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RELATIVE ABUNDANCE AND MICROHABITAT OF FOUR SYMPATRIC ANTPITTAS IN AN INTERANDEAN VALLEY OF SOUTHERN ECUADOR

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Abstract. Exploring mechanisms that determine species coexistence is a key step to understanding community organization and patterns of distribution of biodiversity. Antpittas of the genus *Grallaria* offer a great opportunity to quantify mechanisms of coexistence among closely related species. They are terrestrial insectivores with specialized foraging techniques and limited dispersal abilities, factors that may produce high levels of niche overlap and consequently reduce the chances of stable coexistence. We explored spatial niche partitioning among four sympatric antpitta species –Rufous Antpitta (*Grallaria rufula*), Chestnut-crowned Antpitta (*Grallaria ruficapilla*), Undulated Antpitta (*Grallaria squamigera*), and Tawny Antpitta (*Grallaria quitensis)*–in a tropical Andean valley located in southern Ecuador. We determined the abundance of each antpitta species in native forest, shrub, pasture, and páramo habitats, and gathered data about the microhabitat of each species. Abundance was determined using point counts, territories were located by triangulating on individual calls, and certain microhabitat characteristics were measured within each territory. We found no differences in the abundance or probability of occurrence of species among habitats for the Rufous Antpitta, the Chestnut-crowned Antpitta, or the Undulated Anpitta, but the Tawny Antpitta was restricted to páramo. At the microhabitat level, Rufous and Chestnut-crowned Antpittas shared similar vegetation characteristics, with the presence of shrubs being an important shared microhabitat feature. The Undulated Antpitta occurred in a microhabitat characterized by the presence of trees and a ground cover of mosses. In general, our results suggest that closely related birds could partition habitats into particular niches at different scales, which could promote the coexistence of species in the tropical Andes.

Resumen · Abundancia relativa y microhábitat de cuatro especies simpátricas de *Grallaria* en un valle altoandino del sur del Ecuador.
Explorar los mecanismos que determinan la coexistencia entre especies es un paso clave para entender la organización de comunidades y los patrones de distribución de la biodiversidad. Las aves del género *Grallaria* ofrecen una gran oportunidad para medir los mecanismos de coexistencia entre especies cercanamente emparentadas. Se trata de aves insectívoras de sotobosques que presentan técnicas de forrajeo especializadas y una limitada capacidad de dispersión; estos factores podrían generar altos niveles de solapamiento de nicho y, como consecuencia, reducir la posibilidad de una coexistencia estable. Exploramos la partición de nichos en el espacio entre cuatro especies de gralarias –gralaria rufa (*Grallaria rufula*), gralaria coronicastaña (*Grallaria ruficapilla*), gralaria ondulada (*Grallaria squamigera*) y gralaria leonada (*Grallaria quitensis*)– que coexisten en un valle altoandino ubicado en el sur de Ecuador. Se determinó la abundancia de cada especie en los hábitats de bosque, matorral, pastizal y páramo, y se recopilaron datos del microhábitat de cada una. La abundancia se determinó mediante el método de puntos de conteo: los territorios fueron localizados por el método de triangulación de cantos y algunas características del microhábitat se midieron dentro de cada territorio. No encontramos diferencias en la abundancia o probabilidad de ocurrencia de especies entre los hábitats de la gralaria rufa, la gralaria coronicastaña y la gralaria ondulada, pero la gralaria leonada se encontró restringida al páramo. A nivel de microhábitat, la gralaria rufa y la gralaria coronicastaña comparten características de vegetación similares, con una importante presencia de arbustos. La gralaria ondulada ocurre en un microhábitat caracterizado por la presencia de árboles y con presencia de musgos en la cobertura del suelo, mientras que la gralaria leonada ocupa un microhábitat con una vegetación abierta. En general, nuestros resultados sugieren que las aves cercanamente emparentadas podrían partir su hábitat en nichos a distintas escalas, lo que podría promover la coexistencia de especies en los Andes tropicales.

Key words: Andes · Coexistence · Competition · Grallariidae · Niche partitioning

INTRODUCTION

Studying patterns of species coexistence can provide key information for understanding the organization of communities and the distribution of diversity (MacArthur 1958, Edington & Edington 1972, Kneitel & Chase 2004). This type of research is espe-

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Table 1. Key morphological characteristics of the four sympatric antpitta species co-occurring in the Llaviuco Valley, Ecuador. Data comes from personal observations and other references: [1] Kattan & Beltran 1999, [2] Ridgely & Greenfield 2006, [3] Greeney 2015. Data depicted are means and standard deviations.

Species	Elevation range (m a.s.l.)	Body mass (g)	Culmen (mm)
Grallaria rufula	2700 – 3600[2]	40.1 ± 2.3 (n = 73)	14.6 ± 1.1 (n = 9)
Grallaria ruficapilla	1900 – 3000 [2]	75.9 ± 4.3 (n = 4)	23.8 ± 1.4 [1] (n = 15)
Grallaria squamigera	2400 – 2700 [2]	130.6 ± 29.5 (n = 4)	30 ± 2.0 [1] (n = 5)
Grallaria quitensis	2800 – 4300 [2]	41 (n = 1)	21 [3] (n = 1)

cially relevant in the tropical Andes, where the ability of closely related species to coexist is thought to play a key role in influencing high levels of diversity (Remsen Jr 1985, Brown 2014). Thus, knowledge of variation in the abundance of closely related species across different vegetation types and exploring differences in microhabitat use can provide important insights into the factors that promote species coexistence in the tropical Andes (Kneitel & Chase 2004, Estevo et al. 2017, Reif et al. 2018).

According to niche conservatism theory, closely related species should occupy similar niches (Wiens & Graham 2005), reducing the probability of coexistence due to predicted high levels of competition (Terborgh & Weske 1975, Remsen & Graves 1995, Stenseth et al. 2015). Nonetheless, the coexistence of sympatric species could be promoted if species partition the available niche space (MacArthur 1958, Kelly et al. 2008). There are multiple dimensions in which sympatric and closely related species can partition a niche (Losos et al. 2003, Mahendiran 2016, Trevelline et al. 2018), but variation in space use is one of the most common realizations of niche partitioning (Robinson & Terborgh 1995, Estevo et al. 2017). For example, variation in the capacity of species to use different habitats in a landscape should result in habitat related niche partitioning and, consequently, a stable coexistence (Kneitel & Chase 2004, Harvey et al. 2017, Reif et al. 2018). Moreover, at reduced spatial scales, syntopic species could coexist within the same habitat if they partition a niche through spatial heterogeneity in the conditions and resources at small spatial scales, such as at the level of microhabitats (Urban & Smith 1989, Stratford & Stouffer 2013, Traba et al. 2015).

Studying antpittas (genus *Grallaria*, family Grallaridae) can be useful in exploring patterns of coexistence of closely related species in the Neotropical region. This genus exhibits specialized foraging techniques and limited dispersal abilities (Kattan & Beltran 1999, 2002; Krabbe & Schulenberg 2018, Greeney 2018). They are terrestrial insectivores that commonly feed by searching for prey on the forest floor by tossing dead leaves and other organic material with their bills (Greeney 2018, Krabbe & Schulenberg 2018). In most areas of the Andes, it is possible to find several species of the genus living in sympatry, therefore presenting high levels of niche overlap (Graves 1987, Freile et al. 2010, Snow et al. 2015, Greeney 2018); for example, a study of territory mapping of birds in the Andes of Colombia even found high interspecific overlap in territorial space use of five species of antpittas (Kattan & Beltran 2002)

The Llaviuco Valley is a high elevation, interandean valley located in Cajas National Park, southern Ecuador. Here, four species of *Grallaria* occur in sympatry: the Rufous Antpitta (*Grallaria rufula*), the Chestnut-crowned Antpitta (*Grallaria ruficapilla*), the Undulated Antpitta (*Grallaria squamigera*), and the Tawny Antpitta (*Grallaria quitensis*) (Freile et al. 2010, Astudillo et al. 2015, eBird 2018). These species differ in their body size and bill measurements (Table 1; Greeney 2018), which could facilitate niche partitioning among species (Schoener 1974, Okuzaki et al. 2010, Snow et al. 2015); however, there are no detailed studies about the mechanisms promoting their coexistence (but see Kattan & Beltran 1999).

We thus explored the mechanism promoting species coexistence in birds by studying abundance among habitat types and the microhabitat characteristics of the former four species of antpittas in the Llaviuco Valle, to which we hypothesized that we would find differences in the abundances of species among habitats and that coexistence of these species in the tropical Andes would be explained by variation in their microhabitats.

METHODS

Study area. We conducted this study in the Llaviuco Valley (2°50'S, 79° 8'W), located in Cajas National Park (PNC), Azuay province, southern Ecuador (Figure 1). The ecosystem in this area is an evergreen montane forest (MAE 2012), with an elevational range of 3100–3500 m a.s.l. The monthly mean temperature varies from 5–12°C, with a daily high ranging from -2 to 18°C, and annual rainfall varies from 1100–1800 mm (Celleri et al. 2007). The introduction of cattle farming transformed much of the native forest of this area to pastures prior to incorporation to the national park in 1996, but since that period the natural vegetation has regrown. Today, the valley is covered by a mosaic of early successional shrubs, mature native forest and pastures, whereas the higher sections of the valley are covered by páramo (Chacón 2016).

Species abundance. Sampling areas were selected using an aerial photo of the Llaviuco Valley (SIGTIERRAS-MAG 2010). We created 200 x 200 m grids to cover the entire valley within an elevational range of 3100 to 3500 m a.s.l. Each grid cell was then visually classified as one of four different vegetation types: mature native forest, shrubs, pasture, or páramo. These classifications were later verified in the field.

We performed field observations in order to present a general description of each vegetation type, which is as follows: a) The native forest is mainly composed of trees that reach 17 m in height. In this forest, the structure of the vegetation is homogeneous, with a closed canopy and occasional, small and natural tree gaps. Common tree species in this vegetation type include *Weinmannia fagaroides*, *Escallonia myrtilloides*, *Ocotea heterochroma*, *Valea stipularis*, and

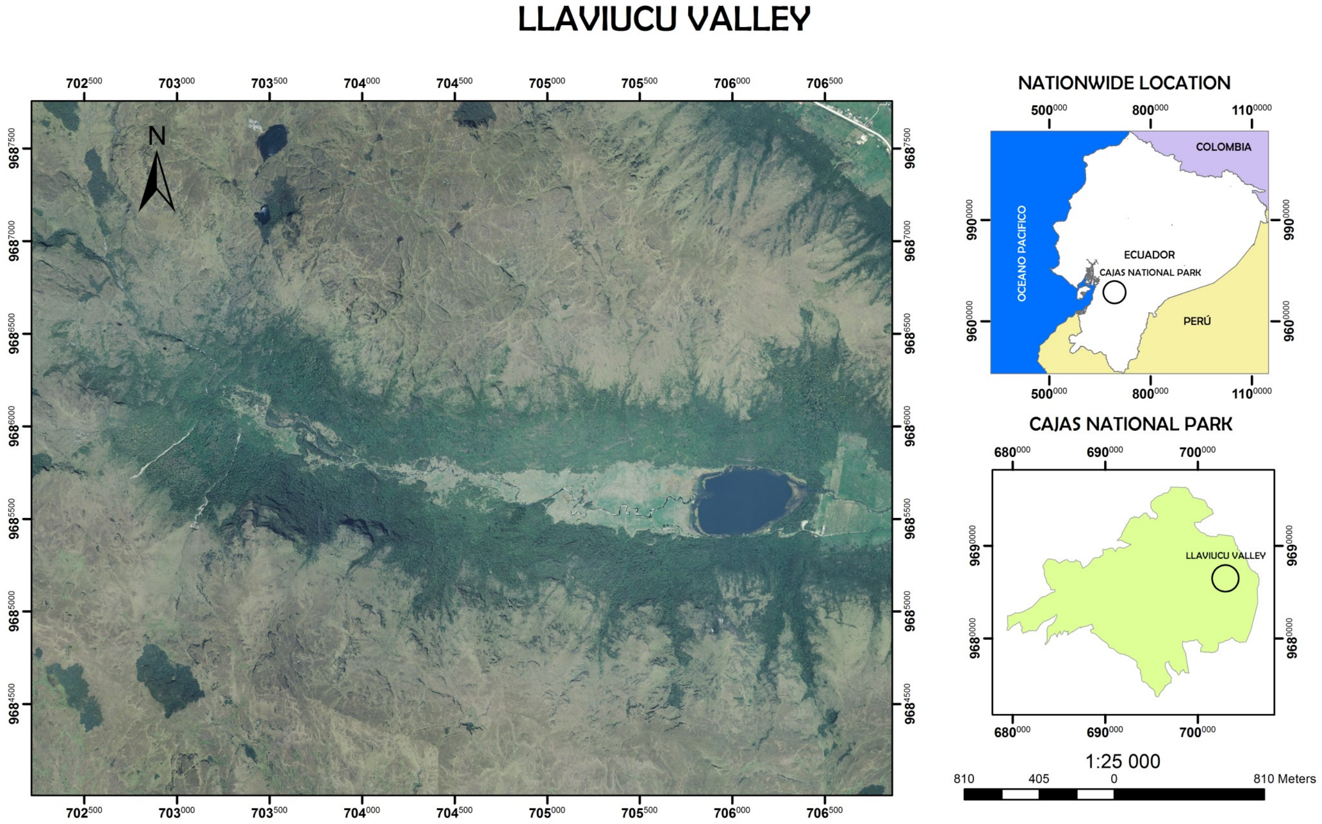

Figure 1. Study area showing the location of the Llaviuco Valley, Cajas National Park, southern Ecuador.

Miconia theaezans; b) the shrub habitat occurs in some areas of the valley floor and especially on the floor margins. Vegetation is composed of shrubs of different sizes, with some isolated trees < 6 m in height. Shrub species common to this habitat include *Myrsine andina*, *Myrsine dependens*, *Barnadesia arborea*, and *Miconia aspergillaris*; c) pasture vegetation is formed by herbaceous plants of < 1 m in height, with little or no presence of shrubs or trees. This type of vegetation is mostly present in the flat floor of the valley, where up to 40 domesticated llamas still graze. Pasture vegetation is dominated by the exotic herb *Holcus lanatus*; d) the páramo is dominated by herbaceous vegetation of < 1 m in height, mainly of the genus *Calamagrostis*, with the presence of scattered shrubs including species of the genus *Brachyotum*, *Gynoxys*, and *Miconia*. Páramo only occurs over 3600 m a.s.l.

Sampled grid cells were selected based on a stratified random sampling design that considered the total coverage represented by the different vegetation types occurring in the valley. As a result of that process, we selected 11 grid cells in shrub habitat, 10 cells in mature, native forest, 7 grid cells in pasture, and 2 cells occurring in páramo. The total number of grids covered 50% of the total area of the valley.

We sampled antpittas in each grid cell using the point count method. Point counts are commonly used to sample terrestrial birds because they are efficient in different types of vegetation and terrain (Ralph et al. 1996, Thomas et al. 2002). Inside each cell, we selected one point count location with a minimum distance of 200 m between points located in adjacent grids. At each point, a single observer recorded all antpittas seen or heard in 10 min within a fixed radius of 30 m. Each point count was re-visited and re-counted for five consecutive days. All point counts were sampled between 06:00 h and 09:00 h, with the starting time changing among visits to reduce the possibility of temporal bias at the same point. Including the five visits to each point count, we performed a total of 150 point counts between April and July 2017.

Microhabitats. To quantify the microhabitat occupied by each species, we used triangulation on calling birds to map the location of individuals in space; this method has been shown previously to work well in territorial vocal birds, such as antpittas (Bell 1964, Naranjo 1995, Martínez 2014). With this method, two observers are placed in two fixed locations and simultaneously record the angle to where a bird is heard singing or calling. The intersection of rays from these points is used as the location of the singing individual.

We established nine transects of 200 m along the whole valley, with each transect located at a minimum distance of 300 m from the next. Along each transect, we placed a total of five fixed points at 50 m intervals. During sampling, two observers were placed at adjacent fixed points to record the angle for all individual antpittas heard during every 10 min census. After 10 min, the observers moved to the next contiguous fixed locations and repeated the census until the entire transect was sampled. Each transect was sampled twice during a day: once in the morning, between 6:00 h and 9:00 h, and once in the afternoon, between 15:00 h and 18:00 h, for five consecutive days. Observers used a protractor to record the angle of the line to where the bird was call-

Table 2. Eigenvectors of the Principal Components Analysis (PCA) analyzing variation in characteristics of the ground cover occurring in the microhabitats of four antpitta species co-occurring in the Llaviuco Valley, Ecuador (S2 = Variance explained by each component).

Variables	PC1 (S^2=35%)	PC2 (S^2=19%)	PC3 (S^2=13%)	PC4 (S^2=12%)
Bare Soil	0.054	0.505	-0.587	0.041
Leaf litter	-0.549	-0.073	0.114	-0.102
Trunks	-0.529	-0.008	0.144	-0.156
Rocks	-0.134	-0.258	-0.118	0.914
Mosses	0.155	-0.535	-0.486	-0.348
Exposed roots	-0.162	0.236	-0.509	0.047
Water	0.327	-0.463	0.048	0.030
Herbs	0.491	0.341	0.333	0.067

ing and were in constant communication with one another using walkie-talkies to make sure that they were registering the same individual at the same time. All sampling took place from August to November 2017.

Once field sampling was completed, all records were plotted using Google Earth (Google Earth 2019) by triangulating the azimuth to the calls noted simultaneously by the two observers. We then determined likely territories of individual birds. To do this, we grouped points of each species that were close in space and within an area of 0.1 ha. This maximum area was chosen based on our records of simultaneous calls of same species individuals in close proximity. After the potential territory was defined, we used a random number generator to select three location points from the ones available within each territory, which were used to describe microhabitats.

Every point was used to center a 5 m radius circular plot, where we quantified the structure of the vegetation and the composition of the ground cover using a protocol modified from James and Shugart Jr (1970). From the center of the plot we placed four 5 m long transects directed north, south, east, and west. In each transect, we counted the number of shrubs (woody plants < 3 cm in diameter at breast height [DBH]), that touched the extended arms of a person walking along the transect. In the same transects, at 1 m intervals, we obtained data on the canopy cover, vertical profile of the vegetation, and leaf litter depth. Canopy cover was estimated visually by looking directly up at the canopy through a paper tube of 10 cm in diameter, which had been divided in into four equal parts; then, by counting the number of quarters covered by vegetation, we estimated canopy cover in a scale from 4 to 1, where 4 was the maximum coverage and 1 the minimum. The vertical profile of the vegetation was measured by estimating the presence–absence of vegetation in different vertical sections using a pole from the ground to the canopy; vertical sections were: 0 – 1 m, 1.1 – 2 m, 2.1 – 3 m, 3.1 – 4 m, 4.1 – 5 m, 5.1 – 6 m, 6.1 – 7 m, 7.1 – 8 m, 8.1 – 9 m, 9.1 – 10 m, 10.1 – 15 m, 15.1 – 20 m, and ≥ 20 m. Leaf litter depth was measured in cm by inserting a ruler in the ground until it hit solid ground. After measuring litter depth, we manually removed the litter to make sure we obtained a precise record. Moreover, we estimated the abundance of trees in each plot by counting the number of trees with a DBH of > 3 cm present in the plot. We also estimated ground cover using a random number generator and randomly tossing four times a frame of 1 x 1 m within each plot, We recorded the percentage of the following cover types: bare soil, leaf litter, fallen trunks, rocks, moss, exposed roots, herbs, and water. Finally, we were also interested in obtaining information about the distance of the location of the bird from the forest border, as this is considered a factor that could influence habitat choice and foraging in anpittas (Greeney 2018); thus, we measured the distance of the center of the plot to the closest native forest border. If the plot was located inside the forest, the distance was measured with a positive sign, while plots located in shrubs, páramo and pastures were recorded with a negative sign.

Using the vertical profile of the vegetation from each plot, we calculated a Shannon diversity index to quantify the vertical complexity of the vegetation (Hays et al. 1981). Ground cover composition data was analyzed using a principal component analysis (PCA), a statistical method that reduces the number of variables and extracts a new set of variables (principal components) that capture the greatest amount of variation (Wold et al. 1987). We chose the first four components of the PCA, which represented 79% of the cumulative variance. PC1 showed a gradient from the ground covered by leaf litter and trunks, to ground covered by abundant herbs. PC2 represented a gradient from the ground covered by mosses and water, to ground dominated by bare soil. PC3 was composed of ground with presence of bare soil and exposed roots to ground covered by herbs, while PC4 showed ground dominated by rocks (Table 2). All of the vegetation structure measurements were averaged among records of the same plot and over the three plots per territory, and were used to depict the microhabitat of each individual.

Data analysis. We used linear models (Kutner et al. 2005) to explore the influence of vegetation types on the abundance of antpittas. To estimate the abundance of each species in each point count, we selected the day in which each species presented its highest number of individuals. We constructed linear models for each species using abundance as a dependent variable and habitat type as a predictor. We could not construct a model for the Tawny Antpitta because it was exclusively recorded in the páramo. For the Rufous Antpitta and the Chestnut-crowned Antpitta, we applied a linear model with normal distribution. In the case of the Undulated Antpitta, due to low values of abundance in most points, we transformed abundance data into presence–absence data, built a generalized linear model with binomial distribution of errors, and explored if there were differences in the probability of presence of this species among habitat types.

To explore if there were differences in the microhabitat of each antpitta species, we used all the vegetation structure variables and the PCA of the composition of the ground in a multivariate PERMANOVA analysis (Anderson 2005). In the PERMANOVA, the dependent variables were all of the microhabitat variables, while the independent variable was the identity of each species. Moreover, to visualize the differences in the microhabitat among species, we created an ordination figure using a non-metric multidimensional scaling

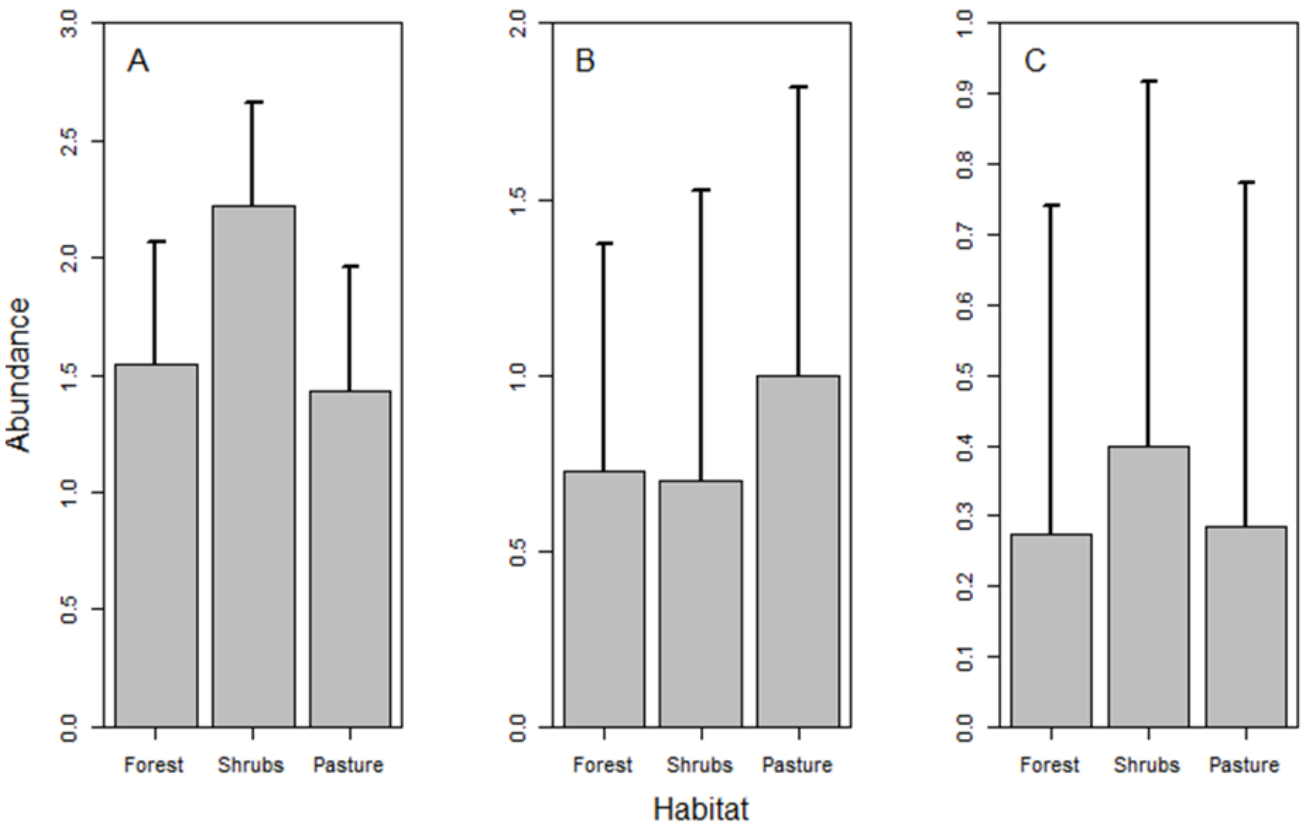

Figure 2. Abundance by counting point of four different antpitta species occurring in different habitat types in the Llaviuco Valley, Cajas National Park. Mean abundance values per point count are shown in the bars. **A)** Rufous Antpitta (*Grallaria rufula)*. **B)** Chesnut-crowned Antpitta (*Grallaria ruficapilla)*. **C)** Undulated Antpitta (*Grallaria squamigera*).

(NMDS). To identify differences in the variables encompassing the microhabitat of each species, we used an ANOVA test in the case of normally distributed variables, or a Kruskal-Wallis test when the variables did not show a normal distribution. All the analyses were performed in R (R Core Team 2015).

RESULTS

Abundance. Considering the abundance of each species in each point count, we recorded a total of 83 individuals, including 49 Rufous Antpittas, 22 Chestnut-crowned Antpittas, 9 Undulated Antpittas, and 3 Tawny Antpittas. The Rufous Antpitta, Chestnut-crowned Antpitta, and Undulated Antpitta were not found in páramo. Among the other habitat types occurring in the valley, the result of the linear models indicated that there were no statistically significant differences in the abundance of the Rufous Antpitta (t = 2.55, df = 2, p = 0.09), as it presented a similar abundance in native forest (mean = 1.54 ± SE = 0.52), shrubs (mean = 2.22 ± SE = 0.44), and pastures (mean = 1.42 ± SE = 0.78) (Figure 2A). A similar result was found for the Chestnut-crowned Antpitta (t = 1.06, df = 3, p = 0.38), which had similar abundances in native forest (mean = 0.72 ± SE = 0.64), shrubs (mean = 0.70 ± SE = 0.82), and pastures (mean = 1 ± SE = 0.81) (Figure 2B). In the case of the Undulated Antpitta, there were no significant differences in occurrence probabilities among native forest, shrubs and pastures (χ^2 = 34.72, df = 2, p = 0.80) (Figure 2C). Lastly, the Tawny Antpitta was only present in the páramo (mean = 1.4 ± SE = 0.55).

Microhabitat. We located a total of 37 probable antpitta territories: 18 for the Rufous Antpitta, 12 for the Chestnut-crowned Antpitta, 3 for the Undulated Antpitta, and 4 for the Tawny Antpitta. The PERMANOVA test indicated that there were significant differences in the microhabitat of the species (R^2 = 0.46, df = 3/33, p = 0.001). Figure 3 revealed that the points belonging to Rufous and Chestnut-crowned antpittas cluster together, suggesting that they had similar microhabitats, while points representing Undulated and Tawny antpittas are isolated from other species, which indicates that they had unique microhabitats. To further explore these results, we analyzed differences among species in each of the measured microhabitat variables. These analyses confirmed that Rufous and Chestnut-crowned antpittas shared a similar microhabitat, which is distinct from the other antpitta species (Table 3). The main differences in the microhabitat of Rufous and Chestnut-crowned antpittas, as compared to the other antpittas, were an intermediate abundance of trees and a mid-height canopy, while the ground litter depth was moderate (Table 3). What was distinctive in the microhabitat of the Undulated Antpitta was the high abundance of trees, a high tree canopy height, and a deep leaf litter (Table 3). In the case of the Tawny Antpitta, its microhabitat was characterized by a low abundance of shrubs and trees, with an open canopy cover and very low vegetation height with little vertical complexity, while on the ground we recorded little leaf litter and a ground cover dominated by rocks and litter

Table 3. Means and standard errors of vegetation variables measured to characterize the microhabitat of the different antpitta species co-occurring in the Llaviuco Valley, Ecuador. PC variables were obtained from a PCA analysis of the composition of the ground cover (Table 2). The results of an ANOVA or Kruskal-Wallis test are presented under each variable. Alphabetical codes denote differences among species based on a Tukey *post hoc* analysis or a Dunn´s test.

Variables	Rufous Antpitta	Chetsnut-crowned Antpitta	Undulated Antpitta	Tawny Antpitta
Abundance of shrubs	14.83 ± 7.25	14.84 ± 6.20	16 ± 8	5.25 ± 1.19
F= 2.48, P= 0.06, Df=3/33	A	A/B	A/B	B
Abundance of tres	32.64 ± 14.95	28.61 ± 9.77	54.31 ± 6	8.33 ± 6.31
F= 8.17 P= 0.001, Df=3/33	A	A	B	C
Canopy heigth	6.81 ± 3.07	5.84 ± 2.59	9.31 ± 1.22	1.45 ± 1.35
F= 5.76, P= 0.002, Df=3/33	A	A	A	B
Canopy cover	1.64 ± 0.97	1.53 ± 1.03	2.30 ± 0.38	0.04 ± 0.08
χ^2= 9.11, P= 0.027, Df=3	A	A	A	B
Leaf litter	7.84 ± 5.31	6.03 ± 4.95	14.49 ± 6.05	2.02 ± 4.05
χ^2= 8.62, P= 0.034, Df=3	A	A/B	B	C
Distance to border	20.01 ± 12.26	24.10 ± 10.26	41.77 ± 7.64	-44.33 ± 37.27
χ^2= 14.74, P= 0.002, Df=3	A	A/C	C	B
Vertical complexity of the vegetation	0.84 ± 0.19	0.89 ± 0.15	0.86 ± 0.11	0.48 ± 0.16
χ^2= 8.37, P= 0.038, Df=3	A	A	A/B	B
PC1	0.12 ± 1.36	0.10 ± 1.19	1.22 ± 0.25	-1.99 ± 0.55
χ^2= 10.08, P= 0.017, Df=3	A	A	A	B
PC2	0.14 ± 0.89	0.20 ± 0.74	-0.16 ± 0.15	-1.16 ± 1.14
χ^2= 6.11, P= 0.106, Df=3	A	A	A	A
PC3	0.20 ± 0.56	-0.02 ± 0.76	-0.03 ± 0.46	-0.51 ± 1.11
F= 1.21, P= 0.321, Df= 3/33	A	A	A	A
PC4	0.05 ± 0.74	-0.3 ± 0.39	0.05 ± 0.84	0.45 ± 0.21
χ^2= 5.98, P= 0.112, Df=3	A	A	A	A

(PC1) (Table 3).

DISCUSSION

This work contributes to increasing our knowledge about the underlying mechanisms that result in coexistence patterns among closely related species living in sympatry in the tropical Andes. In the Llaviuco Valley, the abundance of the Rufous, Chestnut-crowned, and Undulated antpittas was similar in native forest, shrubs, and pasture habitats, while the Tawny Antpitta was limited to the páramo . At a smaller spatial scale, we found differences in the microhabitats used by these species. The Rufous Antpitta and the Chestnut-crowned Antpitta occupied a microhabitat associated with an important presence of shrubs, the Undulated Antpitta’s microhabitat had characteristics of mature forest, and the Tawny Antpitta occupied a microhabitat with open vegetation. In general, these results indicate that sympatric, closely related species can partition their niche either at the level of habitat or microhabitat, a factor that could promote their stable coexistence.

At habitat scale, only one species (Tawny Anpitta) occurred in a habitat different from the other species, demonstrating that there could be high levels of habitat–niche overlap among the Rufous Antpitta, the Chestnut-crowned Antpitta, and the Undulated Antpitta. This result is similar to what was found in the Andes of Colombia (Kattan & Beltran 2002) and indicates that *Grallaria* species may be both sympatric and syntopic across a large and important portion of their distributional range. Nonetheless, it is important to consider that in the valley studied here, forest, shrub, and pasture habitats are highly intermixed, allowing antpittas to move between habitats (Poulsen 1993) and thereby reducing specific associations among species and habitats.

At a smaller spatial scale, we found some evidence of niche partitioning, with Tawny and Undulated antpittas most clearly occupying unique microhabitats. Our results confirm what is known about the habitat of the Tawny Antpitta (Greeney 2018), a species mainly associated with páramo grasslands and the presence of scattered trees and shrubs. We found the Undulated Antpitta occupying as well a unique microhabitat with characteristics corresponding to a mature forest and a forest floor made up of abundant leaf litter. This is generally consistent with what is described by Greeney (2018); however, there are some differences between our results and the typical habitat described in Greeney (2018), as the Undulated Anpitta is most often thought to occur in areas of second growth vegetation, such as shrubs and thickets of bamboo (Fjelsa & Krabbe 1990, Kattan & Beltrán 1999, Snow et al. 2015, Greeney 2018). However, considering that this species has a large distributional range from Venezuela to Bolivia (Greeney 2008), we suspect that there could be a geographical variation in habitat requirements for this species, and more studies are needed across its range to have a clearer idea of the habitat association occupied by it.

At our smaller spatial scale, we also found that the Rufous Antpitta and the Chestnut-crowned Antpitta shared microhabitats with the same characteristics. Rufous and Chestnut-crowned antpittas were present in microhabitats with a partially closed canopy and a moderately dense undergrowth close to the forest border. These microhabitat characteristics also correspond closely to what was described by Greeney (2018) as the habitat for these species. Assuming that interspecific competition for habitats could be important between Rufous and Chestnut-crowned antpittas, the lack of differences in their microhabitats indicates that coexistence between these species could be facilitated by niche partitioning in other dimensions. For example, syntopic insectivorous species could consume different taxa and partition their niches through variation in their diets (Edington & Edington 1972, Leyequién et al. 2007, Trevelline et al. 2018). The Rufous Antpitta and the Chestnut-crowned Antpitta have different body and bill sizes (Table 1), phenotypic characters that can strongly determine diet in birds (Schoener 1974, Dehling et al. 2014), resulting in the consumption of different resources and the maintenance of a stable coexistence despite a high overlap in physical space.

Although our results show that there could be some lev-

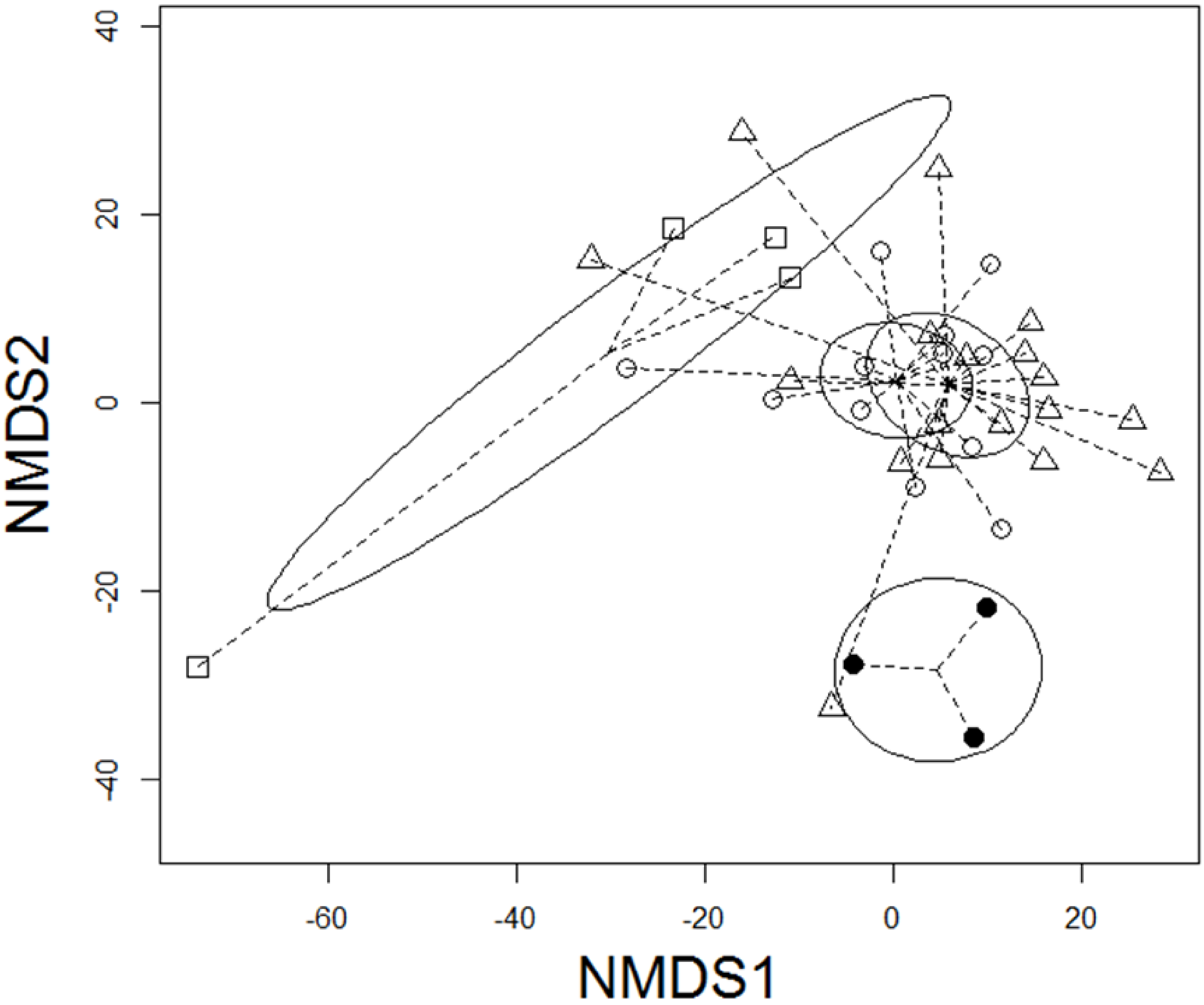

Figure 3. Non-metric multidimensional scaling ordination (NMDS) of microhabitat plots of antpittas in the Llaviuco Valley, Cajas National Park. Species' symbols represent: Δ = Rufous Antpitta (*Grallaria rufula)*; ○ = Chesnut-crowned Antpitta (*Grallaria ruficapilla)*; ● = Undulated Antpitta (*Grallaria squamigera)*; □ = Tawny Antpitta (*Grallaria quitensis)*. The stress value of the NMDS was 0.03.

els of niche partitioning in space among antpittas, there are other mechanisms not considered in this study that could also influence the sympatric and syntopic coexistence of these birds. First, the magnitude of competition in birds could vary over time, perhaps increasing during breeding periods or when the abundance of resources decreases (Morrison & With 1987, Wilson 2010, Pontón-Cevallos et al. 2016). Studies of competition in antpittas are still scarce, but Snow et al. (2015) suggested that there could be temporal variation in interspecific competition among species. Hence, if the competitive interactions vary in time among antpittas, a temporal dynamic in niche partitioning is also to be expected. Because we only sampled antpittas during four months, our results would be strengthened contrasting them with year-round studies exploring any potential temporal dynamics in niche partitioning among these antpitta species.

Second, our study is based on data of species abundance and the location of individuals in different habitats and microhabitats, but we do not know if those sites sustain the populations. Theoretically, there could be source-sink dynamics influencing the presence of the species in the different habitats and allowing their coexistence (Donovan et al. 1995, Mouquet & Loreu 2003); however, in a recent study performed in the Llavicuo Valley and the nearby Mazan reserve (Tinoco et al. 2019), we detected no differences in apparent survival rates of the Rufous Antpitta among native forest, native shrubs, and an exotic forest plantation, but we were unable to obtain survival rates for the other antpitta species that are part of this study. Thus, future studies of the survival and productivity of antpittas in different habitats would be of high interest.

Our study of four sympatric antpitta species in the Llaviuco Valley in southern Ecuador shows that there could be a fine niche partitioning in physical space among closely related species, a factor that could contribute to high avian diversity in the tropical Andes. Future studies could advance these findings through studies of source-sink dynamics and reproductive success and survival, as well as the use of currently available technology, such as diet analyses through DNA metabarcoding or the incorporation of GPS trackers to better understand movements and habitat use. Such tools could be important next steps in understanding coexistence mechanisms among Neotropical bird species at even finer scales.

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