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Elevational patterns and seasonal baseline of bird diversity in the Lomas de Atiquipa, Southern Peru

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Abstract. *Luque-Fernandez CR, Villegas-Paredes LN. 2026. Elevational patterns and seasonal baseline of bird diversity in the Lomas de Atiquipa, Southern Peru. Biodiversitas 27 (6): d270603. https://doi.org/10.13057/biodiv/d270603*. Coastal lomas are fog-dependent vegetation oases in the South Pacific desert, where wet-dry seasonality influences vegetation cover and habitat availability. We characterized bird diversity in the Lomas de Atiquipa, southern Peru, and evaluated its variation along elevation, habitat types, and seasons. We integrated historical records compiled between 2002 and 2018 with standardized surveys conducted in 2018 during the dry and wet seasons. Historical records were used to describe the local avifaunal inventory and broad richness patterns across 100-m elevational bands and habitat types, whereas the standardized surveys were used to evaluate habitat- and season-related variation in community structure based on observed counts. We recorded 110 species belonging to 17 orders and 41 families, including four Peruvian endemics. The highest compiled richness was recorded at mid elevations, particularly between 600 and 700 m asl (55 species), and in open forest, agricultural areas, and herbaceous-shrub habitat. Community composition in the standardized 2018 surveys differed significantly among habitats (ANOSIM R: 0.633, P: 0.003), whereas the overall separation between dry and wet seasons was weak and not significant (R: 0.052, P: 0.258). Although mean Bray-Curtis dissimilarity between seasons was high (78.6%), this reflected shifts in the relative contribution of species within the system rather than a consistent wet-vs-dry grouping of samples. These results identify the mid-elevation fog belt and its habitat mosaic as an evidence-based priority for future monitoring and conservation management in Atiquipa.

Keywords: Bird assemblages, community composition, fog oasis, lomas ecosystem, seasonality

INTRODUCTION

Coastal lomas are discontinuous fog-dependent ecosystems along the Pacific margin of South America, from northern Peru to central Chile. These vegetation "oases" are sustained by marine fog, whose seasonal intensification during the austral winter drives changes in plant productivity and habitat availability. Because they persist within a hyper-arid matrix, lomas concentrate biodiversity and provide habitat for species with coastal, desert, Andean, and endemic affinities, giving them high biogeographic and conservation value (Jiménez et al. 2012; Moat et al. 2021; Gonzales et al. 2023). Their ecological functioning is linked to fog interception and horizontal precipitation, whereby moisture condenses on vegetation, creating moister microenvironments beneath the canopy, increasing soil water availability and supporting plant cover and fauna (Balaguer et al. 2011; Jiménez et al. 2012; Manrique et al. 2014).

Among Peruvian lomas, the Lomas de Atiquipa are notable for including most vegetation strata described for these ecosystems and harbor one of the best-preserved relict forests, dominated by Tara spinosa, with an estimated extent of about 1,260 ha (Vizcarra 2006; Talavera et al. 2017; Pauca-Tanco et al. 2018). Atiquipa extends from the marine littoral to 1,283 m asl forming an elevational gradient where vegetation structure, fog influence, and habitat availability change substantially (Ferreyra 1993; Sotomayor-Melo and Jiménez-Milón 2008; Talavera et al. 2017). Recent studies emphasized its importance for restoration and management under changing conditions, particularly regarding fog dependence, land use, and conservation of Tara-dominated communities (Balaguer et al. 2011; Jiménez et al. 2024).

Birds are useful indicators of ecological responses to environmental gradients because their richness and composition vary with habitat structure, food availability, vegetation complexity, and climate (Blake and Loiselle 2000; Acharya and Vijayan 2017). Along elevational gradients, bird assemblages reflect environmental filters and resource distribution, while productivity changes can alter abundance, habitat use, and community composition (Verea et al. 2000; Ramírez-Albores 2006). In lomas systems, fog-driven moisture pulses rapidly modify vegetation cover, structural complexity, and food and shelter availability, affecting richness, habitat associations, and redistribution of bird assemblages (Goetz et al. 2007; Kim et al. 2018). Thus, evaluating bird communities across spatial and temporal scales is important for understanding avifaunal responses to environmental heterogeneity in these seasonal ecosystems.

Despite their ecological importance, ornithological studies in lomas remain scarce and geographically uneven. Existing work has focused mainly on inventories, faunal accounts, habitat-specific avifauna, or ecological observations for individual species in Atiquipa and other lomas,

including Mejía, Cerro Campana, and Lachay (Brack 1974; Zeballos et al. 2000; Zelada et al. 2014; Pantigoso et al. 2015; Luque-Fernández 2020). A recent systematic review of South American coastal lomas highlighted biodiversity gaps, especially for fauna and studies integrating ecological patterns across space and time (Gonzales et al. 2023). In Atiquipa, previous studies documented bird richness and notable records, but have not integrated elevational, habitat, and seasonal dimensions using long-term records and standardized seasonal surveys. Therefore, this study updates the inventory while combining historical information with standardized surveys to examine spatial patterns and provide a first seasonal baseline for bird diversity in this well-preserved lomas system.

In this context, the present study characterizes bird diversity in the Lomas de Atiquipa and examines how it varies along the local elevational gradient, among habitat types, and between wet and dry seasons. Specifically, we used historical records compiled between 2002 and 2018 to describe the local avifaunal inventory and general richness patterns across elevational bands and habitats, and standardized surveys conducted in 2018 to evaluate habitat and season related variation in community composition. We expected bird richness to be highest at mid elevations, where fog influence and vegetation heterogeneity are greatest; we also expected habitat identity to structure bird assemblages more strongly than season, while seasonal differences would be expressed mainly through localized shifts in relative species contributions rather than through complete community replacement. By combining these two complementary sources of information, this study provides an updated overview of bird diversity in one of the most heterogeneous and best-preserved lomas systems in southern Peru, and offers a baseline for future ecological monitoring and conservation planning.

MATERIALS AND METHODS

Study area

Atiquipa is located in Caravelí Province, Arequipa Department, Southern Peru (15°47′S, 74°22′W). The Lomas de Atiquipa are located in this area and constitute a fog-dependent ecosystem associated with the western Andean foothills. A substantial portion of this system is included within the “Lomas de Atiquipa” Private Conservation Area (ACP), owned by the Atiquipa, Jaqui, and Yauca peasant community and officially recognized by the Peruvian government (MINAM 2011). The study system extends from the coastal littoral belt to 1,283 m asl at Cerro Cahuamarca, forming a short but steep elevational gradient in which fog influence, vegetation structure, and habitat availability change markedly with elevation (Ferreyra 1993; Talavera et al. 2017). Figure 1 shows the location of the study area and the surveyed elevational gradient.

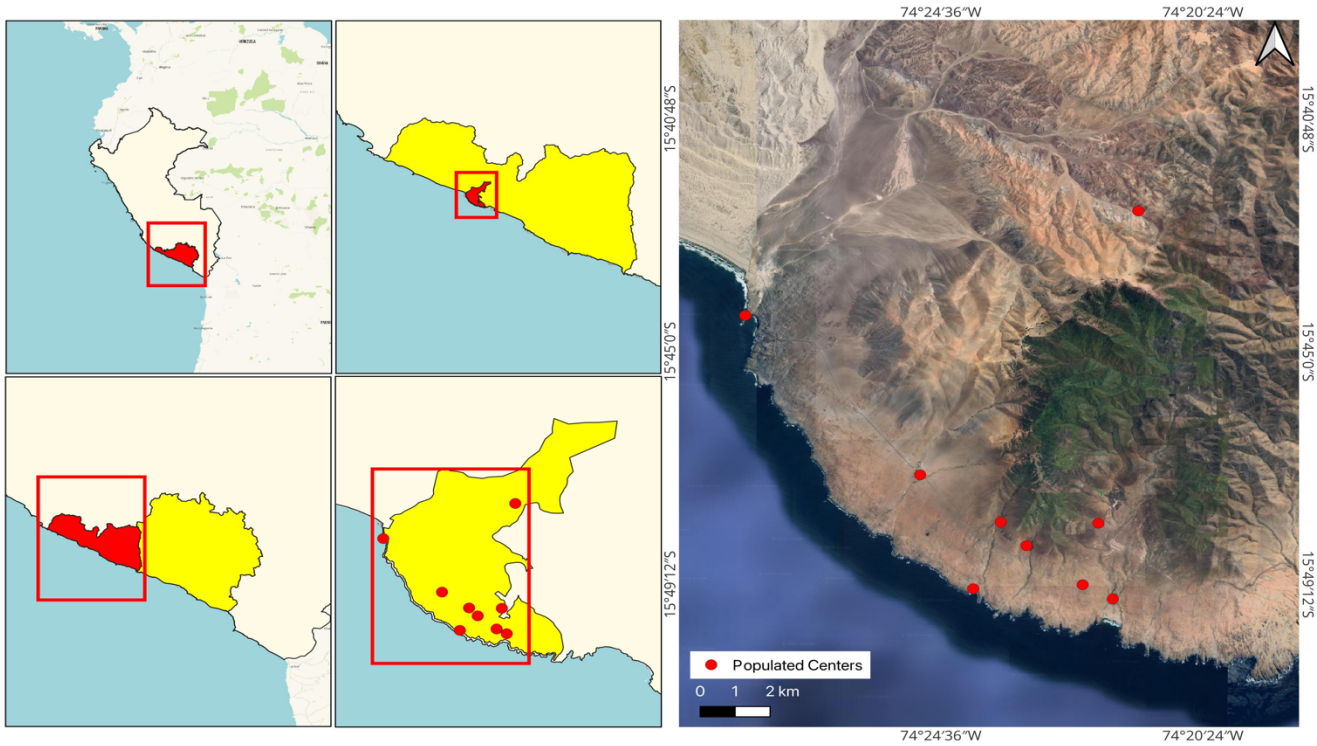

Figure 1. Location of the Lomas de Atiquipa study area in southern Peru

Lomas de Atiquipa is located in a hyper-arid region where water availability depends mainly on fog persistence and, to a much lesser extent, on rainfall. Locally, two well-defined seasons can be distinguished: a cool, wet season with frequent fog from July to November, and a warmer, drier season from December to June (Sotomayor-Melo and Jiménez-Milón 2008). Meteorological monitoring carried out in Atiquipa between February 2005 and February 2006 showed that the wet-cool season had a total precipitation of 60 mm, mean fog capture of 40.9 L m^{-2} day^{-1}, and a mean temperature of 12.8°C, whereas the preceding dry-warm period had 10 mm of precipitation, 8.6 L m^{-2} day^{-1} of fog capture, and a mean temperature of 16.2°C, and the subsequent dry-warm period had 12.7 mm of precipitation, 8.1 L m^{-2} day^{-1} of fog capture, and a mean temperature of 17.5°C. These values indicate that fog is the main driver of seasonal moisture availability and vegetation dynamics in Atiquipa (Sotomayor-Melo and Jiménez-Milón 2008). In addition, annual rainfall in Atiquipa has been reported as very low, whereas fog interception beneath tree canopy can greatly increase local water inputs (Balaguer et al. 2011). These meteorological data are presented to characterize the general seasonal regime of Atiquipa.

Along the elevational gradient, the lomas vegetation is arranged in distinct habitat belts. Desert habitat (0-200 m asl) occupies the driest coastal and leeward sectors and is dominated by annual plants and scattered cacti. Herbaceous vegetation (200-400 m asl) occurs on gentle slopes and small plains, whereas herbaceous-shrub vegetation (400-600 m asl) is found on steeper slopes and is characterized by perennial shrubs mixed with annual species. The main fog belt is represented by forest vegetation (600-1100 m asl), where open and dense stands dominated by *Tara spinosa* can be distinguished. Cactaceous vegetation occurs both in upper sectors (1100-1273 m asl) and on leeward slopes at mid elevations. Agricultural areas are mainly distributed between 200 and 600 m asl, especially along lower stream sectors. The extent of lomas vegetation varies seasonally with fog intensity and may expand markedly during El Niño events (Ferreyra 1993; Talavera et al. 2017).

Bird data collection

Bird data came from two complementary sources with different analytical purposes. The complete species inventory was obtained by integrating unique species records from both sources, whereas richness patterns by elevation and habitat were treated descriptively and community-structure analyses were restricted to the standardized 2018 dataset. First, we compiled historical records obtained by the authors between 2002 and 2018 through non-standardized bird observations, including point counts, transects, incidental observations, and documented evidence (e.g., photographs), along the elevational gradient of the Lomas de Atiquipa from the littoral zone to 1,283 m asl These records were used exclusively to build the local species inventory and to describe broad richness patterns across elevational bands and habitat types. Because all historical records were georeferenced, each observation was subsequently assigned to a 100-m elevational band and to one of nine habitat units present in the locality: marine-coastal (MC), desert (DS), herbaceous (HER), herbaceous-shrub (HER-SHR), open forest (OFOR), dense forest (DFOR), cactaceous (CAC), agricultural areas (AGR), and water bodies (WB). Because these data were compiled from non-standardized observations over multiple years, they provide a broad descriptive basis for the local inventory and for summarizing recorded richness patterns across habitats and elevational bands, while hypothesis-oriented analyses of community structure were based on the standardized 2018 surveys. Because some typically coastal species can move upslope into the lomas during the wet and post-wet seasons, records from the adjacent marine-coastal strip were also included in the inventory.

Second, we conducted a standardized seasonal survey in 2018 during the dry season (May) and wet season (October). During the survey months, climatic conditions were mild and humid. Mean air temperature was 18.09±1.04°C in May and 17.35±1.08°C in October, while mean relative humidity was 86.47±5.98% and 84.98±5.57%, respectively (NASA Power 2026). In each season, all nine habitat types were surveyed using the same two independent linear transects of approximately 1.5 km per habitat, established in different locations representing the same habitat type and separated by at least 2 km. Each transect was surveyed once per seasonal evaluation, resulting in two transects per habitat in May and the same two transects revisited in October. Bird surveys followed the transect-count approach of Emlen (1971). Along each transect, all individuals seen or heard were recorded from 05:30 to 10:00 h using binoculars (Bushnell 10×42) and photographic support when possible. The same observers conducted all standardized surveys. Observers moved continuously along each transect and avoided recounting individuals moving parallel to the observer or birds already registered in the same transect section. Abundance was recorded as the raw number of individuals detected per transect, and these counts were later summed by habitat for multivariate analyses. Pooling was used to obtain one standardized assemblage per habitat and season, matching the scale at which habitat-level community composition was compared. This approach reduced the influence of small within-habitat differences between paired transects, but it also limited the ability to evaluate within-habitat variability and reduced the inferential strength of habitat-season comparisons.

Because detectability likely varied among open coastal, shrub, forest, and agricultural habitats, and because no distance-based correction was applied, counts were interpreted as observed abundances rather than density estimates. Therefore, the standardized 2018 survey provides a balanced baseline for comparing habitat- and season-related community structure based on observed counts. Sampling was conducted under comparable field conditions; in the wet season, days with rainfall, intense fog, or immediately after prolonged fog events were avoided to reduce detectability bias. Consequently, richness values derived from this dataset may reflect both biological occurrence patterns and variation in observation history among habitats and elevational bands.

Data analysis

Analyses were conducted separately according to the evidentiary scope of each dataset. Historical records compiled between 2002 and 2018 were used only for descriptive purposes: to characterize the overall avifaunal inventory, to summarize species richness by 100-m elevational bands and habitat units, and to evaluate broad compositional similarity along the elevational gradient. By contrast, the standardized 2018 transect dataset was used exclusively for inferential analyses of habitat- and season-related community variation. Because historical records were compiled from non-standardized observations over multiple years, richness patterns derived from this dataset summarize recorded occurrence across habitats and elevational bands, whereas effort-balanced community comparisons were restricted to the standardized 2018 dataset. Also, historical records were georeferenced, each observation was assigned to a 100-m elevational band according to its recorded GPS elevation. Only records with sufficiently precise locality information were used for the elevational matrix. A presence/absence matrix of species by elevational band was then constructed for the similarity analyses.

Compositional similarity along the elevational gradient was assessed using presence/absence data and the Sørensen similarity coefficient (Sørensen 1948), calculated as $2a / (2a + b + c)$, where a is the number of species shared by two elevational intervals, and b and c are the species unique to each interval. Following Araneda et al. (2018), similarity values were used to evaluate species turnover patterns among adjacent elevational intervals and to construct a UPGMA clustering dendrogram (Sørensen 1948; Koleff et al. 2003). Because this analysis was based on compiled historical records, the resulting clustering provides a descriptive representation of compositional structure along the elevational gradient, while also reflecting possible differences in sampling intensity among intervals.

For the standardized 2018 surveys, the analytical unit was the habitat-season assemblage. The two transects surveyed within each habitat and season were pooled, producing 18 assemblages in total (nine habitat types × two seasons). Community structure was then explored with non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity on square-root transformed observed abundance data, to reduce the influence of highly dominant species and to down-weight rare species. Differences in community composition between seasons and among habitats were evaluated with ANOSIM using Bray-Curtis dissimilarities and 999 permutations. To assess whether differences between groups could be influenced by heterogeneity in dispersion, we additionally tested homogeneity of multivariate dispersion (betadisper). SIMPER was then used descriptively to identify the species contributing most to average Bray-Curtis dissimilarity between groups (Bray and Curtis 1957; Clarke 1993; Clarke et al. 2014). Given that seasonal comparisons were based on one dry-season and one wet-season survey in 2018, with paired transects pooled by habitat, these analyses provide a standardized baseline of habitat- and season-related community variation.

Finally, species were categorized according to (i) local occurrence status, (ii) relative abundance in the locality, and (iii) conservation status. Based on repeated field observations compiled between 2002 and 2018, each species was assigned a local occurrence status as resident, migrant, occasional, or accidental. Resident species were recorded regularly across years, whereas migrant species showed seasonal occurrence consistent with the status recognized in the national checklist of birds of Peru (Plenge 2022). Occasional species were recorded only sporadically, and accidental species were represented by one or very few exceptional records. Relative abundance was treated as a qualitative index of local commonness based on the frequency of detection and the usual number of individuals observed across years, rather than as a density estimate. Accordingly, species were classified as abundant, common, frequent, scarce, or rare, following checklist- and census-based approaches that use repeated field records to summarize relative commonness. These categories summarize long-term field experience in Atiquipa as qualitative local descriptors of occurrence and commonness, complementing the species inventory without representing standardized estimates of abundance, occupancy, or demographic status (Bibby et al. 2000; Gregory et al. 2004). Conservation status was verified using the IUCN Red List (IUCN 2025) and is presented as the current reference category for each species in the compiled inventory.

RESULTS AND DISCUSSION

Bird richness in the Lomas de Atiquipa

Based on the full locality inventory, which integrated historical records compiled between 2002 and 2018 and the standardized surveys conducted in 2018, the avifauna of Atiquipa comprised 110 species, represented by 17 orders and 41 families. The most represented orders were Passeriformes and Charadriiformes, with 44 and 20 species, respectively, whereas the most represented families were Tyrannidae and Thraupidae, with 12 and 11 species, respectively. Within this richness, we recorded four Peruvian endemic species (*Geositta peruviana*, *Pseudasthenes cactorum*, *Sicalis raimondii*, and *Cinclodes taczanowskii*). Ninety percent of the species are categorized as Least Concern (LC) according to the IUCN, while six species, mainly marine-coastal, are classified as Near Threatened (NT) (*Phalacrocorax gaimardi*, *Phalacrocorax bougainvillii*, *Pelecanus thagus*, *Larosterna inca*, *Progne murphyi*, and *Xenospingus concolor*), and four species fall into threatened categories (*Spheniscus humboldti*, *Vultur gryphus*, *Sternula lorata* and *Chaetura pelagica*). Regarding seasonality, 61% of species (67 spp.) were residents, 20% were migrants (22 spp.), and the remaining species occurred as occasional or accidental records. Based on annual relative abundance for the locality, 14% were abundant, 24% common, 11% frequent, 31% scarce, and 20% (22 spp.) were rare in Atiquipa. Detailed information on conservation status, local occurrence, and relative abundance categories for each species is provided in Table 1.

Table 1. List of birds of Atiquipa, from bird diversity along elevational and seasonal gradients in the Lomas de Atiquipa, Southern Peru

Order	Family	Species	Code species	Status	Seasonality	Relative abundance
Tinamiformes	Tinamidae	*Nothoprocta pentlandii*	Notpen	LC	R	C
Anseriformes	Anatidae	*Spatula cyanoptera*	Spacya	LC	O	R
Sphenisciformes	Spheniscidae	*Spheniscus humboldti*	Sphhum	VU	R	E
Suliformes	Sulidae	*Sula variegata*	Sulvar	LC	R	A
Suliformes	Phalacrocoracidae	*Phalacrocorax gaimardi*	Phagai	NT	R	F
Suliformes	Phalacrocoracidae	*Phalacrocorax bougainvillii*	Phabou	NT	R	F
Suliformes	Phalacrocoracidae	*Phalacrocorax brasilianus*	Phabra	LC	O	E
Pelecaniformes	Pelecanidae	*Pelecanus thagus*	Peltha	NT	R	C
Pelecaniformes	Ardeidae	*Nycticorax nycticorax*	Nycnyc	LC	R	E
Pelecaniformes	Ardeidae	*Bubulcus ibis*	Bubibi	LC	O	R
Pelecaniformes	Ardeidae	*Ardea alba*	Ardalb	LC	O	R
Pelecaniformes	Threskiornithidae	*Plegadis ridgwayi*	Plerid	LC	M	R
Pelecaniformes	Threskiornithidae	*Theristicus melanopis*	Themel	LC	M	R
Cathartiformes	Cathartidae	*Cathartes aura*	Cataur	LC	R	C
Cathartiformes	Cathartidae	*Coragyps atratus*	Coratr	LC	O	R
Cathartiformes	Cathartidae	*Vultur gryphus*	Vulgry	VU	O	R
Accipitriformes	Pandionidae	*Pandion haliaetus*	Panhal	LC	O	E
Accipitriformes	Accipitridae	*Circus cinereus*	Circin	LC	R	E
Accipitriformes	Accipitridae	*Parabuteo unicinctus*	Paruni	LC	R	F
Accipitriformes	Accipitridae	*Geranoaetus melanoleucus*	Germel	LC	R	C
Accipitriformes	Accipitridae	*Geranoaetus polyosoma*	Gerpol	LC	R	C
Gruiformes	Rallidae	*Gallinula galeata*	Galgal	LC	R	E
Charadriiformes	Charadriidae	*Pluvialis squatarola*	Plusqu	LC	M	E
Charadriiformes	Charadriidae	*Vanellus resplendens*	Vanres	LC	A	R
Charadriiformes	Charadriidae	*Oreopholus ruficollis*	Oreruf	LC	M	E
Charadriiformes	Haematopodidae	*Haematopus palliatus*	Haepal	LC	R	C
Charadriiformes	Haematopodidae	*Haematopus ater*	Haeate	LC	R	F
Charadriiformes	Burhinidae	*Burhinus superciliaris*	Bursup	LC	R	F
Charadriiformes	Scolopacidae	*Numenius phaeopus*	Numpha	LC	M	E
Charadriiformes	Scolopacidae	*Calidris alba*	Calalb	LC	M	F
Charadriiformes	Scolopacidae	*Calidris minutilla*	Calmin	LC	M	R
Charadriiformes	Scolopacidae	*Calidris bairdi*	Calbai	LC	M	E
Charadriiformes	Scolopacidae	*Calidris virgata*	Calvir	LC	O	E
Charadriiformes	Scolopacidae	*Phalaropus tricolor*	Phatri	LC	M	R
Charadriiformes	Thinocoridae	*Thinocorus rumicivorus*	Thirum	LC	R	C
Charadriiformes	Laridae	*Chroicocephalus cirrocephalus*	Chrcir	LC	O	E
Charadriiformes	Laridae	*Leucophaeus modestus*	Leumod	LC	R	C
Charadriiformes	Laridae	*Leucophaeus pipixcan*	Leupip	LC	M	R
Charadriiformes	Laridae	*Larus dominicanus*	Lardom	LC	R	C
Charadriiformes	Laridae	*Larus belcheri*	Larbel	LC	R	C
Charadriiformes	Laridae	*Larosterna inca*	Larinc	NT	R	C
Charadriiformes	Laridae	*Sternula lorata*	Stelor	EN	O	R
Columbiformes	Columbidae	*Columbina cruziana*	Colcru	LC	R	C
Columbiformes	Columbidae	*Metriopelia melanoptera*	Metmel	LC	R	E
Columbiformes	Columbidae	*Metriopelia ceciliae*	Metcec	LC	O	R
Columbiformes	Columbidae	*Columba livia*	Colliv	LC	R	F
Columbiformes	Columbidae	*Zenaida meloda*	Zenmel	LC	R	A
Columbiformes	Columbidae	*Zenaida auriculata*	Zenaur	LC	R	A
Cuculiformes	Cuculidae	*Crotophaga sulcirostris*	Crosul	LC	O	E
Strigiformes	Tytonidae	*Tyto alba*	Tytalb	LC	R	E
Strigiformes	Strigidae	*Glaucidium peruanum*	Glaper	LC	R	C
Strigiformes	Strigidae	*Athene cunicularia*	Athcun	LC	R	C
Strigiformes	Strigidae	*Asio clamator*	Asicla	LC	O	R
Caprimulgiformes	Caprimulgidae	*Chordeiles acutipennis*	Choacu	LC	R	E
Caprimulgiformes	Caprimulgidae	*Systellura longirostris*	Syslon	LC	R	C
Apodiformes	Apodidae	*Aeronautes andecolus*	Aerand	LC	M	F
Apodiformes	Apodidae	*Chaetura pelagica*	Chapel	VU	M	R
Apodiformes	Trochilidae	*Myrtis fanny*	Myrfan	LC	R	A
Apodiformes	Trochilidae	*Rhodopis vesper*	Rhoves	LC	R	A
Apodiformes	Trochilidae	*Thaumastura cora*	Thacor	LC	R	E
Apodiformes	Trochilidae	*Amazilia amazilia*	Amaama	LC	O	R
Falconiformes	Falconidae	*Phalcoboenus megalopterus*	Phameg	LC	O	E
Falconiformes	Falconidae	*Falco sparverius*	Falspa	LC	R	C

Falconiformes	Falconidae	*Falco femoralis*	Falfem	LC	R	F
Falconiformes	Falconidae	*Falco peregrinus*	Falper	LC	M	E
Psittaciformes	Psittacidae	*Psilopsiagon aurifrons*	Psiaur	LC	R	C
Passeriformes	Furnariidae	*Geositta peruviana**	Geoper	LC	R	E
Passeriformes	Furnariidae	*Geositta cunicularia*	Geocun	LC	R	A
Passeriformes	Furnariidae	*Geositta maritima*	Geomar	LC	R	E
Passeriformes	Furnariidae	*Cinclodes taczanowskii**	Cintac	LC	R	C
Passeriformes	Furnariidae	*Pseudasthenes cactorum**	Psecac	LC	R	C
Passeriformes	Tyrannidae	*Elaenia albiceps*	Elaalb	LC	R	E
Passeriformes	Tyrannidae	*Anairetes reguloides*	Anareg	LC	R	A
Passeriformes	Tyrannidae	*Anairetes flavirostris*	Anafla	LC	R	C
Passeriformes	Tyrannidae	*Pyrocephalus rubinus*	Pyrrub	LC	R	A
Passeriformes	Tyrannidae	*Muscisaxicola maculirostris*	Musmcr	LC	M	R
Passeriformes	Tyrannidae	*Muscisaxicola rufivertex*	Musruf	LC	M	R
Passeriformes	Tyrannidae	*Muscisaxicola maclovianus*	Musmac	LC	M	F
Passeriformes	Tyrannidae	*Ochthoeca leucophrys*	Ochleu	LC	R	E
Passeriformes	Tyrannidae	*Muscigralla brevicauda*	Musbre	LC	R	C
Passeriformes	Tyrannidae	*Tyrannus savana*	Tyrsav	LC	M	R
Passeriformes	Tyrannidae	*Tyrannus tyrannus*	Tyrtyr	LC	M	E
Passeriformes	Tyrannidae	*Camptostoma obsoletum*	Camobs	LC	A	R
Passeriformes	Hirundinidae	*Pygochelidon cyanoleuca*	Pygcya	LC	R	C
Passeriformes	Hirundinidae	*Progne murphyi*	Promur	NT	M	E
Passeriformes	Hirundinidae	*Riparia riparia*	Riprip	LC	M	E
Passeriformes	Hirundinidae	*Hirundo rustica*	Hirrus	LC	M	F
Passeriformes	Hirundinidae	*Petrochelidon rufocollaris*	Petruf	LC	M	E
Passeriformes	Troglodytidae	*Troglodytes aedon*	Troaed	LC	R	A
Passeriformes	Turdidae	*Turdus chiguanco*	Turchi	LC	R	A
Passeriformes	Mimidae	*Mimus longicaudatus*	Mimlon	LC	R	A
Passeriformes	Motacillidae	*Anthus lutescens*	Antlut	LC	R	E
Passeriformes	Thraupidae	*Conirostrum cinereum*	Concin	LC	R	A
Passeriformes	Thraupidae	*Porphyrospiza alaudina*	Porala	LC	R	A
Passeriformes	Thraupidae	*Xenospingus concolor*	Xencon	NT	R	E
Passeriformes	Thraupidae	*Poospiza hispaniolensis*	Poohis	LC	R	C
Passeriformes	Thraupidae	*Sicalis luteola*	Siclut	LC	R	C
Passeriformes	Thraupidae	*Sicalis raimondii**	Sicrai	LC	R	F
Passeriformes	Thraupidae	*Volatinia jacarina*	Voljac	LC	R	E
Passeriformes	Thraupidae	*Sporophila peruviana*	Spoper	LC	O	R
Passeriformes	Thraupidae	*Sporophila simplex*	Sposim	LC	O	E
Passeriformes	Thraupidae	*Catamenia analis*	Catana	LC	R	E
Passeriformes	Thraupidae	*Asemospiza obscura*	Aseobs	LC	R	E
Passeriformes	Passerellidae	*Zonotrichia capensis*	Zoncap	LC	R	A
Passeriformes	Cardinalidae	*Pheucticus chrysogaster*	Phechr	LC	R	A
Passeriformes	Parulidae	*Setophaga ruticilla*	Setrut	LC	A	R
Passeriformes	Icteridae	*Molothrus bonariensis*	Molbon	LC	O	E
Passeriformes	Icteridae	*Sturnella bellicosa*	Stubel	LC	R	C
Passeriformes	Fringillidae	*Spinus magellanicus*	Spimag	LC	R	C
Passeriformes	Passeridae	*Passer domesticus*	Pasdom	LC	R	C

Note: *Endemic species; Seasonality: R: resident, O: occasional, A: accidental, M: migratory; Relative Abundance: A: Abundant, species seen year-round with high abundances, C: Common, can be seen year-round, F: Frequent, seen regularly, E: Scarce, seen only a few times during the year, R: Rare, rarely observed or no longer observed. Categories are based on repeated local observations compiled between 2002 and 2018 and represent qualitative indices of local commonness rather than standardized density estimates

Bird richness by habitat and variation along the elevational gradient

Elevational richness and range-size patterns were based on georeferenced historical records compiled between 2002 and 2018, including observations from different years and seasons. Compiled species richness increased from sea level up to 200 m, with the highest recorded richness occurring at 600-700 m asl (55 species), and then gradually declined toward 1,200 m, where six species were recorded (Figure 2.A). Because these patterns were derived from non-standardized records, they provide descriptive summaries of recorded occurrence along the elevational gradient. In terms of the elevational ranges occupied by species, those with midpoints close to 500 m tended to show broader recorded ranges, particularly compared with species with lower elevational midpoints (Figure 2.B). Species spanning a wide range of elevations included *Cathartes aura* and several raptors such as *Geranoaetus melanoleucus*, *Geranoaetus polyosoma*, and *Falco sparverius*, as well as other terrestrial birds such as *Anairetes flavirostris*, *Mimus longicaudatus*, and *Porphyrospiza alaudina*. For vultures and raptors, elevational assignment was made cautiously, in these cases individuals flying far from the observer and clearly associated with a different elevational band were

not considered for that band, and many records corresponded to perched individuals or birds observed within the evaluated elevational range. The elevational range-size analysis shown in Figure 2.B included only the 90 species recorded within the terrestrial lomas gradient; marine-coastal species were excluded because they were not part of the inland elevational gradient evaluated.

Among the compiled historical records, the habitats with the highest recorded richness were open forest (OFOR), agricultural areas (AGR), herbaceous-shrub (HER-SHR), and herbaceous (HER). In contrast, dense forest (DFOR) and cactaceous habitat (CAC) showed lower recorded richness, with 17 and 14 species, respectively. Including the adjacent marine-coastal (MC) strip, 23 species were recorded in that habitat unit (Figure 3.A). As with the elevational summaries, habitat richness values should be interpreted as descriptive because they derive from non-standardized records and may partly reflect uneven sampling intensity among habitats.

Presence/absence-based composition along the elevational gradient revealed six main compositional groups, indicating broad changes in species composition with elevation. The highest similarity was observed among intervals between 600 and 1,000 m asl (Figure 3.B), which broadly correspond to the forest and shrub belt. A second zone of relatively high similarity was observed at mid elevations (300-600 m asl), where herbaceous and herbaceous-shrub habitats predominate. By contrast, the lowest similarity occurred near the upper limit of the gradient (1,000-1,200 m asl), where upper cactaceous and herbaceous vegetation dominate. The assemblage recorded at the lower end of the gradient (0-100 m), together with the adjacent marine-coastal strip, was the most distinct from the remaining intervals. Because this clustering was based on compiled historical records, these groups represent broad compositional patterns along the elevational gradient and may also reflect variation in sampling intensity among intervals.

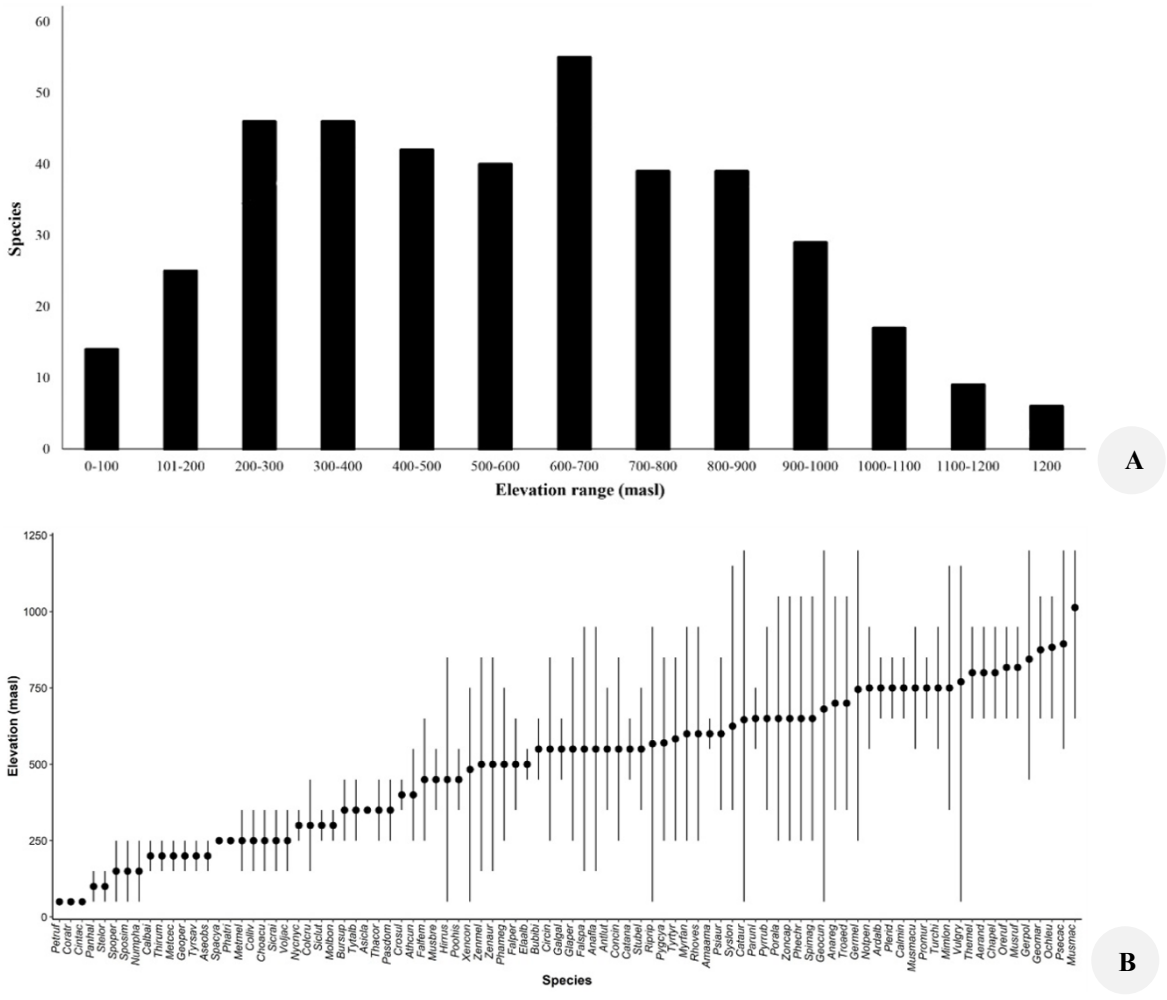

Figure 2. A. Descriptive bird species richness by 100-m elevational bands, B. elevational range sizes for 90 terrestrial species recorded within the inland elevational gradient of the Lomas de Atiquipa, southern Peru. Both panels are based on georeferenced historical records compiled between 2002 and 2018, including observations from different years and seasons. Marine-coastal species were excluded from panel b. Lines indicate the minimum and maximum recorded elevational limits of each species range, and species are ordered along the abscissa by ranked elevational midpoints. See Table 1 for bird-species codes

Habitat- and season-related beta diversity in the 2018 surveys

Based on the standardized dry- and wet-season surveys conducted in 2018, multivariate analyses were performed on 18 habitat-season assemblages (nine habitat types × two seasons), each representing the pooled abundance of the two transects surveyed per habitat in each season. The NMDS ordination based on Bray-Curtis dissimilarity and square-root transformed abundance data yielded a stress value of 0.113 (Figure 4), indicating a good two-dimensional representation of community relationships. Bird assemblages were structured primarily by habitat rather than by season. Accordingly, the global ANOSIM showed significant differences among habitats (R: 0.6333, P: 0.003), whereas the overall separation between seasons was weak and not significant (R: 0.05185, P: 0.258). Seasonal groups also did not differ significantly in multivariate dispersion (betadisper: F: 1.68, P: 0.224). However, SIMPER indicated a mean Bray-Curtis dissimilarity of 78.6% between seasons, showing that seasonal variation was mainly expressed as shifts in the relative contribution of species rather than as a consistent global segregation of assemblages. Seventeen species accounted for 75.9% of this seasonal dissimilarity, mainly *Sicalis raimondii*, *Zonotrichia capensis*, *Sicalis luteola*, *Geositta cunicularia*, *Columbina cruziana*, *Mimus longicaudatus*, *Porphyrospiza alaudina*, *Troglodytes aedon*, and *Spinus magellanicus*. Among habitats, the herbaceous-shrub habitat (HER-SHR) showed the strongest between-season change in the standardized 2018 baseline, with a Bray-Curtis dissimilarity of 0.9079; however, this pattern reflected pronounced seasonal turnover in composition, accompanied by lower abundance (116 to 36 individuals) and richness (16 to 9 species) in the wet season, rather than an increase in wet-season richness or abundance.

Discussion

Bird diversity and specific remarks

The full locality inventory recorded for Atiquipa, including both the inland lomas system and the adjacent marine-coastal strip, highlights the importance of this area for bird diversity in southern Peru. Even when marine-coastal species are excluded, the inland lomas component comprises 89 bird species, exceeding the richness previously reported for Atiquipa by Zeballos et al. (2000), who recorded 59 species for these lomas and 63 species for the Lomas of Mejía during the summer of 1999. Those authors also suggested that bird richness in Atiquipa was likely underestimated and could increase with additional sampling. Lower richness has been reported for other lomas systems, such as Cerro Campana, with 38-52 species (Zelada et al. 2014; eBird 2021). For the Lomas of Lachay, Pantigoso et al. (2015) reported 17 species associated specifically with cacti, whereas overall richness for Lachay has been reported to range from 65 species (SERNANP 2009) to 118 species (eBird 2021). These comparisons should be interpreted cautiously because studies differ in spatial extent, sampling effort, habitat coverage, and the inclusion or exclusion of marine-coastal species. Nevertheless, they indicate that Atiquipa represents one of the most diverse and structurally heterogeneous lomas systems documented in southern Peru.

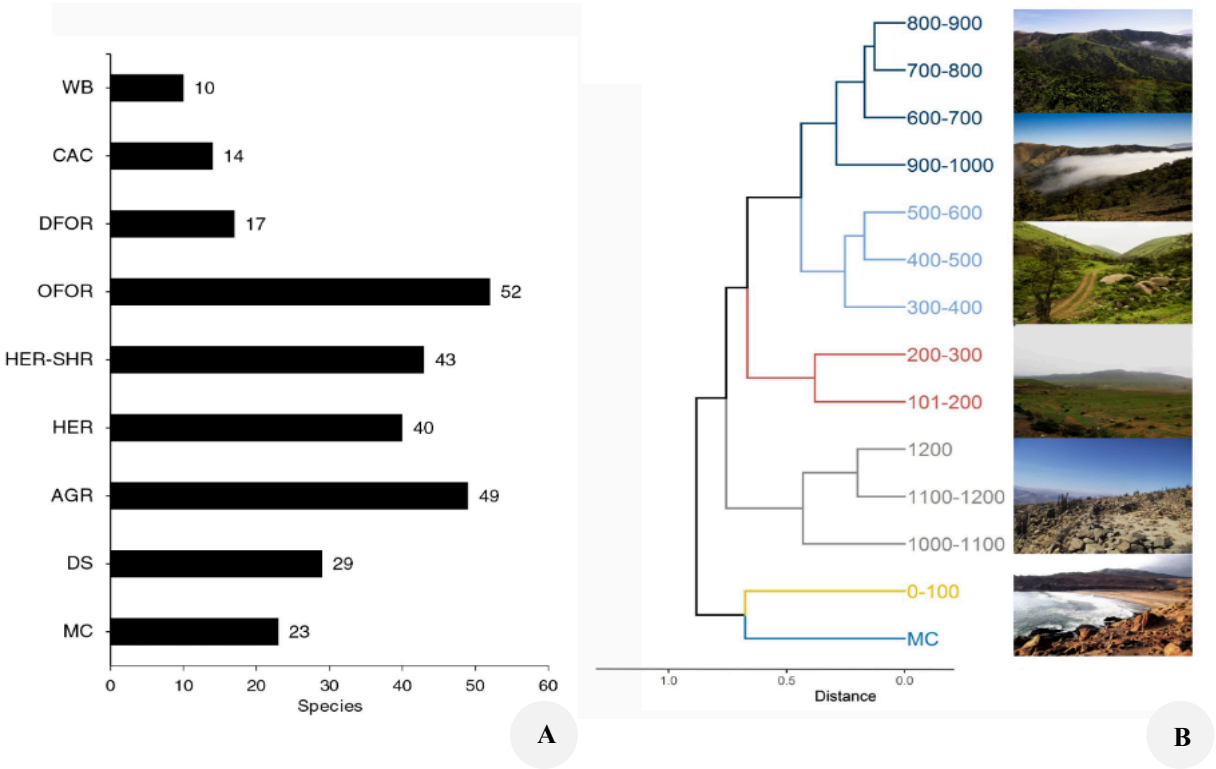

Figure 3. A. Descriptive bird species richness by habitat based on compiled non-standardized records from the Lomas de Atiquipa, southern Peru, B. Cluster analysis based on bird-species composition (presence/absence) across 14 elevational intervals using Sørensen similarity and the Unweighted Pair-Group Method (UPGMA)

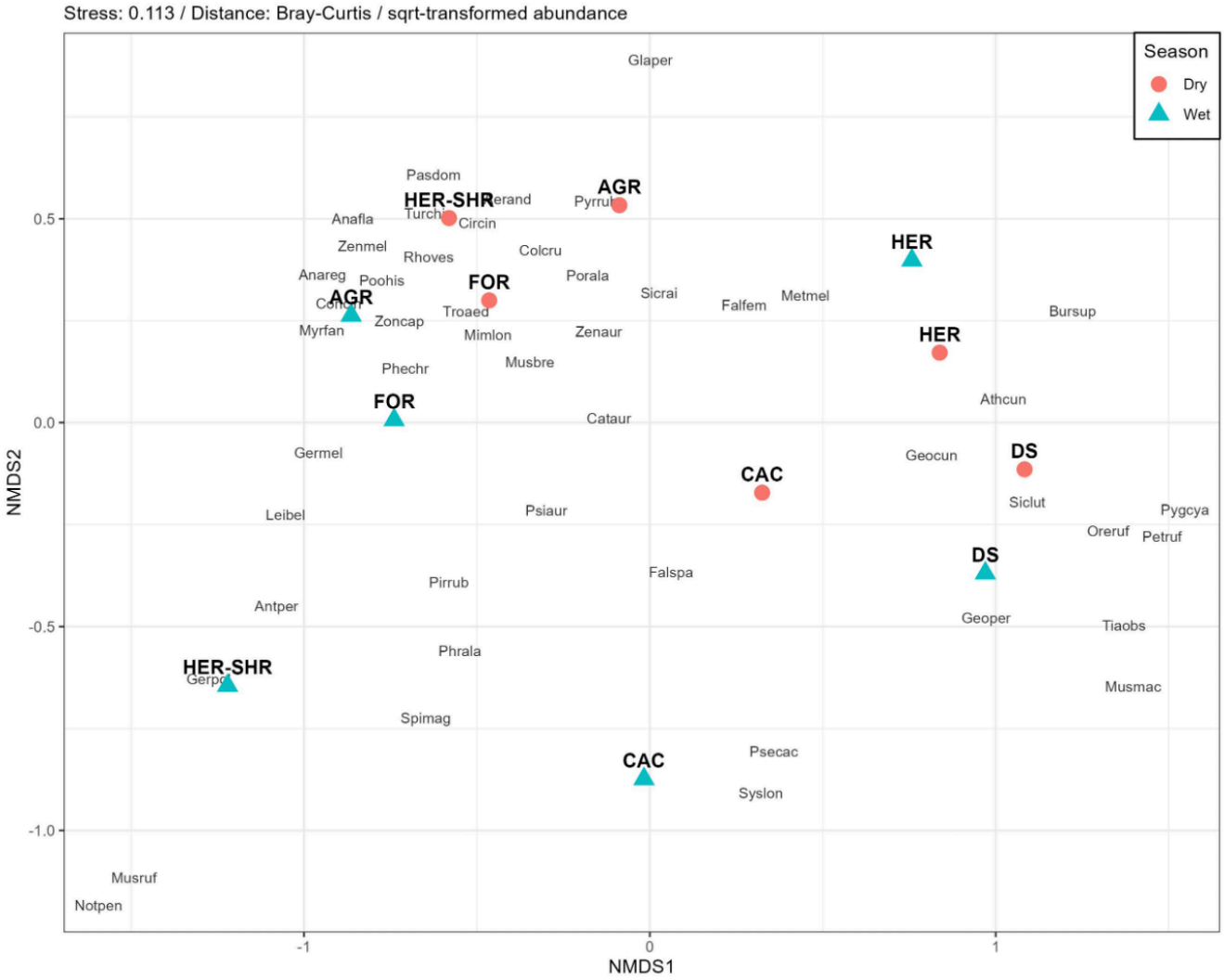

Figure 4. Non-metric multidimensional scaling (NMDS) ordination of bird communities in the Lomas de Atiquipa based on Bray-Curtis dissimilarity of square-root transformed observed abundance data from the standardized dry- and wet-season surveys conducted in 2018. Each point represents one habitat-season assemblage obtained by pooling the two transects surveyed within each habitat and season. The ordination yielded a stress value of 0.113

Among the species recorded in Atiquipa, several Peruvian endemics are noteworthy. Based on the distributional information currently available in the consulted literature, the record of *Geositta peruviana* at Atiquipa may represent one of the southernmost localities documented for the species. Likewise, *Pseudasthenes cactorum* has a restricted distribution in specific areas of the Peruvian highlands and coast (Remsen and Juana 2020), and the record from Atiquipa appears geographically disjunct from the nearest populations reported for the lomas of Lima. However, confirming whether this record represents an isolated population, and its taxonomic correspondence relative to coastal or montane forms, will require additional field and taxonomic evidence. The Lomas of Atiquipa also appear to be an important area for the endemic *Sicalis raimondii*, as large flocks (>50 individuals) were repeatedly observed throughout the year, particularly during the austral summer in desert areas with herbaceous vegetation. A similar pattern was observed for *Pheucticus chrysogaster*, which was consistently recorded in relatively high numbers within the lomas, especially in forest habitats with shrub cover. This species has been recognized as an important seed disperser (Pauca-Tanco et al. 2018), together with other birds recorded in the area such as *Sturnella bellicosa*, *Mimus longicaudatus*, and *Turdus chiguanco*. Based on repeated field observations during the study period, *M. longicaudatus* and *T. chiguanco* were frequently associated with fruits of the endemic “arrayan” tree (*Myrcianthes ferreyrae*), suggesting a potential role in its seed dispersal.

Additional noteworthy records include observations that, according to the consulted literature, may correspond to the southernmost or among the southernmost documented occurrences for species such as *Amazilia amazilia*, *Petrochelidon rufocollaris*, *Sporophila simplex*, *Sporophila peruviana*, *Camptostoma obsoletum*, and *Asio clamator* (Schulenberg et al. 2010; Billerman et al. 2020). In the case of *A. clamator*, the species was consistently detected in the area between 2000 and 2010, but became much less

frequently recorded thereafter. For *Cathartes aura*, field observations suggest the occurrence in Atiquipa of individuals assignable to both the Amazonian form ruficollis and the Andean form jota (Plenge 2022). If confirmed, the occurrence of ruficollis on this slope would be noteworthy, as it has not been commonly referenced for this area in the available literature. This lomas system also provides habitat for some Andean species during migration, and in some cases apparently supports permanent populations, given their recurrent records in the lomas (e.g., *Metriopelia ceciliae*, *Muscisaxicola rufivertex*, *Muscisaxicola maclovianus*), as well as latitudinal migrants such as *Tyrannus tyrannus* and *Tyrannus savana.* Taken together, these records reinforce the biogeographic relevance of Atiquipa as a contact zone between coastal, desert, and lomas-associated bird assemblages, and as a locality of particular interest for future studies on distributional limits, seasonal movements, and taxonomic variation.

Bird diversity in relation to vegetation cover and altitude

To date, no studies have been reported that explicitly address both temporal and spatial variation of birds in lomas systems under the strongly contrasting climatic seasons typical of these ecosystems. Existing studies have largely focused on vegetation dynamics particularly in herbaceous lomas both temporally (Pefaur 1982; Sotomayor and Jiménez 2008; Tovar et al. 2018) and spatially (Manrique et al. 2014). Assessing variability in bird communities is nevertheless important to understand spatiotemporal dynamics and the ecological balance of systems that may depend on species providing services such as seed dispersal or pollination (Loaiza 2017). Furthermore, gradient-based comparisons can be highly useful for identifying zones of high species turnover and for supporting zoning and prioritization in conservation areas such as the one studied (Loaiza 2017).

The highest compiled richness occurred in the middle portion of the gradient (600-700 m asl). In Atiquipa, this pattern is most plausibly associated with a cascade of at least three interrelated factors. First, the mid-elevation belt concentrates fog influence, which likely increases moisture availability and seasonal productivity. Second, this fog-driven productivity promotes vegetation heterogeneity and structural complexity, including forest, shrub, and herbaceous components. Third, these vegetation conditions likely enhance the availability of food, shelter, and nesting sites for birds. Similar relationships between vegetation complexity and bird diversity have been reported in other systems (Blake and Loiselle 2000; Sirami et al. 2009). In this sense, the mid-elevation richness pattern observed in Atiquipa is better interpreted as the result of interrelated local ecological conditions than as the product of a single mechanism. A geometric effect associated with range overlap toward the center of a bounded gradient (Colwell and Lees 2000) may also contribute to this pattern. However, because the present study did not formally test mid-domain expectations, this mechanism should be regarded only as a secondary hypothesis, whereas the observed concentration of fog influence, vegetation heterogeneity, and resource availability at mid elevations is more directly consistent with the patterns documented here.

Livestock-dominated environments can reduce bird diversity when habitat structure is simplified or natural cover is extensively replaced (Macchi et al. 2013). In Atiquipa, however, agricultural and grazing areas occur within a heterogeneous landscape mosaic and are embedded in adjacent natural habitats along the gradient. Under these conditions, the observed richness pattern suggests that modified habitats may add resources or complementary habitat structure without necessarily producing sharp losses in bird richness. Although management intensity and habitat quality were not measured directly, the observed spatial association between productive and natural habitats suggests that modified areas may contribute complementary resources or habitat structure within the Atiquipa landscape mosaic (Rahbek 1997; Patterson et al. 1998; Blake and Loiselle 2001).

Habitat-level analyses are also useful for identifying how birds are distributed among vegetation types along the elevational gradient and for recognizing habitats that concentrate ecologically important species. In Atiquipa, the most diverse habitats were those with greater structural complexity, particularly shrub-dominated habitats and forests with shrub understory. This pattern agrees with reports from other systems in which structurally complex habitats support higher bird diversity than simpler environments (Blake and Loiselle 2000; Coria et al. 2016). Such habitats may be relevant for ecological such as seed dispersal and pollination, because they concentrate species associated with forest and shrub resources (Loaiza 2017).

Vegetation patterns in lomas are largely correlated with the fog gradient, especially during the wet season. This fog-driven seasonality determines habitat availability for many plant species that emerge during this period particularly herbs which in turn condition the distribution of fauna such as birds by providing resources, especially food in the form of insects, fruits, and seeds (Loaiza 2017). Moreover, the mosaic of environments along the lomas likely supports species by enabling may facilitate spatial redistribution in response to changing environmental conditions and resource availability.

Temporal variation in bird diversity

Despite the marked environmental contrast between the wet and dry seasons in Atiquipa, especially in fog frequency and the seasonal development of herbaceous vegetation, the standardized 2018 surveys did not reveal a significant overall seasonal separation in bird community structure (ANOSIM R: 0.05185, P: 0.258). Instead, bird assemblages were structured primarily by habitat, with significant differences among habitat types. At the same time, the mean Bray-Curtis dissimilarity between seasons was high (78.6%), indicating that seasonal variation was expressed mainly as changes in the relative contribution of species within habitats rather than as a consistent global grouping of wet- and dry-season samples across the system. The herbaceous-shrub habitat showed the strongest between-season change (Bray-Curtis dissimilarity: 0.9079), accompanied by lower abundance (116 to 36 individuals)

and richness (16 to 9 species) in the wet season. Thus, in lomas systems where vegetation cover and composition fluctuate seasonally, changes in vegetation may influence bird assemblages mainly through localized shifts in resource availability and habitat structure, rather than through a strong overall seasonal reorganization of communities (Goetz et al. 2007; Kim et al. 2018). This interpretation is consistent with the capacity of birds to track short-term changes in environmental conditions, temporarily shift habitat use, and adjust their distributions according to resource availability and ecological requirements (Hutto 1985; Loaiza 2017). Because these seasonal comparisons were based on one standardized dry-season survey and one wet-season survey conducted in 2018, they provide an initial standardized baseline of seasonal community variation in Atiquipa and a reference point for future interannual monitoring in the lomas system.

This pattern is particularly relevant in zones of persistent fog (600-800 m), where productivity increases during wet and post-wet periods, generating a greater supply of resources and structurally heterogeneous conditions. These patterns are consistent with climate-based hypotheses in species-diversity theory (McCain 2009), because increased resource availability may promote greater habitat heterogeneity and structural complexity. In Atiquipa, however, these conditions appear to facilitate local shifts in bird abundance and habitat use rather than a strong overall seasonal segregation of assemblages across the system. In this sense, the seasonal response of bird communities in the lomas may be expressed more through redistribution among habitats and changes in species contributions than through a complete restructuring of the assemblage.

Finally, under the highly variable conditions typical of lomas ecosystems, where some resources are unstable over time (e.g., herbaceous vegetation and associated insects), birds may compensate through flexible habitat use, opportunistic movements, and adjustments in local abundance, as documented in other arid and semi-arid systems (Poulin et al. 1993; Corcuera and Zavala 2006). In Atiquipa, this flexibility may help explain why seasonal differences were expressed mainly as shifts in the relative contribution of species and in localized habitat turnover, rather than as a strong overall separation between wet- and dry-season bird assemblages. These results suggest that seasonal dynamics in this lomas system operate primarily at the habitat scale, especially in vegetation types with higher short-term variability, such as herbaceous-shrub environments.

Conservation implications

From a conservation perspective, these results suggest that the mid-elevation fog belt, particularly between 600 and 1000 m asl, should be considered a priority for future monitoring and conservation management in Atiquipa. This section of the gradient contained the highest compiled bird richness, showed relatively high compositional similarity among adjacent elevational intervals, and included the habitat mosaic in which forest, shrub, and productive units were most strongly represented. Likewise, the standardized 2018 surveys indicated that bird assemblages were structured primarily by habitat and that seasonal variation was expressed mainly through localized shifts rather than complete community replacement. Taken together, these results support management actions aimed at maintaining habitat heterogeneity and connectivity among fog-influenced forest, shrub, and adjacent semi-managed habitats, while avoiding land-use changes that simplify vegetation structure or reduce the continuity of the mid-elevation belt. In this context, conserving *Tara spinosa* stands and the ecological continuity between natural and semi-managed habitats appears especially relevant for sustaining bird diversity in the lomas system.

In conclusion, the Lomas de Atiquipa support high bird diversity within a relatively short elevational gradient, including endemic, near-threatened, and threatened species. Historical compiled records showed that the highest recorded richness occurred in the mid-elevation fog belt and that bird composition changes markedly along the gradient, whereas the standardized 2018 surveys indicated that community structure was associated more strongly with habitat than with season. Seasonal differences were expressed mainly through localized shifts in relative species contributions rather than through complete community replacement. Because the historical dataset was non-standardized and the seasonal comparisons were based on one dry- and one wet-season survey in 2018, the results should be interpreted as a robust descriptive and baseline framework rather than as a definitive account of long-term ecological dynamics. Even so, the study identifies the mid-elevation fog belt and its associated habitat mosaic as a priority for conservation and provides a useful foundation for future monitoring and management in one of the best-preserved lomas systems of southern Peru.

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