estimates per watershed plotted against the log(area) of each watershed.



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Fig. S2 – Observed (Sobs), Chao2 and Incidence-based Coverage Estimator (ICE) species richness estimates per *Poylepis* patch plotted against the log(area) of each patch.

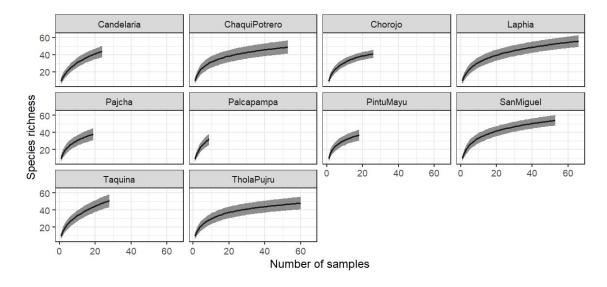


Fig. S3 – Species accumulation curves in the watersheds included in the analyses. One sample corresponds to one 10-species list.

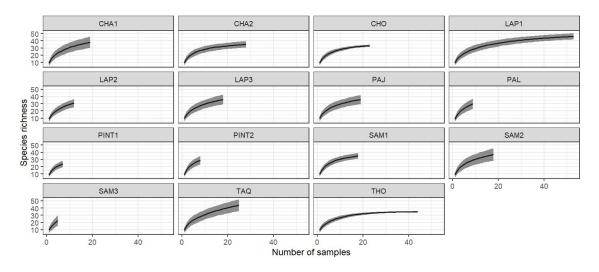


Fig. S4 – Species accumulation curves in the patches included in the analyses. One sample corresponds to one 10-species list.

TABLE S1

Akaike's Information Criterion weights (AIC_w) , values of the coefficient and standard errors (SE) of the variables included in the Generalized Linear Mixed Models analysis with Chao2 and ICE total species richness estimates at watershed and patch levels. Variables with $AIC_w > 0.50$ are shown in bold. * indicates variables which have a coefficient value being larger than their standard errors.

	Variable	AIC _w	Coefficient	SE
Watershed analysis				
Total richness Chao2	Area	0.16	0.53	1.94
	Surrounding exotics	0.10	-0.15	1.23
	NDVI	0.15	0.44	1.78
	Polylepis species	0.12	0.54	3.02
	TopoAxis1	0.11	0.11	0.65
	TopoAxis2	0.17	0.50	1.76
	Topographic Wetness Index	0.62	3.68	3.92
	Tasseled Cap Wetness Index	0.10	0.01	1.42
Total richness ICE	Area	0.28	1.27	2.78
	Surrounding exotics	0.13	-0.36	1.58
	NDVI	0.10	0.12	1.18
	Polylepis species	0.12	0.54	2.99
	TopoAxis1	0.13	0.14	0.71
	TopoAxis2	0.11	0.17	1.19
	Topographic Wetness Index	0.52	2.92	3.60
	Tasseled Cap Wetness Index	0.13	0.09	1.74
Patch analysis	*			
Total richness Chao2	Area	0.23	0.01	1.79
	TopoAxis1	0.08	-0.06	0.55
	TopoAxis2	0.15	0.02	1.48
	TopoAxis3*	0.88	- 8.59	4.95
	VegAxis1	0.60	-2.23	2.27
	VegAxis2	0.13	-0.06	1.14
	VegAxis3*	0.68	-5.11	4.95
	Topographic Wetness Index	0.16	0.01	1.79
	Tasseled Cap Wetness Index	0.26	0.54	2.95
Total richness ICE	Area	0.21	-0.46	1.69
	TopoAxis1	0.06	-0.01	0.31
	TopoAxis2	0.15	-0.12	1.02
	TopoAxis3*	0.87	-6.25	3.61
	VegAxis1*	0.63	-1.78	1.67
	VegAxis2	0.12	-0.11	0.78
	VegAxis3	0.39	-1.41	2.60
	Topographic Wetness Index	0.24	0.42	1.70
	Tasseled Cap Wetness Index	0.22	0.22	1.83

Scientific name	Code	English name	IUCN	Family	Endemism, IBA
Nothoprocta ornata	NOTSP.	Ornate tinamou	LC	Tinamidae	
Nothoprocta pentlandii	NOTSP.	Andean tinamou	LC	Tinamidae	
Nothura darwinii	NOTDAR	Darwin's nothura	LC	Tinamidae	
Patagioenas maculosa	PATMAC	Spot-winged pigeon	LC	Columbidae	
Patagioenas fasciata	PATFAS	Northern band-tailed pigeon	LC	Columbidae	
Leptotila verreauxi	LEPVER	White-tipped dove	LC	Columbidae	
Zenaida auriculata	ZENAUR	Eared dove	LC	Columbidae	
Metriopelia ceciliae	METCEC	Bare-faced ground-dove	LC	Columbidae	IBA BO023
Metriopelia melanoptera	METMEL	Black-winged ground-dove	LC	Columbidae	
Colibri thalassinus	COLTHA	Green violet-ear	LC	Trochilidae	
Colibri coruscans	COLCOR	Sparkling violet-ear	LC	Trochilidae	
Heliangelus amethysticollis	HELAME	Amethyst-throated sunangel	LC	Trochilidae	
Sappho sparganurus	SAPSPA	Red-tailed comet	LC	Trochilidae	
Oreotrochilus estella	OREEST	Andean hillstar	LC	Trochilidae	
Oreotrochilus adela	OREADE	Wedge-tailed hillstar	NT	Trochilidae	IBA BO023; EBA 056
Metallura tyrianthina	METTYR	Tyrian metaltail	LC	Trochilidae	
Aglaeactis pamela	AGLPAM	Black-hooded sunbeam	LC	Trochilidae	Country
Coeligena violifer	COEVIO	Bolivian starfrontlet	LC	Trochilidae	Country
Ensifera ensifera	ENSENS	Sword-billed hummingbird	LC	Trochilidae	
Pterophanes cyanopterus	PTECYA	Great sapphirewing	LC	Trochilidae	
Patagona gigas	PATGIG	Giant hummingbird	LC	Trochilidae	
Chlorostilhon lucidus		Glittering-hellied emerald		Trachilidaa	

TABLE S2

conservation status (LC = Least Concern, NT = Near-Threatened; EN = Endangered) and the Important and/or Endemic Bird Area (IBA/EBA) to which (continued on next five pages). Bird species with their code names observed in Polylepis fragments of the Tunari National Park with their IUCN

Scientific name	Code	English name	IUCN	Family	Endemism, IBA
Amazilia chionogaster	AMACHI	White-bellied humminbird	LC	Trochilidae	
Aulacorhynchus coeruleicinctis	AULCOE	Blue-banded toucanet	LC	Ramphastidae	
Andigena cucullata	ANDCUC	Hooded mountain-toucan	LC	Ramphastidae	
Colaptes melanochloros	COLMEL	Green-barred woodpecker	LC	Picidae	
Colaptes rivolii	COLRIV	Crimson-mantled woodpecker	LC	Picidae	
Colaptes rupicola	COLRUP	Southern Andean flicker	LC	Picidae	IBA BO023
Veniliornis lignarius	VENLIG	Striped woodpecker	LC	Picidae	
Veniliornis nigriceps	VENNIG	Bar-bellied woodpecker	LC	Picidae	
Psilopsiagon aymara	PSIAYM	Grey-hooded parakeet	LC	Psittacidae	
Psilopsiagon aurifrons	PSIORB	Mountain parakeet	LC	Psittacidae	
Bolborhynchus orbygnesius	BOLORB	Andean parakeet	LC	Psittacidae	
Brotogeris chiriri	BROCHI	Yellow-chevroned parakeet	LC	Psittacidae	
Psittacara acuticaudatus	PSIACU	Blue-crowned parakeet	LC	Psittacidae	
Psittacara mitratus	PSIMIT	Mitred parakeet	LC	Psittacidae	
Melanopareia maximiliani	MELMAX	Olive-crowned crescentchest	LC	Rhinocryptidae	
Grallaria rufula	GRARUF	Rufous antpitta	LC	Formicariidae	
Grallaria erythrotis	GRAERY	Rufous-faced antpitta	LC	Formicariidae	Country
Scytalopus parvirostris	SCYPAR	Trilling tapaculo	LC	Rhinocryptidae	
Scytalopus simonsi	SCYSIM	Puna tapaculo	LC	Rhinocryptidae	
Geositta tenuirostris	GEOTEN	Slender-billed miner	LC	Furnariidae	
Xiphocolaptes promeropirhynchus	XIPPRO	Strong-billed woodcreeper	LC	Dendrocolaptidae	
Lepidocolaptes lacrymiger	LEPLAC	Montane woodcreeper	LC	Dendrocolaptidae	
Ochetorhynchus andaecola	OCHAND	Rock earthcreeper	LC	Furnariidae	IBA BO023
Pseudocolaptes boissonneautii	PSEBOI	Streaked tuftedcheek	LC	Furnariidae	

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Scientific name	Code	English name	IUCN	Family	Endemism, IBA
Furnarius rufus	FURRUF	Rufous homero	LC	Furnariidae	
Upucerthia jelskii	UPUJEL	Plain-breasted earthcreeper	LC	Furnariidae	
Cinclodes fuscus	CINFUS	Buff-winged cinclodes	LC	Furnariidae	
Cinclodes atacamensis	CINATA	White-winged cinclodes	LC	Furnariidae	
Syndactyla rufosuperciliata	SYNRUF	Buff-browed foliage-gleaner	LC	Furnariidae	
Margarornis squamiger	Marsqu	Pearled treerunner	LC	Furnariidae	
Sylviorthorhynchus yanacensis	SYLYAN	Tawny tit-spinetail	NT	Furnariidae	IBA BO023
Lepthastenura fuliginiceps	LEPFUL	Brown-capped tit-spinetail	LC	Furnariidae	
Phacellodomus striaticeps	PHASTR	Streak-fronted thornbird	LC	Furnariidae	IBA BO023
Asthenes dorbignyi	ASTDOR	Creamy-breasted canastero	LC	Furnariidae	
Asthenes harterti	ASTHAR	Black-throated thistletail	LC	Furnariidae	Country
Asthenes heterura	ASTHET	Maquis canastero	LΝ	Furnariidae	IBA BO023; EBA 056
Cranioleuca albiceps	Craalb	Light-crowned spinetail	LC	Furnariidae	
Cranioleuca pyrrhophia	Crapyr	Stripe-crowned spinetail	LC	Furnariidae	
Synallaxis azarae	SYNAZA	Azara's spinetail	LC	Furnariidae	
Phytotoma rutila	РНҮКUT	White-tipped plantcutter	LC	Cotingidae	
Ampelion rubrocristatus	AMPRUB	Red-crested cotinga	LC	Cotingidae	
Camptostoma obsoletum	CAMOBS	Southern beardless tyrannulet	LC	Tyrannidae	
Elaenia albiceps	Elalb	White-crested elaenia	LC	Tyrannidae	
Suiriri suiriri	SUISUI	Suiriri flycatcher	LC	Tyrannidae	
Mecocerculus leucophrys	MECLEU	White-throated tyrannulet	LC	Tyrannidae	
Anairetes flavirostris	ANAFLA	Yellow-billed tit-tyrant	LC	Tyrannidae	
Anairetes parulus	ANAPAR	Tufted tit-tyrant	LC	Tyrannidae	
Serpophaga munda	SERMON	White-bellied tyrannulet	LC	Tyrannidae	
Pitangus sulfuratus	PITSUL	Great kiskadee	LC	Tyrannidae	

Scientific name	Code	English name	IUCN	Family	Endemism, IBA
Casiornis rufus	CASRUF	Rufous casiornis	LC	Tyrannidae	
Myiarchus tuberculifer	MYITUB	Dusky-capped flycatcher	LC	Tyrannidae	
Ochthoeca ruftpectoralis	OCHRUF	Rufous-breasted chat-tyrant	LC	Tyrannidae	
Ochthoeca fumicolor	OCHFUM	Brown-backed chat-tyrant	LC	Tyrannidae	
Ochthoeca oenanthoides	OCHOEN	D'Orbigny's chat-tyrant	LC	Tyrannidae	IBA B0023
Ochthoeca leucophrys	OCHLEU	White-browed chat-tyrant	LC	Tyrannidae	
Sublegatus modestus	SUBMOD	Southern scrub-flycatcher	LC	Tyrannidae	
Knipolegus aterrimus	KNIATE	White-winged black-tyrant	LC	Tyrannidae	
Polioxolmis ruftpennis	POLRUF	Rufous-webbed bush-tyrant	LC	Tyrannidae	IBA B0023
Agriornis montanus	AGRMON	Black-billed shrike-tyrant	LC	Tyrannidae	
Myiotheretes striaticollis	Myistr	Streak-throated bush-tyrant	LC	Tyrannidae	
Myiotheretes fuscorufus	Myifus	Rufous-bellied bush-tyrant	LC	Tyrannidae	
Cyclarhis gujanensis	CYCGUJ	Rufous-browed peppershrike	LC	Vireonidae	
Vireo olivaceus	VIROLI	Red-eyed vireo	LC	Vireonidae	
Cyanolyca viridicyanus	CYAVIR	White-collared jay	NT	Corvidae	
Orochelidon murina	Oromur	Brown-bellied swallow	LC	Hirundinidae	
Troglodytes aedon	TROAED	House wren	LC	Troglodytidae	
Mimus dorsalis	MIMDOR	Brown-backed mockingbird	LC	Mimidae	
Catharus ustulatus	CATUST	Swainson's thrush	LC	Turdidae	
Turdus fuscater	TURSP.	Great thrush	LC	Turdidae	
Turdus chiguanco	TURSP.	Chiguanco thrush	LC	Turdidae	
Turdus serranus	TURSER	Glossy black thrush	LC	Turidae	
Turdus amaurochalinus	Turama	Creamy-bellied thrush	LC	Turdidae	
Spinus crassirostris	SPICRA	Thick-billed siskin	LC	Fringillidae	
Spinus magellanicus	SPIMAG	Hooded siskin	LC	Fringillidae	

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Scientific name	Code	English name	IUCN	Family	Endemism, IBA
Spinus atratus	SPIATR	Back siskin	LC	Fringillidae	
Chlorospingus flavopectus	CHLFLA	Common bush-tanager	LC	Thraupidae	
Atlapetes rufinucha	ATLRUF	Bolivian brush-finch	LC	Emberizidae	
Atlapetes fulviceps	ATLFUL	Fulvous-headed brush-finch	LC	Emberizidae	IBA B0023
Zonotrichia capensis	ZONCAP	Rufous-collared sparrow	LC	Emberizidae	
Psarocolius atrovirens	PSAATR	Dusky-green oropendola	LC	Icteridae	
Cacicus chrysonotus	CACCHR	Mountain cacique	LC	Icteridae	
Molothrus bonariensis	MOLBON	Shiny cowbird	LC	Icteridae	
Agelaioides badius	AGEBAD	Greyish cowing	LC	Icteridae	
Oreopsar bolivianus	OREBOL	Bolivian blackbird	LC	Icteridae	
Myioborus brunniceps	MYIBRU	Brown-capped redstart	LC	Parulidae	
Myioborus melanocephalus	MYIMEL	Spectacled redstart	LC	Parulidae	
Pheucticus aureoventris	PHEAUR	Black-backed grosbeak	LC	Cardinalidae	
Saltator aurantiirostris	SALAUR	Golden-billed saltator	LC	Cardinalidae	
Sporophila castaneiventris	SPOCAS	Chestnut-bellied seedeater	LC	Emberizidae	
Poospiza boliviana	POOBOL	Bolivian warbling-finch	LC	Emberizidae	
Compsospiza garleppi	COMGAR	Cochabamba mountain-finch	EN	Thraupidae	Country
Thlypopsis ruficeps	THYRUF	Rust-and-yellow tanager	LC	Thraupidae	
Poospizopsis hypocondria	Роонтр	Rufous-sided warbling-finch	LC	Emberizidae	
Microspingus erythrophrys	MICERY	Rusty-browed warbling-finch	LC	Emberizidae	IBA B0023
Miscrospingus torquatus	MICTOR	Ringed warbling-finch	LC	Emberizidae	
Microspingus trifasciatus	MICTRI	Three-striped hemispingus	LC	Emberizidae	
Conirostrum binghami	CONBIN	Giant conebill	NT	Thraupidae	IBA B0023
Conirostrum ferrugineiventre	CONFER	White-browed conebill	LC	Thraupidae	
Conirostrum cinereum	CONCIN	Cinereous conebill	LC	Thraupidae	

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Scientific name	Code	English name	IUCN	Family	Endemism, IBA
Sicalis flaveola	SICFLA	Saffron finch	LC	Emberizidae	
Sicalis luteocephala	SICLUTO	Citron-headed yellow-finch	LC	Emberizidae	EBA 056
Sicalis olivascens	SICOLI	Greenish yellow-finch	LC	Emberizidae	
Sicalis lutea	SICLUT	Grassland yellow-finch	LC	Emberizidae	IBA B0023
Phrygilus atriceps	PHRATR	Black-hooded sierra-finch	LC	Emberizidae	
Geospizopsis plebejus	GEOPLE	Ash-breasted sierra-finch	LC	Emberizidae	
Idiopsar brachyurus	IDIBRA	Short-tailed finch	LC	Emberizidae	EBA 056
Chionodacryon speculiferum	CHISPE	White-winged diuca-finch	LC	Emberizidae	IBA B0023
Catamenia analis	CATANA	Band-tailed seedeater	LC	Emberizidae	
Catamenia inornata	CATINO	Plain-colored seedeater	LC	Emberizidae	
Diglossa cyanea	DIGCYA	Masked flowerpiercer	LC	Thraupidae	
Diglossa sittoides	DIGSIT	Rusty flowerpiercer	LC	Thraupidae	
Diglossa mystacalis	DIGMYS	Moustached flowerpiercer	LC	Thraupidae	
Diglossa carbonaria	DIGCAR	Grey-bellied flowerpiercer	LC	Thraupidae	IBA BO023; EBA 056
Pipraeidea melanonota	PIPMEL	Fawn-breasted tanager	LC	Thraupidae	
Pipraeidea bonariensis	PIPBON	Blue-and-yellow tanager	LC	Thraupidae	
Pseudosaltator rufiventris	PSERUF	Rufous-bellied mountain-tanager	LΝ	Cardinalidae	IBA BO023 and EBA 056
Dubusia castaneoventris	DUBCAS	Chestnut-bellied mountain-tanager	LC	Thraupidae	
Buthraupis montana	BUTMON	Hooded mountain-tanager	LC	Thraupidae	
Sporathraupis cyanocephala	SPOCYA	Blue-capped tanager	LC	Thraupidae	
Anisognathus somptuosus	ANISOM	Blue-winged mountain-tanager	LC	Thraupidae	
Anisognathus igniventris	ANIIGN	Scarlet-bellied mountain-tanager	LC	Thraupidae	
Lophospingus griseocristatus	Lopgri	Grey-crested finch	LC	Emberizidae	
Tangara sayaca	TANSAY	Sayaca tanager	LC	Thraupidae	

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(continued on five next pages). Bird species observed in the Tunari National Park, reported per watershed (in bold) and Polylepis patch ID (second row), when applicable. Complete bird names and codes are reported in Table S2.2, above. Locations: CAN = Candelaria; CHA = ChaquiPotrero; CHO = Chorojo; ESP = Espital; ICA = Icari; LAP = Laphia; LIR = Liriuni; MOR = Morochata; PAJ = Pajcha; PAL = Palcapamapa; PINT = PintuMayu; SAM = SanMiguel; TAQ = Taquiña; THO = TholaPujru. Data from LIR, ESP and ICA were provided by J. Balderrama.

Ē	СНА	Сно	ESP	ICA		LAP		LIR	Mor	PAJ	PAL	Р	PINT		SAM		TAQ	Тно
2					-	7	3					1	7	1	7	3		
×		x	×	x	x	x	x	×									x	×
				Х				х										
				×														
Х							x			x							x	x
								×									×	
				x				×										
				×				×		×							x	×
				×	x					x				x	x			
			х															
×			×	×	×			×						×				
			Х															
,,	х	Х		Х	Х	Х	х	х		х	х	х	х	Х	Х	Х	Х	х
	×			x	x													
								х			Х							
			x						×									
			х	х					х									
			Х						х									
			×															
			x	х														
	x	x		x	x	x	x	x		x	x	×	×	x	x	x	x	x
							;											

	SAM TAQ THO	2 3	x			X X X		x	X X		X X X X						X X X				X X X X				X		
	PINT	1 2 1						x			x x x	x					x x				x x x				Х		
inued).	MOR PAJ PAL										X X X	x				Х	X X X				X X X				X X	Х	
TABLE S3 (continued).	LAP LIR	1 2 3	x			X X X X		X X X	X		X X X X	x		x	X	X	X X X				X X X				X		x
	CHO ESP ICA		х	x	x		x	x		x	х	x					X	Х	Х	Х	X X X	x	х	x	X X	Х	
	CAN CHA	1 2	I	н	C	L x x	1	P x			f x x		B x	1			X X X	Н	Y	~	f x x x x	7			D x x		×
	Species		AMACHI	AULCOE	ANDCUC	COLMEL	COLRIV	COLRUP	VENLIG	VENNIG	PSIAYM	PSIAUR	BOLORB	BROCHI	PSIACU	PSIMIT	MELMAX	GRARUF	GRAERY	SCYPAR	SCYSIM	GEOTEN	XIPPRO	LEPLAC	OCHAND	PSEBOI	FURRUF

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(continued).
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TABLE

Species	CAN	СНА	Αł	СНО	ESP	ICA		LAP		LIR	MOR	PAJ	PAL	P	PINT		SAM		TAQ	Тно
		1	7				-	7	Э					1	7	1	7	3		
UPUJEL						×														
CINFUS				х	х	х	х	х		х						х	х	х		
CINATA	x	×		x		x	×	x					x	x	x	x	x	x	×	
SYNRUF					Х															
MARSQU					×															
SYLYAN	x	×		x			×	x				×	×	×	×	×	×	×	×	x
LEPFUL		×	×	×		×	×	x	×		×	×	×	×	×	×	×	×	×	x
PHASTR	x	x		×		×	×	×			×	×	x	×	x	×	×		×	×
ASTDOR		x	x	х		x	×	х	x	x	×	×	x	x	x	×	×	×	×	х
ASTHAR	x				x						×									
ASTHET				x		x	×	x			×	×	×						×	
CRAALB											x									
CRAPYR													×							
SYNAZA											x									
PHYRUT		Х	х							Х										
AMPRUB	Х				Х	Х					х	х				х	Х	х	х	
CAMOBS										х										
ELAALB					x					x	×								x	
IUSIUS			x						x										x	x
MECLEU	x	×			x		×		x		×	×		x		x				x
ANAFLA								Х		х		х				х	Х			
ANAPAR		х	Х	Х		Х	х	Х	Х		Х	х	Х	Х	Х	Х	Х	Х	Х	Х
SERMUN										х							х			
PITSUL										Х										
CASRIF					*															

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CAN	0	СНА	Сно	Esp	ICA		LAP		LIR	Mor	PAJ	PAL	PI	PINT		SAM		TAQ	Тно
	1	2				1	2	3					1	2	1	2	3		
									х						х		х	х	
										х									
×				x								x				x	x	x	
x			x		x	x							x	×	×	x			×
×	×	x	x		×	x	×	x	×	×	x	x	x	×	×	x	x	x	×
									×										
	x		х		x				×	×					×			x	
×			x		×		×												
					х														
									×									×	
										×									
								×	×		x						×		
				x															
				Х															
	x	x			x			x	×	×		x			×			x	×
									×										
											х								
x	х	х	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
										x									
								x	x										
					×	x					×	x	x	×	×			x	
Х	х	Х	х		х	х	х		х										
					х	х						х		х					
	Х			Х				х											х
				>						,									

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,	CHO ESP
X X X	Х
Х	Х
X	Х
Х	Х
Х	Х
X	X
х х	
Х	Х
Х	Х
X	Х
х х	
X	Х
Х	Х
Х	X
A A	

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Species	CAN	C	СНА	Сно	ESP	ICA		LAP		LIR	Mor	PAJ	PAL	PINT	LN		SAM		TAQ	Тно
		1	7				1	2	3					1	2	1	2	3		
SICLUT				х			х													
PHRATR	х	×	×	x		x	x	х				x	х	×	x	×	x		x	x
GEOPLE	×			×	×	×	×	×			×	×			x					
IDIBRA						х			Х							x				
CHISPE							×													
CATANA						x	x			x		x								
CATINO	Х	x	x	х		х	x		х	x	х	x		x	x		x		x	×
DIGCYA					x															
DIGSIT					x					x										
DIGMYS					x															
DIGCAR	×	×	×	×	x	×	×	×	x	x	×	×	x	×	x	×	×		x	×
PIPMEL					x															
PIPBON		×					x		x	x									x	
PSERUF	х	×	×	x		x	x	х	x			x	x	×	x	×	x	x	x	×
DUBCAS					x															
BUTMON					x															
SPOCYA					Х															
ANISOM					x															
ANIIGN					х															
LOPGRI										Х										
TANSAY										X		x								

TABLE S4

Results from the NMDS analysis – significant species for each axis at the watershed level with the direction on first axis (Dim1) and on the second axis (Dim2) with the associated p values (pvals1 and pvals2). Bold p-values are significant (< 0.05).

Species	Dim1	pvals1	Dim2	pvals2
NOTSPP	-1	0.61	-1	0.01
NOTDAR	1	0.83	-1	0.012
ZENAUR	1	0.83	-1	0.012
COLCOR	-1	0.279	-1	0.004
SAPSPA	1	0.013	-1	0.314
METTYR	-1	0.013	1	0.314
AGLPAM	-1	0.002	1	0.753
COEVIO	-1	0.004	1	0.442
PTECYA	-1	0.01	-1	0.486
PATGIG	1	0.013	-1	0.314
AMACHI	1	0.572	-1	0.012
PSIAYM	1	0.014	-1	0.984
MELMAX	1	0.019	1	0.003
PSEBOI	-1	0.013	1	0.314
FURRUF	1	0.462	-1	0.035
CINFUS	-1	0.412	-1	0.036
SYLYAN	1	0.017	1	0.212
LEPFUL	1	0.036	1	0.031
ASTDOR	1	0.029	1	0.661
PHASTR	1	0.08	1	0.031
ASTHAR	-1	0.004	1	0.442
PHYRUT	1	0.447	-1	0.049
ANAPAR	1	0.036	1	0.031
TURAMA	1	0.547	-1	0.024
SPIMAG	1	0.85	-1	0.04
ATLRUF	-1	0.013	1	0.314
CONFER	-1	0.004	1	0.442
SICOLI	1	0.009	-1	0.377
PHRATR	1	0.022	1	0.285
GEOPLE	-1	0.032	1	0.223
DIGSIT	-1	0.08	-1	0.031
PSERUF	1	0.022	1	0.285

TABLE S5

Results from the NMDS analysis – significant species for each axis at the patch level with the direction on the first axis (Dim1) and on the second axis (Dim2) with the associated p values (pvals1 and pvals2). Bold p-values are significant (< 0.05).

Species	Dim1	pvals1	Dim2	pvals2
NOTSPP	-1	0.007	1	0.553
PATFAS	-1	0.028	-1	0.354
CHLLUC	1	0.951	-1	0.041
COLMEL	-1	0.001	-1	0.765
MELMAX	-1	0.029	1	0.071
SYLYAN	1	0.007	1	0.485
AMPRUB	1	0.041	-1	0.126
SUISUI	-1	0.005	-1	0.111
MYITUB	1	0.131	-1	0.006
OCHFUM	1	0.22	-1	0.032
TROAED	-1	0.052	-1	0.025
SPIMAG	-1	0.127	1	0.026
CHLFLA	-1	0.027	-1	0.351
POLRUF	-1	0.928	1	0.011
ATLFUL	-1	0.004	-1	0.111
AGEBAD	-1	0.005	1	0.106
MYIBRU	-1	0.504	-1	0.001
COMGAR	-1	0.448	-1	0.008
РООНҮР	-1	0.001	1	0.526
CONBIN	1	0.045	1	0.249
PHRATR	-1	0.951	1	0.041
GEOPLE	1	0.441	1	0.001