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BIRD DIVERSITY AND ITS RELATIONSHIP WITH HABITAT CHARACTERISTICS IN HIGH ANDEAN PEATBOGS

DIVERSIDAD DE AVES Y SU RELACIÓN CON LAS CARACTERÍSTICAS DEL HÁBITAT EN VEGAS DE LOS ALTOS ANDES

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Summary.—High Andean peatbogs are key functional wetlands in the dry Puna region and essential in conserving local biodiversity, including bird communities. We surveyed the bird communities of 18 peatbogs in the Argentinean Puna (Salta and Catamarca Provinces) to describe their species composition, their patterns of species richness and diversity; and their relationship to landscape features and local environmental variables. In total, we registered 60 species belonging to 21 families during summer 2014-2015. Species richness ranged from six to 20 species per peatbog. The Bright-rumped Yellow-finch *Sicalis uropygialis*, Ash-breasted Sierra Finch *Phrygilus plebejus*, Golden-spotted Ground Dove *Metriopelia aymara* and Puna Miner *Geositta punensis* were the most abundant representative species. The change in bird species composition among peatbogs showed a nested structure. The present study is the first one made for the avifauna of peatbogs of the Argentinean Puna and shows that the peatbogs with more irregular forms and more interconnected with other wetlands support more abundance and diversity of birds.

Key words: Argentinean Puna, avifauna, bird richness, High Andean wetlands, multivariate analysis, nestedness pattern.

Resumen.—Las vegas de altura son unidades funcionales claves en la región árida de la Puna y son esenciales para la conservación de la biodiversidad local, incluyendo las comunidades de aves. Se relevó la comunidad de aves de 18 vegas localizadas en la Puna Argentina (Provincias de Salta y Catamarca), para describir su composición de especies, el patrón de la riqueza y diversidad de especies; y la relación con los atributos del paisaje y variables ambientales. En total registramos 60 especies de aves pertenecientes a 21 familias en los veranos de 2014-2015. La riqueza de especies fue de seis a 20 especies por vega. El chirigüe culigualdo *Sicalis uropygialis,* el yal plebeyo *Phrygilus plebejus*, la

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palomita aimará *Metriopelia aymara* y el minero puneño *Geositta punensis*, fueron las especies más representativas en abundancia. El cambio en la composición de especies entre vegas mostró un patrón anidado. El presente estudio es el primero realizado para la avifauna de vegas de Argentina y muestra que las vegas con formas más irregulares y más interconectadas con otros humedales, soportan mayor abundancia y diversidad de aves.

Palabras clave: avifauna, análisis multivariado, humedales, patrón de anidamiento, Puna argentina, riqueza de aves.

Introduction

The Puna ecoregion of South America has a variety of aquatic environments. Peatbogs (locally called "vegas") are among them and represent key functional and particularly distinctive systems within the arid Andean environments (Squeo *et al.*, 2006). Peatbogs represent about 0.7% of the Argentine Puna area (Izquierdo *et al.*, 2015). They contribute a disproportionally high share of the primary productivity (Baldassini *et al.*, 2012), regulate water resources (Reboratti, 2006), and sustain populations of both domestic and wild herbivorous mammals (Halloy, 1991; Seimon *et al.*, 2007). Because of their high soil moisture, peatbogs sustain much of the ecoregional biodiversity (Ruthsatz, 1993; Squeo *et al.*, 2006; Gibbs, 1993).

Bird communities use peatbogs as breeding, feeding and watering sites. Therefore, these sites support species associated with different habitats, such as rivers and lakes, wet meadows or bunch-grass steppes (Tellería *et al.*, 2006). Despite their importance, they have scarcely been studied because of the extreme conditions in which they are found and the difficulty of access (Morrison *et al.*, 1998; Tellería *et al.*, 2006). Their bird communities have been described for some locations in the Argentine and Bolivian Puna, showing high species abundance and richness (Hurlbert & Keith, 1979; Vides Almonacid, 1990; Fjeldså & Krabbe, 1990; Hurlbert & Chang, 1983; Caziani *et al.*, 2001). These studies, however, span a long period and cover sites that are scattered across a large region span. They are mostly focused on shallow lakes and specific groups, such as flamingos.

The High Andean peatbogs appear as green oases in valley bottoms, shallow basins and other areas of concave topography that contrast sharply with the arid and steep landscape (Maldonado Fonkén, 2014). For that reason, they can be regarded as humid and productive "islands" within a matrix of arid environments. From a landscape perspective and according to theories of island biogeography, greater bird species diversity should occur in large and relatively well interconnected peatbogs rather than in small and isolated ones (Caziani *et al.*, 2001; Rosenzweig, 1995; MacArthur & Wilson, 1967; Lossos, 2010). Likewise, in relation to peatbog characteristics, we expected to find higher species richness and abundance in isodiametric peatbogs where the periphery/area relation is small, and therefore, the edge effect is lower (Murcia, 1995; Moser *et al.*, 2002; Andrén, 1994); and in the same way for the larger ones (Tellería *et al.*, 2006). Also, we expect higher diversity in more productive peatbogs since species richness increases from low to intermediate habitat productivity levels (Rosenweigz, 1995; Waide *et al.*, 1999). This latter hypothesis states that primary productivity (i.e. the main input of available energy to ecosystems resulting from plant photosynthesis) limits the number of species present in ecosystems (Mittelbach *et al.*, 2001; Hawkins *et al.*, 2003). Among these studies, those that evaluated both the density of plant growth in terms of the Normalised Difference Vegetation Index (NDVI) and bird-species richness found that mean annual NDVIs were good predictors of avian diversity (Bonn *et al*., 2004; Phillips *et al*., 2010).

In addition to the patterns of bird species number and/or abundance among peatbogs; community descriptions benefit from differentiating whether species composition occurs at random or as a nested pattern (Atmar & Patterson, 1993). Nestedness occurs when the species present at species-poor sites are non-random subsets of those present in species-rich areas (Atmar & Patterson, 1993); reflecting a non-random process of species loss as a consequence of any factor that promotes the orderly disaggregation of assemblages (Gaston & Blackburn, 2000).

In this study, we analysed data from bird communities surveyed in peatbogs of the northwestern Argentinean Puna to describe i) their bird species composition, richness, relative abundance and nestedness, ii) to explore the patterns of change in species composition among peatbogs, and iii) to evaluate which landscape and peatbog characteristics are related to these bird community attributes.

Material and Methods

Study Area

The Puna, the high plateau of the Central Andes, extends over Peru, Bolivia, Chile and Argentina, above 3,000 m a.s.l. In northwestern Argentina it includes areas between 20°S and 30ºS. The climate is arid and cold, with intense solar radiation, strong winds and daily temperature fluctuations that may exceed 30°C (Olson *et al*., 2001). Annual precipitation is scarce (100-400 mm) and occurs between November and February, decreasing to the west and south (Cabrera & Willink, 1973). The hydrographic system of most of the Puna is characterised by the existence of endorreic watersheds with saline depressions that receive input from small rivers and include temporary or permanent shallow salty lakes (Paoli *et al*., 2002).

Peatbogs form in damp hollows where plant matter decomposes slowly because of the low temperature and humidity, forming peat, a deposit of organic material (Maldonado Fonkén & Maldonado, 2010; Segnini *et al*., 2010). The bog vegetation has a cushion-like habit. Large cushions are dominated by *Distichia muscoides, Oxychloe andina* and *Plantago rigida*. Other genera present include *Gentiana, Hypsela, Isoetes, Lilaeopsis, Ourisia* and *Scirpus*. In well-drained areas, some of the cushion plants include Yareta *Azorella compacta* and *Werneria aretioides* (Stotz *et al*., 1996; Salazar, 1999; Nieto *et al*., 2015). These topographic and vegetation characteristics contrast strikingly with the arid surrounding landscape in terms of vegetation cover, which facilitates peatbog spatial delimitation.

Habitat features

We surveyed 18 peatbogs (covering a total of 777.65 ha) in the Salta and Catamarca provinces of northwestern Argentina in 2014 and 2015 (Figure 1, Supplementary material appendix 1, Table S1). We characterised peatbogs according to both landscape and local characteristics. The landscape-scale characterisation was based on the regional peatbog map developed by Izquierdo *et al*. (2015), from which we obtained the exact location (latitude and longitude) and area of each peatbog. In addition, we considered: a) the mean annual temperature and total precipitation from WorldClim (Hijmans *et al*., 2005); b) shape (i.e., perimeter/$2\sqrt{\pi^*}$ area), where a lower value implies more circular shape; c) connectivity; as distance to the closest neighbour peatbog (landscape

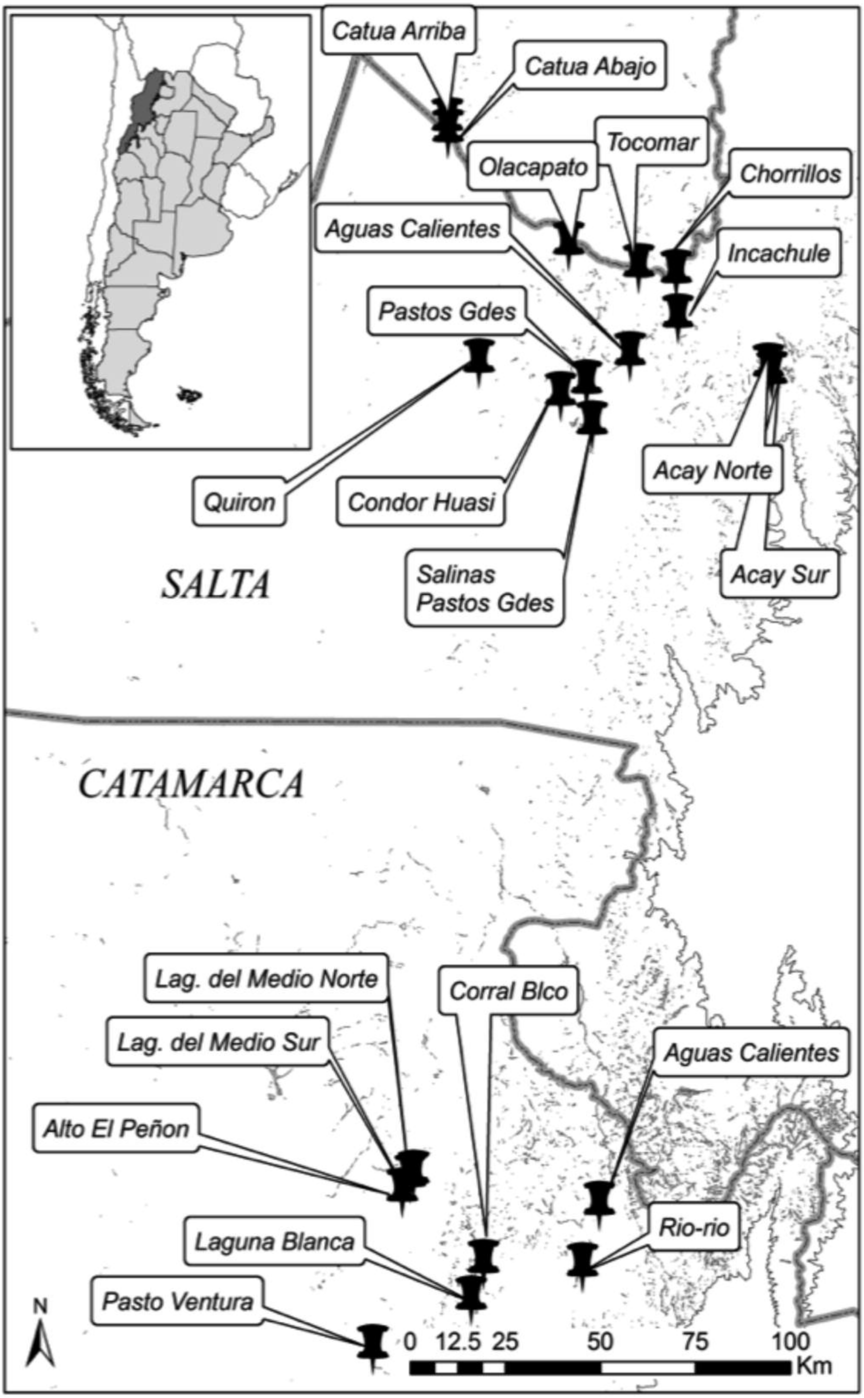

FIG. 1.—Study area and location of visited peatbogs in northwestern Argentina (South America). *[Área de estudio y localización de las vegas visitadas en el noroeste de Argentina (Sudamérica).]*

metrics were calculated with Patch Analysis; continuity with the ‘‘near’’ function, and altitude based on a Digital Elevation Model (DEM) through ESRI@ArcGIS10.1.; Izquierdo *et al.,* 2015); and d) Median NDVI (Normalized Difference Vegetation Index) as a primary productivity proxy calculated from Landsat bands (Supplementary material appendix 1, Table S1).

At local scale, using a “Horiba U52” multiparameter analyzer, we measured the pH, conductivity (NTU) and percentage of dissolved oxygen (DO/mg l) of the peatbog water courses. Altitude was measured in the field using GPS equipment (Supplementary material appendix 1, Table S1).

Bird counts

Point counts across each peatbog were used to estimate bird richness and abundance during single summer visits in 2014 or 2015. Five observation points were separated by 150 to 300 m (depending on peatbog size) from each other to avoid recording the same individuals from neighbouring points (Bibby *et al*., 2000; Naoki *et al*., 2014). During each count we recorded all birds seen or heard during a ten-minute period (Sutherland *et al*., 2004). Since the Puna birds do not show marked peaks of activity, unlike those in the lowlands, observations were carried out between 07:00 and 17:00 hours, unless the weather conditions were unfavorable (rain, wind, hail) (Naoki *et al*., 2014). Species identification followed a standard field guide (Narosky & Yzurieta, 2003).

Statistical analysis

Bird species composition and richness

For each peatbog we calculated the following variables: richness (number of species); abundance (the number of individuals of a given species relative to the other species); the Margalef diversity Index $I = (s-1)/\ln N$, where I = the biodiversity index, ln = natural logarithm, s = species number and N = total number of individuals (Margalef, 1958); Species Evenness (or Pielou’s index) $J = H'/H'_{max}$, where H’ is the number derived from the Shannon diversity index and H'_{max} is the maximum possible value of H’. This latter index quantifies how equal the community is numerically whereas the Margalef index (Margalef, 1958) is a simple measure of species richness.

In addition, we estimated the Relative Importance Index, $RII = (N_i/N_t) * (M_i/M_t) * 100$, where N_i is the number of individuals of species i in all samples, N_t is the total number of individuals of all species, M_i is the number of samples in which species i was present and M_t is the sum of all samples (Gatto *et al*., 2005). This index shows the relative importance of each species across the study area. We decided to use the 16 species with the highest Relative Importance Index values in the subsequent analysis.

Bird assemblage structure compared among peatbogs

Bird assemblage structure was assessed by studying patterns of nestedness. Nestedness occurs when the species composition of any one “island” is a proper subset of the species composition of another larger “island” (Patterson & Atmar, 1986; Cutler, 1994). The nestedness pattern is most often used to explore the structure of communities, such as islands within an archipelago (Patterson & Atmar, 1986), habitat fragments within a landscape (Atmar & Patterson, 1993; Patterson & Atmar, 2000; Ganzhorn & Eisenbeiss, 2001), isolated peaks in mountain ranges (Patterson, 1990; McDonald & Brown, 1992; Cook, 1995), and temporal changes within disturbed habitats (Bloch *et al*., 2007).

We used the weighted nestedness algorithm (Rodríguez-Gironés & Santamaría, 2006) to analyse the distribution pattern of bird species among peatbogs. This method analyses the matrix of abundances of species and calculates its "temperature", which indicates the level of order or disorder of the matrix. Nestedness values of 0 indicate non-nestedness, while 100 indicates perfect nestedness. The lower the temperature of the matrix (level of nestedness of the system), the lower is its disorder and the less stochastic is the distribution of the species in the studied assemblage.

To assess the statistical significance of the nestedness patterns, we used the vaznull model (Vázquez *et al.,* 2007): we compared our result against 1000 randomly generated matrices of the same size (in terms of rows and columns), where the probability of interactions (birds species shared by peatbogs) is proportional to the total interactions (Bascompte *et al*., 2003). The P value was defined as the ratio of the number of random matrices with T value equal to or greater than that of the observed matrix. Nestedness was analysed using the Bipartite v. 2.05 package (Dormann *et al*., 2009) of the R v. 2.15.3 statistical program (R Development Core Team, 2013).

Bird community composition related to habitat characteristics

We performed a multivariate analysis to explore the relationship between bird community composition and the peatbog habitat characteristics. First, we used a Detrended Correspondence Analysis (DCA) with abundance data to determine whether unimodal or linear numerical techniques are most appropriate for modelling the relationships among bird community attributes. Next, Redundancy Analysis (RDA) was performed on the same data matrix and on the $\log_{10}$-transformed peatbog characteristics matrix to examine associations between them and bird community composition. For this purpose, we selected the 16 species with the highest Relative Importance Index values. In the first run, weighted correlations and variance inflation factors VIFs (> 20) were used to identify the inter-correlated variables, and then they were removed. RDA with step-wise forward selection was performed on all samples and the rested variables to identify which peatbog characteristics explained a statistically significant ($P < 0.05$) amount of the variation in bird data. The significance of each variable was tested using an unrestricted Monte Carlo test (999 permutations). Ordinations were performed using the Canoco 4.0 for Windows computer program (Leps & Smilauer, 2003).

Results

We recorded a total of 60 species belonging to 21 families. Species richness ranged from six species in Alto El Peñón to 20 species in Tocomar. The best-represented families were the Emberizidae (11 species), Furnariidae (9 species) and Tyranidae (8 species). The species with highest RII values were the Bright-rumped Yellow-finch *Sicalis uropygialis* and the Ash-breasted Sierra Finch *Phrygilus plebejus* (also the most abundant species), followed by the Golden-spotted Ground Dove *Metriopelia aymara*, Puna Miner *Geositta punensis* and Red-backed Sierra Finch *Phrygilus dorsalis* (Supplementary material appendix 1, Table S2).

The "matrix temperature" of the bird assemblages was 46.91° and was lower than the null model (T mean for vaznull model = 57.54, $P = 0.033$, from 999 randomizations), indicating that bird assemblages (i.e., species composition and abundances) in the surveyed peatbogs exhibited a moderate nested structure.

The bird species with higher RII values the Bright-rumped Yellow-finch, Ash-breasted Sierra finch, Golden-spotted Ground Dove and Puna Miner, were the most abundant and present at most peatbogs. These species are all characteristic of the Puna. The Laguna del Medio (V13), Alto el Peñón (V12) and Aguas Calientes (V3) peatbogs showed greater abundance values, while Tocomar (V1), Salinas Pastos Grandes (V5) and Laguna del Medio (V13) showed most diversity (Figure 2).

To explore which landscape and peatbog characteristics could be associated with bird biodiversity, a DCA with a length gradient (1.805) indicated that a linear model was most appropriate. In the first run of RDA, weighted correlations and variance inflation factors VIFs (> 20) were identified; consequently, the minimum and maximum temperature were eliminated. The RDA was performed on the full data set, and the eigenvalues for axes 1 and 2 ($\lambda 1 = 0.323$ and $\lambda 2 = 0.132$, respectively) explained 64.8% of the variance observed in bird community attributes. The bird community and peatbog characteristics correlations for RDA axes 1 and 2 were high (0.85 and 0.93) (Table 1). Two variables were significant ($P > 0.05$), shape (explaining 20% of the total variance) and connectivity (14%) ($F = 4.006$, $P = 0.009$ and $F = 2.599$, $P = 0.038$ respectively). The first RDA axis explained 46% of this variation, showing high correlation with connectivity, shape and pH. The second axis explained 18.8 % of the variation, showing a high correlation with elevation, peatbog area and Median NDVI. Bird abundance was correlated with connectivity while richness (Margalef Index) was correlated with peatbog shape and area. Also, the ordination graph showed on top, species related to Puna and High Andean steppes (e.g. Red-backed Sierra Finch and Puna Miner) and they correlated with elevation. In contrast, species not distinctive of Puna region (e.g.

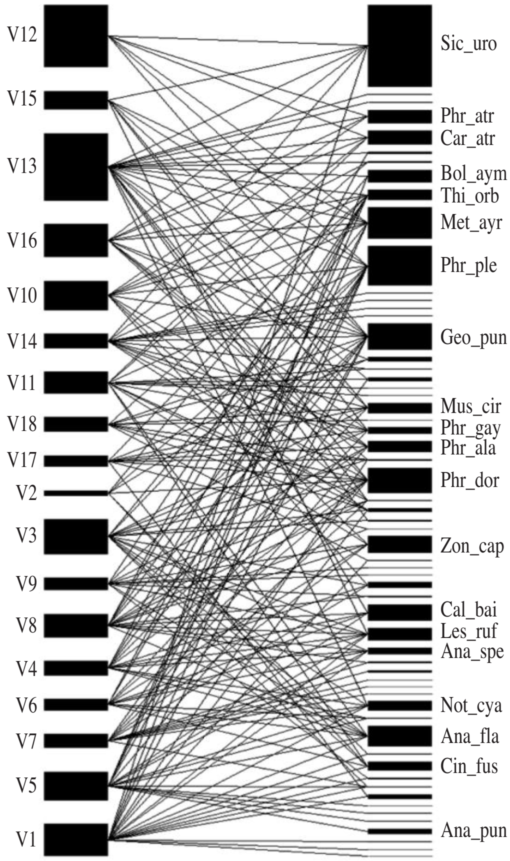

FIG. 2.—Graphical representation of the quantitative species-peatbogs nested pattern. Black rectangles represent bird species (right) and peatbogs (left). Rectangle width is proportional to the number of interactions (species abundance). Lines represent links between species and peatbogs. Only species codes for very frequently recorded species are given (see Supplementary material appendix 1, Table S2, for species codes).
[Representación gráfica del patrón cuantitativo de anidamiento de especies-vegas. Los rectángulos negros representan especies (derecha) y las vegas (izquierda). El ancho del rectángulo es proporcional al número de interacciones (abundancia de especies). Las líneas representan los enlaces entre especies y vegas. Solo se muestran los códigos de las especies con mayores registros (véase el Material suplementario, apéndice 1, Tabla S2 para información sobre el código de las especies de aves).]

Rufous-collared Sparrow *Zonotrichia capensis* and Speckled Teal *Anas flavirostris*, were grouped towards the lower values of this Y axis and they correlated with peatbog area and Median NDVI (Figure 3).

Discussion

The present study shows that the High Andean peatbogs of Argentina sustain a diverse avifauna that differs according to landscape and local environmental characteristics. This highlights the value of an environment that is recognised as highly importance in preserving the biological diversity of this Puna ecoregion. The Argentine Puna peatbog avifauna is more diverse that of Peruvian and Bolivian peatbogs (Tellería *et al*., 2006; Naoki *et al*., 2014 respectively). For example, in Peru the mountain peatbogs seem to be occupied by a subsample of upland birds, totalling 34 species. In contrast, the peatbogs of the Argentine Puna attract many species of the High Andean steppes, grasslands, pre-Puna and Puna, and other common species from wetlands and marshes, totalling 60 bird species. These findings strengthen the view that Argentinian peatbogs may operate as centres of high avian diversity for birds by sustaining species that are also associated with a variety of other habitats (Tellería *et al*., 2006).

According to island biogeography theory (McArthur & Wilson, 1967; Lossos, 2010), it should be expected that large and relatively well interconnected peatbogs attract the greatest avian diversity, and our results partly support this prediction. We found the highest species richness in Tocomar, our largest peatbog. The Laguna del Medio also presented high species richness and abundance; this peatbog is associated with a shallow lake, indicating that landscape

Table 1

Summary of the ordination by redundancy analysis (RDA) for bird community and peatbog variables (see Figure 3).
[Resumen del ordenamiento del análisis de redundancia (RDA) para la comunidad de aves y las variables de las vegas (veáse Figura 3).]

Axes	**1**	**2**	**3**	**4**	**Total variance**
Eigenvalues	0.323	0.132	0.081	0.050	1.000
Species-environment correlations	0.85	0.931	0.924	0.931	
Cumulative percentage variance of species data	32.3	45.4	53.5	58.5	
Cumulative percentage of species-environment relation	46.0	64.8	76.3	83.5	
Sum of all eigenvalues					1.000
Sum of all canonical eigenvalues					0.700

heterogeneity may play a role comparable to peatbog size in determining species richness. In contrast, the smallest and most isolated peatbog, Alto el Peñón, showed low species richness but high abundance of birds, especially such finches as the Bright- rumped Yellow-finch *Sicalis uropigialis* which occur in monospecific flocks.

We expected that isodiametric peatbogs would have higher species diversity, since elongated and irregular peatbogs have more edge effect, thus reducing island functionali-

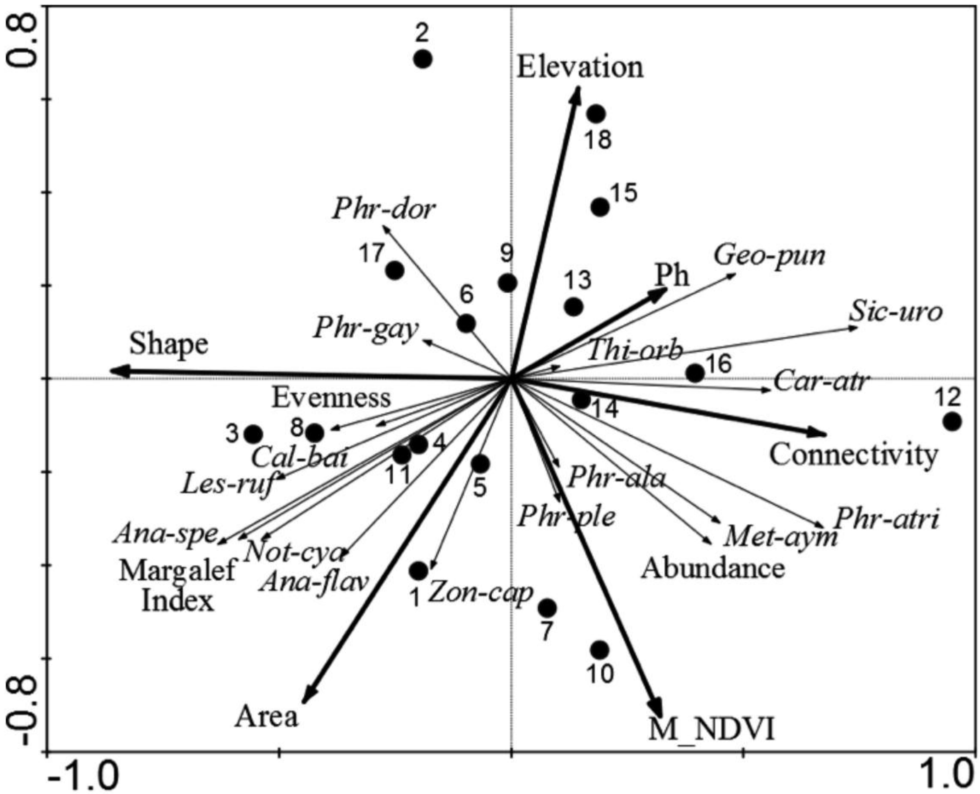

FIG. 3.—Stepwise Redundancy Analysis (RDA) of bird community and peatbog variables. The angle of arrows with the axis indicates their correlation with the axis: variables whose arrows are parallel with one axis are highly correlated with it. Arrow length is proportional to the relative importance of the environmental or species variable. Important variables are represented by longer arrows. The x-axis explained 46% and the y-axis explained 18.8% of the variance. Circles represent peatbog samples. (For peatbog and species codes see Supplementary material appendix 1, Tables S1 and S2, respectively).
[Análisis de Redundancia (RDA) de la comunidad de aves y las variables de las vegas. El ángulo de las flechas con el eje indica la correlación con dicho eje: las variables cuyas flechas están paralelas con el eje presentan una alta correlación con el mismo. El largo de la flecha es proporcional a la importancia relativa de la variable ambiental o especie, variables más importantes están representadas por flechas más largas. El eje x explicó un 46% y, el eje y un 18,8%. Los círculos representan las vegas muestreadas. (Para los códigos de vegas y especies véase el material suplementario, apéndice 1, Tablas S1 y S2, respectivamente).]

ty (Moser *et al*., 2002). However, we found that the more irregularly-shaped peatbogs sustained more bird richness and abundance, probably because peatbogs with more "arms" or an irregular perimeter could offer more microhabitat heterogeneity. As peatbogs appear as green oases within valley bottoms, contrasting sharply with the arid and steep landscape (Maldonado Fonkén, 2014), birds may concentrate there for forage or refuge. This is probably related to the breeding cycle of the Andean avifauna, since peatbogs had a higher abundance of birds in February at the end of the breeding season (Tellería *et al*., 2006), when our sampling was conducted.

Peatbog shape and interconnectivity were nonetheless the main significant and correlated variables. Even though we did not find a relationship between assemblages and peatbog size; species richness (*i.e*. the Margalef index) increased and correlated with peatbog size and shape, indicating that these characteristics are important for birds. In addition, an increase was detected for bird abundance with peatbog interconnectivity and Median NDVI (see Figure 3). Area is the main predictor of species richness, especially in wetlands (Rosenzweig, 1995; Hobaek *et al*., 2002; Paracuellos & Tellería, 2004; Tellería *et al*., 2006). For birds, abundance is strongly determined by peatbog size; larger ones attracting more individuals (Caziani *et al*., 2001; Tellería *et al*., 2006).

The differences in species assemblages between peatbogs indicate a nested pattern, with changes in abundance being more frequent than changes in species diversity. This type of change in biodiversity is most prevalent in fragmented habitat or 'islands' (Patterson & Atmar, 1986; 2000). Nestedness of species assemblages occurs where the biotas of sites with smaller numbers of species are subsets of the biotas at richer sites (Ulrich & Gotelli, 2007), reflecting a non-random process of species loss as a consequence of any factor that promotes the orderly disaggregation of assemblages (Gaston & Blackburn, 2000). Nestedness can occur by two different processes: species-specific colonisation and/or dispersal potential and species-specific vulnerability to extinction (Patterson & Atmar, 1986). For example, the colonisation assumption includes different colonisation capacities of different species, not only in relation to connectivity or distance but also in relation to environmental gradients (altitude, temperature, precipitation, etc.) (Ganzhorn, 1998). For the high Andean Puna peatbogs, environmental gradients and connectivity could have a strong influence on bird communities, as explored in the RDA analysis (see below). Several ecological processes can produce a nested pattern in a community and they are not mutually exclusive (Lomolino, 2007). We cannot address which processes are involved, but nested structure provides guidance on how different species or assemblages could respond to this particular fragmented habitat in the dry Puna.

In Peatbogs are sites of high biodiversity concentration and an important resource for distinctive and endemic species of the puna, some of which are now restricted to fragments of undisturbed natural landscape (Maldonado Fonkén, 2014). However, peatbogs are under-represented among currently protected areas (Caziani *et al*., 2001), despite their rich and unique bird communities, and have hardly been studied from a conservation perspective. During the past decades, human and livestock pressure on the region has decreased (Izquierdo & Grau, 2009), which may have resulted in a recovery of ecosystems and their wildlife (Grau & Aide, 2007). However, a combination of human activities (e.g. mining, mineral extraction from salt-pans) and climatic warming and drying (Carilla *et al.,* 2013) could result in the reduction and fragmentation of regional peatbogs in the coming decades (Squeo *et al*., 2006).

This study is an attempt to contribute to the knowledge of High Andean bird communities in the peatbogs of Northwestern Argentina, by exploring which landscape variables and local peatbog characteristics may be associated with changes in assemblage composition and species richness. Our chief findings regarding the importance of peatbog size and shape, and of interconnectivity among peatbogs and with other wetlands, provide guidelines on how to prioritise peatbog conservation in relation future changes in climate and land use; including mining, urbanisation and roads construction.

In addition to supporting bird communities, the Andean peatbogs are extremely valuable for the conservation of other components of biodiversity, for carbon sequestration, for generating forage for local livestock, and for regulating water resources for human consumption. This study also provides a baseline for elaborated modelling efforts to design conservation and land planning strategies to maximise the sustaining of these environmental benefits in balance with avian conservation.

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REFERENCES

Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos,* 71: 355-366.

Atmar, W. & Patterson, B.D. (1993). The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia,* 96: 373-382.

Bascompte, J., Jordano, P., Melian, C.J. & Olesen, J.M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences USA,* 16: 9383-9387.

Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S. (2000). *Bird census techniques*. Academic Press. London.

Bloch, C.P., Higgins, C.L. & Willig, M.R. (2007). Effects of large-scale disturbance on metacommunity structure of terrestrial gastropods: temporal trends in nestedness. *Oikos,* 116: 395-406.

Bonn, A., Storch, D. & Gaston, K.J. (2004). Structure of the species-energy relationship. *Proceedings of the Royal Society of London B. Biological. Sci*ence, 271: 1685-1691.

Cabrera, A.L. & Willink, A. (1973). *Biogeografía de América Latina*. Secretaria General de la Organización de los Estados Americanos. Washington DC.

Carilla, J., Grau, H.R, Morales, M.S., & Paolini, L. (2013). Lake fluctuations, plant productivity and long-term variability in high-elevation tropical Andean ecosystems. *Arctic, Antarctic and Alpine Research*, 45: 179-189.

Caziani, S.M., Derlindati, E., Talamo, J., Nicolossi, G., Sureda, A.L. & Trucco, C. (2001). Waterbird richness in Altiplano wetlands of northwestern Argentina. *Waterbirds*, 24: 103-117.

Cook, R.R. (1995). The relationship between nested subsets, habitat subdivision, and species diversity. *Oecologia*, 101: 204-210.

Cutler, H.A. (1994). Nested biotas and biological conservation: metrics, mechanisms, and meaning of nestedness. *Landscape and Urban Planning*, 28: 73-82.

Dormann, C.F., Fruend, J., Bluethgen, N. & Gruber, B. (2009). Indices, graphs and null models: analyzing bipartite ecological networks. *Open Ecology Journal*, 2: 7-24.

Fjeldså, J. & Krabbe, N. (1990). *Birds of the High Andes*. Zoological Museum. University of Copenhagen. Copenhagen.

Ganzhorn, J.U. (1998). Nested patterns of species composition and their implications for lemur biogeography in Madagascar. *Folia Primatologica*, 69: 332-334.

Ganzhorn, J.U. & Eisenbeiss, B. (2001). The concept of nested species assemblages and its utility for understanding effects of habitat fragmentation. *Basic and Applied Ecological*, 2: 87-95.

Gaston, K.J. & Blackburn, T.M. (2000). *Pattern and process in macroecology*. Blackwell Science. Oxford.

Gatto, A., Quintana, F.,Yorio, P. & Lisnizer, N. (2005). Abundancia y diversidad de aves acuáticas en un humedal marino del Golfo San Jorge, Argentina. *Hornero,* 20: 141-152.

Gibbs, J.P. (1993). The importance of small wetlands for the persistence of local populations of wetland- associated animals. *Wetlands*, 13: 25-31.

Grau, H.R. & Aide, T.M. (2007). Are rural-urban migration and sustainable development compatible in mountain systems? *Mountain research and development*, 27: 119-123.

Halloy, S.R.P. (1991). Islands of life at 6000 M Altitude-the environment of the highest autotrophic communities on earth (Socompa Volcano, Andes). *Arctic, Antarctic and Alpine Research*, 23: 247-262.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter E.E. & Turner, J.R.G., (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84: 3105-3117.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology,* 25: 1965-1978.

Hobaek, A., Manca, M. & Andersen, T. (2002). Factors influencing species richness in lacustrine zooplankton. *Acta Oecologica*, 23: 155-163.

Hurlbert, S.H. & Chang, C.C.Y. (1983). Ornitholimnology: Effects of grazing by the Andean flamingo (*Phoenicoparrus andinus*). *Proceedings of the National Academy of Science U.S.A.*, 80: 4766-4769.

Hurlbert, S.H. & Keith, J.O. (1979). Distribution and spatial patterning of flamingos in the Andean altiplano. *Auk,* 96: 328-342.

Izquierdo, A.E., Foguet, J. & Grau, H.R. (2015). Mapping and spatial characterization of Argentine High Andean peatbogs. *Wetlands Ecology and Management*, 23: 963-976.

Izquierdo, A.E. & Grau, H.R. (2009). Agriculture adjustment, ecological transition and protected areas in Northwestern Argentina. *Journal Environmental Management,* 90: 858-865.

Leps, J. & Smilauer, P. (2003). *Multivariate Analysis of Ecological Data using CANOCO*. Cambridge University Press. New York.

Lomolino, M.V. (2007). Investigating causality of nestedness of insular communities: selective immigrations or extinctions? *Journal of Biogeography*, 23: 699-703.

Lossos, J.B. (2010). Adaptive Radiation, Ecological Opportunity, and Evolutionary Determinism. *The American Naturalist,* 175: 623-639.

MacArthur, R. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press. Princeton.

Maldonado Fonkén, M.S. (2014). Bofedales of the peruvian high Andes. *Mires and Peat*, 15: 1-13. http://www.mires-and-peat.net/. ISSN 1819-754X.

Maldonado Fonkén, M.S. & Maldonado, L. (2010). L*os Bofedales: "Un oasis en la puna" (Bofedales: "an oasis in the puna")*. Ancash Anuario Cultural. Asociación Ancash, Antamina, Huaraz.

Margalef, D.R. (1958). Information Theory in Ecology. *General Systematic,* 3: 36-7.

McDonald, K.A. & Brown, J.H. (1992). Using montane mammals to model extinctions due to global change. *Conservation Biology*, 6: 409-415.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I., & Gough, L. (2001). What is the observed relationship between species richness and productivity? *Ecology*, 82: 2381-2396.

Morrison, M.L., Marcot, B.G. & Mannan, R.W. (1998). *Wildlife-habitat relationships. Concepts and Applications*. The University of Wisconsin Press. Madison.

Moser, D., Zechmeister, H., Plutzar, C., Sauberer, N., Wrbka, T. & Brabherr, G. (2002). Landscape patch shape complexity as an effective measure of plant species richness in rural landscapes. *Landscape Ecology*, 17: 657-669.

Murcia, C. (1995). Edge Effects in Fragmented Forests: Implications For Conservation. *Trends in Ecology And Evolution*, 10: 58-62.

Naoki, K., Landivar, C.M. & Gómez, M.I. (2014). Bird monitoring to detect changes in the ecosystem quality of High Andean Wetlands. *Ecología en Bolivia*, 49: 73-83.

Narosky, T. & Izurieta, D. (2003). *Guía para la identificación de las aves de Argentina y Uruguay*. Asociación Ornitológica del Plata. Buenos Aires.

Nieto, C., Malizia, A., Carilla, J., Izquierdo, A.E., Rodríguez, J., Cuello, S., Zannier, M. & Grau, H.R. (2016). Patrones espaciales en comunidades de macroinvertebrados acuáticos de la Puna Argentina. *Revista de Biología Tropical*, 64: 747-762.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.J., Ricketts, T. H., Kura, Y., Lamoreux, J.F., Wesley Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001). Terrestrial ecoregions of the World: A new map of life on earth. *BioScience*, 51: 933-938.

Paoli, H., Bianchi, A.R., Yañez, C.E., Volante, J.N., Fernández, D.R., Mattalía, M.C. & Noé, Y.E. (2002). *Recursos Hídricos de la Puna, valles y Bolsones áridos del Noroeste Argentino*. Convenio INTA-EEA Salta-CIED Salta.

Paracuellos, M. & Tellería, J.L. (2004). Factors affecting the distribution of a waterbird community: the role of habitat configuration and bird abundance. *Waterbirds*, 27: 446-453.

Patterson, B.D. (1990). On the temporal development of nested subset patterns of species composition. *Oikos*, 59: 330-342.

Patterson, B.D. & Atmar, W. (1986). Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society*, 28: 65-82.

Patterson, B.D. & Atmar, W. (2000). Analysing species composition in fragments. In: G. Ehinwald (Ed.): *Isolated vertebrate communities in the tropics*. Bonner Zoologische Monographs, 46: 9-24.

Phillips, L.B., Hansen, A.J., Flather, C.H. & Robison-Cox, J. (2010). Applying species-energy theory to conservation: a case study for North American birds. *Ecological Applications*, 20: 2007-2023.

Reboratti, C. (2006). La situación ambiental en las ecoregiones Puna y Altos Andes. In, A.D. Brown, U. Martínez Ortiz, M. Acerbi, J. Corcuera (Eds). *La Situación Ambiental Argentina 2005*. Fundación Vida Silvestre Buenos Aires.

Rodríguez-Gironés, M.A. & Santamaría, L. (2006). A new algorithm to calculate the nestedness temperature of presence-absence matrices. *Journal of Biogeography*, 33: 924-935.

Rodríguez-Gironés, M.L. (1995). *Species diversity in space and time*. Cambridge University Press.Cambridge. New York.

Ruthsatz, B. (1993). Flora and ecological conditions of high Andean peatlands of Chile between 18º00' (Arica) and 40º30' (Osorno) south latitude. *Phytocoenologia*, 25: 185-234.

Salazar, J.M. (1999). Determinación, caracterización y conservación de la diversidad biológica de los bofedales de Toccra a 4.200 msnm (Yanque-Caylloma), 1998. Universidad Nacional de San Agustín. Arequipa.

Segnini, A., Posadas, A., Quiroz, R., Milori, D.M.B.P., Saab, S.C., Martin Neto, L. & Vaz, C.M.P. (2010). Spectroscopic assessment of soil organic matter in wetlands from the High Andes. *Soil Science Society of America Journal*, 74: 2246-2253.

Seimon, T.A., Seimon, A., Daszak, P., Halloy, S.R.P., Schloegel, L.M., Aguilar, C.A., Sowell, P., Hyatt, A.D., Konecky, B. & Simmons, J.E. (2007). Upward range extension of Andean anurans and chytridiomycosis to extreme elevations in response to tropical deglaciation. *Global Change Biology*, 12: 1-12.

Squeo, F.A., Warner, B.G., Aravena, R. & Espinoza, D. (2006). Bofedales: high altitude peatlands of the central Andes. *Revista Chilena de Historia Natural*, 79: 245-255.

Stotz, D.F., Fitzpatrick, J.W., Parker, T.A. & Moskovits, D.K. (1996). *Neotropical birds: ecology and conservation*. University of Chicago Press. Chicago.

Sutherland, W.J., Newton, I. & Green, R.E. (2004). *Bird ecology and conservation: a handbook of techniques*. Oxford.

Tellería, J.L., Venero, J.L. & Santos, T. (2006). Conserving birdlife of Peruvian highland bogs: effects of patch-size and habitat quality on species richness and bird numbers. *Ardeola*, 53: 271-283.

Ulrich, W. & Gotelli, N.J. (2007). Disentangling community patterns of nestedness and species co-occurrences. *Oikos*, 116: 2053-2061.

Vázquez, D.P., Melian, C.J., Williams, N.M., Blüthgen, N., Krasnov, B. R. & Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, 116: 1120-1127.

Vides Almonacid, R. (1990). Observaciones sobre la utilización del hábitat y la diversidad de especies de aves en una laguna de la Puna argentina. *Hornero*, 13: 117-128.

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. (1999). The relationship between productivity and species richness. *Annual Review of Ecology and Systematic*, 30: 257-300.

Supplementary Electronic Material

Additional supporting information may be found in the on-line version of this article. See volume 64(2) on www.ardeola.org

Table S1. Landscape and environmental features of 18 analysed peatbogs in the Argentine Puna Region.

Table S2. List of species recorded in Argentinian peatbogs, their status (ST) and relative importance index (RII).

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