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Habitat heterogeneity rather than the limits of protected areas influence bird communities in an Andean biosphere reserve

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Abstract. The páramo ecosystem harbors a high concentration of restricted range and threatened bird species. However, human modifications to the high Andean landscape have generated habitat loss and fragmentation throughout this ecosystem. Therefore, protected areas in this region are a priority for biodiversity conservation. Buffer zones around protected areas aim to reduce perturbation within them. However, these areas are still not exempt from sources of stress. We used abundance and diversity of birds, recorded by walking transects, in order to compare the community composition occurring in protected areas and adjacent buffer zones in a hotspot of diversity and endemism: the Macizo del Cajas Biosphere Reserve, in the southern high-Andes of Ecuador. The bird community did not vary in its composition between protected areas and buffer zones. However, the habitat characteristics explained differences in the presence and abundance of trophic guilds. Particularly, increasingly heterogeneous páramo grassland with greater woody plant cover and less intervention explained a greater presence and abundance of more specialized trophic guilds such as nectarivores in shrubs and aerial insectivores in trees and shrubs. We conclude that there are heterogeneous páramo habitats in buffer zones that should be considered in more formal conservation planning to maintain the diversity of specialized birds and therefore functionality of the páramo grassland ecosystem.

[Keywords: páramo grassland, Macizo del Cajas Biosphere Reserve, elevation, trophic guilds, specialist birds]

Resumen. La heterogeneidad del hábitat, en lugar de los límites de las áreas protegidas, influye en las comunidades de aves de una reserva de biosfera Andina. El ecosistema de páramo alberga una alta concentración de especies de aves de rango restringido y amenazadas. Sin embargo, las modificaciones humanas al paisaje altoandino han generado pérdida y fragmentación de hábitat en todo este ecosistema. Por lo tanto, las áreas protegidas en esta región son prioritarias para la conservación de la biodiversidad. Las zonas de amortiguamiento en los alrededores de las áreas protegidas tienen por objeto reducir las perturbaciones en éstas; sin embargo, no están exentas de fuentes de estrés. La abundancia y la diversidad de aves, registradas en transectas, se usó para comparar la composición de la comunidad entre áreas protegidas y zonas de amortiguamiento en un *hotspot* de diversidad y endemismo: la Reserva de la Biósfera del Macizo del Cajas, en los altos Andes del sur del Ecuador. La comunidad de aves no varió en su composición entre las áreas protegidas y las zonas de amortiguamiento. No obstante, las características del hábitat sí explicaron diferencias en la presencia y abundancia de grupos tróficos. En particular, el incremento en la heterogeneidad del páramo, con mayor cobertura de plantas leñosas y menos intervención, explicó una mayor presencia y abundancia de gremios tróficos especializados, tales como nectarívoros en arbustos e insectívoros aéreos en árboles y arbustos. En conclusión, hay hábitats heterogéneos de páramo, en zonas de amortiguamiento, que deben considerarse en una planificación de conservación más formal para mantener la diversidad de aves especialistas y, por lo tanto, la funcionalidad del ecosistema de páramo herbáceo.

[Palabras clave: páramo herbáceo, Reserva de la Biósfera Macizo del Cajas, elevación, gremios tróficos, aves especialistas]

Introduction

In a world continuously modified by human activities, biodiversity is increasingly confined to landscapes within altered habitat mosaics (Foley et al. 2005; Laurance et al. 2014). For example, the expansion of the agricultural frontier and the conversion of grasslands to pastures have been identified as some of the main drivers of biodiversity change in natural grasslands of the tropics (Sala et al. 2000; Hamer et al. 2006; Norment et al. 2010; Sylvester et al. 2017). In the tropical Andes, the páramo grassland is a distinctive high mountain ecosystem distributed along the high elevation region of northern South America (Neill 1999; Baquero et al. 2004; Jiménez-Rivillas et al. 2018). In addition, the

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páramo grassland is an important region of avian biodiversity and endemism in the tropical Andes (Fjeldså and Krabbe 1990; Stotz et al. 1996; Stattersfield et al. 1998). However, habitat loss in the region is widespread (Sierra 1999; Hofstede et al. 2002; Sylvester et al. 2017). Consequently, the páramo grassland is considered a conservation priority due to its high concentration of restricted-range bird species and the high concentration of threatened species (Fjeldså and Krabbe 1990; Stattersfield et al.1998; Myers et al. 2000).

Protected areas, such as national parks, recreation areas and reserves are therefore vital for the conservation of the region's species and ecosystems (e.g., Latta et al. 2011; Gary et al. 2016; Astudillo et al. 2019; Tinoco et al. 2019). Protected areas in the high Andes are not exempt from external stressors such as illegal resource extraction and agriculture (Bucheli 2007; Vásconez et al. 2004; Astudillo et al. 2015). In Ecuador, the natural remnants of the páramo grassland ecosystem face alteration through burning to increase pasture for livestock grazing, the introduction of exotic plants, as well as the construction and maintenance of roads, all resulting in habitat loss and fragmentation (Sarmiento 2000; Hofstede et al. 2002; Matson and Bart 2013). In this context, contiguous buffer zones are expected to play an important role in maintaining the function of protected areas. Within buffer zones, restrictions are imposed on the use of resources, and special measures are adopted to reduce the intrusion of anthropogenic activities into the protected area (Carvalho et al. 2012). Consequently, it is important to explore the efficacy of buffer zones through differences, for example, in the composition of páramo bird species that occur in protected areas (e.g., national parks), in comparison to buffer zones outside those protected areas.

Habitat guilds have been proposed as a broad and useful approach to understand the effects of habitat modification on birds in tropical grasslands (Mckinney and Lockwood 1999; Tews et al. 2004) as well as in páramo grassland (Lazo et al. 2019). Avian trophic guilds, defined by habitat affinity and food preferences, are sensitive indicators of land-use change when these modifications impact the structure and composition of natural habitats (Hooper et al. 2012; Grass et al. 2013). For example, the modification of páramo grassland via the introduction of exotic plants along roads and the reduction in grassland cover and lowering of the vegetation profile by livestock grazing, negatively influence the diversity of specialist birds (e.g., páramo specialists, shrubby páramo specialists) (Astudillo et al. 2018; Aguilar et al. 2019). Consequently, analyzing trophic guilds may improve our understanding of the effects of habitat alteration (Latta et al. 2011; Lloyd and Marsden 2011; Astudillo et al. 2019, 2020; Tinoco et al. 2019).

Therefore, in the Macizo del Cajas Biosphere Reserve, a hotspot of diversity and endemism, we used transects to record abundance and diversity of high Andean birds in order to compare the bird community composition between protected areas (i.e., Cajas National Park and the Quimsacocha Recreation Area) and adjacent buffer zones. We hypothesize that generalist trophic guilds (e.g., grass and shrub omnivores, grass and shrub granivores, grass perch gleaners) will be more dominant in buffer zones; while more specialized trophic guilds (e.g., shrub nectarivores, arboreal and shrub frugivores, arboreal and shrub bark-foliage gleaners) will be more common in protected areas due to their conservation status. Finally, we further hypothesize that differences in the avian communities will be explained by variation in the structure of páramo grassland vegetation. In particular, generalist trophic guilds will be dominant in transects with greater habitat homogenization that is characterized by structurally and botanically more simplified grassland with a lower vegetation profile and less cover of native páramo trees and shrubs.

Materials and Methods

Study area

This study was carried out in the Macizo del Cajas Biosphere Reserve, Azuay province, in the high-Andes of south-western Ecuador (2°55′25′′ S - 79°21′57′′ W). The Macizo del Cajas covers an area of 976601 ha, 17% of which is páramo grassland ecosystem (>3500 m a. s. l.) (Rodríguez - Girón et al. 2014). The reserve's core protected areas are the Cajas National Park (PNC; 2°50′45′′ S - 79°14′33′′ W) and the Quimsacocha National Recreation Area (ARQ; 3°00′45′′ S - 79°14′12′′ W) (Figure 1). These two areas are both páramo grassland ecosystems under the control and management of the national system of protected areas and cover an area of 31761 ha (~3% of the biosphere reserve). In addition, the biosphere reserve model considers buffer zones that cover 390596 ha (~40% of the total surface) which are

established around the limits of the protected areas (Rodríguez - Girón et al. 2014). The average monthly temperature ranges from 5 to 12 °C, while the average annual rainfall ranges from 1200 to 1500 mm. The rainy seasons have a bimodal pattern with the greatest rainfall from March to May and a second less intense peak occurring between September and February. The driest period is between June and August (Celleri et al. 2007).

The study area ranges from 3500 to 4400 m a. s. l., where the dominant vegetation is the páramo grassland and represents ~90% of the vegetation cover (Neill 1999; Baquero et al. 2004). The páramo grassland is characterized by an open habitat dominated by various species of tussock grass with cushion plants also occurring in more humid areas (Minga and Verdugo 2007). In addition, the topography of the region is irregular with U-shaped valleys and steep slopes (Harden and Borrero 2005; Delgado et al. 2006). Here, the páramo grassland becomes more heterogeneous with greater presence of trees and shrubs. In these areas the páramo grassland is interspersed with woodland patches that vary in shape and size (<1.0-44 ha) (Benham et al. 2011; Matson and Bart 2013; Astudillo et al. 2020), which are dominated by *Polylepis* (Rosaceae) trees. The páramo grassland shows an evident natural homogenization towards more exposed areas on mountaintops as well as at higher elevations where woody vegetation is replaced by scattered tussocks of grass separated by exposed rocks (Mena-Vásconez and Hofstede 2006; Jørgensen et al. 2011; Astudillo et al. 2018). Throughout the region, modification of vegetation is caused by both natural processes and human activities such as burning to promote pasture and the subsequent livestock grazing that homogenize and fragment the habitat.

As a grassland landscape, the study area suffers burning to promote pasture for cattle forage (Matson and Bart 2013). These activities are prohibited in protected areas but in CNP and ARQ cattle cross the borders through valleys with relatively lower elevation. However, these activities are more common in less controlled buffer zones where the habitat modification by livestock grazing is widespread (Astudillo et al. 2018). There are evident differences in the habitat structure between the protected areas and buffer zones with much greater habitat modification of páramo grassland in the buffer zones.

Habitat structure and composition

We randomly installed 26 transects across the páramo grassland, 13 transects were installed within protected areas (i.e., PNC, ARQ) and 13 transects were installed in buffer zones outside of the protected areas (Figure 1). We consider the buffer zones to be all páramo grassland areas within a maximum distance of 10 km from the boundary of the protected areas. Each transect was 1 km long and separated by at least 350 m from each other. We followed the habitat sampling protocol for birds in páramo habitats used in the study area by Astudillo et al. (2018). Thus, along each transect, 10 circular plots (radius of 20 m) were regularly established (standard plot size used in the study area). In each circular plot, four 12 m transects were established in each cardinal direction. At 3 m intervals the profile of the vegetation was estimated using a 3-metre rod marked at intervals of 0.5 m, in which each interval was counted as long as it was in contact with the vegetation. In addition, an observer with open arms counted and identified the woody vegetation contacted along the transect; shrubs were considered as those plants with a stem diameter at breast height (DBH) <3 cm and trees were defined as DBH >3 cm (James and Shugart 1970). For each transect, the vertical complexity of the vegetation was calculated based on the Shannon index, using the information of vegetation profile across the 10 circular plots; the Shannon index was also calculated to determine plant diversity based on the count of trees and shrubs.

For each circular plot, we visually estimated the proportion of five types of predominant habitat cover. They were: 1) páramo grassland, an open habitat dominated by tussock grass of the genus Calamagrostis (Poaceae) and associated with cushion plants such as *Oreobolus ecuadorensis* (Cyperaceae) and *Plantago rigida* (Plantaginaceae) (Minga and Verdugo 2007); 2) shrubby páramo, a semi-open habitat with a higher vegetation profile and characterized mainly by native woody plants to the genus *Gynoxys*, *Chuquiraga*, *Diplostephium* (Asteraceae), *Brachyotum* and *Miconia* (Melastomataceae) (Minga et al. 2013); 3) water bodies, including ponds and streams; 4) rocky substrates, which are naturally present in the study area, and 5) altered habitat, characterized by the presence of exotic plant species (e.g., *Pinus patula*), eroded soil and cattle feces as evidence of livestock activity (Table S1).

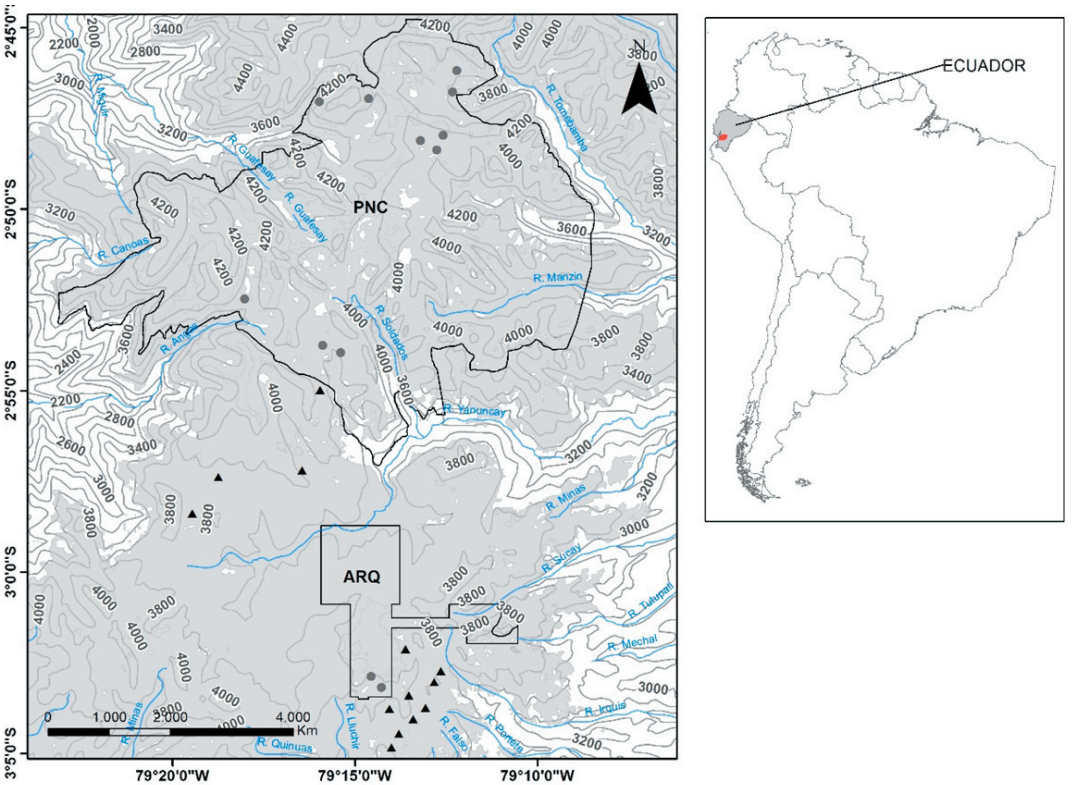

Figure 1. Map of the study area and location of 26 transects (1 km long) in the páramo grassland ecosystem of the Macizo del Cajas Biosphere Reserve, high-Andes of southern Ecuador. Filled circles represent the 13 transects located within the national system of protected areas (PNC: Cajas National Park; ARQ: Quimsacocha National Recreation Area) and filled triangles represent the 13 transects located in the buffer zones. Gray areas represent páramo grassland. On the map of South America, the red polygon represents the Macizo del Cajas Biosphere Reserve.

Figura 1. Mapa del área de estudio y ubicación de 26 transectas (1 km de longitud) en el ecosistema páramo en la Reserva de la Biosfera Macizo del Cajas, en los altos Andes al sur del Ecuador. Los círculos representan 13 transectos ubicados dentro del sistema nacional de áreas protegidas (PNC: Parque Nacional Cajas; ARQ: Área de Recreación Nacional Quimsacocha) y los triángulos representan 13 transectos ubicados en las zonas de amortiguamiento. Las áreas grises representan zonas de páramo. En el mapa de Sudamérica, el polígono rojo representa la Reserva de la Biosfera Macizo del Cajas.

To condense the variability information of habitat measures, a principal component analysis (PCA) was applied. The PCA was based on a correlation matrix with Shannon indices of vertical vegetation complexity, plant diversity and the proportion of the five habitat types across the 26 transects. The first two components of the PCA were selected (total variance explained=55.4%) based on diagrams of the broken-stick method (Jackson 1993). The first component (PCI=33.7%) reflects a gradient of change in páramo habitat from a higher proportion of altered habitat and greater vertical complexity to an increasing proportion of páramo grassland, while the second component (PCII=21.7%) reflects a gradient of change in páramo habitat from a higher proportion of altered habitat to an increasing proportion of shrubby páramo with a higher plant diversity (Figure 2; Table S2). Therefore, PCI is considered a measure of homogeneous habitat with an increase in the proportion of páramo grassland habitat and less vertical complexity, while PCII is considered a measure of less altered heterogeneous habitat with a greater proportion of shrubby páramo associated with a greater diversity of woody plants.

Bird surveys

Each transect was monitored by walking at a constant speed (~0.5 km/h) while recording all birds seen and heard at 50 m on either side of the observer. All birds that overflew transects were excluded. Each transect was repeated four times every year in the months of April, July, October and November between 2016 and 2019. All counts began 15 minutes after sunrise and the order in which they were

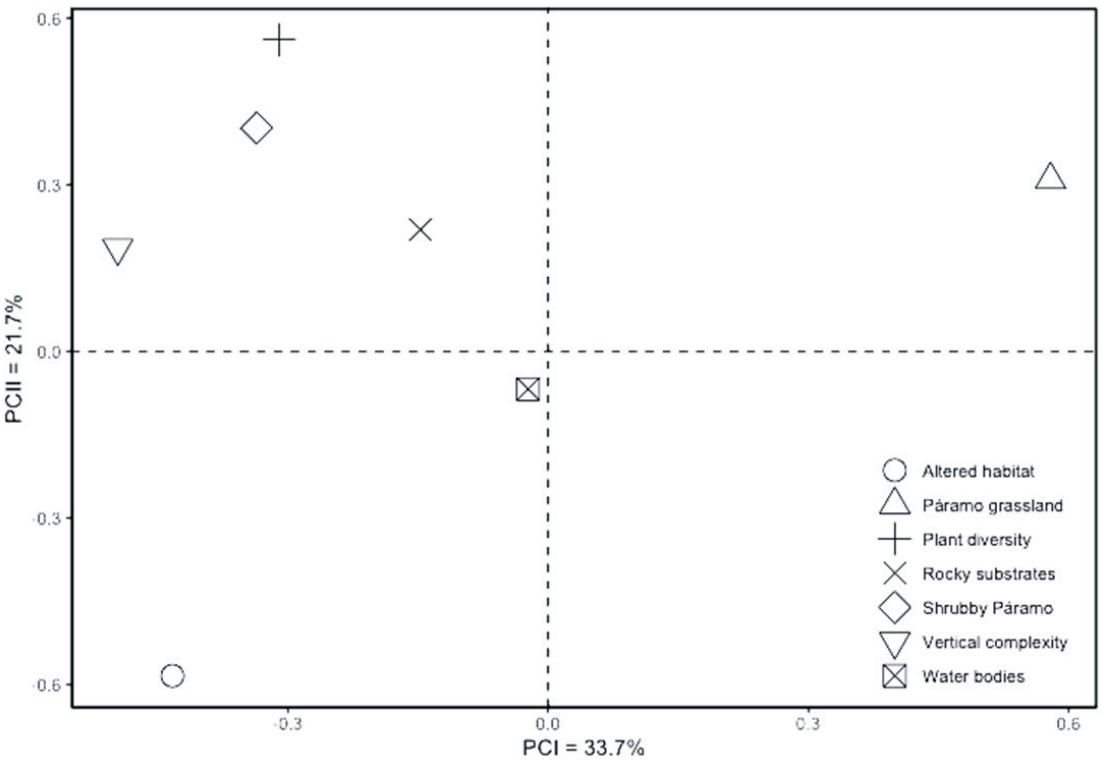

Figure 2. Ordination biplot of principal component analysis (PCA) of seven habitat measures in the páramo ecosystem of the Macizo del Cajas Biosphere Reserve, high-Andes of southern Ecuador.

Figura 2. Ordenación en dos ejes del análisis de componentes principales (ACP) de siete medidas de hábitat en el ecosistema de páramo de la Reserva de la Biósfera del Macizo del Cajas, altos Andes del sur de Ecuador.

Table 1. Trophic guild classification and their description for monitoring páramo birds in the Macizo del Cajas Biosphere Reserve, high-Andes of southern Ecuador.

Tabla 1. Clasificación de los gremios tróficos y su descripción para el monitoreo de aves de páramo en la Reserva de la Biosfera Macizo del Cajas en los altos Andes al sur del Ecuador.

Trophic guild	Code	Description
Arboreal and shrub bark-foliage gleaners	ASB.G	Capture insects directly on the trunk and branches of woody plants in the páramo
Arboreal and shrub frugivores	ASF	Feed at higher levels on fruits of trees and shrubs in the páramo
Arboreal and shrub sally-gleaners	ASS.G	Capture insects in the air sallying from perches on exposed branches of trees and shrubs in the páramo
Grass and shrub granivores	GSG	Feed on seeds at ground level as well as at low height of shrubs in the páramo
Grass and shrub omnivores	GSO	Have a general diet and feed at ground level as well as at medium height of shrubs in the páramo
Grass and shrub raptors	GSR	Birds of prey that perch and feed at ground level as well as in trees and shrubs in the páramo
Grass perch gleaners	GPG	Capture insects at ground level and prefer the open habitat of the páramo grassland
Shrub nectarivores	SN	Feed above ground level on flowers of trees and shrubs in the páramo.

executed was random. The transect method was selected because of its effectiveness in counting birds in open habitats, where the observer can pay attention to detecting birds flushed while walking (Ralph et al. 1993). All transects were performed by two observers. Counts were always conducted by the same observer, while the second zigzagged along the transect to flush birds from the ground. Bird species taxonomy followed the South American Classification Committee (Remsen et al. 2019).

In the study area, trophic guilds have been shown to be good indicators for identifying conservation priorities for specialist birds (Latta et al. 2011; Tinoco et al. 2019). Thus, we followed Lloyd and Marsden (2011) to classify high Andean birds into trophic guilds, taking into account both habitat affinity and food preference. However, adjustments were made to the classification based on personal observations. For example, Lloyd and Marsden classify the genera *Asthenes* and *Leptasthenura* as forest specialist birds, while in the study area *A. flammulata* and *L. andicola* are strongly associated with shrubby páramo. Thus, our trophic guilds reflect this difference and eight trophic guilds were designated (Table 1).

Data analysis

The total number of individuals per transect was used as an abundance value (Nur et al. 1999). We calculated a dissimilarity matrix (trophic guilds x transects) using the Bray-Curtis distance weighted by abundance. In order to evaluate changes in the composition (dissimilarity) of the trophic guilds in the bird community, we further applied a nonmetric multidimensional scaling analysis (NMDS). For this analysis, we used a two-dimensional solution. After ordination, the factor protected areas and buffer zones, habitat variables of structure and composition (derived from the PCA) and terrain elevation were linearly adjusted in order to explain changes in bird composition. We included elevation in the linear adjustment in order to control for the natural homogenization that occurs in the páramo grassland at higher elevations. All explanatory variables were uncorrelated (r-values ranged 0-0.26; *P*-values ranged 0.20-1). The significance of the resulting linear adjustment was evaluated on the basis of 1000 random permutations. Only significant vectors ($P<0.05$) were plotted on the ordination. All analyses were developed in R 3.5.1 (R Core Team 2018) with an alpha=0.05. The 'vegan' package was used for the NMDS (Oksanen et al. 2018).

Results

A total of 2935 individuals associated with 42 species were recorded, 1481 individuals associated with 36 species in the protected areas and 1454 individuals associated with 35 species in the buffer zones. In relation to trophic guilds, grass and shrub omnivores were the most abundant with 38% (1125 individuals) of the records, followed by arboreal and shrub bark-foliage gleaners with 26% (767 individuals) and grass perch gleaners with 17% (504 individuals) of the records. Grass and shrub raptors with 0.51% (15 individuals) and arboreal and shrub frugivores with 0.14% (4 individuals) were the least abundant (Table S3).

Ordination of the community

The NMDS analysis did not show a tendency to separate bird community composition between protected areas and buffer zones (2D solution, stress=0.09, $R^2=0.04$, $P=0.33$). Transects located inside of protected areas and buffer zones were grouped from the center and slightly to the right of the plot ordination (Figure 3).

The components of PCI-homogeneous páramo grassland habitat ($R^2=0.37$, $P<0.001$), PCII-heterogeneous páramo habitat with more woody plants ($R^2=0.26$, $P=0.02$) as well as elevation ($R^2=0.35$, $P<0.001$) significantly influenced the bird composition (Figure 3). Grass perch gleaners (GPG) and arboreal and shrub bark-foliage gleaners (ASB.G) increased along a gradient of increasing elevation; while, arboreal and shrub sally-gleaners (ASS.G), grass and shrub granivores (GSG) as well as arboreal and shrub frugivores (ASF) were associated with lower elevations. Grass and shrub omnivores (GSO) increased along a gradient of increasing PCI; while, arboreal and shrub sally-gleaners (ASS.G), grass and shrub granivores (GSG) and arboreal and shrub frugivores (ASF) were associated with the opposite side of PCI and therefore they increased with decreasing PCI. Finally, shrub nectarivores (SN), grass and shrub granivores (GSG) increased along a gradient of increasing PCII. Arboreal and shrub sally-gleaners (ASS.G) and grass and shrub raptors (GSR)

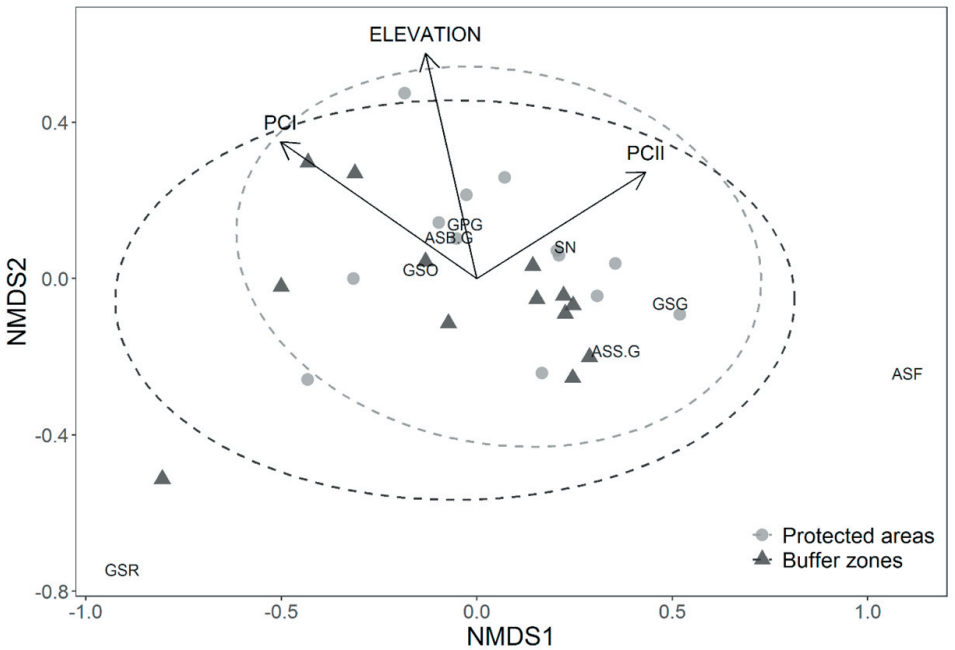

Figure 3. Non-metric multidimensional scaling of the páramo bird community (2D solution) based on the Bray-Curtis distance for the 26 transects located in Macizo del Cajas Biosphere Reserve, high-Andes of southern Ecuador. Filled circles represent 13 transects within protected areas. Filled triangles represent 13 transects in buffer zones. Habitat vectors (arrows) show significant relationships to the ordination ($P<0.05$). PCI reflects a gradient of change in páramo habitat from a higher proportion of altered habitat and greater vertical complexity to an increasing proportion of páramo grassland; PCII reflects a gradient of change in páramo habitat from a higher proportion of altered habitat to an increasing proportion of shrubby páramo with a higher plant diversity. The codes for trophic guilds are: ASB.G=Arboreal and shrub bark-foliage gleaners; ASF=Arboreal and shrub frugivores; ASS.G=Arboreal and shrub sally-gleaners; GSG=Grass and shrub granivores; GSO=Grass and shrub omnivores; GSR=Grass and shrub raptors; GPG=Grass perch gleaners; SN=Shrub nectarivores.

Figura 3. Escalamiento multidimensional no métrico de la comunidad de aves de páramo (solución 2D) basado en la distancia de Bray-Curtis para los 26 transectos ubicados en la Reserva de la Biósfera Macizo del Cajas, altos Andes del sur de Ecuador. Los círculos representan 13 transectos situados dentro de las áreas protegidas. Los triángulos representan 13 transectos en zonas de amortiguamiento. Los vectores del hábitat (flechas) muestran relaciones significativas con la ordenación ($P<0.05$). PCI refleja un gradiente de cambio en el hábitat del páramo desde una mayor proporción de hábitat alterado y una mayor complejidad vertical a una proporción creciente de pastizales de páramo, PCII refleja un gradiente de cambio de una mayor proporción de hábitats alterados a una proporción creciente de páramo arbustivo con una mayor diversidad de plantas. Los códigos para los gremios tróficos son: ASB-G=Insectívoros en corteza en árboles y arbustos; ASF=Frugívoros en árboles y arbustos; ASS-G=Insectívoros aéreos en árboles y arbustos; GSG=Granívoros de páramo y arbustos; GSO=Omnívoros en páramo y arbustos; GSR=Rapaces de páramo y arbustos; GPG=Insectívoros terrestres; SN=Nectarívoros en arbustos.

showed low abundances so they could not be interpreted (Table S3).

Discussion

Buffer zones adjacent to protected areas retain similar bird communities in the páramo ecosystem of the high-Andes of southern Ecuador. As expected, vegetation structure and composition as well as elevation significantly influenced bird community composition in both zones. Trophic guilds such as grass and shrub omnivores were more dominant with the increase of homogeneous páramo grassland and a lower vegetation profile. On the contrary, a more heterogeneous habitat with greater woody plant cover and less intervention, explained a greater dominance of more specialized trophic guilds such as shrub nectarivores as well as arboreal and shrub sally-gleaners. Elevation explains a greater dominance of trophic guilds with greater preference for open habitats such as páramo grassland (i.e., grass perch gleaners) at the higher end, while trophic guilds related to a more developed shrubby páramo (i.e., arboreal and shrub bark-foliage gleaners) are explained by lower elevations.

In general, the presence of specialized birds is expected to be greater in protected areas than in those areas without formal protection (Armenteras et al. 2003; O'Dea et al. 2006; Gray

et al. 2016). However, the bird community did not vary in composition across the boundaries of protected areas in this study; this result was particularly influenced by similar abundance of all trophic guilds across all transects. This last result may be explained by the relatively high level of altered habitat within the protected areas and several unaltered habitats within the buffer zones (e.g., Astudillo et al. 2018). For instance, we found that in protected areas the average percentage of altered habitat is 13% (±SD=10) and the average of altered habitat in buffer zones is 20% (±SD=17). Clearly, some transects in the protected areas are equally or more altered than in buffer zones. This phenomenon suggests that some areas within the protected areas still receive strong impacts from human activities, while at the same time some buffer zones are relatively impact free. Similar levels of alteration lead to an overall resemblance between bird communities inside and outside the protected areas.

In addition, heterogeneous páramo grassland sites with greater shrub coverage and a well-developed vegetation profile are important for maintaining bird diversity and connectivity in our study area (Astudillo et al. 2019). This type of páramo is most often found at mid elevations or towards the bottom of valleys (Ramsay 1992; Suárez and Medina 2001; Mena-Vásconez and Hofstede 2006; Minga et al. 2016). This phenomenon helps explain the occurrence of more specialized trophic guilds (e.g., shrub nectarivores, arboreal and shrub sally-gleaners, and arboreal and shrub bark-foliage gleaners) at relative lower elevations. However, these areas are also generally more accessible by humans, and therefore more susceptible to impacts associated with anthropogenic changes in land use such as burning to promote livestock grazing and introduction of exotic plants via road construction (Young 1997; Koenen and Koenen 2000). Buffer zones with irregular topography are less susceptible to these alterations due to difficult access (Bucheli 2007; Quispe-Melgar et al. 2019) and, therefore, may harbor more heterogeneous habitat associated with less altered páramo that promotes similar diversity patterns among protected areas and buffer zones. Within this framework, our findings indicate that there are indeed parts of the buffer zones that are unaffected by either changes in land use at lower elevations or by natural homogenization associated with higher elevations. As a result, the buffer zones maintain similar overall patterns of bird composition to those recorded within protected areas.

For the Andean forests of this region, secondary habitats recovering from previous impacts are important for the conservation of birds, as they have been shown to maintain similar survival rates for birds as within protected areas (Tinoco et al. 2019). In fact, even small areas of mature vegetation may contain a high diversity of specialized high-Andean birds (Astudillo et al. 2020). For example, forest and shrubby páramo specialist birds use small fragments of *Polylepis* forest surrounded by heterogeneous páramo grassland (Haslem and Bennett 2008; Astudillo et al. 2019). Consequently, the possible influences between protected areas and buffer zones used by the high Andean bird community reinforces the idea that protected areas should not be considered in isolation from what occurs in the buffer zones (DeFries et al. 2005; Hansen and DeFries 2007). Quantity and quality of páramo grassland habitats are important elements to consider for conservation, but habitat quality in zones outside protected areas is especially important to consider (Margules and Pressey 2000; Verboom et al. 2001; Lloyd and Marsden 2008; Astudillo et al. 2018).

Implications for conservation

Given that impacts outside of protected areas may already influence diversity indirectly within the parks, areas of high-quality habitat outside of parks should be prioritized to provide a true buffer against human impacts for the protected area. The páramo grassland ecosystem in the region is often interspersed with natural habitat remnants. This suggests that conservation and management strategies of protected areas would benefit from consideration of land-use process across the adjacent areas in a more regional context (Margules and Pressey 2000). Territories without major pressures from changes in land use by human activities should be considered as important elements contributing to diversity at a regional level, and may play an important role in enhance connectivity across the region, especially for specialized trophic guilds.

This information is especially relevant for the Macizo del Cajas Biosphere Reserve, where only 16% of the páramo grassland is within the national system of protected areas (Rodríguez - Girón et al. 2014). For the high

Andes, the selection criteria for protected areas are frequently based on the protection of water resources or on the concentration of key species (e.g., threatened, endemic; Castaño-Villa 2005; Tinoco et al. 2009), but this approach does not take into account overall diversity of species and habitats. By including trophic groups within analyses for making conservation decisions, their unique associated habitats are automatically considered. This could not only contribute to the conservation of specialist species, but also of habitats that present unique plant composition and structure within the páramo. The results of this investigation are specific to the biogeographically unique Macizo del Cajas Biosphere Reserve (Jiménez-Rivillas et al. 2018); however, this approach may be applicable regionally when adapted to the conditions of each area evaluated.

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