The Andean Ibis (*Theristicus branickii*) in South America: potential distribution, presence in protected areas and anthropic threats

Nivia Luzuriaga-Neira[1], Keenan Ennis[2], Michaël A.J. Moens[3], Jose Leon[3], Nathaly Reyes[1], Agusto Luzuriaga-Neira[4,5], Jaime R. Rau[6] and Roxana Rojas-VeraPinto[7]

[1] Unidad de Estudios de la Vida Silvestre-Facultad de Medicina Veterinaria, Universidad Central del Ecuador, Quito, Pichincha, Ecuador
[2] School of Natural Resources, Knoxville College, Knoxville, TN, United States of America
[3] Fundación de Conservación Jocotoco, Quito, Pichincha, Ecuador
[4] Department of Ornithology, American Museum of Natural History, New York, NY, United States of America
[5] Biology Department, University of Nevada - Reno, Reno, NV, United States of America
[6] Laboratorio de Ecología, Departamento de Ciencias Biológicas & Biodiversidad, Universidad de los Lagos, Osorno, Chile
[7] Proyecto Isnachi, La Libertad, Lima, Peru

ABSTRACT

The avifauna of South America is one of the most widely studied groups of vertebrates. However, certain species, such as the Andean Ibis (*Theristicus branickii*), have received limited attention regarding their ecological patterns, biology, current distribution, and environmental requirements. This study analyzed observation data from the Global Biodiversity Information Facility (GBIF) on the Andean Ibis in four countries to identify and understand critical variables that determine the species' presence, assess the proportion of its habitat within protected areas and identify possible threats to the species. Additionally, this study considered environmental and ecological variables to model ecological niches using the maximum entropy approach in MaxEnt to map the suitable habitat of the species. The findings revealed the extent of suitable Andean Ibis habitats in Ecuador, Peru, Bolivia and Chile. The variables that most determined the presence of the species were: altitude (36.57%), distance to lakes (23.29%) and ecological isothermality (13.34%). The distribution area of the Andean Ibis totaled 300,095.00 km^2, spanning both sides of the Andean mountains range. Human activities have left a significant impact on the Andean Ibis habitat, with 48% of this area impacted by the human footprint and only 10% of the territory falling within protected areas designated by the respective countries. The results of this study show that the Andean Ibis presents characteristics of a specialist species due to its adaptation to the climate conditions of the plateau and highlands, including low temperatures, herbaceous vegetation and the presence of water bodies. The species is distributed in disconnected Andean landscape areas, whose functionality could be compromised by increased human activities. Complementary studies will be necessary to understand the ecological role and effectiveness of protected areas for conserving the species.

INTRODUCTION

The tropical Andes avifauna is a biological group that has been extensively studied (*Vuilleumier, 1969*; *Vuilleumier, 1984*; *Vuilleumier & Simberloff, 1980*; *Fjeldså, 1988*; *Valencia & Franke, 1989*), especially their ability to adaptat and evolve across the bio-regions they inhabit (*Hazzi et al., 2018*). In high mountain ecosystems above 2,500 m a.s.l. (*Sevillano-Ríos, Rodewald & Morales, 2020*), birds have evolved adaptive strategies to cope with extreme environmental conditions (*DuBay & Witt, 2014*; *Sevillano-Ríos, Rodewald & Morales, 2020*; *Anthelme & Peyre, 2020*). As a result, this taxa has a high rate of endemism and habitat specialization (*Long, Crosby & Stattersfield, 1996*). Although high elevation range Andean birds have been extensively studied, there is limited ecological information for some taxons, especially in relation to potential human threats and the effectiveness of protected areas in conserving their habitats (*Bax & Francesconi, 2019*).

High mountain ecosystems of the tropical Andes are highly fragile and susceptible to the adverse effects of climate change and land use alterations (*Anthelme & Peyre, 2020*), which negatively impact the distribution patterns and abundance of functional groups of birds (*Cardenas et al., 2022*), plants (*Carilla et al., 2023*) and insects (*Moret et al., 2016*; *Cuesta et al., 2020*). These changes also disrupt primary production (*Gaglio et al., 2017*; *Rey-Romero, Domínguez & Oviedo-Ocaña, 2022*), thereby influencing the survival of some bird species that are directly dependent on resources such as invertebrates (*Tirozzi et al., 2021*). Climate changes pose a particular threat to bird species with small populations that are restricted to high-altitude areas (*Naveda-Rodríguez et al., 2016*; *Restrepo-Cardona et al., 2022*).

The Andean Ibis (*Theristicus branickii*) is a bird species present in high Andean habitats such as the paramo and the high Andean grassland ecosystems above 3,000 m a.s.l. (*Restall, Rodner & Lentino, 2007*; *Schulenberg et al., 2007*; *Collar & Bird, 2011*). The estimated habitat of the Andean Ibis spans approximately 1,080,000 km² (2023) from northern Chile, Bolivia, Peru and Ecuador (*Fjeldså & Krabbe, 1990*; *Clements, 2019*). The Andean Ibis is known to have particular adaptation and survival strategies (*Bakkeren et al., 2020*; *Dawson et al., 2020*) with specific habitat requirements such as proximity to wetlands in high-humidity areas for feeding, and water bodies adjacent to rocky sites for nesting (*Vizcarra, 2009*; *Collar & Bird, 2011*; *Alcocer, 2014*; *West, 2014*; *Ennis et al., 2019*; *Naveda-Rodríguez et al., 2020*; *Luzuriaga-Neira et al., 2021*; *Muñoz et al., 2021*). The species is categorized as Near Threatened (NT) by the International Union for Conservation of Nature and there is evidence of a declining population trend (*BirdLife International, 2017*). The Andean Ibis was also considered a subspecies of *Theristicus melanopis* until 2019 (*Remsen Jr et al., 2023*), further contributing to the limited knowledge about its ecology, biology, current distribution and environmental requirements.

Ecological niche models are one of the most widely employed methods in ecological studies for identifying the relationship between habitat presence/availability and environmental variables that influence species presence (*Araújo et al., 2019*; *Zurell et al.,*

2020). These models facilitate the construction of geographic distribution maps, providing current and future projections (*Soberon, 2011*). Various statistical methods can be applied to develop ecological models using presence, absence, or pseudo-absence records. The information derived from the analysis and the projection of localities or habitat suitability onto maps plays a crucial role in informing stakeholder decisions and conservation efforts.

This study aims to develop ecological niche models of the Andean Ibis throughout its identified geographic range and cover the following: (1) identification of the environmental variables which significantly influence the presence of the species; (2) generation of potential distribution maps based on the developed model; and (3) identification of distribution overlap with protected areas and the existing human threats impacting the potential species distribution. The results of this study enhance the understanding of the ecological requirements of the Andean Ibis and its current species distribution. This study also identifies potential protection areas and human threats to the Andean Ibis that can aid conservation initiatives and decision-making processes.

MATERIAL AND METHODS

Study area

The scope of the study was restricted to the countries where the presence of the Andean Ibis has been reported (*Schulenberg et al., 2007*; *BirdLife International, 2017*; *Freile & Restall, 2018*; *Clements, 2019*) and the Andean region where previous investigations on the ecology and biology of the species have been conducted (*Vizcarra, 2009*; *Collar & Bird, 2011*; *Alcocer, 2014*; *West, 2014*; *Ennis et al., 2019*; *Naveda-Rodríguez et al., 2020*; *Luzuriaga-Neira et al., 2021*; *Muñoz et al., 2021*; see Table S1).

Occurrences and explanatory variables

Presence records of *T. melanopis branickii* and *T. branickii* from 2003 to 2020 were obtained from the Global Biodiversity Information Facility (GBIF; https://gbif.org; *GBIF, 2019*), a platform that collects e-Bird registration data (https://ebird.org/home). Unreliable records, including those from a dubious source, those with sampling bias and duplicate records, were eliminated from the database. To mitigate potential spatial biases that could impact the models (*Boria et al., 2014*), a spatial filter was applied using the SDM toolbox in ArcMap (*Brown, Bennett & French, 2017*). This filtering procedure eliminated occurrences within less than 10 km from their nearest neighbors. Finally, the database was randomly divided into two groups: 70% of the data was separated for model development, while the remaining 30% was reserved for model evaluation (*Huberty, 1996*). A total of 26 environmental variables were identified that represented the ecological requirements of the species (Table 1). The topographic characteristics such as altitude, slope and roughness index were obtained from digital elevation models at 30 m spatial resolution (*Jarvis et al., 2008*). The hydrographic characteristics were obtained from the HydroSHEDS project (*Lehner & Grill, 2013*; *Messager et al., 2016*) at ~500 m resolution, including the Euclidean distance of lakes (dist_lakes), presence of lakes (pres_lakes) and presence of rivers (pres_river) variables. The bioclimatic conditions were provided by Wordclim version 2.1 and represented 19 variables with a resolution of 1 km (*Fick & Hijmans, 2017*). Vegetation

Table 1 Environmental and climate variables used to the distribution models for Andean ibis (*Theristicus branickii*) in South America.

Enviromental variable	Description	Source
altitude	Mean elevation: meters above the sea level (m a s l.)	SGIAR-CSI SRTM 90m (*Jarvis et al., 2008*)
slope	Average slope in percentage	SGIAR-CSI SRTM 90m (*Jarvis et al., 2008*)
roughness	Roughness index. Field variability	SGIAR-CSI SRTM 90m (*Jarvis et al., 2008*)
dist_lakes	Lakes distance in meters using Euclidean distance	Hydrolake (*Messager et al., 2016*)
pres_lakes	Lakes presence	Hydrolake (*Messager et al., 2016*)
pres_river	River presence	Hydrorivers (*Lehner & Grill, 2013*)
NDVI	Normalized Difference Vegetation Index. Average values 2000-2019	MODIS (*Didan, 2015*)
BIO1	Annual Mean Temperature in °C	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp)) in °C	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO3	Isothermality (BIO2/BIO7) (×100) in °C	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO4	Temperature Seasonality in °C (standard deviation ×100)	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO5	Max Temperature of Warmest Month in °C	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO6	Min Temperature of Coldest Month in °C	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO7	Temperature Annual Range (BIO5-BIO6) in °C	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO8	Mean Temperature of Wettest Quarter in °C	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO9	Mean Temperature of Driest Quarter in °C	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO10	Mean Temperature of Warmest Quarter in °C	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO11	Mean Temperature of Coldest Quarter in °C	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO12	Annual Precipitation in mm	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO13	Precipitation of Wettest Month in mm	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO14	Precipitation of Driest Month in mm	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO15	Precipitation Seasonality (Coefficient of Variation) in mm	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO16	Precipitation of Wettest Quarter in mm	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO17	Precipitation of Driest Quarter in mm	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO18	Precipitation of Warmest Quarter in mm	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)
BIO19	Precipitation of Coldest Quarter in mm	Bio-climate variables WorldClim (*Fick & Hijmans, 2017*)

cover was represented by the average vegetation index (NDVI) for the period 2000–2019, obtained from MODIS Terra Vegetation Indices, whose original resolution is 1 km (*Didan, 2015*). Both the presence records and the environmental variables were edited in ArcGIS 10.5 (Esri, Redlands, CA, USA) to obtain the same spatial projection (WGS84 UTM 19S), model extension (background area) and 1 km spatial resolution.

Data analysis

The maximum entropy method (MaxEnt, (*Phillips et al., 2006*)) in the R program *dismo* package, following the methods outlined by *Hijmans et al. (2022)*, was used to identify the ecological niche of the Andean Ibis. MaxEnt is widely used in ecological studies (*Merow, Smith & Silander, 2013*) because it produces robust models using a small number of samples compared to other methods (*Phillips et al., 2006*; *Merow, Smith & Silander, 2013*). This method requires presence-only records and creates random samples (known as background points) within the landscape to build ecological niches. Another advantage of

MaxEnt is the possibility to choose the characteristic type of the response curves between the variables and the occurrences as well as regularize the complexity of the models (*Phillips et al., 2006*; *Merow, Smith & Silander, 2013*).

Before model development, the background or calibration area (M component), also called the accessible area for the species (*Merow, Smith & Silander, 2013*), was marked using the Andean Ibis presence database, including the southernmost recorded occurrence of the species in Argentina (*Müller, Braslavsky & Chatellenaz, 2021*). These points were used to create a minimal convex polygon. Within this area, 10,000 background points were randomly generated to characterize the environmental context of the background area. To address potential issues of multicollinearity that could affect model performance (*Zurell et al., 2020*), highly correlated environmental variables were identified based on a Pearson coefficient threshold of >0.8 (*Frost, 2020*; Fig. S1). The altitude variable was not eliminated from the selection due to its significance in the species' biogeography. The remaining highly-correlated variables were selected according to their performance (contribution) during model calibration.

During the exploratory phase, calibration models were developed using various settings in the ENMeval package (*Kass et al., 2021*). Three types of model responses linear, quadratic and product were applied both individually and in combination, along with different regularization coefficient values (0, 0.5, 1, 3, and 5). All preliminary models were compared using the lowest Akaike information criterion for small samples (AICc), because of this model's cost-efficiency (*Burnham & Anderson, 2004*). The final model, which exhibited the best fit, was developed through 10 repetitions to obtain the average of its values. Statistical evaluation was conducted using the area under the curve (AUC) and the Boyce Index (*Zurell et al., 2020*; Fig. S2).

The final model was then projected across the four countries that comprise the Andean Ibis's habitat, with the occurrence probability shown in gradients according to the literature. To determine how much of the Andean Ibis's potential distribution is threatened by human disturbance and how much is protected, the "maximization of the sum of sensitivity and specificity" threshold rule (MaxSSS), which has been shown to have high performance value (*Liu et al., 2005*), was used to classify Andean Ibis occurrence probability in a binary map (presence and absence). The map was then overlayed with the boundaries of the protected areas managed by each respective country to assess the extent of the species' potential distribution that fell within protected areas (*Bingham et al., 2019*). To evaluate the anthropic impact on the potential distribution, the map of the Human Footprint Index (represented by population density, land transformation, accessibility and electrical energy infrastructure) was used on the landscapes (*Sanderson et al., 2002*). Human influence impact (HII) is a 0–64 scale with 0 representing theoretically no human impacts and 64 representing the highest human impact. This layer was then overlayed with the potential distribution map to identify the percentage of human disturbance within each protected area along the geographic range.

Table 2 Potential distribution model of the Andean Ibis in South America. The model includes ten replicates and the average values that determined the final model. Evaluation values included are area under the curve with test occurrences (TestAUC), and the Boyce Index (0.93). Mean values are in bold.

	Model replicates										
	1	2	3	4	5	6	7	8	9	10	Mean
Evaluation											
Test AUC	0.91	0.91	0.91	0.93	0.948	0.94	0.92	0.91	0.91	0.91	**0.91**
Boyce Index	0.92	0.92	0.95	0.93	0.95	0.94	0.93	0.98	0.87	0.92	**0.93**
MAXSSS	0.34	0.28	0.33	0.28	0.35	0.28	0.25	0.30	0.32	0.28	**0.30**
Contribution %											
altitude	46.6	31.1	40.0	30.5	47.3	35.6	30	44.1	29.4	31.1	**36.57**
dist_lakes	18.9	24.1	21.7	29.5	17.3	17.6	29.7	19.3	30.7	24.1	**23.29**
bio18 (Precipitation of Warmest Quarter)	0.8	10.4	12.1	4.9	1.5	0.6	1	11	3.9	10.4	**5.66**
pres_river	4.5	4.6	5.3	5.4	4.6	4.6	5.6	5	4	4.6	**4.82**
slope	3.6	3.9	2.2	3.4	2.8	3.4	2.2	3.6	2.2	3.9	**3.12**
bio3 (Isothermality)	7.2	11.7	5.8	17.4	8.3	28.4	17.3	7.3	18.3	11.7	**13.34**
roughness	2.5	1.2	2.2	1.6	2.1	1.3	5.1	1.1	3.3	1.2	**2.16**
bio13 (Precipitation of Wettest Month)	14.6	8.7	8.7	4.8	13.9	6.1	5.2	7.2	5.2	8.7	**8.31**
bio17 (Precipitation of Driest Quarter)	1.4	4.1	2.2	2.6	2.4	2.3	3.8	1.5	2.9	4.1	**2.73**

RESULTS

A total of 2,096 Andean Ibis occurrences were recorded (1,357 for Ecuador, 678 for Peru, 58 for Bolivia, and three for Chile, see supplementary data), covering an altitudinal range of 3,667 to 4,642 m, with an average of 4,108.08 m (SD 169.65 m; Fig. 1). Applying the spatial filter, the occurrences were reduced to 154 (108 for the calibration models and 46 for the evaluation). After exploratory analysis, the best model setting was determined to include only nine variables with a linear and quadratic type of response with a regularization coefficient equal to 1 (Table 2).

The final model showed the contributions made by each of the variables (Table 2), with altitude being the most influential (36.57%) followed by distance to lakes (*dist_lakes*; 23.29%) and isothermality (*bio3*; 13.34%). The response curve showed a heterogeneous relation between the environmental values and the model's prediction. Some variables, such as distance to lakes, slope, precipitation of driest quarter (*bio17*), had a negative association, implying that the probability of the presence of the Andean Ibis decreased as these variables' values increased. Conversely, isothermality (*bio3*) and presence of rivers (*pres_river*) had a positive association, meaning the higher their values, the greater the probability of the presence of the species. On the other hand, altitude, precipitation of the wettest month (*bio13*) and roughness shows bell-shaped response curves all peaking above
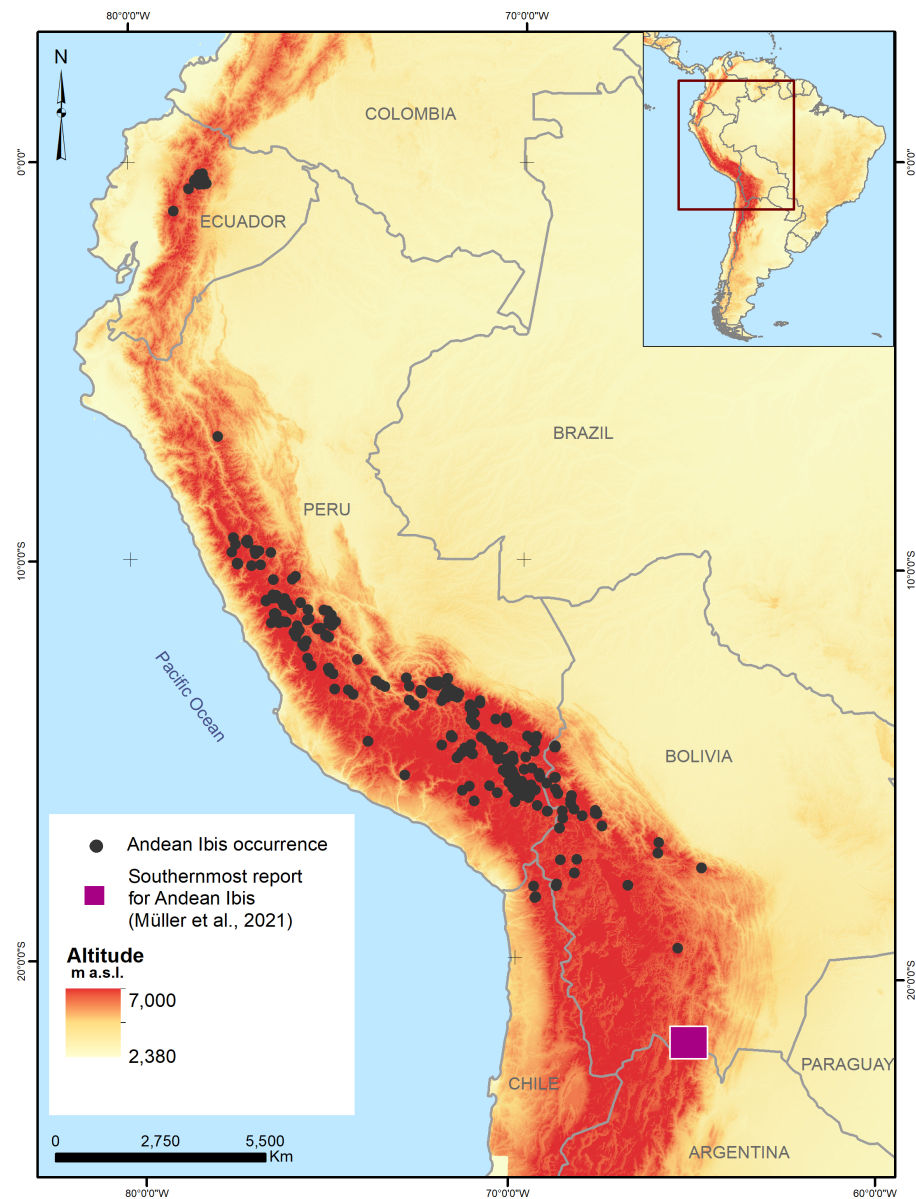
Figure 1 Records of the presence of the Andean Ibis (*Theristicus branickii*) in South America between 2003 and 2020. Data were obtained from GBIF and eBird platforms and specific studies conducted on the species (see references).

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0.8 probability of presence. The statistical evaluation of the model yielded satisfactory results (Test AUC 0.914 and Boyce Index 0.93; Table 2).

Figure 2 shows the model projection of the Andean Ibis in the four countries. The colour gradient map shows that the highest occurrence probability values were located principally in Ecuador and Peru, but the distribution area was fragmented. Bolivia shared a distribution area with Peru and also had some independent locations with high occurrence
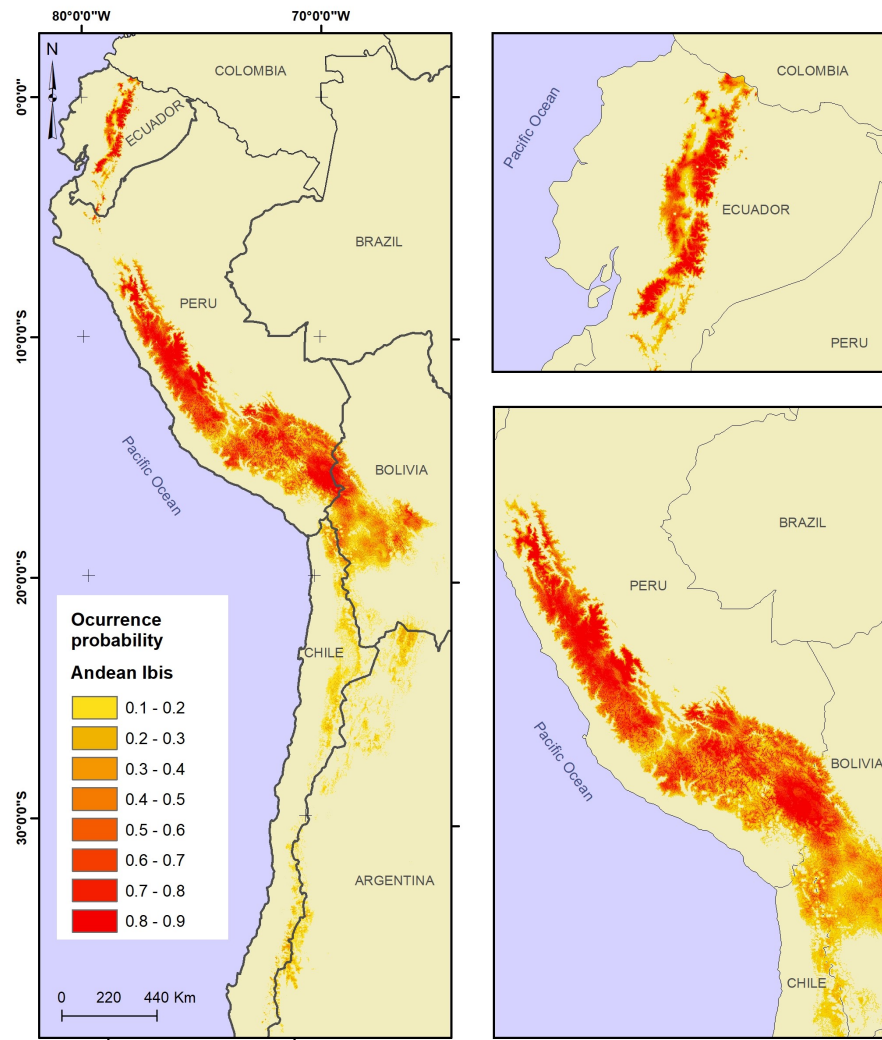
Figure 2 Potential distribution of the Andean Ibis (*Theristicus branickii*) in South America. Occurrence probability is shown in gradient color (from yellow to red).

probability values, while Chile showed a very fragmented distribution with the lowest occurrence probability value.

Finally, the binary classification of the prediction was divided with a threshold value equal to 0.30. Figure 3 shows the extent of the potential distribution of the Andean Ibis was 300,095.00 km^2 at the regional level, with 21,585.85 km^2 (7.19%) in Ecuador, 216,031.33 km^2 (71.99%) in Peru, 57,020.64 km^2 (19.00%) in Bolivia and 5,457.17 km^2 (1.82%) in Chile (Table 3, Fig. 3). Anthropic disturbance (human footprint) covered ∼48% of this potential distribution, while protected areas only covered ∼10% (Table 3). Within national territories, the extent of anthropic disturbance was similar in three of the four countries (45% in Ecuador, 47.12% in Peru, and 53.60% in Bolivia), but was much lower
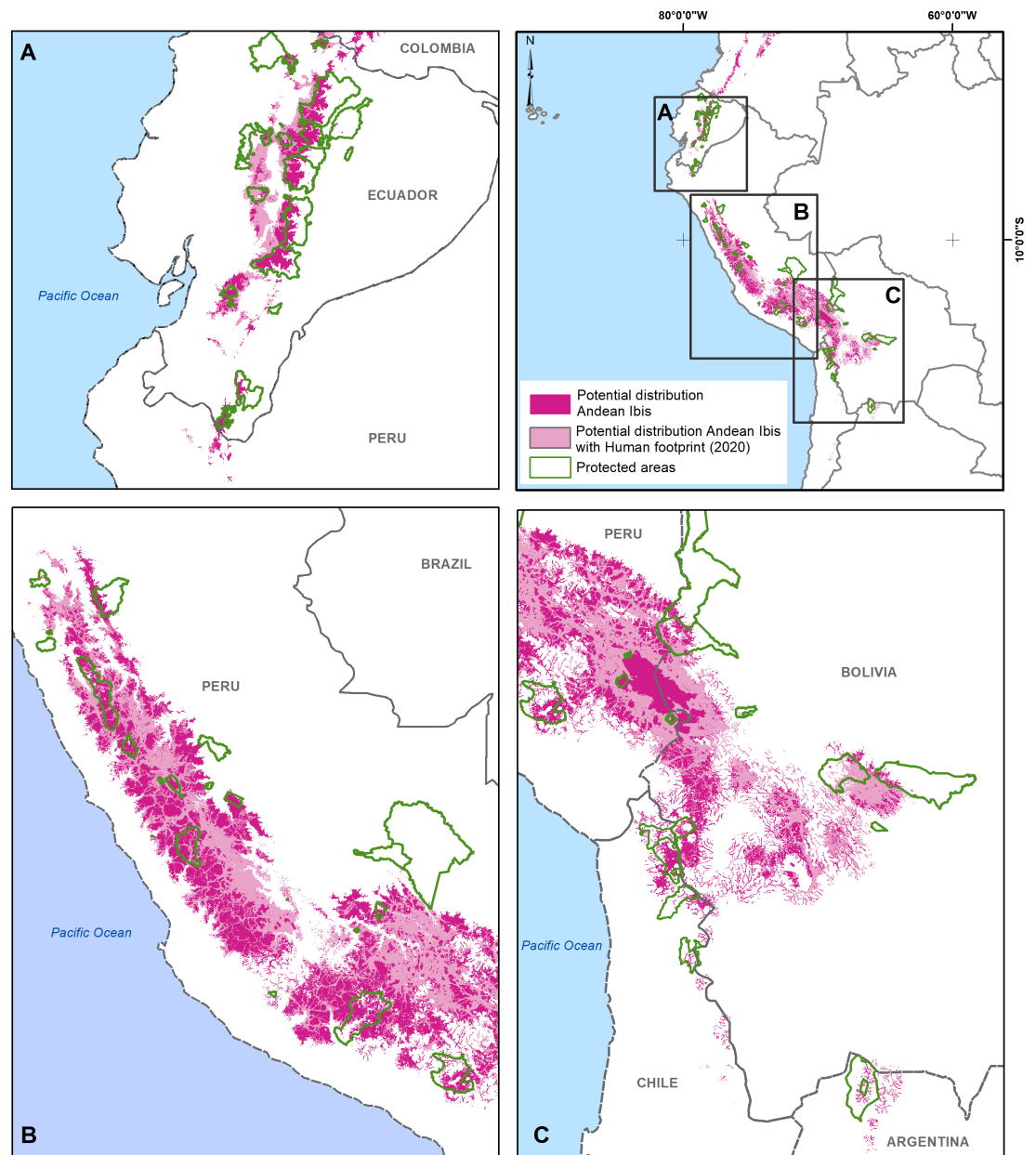
Figure 3 Potential distribution of the Andean Ibis (pink) in South America. (A) Ecuador; (B) Peru; (C) Perú, Chile and Bolivia. National protected areas (green borders) and human footprint areas (light pink; WCS, WC.S. 2005) are included. (A) Human footprint, protected areas and potential distribution in the Ecuadorian and north Peruvian zones; (B) human footprint and protected areas in Peruvian zones, and (C) human footprint, potential distribution and protected areas in southern Peruvian, northeast Bolivia, and north Chile zones.

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Chile (~7%). Ecuador and Chile had the largest percentage of protected areas within the potential distribution areas (35.20% in Ecuador and 34.30% in Chile; Table S3).

Table 3 **Quantification of the potential distribution of the Andean Ibis (*Theristicus branickii*) in South America.** The geographic range, human disturbed areas, and protected zones are described in the national territories of Ecuador, Peru, Bolivia, and Chile.

	Potential distribution of the Andean Ibis					
Country	National territory (km²)	National territory (%)	Anthropogenic disturbance (km²)	Anthropogenic disturbance (%)	Protected areas (km²)	Protected areas (%)
Ecuador	21,585.85	7.19	9,713.12	6.82	8,443.10	28.62
Peru	216,031.33	71.99	101,801.87	71.46	13,642.40	46.25
Bolivia	57,020.65	19.00	30,563.63	21.45	5,540.40	18.78
Chile	5,457.17	1.82	377.18	0.26	1,872.00	6.35
TOTAL	**300,095.00**	**100.00**	**142,455.80**	**100.00**	**29,497.90**	**100.00**

Notes.
Totals are in bold.

DISCUSSION

This study developed ecological niche models to identify the environmental conditions that influence the presence of the Andean Ibis, and map its potential distribution in the tropical Andes. The results of this study reinforce the theory that altitude is a key factor in determining the presence of the species. This study also found that around half (48%) of the Andean Ibis's geographic range is threatened by human activities, while only 10% overlaps with protected areas.

A meticulous review of Andean Ibis occurrences was conducted to ensure the accuracy of this study, taking into account the potential confusion with the records of the *Theristicus melanopis* species. It is worth noting that specific locations in Ecuador, such as Cotopaxi National Park and Antisana National Park, are cited as presence zones for *Theristicus melanopis* in the BirdLife datazone (*BirdLife International, 2023*). However, this published information is likely erroneous, as both species were previously classified as a single species by BirdLife International.

Given the significant disparity in altitudinal habitat ranges between *T. melanopis* and *T. branickii*, it was crucial to carefully scrutinize the occurrence records. The review aimed to ensure that only reliable and accurate data were included in the analysis, thereby minimizing any potential misclassification or confusion between the two species.

The limits of the Andean Ibis occurrence distribution area were determined to be: in the north Lat. −0.2981512, Long. −78.1287425 in Ecuador, in the south Lat. −18.4518884, Long. −70.0663054 in Chile, and in the southeast Lat. −19.6002593, Long. −65.7204267 in Bolivia. Unusual occurrence locations were not considered in the model database. One example of this was the Argentina record (*Müller, Braslavsky & Chatellenaz, 2021*) where the species were registered at about 1,562 m a.s.l. (Lat. −22.283333, Long. −62.683333) in a cloud forest habitat, which is not the typical Andean Ibis habitat. Similarly, records from Ita, Peru, were reported at 157 and 36 m a. s. l. (*Vizcarra, 2009*) and in the Azapa Valley in Chile (Lat. −18.533333, Long. −70.150000; (*Estades, Aguirre & Tala, 2004*)). These recorded occurrences are likely accurate and may represent occasional movements to lower elevation areas during the dry season. These specific occurrences were excluded

from this study's database, but were still considered when designing the background area to ensure an appropriately represented environment context.

The results of the niche model highlight that the most influential variable of the Andean Ibis is altitude (Table 2). Using the threshold of 0.3 (MaxSSS), the current potential distribution area of the Andean Ibis had an altitudinal range of 3,300 and 4,800 m, which is a slightly broader range than the distribution range reported in the literature of 3,700–4,500 m a.s.l. (*BirdLife International, 2017*). High altitude locations in the tropical Andes play an important role for the Andean Ibis and it is important to consider their vulnerability to global warming (*Cuesta et al., 2020*). Modifying the landscape configuration in those localities can shrink the habitat of certain specialist species, like the Andean Ibis, compared to generalist species (*Barnagaud et al., 2012*; *Di Cecco & Hurlbert, 2022*).

Other important variables in Andean Ibis occurrence probability were the distance to lakes and the presence of rivers, which an expected result as lakes and rivers are fundamental foraging sites of the species where its presence has been documented (*Muñoz et al., 2021*). Aquatic microhabitats or wetlands are found in high-altitude locations in the Andes and produce invertebrates and macro-invertebrates. Altitude, bodies of water (*e.g.*, wetlands) and the contribution of annual precipitation (>3,000 mm/year for the paramo and >3,500 mm/year for the puna, respectively; *Flores-López et al., 2016*; *Izquierdo et al., 2018*) are the basic components of the Andean Ibis habitat.

The relationship between altitude, bodies of water and isothermal variables in the high-altitude ecosystems of the Andes, as well as their influence on the potential distribution of the Andean Ibis, aligns with previous research findings on the reproductive patterns of the species. Notably, observations conducted in Antisana National Park provide evidence that the species is present in the volcanic region above 3,500 m a.s.l., with areas close to the Antisana River, wetland areas (lakes) and their tributaries serving as preferred roosting and nesting sites (*West, 2014*; *Luzuriaga et al., 2019*). Similar occurrence and reproductive activity patterns were recorded in Cusco, Peru, at 3,850 m a.s.l., where the species uses the rocky area and the cliffs of the Canepia River to nest (*Alcocer, 2014*).

According to the ecoregion classification of *The Nature Conservancy (2003)*, the potential distribution of the Andean Ibis comprises mainly the paramo highlands in North and Central Andes, the Peruvian Yungas, and the montane dry forest in the south of Bolivia (Fig. 4). Although the statistical evaluation of the model shows it is reliable, the empirical evaluation of the distribution projection indicates that there may be a slight overestimation in some areas, specifically in the southeast of Ecuador (*e.g.*, Podocarpus National Park), where the species has not been observed. This overestimation in models using MaxEnt has been previously reported in rare species, with narrow niches and sampling biases. For example, in the distribution model of the Hose's civet (*Diplogale hosei*) researchers found that the data was biased towards localized areas (easy access) and error-corrected by manipulating the background data (*Kramer-Schadt et al., 2013*). The replicate model shows the potential area, but not the occupied area, of new localities available for the species in the future.

Anthropic activities (human footprint) cover ~48% of the extent of the potential distribution of the Andean Ibis, with the most significant impact in Peru. The impact
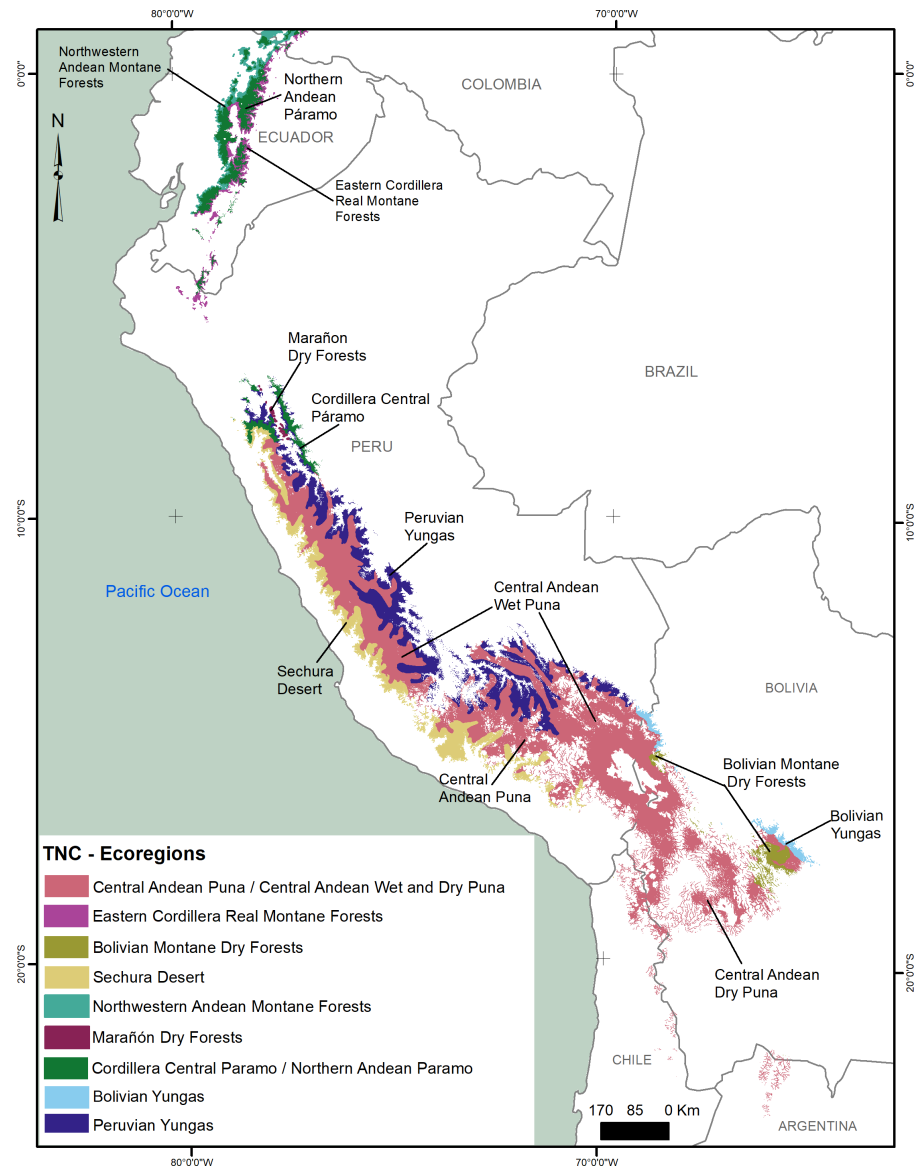
Figure 4 **South American ecoregions (*The Nature Conservancy, 2003*) and the potential distribution of the Andean Ibis.** Eleven ecoregions are in or near the potential distribution areas of the Andean Ibis.

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of anthropogenic pressure on avian species and other functional species such as plants and insects in high Andean ecosystems has been reported in previous studies (*Graham et al., 2009*; *Ocampo-Peñuela et al., 2022*) and is an expected phenomenon considering the high population density and demographic activity of Andean cities, which impose negative impacts on essential resources such as water (*Mulligan, 2009*; *Custodio et al., 2018*). In Ecuador, livestock activities and high-altitude crops such as potatoes, cereals and onions, are leading to habitat transformation of the highlands to farmland at an annual rate of 0.95% (*Gaglio et al., 2017*). Furthermore, scientific evidence shows that this transformation, as well as cultivation processes on a small scale, are associated with a

significant change in water quality indicators (*Rey-Romero, Domínguez & Oviedo-Ocaña, 2022*). Another important factor is climate change, which has a direct impact on altitude zones, influencing the retreat of glaciers (*Francou et al., 2003*) where humidity flows affect the structure and composition of the community of aquatic invertebrates (*Cauvy-Fraunié et al., 2015*), altering the food chain of the species.

CONCLUSIONS

In an ecological niche model, nine environmental variables influenced the distribution of the Andean Ibis, with altitude and distance to lakes contributing a combined 60%. The altitude range of the species distribution was determined to be 975 m, with a higher occurrence probability in high altitude areas (4,108.08 $\pm$ 169.65 SD m a.s.l.) and a distance to lakes of less than 1 km. Thus, the distribution of the Andean Ibis is restricted to Andean ecosystems with water bodies and wetlands, including habitat patches within 11 South American ecoregions. Areas impacted by the human footprint cover nearly half of the distribution area (48%) and the protected area systems in these countries only overlap with a small portion of the distribution area (10%). Moreover, the species has an important potential presence area. However, human activities could threaten Andean Ibis populations by harming their habitats. These factors should be thoroughly studied, focusing on demographic patterns, habitat use and threat identification, to identify the most effective conservation actions. These actions might include reducing the human footprint, promoting connectivity between Andean Ibis distribution zones or including new protected areas for effective species conservation.

Author Contributions

- Nivia Luzuriaga-Neira conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
- Keenan Ennis conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Michaël A.J. Moens conceived and designed the experiments, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Jose Leon conceived and designed the experiments, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Nathaly Reyes conceived and designed the experiments, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Agusto Luzuriaga-Neira conceived and designed the experiments, prepared figures and/or tables, authored or reviewed drafts of the article, english editing, and approved the final draft.
- Jaime R. Rau conceived and designed the experiments, prepared figures and/or tables, authored or reviewed drafts of the article, table and figure editing, and approved the final draft.
- Roxana Rojas-VeraPinto conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the article, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The data is available at GBIF: https://doi.org/10.15468/dl.emayxe.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.16533#supplemental-information.

REFERENCES

Alcocer R. 2014. Nidificación, vigilancia del nido y éxito reproductivo de la bandurria andina *Theristicus melanopis branickii* Berlepsh & Stolzmann, 1894 (Threskiornithidae), en la localidad de Collpamayo, provincia de Espinar, Cusco 2013-2014. Master's thesis, Universidad Nacional de San Agustin de Arequipa, Arequipa, Peru.

Anthelme F, Peyre G. 2020. Biogeography of South American highlands, in earth systems and environmental sciences. In: *Encyclopedia of the World's Biomes*. Amsterdam: Elsevier, 518–529 DOI 10.1016/B978-0-12-409548-9.11811-1.

Araújo MB, Anderson RP, Barbosa AM, Beale CM, Dormann CF, Early R, Garcia RA, Guisan A, Maiorano L, Naimi B, O'Hara RB, Zimmermann NE, Rahbek C. 2019. Standards for distribution models in biodiversity assessments. *Science Advances* **5(1)**:1–12 DOI 10.1126/sciadv.aat4858.

Bakkeren C, Smith E, York JM, Chua B, McCracken KG, Milsom WK. 2020. A morphometric analysis of the lungs of high-altitude ducks and geese. *Journal of Anatomy* **237**:188–196 DOI 10.1111/joa.13180.

Barnagaud JY, Devictor V, Jiguet F, Barbet-Massin M, Viol I, Archaux F. 2012. Relating habitat and climatic niches in birds. *PLOS ONE* **7**(**3**):e32819 DOI 10.1371/journal.pone.0032819.

Bax V, Francesconi W. 2019. Conservation gaps and priorities in the Tropical Andes biodiversity hotspot: implications for the expansion of protected areas. *Journal of Environmental Management* **232**:387–396 DOI 10.1016/j.jenvman.2018.11.086.

Bingham HC, Deguignet M, Lewis E, Stewart J, Juffe-Bignoli D, MacSharry B, Milam AAmy, Kingston N. 2019. *User manual for the world database on protected areas and world database on other effective area-based conservation measures: 1.6.* Cambridge: UNEP-WCMC.

BirdLife International. 2017. Andean Ibis (*Theristicus branickii*). *Available at https://www.iucnredlist.org/species/22697444/112401898#assessment-information* (accessed on 13 January 2019).

BirdLife International. 2023. Ficha técnica de la especie: *Theristicus Branickii. Available at http://datazone.birdlife.org/species/factsheet/andean-ibis-theristicus-branickii* (accessed on 12 April 2023).

Boria RA, Olson LE, Goodman SM, Anderson RP. 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling* **275**:73–77 DOI 10.1016/j.ecolmodel.2013.12.012.

Brown JL, Bennett JR, French CM. 2017. SDMtoolbox 2.0: The next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ* **5**:e4095 DOI 10.7717/peerj.4095.

Burnham KP, Anderson DR (eds.) 2004. *Model selection and multimodel inference.* New York: Springer New York DOI 10.1007/b97636.

Cardenas T, Naoki K, Landivar CM, Struelens Q, Gómez MI, Meneses RI, Cauvy-Frauniè S, Anthelme F, Dangles O. 2022. Glacier influence on bird assemblages in habitat islands of the high Bolivian Andes. *Diversity and Distributions* **28**:242–256 DOI 10.1111/ddi.13458.

Carilla J, Aráoz E, Foguet J, Casagranda E, Halloy S, Grau A. 2023. Hydroclimate and vegetation variability of high Andean ecosystems. *Frontiers in Plant Science* **13**:1–16 DOI 10.3389/fpls.2022.1067096.

Cauvy-Frauniè S, Espinosa R, Andino P, Jacobsen D, Dangles O. 2015. Invertebrate metacommunity structure and dynamics in an andean glacial stream network facing climate change. *PLOS ONE* **10**:1–19 DOI 10.1371/journal.pone.0136793.

Clements JF. University. C and Ornithology. L of, and Association. AB. 2019. *The Clements checklist of birds of the world.* Ithaca: Comstock Pub. Associates/Cornell University Press.

Collar NJ, Bird JP. 2011. Phenotypic discrimination of the andean ibis (*Theristicus branickii*). *The Wilson Journal of Ornithology* **123**:459–463 DOI 10.1676/10-162.1.

Cuesta F, Tovar C, Llambí LD, Gosling WD, Halloy S, Carilla J, Muriel P, Meneses RI, Beck S, Ulloa CUlloa, Yager K, Aguirre N, Viñas P, Jácome J, Suárez-Duque D, Buytaert W, Pauli H. 2020. Thermal niche traits of high alpine plant species and communities across the tropical Andes and their vulnerability to global warming. *Journal of Biogeography* **47**:408–420 DOI 10.1111/jbi.13759.

Custodio M, Peñaloza R, Chanamé F, Yaranga R, Pantoja R. 2018. Assessment of the aquatic environment quality of high andean lagoons using multivariate statistical methods in two contrasting climatic periods. *Journal of Ecological Engineering* **19**:24–33 DOI 10.12911/22998993/92677.

Dawson NJ, Alza L, Nandal G, Scott GR, McCracken KG. 2020. Convergent changes in muscle metabolism depend on duration of high-altitude ancestry across Andean waterfowl. *eLife* **9**:1–35 DOI 10.7554/eLife.56259.

Di Cecco GJ, Hurlbert AH. 2022. Multiple dimensions of niche specialization explain changes in species' range area, occupancy, and population size. *Frontiers in Ecology and Evolution* **10**:921480 DOI 10.3389/fevo.2022.921480.

Didan K. 2015. MOD13A3 MODIS/Terra Vegetation Indices Monthly L3 Global 1km SIN Grid. NASA LP DAAC. DOI 10.5067/MODIS/MOD13A3.006.

DuBay SG, Witt CC. 2014. Differential high-altitude adaptation and restricted gene flow across a mid-elevation hybrid zone in Andean tit-tyrant flycatchers. *Molecular Ecology* **23**:3551–3565 DOI 10.1111/mec.12836.

Ennis K, Leon J, Moens MAJ, Luzuriaga-Neira N. 2019. Mapping ecological niche distribution of *theristicus branickii* in the andean highlands of ecuador, using maximum entropy analysis. In: *XV Congreso Neotropical de Ornitología*. 1.

Estades C, Aguirre J, Tala C. 2004. Theristicus melanopis branickii en el valle de Azapa. *Boletin Chileno de Ornitología* **10**:41–42.

Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**:4302–4315 DOI 10.1002/joc.5086.

Fjeldså J. 1988. High altitude tropical biogeography. François vuilleumier, maximina monasterio. *The Quarterly Review of Biology* **63**:478–478 DOI 10.1086/416089.

Fjeldså J, Krabbe N. 1990. Birds of the high Andes: a manual to the birds of the temperate zone of the Andes and Patagonia, South America the high Andes: a manual to the birds of the temperate zone of the Andes and Patagonia, South America.

Flores-López F, Galaitsi SE, Escobar M, Purkey D. 2016. Modeling of Andean páramo ecosystems' hydrological response to environmental change. *Water* **8(3)**:94 DOI 10.3390/w8030094.

Francou B, Vuille M, Wagnon P, Mendoza J, Sicart JE. 2003. Tropical climate change recorded by a glacier in the central Andes during the last decades of the twentieth century: Chacaltaya, Bolivia, 16°S. *Journal of Geophysical Research: Atmospheres* **108**:1–12 DOI 10.1029/2002jd002959.

Freile J, Restall R. 2018. Birds of Ecuador1. *Nature* **119**:336–336 DOI 10.1038/119336a0.

Frost J. 2020. *Introduction to statistics: an intuitive guide for analyzing data and unlocking discoveries.* Pennsylvania: Jim Publishing, State College Pennsylvania.

Gaglio M, Aschonitis VG, Mancuso MM, Puig JPR, Moscoso F, Castaldelli G, Fano EA. 2017. Changes in land use and ecosystem services in tropical forest areas: a case study in Andes mountains of Ecuador. *International Journal of Biodiversity Science, Ecosystem Services & Management* 13:264–279 DOI 10.1080/21513732.2017.1345980.

GBIF. 2019. GBIF Occurrence Download *Theristicus branickii. Available at* https://www.gbif.org/occurrence/download/ (accessed on 14 March 2020) DOI 10.15468/dl.fljcoc.

Graham CH, Loiselle BA, Velásquez-tibatá J, Cuestan CF. 2009. Species distribution modeling and the challenge of predicting future distributions. In: Herzog SK, Martinez RMP, Tiesse JH, eds. *Climate change and biodiversity in tropical andes.* Montevideo: Inter-American Institute for Global Change Research, 295–310 DOI 10.13140/2.1.3718.4969.

Hazzi NA, Moreno JS, Ortiz-Movliav C, Palacio RD. 2018. Biogeographic regions and events of isolation and diversification of the endemic biota of the tropical Andes. *Proceedings of the National Academy of Sciences of the United States of America* 115:7985–7990 DOI 10.1073/pnas.1803908115.

Hijmans ARJ, Phillips S, Leathwick J, Elith J, Hijmans MRJ. 2022. Species distribution modeling. *Available at* https://rspatial.org/raster/sdm/1_sdm_introduction.html.

Huberty CJ. 1996. *Applied discriminant analysis.* New Delhi: Wiley Interscience.

Izquierdo A, Aragón R, Navarro C, Casagranda E. 2018. Humedales de la Puna: principales proveedores de servicios ecosistémicos de la región. In: Grau HR, Babot MJ, Izquierdo AE, Grau A, eds. *La Puna argentina Naturaleza y cultura.* Argentina: Fundación Miguel Millo, 96–111.

Jarvis A, Reuter HI, Nelson A, Guevara E. 2008. Hole-filled SRTM for the globe Version 4, available from the CGIAR-CSI SRTM 90m Database. *CGIAR Consortium for Spatial Information* 15:5.

Kass JM, Muscarella R, Galante PJ, Bohl CL, Pinilla-Buitrago GE, Boria RA, Soley-Guardia M, Anderson RP. 2021. ENMeval 2.0: redesigned for customizable and reproducible modeling of species' niches and distributions. *Methods in Ecology and Evolution* 12:1602–1608 DOI 10.1111/2041-210X.13628.

Kramer-Schadt S, Niedballa J, Pilgrim JD, Schröder B, Lindenborn J, Reinfelder V, Stillfried M, Heckmann I, Scharf AK, Augeri DM, Cheyne SM, Hearn AJ, Ross J, Macdonald DW, Mathai J, Eaton J, Marshall AJ, Semiadi G, Rustam R, Bernard H, Alfred R, Samejima H, Duckworth JW, Breitenmoser-Wuersten C, Belant JL, Hofer H, Wilting A. 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions* 19:1366–1379 DOI 10.1111/ddi.12096.

Lehner B, Grill G. 2013. Global river hydrography and network routing: baseline data and new approaches to study the world's large river systems. *Hydrological Processes* 27:2171–2186 DOI 10.1002/hyp.9740.

Liu C, Berry PM, Dawson TP, Pearson RG. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**:385–393 DOI 10.1111/j.0906-7590.2005.03957.x.

Long AJ, Crosby MJ, Stattersfield AJ. 1996. Towards a global map of biodiversity: patterns in the distribution of restricted-range birds. *Global Ecology and Biogeography Letters* **5**:281–304 DOI 10.2307/2997796.

Luzuriaga N, Cuichan D, Catagña D, Da Costa M, Reyes N. 2019. Reproductive patterns and nest success rates on the Black-faced Ibis, (*Theristicus branickii*) in the Antisana Ecological Reserve, Ecuador. In: *XV Congreso Neotropical de Ornitología.* Costa Rica, 1.

Luzuriaga-Neira N, Cuichán D, Da Costa M, Reyes N. 2021. Observations on the breeding biology of the Andean Ibis (*Theristicus branickii*) in Ecuador. *Ornithology Research* **29**:22–28 DOI 10.1007/s43388-021-00044-3.

Merow C, Smith MJ, Silander JA. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does and why inputs and settings matter. *Ecography* **36**:1058–1069 DOI 10.1111/j.1600-0587.2013.07872.x.

Messager ML, Lehner B, Grill G, Nedeva I, Schmitt O. 2016. Estimating the volume and age of water stored in global lakes using a geo-statistical approach. *Nature Communications* **7**:1–11 DOI 10.1038/ncomms13603.

Moret P, Á AráuzMdelos, Gobbi M, Á Barragán. 2016. Climate warming effects in the tropical Andes: first evidence for upslope shifts of Carabidae (Coleoptera) in Ecuador. *Insect Conservation and Diversity* **9**:342–350 DOI 10.1111/icad.12173.

Muñoz I, Luzuriaga-Neira N, Heredia A, Gonzalez L, Velastegui J, Olmedo I, Garcìa J, Bonaccorso E. 2021. New records of Andean Ibis *Theristicus branickii* in Ecuador. *Cotinga* **43**:96–98.

Müller G, Braslavsky H, Chatellenaz M. 2021. La Bandurria Andina (*Theristicus branickii*), nueva especie para Argentina. *Hornero* **36**:79–82.

Mulligan M. 2009. The human water quality footprint : agricultural, industrial, and urban impacts on the quality of available water globally and in the Andean region. In: *Procedings of the International Confence on Integrated Water Resource Management and Climate Change, Cali, Colombia.* 11.

Naveda-Rodríguez A, Santander T, Utreras BV, Zapata-Ríos G. 2020. Estimating the abundance of andean ibis (*theristicus branickii*) in the high Andes of Northern Ecuador. *Tropical Conservation Science* **13**:1940082920903185 DOI 10.1177/1940082920903185.

Naveda-Rodríguez A, Vargas FH, Kohn S, Zapata-Ríos G. 2016. Andean condor (*vultur gryphus*) in Ecuador: geographic distribution, population size and extinction risk. *PLOS ONE* **11(3)**:e0151827 DOI 10.1371/journal.pone.0151827.

Ocampo-Peñuela N, Suárez-Castro AF, Díaz-Timoté JJ, Gómez-Valencia B, Olaya-Rodríguez MH, Sánchez-Clavijo LM, Correa-Ayram CA. 2022. Increased exposure of Colombian birds to rapidly expanding human footprint. *Environmental Research Letters* **17**:114050 DOI 10.1088/1748-9326/ac98da.

Phillips SB, Aneja VP, Kang D, Arya SP. 2006. Modelling and analysis of the atmospheric nitrogen deposition in North Carolina. *International Journal of Global Environmental Issues* **6**:231–252 DOI 10.1016/j.ecolmodel.2005.03.026.

Remsen Jr J, Areta J, Bonaccorso E, Claramunt S, Jaramillo A, Lane D, Pacheco J, Robbins M, Stiles F, Zimmer K. 2023. *Una clasificación de las especies de aves de América del Sur. Sociedad Americana de Ornitología (Version octubre 2019)*. Luisiana: EEUU: Museo de Ciencias Naturales, Universidad Estatal de Luisiana.

Restall R, Rodner C, Lentino M. 2007. *Birds of northern South America: an identification guide*. New Haven: Yale University Press.

Restrepo-Cardona JS, Parrado MA, Vargas FH, Kohn S, Sáenz-Jiménez F, Potaufeu Y, Narváez F. 2022. Anthropogenic threats to the Vulnerable Andean Condor in northern South America. *PLOS ONE* **17**:e0278331 DOI 10.1371/journal.pone.0278331.

Rey-Romero DC, Domínguez I, Oviedo-Ocaña ER. 2022. Effect of agricultural activities on surface water quality from páramo ecosystems. *Environmental Science and Pollution Research* **29**:83169–83190 DOI 10.1007/s11356-022-21709-6.

Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G. 2002. The human footprint and the last of the wild. *BioScience* **52**:891–904.

Schulenberg TS, Stotz DF, Lane DF, O'Neill JP, Parker TA. 2007. *Birds of Peru*. Princeton University Press.

Sevillano-Ríos CS, Rodewald AD, Morales LV. 2020. Alpine birds of South America. In: Goldstein MI, DellaSala DA, eds. *Encyclopedia of the world's biomes*. Amsterdam: Elsevier, 492–504 DOI 10.1016/B978-0-12-409548-9.11806-8.

Soberon J. 2011. Mapping species distributions: spatial inference and prediction. *The Quarterly Review of Biology* **86**:219–220 DOI 10.1086/661126.

The Nature Conservancy. 2003. Based on Wiken, E.B. (compiler). 1986. Terrestrial ecozones of Canada. Ecological Land Classification Series No. 19. Environment Canada, Hull, Que. 26 pp. + map.:26 + map. 26 + map *Available at https://databasin.org/datasets/9c7bc177c6154d71b0458391f3177053*.

Tirozzi P, Orioli V, Dondina O, Kataoka L, Bani L. 2021. Species traits drive long-term population trends of common breeding birds in northern italy. *Animals* **11**:1–28 DOI 10.3390/ani11123426.

Valencia N, Franke I. 1989. F. Vuilleumier & M. Monasterio (eds) 1986. High altitude tropical biogeography. Oxford University Press. *Journal of Tropical Ecology* **5**:121–122 DOI 10.1017/S026646740000331X.

Vizcarra J. 2009. Observaciones de *Theristicus melanopis melanopis* y *Theristicus melanopis branickii* en el distrito de Ite, sur de Perú. *Boletín Chileno de Ornitología* **15**:104.

Vuilleumier F. 1969. Pleistocene Speciation in Birds living in the High Andes. *Nature* **223**:1179–1180 DOI 10.1038/2231179a0.

Vuilleumier F. 1984. *Patchy distribution and systematics of Oreomanes fraseri (Aves, Coerebidae) of Andean Polylepis woodlands*. New York: American Museum of Natural History.

Vuilleumier F, Simberloff D. 1980. *Evolutionary biology.* Boston: Springer US DOI 10.1007/978-1-4615-6959-6.

West B. 2014. New observations of the andean ibis (*theristicus branickii*, threskiornithidae): distribution, movements, and behavior near Volcán Antisana. *Available at* https://digitalcollections.sit.edu/isp_collection/2019.

Zurell D, Franklin J, König C, Bouchet PJ, Dormann CF, Elith J, Fandos G, Feng X, Guillera-Arroita G, Guisan A, Lahoz-Monfort JJ, Leitão PJ, Park DS, Peterson AT, Rapacciuolo G, Schmatz DR, Schröder B, Serra-Diaz JM, Thuiller W, Yates KL, Zimmermann NE, Merow C. 2020. A standard protocol for reporting species distribution models. *Ecography* **43**:1261–1277 DOI 10.1111/ecog.04960.