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HAL Id: hal-03481097

https://hal.sorbonne-universite.fr/hal-03481097

Submitted on 15 Dec 2021

RESEARCH ARTICLE

Glacier influence on bird assemblages in habitat islands of the high Bolivian Andes

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Abstract

Aim: Climate projections for the upcoming decades predict a significant loss of ice mass particularly critical for glaciers in tropical mountains. In the dry landscapes of the southern Andes (from Southern Peru to Chile), this global trend has strong ecological impacts on high-altitude wetlands that support a unique avifauna for feeding, roosting and nesting. As glacier runoffs are expected to affect the area and the quality of wetland habitats, these changes may potentially affect bird communities. To address this issue, we studied the structural and functional diversity of bird assemblages in glacier-fed high-altitude wetlands (>4500 m).

Location: Five valleys of the Cordillera Real, Bolivia.

Methods: We surveyed bird communities during dry, wet and intermediate seasons in 40 wetlands (total of 27,720 observations of birds and habitats from 540 transects) showing different degrees of dependence on glacial meltwater. We examined the potential effect of glacier retreat on bird communities through changes in wetland area and environmental quality and heterogeneity.

Results: We found strong relationship between wetland area and taxonomic and functional diversity, but not on phylogenetic diversity. Generalized additive models revealed that avian diversity was influenced by wetland's productivity and elevation and maximized at intermediate levels of glacier influence. Multivariate analysis further showed that habitat productivity and humidity, both potentially influenced by future glacial retreat trends, are the main drivers of bird community composition, with the wettest habitats being crucial for aquatic birds and uncommon species.

Main conclusions: Glacier retreat may significantly affect bird community diversity and composition through changes in both area and quality of high-altitude wetlands, with a particular concern for aquatic birds.

KEYWORDS
bird diversity, glacier retreat, habitat heterogeneity, species–area relationship, tropical Andes, wetlands

1 | INTRODUCTION

Glaciers are sensitive climate indicators and rapidly react to climatic variations with alteration of their mass (Oerlemans, 2001). Glacier retreat has dramatically accelerated during the last decades as a response to a rapid rise of temperatures (Zemp et al., 2019). Worldwide, glaciers have lost ice mass at an average rate of 220 ± 30 Gt/year during the 2006–2015 period (Intergovernmental Panel on Climate Change - IPCC, 2019) and projections for the 21st century indicate a continuing downward trend in glacier cover in almost all regions (Huss & Hock, 2018; IPCC, 2019; Dussaillant et al., 2019). According to the various IPCC scenarios, by 2100, the glacier mass is expected to decrease by 35% to 55% at the global scale and by up to 90% in both Europe and the tropical regions (Huss et al., 2017). A more rapid decline is expected for small glaciers with relatively small accumulation zones (Bosson et al., 2019; IPCC, 2019). Ice loss is the most visible facet of a more profound shift currently underway, affecting multiple components of arctic and alpine systems, from the cryosphere, hydrosphere and pedosphere to the biosphere. Among others, ice loss has vital consequences on the hydrological cycle (flooding/drought), wild and agricultural biodiversity, and human livelihoods (Hock et al., 2019; Huss et al., 2017).

In mountains, glaciers greatly influence downstream systems, through cold meltwater supply, substrate movement and environmental heterogeneity (Jacobsen & Dangles, 2017). Glacier extinction is expected to have both negative and positive consequences on biodiversity (Cauvy-Fraunié & Dangles, 2019). In particular, glacier loss threatens organisms developing on ice (e.g. microorganisms associated with cryoconites; Cauvy-Fraunié & Dangles, 2020), and those dependent on glacier meltwater, such as freshwater microorganisms, invertebrates and fishes (Vincent, 2010, Brighenti et al., 2019, but see Muhlfeld et al., 2020). In turn, recently deglacierized areas offer new colonizable habitats, particularly important for organisms whose lower altitudinal distribution is altered by thermophilization and competition with more competitive taxa (Cauvy-Fraunié et al., 2015; Zimmer et al., 2018).

Birds are prominent and charismatic representatives of mountain biodiversity, in particular in the tropical region (Monasterio & Vuilleumier, 1986), yet we know very little on the potential impacts of glacier retreat on avian communities. While bird richness tends to decrease with elevation (McCain, 2009), they are still abundant and diverse in high-elevation ecosystems in the tropical region (Fjeldså et al.,) and even show peaks of taxonomic and functional diversity at mid-to-high elevations (Altamirano et al., 2020). Birds have adapted their metabolism and behaviour to high-elevation stress related to flight cost, energetic stress and temporal and spatial variation in resource availability (Lague et al., 2017; Wolf & Gill, 1986). In the high tropical Andes, wetland and grassland habitats provide both food resources and stopover sites during bird migration (Fjeldså, 1985; Jacobsen & Dangles, 2017). On glaciers, birds feed on prey that are highly visible, hence easy to detect and catch. Moreover, once the bird dies, feathers and droppings may provide nutrients for ice-dwelling microorganisms (Rosvold, 2016). Birds also fulfil several roles as herbivores, pollinators, predators and dispersers of seeds and invertebrates (Jacobsen & Dangles, 2017). Their presence and activity is therefore crucial for maintaining key ecological functions and ecosystem services (e.g. provisioning and cultural) and reciprocally benefit from habitat type and vegetation heterogeneity interfacing with anthropogenic factors (Araneda et al., 2018).

The decrease in glacier cover and its consequences on water availability may have both direct and indirect effects on mountain birds. Direct effects may concern birds that, regularly or occasionally, nest directly on ice (e.g. the White-winged Diuca-Finch *Idiopsar speculifer* and the White-fronted Gound-Tyrant *Muscisaxicola albifrons*; Figure 1e), roost in crevasses or voids beneath the glacier, foraging on nearby cushion plants (e.g. the seedsnipe *Attagis gayi*) or feed on glacier invertebrates (Hardy et al., 2018; Hotaling et al., 2020). Indirect effects may concern bird assemblages through three main mechanisms: (a) change in habitat area (either an increase in glacier forefield terrestrial habitats or a reduction in wetlands, streams and lakes due to decrease in glacier runoff, Jacobsen & Dangles, 2017), (b) a reduction in habitat heterogeneity (micro-habitats with different characteristics, in particular aquatic ones, Quenta et al., 2016), and (b) a modification of habitat quality (e.g. productivity, temperature and humidity; Huss et al., 2017). The direction and intensity of those effects on bird assemblages would depend on species' life history and functional traits.

Here, we investigated the potential indirect effects of retreating glaciers on avian biodiversity in high-altitude wetlands in the Bolivian Andes (>4500 m). These ecosystems are ideal to look into the effects of changing habitat area, heterogeneity and quality associated with glacier retreat on biodiversity based on the spatial comparisons. First, being "wetlands in drylands," they form well-delimited habitat islands that allow building predictive models linking biological diversity and habitat area (species-area relationships; Anthelme et al., 2014; Rosvold, 2016). Second, the environmental heterogeneity, productivity and moisture of these wetlands are strongly coupled with glacier influence (Cooper et al., 2019; Dangles et al., 2017). It is therefore possible to infer future glacier retreat of these systems from contemporary spatial patterns in wetlands showing a gradient of glacier influence (i.e. space-for-time substitution, Blois et al., 2013). Third, a large number of bird species present on these wetlands are absent from the surrounding habitats and at lower elevation. Finally, these systems are of global conservation relevance as they support important populations of bird species, in particular during the dry season (Gibbons et al., 2016; Tellería et al., 2006). They also serve as stepping-stone ecosystems during the migration and provide connectivity between structurally similar habitats (Venero, 1987; Vuilleumier, 1970). In particular, the role of high-altitude wetlands as migration corridors increases as the quantity and quality of low-elevation riparian habitats decrease (Jacobsen & Dangles, 2017). The specific objectives of this study were to: (a) determine the relationship between habitat area and bird diversity using different metrics (species richness, evenness, functional and phylogenetic diversity) across a range of wetlands with different glacial influence; (b) assess the influence of environmental variables
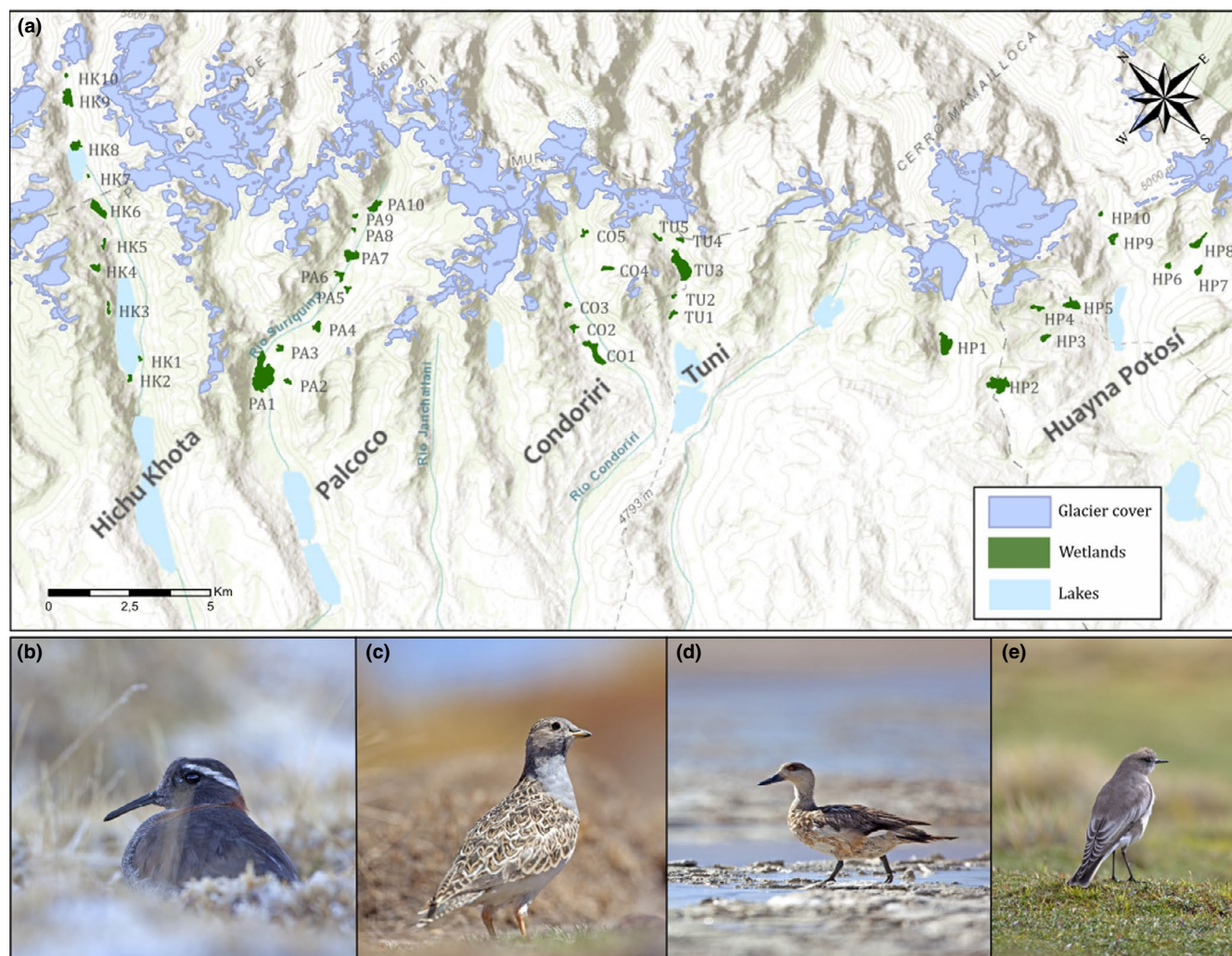
FIGURE 1 (a) Location map of the 40 wetlands studied in the Cordillera Real. Map base data from Esri, ArcGis 10.6 and the GIS User Community. Wetlands code correspond to the first letters to each valley name followed by a number. These habitats host an important avifauna diversity as (b) Diademed Sandpiper-Plover (*Phegornis mitchellii*), (c) Grey-Breasted Seedsnipe (*Thinocorus orbignyianus*), (d) Crested Duck (*Lophonetta specularioides*) and (e) White-Fronted Ground-Tyrant (*Muscisaxicola albifrons*). © Photos O.D

(e.g. elevation, glacier cover in catchment, productivity, heterogeneity) on bird richness at the wetland scale; and (c) determine specific bird assemblages associated with different wetland habitat quality in a context of glacier retreat.

2 | METHODS

2.1 | Study sites

The study area was located in the western side of the Cordillera Real of Bolivia (between 15°45′–16°45′S, and 67°40′–68°40′W, Figure 1a). This mountainous area lengthens over 130 km from south–southeast to north–northwest, with an approximate width of 15 ± 20 km. Several summits rise to over 5000 m a.s.l. and are dominated by relatively small glaciers (80% of glaciers <0.5 km², Dangles et al., 2017). Glaciers of the Cordillera Real represented an area of approx. 324 km² in 1975 but have lost about 48% of

their surface and 43% of their volume between 1975 and 2006 (Soruco et al., 2009, see also deglacierization maps in the study area: Zimmer et al., 2018 and Figure S1). During the last decades, glacier melting has been more intense in this region than outside the tropics (Rabatel et al., 2013) with a relative ice loss rate reaching 3%/year at low latitude between 2006 and 2016 (Zemp et al., 2019). Present and future climatic features in the study region have been described in details by Dangles et al. (2017). Briefly, annual mean temperature is around 5°C and incident solar radiation remains intense all year long due to low latitude. In contrast, seasonal variation in moisture and precipitation produces drier atmosphere conditions and cooler temperatures during the dry season (May–September). The October–December period presents transitional conditions of increasing humidity, followed by slightly warmer temperatures and higher precipitations and moisture during the wet season (December–March). Climatic features can be strongly influenced by the ENSO phenomenon (El Niño Southern Oscillation), which brings considerable variability to the seasonal

patterns as a function of elevation and latitude (Dangles et al., 2017; Rabatel et al., 2013).

High-altitude wetlands of the tropical Andes, locally named *bofedales*, can be described as heterogeneous waterscapes that enclose meadows, marshes, peatlands, ponds and streams perennial or temporary depending on precipitation patterns (Jacobsen & Dangles, 2017; Squeo et al., 2006). In the Andes, reported trends indicate an overall increase in wetlands cover, strongly correlated with precipitation trends (Dangles et al., 2017; Pauca-Tanco et al., 2020). Proportion of different sources of water is highly variable among wetlands as function of topography, size of the watershed, extent of the glacier, infiltration vs. surface circulation of ice runoff (see Cooper et al., 2019; Squeo et al., 2006). There are differences among seasons, as during the dry season up to 40% of the water production in the Tuni-Condoriri valley is of glacier origin (see Soruco et al., 2015). Like other alpine ecosystems, high Andean habitats generally have sparse vegetation cover, dominated by high-elevation adapted plants such as *Festuca rigescens*, *Anatherostipa hans-meyeri* and *Festuca dolichophylla*, along with various species of *Pycnophyllum* and *Deyeuxia* (Ruthsatz, 2012; Squeo et al., 2006). In contrast, the wetland vegetation is dense, mainly composed of cushion-like habitats of different species of *Juncaceae* such as *Oxychloe andina* and *Distichia muscoides*; Cyperaceae such as *Phylloscirpus deserticola*, *Zameioscirpus muticus* and Poaceae as *Deyeuxia spicigera* (Loza Herrera et al., 2015). Wetlands are scattered with ponds, varying in size, shape and depth (Jacobsen & Dangles, 2017). They sustain a high aquatic biodiversity (algae, macrophytes, macroinvertebrates, zooplankton and phytoplankton), with some taxa being highly sensitive to environmental changes and therefore potentially indicators of glacier changes (Quenta et al., 2016).

2.2 | Bird survey

We surveyed 40 wetlands in five valleys of the Cordillera Real: Hichu Khota, Palcoco, Huayna Potosí, Tuni and Condoriri (Figure 1a). We chose wetlands above 4500 m in order to exclude impacts from human activities such as villages, mining activities, overgrazing, water collection and artificial lakes. We selected wetlands across a wide range of areas (from 0.3 to 42.3 ha) and glacier influence (from 0 to 22% of glacier cover in the catchment) to estimate the indirect effects of glacier retreat through changes in habitat area and quality. All wetlands were separated by at least 500 m and therefore considered as independent units (Ralph, 1993). Bird census was carried out between October 2013 and July 2014 to encompass the wet, transitional and dry seasons. Bird richness and abundance were determined by the point count method (Bibby et al., 2000), with unlimited observation distance and three equidistant observation points and six temporal repetitions per wetland. Count duration was 10 min at each observation point, that is 30 min per wetland per visit. In view of the openness

of the habitat, this sampling effort allows to survey different area keeping a satisfactory detectability of species present (Hutto et al., 1986; Savard & Hooper, 1995; Wunderle, 1994). In total, we obtained 720 observation points over the 40 wetlands. We alternated the order of visit to cover a broad daytime range in each wetland and minimize potential bias resulting from daily variation in bird occurrence (Naoki et al., 2014).

2.3 | Environmental variables

We characterized wetlands using both field measurements and database compilations. First, we evaluated environmental features in the field by recording habitat types along 10 randomly oriented transects of 50-m long for small wetlands (<5 ha) and 20 transects for larger ones. Every 1 m in each transect, 21 categories were considered as representative of habitat diversity and recorded in a total of 27,000 points from 540 transects, corresponding to a sampling effort of 240 observer-hour (Naoki et al., 2014). We regrouped habitat types in 11 resuming categories as follows: *Distichia* cushion, *Oxychloe* cushion, *Phylloscirpus/Aciachne* cushion, *Pycnophyllum* cushion, forbs, graminoid peatland, bryophyte, marsh (marsh and macrophytes), water bodies and flowing water (see Table S1).

Second, area and perimeter of the 40 wetlands were extracted from 2013 PLEIADES images using ArcGis 10.6 (see Dangles et al., 2017). In addition, we considered the following environmental variables: (a) watershed area, calculated for each wetland with the hydrological tools of ArcGis 10.6 from the 30-Meter SRTM Elevation Model (DEM downloaded from srtm.csi.cgiar.org/srtmdata); (b) glacier cover in the catchment area (%GCC, from dry season LANDSAT images, see Dangles et al., 2017), as an index signifying the potential glacier's influence of on aquatic systems; (c) distance to the nearest lake, calculated in meters with the distance tool in ArcGis10.6; (d) productivity index, using the median normalized difference vegetation index (NDVI) as a proxy (Bonthoux et al., 2018; Paruelo et al., 1997) and calculated from Pleiades satellite images near infra-red and red bands, ranging from –1 to 1 (see Kraemer, 2014); (e) shape index (SI), a proxy of stability that quantifies irregularly shaped fragments of wetlands that would be more susceptible to changes (Dangles et al., 2017). SI was calculated by dividing the unit perimeter by that of an equal-sized circle $SI = P/2\sqrt{\pi A}$, P being the perimeter of each wetland and A the area; (f) wetland environmental heterogeneity, calculated as the Simpson diversity index (Lande, 1996; Yoshioka et al., 2017). Heterogeneity index was calculated on 11 reclassified groups of habitat types from the 21 original categories measured on the field transects (see Table S1). Ranging from 0 to 1, this index reflects the inverse probability of each habitat types to be present in the same wetland: the highest value meaning a higher diversity of habitats and thus a lower probability to come across the same habitat within a given wetland.

2.4 | Data analyses

2.4.1 | Bird taxonomic, phylogenetic and functional diversity

We calculated bird diversity as the total number of bird species per wetland and quantified the evenness using the probability of interspecific encounter (PIE, Hurlbert, 1971). Data were log-transformed to meet normality criteria. We assessed phylogenetic and functional diversity following the mean pairwise distance (MPD) approach from Swenson (2014) using the Picante R package (v1.8 Kembel et al., 2010). On one side, MPD is a measure of phylogenetic diversity based on the average of all distances connecting species together in a sample (Cadotte et al., 2012; Webb et al., 2002). For phylogenetic data, we used a subset of phylogenetic trees downloaded from bird-tree.org (Jetz et al., 2012). These trees were constructed from the wetlands species' total pool and pruned to include corresponding species present in each wetland. We calculated phylogenetic diversity (PD) as the mean pairwise distance (MPD) between the species of the consensus tree elaborated from 1000 phylogenetic trees with the Rphylip package version 0.1-23 (Felsenstein, 2013). On the other side, for functional diversity (FD), we assembled data of functional traits based on resource requirements (habitat), dietary composition, body size and migration from Stotz et al. (1996), Stotz et al. (2019), Jetz et al. (2014), Wilman et al. (2014) and del Hoyo et al. (2019). Foraging stratum and body weight were not part of the trait analysis as there is no significant vertical structure in the studied ecosystems and because weight incorporates variation in both size and fitness and may therefore be redundant with other traits (Gosler, 2004).

We calculated the dominant principal components of the functional distance matrix with the Gower distance measure (Gower, 1971) and performed a principal coordinates analysis (PCoA) to reduce dimensionality of functional diversity (Maire et al., 2015). We then performed the FD_{MPD} analysis on the subset of the PCoA as described on Swenson (2014) and obtained a FD_{MPD} value for each wetland. MPD represents a measure of functional diversity weighted by species relative abundance in the community (Laliberté & Legendre, 2010; Mouchet et al., 2010), that is the deviation of trait values from the centre of the functional space.

2.4.2 | Species–area relationship

Considering the classical biogeography study on the relationship between the number of species and the area of islands (Species-area Relationship, SAR; MacArthur & Wilson, 2016), we evaluated different model fits and slopes on the relationship between bird diversity and wetlands area. Using the sars R package (Matthews et al., 2019), we tested 20 different functions to linear and non-linear model fitting (linear, convex or sigmoid shapes) of the SAR and evaluated their performance through the second-order Akaike information criterion (AICc, Burnham & Anderson, 2002). Model validation was also based on tests of the normality and homoscedasticity of the residuals (see Table S2).

Additionally, we tested for differences in the SAR among models using analyses of covariance (ANCOVAs) on species richness as a function of season while keeping area as a covariate (Fattorini et al., 2017). Finally, we tested the small-island effect (SIE) using the sar_threshold function of the sars R package v1.3.5 (Matthews et al., 2019). This pattern describes SAR changing below a certain threshold area at which species richness varies independently of area (Lomolino & Weiser, 2001), and the pattern of species richness increasing at lesser rate in small than in larger islands (Dengler, 2010; Wang et al., 2018).

We also assessed diversity–area relationship patterns with three other dimensions of diversity: evenness (PIE), phylogenetic (PD_{MPD}) and functional (FD_{MPD}) (see metric calculation above). We used log-transformed values of each variable to fit the log-log linear relationship of the Poisson distribution and fitted linear regression models using generalized least squares (GLS) to determine whether wetland area predicted each diversity variable (significance threshold of 5%). Since the MPD measures of diversity are hardly comparable and their variance not independent from species richness (Swenson, 2014), we used a null model approach to determine whether observed patterns adjusted significantly differently than expected from a random distribution. For the null model, species composition was randomly reshuffled using an unconstrained phylogenetic swapping for PD_{MPD} and independent swap maintaining species occurrence frequency and shifting trait expressions in the randomized community matrix for FD_{MPD} (Kembel et al., 2010). We compared observed values in each wetland to its respective null distribution values to determine both phylogenetic and functional diversity–area relationships. Additionally, we tested for competitive or trait-based processes structuring species assembly by calculating the standardized effect sizes (SES) as the difference between the observed and expected values divided by the standard deviation of null distributions (Swenson, 2014). For PD_{MPD} and FD_{MPD}, SES and slope estimates can be used as proxy to qualify community composition. Communities are considered as overdispersed when the observed slope is significantly lower than the mean slopes from the null model and the SES score values higher than 1.96, implying competitive exclusion. Inversely, communities are considered as underdispersed when the observed slopes is greater than the mean slopes from the null model and SES score values lower than −1.96, suggesting trait-based assembly (Petchey et al., 2007; Ross et al., 2019). SES also allows evaluating the relative strength of the assembly processes (i.e. the effect of area on diversity), with the significance threshold value fixed to 1.96 corresponding to the 95% confidence interval for the null distribution (Veech, 2012). Thus, in the case of phylogenetic assembly, species might occur with closely related species more than expect by chance (Webb 2000). Likewise, non-random functional distribution indicates assembly processes like environmental filtering or competitive exclusion (Concepción et al., 2017).

2.4.3 | Generalized additive models

We used generalized additive models (GAMs) to explore the links between bird diversity and the environmental factors associated with

wetlands (Hastie & Tibshirani, 1987). These models allow considering environmental factors through a range of nonparametric trends of increasing complexity, leading to understand relationships patterns between predictors and response variables (Wood, 2015). We ran the GAMs with the gam function of the mgcv R package (Wood & Wood, 2015), using species richness as a response variable and environmental data as predictors, including the following: elevation, nearest distance to lakes, glacier cover (%GCC), productivity, heterogeneity and shape index (see index description above and Table S5). After controlling for multicollinearity among predictors (concurvity function; Wood 2017), we set different GAMs under Poisson distribution and log link functions with four variables: elevation, glacier cover, heterogeneity and productivity. After evaluating correlation coefficients between predictor variables using pairwise diagnostic tools, two variables (shape index and nearest distance to lakes) were excluded for having marginal contribution (i.e. variables not bringing additional significant information to the model).

2.4.4 | Canonical correspondence analysis

We assessed the response of bird species and guilds (see below) to changes in specific habitat variables (21 habitats within wetlands) by performing a canonical correspondence analysis (CCA) (Ter Braak, 1986). We first transformed bird abundances into presence/absence data to better capture the influence of environmental predictors on species composition among and within wetlands (Cushman & McGarigal, 2004). We defined seven groups of birds (guilds) based on their use of environmental resources, that is "aquatic" and "terrestrial" and their feeding guilds (see Table S4). We then used the cca function of the Vegan package (Oksanen et al., 2019) to pair the matrix of presence/absence of bird species with six environmental variables (area, glacier cover, elevation, productivity, heterogeneity, distance to lake), then with the 11 habitats type matrix of each wetland. We tested CCA significance with an ANOVA. For the habitat matrix, we included the 11 habitat types regrouping the 21 coverage recorded on field transects (see above, *Environmental variables*).

3 | RESULTS

Across the 40 study wetlands, we recorded a total of 2858 individuals from 41 species, representing 22 families of birds (Table S4). Species richness ranged from 3 to 21 per wetland. Overall abundances varied among wetlands between 10 and 221 individuals, the most abundant species being the passerine species *Idiopsar speculifer* and *Muscisaxicola albifrons* (Figure 1e). Those with the lowest abundances were *Nothoprocta ornata* and *Phegornis mitchellii* (Figure 1b), the latter classified as near threatened in the IUCN red list (BirdLife International, 2016). The most common feeding guilds were invertebrate feeders for both aquatic and non-aquatic species.

Among the SAR models fitted to our data (see Tables S2.a and S2.b), the linear function better described the relationship between species richness and wetland area (slope = 0.18, intercept = 0.17, p-value = .002, Figure 2a). Species evenness (PIE index) also showed a positive linear relationship with wetland area (slope = 0.04, intercept = −0.69, p-value = .003; Figure 2b). The results of the linear models on the phylogenetic and functional diversity mean pairwise distances (MPD) showed a stronger relationship with wetland area for the functional diversity (FD$_{MPD}$ slope = 0.12, intercept = −1.32, p-value = .0001; Figure 2c) than for the phylogenetic diversity (PD$_{MPD}$ slope = 0.07, intercept = −5.73, p-value = .001; Figure 2d). SES of phylogenetic diversity tended barely to underdispersion from the null model (PD$_{MPD}$ SES mean = −0.21), while SES of functional diversity approached underdispersed and converging on null distribution (FD$_{MPD}$ SES mean = −1.28). As seasonality may both affect both wetland characteristics and bird communities, we assessed its effect on species richness and SAR. After adjusting for area as a covariate, species richness was not significantly different among sampling seasons ($F(2.113) = 0.929$, p-value = .398; see Figure S2a,b). Interestingly, SAR had a significantly higher slope value when only aquatic bird species were considered (slope = 0.32, intercept = −2.68, p-value = .002; see Figure S2c), while SAR for terrestrial species became non-significant (slope = 0.09, intercept = 0.83, p-value = .1). For the small-island effect, there was no conclusive difference in breakpoint regression slope values (see Figure S3 and Table S3).

Among the four environmental variables considered, GAMs showed significant non-linear relationship between species richness and glacier cover and elevation (Figure 3; Table 1). The first model, built with one parametric term, productivity and three smooth terms, heterogeneity, elevation and glacier cover, explained 60% of the variance (R-sq.(adj) = 0.56, p-value < .05, AICc = 204.08). However, the second model including the variables productivity (p-value < .01, Figure 3a), glacier cover (p-value .09, Figure 3b) and elevation (p-value < .01, Figure 3c) had lower AICc, still explaining 59.8% of the variance (R-sq.(adj) = 0.57, p-value < .05, AICc = 201.17). For this model, productivity showed scattered data, glacier cover displayed a unimodal function form with bird richness, and elevation exhibited a broadly monotonic negative response (Figure 3b,c).

A preliminary CCA aimed to explore global patterns influencing bird communities, while a second CCA (Figure 4) further explored differences within habitat types. The first CCA with environmental factors explained 23% of the total inertia of bird communities, with the most influential factors being elevation, area and productivity (p = .001; see Figure S6). The second CCA with wetland habitat types explained 37% of the total inertia in bird communities across wetlands (p < .001; Figure 4). In this CCA, the first axis (eigenvalue 0.21) reflected a gradient of habitat productivity from graminoids to peat. The second axis (eigenvalue 0.17) was mainly related to a humidity gradient, from water habitats and humid cushions to drier grasslands and graminoid covers. Overall, our CCA revealed that the high Andean bird community was distributed among three habitat types: bog (upper-left part, dominated by cushions and peat), aquatic (upper right part, aquatic-dominated coverages) and drier puna (bottom part, dominated by drier cushions, forbs and gramineae); the most productive plant communities being observed in
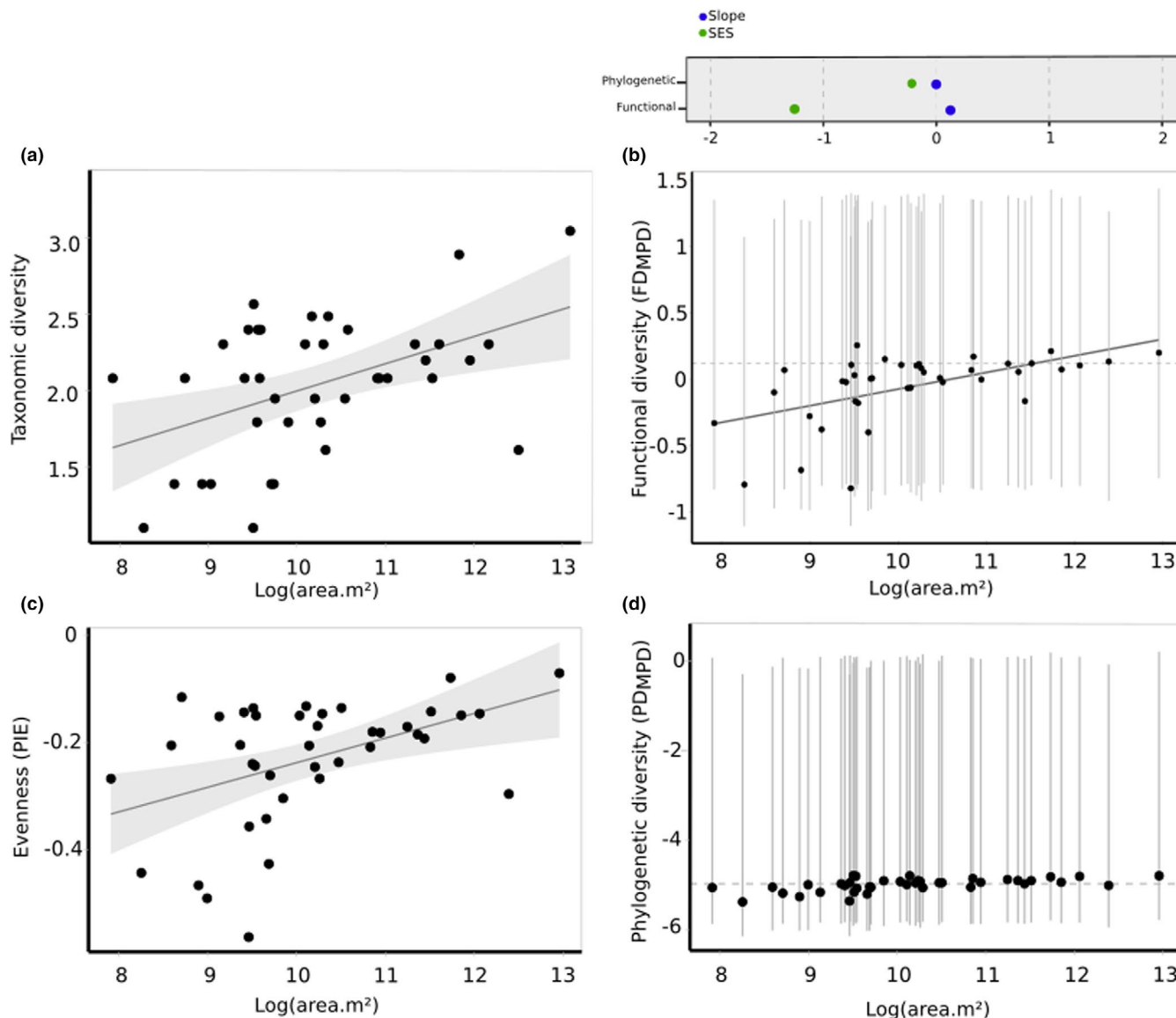
FIGURE 2 Diversity–area relationship models for four diversity components. (a) Taxonomic diversity (S). (b) Evenness index (PIE). (c) Functional diversity (FD_{MPD}). (d) Phylogenetic diversity (PD_{MPD}). Dark points are the observed diversity values for each wetland and grey bands correspond to the 95% confidence intervals of the models and grey vertical lines the confidence intervals of PD and FD null distributions. For c and d, grey dashed lines represent the mean value from the null distribution model. Inset plot represents the SES values of PD and FD_{MPD} and the slope of the diversity–area relationship relative to null distributions

the largest bofedales at lower elevations. The CCA further suggests that changes in habitat productivity (first axis) and water availability (from dry terrestrial habitats to wetlands to lakes, second axis)—as it is expected with glacier retreat—would have marginal consequences for bird species using a wide array of habitats in the Andean highlands as scrub, grasslands or lower forest edge (many species were distributed around the centre of the biplot). However, certain species will be more affected by the loss of aquatic habitats as glaciers retreat, like the Diademed Sandpiper-Plover (*P. mitchellii*, Figure 1b) and the South American Crested Duck (*Lophonetta specularioides*, Figure 1d), both related to water-dominated habitats (top-right part of the biplot). Contrastingly, many other *species* as

Cinclodes albiventris did not seem affected by wetland habitat quality as they were positioned around the central part of the CCA. Lastly, other relatively common bird species (e.g. *Geospizopsis unicolor* and *Asthenes modesta*) were associated with habitats dominated by drier grasslands (bottom part of the biplot).

4 | DISCUSSION

Following the objectives of our study (see introduction), we found (a) strong relationship between wetlands area and species richness, evenness and functional diversity, (b) glacier cover, productivity and
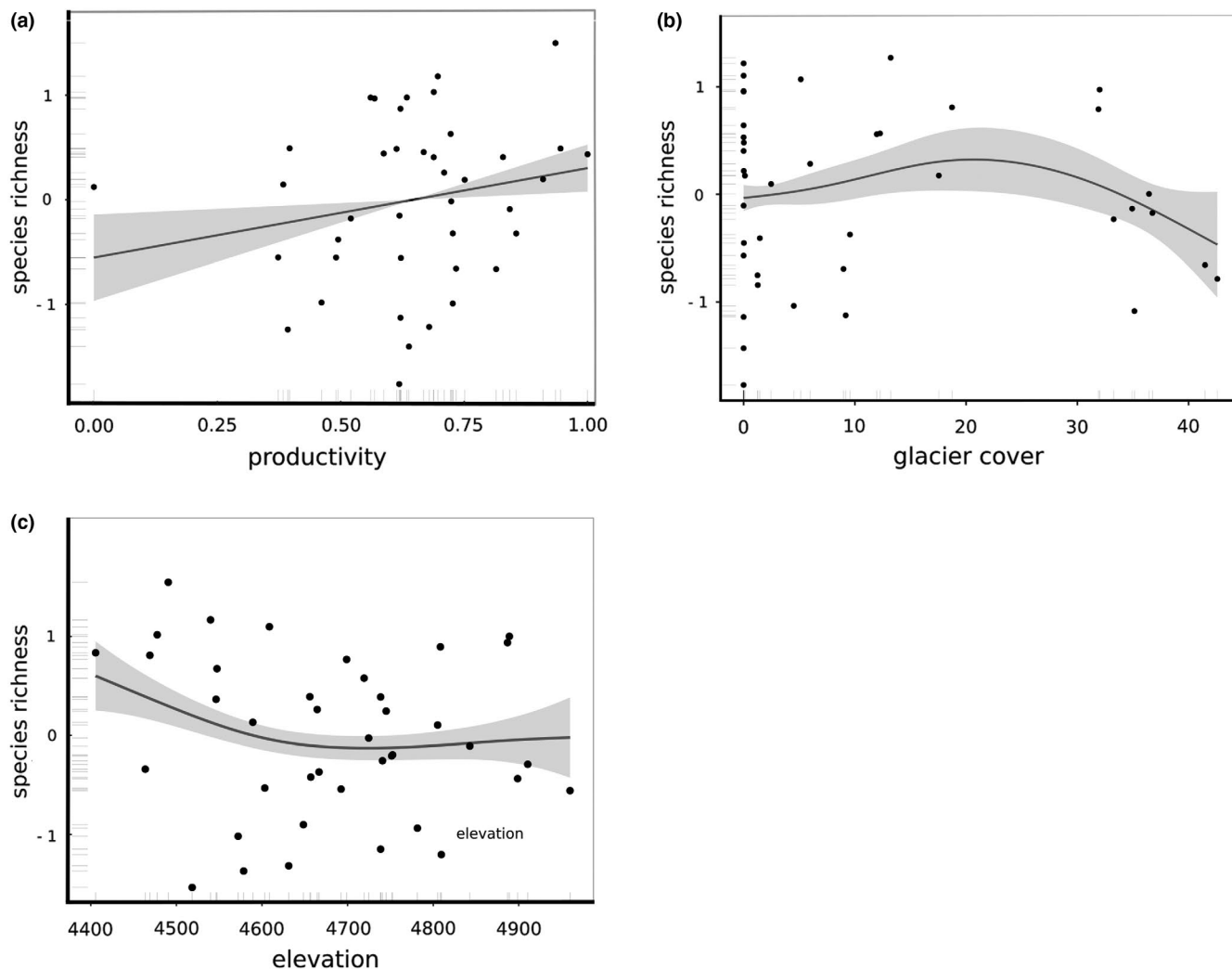
FIGURE 3 Generalized additive model (GAM) of bird richness vs. environmental parameters in high Andean wetlands. For each variable grey points are the observed values, dark lines show the fitted GAM model and grey shaded areas represent the 95% confidence intervals around the response curve. Y-axis is scaled for each predictor units on the model, indicating the smoothing term for: (a) s(productivity, 1), (b) s(glacier cover, 2.4), (c) s(elevation, 2.4)

elevation had a non-linear influence on bird richness; and (c) at a wetland scale, we found bird assemblages shaped by environmental gradients of humidity and productivity from wetter to drier habitats. Hereafter, these results are discussed in light of the relationship between wetland area and bird communities in melting Andes and the extent and quality of habitats. Last, we discuss the implications of our study in terms of bird conservation in the region.

4.1 | Wetland area and bird communities in melting Andes

Building models depicting species–area relationship (SAR) is a key preliminary step to assess the potential effect of wetland area changes on bird communities. In the Bolivian Andes, an increase in high-elevation wetland surfaces over the last 30 years has coincided with an increase in water availability due to glacier melting rates (Dangles et al., 2017). This observed positive trend in wetland cover

is likely to be reversed in a near future as the current increase in glacier runoff is expected to slow until it reaches its maximum and then start a pronounced decline diminishing glacier influence on outflows (Baraer et al., 2012; Huss & Hock, 2018). Wetland area will also depend on future trends in precipitations, which are highly uncertain in the tropical Andes (Vuille et al., 2008, also see Jacobsen & Dangles, 2017). While waterbirds may benefit glacier melting and associated increase in wetland area, annual glacial runoff is expected to decrease after a critical threshold of reduction in ice volume (Baraer et al., 2012; Rabatel et al., 2013). This would induce an increase in low-flow period frequency and intensity followed by continuous low flows until the complete loss of glacier outflow when the glacier disappears. In this case, the future of waterbirds in bofedales will tightly associate with precipitation patterns.

Our study revealed that wetland area is a good predictor of species richness, at a rate of 0.18 species/m². This value falls below the range of values of 0.2–0.4 most commonly documented in SAR literature (Triantis et al., 2012), probably because habitat islands are

TABLE 1 Summary of four fitted generalized additive models (GAMs) from the diversity–environment relationship analysis

Model	Parameters	Deviance explained	AICc	mgcv (RemL)	p-Value	edf (k)
Model 1 Sp.richness ~	**All var**	60%	204.0897	110.65	3.91e−07***	
Family: Poisson	Productivity				.00764**	
Link fun: log	s(glacier cover)				.11393	2.39 (4)
	s(heterogeneity)				.54258	1.00 (9)
1 parametric term, 3 smooth terms	s(elevation)				.00665**	2.449 (9)
Model 2 Sp.richness ~	**Prod. + glac. c. + elev.**	59.8%	201.1708	102.24	<2e−16***	
Family: Poisson	s(productivity)				.00844**	1.00 (9)
Link fun: log	s(glacier cover)				.09762·	2.49 (4)
3 smooth terms	s(elevation)				.00568**	2.42 (9)
Model 3 Sp.richness ~	**Prod. + het. + glac.**	47.5%	206.8046	105.18	<2e−16***	
Family: Poisson	s(productivity)				.000216***	2.63 (9)
Link fun: log	s(heterogeneity)				.453315	1.00 (9)
3 smooth term	s(glacier cover)				.035324*	2.18 (4)
Model 4 Sp.richness ~	**heterogeneity**	24.5%	214.8838	109.2	.0368*	3.62 (6)
Family: Poisson	s(heterogeneity)					
Link fun: log						

Note: Per cent deviance explained refers to the whole model scores, the *p*-value is indicated for each descriptor and k refers to the basis dimension of each parameter. The models tested species richness as response for the follow predictor variables: glacier cover (percentage of glacier in the catchment area), elevation (m.a.s.l.), productivity (NDVI index) and heterogeneity (heterogeneity index).

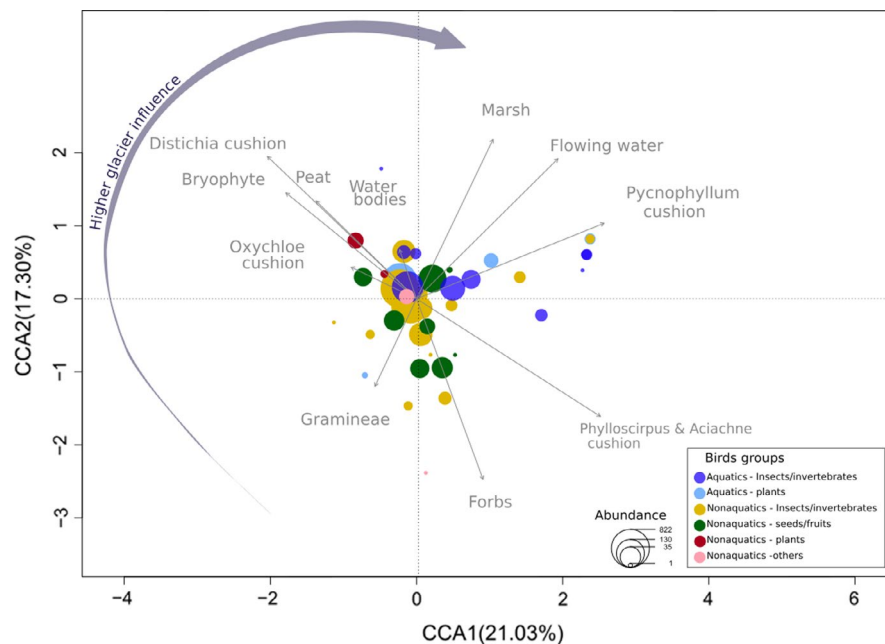Bold text indicates variables included in each model

FIGURE 4 Canonical correspondence analysis (CCA). The biplot displays the ordination of Andean wetlands bird species (points) along the first two canonical axis and their correlation with local habitat variables (arrows). Arrows' direction and length show the degree of correlation between bird's species and habitat types. Point size and colour reflect species total abundances on log(1+x) scale and birds' guilds, respectively. Feeding groups are listed in Supporting Information (Table S4). First axis present habitat productivity gradient and second axis water availability gradient. The blue arrow represents the glacier loss gradient. Decrease in water availability display changes in vegetation, with partial drying, more compact soils and less water storage capacity of *Phylloscirpus* and *Aciachne* cushions and their associated plants. Changes in wetland vegetation affects diversity indirectly through changes in dominant species and resource availability

less isolated compared to oceanic islands (Matthews et al., 2016). It was also lower compared to previous studies on birds in the northern Andes páramo (0.28; Vuilleumier, 1970) and Argentinian Sierras Pampanas (0.36; Nores, 1995). These SAR concern different spatial scales (within mountain-top habitats) and ecological realities (viable populations, habitat selection), which implies that z values can be expected to vary greatly. These lower values may also reflect the overall low species richness in this part of the Andes, compared to other elevations (Araneda et al., 2018). SAR can also be influenced by the taxonomic group (Triantis et al., 2012, Sólymos & Lele 2012), with different responses to SAR between specialist and generalist species (Lehikoinen et al., 2019; Matthews et al., 2016). Thus, our results suggest that wetland area reduction resulting from glacier retreat would have higher consequences for the conservation of aquatic birds, as reflected by its higher z value (0.32) (see Figure S2). Despite slight differences among fitted SAR models, the log-log linear parameters are more easily interpretable (Rosenzweig 1995) and can help potential subsequent comparisons with other environmental contexts and taxonomic groups on regional or global scales. Last, SAR can also be influenced by the scale of the area parameter, notably on smaller islands deviating from the overall pattern (SIE; Lomolino, 2000). However, we found no conclusive evidence of such effect for the studied wetlands (see Figure S3).

Standardized effect size (SES) and slope values on FD and PD MPD analyses suggest that bird communities of high Andean wetlands were not phylogenetically different from randomly assembled communities nor that functional assembly was non-random, however suggesting a trend towards trait-driven arrangement. The scaling of functional diversity with area might reflect different assembly processes that are expected to occur at different spatial scales (Concepción et al., 2017). As differences in food preferences and in use of habitat space may reduce competition and permit coexistence (Jacobsen & Dangles, 2017), competition among ecologically similar species might involve stronger selection pressure in smaller wetlands because of lower niche availability within wetlands (Si et al., 2016; Zhang et al., 2020). This may affect range-restricted species as those restricted to glacier and periglacier margins (e.g. the White-winged Glacier Finch, *Idiopsar speculifer*). At a larger scale, increasing proportions of certain traits could lead to amplify the homogenization of high Andean bird communities (increasing levels of functional redundancy; Altamirano et al., 2020; Mouillot et al., 2013; Petchey et al., 2007). Thus, rising abundance of species related to puna gramineae habitat and feeding on seeds (e.g. the Sierra Finches *Geospizopsis unicolor* and *G. plebejus*) might indicate the progression of drier habitats and loosing of typical wetland conditions. When related to glacier retreat, this situation suggests that ongoing changes in functional diversity might be part of the environmental filtering on some specific traits such as those related to high glacier influenced environments (e.g. aquatic plants and invertebrate-feeding species or ice-breeding). This calls attention to the importance of ecosystem resilience assured by functional diversity adjusting shared similar functions among species in response to environmental change

and hence buffer ecosystem function diminution (Concepción et al., 2017).

4.2 | Extent and quality of habitats

While area appears to be a key driver of bird assemblages in high-altitude wetlands, other environmental variables may come into play. In particular, environmental factors related to temperature and system stability (e.g. water provision by the glacier) may influence species composition through resource constraints and habitat complexity (McCain, 2009; Worm & Tittensor, 2018; Zhang et al., 2020). NDVI has been long used as proxy of productivity of Andean wetlands as it is sensitive to the greenness of photosynthetically active biomass (Anderson et al., 2021; Chávez et al., 2019; Moreau et al., 2003). However, these satellite image analyses do not allow quantifying wetland value as direct feeding habitat for waterbirds. Thus, further investigation might lead to generate better indicators for aquatic birds feeding exclusively water organisms. Other factors may also influence bird community composition, such as relationship between productivity and plant species as glacial retreat may indirectly affect plant diversity through changes in dominant species (Loza Herrera et al., 2015). Our results indicate that bird diversity was higher at intermediate levels of glacier influence (Figure 3), in line with similar trends recorded in previous studies on several freshwater taxa in the Andes (Cauvy-Frauinié et al., 2014; Quenta et al., 2016). Our GAM model also suggests interactive mechanisms between heterogeneity, glacier cover and elevation variables. This is consistent with the glacier-heterogeneity-biodiversity paradigm (Jacobsen et al., 2012), where glaciers drive indirect effects on environmental heterogeneity through changes in abiotic and biotic features and community turn over. In aquatic systems for example, local and regional diversity can be influenced by glacier retreat along a gradient from environmental conditions restricted to a few adapted species, to lower or deglacierized environmental conditions (Cauvy-Frauinié et al., 2015; Quenta et al., 2016). Likewise, we found higher bird richness in wetlands with intermediate environmental heterogeneity levels (see Figures S4 and S5), suggesting that species richness might increase with increasing heterogeneity as species coexistence is favoured by space availability and resource variety (de Souza-Júnior et al., 2014). As proposed by the area–heterogeneity trade-off hypothesis (Allouche et al., 2012), species may be affected differently according to their niche width as higher heterogeneity of habitats involves competitive dynamics under limiting resource conditions (e.g. the Crested Duck *Lophonetta specularioides* or the Andean Goose *Oressochen melanopterus*, found in large water bodies and dislodged from smaller ponds and the Grey-Breasted Seedsnipe *Thinocorus orbignyianus*, Figure 1c, nesting in grasslands near water). In this sense, it is likely that harsh environmental conditions in high-elevation ecosystems drive stronger environmental filtering on species with narrower niche as heterogeneity could increase the likelihood of

stochastic extinctions, as previously demonstrated for plants of the Cordillera Real (Raevel et al., 2018).

4.3 | Conservation implications in melting Bolivian Andes

Bird survey in high-altitude wetlands might be an initial step for long-term ecosystem monitoring under climate change context. We hypothesized that glacier retreat may affect bird assemblages through changes in wetland area and habitat quality. Larger wetlands showed greater number of individual bird species, although with different occurrences (see Figure S7). Within wetlands, some habitats such as ponds or cushions (e.g. *Distichia muscoides)* may contribute more to total bird diversity than other habitats (Josens et al., 2017; Servat et al., 2018). We indeed found that local habitat complexity (i.e. forbs, shrubland or aquatic habitats) explains the composition of bird communities through a gradient of productivity and humidity (Figure 4), two features that may be affected by glacier retreat. Bird species from different feeding guilds would colonize wetlands having different vegetation stages (i.e. wetter/drier cushions or vegetation), but birds feeding on aquatic organisms (invertebrates, plants and fishes) would remain only in wetlands where ponds are available. This may have important implications for the conservation of bird species loosing substantial portions of their core habitat, or with reported decreasing population (IUCN, 2016), such as the Lesser Yellowlegs (*Tringa flavipes*), or the Diademed Sandpiper-Plover (*P. mitchellii*, Figure 1b) whose total number of mature individuals is estimated between 1500 and 7000 (https://www.iucnredlist.org/species/22693931/93430667). Furthermore, facing an increasing dominance of birds of the drier habitats, rare or low-dispersion species might deeply affect wetland functioning with potential cascading effects at higher and lower trophic levels (Franzén et al., 2012; Holt, 2010). Under this scenario, the interplay between habitat productivity (as a response to increasing temperature) and humidity (dependent on future precipitation patterns) will be key to predict the fate of bird communities in high Andean wetlands with decreasing runoff from glaciers. In this context, it is important to document ongoing changes in alpine plant communities (such as tussock and cushion plants; Meneses et al., 2014; Zimmer et al., 2018) as vegetation provides fundamental feeding resources for many birds, both in terrestrial and in aquatic habitats. Andean bogs also increase habitat suitability for specific wetland bird species (aquatic invertebrates and plants feeding gilds) and might help several species to resist extinction (Gibbons et al., 2016; Tellería et al., 2006). All this advocates for a more integrating and across-taxa analysis of the ecological consequences of glacier retreat.

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BIOSKETCH

The authors are part of a French-Bolivian research team with various expertise (ornithology, botany, entomology, glaciology, hydrology, geography, statistics) that has been working for the last eight years on biodiversity and conservation issues in high-altitude wetlands of the tropical Andes.

Author contributions: KN, RIM, FA and OD conceived the ideas and monitoring design; KN, CML MIG, RIM, FA, and OD collected data; TC, QS, KN, SC-F organized and analysed data; TC and OD led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

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