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RESEARCH ARTICLE

Taxonomic and functional diversity of birds in a rural landscape of high Andean forest, Colombia

Lina P. Sarmiento-Garavito[1], Juan S. García-Monroy[1], Juan E. Carvajal-Cogollo[1]

1 *Grupo de Investigación Biodiversidad and Conservación, Museo de Historia Natural Luis Gonzalo Andrade Natural, Facultad de Ciencias, Universidad Pedagógica y Tecnológica de Colombia, Address Avenida Central del Norte 39-115, 150003 Tunja, Boyacá, Colombia*

Corresponding author: Juan E. Carvajal-Cogollo (juancarvajalc@gmail.com)

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Abstract

We evaluated the taxonomic and functional diversity of birds in a rural landscape in the north-eastern Andes of Colombia. We carried out seven field trips and used transects of 300 m, separated from each other by 500 m in the dominant plant cover of the rural landscape. We measured alpha (α) and beta (β) diversity at both the taxonomic and functional levels. We registered 10 orders, 21 families, 56 genera and 63 species of birds. In wooded pasture, we recorded 55 species and a relative abundance of 66% and 44 and 34% for an Andean forest fragment. The species that contributed the most to the dissimilarity between the covers were *Zonotrichia capensis*, *Turdus fuscater*, *Mecocerculus leucophrys*, *Atlapetes latinuchus* and *Crotophaga ani*. We identified nine functional types, where G1 was made up of small species with anissodactyl and pamprodactyl legs that were insectivorous, frugivorous and nectarivorous as the best represented. The FEve and FDiv were 0.51 and 0.74, respectively in the Andean forest fragment plant cover and, for the wooded pasture, the FEve was 0.45 and the FDiv was 0.81. Both cover types contributed to the diversity of the rural landscape and the dynamics that existed between them formed a complementary factor that favoured the taxonomic and functional richness of the characterised rural landscape.

Keywords

Colombian Andes, countryside, functional traits, species composition, species richness, transformed landscape

Introduction

The transformation of landscapes by the loss and fragmentation of land-cover types results in a mosaic of native plant cover, surrounded by extensive areas of anthropogenic cover types (Collinge 2009; IPBES 2019). Agriculture and pastures, destined for livestock, form a large part of these new land covers and their unplanned extension does not allow sustainable use to be recognised as one of the current threats to biodiversity, both at the taxonomic scale (richness, composition and abundance) and at the functional level (diversity of functional traits) (Tscharntke et al. 2012; Freedman 2014). The extension of agricultural activities and livestock affect biological communities in their structure and composition and leads to functional and ecological destabilisation of natural systems (Bilenca et al. 2017). This conglomerate of effects on arable land fractions without buildings, but not containing agricultural land, crops, plantations and managed forests, as well as remnants of native vegetation, is what has been defined as rural landscape (Daily et al. 2001; Ranganathan and Daily 2008).

Rural landscapes favour positive and negative responses from biodiversity, depending on the intensity of habitat loss or fragmentation and the study group (Lawton et al. 1998; Newbold et al. 2013). For flocks of birds, studies show that they respond positively to habitat fragmentation (Villard et al. 1999; Lampila et al. 2005). In this way, when evaluating the responses of taxonomic diversity (species richness, composition and abundance) and functional variety, we understand the connection between species and how these are integrated into ecosystems (Villéger et al. 2008; Cadotte et al. 2011; López-Ordoñez et al. 2015). At the taxonomic level, the evaluation of specific diversity (alpha) through the analysis of species richness, relative abundance (structure) and species composition added to the quantification of diversity functional traits of species provides new and complementary information for the conservation of species in rural landscapes (Oldeland et al. 2010). This fact becomes relevant if we consider the changes that species undergo at the level of behavioural and functional attributes with habitat disturbance, as seen in the Andes of Colombia, where severe transformation patterns linked to human occupation have been documented (Cavelier and Etter 1995; Morante-Filho et al. 2016).

Rural landscapes modify positive and negative responses from biodiversity, depending on the intensity of the loss and/or fragmentation of the habitats and the study group (Lawton et al. 1998; Newbold et al. 2013). For many bird flocks, there are studies that demonstrate positive responses to habitat fragmentation (Villard et al. 1999; Lampila et al. 2005). In this way, when evaluating the responses of diversity from the taxonomic and functional dimensions, it allows us to understand the connection between species and the functioning of ecosystems (Cadotte et al. 2011; López-Ordoñez et al. 2015). At the taxonomic level, the evaluation of specific diversity (alpha), through species richness analysis, relative abundance (structure) and species composition added to the quantification of the diversity of functional features of species (functional dimension) provides new and complementary information for the conservation of species in rural landscapes, but especially for those that have suffered severe patterns of transformation linked to human occupation of regions like the Andean cordillera of Colombia (Cavelier and Etter 1995; Oldeland et al. 2010; Morante-Filho et al. 2016).

The landscapes of the Andean region of Colombia are the most diverse on the planet, with species that have limited ranges of distribution generating elements where the alpha and beta diversity of various taxonomic groups, such as birds, are highly expressed (Carvajal-Castro et al. 2019). Birds have been widely used as a biological model, thanks to their biological and ecological qualities (Veríssimo et al. 2009; Larsen et al. 2012); and the evaluation of different parameters of their assemblages can be used as inputs for the establishment of areas of importance or conservation strategies in each area (Westgate et al. 2014). In addition, birds have wide distribution, high taxonomic diversity and functional levels and an ability to attract attention and arouse the fascination of people making them a model for study (Veríssimo et al. 2009; Ikin et al. 2016).

We evaluated the taxonomic and functional diversity of birds in wooded grasslands and forest fragments in a rural landscape in the Colombian Andes. We started from the premise that grasslands with trees with a simple plant structure would have lower values of alpha diversity, both taxonomic and functional, in relation to forest fragments, whose plant structure is complex and stratified and provides greater availability of resources for the species. Similarly, beta diversity between assemblages will be structured by high turnover in species composition.

Materials and methods

Study area

The research was carried out in an Andean rural landscape of the Eastern Cordillera of Colombia (5°42'20"N, 73°30'35"W), at 2583 m a.s.l., in the Department of Boyacá. The study area has temperatures between 11 °C and 15 °C, relative humidity between 80% and 82% and a mean annual rainfall between 1000 mm and 1900 mm with two rainfall peaks per year, the first between March and April and the second between October and November (Galindo 2000).

The study area (Fig. 1A–D) was a landscape dominated by two types of cover, namely Andean forest fragments and wooded grasslands. The forest fragments are remnants of the original vegetation, composed of *Quercus humboldtii* or oak, with arborescent elements that have colonised the spaces made available by logging, giving space to *Pinus patula* plantations, *Acacias melanoxylon* and *Acacia decurrens* (Rangel-Ch et al. 1997). The second dominant cover of wooded grasslands are defined as open areas with isolated Melastomataceae and Clusiaceae trees, with herbaceous and shrub elements (70%), dedicated to cattle grazing (Rangel-Ch. et al. 1997).

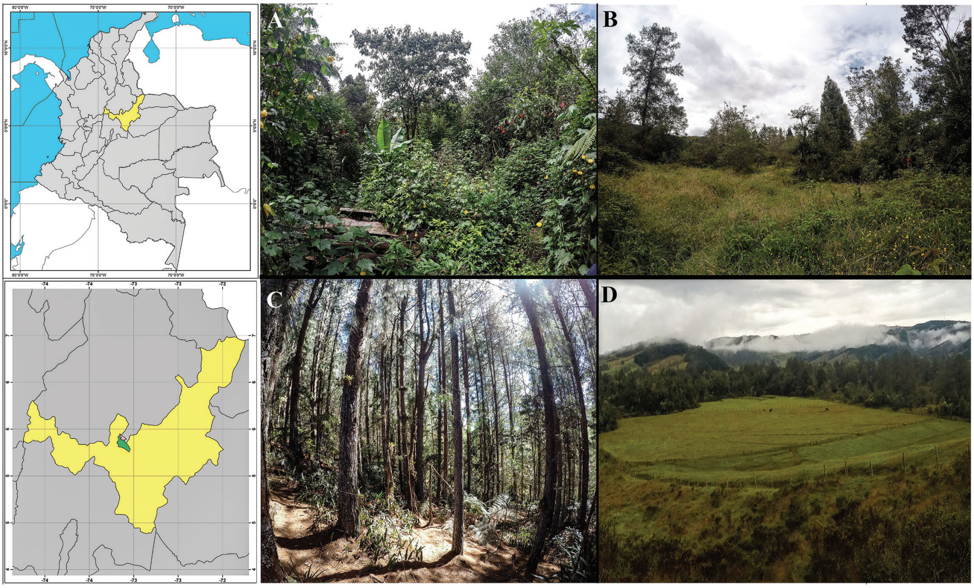

Figure 1. Location of the study area, an Andean rural landscape of the Eastern Cordillera of Colombia. The sampled landscape units are highlighted **A, B** wooded pasture **C, D** Andean Forest.

Research design and sampling

We established transects in an Andean forest fragment of 17.57 ha and a wooded pasture of 12.13 ha, both at an altitude of 2527 m above sea level. For each of the sampled covers (fragment of Andean forest and wooded pasture), we carried out two free travel transects with a length of 300 m each, separated from each other by 500 linear m, a distance documented as optimal for data collection in linear transects and that for the study area guaranteed the independence of samples, due to the topography of the area with steep slopes that spatially increased the real distance across the land surface (Gale et al. 2009). Each transect was replicated in space and time and represented the minimum sampling unit. The order of sampling of each transect was carried out randomly to eliminate the correlation between the observations and avoid overestimations in the richness and abundance of the species (Ralph et al. 1996). In each transect, all bird species that were visually detected within an unlimited radius, for 10 minutes in the morning sampling and eight minutes in the evening sampling, for a total of 18 minutes per point/day (Howe et al. 1997; Leach et al. 2016).

We carried out seven field trips between June and December 2017. During this period, we registered the birds for the climatic seasons that characterise the area and a migration peak, to obtain real estimates of alpha diversity. During each field trip, we walked a daily transect two times, one in the morning from 5:30 h to 10:30 h and another in the mid- to late afternoon between 15:00 h and 17:30 h. We rotated these schedules throughout the field trips to obtain records of most species, given their activity peaks (Ralph et al. 1996). For bird watching, we used 10 × 50 binoculars and reflex cameras with a 150–600 mm super telephoto lens and a 75–300 mm lens. The sampling effort was 420 hours/person.

For recording information, formats were used daily during each field trip. In these formats, we recorded the data of the coordinates of the place of each observation, the altitude, the date and the time of the sighting, the foraging stratum and the social behaviour (López-Ordoñez et al. 2015). In addition, the number of individuals observed (detections) made up the basic input for the analysis of alpha and beta diversity.

Taxonomic determination was carried out with specialised pictorial keys for neotropical and Colombian birds (Restall et al. 2007; Ridgely and Tudor 2009; McMullan and Donegan 2014). The taxonomic arrangement followed Remsen et al. (2020).

Analysis of data

We evaluated the alpha diversity (α) of each vegetation type (cover type) from data of relative richness and abundance. We used the sample´s completeness method (Chao and Jost 2012) that measures the proportion represented by the individuals of each species in the sample with respect to the total number of individuals with which the expected species could be quantified through accumulation curves. Sampling coverages were evaluated through accumulation curves (rarefaction and extrapolation) and with the Hill numbers and the evaluation of $q = 0$ that measured the total species richness (true diversity), the $q = 1$ that expressed the exponential of the Shannon Entropy Index and $q = 2$, corresponding to the inverse of the Simpson Index (Chao et al. 2014). For each analysis, we used the procedure of Chao and Jost (2012) in the iNEXT programme (Hsieh et al. 2013). In addition, we applied non-parametric estimators of Chao 1 and bootstrap for a better approach to the structure of the bird assemblage (Chao and Lo 1994), since there were species that were represented by few individuals. We quantified the values of singletons and doubletons and of any unique and duplicate samples using the programme EstimateS version 9.0 (Colwell et al. 2019).

The structure of the bird assemblage, expressed by the relative abundance of the species, was obtained from the division of the number of individuals counted for each species and the total numbers per cover type taken as a percentage (Pettingill 1985; Issa 2019). We applied analysis of similarity of the abundance matrix (ANOSIM) to determine if there were differences in the composition of birds between cover types and a SIMPER analysis to identify the taxa that contributed to the differentiation or similarity between the groups through the percentages of contribution (PC) and accumulation (AC) of the detections in each of the vegetation cover types (Clarke 1993). Beta diversity (β) was analysed by means of the turnover of species between the two vegetation cover types with the complementarity index. Exclusive and shared species between both cover types were also identified (Colwell and Coddington 1994).

For the functional diversity analyses, we considered four ethological functional traits related to the ecological role of nutrient and energy flow within the ecosystem (Stotz et al. 1996; López-Ordoñez et al. 2015): 1. Type of diet (carnivore, scavenger, folivore, frugivore, granivore, insectivore, nectarivore) (Stotz et al. 1996; Wilman et al. 2014); 2. Feeding strategy (catcher, forager, robber) (López-Ordoñez et al. 2015), 3. Foraging stratum (arboreal, shrub, herbaceous and soil) (Rangel-Ch and Lozano-C 1986); and 4. Social behaviour (mixed flock, monospecific flock and solitary). Furthermore, we took into account four morphometric traits, related to the selection of foraging sites and seed dispersal (Sekercioglu 2006): 1. Type of legs (anissodactyls, pamprodactyls, sydactyls, totipalmos, zygodactyls); 2. Beak shape (tall and compressed, conical, short and robust, recurved, curved, fine and pointed, hooked, slightly curved, pointed, straight, straight and fine, straight and pointed) and 3. Body size (large, medium, small) (Herrel et al. 2005; López-Ordoñez et al. 2015). The values of the functional traits were obtained in the field and supplemented by secondary information.

To quantify functional diversity, we performed a cluster analysis to identify functional types of birds in each of the sampled habitats (Petchey and Gaston 2002; Casanoves et al. 2011). We also calculated two multidimensional-multifunctional indices, functional equity (FEve) and functional dispersion (FDis) (Mouillot et al. 2005; Laliberté and Legendre 2010). For these analyses, we used the statistical packages infoStat and FDiversity that connects to the statistical programme R with an interface written in Delphi with DCOM-R (Di Rienzo 2009; Casanoves et al. 2011).

Results

Richness and composition of bird assemblages

We registered 10 orders, 21 families, 56 genera and 63 species of birds (Table 1). In the wooded pasture, the richness was 55 species, followed by the Andean forest fragment with 44 species. The families with the highest abundances were Passerellidae with 282 individuals, followed by Parulidae with 185 and Trochilidae with 179. The genera with the highest number of individuals were *Atlapetes* (183), *Myioborus* (103) and *Coeligena* (103). In the Andean forest fragment, the two best represented families were Trochilidae with eight genera and Passerellidae with four and, in the wooded pasture, they were Trochilidae with seven genera and Tyrannidae with five.

We obtained a high proportion of avian species richness from the two cover types. The percentage of representativeness was 94.39% and 94.38%, for the wooded pastureland and the Andean forest fragment, respectively (Fig. 2A–C).

Structure of the bird assemblage

In the wooded pasture, we obtained a relative abundance of 66% (838 individuals), with nine species represented by only one individual and 10 species with two

Table 1. Composition and richness of birds and their respective absolute and relative abundances in an Andean rural landscape of the Eastern Cordillera of Colombia. The five most abundant species for each cover are highlighted in bold.

Taxon name	English name	Code	Absolute Abundance (AA)		Relative abundance (RA%)		Functional group
			Fragments of Andean forest	Wooded pasture	Fragments of Andean forest	Wooded pasture	
Galliformes							
Cracidae							
Penelope montagnii	Andean Guan	Pem	3	0	0.718	0	G9
Columbiformes							
Columbidae							
Patagioenas fasciata	Band-tailed Pigeon.	Paf	0	15	0	1.789	G4
Zenaida auriculata	Eared Dove	Zea	0	3	0	0.358	G4
Cuculiformes							
Cuculidae							
Crotophaga ani	Smooth-billed Ani	Cra	0	33	0	3.938	G8
Piaya cayana	Squirrel Cuckoo	Pic	4	0	0.957	0	G8
Coccyzus americanus	Yellow-billed Cuckoo	Coa	2	5	0.478	0.597	G8
Apodiformes							
Trochilidae							
Adelomyia melanogenys	Speckled Humming-bird	Adm	18	6	4.307	0.716	G1
Chaetocercus heliodor	Gorgeted Woodstar	Chh	1	1	0.240	0.120	G1
Chaetocercus mulsant	White-bellied Woodstar	Chm	0	8	0	0.955	G1
Campylopterus falcatus	Lazuline Sabrewing	Caf	10	0	2.393	0	G1
Chlorostilbon poortmani	Short-tailed Emerald	Chp	1	1	0.240	0.120	G1
Coeligena prunellei	Black Inca	Cop	**30**	**40**	**7.177**	4.773	G1
Colibri coruscans	Sparkling violet-ear	Coc	2	4	0.479	0.478	G1
Colibri cyanotus	Lesser Violetear	Coy	18	14	4.307	1.671	G1
Heliangelus amethysticollis	Amethyst-throated Sunangel.	Hea	11	2	2.632	0.239	G1
Metallura tyrianthina	Tyrian Metaltail.	Met	3	9	0.718	1.074	G1
Pelecaniformes							
Ardeidae							
Ardea alba	Great White Egret	Ara	0	1	0	0.120	G9
Cathartiformes							
Cathartidae							
Coragyps atratus	Black Vulture	Cga	2	2	0.479	0.239	G9
Cathartes aura	Turkey Vulture	Caa	0	2	0	0.239	G9
Accipitriformes							
Accipitridae							
Rupornis magnirostris	Roadside hawk.	Rum	3	7	0.718	0.836	G4
Coraciiformes							
Alcedinidae							
Megaceryle torquate	Ringed Kingfisher	Meq	0	2	0	0.239	G9
Piciformes							
Picidae							
Colaptes rivolii	Crimson-mantled Woodpeck-er.	Cor	6	1	1.436	0.120	G7
Melanerpes formicivorus	Acorn Woodpeck-er	Mef	0	2	0	0.239	G7
Ramphastidae							
Aulacorhynchus prasinus	Emerald Toucanet	Aup	0	2	0	0.239	G6
Passeriformes							
Passerellidae							
Arremon brunneinucha	Chestnut-capped Brush-finch	Arb	4	0	0.957	0	G3

Taxon name	English name	Code	Absolute Abundance (AA)		Relative abundance (RA%)		Functional group
			Fragments of Andean forest	Wooded pasture	Fragments of Andean forest	Wooded pasture	
Atlapetes albofrenatus	Moustached Brush-finch	Ata	**26**	**54**	**6.221**	**6.444**	G2
Atlapetes latinuchus	Yellow-breasted Brush-finch	Atl	**32**	**71**	**7.656**	**8.473**	G2
Chlorospingus canigularis	Ashy-throated Chloro-spingus	Chc	13	5	3.111	0.597	G2
Chlorospingus flavopectus	Common Chloro-spingus	Chf	17	2	4.067	0.239	G2
Zonotrichia capensis	Rufous-collared Sparrow	Zoc	2	**56**	0.479	**6.683**	G2
Turdidae							
Catharus ustulatus	Swainson's Thrush	Cau	0	4	0	0.478	G3
Turdus ignobilis	Black-billed Thrush	Tui	0	3	0	0.358	G3
Turdus fuscater	Great Thrush	Tuf	8	**65**	1.914	**7.757**	G4
Thraupidae							
Diglossa albilatera	White-sided Flower-piercer	Dia	18	31	4.307	3.701	G4
Diglossa caerulescens	Bluish Flower-piercer	Dgc	0	1	0	0.120	G3
Diglossa cyanea	Masked Flower-piercer	Dic	5	8	1.197	0.955	G1
Stilpnia heinei	Black-Capped Tanager	Tah	4	7	0.957	0.836	G2
Sporathraupis cyanocephala	Blue-capped Tanager	Spc	13	35	3.111	4.177	G1
Tyrannidae							
Elaenia frantzii	Mountain Elaenia	Elf	2	18	0.479	2.148	G1
Mecocerculus leucophrys	White-banded Tyrannulet	Mel	11	**51**	2.632	**6.086**	G1
Pitangus sulphuratus	Great Kiskadee	Pis	0	6	0	0.716	G4
Pyrrhomyias cinnamomeus	Cinnamon Flycatcher	Pyc	1	0	0.240	0	G3
Tyrannus melancholicus	Tropical Kingbird	Tym	0	10	0	1.194	G1
Zimmerius chrysops	Golden-faced Tyrannulet	Zic	3	5	0.718	0.597	G1
Troglodytidae							
Troglodytes aedon	House Wren	Tra	0	13	0	1.552	G1
Henicorhina leucophrys	Grey-breasted Wood Wren	Hel	9	10	2.154	1.194	G1
Pheugopedius mystacalis	Whiskered Wren	Phm	1	0	0.240	0	G3
Icteridae							
Icterus chrysater	Yellow-backed Oriole	Icc	**26**	**44**	**6.221**	**5.251**	G1
Sturnella magna	Eastern Meadow-lark	Stm	0	6	0	0.716	G4
Furnariidae							
Lepidocolaptes lacrymiger	Montane Wood-creeper.	Lel	2	0	0.479	0	G5
Synallaxis azarae	Azara´s Spinetail	Sya	12	**44**	2.871	5.251	G1
Xenops rutilans	Streaked Xenops	Xer	2	1	0.479	0.120	G5
Parulidae							
Mniotilta varia	Black-and-white Warbler	Mnv	**1**	**2**	0.240	0.239	G5
Myioborus miniatus	Slate-throated Redstart	Mym	**39**	**45**	**9.331**	**5.370**	G1
Myioborus ornatus	Golden-fronted Whitestart	Myo	13	6	3.111	0.716	G1
Myiothlypis coronate	Russet-crowned Warbler	Myc	9	0	2.154	0	G1
Setophaga fusca	Blackburn-ian Warbler	Sef	20	**49**	4.785	5.848	G1
Parkesia noveboracensis	Northern Waterthrush	Pan	0	1	0	0.120	G3

Taxon name	English name	Code	Absolute Abundance (AA)		Relative abundance (RA%)		Functional group
			Fragments of Andean forest	Wooded pasture	Fragments of Andean forest	Wooded pasture	
Fringillidae							
Spinus psaltria	Lesser Goldfinch	Spp	1	2	0.240	0.239	G3
Spinus spinescens	Andean Siskin	Sps	1	1	0.240	0.120	G3
Virionidae							
Vireo leucophrys	Brown-capped Vireo	Vil	9	19	2.154	2.268	G4
Vireo olivaceus	Red-eye Vireo	Vio	0	2	0	0.239	G3
Cardinalidae							
Piranga rubra	Summer Tanager	Pir	0	1	0	0.120	G3

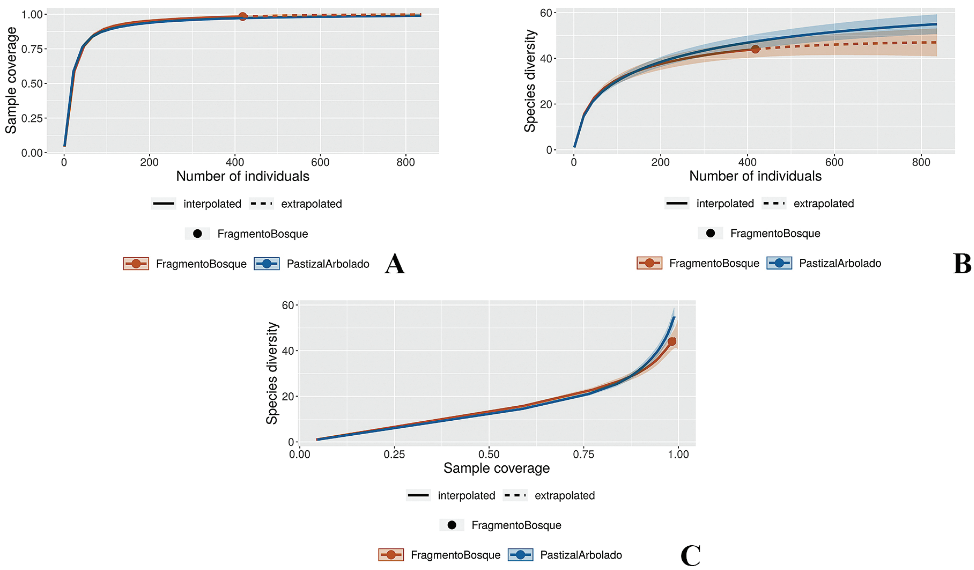

Figure 2. **A** Sampling coverage by number of bird individuals in a rural Andean landscape of the Eastern Cordillera of Colombia. Rarefaction (solid lines), and extrapolated (dotted lines). **B** Diversity of species by number of individuals in a rural Andean landscape of the Eastern Cordillera of Colombia. Interpolation (solid line) and extrapolation (dashed line). **C** Sampling coverage by number of bird species in a rural Andean landscape of the Eastern Cordillera of Colombia. Interpolation (solid line) and extrapolation (dashed line). The shadows on the curves correspond to the 95% confidence intervals.

(Table 1). In the Andean forest fragment, the relative abundance was 34% (418), represented by seven unique individuals and seven species with two individuals (Table 1). The hierarchical distribution of the species abundance was different between the two vegetation covers (Fig. 3). For the wooded pasture, the species with the highest relative abundances were *Atlapetes latinuchus*, *Turdus fuscater*, *Zonotrichia capensis*, *Atlapetes albofrenatus* and *Mecocerculus leucophrys* and, for the Andean forest fragment, they were *Myioborus miniatus*, *Atlapetes latinuchus*, *Coeligena prunellei*, *Atlapetes albofrenatus* and *Icterus chrysater*. The species *Atlapetes latinuchus* and *Atlapetes albofrenatus* had high relative abundances in both plant cover types (Fig. 3).

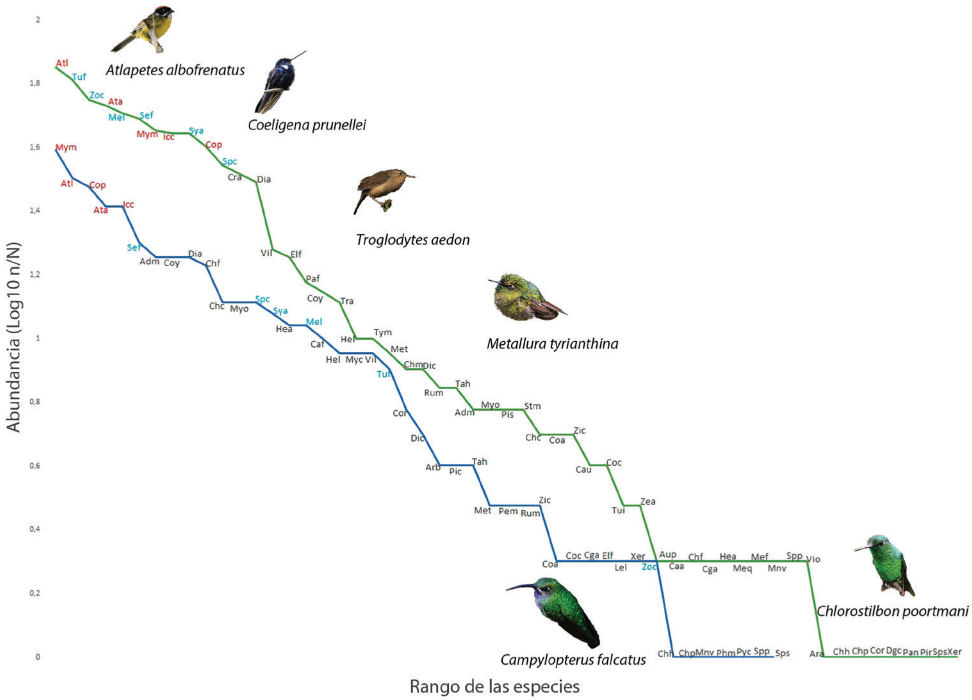

Figure 3. Range-abundance curve of the bird species for two covers evaluated in a rural landscape an Andean rural landscape of the Eastern Cordillera of Colombia. The green line corresponds to the cover of wooded grassland. Reference the codes in relation to Table 1.

The species that contributed the most to the dissimilarity between the vegetation covers were *Zonotrichia capensis* (SIMPER: 7.865%), *Turdus fuscater* (SIMPER: 7.445%), *Mecocerculus leucophrys* (SIMPER: 5.605%) and *Atlapetes latinuchus* (SIMPER: 5.132%), as well as species *Crotophaga ani* (SIMPER: 4.944%), *Synallaxis azarae* (SIMPER: 4.788%), *Setophaga fusca* (SIMPER: 4.627%), *Diglossa albilatera* (SIMPER: 3.957%) and *Atlapetes albofrenatus* (SIMPER: 3.935%).

Beta diversity

Of 63 species found, 19 were exclusive to the wooded grassland cover and eight were exclusive to the plant cover type of the Andean forest fragment (Table 1). The dissimilarity between the coverages was 43%. The transects of each cover was also a high dissimilarity, 48% amongst the transects of the Andean forest fragment and 43% amongst those of the wooded pasture. We did not find differences between the richness and composition of the Andean forest fragment and the wooded pasture (ANOSIM: R = 1, p = 0.32).

Table 2. Groups or functional types of birds in a rural Andean landscape of the Eastern Cordillera of Colombia. Each group was generated from cluster analysis for coverage type.

Group	Number of species	Characteristics	Coverage
G1	23	Mainly small, anisodactyl and pamprodactyl legged species, with diets based mostly on insects, fruits and/or nectar.	Fragment of Andean forest and wooded pasture.
G3	12	Species of small size, of trapping and foraging habits, with anisodactyl and pamprodactyl legs, which can occupy the arboreal, shrubby and herbaceous levels.	Fragment of Andean forest and wooded pasture.
G4	8	Small and medium-sized species, which present anisodactyl legs, are mostly catchers and scavengers, with straight beaks dominating, followed by hooked ones.	Fragment of Andean forest and wooded pasture.
G2	6	Species of small size, with anisodactyl legs, this group is dominated by species with a not very specific diet, which includes fruits, seeds, insects and leaves, most of the species in this group presented conical beaks.	Fragment of Andean forest and wooded pasture.
G9	5	Large species, almost all of which occupy mainly the arboreal stratum, their diets include the ingestion of carrion, meat and fruits.	Fragment of Andean forest and wooded pasture.
G5	3	Small species, with insectivorous diet of curved beak, that occupy the shrub and sapling levels.	Fragment of Andean forest and wooded pasture.
G8	3	Medium-sized, curved-billed, zygodactyl, trappers or foragers, living in monospecific and/or solitary flocks.	Fragment of Andean forest and wooded pasture.
G7	2	Species of various sizes, of foraging habits, insectivorous, with zygodactyl legs, with straight beaks, they mainly occupy the arboreal and shrub levels.	Fragment of Andean forest and wooded pasture.
G6	1	A single, medium-sized, foraging species with zygodactyl legs and a high, compressed beak that occupies the arboreal stratum and bases its diet on fruit and insects.	Wooded pasture.

Functional diversity

We identified nine functional types: Group 1 (G1) was the best represented, made up of mainly small species, with anissodactyl and pamprodactyl legs and diets based on the ingestion of insects, fruits, nectar or both. Group 2 (G2) was represented by species of small size, trappers and foragers with anissodactyl and pamprodactyl legs that can occupy the shrub and herbaceous strata (Table 2). In the Andean forest fragment, we recorded eight of the nine groups identified in the entire study and, in the wooded pasture, all nine groups were represented. The functional equity (FEve) was 0.51 in the Andean forest fragment cover and differences are shown between the roles played by the dominant species (FDiv = 0.74). In the wooded pasture, we obtained a lower functional equity (FEve = 0.45) than in the Andean forest fragment. Similarly, role differentiation was presented by the dominant functional species (FDiv = 0.81).

Discussion

Taxonomic diversity of birds

The diversity of birds in the rural landscape for each of their representative cover types was low in relation to other fragmented landscapes in Colombia, such as those found in the tropical and sub-Andean region of the Las Quinchas Mountain range in the Eastern Cordillera of Colombia (García-Monroy et al. 2020). Although the rural landscape of our study was completely in the Andean life region, for these sectors, there are records of a higher number of species (Córdoba-Córdoba and Echeverry-Galvis 2006; Jiménez 2010). In this regard, Trzcinski et al. (1999) hypothesise that the presence of bird species in the landscape is more related to the amount of habitat present than to the degree of fragmentation. Our rural landscape, despite being in areas bordering a protected area, has had a history of transformation in the last century, where most of the original coverage has diminished to critical points or has even disappeared (Etter 1993). This fact shows a configuration of the current landscape made up mostly of pastures for livestock, crops and small fragments of intervening forest, many of them the product of natural regeneration in the last four decades (Chavarro 2005).

The fact that, in the wooded pasture, the highest species richness value was recorded compared to the Andean forest fragment shows several ecological aspects of landscapes, as documented by Tabarelli et al. (2010), for fragmented landscapes of the Atlantic Forest. First, the greater heterogeneity of the wooded pastures gives rise to various areas that offer more resources, both for specialist species and generalists in choice of habitat. Second, the greatest amount of edge habitats are found for the wooded grasslands, facilitating edge effects: higher richness and higher detection values for the ecotonal area (e.g. for the study area the forest edges, areas around roads or living fences), as documented in multiple studies (García-Romero et al. 2019). Third, the structure of vegetation in Andean forests with the presence of foreign species, such as *Pinus radiata* (Don, 1836) and *Eucalyptus globulus* (Labill, 1800), limits food resources and nesting sites for many bird species (Zurita et al. 2006); and this is directly related to the alpha diversity for these plant cover types.

Another ecological aspect that has a direct effect on the species richness values in the sample cover types and that is often not considered because of inferences towards a specific taxonomic group is the detection capacity. This can be managed with other methodologies. However, for the purpose of this study and that of observing the functional attributes, direct observation of the species was necessary. This fact together with the fact that the wooded grassland area had more heterogeneity than the Andean forest fragment and given the complex plant structure and homogeneous nature of the latter, the type of plant cover limited observations, while they were facilitated in areas of wooded grasslands with open areas (Enríquez-Lenis et al. 2007).

In terms of composition and structure, the differences recorded between the plant cover types are due, like the species richness, to the structural complexity in terms of the vegetation of each of the plant cover type. This is a general pattern identified in rural landscapes (Cook et al. 2002). In contrast, the conjunction of remnant vegetation, living fences and production areas with isolated trees in wooded pastures creates suitable locations for the establishment and occupation of sites corresponding to species with a wide spectrum of habitat, generalists in the choice of resources, such as *Turdus fuscater*, *Zonotrichia capensis* and *Tyrannus melancholicus*

(Ocampo-Peñuela and Pimm 2015). In the case of the Andean forest fragment, the assemblage has generalist species, but also there are others with some degree of specialisation, for example, *Pyrrhomyias cinnamomeus* and *Colaptes rivolii* (Avendaño et al. 2013). This is a pattern like that recorded in other fragmented natural systems (Zurita et al. 2006; Tabarelli et al. 2010; Hadley et al. 2018).

The contrasting plant cover in the landscape contributes to the turnover of species within the types of cover observed in the wooded pasture, as it is the dominant cover in the north-eastern Andean landscapes after grasslands (Etter 1998). In this way, wooded grasslands serve as a transition zone between the open areas and the Andean forest fragment. However, it is important to bear in mind that both plant covers have a different structure and contribute unique species to the assemblage of birds in the landscape. This is a basic input when taking conservation actions in this type of region since this contrast of areas contributes greatly to the maintenance of biodiversity in these transformed landscapes (Lôbo et al. 2011).

The exchange of species found in the study area can be linked to the heterogeneity that is present in tropical landscapes altered by changes in land use. The land-use changes directly affect the composition of birds within the landscape vegetation coverage; and according to the spatial scale of the analysis, it can generate variations within the analysed coverage, together with other filters and biotic variables of each landscape (Morante-Filho et al. 2016).

Functional diversity

From the results, we observe that there is higher functional diversity in the wooded pasture with respect to the Andean forest cover. There is also a marked relationship between functional equity and the distribution of wealth between functional attributes (Luck et al. 2013). However, the fact that functional diversity does not decrease with the degree of simplification of the structure of the plant cover reflects a result that is observed infrequently in fragmented landscapes, when the biodiversity values are congruent with the complexity of the structure of the vegetation that is evaluated. It also provides information on the response of the assemblages to these new landscapes, where the greater heterogeneity of the wooded landscapes could provide a greater number of resources for the maintenance of the bird assemblage and the history of disturbances of the fragments clearly reflects the composition and structure of current assemblages. In this way, the fragments of secondary forests that form the rural landscapes of the north-eastern Andes of Colombia are the product of regeneration, restoration or both during the last three decades, where the vegetation has reached structural maturity, but perhaps the faunal groups that occupy these areas do not follow the same maturity line (Etter 1993). This fact represents a priority topic for evaluation in this type of rural landscape.

Regarding functional divergence, the values obtained for the two vegetation types reflect high niche differentiation, allowing better use of the resources that the plant cover type provides and reduces the levels of competition (Ding et al. 2017).

In addition to this, we found a higher abundance of frugivorous and nectarivorous birds in the plant cover of the wooded grasslands. These species may be closely related to the passive restoration of the site since they influence pollination and seed dispersal, like that documented by Tscharntke et al. (2012). In addition, the absence of group G6 in the Andean forest fragment cover, represented only by *Aulacorhynchus prasinus* (Gould, 1833) in wooded pasture, may be attributed to the scarcity of fruits in the forest. This scarcity of food could generate a differential effect on the distribution of the functional attributes and, therefore, a functional contrast between the coverages.

Implications for landscape management and bird conservation

Although the wooded pasture presented a better state at a taxonomic and functional level, it is important to maintain the remnants of Andean forests, since they contribute to the functional richness of the area, in general and to an increase in the diversity of a landscape with contrasting hedges. The heterogeneity of the landscape generated a differential effect on the patterns of species richness and also on the patterns of species turnover and positively affected birds, along with the effect of a system that included semi-natural habitats, low-intensity agriculture and various mosaics of small-scale land-use types.

The contrast of cover allowed the birds´ greater mobility with fewer interruptions within the landscape since bird assemblages tended to avoid clearly-defined forest edges and completely open areas. A strategy for the study area is the enrichment of living fences and wooded pastures that, due to their high heterogeneity, provide good resource availability for birds in the rural landscape.

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